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Research Article

Morphofunctional segregation in molossid bat species (Chiroptera: Molossidae) from the South American Southern Cone

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Abstract

Molossid bats exhibit a great diversity of size and skull morphology which likely reflects differences in diet a trophic function and may be indicative of the degree of resource partitioning and ecological overlap in the group. We explored the morphofunctional variation of the skull in molossids from Argentina, where 18 species occur, and are representative of the vast South American Southern Cone region. We measured 18 craniodental variables in 377 specimens representing all 18 species. We performed a multivariate analysis using craniodental variables, with and without correcting for body mass variation, and applied a comparative phylogenetic method to determine the importance of phylogeny in morphofunctional variation. The specimens distribution in morphospace showed a clear segregation between species on the basis of skull size and morphological differences that related with prey selection, and associated with other important factors such as echolocation and flight. Our results highlighted that the morphological pattern observed was determined principally by the evolutionary history of the family, as we identified major events of expansion of occupied morphospace with the origination of large species such as those in *Eumops* as well as small species of *Molossops* and *Cynomops*. Our findings suggest that the joint effects of history, size and functional morphology boosted the evolution of Neotropical molossids and facilitated the coexistence of related species.

Introduction

The Molossidae Gervais, 1856 includes over 110 species assigned to 17 genera (Ammerman et al., 2012) in subfamilies Tomopeatinae Miller, 1900 and Molossinae Gervais, 1856 (Simmons, 2005; Eger, 2007; Vaughan et al., 2011). The narrow Peruvian endemic *Tormopeas ravus* (see Eger, 2007) is the single member of the first subfamily, the remaining diversity is classified in the Molossinae which shows an extended pantropical distribution (Ammerman et al., 2012). Molossid bats are insectivorous and are diagnosed by a free tail extending well beyond the trailing edge of the uropatagium among other characters (Freeman, 1981a; Vaughan et al., 2011). Molossids exhibit an impressive range of body size (e.g., forearm length varies between 27–85 mm or >300% size difference; Nowak, 1994) and significant anatomical variation, including contrasting skull morphologies (e.g. short versus long rostrum, well-developed versus absent sagittal crest, and low versus high coronoid process of the mandible; Freeman, 1979, 1981a). These morphologies are believed to reflect general relationships between skull structure and trophic function (Freeman, 1979, 1981a, 1998; Swartz et al., 2003). The specific hardness of a given food item, and the bite force required to cope with it can play an important role in resource partitioning within vertebrate communities, including bats (see Freeman, 1979, 1981a; Wainwright, 1987; Van Valkenburgh, 1996; Aguirre et al., 2003; Dumont, 2007). According to Freeman (1981a) bats with robust skulls and thick jaws tend to consume hard-shelled insects (e.g., beetles), and bats with gracile skulls and thin jaws select soft-bodied insects (e.g., moths). These morphological differences may indicate resource partitioning at the ecological level or at least some decrease in resource use overlap (Aldridge and Rautenbach, 1987).

An important factor that may help understand the ecological segregation and coexistence of species is evolutionary history, but phylogenetic relationships within the subfamily Molossinae are still unclear (Ammerman et al., 2012). Freeman (1981b), on the basis of external and skull characters, distinguished two groups of molossines: the *Mormopterus* and the *Tadarida* groups. Gregorin (2000) using a cladistic analysis recovered two subfamilies, Tomopeatinae and Molossinae, and two tribes within the latter, Molossini and Tadaridini. More recently, Ammerman et al. (2012) carried out the first molecular phylogenetic analysis of the subfamily Molossinae using DNA sequence and proposed four tribes: Molossini (New World taxa), Tadarini (Old World taxa), Cheiromelini and Mormopterini. Some conflicting and some congruent groups were recovered in the morphological phylogeny of Gregorin and Cirranello (2015). These phylogenetic relations among molossid species may have implications for the segregation of species in morphofunctional space and the way it maps onto the ecological space.

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In this study, we explore the morphofunctional variation of molossid species that occur in Argentina. Here the family is widely distributed and seven genera have been recorded (*Cynomops*, *Eumops*, *Molossops*, *Molossus*, *Nictynomops*, *Promops* and *Tadarida*) which include 18 currently recognized species (Barquez, 2006; Barquez and Díaz, 2009). The greatest diversity of molossid species of the country is found in the northern subtropical regions, but at least two species were recorded in Patagonia (i.e. *Tadarida brasiliensis* and *Eumops patagonicus*, Barquez et al., 1999). This fauna is highly representative of the South American Southern Cone (see Díaz et al., 2011), a vast extratropical region of the Neotropics with a wide variety of environments that harbor a rich mammalian fauna, including molossid bats. For these species, we defined a multivariate morphofunctional space using linear variables of the skull dentition and mandible. We hypothesized that given the wide geographic overlap among species, these would segregate in the functional morphospace in order facilitate their ecological coexistence (hypothesis 1). The molossid species that inhabit Argentina belong in the New World clade Molossini, with one representative taxon of the Old World Tadarini (*T. brasiliensis* from Tadarini: Ammerman et al., 2012). Therefore, we hypothesized that the resulting morphospace structure was determined chiefly by the contrasting biogeographic component of the main and oldest tree partition (i.e., the New vs. Old World tribes, or hypothesis 2), and consequently that phylogeny was a key factor in structuring the functional morphospace (hypothesis 3). We dealt with aspects of limited sample size in rare species, for which few specimens with intact skulls are available in collections worldwide but nonetheless were included here, by means of a sensitivity analysis. Then we related the perceived morphofunctional patterns with the phylogeny of molossid bats and the distribution of their species (sympatry vs. allopatry) in an attempt to identify functional conditions that may allow for their coexistence at the regional scale and predict specific differences in trophic niche space.

Materials and methods

Study region

A complex mosaic of habitat covers the Argentinean territory given the variety of topographic, climatic and vegetation conditions available (Ojeda et al., 2002). According to the scheme of Burkart et al. (1999), 18 eco-regions are represented in Argentina, grouped into 11 of the 14 broad biomes of the World (missing only manglars, taiga and Mediterranean scrubland; see Olson et al., 2001). Molossid bats inhabit the majority of these environments, including subtropical wet forests (e.g., Yungas montane rainforests, Paranaense lowland rainforest), temperate rainforests (Andean Subantartic forests), xeric forests and savannas (e.g., Chaco, Espinal), and both lowland (e.g., Pampas, Monte, Patagonian steppe) and highland (e.g., Puna), grasslands and scrublands (Burkart et al., 1999). This biome classification was the basis of our biogeographic analysis (see below).

Specimens and measurements

We studied the craniodental morphology of 377 specimens from the 18 species of molossid bats of regular presence in Argentina (Fig. 1): *Cynomops abrasus* (n=5), *Cynomops paranus* (n=2), *Cynomops planirostris* (n=6), *Eumops auripendulus* (n=4), *Eumops bonariensis* (n=25), *Eumops dabbenei* (n=1), *Eumops glaucinus* (n=10), *Eumops patagonicus* (n=36), *Eumops perotis* (n=26), *Molossus molossus* (= *Molossus currentium* for some authors including Barquez, 2004; n=51), *Molossus rufus* (= *Molossus ater* for some authors including Díaz et al., 2011; n=23), *Molossops neglectus* (n=1), *Molossops temminckii* (n=33), *Nyctinomops laticaudatus* (n=3), *Nyctinomops macrotis* (n=8), *Promops centralis* (n=7), *Promops nasutus* (n=26) and *Tadarida brasiliensis* (n=110). The specimens are stored in seven Mammal Collections from Argentina: Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN), Ciudad Autónoma de Buenos Aires, Buenos Aires; Colección de Mamíferos Lillo (CML), San Miguel de Tucumán, Tucumán; Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA), Mendoza Capital, Mendoza; Museo La Plata (MLP), La Plata, Buenos Aires; Colección Felix de Azara (CFA), Ciudad Autónoma de Buenos Aires, Buenos Aires; Museo Municipal de Ciencias Naturales Lorenzo Scaglia (MMMP), Mar del Plata, Buenos Aires; Colección Laboratorio de Investigaciones en Evolución y Biodiversidad (LIEB), Facultad de Ciencias Naturales, Universidad Nacional de la Patagonia San Juan Bosco, Esquel, Chubut. The list of specimens and their localities are provided in Appendix 1. This set represented all the specimens from the study area available to us. To this set we added 75 specimens of 13 species with relatively small samples from localities outside the study area, which represented a c. 20% increase in overall sample size; we used these specimens in the sensitivity analysis described below (additional specimens and provenance in Supplementary Material as Appendix S1).

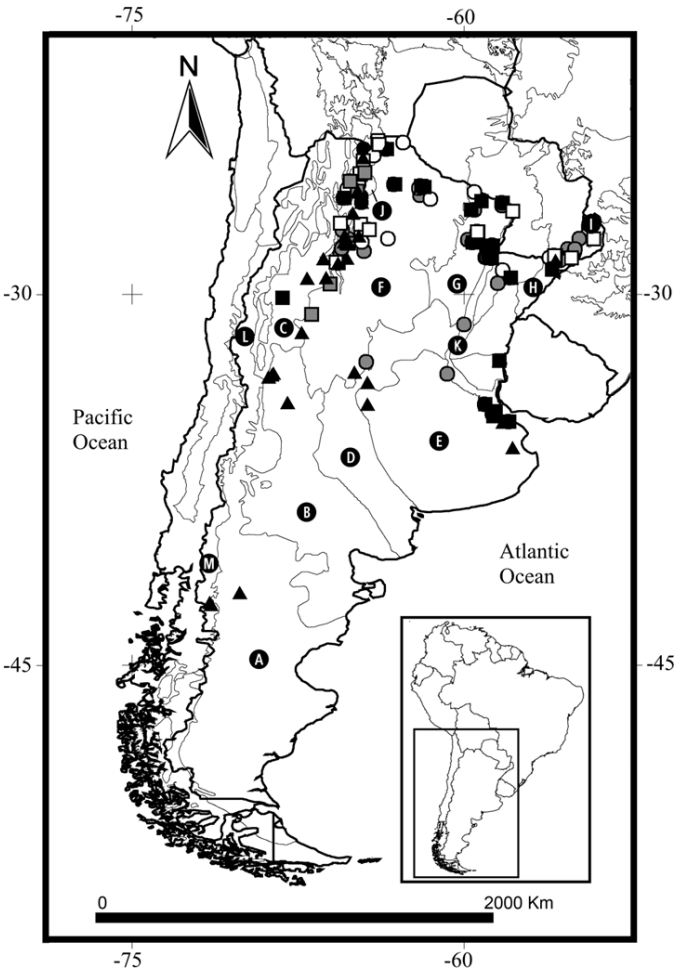

Figure 1 – Localities of the studied specimens of the molossid bats from Argentina. *Cynomops* (●), *Eumops* (●), *Molossops* (○), *Molossus* (■), *Nyctinomops* (■), *Promops* (□), *Tadarida brasiliensis* (▲). A: Patagonian Steppe; B: Low Mont; C: High Mont; D: Espinal; E: Humid Pampas; F: Dry Chaco; G: Humid Chaco; H: Campos y Malezales; I: Paranaense; J: Yungas; K: Delta e Isla del Parana; L: High Andes; M: Patagonian Forest. Scale=2000 km.

