



TEXAS TECH UNIVERSITY

Natural Science Research Laboratory

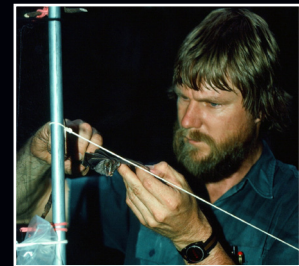
SPECIAL PUBLICATIONS

Museum of Texas Tech University

Number 71

11 October 2019

FROM FIELD TO LABORATORY: A MEMORIAL VOLUME IN HONOR OF ROBERT J. BAKER



EDITED BY

ROBERT D. BRADLEY, HUGH H. GENOWAYS, DAVID J. SCHMIDLY, AND LISA C. BRADLEY

MORPHOMETRIC VARIATION OF THE GENUS *Lonchorhina* (CHIROPTERA, LONCHORHININAE), WITH NOTEWORTHY COMMENTS ON TAXONOMY AND DISTRIBUTIONAL RANGE EXTENSIONS

HUGO MANTILLA-MELUK, NATALIA PEREZ-AMAYA, AND PAÚL M. VELAZCO

ABSTRACT

Insectivorous sword-nose bats *Lonchorhina* (Phyllostomidae: Lonchorhininae) are characterized by the most hypertrophied telic structures (noseleaf and pinna) within the family. Internally, enlarged ears and noseleaf are supported by a skull morphology that differs from that in other closely related genera. Except for *L. aurita*, widely distributed across both Central and South America, species in the genus *Lonchorhina* have relatively restricted distributions and are represented in museum collections by a limited number of specimens. Herein, morphological and morphometric variation is assessed in 115 *Lonchorhina* specimens representing the six recognized species in the genus from a significant portion of its geographic range, from Belize to Brazil, including the recently described *L. mankomara* from the isolated mountain range of Serranía de Chiribiquete in the Colombian Guayana. The first Peruvian records of *L. inusitata*, collected 9 km N of Aucayacu, province of Leoncio Prado, department of Huánuco in the piedmonts of the Peruvian Amazon, are reported herein; these records represent a significant extension in the geographic and ecological distribution of this taxon. In addition, the distribution of *L. mankomara* is extended into the northern portion of Colombian Guianan-Amazon. Finally, the morphometric affinities of medium-size representatives of the genus *L. aurita*, *L. inusitata*, and *L. orinocensis* are discussed and comments are made on the external and cranial morphological differentiation between *L. mankomara* and *L. marinkellei*.

Key words: cranial morphology, distribution extension, geographic variation, *Lonchorhina inusitata*, *Lonchorhina mankomara*, sword-nosed bats

RESUMEN

Los murciélagos insectívoros de hoja de espada en el género *Lonchorhina* (Phyllostomidae: Lonchorhininae), se caracterizan por poseer las estructuras télicas (hoja nasal y pina) más hipertrofiadas en la familia. Internamente, estas estructuras están soportadas por una morfología craneal que difiere significativamente de aquella en los géneros más cercanos. Con excepción de *L. aurita*, ampliamente distribuida a lo largo de Centro y Sur América, las especies de *Lonchorhina* presentan distribuciones restringidas y están pobremente representadas en colecciones científicas. En este estudio investigamos la variación geográfica en la morfología y morfometría craneal en *Lonchorhina* a través del análisis de 115 especímenes representando las seis especies descritas para el género, provenientes de una porción significativa de su rango de distribución desde Belice a Brasil, incluyendo material de la recientemente descrita *L. mankomara* del sistema montañoso aislado de la Serranía de Chiribiquete en la Guayana Colombiana. Presentamos los primeros registros peruanos de *L. inusitata* colectados 9 km N de Aucayacu, en la provincia de Leoncio Prado, departamento de Huánuco, en el piedemonte de la

Amazonía peruana, que constituyen una extensión geográfica y ecológica significativa en la distribución de este taxón; y extendemos la distribución de *L. mankomara* al norte de la Guayana-Amazónica de Colombia. Finalmente discutimos sobre las afinidades morfológicas de representantes de talla media en el género: *L. aurita*, *L. inusitata* y *L. orinocensis*; y se adición comentarios sobre la diferenciación craneal y en caracteres externos entre *L. mankomara* y *L. marinkellei*.

Palabras clave: extensión en distribución, *Lonchorhina inusitata*, *Lonchorhina mankomara*, morfología craneal, murciélagos de hoja de espada, variación geográfica

INTRODUCTION

The phyllostomid genus *Lonchorhina* (sword-nosed bats) is the sole member of the subfamily Lonchorhininae (Baker et al. 2012; Dávalos et al. 2012) and is characterized by the most hypertrophied telic structures (noseleaf, ear, and tragus) within the family (Fig. 1) and a unique skull morphology. The genus *Lonchorhina* currently includes six species—*L. aurita* Tomes, 1863; *L. orinocensis* Linares and Ojasti, 1971; *L. marinkellei* Hernández-Camacho and Cadena, 1978; *L. fernandesi* Ochoa and Ibañez, 1984; *L. inusitata* Handley and Ochoa, 1997; and *L. mankomara* Mantilla-Meluk and Montenegro, 2016—that exhibit considerable variation in size and distributional patterns (Williams and Genoways 2008; Mantilla-Meluk and Montenegro 2016; Mantilla-Meluk et al. 2017). Except for *L. aurita*, species in the genus are poorly represented in museum collections and little is known about their morphometric variation. To date, the only available revision of the genus (Hernandez-Camacho and Cadena 1978) included three of the six currently recognized species. Although that revision provides one of the most detailed morphological assessments of a phyllostomid genus, it was limited in scope in terms

of the localities examined and lacked information on geographic variation in skull morphology and morphometrics (Hernandez-Camacho and Cadena 1978).

In the present work, the skull morphometric variation in all currently recognized species in the genus was analyzed, with attention given to variation displayed by *L. aurita*. In addition, while examining *Lonchorhina* specimens deposited at two natural history museums in the USA, two relatively larger male specimens (GLS > 22 mm) were found from Peru, where only *L. aurita* (GLS < 21.5 mm) is known to occur. These two specimens were within the morphometric ranges of measurements reported for *L. inusitata*. The discrete character variation of these two *Lonchorhina* specimens from Peru was analyzed in order to determine their taxonomic status. Similarly, new material of *L. mankomara* was analyzed that not only extended this species' distribution into the northern portion of the Serranía de Chiribiquete in the department of Guaviare, Colombia, but also allowed an opportunity to document the external morphology of the largest species in the genus (Fig. 1).

MATERIALS AND METHODS

Specimens examined.—A total of 115 adult specimens of *Lonchorhina* representing the six species of the genus were examined: 83 specimens of *L. aurita*, 6 of *L. inusitata*, 1 of *L. fernandesi*, 9 of *L. mankomara*, 2 of *L. marinkellei*, and 14 of *L. orinocensis* (see Appendix for complete specimen data). The specimens examined in this study are deposited in the American Museum of Natural History (AMNH, New York, USA); Carnegie Museum of Natural History (CM, Pittsburgh,

USA); Collection of Mammals of the University of Quindío (CMUQ, Armenia, Colombia); Field Museum of Natural History (FMNH, Chicago, USA); Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN, Bogotá, Colombia); Museum of Texas Tech University (TTU, Lubbock, USA); and National Museum of Natural History (formerly the United States National Museum), Smithsonian Institution (USNM, Washington, DC, USA).



Figure 1. Images of various species of *Lonchorhina*, representing: *L. aurita* from Costa Rica, Central America (top left; photo courtesy of M. Tschapka) and Brazil (top center; photo courtesy of Tekbio); *L. inusitata* from Suriname (top right; photo courtesy of B. Lim); *L. orinocensis* from Serranía de La Lindosa, Guaviare, Colombia (bottom left; photo courtesy of R. Agudelo); *L. mankomara* from Serranía de Chirbiquete, Guaviare, Colombia (bottom center; photo courtesy of H. Mantilla-Meluk); and *L. marinkellei* from Serranía de La Lindosa, Guaviare, Colombia (bottom right; photo courtesy of D. Martínez-Morales).

Morphology and morphometrics.—External and osteological characters examined were defined based on, but not restricted to, Ochoa and Ibañez (1984) and Handley and Ochoa (1997). Dávalos et al. (2014) was followed in assigning homology for the premolars: first upper premolar (P4), second upper premolar (P5), first

lower premolar (p1), second lower premolar (p4), and third lower premolar (p5).

Digital calipers were used to take 10 craniodental measurements to the nearest 0.01 mm on each specimen. Only adult specimens were used in this study and

age was determined based on the presence of closed phalangeal epiphyses. Descriptive statistics (mean and observed range) were calculated for all samples (Table 1). The craniodental measurements used in this study include: greatest length of skull (GLS): measured from the most posterior edge of the skull at the occipital crest to the most anterior point of the maxillary bone; condylobasal length (CBL): measured from the most posterior edge of the condyles to the most anterior point of the maxillary bone; palatal length (PAL): distance from the most anterior point of the palatal, usually in between the incisor (in ventral view), to the inflexion point of the arc drawn by the joint of the palatines in the so-called mesopterygoid fossa; postorbital constriction (PO): smallest distance across the maxilla at the interorbital region; rostrum width (RO): maximum distance on the maxilla, across the base of the canines; braincase length (BL): distance between the point of inflexion delimiting the braincase anteriorly and the posterior end of the occipital; distance across tympanic bullae (BL–BL): maximum distance across the most lateral points of the tympanic bullae in dorsal view; braincase height (BCH): distance from the base of the cranium at the basisphenoidal region to the highest point at the joint of the parietals; tooth-row length (LTR): distance from the posterior edge of the third upper molar to the most anterior edge of the canine in the maxillary toothrow; distance across third upper molars (M–M): maximum distance across the third upper molars; and distance across canines including cingula (C–C): distance across the cingula of the upper canines.

