

Diversity, morphological phylogeny,
and distribution of bats of the genus *Molossus*
E. Geoffroy, 1805 (Chiroptera, Molossidae) in Brazil

Livia Oliveira LOUREIRO,
Renato GREGORIN & Fernando Araujo PERINI



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Molossus molossus (Pallas, 1766). Photo courtesy of Dr Marco A. R. Mello.

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Diversity, morphological phylogeny, and distribution of bats of the genus *Molossus* E. Geoffroy, 1805 (Chiroptera, Molossidae) in Brazil

Livia Oliveira LOUREIRO

University of Toronto, Department of Ecology and Evolutionary Biology,
25 Willcocks Street, Toronto, ON, M5S 3B2 (Canada)
and Universidade Federal de Minas Gerais, Avenida Presidente Antônio Carlos,
6627 – Pampulha, Belo Horizonte – MG, 31270-901 (Brazil)
(corresponding author) livia.loureiro@mail.utoronto.ca

Renato GREGORIN

Universidade Federal de Lavras. Campus Universitário,
Caixa Postal 3037, Lavras – MG, 37200-000 (Brazil)
rgregorin@dbi.ufla.br

Fernando Araujo PERINI

Universidade Federal de Minas Gerais,
Avenida Presidente Antônio Carlos,
6627 – Pampulha, Belo Horizonte – MG, 31270-901 (Brazil)
faperini@ufmg.br

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ABSTRACT

Tenuous descriptions of many species and subspecies of mastiff bats make the taxonomy of *Molossus* E. Geoffroy, 1805 confusing and unstable. *Molossus* is one of the most diverse genera of free tailed bats in the pantropical family Molossidae Gervais, 1856. Given their impressive variation due to geography, sex, and ontogeny, and incomplete knowledge about species boundaries, a comprehensive taxonomic revision of the genus is needed. In addition, the level of genetic divergence, even among morphologically well-characterized species is low, often making diagnosis of groups difficult and likely resulting in an underestimation of the number of species. Brazil has a wide territory harboring many different physiognomies, but with no study focusing on the morphological variation and taxonomy of *Molossus* available. Therefore, we have analyzed qualitative and quantitative characters from 493 specimens belonging to nine species of *Molossus*, and conducted a wide comparative morphological analysis of the species occurring in Brazil. In addition, we propose a hypothesis of phylogenetic relationships within *Molossus* based on morphology, establishing the morphological characters for diagnosis and identification of species, and update the geographic distribution of *Molossus* species in Brazil, with range extensions for four taxa. Six species, *Molossus rufus* E. Geoffroy, 1805, *Molossus molossus* (Pallas, 1776), *Molossus coibensis* Allen, 1904, *Molossus aztecus* Saussure, 1860, *Molossus currentium* Thomas, 1901, and *Molossus pretiosus* Miller, 1902 occur in Brazil. We bring support for the synonymy of *Molossus bondae* Allen, 1904 with *M. currentium*, as suggested by several authors.

KEY WORDS

Brazil,
Mastiff bats,
morphology,
identification key,
phylogenetic relationships.

RÉSUMÉ

Diversité, phylogénie morphologique et répartition des chauves-souris du genre Molossus E. Geoffroy, 1805 (Chiroptera, Molossidae) au Brésil.

Les vagues descriptions de nombreuses espèces et sous-espèces de chauve-souris molosses rendent la taxonomie de *Molossus* E. Geoffroy, 1805 confuse et instable. *Molossus* est l'un des genres les plus divers de chauves-souris à queue libre de la famille pantropicale Molossidae Gervais, 1856. Du fait de son impressionnante variation liée à la géographie, au sexe et à l'ontogénie, et de la connaissance incomplète des limites entre espèces, une révision taxonomique complète du genre est nécessaire. En outre, le niveau de divergence génétique, même entre les espèces morphologiquement bien caractérisées, est faible, ce qui rend souvent difficile la diagnose des groupes et conduit probablement à une sous-estimation du nombre d'espèces. Le Brésil couvre un vaste territoire présentant de nombreuses physionomies différentes, mais aucune étude portant sur la variation morphologique et la taxonomie de *Molossus* n'a été réalisée. Par conséquent, nous avons analysé les caractères qualitatifs et quantitatifs de 489 spécimens appartenant à neuf espèces de *Molossus*, et effectué une large analyse morphologique comparative des espèces présentes au Brésil. En outre, nous proposons une hypothèse de relations phylogénétiques des espèces de *Molossus* basée sur la morphologie, établissant les caractères morphologiques pour la diagnose et l'identification des espèces, et actualisons la répartition géographique des espèces de *Molossus* au Brésil; quatre taxons ont leur aire de répartition étendue. Six espèces, *Molossus rufus* E. Geoffroy, *Molossus molossus* (Pallas, 1776), *Molossus coibensis* Allen, 1904, *Molossus aztecus* Saussure, 1860, *Molossus currentium* Thomas, 1901 et *Molossus pretiosus* Miller, sont présentes au Brésil. Nos données confirment la synonymie de *Molossus bondae* Allen, 1904 avec *M. currentium*, suggérée par plusieurs auteurs.

MOTS CLÉS

Brésil,
Mastiff bats,
morphologie,
clé d'identification,
relations phylogénétiques.

INTRODUCTION

Molossidae Gervais, 1856 represent the fourth most diverse family of bats (Chiroptera) with more than 100 species (Simmons 2005) occurring mostly in tropical regions around the World. Although some Neotropical genera have been recently reviewed, such as *Promops* Gervais, 1856 (Gregorin & Chiquito 2010), *Eumops* Miller, 1906 (Gregorin *et al.* 2016), and *Cynomops* Thomas, 1920 (Moras *et al.* 2016, 2018), some highly diverse genera, such as *Molossus* E. Geoffroy, 1805, still lack a comprehensive taxonomic revision. The distribution of *Molossus* is Neotropical, occurring from Mexico to southern Argentina, including several Caribbean islands (Simmons 2005), which makes the study of this taxon difficult.

Molossus is characterized by a set of morphological traits, such as slightly triangular ears, divergent upper incisors in line with canines, smooth upper lips, obtuse rostrum, and well developed sagittal crest, especially in males (Dolan 1989; Fabián & Gregorin 2007; Gregorin 2009; Gregorin & Cirranello 2016). However, several morphological and physiological characteristics vary among geographic regions (Davison & Wilkison 2002), and only part of this variation has been analyzed (Willig 1983; Dolan 1989; Jennings *et al.* 2000; López-González & Presley 2001; Souza 2011; Gregorin *et al.* 2011; Catzefflis *et al.* 2016).

Molossus has been reviewed by Miller (1913) and Dolan (1989), but its taxonomy has been in a state of constant flux, and the actual number of species is not a consensus among authors. For example, Miller (1913) recognized 18 species while Goodwin (1956, 1959) added one species and one subspecies to the genus. In the most influential review of

Molossus, Dolan (1989) recognized seven species: *Molossus molossus* (Pallas, 1776), *Molossus aztecus* Saussure, 1860, *Molossus rufus* Geoffroy, 1805, *Molossus pretiosus* Miller, 1902, *Molossus coibensis* Allen, 1904, *Molossus bondae* Allen, 1904, and *Molossus sinaloae* Allen, 1906. However, this author examined specimens almost exclusively from Central America. Other studies recognized eight species with the revalidation of *Molossus barnesi* Thomas, 1905 (Simmons & Voss 1998; Simmons 2005), but its synonymy with *M. coibensis* was suggested by Gregorin *et al.* (2011) and endorsed by Catzefflis *et al.* (2016) based on both morphological and molecular characters. Recently, two new species, *Molossus alvarezii* Gonzalez-Ruiz, Ramirez-Pulido & Arroyo-Cabrales, 2011 from Mexico and *Molossus fentoni* Loureiro, Lim, Engstrom, 2018 from Guyana and Ecuador were described (González-Ruiz *et al.* 2011; Loureiro *et al.* 2018). However, studies focusing on morphological variation are scarce and the distributional range of the species is poorly known, especially in South America. Due to the description of many species and subspecies, and because the morphological differences are tenuous in many cases, taxonomy of *Molossus* is confusing and unstable (Dolan 1989; Simmons 2005; Eger 2008). Additionally, the level of genetic divergence, even among morphologically well-characterized species, such as *M. molossus* and *M. rufus*, is low (Lindsey & Ammerman 2016; Lim *et al.* 2017, Loureiro *et al.* 2018), often making diagnosis of groups based on molecular markers difficult, and likely resulting in an underestimation of the number of species. The combination of these factors makes the taxonomy of *Molossus* a challenge.

In Brazil, species of *Molossus* occur in all six major Brazilian biomes (Eger 2008), from the state of the Amazonas to Rio

Grande do Sul, encompassing a wide latitudinal range. *Molossus* is also commonly found in urban areas and in houses, making it one of the most frequently observed free-tailed bats in Brazil. Six species of *Molossus* are currently recognized for the country (Dolan 1989; Gregorin & Taddei 2000; López-González & Presley 2001; Gregorin *et al.* 2011), but the diversity of *Molossus* was historically underestimated, with only two species being recognized for a long time: the small-sized *M. molossus* and the larger *M. rufus* (synonym of *M. ater*). Dolan (1989) recorded *M. coibensis* as occurring in the state of Mato Grosso (under the name *M. cherriei* Allen, 1916); however, this record was not mentioned by subsequent authors (e.g. Gregorin & Taddei 2002). In the 2000's, some publications improved our knowledge about *Molossus* in Brazil, with the addition of four species recognized for the country: *M. pretiosus* (Gregorin & Taddei 2000; Nogueira *et al.* 2008), *M. currentium* (López-González & Presley 2001; Tavares *et al.* 2010; Bernard *et al.* 2011), *M. aztecus* (Gregorin *et al.* 2011), and *M. coibensis* (Dolan 1989; Costa *et al.* 2013).

Therefore, due to presence of many species of *Molossus* in Brazil, the high phenotypical variation in some species, such as in *M. molossus* (Souza 2011) and to the uncertainties that surround its taxonomy in the large and ecologically diverse Brazilian territory, an overview of the taxon is necessary to determine the number of species of *Molossus* currently present in Brazil, establishing morphological diagnostic traits and defining the limits of their geographical range. It can be expected that the hidden taxonomic diversity found in Brazilian *Molossus* will occur in other ecological, geological and environmental complexes countries such as Peru, Ecuador, and Colombia). In addition, *Molossus* has been divided into two morphogroups based on several morphological traits such as banding pattern in the dorsal hairs and cranio-dental morphology (Dolan 1989; Gregorin *et al.* 2011). However, there are no studies addressing the relationships within *Molossus* using a cladistic approach neither discussing the diagnosis of species-group based on a cladistic view (e.g. apomorphies). Therefore, this study aims at: 1) making a comparative morphological analysis of the species within *Molossus* from Brazil; 2) establishing morphological characters for definition and identification of species based mainly in apomorphic states of characters as recovered by phylogeny; and 3) updating the geographic distribution of several species of *Molossus* in Brazil.

MATERIAL AND METHODS

EXAMINED MATERIAL

We examined 493 specimens from nine species of *Molossus* including nine *M. bondae* from Colombia, 26 *M. coibensis* (including three individuals previously identified as *M. barnesi*) from Brazil, Panama, French Guiana, and Guatemala), 253 *M. molossus* (mainly from several Brazilian localities), 59 *M. aztecus* (from Mexico and Brazil), 11 *M. currentium* (from Colombia, Brazil, and Panama), 32 *M. pretiosus* (from some Mexico, Brazil, and Venezuela), 80 *M. rufus* (mainly from several Brazilian localities), 10 *M. sinaloae* (from Central

America) and a single indeterminate specimen of *Molossus* sp. from Brazilian Caatinga, state of Bahia, Northeastern Brazil (possibly a new taxon). Additionally we have also examined six specimens of *Promops centralis* Thomas, 1915 and seven of *Eumops auripendulus* Shaw, 1800 to use as outgroup in the phylogenetic analysis. The choice of these species was based on the phylogeny proposed by Ammerman *et al.* (2012) and Gregorin & Cirranello (2016). The specimens were initially identified based on the taxonomic identification keys of Gregorin & Taddei (2002) and Eger (2008), and on the characteristics described by Dolan (1989) and Gregorin *et al.* (2011). Only adults, defined as having all cranial sutures closed and complete epiphyseal ossification of metacarpal and phalanx, of both sexes were examined. We have also analyzed the holotypes of *M. coibensis* (AMNH 18731), *M. bondae* (AMNH 23661), *M. sinaloae* (AMNH 24524), *M. molossus verrilli* Allen, 1908 (AMNH 25764), and *M. pretiosus* (USNM 102761), and photographs of the holotype of *M. rufus* (MNHN-ZM-MO-1997-1847). In addition, topotypes of *M. alvarezi*, *Molossus molossus milleri* Johnson, 1952, *M. molossus*, and *Molossus molossus pygmaeus* Miller, 1900 were also included in our study. *M. aztecus* was originally described for Amecameca, Mexico (Saussure, 1860). Although we did not include in our sampling topotypes of this species, we have examined *M. aztecus* from the state of Oaxaca and Colima in Mexico (Appendix 1), which are located in south and north-western from Tlaxaca respectively, englobing the geographic distribution of this taxa. The list of the analyzed specimens, their geographic locations and institutions in which they are deposited are presented in Appendix 1.

MORPHOLOGICAL ANALYSIS

Qualitative characters included those from external, cranial and dental morphology. The morphometric analyses included one external and 12 cranial variables, all taken using digital calipers with 0.01 mm of accuracy (Giannini & Simmons 2005; Tavares 2008; Fracasso *et al.* 2011). The measurements were: Forearm length (FA); Greater length of skull with incisors (GSLI); Greater length of skull excluding incisors (GSL); Braincase width (BCW); Condylar-incisor length (CIL); Zygomatic breadth (ZB); Palatal length (PAL); Width across upper molars (M-M); Width across upper canines (C-C); Width across upper incisors (I-I); Length of maxillary toothrow (C-M); Height of the sagittal crest (SAR); and Interorbital width (IOW) (Fig. 1).

DATA ANALYSIS

A Student *t*-test was carried out to test for sexual differences within each species. Because not all variables were normally distributed, the data were log-transformed prior to the analysis. Significant sexual differences were observed for all species ($P < 0.05$) and, therefore, males and females were treated separately in subsequent analyses. A Principal Component Analysis (PCA) was carried out using the correlation matrix for 13 variables and a Multiple Analysis of Variance (MANOVA) was performed based on the same set of characters to test if there were significant differences among species.

