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Allometric patterns and evolution in Neotropical nectar-feeding bats (Chiroptera, Phyllostomidae)

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Within the neotropical bat family Phyllostomidae, species of the subfamilies Glossophaginae and Lonchophyllinae have many derived traits adapted to nectarivory, including elongated snouts and jaws and the ability to perform hovering flight. We compared patterns of cranial variation within and between these groups with respect to within-group allometric trajectories, based on 19 linear morphometric variables collected from 221 specimens representing all genera and 62% of the species in the two subfamilies. In a pooled principal component analysis, species belonging to Lonchophyllinae and Glossophaginae occupy similar regions in morphospace, though the latter species have a greater variance. Principal components and common principal components analyses for separate taxonomic lineages (subfamilies, tribes and subtribes) revealed distinct static allometric trajectories among these groups, with variables associated with elongation of the rostrum having distinct allometric coefficients. Our results indicate that distinct cranial morphotypes associated with the degree of elongation of the rostrum in phyllostomid nectarivores are allometrically characteristic of each lineage. The patterns suggest that cranial integration in phyllostomid nectarivores reflects primarily their phylogenetic history rather than adaptive pressures resulting from specialization to particular feeding resources.

Key words: allometry, craniometry, Glossophaginae, Lonchophyllinae, multivariate analysis

Introduction

The order Chiroptera is unique among mammals due to the presence of exclusive traits such as true flight abilities and a vast diversity of feeding habits. Bats represent the largest radiation of nectarivorous mammals (Feldhamer *et al.*, 2007) and are the main agents of pollination for hundreds of plant species, some of which are completely dependent on them for reproduction (Sazima *et al.*, 1999; Muchhala, 2006).

Among the order's 21 families, three include representatives that feed on pollen and nectar: Phyllostomidae Gray, 1825, Mystacinidae Dobson, 1875, and Pteropodidae Gray, 1821 (Nowak, 1994; Altringham, 1996; Arkins *et al.*, 1999). Within the Phyllostomidae, species of two subfamilies evolved a diet based mainly on nectar and show important morphological aspects correlated to this food strategy. Species belonging to subfamilies Glossophaginae Bonaparte, 1845 and Lonchophyllinae Griffiths, 1982 have elongated snouts, reduced teeth, long and extensible tongues, and the ability to perform hovered flight, among other derived traits (Nowak, 1994; Freeman, 1995; Nogueira *et al.*, 2007).

Glossophaginae and Lonchophyllinae are represented by 19 genera and 53 extant species, ranging from southwestern United States to South America as far as southern Brazil and northern Argentina (Simmons, 2005; Griffiths and Gardner, 2008*a*, 2008*b*; Mantilla-Meluk and Baker, 2010; Nogueira *et al.*, 2014; Parlos *et al.*, 2014). They have been the object of various studies in taxonomy (Dias *et al.*, 2013; Parlos *et al.*, 2014), ecology (Sampaio *et al.*, 2003; Faria, 2006), conservation (Arita and Santos-del-Prado, 1999; Hutson *et al.*, 2001) and phylogeny (Wetterer *et al.*, 2000; Baker *et al.*, 2003; Datzmann *et al.*, 2010).

The current classification of the phyllostomid nectar-feeding bats reflects the monophyletic groups identified by Baker *et al.* (2003), who recognized independent genetic lineages in the family as

subfamilies, tribes, and subtribes. Their study supported an independent origin for nectarivory among the Phyllostomidae, since Glossophaginae and Lonchophyllinae do not form a monophyletic group (Baker *et al.*, 2003). Based on molecular data, Datzmann *et al.* (2010) later suggested an earlier divergence for Glossophaginae with respect to the Lonchophyllinae.

Recent studies have focused on the association between cranial morphology and diet of nectar-feeding bats, as well as on their phylogenetic relationships (e.g., Freeman, 1995; Wetterer *et al.*, 2000; Baker *et al.*, 2003; Winter and von Helversen, 2003; Dumont, 2004; Muchhala, 2006; Tschapka *et al.*, 2008; Datzmann *et al.*, 2010; Mancina and Balseiro, 2010; Monteiro and Nogueira, 2011). However, no study has addressed the cranial variation of Neotropical nectar-feeding bats using an explicit allometric framework. A comprehensive sampling of the taxonomic diversity within and among the genetic lineages of nectarivorous bats would allow a comparative analysis of cranial allometries from an evolutionary perspective.

Against this background, the objective of this study was to identify the main trends of cranial morphometric variation based on the widest possible sampling of Neotropical nectar-feeding bats, in order to allow comparisons between the two subfamilies with respect to the diversity of cranial variation patterns and the allometric relationships in each group.

Materials and Methods

A total of 221 adult specimens belonging to 19 genera and 33 species of Neotropical nectar-feeding bats were analyzed (Table 1 and Appendix). This sample includes all genera and 62% of the species described for the group. Sample size varied from two to ten specimens for each species except for *Hsunycteris thomasi*, *Lonchophylla handleyi* and *Scleronycteris ega*, which are represented by single specimens.

The identification of specimens was confirmed by consulting taxonomic keys, revisions of genera, species descriptions, and other taxonomic studies (e.g., Handley, 1960; Arroyo-Cabrales *et al.*, 1987; Pfrimmer Hensley and Wilkins, 1988; Webster, 1993; Timm and Genoways, 2003; Woodman, 2007; Reid, 2009). External, cranial and dental characters that had been reported as diagnostic in previous studies were investigated. Cranial and dental characters were measured with the use of a stereoscopic microscope.

Analyzed specimens are deposited in the following scientific collections: Coleção Adriano Lúcio Peracchi, Universidade Federal Rural do Rio de Janeiro, Seropédica, Brasil (ALP); Museum of Texas Tech University, Lubbock, USA (TTU); American Museum of Natural History, New York, USA (AMNH); and National Museum of Natural History, Washington, DC, USA (USNM).

Nineteen cranial characters were measured (in mm) for each specimen using a digital caliper accurate to 0.01 mm, based on descriptions of Taddei *et al.* (1998), Van Cakenberghe *et al.* (2002) and De Blase and Martin (1981). The characters and their abbreviations are defined as follows: greatest length of skull (GLS), from the most anterior region of the upper internal incisors to the most posterior region of the occipital; condyle-incisive length (CIL), from the distal point of the occipital condyles to the tips of the upper internal incisors; zygomatic breadth (ZB), the greatest distance across the outer margins of the zygomatic arches; mastoid breadth (MAB), the greatest

Table 1. Species of Neotropical nectar-feeding bats analyzed in the present study

Taxon	Total
Subfamily Glossophaginae	
Tribe Brachyphyllini	
Brachyphylla cavernarum Gray, 1834	10
Tribe Choeronycterini	
Subtribe Anourina	
Anoura caudifer (E. Geoffroy, 1818)	10
A. geoffroyi Gray, 1838	10
Subtribe Choeronycterina	
Choeroniscus godmani (Thomas, 1903)	3
C. minor (Peters, 1868)	10
C. mexicana Tschudi, 1844	10
Dryadonycteris capixaba Nogueira, Lima, Peracchi and Simmons, 2012	3
Hylonycteris underwoodi Thomas, 1903	5
Lichonycteris obscura Thomas, 1895	10
Musonycteris harrisoni Schaldach and McLaughlin, 1960	5
Scleronycteris ega Thomas, 1912	1
Tribe Glossophagini	
Glossophaga commissarisi Gardner, 1962	8
G. leachii (Gray, 1844)	10
G. longirostris Miller, 1898	3
G. morenoi Martínez and Villa-R., 1938	8
G. soricina (Pallas, 1766)	10
Leptonycteris nivalis (Saussure, 1860)	10
L. yerbabuenae Martínez and Villa-R., 1940	10
Monophyllus plethodon Miller, 1900	10
M. redmani Leach, 1821	10
Tribe Phyllonycterini	
Erophylla bombifrons (Miller, 1899)	10
E. sezekorni (Gundlach, 1861)	6
Phyllonycteris aphylla (Miller, 1898)	10
P. poeyi Gundlach, 1861	5
Subfamily Lonchophyllinae	
Tribe Hsunycterini	
Hsunycteris cadenai (Woodman and Timm, 2006)	5
H. thomasi (J. A. Allen, 1904)	1
Tribe Lonchophyllini	
Lionycteris spurrelli Thomas, 1913	4
Lonchophylla concava Goldman, 1914	3
L. handleyi Hill, 1980	1
L. peracchii Dias, Esbérard and Moratelli, 2013	10
L. robusta Miller, 1912	5
Platalina genovensium Thomas, 1928	3
Xeronycteris vieirai Gregorin and Ditchfield, 2005	2
Total	221

