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Ecomorphological diversity in the Patagonian assemblage of bats from Argentina

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Patagonian bats are represented by only insectivorous species, five vespertilionids and one molossid species. They constitute an interesting assemblage of temperate species that remains poorly studied. Here we uncover ecomorphological patterns of Patagonian bats using craniodental morphology, aerodynamic measurements, and external bodily characters. Multivariate analysis was applied to characterize morphometric variation of each dataset separately and in combination. We explored the segregation of species in morphospace, and the importance of phylogeny in the assemblage organization. We used a phylogenetic comparative method to evaluate historical effects on the morphofunctional structure. Our results indicated that the species of the Patagonian assemblage segregate in dimensions of morphospace by size and morphology, which would be related to prey selection (trophic differences) and habitat use (different styles of flight). We also demonstrated the impact of different cladogenetic events of the evolutionary history of species on the structuring of the Patagonian assemblage, with the successive addition of non-overlapping, well-defined morphofunctional types imported from other South American regions, and whit speciation events that resulted in species-level endemisms (*Myotis chiloensis*, *Histiotus magellanicus*, and *Lasiurus varius*).

Key words: ecomorphology, Vespertilionidae, Molossidae, Patagonia, morphospace

INTRODUCTION

The vast region of Patagonia in the Southern Cone of South America is characterized by severe climatic conditions with extreme annual rainfall regimes, low temperatures and strong winds (León *et al.*, 1998; Paruelo *et al.*, 1998; Mancini *et al.*, 2005). These climatic conditions might impact on the low bat diversity recorded in the area by generating seasonal fluctuations in the insects abundance throughout the year (Glanz, 1982; McNab, 1982; Racey and Speakman, 1987; Grinevitch *et al.*, 1995; Speakman and Thomas, 2003; Boyles *et al.*, 2008) that might not allow the maintenance of a great species number. Patagonian bats are represented by a few insectivorous species in the Vespertilionidae and Molossidae, which are the only bats that have successfully colonized Patagonia (Kunz, 1988). Nonetheless, Patagonia is interesting for the study of bats particularly due to the endemic status of some of its species, and the fact that the non-endemic species reach their

austral distributional limits in the region. In northwestern Central Patagonia (Argentina), only seven bat species have been recorded: *Histiotus macrotus*, *H. magellanicus*, *H. montanus*, *Myotis aelleni*, *M. chiloensis*, and *Lasiurus varius* in the family Vespertilionidae, and *Tadarida brasiliensis* in Molossidae (Barquez *et al.*, 1993, 1999; Barquez, 2006; Giménez, 2010; Giménez *et al.*, 2012). Four of these species are endemic to Patagonian environments: *L. varius*, *H. magellanicus*, *M. aelleni* and *M. chiloensis* (Barquez, 2006). Contrarily, *H. macrotus*, *H. montanus* and *T. brasiliensis* are widely distributed beyond the region (Barquez *et al.*, 1999; Giménez, 2010; Giménez *et al.*, 2012, 2015).

The Patagonian bat assemblage has been poorly studied, and little is known of the ecological interaction patterns among these species. In this study, we analyzed the Patagonian bat assemblage using an ecomorphological approach. Ecomorphology is the study of the relationship between the functional design of organisms and the environment (Wainwright,

1991, 1994; Swartz *et al.*, 2003), and investigates how these relationships influence the organism's ability to exploit environmental resources (Swartz *et al.*, 2003). It is assumed that the concurrent effects of ecological requirements and evolutionary histories have determined the size and shape of living organisms (Wainwright, 1994). A variety of studies on bat assemblages have applied the ecomorphological approach, and have satisfactorily demonstrated the relationships between ecology and functional morphology in these animals (Freeman, 1979; Findley and Black, 1983; Norberg and Rayner, 1987; Fenton and Bogdanowicz, 2002; Swartz *et al.*, 2003). Examples prominently include insectivorous bats, which in sympatry have shown differences in foraging behaviour (Aldridge and Rautenbach, 1987; Barclay and Brigham, 1991; Fullard *et al.*, 1991) and habitat use (Herd and Fenton, 1983; Saunders and Barclay, 1992), or both (Kunz, 1973). Bats may also differ in types and/or sizes of insects consumed, as predicted by ecomorphological theory (e.g., Freeman, 1981; Barclay and Brigham, 1991). Such differences promote coexistence of species and hence maintenance and evolution of diversity, which has been attributed to some crucial ecomorphological features or behavioral differences (Norberg and Rayner, 1987; Jones and Rydell, 1994).

The evolutionary history is an important factor that can determinate the structure of a contemporary assemblage (Simmons, 2000). This becomes apparent when we consider that aspects of an organism's performance, such as functional morphology, ecology, and behavior, may have been shaped by adaptive evolution since the origin of a given lineage, and preserved by common ancestry in descendant species. Therefore to understand the modern patterns of diversity and the biology of living organisms requires an evolutionary perspective that can only be gained by reference to phylogeny (Simmons, 2000). Recent studies have shown the importance of evolutionary history in the structure of insectivorous bat assemblages (Giménez and Giannini, 2016a, 2016b).

The aims of this study were: 1) explore the ecomorphological patterns of the Patagonian bat assemblage using complementary morphofunctional datasets (external, aerofoil and craniodental morphology); 2) examine whether any pattern of segregation between species is manifested in morphospace structure; and 3) assess the effect of phylogeny on morphological traits and, ultimately, in structure of morphospace.

MATERIALS AND METHODS

Study Area

Patagonia is localized to south of the Río Colorado from 39° to 55°S latitudes (León *et al.*, 1998). This vast region has a temperate cold climate (Leon *et al.*, 1998; Paruelo *et al.*, 1998) with a mean annual temperature decreasing from east to west (8–10°C to 5–6°C — Mancini *et al.*, 2005) and rainfall decreasing from west to east (2,000 mm to 125 mm — León *et al.*, 1998; Mancini *et al.*, 2005), which influences one of the strongest precipitation gradients in southern South America (Mancini *et al.*, 2005). Strong eastward winds are also one of the climatic features that characterize the region (León *et al.*, 1998; Paruelo *et al.*, 1998). The Patagonian Region contains the biomes Temperate Forest, and Steppe (Olson *et al.*, 2001), with the corresponding ecoregions Patagonian Forest and Steppe, respectively (León *et al.*, 1998; Burkart *et al.*, 1999). A narrow ecotonal (i.e., transitional) zone separates both ecoregions (Schlichter and Laclau, 1998). In this study, the locality records are concentrated in the northwestern part of Patagonia in Argentina (Fig. 1), including Neuquén, Río Negro and Chubut provinces.

Study Specimens

In this study we excluded *M. aelleni* from the analysis given that its identity has been repeatedly questioned and it has been considered a synonym of *M. chiloensis* (Pearson and Pearson, 1989; Barquez *et al.*, 1999). In the analysis we include six bat species that inhabit northwestern Patagonia in Argentina: *Histiotus macrotus* (Poeppig, 1835); *H. magellanicus* (Phillipi, 1866); *H. montanus* (Philippi and Landbeck, 1861); *Lasiurus varius* Poeppig, 1835; *Myotis chiloensis* (Waterhouse, 1840; family Vespertilionidae); and *Tadarida brasiliensis* (Geoffroy Saint-Hilaire, 1824; family Molossidæ). We examined only adults — 92 specimens with external and 91 specimens with wing measurements [*H. macrotus*, $n = 31$, *H. magellanicus* = 11, *H. montanus* = 8, *L. varius* = 4, *M. chiloensis* = 31, and *T. brasiliensis* = 7 or 6 (external and wing measurements, respectively)]. These adult specimens were measured after being captured in 2010–2015 and later deposited in the Colección de Mamíferos del Laboratorio de Investigaciones en Evolución y Biodiversidad (LIEB), CIEMEP (CONICET-UNPSJB), Esquel, Chubut (Appendix I). Likewise, we examined 74 adult specimens with craniodental measurements in *H. macrotus* = 21, *H. magellanicus* = 8, *H. montanus* = 5, *L. varius* = 9, *M. chiloensis* = 25, and *T. brasiliensis* = 6. These specimens are stored in four mammal collections in Argentina: Colección de Mamíferos del Laboratorio de Investigaciones en Evolución y Biodiversidad (LIEB), CIEMEP (CONICET-UNPSJB), Esquel, Chubut; Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires (MACN); Colección de Mamíferos Lillo, Tucumán (CML); and Instituto Argentino de las Zonas Áridas, Mendoza (IADIZA). The specimen list with corresponding localities of occurrence is given in Appendix I.