Eighteen craniodental measurements (Fig. 2) were taken to the nearest 0.01 mm using a digital caliper. These included: condylobasal length (CBL); zygomatic breadth (ZB); height of braincase (HB); mastoid breadth (MB); maximum external width between left and right upper molars (WUM); length of maxillary toothrow (CM^3); postorbital constriction (PO); length of rostrum (LR); length of palatal (LP); length of upper canine (LUC); width across upper canines (CC); height of mandibular body at lower third premolar (HM); length of lower canine (LLC); length of mandible (LM); length of mandibular toothrow, (CM_3); and three measurements of the coronoid process (HC1, HC2, HC3, see Fig. 2). These variables were modified from Simmons and Voss (1998), Barquez et al. (1999) and Giménez and Giannini (2011). Average minimum and maximum values for these measurements are included in Tab. 1.

Table 1 – Average, minimum and maximum values (in small text respectively) of craniodental meaurements (in mm) and weight (in g, taken from Barquez et al., 1999; Best et al., 2002; McWilliams et al., 2002; Avila-Flores et al., 2002; Eger, 2007) for molossids species from the South American Southern Cone.

Species	Mass	CBL	ZB	HB	BM	WUM	CM^3	PO	LR	LP	CC	LUC	LM	HM	LLC	CM_3	HC1	HC2	HC3
E. auripendulus	30.57	22.99	15.09	9.17	12.8	10.49	9.91	4.93	6.51	9.89	6.44	4.37	18.31	2.78	4.37	10.89	5.22	5.30	5.39
	26–37.8	22.11–24.36	14.9–15.98	8.71–9.84	12.15–13.59	9.89–11.11	9.38–10.54	4.63–5.34	6.01–7.04	9.01–10.87	5.81–5.96	3.52–5.04	17.52–19.41	2.36–3.44	3.84–5.04	10.9–11.6	4.61–5.76	4.79–5.83	4.91–6.11
E. patagonicus	12.1	16.56	10.9	6.55	10.35	7.81	6.82	4.28	4.50	6.78	4.29	2.43	12.44	1.98	2.23	7.37	3.53	3.30	3.56
	7–16	15.85–17.69	10.42–11.41	6.21–7.15	9.92–10.92	7.39–8.19	6.21–7.29	3.97–4.57	3.83–4.97	5.91–7.77	3.93–4.69	1.58–2.81	11.41–13.28	1.59–2.54	1.38–2.61	6.66–7.78	3.02–3.92	3.01–3.74	3.11–3.94
E. glaucinus	26	23.36	14.99	8.93	13.31	10.34	9.82	5.21	6.22	9.49	6.16	4.15	18.11	2.71	4.14	10.86	5.21	4.88	5.35
	24–28	22.91–24.73	13.72–15.74	8.23–9.41	12.61–14.24	9.45–11.39	9.42–10.23	4.91–5.41	5.89–6.78	8.39–10.41	5.66–6.58	3.35–4.69	17.38–19.14	2.21–3.18	3.64–4.68	10.41–11.32	4.93–5.58	4.48–5.25	5.01–5.82
E. bonariensis	17.5	17.86	11.51	6.88	10.89	8.24	7.34	4.33	4.84	7.22	4.81	2.60	13.48	2.05	2.49	7.93	3.84	3.63	3.92
	16–20	16.01–18.83	10.58–12.21	5.64–7.54	10.21–11.39	7.26–8.84	6.66–7.79	3.92–4.69	4.32–5.32	6.63–7.95	4.09–5.23	1.28–3.19	11.97–14.62	1.59–2.55	1.68–2.94	7.16–8.39	3.35–4.21	3.23–3.99	3.39–4.33
E. dabbenei	100	28.82	19.54	10.76	16.56	13.45	12.13	6.25	7.88	11.95	8.23	4.72	23.47	3.47	5.09	14.07	7.23	7.45	7.36
E. perotis	68.1	30.69	18.75	9.78	15.40	13.07	13.03	5.56	8.36	12.89	8.54	5.37	23.62	3.37	5.42	14.09	7.14	6.00	7.28
	60–76	29.75–31.71	18.12–19.61	8.24–10.69	14.76–16.28	12.2–13.72	12.4–13.53	5.24–6.03	7.82–8.78	11.76–13.97	8.11–9.11	4.14–6.34	22.63–25.07	2.65–4.08	4.64–6.33	12.24–14.82	6.63–7.78	5.43–6.61	6.88–7.83
C. abrasus	31.7	19.41	14.24	7.18	12.04	9.57	7.74	5.18	5.57	8.02	5.70	3.28	15.23	2.48	2.76	8.68	4.64	4.83	4.71
	24.4–37.8	18.64–20.64	13.71–14.94	6.47–7.72	11.76–12.69	9.27–10.03	7.44–8.61	4.95–5.48	5.27–5.99	7.51–8.45	5.25–6.29	3.01–3.67	14.41–16.05	2.09–2.69	2.53–3.65	8.35–9.19	4.39–4.94	4.36–5.11	4.36–4.95
C. paranus	11.5	15.50	11.0	5.89	9.52	7.57	6.40	4.45	4.52	6.91	4.61	2.72	12.25	2.08	2.31	7.0	3.60	3.59	3.63
	10.5–12.5	14.91–16.82	10.19–11.84	5.34–6.39	9.11–10.12	6.78–8.17	5.19–7.29	4.25–4.93	4.08–5.06	6.39–7.49	4.08–5.12	2.08–3.55	11.55–13.37	1.73–2.81	1.59–3.05	6.45–7.84	3.21–4.02	3.11–4.08	3.23–4.22
C. planirostris	-	15.36	10.55	5.62	9.44	7.35	6.23	4.30	4.58	6.83	4.48	2.59	12.0	2.13	2.29	6.90	3.55	3.53	3.57
	-	14.43–16.76	9.69–11.34	4.72–6.02	9.15–9.98	6.87–7.94	5.88–6.75	4.15–4.62	4.25–5.08	6.41–7.54	4.14–4.84	1.99–3.25	11.41–12.89	1.86–2.54	1.39–2.88	6.59–7.47	3.19–3.98	3.26–4.01	3.34–3.96
M. neglectus	11	14.22	10.66	6.01	8.81	7.14	6.04	4.81	4.24	6.79	4.21	1.94	10.93	1.69	1.77	6.35	3.11	3.62	3.19
	10.5–11.5																		
M. temminckii	6.2	13.42	9.14	5.16	8.35	6.64	5.46	4.01	4.1	6.23	3.91	2.17	10.18	1.81	1.93	5.96	3.11	3.12	3.13
	5–8	12.82–14.13	8.18–9.79	4.64–5.70	7.62–9.06	6.23–7.32	5.15–5.96	3.54–4.29	3.51–4.71	5.58–6.79	3.48–4.26	1.33–2.73	9.61–10.83	1.41–2.22	1.06–2.38	5.57–6.67	2.81–3.48	2.85–3.38	2.75–3.49
M. rufus	30.7	19.82	13.91	8.47	13.07	10.09	8.17	4.56	5.35	7.35	5.94	3.70	15.58	2.74	3.39	9.22	4.71	5.03	4.65
	21–43	18.73–20.91	13.25–14.74	7.61–9.41	11.99–14.49	9.49–10.69	7.66–8.71	4.31–4.78	4.87–5.76	6.36–8.53	5.39–6.63	2.94–4.24	14.45–16.61	1.97–3.46	2.83–3.97	8.77–9.68	4.34–5.18	4.53–5.46	4.24–5.08
M. molossus	14.7	15.70	10.97	6.91	10.58	7.97	6.31	3.93	4.1	5.77	4.47	2.56	11.91	2.07	2.35	7.03	3.53	3.67	3.53
	12–18	14.47–17.01	10.03–12.23	5.99–8.06	9.71–11.57	7.19–8.89	5.84–6.84	3.38–4.41	3.53–4.62	5.08–6.32	3.93–5.15	1.55–3.27	11.01–13.01	1.63–2.55	1.22–2.92	6.57–7.77	3.07–3.99	3.11–4.37	3.08–4.12
P. nasutus	15.7	16.47	11.03	7.41	10.63	8.12	6.59	4.2	4.36	6.45	4.31	2.87	12.05	2.09	2.71	7.37	3.33	3.50	3.33
	13–22	15.61–17.77	10.51–11.91	7.03–8.12	10.21–11.56	7.62–8.95	5.97–7.31	3.94–4.54	3.95–4.78	5.66–7.01	3.99–4.81	2.06–3.38	11.34–13.25	1.71–2.47	2.08–3.24	6.97–8.15	2.99–3.72	3.19–3.91	3.01–3.82
P. centralis	24.2	18.70	12.50	8.10	11.75	9.10	7.53	4.29	5.12	7.70	5.05	3.23	14.01	2.24	3.10	8.57	3.99	4.30	3.94
	23.5–25	18.25–19.77	11.73–13.21	7.65–9.01	11.41–12.27	8.69–9.65	7.15–8.01	3.99–4.57	4.84–5.46	7.35–8.06	4.81–5.36	2.32–3.62	13.17–14.76	1.94–2.83	2.68–3.43	8.29–9.02	3.72–4.28	3.62–4.71	3.64–4.21
N. laticaudates	11.33	16.69	10.18	6.38	9.95	7.36	6.77	3.78	4.49	7.73	3.96	2.29	12.56	2.00	2.24	7.26	3.42	3.04	3.44
		15.79–17.78	9.62–10.71	5.85–6.75	9.26–10.63	6.19–7.87	6.31–7.16	3.31–4.58	4.26–4.98	6.76–8.62	3.68–4.36	1.82–2.66	12.02–13.41	1.71–2.23	1.65–2.67	6.87–7.64	3.17–3.66	2.97–3.14	3.24–3.74
N. macrotis	20	21.78	12.13	7.44	11.35	8.48	8.80	4.12	5.66	9.38	4.75	2.82	16.08	2.20	2.79	9.42	4.58	3.19	4.57
		21.11–22.69	11.59–12.56	7.15–7.77	10.63–11.72	8.07–8.74	8.31–9.09	3.91–4.26	5.09–6.01	8.38–10.01	4.38–5.21	2.57–3.16	15.21–16.76	2.03–2.46	2.39–3.09	9.05–9.79	4.19–4.91	3.01–3.42	4.18–4.95
T. brasiliensis	11.6	16.02	9.94	5.92	9.39	7.13	6.23	4.21	4.55	6.88	4.28	2.13	11.66	1.72	1.91	6.74	3.18	3.32	3.12
	8.2–19	15.01–17.69	8.84–10.96	5.52–7.02	8.56–10.03	6.67–7.44	5.78–7.21	3.91–4.53	4.14–5.29	6.13–8.09	3.76–4.78	1.36–2.92	11.09–12.39	1.21–2.27	1.19–2.52	6.11–7.27	2.83–3.44	2.77–3.67	2.75–3.71

