

Argentinean *Myotis* (Chiroptera, Vespertilionidae), including the description of a new species from the Yungas

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Abstract

Myotis is the most speciose genus of mammals in the world and recent taxonomic revisions have revealed an impressive diversity of species in South America. Even so, the phenotypic conservatism of some taxa makes taxonomic delimitation difficult. We perform a taxonomic review of *Myotis* from Argentina based on qualitative and quantitative morphological characters. Our results confirm the occurrence of 12 species (*M. albescens*, *M. chiloensis*, *M. dinellii*, *M. izecksohni*, *M. keaysi*, *M. lavalii*, *M. levis*, *M. nigricans*, *M. oxyotus*, *M. riparius*, *M. ruber*, and *M. cf. simus*) and revealed an additional new species for the Yungas Forest. The new species is small to medium (forearm length ~ 35 mm) and can be distinguished from its congeners by a set of characters that includes forearm length, cranial measurements, discrete craniodental characters, and fur color. This review does not exhaust the need for new systematic studies with Argentinean *Myotis*, considering the possibility of occurrence of new species and the great morphological variation found for some complex taxa.

Keywords

Argentina, morphology, Myotinae, Neotropics, systematics

Introduction

Myotis Kaup, 1829 currently comprises more than 140 species distributed worldwide, and 24 are recognized from South America (Moratelli et al. 2019a, 2019b; Carrón-Bonilla and Cook 2020; Novaes et al. 2021a, 2021b,

2021c; MDD 2022). Recent taxonomic reviews revealed a high diversity within *Myotis* (e.g., Moratelli et al. 2011a, 2013, 2016, 2017, 2019b; Novaes et al. 2021a, 2021b, 2021c), refuting the hypothesis of LaVal that indicated a

relatively low number of species in South America due to late colonization, and competition with other well-established insectivorous bat lineages (LaVal 1973). Although the arrival of *Myotis* in South America is estimated for the Plio-Pleistocene interval, the genus has undergone a fast and wide-ranging process of diversification (Stadelmann et al. 2007). Therefore, the hypothesis of LaVal was skewed by incomplete taxonomic knowledge in the past, and has no biological correspondence, as shown by most recent phylogenetic and taxonomic studies (Stadelmann et al. 2007; Larsen et al. 2012; Moratelli et al. 2011a, 2017; Carrión-Bonilla and Cook 2020; Novaes et al. 2021a, 2021b).

Taxonomic reviews of South American *Myotis* have been frequent over the last decades (i.e., LaVal 1973; López-González et al. 2001; Mantilla-Meluk and Muñoz-Garay, 2014; Moratelli et al. 2011a, 2013, 2016, 2017, 2019b; Carrión-Bonilla and Cook 2020; Novaes et al. 2018, 2021a, 2021b); however, most studies have focused on the northern portion of the continent and only a few studies have included taxa occurring in the Southern Cone (q.v., López-González et al. 2001; Moratelli et al. 2013; Novaes et al. 2018).

Specifically, no reviews focusing on the species of *Myotis* from Argentina have been carried out so far. Nevertheless, several studies have made important contributions to our knowledge on the genus in this region (e.g., Barquez et al. 1999, 2017; Lutz et al. 2016; Urquiza et al. 2017; Novaes et al. 2018). Currently, 12 species of *Myotis* are known for Argentina (Barquez and Díaz 2009, 2020; Barquez et al. 2017; Urquiza et al. 2017), even though taxonomic limits are still poorly defined for some species (Novaes et al. 2018).

Based primarily on the large samples of *Myotis* available in scientific collections, we provide an overview of the taxonomic diversity of *Myotis* in Argentina, and describe a new species from Yungas Forest.

Methods

This research is part of a critical review of Neotropical *Myotis*, and more than 7,500 specimens from different localities in South America and Central America have been examined, covering all species currently recognized and their type specimens. Our analyses here were based on 187 specimens from Argentina, deposited in 11 scientific collections: American Museum of Natural History (AMNH, New York, USA), Carnegie Museum of Natural History (CM, Pittsburgh, USA), Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN, Buenos Aires, Argentina), Colección Mamíferos Lillo (CML, Tucumán, Argentina), Muséum d'Histoire Naturelle (MHNG, Geneva, Switzerland), Museum of Natural Science, Louisiana State University (LSUMZ, Baton Rouge, USA), Museum of Texas Tech University (TTU, Lubbock, USA), Museum of Vertebrate Zoology (MVZ, Berkeley, USA), Sam Noble Oklahoma Museum of Natural History (OMNH, Norman, USA), Smithsonian's National Museum of Natural History (USNM, Washington, D.C., USA). Additionally, for comparison purposes, we examined 772 specimens of 19 *Myotis* species from other South American countries. See the complete list of specimens examined in this study in Appendix 1.

Intra- and interspecific morphological variation were evaluated from qualitative and quantitative analyses based on adult specimens, classified from ossified epiphyses (q.v., Brunet-Rossini and Wilkinson 2009). 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. Skull and other external dimensions were taken using digital callipers accurate to 0.01 mm, including: forearm length (FA), length of dorsal hair (LDH), length of ventral hair (LVH), greatest length of

Table 1. Description of cranial, mandibular, and external dimensions (and their abbreviations) used in this study.

Measurements	Acronyms	Descriptions
Greatest length of skull	GLS	From the apex of the upper internal incisors to the occiput.
Condyle-canine length	CCL	From the anterior surface of the upper canines to a line connecting the occipital condyles.
Condyle-incisive length	CIL	From the apex of upper internal incisors to a line connecting the occipital condyles.
Basal length	BAL	Least distance from the apex of upper internal incisors to the ventral margin of the foramen magnum.
Mastoid breadth	MAB	Greatest breadth across the mastoid region.
Braincase breadth	BCB	Greatest breadth of the globular part of the braincase.
Interorbital breadth	IOB	Least breadth between the orbits.
Postorbital breadth	POB	Least breadth across frontals posterior to the postorbital bulges.
Breadth across canines	BAC	Greatest breadth across outer edges of the crowns of upper canines, including cingulae.
Breadth across molars	BAM	Greatest breadth across outer edges of the crowns of upper molars.
Maxillary toothrow length	MTL	From the upper canine to M3.
Molariform toothrow length	M13	From M1 to M3.
Mandibular length	MAL	From the mandibular symphysis to the condyloid process.
Mandibular toothrow length	MAN	From the lower canine to m3.
Forearm length	FA	From the elbow to the distal end of the forearm including carpal.
Length of the dorsal hairs	LDH	From the base to the tip of the hair in fur between scapulae.
Length of the ventral hairs	LVH	In fur at mid thorax.
Ear length	EL	From the base to the apex of the pinna

skull (GLS), condylocanine length (CCL), condylobasal length (CBL), condyloincisive 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). See Table 1 for a detailed description of each measurement.

To characterize and discriminate samples, Principal Component (PCA) and Discriminant Function (DFA) analyses were performed in R platform, with ‘MASS’ (Venable and Ripley 2002) and ‘Lattice’ (Sarkar 2008) packages. For these morphometrical analyses, we selected a subset of the skull dimensions (GLS, CIL, MAB, BCB, POB, IOB, BAM, MTL, M1-3, MAN, MAL) representing different axes of length and width of skull, rostrum, and mandible. As multivariate procedures require complete data sets, missing values (less than 5% of the total dataset) were estimated from the existing raw data using Amelia II package (Honaker et al. 2011) implemented in R platform. Measurements were transformed to natural logs, and covariance matrices were computed considering all variables. Due to the disparity among samples, we randomly selected a maximum of 10 individuals per species, covering almost all *Myotis* species from Argentina, except for *M. izecksohni* and *M. oxyotus*, with only one specimen available each. Qualitative traits employed here to characterize and distinguish species follow Moratelli et al. (2013) and Novaes et al. (2021b), being: (i) presence and height of the sagittal crest; (ii) presence and height of lambdoidal crests; (iii) shape of the braincase roof, being the upper portion formed by the sagittal and parietal suture; (iv) shape of the posterior region of the braincase, being formed by the interparietal and supraoccipital bones; (v) development of the mastoid process; (vi) fur on the leg and dorsal surface of the uropatagium; and (vii) fur texture and coloration. The dental nomenclature follows Miller (1897) and capitalized color nomenclature follows Ridgway (1912).

Results

Our systematic review of Argentinean *Myotis* confirms the occurrence of 12 recognized species (*M. albescens*, *M. chiloensis*, *M. dinellii*, *M. izecksohni*, *M. keaysi*, *M. lavalii*, *M. levis*, *M. nigricans*, *M. oxyotus*, *M. riparius*, *M. ruber*, *M. cf. simus*), and a new taxon, morphologically distinct from its congeners, representing an undescribed species.

Principal Component Analysis (Fig. 1) showed that 86% of the variation is related to skull size (PC1), especially in measurements associated with skull and mandible length (GLS, CIL, MAL), mastoid and braincase breadth (Table 2). Vector correlation loadings on PC2 indicate that this component is related to the shape, and

Table 2. Vector correlation loadings with original variables of principal components (PC1 and PC2) and discriminant functions (DF1 and DF2) for selected samples of the Argentinean *Myotis*.

Measurements	PC1	PC2	DF1	DF2
GLS	0.573	-0.538	0.367	-0.847
CIL	0.555	-0.194	0.732	-0.839
MAB	0.260	0.512	0.589	-0.137
BCB	0.240	0.540	0.469	-0.030
POB	0.093	0.491	0.468	0.017
IOB	0.187	0.254	0.336	0.018
BAM	0.248	0.085	0.352	-0.463
MTL	0.199	-0.380	0.237	-0.563
M1-3	0.124	-0.222	0.173	-0.461
MAN	0.176	-0.495	0.142	-0.665
MAL	0.384	0.095	0.729	-0.591

represented 30% of the variation. This analysis indicates a wide overlap along the first and second axes. The first two discriminant functions (DF1 and DF2) of the Discriminant Function analysis represented 41% and 29% of the skull variation, respectively. There is partial discrimination among the species samples, except for *M. dinellii* and *M. levis*, which are totally overlapping, and *M. nigricans* and *M. lavalii* which are partially overlapping. Along these axes, *Myotis* sp. nov. is fully distinct from all other analyzed species.

Skull and external linear morphometric measurements indicated that *Myotis* sp. nov. is consistently smaller than most species found in Argentina; but there is partial overlap for forearm length and some cranial measurements with *M. lavalii*, *M. nigricans*, and *M. riparius* (Tables 3–7). Additionally, qualitative morphological characters unequivocally distinguish these species. We present here the description of a new species from Salta Province, including a morphological diagnosis and comparisons with other Neotropical *Myotis* species.

Family Vespertilionidae Gray, 1821

Subfamily Myotinae Tate, 1942

Genus *Myotis* Kaup, 1829

Myotis barquezi sp. nov.

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Holotype. Dried skin, skull, and mandible of an adult female (CML 7623; Figs 2 and 3), collected by M. D. Miotti (field number 540) on September 14, 2006. The specimen is deposited in the Colección Mamíferos Lillo (CML, Tucumán, Argentina).

