

A new species of *Lonchorhina* (Chiroptera: Phyllostomidae) from Chiribiquete, Colombian Guayana

Nueva especie de *Lonchorhina* (Chiroptera: Phyllostomidae) de Chiribiquete, Guayana colombiana

Hugo Mantilla-Meluk^{1,2}, Olga Montenegro¹

Abstract

Sword-nose bats genus *Lonchorhina* are characterized by the most developed telic structures among representatives of the Neotropical family Phyllostomidae, including the longest noseleaf, ear pinna, and tragus in respect to their body sizes. Species in the genus *Lonchorhina* are usually rare in mist-netting inventories, and most of the currently recognized species are represented in museum collections by few specimens from a limited number of localities, preventing a better appreciation of its diversity. The last comprehensive study on the taxonomy of the genus was conducted almost four decades ago based upon a limited number of specimens that did not include all currently recognized species. In this work we evaluate the phenetic affinities and taxonomic placement of divergent *Lonchorhina* specimens recovered from the Colombian Guayana, through the analysis of both discrete and morphometric skull characters. Our analyses included 105 *Lonchorhina* specimens, representing the five currently recognized species, from a substantial portion of the distribution of the genus. As a result of our evaluation, we introduce a new species of sword-nose bat, representing the phyllostomid species with the largest known noseleaf and tragus (noseleaf >41.5 mm, tragus >22.3 mm). The newly introduced taxon is part of the large skull *Lonchorhina* (Greatest Skull Length, GSL >21.5 mm) and it is closely related in its morphology to *L. marinkellei* and *L. inusitata* from which it is easy to tell apart by its unique morphology, overall larger size (GSL media=27.31; StDev=0.5) and more massive dentition. The holotype of *Lonchorhina* sp. nov. was collected at an inselberg formation, adjacent to Río Mesay, Puerto Abeja in the Southwestern portion of the National Natural Park Chiribiquete, in the Colombian department of Caquetá, at 340 masl. The National Park Chiribiquete, corresponds to one of the most unexplored areas in the country, enclosing the oldest and largest series of Amazon pictograms (20.000 years bc) registered on the outcrops of the numerous tepuis, in which images of bats are of particular cultural importance, in that sense the new species is a tribute to the Karijona people who inhabited the area of Chiribiquete.

Keywords: Chiribiquete, Guayana, Karijona, Sowrd-nose bat.

Resumen

Los murciélagos de hoja nasal de espada del género *Lonchorhina* se caracterizan entre los miembros de la familia Phyllostomidae por poseer las estructuras téllicas más desarrolladas, incluyendo la hoja nasal, trago, y pina más largos con respecto a su tamaño corporal. Las especies del género *Lonchorhina* son usualmente difíciles de registrar en muestreos con redes de niebla y están representadas en colecciones científicas, por pocos individuos de algunas localidades, impidiendo una mejor apreciación de su diversidad. La última revisión del género se realizó hace casi cuatro décadas, e incluyó un número limitado de especímenes de pocas localidades, sin considerar todas las especies reconocidas en la actualidad. En este estudio se analiza la morfología y variación morfométrica craneal de 105 especímenes de *Lonchorhina*, representando todas las especies del género reconocidas a la fecha, provenientes de una porción significativa de su rango geográfico conocido. Como resultado de la presente evaluación, se describe una nueva especie de murciélago de hoja nasal de espada proveniente de la región biogeográfica de la Guayana colombiana, que representa el murciélago filostómido con la hoja nasal y trago más largos documentados (hoja nasal >41.5 mm, trago >22.3 mm). La nueva especie es parte del grupo de *Lonchorhina*

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de cráneo grande (longitud máxima del cráneo, LMC >21.5 mm) y está cercanamente relacionada en su morfología con *L. marinkellei* y *L. inusitata*, de las cuales es fácilmente distinguible por su morfología única, mayor tamaño (LMC media 27.31; DE=0.5) y dentición masiva. El holotipo de *Lonchorhina* sp. nov. se recolectó en una formación de Inselberg adyacente al río Mesay, Puerto Abeja, a 340 msnm en la porción suroccidental del Parque Natural Nacional Chiribiquete, en el departamento de Caquetá, Colombia. El PNN Chiribiquete corresponde a una de las áreas más inexploradas del país, de particular interés antropológico al contener la serie más extensa y antigua (20.000 AP) de pictogramas amazónicos sobre los escarpes de sus números tepuis, donde las representaciones de quirópteros son de particular importancia cultural. La nueva especie es en este sentido un tributo a la gente Karijona que habitó el área de Chiribiquete.

Palabras clave: Chiribiquete, Guayana, Karijona, Murciélago de hoja de espada.

Introduction

Sword-nose bats in the genus *Lonchorhina* are characterized by the most developed telic structures among representatives of the Neotropical family Phyllostomidae, including the longest noseleaf, ear pinna, and tragi in respect to their body sizes (Hernández-Camacho and Cadena 1978). These extraordinary morphological adaptations have been associated with a hyper-developed echolocation system that allows these bats to forage for their prey in stratified forests. The genus *Lonchorhina* Tomes 1863, currently comprises five species, three of them present in Colombia (marked with an asterisk) (Mantilla-Meluk *et al.* 2009): *L. aurita** Tomes 1863, *L. orinocensis** Linares and Ojasti 1971, *L. marinkellei** Hernández-Camacho and Cadena 1978, *L. fernandezi* Ochoa and Ibañez 1984, and *L. inusitata* Handley and Ochoa 1997 (Williams and Genoways 2007).

Species in the genus *Lonchorhina* differ in terms of size. *Lonchorhina fernandezi*, the smallest species in the genus (greatest skull length, GSL <18.00 mm) is only known from its type locality; medium size *L. aurita* and *L. orinocensis* (GSL >19.0 and <21.5 mm) have relatively wide distributions (Williams and Genoways 2007) and are relatively well represented in museum collections; and finally, large *L. inusitata* and *L. marinkellei* (GSL >21.5 mm) have restricted distributions and are considered rare animals poorly represented in museum collections. The largest species, *L. marinkellei*, is only known from two locali-

ties in Colombia: Mitú, department of Vaupés, type locality (Hernández-Camacho and Cadena 1978); and Serranía de Chiribiquete, department of Caquetá (Montenegro and Romero 2000) (Figure 1). In a revision of material of *Lonchorhina* deposited at the Instituto de Ciencias Naturales of the Universidad Nacional de Colombia (ICN), we found that some specimens (ICN 14584-87♀) previously identified as *L. marinkellei* due to their larger size (mean of GSL=27.3; Std. Dev.=0.5), were morphologically divergent with respect to the holotype of this taxon (mean of GSL=25.5). Divergent specimens were collected at the National Natural Park (PNN) Chiribiquete, on the rock outcrops of Serranía de Chiribiquete, Department of Caquetá; a remote and unexplored area in the Colombian Guayana Biogeographic Region (Figure 1). To understand the phenetic affinities and taxonomic placement of divergent *Lonchorhina* from PNN Chiribiquete, their morphological variation was investigated through the analysis of both discrete and morphometric characters.

Materials and methods

Analysis of discrete characters. Phenetic affinities of divergent *Lonchorhina* specimens from Serranía de Chiribiquete were evaluated through comparative analyses of discrete characters with respect to 105 *Lonchorhina* specimens representing the five recognized species in the genus from a substantial portion of its distribution. Our morphological analyses comprise the largest dataset of specimens used in a single publication for this genus and included comparisons with the holotype of *L. marinkellei* (ICN 5459♂) and material of this species from near the type locality in Mitú, department of Vaupés, Colombia; as well as material of *L. aurita* from Trinidad, collected near the type locality of the species; specimens from several localities across its distributional range (Belize, Honduras, Panamá, Colombia, Venezuela, Perú and Brazil); images of the holotype of *L. a. occidentalis* (Ecuador); specimens of *L. inusitata* from Brazil and Venezuela; a specimen of the rare *L. fernandezi* from the only known collecting locality of the species in Venezuela; and representatives of *L. orinocensis* from several localities in Colombia and Venezuela (Appendix I). Although resolving the phylogeny of the genus is beyond the scope of this work, since we