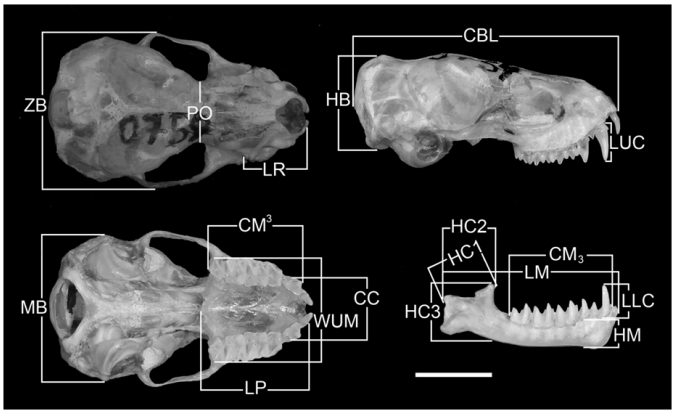

Figure 2 – Skull variables measured in molossid bats from Argentina, show on a *Tadarida brasiliensis* specimen (LIEB-M 0759). See text for abbreviations. Scale 5 mm.

Data analysis

We performed a Principal Components Analysis (PCA) for all 377 specimens based on a covariance matrix of untransformed measurements; we aimed at determining the patterns of morphofunctional variation among the 18 molossid species studied, as perceived in the multivariate data structure of the 18 × 377 morphometric matrix. On the PCA ordination diagram (plot of axes 1 and 2) we traced minimum polygons joining conspecifics. Additionally, we performed a size-corrected PCA; we used the ratio between each variable value and the geometric mean of the individual to transform the original variables (e.g., Meachen-Samuels and Van Valkenburgh, 2009; Morales and Giannini, 2010, 2013, 2014). We applied Multivariate Analysis of Variance (MANOVA) for all 377 specimens to evaluate morphometric differences across species. All analyses were executed using the program InfoStat v.2011 (Di Rienzo et al., 2010).

To assess the effect biogeographic on morphological pattern we performed a redundancy analysis (RDA; Rao, 1964; ter Braak, 1995). RDA is the canonical form of PCA (Rao, 1964; ter Braak, 1995), an ordination technique with a linear constraint represented by the exploratory variables of an external matrix (ter Braak, 1995). The main matrix was our morphological matrix with 377 measured specimens by the 18 craniodental variables. The external matrix was composed by variables that contained the binary assignment of the 377 specimens to each of 18 eco-regions of Argentina (*sensu* Olson et al., 2001). In this analysis we first tested each eco-region individually with 4999 Monte Carlo unrestricted permutations (alpha level set at 0.01), and then we included the significant eco-regions in a model using a forward stepwise selection procedure (see ter Braak and Šmilauer, 1998).

We used a comparative phylogenetic method, Canonical Phylogenetic Ordination (CPO; Giannini, 2003), to assess the importance of phylogenetic relationships on the morphofunctional variation of the molossid species. CPO is a form of canonical ordination that was designed to detect the most important associations between data and phylogenetic tree partitions. The method is a multivariate linear model that uses two basic matrices Y and X, main and external, respectively (see below). CPO was carried out as a variance-covariance Redundancy Analysis (RDA) using CANOCO 4.5 (ter Braak and Šmilauer, 1998), with the main matrix represented by the craniodental data (the 18 × 377 morphometric matrix), and the external matrix represented by phylogenetic information of the relationship among taxa (Giannini, 2003; Morales and Giannini, 2010). The external matrix was built as a exhaustive set of binary variables coding clade membership of each specimen and species (see Giannini, 2003). Therefore the method is ideally suited for testing our second (alternative) hypothesis given that the relative importance of each tree partition (one of which was Tadaridini vs. Molossini) can be evaluated directly. For building the external matrix we used trees from Jones et al. (2002), Peters et al. (2002), Gregorin (2009), Ammerman et al. (2012), and Gregorin and Cirranello (2015), pruned to included only the 18 species from Argentina. This matrix contained clade variables 1–17 (Fig. 3). To this tree and matrix we added three species that were not included in phylogenetic studies (*M. neglectus*, *N. laticaudatus* and *P. nasutus*, see Fig. 3). We placed the missing species as sister to their congeners, i.e., *M. neglectus* was placed as sister to *M. temminckii*, *N. laticaudatus* as sister to *N. macrotis*, and *P. nasutus* as sister to *P. centralis*. CPO tests tree partitions; i.e., it uses an unrooted network to define opposing sets of terminals whose values (e.g., morphological measurements) are compared; these partitions coincide with clades when the network is rooted (as here using *Tadarida*), except for the root itself (not given in the data), which is not tested (Giannini, 2003). The significance of each tree partition was tested individually using 4999 unrestricted Monte Carlo permutations. A forward stepwise selection of clades from the external matrix was then performed in order to obtain a reduced tree matrix that best explained the phylogenetic association with morphofunctional total variation without redundance (see Giannini, 2003). This analysis was replicated for the size-corrected data set, as was the RDA analysis (see above).

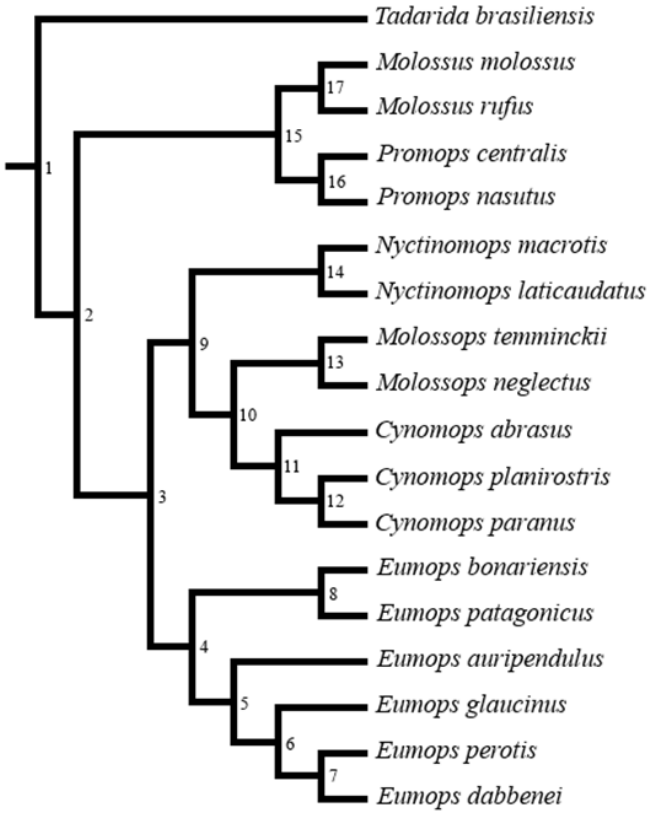

Figure 3 – Cladogram of molossid bats from Argentina based on Jones et al. (2002), Peters et al. (2002), Gregorin (2009), Ammerman et al. (2012) and Gregorin and Cirranello (2015). Tree partitions are indicated with numbers and correspond to clades when rooted in *Tadarida brasiliensis* as here, used in canonical phylogenetic ordination (CPO). As guide to interpretation, tree partition #1 is trivial and includes all descendants, tree partition #2 separates *T. brasiliensis* from all other bats, #3 separates *Tadarida, Molossus* and *Promops* from all other bats, and so forth. See Materials and Methods.

Some of the molossid species included in our sample had critically small sample size because these are relatively rare species poorly represented in collections with intact skulls. We implemented a sensitivity analysis in order to evaluate the effect of small samples in the patterns we recovered for the molossid assemblage from the South American Southern Cone. Four additional analyses were done, as follows. First, we included more specimens for 13 species with the smallest samples, from localities outside the study area and applied the same analyses as above (Tab. 2). Because the dataset with more specimens introduced additional variation from a broad geographic coverage, this analysis represented a strong test on the observed patterns of our study area. Second, because two species (*Molossops neglectus* and *Eumops dabbenei*) still were represented by a single specimen each, we removed these two specimens and species from the data and performed the same

analyses as above (Tab. 2). For the third and fourth analysis, we used these same criteria including specimens of other localities from South America (third analysis); and, removing *M. neglectus* and *E. dabbenei* (four analysis), but with the size-corrected data. Then we compared the results with respectively more and less specimens/species with our main analysis, and evaluated the strength of the patterns so obtained in the light of these additional analyses. The Tables and Figures of these results were included in Supplementary Material.

Results

Main analysis

Both Principal Component Analysis (data set corrected and not corrected for body size) showed a similar pattern in the molossid species morphofunctional distribution. The PCA using dataset not corrected for body size showed that the first two principal components (PC) explained 98.1% of total variation (PC1 95.9% and PC2 2.2% respectively; Tab. 3). All variables were positively correlated with PC1, and variously so with PC2. The variable best correlated with PC1 was condylobasal length (CBL; Tab. 3). PC2 showed the highest positive correlation with length of palate (LP) and the highest negative correlation with mastoid breath (MB) and height of braincase (HB; Tab. 3). The correlation of variables (Fig. 4A-B) structured the morphospace such that bats placed on the negative end of PC1 and PC2 have small and robust skulls and mandibles; bats on the positive end of PC1 and negative end PC2 have large and robust skulls and mandibles; bats on the negative end of PC1 and positive end PC2 have small and gracile skulls and mandibles; bats on the positive end of PC1 and PC2 have large and gracile skulls and mandibles. However, not all of these possibilities are realized in the observed craniodental space of Argentinean molossid species (e.g., there were no very small species with robust skulls). An axis-wise interpretation follows.