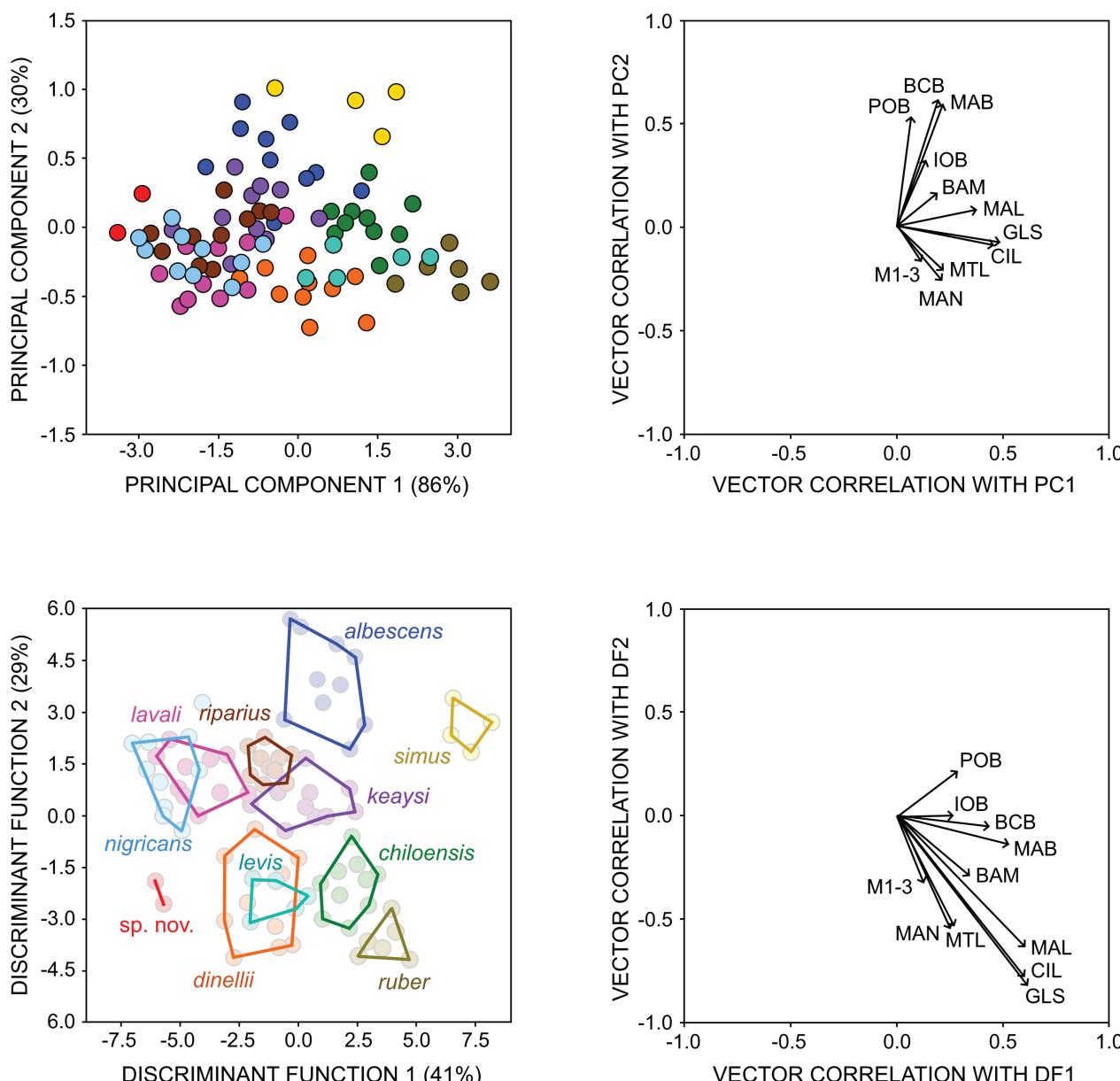


Figure 1. Plots showing dispersion points and vector correlation of skull measurements of Principal Component Analysis (upper) and Discriminant Function Analysis (lower) for *Myotis* species from Argentina.

Type locality. Finca Alto Verde, ca. 20 km SW San Ramón de La Nueva Orán, Orán Department, Salta Province, Argentina ($23^{\circ}13'S$, $64^{\circ}32'W$; 670 m elevation).

Paratype. Dried skin, skull and mandible of an adult female (CML 7622), collected by M. D. Miotti (field number 539) on September 14, 2006 at the type locality.

Distribution and habitat. *Myotis barquezi* is known only from the type locality, in Salta Province, northern Argentina, where it inhabits lowland tropical forests inside the Southern Andean Yungas ecoregion (Fig. 4). This vegetational domain is classified as tropical and subtropical moist broadleaf forest (Olson et al. 2001) and is located between the Eastern slope of the Andes and the lowlands of the Alto Chaco ecoregion. The locality where *M. barquezi* was captured is close to Orán city and consists of a Premontane Forest (“selva pedemontana palo blanco

and palo amarillo”) of the Upper Bermejo River Basin distributed altitudinally between 400 and 900 m, with dominance of *Calycophyllum multiflorum* and *Phyllostylon rhamnoides* (Jayat and Ortiz 2010). Some dominant species of trees in the area include pink lapacho (*Tabebuia impetiginosa*), pink cedar (*Cedrela balansae*), oak (*Amburana cearensis*), red cedar (*Anadenanthera colubrina*), cinchona (*Myroxylon peruferum*), afata (*Cordia tricotoma*), palo lanza (*Patagonula americana*), and urundel (*Astronium urundeuva*) (Brown 1995). The area is closely related to the Eastern Cordillera and the piedmont forest reaches only 700 m, bordering extensively with the Montane Forest of Argentina and Bolivia; to the east it is bordered by areas of highly disturbed Premontane Forests and highland Chaco environments (Jayat and Ortiz 2010).

The climate presents hot, rainy summers and cold, dry winters, and the annual mean temperature exceeds 21°C (Adámoli et al. 1972; Ojeda and Mares 1989). Summer

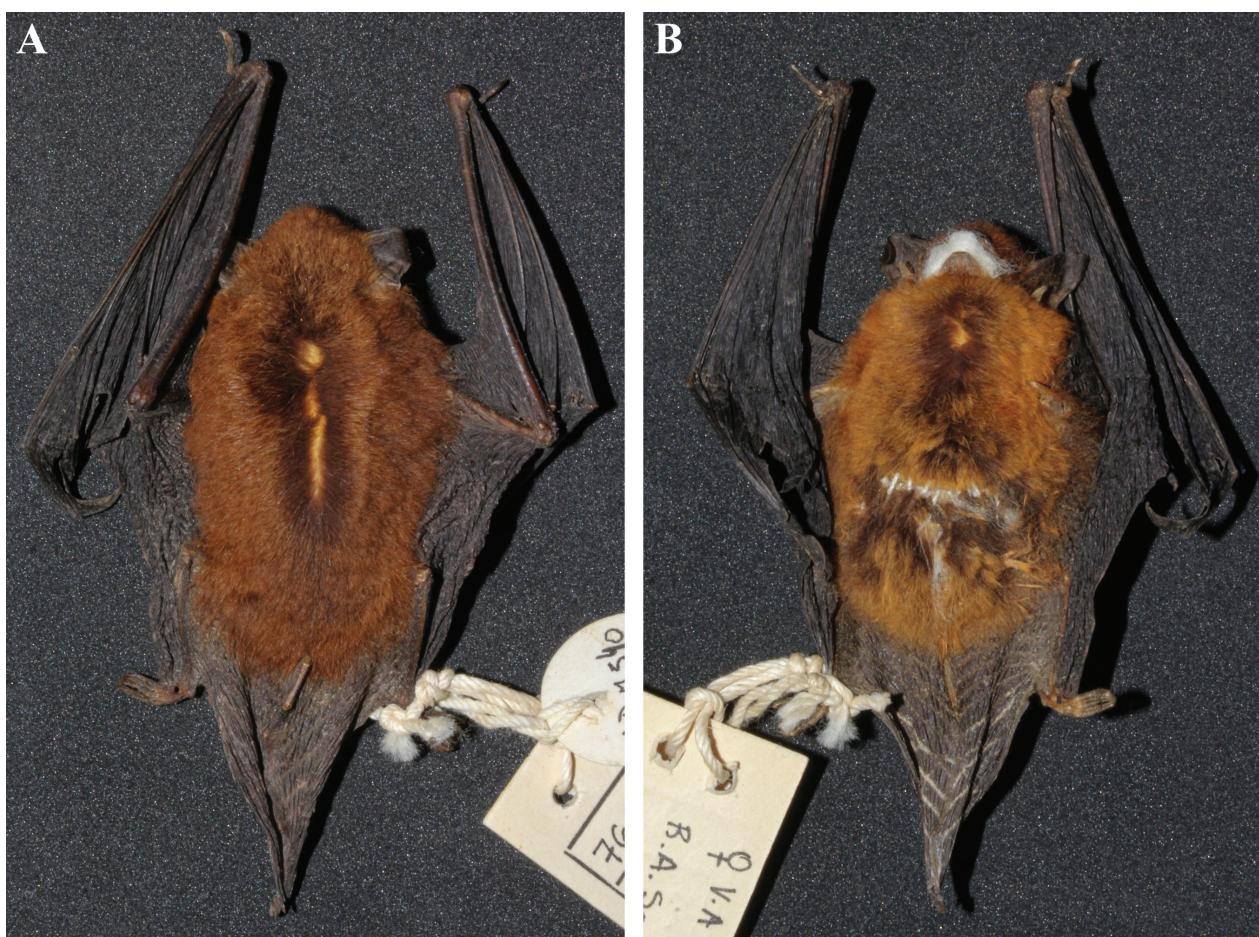


Figure 2. Dorsal (A) and ventral (B) views of the skin of the holotype of *Myotis barquezi* (CML 7623).

temperatures (December to March) may approach 40°C, whereas winter minima (June to September) are near 6°C; annual rainfall mean ranges from 500 to 800 mm (Adámoli et al. 1972; Cabrera 1976; Ojeda and Mares 1989). During the cooler months, the condensed water mist that characterizes these “cloud forests” is captured and cooperates to partially compensate for the lack of rains in that season (Burkart et al. 1999).

Etymology. *Myotis barquezi* is named in honor of Dr. Rubén M. Barquez, in recognition of his outstanding contributions to Neotropical mammalogy, especially on the bat fauna from Argentina. This species 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. Barquez’s Myotis [English]; Myotis de Barquez [Spanish].

Diagnosis. Small to medium sized species (FA 35.1–35.2 mm; GLS 13.1–13.5 mm); sagittal crest present but low; robust and broad skull; braincase inflated and remarkably high in lateral profile; braincase roof formed by the parietal bone strongly inclined forward; frontal bone with a slight slope towards the rostrum; posterior region of the braincase flattened and non-projected beyond the limit of the occipital condyles; well-developed mastoid processes; dorsal fur moderately long (LDF 5–6 mm), woolly

and clearly bicolored, with tips ranging from Dresden Brown to Snuff Brown, and darker bases (Natal Brown); legs and dorsal surface of the uropatagium covered by fur that extend up to the knees or just beyond; plagiopatagium inserted into the foot by a broad band of membrane.

Morphological description and comparisons. *Myotis barquezi* is a small to medium species of *Myotis* (Table 3), and fur texture and cranial morphology reassembles species allocated to the ruber-group (q.v., Moratelli et al. 2013, 2019a). Ears dark brown and comparatively medium-sized (EL 13–15 mm), reaching the portion of the rostrum between the eyes and nostrils when extended forward. Tragus long and slender, with a wide base and narrower spear-shaped terminal half, almost straight anterior edge, and rounded tip. Similar to *M. armiensis* and *M. keaysi*, membranes are Bone Brown, the dorsal surface of elbow, tibia, and uropatagium are densely furred, with hairs extending to the level of the knees or just beyond. The uropatagium lacks the fringe of hairs along the trailing edge. Plagiopatagium attached to the foot at the level of the toes by a broad band of membrane; toe nails are light brown.

Dorsal and ventral fur woolly and medium-sized (LDH 5–6 mm, LVH ~4.5 mm). Dorsal pelage clearly bicolored with medium-brown bases (near Natal Brown) and reddish tips, ranging from Dresden Brown to Snuff Brown. Darker bases comprise 2/3 of total hair length and



Figure 3. Dorsal, ventral and lateral views of the skull, and lateral view of the mandible of the holotype of *Myotis barquezi* (CML 7623). Scale bar = 10 mm.

changes abruptly from darker to lighter, with lighter tips comprising about 1/3 of hair length. Ventral pelage is also strongly bicolored, with Natal Brown bases (2/3 of hair length) and bright orangish tips (1/3 of hair length [near Clay Color]). The orangish venter contrasts with the reddish-brown dorsum.