Eleven craniodental measurements (GLS, CBL, PAL, PO, RO, BL, BL–BL, BCH, LTR, M–M, and C–C) of 115 *Lonchorhina* specimens from eight countries, including all recognized species from most of the known geographic range of the genus from Belize to Brazil, were tested for normality and homogeneity of variances using a Shapiro-Wilks and a Bartlett's, tests respectively, in the software R versión 3.4.3 (R Core Team 2017), with the package stats (R Core Team 2017) and car (Fox and Weisberg 2011). Two principal components analyses (PCA) were performed on the data. The first PCA included all species of *Lonchorhina*. For the second PCA, *L. fernandesi* (smallest species of the genus) and *L. mankomara* and *L. marinkellei* (largest species) were excluded. The range of size variation in the first PCA analysis was such that *L. aurita*, *L. inusitata*, and *L. orinocensis* were partially obscured by overlap. Therefore, a second PCA analysis of these

three species was performed in an effort to ascertain the degree to which these taxa differed within the morphospace. Size discrimination follows the criteria in Williams and Genoways (2008). Subsequently, Discriminant Function Analyses (DFA) were performed in order to statistically determine the morphometric independence among medium-sized species: *L. aurita*, *L. inusitata*, and *L. orinocensis*. In addition, because previous publications had misidentified medium-sized *L. inusitata* as the large-sized *L. marinkellei* (Brosset and Charles-Dominique 1991; Brosset et al. 1996), a second DFA was performed in order to test for morphometric independence among *L. inusitata* (N = 6), and *L. marinkellei* (N = 2), and *L. mankomara* (N = 9). Finally, a DFA was conducted to assess the variation of the widespread *L. aurita* across its geographic range. Seventy-three specimens assigned to *L. aurita* from eight countries were included in this analysis: Belize (1), Brazil (10), Colombia (32), Guatemala (13), Honduras (2), Panama (1), Peru (3), and Trinidad (11). Morphometric analyses were performed using the statistical packages PAST (Hammer et al. 2001) for the PCA analyses, and Statgraphics Centurion XV (StatPoint Technologies Inc.) was used for the DFA analyses. Because *L. aurita* was the species with the highest number of individuals, a U-Mann-Whitney test was conducted to account for sexual dimorphism in the software R (R Core Team 2017).

To confirm the identification of *L. inusitata* specimens from Huánuco, Peru (TTU 46137♂ and CM 98592♂), cranial morphological affinities were analyzed among the *L. inusitata* specimens and representatives of all recognized species in the genus, in particular with the morphometrically closely related *L. aurita*. These analyses included the following localities and specimens: comparisons with *L. aurita* material from Trinidad, collected near the type locality of the species; specimens of *L. aurita* from several localities across its distributional range (Belize, Honduras, Panama, Colombia, Venezuela, Peru, and Brazil); the holotype of *L. a. occidentalis* (Ecuador); specimens of *L. inusitata* from Brazil and Venezuela; a specimen of the rare *L. fernandesi* from the only known locality of this species in Venezuela; representatives of *L. orinocensis* from several localities in Colombia and Venezuela; and the holotypes of the rare *L. mankomara* and *L. marinkellei* in Colombia, including new putative collecting localities for the species.

RESULTS

Craniometric variation in the genus Lonchorhina.—For the PCA analysis of all species of *Lonchorhina* (Fig. 2), the first two principal components (PC1 = 92.8%, PC2 = 2.9%) explained most of the variation, with GLS, CBL, and PAL having the highest loadings on PC1, reflecting the skull length variation among all the species of the genus. On PC2, BL-BL showed the highest loading, thus illustrating differences in skull width of *L. fernandesi* with respect to the other species in the genus (Fig. 2). The three medium-sized species (*L. aurita*, *L. inusitata*, and *L. orinocensis*) grouped in the same area of the morphospace, with some degree of overlap between *L. aurita* and *L. inusitata*, and *L. orinocensis* being the smallest of the three. Large species *L. mankomara* and *L. marinkellei* show no overlap with each other or with the rest of species in the genus.

Craniometric variation among medium-sized species of Lonchorhina.—The PCA analysis of *L. aurita*, *L. inusitata*, and *L. orinocensis* revealed the highest variation for the first principal component (PC1 = 85%, PC2 = 8.5%), with CBL showing the highest loading (CBL = 0.333, M-M = 0.329, GLS = 0.327). Correspondingly, three clusters were observed along PC1, representing samples of: *L. orinocensis*, placed at the negative end of the axis (lower scores); *L. aurita*, placed in the middle of the axis with some individuals presenting negative and other positive scores; and *L. inusitata*, with all its individuals grouped at the positive end of the axis.

Craniometric comparison of medium-sized Lonchorhina from Peru.—Measurements of the two

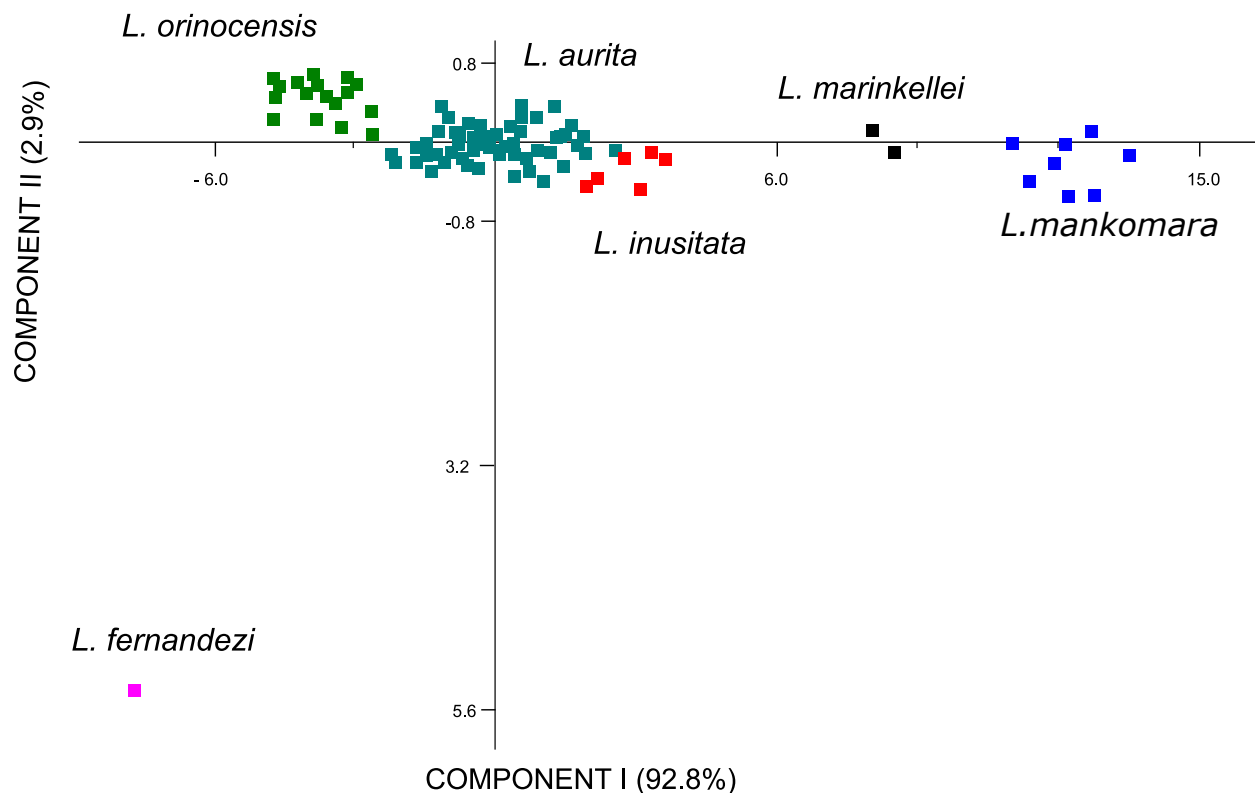


Figure 2. Principal Component Analysis of 10 cranial measurements of 115 individuals of the genus *Lonchorhina*, representing the six recognized species: *L. aurita* (aquamarine squares); *L. fernandesi* (pink square); *L. inusitata* (red squares); *L. mankomara* (blue squares); *L. marinkellei* (black squares); and *L. orinocensis* (green squares).

male specimens (TTU 46137 and CM 98592) from Peru fell within the range of *L. inusitata* proposed by Handley and Ochoa (1997) (see Table 1), and clustered together with other *L. inusitata* specimens from Brazil and Venezuela in the factorial plane of both PCA's (PCA of all species in the genus and PCA on medium-sized species). The DFA of the medium-sized species indicated that all the specimens *a priori* identified as *L. inusitata*, *L. aurita*, and *L. orinocensis* were correctly assigned (Wilks's $\lambda=0.66, 0.64$; $\chi^2=201.71, 33.2$; $P > 0.001, 0.001$) and showed no overlap on the factorial plane (Fig. 3). Based on these analyses, *L. aurita* and *L. inusitata* were more morphologically aligned relative to *L. orinocensis*.

The discriminate function analysis that included *L. inusitata* and the larger species *L. mankomara* and *L. marinkellei* indicated that all the specimens identified *a priori* were correctly assigned to their taxonomic groups (Wilks's $\lambda=0.78, 0.73$; $\chi^2=231.014, 47.2$; $P >$

0.001, 0.001) and showed no overlap on the factorial plane (Fig. 4).

Evaluation of the status of divergent Lonchorhina specimens from Peru.—Specimens TTU 46137 and CM 98592 from Peru were within the morphometric ranges established for *L. inusitata*, and were placed with other specimens of *L. inusitata* from Brazil and Venezuela in both PCA analysis (Figs. 2, 3), as well as confirmed as part of this taxon in our DFA analysis (Fig. 4).

Geographic craniometric variation of the widespread L. aurita.—The U-Mann-Whitney test conducted to account for secondary sexual dimorphism showed no statistical differences in this taxon. The DFA revealed high variability and some geographic structure in the skull morphology of *L. aurita* (Fig. 5). Based on the DFA, specimens from Trinidad, the type locality of *L. a. aurita*, were morphologically different from specimens from Central America and Brazil.