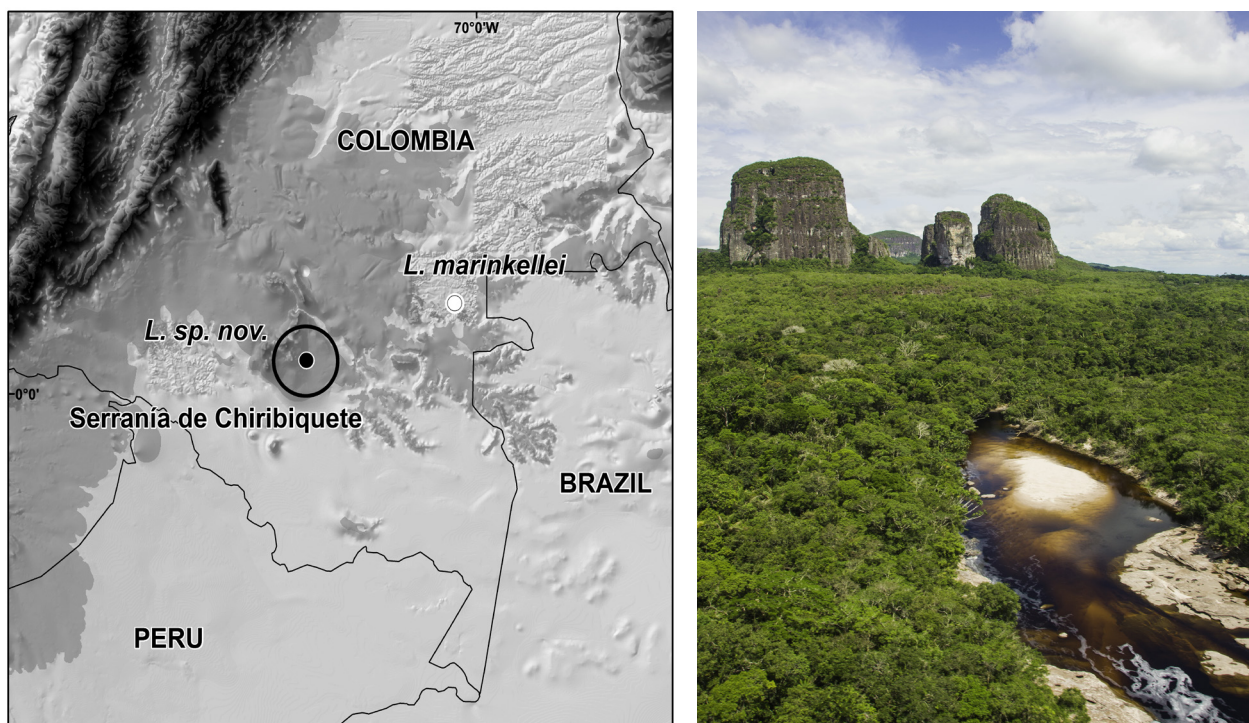


Figure 1. Type locality of *L. sp. nov.* (back circle), in río Mesay, Puerto Abeja southern portion of Serranía de Chiribiquete in the Colombian tepuis. Shaded area represents terraces above 200 m. White circle represents the type locality of *L. marinkellei* (left). Rock outcrops of PNN Chiribiquete (Photo, J. Arango Fundaherencia-SPNN, 2015) (right).

were able to include all currently recognized species in the genus in our dataset, we wanted to present a preliminar evaluation of the phylogenetic affinities of *Lonchorhina* species. Seventeen discrete external and cranial characters were evaluated and codified for all recognized species in the genus (*L. fernandesi*, *L. orinocensis*, *L. aurita*, *L. inusitata*, *L. marinkellei*, and *L. sp. nov.*) (matrix of characters presented in Appendix II) and a cladistic analysis was performed using the maximum parsimony and bootstrap search option of Winclada (Nixon 1999) and NONA 2.0 (Goloboff *et al.* 2008); and using *Micronycteris hirsuta* as outgroup. In all analyses, 10,000 replicates were performed. To guarantee independence among characters morphometric data were excluded from the analysis. We report only the most parsimonious tree.

Morphometric analysis. The morphometric variation of divergent specimens from the PNN Chiribiquete, were also evaluated through a principal components analysis (PCA) performed on 10 cranial measurements including: greatest skull length (GSL); condylobasal length (CBL); palatal length (PAL); postorbital constriction width (PO); rostrum width (RW); braincase height (BCH); distance across tympanic

bullae (BL-BL); tooth row length (TR); distance across third upper molars (M-M); distance across canines including cingula (C-C) of 105 *Lonchorhina* specimens from eight countries including all recognized species in the genus from most of its known geographic range from Belize to Brazil. Only adult specimens were used in the analyses and age was determined based on the presence of closed epiphyses. All measurements are in millimeters to 0.01 mm and were tested for normality and homogeneity of variances using a Shapiro-Wilks and a Bartlett's tests respectively. Measurements are summarized in Table 1. Analyzed specimens are deposited at the following institutions: Field Museum of Natural History (FMNH); National Museum of Natural History of the Smithsonian Institution (USNM); Instituto de Ciencias Naturales of the Universidad Nacional de Colombia (ICN); and the Natural Science Research Laboratory of the Texas Tech Museum (TTU). Specimens included in the analysis and collecting localities are compiled in Appendix I.

Hypothesis testing. To test our hypothesis of a morphometric differentiation between our samples from Serranía de Chiribiquete and large representatives in the genus (*L. inusitata* and *L. marinkellei*) a

Table 1. Cranial measurements analyzed among representatives of the five recognized species in the genus *Lonchorhina*

GSL	CBL	PAL	PO	RO	BL	BL-BL	BCH	LTR	MM	CC
<i>L. mankomara</i> N=4										
27,53	26,22	13,12	6,66	8,60	13,64	11,72	7,89	9,50	9,55	6,07
0,19	0,22	0,31	0,09	0,15	2,20	0,38	0,31	0,22	0,20	0,10
<i>L. aurita</i> N=75										
20,46	19,01	9,62	4,95	5,86	10,49	11,22	6,86	6,84	7,27	4,55
0,60	0,62	0,51	0,22	0,36	1,39	0,38	0,22	0,31	0,55	0,24
<i>L. fernandesi</i> N=1										
17,92	15,53	6,7	3,9	4,7	11,64	3,95	6,53	5,46	5,81	3,45
<i>L. inusitata</i> N=6										
22,21	20,65	10,75	5,26	6,39	12,56	11,87	7,10	7,64	7,91	5,08
0,43	0,42	0,27	0,22	0,12	0,48	0,23	0,22	0,14	0,17	0,07
<i>L. marinkellei</i> N=2										
26,62	25,45	12,63	6,44	8,41	14,19	9,30	7,72	8,98	9,40	5,99
1,05	1,03	0,71	0,26	0,22	1,78	2,26	0,30	0,54	0,37	0,19
<i>L. orinocensis</i> N=17										
18,67	16,81	8,07	4,04	4,64	11,10	10,51	6,32	6,04	6,03	3,53
0,24	0,29	1,01	0,08	0,11	0,28	0,26	0,22	0,09	0,14	0,10

Abbreviations of measurements: Greatest length of skull (GSL); 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 (MM); distance across canines, including cingula (CC).

Discriminant Function Analysis (DFA) was performed on the ten recorded cranial measurements in the statistical package Statistica Centurion XV.

Results

Principal components analysis. In our principal components analysis, the first two components accounted for most of the observed variation (PC1=92.8%; PC2=2.9%) with GSL, CBL, PAL presenting the highest loadings on the first component and explaining the variation among *L. orinocensis*, *L. aurita*, *L. inusitata*, and *L. marinkellei*; while distances across bullae presented the highest loadings on the second component, explaining the variation in size of *L. fernandesi* with respect to other species in the genus (Figure 2). Large *Lonchorhina* (ICN 14584-87♀) from PNN Chiribiquete, were separated from other species in the genus, in the factorial plane of our PCA, including the holotype of *L. marinkellei* and samples of this taxon from Mitú, Vaupés (near the type locality of the species) (Figure 2).

Hypothesis testing. Discriminant function analysis, performed on analyzed specimens of large representatives of the genus falsified the hypothesis of a morphological homogeneity among specimens identified as *L. inusitata*, *L. marinkellei*, and specimens from PNN Chiribiquete (Wilks's $\lambda=0.0017$; 0.05; $\chi^2=163.5$; 11.8; $p>0.001$; 0.001) (Figure 3). In our DFA all specimens from PNN Chiribiquete were correctly assigned in its own group, separated from specimens of *L. inusitata* and *L. marinkellei*, which were also correctly assigned in their own groups.

Taxonomic results. We interpret morphological differences observed in our samples from Serranía de Chiribiquete as a distinct taxon deserving consideration as a new species in the genus which is described in this work.