Dental formula is I 2/3, C 1/1, PM 3/3, M 3/3 (2x) = 38, typical of most species of *Myotis*. Skull robust and medium-sized in length, resembling *Myotis* species of

the ruber-group (GLS 13.1–13.5 mm). The second upper premolar (P3) aligned with toothrow, not displaced to the lingual side, and barely smaller than first upper premolar (P2). First lower molar (m1) myotodont, with postcristid connecting hypoconid and entoconid (Menu 1987). Braincase robust and globose; sagittal and lambdoidal crests presents, but sagittal crest does not reach the posterior edge of the skull or join the lambdoidal crests, although there is a triangular-shaped elevation between

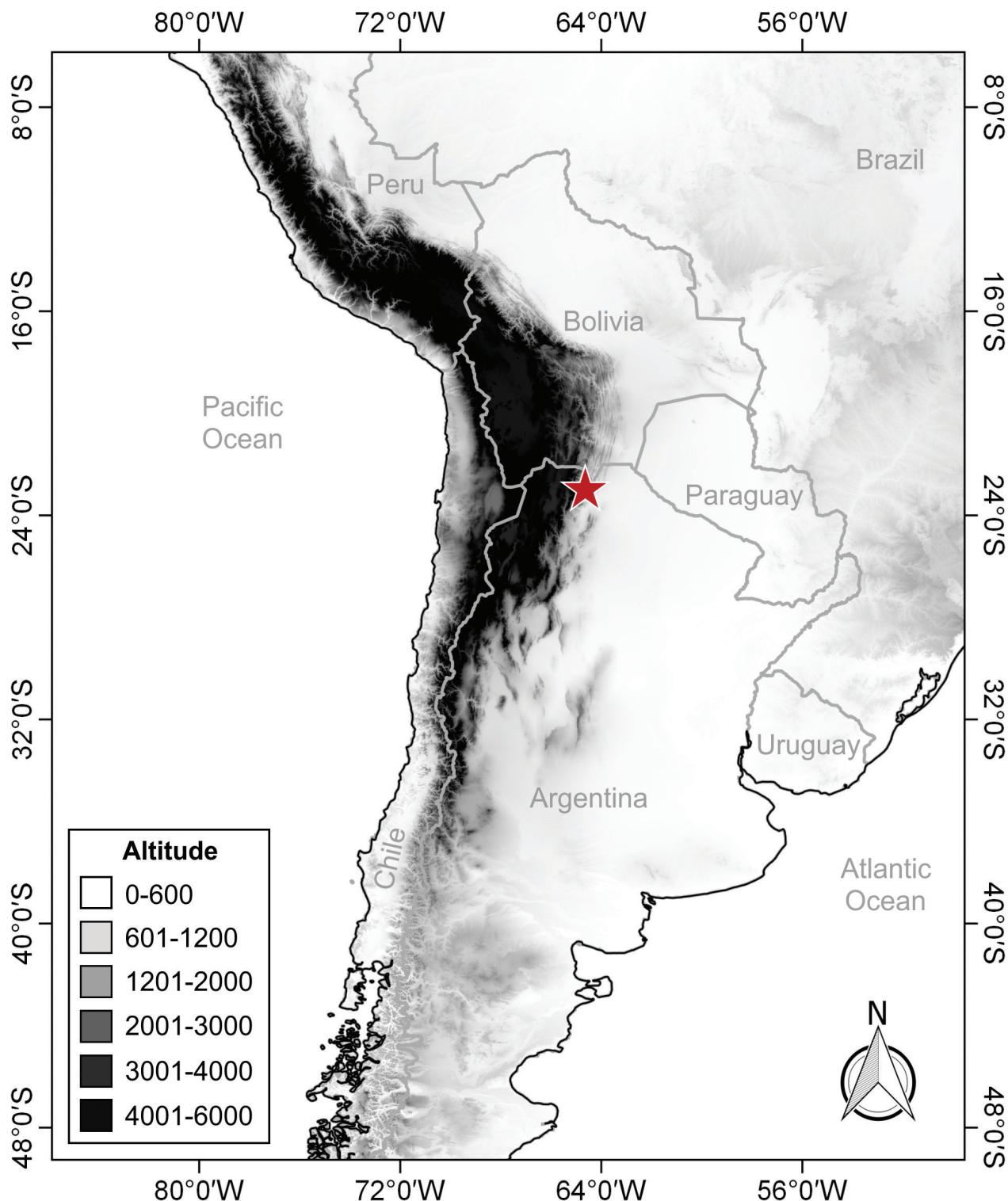


Figure 4. Map of part of South America with type locality of *Myotis barquezi* (red star).

them; occipital region flattened and not projecting beyond the posterior limits of occipital condyles; well-developed mastoid processes. Frontal bone slightly sloping; rostrum comparatively short.

Myotis barquezi can be distinguished from all the species in the ruber-group (*armiensis*, *elegans*, *keaysi*, *midastactus*, *moratellii*, *pampa*, *pilosatibialis*, *riparius*, *ruber*, and *simus*), and species from the albescens-group that confirmedly or potentially occur in the South American southern cone (*albescens*, *chiloensis*, *dinellii*, *izeck-*

sohni, *lavalii*, *levis*, *nigricans*, and *oxyotus*), by the set of diagnostic traits reported above.

Among species from the ruber-group, *M. barquezi* most resembles *M. keaysi* from the Central Andes (see Novaes et al. 2021b), but it is much smaller, and differs in all external and cranial dimensions (e.g., FA > 38 mm and GLS > 13.5 mm in *M. keaysi*; whereas FA ~ 35 mm and GLS < 13.5 mm in *M. barquezi*), it also has shorter fur, and a lower sagittal crest. In addition, *M. barquezi* differs conspicuously from *M. keaysi* from Argentina by

Table 3. Selected measurements (mm) and body mass (g) of the holotype (CML 7623) and paratype of *Myotis barquezi* (CML 7622) from Salta, Argentina.

Measurements	Holotype CML 7623	Paratype CML 7622
FA	35.1	35.2
EL	15.0	14.0
Body mass	5.0	6.0
LDF	6.0	5.0
LVF	5.3	4.5
GLS	12.9	13.4
CCL	11.8	11.7
CBL	12.3	12.4
CIL	12.6	12.7
BAL	11.2	11.6
ZYG	—	—
MAB	6.7	6.7
BCB	6.6	6.3
POB	3.4	3.4
IOB	4.5	4.6
BAC	3.4	3.4
BAM	5.4	5.3
MTL	5.1	5.0
M1–3	3.0	3.0
MAN	5.3	—
MAL	—	—

its reddish fur color, in contrast to brownish in *M. keaysi* populations from Argentina.

Myotis barquezi differs from *M. ruber* by its smaller size (both external and cranial; FA > 37.5 mm and GLS > 14.0 mm in *M. ruber*), shorter and clearly bicolored dorsal fur, dense fur along the leg and dorsal surface of the uropatagium, narrower interorbital constriction, and more developed mastoid processes. It differs from *M. armiensis* by its smaller size (FA > 36.0 mm in *M. armiensis*), clearly bicolored dorsal fur, lower sagittal crest, posterior region of the braincase flattened and non-projected beyond the limit of the occipital condyles. It differs from *M. pilosatibialis* by its smaller size (both external and cranial; FA > 36.0 mm in *M. pilosatibialis*), clearly bicolored dorsal fur, globose braincase (elongated in *pilosatibialis*), parietal bone strongly inclined forward, and shorter and broader rostrum. It differs from *M. moratellii* by its general smaller size (FA > 35.0 and GLS > 13.8 in *moratellii*), clearly bicolored dorsal fur, braincase lower in profile, posterior region of the braincase flattened and not projected beyond the limit of the occipital condyles, and sagittal crest lower.

Myotis barquezi can be distinguished from *M. riparius* by its clearly bicolored and reddish dorsal fur, presence of dense fur along the leg and dorsal surface of the uropatagium, parietal bone strongly inclined forward, posterior region of the braincase flattened and not projected beyond the limit of the occipital condyles, narrower interorbital constriction, and more developed mastoid processes. It differs from *M. elegans* by its larger size (both external and cranial; FA < 34.5 mm and GLS < 13.0 mm in *M. el-*

egans), more robust skull, higher sagittal crest, posterior region of the braincase flattened and not projected beyond the limit of the occipital condyles, narrower interorbital constriction, and more developed mastoid processes. It differs from *M. pampa* by its shorter fur (LDF < 6 in *M. barquezi*, LDF > 7 in *M. pampa*), ventral fur bicolored (being tricolored in *M. pampa*), skull more robust, sagittal crest present, posterior region of the braincase flattened and not projected beyond the limit of the occipital condyles, and more developed mastoid processes.

Myotis barquezi can be easily distinguished from *M. simus* and *M. midastactus* by its smaller size (FA > 36.0 mm and GLS > 13.5 mm in *M. simus* and *M. midastactus*), longer and clearly bicolored dorsal fur (being shorter [LDF < 4] and unicolored in *M. simus* and *M. midastactus*), legs and dorsal surface of the uropatagium covered by fur that extend up to the knees, plagiopatagium inserted into the foot by a broad band of membrane (attached at ankles in *M. simus* and *M. midastactus*); and narrower skull. In addition, tympanic bullae are comparatively larger in *M. barquezi* than in any other species from rubber-group, except *M. elegans*.

In comparison to the species from the albescens-group, *M. barquezi* can be easily distinguished from *M. albescens* by the absence of a fringe of hairs on the posterior margin of the uropatagium, reddish dorsal fur clearly bicolored (brownish with frosted appearance in *albescens*), yellowish ventral fur (whitish in *albescens*), frontal bone slightly sloping, sagittal crest present, and posterior region of the braincase flattened and not projected beyond the limit of the occipital condyles. It differs from *M. dienellii* and *M. levis* by its smaller size, absence of a fringe of hairs on the posterior margin of the uropatagium, comparatively shorter ears, narrower skull, posterior region of the braincase flattened and not projected beyond the limit of the occipital condyles. It differs from *M. izecksohni* and *M. nigricans* by the reddish and clearly bicolored dorsal fur, parietal bone strongly inclined forward, posterior region of the braincase flattened and not projected beyond the limit of the occipital condyles, and well-developed mastoid processes.

Myotis barquezi can be distinguished from *M. chiloensis* from its general smaller size (FA < 35.2 in *M. barquezi*; FA > 37 mm in *M. chiloensis*), ventral fur strongly bicolored with bright orange tips, shorter and broader skull, less inflated braincase, parietal bone strongly inclined forward, posterior region of the braincase flattened and not projected beyond the limit of the occipital condyles. It differs from *M. lavalii* by its shorter and reddish fur, broader skull, parietal bone strongly inclined forward, posterior region of the braincase flattened and not projected beyond the limit of the occipital condyles, and well-developed mastoid processes. Differs from *M. oxyotus* by its smaller size (FA > 37 mm), shorter dorsal fur, ventral fur strongly bicolored with bright orange tips, shorter and broader skull, broader skull, parietal bone strongly inclined forward, posterior region of the braincase flattened and not projected beyond the limit of the occipital condyles. In addition, *M. barquezi* can be distinguished from all species of the albescens-group by its woolly fur (silky fur in albescens-group species, except

Table 4. External and craniodental measurements of Argentinean populations of *Myotis albescens*, *M. ruber*, and *M. nigricans*, including morphometric variation and number of samples (N). The measurements are in millimeters. Acronyms and descriptions are available in Table 1.