Measurements

We studied the morphology of Patagonian bats using three datasets: external, wing, and craniodental measurements. The external measurements (in mm; following Simmons and Voss,

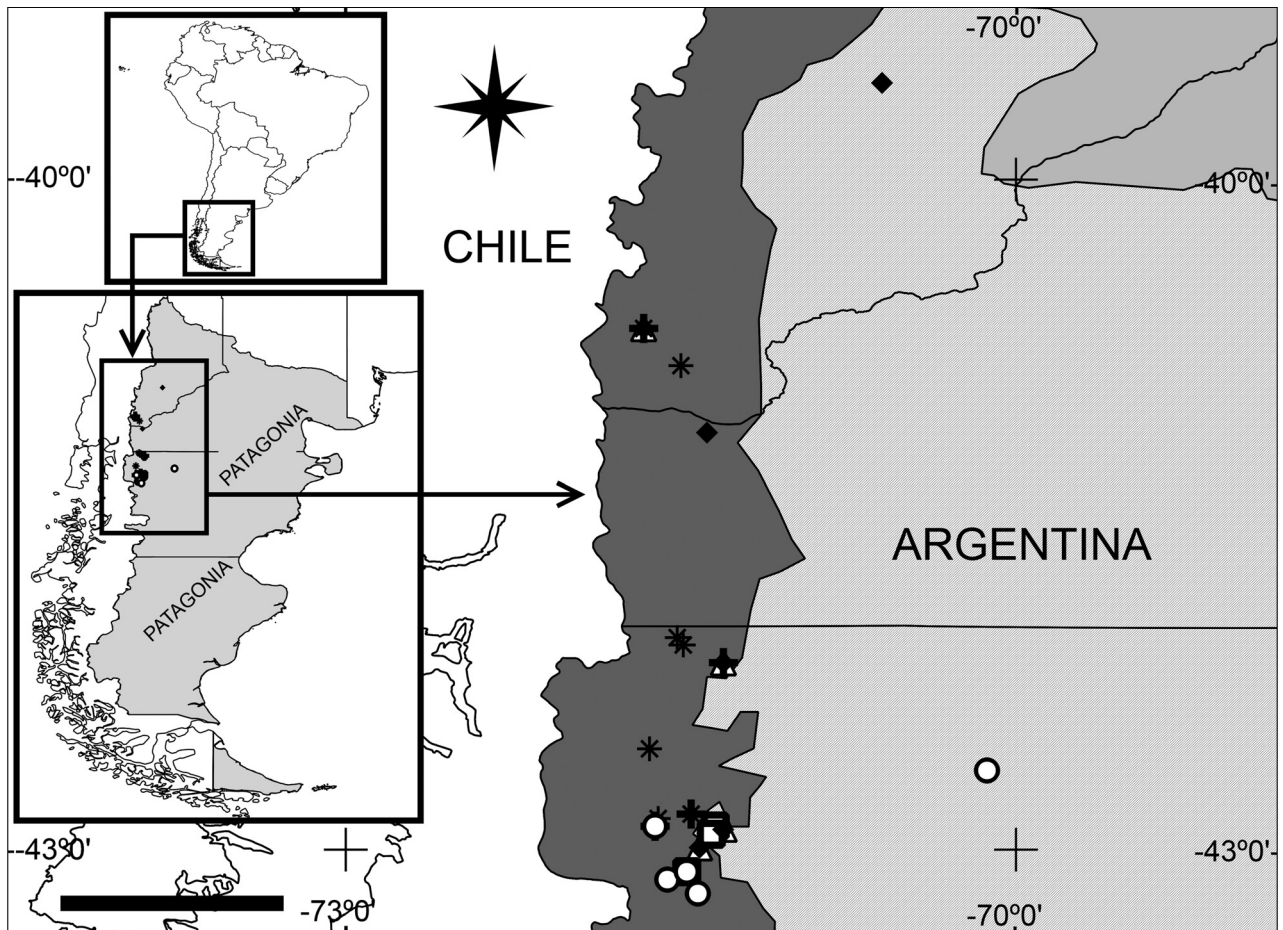


FIG. 1. Localities of study specimens of Patagonian bats from Argentina. Eco-regions from Argentina are coded as follows: Patagonian Steppe (clear gray); Patagonian Forest (dark gray); Low Monte (gray). *Histiotus macrotus* (Δ), *H. magellanicus* (+), *H. montanus* (\square), *L. varius* (\blacklozenge), *M. chiloensis* (*), and *T. brasiliensis* (\circ). Scale in map (black bar) = 100 km

1998; Barquez *et al.*, 1999) included: head and body length (LCC), distance from tip of the snout to the point of insertion of the tail into the body; tail length (TL), distance between the point of insertion of the tail into the body and the last caudal vertebra; ear length (EL), distance between the notch and the tip of the pinna; tragus length (TrL), distance between the notch and the tip of tragus; forearm (FA), distance between the elbow and the wrist when the wing is folded; and tibia length (TbL), from the proximal end of the tibia to the posterior base of the calcus. External measurements were taken with a ruler to the nearest 0.5 mm.

The wing measurements (in mm, S in mm²; taken from Norberg and Rayner, 1987) included: wing span (B); wing chord (c); length of hand wing (Lh); and wing area (S, see measurements definition in Table 1). Three wing indexes were obtained from these basic measurements: aspect ratio (AR), wing loading (WL) and tip shape index (I, see indexes definition in Table 1). High AR usually corresponds with greater aerodynamic efficiency and lower energy losses in flight; high WL corresponds with fast flight and long-distance commuting, and low WL allows slow, maneuverable flight. Wing tip index of 1 corresponds to wider triangular wingtips, and lower values indicate pointed wingtips (Norberg and Rayner, 1987). Wing measurements were taken with a ruler accurate to the nearest 0.5 mm and body mass with

a precision balance (Pesola ® 30 g). We obtained the wing silhouette of each bat by tracing it on a white sheet of paper and scanning it to obtain a digital image. Each wing silhouette in digital format was analyzed with the ImageJ 1.46r software (Rasband, 2012) to calculate the wing area.

The craniodental measurements (in mm; taken from Simmons and Voss, 1998; Barquez *et al.*, 1999; Giménez and Gianini, 2011, 2016a, 2016b — see Fig. 2) included: condylobasal length (CBL); postorbital constriction (PC); zygomatic breadth (ZB); mastoid breadth (MB); length of rostrum (LR); height of braincase (HB); length of paladar (LP); length of maxillary tooththrow, from the anterior margin of the canine to the posterior margin of the last molar (CM³); breadth across molar, greatest breadth across the outer edges of the crowns of the upper molars (MM); breadth across canines, greatest breadth across the outer edges of the crowns of the upper canines (CC); length of mandibular, from incisive insertion to the mandibular condyle (LM); length of mandibular tooththrow (CM₃); height of mandibular body, at lower third premolar (HM); length of upper canine (LUC); length of lower canine (LLC); height of coronoid process 1, from the mandibular condyle to the extreme of the coronoid process (HC1); height of coronoid process 2, from the mandibular posterior base to extreme of the coronoid process (HC2); height of coronoid process 3, from the mandibular

TABLE 1. Definition of wing measurements taken on the specimens studied

Wing measurements	Definition
Wing span (B)	Distance between the wingtips of a bat with wing extended so that the leading edge is straight
Wing chord (c)	Width of wing estimated by length of fifth finger
Length of hand wing (Lh)	Length of third finger
Wing area (S)	Combined area of the two wings, the entire tail membrane and portion of the body between the wings
Aspect ratio (AR)	Square of the wingspan divided by the wing area, $AR = B^2 / S$ (adimensional)
Wing loading (WL)	Weight (product of the mass and gravitational acceleration) divided by wing area, $WL = w / S$ (measured in Pascals)
Tip shape index (I)	Defined as $Ts/(Tt-Ts)$ where Ts is the average of the surface of the hand divided the surface of the arm (Shw/Saw), and Tt is the average length of the wing hand over the long wing arm (Ihw/Iaw)

condyle to the anterior edge of the coronoid process (HC3). These variables were taken with digital calipers to the nearest 0.01 mm.

Morphometric Analysis

We used Principal Components Analysis (PCA) to summarize morphometric variation of each data set, based on a correlation matrix for the wing data set, and on a variance-covariance matrix for the external and craniodental data sets, and all variables together based on a correlation matrix. We traced polygons joining conspecific individuals on each PCA ordination plot to record position of each species in the

morpho-space and their relationship with the different variables. Additionally, we performed a size-corrected PCA for each data set, using the geometric mean transformation (the ratio between each value and the geometric mean of the corresponding variable — e.g., Meachen-Samuels and Van Valkenburgh, 2009; Morales and Giannini, 2010, 2013, 2014). All analyses were performed with the InfoStat software ver. 2010 (Di Rienzo *et al.*, 2010).