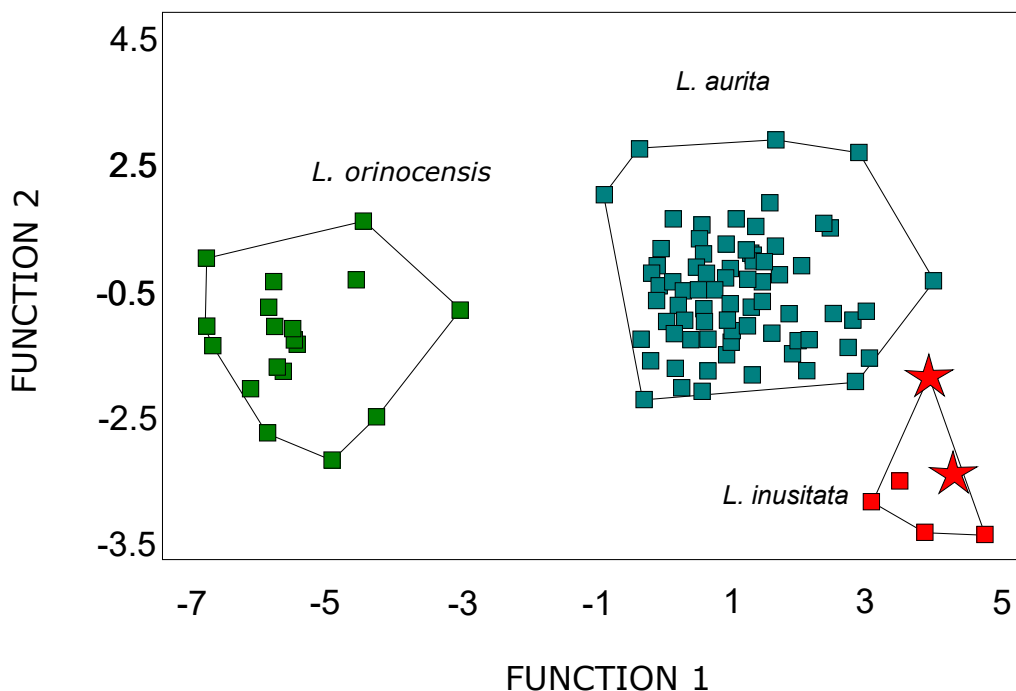


Figure 3. Discriminant Function Analysis performed on 10 cranial measurements of *Lonchorhina aurita* (blue squares), *L. orinocensis* (green squares), and *L. inusitata* (red squares). Red stars represent Peruvian specimens of *L. inusitata* (TTU 46137 ♂ and CM 98592 ♂).

Table 1. Cranial measurements analyzed among representatives of the five recognized species in the genus *Lonchorhina*. Abbreviations of measurements: Greatest length of skull (GLS); condylobasal length (CBL); palatal length (PAL); postorbital constriction (PO); rostrum (RO); braincase length (BL); distance across tympanic bullae (BL-BL); braincase length (BCH); tooth row length (LTR); distance across third upper molars (M-M); distance across canines, including cingula (C-C).

Statistics or catalog number	GLS	CBL	PAL	PO	RO	BL	BL-BL	BCH	LTR	M-M	C-C
<i>Lonchorhina aurita</i> (N = 83)											
Mean±SD	20.46±0.60	19.01±0.62	9.62±0.51	4.95±0.22	5.86±0.36	10.49±1.39	11.22±0.38	6.86±0.22	6.84±0.31	7.27±0.55	4.55±0.24
Range	19.3–21.55	17.56–20.09	8.40–10.87	4.38–5.50	5.13–6.84	8.51–12.30	10.47–11.96	6.28–8.32	6.18–7.54	6.50–7.89	4.12–5.12
<i>Lonchorhina fernandezi</i> (N = 1)											
ICN 12276♂	17.92	15.53	6.70	3.90	4.70	11.64	3.95	6.53	5.46	5.81	3.45
<i>Lonchorhina inusitata</i> (N = 6)											
Mean±SD	22.21±0.43	20.65±0.42	10.75±0.27	5.26±0.22	6.39±0.12	12.56±0.48	11.87±0.23	7.10±0.22	7.64±0.14	7.91±0.17	5.08±0.07
Range	21.04–22.69	19.96–21.09	10.28–11.20	5.02–5.59	6.04–6.59	12.11–13.36	11.38–12.15	6.89–7.43	7.08–7.78	7.45–8.20	4.81–5.17
<i>Lonchorhina mankomara</i> (N = 9)											
Mean±SD	27.78±0.08	25.87±0.46	13.11±0.34	6.89±0.08	8.69±0.14	14.61±0.45	14.35±0.15	8.04±0.03	9.19±0.29	9.44±0.31	6.02±0.11
Range	26.54–27.95	25.57–26.59	12.20–13.71	6.26–6.96	8.39–8.83	14.00–15.23	14.25–14.62	8.02–8.09	8.73–9.43	9.35–9.91	5.92–6.12
<i>Lonchorhina marinkellei</i> (N = 2)											
ICN 12587♂	25.08	24.00	11.81	6.07	8.26	14.40	13.79	7.35	8.08	8.82	5.70
ICN 5459♀	25.91	24.31	12.00	6.11	8.25	14.47	13.81	8.11	8.63	9.17	5.52
<i>Lonchorhina orinocensis</i> (N = 14)											
Mean±SD	18.67±0.24	16.81±0.29	8.07±1.01	4.04±0.08	4.64±0.11	11.10±0.28	10.51±0.26	6.32±0.22	6.04±0.09	6.03±0.14	3.53±0.10
Range	18.33–19.82	16.24–17.64	7.07–9.05	3.87–4.87	4.09–5.30	10.53–11.74	9.82–10.90	5.94–6.97	5.92–6.32	5.76–6.69	3.37–4.35

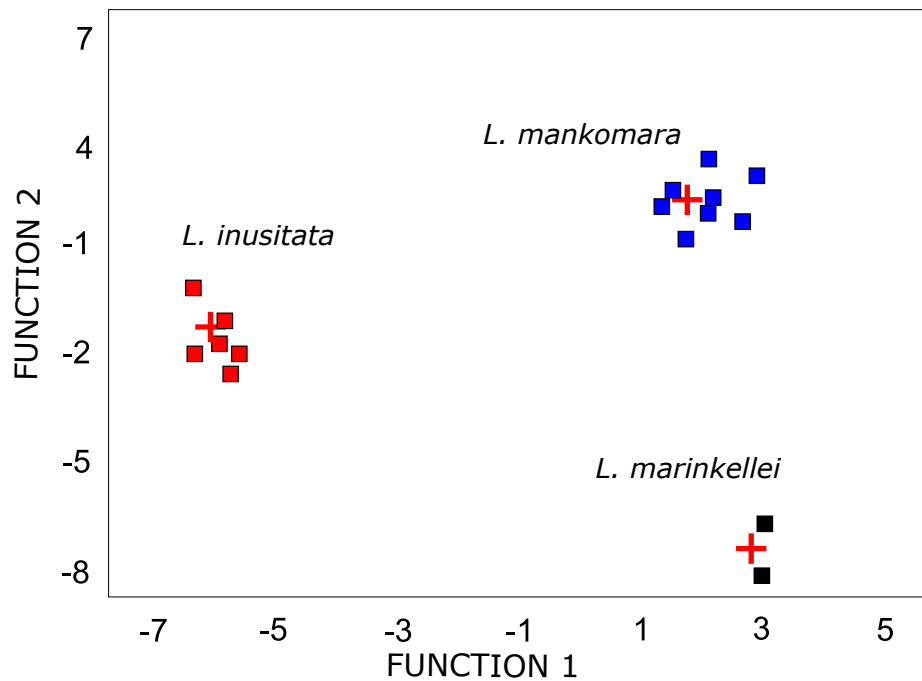


Figure 4. Discriminant Function Analysis of large species *L. mankomara* (blue squares) and *L. marinkellei* (black squares), as well as the medium sized *L. inusitata* (red squares). Centroids are designated by a plus symbol (+).

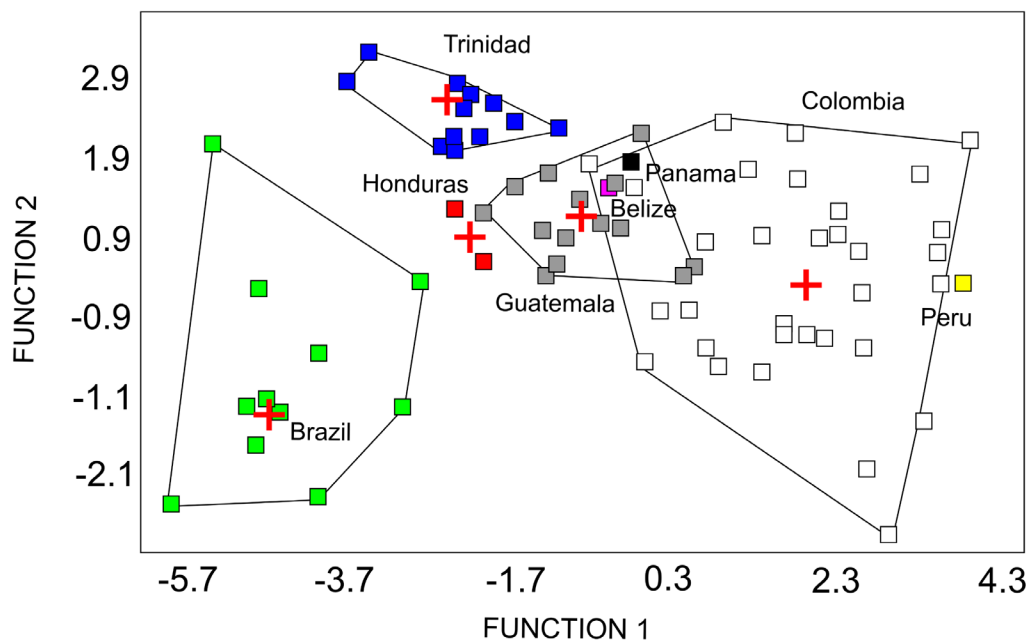


Figure 5. Discriminant Function Analysis (DFA) performed on 10 cranial measurements of analyzed specimens of *Lonchorhina aurita* across its distributional range: Belize (pink square); Brazil (green squares); Colombia (white squares); Guatemala (grey squares); Honduras (red squares); Panama (black square); Peru (yellow square); and Trinidad (blue squares). Centroids are designated by a plus (+) symbol.