An increasing segregation based on size appeared along the PC1 with five recognizable groups (Fig. 4A): very small (*M. temminckii*); small (*M. neglectus*, *T. brasiliensis*, *E. bonariensis*, *E. patagonicus*, *C. planirostris*, *C. paranus*, *N. laticaudatus*, *M. molossus* and *P. nasutus*); mid-sized (*N. macrotis*, *C. abrasus*, *M. rufus* and *P. centralis*); large (*E. auripendulus* and *E. glaucinus*); and very large (*E. perotis* and *E. dabbenei*). These groups mapped actual size only approximately, suggesting additional variation of importance (see below). The group of small bats showed the greatest degree of interspecific overlap.

PC2 separated three groups (Fig. 4A-B): group I composed only by specimens of *N. macrotis*, placed on the positive side of PC2, having elongate (longer LP-LR), narrow (lesser MB, ZB, WUM) and low skulls (lesser HB), low mandible (lesser HM), and little developed coronoid process (HC3); group II made of six species (*M. molossus*, *M. rufus*, *P. nasutus*, *P. centralis*, *C. abrasus* and *E. dabbenei*) placed on the negative side of PC2 which exhibit a short, wide and high, stout skull, estimated to generate the greatest bite force with a thick mandible (HM higher) and well developed coronoid process (HC3 higher); and group III with the remainder 11 species placed in an intermediate position along PC2: *M. neglectus*, *M. temminckii*, *T. brasiliensis*, *N. laticaudatus*, *C. planirostris*, *C. paranus*, *E. bonariensis*, *E. patagonicus*, *E. auripendulus*, *E. glaucinus* and *E. perotis*. The latter species have skulls and mandibles of shape intermediate between the previous groups.

Still, a more accurate interpretation emerged from the joint analysis of PC1 and PC2. The following groupings were recognized. The very small species (members of *Molossops*) occupied the negative extreme of PC1, centered on PC2. Next a heterogeneous group composed of *Tadarida*, the two mid-sized *Eumops* (*E. patagonicus* and *E. bonariensis*), *Cynomops planirostris* and *C. paranus*, and *Nyctinomops laticaudatus* shared the space near the centroid with varying degrees of overlap. These two groups exhibited skulls of intermediate structure and were of very small to small size. *Nyctinomops macrotis* separated as a mid-sized bat with the most gracile skull. On the opposite side of the morphospace appeared the robust-skulled, mid-sized bats members of *Molossus* and *Promops*, to which *Cynomops abrasus* joined as the largest member of its genus. The next two groups, clearly segregated along PC1, represent the other two size classes within *Eumops*, i.e., large *E. auripendulus* and *E. glaucinus*, and further away along PC1 the very large *E. perotis* and *E. dabbenei*. Some of these groupings were highly significant associated to clades (see below). Additionally, interesting pairings of functionally similar species of different genera were evident, including small or large *Molossus* versus *Promops*, and *Tadarida* versus *Nyctinomops* and mid-sized *Eumops*.

The first two principal components (PC) of the analysis using the size-corrected dataset explained 95.3% of variation (PC1 92.5% and

Table 2 – Number of adult specimens with intact skulls used in each of three multivariate analyses. Main analysis includes all specimens available to us from the 18 species of molossid bats that occur in the Southern Cone (extra-tropical Neotropics). Specimen details in Appendix 1. The first sensitivity analysis includes all the former specimens plus 75 additional specimens from other regions of the Neotropics of species represented in the previous sample by <10 specimens. Specimen details in Appendix S1. The second sensitivity analysis includes all the specimens in the first sensitivity analysis minus the species *Eumops dabbenei* and *Molossops neglectus*, each represented by a single specimen.

		Sensitivity analysis	
Species	**Main analysis**	**More specimens**	**Less specimens**
Tadarida brasiliensis	110	110	110
Nyctinomops macrotis	8	4	4
Nyctinomops laticaudatus	3	14	14
Promops nasutus	26	5	5
Promops centralis	7	6	6
Molossus rufus	23	23	23
Molossus molossus	51	51	51
Molossops neglectus	1	1	-
Molossops temminckii	33	4	4
Cynomops planirostris	6	6	6
Cynomops paranus	2	7	7
Cynomops abrasus	5	5	5
Eumops perotis	26	3	3
Eumops patagonicus	36	4	4
Eumops glaucinus	10	6	6
Eumops dabbenei	1	1	-
Eumops bonariensis	25	5	5
Eumops auripendulus	4	6	6

Table 3 – Results of Principal Components Analysis (PCA), for molossid bats from Argentina (dataset not corrected and corrected size). Loading of each variable on the first two axes extracted and corresponding eigenvalues, and percentage of total variation per axis. See text for abbreviation.

	Dataset not corrected size		**Dataset corrected size**	
	PC1	**PC2**	**PC1**	**PC2**
% explained	**95.9**	**2.2**	**92.5**	**2.8**
Variables				
CBL	0.54	0.32	0.22	0.23
ZB	0.32	∓0.30	0.21	∓0.02
HB	0.15	∓0.40	0.16	∓0.22
MB	0.23	∓0.45	0.16	∓0.12
WUM	0.21	∓0.26	0.19	∓0.07
CM^3	0.24	0.11	0.25	0.21
PO	0.05	0.03	0.09	0.10
LR	0.14	0.17	0.21	0.31
LP	0.22	0.50	0.22	0.48
CC	0.15	∓0.05	0.23	0.08
LUC	0.11	∓0.13	0.32	∓0.42
LM	0.43	0.10	0.24	0.17
HM	0.06	∓0.11	0.21	∓0.32
LLC	0.12	∓0.10	0.38	∓0.35
CM_3	0.26	0.01	0.25	0.13
HC1	0.14	∓0.02	0.27	0.11
HC2	0.10	∓0.18	0.20	∓0.15
HC3	0.14	∓0.02	0.28	0.12

Table 4 – Results of Canonical Phylogenetic Ordination (CPO) for molossid bats from Argentina (dataset corrected and not corrected size). Clades are numbered as in Fig. 1. Values significant at the p=0.01.

	Dataset not corrected size				Data corrected size			
Analysis	**Variables**	**Variance**	***F*-value**	***p*-value**	**Variables**	**Variance**	***F*-value**	***p*-value**
Individual	5	0.735	1053.070	0.0002	7	0.808	1574.508	0.0002
	6	0.705	906.485	0.0002	5	0.649	692.378	0.0002
	7	0.681	809.741	0.0002	6	0.649	690.396	0.0002
	4	0.296	159.793	0.0002	4	0.208	98.312	0.0002
	3	0.121	52.397	0.0002	3	0.101	41.921	0.0002
	2	0.115	49.356	0.0002	2	0.037	14.560	0.0006
	13	0.087	36.040	0.0002	15	0.025	9.611	0.001
	10	0.066	26.858	0.0002	8	0.017	6.648	0.0062
	9	0.041	16.355	0.0002	9	0.017	6.449	0.008
	15	0.017	6.767	0.0068	10	0.014	5.250	0.0102
	17	0.013	4.907	0.0266	17	0.014	5.495	0.0128
	14	0.008	2.940	0.0668	13	0.010	3.819	0.0256
	8	0.005	1.945	0.1516	16	0.008	3.141	0.0520
	16	0.004	1.646	0.1958	11	0.003	1.163	0.2622
	12	0.003	1.173	0.2674	12	0.002	0.705	0.4528
	11	0.001	0.346	0.5824	14	0.002	0.887	0.3560
Forward stepwise	5	0.735	1053.070	0.0002	7	0.808	1574.508	0.0002
selection	7	0.056	102.437	0.0002	5	0.055	149.481	0.0002
	13	0.042	95.566	0.0002	6	0.011	31.360	0.0002
	2	0.046	142.502	0.0002	17	0.004	11.569	0.0002
	14	0.011	37.791	0.0002				
	3	0.005	18.020	0.0002				
	4	0.002	6.146	0.0094				
	12	0.007	28.446	0.0002				
	16	0.002	6.416	0.0038				

PC2 2.8% respectively; Tab. 3). All variables were positively correlated with PC1, but not with PC2. The variable best correlated with PC1 were length of lower and upper canine (LLC and LUC), and two measurements of the coronoid process (HC2 and HC1; Tab. 3). These variables can be related with the diet of species (see below). Variables best correlated with PC2 were length of palatal (LP) and length of rostrum (LR), positively; and length of low and upper canine (LLC and LUC), and height of mandibular body (HM), negatively. The general segregation pattern among molossid species was similar to previous analysis, although overlap among several species was greater (see Fig. 5A-B). Comparing this result with that of the previous PCA, we conclude that the size is an important factor in morphofunctional species segregation. The size-corrected analysis also accentuated differences between several overlapping species in the first PCA, mainly due to differences in the length of the canines and the width of coronoid process (e.g., *E. glaucinus* vs. *E. auripendulus*; *C. abrasus* vs. *P. centralis*).

Additionally, MANOVA showed significant differences between the 18 molossid species using all variables for $p \leqslant 0.001$ (F=27.63). This result confirmed the differences seen in the PCA.

The RDA model retained only two eco-regions, Southern Andean Yungas and Low Monte (*sensu* Olson et al., 2001) that jointly explained (with $p \leqslant 0.001$) part (7.7%; Tab. S2) of morphological variation. A similar result was obtained using the size-corrected dataset, although in this case, only the Southern Andean Yungas eco-region was important and explained 5.6% of total morphogical variation (Tab. S3).

CPO results indicated that most tree partitions were individually significant in explaining some of the morphological variation observed, with $p \leqslant 0.01$ (exceptions were clades 17, 14, 8, 16, 12 and 11 of tree in Fig. 3; see Tab. 4). Nine partitions were included in the reduced external matrix (clades 5, 7, 13, 2, 14, 3, 4, 12, and 16 of tree in Fig. 3; with values significant at α=0.01). In this analyses the five most important tree partitions, explaining together the largest fraction (as much as 89%) of total morphological variation, were: partition of clade 5 separating the four large *Eumops* from all other bats (*E. auripendulus*, *E. dabbenei*, *E. glaucinus*, and *E. perotis*); clade 7 separating the two largest *Eumops* (*E. dabbenei* and *E. perotis*); clade 13 separating *Molossops*; clade 2 separating *T. brasiliensis* specimens from the remainder of species; and clade 14 separating *Nyctinomops* (see Fig. 3 and Tab. 4). The total variation explained by the full model including 4 additional significant clade variables was 90.6%, that is just 1.6% above the model with the five clade variables considered above (Tab. S4). The second CPO performed with data set corrected for size body showed similar results, the most important tree partitions were clade 7, 5 and 6 (Tab. 4), and the total variation explained by the model including these clade variables was 87.7% (see Tab. S4).