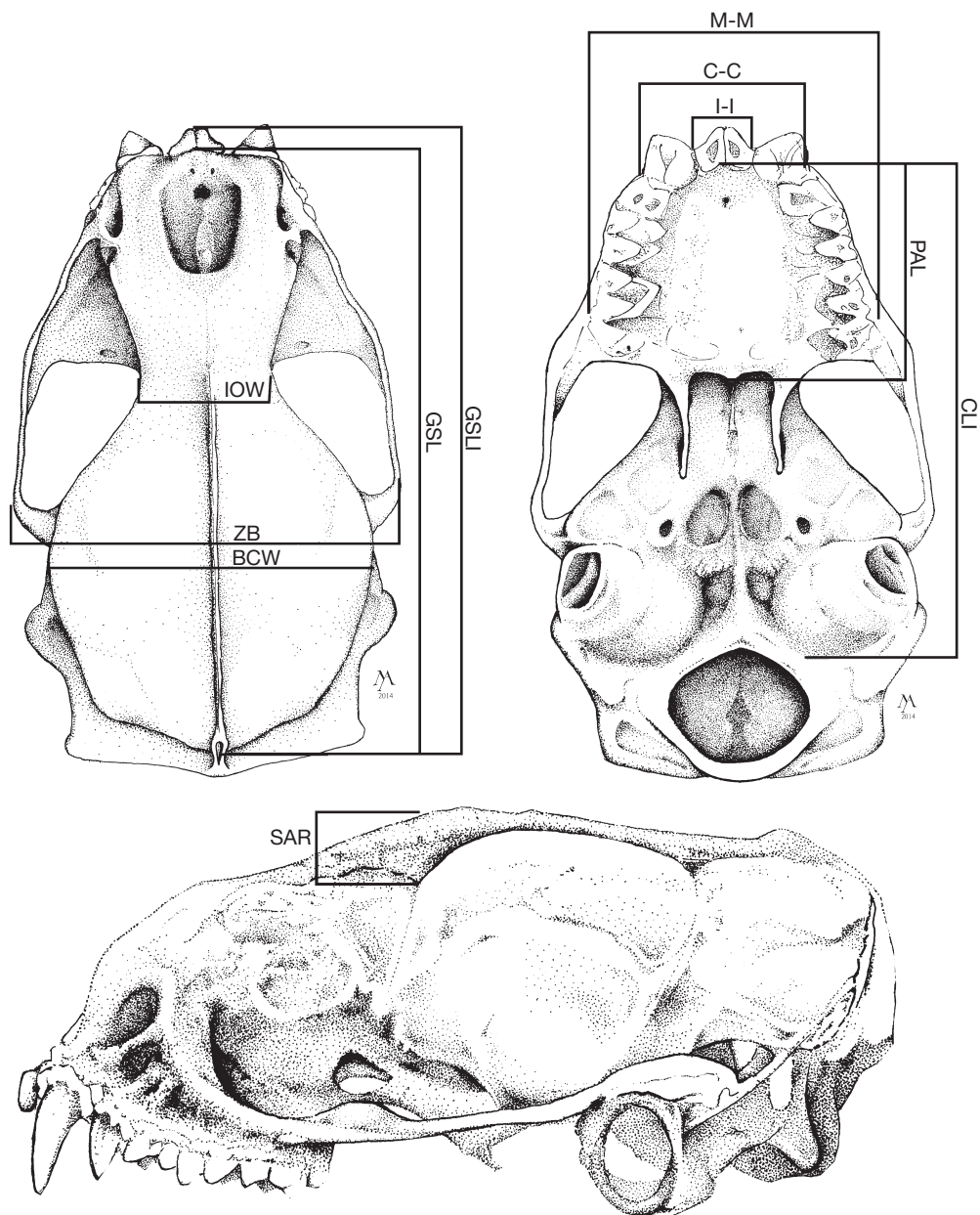


FIG. 1. — Definition of skull measurements used in this study of *Molossus* E. Geoffroy, 1805. Abbreviations: see Material & Methods. Reprinted from Loureiro *et al.* 2018, copyright (2018), with permission from Elsevier.

The pattern of morphology within species can vary due to environmental conditions, which are differentiated along the latitudinal gradient (Brown 1995; Ashton *et al.* 2000; Salewski & Watt 2017). In Brazil, several environmental variables, such as temperature and humidity, vary greatly between north and south (Souza 2011). Therefore, a multiple regression analysis within species was conducted to verify the relationship between latitude and body size. Only *M. molossus*, *M. aztecus*, and *M. rufus* were analyzed because only these species had enough individuals and localities to provide robust analyses (see Appendix 1). PCA and MANOVA within each of these species were also used to verify the differences among populations at

different latitudes. Missing data (due to damaged skulls) were estimated using the algorithm “estimation-maximization” (Little & Rubin 1987) for skulls with a maximum 20% of missing data. The significance level for all statistical tests was $P = 0.05$. Statistical analyses were performed using Systat 11, R 3.1.0 (R Core Team 2005) and Past 2.17 (Hammer *et al.* 2001).

GEOGRAPHICAL DISTRIBUTION

For estimation of geographic distribution of *Molossus* species in Brazil only material with voucher specimens was considered. The maps were built in Quantum Gis 2.0.1 (QGIS Development Team 2009).

PHYLOGENETIC ANALYSIS

A total of 40 morphological characters were coded, of which 13 are new characters for phylogenetic relationships within bats, and 27 represent modified versions from previous papers (Wetterer *et al.* 2000; Tavares 2008; Gregorin 2009) (Fig. 2; Appendix 2). The characters were equally weighted and multi-state characters were treated as unordered. The coded characters were included in a data matrix for analysis (Appendix 3), where missing data were denoted as “?”. A parsimony analysis was performed in the Tree analysis using New Technology (TNT) program (Goloboff *et al.* 2008) using implicit enumeration to evaluate the congruence among morphological characters (Hennig 1966; Farris 1983). The definition of character states and coding were based on the outgroup method (Farris 1983; Nixon & Carpenter 1993). Tree statistics, including consistency index (CI) and retention index (RI), were also calculated using TNT. Clade stability was assessed using bootstrap analysis (Felsenstein 1985), conducted with 5000 replicates, and Bremer support (Bremer 1994).

IDENTIFICATION KEY

An identification key was elaborated based on the characters obtained for the phylogenetic reconstruction and on the morphological comparisons used to identify and differentiate species of *Molossus*. We highlight that the identification key does not reflect the phylogeny, but each entry contains a set of both derived and plesiomorphic characters, that just permits the accurate identification of taxa.

RESULTS

QUALITATIVE CHARACTERS

A set of external, cranial, and dental characters (Figs 1; 2) allowed us to recognize at least six morphologically well-defined species of *Molossus* occurring in Brazil (*M. coibensis*, *M. molossus*, *M. aztecus*, *M. currentium*, *M. pretiosus*, and *M. rufus*), and a putative new species from Caatinga. Based on morphological similarity, we can cluster these species in three phenetic groups: (*M. aztecus* + *M. coibensis* + *M. rufus*); (*M. molossus* + *M. currentium*); and (*M. pretiosus*). *Molossus sinaloae* does not occur in Brazil and it was not included in this species account.

The group composed of *M. aztecus*, *M. coibensis*, and *M. rufus* has monochromatic dorsal hairs or with a basal band slightly paler and not covering more than 1/3 of the hair, and the pelage is usually dark or blackish. The skull is robust with short and inflated rostrum and a broad braincase (Fig. 2B). The sagittal and lambdoidal crests are well developed and the occipital complex is square-shaped (Fig. 2F). Dental variation is restricted to upper incisors for all species of the genus, as noted by Dolan (1989) and Gregorin & Taddei (2000). The upper incisors are spatulate with pincer-like and convergent tips (Fig. 2H) and do not project beyond the canines in lateral view (Fig. 2A). However, the body and skull dimensions of these species are very different. *M. coibensis* is the smallest species of *Molossus*, followed by *M. aztecus* with an intermediate size within the group, and *M. rufus*, which is

the largest species of the genus (Table 1). In addition, some characteristics of the skull also differ among these taxa. The infraorbital foramen in *M. coibensis* opens frontally in rostral view (Fig. 2G), and the rostrum is more robust (Fig. 2G), whereas, in *M. aztecus* and *M. rufus* the infraorbital foramen opens laterally (Fig. 2H), while the rostrum is triangular and more gracile (Fig. 2E). The basisphenoid pits are very shallow or absent in *M. coibensis* (Fig. 2C) and of moderate depth in the other two species (Fig. 2D). In addition, the mastoid process is directed towards the foramen magnum in *M. rufus* (Fig. 2F), and ventrally directed in *M. coibensis* and *M. aztecus* (Fig. 2E).

The group composed of *M. currentium* and *M. molossus* has marked bicoloured cocoa to cinnamon brown dorsal hairs with a whitish basal band reaching 1/2 to 1/4 of the total length of the hair. However, *M. currentium* tends to have a shorter band than *M. molossus*. In these species, the skull is more elongated (Fig. 2A) and the upper incisors are long and tapered (Fig. 2G). In addition, the basisphenoid pits are moderate in depth (Fig. 2B), and the mastoid process is directed ventrally (Fig. 2E). Despite some overlap in measurements between *M. molossus* and *M. currentium*, the latter tends to have larger external and cranial measurements than *M. molossus* (Table 1). These species also differ in qualitative cranial characters: *M. currentium* has the infraorbital foramen directed laterally (Fig. 2H) and very well developed sagittal and lambdoidal crests (Fig. 2F, B), whereas *M. molossus* has the infraorbital foramen directed frontally (Fig. 2G) and undeveloped sagittal and lambdoidal crests (Fig. 2A, E).

M. pretiosus is unique within the genus, with many characters showing an intermediate state between both previous groups. *M. pretiosus* overlaps *M. currentium* and *M. rufus* in forearm and cranial measurements. However, in general it is slightly larger than *M. currentium* and smaller than *M. rufus* (Table 1). In *M. pretiosus* the upper incisors are thin and elongated, but often they are convergent at the tips and project beyond the canines, an intermediate condition when compared to other species of the genus. *M. pretiosus* also has an evident crest between the basisphenoid and basioccipital pits, due to the very deep basisphenoid pits, which also differentiates this species from other *Molossus*.

MORPHOMETRIC VARIATION

One external and 12 cranial variables were measured from six recognized species of *Molossus* and from one undetermined individual from the Brazilian Caatinga (*Molossus* sp.) (Table 1). Males are statistically larger than females with different variables showing significant differences in each species. Most of the species have males with larger GLSI, GSL, SAR, and ZB (Table 2). Additionally, some qualitative characters, such as the development of sagittal and lambdoidal crests are sexually dimorphic. Therefore, males and females were treated separately in subsequent analyses.

The interspecific variation indicated by the PCA was similar for males and females (Fig. 3). Two main groups, distinguished by size, were evident in analyses of both sexes.

TABLE 1. — Measurements in mm of species of *Molossus* E. Geoffroy, 1805 occurring in Brazil. *Molossus* sp. refers to the putative new species capture in the Brazilian Caatinga. Abbreviations: see Material & Methods.

	GSLI	GSL	CIL	CM	M-M	C-C	I-I	PAL	IOW	BCW	SAR	ZB	FA
<i>M. coibensis</i> Allen, 1904													
Females (n=9)													
Minimum	14.86	14.46	11.88	5.50	7.07	7.07	1.32	4.55	4.55	8.10	0.25	9.49	34.33
Maximum	16.70	16.25	13.57	6.19	7.45	7.45	1.74	5.30	5.30	8.70	0.93	10.55	37.5
\bar{x}	15.50	15.28	12.81	5.71	7.22	7.22	1.61	5.00	5.00	8.44	0.52	9.76	37.00
Males (n=14)													
Minimum	15.71	15.21	12.67	5.20	7.17	4.01	1.54	4.81	3.21	8.11	1.84	10.57	36.10
Maximum	16.94	16.43	13.96	6.24	7.84	4.76	1.97	5.36	3.85	8.84	0.50	10.57	37.90
\bar{x}	16.43	15.91	13.14	5.99	7.50	4.41	1.75	5.11	3.63	8.65	0.88	10.57	36.60
<i>M. molossus</i> (Pallas, 1766)													
Females (n=120)													
Minimum	15.60	15.39	12.52	5.43	5.98	3.82	1.32	2.28	3.08	8.01	0.28	8.57	36.43
Maximum	18.59	18.47	15.49	6.99	8.65	6.16	2.24	8.62	4.36	9.60	1.37	12.03	42.56
\bar{x}	16.95	16.49	13.49	6.13	7.65	4.36	1.73	5.39	3.70	8.84	0.80	10.26	39.45
Males (n=111)													
Minimum	16.40	15.73	12.83	5.41	6.24	4.07	1.30	4.45	3.07	8.29	0.49	9.68	36.20
Maximum	18.66	19.53	18.63	7.75	9.10	5.90	2.33	6.34	8.86	10.33	2.62	13.52	42.60
\bar{x}	17.65	17.22	14.04	6.30	7.92	4.58	1.78	5.54	3.80	9.05	1.16	11.02	40.21
<i>M. aztecus</i> Saussure, 1860													
Females (n=9)													
Minimum	16.14	15.50	12.55	5.77	7.23	4.17	1.44	4.79	3.40	8.34	0.41	9.53	35.00
Maximum	18.16	17.56	15.32	7.98	8.77	5.67	2.35	6.97	4.56	10.56	2.07	11.96	41.90
\bar{x}	16.68	16.41	13.37	6.04	7.62	4.32	1.68	5.29	3.78	9.02	0.80	10.65	39.00
Males (n=13)													
Minimum	16.25	15.92	13.06	5.66	7.08	4.29	1.40	4.81	3.57	8.58	0.44	10.15	35.94
Maximum	18.28	18.34	14.74	6.64	8.75	6.12	2.30	6.30	4.18	9.61	1.90	12.36	41.50
\bar{x}	17.62	17.28	14.01	6.21	7.88	4.66	1.83	5.53	3.85	9.10	1.28	10.91	39.50
<i>M. currentium</i> Thomas, 1901													
Females (n=4)													
Minimum	17.87	17.45	14.29	6.56	8.21	4.65	1.82	5.33	3.90	8.66	1.20	11.47	38.00
Maximum	18.32	17.63	14.36	6.63	8.26	5.66	2.11	5.57	4.33	9.65	1.54	11.78	43.00
\bar{x}	17.97	17.57	14.34	6.61	8.25	4.82	1.94	5.54	4.13	9.32	1.40	11.62	41.90
Males (n=6)													
Minimum	18.61	17.92	13.85	6.48	8.19	4.93	1.99	5.58	3.75	9.42	1.22	11.70	39.00
Maximum	19.35	18.66	15.23	7.04	8.51	5.18	2.18	6.21	4.27	9.87	2.14	12.24	43.50
\bar{x}	18.89	18.27	14.91	6.78	8.38	5.04	2.02	5.72	3.92	9.64	1.57	11.85	41.25
<i>M. pretiosus</i> Miller, 1902													
Females (n=10)													
Minimum	18.91	18.65	15.39	7.02	8.37	4.85	1.69	5.91	3.98	9.67	1.07	12.04	45.00
Maximum	20.95	20.39	16.98	7.61	9.56	5.40	2.40	6.73	4.66	10.69	2.22	13.57	49.01
\bar{x}	19.61	19.27	15.94	7.35	9.22	5.25	2.03	6.30	4.11	10.06	1.68	12.45	47.00
Males (n=13)													
Minimum	19.88	19.54	15.68	5.62	8.92	5.21	1.86	6.22	3.91	9.98	1.79	12.57	44.65
Maximum	22.36	29.34	17.61	8.12	10.12	6.11	2.35	6.89	4.53	10.78	2.66	13.71	48.50
\bar{x}	21.40	20.99	16.86	7.70	9.51	5.63	2.17	6.73	4.30	10.44	2.10	13.29	47.50
<i>M. rufus</i> (E. Geoffroy Saint-Hilaire, 1805)													
Females (n=43)													
Minimum	19.89	19.62	16.00	6.96	8.52	5.19	2.01	6.25	3.93	9.83	0.97	12.02	46.76
Maximum	23.26	22.65	18.54	8.40	10.28	7.57	3.01	8.17	4.83	11.17	2.98	14.52	54.00
\bar{x}	21.30	20.69	17.07	7.74	9.67	5.58	2.31	6.78	4.38	10.62	1.73	12.90	50.00
Males (n=37)													
Minimum	20.77	20.01	17.05	7.00	8.86	5.00	2.11	6.72	3.60	9.92	1.41	12.61	47.69
Maximum	23.80	23.30	19.05	8.63	10.40	6.50	3.00	7.70	5.00	11.74	3.40	14.76	55.20
\bar{x}	22.90	22.19	17.85	8.04	9.95	6.07	2.46	7.09	4.54	10.91	2.58	14.05	49.55
<i>Molossus</i> sp.													
Female	19.16	18.36	15.76	6.90	8.45	5.22	2.15	5.73	4.17	10.07	0.59	–	45.78

One group is formed by larger individuals representing *M. pretiosus*, *M. sinaloae*, and *M. rufus*, while the other one is composed of individuals of small to medium size representing *M. currentium*, *M. aztecus*, *M. molossus*, and *M. coibensis*. For the females, *Molossus* sp. is placed between the two groups

in the PCA (Fig. 3). The first two principal components explain 84.81% of the total variation in males and 86.99% in females (Table 3). The MANOVA corroborates the PCA and shows significant differences among species for both males ($P < 0.001$, $F = 56.70$) and females ($P < 0.001$, $F = 47.50$).