DISCUSSION

Molecular data place the genus *Lonchorhina* in its own subfamily Lonchorhininae with a deep node that probably diverged from other phyllostomids between 24.7 and 21.6 mya (Baker et al. 2003, 2012). As mentioned, species in the genus *Lonchorhina* are characterized by extreme morphological modifications, including hypertrophied telic structures, with an enormous and extremely complex sword-shaped noseleaf, that in some species could reach one and a half times the dimensions of the skull (Hernández-Camacho and Cadena 1978; Mantilla-Meluk and Montenegro 2016) (Figs. 1, 7). Modifications of external features in *Lonchorhina* are accompanied by a unique skull morphology, found only in this genus. In *Lonchorhina*, the anterior portion of the skull, particularly the nasal and maxillae bones, are enlarged, providing support to the hypertrophied noseleaf, a structure that has been associated with the direction and intensity of the echolocation among bats in the family Phyllostomidae. The noseleaf among phyllostomids aids in echolocation and navigation inside a complex understory of Neotropical mature stratified forests. In addition, although poorly investigated, a larger and more complex noseleaf is a characteristic of some of the most specialized insectivore phyllostomid genera (i.e., *Gardnerycteris*, *Lophostoma*, *Macrophyllum*, and *Mimon*), suggesting that prey detection may play an important role in the evolution of more elaborate nose leaves and consequently can be associated with the accumulation of differences in skull morphologies in the genus *Lonchorhina*. Therefore, two non-excluding hypotheses can be suggested for the origin of the unique morphology in *Lonchorhina*: 1) a red queen effect, that includes a rapid channelization of the echolocation system (external and internal) in a predator-prey arms race (Mantilla-Meluk and Montenegro 2016); and 2) trophic niche displacement. Based on these arguments, prey size could be one of the drivers of the skull morphometric variation among recognized species in the genus.

Currently, the genus includes six species, five of which were subdivided by Williams and Genoways (2008) into three size groups: 1) large-sized (greatest length of the skull, GLS > 25 mm), including *L. marinkellei* and, in the study reported herein, the recently described *L. mankomara*, which is the largest

species in the genus; 2) medium-sized (GLS 19–23 mm), which includes *L. aurita*, *L. inusitata*, and *L. orinocensis*; and 3) small-sized (GLS < 19 mm), *L. fernandezi*. The analyses reported herein support the proposed size classes among *Lonchorhina* species, and point to the extreme divergence between the smallest, *L. fernandezi*, and the largest, *L. mankomara* and *L. marinkellei*, with a greater morphometric overlap among medium-sized taxa. In addition, the results of this study suggest an association between size of the noseleaf and complexity of its ornamentations and species body size. This is partially explained by the need for major structural support of larger noseleaves, represented by an also larger and more elaborate sellas (for images and nomenclature of *Lonchorhina* noseleaf structures see Hernández-Camacho and Cadena 1978; Mantilla-Meluk and Montenegro 2016). Based on the general morphology of the sellas, three groups can be differentiated: 1) the simplest sella expressed in *L. fernandezi*; 2) intermediate ornamentation of the sella, expressed in *L. orinocensis*, which also has a distinctly characteristic serrate border of the ear pinna; and hyperelaborated sellas in *L. aurita*, *L. inusitata*, *L. mankomara*, and *L. marinkellei*, species that exhibit size differences in noseleaf and ear pinna (Fig. 1).

Although analyses herein provide evidence of morphological separation of the six recognized species of *Lonchorhina*, except for *L. aurita*, most species (especially *L. fernandezi*, *L. inusitata*, *L. mankomara*, and *L. marinkellei*) are known from a few specimens and a limited number of localities. This makes a detailed morphological assessment of intraspecific variation and delineation of the distribution of species challenging (see Williams and Genoways 2008; Mantilla-Meluk and Montenegro 2016; Mantilla-Meluk et al. 2017).

Variation in Lonchorhina aurita and taxonomic remarks.—Morphometric analyses in this study indicated that specimens of *L. aurita* from near the type locality of the species in Trinidad were differentiated as an independent unit from two groups showing no overlap on the factorial plane—specimens from Brazil that were consistently smaller with respect to the hypodigm of *L. aurita* but clearly differentiated from *L. orinocensis*; and a group including representatives

in the remainder of the geographic range of the species (Central and northern South America). To better understand the morphological relationships among populations of *L. aurita*, a discriminant function analysis was performed on the *L. aurita* subset of specimens. *Lonchorhina aurita* from Brazil proved to be morphologically different from *L. aurita* from several localities across its distribution, including material from near the type locality of the species in Trinidad (Fig. 5). These morphometric differences suggest that *Lonchorhina* specimens from Brazil may represent a distinct species.

The only species in the genus that has a wide distribution is *Lonchorhina aurita*, originally described from Trinidad (Tomes, 1863), with a distribution extending from Oaxaca, Mexico, south to South America (Colombia, Ecuador, Peru, Bolivia, and Brazil), and a portion of the Caribbean (Trinidad; and the New Providence Islands [Bahamas Islands]) (Jones and Carter 1976; Lassieur and Wilson 1989; Nogueira et al. 2007; Williams and Genoways 2008; Reid 2009). Intraspecific variation in the genus has been suggested only for *L. aurita*. Anthony (1923) described the subspecies *L. a. occidentalis* based on three specimens collected in Guayas, Ecuador, claiming that this taxon could be differentiated from *L. a. aurita* (from Trinidad) by external characters (e.g., presence of white markings on the wings and length of the noseleaf). Soon after the description, several authors treated *occidentalis* as a subspecies of *L. aurita* (Goodwin and Greenhall 1961; Koopman 1978; Sanborn 1932; Tuttle 1970), with Linares and Naranjo (1973) and Hernández-Camacho and Cadena (1978) accepting *L. a. occidentalis* as a subspecies of *L. aurita* but restricting this consideration until additional material was available to test its specific status. However, since Cabrera (1958) overlooked this taxon in his revision of mammals from South America, other researchers considered it as a junior synonym of *L. aurita*, which is its currently accepted taxonomic status (Solmsen 1985; Williams and Genoways 2008). Based on the results of this study, some degree of morphometric differentiation is recognized between northern South American and Central American specimens of *L. aurita* and representatives of this taxon from Trinidad.

Also noteworthy is that Colombian specimens of *L. aurita*, particularly those from the departments of Caqueta and Meta, in the northeastern portion of the

Colombian Amazon, proved to have larger skulls than typical *L. aurita* from Trinidad, Brazil, and Ecuador but were part of a group including specimens from Central and northern South America, on the factorial plane. Although larger than typical *L. aurita* from Trinidad, the overall skull morphology of *L. aurita* material from Caqueta differed from that of herein analyzed *L. inusitata* specimens from Brazil, Peru, and Venezuela. These results point again to the need to conduct more detailed analyses using data sets other than morphology, including DNA analyses, to better understand the phylogenetic and phylogeographic affinities within the genus.

Large-sized Lonchorhina.—*Lonchorhina* species with a larger skull size in this study (medium-sized *L. inusitata* and large-sized *L. mankomara* and *L. marinkellei*) have a height of the rostrum comparable to braincase height, a character associated with size increase and complexity of the noseleaf supporting structures (cartilage and muscles). The overall enlargement of the rostrum (rostrum width, depth, and degree of swollen) is one of the major and consistent modifications separating medium-sized *L. inusitata* from *L. aurita* and *L. orinocensis*, and also works as diagnostic characters distinguishing *L. mankomara* from *L. marinkellei* (Figs. 6, 7). In addition, Mantilla-Meluk and Montenegro (2016) mention the following as modifications of the anterior portion of the skull in *L. mankomara*—the presence of projections of palatine; a massive hamulus pterygoideus; and an angled occipital region (all characters observed from a ventral view; see images in Mantilla-Meluk and Montenegro 2016). *Lonchorhina mankomara* has an overall more massive dentition than *L. marinkellei*; central upper incisors longer and wider; massive canines with wide cingula; enlarged first upper premolar, double the size of that in *L. marinkellei* (Fig. 6); wide molars with elongated lingual bases (Fig. 6); and bilobed lower incisors (Figure 8b in Mantilla-Meluk and Montenegro 2016). From a craniometric standpoint, significant values in the DFA's of medium and large size *Lonchorhina* support the currently accepted taxonomic differentiation and the recognition of *L. inusitata*, *L. mankomara*, and *L. marinkellei* as craniometrically distinct groups, also supported by discrete morphological characters.

In their assessment of representatives of the genus *Lonchorhina* from Colombia, Morales-Martínez and