SYSTEMATICS

FAMILY PHYLLOSTOMIDAE

Subfamily Lonchorhininae, Baker *et al.* 2003

Genus *Lonchorhina* Tomes 1863

***Lonchorhina mankomara* sp. nov.**

Lonchorhina marinkellei

(Montenegro and Romero 2000)

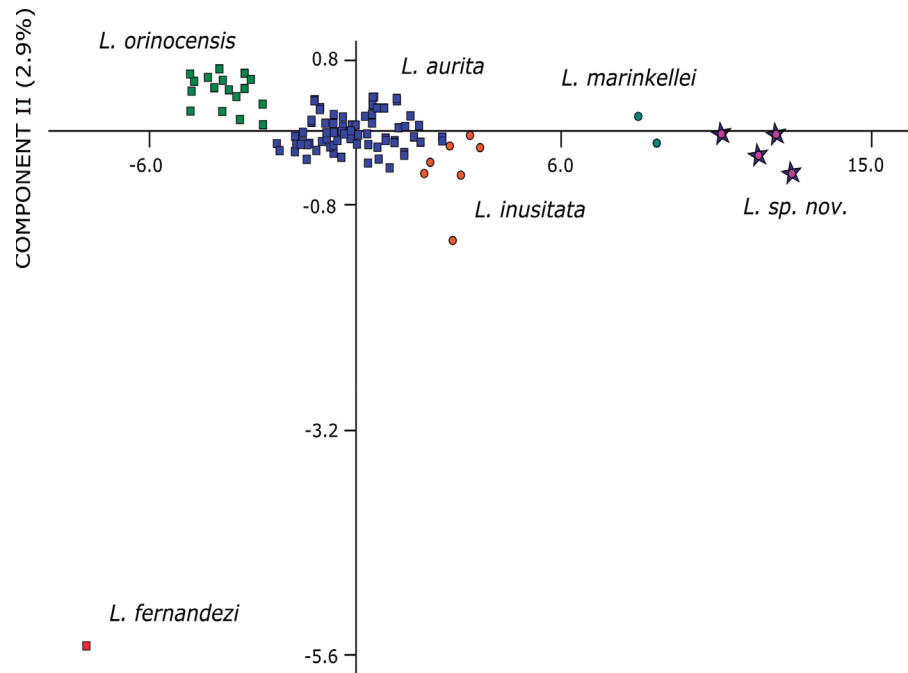


Figure 2. Principal components analysis (PCA) performed on 10 cranial measurements of 105 *Lonchorhina* specimens representing all recognized species in the genus. *Lonchorhina aurita* (blue squares); *L. fernandezi* (red square); *L. inusitata* (orange circles); *L. orinocensis* (green squares); *L. marinkellei* (light green circles); and *L. sp. nov.* (blue stars with a pink circles).

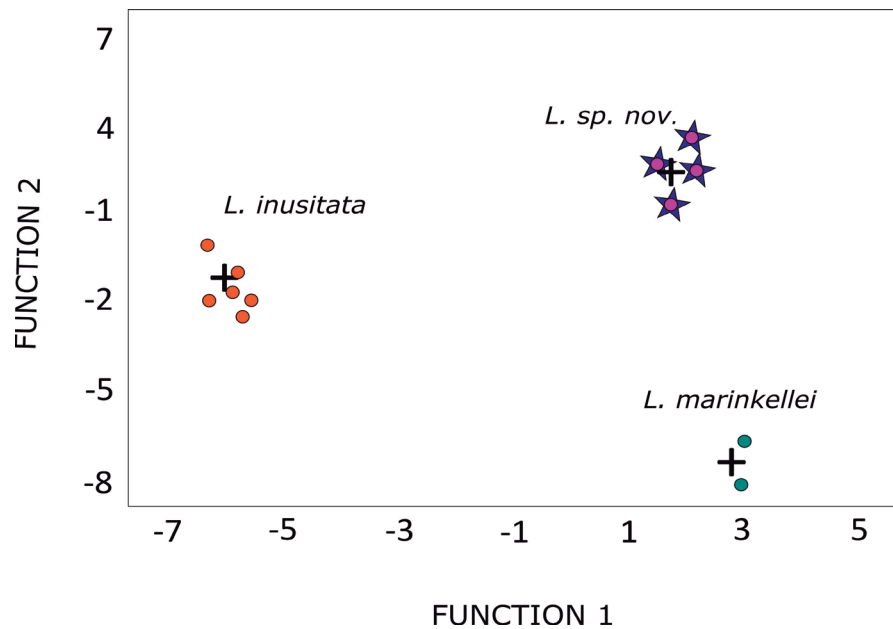


Figure 3. Discriminant function analysis performed on large representatives of the genus *Lonchorhina*: *L. inusitata* (orange circles), *L. marinkellei* (green circles), and *L. sp. nov.* (blue stars with pink circles); black crosses represent centroids of recovered groups.

Lonchorhina marinkellei
(Marín-Vasquez and Aguilar-González 2005)

Lonchorhina marinkellei
(Mantilla-Meluk *et al.* 2009)

Holotype. Adult female specimen ICN 14586, deposited at the mammal collection of the Instituto de Ciencias Naturales of the Universidad Nacional de Colombia; holotype preserved as skin with skull

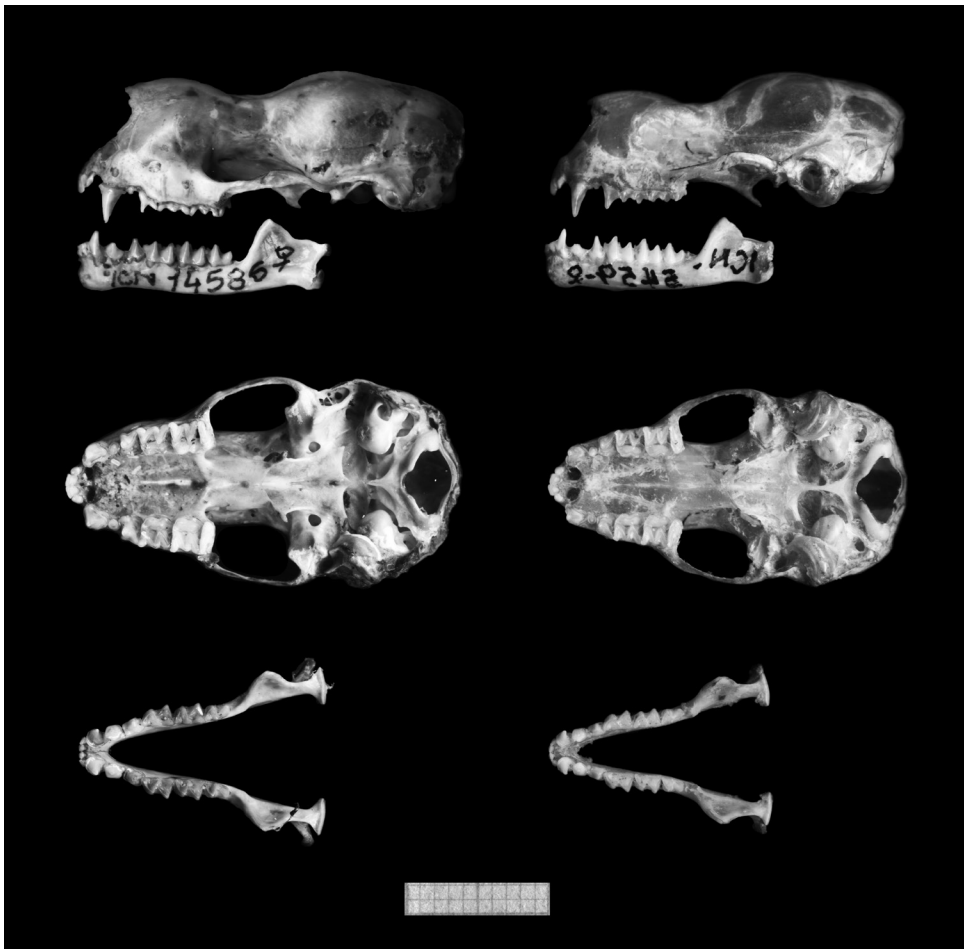


Figure 4. Lateral (top) and ventral (bottom) views of skull and mandibles of *Lonchorhina mankomara* (ICN 14586♀, (left) and *L. marinkellei* (ICN 5459♀) holotypes.

extracted in general good condition, tympanic bullae detached from skull (Figure 4). Specimen collected by M. Romero and O. Montenegro (collectors number: MRR 029) on July 12, 1993; measurements as recorded on tag: Total length=144.6 mm; Tail: 68.7 mm; Hind foot=41.1mm; Forearm=64.3mm; Weight=33.0 g. Cranial and appendicular measurements of holotype ICN 14586♀ are presented in Table 1.

