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Comparative Study of the Cranio-osteology of Two *Lonchophyllinae* from Colombia

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Author's contribution

The sole author designed, analysed, interpreted and prepared the manuscript.

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ABSTRACT

Lonchophyllinae comprises four genera of Neotropical nectarivorous bats. Inside this subfamily the genus *Lonchophylla* is one of the most diverse. A total of 51 *Lonchophylla* skulls from Colombia (*L. robusta* n=34 and *L. thomasi* n=17) was studied by means of geometric morphometric methods with the aim to determine their morphological differential characteristics. For this purpose, viscerocranium and neurocranium were evaluated with 12 landmarks on the dorsal aspect of left hemicranium. The two species were statistically different according to size (expressed as skull length) but also to shape (expressed as the set of Procrustes coordinates). Skulls in *L. robusta* were clearly bigger, with shorter braincase and longer rostra, and their zygomatic process was more latero-caudally displaced, whereas *L. thomasi* presented a zygomatic process which was displaced more rostrally as well longer braincases. All these detected skull form dissimilarities between both species would be explained by their different alimentary habits, but a combination of dietary analysis and morphological analysis is needed to make stronger inference about diet preferences.

Keywords: *Lonchophylla robusta*; *Lonchophylla thomasi*; neurocranium; viscerocranium.

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1. INTRODUCTION

Lonchophyllinae comprises four genera of Neotropical nectarivorous bats. Inside this subfamily, the genus *Lonchophylla* Thomas, 1903, one of the most diverse [1], is small to medium-sized (forearm 30–48 mm), pale brown to reddish-brown, and can be distinguished on the basis of its broad, pale basal band on the body pelage, the lack of conspicuous fur on uropatagium, and the large, forwardly projecting inner upper incisors. On the skull, the anterior margin of the mesopterygoid fossa is relatively shallow and V-shaped, the central upper incisors are long and larger than lateral ones, the premolars are narrow and anteroposteriorly elongated, and the zygomatic arch is absent [2,3]. *Lonchophylla* bats are nectar-feeding bats, and occur primarily in tropical lowland and mid-elevation forests from near sea level to at least 1,350 m. Their geographic distribution extends from southern Nicaragua south to southern Peru and Bolivia, and southeastern Brazil [4,5].

Lonchophylla genus has recently been the source of taxonomic revisions, with changes in species descriptions, taxonomic rearrangements, and species distribution limits. There are ten species currently recognized in the genus, of which eight are known to occur in Colombia, and three of them have type localities in the country. “Large” species include, among others, Big Nectar Bat (*Lonchophylla robusta* Miller, 1912) [6], while the group of “small” species is composed, among others, of Thomas’s Nectar Bat (*L. thomasi* Allen, 1904) [6].

It is in the interest of the individual species to specialize on prey that are most abundant or are not available for competitors. The large differences in skull morphology among species is an important factor in predicting and understanding the diets of bats and could find their origin within resource partitioning. *Lonchophylla* species are often separated into larger-bodied and smaller-bodied forms [6], which differ also to some extent in the relative length of the rostrum [6]. Here we present a study to establish if there are skull form (size and shape) differences between the big *L. robusta* and the smaller *L. thomasi* from Colombia. We expected to find morphological differences that could be explained by their feeding different characteristics. In comparison to other studies, this study focuses on geometric morphometric techniques.

2. MATERIALS AND METHODS

2.1 Data Collection

We examined 51 specimens of *Lonchophylla* archived in the collections of the *Instituto de Ciencias Naturales* (ICN) of the Universidad Nacional de Colombia in Bogotá and the *Departamento de Biología* of the *Universidad del Valle* in Cali. Species studied were *L. robusta* (n=34) and *L. thomasi* (n=17). Individual information of studied specimens can be obtained from author upon request. Study was done using standard geometric morphometric techniques, as it will be described. Briefly, this consisted of an initial step in which individual landmark configurations were aligned, translated and rotated. Then, they were scaled to a unit centroid size (the square root of the sum of squared distances of all landmarks to the centroid of the object). This procedure eliminates “size” as a factor (although size-related shape differences may remain) and “shape” can therefore be analysed separately from “size”. Shape was retained as Procrustes coordinates.

2.2 Obtention of Images and Digitalization

Pictures of skulls (on their dorsal aspect) were taken using a Nikon D1500 digital camera equipped with an 18-105 mm Nikon DX telephoto lens and tripod. Images were taken at an opening of 10 and sensitivity of 1,000. Ulteriorly, a total of 12 landmarks were situated on each skull image (Fig. 1). Landmarks used in this study were primarily chosen to describe major cranium functional regions: both viscerocranium and neurocranium. To avoid undesirable variation due to potential asymmetry, only the left side was measured. A ruler was used in order to obtain real distances between landmarks. The x and y co-ordinates of all landmarks for the views photographed were obtained using TpsDig v. 2.21 software [7].

