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A New Chocoan Species of *Lonchophylla* (Chiroptera: Phyllostomidae)

LILIANA M. DÁVALOS¹

ABSTRACT

Lonchophylla is a diverse genus of glossophagines characterized by large, forwardly projecting inner upper incisors and the absence of zygomatic arches. Seven species are currently recognized, including the large-bodied (greatest length of skull >24.5 mm) *robusta*, *handleyi*, *hesperia*, and *bokermanni* and the small-bodied (greatest length of skull <24.5 mm) *thomasi*, *dekeyseri*, and *mordax*. *Lonchophylla* species range throughout the Neotropics and include endemics in Amazonia, the Cerrado, and the arid regions of coastal Peru and Ecuador. In this paper I describe a new large-bodied species, *Lonchophylla chocoana*, from the subtropical rainforests of the Chocó in southwestern Colombia and northwestern Ecuador. I also document the diagnostic external, craniodental, and mitochondrial characters of the new species and summarize morphological characteristics for the new species and its sympatric congeners.

INTRODUCTION

The genus *Lonchophylla* Thomas includes seven species of glossophagines characterized by large, forwardly projecting inner upper incisors and the absence of zygomatic arches (Taddei et al., 1983; Thomas, 1903). Two closely related monotypic genera distinguished primarily by larger size and the morphology of premolars are *Platalina* Thomas and *Lionycteris* Thomas. Together, these

three genera constitute the phyllostomid tribe Lonchophyllini. Recent analyses of morphological and mitochondrial DNA-sequence characters from lonchophyllines have recovered a paraphyletic *Lonchophylla*, although low support values indicate that new evidence might easily overturn this conclusion (Dávalos and Jansa, 2004).

As members of the phyllostomid subfamily Glossophaginae, species of *Lonchophylla* have a rostrum roughly equal in length to the

¹ Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History; and Department of Ecology, Evolution, and Environmental Biology, Columbia University. e-mail: davalos@amnh.org

braincase and a small but well-developed nose leaf (Koopman, 1994). *Lonchophylla* species range from Nicaragua to Peru, Bolivia and southeastern Brazil, and west of the Andes through the Chocó south to the arid regions of Ecuador and northwestern Peru. Large-bodied *Lonchophylla* species (greatest length of skull >24.5 mm) include *robusta*, *handleyi*, *hesperia*, and *bokermanni*. *Lonchophylla thomasi*, *dekeyseri*, and *mordax* are comparatively smaller (greatest length of skull <24.5 mm, Taddei et al., 1983). *Lonchophylla* species are typically found in forests, gardens, and plantations, with *L. hesperia* restricted to deciduous forest, *L. bokermanni* to the Cerrado, and *L. handleyi*, *L. robusta*, and *L. mordax* ranging to cloud-forest habitat (Cadena et al., 1998; Handley, 1976; Koopman, 1994; Sazima et al. 1978). *Lonchophylla* feed predominantly on nectar, although insects, fruit, and pollen are also part of their diet (Gardner, 1977; Sazima et al., 1978).

The lowland *Lonchophylla* species are easily captured by mistnetting (Handley, 1976; Sazima et al., 1978; Simmons and Voss, 1998), and *L. thomasi* is widespread throughout its range and appears to be the most common glossophagine found in Amazonia (Emmons, 1997). *Lonchophylla* congeners, however, have not been found in sympatry at well-sampled lowland localities (Simmons and Voss, 1998; Voss and Emmons, 1996), although *mordax* and *robusta* were recently collected together at 1400 m above sea level in Altaquer, southwestern Chocó of Colombia (Cadena et al., 1998).

In 1999 Sharon A. Jansa and I initiated a collaboration to sequence cytochrome *b* from lonchophyllines to resolve relationships among the bats in this tribe. Among others, we obtained samples from 11 individuals representing five species of *Lonchophylla* (for details and results see Dávalos and Jansa, 2004). One of those species is an undescribed large *Lonchophylla* resembling *L. robusta* and *L. handleyi* in size, but differing from these and other known congeners by a unique combination of traits. I describe this new species below, document its diagnostic morphological and molecular attributes, and summarize available observations in a comparative context.