Type locality. Río Mesay, Puerto Abeja (Tepui), Southeastern portion of Serranía de Chiribiquete The National Park Chiribiquete (PNN Chiribiquete), at 340 masl, department of Caquetá, Colombia; coordinates: 00°04'N, 72°26'W (Figure 1). The PNN Chiribiquete, corresponds to one of the most pristine and unexplored areas in the country, enclosing the oldest and largest series of Amazon pictograms (20.000 years bc) registered on the outcrops of the numerous inselbergs and tepuis, in which images of bats are of particular cultural importance.

Type series. Three adult females collected at the same locality of the holotype on different days were included in the type series: ICN 14584♀, collected by O. Montenegro (collectors number OMD 138) on July 10, 1993; preserved as skin, skull extracted, partially damaged; nasals and basicranium broken; ICN 14585♀, O. Montenegro (collectors number: OMD 173) on July 12, 1993; preserved as skin, skull extracted in good condition; ICN 14587♀, collected by O. Montenegro (collectors number OMD 169) on 20 of July, 1993; preserved as skin, skull extracted in good condition at the moment of the description, but accidentally destroyed during the plague control process of the collection of the ICN (Figure 5).

Distribution. *Lonchorhina mankomara* is only known from the type locality, and presumably confined to the lowland rocky outcrops of the PNN Chiribiquete, at department of Caquetá, in Colombia (Figure 1) Such lowland outcrops (also called insel-

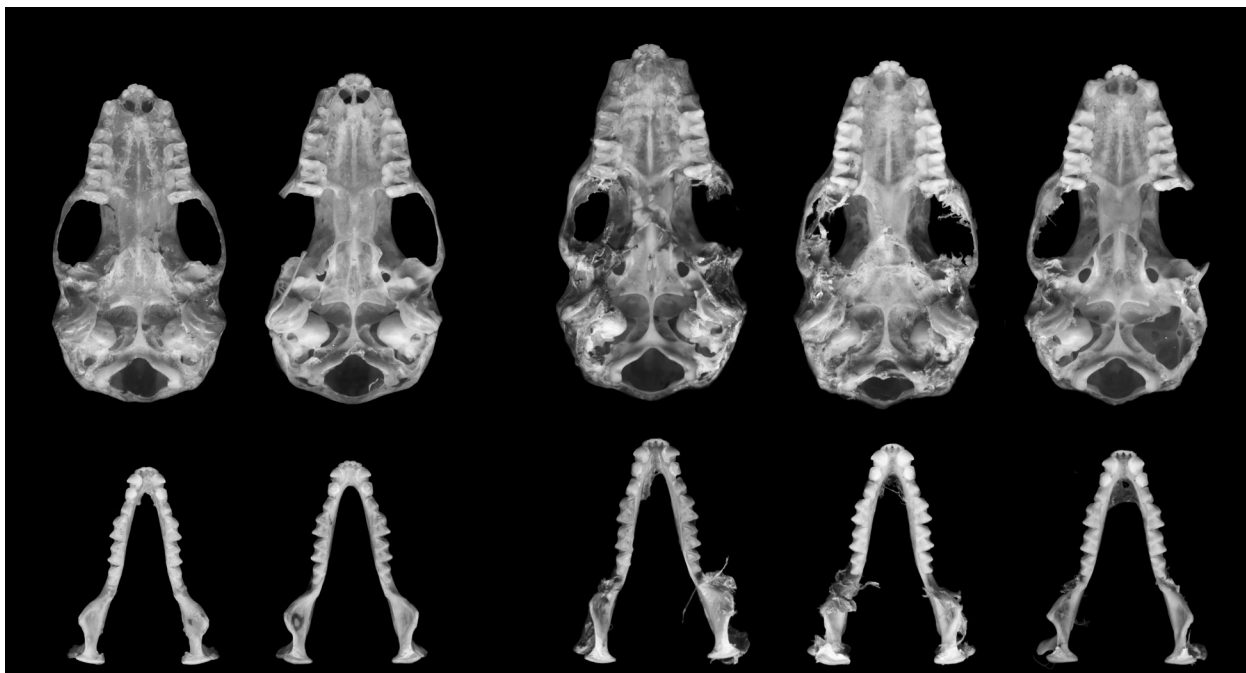


Figure 5. Skull comparison of the largest representatives of the genus *Lonchorhina*, *marinkellei* holotype ICN 5459♀, and specimen of ICN 12557 ♀, and female specimens ICN 14584-85 and ICN 14587 in *L. mankomara* type series.

bergs) belong to the *Guayana Region*, the recognized biogeographical entity assigned to the outcrops of the Guayana Shield (Maguire 1979, Huber 1994, Berry *et al.* 1995).

Etymology. The name *mankomara* is composed of two parts; the first refers to the indigenous Karijona word *manko* (*ma-nü-ko*), meaning mother. Karijona or Carijona is an indigenous culture that inhabited the area of Chiribiquete and were virtually extinct after the genocide of indigenous people promoted by the rubber trading. Karijonas are currently represented by no more than 350 survivors that lost their own language. We wanted to honor Karijonas as documenters of the nature of Chiribiquete. The new species is named after Mara Meluk de Mantilla, mother of the senior author. My mother always encourage me to appreciate the wonders of nature and to appreciate cultural diversity. The name is also an extended recognition to all mothers, that have play the role of being keepers of knowledge and to promote curiosity and science in our societies.

Diagnosis. The largest species known in the genus *Lonchorhina* (holotype: FA=64.1 mm; GSL=27.62 mm), closely related to *L. marinkellei* (Table 1). Telic structures enormously developed. Long noseleaf broad at the base (noseleaf length 40.15 mm; width at

noseleaf base 12.2 mm) compared with *L. marinkellei* noseleaf (37 and 11.32 mm respectively), ear pinna (44.86 mm from notch), and tragus (22.3 mm).

Skull characters. Skull larger than in other species of the genus (GSL>26.5); height of the braincase almost the same size of the rostrum; sagittal crest present, absent in *L. marinkellei*; in *L. mankomara*, the observed area of the basisphenoid from a ventral view has a rectangular appearance, longer than wider (width representing a 66% of its length), with the lateral sides concave (lateral sides delimited by the medial pterigoid plates); while in *L. marinkellei* the structure looks almost squared (width representing 86% of its length) and lateral sides convex (Figure 6).

Dental characters. *Lonchorhina mankomara* has an overall more massive dentition than *L. marinkellei*; enlarged first premolar double the size of that in *L. marinkellei*; wide molars with elongated lingual bases; holotype of *L. mankomara* has an extra cusp on the hypoconal basin of the first and second upper molars, absent in other specimens of the type series and representatives of the other species in the genus (Figure 7). Lower incisors bilobed, contrasting the trilobed incisors of *L. inusitata* and *L. marinkellei* (Figure 8).