Measurements	<i>Myotis albescens</i>	<i>Myotis ruber</i>	<i>Myotis nigricans</i>
	mean (min–max) N	mean (min–max) N	mean (min–max) N
FA	35.0 (33.7–36.8) 22	38.5 (37.5–40.5) 5	33.8 (33.0–35.0) 7
EL	14.0 (12.0–15.5) 22	14.2 (13.0–15.0) 4	13.0 (11.0–15.0) 7
Body mass	6.0 (5.5–7.0) 18	7.0 (4.0–8.0) 4	4.5 (3.5–6.0) 7
LDF	6.5 (5.5–7.5) 17	7.0 (6.5–8.0) 4	7.0 (6.0–7.5) 7
LVF	5.0 (4.5–6.0) 17	5.5 (5.0–6.0) 4	5.5 (5.0–6.5) 7
GLS	14.3 (13.9–15.0) 20	15.3 (15.1–15.6) 5	13.5 (12.4–14.3) 7
CCL	12.7 (12.1–14.2) 20	13.5 (13.5–13.7) 5	12.0 (11.6–12.7) 7
CBL	13.1 (12.6–13.8) 20	14.2 (14.0–14.4) 5	12.7 (12.3–13.5) 7
CIL	13.4 (12.9–14.0) 20	14.5 (14.4–14.8) 5	12.8 (12.4–13.5) 7
BAL	12.1 (11.5–13.4) 20	13.0 (12.8–13.2) 5	11.5 (11.0–12.3) 7
ZYG	8.8 (8.6–9.0) 11	9.5 (9.4–9.6) 3	8.3 (8.1–8.4) 4
MAB	7.4 (7.0–7.7) 20	7.8 (7.7–8.2) 5	6.9 (6.6–7.1) 7
BCB	7.1 (6.8–7.4) 20	7.0 (6.7–7.2) 5	6.4 (6.2–6.6) 7
POB	4.1 (3.9–4.2) 20	3.7 (3.6–3.9) 5	3.5 (3.3–3.8) 7
IOB	4.8 (4.5–5.0) 20	4.9 (4.7–5.2) 5	4.5 (4.1–4.7) 7
BAC	3.8 (3.5–4.0) 20	4.1 (4.0–4.3) 5	3.4 (3.2–3.5) 5
BAM	5.5 (5.2–5.7) 20	6.0 (5.8–6.2) 5	5.2 (4.9–5.6) 7
MTL	5.1 (4.9–5.5) 20	5.9 (5.9–5.9) 5	5.0 (4.8–5.2) 7
M1–3	2.9 (2.8–3.1) 20	3.3 (3.2–3.3) 5	2.8 (2.7–3.0) 7
MAN	5.8 (5.1–6.1) 20	6.3 (6.2–6.4) 4	5.3 (5.1–5.5) 7
MAL	10.0 (9.5–10.4) 20	11.1 (10.9–11.4) 4	9.4 (9.0–9.7) 7

M. chiloensis), dense fur on dorsal surface of the uropatagium (absent in all species of albescens-group), and tympanic bullae comparatively larger.

Remarks. The specimens used here to describe *M. barquezi* (CML 7622 and 7623) were originally misidentified as *Myotis lavalii* (Barquez et al. 2017: 291).

Other *Myotis* species from Argentina

Myotis albescens (É. Geoffroy, 1806)

Comments. Medium-sized species (FA 33.5–37.5 mm, body mass 4–8 g; Table 4, Fig. 5), with silky, moderately long fur (LDF 5–8 mm, LVF 4–6 mm). Ears comparatively short (length 12–15 mm). Dorsal fur Mummy Brown from basis almost to the tip (ca. 4/5 of hairs length); tips (ca. 1/5) Antimony Yellow or paler usually strongly contrasting with the basal color, giving a yellowish or grayish frosting appearance. Yellowish tips can be less evident in a few specimens in which the dorsal fur seems nearly unicolored (especially in northeastern Argentina). Ventral fur strongly bicolored, with blackish bases (2/3 hair length) and whitish tips (1/3 hair length). Ventral fur often becomes progressively paler (whiter) from upper thorax to pelvic region. Membranes and ears Mummy Brown. Legs and dorsal surface of uropatagium naked. Fringe of hairs along the trailing edge of the uropatagium always present. Plagiopatagium attached to feet on the level of

the base of the toes by a wide band of membrane. Skull moderate in size (GLS 13.8–15.2 mm, BCB 6.8–7.3 mm), rostrum comparatively short and broad, and frontal bone strongly sloping. P3 smaller than P2 and usually aligned to the toothrow, and visible in labial view. Sagittal crest absent; lambdoidal crests usually present and ranging from low to medium. Parietals slope anteriorly; occipital region rounded and projecting beyond the occipital condyle limits; braincase globular in dorsal view; postorbital and interorbital constrictions comparatively wide.

Occurs from southern Veracruz, Mexico, southward through Central America into Uruguay, northern Argentina and eastern Brazil, from humid tropical forests to savannas and semi-arid environments (Braun et al. 2009; Moratelli and Oliveira 2011; Moratelli et al. 2019a; Díaz et al. 2021). In Argentina, it occurs in Northwestern (Provinces of Jujuy, Salta, and Tucumán), Gran Chaco (Chaco, Formosa, and Santiago del Estero Provinces), Littoral regions (Provinces of Corrientes, Entre Ríos, and Misiones), and the Pampa area (Buenos Aires Province) (Barquez and Díaz 2020), from humid forests (Southern Andean Yungas) to scrublands (Dry Chaco) in an altitudinal range from 5 to 1,400 m.

Myotis ruber (É. Geoffroy, 1806)

Comments. Medium to large-sized species (FA 35.8–40.5 mm; body mass 4–8 g; Table 4, Fig. 6); with woolly, moderately long fur (LDF 6–8 mm, LVF 5–6 mm). Ears comparatively short (length 13–15 mm). Dorsal fur



Figure 5. Adult female of *Myotis albescens* (CML 5108) from Salta, Argentina.

reddish and varying from Cinnamon Brown to Ochreaceous Tawny, with slightly darker bases (1/3 hair length). The ventral fur strongly bicolored, with Prout's Brown bases (2/3 hair length) and yellowish red tips (1/3 hair length). Membranes and ears are Mummy Brown. Legs and dorsal surface of uropatagium naked. Fringe of hairs along the trailing edge of the uropatagium absent. The plagiopatagium is attached to feet on the level of the base of the toes by a wide band of membrane. Skull robust and moderate in size (GLS 15.1–15.6 mm; BCB 6.7–7.2 mm); rostrum comparatively elongated; mastoid process

well-developed. The P3 is smaller than P2 and can be aligned or displaced to lingual side in the toothrow. Sagittal crest present and usually low to medium; lambdoidal crests usually present and ranging from medium to high. Parietal straight or slightly inclined forward; occipital region flattened and not projected beyond the occipital condyle limits in most specimens; braincase elongated in dorsal view; postorbital and interorbital constrictions are comparatively narrow.

The distribution is associated with ombrophilous and seasonal tropical forests from Northeastern Brazil to



Figure 6. Adult male of *Myotis ruber* (MACN 18035) from Misiones, Argentina.

northern Argentina and Paraguay, where it appears to be strongly associated to humid and dense forested environments (Weber et al. 2010; Moratelli et al. 2019a). In Argentina, we confirm the occurrence throughout ombrophilous tropical forests in Humid Chaco (Formosa Province) and moist Atlantic Forest (Misiones Province), in an altitudinal range from 70 to 550 m. However, literature indicates a wider distribution, with records in Buenos Aires, Corrientes, Entre Ríos, and Santa Fe provinces (Barquez and Díaz 2020).

Myotis nigricans (Schinz, 1821)

Comments. Recent studies have indicated that *M. nigricans* is a complex of allopatric species (Moratelli et al. 2011a, 2016, 2017, 2019b). The name *nigricans* applies to populations from the Atlantic Forest in Southeastern Brazil to northern Argentina. Forms from northern South America previously identified as *M. nigricans* have received new names, or their subspecies have been raised to the species level (Moratelli and Wilson, 2011; Moratelli et



Figure 7. Adult male of *Myotis nigricans* (MACN 18487) from Misiones, Argentina.

al. 2013, 2017). Argentinean populations are small-sized (FA 33.0–35.1 mm; body mass 3.5–6.0 g; Table 4, Fig. 7); with silky, moderately long fur (LDH 6–8 mm, LVH 5–6 mm). Ears comparatively short (length 13–15 mm). Dorsal fur without contrast between bases and tips or slightly bicolor, with blackish bases and Mummy Brown tips. Ventral fur strongly bicolored, with blackish bases (1/2 hair length) and tips ranging from Buffy Brown to Citrine Drab (1/2 hair length). Membranes and ears are Mummy Brown or darker. Legs and dorsal surface of uropatagium naked. Fringe of hairs along the trailing edge of the

uropatagium absent. The plagiopatagium is attached to feet on the level of the base of the toes by a wide band of membrane. Skull delicate and small in size (GLS 12.4–14.2 mm, BCB 6.2–6.6 mm); rostrum comparatively elongated; the mastoid process is weakly-developed. The P3 is smaller than P2 and usually aligned to the toothrow. Sagittal crest usually absent or, when present, very low; lambdoidal crests usually present and ranging from medium to high. Parietal straight or slightly inclined forward; occipital region rounded and generally projected much beyond the posterior limit of the occipital condyles;

Table 5. External and craniodental measurements of Argentinean populations of *Myotis levis*, *M. chiloensis*, and *M. oxyotus*, including morphometric variation and number of samples (N). The measurements are in millimeters. Acronyms and descriptions are available in Table 1.

Measurements	<i>Myotis levis</i>	<i>Myotis chiloensis</i>	<i>Myotis oxyotus</i>
	mean (min–max) N	mean (min–max) N	CML 10860
FA	38.6 (36.6–40.1) 5	38.5 (37.0–41.2) 30	40.9
EL	17.0 (16.0–19.0) 5	15.0 (14.0–16.0) 22	19.0
Body mass	7.0 (6.0–8.0) 4	7.5 (5.5–9.5) 20	4.0
LDF	7.0 (6.0–8.0) 5	7.0 (6.0–8.5) 20	9.5
LVF	6.0 (4.5–7.0) 5	6.0 (5.0–7.5) 20	7.5
GLS	15.1 (14.4–15.5) 5	14.7 (13.8–15.3) 30	14.7
CCL	13.2 (12.7–13.5) 5	13.0 (12.4–13.7) 30	12.8
CBL	13.9 (13.5–14.2) 5	13.7 (13.3–14.4) 30	13.5
CIL	14.1 (13.6–14.5) 5	14.0 (13.6–14.6) 30	13.9
BAL	12.7 (12.1–13.2) 5	12.6 (12.1–13.1) 30	12.5
ZYG	9.0 (8.5–9.3) 4	-	8.7
MAB	7.6 (7.2–7.8) 5	7.6 (7.3–7.8) 30	7.1
BCB	7.1 (6.8–7.5) 5	7.0 (6.4–7.5) 30	6.9
POB	3.7 (3.5–3.8) 5	3.8 (3.5–4.0) 30	3.8
IOB	4.7 (4.3–4.5) 5	4.7 (4.6–5.0) 30	4.9
BAC	3.7 (3.5–3.9) 5	3.8 (3.6–4.0) 30	3.5
BAM	5.8 (5.6–6.0) 5	5.8 (5.4–6.1) 30	5.5
MTL	5.5 (5.4–5.6) 5	5.7 (5.5–5.8) 30	5.6
M1–3	3.2 (3.1–3.2) 5	3.2 (3.1–3.3) 30	3.6
MAN	6.0 (5.8–6.1) 4	6.0 (5.6–6.2) 30	5.8
MAL	10.6 (10.0–10.8) 4	10.6 (10.1–11.1) 30	11.0

braincase elongated in dorsal view; the postorbital and interorbital constrictions are comparatively broad.

In Argentina, they occur in ombrophilous tropical forests from Humid Chaco (Provinces of Chaco and Corrientes) and moist Atlantic Forest (Misiones Province), in an altitudinal range from 40 to 400 m. The distribution of this species still needs to be reviewed considering the recent taxonomic changes in populations originally identified as *M. nigricans*. Thus, records for other Argentinean provinces (e.g., Barquez and Díaz 2020) should be revised in light of new knowledge about *Myotis* systematics.