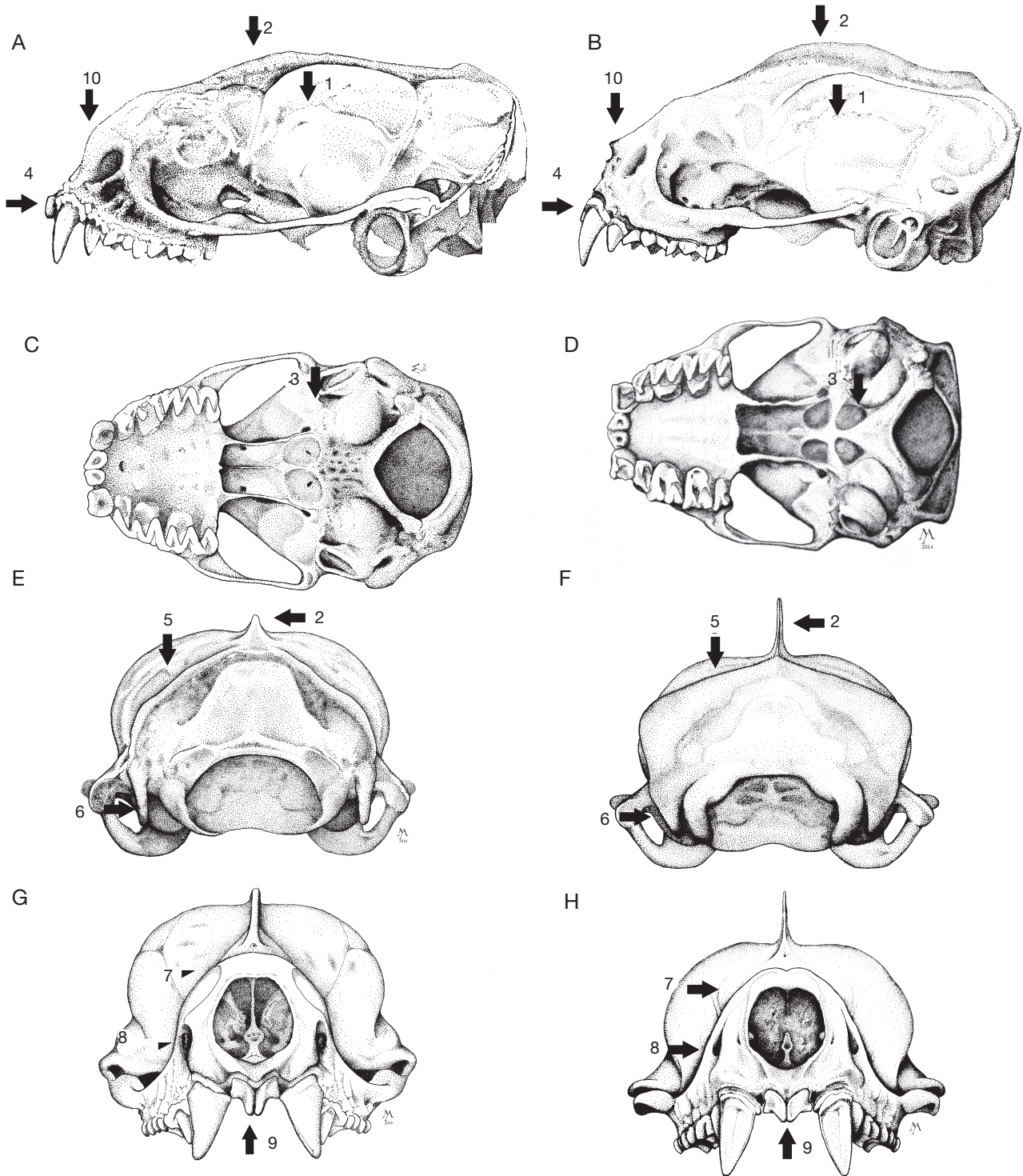


FIG. 2. — Variable characters in skull morphology within *Molossus* E. Geoffroy, 1805 (Pallas, 1766): **A, B**, lateral views; **C, D**, ventral views; **E, F**, posterior view; **H, G**, frontal view. Numbers represents characters described in the text: **1**, skull robustness; **2**, sagittal crest; **3**, basioccipital pits; **4**, projection of the canines; **5**, lambdoidal crest and occipital complex; **6**, mastoid process; **7**, rostrum shape; **8**, infraorbital foramen; **9**, upper incisors; **10**, nasal process. Not to scale.

Multiple regression analysis revealed that the samples from lower latitudes have smaller body and cranial sizes than populations at higher latitudes in *M. molossus*. In males, the measurements GLS, CI, I-I, and FA showed a high correlation with latitude ($P < 0.001$). In contrast,

the variables correlated in females were GLS ($P = 0.003$), ZB ($P = 0.001$), SAR ($P = 0.003$), and FA ($P = 0.008$). In males of *M. aztecus* GLS ($P < 0.001$) was the only variable correlated with latitude. However, this relationship in females is supported by ZB ($p = 0.009$) and SAR ($P = 0.042$).

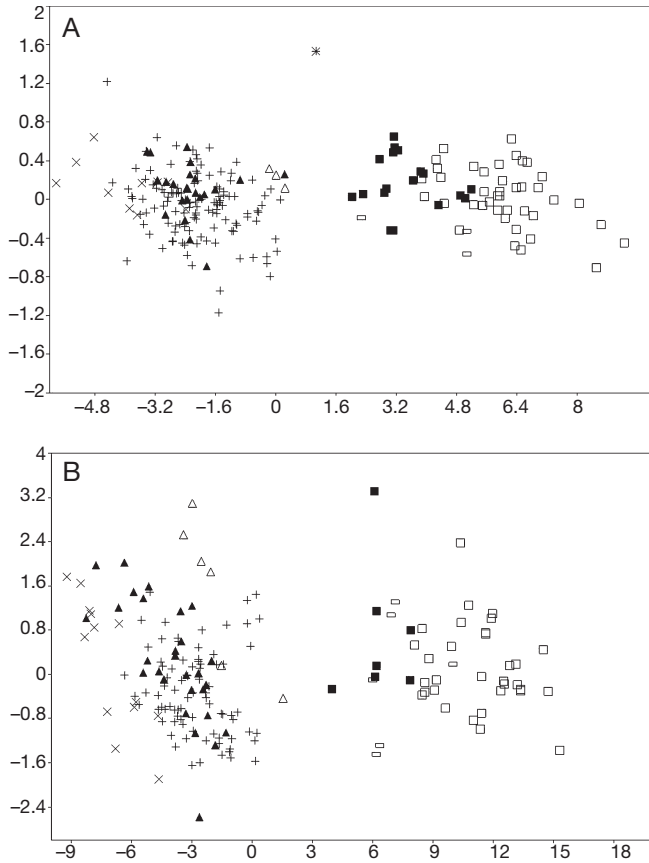


FIG. 3. — Principal Components Analysis plot of PC1 and PC2 based on 13 cranial and external variables of *Molossus* E. Geoffroy, 1805: **A**, females, **B**, males. Symbols: ■, *M. pretiosus* Miller, 1902; □, *M. rufus* (E. Geoffroy, 1805); △, *M. currentium* Thomas, 1901; +, *M. molossus* (Pallas, 1766); X, *M. coibensis* Allen, 1904; ▲, *M. aztecus* Saussure, 1860; □, *M. sinaloa* Allen, 1906; *, and *Molossus* sp.

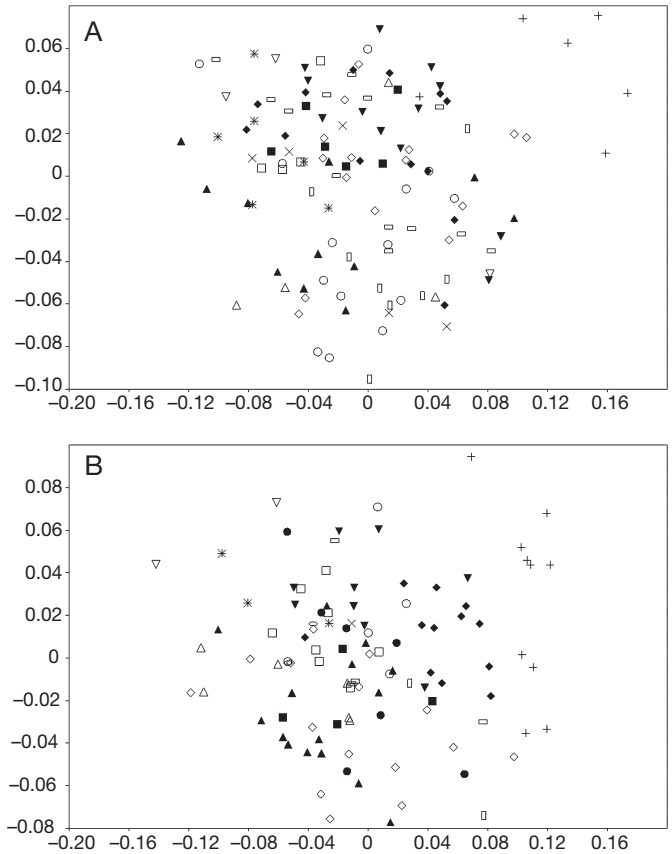


FIG. 4. — Principal component analysis of the first two main components (PC1 and PC2) based on 13 cranial and external variables of *Molossus molossus*: **A**, males, **B**, females. Symbols: ■, Rio de Janeiro; ▲, Ceará; ▼, Pará; +, Rio Grande do Sul; △, Piauí; ○, Mato Grosso do Sul; ◇, Minas Gerais; *, Bahia; ◆, Amazonas; ●, Paraíba; □, São Paulo; □, Mato Grosso; x, Paraíba; ▽, Acre; ○, Piauí.

TABLE 2. — P-values of t-test of measurements between male and female *Molossus*. Abbreviations: see Material & Methods.

Variables	<i>M. coibensis</i> Allen, 1904	<i>M. molossus</i> (Pallas, 1766)	<i>M. aztecus</i> Saussure, 1860	<i>M. currentium</i> Thomas, 1901	<i>M. pretiosus</i> Miller, 1902	<i>M. rufus</i> (E. Geoffroy, 1805)
GSLI	0.014	0.637	0.013	0.000	0.005	0.000
GSL	0.011	0.638	0.001	0.033	0.008	0.542
CIL	0.123	0.000	0.394	0.001	0.012	0.000
CM	0.629	0.001	0.510	0.304	0.866	0.009
M-M	0.023	0.000	0.172	0.300	0.052	0.001
C-C	0.461	0.000	0.000	0.902	0.007	0.020
I-I	0.020	0.024	0.114	0.394	0.100	0.015
PAL	0.228	0.002	0.666	0.527	0.010	0.010
IOW	0.235	0.000	0.296	0.094	0.816	0.004
BCW	0.110	0.000	0.140	0.431	0.030	0.000
SAR	0.001	0.000	0.000	0.303	0.000	0.000
ZB	0.024	0.000	0.006	0.133	0.000	0.000
FA	0.362	0.001	0.751	0.300	0.474	0.912

Males of *M. rufus* only have I-I ($P = 0.043$) associated with the latitude, while the females showed a differentiation in IOW ($P = 0.015$), PAL ($P = 0.040$), M-M ($P = 0.006$), and SAR ($p = 0.006$).

The PCAs carried out within each species of *Molossus* shows no differentiation among samples, except for a

male sampling of *M. molossus* from southern Brazil (Fig. 4; Table 4). This sample grouped separately and showed larger body and cranial measurements than other individuals. PC1 and PC2 explain 90% of the total variation and are both driven by size (Table 4). The ANOVA confirms that the samples from southern Brazil are morphometrically

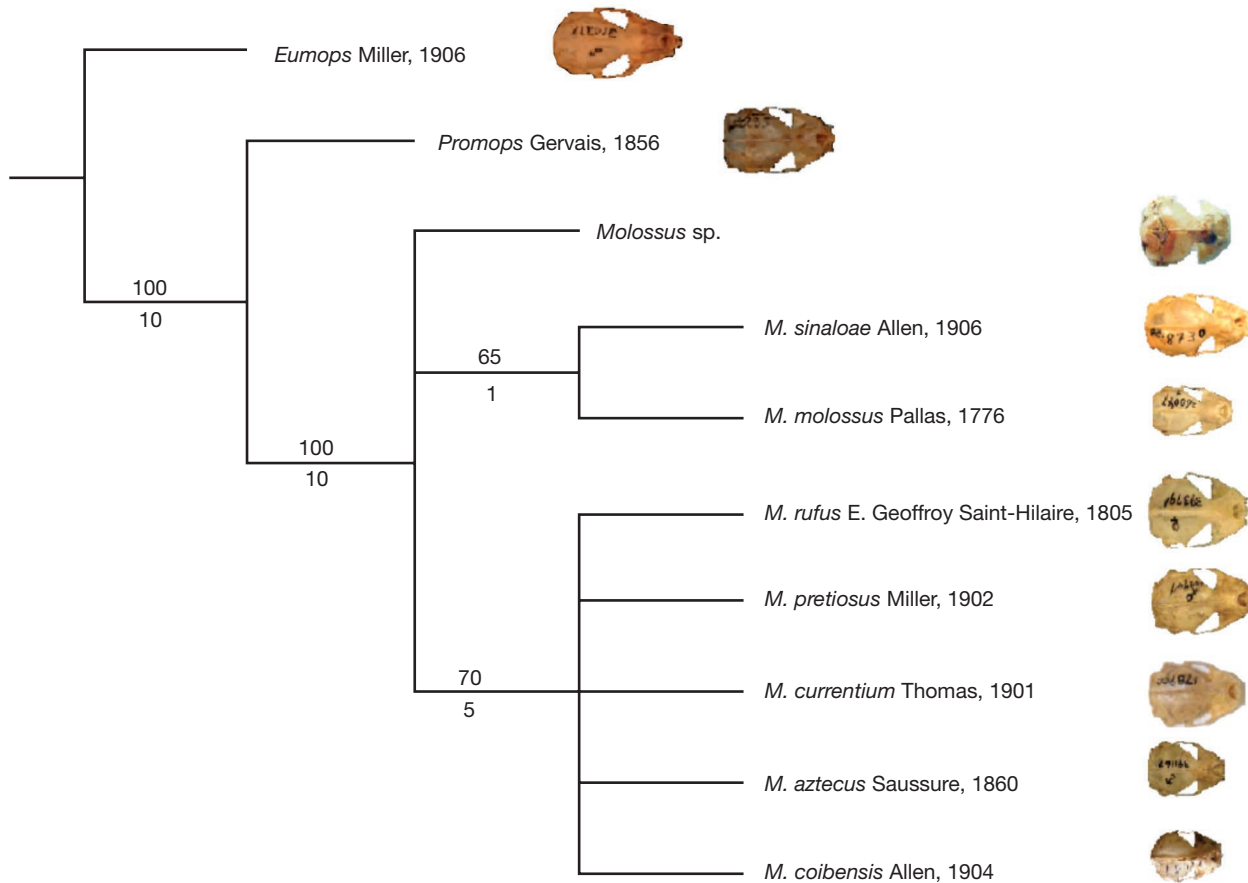


FIG. 5. — Strict consensus tree from eight most parsimonious trees recovered for *Molossus* E. Geoffroy, 1805. Numbers above the branches indicate Bootstrap values and bottom numbers indicate Bremer support values.

TABLE 3. — Eigenvalue and PCA loading for the first and second components. Abbreviations: see Material & Methods.

	PC1		PC2	
	Females	Males	Females	Males
Eigenvalue	2.10	2.47	0.31	1.70
IOW	0.31	0.27	0.24	0.16
I-I	0.57	0.21	-0.21	-0.12
C-M	0.17	0.41	0.32	-0.05
GSLI	0.19	0.32	0.22	0.19
GSL	0.18	0.30	0.25	0.15
BCW	0.14	0.31	0.16	0.16
CIL	0.20	0.23	0.25	0.05
C-C	0.31	0.30	0.28	0.17
M-M	0.19	0.31	0.25	0.02
ZB	0.13	0.28	0.28	0.10
PAL	0.31	0.30	0.28	0.19
FA	0.49	0.29	0.19	0.25

TABLE 4. — Eigenvalue and PCA loading for the first and second components in *M. molossus*. Abbreviations: see Material & Methods.