Description. Largest species in the genus (Table

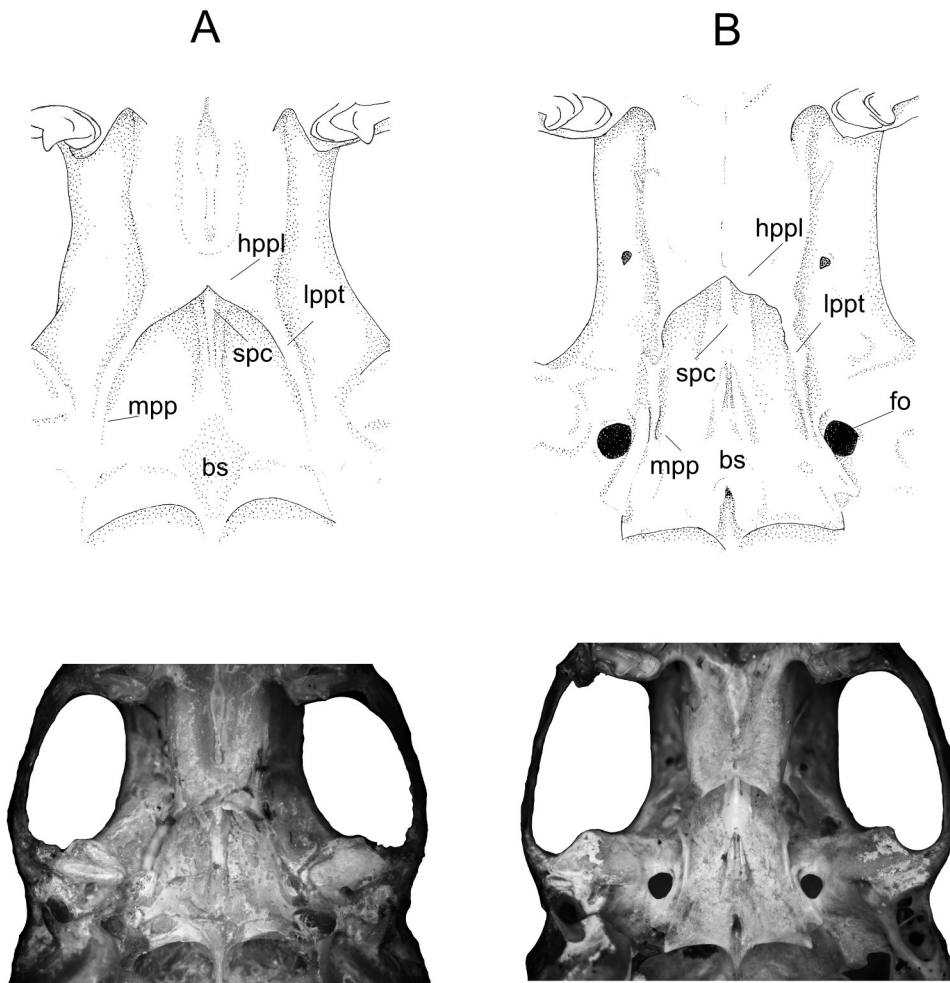


Figure 6. Detail of the basicranium of *Lonchorhina marinkelle* (A) and *L. mankomara* (B).

Abbreviations as follows: bs. Basisphenoid; hppl. Fo. Foramen ovale; Horizontal plane of the postpalatal bone; mpp. Medial plane of the pterigoid process; spc. Sphenoidal crest.

1); noseleaf enormously developed (0.9 to 1.49 the length of the skull; width 1/3 of the length of the skull) free margins not crenulated or waved, revolved on the anterior surface of its base accompanied with ribs (*costae foliae nasalis*), and a medial costae on both the anterior and posterior surfaces of the noseleaf, formed by two muscular bands (*sulcus medialis costae*), absent in *L. orinocensis*. Presence of two nasal fossae (*vestibule narium*) separated by a septum (*connectivum sellae*), which in its posterior parts extends into the *sella*. The *sella* is constituted by the *basis sellae*, expanded anteriorly and laterally to form two mobile laminar expansions (*alae sellae*), on top of which the *sellae* is thinner forming the *pedunculum sellae* which is terminated in *tuberculum sellae*. On each side, the basal portion of the noseleaf is extended forming a *plica praenarialis*, which is extended to

the *basis sellae* delimiting the *vestibule narium*. The narina are narrow and opened upwards inside the *vestibuli* close to a conspicuous excrescence (*cornu praenariale major*) of the *plica praenarialis*; lateral to that excrescence there is a second one, smaller in size (*cornu praenariale minimus*). All described ornamentations are absent in *L. ferenandezii*. In *L. mankomara* all ornamentations are enlarged compared to those in other species in particular the *pedunculum sellae* is longer and the *tuberculum sellae* is more expanded and simple than that of *L. marinkellei*. A representation of the ornamentations of noseleaf of *L. mankomara* and structure's nomenclature used (Hernández-Camacho and Cadena 1978) is presented in Figure 9.

Lonchorhina mankomara holotype has a dorsal pelage bicolored, white at the base and axial two

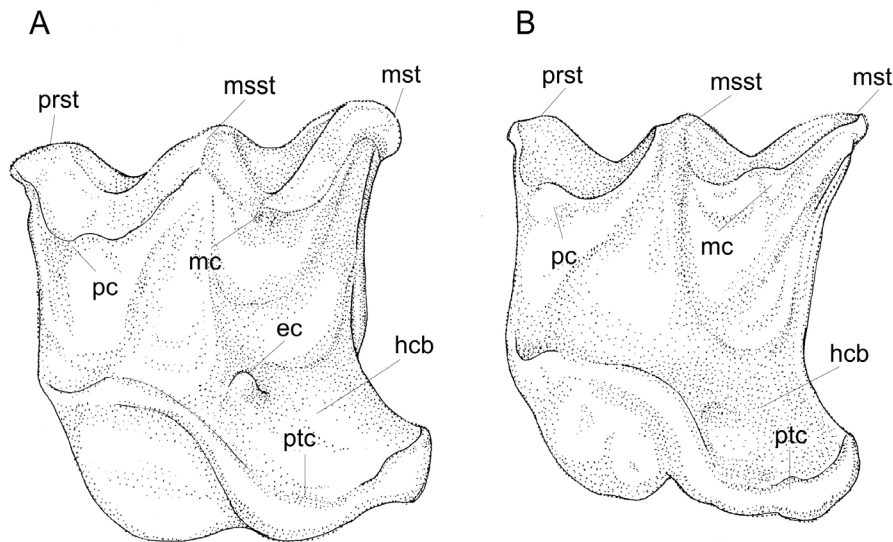


Figure 7. Lingual view of the first upper molar (M1) of holotype of *Lonchorhina marae* (right) and holotype of *L. marinkellei* (left), showing the presence of an extra cusp on the hypoconal basin of *L. mankomara*, which is absent in *L. marinkellei*. Abbreviations: ec. Extra cusp; hcb. Hypoconal basin; mc. Metacone; msst. Mesostyle; mst. Metastyle; pc. Paracone; prst. Parastyle; ptc. Protocone.

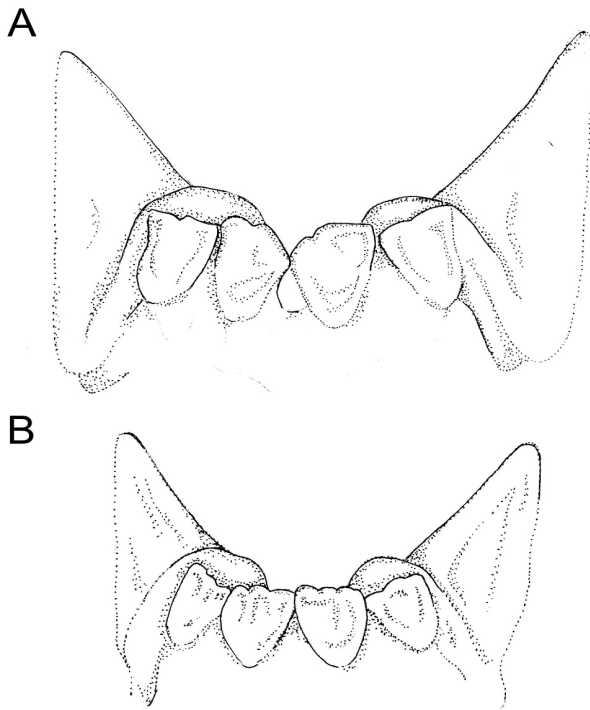


Figure 8. Bilobed lower incisors of *Lonchorhina mankomara* (A) and trilobed lower incisors *L. marinkellei* (B).

thirds sepiia 219 (Smithe 1975) (Figure 10); contrasting the unicolored amber 36 (Smithe 1975) dorsal pelage of *L. marinkellei* holotype. Dense and longer bicolored hair on the chest, olive brown 28 (Smithe 1975) at the base and drab 27 (Smithe 1975) on the

tips; contrasting the shorter hair cinnamon brown 33 (Smithe 1975) at the base and drab 27 (Smithe 1975) on the tips of *L. marinkellei* holotype. In *L. mankomara*, there are long hairs (14.55 mm) extended laterally on the chest, that can be observed ventrally, absent in *L. marinkellei* holotype. Dense and long facial and ear hairs (>6.9 mm at the base of the ear) contrasting the shorter hair of *L. marinkellei* holotype. Membranes are black to dark brown. Holotype of *L. mankomara* has a dense pillow of short hairs on the anterior margins of the ear pinna; structure that may prevent the friction between the noseleaf and the pinna, also present in other representatives of the genus, as well as other long eared bats such as some representatives of *Micronycteris* (Simmons *et al.* 2000).