distance across the mastoid region; braincase breadth (BCB), the greatest breadth of the globular part of the braincase; interorbital breadth (IOB), the smallest distance between the orbits; braincase height (BCH), from the deepest point of basioccipital to the highest point of the parietal, sagittal crest discarded; palatal length (PAL), from the posterior margin of the hard palate to the tips of the upper internal incisors; maxillary toothrow length (MTL), from the anterior surface of the upper canine to the posterior surface of M^3; breadth across molars (BAM), the greatest distance across outer edges of the crowns of the last upper molars; breadth across canines (BAC), the greatest distance across outer edges of the crowns of upper canines; postpalatal length (PPL), from the anterior margin of the foramen magnum to the posterior margin of the bony palate; tympanic bullae length (TBL), the greatest length of the bulla; tympanic bullae breadth (TBB), the greatest breadth of the bulla; mandibular length (MAL), from the most anterior region of the internal incisors to the condyle process; mandibular toothrow length (MAN), from the anterior surface of the lower canine to the posterior surface of M_3; coronoid height (CH), from the highest point of the coronoid process to the inferior surface of the mandible; coronoid-condyle distance (CCD), from the coronoid process to a line connecting the condyle processes; and condyle-angular distance (CAD), from a line connecting the condyles processes to the angular process.

All variables were log-transformed prior to statistical analyses. Because multivariate analyses require complete datasets, missing data (1.86% of total dataset) were imputed from the original data using the Expectation Maximization (EM) algorithm (Strauss *et al.*, 2003). A principal components analysis (PCA) of the entire data matrix, including the species of both subfamilies, was performed to summarize trends of variation in cranial size and shape. Confidence intervals (95%) for PCA loadings were estimated from sampling distributions based on 1000 bootstrap iterations.

Another PCA was implemented separately for each taxonomic lineage represented in the total sample (Anourina, Choeronycterina, Glossophagini, Lonchophyllinae, Brachyphyllini and Phyllonycterini) to estimate multivariate allometric coefficients for each lineage. To the extent that the first principal component (PC) represents a size axis, allometric relationships among variables and the latent variable size can be estimated from the loadings (scaled coefficients) of the first PC (Jolicoeur, 1963). Isometry is the special case in which all loadings have the same magnitude, estimated by dividing 1 by the square root of p, where p is the number of variables in the analysis (Jolicoeur, 1963; Weston, 2003). In order to facilitate the interpretation of the results, we followed Strauss and Bookstein (1982) in scaling the coefficients of the first PC to a mean of 1 and considering a variable to be isometric when its allometric coefficient is equal to 1 ($\alpha = 1$), positively allometric when its coefficient is greater than 1 ($\alpha > 1$), and negatively allometric when its coefficient is between 0 and 1. Confidence intervals (95%) for the allometric coefficients were scaled from corresponding bootstrapped confidence intervals for the coefficients of the first PC. If a confidence interval does not include the isometric value 1, then the corresponding allometric coefficient can be considered to be significantly allometric. Multivariate allometric coefficients can be compared among groups only if the loadings of the first PC have similar signs and magnitudes for all groups in the analysis. This condition can be verified for each pair of groups by estimating the vector correlation coefficient, defined as the inner product of their first PCs (Morrison, 1990), which approaches 1 when vectors are similar and zero when vectors are orthogonal (Reis *et al.*, 1988).

A reduced matrix including the lineages with comparable multivariate allometric coefficients was then submitted to a common principal component analysis (CPCA) to examine the trajectories of static cranial allometry in these lineages. CPCA is more suitable for data from extrinsically defined groups (the lineages in this case) to take into account both the variance contained among and within groups (Flury, 1984; Eslami *et al.*, 2013). Allometric trajectories for each lineage were estimated by major axis regression of scores in the first two CPCs, following Warton *et al.* (2006). Statistical procedures were performed using the program R v3.0.1 (2013-05-16), using function Amelia, in package Amelia (King *et al.*, 2001; Honaker *et al.*, 2011) for missing data imputation; function prcomp, in package Stats (Mardia *et al.*, 1979; Becker *et al.*, 1988; Venables and Ripley, 2002) for PCA; and function fcpca, in package Multigroup (Flury, 1984; Eslami *et al.*, 2013) for CPCA.

Results

Principal Components Analysis

The first two PCs of the complete matrix (PC1 and PC2) account for 91.0% of the total variation (Table 2). PC1 accounts for 76.4% of the total variation. All PC1 loadings are positive and of high magnitude, and thus can be interpreted as a general size axis. Confidence intervals for loadings do not overlap with zero for any of the 19 variables,

Table 2. Eigenvector coefficients (loadings) for the first two principal components (PC1 and PC2) for the pooled sample of Glossophaginae and Lonchophyllinae species. Bounds in brackets are 95% confidence intervals for loadings; values in parentheses are percentages of variance accounted for by principal components

Characters	PC1 (76.4)	PC2 (14.6)
GLS	0.20 [0.18–0.22]	0.23 [0.20–0.24]
CIL	0.19 [0.17–0.22]	0.28 [0.26–0.30]
ZB	0.23 [0.21–0.24]	-0.15 [-0.17– -0.13]
MAB	0.21 [0.20–0.22]	-0.09 [-0.12– -0.06]
BCB	0.17 [0.15–0.19]	-0.03 [-0.06–0.01]
IOB	0.28 [0.25–0.30]	-0.28 [-0.31– -0.25]
BCH	0.18 [0.16–0.20]	-0.10 [-0.13– -0.08]
PAL	0.14 [0.11–0.19]	0.55 [0.53–0.58]
MTL	0.21 [0.19–0.24]	0.34 [0.32–0.36]
BAM	0.29 [0.26–0.31]	-0.26 [-0.30– -0.23]
BAC	0.27 [0.26–0.29]	-0.20 [-0.24– -0.17]
PPL	0.26 [0.24–0.29]	-0.08 [-0.14– -0.04]
TBL	0.18 [0.16–0.20]	-0.01 [-0.04–0.03]
TBB	0.16 [0.15–0.17]	-0.03 [-0.06– -0.01]
MAL	0.21 [0.19–0.24]	0.32 [0.30–0.34]
MAN	0.22 [0.20–0.25]	0.29 [0.26–0.31]
CH	0.28 [0.25–0.30]	-0.03 [-0.07–0.01]
CCD	0.26 [0.24–0.27]	-0.06 [-0.11–0.00]
CAD	0.32 [0.28–0.35]	-0.12 [-0.18– -0.07]

indicating that all individual loadings are statistically significant. The seven characters having the highest loadings are: condyle-angular distance (CAD), breadth across molars (BAM), coronoid height (CH), interorbital breadth (IOB), breadth across canines (BAC), postpalatal length (PPL) and coronoid-condyle distance (CCD). These characters contribute to the distinction of species in three main groups of clusters in relation to PC1 (as numbered in Fig. 1), the first including smaller- to medium-sized nectarivorous (*Lichonycteris obscura* [8], *Monophyllus redmani* [19], *Lionycteris spurrelli* [22], *Choeroniscus godmani* [3], *Dryadonycteris capixaba* [6], *Scleronycteris ega* [10], *Hylonycteris underwoodi* [7], *Choeroniscus minor* [4], *Glossophaga commissarisi* [11], *G. leachii* [12], *G. longirostris* [13], *G. morenoi* [14], *G. soricina* [15], *Hsunycteris cadenai* [20], *H. thomasi* [21], *Monophyllus plethodon* [18], *Anoura caudifer* [1], *Lonchophylla concava* [23], *L. peracchii* [25] and *Xeronycteris vieirai* [28]); the second cluster including larger species (*Musonycteris harrisoni* [9], *Choeronycteris mexicana* [5], *Platalina genovensium* [27], *Lonchophylla robusta* [26], *L. handleyi* [24], *Leptonycteris nivalis* [16], *L. yerbabuenae* [17], *Anoura geoffroyi* [2], *Erophylla bombifrons* [30], *E. sezekorni* [31], *Phyllonycteris aphylla* [32] and *P. poeyi* [33]); and the third cluster separating *Brachyphylla cavernarum* [29] from all other species. Individual PC scores for *B. cavernarum* are the largest on PC1 and are quite separated along this axis from those of remaining species (Table 2 and Fig. 1).