	PC1		PC2	
	Females	Males	Females	Males
Eigenvalue	3.46	3.43	1.62	1.27
IOW	0.28	0.23	0.12	0.23
I-I	0.39	0.35	-0.33	-0.26
C-M	0.18	0.20	0.31	0.24
GSLI	0.20	0.16	0.21	0.25
GSL	0.19	0.15	0.24	0.23
BCW	0.14	0.14	0.15	0.14
CIL	0.21	0.18	0.24	0.31
C-C	0.31	0.22	0.26	0.24
M-M	0.20	0.18	0.25	0.22
ZB	0.12	0.20	0.27	0.28
PAL	0.32	0.25	0.28	0.28
FA	0.36	0.15	0.19	0.20

distinct from other groups previously identified as *M. molossus* ($P < 0.01$; $F = 0.6$). In the MANOVA, the effect of variation among samples is highly significant for males of *M. molossus* ($P = 0.001$), but not significant for females of *M. molossus*, *M. aztecus*, and *M. rufus* ($P > 0.6$), consistent with the PCA.

PHYLOGENY

Parsimony analysis resulted in eight most parsimonious trees with 56 steps each ($CI = 0.84$; $RI = 0.83$). A strong support (Bootstrap = 100% and Bremer = 10) was found for *Promops* as the sister group to *Molossus*, instead of *Eumops*, and for the monophyly of *Molossus*. The consensus tree (Fig. 5) shows

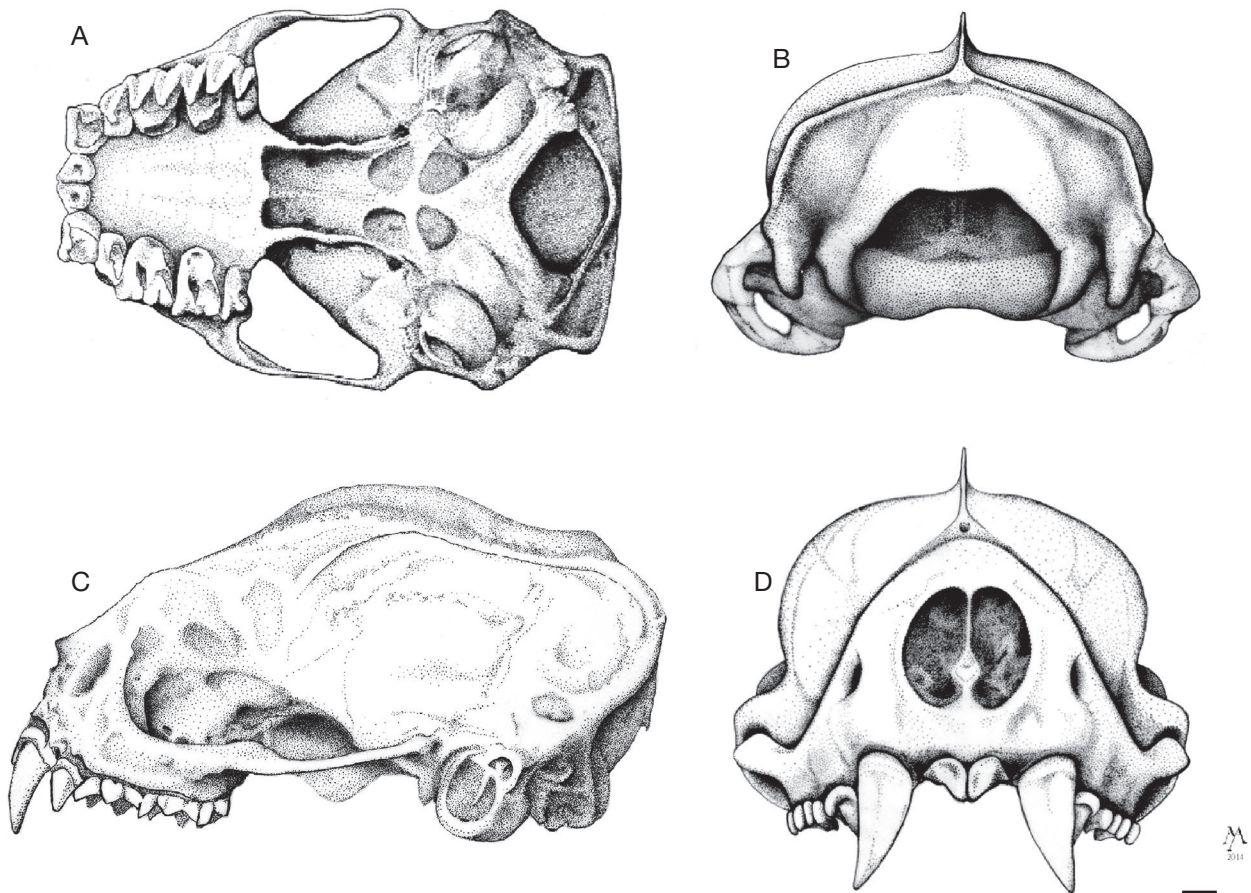


FIG. 6. — *Molossus aztecus* Saussure, 1860 skull: **A**, ventral view; **B**, posterior view; **C**, lateral view; **D**, frontal view. Scale bar: 1 mm.

low support for the relationships within *Molossus*. However, the clade composed of *M. coibensis* + *M. rufus* + *M. pretiosus* + *M. currentium* + *M. aztecus* is divergent from the clade *M. molossus* + *M. sinaloae*. In addition, the individual from Caatinga (*Molossus* sp.) does not occupy a defined position within the genus and we consider it as a soft polytomy in the consensus tree (Coddington & Scharff 1996). Based on this phylogenetic hypothesis, synapomorphies of *Molossus* include incisors with convergent tips or ventrally directed (character 10, states 1 and 2), one upper premolar (*c.* 11), a reduced third lower premolar (*c.* 12), and a domed occipital complex (*c.* 18). The clade composed by *M. coibensis* + *M. currentium* + *M. aztecus* + *M. pretiosus* + *M. rufus* is supported by pincer-like incisors (*c.* 10, state 1), quadrangular occipital complex (*c.* 38, state 1), and well developed lambdoidal and sagittal crests (*c.* 36, state 2 and *c.* 37, state 1). The clade *M. molossus* and *M. sinaloae* is supported by triangular occipital complex (*c.* 38, state 0), thin and elongated incisors (*c.* 10, state 2) and low sagittal crest (*c.* 36, state 1) (see Appendix 2). These two branches reflect partially the previous phenetic grouping of species (Dolan 1989). A third lineage is composed solely by *Molossus* sp and this branch is defined by characters such as low sagittal crest, triangular occipital complex, thin and elongated incisors, moderate occipital pits.

SYSTEMATICS

Family MOLOSSIDAE Gervais, 1856
Genus *Molossus* E. Geoffroy, 1805

Molossus aztecus Saussure, 1860

Molossus aztecus Saussure, 1860: 285.

Molossus molossus – Willig *et al.* 1986: 671.

EMENDED DIAGNOSIS. — Medium-sized *Molossus* with dense and long dark dorsal fur. Dorsal hair reaching 6.0 mm and varying from dark cocoa brown to blackish. Monochromatic dorsal hairs or with a small pale basal band covering no more than ¼ of the total length. Forearm length averages 39.5 mm in males (35.9–41.5) and 39.0 mm in females (35.0–41.9). Greatest length of skull averages 17.6 mm (16.3–18.3) in males and 16.7 mm (16.1–18.6) in females (Table 1). Basioccipital pits moderate in depth (Fig. 6A). Occipital complex rectangular in posterior view due to the development and inclination of the lambdoidal crests (Fig. 6B). Inflated rostrum and rounded braincase (Fig. 6C). Infraorbital foramen opening laterally in frontal view (Fig. 6D). Nasal process of the premaxilla well developed in males, protruding over the nasal cavity (Fig. 6C). Skull with mastoid processes oriented ventrally in posterior view. Triangular rostrum in frontal view with narrow dorsal portion (Fig. 6D). Upper incisors spatulated with convergent tips (Fig. 6D).

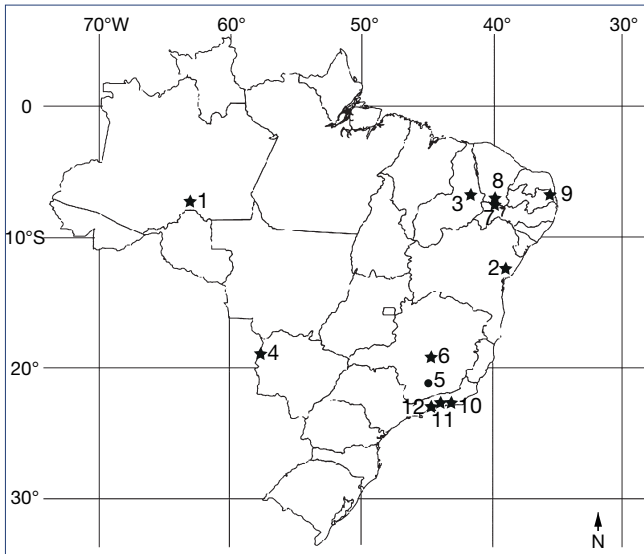


FIG. 7. — Geographic range of *Molossus aztecus* Saussure, 1860 in Brazil (Gregorin *et al.* 2011). ★, represents new records for the country, the numbers represent the localities described in Appendix 1.

VARIATION. — The dorsal pelage varies from dark grayish to blackish. In females, the occipital complex may be less distinctly squared due to smaller lambdoidal crests. Sagittal crests in females are also lower and less robust than males, and the nasal process of the premaxilla is less developed. The upper incisors vary among individuals with some specimens being less spatulated and more elongated than average (AMNH 10245).

DISTRIBUTION. — *M. aztecus* is widely distributed from Mexico and Central America (Dolan 1989) to South America, in Venezuela (Handley 1976; Ochoa *et al.* 1993; Lim & Engstrom 2001) and southeastern Brazil (Gregorin *et al.* 2011). This study extends the distribution of *M. aztecus* to nine Brazilian states confirming the occurrence of the species in Mammanguapé (Paraíba), Huimata (Amazonas), Rio de Janeiro (Rio de Janeiro), São José do Piauí (Piauí), Corumbá (Mato Grosso do Sul), Crato (Ceará), Lavras and Sete Lagoas (Minas Gerais), Exu (Pernambuco), Salvador (Bahia), and Ilha dos Búzios (São Paulo) (Fig. 7).

REMARKS

The body size of *M. aztecus* is very similar to *M. molossus* and therefore, these two taxa are frequently confused. However, both species are distinguished by several qualitative characters, such as a pale band at the base of the dorsal hair, which is discrete or imperceptible in *M. aztecus*, and long and obvious in *M. molossus*. The dorsal fur of *M. aztecus* is grayish to blackish, while *M. molossus* usually has a cocoa to cinnamon brown colouration. *M. aztecus* has a shorter and inflated braincase and domed skull (Fig. 6C), while in *M. molossus* the skull is more elongated. The sagittal and lambdoidal crests in *M. aztecus* are more developed (Fig. 6B) than in *M. molossus*. In *M. aztecus*, the rostrum is triangular (Fig. 6D), whereas in *M. molossus* it is rectangular. The infraorbital foramen in *M. aztecus* opens laterally (Fig. 6D) while in *M. molossus* it opens frontally. The occipital in *M. aztecus* has a clear quadrangular format (Fig. 6B), while in *M. molossus* this structure is triangular or rounded. The upper incisors in *M. aztecus* are flat and spatulated (Fig. 6D),

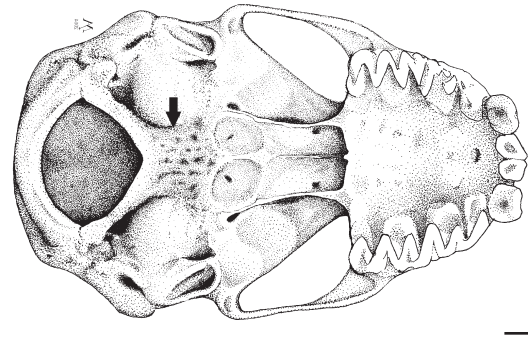


FIG. 8. — Ventral view of skull of *Molossus coibensis* Allen, 1904. The arrow shows the absence of the basioccipital pits.

unlike *M. molossus*, which has elongated and tapered upper incisors with parallel tips. Although some authors do not consider *M. aztecus* as a valid species (Jennings *et al.* 2000; Eger 2008), our data indicate that it is consistently distinguishable from *M. molossus* and *M. coibensis* based on morphological characters, corroborating Dolan (1989) and Gregorin *et al.* (2011).

Molossus coibensis Allen, 1904

Molossus coibensis Allen, 1904: 227.

Molossus barnesi Thomas, 1905: 584 (type locality: French Guiana: Cayenne).

Molossus burnesi – Thomas 1905: 584 (type locality: Cayene, French Guiana; misspelling of *Molossus barnesi* Thomas, 1905). — Husson 1962: 251 (misspelling of *Molossus barnesi* Thomas, 1905).

Molossus cherriei Allen, 1916: 35 (type locality: Tapirapoan, Mato Grosso, Brazil).

Molossus burnsi – Hershkovitz 1949: 454 (misspelling of *Molossus barnesi* Thomas, 1905).

Molossus burnsi *Molossus aztecus lambi* Gardner, 1966: 1 (type locality: 11 km, Northeast of Esquintla, Chiapas, Mexico).

EMENDED DIAGNOSIS. — Smallest species of *Molossus*, usually with dark dorsal hairs varying from cocoa brown to blackish. Monochromatic dorsal hair or, if bicoloured, with a pale brown or grayish short basal band not exceeding one third of the total length. Dorsal hairs from 2.0 to 4.0 mm long. Forearm length averaging 36.9 mm (36.1–37.9) in males and 37.0 mm (34.3–37.5) in females; skull length averages 16.4 mm (15.7–16.9) in males and 15.5 mm (14.9–16.7) in females (Table 1). Relatively massive skull with inflated braincase (Fig. 2B). Infraorbital foramen opens frontally (Fig. 2G). Very shallow or absent basioccipital pits (Figs 2C, 8). Nasal process of the premaxilla not protruding over the nasal cavity (Fig. 2A). Mastoid process oriented ventrally in dorsal view (Fig. 2E). Quadrangular occipital complex (Fig. 2F) and upper incisors with convergent tips (Fig. 2H).

VARIATION. — Only a single specimen (UFMG 3350) had grayish dorsal pelage instead of brown, and Gager *et al.* (2016) recorded cinnamon dorsal fur in specimens from Panama. The basioccipital pits are shallow or absent. Upper incisors can vary from short and

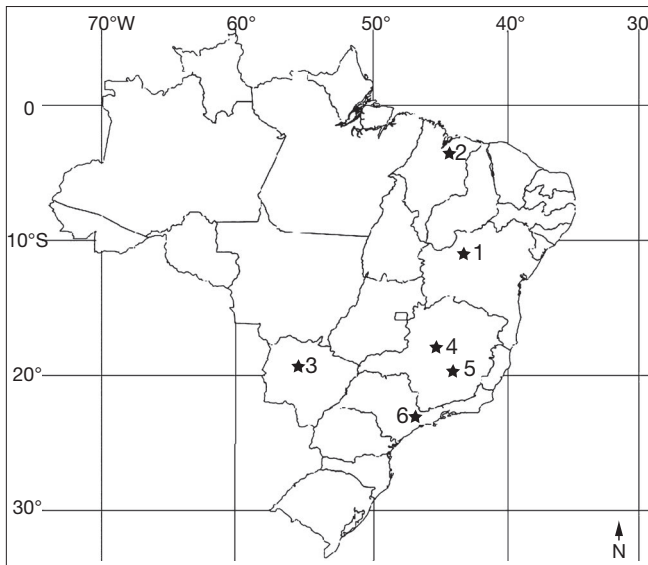


FIG. 9. — Geographic range of *Molossus coibensis* Allen, 1904 in Brazil: ★, Represents new records for the country. The numbers represent the localities described in Appendix 1.

spatulated to slightly elongated, but always have convergent tips (AMNH 217448 and AMNH 217449).