Sensitivity analyses

The first additional analysis with more specimens of rare species from localities outside the South American Southern Cone recovered essentially the same pattern of species in multivariate morphofunctional space (cf. Fig. 4 with Fig. S5). The amount of variation explained by PC axes 1 and 2 was virtually the same (indicated in Fig. 4 and Fig. S5). RDA showed similar result, Southern Andean Yungas, Low Monte and Humid Pampa being the eco-regions selected in the model and together explained 7.7% of total morphological variation (Tab. S6). The phylogenetic influence on the data was strong and mostly due to the same tree partitions. The first five clades selected (those that explained c. 1% or more each) were the same, with clade 5 (which includes the largest species of *Eumops*, *E. auripendulus*, *E. dabbenei*, *E. glaucinus*, and *E. perotis*) explaining the great majority (some 69%) of morphofunctional variation, only slightly less than in the main analysis (c. 73%; see Tab. S7).

The second additional analysis consisted in use the same dataset as the first additional analysis without two specimens, those representing *Molossops neglectus* and *Eumops dabbenei* in the sample. As in the previous analysis, the pattern of species in morphofunctional space was identical (cf. Fig. S8 with Fig. 4 and Fig. S5), as was the amount of variation explained by PC axes 1 and 2 (indicated in Fig. 4 and Fig. S8). RDA indicated results similar to the previous analysis, with the model

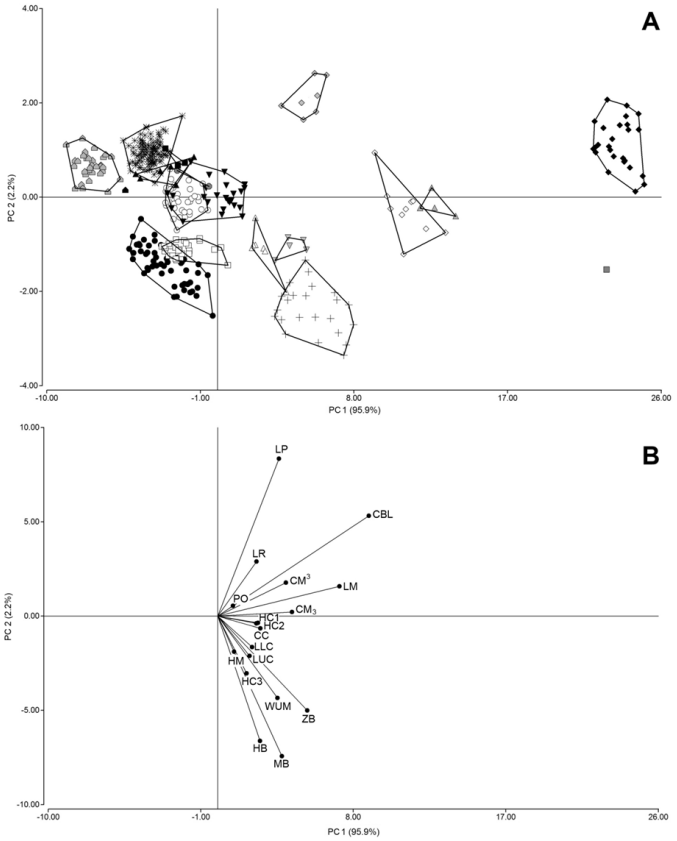

Figure 4 – Ordination diagram of the principal components analysis. A) segregation of the specimens of molossid species from Argentina using dataset not corrected size; polygons include specimens from each species. *C. abrasus* (▼), *C. paranus* (●), *C. planirostris* (▲), *E. auripendulus* (▲), *E. bonariensis* (▼), *E. dabbenei* (■), *E. glaucinus* (○), *E. patagonicus* (○), *E. perotis* (◆), *M. neglectus* (⌂ black), *M. temminckii* (⌂ gray), *M. molossus* (●), *M. rufus* (+), *N. laticaudatus* (■), *N. macrotis* (♦), *P. centralis* (△), *P. nasutus* (□), *T. brasiliensis* (×). B) Vectors shown the strengh of correlation of each variable to the plane of PCl and PC2. See text for abbreviations.

including three most important eco-regions (Southern Andean Yungas, Low Monte and Humid Pampa) that together explained 7.8% of total variation (Tab. S9). And again, the influence of phylogeny was strong and the clade explaining most variation (c. 68%) was that of the large *Eumops* (clade 5), even when *E. dabbenei* (member of this clade) was removed from the analysis (Tab. S10). The other clades that explained a minor fraction of variation (between 1–3%) were similar except for clade 6 recovered among the first five groups (instead of clade 2, which appeared in the 8th order; Tab. S10).

The third and fourth analyses showed similar patterns of species segregation in morphofunctional space (cf. Fig. 5 with Fig. S11 and Fig. S12), as were similar the contribution of PC axes 1 and 2 (see Fig. 5, Fig. S11 and Fig. S12). The eco-regions influence was similar to previous analysis, with the Southern Andean Yungas (for third and four analysis) and Dry Chaco (only for four analysis) selected as most important explaining 7% and 7.5% of total morphological variation respectively (see Tab. S13 and Tab. S14). Likewise, the phylogeny also was an important factor in both analysis (explained c. 88% and 62% respectively), the most important clades were 7, 5 and 6 (see Tab. S15 and Tab. S16). In conclusion, our four additional analyses, which constituted effective tests of the results seen in our main analyses, demonstrated that neither the species patterns in morphospace nor the magnitude of historical effects were affected by the small sample of some species in the study region.

Discussion

The distribution of molossid specimens in the morphospace expanded by our set of craniodental variables showed a clear segregation of species that inhabit Argentina. This result, validated by our sensitivity analysis, supports our first hypothesis by which a pattern of species segregation in functional morphospace was expected, and allows discarding the New vs. Old World tribal partition as the expected, major organizer of morphospace structure. The pattern recovered is still strongly phylogenetic, which led us to accept our hypothesis 3, but with a different structure that has wide ecological implications (see below) but no specific global biogeographic component (rejection of hypothesis 2). The biome-level biogeographic effect was also of limited importance. Molossids span a wide size range with at least five groups fairly well differentiated along the PC1; and the variation along PC2 showed that the study species graded along three major types of morphologies (see below). The combined differences in size and morphotypes likely were related with prey selection, given the nature of the variables involved, as discussed in the following.

Typically, mammalian predators of small size are limited with respect to the range of prey they can capture, whereas larger predators are able to use both small and large prey (e.g., Morales and Giannini, 2010). Body size also is a key factor in prey selection in bats (Aldridge and Rautenbach, 1987; Barclay and Brigham, 1991; Swartz et al., 2003), and in this study the analyzed species present an important size range (i.e., forearm length range: 31–78.5 mm; weight: 6.2–76 g; Barquez et al., 1999; and see Tab. 1). Therefore the expectation of prey use by these molossid species would be the same as for other mammals, i.e., small bats restricted to small prey, larger bats using a wide range of prey sizes, from small to large. However, interpretation of size variation seen in these molossids requires careful consideration of additional factors, particularly the mutual effects of echolocation and flight on scaling, and vice versa. Molossid bats are insectivorous predators, and just as with all other aerial hawking bats, they rely on echolocation to detect and capture prey (Schnitzler and Kalko, 1998). Echolocation is a sophisticated key adaptation that is nevertheless a short-range sensory system highly restricted by physical factors (Schnitzler and Kalko, 1998). Flight speed and pulse duration scale positively with body size,

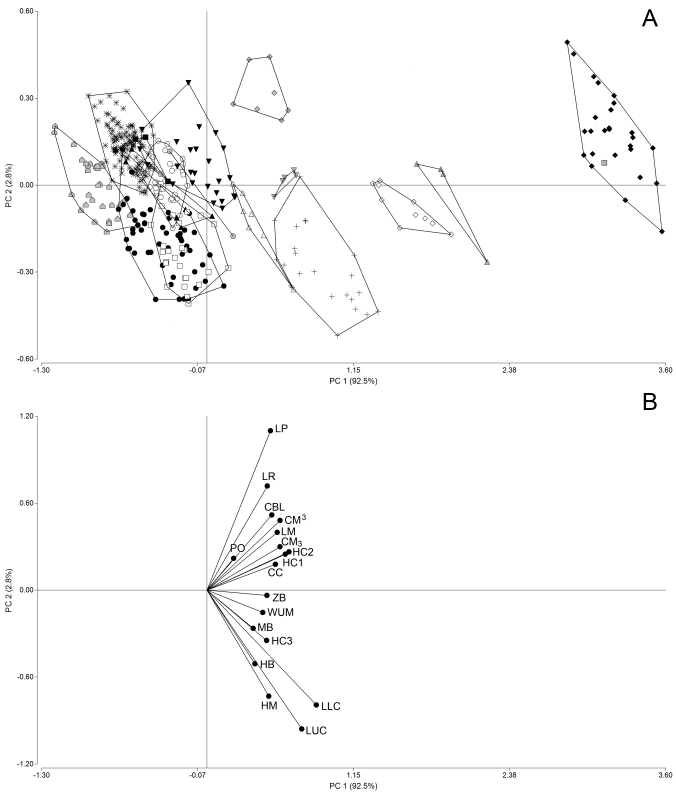

Figure 5 – Ordination diagram of the principal components analysis. A) segregation of the specimens of molossid species from Argentina using dataset corrected size; polygons include specimens from each species. *C. abrasus* (▼), *C. paranus* (●), *C. planirostris* (▲), *E. auripendulus* (▲), *E. bonariensis* (▼), *E. dabbenei* (■), *E. glaucinus* (○), *E. patagonicus* (○), *E. perotis* (♦), *M. neglectus* (⌂ black), *M. temminckii* (⌂ gray), *M. molossus* (●), *M. rufus* (+), *N. laticaudatus* (■), *N. macrotis* (◆), *P. centralis* (△), *P. nasutus* (□), *T. brasiliensis* (×). B) Vectors shown the strengh of correlation of each variable to the plane of PCl and PC2. See text for abbreviations.

whereas frequency parameters (peak frequency, pulse repetition rate, wing beat frequency) scale inversely with body size (Jones, 1999), as expected in the case of all biological frequencies (Calder, 1996). These constraints translate into large bats flying fast while emitting low frequency calls at low repetition rates, a combination that is unsuited for detection and capture of small airborne prey (Jones, 1999). That is, small prey pass undetected for large bats, and this has a direct consequence in the interpretation of body size pattern seen in the molossids of our study. Specifically, bats such as large *Eumops* species may not exhibit the expected wide dietary range from small to large prey; therefore, on the basis of Jones (1999) scaling data, and contrary to other mammalian predators, large bats would be restricted to detectable large prey (instead of having access to a wide range of prey). The consequence is that, perceived size groups in morphospace may not overlap much in actual prey use. We predict that the size structure in morphospace may map well onto trophic space, and this may be general for assemblages of aerial hawking bats with size range wide enough to express differences due to echolocation constraints.