Tps Small v. 1.29 software [8] was then used to assess the correlation between the 2D Procrustes distances and the Euclidean distances in that tangent space. The correlation was very close to linear for all of the data ($r=0.999$; slope $b=0.898$), suggesting that tangent space was an adequate approximation to Kendall and that no specimens deviated appreciably from the linear regression line. Thus, although the dorsal view of the skull is not a flat object, author considered that the two-dimensional approach implied a limited loss of

information, and we proceeded with the morphometric analyses. As no sexual dimorphism was found in a preliminary analysis ($p>0.215$), sexes were pooled for each species.

Skull length was interpreted as the distance between landmarks 1 and 2 and compared with a Mann-Whitney test. A canonical variate analysis (CVA) was used to separate species in the data. CVA provides an ordination that maximizes the

separation of the group means relative to the variation within groups.

Procrustes values were obtained with MorphoJ 1.06c [9] and data were analysed using PAST - Paleontological Statistics Software Package for Education and Data Analysis [10]. All this software is available over the Internet by FTP from the "morphmet" directory via the WWW at <http://life.bio.sunysb.edu/morph/>.

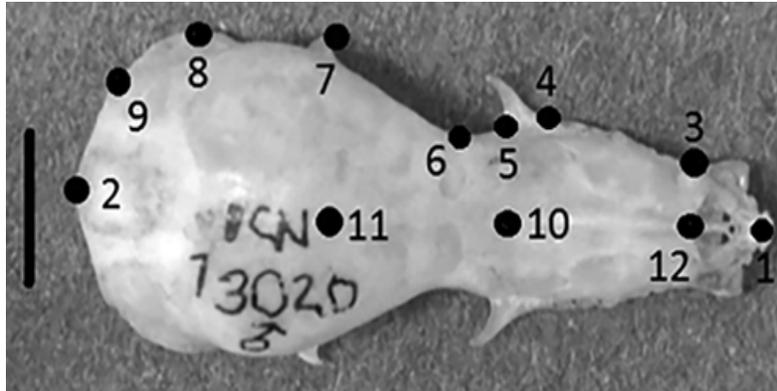


Fig. 1. Dorsal skull view of *Lonchophylla*. Skulls were placed on a stage and aligned by their maxillary tooth rows to a stable plane. Twelve landmarks were used to capture cranial shape (on left hemicranium). Left vertical bar corresponds to a 5 mm line and was used to estimate real skull length (distance from landmark 1 to 2)

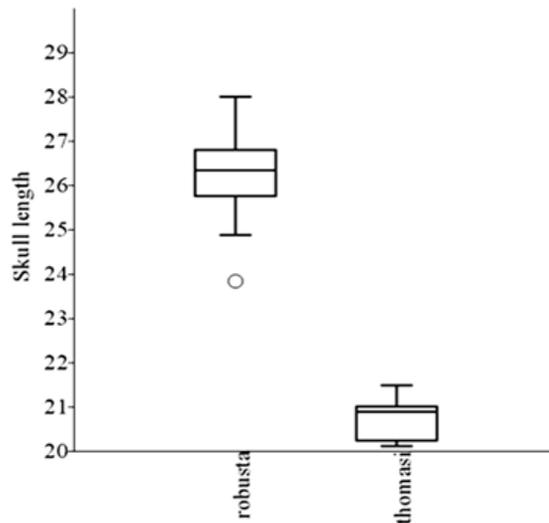


Fig. 2. Skull length (expressed in mm) in *Lonchophylla*: *L. robusta* (n=34) and *L. thomasi* (n=17). For each species, the 25-75 per cent quartiles are drawn using a box. The median is shown with a horizontal line inside the box. The short horizontal lines were drawn from the top of the box up to the largest data point less than 1.5 times the box height from the box (the "upper inner fence"), and similarly below the box. The circle shown outside the inner fence for *L. robusta* is an outlier (23.8 mm). The Mann-Whitney test reflected statistical differences between the two species ($U=0, p<0.01$)

3. RESULTS

The Mann-Whitney test reflected statistical differences between both species for skull length ($U=0$, $p<0.01$) (Fig. 2). According to Procrustes distances, shape differences also appeared (Procrustes distance: 0.04548400, $p<0.0001$) (Fig. 3). From Fig. 4, it can be observed that both

viscerocranium and neurocranium play a role in the discrimination between the two species: deviations in *L. robusta* yielded shorter braincase and longer rostra, zygomatic process more latero-caudally displaced, whereas *L. thomasi* deviations included forms with zygomatic process displaced more rostrally and longer braincases.