Phylogenetic Comparative Method

We used a phylogenetic comparative method, Canonical Phylogenetic Ordination (CPO — Giannini, 2003) to evaluate

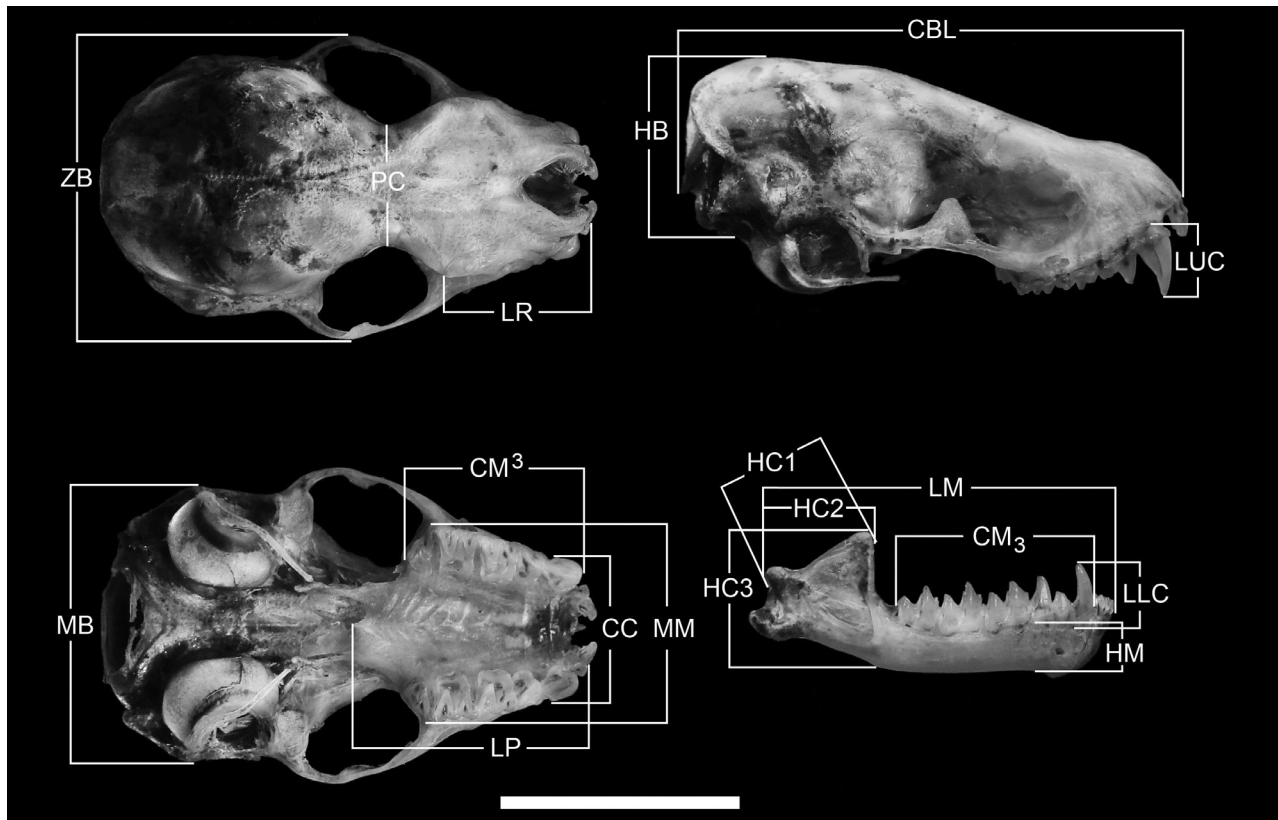


FIG. 2. Skull variables measured in Patagonian bats from Argentina, shown on a *H. macrotus* specimen (LIEB-M 851 ♀). See text for abbreviations. Scale bar is 10 mm

historical effect on the morphofunctional variation of Patagonian bats. CPO is a form of canonical ordination that uses two basic matrices (main and external), as the ones used in Redundancy Analysis (RDA = the Canonical form of PCA — see Giannini, 2003 and citations therein). The main matrix is the dependent data (here morphometric variation); the external matrix codes for clade membership; i.e., it is composed of as many binary variables as clades present in the phylogenetic tree, coding 1 as a species that belongs in the clade and 0 as a species that does not belong in the clade. CPO fits a multivariate linear model using the main and external matrices (Giannini, 2003). We used four main matrices that corresponded to external, wing, cranial, and combined data sets (standardized values). The first main matrix included 92 specimens and seven external variables; the second matrix included 91 specimens and seven wing variables; the third matrix included 74 specimens and 18 craniodental variables; and the fourth matrix included 51 specimens and 31 variables. Each main matrix was analyzed with the external matrix. Clades were defined as in Fig. 3 following phylogenetic trees from Jones *et al.* (2002), Hooper and Van Den Bussche (2003), Bickham *et al.* (2004), Stadelmann *et al.* (2007), Lack and Van Den Bussche (2010), Lack *et al.* (2010), Roehrs *et al.* (2010), Ammerman *et al.* (2012), and Amador *et al.* (2016), that were pruned to include only the species that inhabit Patagonia. In the case of species not included in references

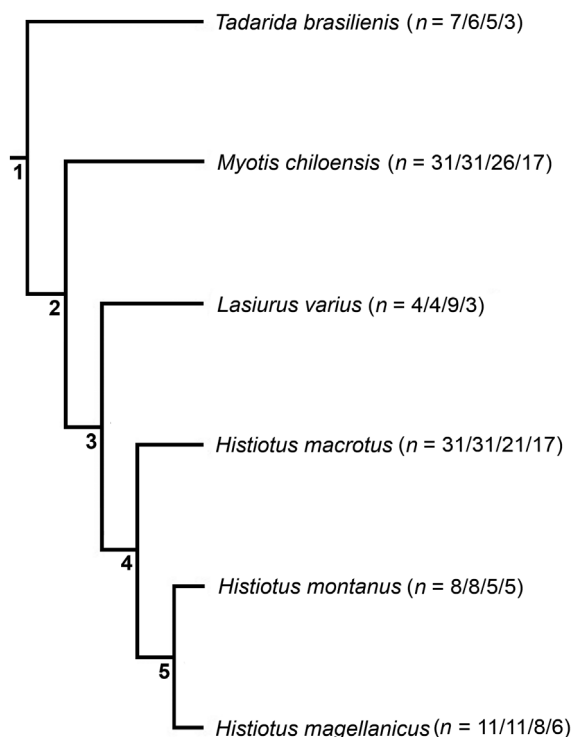


FIG. 3. Cladogram of Patagonian bats from Argentina based on Jones *et al.* (2002), Hooper and Van Den Bussche (2003), Bickham *et al.* (2004), Stadelmann *et al.* (2007), Lack and Van Den Bussche (2010), Lack *et al.* (2010), Roehrs *et al.* (2010), Ammerman *et al.* (2012) and Amador *et al.* (2016). Tree partitions are indicated with numbers and correspond to clades used in Canonical Phylogenetic Ordination. Partition 1 is trivial and indicates the whole tree. The number of specimens per species for each data set (external, wing, craniodental, and all combined variables) is indicated in parentheses

trees, these were placed in the most plausible position (within the genus, i.e. *L. varius*). The level of significance of each clade was tested individually using 4999 unrestricted permutations of Monte Carlo (Giannini, 2003). Clades were included manually in the model using forward stepwise selection (ter Braak and Smilauer, 1998). The reduced tree matrix obtained is expected to be the variable set that best explains the phylogenetic effect on morphofunctional total variation without redundancy (see Giannini, 2003).

RESULTS

Morphological Patterns

The PCA showed a clear segregation among Patagonian bat species in each of the three variables sets (external, wing, craniodental variables) independently and combined. The first PCA (with external variables) explained 94.1% of the variation including the two first components (PC1 = 79.4%, PC2 = 14.7% — see Supplementary Table S1). All variables were positively correlated with the PC1; EL, LCC, and TL were the best correlated variables. LCC (positively) and TL (negatively) were best correlated with PC2. The species dispersion showed a clear separation on PC1 based on body size differences. The largest species were *H. macrotus*, *H. magellanicus* and *H. montanus* on the most positive end of PC1; medium sized species were *T. brasiliensis* and *L. varius*; specimens of the smallest species, *M. chiloensis*, was positioned on the negative end of PC1 (Fig. 4A). Species segregation was less important on PC2, with only two groups: specimens of *T. brasiliensis* (on the positive side) and all vespertilionid bats (Fig. 4A). The size-corrected PCA explained 94.8% of the variation in the first two components (PC1 = 90.5%, PC2 = 4.3% — see Supplementary Table S1). The variables best correlated positively with PC1 were EL and TrL, while LCC (positively) was the variable best correlated with PC2. The species were clearly segregated in the morphospace principally by contributions of EL and TrL on the PC1 (see Fig. 4B). Specimens of *H. magellanicus* were clearly segregated from other *Histiotus*, and *T. brasiliensis* separated from vespertilionids along PC2, as in the first PCA (Fig. 4B).