Myotis levis (I. Geoffroy, 1824)

Comments. Medium-sized species (FA 36.5–40.1 mm, body mass 6–8 g; Table 5, Fig. 8), with silky, moderately long fur (LDH 6–8 mm, LVH 4–7 mm). Ears comparatively long (length 16–19 mm). Dorsal fur bicolored, with blackish bases (2/3 hair length) and the tips (1/3 hair length) ranging from Mummy Brown to Bister. The ventral fur is strongly bicolored, with blackish bases (1/2 hair length) and tips (1/2 hair length) Ivory Yellow or Drab Gray. Membranes and ears Mummy Brown. Legs and dorsal surface of uropatagium naked. A fringe of hairs along the trailing edge of the uropatagium present. The plagiopatagium attached to feet on the level of the base of the toes by a wide band of membrane. Skull medium to large in size (GLS 14.4–15.5 mm, BCB 6.8–7.5 mm), and the rostrum is comparatively long and broad. The P3

is approximately the same size as P2, or slightly smaller, and usually aligned in the toothrow and visible in labial view. Sagittal crest absent or very low; lambdoidal crests usually present and ranging from low to medium. Parietals incline subtly forward to the frontal bone; occipital region rounded and projecting beyond the occipital condyle limits; braincase elongated in dorsal view; the postorbital and interorbital constrictions are comparatively narrow.

This species occurs from Southeastern Brazil southward to Uruguay, Paraguay, and eastern Argentina, from ombrophilous Atlantic Forest to Pampa grasslands (LaVal 1973; Wilson 2008; Moratelli et al. 2019a). In Argentina it is present in the Provinces of Buenos Aires, Corrientes, Entre Ríos, Misiones, and Santa Fe, occurring in scrubland savannas in an altitudinal range from sea level to 200 m (Barquez and Díaz 2020).

Myotis chiloensis (Waterhouse, 1840)

Comments. Medium to large-sized species (FA 37.0–41.2 mm, body mass 5.5–9.5 g; Table 5; Fig. 9), with wolly, long fur (LDF 6.0–8.5 mm, LVF 5.0–7.5 mm). Ears comparatively short (length 14–16 mm). Dorsal fur subtly bicolored, with medium-brown bases (near Mummy Brown) and tips generally Brussels Brown or Cinnamon Brown. The ventral fur is strongly bicolored, with Mummy Brown bases (2/3 hair length) and Dresden Brown tips (1/3 hair length). Membranes and ears Mummy Brown. Legs and dorsal surface of uropatagium



Figure 8. Adult male of *Myotis levis* (CML 4127) from Buenos Aires, Argentina.

naked. The few hairs on the trailing edge of the uropatagium do not constitute the fringe of hairs characteristic of other species, such as *M. albescens*. The plagiopatagium attached to feet on the level of the base of the toes by a wide band of membrane. Skull medium to large in size (GLS 13.8–15.3 mm, BCB 6.3–7.4 mm), and the rostrum comparatively long and narrow. The P3 is approximately the same size than P2, aligned in the toothrow, and visible in labial view. Sagittal crest absent or, when present, very low; lambdoidal crests present and low. Parietals decay subtly forward to frontal bone; occipital region projects

beyond the occipital condyle limits; braincase elongated in dorsal view; the postorbital and interorbital constrictions are comparatively narrow.

Myotis chiloensis occurs from Southern Chile, eastward into western Argentina and southward to Tierra del Fuego, in evergreen-deciduous forests, montane temperate forests, and Patagonian scrublands (Ossa and Rodríguez-San Pedro 2015; Moratelli et al. 2019a). In Argentina, it is present in the Provinces of Neuquén, Río Negro, Chubut, Santa Cruz, and Tierra del Fuego, in Valdivian Temperate Forests, Patagonian Steppes, and Magellanic



Figure 9. Adult female of *Myotis chiloensis* (MACN 16524) from Chubut, Argentina.

Subpolar Forests in an altitudinal range from sea level to ca. 1,000 m.

Myotis oxyotus (Peters, 1866)

Comments. Among all *Myotis* specimens from Argentina analyzed, only one voucher was identified as *M. oxyotus* (CML 10860). It is a medium-sized bat (FA 40.9 mm, body mass 4.0 g; Table 5; Fig. 10), with silky long fur (LDF 9.5 mm, LVF 7.5 mm). Ears comparatively short (length 19

mm). Dorsal fur strongly bicolored, with Blackish Brown bases (2/3 hair length) and Dresden Brown tips (1/3 hair length). The ventral fur strongly bicolored, with Blackish Brown bases and Light Grayish Olive tips. Membranes and ears are Mummy Brown. Legs and dorsal surface of uropatagium naked. A fringe of hairs along the trailing edge of the uropatagium absent. The plagiopatagium attached to feet on the level of the base of the toes by a wide band of membrane. The skull is large in size (GLS 14.83 mm, BCB 6.97 mm), and the rostrum comparatively short and narrow. The P3 is smaller than P2 and aligned



Figure 10. Adult female of *Myotis oxyotus* (CML 10860) from Jujuy, Argentina.

in the toothrow and visible in labial view. Sagittal crest and lambdoidal crests very low. Parietals decay steeply to frontal bone; occipital region rounded and slightly projected beyond the occipital condyle limits; braincase globular in dorsal view; the postorbital and interorbital constrictions comparatively wide.

Myotis oxyotus is divided in two allopatric subspecies: *Myotis o. oxyotus* from South America and *M. o. gardneri* from Central America. *Myotis o. oxyotus* occurs along the Andes, from Venezuela southward to northern Argentina (Wilson 2008; Moratelli et al. 2019a). The only spec-

imen recorded for Argentina is from El Mirador, 1 km NW Yavi (Yavi Department, Jujuy Province, 22°07'41"S, 65°27'58"W; 3,450 m a.s.l.), in Puna ecoregion (Urquiza et al. 2017)

***Myotis dinellii* Thomas, 1902**

Comments. Medium to large-sized species (FA 34.7–39.4 mm, body mass 5–6 g; Table 6, Fig. 12), with silky, long fur (LDF 7–9 mm, LVF 6–8 mm). Ears compara-

Table 6. External and craniodental measurements of Argentinean populations of *Myotis* cf. *simus*, *M. dinellii*, and *M. keyesi*, including morphometric variation and number of samples (N). The measurements are in millimeters. Acronyms and descriptions are available in Table 1.

Measurements	<i>Myotis</i> cf. <i>simus</i>	<i>Myotis</i> <i>dinellii</i>	<i>Myotis</i> <i>keyesi</i>
	mean (min–max) N	mean (min–max) N	mean (min–max) N
FA	39.1 (38.0–41.3) 4	36.8 (34.7–39.4) 51	39.4 (38.7–40.0) 8
EL	10.5 (10.0–12.0) 4	15.5 (14.0–17.0) 33	13.5 (13.0–14.0) 4
Body mass	9.0 (8.0–9.5) 3	5.0 (5.0–6.0) 33	7.0 (6.0–8.0) 4
LDF	3.1 (2.7–3.4) 4	8.0 (7.0–9.1) 33	7.5 (6.5–8.0) 3
LVF	2.8 (2.5–2.9) 4	6.5 (6.0–8.8) 33	5.5 (5.0–6.0) 3
GLS	14.5 (14.0–15.0) 4	14.5 (13.9–15.3) 51	13.7 (13.5–13.9) 8
CCL	12.6 (11.8–13.0) 4	12.8 (12.3–13.8) 51	12.4 (12.3–12.6) 8
CBL	13.3 (12.9–13.8) 4	13.5 (12.9–14.5) 51	13.0 (12.8–13.1) 8
CIL	13.7 (13.2–14.2) 4	13.7 (13.0–14.7) 51	13.3 (13.1–13.4) 8
BAL	12.3 (11.8–13.0) 4	12.3 (11.7–13.2) 51	11.9 (11.7–12.0) 8
ZYG	9.4 (9.3–9.5) 3	8.7 (8.4–9.4) 39	8.9 (8.8–9.0) 5
MAB	7.7 (7.5–7.9) 4	7.2 (6.8–7.7) 51	7.3 (7.0–7.6) 8
BCB	7.1 (6.8–7.5) 4	6.8 (6.5–7.1) 51	6.8 (6.7–7.0) 8
POB	3.8 (3.6–4.1) 4	3.6 (3.3–3.8) 51	3.7 (3.6–3.8) 8
IOB	4.9 (4.7–5.1) 4	4.6 (4.0–5.0) 51	4.5 (4.5–4.5) 8
BAC	4.0 (3.7–4.1) 3	3.6 (3.1–3.9) 51	3.6 (3.6–3.6) 8
BAM	5.7 (5.2–6.0) 4	5.6 (5.2–6.0) 51	5.5 (5.3–5.7) 8
MTL	5.4 (5.1–5.8) 3	5.5 (5.2–5.8) 51	5.3 (5.1–5.4) 8
M1–3	3.1 (2.8–3.3) 4	3.2 (3.0–3.3) 50	2.9 (2.9–3.1) 8
MAN	5.7 (5.4–6.2) 3	5.9 (5.6–6.2) 51	5.7 (5.6–5.8) 8
MAL	10.8 (10.5–11.3) 4	10.3 (9.8–11.0) 51	9.9 (9.8–10.1) 8

tively long (length 14–17 mm). Dorsal fur strongly bicolored, with blackish bases (1/2 hair length) and tips ranging from Buff Brown to Aniline Yellow, forming two clearly color bands in the dorsal fur. The ventral fur is strongly bicolored, with blackish bases (2/3 hair length) and tips (1/3 hair length) ranging from Ivory Yellow to Pale Olive Buff. Membranes, rostrum, and ears are blackish, contrasting strongly with the body coloration. Legs and dorsal surface of uropatagium naked. A fringe of hairs along the trailing edge of the uropatagium present, but with scattered hairs, less evident than *M. albescens* and *M. levis*. The plagiopatagium attached to feet on the level of the base of the toes by a wide band of membrane. Skull medium to large in size (GLS 13.9–15.2 mm, BCB 6.5–7.1 mm), and the rostrum comparatively long and broad. The P3 is smaller than P2 and always aligned in the toothrow and visible in labial view. Sagittal crest absent in most specimens, but when present, is very low; lambdoidal crests usually very low. Parietals decay subtly forward to frontal bone; occipital region rounded and projects beyond the occipital condyle limits; braincase elongated in dorsal view; postorbital and interorbital constrictions comparatively narrow.

This species occurs from southern Bolivia southward through Argentina, occupying deciduous forests, savannas, and semiarid open environments (Wilson 2008; Sandoval and Barquez 2013; Gamboa-Alurralde et al. 2017; Moratelli et al. 2019a). In Argentina it is present from Southern Andean Yungas (Provinces of Tucumán and Salta), southward to High Monte, Southern Andean Steppe, Low Monte, and Patagonian Steppe (Provinces

of Catamarca, Chubut, San Juan, and Mendoza), extending eastward to Dry Chaco, Espinal, and Humid Pampas (Provinces of Buenos Aires and Córdoba), occupying an altitudinal range from 50 to 2,500 m (Barquez and Díaz 2020).