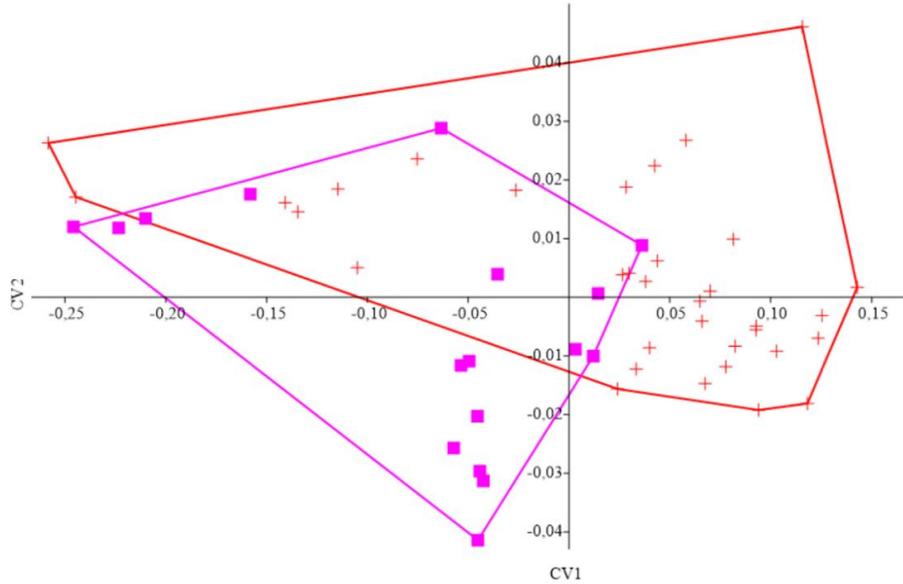


Fig. 3. Canonical analysis (CV1 and CV2) for *Lonchophylla robusta* (n=34, crosses) and *L. thomasi* (n=17, filled squares) based on their skull shape variations. According to Procrustes distances, differences appeared between the two species (Procrustes distance: 0.04548400, $p<0.0001$)

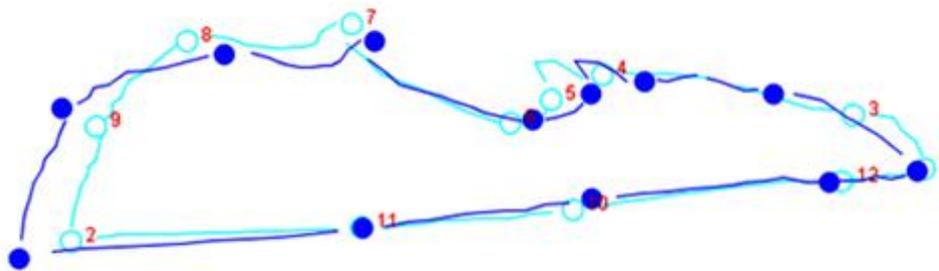


Fig. 4. Average warped outline graph for *Lonchophylla robusta* (empty circles) and *L. thomasi* (filled circles). Both viscerocranium and neurocranium play an important role in the discrimination between species. *L. robusta* yielded shorter braincase, longer rostra, and a zygomatic process more latero-caudally displaced, whereas *L. thomasi* deviations included forms with zygomatic process displaced more rostrally and longer braincases

4. DISCUSSION

Specific identification of skulls from *L. robusta* and *L. thomasi* from Colombia cannot be made consistently on the basis of a single cranial characteristic, as differences rely on both viscerocranium and neurocranium traits. Therefore, on the basis of their global shape, *L. thomasi* and *L. robusta* can be differentiated according to braincase, rostra and zygomatic process. Although there are many researches on the skull morphology of this species, none (at least at author's knowledge) has focused on the form (size and shape) applying geometric morphometric techniques. A few studies have combined the data related to biological characteristics such as skull morphology.

The morphology and biomechanics of the vertebrate skull reflect the physical properties of diet and behaviour used in food acquisition and processing [11]. Bats do specialize and prefer certain food. Preference of certain items can explain certain characteristics of the skull. For instance, food hardness, for example, would be related to the bite force (and the cranial length represents bite force). The skull form dissimilarities detected between *L. robusta* and *L. thomasi* would thus be explained by different alimentary factors in these two species: mainly insectivore for the former and mainly nectar and pollen for the latter [3]. It is not just the size of the bat determines the diet but that certain morphological characteristics of the skull are much more important. The differentiation of these skull characteristics in both species is likely to have evolved from trophic specialization and had made that *Lonchophylla* bats can exploit a different range of niches sympatrically.

5. CONCLUSION

- Geometric morphometric analysis shows that skulls in *Lonchophylla robusta* are clearly bigger, with shorter braincase and longer rostra, and the zygomatic process more latero-caudally displaced, whereas *L. thomasi* presents a zygomatic process which is displaced more rostrally, also having longer braincases.
- These dissimilarities can be explained by different alimentary factors in the two species.
- These differences in skull morphology make *Lonchophylla* bats can exploit a different range of niches sympatrically.

ETHICAL APPROVAL

Animal Ethic committee approval has been taken to carry out this study.

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COMPETING INTERESTS

Author has declared that no competing interests exist.

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