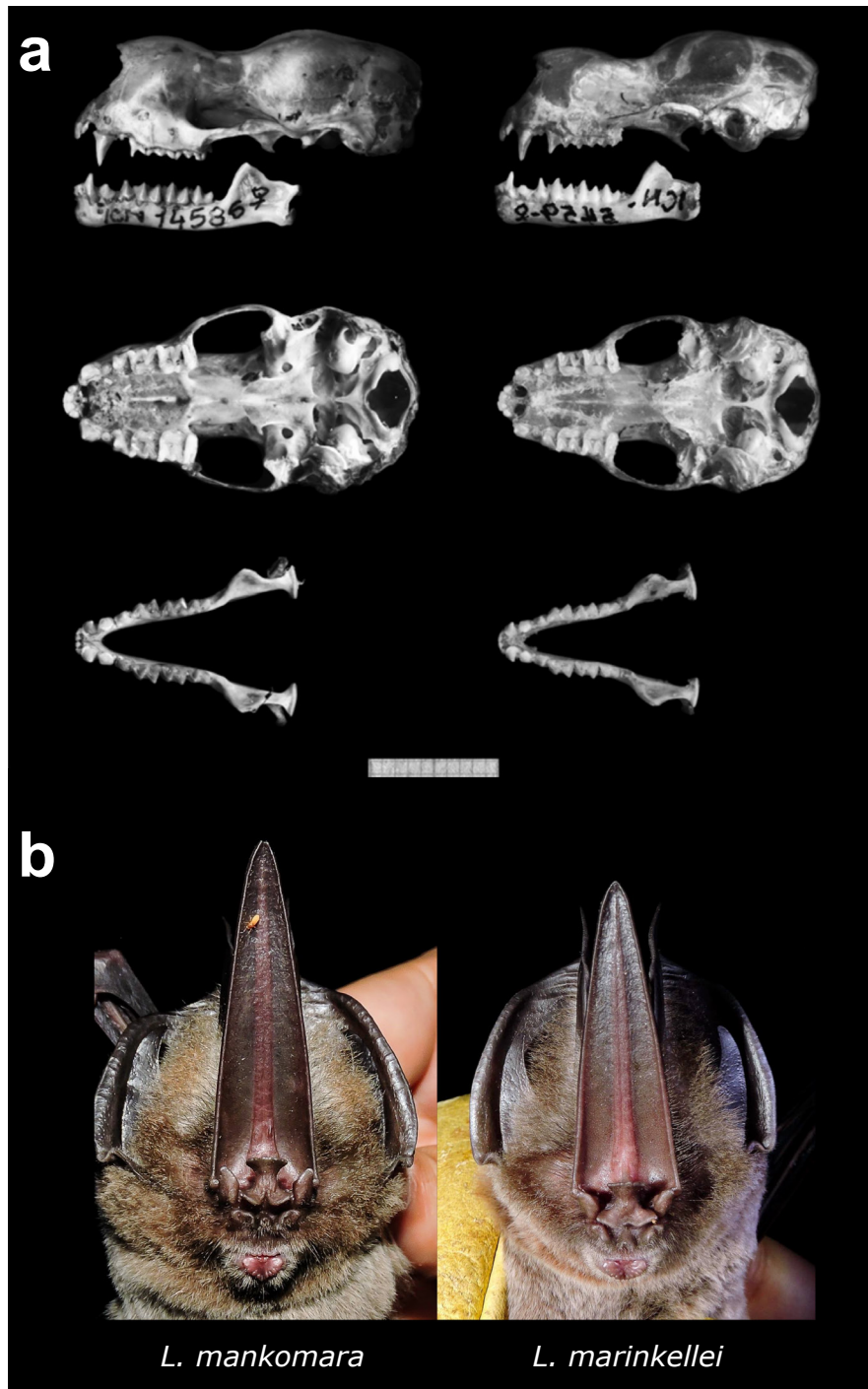


Figure 6. a) Comparison of lateral (top) and ventral (bottom) skull views of the holotypes of the recently described *Lonchorhina mankomara* (ICN 14586♀; Mantilla-Meluk and Montenegro 2016) (left) and *L. marinkellei* (ICN 5459; Hernandez-Camacho and Cadena 1978) (right). b) Comparison of external characters distinguishing *L. mankomara* and *L. marinkellei*, showing differences in size and shape of the nose-leaf, tragus, and pinna documented at the Serrania de la Lindosa where these two species occur in sympatry.

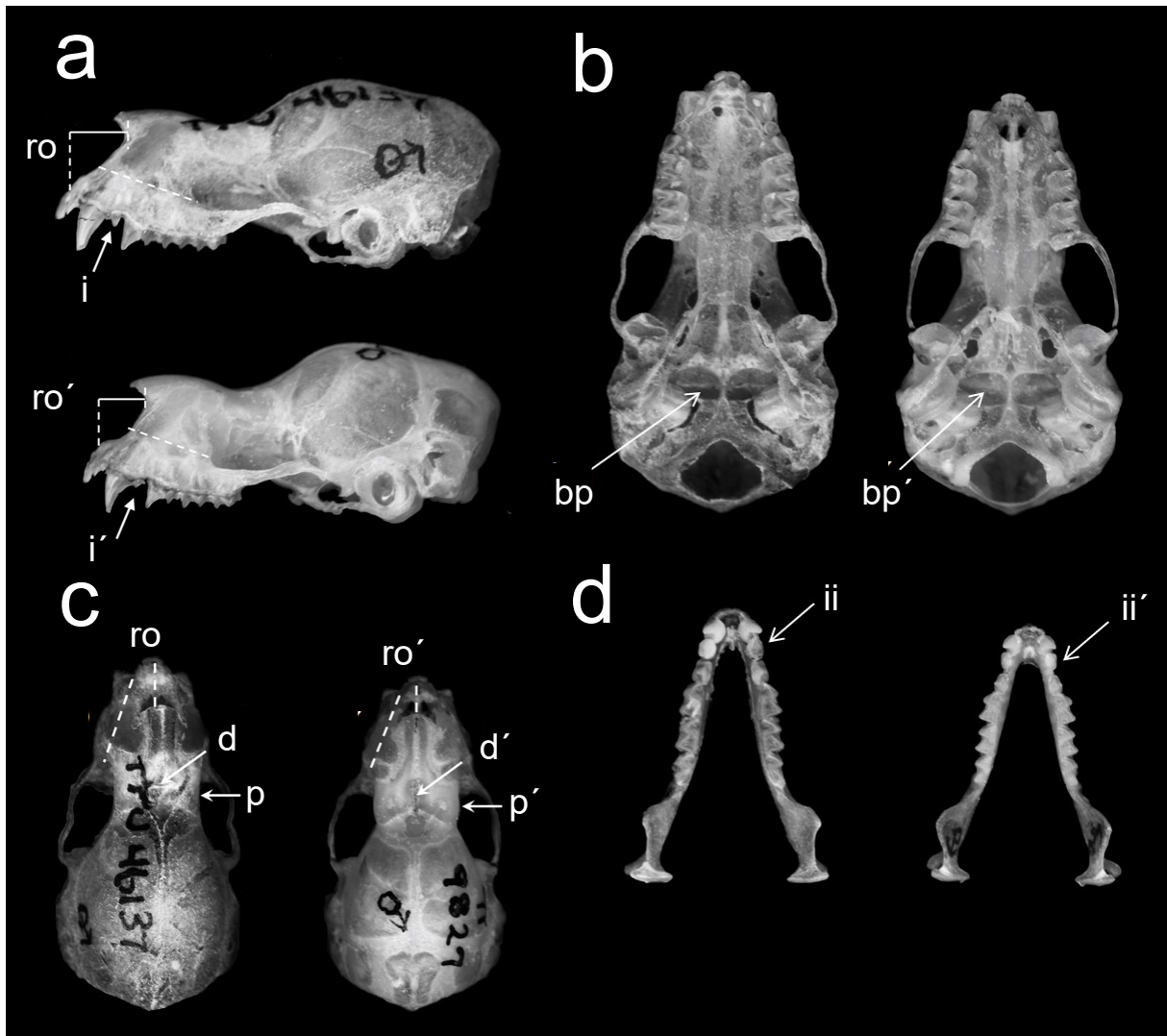


Figure 7. Comparison of discrete skull characters between the *Lonchorhina inusitata* (TTU 46137 ♂) from Peru and *L. aurita* (TTU 9827 ♂) from the island of Trinidad, type locality of the species: a) lateral view, showing the enlarged second premolar in *L. inusitata* (i) versus the small upper premolar in *L. aurita* (i'); b) ventral view, showing the wide and deep basisphenoid pits in *L. inusitata* (bp) versus the narrow and shallow basisphenoid pits in *L. aurita* (bp'); c) dorsal view showing the deep postorbital depression in *L. inusitata* (dp) versus a shallow postorbital depression in *L. aurita* (dp'), and a flat postorbital lateral profile in *L. inusitata* (p) versus a swollen postorbital region in *L. aurita* (p'); d) dorsal view of the mandible showing the enlarged first lower premolar in *L. inusitata* (ii) versus the small lower premolar in *L. aurita* (ii'). Dashed lines in 7a and 7c show deeper rostrum in *L. inusitata* (ro) versus a shallow rostrum in *L. aurita* (ro').

López-Arévalo (2018) omitted records of *L. mankomara* and *L. marinkellei* that were reported in Agudelo et al. (2018) and Mantilla-Meluk et al. (2017), alluding that: “being these two species externally undistinguishable, we consider that records in Agudelo et al. (2018) and Mantilla-Meluk et al. (2017) do not count with enough certainty to be considered within our work.” In the present assessment we verified not only the already reported differences in size of telic structures recorded for these two taxa (Mantilla-Meluk and Montenegro 2016) but also differences in shape and complexity of the sella, the cornus minus, and majus, as well as general shape of the excrescences at the base of the noseleaf López-Arévalo (2018). Herein, the lack of resolution in Morales-Martínez and López-Arévalo (2018) is interpreted as a potential consequence of the limited number (or absence) of *in vivo* specimens. However, although Morales-Martínez and López-Arévalo (2018) included a table with a detailed analysis of the external morphology of representatives of the genus, they failed to identify conspicuous external differences between *L. mankomara* and *L. marinkellei* (Fig. 6).

Finally, it is important to mention that the morphology of external characters is compromised in museum specimens preserved as dry skins, preventing an appropriate description of the actual complexity of soft anatomy structures.

First record of Lonchorhina inusitata for Peru.—To date, the only species of the genus *Lonchorhina* reported in official lists of mammals from Peru is *L. aurita* (Pacheco et al. 2009); however, specimens from Huánuco (TTU 46137 and CM 98592) proved to differ in all craniometric measurements but to have a distinct morphology when compared with typical *L. a. aurita* from Trinidad and the holotype of *L. a. occidentalis* (AMNH 62101♂). The craniometric ranges of specimens TTU 46137 and CM 98592 fell into those described for *L. inusitata*. As mentioned, *L. inusitata* is among the medium-sized species in the genus (Table 1) and it can be distinguished easily by forearm and skull size from the smaller *L. fernandesi* and *L. orinocensis* and the much larger *L. mankomara* and *L. marinkellei* (Williams and Genoways 2008; Mantilla Meluk and Montenegro 2016). No differences were found in overall craniometrics of specimen TTU 46137 in comparison to analyzed specimens of *L. inusitata* from Brazil and Venezuela (Figs. 2, 3).