In addition, larger body size may scale a greater bite force (Aguirre et al., 2002), so within dietary categories, an increase in size may facilitate dietary divergence (Aldridge and Rautenbach, 1987). This may be accentuated by differences in morphology. The molossid species that inhabit the Southern Cone exhibit three morphotypes as expressed along PC axis 2 (and also in the size-corrected PCA), including species with robust skulls and mandibles, species with gracile skulls and mandibles (i.e. *Nyctinomops macrotis*), and intermediate species (see above). Species in the first group often are associated with a durophagous diet (i.e., composed mainly of hard shelled prey such as beetles; Freeman, 1979, 1981a,b, 2000; Swartz et al., 2003). These species (in *Molossus*, *Promops* and larger *Cynomops*) have short, tall and wide faces often with a vaulted palate (more so in *Promops*; pers. obs.) that bring the dentition backward and closer to the temporomandibular joint, thus allowing an increase in force of the masseter and anterior temporal muscles (Freeman, 1979; Swartz et al., 2003; Santana et al., 2010). Correspondingly, these skulls have greater development of cranial crests and higher coronoid processes (Freeman, 1979, 1981a; Nogueira et al., 2009), providing greater origin areas for masticatory muscles (Freeman, 1979, 1981a). Morphologically, the species of *Cynomops*, *Molossus* and *Promops* are similar but are differentiated by their size and degree of development of sagittal and lambdoidal crests (Freeman, 1981b). Dietary data are still lacking for *Cynomops* and *Promops*, but studies on *Molossus molossus* and *M. rufus* indicated a diet composed mainly of beetles, that is a durophagous diet in correspondence with their morphology (Pine, 1969; Howell and Burch, 1974; Freeman, 1981a,b; Bowles et al., 1990; Fenton et al., 1998; Ramírez-Chaves et al., 2008).

Species with very gracile skull and mandibles for their size, here represented by *Nyctinomops macrotis*, are associated with eating soft-bodied insect (Freeman, 1979, 1981a,b, 2000; Swartz et al., 2003). These species have low skulls with long and narrow faces (Freeman, 1981a,b). The mandible is thin with poorly developed coronoid process. Diverse studies indicated that *N. macrotis* eats soft-bodied insects, principally moths (Ross, 1967; Easterla and Whitaker, 1972; Freeman, 1981a,b; Milner et al., 1990).

The species with intermediate although rather heterogeneous morphology were clearly differentiated along a size gradient. Likely these species have access to a greater spectrum of prey, capturing diverse types of insects, depending on their own echolocation range. The degree of overlap among these molossids in craniodental morphospace was low and occurred among small to medium sized species of intermediate morphology. It was remarkable that several pairs of closely related species, in all likelihood very similar functionally, segregated in contiguous regions of morphospace (e.g., *Molossus molossus* vs. *M. rufus*, *Promops centralis* vs. *P. nasutus*). Regarding the group of intermediate species with some degree of overlap, they showed limited geographic co-occurrence; e.g., species pairs such as *Tadarida brasiliensis* and *Nyctinomops laticaudatus* only coexist in the Northern Yungas forest in the study region, with the former widely distributed in many different habitats, and the latter specialized in rain forests.

Another pattern of great interest was the fact that not all space available was realized. Regions of morphospace lacked occupant species, and so the associated morphofunctional niche was vacant; for instance, there were no very small and durophagous species (corner of negative axes 1 and 2 vacant). We believe that the unoccupied space is as important as the realized space in that the former may reflect functional constraints to the evolution of morphology and function in those directions.

The local, eco-regional influence in structuring the morphological pattern among molossid species was limited, with Southern Andean Yungas being the principal eco-regions explaining some of the morphological variation with one or two additional eco-regions depending of the analysis, together explaining up to only 7.8% of total variation. The Southern Andean Yungas is home to a great diversity of bats in general, and is one of the richest environments of Argentina (Barquez et al., 1999; Barquez, 2006). It is clear that biome variation is less important than other factors and this may be due to the fact that molossid bats fly and capture prey in open environments and above the canopy in forested habitats (see Kunz and Pierson, 1994), so the actual habitat structure does not so directly influence their habitat use.

Our phylogenetic comparative analysis indicated that morphological variation in morphospace was highly correlated with evolutionary history, but in a way different to that predicted by our second hypothesis. That is, support for a great impact of phylogeny on the morphofunctional pattern did not originate in the main tree partition, Tadaridini vs. Molossini, as we expected. Instead, the clade that separated the four largest species of *Eumops* (*E. auripendulus*, *E. glaucinus*, *E. dabbenei* and *E. perotis*) from all other molossid species explained the greatest proportion of variation (as much as 73.5% of total variation). *Eumops* originated ca. 24 mya, whereas the divergence of the larger species was ca. 19 mya (Ammerman et al., 2012). This cladogenetic event represented the emergence of a new size spectrum in the group that was reflected in the great expansion of craniodental morphospace along the size axis. Similar results has been reported for other groups of mammals such as primates (Marroig and Cheverud, 2005; Meloro et al., 2015) and carnivores (Meloro and Raia, 2010; Morales and Giannini, 2013, 2014). The effect size was the chief determinant of the perceived morphospace structure, an event deeply rooted in time that opened the exploitation of large insect prey to the Neotropical molossid lineage. A further split in this evolutionary lineage, separating the largest *Eumops* (*E. dabbenei* and *E. perotis*) was the next important clade, among other clades that also explained <10% of the morphological variation. This event only deepened the size expansion originated in the previous important node. A third important clade was *Molossops* with *M. neglectus* and *M. temminckii* as member species. Cleary different from its sister *Cynomops* (see Peters et al., 2002), *Molossops* is endemic to South America (Eger, 2007) and includes the smaller bats in our sample. The divergence between these genera was estimated at ca. 20 mya (Ammerman et al., 2012), with clear morphological (Williams and Genoways, 1980; Peters et al., 2002), and chromosomal differences (Gardner, 1977). Lastly, the tree partition that included all specimens of *Tadarida brasiliensis* was also significant but with a small influence in explaining the observed variation. *Tadarida* is polyphyletic and the divergence of the *brasiliensis* lineage is estimated at ca. 18 mya (Ammerman et al., 2012). We predicted that this tree partition would be the most relevant one on the basis of its deep biogeographic divergence with the remainder of taxa included in this study. Now this hypothesis can be safely rejected with our data and replaced by one stating that much of the morphofunctional evolution that structured the craniodental space of Southern Cone molossids took place in the Neotropics, had a strong functional basis that determined expansion of the morphospace in the direction of increasing size, and retained a strong phylogenetic signal that likely is as old as the early Miocene.

In conclusion, our analyses showed a clear segregation in morphospace among the majority of molossid species that inhabit Argentina and the vast region of the Southern Cone. This perceived

segregation in morphospace was the product of differences principally in size and also relevant differences in craniodental morphology that likely translates into the predatory function of these aerial hawking bats. Given the echolocation constraints affecting prey detection and capture, we predict that these differences will map with fidelity onto the trophic space of these species. In addition, we showed that the observed morphofunctional pattern was determined principally by the evolutionary history of the family in the Neotropic, with major events of expansion of occupied space beginning some 20 mya with the emergence of the larger species (*Eumops*) and well as the smallest species (such as *Molossops* and *Cynomops*). We propose that the joint effects of history, size and functional morphology drove the evolution of Neotropical molossids along functional size and shape axes and allowed the coexistence among species as they appeared in the early Miocene.

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Appendix 1

Molossid specimens examined from Argentina

***Cynomops abrasus* (5)** Argentina: Misiones Province, Zaimán (CFA-MA-06201, ♀); Misiones Province, Villa Miguel Lanús (CML 5325, ♀); Misiones Province, Tacuaruzú (MACN 16612, ♀); Misiones Province, Posadas (MACN 18063, ♀); Misiones Province, Bompland Arroyo Mártires (MACN 18065, ♀).

***Cynomops paranus* (2)** Argentina: Corrientes Province, Laguna Paiva Barrio Las Lomas (CML 4568, ♂); Corrientes Province, Barrio Las Lomas (MACN 2239, ♀).

***Cynomops planirostris* (6)** Argentina: Jujuy Province, Río Las Capillas 15 km N of Las Capillas (CML 4177, ♀); Salta Province, Tartagal, Quebrada de Acambuco, Dique Itiyuro (CML 1207); Salta Province, 48.9 km NW of cross roads n° 50 and 18 road to Islas de Caña (CML 5146, ♀); Salta Province, Río El Naranjo 14 km of road n° 5 (access to the Parque Nacional El Rey) (CML 5991, ♂); Salta Province, Arroyo La Sala, Administración Parque Nacional El Rey (CML 6054, ♂); Salta Province, Serranía de Las Pavas (MACN 16613, ♂).

***Eumops auripendulus* (4)** Argentina: Chaco Province, Barranqueras, Resistencia (MLP 8.VII.44.6, ♂); Misiones Province, Hipólito Irigoyen (MACN 18072, ♂; MACN 18073, ♀); Santiago del Estero Province, Nueva Esperanza (MACN 21074).