PC2 accounts for 14.6% of the total variation; loadings are both positive and negative and PC2 can therefore be interpreted as a shape axis. Except for braincase breadth (BCB), tympanic bullae length (TBL), coronoid height (CH) and coronoid-condyle distance (CCD), which are not statistically

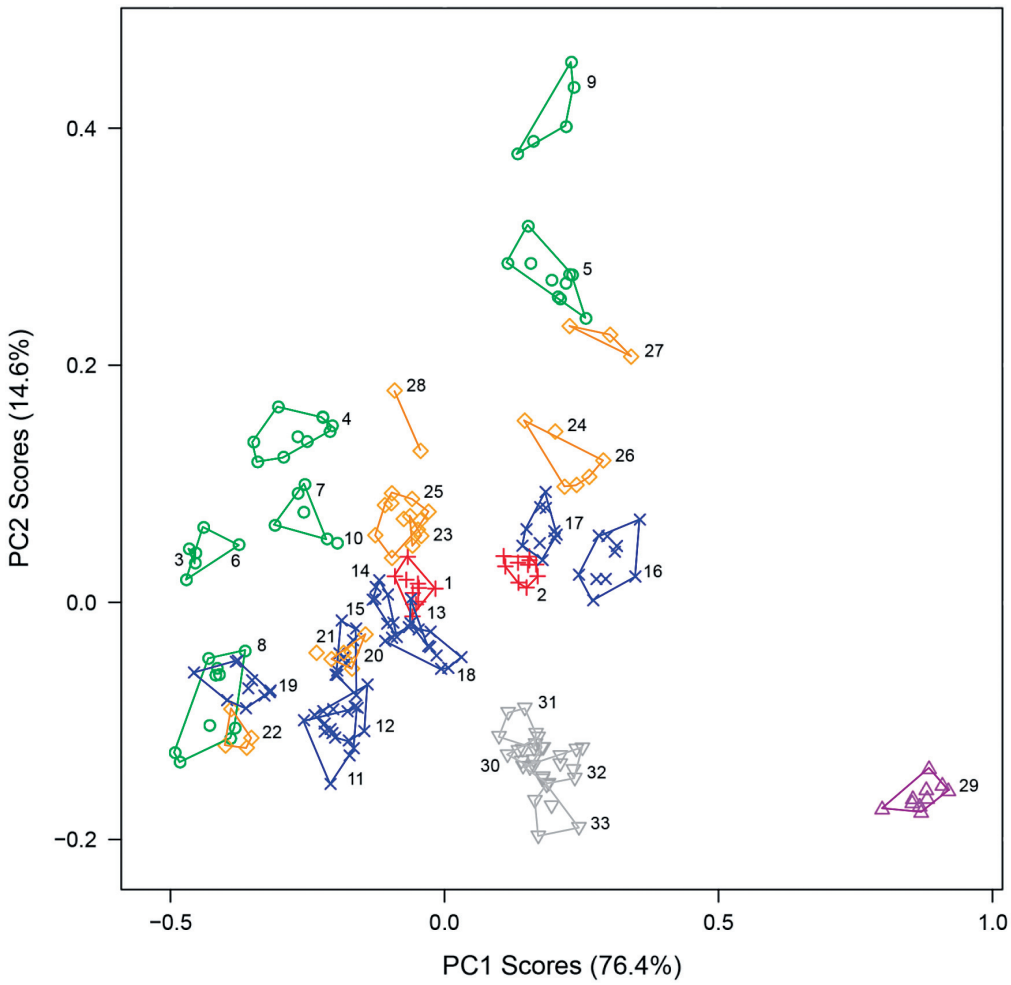

FIG. 1. Scatter plot of PCA for the pooled sample of Glossophaginae and Lonchophyllinae species. Symbols and colors represent lineages of Neotropical nectar-feeding bats as follows: + Anourina, ○ Choeronycterina, × Glossophagini, ◇ Lonchophyllinae, △ Brachyphyllini, ▽ Phyllonycterini. See group numbers in text

significant, all 15 other cranial characters have confidence intervals for loadings not overlapping with zero. Five of these present the highest positive loadings: palatal length (PAL), maxillary toothrow length (MTL), mandibular length (MAL), mandibular toothrow length (MAN) and condyle-incisive length (CIL). Interorbital breadth (IOB) has the highest negative loading. These characters contribute to differentiation along PC2, with clusters belonging to *M. harrisoni* [9], *C. mexicana* [5], and *P. genovensium* [27] separated from all other species (Table 2 and Fig. 1).

Although the inclusion of *B. cavernarum* [29] in this analysis notably influenced the variance summarized by PC1 and evidently hampered a clearer pattern of distribution of PC scores of the remaining species, it is possible to identify a pattern of craniometric variation in the assemblage analyzed. PC scores of each species are grouped in distinct clusters with the multivariate space defined by PC1 × PC2, despite some overlap in scores (Fig. 1). Among the smallest forms, *L. obscura* [8] partially overlaps with *M. redmani* [19] and *L. spurrelli* [22], while *C. godmani* [3] overlaps with *D. capixaba* [6], and *S. ega* [10] overlaps with *H. underwoodi* [7]. Scores of *G. commissarisi* [11] overlap with those of *G. leachii* [12], while *G. soricina* [15] scores overlap with those of *H. cadenai* [20], and scores of *G. longirostris* [13] and *G. morenoi* [14] form a cluster that overlap with scores of *A. caudifer* [1] and *M. plethodon* [18]. Scores of *L. concava* [23] overlap with those of *L. peracchii* [25], and scores of *L. handleyi* [24] overlap with those of *L. robusta* [26]. Scores of *L. yerbabuenae* [17] overlap with those of *A. geoffroyi* [2] rather than to those of *L. nivalis* [16]. Finally, scores of *E. bombifrons* [30] overlap with those of *E. sezekorni* [31] and *P. aphylla* [32].

As expected, PC scores of some congeneric species are distributed into separate clusters. This is the case for species pairs *C. godmani* [3]/*C. minor* [4], *M. plethodon* [18]/*M. redmani* [19], and *A. caudifer* [1]/*A. geoffroyi* [2], reflecting the remarkable intrageneric morphological variation present in skulls of these species.

It is also noteworthy that PC scores belonging to species of distinct subfamilies occupy similar regions in the PC1 × PC2 space. Thus, among the smallest forms, scores of *L. spurrelli* [22] of the subfamily Lonchophyllinae overlap with scores of *L. obscura* [8] of the subfamily Glossophaginae. Likewise, among medium-sized forms, *H. cadenai* [20] scores overlap with those of *G. soricina* [15].