The PCA using wing variables explained 78.3% of the variation (PC1 = 52.8%, PC2 = 25.5% — Supplementary Table S2). All variables were positively correlated with PC1, except I, which was negatively correlated. The variables best correlated with PC1 were B and Lh, while AR, WL (positively) and I (negatively) were the variables best correlated with PC2. This analysis showed on PC1 a great

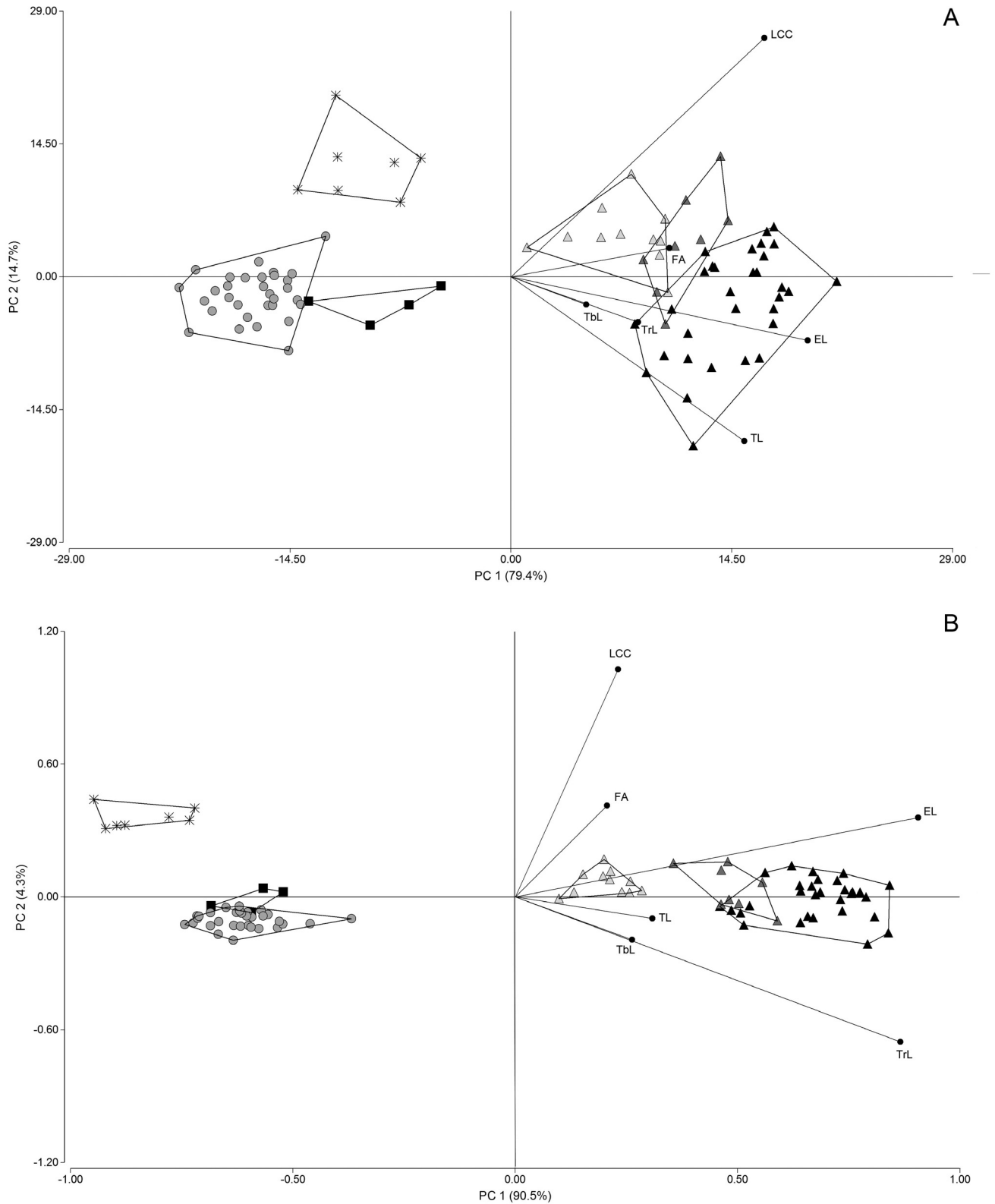


FIG. 4. Ordination diagram of PCA of the Patagonian bat assemblage for external variables using A) data set not size-corrected; and B) data set size-corrected. Polygons include specimens from each species: *H. macrotus* (\blacktriangle), *H. magellanicus* (\triangle), *H. montanus* (\blacktriangle), *L. varius* (\blacksquare), *M. chiloensis* (\bullet), and *T. brasiliensis* (\square). Vectors show the strength of correlation of each variable with the plane of PC1 and PC2. See text for abbreviations

segregation as a function of wing dimensions (size) and a clear segregation by genus; with *Histiotus* species (larger) forming a compact group on the positive extreme of the PC1, *M. chiloensis* in the

opposite position (smaller), and *T. brasiliensis* and *L. varius* in a intermediate position (Fig. 5A). On the PC2 the species were segregated by aerodynamic-derived indices and showed a clear segregation by

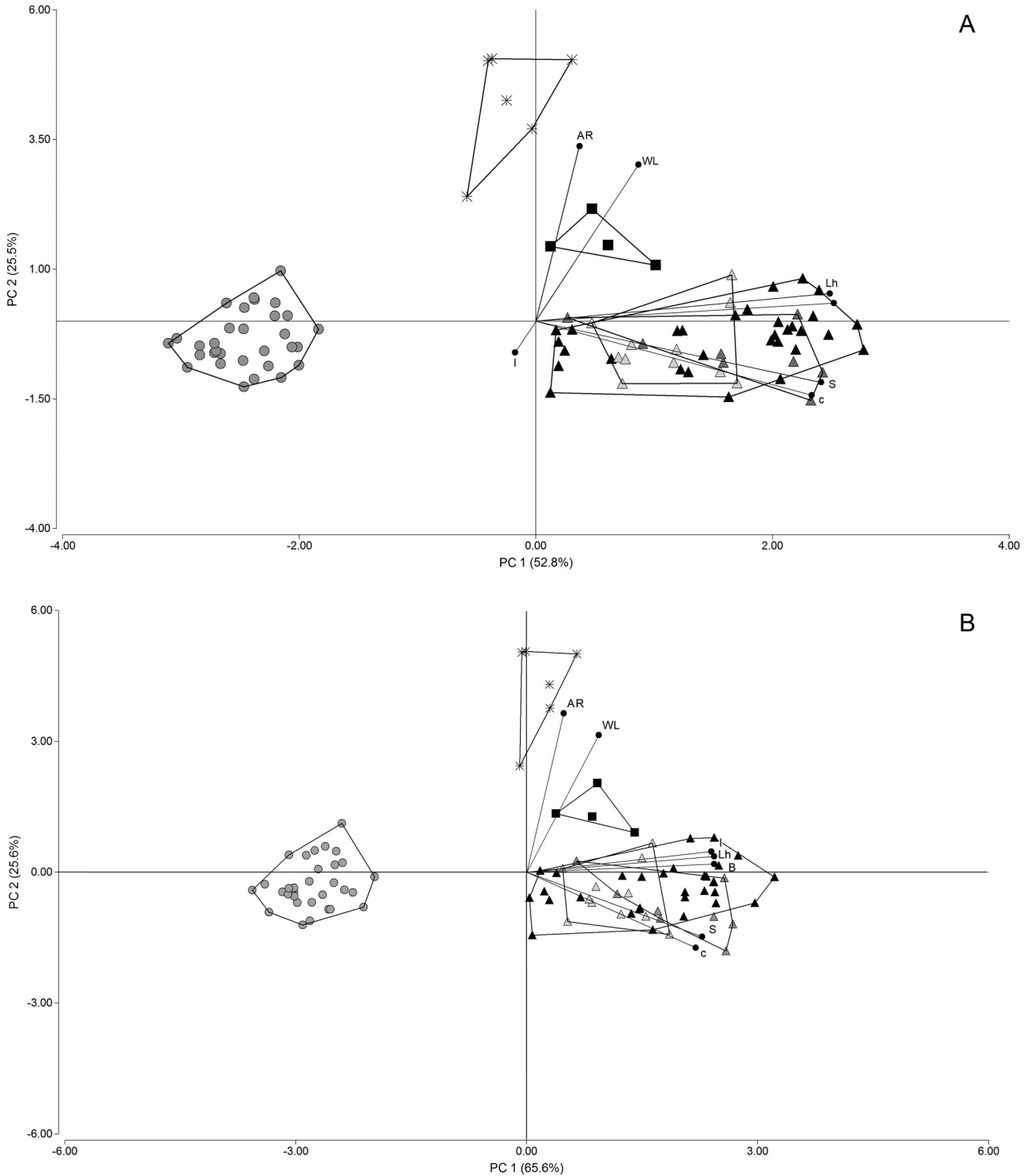


FIG. 5. Ordination diagram of PCA of the Patagonian bats assemblage for wing variables using A) data set not size-corrected; and B) data set size-corrected. Polygons include specimens from each species: *H. macrotus* (▲), *H. magellanicus* (△), *H. montanus* (▲), *L. varius* (■), *M. chiloensis* (●), and *T. brasiliensis* (□). Vectors show the strength of correlation of each variable with the plane of PC1 and PC2. See text for abbreviations

morphotypes (Fig. 5A), with *Histiotus* species and *M. chiloensis* on the negative side of PC2, *T. brasiliensis* separated on the positive side of PC2 (with greater AR and WL), and *L. varius* in an intermediate position (Fig. 5A). These three morphotypes determine different flight styles: *T. brasiliensis* presented morphological characteristics of a fast (high WL) and economic flight (high AR) in open spaces. Both *Histiotus* and *Myotis* species presented features for slow and maneuverable flight (low WL), but they were clearly distinguished along the size axis (PC1; higher Lh, B, c, and S in *Histiotus*); while *L. varius* presented an intermediate flight style among these two groups. The sized-corrected PCA showed the same segregation pattern between the species (Fig. 5B). In this case the two first component explained the 91.2% of total variation (PC1 = 65.6%, PC2 = 25.6% — Supplementary Table S2).