Skull characters. Large and elongated skull compared with skulls in other species of the genus. Braincase height same as rostrum height (subequal) (character shared with *L. inusitata* and *L. marinkellei*); nasal aperture broad and piriform, compared to the narrow nasal aperture of *L. marinkellei*; wide rostrum; projections of palatine swollen; massive hamulus pterigoideus; angled occipital region observed from a ventral view.

Dental characters. Dental formula: I 2/2; C1/1; PM; 2/3; M3/3. *Lonchorhina mankomara* has an overall more massive dentition than *L. marinkellei*; central upper incisors longer and wider; massive

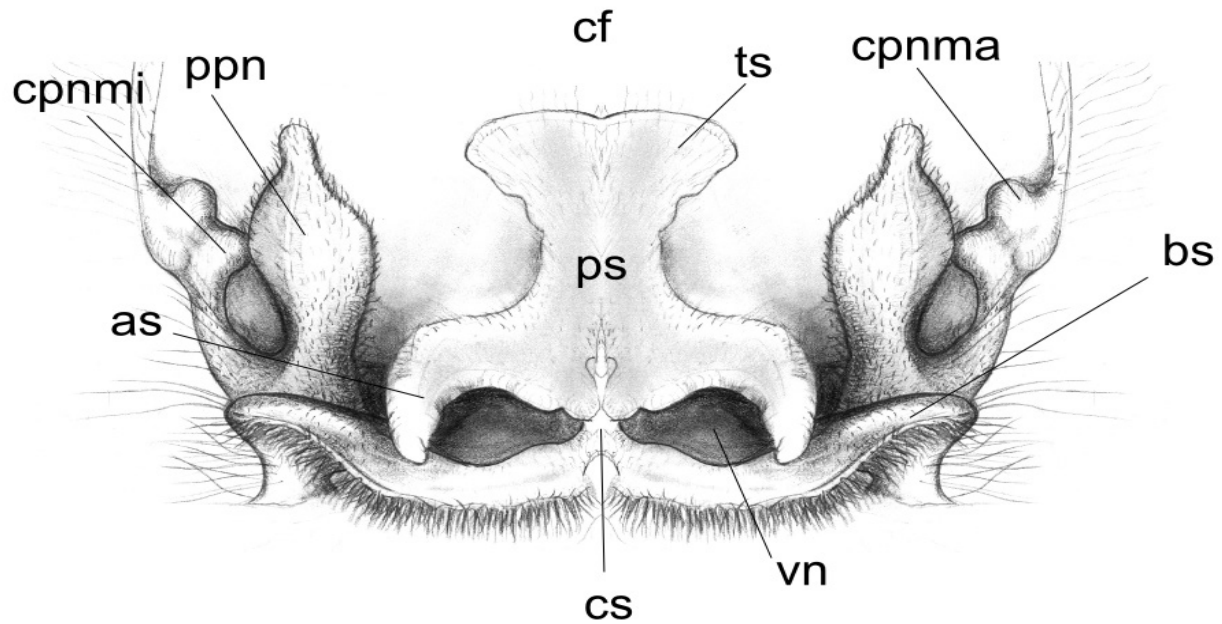


Figure 9. Reconstruction of the leaf nose base of *L. mankomara* from material preserved as dry skins. Nomenclature follows Hernández-Camacho and Cadena (1978).

Abbreviations: cf. *costae foliae nasalis*, vn. *vestibule narium*; cs. *connectivum sellae*; bs. *basis sellae*, as. *alae sellae*; ps. *pedunculum sellae*; ts. *tuberculum sellae*; ppn. *plica praenariale*, cpnma. *cornu praenariale major*, cpmi. *cornu praenariale minus*.



Figure 10. Dorsal (left) and ventral (right) views of skin of the holotype of *Lonchorhina mankomara* (ICN 14586♀). Long hairs on the chest of the holotype (ventral view) of *L. mankomara* absent in *L. marinkellei* (ICN 5459♀).

canines with a wide cingula; enlarged first upper premolar, double the size of that in *L. marinkellei* (Figure 4) wide molars with elongated lingual bases; presence of an extra cusp on the hypoconal basin of the first and second upper molars (Figure 7); bilobed lower incisors (Figure 8b).

Discussion

Molecular data (Baker *et al.* 2003), 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.* 2012). Species in the genus *Lonchorhina* are characterized by extreme modifications of external characters, represented by the largest telic structures found in the family: ears, tragus, and an enormous and extremely complex sword nose-leaf, that in some species could reach one and a half the dimensions of the skull, as well as a skull morphology, only found in this genus (Hernández-Camacho and Cadena 1978). The combination of discrete skull characters in the genus is unique among phyllostomids (Hernández-Camacho and Cadena 1978). These modifications are suggested to be adaptations associated with echolocation and insect prey detection inside mature stratified forests. Lowland forests in South and Central America are interrupted by several natural barriers isolating natural populations and eventually promoting speciation. Four of the five currently recognized species in the genus (*L. fernandezi*, *L. inusitata*, *L. orinocensis*, and *L. marinkellei*) are apparently restricted to the lowland forest of Northern South America in the Amazon and Guianan biogeographic provinces (Williams and Genoways 2007 for marginal localities). The environments typically inhabited by these bats, rocky outcrops of tepuis formations, are also unique. Representatives of the genus are considered cave bats, condition which imposes extra restrictions in terms of their expansion. Natural environments of *Lonchorhina*, and particularly large members of the genus (*L. inusitata*, *L. mankomara*, and *L. marinkellei*) are, in general, difficult to access. Bats in the genus *Lonchorhina* are rare in museum collections and some species such as *L. fernandezi* are only known from its holotype, or few specimens, such as *L. marinkellei* (Williams and Genoways 2007) preventing a full understanding of their biogeographic

patterns and morphological variation.

The only species that has a wide distribution is *L. aurita* described from Trinidad (Tomes 1863) which exists from Oaxaca, México south to South East Brazil, Bolivia, Perú and Ecuador; Trinidad and the New Providence Islands (Bahamas Islands) (Jones and Carter 1976). *Lonchorhina aurita* is currently considered a monotypic species (Williams and Genoways 2007). However, Anthony (1923) described the subspecies *L. a. occidentalis* based on three specimens collected in Guayas, Ecuador. Currently, *L. a. occidentalis* is considered as a junior synonym of *L. aurita* since Cabrera (1958) overlooked this taxon in his revision of mammals from South America. Nevertheless, Linares and Naranjo (1973) and Hernández-Camacho and Cadena (1978) suggested that *L. a. occidentalis* should be treated as a subspecies of *L. aurita* until additional material will be available to test its specific status.

Unfortunately, Anthony (1923) did not provide a description of discrete skull characters to differentiate *L. aurita* from Guayas from its conspecific from Trinidad, and the author refer to the skull of *L. a. occidentalis* as “normal for the genus *Lonchorhina*, and very similar to that of *L. aurita*”, line that constitutes the only reference for skull morphology in Anthony’s (1923) description of the species. Although large skull *L. inusitata* is “similar to *L. marinkellei* in shape of the rostrum, there are differences in skull size. In *L. inusitata* the basisphenoid pits are shallow anteriorly contrasting the anteriorly deep basisphenoid pits of *L. marinkellei*. These two species also differ in shape and degree of hairiness of ears, noseleaf, and facial excrescences; underparts of *L. inusitata* are dark, while in *L. marinkellei* the venter is heavily washed (Williams and Genoways 2007). The same authors mentioned that the rostrum in *L. marinkellei* is higher than the braincase, while in *L. inusitata* the rostrum is about of equal height or slightly lower than the braincase.” 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).

The combination of discrete skull characters of *L. mankomara* holotype are unique among recognized species of *Lonchorhina* and represent a significant

morphological evolution of characters historically assumed as conserved among mammals such as modifications in size and placement of dental elements.

Biogeography. The morphological variation observed in our new species in conjunction with the geographic location of the holotype open a series of interesting questions about the biogeography of the genus. The Guayana Region is a discontinuous biogeographical area, formed by the rock outcrops of the Guayana Shield, one the oldest geological formation of South America. This formation of Precambrian origin is located in northern South America and spans close to two million square kilometers. However, outcrops of this formation are of insular character and form a complex landscape of lowland, upland and highland ecosystems (Gröger and Huber 2007), surrounded by tropical forest or savannas. Such a discontinuous arch of inselbergs (lowlands, about 300-500 masl) hills (uplands, >500 masl), and tepuyes (highlands, >3000 masl) form insular habitats with a highly endemic biota. The Guayana region has been subdivided into four major provinces: Eastern, Central, Pantepui, and Western (where Chiribiquete is located) (Huber 1994, Berry *et al.* 1995).