A wider spectrum of morphometric variation was revealed within the Glossophaginae than in the Lonchophyllinae sampled in our study (Fig. 1). PC scores of the Lonchophyllinae (*L. spurrelli* [22], *H. cadenai* [20], *H. thomasi* [21], *L. concava* [23], *L. peracchii* [25], *L. robusta* [26], *L. handleyi* [24], *X. vieirai* [28] and *P. genovensium* [27]) are distributed along the same direction in the multivariate space defined by PC1 × PC2. On the other hand, Glossophaginae forms are distributed more widely in this multivariate space. PC scores of *Monophyllus* spp. [18 and 19], *Glossophaga* spp. [11 to 15], *Anoura* spp. [1 and 2] and *Leptonycteris* spp. [16 and 17] are distributed in a similar direction occupied by the Lonchophyllinae, but occupy a lower part of the multivariate space defined by PC1 × PC2. PC score groups referable to *L. obscura* [8], *H. underwoodi* [7], *Choeroniscus* spp. [3 and 4], *D. capixaba* [6], *S. ega* [10], *C. mexicana* [5] and *M. harrisoni* [9], also distributed along a straight line almost parallel to that of the Lonchophyllinae, occupy the upper part of PC1 × PC2 plot. Finally, *Erophylla* spp. [30 and 31] and *Phyllonycteris* spp. [32 and 33], large Glossophaginae that presented low PC scores in PC2, occupy a distinct part of the morphometric space, nearer to that occupied by PC scores of *B. cavernarum* [29], representing a distinct cranial morphology in this subfamily.

These results prompted an investigation of the static cranial allometric trajectories of the distinct lineages of Neotropical nectar-feeding bats represented in our sample, namely the Choeronycterini (including Anourina and Choeronycterina), Glossophagini, Lonchophyllinae, Brachyphyllini and Phyllonycterini (Table 1).

Principal Components Analysis and Multivariate Allometric Coefficients

Separate PC1 axes accounted for 81.9% of the total variation in Anourina, 90.3% in Choeronycterina, 85.5% in Glossophagini, 83.8% in Lonchophyllinae. For Brachyphyllini and Phyllonycterini the variation summarized by PC1 was lower (respectively 40.0% and 51.1%). All PC1 loadings within these five samples have the same signs (but being negative for Brachyphyllini), and can therefore be interpreted as a general size axis. PC1 loadings differ for Phyllonycterini by the presence of variable signs, and can therefore be interpreted as a shape axis (Table 3).

Vector correlation coefficients confirm that loadings of PC1 are similar among all lineages consid-

TABLE 3. Eigenvector coefficients (loadings) for the first principal component (PC1) for each lineage of Neotropical nectar-feeding bats. Values of percent variance explained are in parentheses

Characters	Anourina (81.9)	Choeronycterina (90.3)	Glossophagini (85.5)	Lonchophyllinae (83.8)	Brachyphyllini (40.0)	Phyllonycterini (51.1)
GLS	0.21	0.29	0.25	0.26	-0.27	0.13
CIL	0.22	0.29	0.28	0.27	-0.25	0.11
ZB	0.21	0.12	0.17	0.16	-0.17	-0.02
MAB	0.20	0.12	0.22	0.19	-0.26	0.12
BCB	0.19	0.11	0.21	0.15	-0.01	0.05
IOB	0.18	0.10	0.16	0.22	-0.21	0.22
BCH	0.19	0.11	0.13	0.12	-0.04	-0.33
PAL	0.05	0.35	0.30	0.36	-0.27	0.03
MTL	0.31	0.38	0.21	0.33	-0.14	-0.06
BAM	0.14	0.13	0.22	0.15	-0.20	0.20
BAC	0.26	0.15	0.22	0.16	-0.26	0.33
PPL	0.48	0.21	0.28	0.17	-0.29	0.09
TBL	0.19	0.17	0.25	0.16	-0.27	0.10
TBB	0.12	0.14	0.16	0.16	-0.05	0.28
MAL	0.17	0.33	0.27	0.31	-0.24	0.00
MAN	0.30	0.37	0.21	0.34	-0.26	0.00
CH	0.25	0.20	0.23	0.24	-0.35	0.28
CCD	0.10	0.21	0.23	0.23	-0.31	0.55
CAD	0.26	0.19	0.27	0.16	-0.17	0.40

ered in the analyses except Phyllonycterini, which was then excluded from subsequent analysis (Table 4). Brachyphyllini was also excluded due to its peculiar and more generalist cranial morphology, since the purpose here was to show allometric pattern for more specialized nectar-feeding species. Results for remaining lineages (Table 5) are as follows: 1) In Anourina, variables postpalatal length (PPL), maxillary toothrow length (MTL) and mandibular toothrow length (MAN) have high positive allometric coefficients and variables palatal length (PAL) and coronoid-condyle distance (CCD) have high negative allometric coefficients; 2) Multivariate allometric coefficients obtained for Choeronycterina indicated that variables maxillary toothrow length (MTL), mandibular toothrow length (MAN), palatal length (PAL) and mandibular length (MAL) have the highest positive allometric coefficients; variables interorbital breadth (IOB) and braincase breadth (BCB) have the highest negative allometric coefficients; 3) The same pattern of positive allometry observed for Choeronycterina was found for Lonchophyllinae, and the highest negative allometric coefficients were observed in variables braincase height (BCH) and braincase breadth (BCB); 4) For Glossophagini, variables palatal length (PAL), condyle-incisive length (CIL), postpalatal length (PPL) and mandibular length (MAL) have high positive allometric coefficients and variables braincase height (BCH) and interorbital breadth (IOB) have high negative allometric coefficients.

Our data show distinct static allometry patterns among the lineages analyzed. It is also noteworthy that variables associated with the elongation of the rostrum, such as palatal length (PAL), maxillary toothrow length (MTL), mandibular length (MAL) and mandibular toothrow length (MAN), have high positive allometric coefficients in most lineages, except for Glossophagini, which shows isometric coefficients for the variables maxillary toothrow length (MTL) and mandibular toothrow length (MAN), and

TABLE 4. Vector correlation coefficients for all pairs of lineages of Neotropical nectar-feeding bats studied

Lineages	Anourina	Choeronycterina	Glossophagini	Lonchophyllinae	Brachyphyllini	Phyllonycterini
Anourina	1					
Choeronycterina	0.86	1				
Glossophagini	0.91	0.94	1			
Lonchophyllinae	0.87	0.98	0.96	1		
Brachyphyllini	-0.87	-0.90	-0.94	-0.92	1	
Phyllonycterini	0.47	0.45	0.59	0.51	-0.65	1

TABLE 5. Multivariate allometric coefficients for each lineage of Neotropical nectar-feeding bats. Confidence intervals under the null hypothesis of isometry are provided