The PCA performed with craniodental variables showed a clear segregation among Patagonian bat species. The first two components explained 94.3% of total variation (PC1 = 84.2%, PC2 = 10.1% — Supplementary Table S3). All variables were positively correlated with PC1 and the best correlated variables were CBL, LM and ZB. The best correlated variables with PC2 were LR and LP (positively) and CC (negatively — Fig. 6A). The species were separated primarily by size along the PC1, and less so by morphology along PC2. PC1 reflects the pattern seen in external variables (see above), while along the PCA2 the species were segregated into three different morphotypes: species with short and wide rostrum such as *L. varius* (negative side); species with long and narrow rostrum such as *M. chiloensis* (positive side); and species with relatively intermediate morphology in the genera *Histiotus* and *Tadarida* (Fig. 6A). The size-corrected PCA showed the same pattern (see Figs. 6A and 6B). The first two components explained 90.7% of total variation (PC1 = 74%, PC2 = 16.7%) and the variables best correlated positively with PC1 were LLC and LUC, while the best correlated with PC2 were LR and LP (positively), and CC (negatively — Supplementary Table S3).

The PCA performed with all variables combined explained 78.5% of total variation (PC1 = 68.1%, PC2 = 10.4% — Supplementary Table S4 and Fig. 7A). All variables were positively correlated with PC1, and the variables best correlated were: FA, CBL, ZB, HB, MB, and MM; while LR, I (positively), A and WL (negatively) were the variables best correlated with the PC2 (Supplementary Table S4 and Fig. 7A). The position of the species in

morphospace was somewhat different to previous analysis and certainly due to the combination of variables; however, the species were clearly segregated principally by size along PC1 (Fig. 7A). On the PC2 the species were segregated by various morphological aspects. Specimens of *M. chiloensis*, having long rostrum, high I, and lowest AR and WL, were positioned toward the positive end of PC1. By contrast, *L. varius* specimens, having short rostrum and lowest I, but with high AR and WL, were positioned toward the negative end of PC1. Specimens of three *Histiotus* species and *T. brasiliensis* were in an intermediate position, although *Histiotus* species were closest to *M. chiloensis*, and *T. brasiliensis* to *L. varius*. The size-corrected PCA performed with all variables combined showed a similar pattern of species in morphospace (Fig. 7B). The first two components together explained 83.8% (PC = 73.6%; PC2 = 10.2% — Supplementary Table S4) of total variation. All variables were positively correlated with PC1; FA, B, CBL, ZB, HB, MB, MM, LM, HC1, HC2, and HC3 were the best correlated variables with this component (Fig. 7B). PC2 scores correlated best with LR, LP (positively), AR, and WL (negatively — Supplementary Table S4).

Phylogenetic Effect

The CPO analyses showed that the evolutionary history of the assemblage was an important factor in determining the ecomorphological pattern of Patagonian bats. In the first analysis (external variables), phylogeny explains 85.5% of total variation through selection of clades 4 (*Histiotus*, 75.8%) and 2 (Vespertilionidae, 5.8% — Table 2). The second CPO on wing variables explained 49.1% of total variation and selected the clades 2 (Vespertilionidae, 38%) and 3 (*Lasiurus* + *Histiotus*, 6.8%). The third CPO on craniodental variables explained 87.5% of total variation and the most important tree partitions were the clades 4 (*Histiotus*, 67.6%) and 3 (*Lasiurus* + *Histiotus*, 11.5%). Finally, the CPO on all variables selected three tree partitions: clade 4 (*Histiotus*, 27.6%), clade 5 (*H. montanus* + *H. magellanicus*, 14%) and clade 2 (Vespertilionidae, 4.3% — Table 2). The model including these tree partitions explained 45.9% of the total variation.

DISCUSSION

Morphological Pattern

Patagonian bats exhibited a clear pattern of species segregation on the basis of the relative position

of specimens in morphospace in each of the data sets analyzed and in the combination of all variables. The morphofunctional space covered by the variables was structured mainly by size and to a lesser extent

by other morphological features (see below). Size is a key variable known to have a profound influence in aspects of bat biology, including roosting behavior, physiology, and echolocation, among other

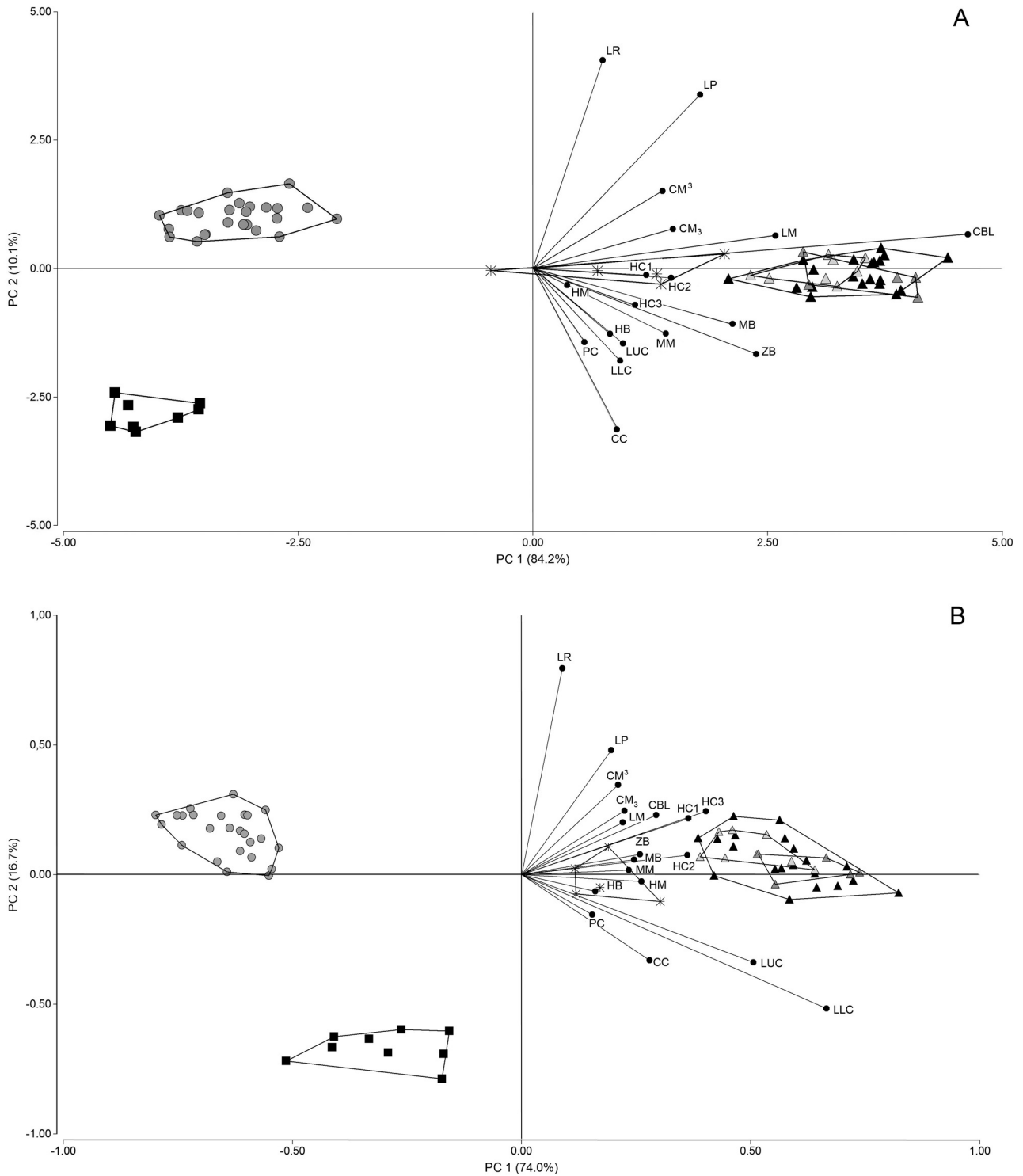


FIG. 6. Ordination diagram of PCA of the Patagonian bat assemblage for craniodental variables using A) data set not size-corrected; and B) data set size-corrected. Polygons include specimens from each species: *H. macrotus* (▲), *H. magellanicus* (△), *H. montanus* (▲), *L. varius* (■), *M. chiloensis* (●), and *T. brasiliensis* (□). Vectors show the strength of correlation of each variable with the plane of PC1 and PC2. See text for abbreviations

factors (e.g., Aldridge and Rautenbach, 1987; Barclay and Brigham, 1991; Fenton and Bogdanowicz, 2002; Kunz and Lumsden, 2003). In particular, size can affect several of the variables related to flight performance and so define foraging styles (Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987; Ranivo and Goodman, 2007). Diet selection depends to a great extent on flight performance in aerial hawking and gleaning bats (see