DISTRIBUTION. — *M. coibensis* is widely distributed in Colombia, Peru, Ecuador, Venezuela, and Guyana (Eger 2008). The presence of *M. coibensis* in Brazil was firstly recorded by Dolan (1989) under the name *Molossus cherriei* based on a specimen (holotype) from the state of Mato Grosso, and subsequently extended by Costa *et al.* (2013) to the state of Pará based on six adults and one juvenile female. In this study records of *M. coibensis* were obtained for Cidade da Barra (Bahia), Belo Horizonte (Minas Gerais), São Luís (Maranhão), São Paulo (São Paulo), and Corumbá (Mato Grosso do Sul) (Fig. 9).

REMARKS

Our morphological analyses indicate that the differences between *M. barnesi* and *M. coibensis* described by Simmons & Voss (1998) represent intraspecific variation, as suggested by Gregorin *et al.* (2011) and Catzefflis *et al.* (2016). Some individuals of *M. barnesi* (e.g. AMNH 26905) have dark dorsal fur with a pale band at the base of the dorsal hairs, not exceeding 1/3 of its length. This pattern of variation also occurs in *M. coibensis*, as described in the account of that species. Both the mesopterygoid canal and the crest between the basisphenoid and basioccipital pits are variable in *M. coibensis*, and the range of variation includes values described for *M. barnesi* (Gregorin *et al.* 2011). Simmons & Voss (1998) based on the species distributions available at the time, also suggested that there was a large gap in the distribution of these two species: *M. coibensis* would be present in Central America and northwestern South America while *M. barnesi* would be restricted to French Guiana. However, the extension of the distributional range of *M. coibensis* to eastern South America (Lim & Engstrom 2001) and northern Brazil (Costa *et al.* 2013), together with the small morphological differences found between these two taxa, support *M. barnesi* as junior synonym of *M. coibensis* (Catzefflis *et al.* 2016).

***Molossus rufus* E. Geoffroy, 1805**

Molossus rufus E. Geoffroy, 1805: 279.

Molossus castaneus E. Geoffroy, 1805: 279.

Molossus ursinus Spix, 1823: 59 (type locality: Suburbis Para, Brazil).

Dysopes alecto Temminck, 1826: 231 (type locality: Brazilian lowlands).

Dysopes albus Wagner, 1843: 368 (type locality: Mato Grosso, Brazil).

Dysopes holosericeus Wagner, 1843: 368 (type locality: Rio de Janeiro, Brazil).

Molossus myosurus Tschudi, 1845: 83 (type locality: Cejaregion farm, Ostabhang der Binnencordillera, Peru).

Molossus molossus rufus – Peters 1866: 575 (name combination).

Molossus albus – Pelzeln 1883: 43 (name combination).

Molossus fluminensis Lataste, 1891: 658 (type locality: Rio de Janeiro, Rio de Janeiro, Brazil).

Molossus molossus fluminensis – Trouessart 1897: 143 (name combination).

Molossus nigricans Miller, 1902: 395 (type locality: Acaponeta, Tepic [Nayarit], Mexico).

Molossus pretiosus macdougalli Goodwin, 1956: 3 (type locality: San Blas, Tehuantepec, Oaxaca, Mexico).

Molossus ater – Goodwin 1960: 4 (not from E. Geoffroy, 1805).

EMENDED DIAGNOSIS. — Largest species of *Molossus* with a dark dorsal pelage varying from dark brown to blackish (Fig. 10). Monochromatic dorsal hairs or, when dichromatic, with a small pale basal band covering no more than 1/4 of the total length. Dorsal hairs reaching 4.0 mm. Forearm length averaging 50.3 mm in males (47.7-55.2) and 50.0 mm in females (46.7-54.0). Greatest length of skull averaging 22.9 mm (20.8-23.8) in males and 21.3 mm (19.9-22.6) in females (Table 1). Skull with inflated rostrum and elongated braincase (Fig. 11A, C). Mastoid process directed laterally in posterior view and occipital square-shaped with highly developed and inclined lambdoidal crests (Fig. 11B). High sagittal crest, particularly in males (Fig. 11B, D). Infraorbital foramen opening laterally in frontal view (Fig. 11D). Basioccipital pits with moderate depth. Triangular rostrum in frontal view (Fig. 11D). Pincer-like upper incisors with convergent tips (Fig. 11D).

VARIATION. — The dorsal fur is always very dark, ranging from dark brown to blackish. In some individuals, the entire dorsal hair or just the tips are reddish brown (hence the specific epithet). In females, the sagittal and lambdoidal crests are less robust and the nasal process of the pre-maxilla, although also projecting over the nasal cavity, is less developed than in males.

DISTRIBUTION. — *M. rufus* is widely distributed in South America, occurring from Trinidad to Bolivia, Paraguay, Argentina, and in a large portion of Brazil (Eger 2008) (Fig. 12).

REMARKS

M. rufus resembles *M. pretiosus* in having dark pelage, and similar body and cranial size. However, *M. pretiosus* tends to be smaller (Table 1). *M. rufus* has higher sagittal crest when compared to *M. pretiosus*; the mastoid process in *M. rufus*



FIG. 10. — *Molossus rufus* (E. Geoffroy, 1805). Photo courtesy of Dr Marco A. R. Mello (<https://marcoarmello.wordpress.com>).

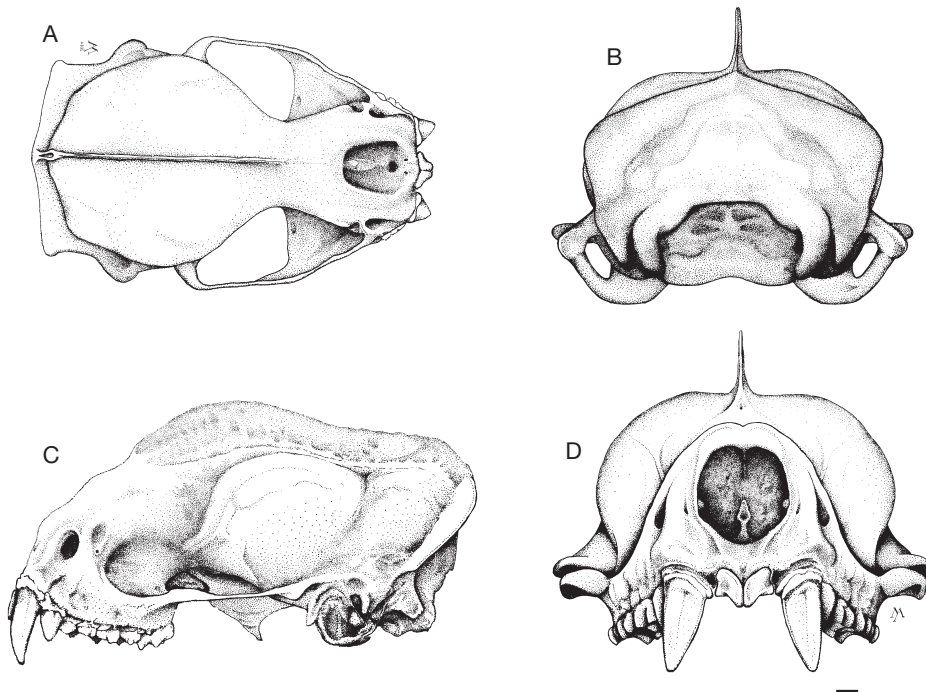


FIG. 11. — Skull of *Molossus rufus* E. Geoffroy, 1805: A, dorsal view; B, posterior view; C, lateral view; D, frontal view. Scale bar: 1 mm.

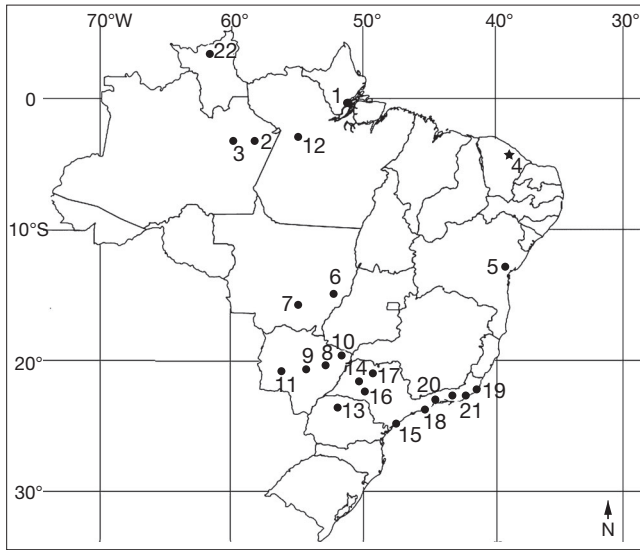


FIG. 12. — Geographic range of *Molossus rufus* (E. Geoffroy, 1805) in Brasil. The numbers represent the localities described in Appendix 1.

is laterally oriented in posterior view (Fig. 11B), while it is ventrally oriented in *M. pretiosus* (Fig. 2E); and *M. rufus* has spatulate incisors (Fig. 11H) whereas they are elongated and thin in *M. pretiosus* (Fig. 2G) (although there are variation among samples).

Molossus molossus (Pallas, 1766)

Vespertilio molossus Pallas, 1766: 49 (type locality America). — Husson 1962: 251 (restricted to Martinique, Antilles).

Vespertilio molossus major Kerr, 1792: 97 (type locality Martinique, Antilles). — Miller 1913: 90.

Vespertilio molossus minor Kerr, 1792: 97 (type locality Antilles).

Molossus obscurus E. Geoffroy, 1805: 279 (type locality: not specified). — Husson 1962: 258 (restricted to Martinique).

Molossus longicaudatus E. Geoffroy, 1805: 279 (type locality: not specified).

Molossus fusciventer E. Geoffroy, 1805: 279 (type locality: not specified). — Husson 1962: 257 (restricted to Martinique).

Molossus crassicaudatus E. Geoffroy, 1805: 279 (type locality: not specified).

Molossus acuticaudatus Desmarest, 1820: 116 (type locality: Brazil).

Dysopes velox Temminck, 1826: 234 (type locality: Brazil).

Molossus moxensis D'Orbigny, 1835: pl. 11, figs 1-4 (type locality: Moxos, Beni, Bolivia).

Dysopes olivaceo-fuscus Wagner, 1847: 202 (type locality: Cuiaba, Mato Grosso, Brazil).

Dysopes amplexicaudatus Wagner, 1847: 203 (type locality: Caiçara, Mato Grosso, Brazil).

Molossus tropidorhynchus Gray, 1839: 6 (type locality: Cuba).

Molossus molossus obscurus — Peters 1866: 575 (name combination).

Molossus pygmaeus Miller, 1900: 162 (type locality: Curaçao, Antilles).

Molossus debilis Miller, 1913: 90 (type locality: Saint Kitts, Antilles).

Molossus fortis Miller, 1913: 89 (type locality: Luquillo, Puerto Rico).

Molossus daulensis Allen, 1916: 530 (type locality: Daule, Los Rios, Equador, Ceara, Brazil).

Molossus major crassicaudatus — Hershkovitz 1949: 454 (name combination).

Molossus molossus crassicaudatus — Koopman 1978: 21 (name combination).

Molossus molossus — Willig 1985: 671 (misspelling).

Molossus molossus — Polanco-Ochoa *et al.* 2000: 675 (misspelling).

EMENDED DIAGNOSIS. — Medium-sized *Molossus* with brown dorsal fur varying from cinnamon to cocoa brown (Fig. 13). Dorsal hairs noticeably bicoloured, with pale basal band reaching $\frac{1}{2}$ to $\frac{1}{4}$ of total length of the hair. Forearm length averaging 40.2 mm in males (36.2–42.6) and 39.5 mm in females (36.4–42.6). Greatest length of skull averaging 17.7 mm (16.4–18.7) in males and 16.9 mm (15.6–18.6) in females (Table 1). Elongated skull (Fig. 2A) and infraorbital foramen facing anteriorly when observed in frontal view (Fig. 14B). Basioccipital pits moderately deep (Fig. 14C) and mastoid process ventrally oriented (Fig. 14D). Triangular or rounded occipital with underdeveloped lambdoidal crests (Fig. 14D), and low sagittal crest (Fig. 2B, E). Elongate upper incisors with parallel tips (Fig. 14B). Nasal process of pre-maxilla undeveloped, not protruding over the nasal cavity (Fig. 14E).

VARIATION. — Dorsal pelage in *M. molossus* is highly variable, from cinnamon to cocoa brown. Some individuals have a very dark pelage, while others, mostly young specimens, have a grayish fur. The incisor thickness may also vary within series, going from tapered (AMNH 235285) to moderately wide and somewhat spatulated (AMNH 238351).

DISTRIBUTION. — *M. molossus* is one of the most widely distributed bat species in the Neotropics, occurring from southeastern United States to Argentina, and throughout the Caribbean islands (López-González & Presley 2001). In Brazil, this species has been recorded from the state of Amazonas to Rio Grande do Sul (Eger 2008). In the present study, we added a new record from Alagoinha, state of Alagoas (Fig. 15).

REMARKS

There is a clear morphometric difference between samples of *M. molossus* males from state of Rio Grande do Sul, southern Brazil, and other localities. However, no single qualitative morphological character corroborates the distinction of these samples other than the overall size. Therefore, the difference in size may be an intraspecific variation explained by latitude (Bergmann 1847; Brown 1995; Ashton *et al.* 2000; Souza 2011). Future studies analyzing genetic divergence should be made to test the hypothesis that these samples are significantly different from each other.



FIG. 14. — *Molossus molossus* (Pallas, 1766). Photo courtesy of Dr Marco A. R. Mello (<https://marcoarmello.wordpress.com>).

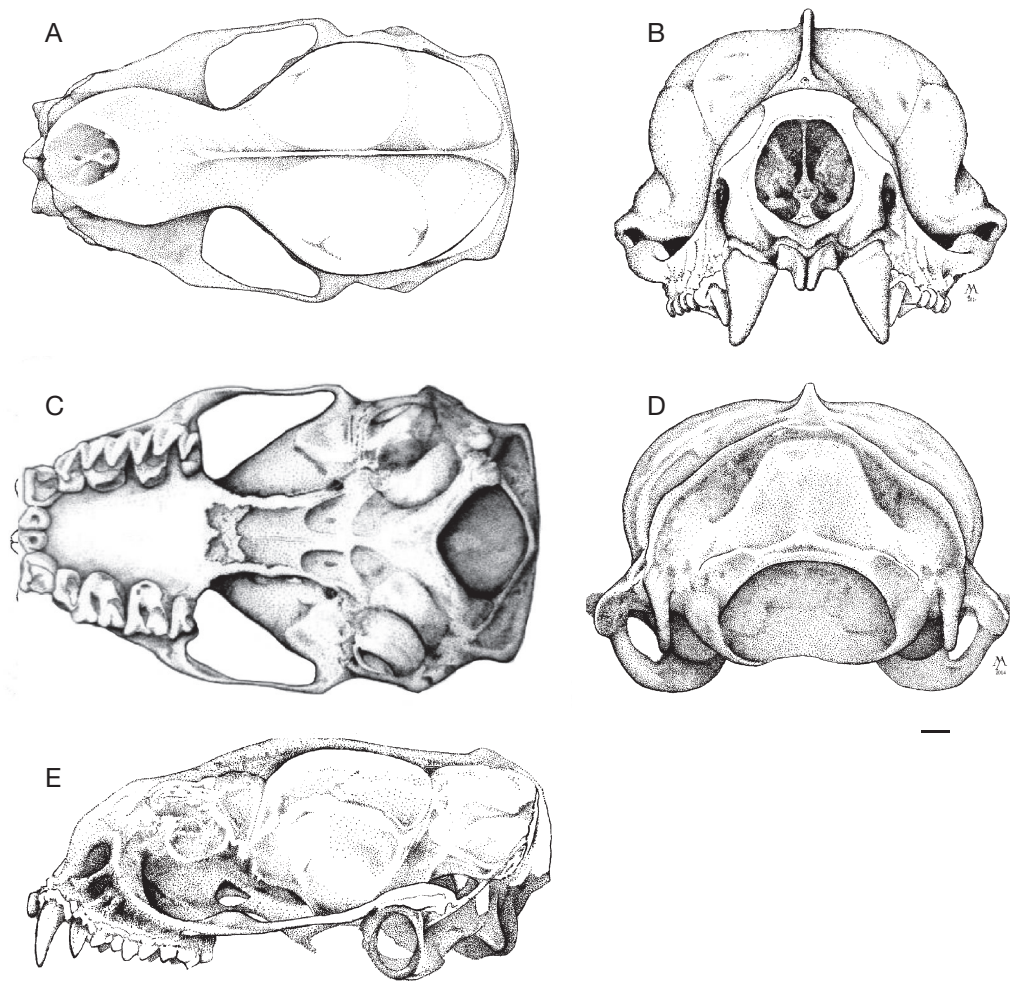


FIG. 13. — *Molossus molossus* (Pallas, 1766) skull: **A**, dorsal view; **B**, frontal view; **C**, ventral view; **D**, posterior view; **E**, lateral view. Scale bar: 1 mm.