METHODS

STUDY SITE AND COLLECTION METHODS

The known specimens of this new species were collected 2 km south of Alto Tambo (00°54'N, 78°33'W; 700 m) in Provincia Esmeraldas, Ecuador, and at La Guarapería, ca. 3 km NW of Junín (1°21'N, 78°08'W; ca. 900 m) in Departamento Nariño, Colombia (fig. 1; Burton Lim, personal commun.; Cadena et al., 1998). The average annual rainfall at the elevation belt encompassing both Alto Tambo and La Guarapería (fig. 1) is estimated to be around 2800 mm (ESRI, 1997), and the average annual temperature is estimated to be around 25°C (ESRI, 1999). The Alto Tambo locality comprised humid disturbed secondary forest (Burton Lim, personal commun.). The vegetation at La Guarapería had been selectively logged without ever being fully cleared (Cadena et al., 1998).

Both specimens were captured using mist nets. At Alto Tambo, nets were set along a trail and along a river surrounded by disturbed secondary growth, and there was rain before the capture of the specimen (B. Lim, personal commun.). At La Guarapería nets were set across a stream, a trail, and in a cleared area (Cadena et al., 1998). Mist nets were opened at 1700 hours and stayed open overnight until 0500 hours at Alto Tambo, while at La Guarapería nets were open at dusk and closed around 2200 hours (B. Lim, personal commun.; Cadena et al., 1998). Nets varied from 10 to 18 m in length and were set to reach 3 m above ground at both localities.

MEASUREMENTS AND ABBREVIATIONS

All measurements reported here are from adult individuals with closed epiphyses. The first five measurements listed below were taken from skin tags or other records made by the collector, but other dimensions were measured using digital calipers. Linear measurements of external and craniodental dimensions are reported in millimeters (mm); weights are reported in grams (g). Measurements follow Simmons et al. (2002), and are described below:

Total length: Distance from the tip of the snout to the tip of the last caudal vertebra.