Barclay and Brigham, 1991; Swartz *et al.*, 2003; Ranivo and Goodman, 2007), as is the case for all Patagonian species. It is expected that larger bats capture a wider range of prey size (from small to large), whereas small bat species would be restricted to small prey (Barclay and Brigham, 1991; Swartz *et al.*, 2003; Ranivo and Goodman, 2007). Size affects bite force which increases with bat size in absolute terms (Aguirre *et al.*, 2002), thus generating

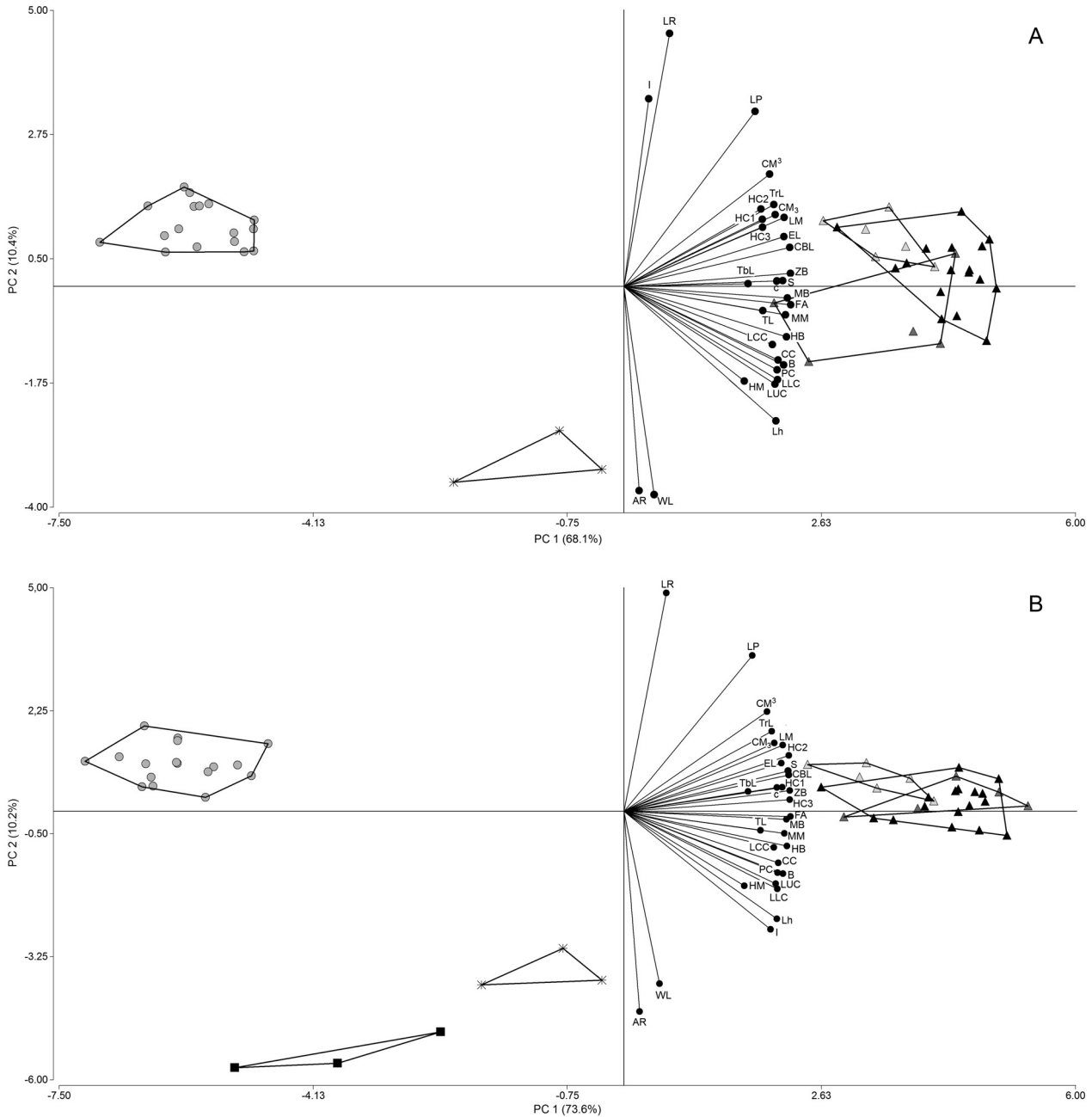


FIG. 7. Ordination diagram of PCA of the Patagonian bat assemblage for combined three data sets using A) data set not size-corrected; and B) data set size-corrected. Polygons include specimens from each species: *H. macrotus* (▲), *H. magellanicus* (△), *H. montanus* (▲), *L. varius* (■), *M. chiloensis* (●), and *T. brasiliensis* (□). Vectors show the strength of correlation of each variable with the plane of PC1 and PC2. See text for abbreviations

TABLE 2. Results of the Canonical Phylogenetic Ordination (CPO) for three data sets (external, wing and craniodental variables). Clades are numbered as in Fig. 3. Values are significant at $P = 0.01$

Analysis	Variables	Variance	F-value	P-value	
	External variables				
Individual	4	0.758	282.237	0.0002	
	3	0.726	238.732	0.0002	
	5	0.115	11.708	0.0002	
Forward stepwise selection	4	0.758	282.237	0.0002	
	2	0.058	28.102	0.0002	
	3	0.037	22.225	0.0002	
		5	0.027	19.892	0.0002
	Wing variables				
Individual	2	0.380	54.633	0.0002	
Forward stepwise selection	2	0.380	54.633	0.0002	
	3	0.068	10.835	0.0002	
	4	0.043	7.265	0.0018	
	Craniodental variables				
Individual	4	0.676	148.358	0.0002	
	3	0.341	36.666	0.0002	
	5	0.155	12.996	0.0004	
Forward stepwise selection	4	0.676	148.358	0.0002	
	3	0.115	38.834	0.0002	
	2	0.077	40.219	0.0002	
	5	0.006	3.273	0.0002	
	All variables together				
Individual	4	0.276	18.636	0.0002	
	3	0.177	10.563	0.0002	
Forward stepwise selection	4	0.276	18.636	0.0002	
	5	0.140	11.529	0.0002	
	2	0.043	3.756	0.0080	

differences in foraging habits (hard-eating versus soft-eating) of the species with similar morphologies, but with different sizes. In the Patagonian ensemble in particular, a species gradient was evident in all datasets analyzed, which indicates a rather global impact of size and phylogeny on the pattern of species, and in the way they segregate morpho-functionally. The ordering of species in projected multivariate space indicated a gradient of vespertilionid species (*Myotis* — *Lasiurus* — *Histiotus*), an intermediate position of the molossid *Tadarida*, and a segregation of the latter along a second axis (PC2) when external, more specifically aerodynamic variables, are included in the analysis. Interestingly, *L. varius* also segregated to some extent in the same dimension chiefly due to the higher wing loading (WL) and aspect ratio (AR) as compared to the other vespertilionids, but also in the secondary skull dimension given its wide and short rostrum.

The external morphology reflected the highly derived morphology of *Histiotus*, which is considered a subgenus of *Eptesicus* (Hooper and Van Den

Bussche, 2003). Ear size was an important factor for species segregation mainly for *Histiotus* species, which are very similar. The Patagonian *Histiotus* species differentiate by ear length (*H. macrotus* > 30 mm, *H. montanus* between 27–30 mm and *H. magellanicus* < 25 mm — Barquez *et al.*, 1993, 1999; Barquez and Díaz, 2009; Giménez, 2010; Giménez *et al.*, 2012). Ear size and shape affect reception of echolocation calls (Obrist *et al.*, 1993; Fuzessery, 1996) but also species with larger ears are more sensitive to low frequency sounds such as those from the movements of their prey, i.e., passive listening of prey generated sounds (Obrist *et al.*, 1993; Fenton and Bogdanowicz, 2002). Ear size also affects flight through an increase in parasitic drag (Speakman and Thomas, 2003; Canals *et al.*, 2005). Although the hunting habits of these long-eared species are not documented, the two variables that correlated with the positive scores of *Histiotus* specimens in external PC1, ear length and tail length, indicate gleaning as the main foraging habit (Schnitzler and Kalko, 1998). A long tail with extensive uropatagium is used as a flexible basket to catch insects both in flight (aerial hawking) and by gleaning from vegetation (Norberg, 1994).