Characters	Anourina	Choeronycterina	Glossophagini	Lonchophyllinae
GLS	0.98 [0.88–1.08]	1.39 [1.34–1.43]	1.10 [1.04–1.16]	1.18 [1.06–1.28]
CIL	1.05 [0.97–1.12]	1.40 [1.34–1.44]	1.23 [1.16–1.30]	1.24 [1.13–1.33]
ZB	0.99 [0.81–1.17]	0.58 [0.48–0.69]	0.77 [0.72–0.81]	0.73 [0.60–0.86]
MAB	0.97 [0.82–1.10]	0.58 [0.49–0.66]	0.99 [0.93–1.04]	0.88 [0.78–0.97]
BCB	0.88 [0.78–0.97]	0.51 [0.42–0.60]	0.94 [0.73–1.34]	0.67 [0.54–0.79]
IOB	0.86 [0.57–1.12]	0.47 [0.34–0.62]	0.70 [0.62–0.78]	1.02 [0.88–1.17]
BCH	0.91 [0.59–1.20]	0.54 [0.45–0.63]	0.58 [0.51–0.66]	0.53 [0.43–0.64]
PAL	0.23 [0.00–0.47]	1.67 [1.51–1.81]	1.32 [1.24–1.40]	1.64 [1.40–1.83]
MTL	1.46 [1.30–1.61]	1.82 [1.74–1.88]	0.95 [0.88–1.03]	1.52 [1.42–1.65]
BAM	0.65 [0.38–0.88]	0.60 [0.44–0.75]	0.99 [0.90–1.08]	0.70 [0.41–1.02]
BAC	1.21 [0.98–1.39]	0.72 [0.63–0.82]	0.98 [0.90–1.06]	0.76 [0.57–0.89]
PPL	2.26 [1.81–2.59]	1.03 [0.89–1.17]	1.22 [1.02–1.42]	0.78 [0.55–1.01]
TBL	0.91 [0.68–1.16]	0.80 [0.70–0.92]	1.09 [1.00–1.16]	0.72 [0.53–0.92]
TBB	0.57 [0.37–0.79]	0.66 [0.57–0.76]	0.72 [0.63–0.80]	0.71 [0.62–0.80]
MAL	0.80 [0.67–0.91]	1.57 [1.49–1.63]	1.22 [1.16–1.27]	1.44 [1.29–1.57]
MAN	1.42 [1.30–1.54]	1.79 [1.72–1.85]	0.95 [0.90–1.01]	1.56 [1.46–1.67]
CH	1.17 [0.84–1.44]	0.95 [0.83–1.06]	1.00 [0.86–1.14]	1.13 [0.86–1.35]
CCD	0.47 [0.12–0.78]	1.01 [0.89–1.13]	1.02 [0.95–1.09]	1.04 [0.67–1.32]
CAD	1.22 [0.85–1.58]	0.90 [0.78–1.01]	1.21 [1.08–1.33]	0.73 [0.55–0.87]

Anourina, which shows negative allometry in the variables palatal length (PAL) and mandibular length (MAL).

Common Principal Components Analysis and Trajectories of Static Allometry

The first two CPCs of the partial data matrix (CPC1 and CPC2) accounted for 78.2% of the total variation in Anourina, 93.9% in Choeronycterina, 84.2% in Glossophagini, and 85.3% in Lonchophyllinae (Table 6). All CPC1 loadings have the same sign, and can therefore be interpreted as a general size axis. The variables heavily loaded on CPC1 are maxillary toothrow length (MTL) and mandibular toothrow length (MAN). CPC2 loadings are both positive and negative, and can therefore be interpreted as a shape axis. The variable palatal length (PAL) presents the highest negative loadings and the variable postpalatal length (PPL) presents the highest positive loadings on CPC2 axis (Table 6).

CPC scores of three lineages (Choeronycterina, Glossophagini and Lonchophyllinae) distributed along the multivariate space defined by CPC1 × CPC2 partially overlap among the smaller nectarivorous species. Conversely, CPC scores of Anourina overlap with those of Glossophagini and Lonchophyllinae, rather than to those of Choeronycterina (Fig. 2).

The major axis regression of scores of CPCA for each lineage of this partial data matrix reveals that the slope of the regression line in Choeronycterina is steeper than the others, followed by the Lonchophyllinae, which has similar but smaller slope, and by the Glossophagini and Anourina, in

TABLE 6. Eigenvector coefficients (loadings) for the first two common principal components (CPC1 and CPC2) for lineages of Neotropical nectar-feeding bats. Percentages of variance explained are also provided

Characters	CPC1	CPC2
GLS	0.25	-0.17
CIL	0.27	-0.17
ZB	0.17	0.20
MAB	0.18	0.17
BCB	0.15	0.13
IOB	0.17	0.24
BCH	0.13	0.12
PAL	0.26	-0.51
MTL	0.33	-0.19
BAM	0.16	0.09
BAC	0.22	0.31
PPL	0.28	0.32
TBL	0.20	0.17
TBB	0.15	0.08
MAL	0.27	-0.30
MAN	0.33	-0.19
CH	0.26	0.30
CCD	0.21	-0.14
CAD	0.22	0.08
Anourina (%)	71.7	6.5
Choeronycterina (%)	86.2	7.7
Glossophagini (%)	81.7	2.5
Lonchophyllinae (%)	80.7	4.6

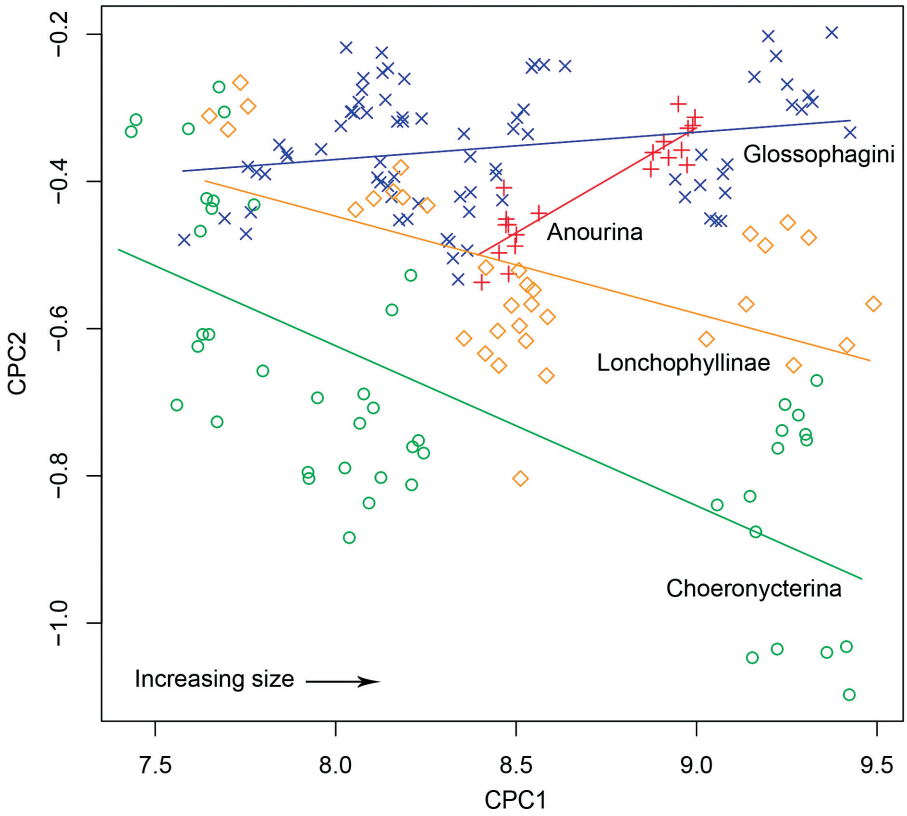

FIG. 2. Trajectories of static allometry for each lineage of Neotropical nectar-feeding bats described through major axis regression of scores in the first two common principal components. Symbols and colors represent lineages of Neotropical nectar-feeding bats as follows: + Anourina, ○ Choeronycterina, × Glossophagini, ◇ Lonchophyllinae

which the trajectories vary from almost horizontal to tightly positive (Fig. 2).

It is interesting to note that the static allometric trajectory of Anourina is more similar to that of Glossophagini than to the Choeronycterina. Finally, it is also noteworthy that the trajectories for the four lineages are divergent, with smaller species being more similar in cranial morphology than the large ones, presenting therefore larger shape differences with increasing size (Fig. 2).

DISCUSSION

This study investigated the main trends of cranial morphometric variation in Neotropical nectar-feeding bats, by comparing cranial variation patterns and allometric relationships among its distinct taxonomic lineages.

Cranial Variation Patterns

A PCA of the complete data matrix showed that the position of *B. cavernarum* [29], which is completely separated from all other species, can be related to its broad rostrum and robust mandibular processes (Table 2 and Fig. 1). This unusual cranial pattern indicates a less specialized form of nectarivorous bat. This species has been reported as a bat that feeds on pollen, fruit and insects (Gardner, 1977; Swanepoel and Genoways, 1983). Morphological similarities between *B. cavernarum* and frugivorous species have been discussed in previous studies (e.g., Griffiths, 1985; Freeman, 1995). In addition, *B. cavernarum* was positioned between frugivorous and insectivorous species in a recent geometric morphometric analysis (Monteiro and Nogueira, 2011).