Comparative analysis of discrete skull characters between L. inusitata and L. aurita.—The combination of discrete skull characters of *L. inusitata* are unique among recognized species of *Lonchorhina* and represent significant morphological evolution of characters historically assumed as conserved among mammals, such as modifications in size and placement of dental elements, as well as cusp development. Many specimens of *L. inusitata* have been either misidentified with the smaller and more common *L. aurita* (Genoways et al. 1981, material from Suriname) or with the much larger and less common *L. marinkellei* (Brosset and Charles-Dominique 1991; Brosset et al. 1996; material from French Guiana).

Besides differences in size between *L. aurita* and *L. inusitata* (Table 1), specimen TTU 46137 herein identified as *L. inusitata* is morphologically different from the typical *L. aurita* from Trinidad and Ecuador (countries from where the two subspecies of *L. aurita* have been described—*L. a. aurita* and *L. a. occidentalis*), and proved to be closely related in its morphology with typical *L. inusitata* from Brazil and Venezuela. However, in the Peruvian *L. inusitata* the anteriorly excavated portion of the basisphenoidal pits, also called inter-auditory pits in Handley and Ochoa (1997), were deeper than those of analyzed *L. inusitata* specimens from Brazil and Venezuela. Peruvian specimens of *L. inusitata* can be distinguished easily from the morphometrically closely related *L. aurita* by a suite of discrete characters. These include a more robust dentition, with particularly enlarged canines and premolars which are almost double the size of those in *L. aurita* (Figs. 7, 8), and bilobed inner incisors that contrast the entire cutting edges of the inner incisors of *L. aurita*. Although both *L. inusitata* and *L. aurita* have subequal lateral incisors (I2s), the inner lobes on I2 in *L. inusitata* are more acute than those in *L. aurita*, with the inner lobes almost twice the size of the lateral lobes. The canines of the Peruvian *L. inusitata* are larger than those in *L. aurita* and have a wider frontal surface. Some of the most contrasting characters between Peruvian *L. inusitata* and typical *L. aurita* from Trinidad are found on P4. Size, placement, shape, and disposition of the cusps on P4 differ substantially as follows—the paracone of P4 in Peruvian *L. inusitata* is larger in comparison with the paracone of *L. aurita*; and, the P4s in Peruvian *L. inusitata* are in contact with the canines and P5, whereas in *L. aurita* from Trinidad the P4 possesses diastemata between adjoining teeth (Figs. 7, 8).

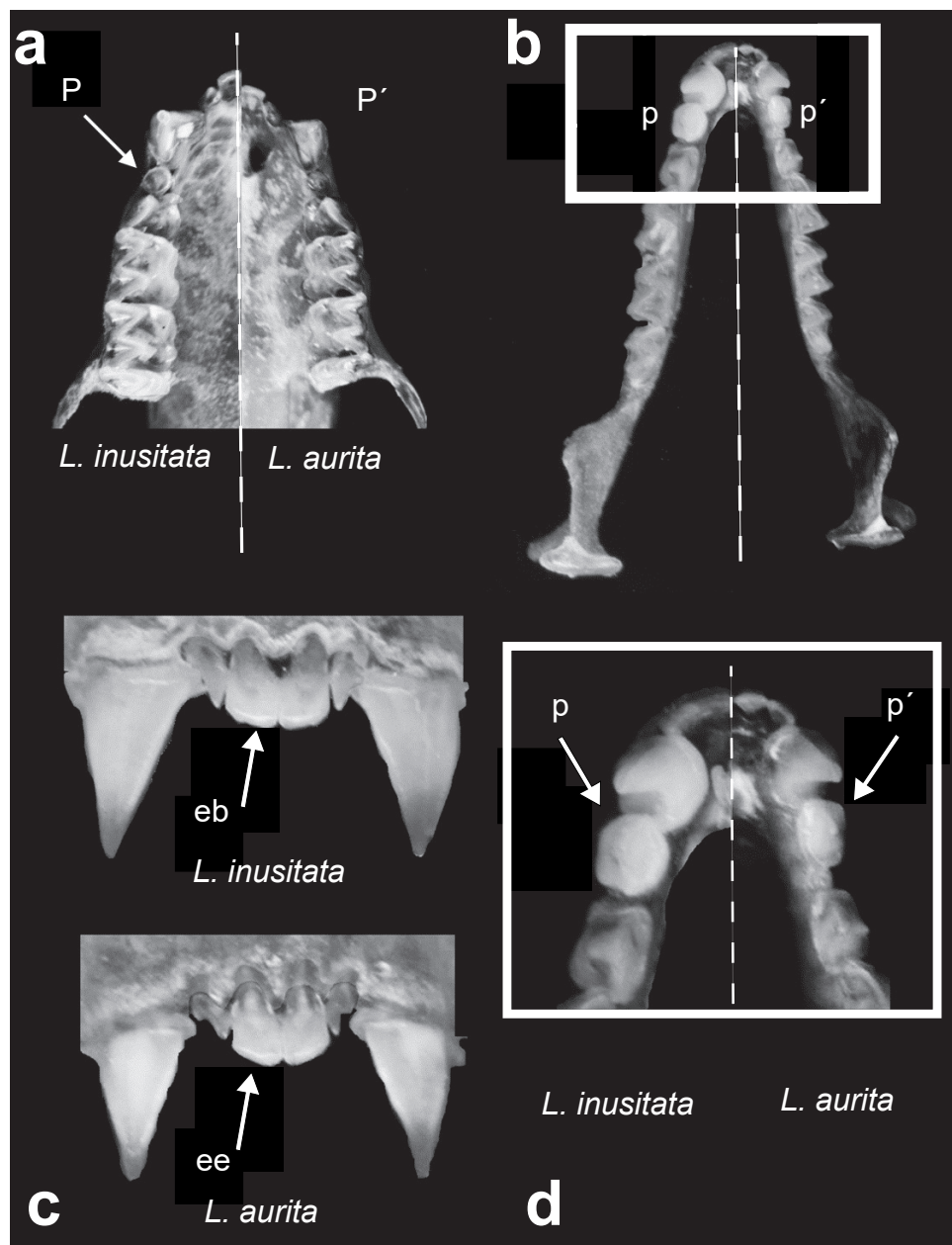


Figure 8. Comparison of discrete skull characters differentiating *L. aurita* from Trinidad and *L. inusitata* from Peru (TTU 46137). Skull images are composites, in which the left half of the axis (dashed line) corresponds to *L. inusitata*, while the right half corresponds to *L. aurita*: a) skull ventral view showing the enlarged first upper premolar in *L. inusitata* (P) versus the smaller first upper premolar in *L. aurita* (P'); b) dorsal view of the mandible showing the enlarged first lower premolar in *L. inusitata* (p) versus the smaller lower premolar of *L. aurita* (p'); c) frontal view of the bilobed edge inner incisors of *L. inusitata* (upper) (eb) versus the entire edge of inner incisors in *L. aurita* (bottom) (ee); and d) detail of the first lower premolars of *L. inusitata* (left of the axis) versus *L. aurita* (right of the axis) showing differences in size of the paracone of P4, larger *L. inusitata* (p) and in contact with the canines and P5, than that in *L. aurita* (p'), which also has a diastemata between adjoining teeth.

In addition to size differences in all measurements analyzed between *L. inusitata* and *L. marinkellei* (Table 1), Williams and Genoways (2008:264) mentioned that *L. inusitata* is internally similar to *L. marinkellei* in shape of rostrum, with the basisphenoid pits shallow anteriorly, in contrast to the deep anteriorly pits in *L. marinkellei*. In addition, the rostrum is higher than the braincase in *L. marinkellei*, but of about equal height or slightly lower than the braincase in *L. inusitata*. Externally, both species are similar in the size, shape, and degree of hairiness of ears, noseleaf, and facial excrescences; however, the underparts are dark in *L. inusitata*, while in *L. marinkellei* the venter is heavily washed with white. All the above-mentioned characters were identified in both *Lonchorhina* specimens from Huánuco (TTU 46137 and CM 98592).

Based on the evidence provided herein from the craniometric analyses, as well as morphological comparison of discrete characters, the Peruvian specimens TTU 46137 and CM 98592 from the department of Huánuco, previously identified as *L. aurita*, should be recognized as *L. inusitata*. Thus, they represent the first record of the species in the country, as well as a significant distribution extension in its range of more than 1,360 km (860 mi) southeast from records in Venezuela (Fig. 9). Pacheco et al. (2018) reported 181 bat species occurring in Peru. With the new records of *L. inusitata* for Peru, the bat diversity increases to 182 species.

The specimens of *L. inusitata* from Peru (TTU 46137 and CM 98592) were caught the same night in the same mist net, and are in good condition and preserved as study skins with clean skulls. The specimens were the product of a field trip organized by D.

E. Wilson as Director of Biodiversity Programs at the National Museum of Natural History (NMNH). The trip was conducted under the auspices of the Smithsonian Institution/Man and the Biosphere Program, with Francisco Dallmeier as Director of that program. Don Wilson invited Robert Baker, curator of mammals at the and director of the Natural Science Research Laboratory of the Museum of Texas Tech University at the time, to go to a Shell Oil Company drilling platform in the lower Urubamba region of Peru, in the company of M. O'Connell of the Carnegie Museum of Natural History, which is the institution that houses one of the two collected *L. inusitata* specimens. Robert had wanted to go to the field with his good friend Don Wilson, and the trip to Urubamba seemed like a good opportunity. The site was very isolated, and accessible only by helicopter. The trip was very successful in terms of the number collected specimens (D. Wilson, comm. pers.). As a result of Dr. Baker's and Dr. Wilson's commitment to science, and their profound personal and academic friendship, herein we add another species to the list of Peruvian mammals. One author of this publication (H. Mantilla-Meluk), had been introduced to R. J. Baker (his former PhD advisor) by D. Wilson, who also supported the visit to the NMNH mammal collections that allowed the *Lonchorhina* craniometric data gathering years later. The authors chose to include this manuscript as part of this memorial volume, in honor of Dr. Robert J. Baker, because it depicts a crucial aspect of mammalogy as a science, as well as our academic family bonds. In his life, Robert J. Baker understood what academia is, a web of bridges that facilitate the construction of knowledge; connections that can only be generated with generosity, as he used to say: "as many brains as you need" (R. J. Baker 1942–2018).