The Western Guianan Province is represented by a mosaic of forests of Amazon and Guianan elements, hills and isolated mountain ranges, and savannas located between the Rivers Guaviare and Caquetá (Cortés and Franco 1997). Hernández-Camacho *et al.* (1992) recognized the area of Chiribiquete as part of the “Complejo Vaupés” (VII.4) biogeographic district. This is a mosaic of landscapes including both inundated as well drained forests in areas interrupted by rocky outcrops of granitic and basaltic origin. This isolated mountain ranges and plateaus differ considerably in their floristic composition from the matrix of lowland rainforest and are characterized by a number of endemic elements. It has been difficult to determine the eastern limits of the biogeographic unit, but Hernández-Camacho *et al.* (1992) propose the Apaporis River as the eastern boundary of lowland forest of the district, based on distributional patterns of primates and bird subspecies. The natural ecological isolation of the region, as well as the heterogeneity of their landscapes may result in restriction of gene flow among *Lonchorhina* populations, and might be associated to the radiation of the genus. Except for *L. aurita*, the other known species of *Lonchorhina*

seem to be restricted or associated to other localities of the Guayana Region. For example, *L. marinkellei*, was described from rocky outcrops in Vaupés, Colombia (Hernández-Camacho and Cadena, 1978), *L. inusitata*, was found at low elevations on the Guayana Shield in central French Guiana, west-Central Surinam, and southern Venezuela and Rondônia, Brazil), *L. fernandesi* was collected at El Burro, 40-50 km NE of Puerto Ayacucho, Venezuela (Ochoa and Ibañez 1984) and *L. orinocensis* was described from the Orinoco basin in Venezuela and NE Colombia (Linares and Ojasti 1971).

In Colombia collection localities of *L. orinocensis* are associated with the Serranía de la Macarena, Vaupés, Araracuara, Tuparro y Chiribiquete, all of them sites of the Guayana region. All these sites are surrounded by either open savannas of the Orinoco region or tropical rainforest of the Amazon region. For example, the habitat of *L. fernandesi* was described as open savannas mixed with granitic formations or “lajas” (Spanish word for inselbergs) (Ochoa and Sánchez (1988), which is the same habitat type dominating the Tuparro site in Colombia, which is within *L. orinocensis* range. The larger *L. marinkellei*, *L. inusitata* and *L. mankomara* are found in Guyana inselbergs surrounded by Amazonian rainforest. The inselbergs are described as outstanding biomas consisting of huge, dark black, rocky boulders and hills with a characteristically dome-like appearance, rarely more than 300-400 m high, but of variable horizontal extension” (Gröger and Huber 2007). A very important feature of the Guayana region, besides its insular distribution, is its remarkable low content of soil nutrients, which pose a challenging environment to its high endemic biota (Cortés and Franco 1997, Hollowell and Reynolds 2005, Rodríguez *et al.* 2012). The unique morphological features of *Lonchorhina* species, especially those related to echolocation, might be associated to their life in such a prohibitive and astonished landscape.

Taxonomic remarks. In spite of the limited number of characters considered in our phylogenetic analysis (N=17), we recovered the morphological independence of some species in the genus (Figure 11). *Lonchorhina fernandesi* with the less complex noseleaf seems to be the basal living form of the genus as shown in our cladistics analysis, in where the evolutionary independence of this taxon was well

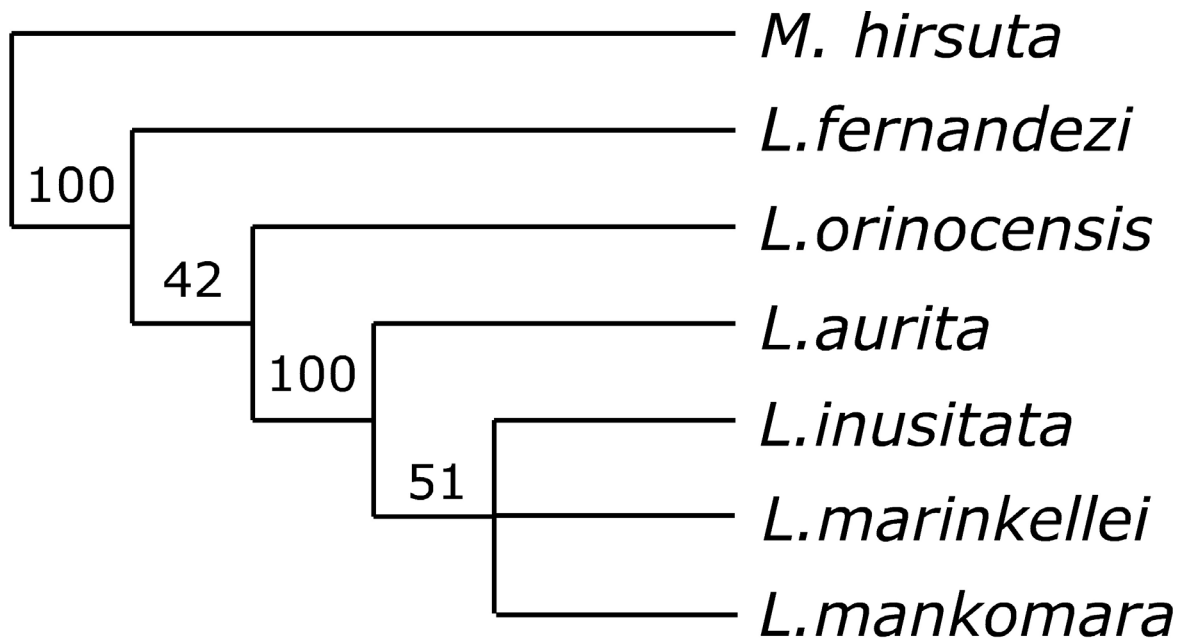


Figure 11. Parsimony analysis of 17 discrete external and cranial characters showing the phylogenetic affinities of representatives of the genus *Lonchorhina*, including *L. mankomara*. Numbers in the nodes represent GC values.

supported. The remarkable morphological differences of *L. fernandezii* with respect to rest of the species of *Lonchorhina* lead us to suggest the placement of this taxon in an independent subgenus. However, further analyses using other set of characters rather than morphology are needed to test this hypothesis. Morphological differences of *L. fernandezii* are not only represented by its smaller size. The basicranial region has divergent features such as a deeply notched posterior edge of the horizontal palatal process, a character shared with other basal phyllostomids such as *Macrotus* and *Micronycteris* absent in other species of *Lonchorhina*. *Lonchorhina orinocensis* seems to represent an intermediate stage between basal *Lonchorhina* and large representatives of the genus, but this relationship was poorly supported in our cladistics analysis. *Lonchorhina aurita* appears as sister taxa of large representatives of the genus (*L. inusitata*, *L. mankomara*, *L. marinkellei*) with full support. However, it is important to mention that a great deal of morphological variation among representatives of *L. aurita* was revealed in our morphometric analysis suggesting the presence of cryptic diversity within this taxon. Finally, *L. inusitata*, *L. mankomara* and *L. marinkellei* appear as part of a single clade with low support. The close relationship between *L. inusitata* and *L. marinkellei* was previously suggested

by Williams and Genoways (2007).

Conservation remarks. Following the criteria of the International Union for the Conservation of Nature (IUCN) Muños and Mantilla (2008) placed *L. marinkellei* as an endangered species [Endangered B1ab(ii,iii) version 3.1]. In their analysis Muños and Mantilla (2008) still considered the populations from Chiribiquete as *L. marinkellei*. As product of this work the distribution of *L. marinkellei* is restricted to collecting localities in the department of Vaupés; and as previously described, populations from Serranía de Chiribiquete correspond to the herein described new species *L. mankomara*. The area of Chiribiquete corresponds to a Natural National Park (1'280.000 ha), protected since 1989 (<http://www.parquesnacionales.gov.co/PNN/portel/libreria/php/decide.php?patron=01.0107>). However, several threats exist in Chiribiquete. The surrounded areas of the park are experiencing a great deal of transformation of the forest coverage into grass for cattle ranching and expansion of illegal crops. Such deforestation at the Colombian Guayana might speed over time as settlements become larger. The current political situation of the country, with major armed groups in a process of negotiation, will result in a massive migration of people as well as multinationals into the forested areas. Also, mining may be a future threat, since several

areas of the Colombian Guayana Region are under legal and illegal mineral extraction. Examples of such extracting activities are currently underway at the Puinawai Reserve, another Colombian Guayana site, northeastern of Chiribiquete. Mining operations are also underway in other sites of the Guayana Region and it is in the development agendas of the region (Hammond 2005).