Myotis keyesi J.A. Allen, 1914

Comments. Medium to large-sized species (FA 38.7–42.0 mm, body mass 6–8 g; Table 6, Fig. 13), with woolly long fur (LDF 7–8 mm, LVF 5–6 mm). Ears comparatively short (length 11–14 mm). Dorsal fur slightly bicolored, ranging from Mummy Brown and Cinnamon Brown to Ochraceous Tawny, with darker bases. Ventral fur strongly bicolored, with Clove Brown bases, and tips ranging from Ivory Yellow to Light Drab. Membranes and ears are Mummy Brown. Legs and dorsal surface of uropatagium covered by a dense pelage that extends to the knees (or just beyond). A fringe of hairs along the trailing edge of the uropatagium absent. Plagiopatagium attached to feet on the level of the base of the toes by a wide band of membrane. Skull moderate in size (GLS 13.5–13.8 mm, BCB 6.7–6.9 mm), and the rostrum comparatively elongated. The P3 is smaller than P2 and aligned in the toothrow and visible in labial view. Sagittal crest present and varying from low to medium; lambdoidal crests present and ranging from medium to high. Parietal subtly inclined forward in most individuals; posterior region of the braincase rounded and projected beyond the limit of the occipital condyles in most individuals; braincase

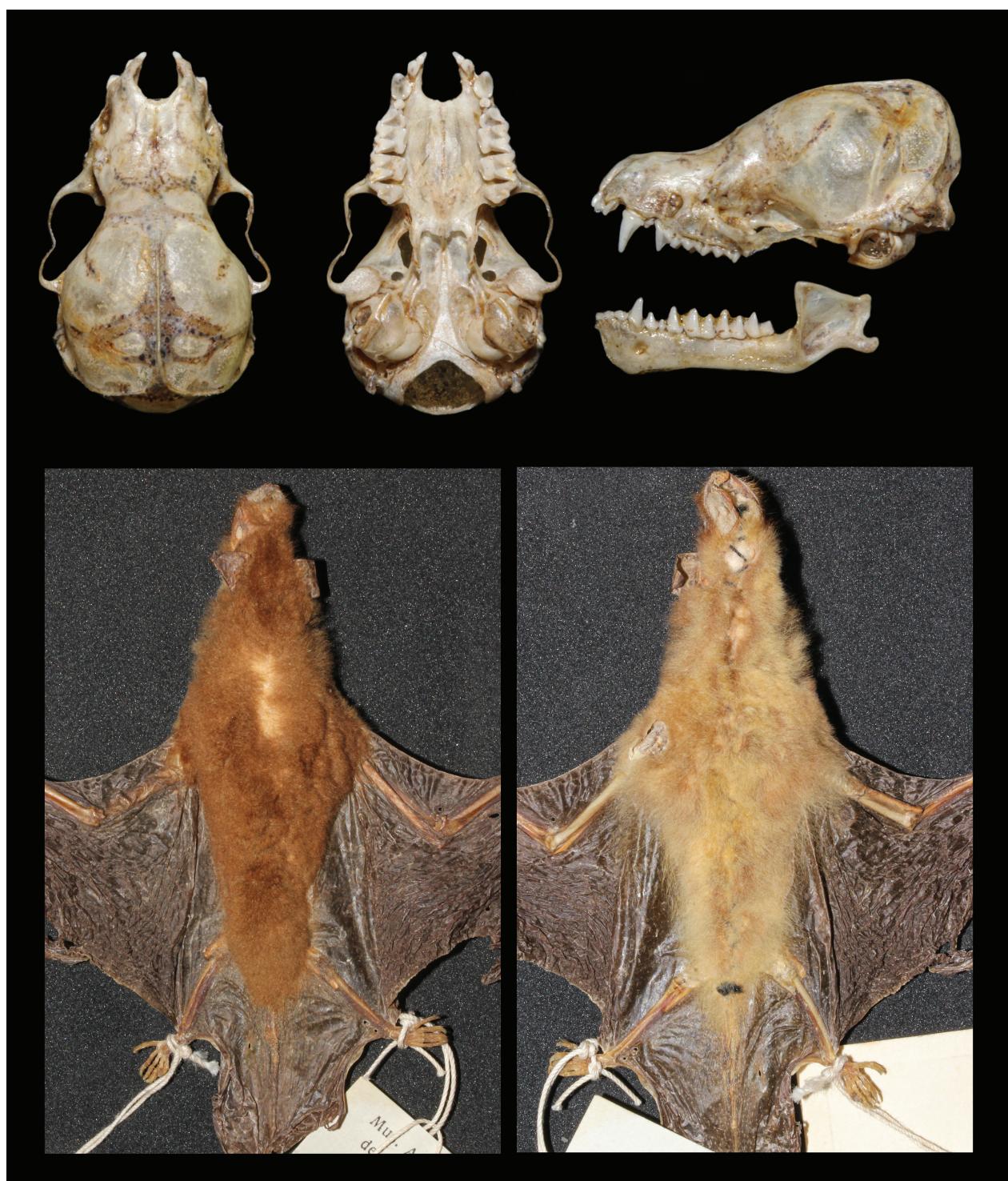


Figure 11. Adult male of *Myotis* cf. *simus* (MACN 18033) from Corrientes, Argentina.

is narrow in dorsal view; the postorbital and interorbital constrictions are comparatively wide. Specimens from Argentina are smaller and have darker fur than those of the Central Andes.

Endemic to South America and strongly associated with highlands in the Andes, from Venezuela to northern Argentina, where it is present in habitats formed by Dense Ombróphyllous Forest, Montana Nebular Forest and, in the areas of higher altitude, in Seasonal Forests dominated by shrubby vegetation and with sparse patches of arboreal vegetation (LaVal 1973; Moratelli et al.

2019a; Novaes et al. 2021b). In Argentina, it is recorded in Jujuy, Salta, Tucumán, and Catamarca, in Yungas Forest (450–1,700 m; Barquez and Díaz 2020).

Myotis riparius Handley, 1960

Comments. Small to medium-sized species (FA 33.4–36.3 mm, body mass 4–5 g; Table 7; Fig. 14), with woolly, moderately long fur (LDF 6.5–7.5 mm, LVF 5.5–7.0 mm). Ears comparatively short (length 12–15 mm). Most indi-



Figure 12. Adult male of *Myotis dinellii* (MACN 14747) from Córdoba, Argentina.

viduals have dorsal fur subtly bicolored, with Bone Brown bases (2/3 hair length) and tips (1/3 hair length) ranging from Cinnamon-Brown to Snuff Brown, with a burnished aspect (e.g., CML 3155). However, some specimens have unicolored dorsal fur generally Cinnamon-Brown (e.g., CML 5412). Ventral fur strongly bicolored, with Clove Brown bases (2/3 hair length) and generally Deep Olive Buff tips (1/3 hair length). Membranes and ears are Mummy Brown. Legs and dorsal surface of uropatagium naked. Lack of a fringe of hairs along the trailing edge of the uropatagium. Plagiopatagium attached to feet on the

level of the base of the toes by a wide band of membrane. Skull moderate in size (GLS 13.3–13.8 mm, BCB 6.3–6.4 mm), and the rostrum comparatively short and broad. The P3 is smaller than P2 and can be aligned in the toothrow or displaced to lingual side, but always visible in labial view. Sagittal crest present, ranging from low to medium; lambdoidal crests present and ranging from low to medium. Parietals decay anteriorly; occipital region is almost flattened, but projects beyond the occipital condyle limits; braincase elongated in dorsal view; postorbital and interorbital constrictions comparatively wide.



Figure 13. Adult female of *Myotis keaysi* (CML 9839) from Tucumán, Argentina.

Myotis riparius occurs from Honduras, southward through South America into northern Argentina and eastern Brazil, occupying humid tropical forests to savanna environments (Novaes et al. 2017; Moratelli et al. 2019a). *Myotis riparius* has a marked geographic variation in relation to fur coloration and skull features, which has raised suspicions that this species is, in fact, a cryptic taxonomic complex (Novaes et al. 2017). Most specimens from Argentina have morphological features that are subtly distinct from those from Panama (including the type

series) and northern South America, such as bicolored dorsal fur, skull with lower sagittal and lambdoid crests, and smaller skull and external size. On the other hand, a few specimens have fur color and cranial traits more similar to the forms from Central America and northern South America. We do not reject the hypothesis that Argentinean populations currently under the name *riparius* might be a distinct species; it is also not impossible that populations of *M. riparius* from Argentina may be hiding two sympatric cryptic species. However, more investiga-

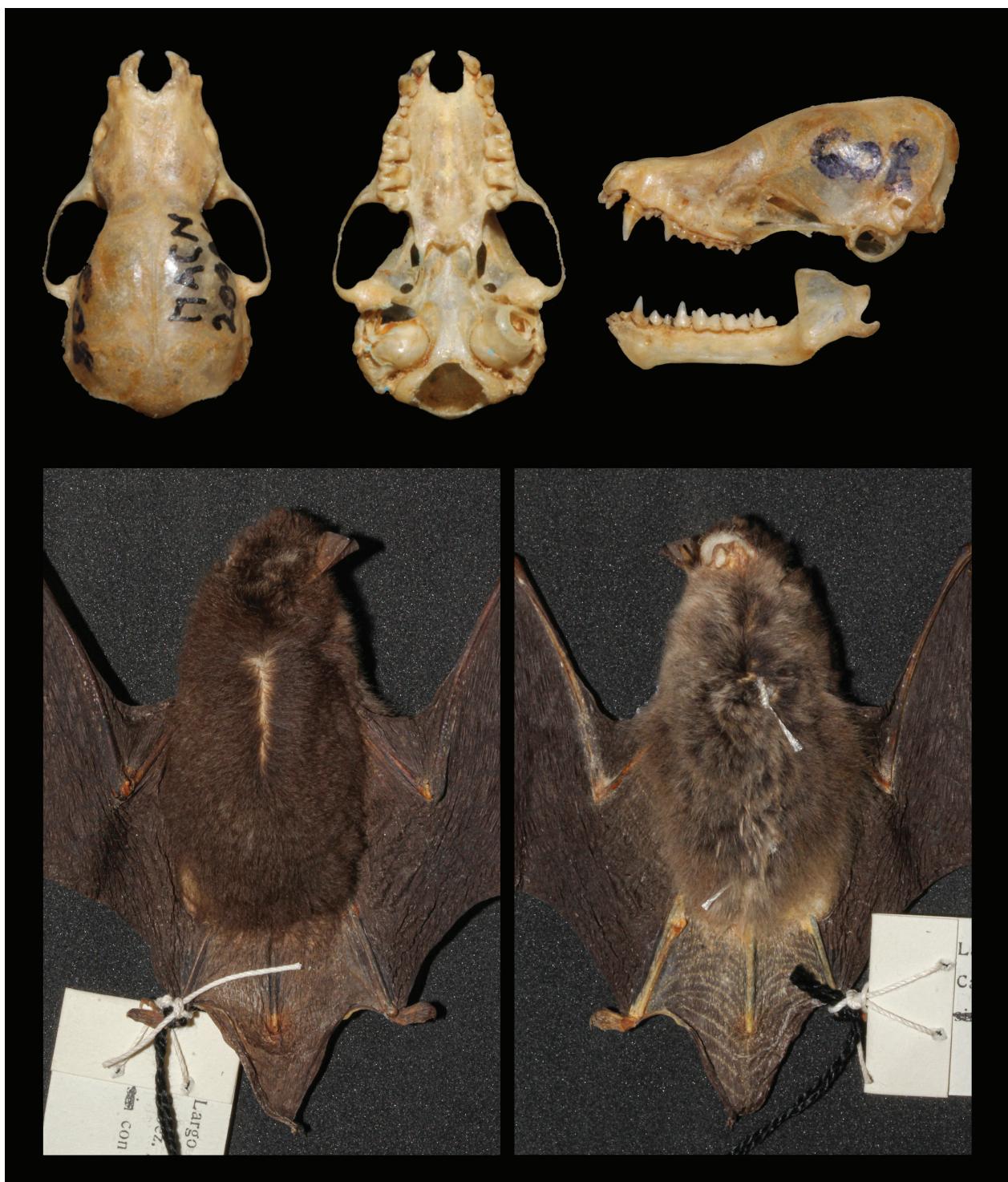


Figure 14. Adult female of *Myotis riparius* (MACN 20906) from Formosa, Argentina.

tions are needed to understand the taxonomic status of the Argentinean populations currently named as *M. riparius*, and molecular data are needed to understand whether these patterns of variation represent independent evolutionary lineages.