Other cranial and aerodynamic variables are also important, particularly wing loading (WL) and aspect ratio (AR). These values are lowest in *Histiotus* and also in *Myotis*, which probably hunt for prey in cluttered microhabitats, and highest for *Tadarida* and *Lasiurus*, which likely are fast, enduring fliers (Norberg, 1994). So Patagonian bats were also segregated on the basis of derived aerodynamic features (AR, WL, and I), with *T. brasiliensis* being the most aerodynamically efficient bat (values $AR > 7$ — Norberg and Rayner, 1987) and swift flier (higher WL — Norberg, 1994) within the ensemble, which would allow this species to fly in open areas and above the canopy (Norberg and Rayner, 1987; Iriarte Díaz *et al.*, 2002; Canals *et al.*, 2005). This wing design also meets the requirements of a migratory species: migratory circuits up to 1,000 km long have been recorded for *T. brasiliensis* (Villa-R and Cockrum, 1962; Glass, 1982; Norberg, 1994). *Myotis* and *Histiotus* have similar morphologies but with major differences in wing size (*Histiotus* species have larger wing span and surfaces). This morphology (short and wide wing) allows a highly maneuverable flight at low speed (lowest WL values — Norberg and Rayner, 1987; Iriarte Díaz *et al.*, 2002; Canals *et al.*, 2005). These species fly in forested environments and capture prey near vegetation (Iriarte Díaz *et al.*, 2002; Canals *et al.*, 2005).

Myotis chiloensis seems to inhabit both the inside and edge of the forest, and to prey on soft insects (e.g., nematocerans — Galaz *et al.*, 2009). Finally, *L. varius* presents a relatively intermediate morphology (narrow and long wing, and intermediate AR and WL values). Similar values were obtained for the congener *L. cinereus* (Norberg and Rayner, 1987; Canals *et al.*, 2005). As with other *Lasiurus* species from temperate regions, *L. varius* is a possible migrant, and this morphotype permits long-distance, enduring flight (Norberg and Rayner, 1987).

Different flight styles generally indicate differential habitat use across species within the same environment (Norberg and Rayner, 1987). Our results indicate that the Patagonian bats partition their habitat with *T. brasiliensis* foraging in open environments (e.g., Patagonian steppe) and above the canopy in forested areas, while vespertilionids move in forested areas where a slow and maneuverable flight is required (Norberg and Rayner, 1987; Iriarte Diaz *et al.*, 2002; Canals *et al.*, 2005). *Lasiurus* in particular probably has the most flexible behavior, alternating forested habitats and long-distance movements such as migration.

Regarding the craniodental morphology, three clearly different morphotypes segregated in morphospace. *Myotis chiloensis* presented a gracile skull with elongate and narrow rostrum and palate. By contrast, *L. varius* exhibited a short, wide and robust skull which are features usually associated with greater bite force in species of comparable size (Freeman, 1979, 1981; Aguirre *et al.*, 2002; Swartz *et al.*, 2003; Nogueira *et al.*, 2009), such as *M. chiloensis*. These two species also show a globose, tall cranium. *Tadarida brasiliensis* and *Histiotus* species presented a rather similar and intermediate morphology between *L. varius* and *M. chiloensis*, with a relatively elongate and characteristically low skull. *Tadarida brasiliensis* and *Histiotus* differ in size and in details of skull architecture such as the development of coronid process, which is more developed in *Histiotus*. This gives *Histiotus* a greater insertion surface for the temporalis muscle, which is the main jaw-closing and prey-seizing muscle in bats (Freeman, 1979). Therefore, all species exhibited marked differences in skull dimensions with functional implications.

Historical Effects

Our phylogenetic comparative analysis showed that the segregation in morphospace among

Patagonian bats is associated with variation around three historical events represented by tree partitions 2, 3 and 4, with different importance in each dataset analyzed. Tree partition 2 represents the separation between *T. brasiliensis* and vespertilionid bats and it was important when wing variables were analyzed but less important for external variables. *Tadarida brasiliensis* diverged from the rest of molossids and its African sister taxa at ca. 18 Mya (Ammerman *et al.*, 2012) or ca. 14 Mya (Amador *et al.*, 2016). This genus may have originated in Eurasia and migrated to North America during the Miocene, and subsequently dispersed into South America during the late Pliocene at the beginning of the Great American Biotic Interchange (GABI — Czaplewski *et al.*, 2003). This molossid successfully expanded its distribution to Patagonia with a morphotype clearly different externally and aerodynamically from vespertilionid bats, allowing it to exploit an empty niche in Patagonian environments. Tree partition 4 (*Histiotus*) was also important when external and craniodental morphology were evaluated. *Histiotus* is endemic to South America and its origin is estimated to date from the Miocene (Lim, 2009), splitting from other American *Eptesicus* ca. 8 Mya (Amador *et al.*, 2016). This genus is the most diverse in Patagonia with three species and one of them is endemic (*H. magellanicus* — Barquez *et al.*, 1999; Giménez *et al.*, 2012). Finally, the partition tree 3 that separates *Histiotus* and *Lasiurus* was moderately important when wing and craniodental variables were analyzed. The emergence of *Myotis* in South America is estimated at 7–10 Mya in the middle Miocene (Stadelmann *et al.*, 2007), before the GABI maximum; while *M. chiloensis* split from its sister group in the early Pliocene at ca. 5 Mya (Stadelmann *et al.*, 2007; Amador *et al.*, 2016).

Considering all historical data together, Patagonian bats were assembled from previously existing morphotypes, which resulted in the strong phylogenetic signals that are generally older than the time when all species were together in Patagonia (estimated as the age of the youngest clade), and the lack of genus- or higher-level endemism in the region. This translates into the morphofunctional aspect of the Patagonian assemblage, which can be described as the successive addition of non-overlapping, well-defined morphofunctional types imported from other South American regions. Then speciation took place in Patagonia and resulted in species-level endemisms (*M. chiloensis*, *H. magellanicus*, *L. varius*). It is expected that some degree of fine-grained niche partitioning occurred among the Patagonian

bats, but ecological and echolocation data are needed to test these hypotheses.

SUPPLEMENTARY INFORMATION

Contents: Table S1. Results of Principal Components Analysis (PCA) performed with external variables including dataset not corrected and corrected for 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; Table S2. Results of PCA performed with wing variables including dataset not corrected and corrected for 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; Table S3. Results of PCA performed with external variables including dataset not corrected and corrected for 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; Table S4. Results of PCA performed with all variables combined including datasets not corrected and corrected for 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. Supplementary Information is available exclusively on BioOne.

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APPENDIX I

List of the specimens examined in the morphological analysis of Patagonian bats

Histiotus macrotus ($n = 31$) — Argentina: Chubut Province, Ea. El Principio, 10 km of Esquel (LIEB-M 746, ♀; LIEB-M 747, ♀; LIEB-M 748, ♀; LIEB-M 749, ♀; LIEB-M 750, ♀; LIEB-M 751, ♀; LIEB-M 752, ♀; LIEB-M 754, ♀; LIEB-M 756, ♀; LIEB-M 773, ♂; LIEB-M 774, ♀; LIEB-M 775, ♀; LIEB-M 847, ♀; LIEB-M 848, ♂; LIEB-M 849, ♀; LIEB-M 850, ♂; LIEB-M 851, ♀; LIEB-M 852, ♀); Chubut Province, Trevelin, Wales School (LIEB-M 757, ♀; LIEB-M 761, ♀; LIEB-M 763, ♀; LIEB-M 768, ♀; LIEB-M 772, ♀; LIEB-M 1100, ♀; LIEB-M 1101, ♀); Chubut Province, Esquel (LIEB-M 845, ♂; LIEB-M 846, ♂); Chubut Province, El Coihue Reserve (LIEB-M 853, ♀); Neuquén Province, Villa La Angostura (CML 3230, ♀); Neuquén Province, 19 km of Villa La Angostura (ICM 4557, ♀).

Histiotus magellanicus ($n = 13$) — Argentina: Chubut Province, Arroyo La Camioneta, Cerro La Torta (LIEB-M 854, ♀; LIEB-M 855, ♀; LIEB-M 856, ♀; LIEB-M 1107, ♀; LIEB-M 1108, ♀; LIEB-M 1109, ♀); Chubut Province, El Coihue Reserve (LIEB-M 857, ♀; LIEB-M 858, ♀; LIEB-M 859, ♀; LIEB-M 860, ♀; LIEB-M 861, ♀); Chubut Province, National Park Los Alerces (LIEB-M 1111, ♀); Neuquén Province, Villa La Angostura 19 km to N (CML 3231).

Histiotus montanus ($n = 8$) — Argentina: Chubut Province, Trevelin, Wales School (LIEB-M 744, ♀; LIEB-M 745, ♀); Chubut Province, Laguna La Zeta, 4 km of Esquel (LIEB-M 1113, ♂; LIEB-M 1115, ♂; LIEB-M 1116, ♂; LIEB-M 1117, ♀); Chubut Province, Esquel, National University of the Patagonia San Juan Bosco, 4 km of Esquel on road N° 259 (LIEB-M 1118, ♀; LIEB-M 1119, ♀).