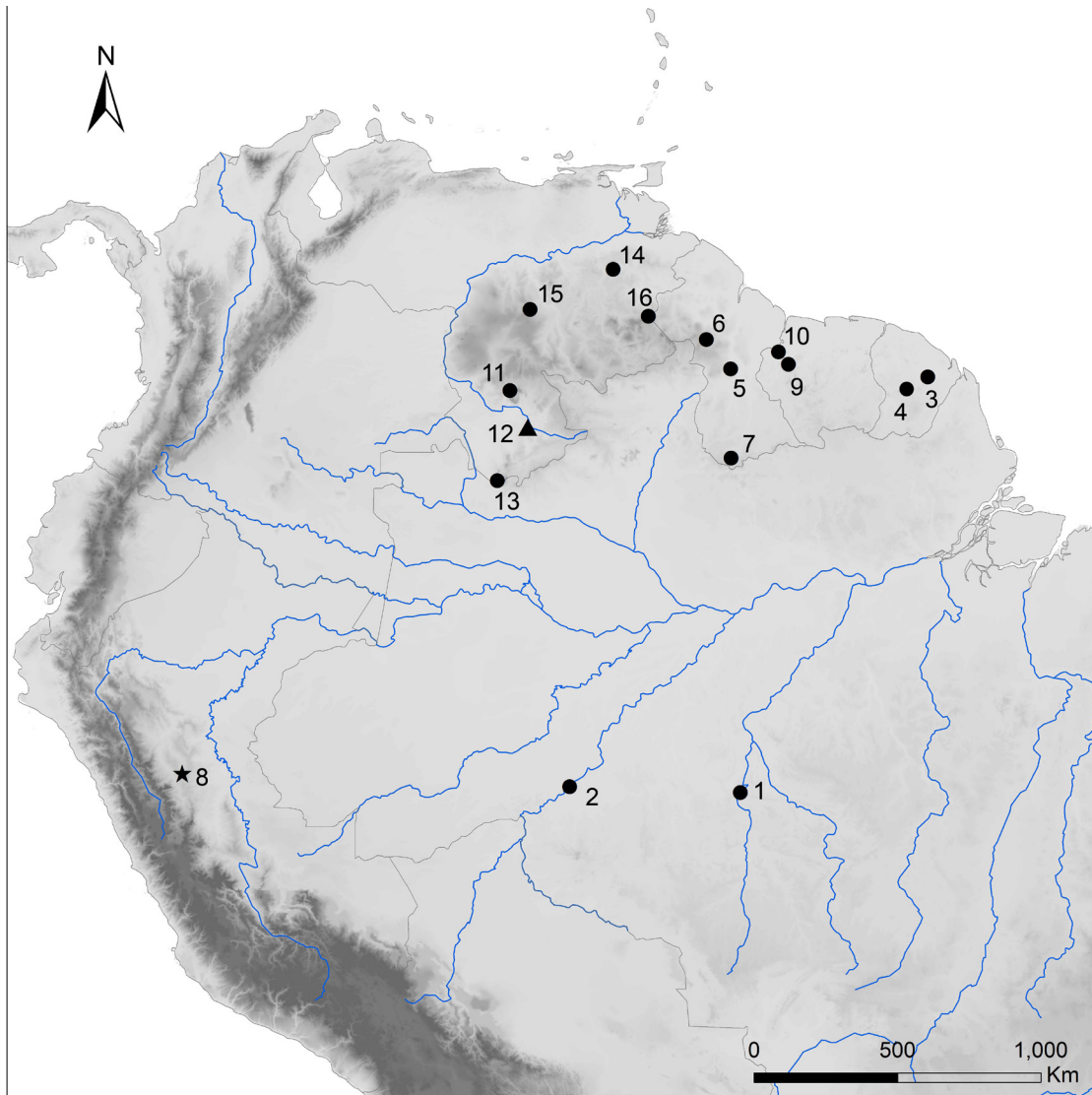


Figure 9. Map showing known localities of *Lonchorhina inusitata*, including the first record of this taxon for Peru (black star). 1) Brazil: Mato Grosso, Juruena National Park, São João River trail; 2) Brazil: Rondônia, Pôrto Velho [“19 km da Cidade”]; 3) French Guiana: Cayenne, 100 km SSW Cayenne, Aratoi, Estación les Nouragues; 3) French Guiana: Cayenne, Grotte du Bassin du Tapir, Les Nouragues; 4) French Guiana: St. Laurent Du Maroni, Saül; 5) Guyana: Potaro-Siparuni, 30 Km NE of Surama; 6) Guyana: Potaro-Siparuni, Kaieteur National Park, Kaieteur Falls; 7) Guyana: Upper Takutu-Upper Essequibo, Kamoá River, 50 Km SWW of Gunn's Strip; 8) Peru: Huánuco, Leoncio Prado, 9 km N Aucayacu; 9) Suriname: Nickerie, Sipaliwini, Bakhuis, Transect 9; 10) Suriname: Sipaliwini, Avanavero; 11) Venezuela: Amazonas, 56 km NNW La Esmeralda, Caño Culebra, Belén; 12) Venezuela: Amazonas, Boca Mavaca, 84 km SSE Esmeralda; 13) Venezuela: Amazonas, Río Mawarinuma, Parque Nacional Serranía de la Neblina; 14) Venezuela: Bolívar, 12 km S of El Manteco; 15) Venezuela: Bolivar, Alto Rio Tawadu, Monumento Natural Sierra de Maigualida; and 16) Venezuela: Bolivar, Km 85, about 65 km SSE El Dorado.

ACKNOWLEDGMENTS

We would like to thank the late R. J. Baker, H. Garner, L. Bradley, J. P. Carrera, and personnel of the Natural Science Research Laboratory and the Texas Tech Museum; S. McLaren and the Carnegie Museum for access to specimen CM 89582; B. D. Patterson, L. Heaney, R. Banasiak, N. Upham, the late W. Stanley, and the Field Museum of Natural History short-term visitors program; D. E. Wilson, A. L. Gardner, K. Helgen, and L. Gordon for their help at the collections of the United States National Museum of the Smithsonian Institution; G. Amat, J. Aguirre, H. López, and J.

Muñoz-Garay for their help at the mammal collection of the Instituto de Ciencias Naturales of the Universidad Nacional de Colombia; and F. Mosquera-Guerra, F. Trujillo, A. Velasquez, and the team of the Expeditions to the Chiribiquete, National Natural Park at the Colombian Guayana (2015–2017). R. Agudelo, B. Lim, D. Morales-Martínez, and M. Tschapka kindly allowed us to reproduce photographs of *Lonchorhina*. Data collection in Colombia was possible thanks to the Posdoctoral program of the Universidad Nacional de Colombia and the Instituto de Ciencias Naturales.

LITERATURE CITED

- Agudelo R., V. Giraldo, and V. J. Setina. 2018. Murciélagos de San José del Guaviare. Field Guides of Field Museum # 1006. [Reviewed on: 15 June 2018] https://fieldguides.fieldmuseum.org/sites/default/files/rapid-color-guides-pdfs/1006_colombia_bats_of_san_jose_del_guaviare.pdf.
- Anthony, H. E. 1923. Preliminary report on Ecuadorean mammals, no. 3. American Museum Novitates 55:1–14.
- Baker, R. J., O. R. P. Bininda-Emonds, H. Mantilla-Meluk, C. A. Porter, and R. A. Van den Bussche. 2012. Molecular timescale of diversification of feeding strategy and morphology in New World leaf-nosed bats (Phyllostomidae): a phylogenetic perspective. Pp. 385–409 in *Evolutionary history of bats: fossils, molecules and morphology* (G. F. Gunnell and N. B. Simmons, eds.). Cambridge University Press, Cambridge, United Kingdom.
- Baker, R. J., S. R. Hooper, C. A. Porter, and R. A. Van den Bussche. 2003. Diversification among New World leaf nosed bats: an evolutionary hypothesis and classification inferred from digenomic congruence of DNA sequence. Occasional Papers, Museum of Texas Tech University 230:1–32.
- Brosset, A., and P. Charles-Dominique. 1991. The bats from French Guiana: a taxonomic, faunistic, and ecological approach. *Mammalia* 54:509–560.
- Brosset, A., J. -F. Cosson, P. Gaucher, and D. Masson. 1996. Les chiropteres d'un marecagecotier de Guyane; composition du peuplement. *Mammalia* 59:527–537.
- Cabrera, A. 1958. Catalogo de los mamíferos de America del Sur. I (Metatheria, Unguiculata, Carnivora). *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* 4:1–307.
- Dávalos, L. M., A. L. Cirranello, J. H. Geisler, and N. B. Simmons. 2012. Understanding phylogenetic incongruence: lessons from phyllostomid bats. *Biological Reviews* 87:991–1024.
- Dávalos, L. M., P. M. Velazco, O. M. Warsi, P. D. Smits, and N. B. Simmons. 2014. Integrating incomplete fossils by isolating conflictive signal in saturated and non-independent morphological characters. *Systematic Biology* 63:582–600.
- Fox, J., and S. Weisberg. 2011. An {R} companion to applied regression, Second Edition. Thousand Oaks California: Sage. URL:<http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>.
- Genoways, H. H., S. L. Williams, and J. A. Groen. 1981. Results of the Alcoa Foundation–Suriname expeditions. V. Noteworthy records of Surinamese mammals. *Annals of Carnegie Museum* 50:319–332.
- Goodwin, G. G., and A. M. Greenball. 1961. A review of the bats of Trinidad and Tobago. *Bulletin of the American Museum of Natural History* 122:187–302.
- Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4:1–9.
- Handley, C. O., Jr., and J. Ochoa G. 1997. New species of mammals from northern South America: a sword-nosed bat, genus *Lonchorhina* Tomes (Chiroptera: Phyllostomidae). *Memoria Sociedad de Ciencias Naturales La Salle* 57:71–82.
- Hernández-Camacho, J., and A. Cadena G. 1978. Notas para la revisión del género *Lonchorhina* (Chiroptera, Phyllostomidae). *Caldasia* 7:199–251.
- Jones, J. K., Jr., and D. C. Carter. 1976. Annotated checklist, with keys to subfamilies and genera. Pp. 7–38 in *Biology of bats of the New World family Phyllostomatidae*. Part I (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.).