In contrast, extreme nectarivory is traditionally associated with a long and narrow rostrum (Freeman, 1995; Dumont, 2004). Among the species included in this study, a pattern of extreme cranial elongation was shown for *M. harrisoni* [9], followed by *C. mexicana* [5] and *P. genovensium* [27] (Table 2 and Fig. 1). These results corroborate previous studies that indicated a nectarivorous diet for *M. harrisoni* and *C. mexicana* (Gardner, 1977; Arroyo-Cabrales *et al.*, 1987; Tschapka *et al.*, 2008), despite recent findings of soft parts of insects (Lepidoptera) in fecal samples of two *M. harrisoni* (see Tschapka *et al.*, 2008) and remains of cacti fruit

inside the mouths of four individuals of *C. mexicana* (see Villa-R., 1967). These animals could have eaten these items by chance while feeding on nectar. Skull morphology varies greatly between species that feed on hard items and soft items (Freeman, 1979). Therefore, even if these bats feed on fruit and insects, they most likely concentrate on the soft parts of these items. Little is known about the diet of the rare *P. genovensium*, but studies have shown that it is associated with flowers of columnar cacti (Sahley and Baraybar, 1996; Velazco *et al.*, 2013).

Xeronycteris vieirai [28] also shows a great elongation of the rostrum, despite the fact that it is smaller than *M. harrisoni* [9], *C. mexicana* [5] and *P. genovensium* [27] (Table 2 and Fig. 1). The diet of this species is unknown (Gregorin and Ditchfield, 2005; Nogueira *et al.*, 2007). However, based on lingual characters and extreme reduction of teeth, Gregorin and Ditchfield (2005) stated that *X. vieirai* may have a predominantly liquid diet. The pattern shown in the present study corroborates their hypothesis.

The remaining species occupying a gradient along PC2 between the morphological extremes represented by *Musonycteris* [9], *Choeronycteris* [5], *Platalina* [27] and *Brachyphylla* [29], *Erophylla* [30 and 31], *Phyllonycteris* [32 and 33], show a less specialized nectarivore morphology, which probably allows them to complement their diet with fruit and insects (Table 2 and Fig. 1). These inferences are in agreement with previous studies based on the analysis of stomach contents, fecal samples and literature review (e.g., Fleming *et al.*, 1972; Gardner, 1977; Rivas-Pava *et al.*, 1996; Tschapka, 2004; Soto-Centeno and Kurta, 2006; Mancina, 2010; Barros *et al.*, 2013).

PC scores of species belonging to subfamilies Lonchophyllinae and Glossophaginae occupy similar regions in the morphometric space defined by PC1 × PC2, although PC scores of Glossophaginae are of greater variance (Fig. 1). Based on molecular data, Baker *et al.* (2003) classified the phyllostomid nectar-feeding bats in two subfamilies, Glossophaginae and Lonchophyllinae, and postulated an independent origin for nectarivory (Fig. 3). These findings were later corroborated by Datzmann *et al.* (2010), who suggested an earlier divergence for Glossophaginae than for Lonchophyllinae, with different genera of Glossophaginae appearing in the Late Oligocene, while genera in Lonchophyllinae originated later in the Middle Miocene. The evolutionary history of Glossophaginae produced three times more genera and twice the number of species (14 genera and 35 species) than the subfamily Lonchophyllinae (five genera and 18 species). Glossophaginae also shows a broader geographical distribution, ranging from United States through Central America and Antilles to South America, whereas Lonchophyllinae species range from Central to South America (Simmons, 2005; Griffiths and Gardner, 2008*a*, 2008*b*; Mantilla-Meluk and Baker, 2010; Nogueira *et al.*, 2014; Parlos *et al.*, 2014). Similar distributions of PC scores observed in the morphometric space reflect convergence with respect to the nectarivore feeding habit between Glossophaginae and Lonchophyllinae. Likewise, the wider dispersion of PC scores of Glossophaginae with respect to those of the Lonchophyllinae is in agreement with its earlier divergence and greater taxonomic diversity.

It is also noteworthy that the distribution of PC scores observed for Glossophaginae and Lonchophyllinae partially reflects phylogenetic relationships for these groups (Baker *et al.*, 2003; Fig. 3). Two main clades are recognized in Glossophaginae: one containing *Anoura*, *Hylonycteris*, *Choeroniscus*, *Choeronycteris*, *Musonycteris*, *Lichonycteris* and *Scleronycteris*, and the other formed by *Brachyphylla*, *Erophylla*, *Phyllonycteris*, *Monophyllus*, *Glossophaga* and *Leptonycteris*. Members of the former molecular clade are classified in tribe Choeronycterini. Morphologically, members of this tribe share the absence of lower incisors. Members of the other molecular clade are classified in tribes Brachyphyllini (*Brachyphylla*), Phyllonycterini (*Erophylla* and *Phyllonycteris*) and Glossophagini (*Monophyllus*, *Glossophaga* and *Leptonycteris*) in agreement with their morphological distinctiveness observed in previous classifications (e.g., Wetterer *et al.*, 2000). Within Choeronycterini, two subtribes are recognized: Anourina, which contains *Anoura* and is differentiated from the other genera by the presence of three upper premolars, and Choeronycterina, which contains the remaining genera. One clade is recognized in Lonchophyllinae, containing *Lionycteris*, *Lonchophylla* and *Platalina*. Although there were no samples available for *Lichonycteris*, *Scleronycteris*, *Phyllonycteris* and *Platalina* in analyses of Baker *et al.* (2003), the authors considered that the classification above is appropriate for these genera due to morphological similarities. The genera *Dryadonycteris*, *Hsunycteris* and *Xeronycteris* were described after 2003, but the former is classified into Choeronycterina and the latter into Lonchophyllinae (Gregorin and Ditchfield, 2005; Nogueira *et al.*, 2012; Parlos *et al.*, 2014).