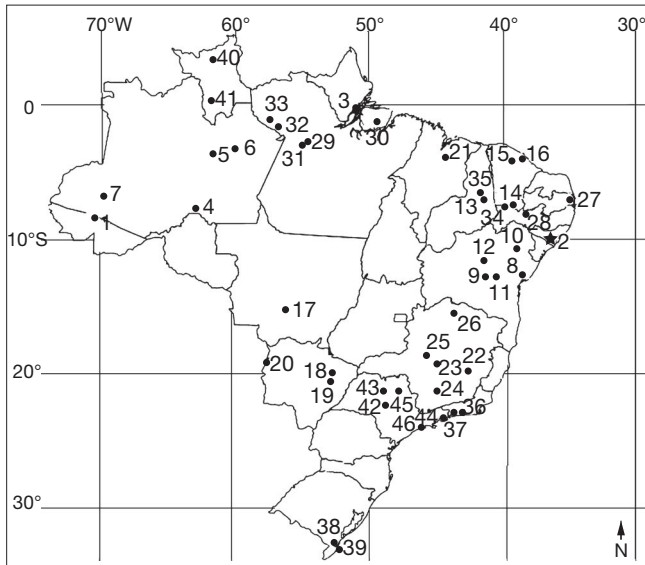


FIG. 15. — Geographic range of *M. molossus* (Pallas, 1766) in Brazil: ★, represents new records for the country. The numbers represent the localities described in Appendix 1.

Molossus currentium Thomas, 1901

Molossus obscurus currentium Thomas, 1901: 438 (type locality: Goya, Corrientes, Argentina).

Molossus currentium – Miller 1913: 89 (first use of the current name).

Molossus major currentium – Hershkovitz 1949: 454 (name combination).

Molossus major crassicaudatus – Cabrera 1958: 130 (name combination).

Molossus molossus currentium – Koopman 1993: 235 (name combination).

Molossus molossus crassicaudatus – Barquez *et al.* 1999: 221 (name combination).

Molossus currentium currentium – López-González & Presley 2001: 771 (name combination).

Molossus bondae Allen, 1904: 228 (junior synonym of *Molossus currentium*).

DIAGNOSIS. — Medium size *Molossus* with dark dorsal pelage, ranging from coffee brown to blackish. Dorsal hair with a pale band at the base, varying from 1/3 to 1/2 of the length. Short dorsal hairs, 4.0 mm long on average. Forearm length averages 41.3 mm in males (39.0–44.7) and 41.9 mm in females (40.0–43.5). Greatest length of skull averages 18.9 mm in males (18.6–19.4) and 17.9 mm in females (17.9–18.3). Relatively massive skull with elongated rostrum (Fig. 16A) and infraorbital foramen opening laterally in frontal view (Fig. 16D). Basioccipital pits moderately deep (Fig. 16B). Mastoid process oriented ventrally in posterior view (Fig. 16C). Triangular occipital due to the development and inclination of the lambdoidal crest, and well-developed sagittal crest, both more pronounced in males (Fig. 16C).

VARIATION. — The size of the pale band at the base of the dorsal hairs can vary in *M. currentium* even in the same geographic series. In some individuals, this band may be short, almost imperceptible, whereas in others it extends about 1/3 of the total length of the hair. In addition, most of the individuals had small, wide, and spatulate upper incisors but, in a few cases, they may be elongated. Females of *M. currentium* have cranial features less pronounced compared to males, such as the sagittal and lambdoidal crests.

DISTRIBUTION. — In South America *M. currentium* was recorded in Colombia, Ecuador, Venezuela, Argentina, Paraguay, and Brazil (López-González & Presley 2001; Eger 2008). The occurrence of this species in Brazil was first reported based on a juvenile female from Manaus, Amazonia (AMNH 40724) (López-González & Presley 2001). However, the identification of this individual remains uncertain as noted by Eger (2008) and confirmed by us. For this reason, this record is not considered in the present study. Tavares *et al.* (2010) identified several specimens as *M. currentium* in the state of Minas Gerais. However, these individuals have small cranial and external measurements, the dorsal hairs have an evident pale band at the base, and several cranial features are more similar to *M. molossus* than *M. currentium*. Therefore, these specimens are herein assigned to *M. molossus*. In this paper, an adult male of *M. currentium* from Corumbá, Brazilian state of Mato Grosso do Sul, was recorded (Fig. 17).

REMARKS

Thomas (1901) described the subspecies *Molossus obscurus currentium* Thomas, 1901 from a series of specimens earlier assigned to *Molossus obscurus* Geoffroy Saint-Hilaire, 1805 from Goya, Corrientes, Argentina. Further analyses considered *M. obscurus obscurus* as a junior synonym of *M. molossus* (Dolan 1989; Freeman 1981) and *M. obscurus currentium* as *Molossus bondae* (López-González & Presley 2001). López-González & Presley (2001) argued that the name *M. bondae* Allen 1904 is a junior synonym, and that the valid name for the species should be *Molossus currentium* Thomas, 1901. However, some authors suggest that *M. currentium* and *M. bondae* should be considered different species. Simmons & Voss (1998) and Eger (2008) argued that the pelage of *M. bondae* is monochromatic or with a short, almost indistinguishable pale band at the base of the dorsal hairs, while in *M. currentium* the dorsal fur is markedly bicoloured with a long whitish basal band. These authors also suggest that the upper incisors of both species are distinct, and *M. bondae* resembles *M. aztecus* and *M. rufus* with pincer-like upper incisors, while *M. currentium* resembles *M. molossus* with elongated and tapered incisors.

In this study, we have analyzed several specimens identified as *M. bondae* including the holotype, and specimens of *M. currentium* from Colombia, Brazil, and Panama. According to our morphological analyses, there are high levels of variation in dorsal pelage colouration as well as upper incisor shape and other cranial and external characters among specimens representing both taxa, with much overlapping. Indeed, the holotype of *M. bondae* (AMNH 23661) has short, brownish dorsal hairs, with a small paler basal band, like several individuals assigned to *M. currentium* (e.g. AMNH 212908, 185000, 184999). In the holotype of *M. bondae*, the incisors have an intermediary shape between pincer-like (as seen in *M. coibensis* and *M. rufus*) and tapered, as observed in some individuals of *M. currentium* (e.g. AMNH 34235 and 34236). In addition, several cranial features, such as opening of the infraorbital foramina and the shape of the occipital complex, are invariable in all samples representing *M. currentium* and *M. bondae*. Therefore, we consider *M. bondae* as a junior synonym of *M. currentium*, in agreement with López-González & Presley (2001) and Simmons (2005), and against Eger (2008).

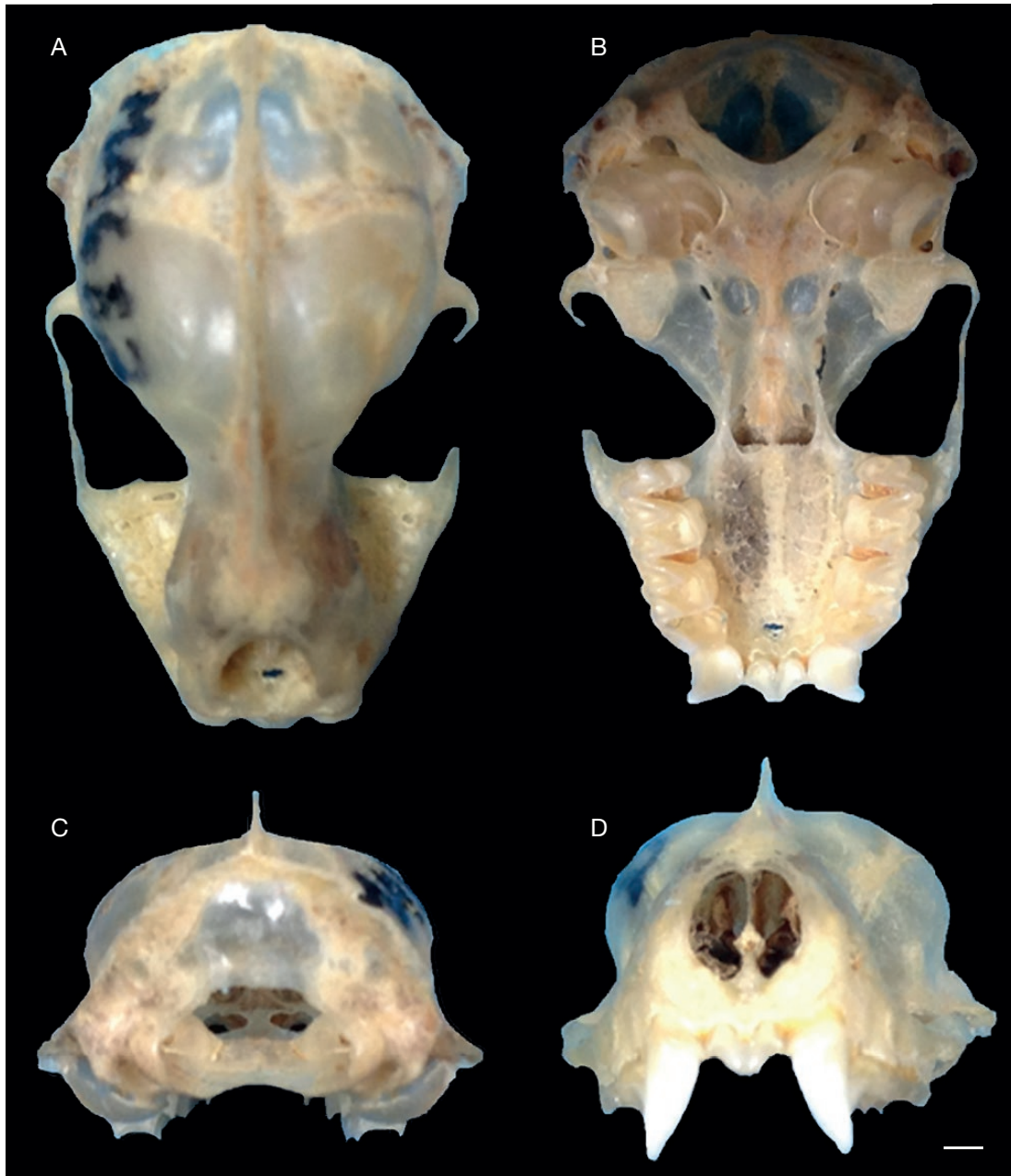


FIG. 16. — *Molossus currentium* Thomas, 1901 skull: **A**, dorsal view; **B**, ventral view; **C**, posterior view; **D**, frontal view. Scale bar: 1 mm.

Molossus pretiosus Miller, 1902

Molossus pretiosus Miller, 1902: 396 (type locality: La Guaira, Distrito Federal, Venezuela).

EMENDED DIAGNOSIS. — Large-sized *Molossus* with dark dorsal pelage from medium brown to blackish, and an absent or narrow, usually grayish, basal band. Short dorsal hairs varying from 2.0 to 4.0 mm. Forearm length averaging 47.5 mm in males (44.6-48.5) and 47.0 mm in females (44.9-49.0). Greatest length of skull averaging 21.4 mm in males (19.8-22.7) and 19.1 mm in females (18.9-20.9). Short and inflated rostrum and domed braincase (Fig. 2B). Infraorbital foramen opening laterally in frontal view (Fig. 2H). Noticeable crest between the basisphenoid and

basioccipital pits due to the very deep basisphenoid pits (Fig. 18). Nasal process of the premaxilla not protruding over the nasal cavity (Fig. 2A). Squarish occipital complex due to the large development and inclination of the lambdoidal crests. Quadrangular rostrum in frontal view. Incisors projecting beyond the canines, an intermediate condition when compared to other species of *Molossus*.

VARIATION. — The dorsal fur is dark, ranging from cocoa brown to blackish. Some individuals are orange in the entire dorsal hair or just in the tips (e.g. USNM 102780, 102767, 102768). Individual variation in the upper incisors exist within samples (Nogueira *et al.* 2008), and although most individuals have the incisors with parallel tips (tapered), others have pincer-like incisors (e.g. ALP 6896, 6875, 6946, 6943).



FIG. 17. — Geographic range of *Molossus currentium* Thomas, 1901 in Brasil: ★, represents new records for the country. The numbers represent the locality described in Appendix 1.



FIG. 19. — Geographic range of *Molossus pretiosus* Miller, 1902 in Brasil. The numbers represent the localities described in Appendix 1.

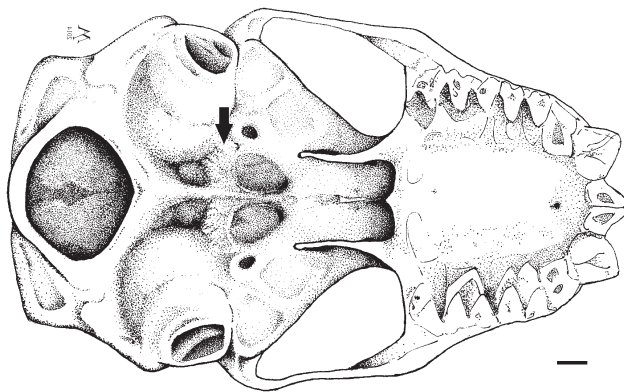


FIG. 18. — Ventral view of the skull of *Molossus pretiosus* Miller, 1902. Note the crest between the occipital and the basisphenoid pits. Scale bar: 1 mm.

DISTRIBUTION. — *M. pretiosus* presently has a disjunct distribution, occurring in Nicaragua, Colombia, Venezuela and Guyana (Koopman 1982; Dolan 1989; Eisenberg 1989; Lim & Engstrom 2001); in Brazil, this species was reported from Campo Grande, Mato Grosso do Sul (Gregorin & Taddei 2000), and Jaíba, northern Minas Gerais (Nogueira *et al.* 2008). These specimens were examined by us and are assigned to *M. pretiosus* (Fig. 19).

REMARKS

Some studies have showed that there are two large species of *Molossus* in Brazil (Dolan 1989; Jennings *et al.* 2000; Gregorin & Taddei 2000; Nogueira *et al.* 2008). This study corroborates with these authors and *M. pretiosus* can be distinguished from *M. rufus* based on qualitative and quantitative traits (see comparisons in *M. rufus* account).

DISCUSSION

Prior to our study, evolutionary relationships based on morphological phylogenetic studies have not been explicitly proposed for *Molossus*. However, several authors have suggested phenetical groupings within the genus based on similarity of a few characters (Miller 1913; Freeman 1981; Dolan 1989; Simmons & Voss 1998; López-González & Presley 2001; López-González-Ruiz *et al.* 2010; Gregorin *et al.* 2011). Our analysis supports the monophyly of *Molossus* (Fig. 5) based on morphological characters corroborating Ammerman *et al.* (2012) and Gregorin & Cirranello (2016). Although weakly supported, the phylogeny also clusters *M. coibensis*, *M. currentium*, *M. aztecus*, *M. pretiosus*, and *M. rufus* in one branch, and *M. sinaloae* and *M. molossus* in another. These results differ slightly from the grouping proposed by Dolan (1989), which clustered *M. currentium* with *M. molossus* and *M. sinaloae*. However, the analysis shows weak support for relationships within the genus and other clades within *Molossus* could not be supported.