In general, the unique environmental features of Chiribiquete as well as the other Guayana sites, make of these sites a very fragile habitat. The animal populations in the Guayana Region are poorly known, but the few information available indicates high diversity and endemism (Hollowell and Reynolds 2005), contrasting with very low population densities (Gómez and Montenegro 2012). Global warming is also considered as a considerable threat to areas of the Guiana Region, especially the highland tepuis, because of the predicted habitat loss by upward displacement projected by the end of this century (Rull and Vegas 2006). Preliminary estimations project losses around one-tenth to one-third of endemic vascular plants of Guayanan highlands. Such losses would be of a global extent due to the high endemism in the Guayana Region (Rull and Vegas 2006). It is urgent to investigate the ecology and natural history of *L. mankomara* at Chiribiquete to better understand the biological meaning of extreme adaptations of this species. It is also important to recover material that allows us to investigate the genetic bases of unique skull and external morphological features of *L. mankomara*, presumably associated with a hyper developed hearing system.

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Appendix I

Lonchorhina specimens used in morphometric and morphological analyses. Specimens are deposited in the following institutions: Carnegie Museum (CM); Instituto de Ciencias Naturales (ICN); Field Museum of Natural History (FMNH); National Museum of Natural History of the Smithsonian Institution (USNM); Texas Tech Museum (TTU).

Lonchorhina aurita (N=48): BELIZE (N=1): Toledo, Bladen Nature Reserve, Teakettel Camp, on Bladen Branch USNM 583007♂; BRAZIL (N=10): Maranhao, Alto Parnaiba FMNH-26449 ♂; Pernambuco, Toritama, Fazenda Matumbo, Pedrao Dos Pontais USNM 536441♂; Para, Altamira 9 km SE (by road) Caverna do Valdeci USNM 549340, USNM 549343-45♀, USNM 549339♂, USNM 549341-42♂; Para, Altamira 85 km SW Eastern bank Rio Iriri USNM 549346♀; COLOMBIA (N=32): Antioquia, Zaragoza 26 km W Aljibes USNM 799290-92♂; 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 14306-07♀; Samana, Corregimiento Norcaia, surroundings Campamento CHEC, ICN 15953♀; Samana, Corregimiento Norcasia, Vereda La Pradera, Campamento CHEC, Corporación Hidroeléctrica de Caldas, La Miel I, ICN 12488-89♀, ICN 12490♂, ICN 12571♂; Caqueta, Municipio Montañitas; Vereda Santuario, Finca Ceilán, ICN 16896-97♀; Rio Cuñare, Raudal El Tubo, E Serrania de Chiribiquete, Parque Nacional Natural (PNN) Chiribiqueté, ICN 14716♀, ICN 14584-87♀; Rio Mesay, Puerto Abeja, SE Serranía de Chiribiquete, ICN 14583♂; Meta, San Juan de Arama, Northern portion Serranía La Macarena, Caño Guamalito, ICN 12041-42♀; 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 11458-59♂; Valle del Cauca, 29 km SE Buenaventura USNM 483327♂; GUATEMALA (N=13): Izabal, Quebrados, FMNH-41891-92 ♂, FMNH-41893 ♀, FMNH-41894-97 ♂, FMNH- 41898-00 ♂, FMNH-41901-04, FMNH-41906 ♀, FMNH-41911-13 sex undetermined; HONDURAS (N=2): Colon, Trujillo, Parque Nacional Caprio y Calenturas, TTU 104255-56♀; TRINIDAD AND TOBAGO: Saint George, TTU 5233♀; TTU 5221♂; TTU 5223♂; TTU 5224♀; TTU 8983♂; TTU 8984♂; TTU 9826-9829♂; PANAMA (N=2): Canal zone, Mine Shaft, Coco Plantation, Gamboa, FMNH-92642 ♂; Canal zone, Fort Sherman FMNH-92663 ♂; PERU (N=7): Cusco, Paucartambo; Consuelo, 15.9 km SW Pilcopata, FMNH-174715 ♂, FMNH-174717-18 ♀; Madre de Dios, Maskoitania, 13.4 km NNW Atalaya, left bank Rio Alto Madre de Dios FMNH-174716 ♀; Pasco, Oxapampa, San Juan USNM 364269-70♀, USNM 364268♂; VENEZUELA: FMNH-20637 sex undetermined.

Lonchorhina inusitata (N=6): BRAZIL (N=1): Rondonia, Porto Velho NMNH 554575 ♀; PERU (N=1): Huánuco, Leoncio Prada TTU 46137♂ (tissues available, TK 22878), CM 98592♂; VENEZUELA (N=3): Amazonas, Belén, 56 Km NNW Esmeralda, Caño Culebra, USNM 388736♂; Cerro Neblina, Base Campamento, USNM 560553♀, USNM 560774♀.

Lonchorhina fernandezii (N=1): VENEZUELA: Bolivar, Puerto Cedeño, 12276♂.

Lonchorhina mankomara (N=4): COLOMBIA: Caquetá, Rio Mesay, Puerto Abeja, SE Serrania de Chiribiquete, ICN 14584-87♀.

Lonchorhina marinkellei (N=5): COLOMBIA: Vaupes, Mitu, 10 km E Durania, ICN 5459♀; Mitu, Cueva Superior Primer Cerro, Finca Urania, ICN 12587♂, ICN 12588♀, ICN 12589♂, ICN 12590♀.

Lonchorhina orinocensis (N=10): COLOMBIA: Meta, Serranía de la Macarena, Caño Cristales, FMNH-58672♂, FMNH-58675♂, FMNH-58676♀; VENEZUELA: Apure, Hato Cariben, 32 km NE Puerto, USNM 373290-92, USNM 373293♂, USNM 373294♀, ICNUSNM 373295♂, USNM 373296-98♀, USNM 373299♂, USNM 373302♀.

Lonchorhina inusitata (N= 6): BRAZIL: Rondonia, Porto Velho; USNM 554575; VENEZUELA: Amazonas, Belén, USNM 388736; Neblina, USNM 560553♀; USNM 560556; USNM 560774♀; PERU: Huánuco, Leoncio Prada TTU 46137♂.

Appendix II

Discrete characters used in the cladistic analysis. Character 1: rostrum height as same as braincase height; Character 2: sagittal crest present; Character 3: projection of the basicranium at the basisphenoidal pits; Character 4: posterior border of the palate U shaped; Character 5: lower incisors bilobed; Character 6: pm3 within the tooth-row line; Character 7: lateral incisors conical in shape; Character 8: basisphenoidal pits, deep posteriorly; Character 9: ear border granulated; Character 10: presence of a patch of hairs on the ears; Character 11: presence of a sella; Character 12: forearm naked; Character 13: proximal portion of the noseleaf naked; Character 14: long hairs on the chest; Character 15: presence of a medial sulcus; Character 16: enlarged tuberculum; Character 17: large body size.

Matrix of analyzed characters

	Characters				
	1	2	3	4	5
<i>L. fernandesi</i>	0	0	1	1	1
<i>L. orinocensis</i>	0	0	0	0	0
<i>L. aurita</i>	0	0	0	0	1
<i>L. inusitata</i>	1	0	0	0	1
<i>L. marinkellei</i>	1	0	0	0	1
<i>L. marae</i>	1	1	0	0	0

	Characters					
	6	7	8	9	10	
<i>L. fernandesi</i>	1	1	1	0	0	
<i>L. orinocensis</i>	0	0	1	1	0	
<i>L. aurita</i>	0	0	0	0	0	
<i>L. inusitata</i>	0	0	0	0	1	
<i>L. marinkellei</i>	0	0	0	0	1	
<i>L. mankomara</i>		0	0	0	0	1

	Characters					
	11	12	13	14	15	
<i>L. fernandesi</i>	0	0	0	0	0	
<i>L. orinocensis</i>	0	0	0	0	0	
<i>L. aurita</i>	1	1	1	0	1	
<i>L. inusitata</i>	1	1	1	0	1	
<i>L. marinkellei</i>	1	1	1	0	1	
<i>L. mankomara</i>		1	1	1	1	1

	Characters		
	16	17	
<i>L. fernandesi</i>	0	0	
<i>L. orinocensis</i>	0	0	
<i>L. aurita</i>	1	1	
<i>L. inusitata</i>	1	1	
<i>L. marinkellei</i>	1	1	
<i>L. mankomara</i>		1	1