In Argentina, *M. riparius* occurs in the northern portion, from Southern Andean Yungas (Jujuy, Salta, and Tucumán Provinces) throughout ombrophilous tropical forests in Humid Chaco (Province of Chaco and Formosa), Dry Chaco (Santiago del Estero), and moist Atlantic

Forest (Misiones Province), in an altitudinal range from 70 to 2,000 m (Barquez and Díaz 2020). It is possible that records of *M. riparius* from the Pampa and Espinal ecoregions, in the provinces of Buenos Aires, Corrientes, and Entre Ríos, may represent the newly described *Myotis pampa* Novaes, Wilson & Moratelli, 2021. Therefore, specimens that resemble *M. riparius* from these regions need to be revised.

Table 7. External and craniodontal measurements of Argentinean populations of *Myotis riparius*, *M. izecksohni*, and *M. lavalii*, including morphometric variation and number of samples (N). The measurements are in millimeters. Acronyms and descriptions are available in Table 1.

Measurements	<i>Myotis riparius</i>	<i>Myotis izecksohni</i>	<i>Myotis lavalii</i>
	Mean (min–max) N	CML 10200	Mean (min–max) N
FA	34.3 (32.3–35.6) 10	37.8	34.0 (33.2–35.1) 9
EL	13.0 (12.0–15.0) 7	12.1	14.0 (13.0–15.0) 5
Body mass	5.0 (4.0–5.0) 7	4.0	6.5 (6.0–7.0) 5
LDF	7.1 (6.5–7.5) 7	6.5	7.0 (6.5–7.5) 5
LVF	6.0 (5.5–7.0) 7	5.3	6.0 (5.5–6.5) 5
GLS	13.6 (13.4–13.8) 10	14.6	13.9 (13.6–14.3) 9
CCL	12.1 (11.8–12.3) 10	12.6	12.3 (12.1–12.7) 9
CBL	12.7 (12.4–12.8) 10	13.4	13.0 (12.7–13.3) 9
CIL	12.9 (12.6–13.1) 10	13.8	13.2 (12.9–13.5) 9
BAL	11.5 (11.3–11.7) 10	12.1	11.7 (11.4–12.1) 9
ZYG	8.7 (8.6–8.7) 6	8.7	8.3 (8.3–8.3) 4
MAB	7.0 (6.9–7.0) 10	7.1	7.0 (6.7–7.4) 9
BCB	6.4 (6.3–6.4) 10	6.8	6.6 (6.1–6.9) 9
POB	3.5 (3.4–3.6) 10	3.5	3.5 (3.4–3.6) 9
IOB	4.4 (4.3–4.7) 10	4.5	4.5 (4.2–4.7) 9
BAC	3.6 (3.5–3.6) 10	3.7	3.4 (3.3–3.6) 9
BAM	5.4 (5.2–5.6) 10	5.7	5.4 (5.2–5.5) 9
MTL	5.1 (4.9–5.2) 10	5.5	5.0 (4.9–5.2) 9
M1–3	2.9 (2.8–3.0) 10	3.1	2.9 (2.8–2.9) 9
MAN	5.5 (5.2–5.7) 10	5.7	5.4 (5.2–5.5) 8
MAL	9.8 (9.5–10.1) 10	10.5	9.7 (9.3–10.1) 8

Myotis izecksohni Moratelli, Peracchi, Dias & Oliveira, 2011

Comments. Among all *Myotis* specimens from Argentina analyzed, only one voucher (CML 10200) was identified as *M. izecksohni*. It is a medium-sized species (FA 37.8 mm, body mass 4 g; Table 7, Fig. 15). Ears comparatively short (length 12.1 mm). Silky, moderately long fur (LDH 6–8 mm, LVH 5–6 mm). Dorsal fur slightly bicolor, with blackish bases (2/3 hair length) and Bone Brown tips (1/3 hair length). Ventral fur strongly bicolored, with blackish bases (2/3 hair length) and Buffy Brown tips (1/3 hair length). Membranes and ears are Mummy Brown. Legs and dorsal surface of uropatagium naked. A fringe of hairs along the trailing edge of the uropatagium is absent. The plagiopatagium attached to feet on the level of the base of the toes by a wide band of membrane. Skull delicate and small in size (GLS 14.6 mm, BCB 6.8 mm); the rostrum comparatively elongated; mastoid process weakly developed. The P3 is smaller than P2 and usually aligned to the toothrow. Sagittal crest and lambdoidal crests very low. Parietal straight or slightly inclined forward; occipital region is rounded and projected beyond the posterior limit of the occipital condyles; braincase elongated in dorsal view; the postorbital and interorbital constrictions comparatively broad.

This species occurs from southeastern Brazil to northern Argentina, in dense ombrophilous forests (Moratelli et al. 2019a). The only record in Argentina is from humid and dense forests from Misiones (210 m) in the Alto Paraná Atlantic Forest (Barquez et al. 2017).

Myotis lavalii Moratelli, Peracchi, Dias & Oliveira, 2011

Comments. Small to medium-sized species (FA 33.8–39.6 mm, body mass 5–6 g; Table 7, Fig. 15), with silky and long fur (LDH 5–8 mm, LVH 4–6 mm). Ears are moderate in length (13–14 mm). Dorsal fur strongly bicolored, with Clove Brown bases (1/2 hair length) and Buffy Brown tips (1/2 hair length). The ventral fur strongly bicolored, with Bone Brown bases (1/2 hair length) and generally Pale Olive-Buff tips (1/2 hair length). Membranes and ears are Mummy Brown or lighter. Legs and dorsal surface of uropatagium naked. A fringe of hairs along the trailing edge of the uropatagium is absent. The plagiopatagium attached to feet on the level of the base of the toes by a wide band of membrane. Skull small to moderate in size (GLS 13.6–13.8 mm, BCB 6.5–6.7 mm), and the rostrum comparatively short and narrow. The P3 is smaller than P2 and usually aligned in the toothrow and visible in labial view. Sagittal crest usually present and very low, or even absent in some individuals; lambdoidal crests usually present and very low. Parietals decay anteriorly; occipital region rounded and projected beyond the occipital condyle limits; braincase is elongated in dorsal view; the postorbital and interorbital constrictions are comparatively narrow.

Myotis lavalii occurs from Northeastern Brazil, throughout South American diagonal of open formations, to Paraguay and northern Argentina, in savannas, semi-arid fields, and seasonal forests (Moratelli et al. 2019a; Weber et al. 2019). In Argentina, it is present in



Figure 15. Adult female of *Myotis izecksohni* (CML 10200) from Misiones, Argentina.

Dry Chaco scrublands and Yungas Forest from Salta and Santiago del Estero Provinces, in an altitudinal range from 120 to 800 m.

Myotis cf. simus

Comments. The *M. simus* complex was taxonomically revised resulting in the recognition of the recently described species *Myotis midastactus* Moratelli & Wilson, 2014, based on individuals originally identified as *M. si-*

mus from Bolivia (Moratelli et al. 2011b; Moratelli and Wilson 2014). Subsequently, populations of *M. simus* from Paraguay were reidentified as *M. midastactus* based on morphological traits (Moratelli et al. 2015). Moratelli et al. (2019a) considered that *M. simus* has two disjunct populations, one in dense humid forests along the Amazon Basin and the other in Brazilian Pantanal and Humid Chaco from Argentina and Paraguay. However, specimens from Argentina can be distinguished from *M. simus* from the Amazon Basin by paler pelage, and larger skull with lower sagittal crest. Considering the geographic



Figure 16. Adult female of *Myotis lavalii* (CML 5404) from Santiago del Estero, Argentina.

discontinuity (Moratelli et al. 2011c) and morphological differences, it is likely that samples from Argentina represent a distinct taxon from *M. simus* from the Amazon Basin. On the other hand, one specimen from Argentina is more similar to *M. midastactus* in fur color (MACN 18033) but differs slightly in cranial traits. Other specimens from Argentina differ conspicuously from *M. simus* and *M. midastactus* in fur color. Thus, samples from Argentina may (i) represent a population of *M. midastactus* (with subtle geographic variation in relation to fur color); (ii) represent *Myotis guaycuru* Proen  a, 1943, a species

described for the Brazilian Cerrado-Pantanal transition and currently considered a junior synonym of *M. simus*; (iii) represent a third and unnamed species, with occurrence restricted to the Argentinean Humid Chaco. If the third hypothesis is confirmed, *M. guaycuru* could be the valid name for the populations currently considered as *M. midastactus* from Bolivia and Paraguay. However, due to morphological similarity and the absence of phenotypic discontinuity, the resolution of this issue depends on the analysis of new specimens from all ecoregions based on morphological and molecular approaches.

In Argentina, this taxon is medium to large-sized (FA 38.0–41.3 mm, body mass 8.0–9.5 g; Table 6; Fig. 11), with wooly and very short fur (LDF 2.7–3.4 mm, LVF 2.5–2.9 mm). Ears are comparatively short (length 10–14 mm). Dorsal fur ranges from Clay Color to Wood Brown, without contrast between bases and tips. The ventral fur weakly bicolored, with Drab bases (1/2 hair length) and tips (1/2 hair length) ranging from Colonial Buff to Pale Olive-Buff. Membranes and ears are Clove Brown or lighter. Legs and dorsal surface of uropatagium are naked. A fringe of hairs along the trailing edge of the uropatagium is absent. The plagiopatagium attached to feet at the ankles level or on the base of the toes by a narrow band of membrane. Skull medium to large in size (GLS 14.0–15.0 mm, BCB 6.8–7.5 mm), and the rostrum comparatively short and broad. The P3 smaller than P2 and usually displaced to lingual side in the toothrow. Sagittal crest and lambdoidal crests present and ranging from low to medium. Parietals slope anteriorly; occipital region flattened and subtly projects beyond the occipital condyle limits; postorbital and interorbital constrictions comparatively wide.

Argentinean populations of *M. cf. simus* are present in Humid Chaco and Mesopotamian Savanna from Formosa and Corrientes Provinces, and in the Delta e Islas del Paraná in Santa Fe Province, occupying an altitudinal range from 46 to 200 m (Pavé and Gavazza 2022).

Discussion

Myotis barquezi occurs in humid seasonal forests from Southern Andean Yungas, an ecoregion with a high richness of mammals, including endemic species (Ojeda and Mares 1989; Barquez and Díaz 2001; Ojeda et al. 2008; Sandoval et al. 2010; d'Hiriart et al. 2015). Our revision of museum specimens indicates the occurrence of another five *Myotis* species for the Yungas Forest (*M. albescens*, *M. dinellii*, *M. keaysi*, *M. lalavi*, and *M. riparius*). Historical records of *M. nigricans* for this ecoregion (i.e., Ojeda and Mares 1989; Barquez and Díaz 2001) need to be revised, considering that recent taxonomic revisions have indicated that this species corresponds to a cryptic complex (Moratelli et al. 2011a; Novaes et al. 2022). Although the Argentine Yungas have received an extensive sampling effort for the bat assemblage during the past 50 years (Barquez and Díaz 2001; Gamboa-Alurralde et al. 2017), the discovery of *M. barquezi* reveals the need for continued field sampling, associated with careful taxonomic investigations. In addition, there is the possibility of occurrence of other *Myotis* in Argentina not included in this study, for example *M. pampa*, a species recently described from pampa grassland in Uruguay close to the Argentina boundary (Novaes et al. 2021c).

Despite recent taxonomic revisions of Neotropical *Myotis*, we consider that a large part of *Myotis* species from Argentina have insufficient taxonomic knowledge. Of the 13 species listed for Argentina, three (*M. keaysi*,

M. riparius, and *M. simus*) show strong morphological variation in relation to the type specimens and topotype series (Moratelli et al. 2011b; Novaes et al. 2017, 2021b), with poorly delimited taxonomic limits, which may hide cryptic diversity; and three are known from few specimens (*M. barquezi*, *M. izecksohni*, and *M. oxytous*).