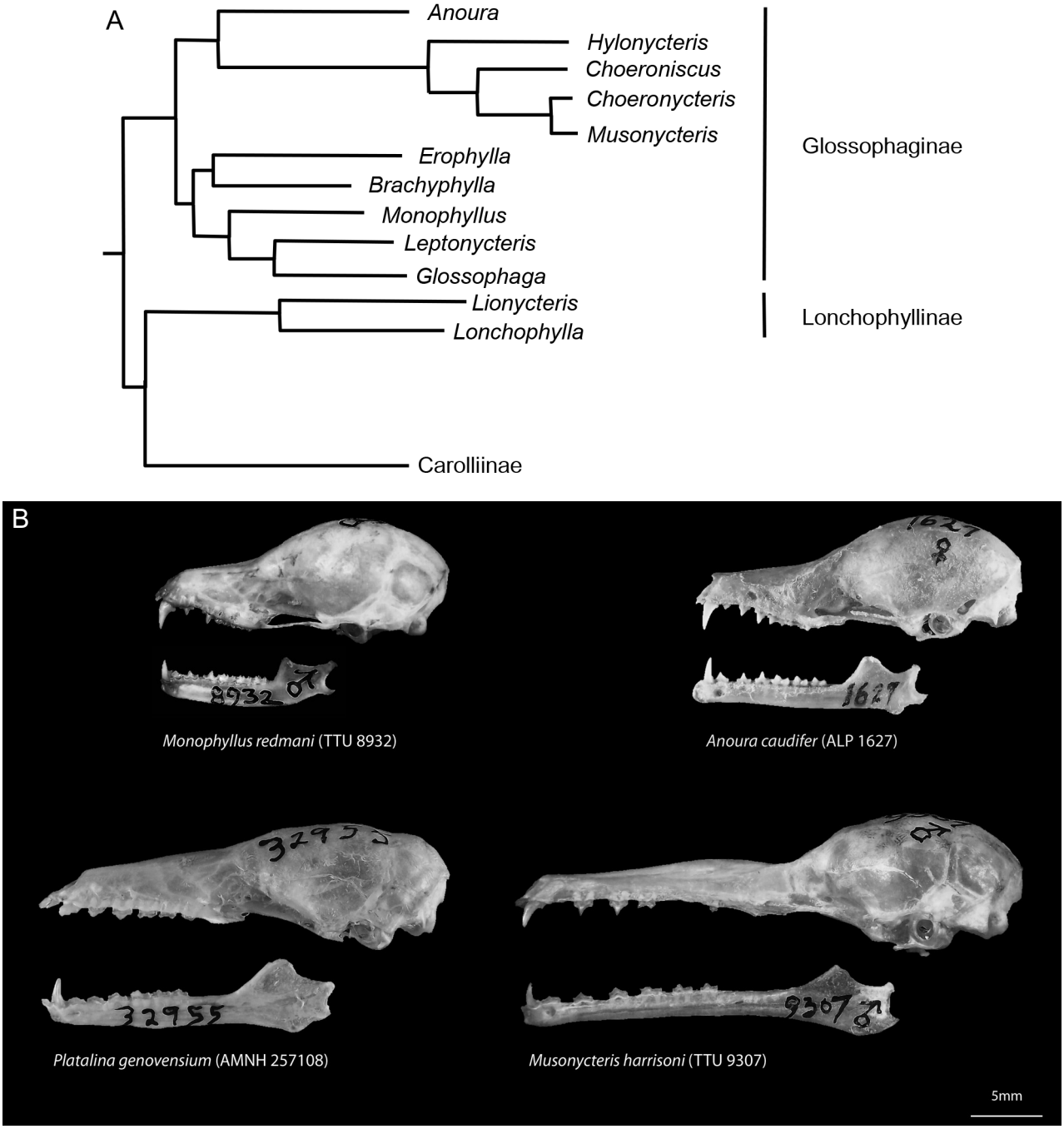

FIG. 3. A — Relationships among phyllostomid nectar-feeding bats redrawn from Baker *et al*. (2003); B — lateral view of the skull of some species of phyllostomid nectar-feeding bats

Allometric Relationships

The distinct static allometric patterns found among nectarivore lineages reveal variables strongly associated with the elongation of the rostrum in the subtribe Choeronycterina and in the subfamily Lonchophyllinae, but less markedly in species of the tribe Glossophagini and in *Anoura*, which have convergent allometric trajectories (Table 5 and Fig. 2). Molecular data places *Anoura* as an early offshoot of the Choeronycterini, and this fact seems to be reflected on the allometric trajectory of the species in this genus in relation to the remaining Choeronycterini.

Previous studies addressed the relationship between rostrum extension in nectarivores bats and degree of nectarivory, as well as on ability to feed on flowers with equally long corollas (e.g., Muchhala,

2006; Tschapka *et al.*, 2008). However, species like *M. harrisoni*, which exhibit very elongated snout and consequently large rostrum, are known for feeding mainly on plants with short corollas (Tschapka *et al.*, 2008). This incongruence led to the hypothesis that the main selective pressures involved in the elongation of the rostrum and related rostral characters rest upon other factors, such as variation in annual availability of nectar. Thus, a more elongated snout and tongue would allow the extraction of even small amounts of nectar, which are beyond the reach of less specialized species, thus favoring efficient use of this resource in periods of low availability. Such an adaptation would avoid seasonal shifts in diet or migration (Tschapka, 2004; Tschapka *et al.*, 2008).

Our results suggest that distinct cranial patterns associated with degree of elongation of the rostrum in phyllostomid nectarivores are allometrically characteristic of each lineage. The allometric coefficients are strongly positive in Lonchophyllinae and Choeronycterina and isometric to negatively allometric in Glossophagini and *Anoura*. These patterns suggest that cranial integration in phyllostomid nectarivores reflects primarily their phylogenetic history rather than adaptive pressures resulting from specialization to particular feeding resources. Differences in skull shape among species of Neotropical nectar-feeding bats could then be accounted for by static allometric trajectories within each lineage, which eventually maintain the functionality of the organisms at different sizes.

These results do not imply that all morphological differences among nectarivorous bats are restricted to the allometric trends reported here. *Anoura fistulata* Muchhala, Mena and Albuja, 2005 has a huge tongue that can reach 1.5 times its body length. Although maximum tongue extension is generally correlated with length of rostral components in nectarivorous mammals (e.g., Winter and von Helversen, 2003), *A. fistulata* seems to be an exception: morphological analyses showed that while the base of the tongue is generally inserted in the hyoid bone in mammals, in this species the base of the tongue is housed in the sternum, in the thoracic cavity (Muchhala, 2006). This species was documented as the only pollinator for flowers of *Centropogan nigricans*, a plant that has very long corollas. This is a rare case of an angiosperm species specializing on a single pollinator, and may represent an example of coevolution between a bat and a plant species (Muchhala, 2006). It is interesting that this is a species of the genus *Anoura*, which was characterized as a less specialized Choeronycterini in our study. Apparently, allometric restrictions in the skull development of Anourina lineage over time prevented the elongation of rostral parts in *A. fistulata*, despite selective pressure for elongation of the tongue.

It is possible to conceive that lineages showing more isometric coefficients of rostral components will be more prone to small dietary shifts than those presenting more extreme allometric trajectories, as revealed among members of the subtribe Choeronycterina. Phyllonycterini and *Brachyphylla* show relatively generalized cranial morphologies, which would allow them to opportunistically use nectar resources. It may be relevant to note that *B. cavernarum* is the more widespread insular species in 13 of the 19 major islands in the Antillean range, a success that has been ascribed both to its large, robust size and varied diet (Baker *et al*., 1978).

Allometry should be investigated as a null hypothesis to evaluate whether morphological traits can be regarded as true adaptations or could be more simply explained as the outcome of a more general allometric trend. Future studies on the association between cranial morphology and diet should contemplate other lineages and guilds of bats under the perspective of allometry in order to objectively evaluate adaptations to a specific diet.

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Appendix

Specimens examined. The list of specimens is organized in alphabetical order. See names and acronyms of institutions in the Materials and Methods section

Anoura caudifer (10) — Brazil, Rio de Janeiro, Seropédica: km 49 (ALP 1626, 1627, 1716, 2057, 2060, 2062, 2083), Fazenda do Sá Freire (ALP 2191); Brazil, Rio de Janeiro, Teresópolis: Fazenda Santo Afonso (2315, 2316).

Anoura geoffroyi (10) — Trinidad, St George: San Rafael (TTU 37664), Las Cuevas (TTU 5464, 8979, 26787); Trinidad, St Andrew: 2 mi N, 2 mi W Valencia (TTU 26786), Tamana Cave (TTU 26463, 26465, 26468), Mt. Tamana Cave (TTU 26475, 26478).

Brachyphylla cavernarum (10) — United States of America, Puerto Rico: 1 mi W Corozal (TTU 8892, 8893, 8894, 8896, 9818, 9819, 9820);United States of America, Puerto Rico, Naguabo: Base of El Toro Trail, Caribbean National Forest (TTU 43512, 43514, 62107).

Choeroniscus godmani (3) — El Salvador, La Paz: Volcan de San Vicente (TTU 63592, 63593, 63594).

Choeroniscus minor (10) — Trinidad, St George: Las Cuevas (TTU 8994, 8996, 8998, 8999, 9782, 9784), Blanchisseuse (TTU 5319, 5496, 9006, 9007).

Choeronycteris mexicana (10) — Mexico, Tamaulipas: Rancho San Jose, 19 mi NW San Carlos (TTU 44733, 44736, 44737, 44743); Mexico, Tlaxcala: 3 km N, 5 km E Tlaxcala (TTU 25343); Mexico, Hidalgo: 11 km S, 1 km W Zacualtipan (TTU 24191),7 km S Zacualtipan (TTU 24190); Mexico, Puebla: 5 km SE San Antonia (TTU 82613, 82614); Mexico, San Luis Potosi: 15 mi S, 1 mi E Huizache, Hwy 57 (TTU 36118).