- Special Publications, Museum of Texas Tech University 10:1–218.
- Koopman, K. F. 1978. Zoogeography of Peruvian bats with special emphasis on the role of the Andes. *American Museum Novitates* 2651:1–33.
- Lassieur, S., and D. E. Wilson. 1989. *Lonchorhina aurita*. *Mammalian Species* 347:1–4.
- Linares, O. J., and C. J. Naranjo. 1973. Notas acerca de una colección de murciélagos del género *Lonchorhina* de la cueva de Archidona, Ecuador (Chiroptera). *Boletín de la Sociedad Venezolana de Espeleología* 4:175–180.
- Linares, O. J., and J. Ojasti. 1971. Una nueva especie de murciélago del género *Lonchorhina* (Chiroptera: Phyllostomatidae) del sur de Venezuela. *Novedades Científicas, serie zoológica* 36:1–8.
- Mantilla-Meluk, H., and O. L. Montenegro. 2016. A new species of *Lonchorhina* (Chiroptera: Phyllostomidae) from Chiribiquete, Colombian Guayana. *Biodiversidad Neotropical* 6:171–187.
- Mantilla-Meluk, H., F. Mosquera-Guerra, F. Trujillo, N. Pérez-Amaya, A. Velásquez-Valencia, and A. Vargas Pérez. 2017. Mamíferos del Sector Norte del Parque Nacional Natural Serranía de Chiribiquete. *Colombia Amazónica* 10:99–134.
- Morales-Martínez, D. M., and H. F. López-Arévalo. 2018. Distribución y conservación de los murciélagos del género *Lonchorhina* (Chiroptera: Phyllostomidae) en Colombia. *Caldasia* 40:349–365.
- Nogueira, M. R., A. L. Peracchi, and R. Moratelli. 2007. Subfamilia Phyllostominae. Pp. 61–97 in *Morcegos do Brasil* (N. R. Reis, A. L. Peracchi, W. A. Pedro, I. P. Lima, eds.). Nélio Roberto dos Reis, Londrina, Brazil.
- Ochoa G., J., and C. Ibañez. 1984. Nuevo murciélago del género *Lonchorhina* (Chiroptera: Phyllostomidae). *Memoria de la Sociedad de Ciencias Naturales La Salle* 118:145–159.
- Pacheco, V., R. Cadenillas, E. Salas, C. Tello, and H. Zeballos. 2009. Diversidad y endemismo de los mamíferos del Perú. *Revista Peruana de Biología* 16:5–32.
- Pacheco, V., P. Sánchez-Vendizú, and S. Solari. 2018. A new species of *Anoura* Gray, 1838 (Chiroptera: Phyllostomidae) from Peru, with taxonomic and biogeographic comments on species of the *Anoura caudifer* complex. *Acta Chiropterologica* 20:31–50.
- R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Reid, F. A. 2009. A field guide to the mammals of Central America and Southeast Mexico. 2nd ed. Oxford University Press, New York.
- Sanborn, C. C. 1932. Neotropical bats in the Carnegie Museum. *Annals of the Carnegie Museum* 21:171–183.
- Solmsen, E.-H. 1985. *Lonchorhina aurita* Tomes, 1863 (Phyllostominae, Phyllostomidae, Chiroptera) im westlichen Ecuador. *Zeitschrift für Säugetierkunde* 50:329–337.
- Tomes, R. F. 1863. On a new genus and species of leaf-nosed bats in the Museum at Fort Pitt. *Proceedings of the Zoological Society of London* 1863:81–84.
- Tuttle, M. D. 1970. Distribution and zoogeography of Peruvian bats, with comments on natural history. *The University of Kansas Science Bulletin* 49:45–86.
- Williams, S. L., and H. H. Genoways. 2008 (2007). Subfamily Phyllostominae Gray, 1825. Pp. 255–300 in *Mammals of South America, Volume 1: Marsupials, xenarthrans, shrews, and bats* (A. L. Gardner, ed.). The University of Chicago Press, Chicago, Illinois.

Addresses of authors:

HUGO MANTILLA-MELUK

*Centro de Estudios de Alta Montaña (CEAM)
Universidad del Quindío
Armenia, Quindío
Colombia
ceam@uniquindio.edu.co*

NATALIA PEREZ-AMAYA

*Departamento de Biología
Posgrado en Ciencias-Biología
Universidad del Valle
Cali, Valle del Cauca
Colombia
natalia.prez7@gmail.com*

PAÚL M. VELAZCO

*Department of Mammalogy
American Museum of Natural History
New York, NY 10024 USA
pvelazco@amnh.org*

APPENDIX

Specimens of *Lonchorhina* used in this study. See Materials and Methods for collection acronyms.

Lonchorhina aurita (83).—BELIZE: Toledo: Bladen Nature Reserve, Teakettel camp, on Bladen Branch (USNM 583007♂). BRAZIL: Maranhão: Alto Parnaíba (FMNH 26449♂). Para: Altamira 9 km SE (by road) Caverna do Valdeci (USNM 549340, USNM 549343–549345♀, USNM 549339♂, USNM 549341–549342♂); Altamira 85 km SW Eastern bank Rio Iriri (USNM 549346♀). Pernambuco: Toritama, Fazenda Matumbo, Pedrao Dos Pontais (USNM 536441♂). COLOMBIA: Antioquia: Zaragoza 26 km W Aljibes (USNM 799290–799292♂); 26 km S, 22 km W of Zaragoza (Aljibes) (ICN 12697♂, 12698♂); Zaragoza 25 km W La Tirana (USNM 549340♀). Caldas: Samana, Norcasia, Campamento Profesionales I, Proyecto La Miel I (ICN 14277♀); Samana, Vereda La Miel, near Campamento Tasajos (ICN 14306–14307♀); Samana, Corregimiento Norcasia, surroundings Campamento CHEC (ICN 15953♀); Samana, Corregimiento Norcasia, Vereda La Pradera, Campamento CHEC, Corporación Hidroeléctrica de Caldas, La Miel I (ICN 12488–12489♀, ICN 12490♂, ICN 12571♂). Caqueta: Municipio Montañitas; Vereda Santuario, Finca Ceilán (ICN 16896–16897♀); Rio Cuñare, Raudal El Tubo, E Serranía de Chiribiquete, Parque Nacional Natural (PNN) Chiribiqueté (ICN 14716♀, ICN 14584–14587♀); Rio Mesay, Puerto Abeja, SE Serranía de Chiribiquete (ICN 14583♂). Meta: San Juan de Arama, Northern portion Serranía La Macarena, Caño Guamalito (ICN 12041–12042♀); San Juan de Arama, northern portion Serranía La Macarena, Caño La Curia (ICN 10215♂, ICN 10217♂, ICN 10218♀, ICN 10219♂). Risaralda: Pueblo Rico, camino a la Bocatoma (ICN 11458–11459♂). Valle del Cauca: 29 km SE Buenaventura (USNM 483327♂). ECUADOR: Chimborazo: Chunchi, Puente de Chimbo (AMNH 62101♂ [holotype of *Lonchorhina aurita occidentalis*]). GUATEMALA: Izabal: Quebrados (FMNH 41891–41892♂, 41893♀, 41894–41897♂, 41898–41900♂, 41901–41904, 41906♀, 41911–41913 sex undetermined). HONDURAS: Colón: Trujillo, Parque Nacional Caprio y Calenturas (TTU 104265–104266♀). PANAMA: Colón: Gamboa, Coco Plantation, Mine Shaft (FMNH 92642♂); Fort Sherman (FMNH 92663♂). PERU: Cuzco: Paucartambo, Consuelo, 15.9 km SW Pilcopata (FMNH 174715♂, 174717–174718♀). Madre de Dios: Maskoitania, 13.4 km NNW Atalaya, left bank Rio Alto Madre de Dios (FMNH 174716♀). Pasco: Oxapampa, San Juan (USNM 364269–364270♀, 364268♂). TRINIDAD: Saint George: (TTU 5233♀, 5221♂, 5223♂, 5224♀, 8983♂, 8984♂, 9826–9829♂). VENEZUELA: (FMNH 20637 sex undetermined).

Lonchorhina inusitata (6).—BRAZIL: Rondônia: Porto Velho (NMNH 554575♀). PERU: Huánuco: Leoncio Prado, 9 km N Aucayacu (TTU 46137♂ [tissues available, TK 22878]; CM 98592♂). VENEZUELA: Amazonas: Belém, 56 Km NNW Esmeralda, Caño Culebra (USNM 388736♂); Cerro Neblina, Base Campamento (USNM 560553♀, 560774♀).

Lonchorhina fernandesi (1).—VENEZUELA: Bolívar: Puerto Cedeño (ICN 12276♂).

Lonchorhina mankomara (9).—COLOMBIA: Caqueta: Rio Mesay, Puerto Abeja, SE Serranía de Chiribiquete (ICN 14584–14587♀). Guaviare: Serranía de Chiribiquete, Sector Norte (UQ-HMM 1049♀, 1960♀, 1062♀, 1072♀, 1081♂).

Lonchorhina marinkellei (2).—COLOMBIA: Vaupés: Mitu, 10 km E Durania (ICN 5459♀); Mitu, Cueva Superior Primer Cerro, Finca Urania (ICN 12587♂).

Lonchorhina orinocensis (14).—COLOMBIA: Meta: Serranía de la Macarena, Caño Cristales (FMNH 58672♂, 8675♂, 58676♀). VENEZUELA: Apure: Hato Cariben, 32 km NE Puerto (USNM 373290♀, 373291♀, 373292♀, 373293♂, 373294♀, 373295♂, 373296–373298♀, 373299, 373302♀).

Suggested citation format:

Mantilla-Meluk, H., N. Perez-Amaya, and P. M. Velazco. 2019. Morphometric variation of the genus *Lonchorhina* (Chiroptera, Lonchorhininae), with noteworthy comments on taxonomy and distributional range extensions. Pp. 149–168 in *From field to laboratory: a memorial volume in honor of Robert J. Baker* (R. D. Bradley, H. H. Genoways, D. J. Schmidly, and L. C. Bradley, eds.). Special Publications, Museum of Texas Tech University 71:xi+1–911.