The phylogeny proposed in this study shows that morphology by itself is not sufficient to resolve the relationships within the genus and many characters demonstrated degrees of homoplasy. The number of palatal streaks, the position of the upper incisors relative to the canines, the position of the opening of the infraorbital foramen, and the shape of the rostrum in rostral view appear at least twice in the evolutionary history of the group. However, different combinations of morphological characters have shown to be reliable for species identification (Dolan 1989; Gager *et al.* 2016).

Molecular phylogenies of *Molossus* have been proposed (Lindsey & Ammerman 2016; Lim *et al.* 2017; Loureiro *et al.* 2018), but genetic data alone also seems not be enough to resolve the relationships within the genus. Gager *et al.* (2016), based on the mitochondrial CO1 gene and the control region

KEY FOR IDENTIFICATION OF RECOGNIZED SPECIES OF *MOLOSSUS* E. GEOFFROY, 1805 IN BRAZIL

1. Forearm length between 44.6 and 56.0 mm; length of maxillary tooththrow between 7.5 and 8.7 mm; greatest length of skull without incisors from 18.0 to 23.5 mm; palatal length between 6.3 and 7.8 mm 2
 - Forearm length between 33.0 and 44.0 mm; Length of maxillary tooththrow between 5.0 and 7.5 mm; greatest length of skull without incisors from 14.0 to 18.0 mm; palatal length between 4.5 and 6.3 mm 3
2. Upper incisors short and spatulated, with convergent tips (Fig. 2H); depth of the basioccipital pits moderate, without formation of crest between the basioccipital and the basisphenoid (Fig. 2B); nasal process highly developed (Fig. 2B); mastoid process facing toward the foramen magnum in posterior view (Fig. 2F). Larger size, forearm between 47.7 and 55.2 mm in males and 46.7 and 54.0 mm in females. Greatest length of skull between 20.8 and 23.8 mm in males and 19.9 and 22.6 mm in females *M. rufus* E. Geoffroy, 1805
 - Elongated upper incisors without converging tips; deep basioccipital pits, with the formation of a crest between the basioccipital and the basisphenoid; nasal process undeveloped (Fig. 2A); mastoid process directed ventrally in posterior view (Fig. 2F). Smaller size, forearm between 44.6 and 48.5 mm in males and 45.0 and 49.0 mm in females. Greatest length of skull without incisors between 19.8 and 22.7 mm in males and 18.9 and 21.0 mm in females *M. pretiosus* Miller, 1902
3. Dorsal hair with a long and pale, and usually whitish, band at the base, covering from ¼ to ½ of the total length of the hair; dorsal pelage colouration varying from medium to dark brown; triangular occipital complex (Fig. 2E); elongated incisors with parallel tips (Fig. 2G) 4
 - Dorsal hair without a pale band at the base, if present, the basal band is incipient, usually greyish or buff, and not extending more than 1/3 of the total length of the hair; dark dorsal pelage that may vary from dark brown, grayish to blackish brown; occipital complex quadrangular in shape (Fig. 2F); small and spatulated upper incisors (Fig. 2H) 5
4. Infraorbital foramen directed laterally (Fig. 2H); very well-developed sagittal and lambdoidal crests (Fig. 2F, B) *M. currentium* Thomas, 1901
 - Infraorbital foramen directed frontally (Fig. 2G); undeveloped sagittal and lambdoidal crests (Fig. 2A, E) *M. molossus* (Pallas, 1776)
5. Infraorbital foramen opens frontally in rostral view (Fig. 2G); shallow or absent basioccipital pits (Fig. 2A). Smaller size, forearm between 36.1 and 37.9 mm in males, and 34.3 and 37.5 mm in females. Greatest length of skull between 15.7 and 16.9 mm in males and 14.9 and 16.7 mm in females *M. coibensis* Allen, 1904
 - Infraorbital foramen directed laterally in rostral view (Fig. 2G); basioccipital pits with moderate depth (Fig. 2B). Larger size, forearm between 35.9 and 41.5 mm in males, and 35.0 and 41.9 mm in females; greatest length of skull between 16.2 and 18.3 mm in males, and 16.4 and 18.6 mm in females *M. aztecus* Saussure, 1860

D-loop, examined the relationships of *M. molossus*, *M. rufus*, and *M. coibensis* in Panama, and recognized all as valid taxa. However, the resulting phylogenetic tree included numerous polytomies with most nodes having low statistical support (<70%). Lindsey & Ammerman (2016) reconstructed the phylogeny of some species of *Molossus* based on partial CytB sequences. In their study, *Molossus molossus tropidorrhynchus* Gray, 1839 from Cuba formed a divergent monophyletic lineage, but the branches comprising the samples of *M. molossus*, *M. rufus*, and *M. coibensis* had low support. A more recent study by Loureiro *et al.* (2018) described a new, highly divergent species of *Molossus* from Guyana and Ecuador (*M. fentoni*) based on morphology, mitochondrial and nuclear genes. However, in their phylogeny, the support for the relationships among some terminal taxa, such as *M. rufus*, *M. coibensis*, and *Molossus* sp from Guyana and Venezuela, is very low.

Morphometric variation of some cranial and external measurements are correlated with latitude in at least three species of *Molossus*, corroborating with trends hypothesized by Bergmann (1847), Brown (1995), Ashton *et al.* (2000), and Salewski & Watt (2017). However, these variables are

not the same among species or between sexes, and perhaps different ecological variables, such as temperature (Bergmann 1847), food availability (Millar & Hickling 1990), prey size (Erlinge 1987), and competition (Damuth 1993) could affect each species differently. For example, Medeiros *et al.* (2018) noted rapid body dimensions divergence in *Artibeus planirostris* Spix, 1823 linked to anthropogenic alterations of environment. Some individuals of *M. molossus* from southern Brazil have significant larger cranial and external measurements, and further molecular analyses may be required to investigate the possibility of this population being distinct from other *M. molossus*. In addition, a single individual of *Molossus* sp. from the Caatinga of northeastern Brazil was analyzed. However, the combination of characters found in this individual is unique, which suggest that it may be assignable to a new species. Therefore, we emphasize the need for molecular analysis and more field work focusing to collect additional material in order to solve its taxonomic status.

Morphologically, many species within *Molossus* are highly similar and the lack of traditional characters (pelage, skull, and dentition) to distinguish them resulted in an unsatisfactory identification of specimens of this genus. Furthermore, some

characters showed high levels of variation within samples or between sexes, which results in difficulty in the identification and delimitation of species. The level of genetic divergence, even among well characterized species of the genus, is low (Clare *et al.* 2007; Borisenko *et al.* 2008; Lim *et al.* 2017; Loureiro *et al.* 2018), often making characterization of biologically meaningful subunits difficult, and likely resulting in an underestimation of the actual species richness in the genus. The combination of these factors makes *Molossus* a taxonomic challenge. We suspect that the diversity within *Molossus* is underestimated, and new molecular analyses (e.g., multi-genes, and single nucleotide polymorphism – SNPS) will be important for resolving its relationships. However, morphological analysis are also crucial for the understanding of this complex genus and should be used in combination with other data sets. Echolocation calls have been providing a good dataset to distinguish species of *Molossus* (Jung *et al.* 2014; Gager *et al.* 2016; Mischiatti 2018; Aguilar *et al.* 2018), and it is proven to help deciphering cryptic species complex (Ramasindrazana *et al.* 2011, Thoisy *et al.* 2014). Therefore, acoustics could also help to bring information about cryptic species within *Molossus* an understand the taxonomy of the genus. In a recent example, CytB variation in *M. molossus* as recovered by Lindsey & Ammerman (2016) suggests that two subspecies, *M. m. tropidorhynchus* and *M. m. daulensis* Allen, 1916 may be considered as full species, agreeing with previous recorded morphological differences diagnostic of both subspecies. . Despite their ubiquitous distribution in Brazil, we have presented a large number of external, cranial, and dental characters, which we expect to be useful for the diagnosis of the six species of *Molossus* identified for the country.

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APPENDICES

APPENDIX 1. — Specimens examined.

We examined a total of 493 specimens, 258 females and 235 males. The material studied is housed in the following institutions: American Museum of Natural History, New York City (AMNH); National Museum of Natural History, Washington DC (USNM); Universidade Estadual Paulista, São José do Rio Preto (DZSJRP); Universidade Federal Rural do Rio de Janeiro, Seropédica (ALP); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP); Universidade Federal de Lavras, Lavras (CMUFLA); Universidade Federal de Minas Gerais, Belo Horizonte (UFMG); Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro (MNRJ); Universidade Federal do Mato Grosso do Sul, Campo Grande (ZUFMS); Centro de Zoonoses da Cidade de São Paulo, São Paulo (CCZSP); Museu de História Natural da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte (MCN).

Molossus aztecus: Brazil: Amazonas: 1. — Humaitá (DZSJRP 13271, 12176, 12781, 12788; CMUFLA DZSJRP13180, DZSJRP13264, DZSJRP13269, DZSJRP13272-DZSJRP13274, DZSJRP13276); Bahia: 2. — SALVADOR (MZUSP 1309); CEARÁ: 3. — Crato (MZUSP 16834, 16841, 16861, 14896, 14897, 14904); MATO GROSSO DO SUL: 4. — Corumbá (ZUFMS 35, CHI00635, CHI01539, CHI01545); MINAS GERAIS: 5. — Lavras (CMUFLA 356, 399, 400, 408, 414-416), 6. — Sete Lagoas (USNM 314301, 391162-391164, 391167, 391171, 39174, 391175); Piauí: 7. — São José do Piauí (CMUFLA 1051); Paraíba: 8. — Mamanguape (MZUSP 8329, 8346); Pernambuco: 9. — Exú (MZUSP 16800, 16814); Rio De Janeiro: 10. — Rio de Janeiro (MNRJ 23063), 11. — Reserva Biológica do Tinguá (ALP 6294, 6295, 6298), 12. — Seropédica, Universidade Rural do Rio de Janeiro (ALP 420, 424, 425, 646); São Paulo: 13. — Ilha dos Búzios (MZUSP 10269, 10270). Mexico: Colima, Etijó Tepextles (AMNH 172045), Colma (AMNH 172044), OAXACA: Oaxaca (AMNH 171605, 171639, 171640, 206873, 206876), Temuaratepec (AMNH 171597).

Molossus barmesi: French Guiana: Cayenne (AMNH 267262, 269105).

Molossus bondae: Colombia: Magdalena: Bonda (AMNH 14922, 14924, 23661), Vale Del Cauca (USMN 83959-483964).

Molossus coibensis: Brazil: 1. — Bahia: Cidade da Barra (MZUSP 2672); Maranhão: 2. — Parque Estadual do Bacanga, São Luis, Ma (UFMG 3404, 3405); Mato Grosso Do Sul: 3. — Brasilândia (MZUSP 28782, 28689); Minas Gerais: 5. — Belo Horizonte (UFMG 3350), 6. — Três Marias (UFMG 3411); São Paulo: 7. — São Paulo (CCZSP15). Guatemala: Dept. Tutiapa (AMNH 217443-217446, 217448, 217449). Panama: Chagres River (AMNH 173919), CHIRIQUI: Coiba Island (AMNH 18731), Veraguas: Mon-

tijo (AMNH 18732, 18733); Canal Zone (USNM 314299, 314300, 317648).

Molossus currentium: Colombia: Nariño Department: Barbacoas (AMNH 34235, 34236), Magdalena: Bonda (AMNH 23661). Brazil: Mato Grosso Do Sul: 1. — Corumbá (ZUFMS CHI00682). Panama: Canal Zone (AMNH 212908), Chagres River (AMNH 178900, 178899, 184999, 185000), LA Chorrera: La Chorrera (AMNH 31676).

Molossus molossus: Brazil: 1. — Acre (MZUSP 8228, 8231, 8232, 8235, 8239-8241, 8244); 2. — Alagoas: Alagoinha (MNRIO 42839); Amapá: 3. — Macapá: (ALP 4019, 4025, 4051, 4097, 4100, 4140); Amazonas: 4. — Humaitá (DZSJRP 11904, 11906, 12781, 12783, 12786, 12787, 12911, 13268, 13270, 13273, 13178, 13190), 5. — Manaus (AMNH 40724; AMNH 77669-77671, 77673-77675, 77677, 77680, 91462, 91463); 6. — João Pessoa (MZUSP 4427, 4432, 4464), 7. — Eirunepé (MZUSP 4443, 4465); Bahia: 8. — Salvador (MZUSP 501; MNRJ 3601, 23052, 23057, 23058, 23060, 23062, 23064, 20962, 23065, 30665, 30666), 9. — Cidade da Barra (MZUSP 2672), 10. — Canudos (MZUSP 15577), 11. — Santo Inácio (MZUSP 26807), 12. — Vila Nova (MZUSP 5849); Ceará: 13. — Chapada do Araripe (CMUFLA 1049, 1050), 14. — Crato (MZUSP 4972, 14899, 14901, 14902, 15036-15038, 15046, 15048, 16808, 16809, 16830, 16832, 16833, 16835, 16840, 16842, 16843, 16845, 16847, 16849, 16852-16854, 16857, 16858, 16860, 16862), 15. — Pacoti (MZUSP 8730), 16. — Fortaleza (MCN 92); Mato Grosso: 17. — Cuiabá (3661, 3662); Mato Grosso Do Sul: 18. — Águas Claras (DZSJRP 11894, 11895, 11896, 11898, 11900, 11901, 11916, 16457, 16458), 19. — Corumbá (ZUFMS CHI00699, CHI00698, CHI01523, CHI01530, CHI01532, CHI01536, CHI01538, CHI01548), 20. — Inocência (UFMG 1275); Maranhão: 21. — Parque Estadual do Bacanga, São Luis, MA (UFMG 3402, 3403); Minas Gerais: 22. — Parque Estadual do Rio Doce (CMUFLA 977, 988), 23. — Belo Horizonte (MCN 29, 139, 273), 24. — Lavras (CMUFLA 356, 408, 414-416), 25. — Pompeu (MNC 274, 275-284, 296, 376), 26. — Jaíba (ALP 6851, 6878, 6916, 1730); Paraíba: 27. — Mamanguape (MZUSP 8327, 8330, 8335, 8339, 8343-8345, 8347, 8348, 8353, 15633); Pernambuco: 28. — Exu (MZUSP 16792, 16793, 16804, 16806, 16807, 16817-16825); PARA: (MNRJ 23057), 29. — Caxiricatuba (MZUSP 4407, 4422, 4423, 4431, 4435, 4441, 4447, 4461, 4462, 4386, 4387, 23804), 30. — Ilha de Marajó (MZUSP 8656, 8665, 8661, 8667, 8671, 8673), 31. — Santarém (MZUSP 15483, 15484); 32. — Reserva biológica do rio Trombetas (MZUSP 19460, 19461), 33. — Rio Trombetas (MZUSP 15496, 15488, 15502, 15505, 15506, 15509); PIAUÍ: 34. — Fronteiras (DZSJRP 11447, 11448), 35. — Valença do Piauí (MZUSP 16866, 16868); Rio De Janeiro:

APPENDIX 1. — Continuation.

36. — Reserva Biológica do Tinguá: (6229, 6233, 6238, 6241-6243), 37. — Seropédica, Universidade Rural do Rio de Janeiro (ALP 887); Rio Grande Do Sul: 38. — Quinta (AMNH 235381-235390), 39. — Taim (DZSJRP 14565-14570); Roraima: 40. — Ilha de Macará (DZSJRP 11493), 41. — Santa Maria do Boiaçu (MZUSP 27897, 27898, 27901, 27902, 27905); São Paulo (MZUSP 21093), 42. — Boracéia (MZUSP 15039), 43. — Catanduva (DZSJRP 16456), 44. — Ilha de Búzios (MZUSP 10268, 10271 -10273), 45. — Ribeirão Preto (MZUSP 17597), 46. — Bertioiga (MZUSP 26410); Venezuela: (MNRS 23052); Argentina: Corrientes: Goya (MCN286).

Molossus pretiosus: Brazil: Mato Grosso Do Sul: 1. — Corumbá (ZUFMS CHI00682, CHI01360); Minas Gerais: 2. — Jaíba (ALP 6875, 6896, 6911, 6912, 6914, 6915, 6943-6946, 6963); Mexico: Oaxaca: San Blas: (AMNH 14515), Oaxaca (145150); Venezuela: Juapure (AMNH 17037, 17039-17043, 102752, 102754), São Francisco de Cara (USNM 303852), VARGAS: La Guaira (USNM 102744, 102745, 102747-102749, 102761); Macuto (USNM 143832-143835, 102767, 102768); Distrito Federal: (USMN 102780).