Dryadonycteris capixaba (3) — Brazil, Espírito Santo, Linhares: Reserva Florestal da Cia Vale do Rio Doce (ALP 9599 [parátipo], ALP 9667 [holótipo]); Brazil, Sergipe, Capela: Refúgio de Vida Silvestre Mata do Junco (ALP 9740).

Erophylla bombifrons (10) — United States of America, Puerto Rico: El Verde Research Station (TTU 8901, 8919, 8920, 8922, 9027), El Toro, El Yunque National Forest (TTU 8906, 8907), 1 mi W Corozal (TTU 8938, 8939, 8941).

Erophylla sezekorni (6) — Jamaica, St. Ann: Orange Valley (TTU 21894, 21895, 21896, 21897), 4 mi E Runaway Bay (TTU 21898), 2 km SW Priory (TTU 45329).

Glossophaga commissarisi (8) — El Salvador, Cabanas: 4 km W Ilobasco (TTU 63598, 63600); El Salvador, La Libertad: Deininger Park (TTU 63603, 63605); El Salvador, La Paz: 3 mi W Zacatecoluca (TTU 63611),Volcan de San Vicente (TTU 63609, 63610), Playa El Zapote (TTU 60893).

Glossophaga leachii (10) — El Salvador, La Libertad: Deininger Park, over Amayo River (TTU 63615, 63616, 63617), La Libertad to Sonsonate Road (TTU 63620, 63623, 63625); El Salvador, La Paz: 4.5 mi NW San Luis Talpa Hacienda la Soledad (TTU 63629, 63630, 63632); El Salvador, San Salvador: Near El Guaje (TTU 60919).

Glossophaga longirostris (3) — Grenada, St John: 0.75 km S, 0.5 km W Concord (TTU 35695, 35696); Venezuela, Guarico: Guatopo National Park, Aqua Blanco Campground (TTU 33315).

Glossophaga morenoi (8) — Mexico, Chiapas: 8.2 mi SE, 2.5 mi E Tonala, Rio Ocuilapa (TTU 36137, 36138, 36140, 36141, 36142, 36143, 36144), 8.9 mi E Tehuantepec, Hwy 190 (TTU 36146).

Glossophaga soricina (10) — Brazil, Rio de Janeiro, Seropédica: Universidade Federal Rural do Rio de Janeiro (ALP 563, 568, 580, 612, 674, 675, 676), Fazenda do Sá Freire (ALP 2193); Brazil, Rio de Janeiro, Itaguaí: Sá Freire (ALP 727, 729).

Hsunycteris cadenai (5) — Ecuador, Esmeraldas: San Jose Farm, E San Lorenzo, towards Lita (TTU 85448, 85451), Terrenos aledanos de la comuna San Francisco de Bogota (TTU 103183, 103195), Comuna San Francisco de Bogota (TTU 102942).

Hsunycteris thomasi (1) — Ecuador, Pastaza District: 5 km E Puyo, Safari Hosteria Park (TTU 84784).

Hylonycteris underwoodi (5) — Mexico, Oaxaca, Tuxtepec: 5 mi W San Jose Chiltepec (AMNH 189688); Mexico, Tabasco: 3 km E Teapa, Grutas de Cocona (TTU 36152); Costa Rica, Heredia: 1 mi W Vara Blanca (TTU 13142), Parque Nacional Braulio Carrillo, San Miguel (USNM 562798, 562800).

Leptonycteris nivalis (10) — Mexico, Hidalgo: 11 km S, 1 km W Zacualtipan (TTU 24195, 24196, 24197), 11 km S Zacualtipan (TTU 24200, 24201); Mexico, Nuevo Leon: Ojo de Agua, 7 km NW Dr. Arroyo (TTU 37574, 37576, 37577, 37578, 37579).

Leptonycteris yerbabuenae (10) — Mexico, Hidalgo: 0.5 km W Huejutla (TTU 38040, 38041), 4 km E San Felipe Orizatlan (TTU 15483, 15485, 15486, 15487); Mexico, Oaxaca: Las Minas (TTU 82605, 82620, 82622, 82623).

Lichonycteris obscura (10) — Nicaragua, Zelaya: 4.5 km NW Rama (TTU 13117, 13119, 13120, 13121), 7.3 mi NW Rama (TTU 13125, 13126), 9 mi E Rama at Dos Bocas (TTU 13128, 13130, 13131), 10 km W Rama (TTU 9870).

Lionycteris spurrelli (4) — Panama, Darien: Cana (TTU 39121, 39122, 39123, 39124).

Lonchophylla concava (3) — Ecuador, Esmeraldas: E San Lorenzo, banana plantation (TTU 85360), Comuna San Francisco de Bogota (TTU 102960), Mataje, navy base (TTU 103120).

Lonchophylla handleyi (1). Peru, Huanuco Dept, Leoncia Prado: 6 km N Tingo Maria (TTU 46164).

Lonchophylla peracchii (10). Brazil, Rio de Janeiro, Rio de Janeiro: Parque Estadual da Pedra Branca (5860); Brazil, Rio de Janeiro, Nova Iguaçu: Reseva Biológica do Tinguá (ALP 6265, 6283, 6284, 6556, 6557, 6558, 6559, 6560, 6561).

Lonchophylla robusta (5). Ecuador, Esmeraldas: E San Lorenzo, banana plantation (TTU 85353, 85366), E San Lorenzo, La Guarapera banana farm and pasture (TTU 85391), Comuna San Francisco de Bogota (TTU 102941, 102959).

Monophyllus plethodon (10). Dominica, St Joseph: Clarke Hall (TTU 31331, 31337); Dominica, St Paul: Springfield (TTU 31333, 31341); Dominica, St Paul Par: Mt. Joy State (TTU 63357); Dominica, St. Joseph Par: York Valley State, 4.25 km by Rd Coast Rd, S side Layou River (TTU 63353); France, Guadeloupe, Basse-Terre: 1 km W Vernou (TTU 20798, 20800), Bains Jaunes, 2.5 km E Saint-Claude (TTU 20795, 20796).

Monophyllus redmani (10) — United States of America, Puerto Rico, Naguabo: Base El Toro Trail, Caribbean National Forest, 13.5 km, Route 191 (TTU 43399); United States of America, Puerto Rico, Rio Grande: El Verde Field Station near Rt. 186 Caribbean National Forest (TTU 46364, 46365, 46366, 46367); United States of America, Puerto Rico: 1 mi W Corozal

APPENDIX. Continued.

(TTU 8932, 8933, 9817), East Peak El Yunque National Forest (TTU 8928), El Toro Trail, El Yunque National Forest (TTU 9797).

Musonycteris harrisoni (5) — Mexico, Colima, Armería: Las Juntas, 5 km SE Pueblo Juarez (AMNH 235179, TTU 9307); Mexico, Colima: Pueblo Juarez (USNM 314689); Mexico, Colima: Mixcuate, near Pueblo Nuevo (USNM 324971); Mexico, Jalisco: 2 km W Tomatlan (TTU 36433).

Phyllonycteris aphylla (10) — Jamaica, St. Ann: Orange Valley (TTU 21901, 21902, 21903, 21904, 21905, 21907, 21908, 21923, 21925, 21926).

Phyllonycteris poeyi (5) — Haiti, Dept. du Sud: 1 km S Lebrun (TTU 22782, 22783), 1 km S, 1 km E Lebrun (TTU 22795, 22796, 22797).

Platalina genovensium (3) — Peru, Piura, Talara: La Brea, 12.9 km N Tamarindo (AMNH 278520); Peru, Arequipa: Caravelli (AMNH 257108); Peru: Carivelli (USNM 268765).

Scleronycteris ega (1) — Venezuela, Amazonas: Tamatama, Rio Orinoco (USNM 407889).

Xeronycteris vieirai (2) — Brazil, Sergipe: Monumento Natural Grota de Angico (ALP 9760, 10092).