Until recently, *M. dinellii* was considered a subspecies of *M. levis* (LaVal 1973; Barquez et al. 1999; Wilson 2008). The elevation of *M. dinellii* to species level was based on morphological and morphometric evidence (Barquez et al. 2006; Miranda et al. 2013). However, the decision taken by Miranda et al. (2013) may have been biased by misidentified specimens, since samples of *M. dinellii* recorded for southern Brazil by these authors are actually *M. albescens*. Moratelli et al. (2019a) considered *M. dinellii* as a full species based on external and skull features, but the geographic limits remain poorly understood.

The present study indicates the occurrence of 13 species of *Myotis* in Argentina but does not end the need for further revisions. On the contrary, the pattern of variation found in several taxa suggests that the diversity of Argentinian *Myotis* may be underestimated and the taxonomic status of some populations need to be revised, especially in light of new morphological and, mainly, molecular evidence. We suggest that further studies of *Myotis* from Argentina should focus on investigating the morphological and genetic variation of the forms currently named *M. riparius*, *M. simus*, and *M. keaysi*.

With the description of *M. barquezi*, we recognize 25 species of South American *Myotis*, 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. oxytous* (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. lalavi* Moratelli, Peracchi, Dias & Oliveira, 2011, *M. izecksohni* Moratelli, Peracchi, Dias & Oliveira, 2011, *M. handleyi* Moratelli, Gardner, Oliveira & Wilson, 2013, *M. midastactus* Moratelli & Wilson, 2014, *M. clydejonesi* Moratelli, Wilson, Gardner, Fisher & Gutiérrez, 2016, *M. attenboroughi* Moratelli, Wilson, Novaes, Helgen & Gutiérrez, 2017, *M. bakeri* Moratelli, Novaes, Carrión-Bonilla & Wilson, 2019, *M. armiensis* Carrión-Bonilla & Cook, 2020, *M. pampa* Novaes, Wilson & Moratelli 2021, and *M. moratellii* Novaes, Cláudio, Carrión-Bonilla, Abreu, Wilson, Maldonado & Weksler, 2021. In line with other taxonomic revisions (i.e., Larsen et al. 2012; Novaes et al. 2018, 2021a, 2021b), our results demonstrate morphological complexes that correspond to undescribed species in South America. Despite its recent arrival at the Neotropics (Stadelmann et al. 2007), *Myotis* is the most speciose bat genus in South America and should be considered an important model for biogeographic and evolutionary studies that focus on colonization, dispersal, and diversification of the South American bat fauna.

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Appendix 1

Listed below are localities with specimens examined from following collections: American Museum of Natural History (AMNH, New York, USA), Carnegie Museum of Natural History (CM, Pittsburgh, USA), Coleção Adriano Lucio Peracchi da Universidade Federal Rural do Rio de Janeiro (ALP, Seropédica, Brazil), Coleção Científica de Mastozoologia da Universidade Federal do Paraná (CCMZ-DZUP, Curitiba, Brazil), Field Museum of Natural History (FMNH, Chicago, USA), Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN, Buenos Aires, Argentina), Colección Mamíferos Lillo (CML, Tucumán, Argentina), Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, Brazil), Muséum d'Histoire Naturelle (MHNG, Geneva, Switzerland), Museum of Natural Science, Louisiana State University (LSUMZ, Baton Rouge, USA), Museum of Texas Tech University (TTU, Lubbock, USA), Museum of Vertebrate Zoology (MVZ, Berkeley, USA), Royal Ontario Museum (ROM, Toronto, Canada), Sam Noble Oklahoma Museum of Natural (OMNH, Norman, USA), Smithsonian's National Museum of Natural History (USNM, Washington, D.C., USA), Universidade Federal de Pernambuco (UFPE, Recife, Brazil). Localities are arranged by species and alphabetically by major political unit (region/department/province), and may include precise locality.

Myotis albescens ($N = 64$): 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, Orán, 40 km NW del cruce de ruta 50 y ruta provincial 18, sobre camino a San Andrés (CML 7601); Salta, San Martín, 12 km W Piquirenda Viejo (CML 5108); Salta, Iruya, 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 del 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).

Myotis armiensis ($N = 14$): Ecuador: Tungurahua, Baños (TTU 85060, FMNH 47593). Panamá: 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 barquezi ($N = 2$): Argentina: Salta, Orán, ca. 20 km SW San Ramón de La Nueva Orán, Finca Alto Verde (CML 7622 [paratype], CML 7623 [holotype]).

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, Estancia Chacabuco, 62 km SE San Martín de Los Andes (MVZ 150868, 150869, 150883, 150884, 150892); Neuquén, Parque Nacional Nahuel Huapi, 10 km W Villa Traful, Arroyo Medina (CML 10855); Río Negro, Bariloche, Isla Victoria, 10 km al E de Piedras Blancas (CML 5219).

Myotis dinellii ($N = 73$): Argentina: Buenos Aires, General Guido, Cañal 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, MACN 14747); 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); 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 (MVZ 150861); Mendoza, La Valle, 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 Siambón (OMNH 36216).

Myotis elegans ($N = 25$): Costa Rica (KU 158651); El Salvador (ROM 101293, 101319); Honduras: Olancho (TTU 13299, 13345, 47926); Santa Barbara (TTU 13348); Atlantida (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, Apóstoles, Parque Provincial de la Sierra, Colonia Taranco (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 ($N = 36$): Argentina: Tucumán, Burruyacú, Piedra Tendida, 8 km W Dique El Cajón (CML 6177, 7600, 9839); Tucumán, Burruyacú, Reserva Provincial Aguas Chiquitas, Arroyo Aguas Chiquitas (CML 8938); Tucumán, Burruyacú (MACN 16795, 16855, 16857, OMNH 23499, 36207, TTU 32588). Peru: 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).

Myotis lavalii ($N = 58$): Argentina: Salta, 1 km al E de Tonono sobre río Itiyuro (CML 5324); Santiago del Estero, Pellegrini, Santo Domingo (OMNH 23768, 23769, 23770, CML 3265, 5404, 5469, 5470, 5471, 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, La Valle (USNM 236236, 236237); Buenos Aires, Maipú (TTU 32555); Entre Ríos, Puerto Constanza, Estancia El Tara (USNM 582461); Santiago del Estero, Pozo Hondo, Finca El Duende (CML 4127). 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: Camaquã (AMNH 235863, 235864, 235865, 235866, 235867, 235868, 235869, 235870, 235871, 235872, 235873, 235874).

235875, 235876, 235877, 235878, 235879, 235880, 235881). Uruguay: Lavalleja, Piraraja (AMNH 205477, 205478, 205503, 205504, 205505, 205508, 205509, 205510, 205511, 205512, 205513, 205514, 205515); Colón (USNM 252599); Tacuarembó, Arroyo Yaguarí (MZUSP 28979, 28981).

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 Rayes (MVZ 144481–144484).

Myotis moratellii ($N = 9$): Ecuador: Los Ríos, Abras de Mantequilla, Hacienda Santa Teresita (USNM 513482); Vincos, 3 km NE, Puerto Nuevo (USNM 513482 [holotype]); Santo Domingo, 47 Km S (by road), Rio Palenque Science Center (USNM 528568, USNM 522575). El Oro, Reserva Militar Arenillas (TTU 102438, 102681, 102691, 102707); Esmeraldas, Cristal (CM 112857).

Myotis nigricans ($N = 72$): Argentina: Chaco, Sargent Cabral, La Forestal, 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 oxyotus ($N = 26$): Argentina: Jujuy, Yavi, el Mirador (CML 10860). Colombia: Nariño: El Guabo (USNM 309019). Ecuador: Chimborazo, Pallatanga (USNM 513480); Pastaza, Mera (USNM 548337, 548339); Pastaza, Mirador USNM 513491, 513492, 513493, 513494). PERU: Cuzco, Iquente (USNM 195196); Cuzco, Santa Ana (USNM 194452, 194453, 195141, 195147, 195149); Junín, Rio Palca (USNM 507204). Venezuela: Amazonas, Cerro Duida, Cano Culebra, 50 km NW Esmeralda (USNM 405799); Amazonas, Cerro Neblina, Camp VII (USNM 560809–560811); Bolívar, Km. 125, 85 km SE El Dorado (USNM 387712); Bolívar, El Pauji, 21 km NE Icabaru, El Pauji (USNM 441750); Distrito Federal, Alto Ño León, 33 km SW Caracas (USNM 409427); Merida, La Mucuy, 4 km E Tabay (USNM 373919, 387705).

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

Myotis pilosatibialis ($N = 32$): El Salvador: Ahuachapan, El Imposible, San Francisco Menendez (ROM 101273), Santa Ana, Parque Nacional Montecristo (ROM 101352, 101353, 101356, 101357, 101430, 101433, 101465–101467, 101524). Honduras: Francisco Morazan, 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). Mexico:

Oaxaca (KU 99731, LACM 14244, 14245, 26159, 26127, 26128); Taumalipas, Ocampo (AMNH 164969, 164945, 164967, 164971, 164972, 164939, 144988); Veracruz, Coatepec, Ojo de Agua (AMNH 254676, 254677).

Myotis riparius ($N = 63$): Argentina: Corrientes, Capital, Laguna Páivias, Barrio Los Lomas (CML 2994); Formosa, Rio Porteña, km 64, a 5 km al sur de Estancia Sta. Catalina (OMNH 18889); Formosa, Río Bermejo, 10 millas al S de Colonia km 503 (CML 5412); Formosa, Parque Nacional Pilcomayo (MACN 20881, 20895, 20906); 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, 5092); 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: Amazonas, Barcelos (CRB 2871); 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); Caqueta, Río Caqueta (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). Panama: Bocas del Toro, Isla Popa (USNM 464368, 575586); Chiriquí, Cotito Near (USNM 331916); Panama, Cerro Azul (ROM 99936); Panama, Cerro Campana (USNM 306795); Panama, 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 ($N = 60$): Argentina: Formosa, Laguna Blanca, Parque Nacional Pilcomayo (CML 4666, 4673, 4676, 4686); Misiones, Guarani, jat. Hwy 21, Arroyo Oveja Negra, ~2 km W Parque Provincial Moconá (CML 3877); Misiones, Parque Nacional Iguazú, Ayui (MACN 18490); Misiones, Loreto (MACN 18035); Misiones, Parque Nacional Iguazú, Seccional Mbocay (OMNH 18882). Brazil: Pernambuco, Brejo da Madre de Deus (UFPE 1022, 1026, 1089), Caruaru (UFPE 1105, 1285, 1361); Bahia, Alagoas (MHNG 1884-50); 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); Macaé de Cima (JAO 1751, 1756, 1773); 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 Teotonio (MHNG 1916-71); Rio Grande do Sul, São Lourenço da Mata (MZUSP 1988). Paraguai: Sapucay, Sapucay (USNM 115097 [holotype], 121478); Itapúa, Arroyo Pirayu (MHNG 1747-56); Santo Temembey, 4 km amont (MHNG 1695-27); Misiones, Iguazu (OMNH 18882). Uruguay: Arroyo Grande (MHNG 1748-47).

Myotis simus ($N = 68$): Brazil: Amazonas, Manaus (AMNH 91475–91478, 91500); Amazonas, Borba (AMNH 91886, 91888–91891, 94224, 94225, 94227, 94230–94234); Amazonas, Parintins (AMNH 92983, 93490, 93492–93496, 93922, 93923); Amazonas, Rio Juruá (MZUSP 638, 1062, 1074); Amazonas, Itacoatiara (MZUSP 4372). Colombia: Amazonas (TTU 9073, 9076–9078). Ecuador, Pastaza, Río Capahuari (FMNH 43143). Peru: 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).

Myotis cf. simus ($N = 4$): Argentina: Corrientes, Isla Apipé (MACN 18033); Corrientes, Parque Nacional Mburucuyá (MACN 20914); Formosa, Parque Nacional Pilcomayo, Paso Pomelo, Laguna Blanca (CML 4680, MACN 20901).