Lasiurus varius ($n = 9$) — Argentina: Chubut Province, El Coihue Reserve (LIEB-M 862, ♀); Chubut Province, Arroyo Esquel ca. 10 km of Esquel (LIEB-M 863, ♀); Chubut Province, Esquel (LIEB-M 1103, ♀); Chubut Province, on Río Percey

road to Los Alerces National Park (LIEB-M 1527); Neuquén Province, Catán Lil, Las Coloradas (MACN 13617, ♂; MACN 13621, ♂; MACN 13626, ♂); Neuquén Province, 19 km of N of Villa La Angostura (CML 3234); Río Negro Province, Bariloche, Isla Victoria Instruction Center (CML 2005).

Myotis chiloensis ($n = 39$) — Argentina: Chubut Province, El Hoyo (CML 5218, ♀; MACN 16522, ♀; MACN 16523, ♀; MACN 16524, ♀; MACN 16525, ♂; MACN 16527, ♀); Chubut Province, Cascada Irigoyen in National Park Los Alerces (LIEB-M 812, ♂; LIEB-M 813, ♀; LIEB-M 814, ♀; LIEB-M 815, ♂); Chubut Province, Ea. Las Vacas Pampas (LIEB-M 816, ♀; LIEB-M 818, ♀; LIEB-M 819, ♀; LIEB-M 820, ♀; LIEB-M 821, ♂; LIEB-M 822, ♂; LIEB-M 823, ♀; LIEB-M 824, ♂; LIEB-M 825, ♂; LIEB-M 826, ♀; LIEB-M 827, ♂; LIEB-M 828, ♂; LIEB-M 829, ♀; LIEB-M 830, ♀; LIEB-M 831, ♂; LIEB-M 832, ♀; LIEB-M 833, ♂; LIEB-M 834, ♂; LIEB-M 835, ♂; LIEB-M 836, ♀; LIEB-M 837, ♀; LIEB-M 838, ♀); Chubut Province, Arroyo La Camioneta road to Cerro La Torta near Esquel (LIEB-M 840, ♀); Chubut Province, Río Rivadavia near Villa Lago Rivadavia (LIEB-M 841, ♀); Chubut Province, El Hoyo, La Sequoia Ranch (LIEB-M 842, ♂; LIEB-M 843, ♂; LIEB-M 844, ♀); Neuquén Province, 19 km N of Villa La Angostura on road N° 234 (CML 3242, ♂); Río Negro Province, Bariloche Isla Victoria 10 km E of Piedras Blancas (CML 5219).

Tadarida brasiliensis ($n = 9$) Argentina: Chubut Province, Trevelin in Welsh Chapel (LIEB-M 753, ♂; LIEB-M 758, ♂; LIEB-M 759, ♂; LIEB-M 760, ♂); Chubut Province, Ea. Las Vacas Pampas (LIEB-M 865, ♂); Chubut Province, National Park Los Alerces, Villa Futalauquen (LIEB-M 866, LIEB-M 1114, ♂); Chubut Province, Aldea Escolar, Provincial School N° 740 (LIEB-M 881, ♂); Chubut Province, Piedra Parada (MLP 31.XII.02.84).

APPENDIX II

Table with average, minimum and maximum values of the three data sets (external, wing and craniodental measurements in mm; S in mm² and body mass in g) for Patagonian bat species. Each data set is indicated with different shading. The number of specimens per species for each data set (external, wing and craniodental) is indicated in parentheses

Variables	<i>H. macrotus</i> (n = 31/31/21)			<i>H. magellanicus</i> (n = 11/11/8)			<i>H. montanus</i> (n = 8/8/5)			<i>L. varius</i> (n = 4/4/9)			<i>M. chiloiensis</i> (n = 31/31/25)			<i>T. brasiliensis</i> (n = 7/6/6)		
	X	Range	X	Range	X	Range	X	Range	X	Range	X	Range	X	Range	X	Range		
Weight	13.74	8.6–20	12.62	10.3–17.6	14.88	12–18	11.125	10.1–12.4	7.31	5.4–8.6	12.09	11–13.45						
LCC	61.89	53–70	64.45	59–69	64.88	57–74	52.25	49–57	46.48	39.5–54	61.43	56–66						
TL	54.18	47–62	48.82	43–57	49.00	45–53	50	45–53	39.37	34–45	37.43	31–42						
EL	32.48	30–35	24.18	23–25	28.50	27–30	12.75	12–14	13.52	11.5–15.5	13.71	12–16						
TrL	14.92	12–17	12.05	11–13	14.06	12–15	6.375	6–7	7.49	6.5–10	3.57	3–4						
FA	48.43	45.9–52.5	47.00	44.58–48.67	49.02	46.4–50.78	40.66	39.83–41.63	38.44	36.68–40.17	43.77	42–44.9						
TbL	20.38	18.5–22.11	20.60	18.68–22.03	20.82	18.3–21.78	20.16	19.49–21.62	16.25	14.82–17.22	13.13	12–14						
c	62	56–70	63	60–67	65	59–69	56	55–57	48	46–51	45	41–47						
B	321	288–346	307	297–318	305	287–329	294	283–305	240	223–251	296	271–308						
Lh	82	71–88	79	74–83	83	77–87	84	82–89	61	56–65	79	75–82						
S	15444	12072–17445	14467	12653–16732	15765	12399–17914	11269	10340–12109	9251	7821–10304	9372	8854–10144						
AR	6.69	5.93–7.26	6.55	5.85–7.21	5.96	5.40–6.75	7.66	7.43–7.97	6.22	5.56–7.04	9.42	7.59–10.64						
WL	8.70	6.17–12.39	8.54	7.05–11.38	9.25	8.21–9.96	9.81	8.51–10.90	7.76	6.30–9.81	12.69	11.65–13.99						
I	2.75	1.58–3.85	2.71	1.36–3.5	1.66	1.11–3.36	1.36	1.23–1.61	2.51	1.37–3.62	2.16	1.97–2.56						
CBL	17.96	17.09–18.69	17.38	17.01–17.84	17.97	17.58–18.24	12.93	12.22–13.32	13.88	13.46–14.44	16.53	15.75–17.69						
ZB	11.37	10.76–12.01	11.56	11.37–11.79	11.45	10.98–11.91	9.59	8.71–9.98	9.12	8.51–9.61	10.33	9.88–10.96						
HB	6.17	5.99–6.41	6.14	5.96–6.35	6.25	6.02–6.50	5.80	5.54–6.06	5.28	4.99–5.61	5.83	5.52–6.16						
MB	9.71	9.34–10.22	9.38	9.13–9.58	9.70	9.25–9.93	7.84	7.28–8.14	7.65	7.42–8.03	9.52	9.19–9.88						
MM	7.22	6.86–7.55	7.33	7.01–7.68	7.14	6.99–7.39	6.25	5.64–6.65	5.85	5.39–6.31	7.22	6.92–7.41						
CM3	6.55	6.15–6.81	6.72	6.53–6.95	6.59	6.48–6.69	4.64	4.41–4.79	5.62	5.31–5.81	6.34	6.11–6.51						
PC	4.69	4.37–4.93	4.57	4.41–4.73	4.72	4.58–4.82	4.62	4.38–4.76	3.98	3.71–4.17	4.26	4.12–4.44						
LR	4.87	4.51–5.45	5.03	4.83–5.26	4.90	4.64–5.05	2.64	2.35–3.18	4.86	4.56–5.48	4.72	4.59–4.91						
LP	8.49	8.03–8.85	8.41	7.87–8.91	8.43	8.18–8.79	5.48	4.71–6.16	7.35	6.77–7.99	7.21	6.92–7.47						
LUC	2.53	2.11–2.81	2.42	2.09–2.75	2.73	2.34–2.91	2.20	1.62–2.41	1.54	1.26–1.89	2.18	2.08–2.32						
CC	5.11	4.67–5.52	5.18	4.82–5.35	5.13	4.88–5.37	5.20	4.58–5.53	3.79	3.58–3.99	4.28	3.89–4.71						
HM	1.54	1.15–2.01	1.58	1.45–1.85	1.72	1.59–1.85	1.44	1.26–1.59	1.32	1.02–1.75	1.79	1.52–2.08						
LM	12.76	12.16–13.31	12.78	12.44–13.04	12.86	12.31–13.24	9.87	9.10–10.33	10.66	10.14–11.07	11.86	11.28–12.39						
LLC	2.25	1.82–2.88	2.18	1.94–2.33	2.30	2.18–2.44	1.95	1.69–2.22	1.15	0.77–1.53	2.10	1.86–2.31						
CM ₃	7.08	6.87–7.69	7.23	6.95–7.57	7.26	7.03–7.38	5.33	4.96–5.45	5.97	5.32–6.26	6.94	6.56–7.27						
HC1	4.04	3.75–4.36	3.97	3.81–4.11	4.01	3.86–4.11	2.83	2.13–3.17	2.93	2.75–3.23	3.33	3.24–3.44						
HC2	4.59	4.37–4.77	4.41	4.21–4.63	4.55	4.22–4.78	3.06	2.61–3.31	3.20	2.93–3.45	3.53	3.32–3.64						
HC3	3.75	3.46–4.09	3.72	3.51–4.04	3.74	3.49–3.87	2.88	2.65–3.39	2.69	2.54–2.91	3.25	3.09–3.46						