***Eumops bonariensis* (25)** Argentina: Buenos Aires Province, Delta Canal 6 (CFA-MA-04780, ♂); Buenos Aires Province, La Plata (CML 4841, ♂; CML 4842, ♂; CML 4843, ♂; MLP 7.VIII.35.9; MLP 7.VIII.35.13, ♂; 7.VIII.35.14, ♂); Bella Vista (MACN 50.5, ♂); Corrientes Province, Rincón de Luna (MACN 14.036, ♀); Barrio Cadenas Departamento Capital (MACN 22.422, ♂); Misiones Province, Cainguás 10 km W of Aristóbulo del Valle (CML 3267, ♀); Misiones Province, Posadas (MACN 18.076, ♀; MACN 18.079, ♂); Santa Fé Province Puerto San Martín, Rosario San Lorenzo (CFA-MA-07777); Tucumán Province, El Cadillal 28 km of the capital city, Aguas Chiquitas (CML 2073, ♀; CML 2074, ♀; CML 2075, ♀); Tucumán Province, Reserva Provincial Aguas Chiquitas, Arroyo Aguas Chiquitas (CML 5284, ♀; CML 5285, ♂; CML 5286, ♂; CML 5287, ♂; CML 5288, ♂); Tucumán Province, Piedra Buena (MACN 16.610, ♂; MACN 16.754, ♀; MACN 16.761, ♀).

***Eumops dabbenei* (1)** Argentina: Santa Fé Province, San Javier (CFA-MA-04954, ♀).

***Eumops glaucinus* (10)** Argentina: Jujuy Province, Yuto (CML 492); Jujuy Province, Río Las Capillas 15 km N of Las Capillas by road n° 20, 957 m (CML 4318, ♂; CML 4319, ♀); Jujuy Province, Río Lavayén ca. 1 km N of Santa Rita (CML 4175, ♀); La Rioja Province (MACN 28.200, ♂); Misiones Province, Caraguatay (MACN 18078, ♂); Salta Province, 5 km E of Tonono on Río Itiyuro (CML 5306, ♀; CML 5307, ♂); Tucumán Province, San Miguel de Tucumán (CML 6171, ♂; CML 5437).

***Eumops patagonicus* (36)** Argentina: Chaco Province, General Vedia, Río de Oro (CML 2856, ♀); Chaco Province, Barranqueras (CML 2860, ♀); Chaco Province, Pozo del Gato sobre Río Bermejito 8 km E of Campo Grande (CML 5373, ♂); Chaco Province, Parque Nacional Chaco (MACN 20.858, ♂); Chaco Province, Department Capital, School Nº 599 (CML 5461, ♀; CML 5463, ♂); Formosa Province (MACN 20.898, ♀); Formosa Province, Parque Nacional Pilcomayo, Santa Librada (MACN 20.911, ♀); Formosa Province, Parque Nacional Mburucuyá (MACN 20.915, ♀); Formosa Province, El Colorado (CFA-MA-03167, ♂; CFA-MA-04154, ♂; CFA-MA-05152, ♂; CFA-MA-05153, ♂); Formosa Province, Laguna Blanca, Pilcomayo (CFA-MA-05208, ♀); Formosa Province, Comandante Fontana (CML 1818, ♂); Formosa Province, Pirané, El Colorado (CML 1819, ♀); Formosa Province, Bermejo 35 km S, 5 km E Ingeniero Guillermo N Juarez Puesto Divisadero (CML 3858, ♂); Formosa Province, Reserva Natural Formosa, Río Teuco (MACN 20.930, ♂; MACN 20.937, ♂; MACN 20.941); Jujuy Province, San Pedro Río Lavayén ca. 1km N of Santa Rita (CML 7057, ♂); Misiones Province, Villa Miguel Lanús, INTA (CFA-MA-02827, ♀; CFA-MA-04755); Misiones Province, Cainguás (ICM 4494, ♂); Salta Province, 1 km E of Tonono on Río Itiyuro (CML 5290, ♂; CML 5293, ♀; CML 5294, ♀; CML 5295, ♀; CML 5296, ♀; CML 5298, ♀; CML 5299, ♂); Salta Province, Santa Rosa (CML 5378, ♂; CML 5382, ♀; CML 5403, ♀); Tucumán Province, San Miguel de Tucumán (CML 6170, ♂; CML 6172, ♀).

***Eumops perotis* (26)** Argentina: Córdoba Province, Embalse Río Tercero, Grietas Murallón (CFA-MA-07693); Córdoba Province, Embalse Río Tercero, 2° Usina (CFA-MA-08084); Formosa Province, El Colorado (CFA-MA-05145, ♀; CFA-MA-05146, ♀; CFA-MA-05147, ♀); Salta Province, Capital (MACN 16.590, ♂); Santiago del Estero Province, Pozo Hondo (MACN 16601, ♀; MACN 16602, ♀); Santiago del Estero Province, Nueva Esperanza (MACN 21071; MACN 21073); Tucumán Province, Caspichango (CFA-MA-03100, ♂; CFA-MA-03101, ♂; CFA-MA-03129, ♀; CFA-MA-03130, ♀; CFA-MA-03134, ♀; CFA-MA-03145, ♀); Tucumán Province, Famaillá Caspichango (CFA-MA-03321, ♀); Tucumán Province, San Miguel de Tucumán (CML 707, ♂; CML 716, ♂; CML 7246); Tucumán Province, San Pedro de Colalao (CML 1476); Tucumán Province, Las Talitas, Tafí Viejo (CML 2227, ♀); Tucumán Province, Dique San Ignacio (CML 2876, ♀); Tucumán Province, Departamento Capital (CML 3012, ♀); Tucumán Province, Concepción (MACN 29.743,♀; MACN 29.744, ♀).

***Nyctinomops laticaudatus* (3)** Argentina: Formosa Province, Bañados Palmas (CML 1913); Jujuy Province, Río Lavayén ca.1 km N of Santa Rita (CML 7074, ♂; CML 7075, ♀).

***Nyctinomops macrotis* (8)** Argentina: Catamarca Province, Capayán, 1.5 km N of Concepción, Balneario Municipal Gancho del Bino (CML 7688, ♂; CML 7689, ♀); Jujuy Province, Laja Morada 15 km N of Finca Las Capillas by provincial road nº 20 (CML 7737, ♀); Jujuy Province, Yuto (MACN 13217); La Rioja Province, Patquía (MMPMa 1027); Tucumán Province, San Miguel de Tucumán (CML 1082, ♀; CML 1083, ♂; CML 1084, ♂).

***Molossops neglectus* (1)** Argentina: Misiones Province, Parque Nacional Iguazú (CML 2258, ♀).

***Molossops temminckii* (33)** Argentina: Buenos Aires Province, La Plata (CML 4846, ♀); Chaco Province: Río Teuco 10 km W of Tartagal (CML 5395, ♀); Chaco Province, Misión Nueva Pompeya (CML 5457, ♂; CML 5462, ♀); Corrientes Province, Ituzaingó, Ea. San Borgita (CFA-MA-02829, ♀; CFA-MA-02830, ♀); Corrientes (MACN 16614); Corrientes Province, Parque Nacional Mburucuyá, El Quebrachal (MACN 20923, ♂; MACN 20924, ♀; MACN 20925, ♀); Formosa Province, El Colorado (CFA-MA-03173, ♀; CFA-MA-05123, ♂; CFA-MA-05127, ♂); Formosa Province, Santa Catalina (CML 2054, ♀; CML 2055, ♀; CML 2057, ♂); Formosa Province, Parque Nacional Pilcomayo Estero Abadie (CML 4678); Formosa Province, Parque Nacional Pilcomayo, Santa Librada (MACN 20909, ♂); Jujuy Province, Río Lavayén on road nº 6 to N of Santa Clara (CML 5331, ♂); Jujuy Province, 3km N of Oyeros, road between road 61 and 43 (CML 7062, ♀); Jujuy Province, Río Lavayén ca. 1km N of Santa Rita (CML 7063, ♂; CML 7064, ♀; CML 7065, ♀; CML 7066, ♂); Misiones Province, Candelaria, Tacuarusú (MACN 18066, ♀); Misiones Province, Reserva Nacional Formosa, ex-población Tolaba on Río Teuco (MACN 20948, ♂); Misiones Province, Departamento Candelaria, Campo San Juan (MACN 22431, ♂); Salta Province, Santa Victoria Este (CFA-MA-00652, ♀); Salta Province, Agua Linda (MACN 36582); Tucumán Province, Departamento Burruyacú, Puesto Cortadora (MACN 16615, ♂); Santiago del Estero Province, San Antonio (MACN 16616, ♀; MACN 16617, ♂); San del Estero Province, San Félix (MACN 16619, ♂).

***Molossus molossus* (51)** Argentina: Buenos Aires Province, Delta, Canal 6 INTA (CFA-MA-02929, ♂; CFA-MA-02932, ♀; CFA-MA-04771, ♀; CFA-MA-08117); Buenos Aires province, Castelar INTA (CFA-MA-02992, ♂); Buenos Aires Province, Villa Udaondo (CFA-MA-05231, ♂); Buenos Aires Province, Partido of San Fernando, Canal Arana and Arroyo Méndez Chico (MLP 8.10.02.3, ♂; MLP 8.IV.02.4; MLP 8.IV.02.6, ♀; MLP 8.IV.02.7, ♀; MLP 8.IV.02.8; MLP 8.IV.02.9, ♀); Buenos Aires Province, La Plata (MLP 25.IV.01.26; MLP 26.XII.02.18); Chaco Province, Río de Oro, General Veida (CFA-MA-00611, ♂); Entre Ríos Province, Department Colón, Arroyo Petucho Verna (MLP 25.IV.01.27); Formosa Province (CFA-MA-03256, ♀; CFA-MA-03257, ♂; CFA-MA-03258, ♀); Formosa Province, El Colorado (CFA-MA-03214, ♀; CFA-MA-03225, ♀; CFA-MA-04151, ♀; CFA-MA-05140, ♀; CFA-MA-05141, ♀; CFA-MA-05166, ♀; CFA-MA-05168, ♂; CFA-MA-04137, ♀; CML 1816; CML 1817, ♀; MACN 16664); Formosa Province, Department Patiño, Ea. Santa Catalina 5 km of Cogoi (CML 2048, ♂); Formosa Province, Bermejo 35 km S, 5 km E of Ingeniero Guillermo N Juarez puesto divisadero (CML 3870, ♀); Formosa Province, Reserva Natural Formosa (MACN 20929, ♀); La Rioja Province (MACN 34.431, ♀); Salta Province, 12.6 km W of Piquirienda Viejo (CML 7297, ♀; CML 5111, ♀); Salta Province, Capital (MACN 16654, ♀; MACN 16.652, ♀); Salta Province, 1 km E of Tonono on Río Itiyuro (CML 5310, ♀); Salta Province, Santa Rosa (CML 5335, ♂; CML 5339, ♂; CML 5354, ♀; CML 5356, ♀); Santiago del Estero Province, (MACN 16737, ♀); Santiago del Estero Province, Nueva Esperanza (MACN 16.633, ♀). Tucumán Province, San Miguel de Tucumán (CML 6114, ♂; CML 6173, ♂; CML 6079, ♂); Tucumán Province, Yerba Buena (CML 6180, ♀); Dique San Ignacio (ICM 3482, ♂; ICM 3483, ♀).