Molossus sinaloae: Honduras: Francisco Morazan (USNM 461105); San Pedro Sula: Chamelecón (USNM 148773). Guatemala: Izabal: Bobos (USNM 260048, 260047). Mexico: Guerrero (USNM 5598020); Nayarit (USNM 508997, 509001, 508996, 508998); Sinaloa: Escuinapa (AMNH 24524).

Molossus: Brazil: Bahia: São Félix do Coribe (CMUFLA 3453).

Molossus rufus: Brazil: Amapá: 1. — Rio Maruanum (MZUSP 17595); Amazonas: 2. — Itacoatiara (MZUSP 4437), 3. — Manaus (AMNH 77669-77671, 77673-77675, 91462, 91463, 77677, 77680); Ceará: 4. — Pacoti (MZUSP 8729); Bahia: 5. — Salvador: (MNRJ 3603, 11198); Mato Grosso: 6. — Serra do Roncador (USNM 393787-393792), 7. — Xavantina (AMNH 393786, 393793); Mato Grosso Do Sul: 8. — Águas Claras (DZSJRP 11918, 11919, 11923, 11925), 9. — Campo Grande (ZUFMS CHI01318), 10. — Inocência (MNRJ 12482), 11. — Miranda (UFMS CHI00649); Pará: 12. — Caxiricatuba (MZUSP 4381, 4428, 4439, 4450, 4463, 5630,); Paraná: 13. — Floriano (DZSJRP 10439, 10447, 10449, 10453); São Paulo: (10766, 11917), 14. — Bilac (DZSJRP 10735, 10736), 15. — Iguape (MZUSP 21036, 21083, 21085), 16. — Marília (DZSJRP 10740, 10745, 10747-10749, 10767), 17. — São José do Rio Preto (CMUFLA 979; DZSJRP 16474, 16477, 16478), 18. — São Paulo (DZSJRP 15988 -15990); Rio De Janeiro: (MNRJ 3505), 19. — Niterói (MN 3296, 3996), 20. — Reserva Biológica do Tinguá (6228-6232, 6299-6302), 21. — Rio de Janeiro (MZUSP 1489); Roraima: 22. — Ilha do Maracá (DZSJRP 11493). French Guiana: Cayene (MNHN-ZM-MO-1997-1847), Paracou (AMNH 267263, 267264, 267267, 267268, 267270, 267539).

APPENDIX 2. — Description of characters used in the phylogenetic analysis.

FACIAL, PELAGE, AND SOFT PALATE

0. — *Size of the forearm*

Large, measuring 57-61 mm (0); Average, measuring 49-45 mm (1); Small, less than 45 mm (2). *Eumops* has a large forearm while *Promops* and *Molossus rufus* have the forearm of an average size. The other species of *Molossus* have a small forearm, measuring up to 46 mm.

1. — *Presence of hair on the top edge of the nostril*

Covered with small hairs (0); without any structure (flat) (1). While *Eumops* has the region on top edge of the nostril covered with small hairs, the species of *Promops* and *Molossus* have a smooth region.

2. — *Fur density in the internarial rib*

High density of fur (0); Small density of fur (1). The intranasal rib is densely covered with fur in *Eumops*, but with sparse fur in *Molossus* and *Promops*.

3. — *Shape of ears*

Rounded (0); Triangular (1). The ears of *Eumops* and *Promops* have a rounded shape, whereas in *Molossus* the ears are triangular.

4. — *Form of antitragus*

Longer than wide, with a tapered base (0). As long as broad, quadrangular in shape (1). While in *Eumops auripendulus* the antitragus tends to be long and tapered, in the species of *Promops* and *Molossus* it tends to be quadrangular.

5. — *Banding pattern of dorsal fur*

Dorsal fur uncoloured or partially bicolour, with a pale base covering up to ¼ of the length (0); Dorsal fur bicolour with a pale base covering ¼ to ½ of the length (1). Some species such as *M. aztecus*, *M. pretiosus*, *M. rufus*, *M. currentium*, and *M. coibensis* might have a unicolour fur or have a narrow pale band, but rarely white, not reaching more than a quarter of the length of the fur. However, other species such as *M. sinaloae* and *M. molossus* have a wide basal band in the dorsal hair, whitish or rarely yellowish, occupying about half the length of the hair.

6. — *Number of palatal streaks*

Seven (0); Eight (1); Nine (2). *Molossus* species have different amounts of palatal streaks, ranging from seven to nine.

DENTITION

7. — *Height of metaconule on first and second molars*

High (0); Low (1). *Eumops* presents the two first upper molars with a metaconule detached from the post-protocrista while *Molossus* has a low cusp positioned on the crest.

8. — *Shape of upper incisors*

Conical (0); Flattened anterior posteriorly (1). In *Eumops* and *Promops* the incisors are conical while *Molossus* have flattened upper incisors.

9. — *Upper incisors position relative to vertical plane*

Upper incisors project forward in a plane not parallel to the anterior face of canines (0); Aligned to the anterior plan of canines (1). In side view, the incisors may be projected beyond the line of canines (e.g. *Eumops*, *Promops*, and *M. molossus*) (Fig. 2A) or in the same line of canines (e.g. *M. rufus* and *M. aztecus*) (Fig. 2B).

10. — *Orientation of the upper incisors*

Upper incisors tips divergent (0); Upper incisors tips convergent (1); Upper incisors tips directed ventrally (2). The tips of the upper incisors are divergent in *Eumops* and *Promops*. In contrast, the upper incisors are directed medially in some species of *Molossus* (*M. rufus* and *M. aztecus*) (Fig. 2H) and parallels in other (*M. molossus* and *M. sinaloae*) (Fig. 2G)

11. — *Number of upper premolars*

Two (0); One (1). *Eumops* and *Promops* present two premolars on each hemimaxilla while *Molossus* has one (Fig. 2C, D).

12. — *Size of the third lower premolar*

Large and developed, greater than half of the fourth inferior premolar (0); Median size, measuring about half of the fourth premolar (1); Small and undeveloped, with less than half of the length of the fourth premolar (2). In *Eumops* the third premolar is large and developed and in *Promops* it is of median size. In *Molossus* the third premolar is undeveloped, not having more than half the size of fourth inferior premolar.

13. — *Development of metaconid of the third and fourth lower premolars*

Undeveloped, not forming projections (0); Well-developed, forming a distinct cusp (1). In *Eumops* the metaconid of the third and fourth premolars is undeveloped. In contrast, in *Molossus* there is a large and developed metaconid forming a distinct cusp.

14. — *Presence of hypoconulid in the first lower molar*

Present (0); Absent (1). The hypoconid of the first molar is present in *Eumops auripendulus* and absent in *Molossus*.

15. — *Number of lower incisors*

Two (0); One (1). *Eumops* and *Promops* have two incisors in each hemimandible. In contrast, *Molossus* has only one.

16. — *Development of the entoconid on first lower molar*

Developed forming a lateral projection (0); Reduced, not forming a lateral projection (1). The entoconid in *Eumops* is large and developed creating a side projection, while *Molossus* and *Promops* have this crest weak and barely noticeable.

17. — *Size of entoconid on the lower third molar*

Small and poorly developed (0); Large and developed projecting distally (1). The entoconid on the lower third molar in *Eumops* and *Promops* is small and barely noticeable, while in species of *Molossus* is large and developed forming a lateral projection.

SKULL

18. — *Opisthocranium in posterior view*

Straight (0); Curved dorsally and anteriorly (1). In *Eumops* the occipital in posterior view is straight and flat, while in *Molossus* it is curved, which gives the appearance of a dome.

19. — *Palate arching*

Palate moderately arched. The distance between midline of the palate and the toothrow is about the size of the first molar (0); Palate strongly arched. The distance between the midline of the palate and tooth row is greater than the size of the first molar (1). Palate slightly arched without significant space between the center of the palate and toothrow (2); The hard palate is a complex association of the palatal process of the premaxilla, maxilla, and horizontal process of the palatine bone. In Microchiroptera, the arching palate can range from straight to strongly curved, depending on the diet. In the case of *Promops*, *Eumops*, and *Molossus* this arching decreases, respectively, with *P. centralis* having the most arched palate.

20. — *Posterior border of hard palate*

V-shaped, with the anterior end tapered (0); U-shaped, with rounded anterior end (1). *Eumops auripendulus* has the V-shaped palate, while *P. centralis* and *Molossus* (Fig. 2C and D) have an U shaped palate.

21. — *Shape of the basisphenoid pits*

Basisphenoid pits long and oval (0); Basisphenoid pits circular (1). In *E. auripendulus*, the basisphenoid pits are elongated and oval compared to the genus *Molossus* (Fig. 2D).

22. — *Relative width of zygomatic arch along its length*

Zygomatic arch with gentle decrease in width along the length (0); Zygomatic arch with a sudden decrease in width along the length (1). The transition from the jugal to squamosal can be abrupt or smooth, making the width of the zygomatic arch along its length homogeneous or variable. In the outgroup taxa there is a gentle decrease in this thickness along its length, while in *Molossus* there is a sudden decrease in this width, forming a process near to the process of the maxilla (Fig. 2A, B).

23. — *Depth of basicochlear fissure*

Wide (0); Shallow (1). The basicochlear fissure separates the complex of the tympanic bulla from the palatal portion formed by basisphenoid and basioccipital plates. This structure is remarkably deep in *Eumops* and *Promops*, while in *Molossus* it is shallow. The shallow state of this character implies in a contact zone between the bulla and other parts of the skull (Gregorin, 2009).

24. — *Number of incisive foramina*

One (0); Two (1). *Eumops* and *Promops* have only one incisor foramen while the species of *Molossus* have two.

APPENDIX 2. — Continuation.

25. — *Size of the spheno-orbital process*

Spheno-orbital process small and truncated (0); Spheno-orbital process large, long and tapered (1). The spheno-orbital process is small and truncated in *Eumops* and *Promops* and very thin and elongated in *Molossus*.

26. — *Position the optical channel*

Anterior part of the optical channel located at the level of the third molar (0); Anterior part of the optical channel located at the level of the tooththrow end (1). In *Eumops* the posterior part of the optic canal extends to the height of the third molar, while in *Promops* and *Molossus* this structure reaches only the end of the dental series (Fig. 2A, B).

27. — *Length of the rostrum*

Long compared to the braincase (0); Short compared to the braincase (1). *Eumops* has a proportionately more elongate rostrum, while *Promops* and *Molossus* have this region more shortened (Fig. 2A, B).

28. — *Basisphenoid pits depth*

Basisphenoid pits deep (0); Basisphenoid pits shallow (1); In *Molossus* and *Promops* the basisphenoid pits are relatively shallow when compared to *E. auripendulus*.

29. — *Basioccipital pits depth*

Shallow (0); Moderate (1); Deep (2). Within species of *Molossus*, the depth of the basioccipital pit varies considerably. In *M. coibensis* the pits are extremely shallow (Fig. 2C), while in *M. pretiosus* they are quite deep. Other species of the genus have cavities with moderate depth (Fig. 2D).

30. — *Position of the opening of the infra-orbital foramen*

Opening of the infra-orbital foramen forward directed (0); Opening of the infra-orbital foramen directed laterally (1). In frontal view, the skull of some species of *Molossus*, as *M. aztecus* and *M. rufus* (Fig. 2H), show the infra-orbital foramen laterally directed, whereas in other species, such as *M. molossus*, it opens frontally (Fig. 2G).

31. — *Height of braincase*

In the same plane as the dorsal region of the rostrum (0); Above the dorsal surface of the rostrum (1); The braincase may be less developed and in the same plane as the dorsal region of the rostrum, giving a flattened appearance to the skull (*E. auripendulus*), or it may be well developed, extending above the dorsal surface of the rostrum, which gives the appearance of a globose skull (*Molossus*).

32. — *Presence of the crest between the basisphenoid and basioccipital pits*

Absent (0); Present (1). Due to the deepening of basisphenoid and basioccipital pits, a crest is formed between these concavities in *Molossus pretiosus*.

33. — *Projection of the nasal process of premaxilla*

The nasal process of premaxilla does not project over the nasal cavity (0); The nasal process of premaxilla project over the nasal cavity (1). In some species of the genus *Molossus* such as *M. aztecus* and *M. rufus*, the nasal process of the premaxilla is well developed and it is projected over the nasal cavity (Fig. 2B). In other species, such as *M. molossus*, this structure is less developed not projecting over the nasal cavity (Fig. 2A).

34. — *Format of the rostrum in rostral view*

Square, with a uniform width along its length (0); Triangular with the width of the dorsal portion narrow (1). In frontal view, the skull of some species have a quadrangular nasal aperture, as in the case of *M. coibensis* and *M. molossus* (Fig. 2G). In other species, such as *M. aztecus*, the shape of the nasal aperture is triangular, giving the appearance of a slender rostrum (Fig. 2H).

35. — *Robustness of the skull*

Slender and elongated skull (0); Robust skull (1). In *M. molossus* the skull is elongated with an elongated braincase and an inflated rostrum, giving it a slender look. In *M. coibensis* and *M. aztecus*, the braincase is more globular and they have a more inflated rostrum, giving it a more robust appearance.

36. — *Development of medial sagittal crest in males*

Absent (0); Undeveloped (1); Well developed (2). *Eumops auripendulus* do not have a sagittal crest, while *Molossus* species have it with variable sizes. In some species such as *M. coibensis*, *M. aztecus*, and *M. rufus*, the sagittal crest is well developed (Fig. 2B, F and H), while in other species such as *M. molossus* the crest is less developed when compared with the size of the skull (Fig. 2A, E, G).

37. — *Development of lambdaoidal crest in males*

Low (0); Very high (1). In *Eumops*, *Promops* and in some species of *Molossus*, such as *M. molossus* and *M. sinaloae*, the lambdaoidal crest is poorly developed (Fig. 2E), whereas in *M. aztecus*, *M. currentium*, and *M. rufus* the crest is high and detached from the occipital (Fig. 2F).

38. — *Shape of occipital complex in dorsal view*

Triangular (0); Quadrangular (1). *Eumops auripendulus*, *P. centralis*, and some species of *Molossus*, such as *M. molossus* and *M. sinaloae* (Fig. 2E), have a triangular or rounded occipital, whereas other species of *Molossus* have an occipital more robust and quadrangular (Fig. 2F).

39. — *Projecting of mastoid process*

Paraoccipital process projects laterally (0); Paraoccipital process projects frontally (1). The paraoccipital process in *E. auripendulus*, *P. centralis*, *Molossus* sp., and *M. rufus* projects laterally and can be easily visualized in dorsal view (Fig. 2F). In contrast, in other species of *Molossus*, the paraoccipital process projects ventrally (Fig. 2E).

APPENDIX 2. — Morphological character matrix used in the phylogenetic analysis. “?” denotes missing data.

Taxon/ Character	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39		
<i>E. auripendulus</i>	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>P. centralis</i>	1	1	1	0	1	0	?	0	0	0	0	0	1	1	0	0	1	0	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0
<i>M. coibesis</i>	2	1	1	1	1	0	0	1	1	1	1	1	2	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	0	1	2	1	1	1	1	
<i>M. molossus</i>	2	1	1	1	1	1	1	1	0	2	1	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	1	0	0	1	0	0	1
<i>M. aztecus</i>	2	1	1	1	1	0	1	1	1	1	1	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	2	1	1	1	1	
<i>M. currentium</i>	2	1	1	1	1	0	1	1	1	1	1	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	2	1	1	1	
<i>M. sinaloae</i>	2	1	1	1	1	?	1	1	0	2	1	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	1	0	0	1		
<i>M. pretiosus</i>	1	1	1	1	1	0	2	1	1	1	1	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	2	0	1	1	0	0	0	2	1	1	1		
<i>M. rufus</i>	1	1	1	1	1	0	2	1	1	1	1	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	2	1	1	0	0		
<i>Molossus sp.</i>	2	1	1	1	1	?	1	1	0	2	1	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	?	?	1	0		