***Molossus rufus* (23)** Argentina: Chaco Province, Puente Libertad, General San Martín (CFA-MA-04185, ♂); Chaco Province, along Hwy 90, 15 km NW of Ea. San Miguel (CML 3270, ♂; CML 4491, ♂); Chaco Province, Parque Nacional Chaco (MACN 20857, ♂); Corrientes Province, Capital, School Nº 599 (CML 4066, ♂; CML 5423, ♀; CML 5466, ♀); Corrientes Province, Las Marías (CML 3007, ♂); Corrientes Province, Department Capital, Barrio Las Lomas (MACN 22397, ♀); Corrientes Province, Department Concepción, Ea. Pira (MLP 1.X.01.17); Formosa Province, Bartolomé de las Casas (CML 1815, ♀); Formosa Province, road nº 11, 13 km S of Clorinda (CML 2049, ♀); Formosa Province, Parque Nacional Pilcomayo Lata-Cue (CML 4681, ♂; CML 4682, ♂); Formosa Province, El Colorado (MACN 16662, ♂); Formosa Province, Reserva Natural Formosa (MACN 20934, ♀); Jujuy Province, cross between Río de Zora and road nº 34 (CML 5330, ♀); Misiones Province (MACN 18093, ♀; MACN 18085, ♂); Misiones Province, Ea. Santa Inés (CFA-MA-05428, ♀; CFA-MA-05433, ♀; CFA-MA-05434, ♀); Misiones Province, Posadas (MACN 18086, ♀).

***Promops nasutus* (26)** Argentina: Jujuy Province, Parque Nacional Calilegua, Arroyo Sauzalito (CML 2940, ♂); Misiones Province, Posadas (MACN 49.21, ♂); Misiones Province, San Pedro, Boca Pepirí Miní (MACN 18080, ♀); Misiones Province, Oberá Arroyo Barrero (MACN 18081, ♀; MACN 18082, ♀; MACN 18084, ♂); Salta Province, 3 km N of Las Mercedes Finca Santa Cruz (CML 2346, ♀; CML 6064, ♀); Salta Province, Quebrada de Acambuco 5 km W of Dique Itiyuro (CML 2866, ♀); Salta Province, Department Orán road to Isla de Cañas (CML 5094, ♂); Salta Province, 6 km W of Piquirienda Viejo (CML 5370, ♂); Salta Province, San Antonio (MACN 167.12, ♀; MACN 167.13, ♀; MACN 167.15, ♀); Santiago del Estero Province, (MACN 16701, ♀); Santiago del Estero Province, Nueva Esperanza (MACN 166.92, ♂; MACN 166.93, ♀; MACN 166.95, ♀; MACN 166.98, ♀; MACN 167.03, ♂; MACN 16680, ♂; MACN 166.85, ♀; MACN 166.86, ♂); Tucumán Province, Department Alberdi, Hostería Escaba (CML 6158, ♀; CML 6159, ♀; CML 6160, ♀).

***Promops centralis* (7)** Argentina: Formosa Province, by road nº 11, 13 km S of Clorinda (CML 2050, ♂); Formosa Province, El Colorado (MACN 167.04, ♀; MACN 167.05, ♀; MACN 167.08, ♀; MACN 167.07, ♀; MACN 16719, ♀; MACN 16720, ♀).

***Tadarida brasiliensis* (I10)** Argentina: Buenos Aires Province, (MACN 164, ♀); Buenos Aires Province, Capital Federal (MACN 34.617, ♀; MACN 41.397, ♂); Buenos Aires Province, Partido Castelli, Ea. San Pedro (MLP 5.V.99.12; MLP 3.XII.02.9; MLP 3.XII.02.10; MLP 3.XII.02.11; MLP 3.XII.02.12; MLP 3.XII.02.13; MLP 3.XII.02.30; MLP 3.XII.02.27; MLP 3.XII.02.28; MLP 3.XII.02.29); Buenos Aires Province, La Plata (MLP 28.IX.98.1); Buenos Aires Province, Sierra Paititi (MMPMa 4051, ♂); Catamarca Province, Pomán 95 km S of Andalgalá near of balneario (CML 3278, ♀); Catamarca Province, Pomán 95 km S of Andalgalá (ICM 4064, ♀; ICM 4065, ♀); Catamarca Province, Dique El Potrero 13 km N of Andalgalá (CML 5417); Chubut Province, Trevelin, Capilla Galesa (LIEB-M 758, ♂; LIEB-M 759, ♂); Chubut Province, Ea. Las Vacas Pampas (LIEB-M 865, ♂); Chubut Province, Villa Futalaufquen, Parque Nacional Los Alerces (LIEB-M 866); Chubut Province, Aldea Escolar, School Nº 740 (LIEB-M 881, ♂); Chubut Province, Piedra Parada (MLP 31.XII.042.84); Córdoba Province, (CFA-MA-08086, CFA-MA-08087); Córdoba Province, Río Cuarto (MLP 31.XII.02.47, ♀; MLP 31.XII.02.48, ♂; MLP 31.XII.02.49, ♀; MLP 31.XII.02.50, ♀; MLP 31.XII.02.51, ♀; MLP 31.XII.02.52, ♀; MLP 31.XII.02.53, ♀; MLP 31.XII.02.54, ♂; MLP 31.XII.02.56, ♀); Córdoba Province, Banda Norte, Río Cuarto (CFA-MA-07760; CFA-MA-07761; CFA-MA-07762; CFA-MA-07763; CFA-MA-07764; CFA-MA-07765; CFA-MA-07766; CFA-MA-07767; CFA-MA-07768); Entre Ríos Province, Villa Elisa (MLP 11.VIII.99.53); Jujuy Province, Río Lavayén ca. 1 km N of Santa Rita (CML 7077, ♀); Mendoza Province, Lavalle (MACN 39.980); Mendoza Province, Mendoza City (ICM 303, ♂; ICM 304, ♂; ICM 305, ♀; ICM 306; ICM 307, ♂; ICM 309, ♀; ICM 310, ♂; ICM 311, ♂; ICM 312, ♀; ICM 319, ♂; ICM 313, ♂; ICM 320, ♂; ICM 322, ♀; ICM 323, ♀); Mendoza Province, La Pega (ICM 684, ♂; ICM 686, ♂); Mendoza Province, Reserva de la Biosfera Ñacuñan (ICM 2096, ♂; ICM 2270, ♂; ICM 2272, ♂; ICM 2273, ♂; ICM 2276, ♂; ICM 2278, ♀; ICM 2281, ♀; ICM 2282, ♂; ICM 2283, ♂; ICM 2286, ♂; ICM 2287, ♀; ICM 2288, ♀; ICM 2289, ♂; ICM 2290, ♂; ICM 2586, ♀; ICM 2587, ♂; ICM 2589, ♀; ICM 2590, ♀); Mendoza Province, Cerro La Gloria (ICM 3832, ♀); Misiones Province (MACN 259); Misiones Province, Capital, Parada Leis (MACN 18069, ♂; MACN 18071, ♂); La Rioja Province, 4 km SE of San Blas (CML 5446, ♂; CML 5447, ♂); San Luis Province, Rincón de Papagayos (ICM 4509, ♂); San Juan Province, Valle Fértil, Las Tumanas (ICM 4496, ♂); Salta Province, Río de Las Conchas, 2 km N and 6 km W of Metán (CML 5144, ♀; CML 5152, ♀; CML 5153, ♂); Salta Province, 48.9 km NW of cross between road nº 50 and 18, road to Islas de Caña (CML 5148, ♀); Salta Province,1 km E of Tonono on Río Itiyuro (CML 5309, ♀); Salta Province, Río El Naranjo 14 km by road nº 5, access to Parque Nacional El Rey, (CML 5993, ♂); Tucumán Province, (MACN 16741, ♀; MACN 16.745, ♂; MACN 16746, ♂); Tucumán Province, Ea. San Pedro Vipos (CML 697, ♂); Tucumán Province, Cerro San Javier (CML 1694, ♂); Tucumán Province, La Cocha, Dique San Ignacio (CML 5263, ♂; CML 5270, ♀; CML 5272, ♀); Tucumán Province, Horco Molle, Residence UNT Parque Biológico (CML 5266, ♀; CML 5267, ♀); Tucumán Province, Department Capital (CML 6720, ♂); Tucumán Province, Monteagudo (MMPMa 125; MMPMa 130; MMPMa 262).

Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Appendix S1 Additional molossid specimens from South America.

Table S2 Results of Redundancy Analysis for molossid bats from Argentina.

Table S3 Results of Redundancy Analysis for molossid bats from Argentina, dataset corrected size.

Table S4 Results of Canonical Phylogenetic Ordination (CPO) for molossid bats from Argentina (dataset corrected and not corrected size), total variation explained by the final model.

Figure S5 Ordination diagram of the Principal Component Analysis (PCA). I

Table S6 Results of Redundancy Analysis for molossid bats including additional specimens from South America.

Table S7 Results of Canonical Phylogenetic Ordination (CPO) for molossid bats including additional specimens from South America.

Figure S8 Ordination diagram of the Principal Component Analysis (PCA). II

Table S9 Results of Redundancy Analysis for molossid bats including additional specimens from South America, and excluding species with only one specimen (*E. dabbenei* and *M. neglectus*).

Table S10 Results of Canonical Phylogenetic Ordination (CPO) for molossid bats including additional specimens from South America, and excluding species with only one specimen (*E. dabbenei* and *M. neglectus*).

Figure S11 Ordination diagram of the Principal Component Analysis (PCA). III

Figure S12 Ordination diagram of the Principal Component Analysis (PCA). VI

Table S13 Results of Redundancy Analysis for molossid bats including additional specimens from South America, dataset corrected size.

Table S14 Results of Redundancy Analysis for molossid bats including additional specimens from South America, and excluding species with only one specimen (*E. dabbenei* and *M. neglectus*), dataset corrected size.

Table S15 Results of Canonical Phylogenetic Ordination (CPO) for molossid bats including additional specimens from South America, dataset corrected size.

Table S16 Results of Canonical Phylogenetic Ordination (CPO) for molossid bats including additional specimens from South America, and excluding species with only one specimen (*E. dabbenei* and *M. neglectus*), dataset corrected size.