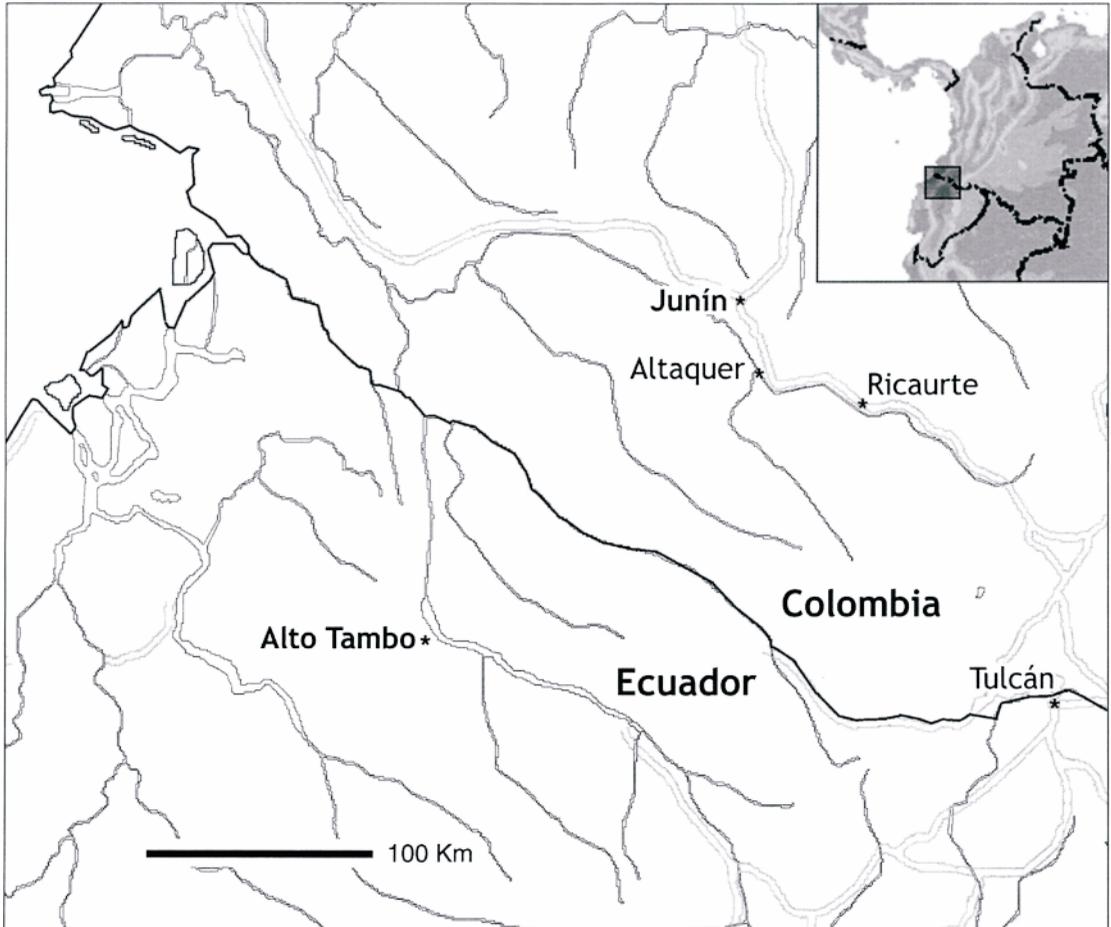


Fig. 1. Southern Chocó of Colombia (Departamento Nariño) and Ecuador (Provincia Esmeraldas), showing the towns closest to the localities at Alto Tambo (Alto Tambo) and La Guarapería (Junín). Gray outlines indicate major roads, black outlines correspond to rivers. See text for map coordinates.

Tail length: Measured from the point of dorsal flexure of the tail with the sacrum to the tip of the last caudal vertebra.

Hindfoot length: From the anterior edge of the base of the calcar to the tip of the claw of the longest toe.

Ear length: From the notch to the fleshy tip of the pinna.

Forearm length: From the elbow (tip of olecranon process) to the wrist (including the carpals), measured with the wing partially folded.

Thumb length: From the metacarpal-phalangeal joint to the tip of the claw of the thumb.

Tibia length: From the proximal end of the tibia to the posterior base of the calcar.

Greatest length of skull: From the posteriormost point on the occiput to the anteriormost point on the premaxillae (excluding the incisors).

Palatal length: From the anteriormost point behind the incisors to the edge of the bony palation.

Condylar-incisive length: From the posteriormost point on the occipital condyles to the anteriormost point on the upper incisors.

Postorbital breadth: Least breadth across frontals posterior to the postorbital bulges.

Braincase breadth: Greatest breadth of the globular part of the braincase.

Mastoid breadth: Greatest cranial breadth across the mastoid region.

Maxillary toothrow length: From the anteriormost edge of the canine crown to the posteriormost edge of the crown of M3.

Breadth across molars: Greatest breadth across the outer edges of the crowns of the upper molars.

Height of upper canine: Dorsoventral height from the anterior base of the crown of the upper canine to the tip.

Breadth at the base of upper canine: Greatest anteroposterior breadth at the base of the upper canine.

In attempting to make taxonomic identifications I compared the vouchers from Alto Tambo and La Guarapería with original descriptions, notes on distribution, and comparative series of specimens of all other *Lonchophylla* species. The following institutional acronyms correspond to museums in which vouchers and other specimens examined are preserved: AMNH, American Museum of Natural History (New York); ICN, Instituto de Ciencias Naturales (Bogotá); MHN, Museo de Historia Natural (Popayán); ROM, Royal Ontario Museum (Toronto); TTU, The Museum, Texas Tech University (Lubbock); USNM, National Museum of Natural History (Washington, DC).

SYSTEMATICS

FAMILY PHYLLOSTOMIDAE GRAY, 1825

SUBFAMILY GLOSSOPHAGINAE BONAPARTE,
1845

GENUS *LONGHOPHYLLA* THOMAS, 1903

Lonchophylla chocoana, new species

Figures 2, 3

TYPE MATERIAL: The holotype (ROM 105786), an adult female preserved as skin, skull, skeleton, and tissue, was collected in the vicinity of Alto Tambo by Mark Engstrom, Burton Lim, and Francisco Sornoza (original number F40079) on 3 March 1996. One paratype is an additional female (ICN 13649) collected by Alberto Cadena, Pilar Rivas, and Robert P. Anderson (original number ACG 2765) at La Guarapería on 12 March 1995.

DISTRIBUTION: Currently known only from northwestern Ecuador and southwestern Colombia (fig. 1), but perhaps widespread throughout the lower to middle elevations of the southern biogeographic Chocó. Because

exhaustive mammal inventories in neotropical forests west of the Andes have been restricted to Barro Colorado, Panama, and La Selva, Costa Rica (Voss and Emmons, 1996), it is likely that the known distribution is just an artifact of inadequate collecting, compounded with superficial similarities to *L. robusta* and *L. handleyi*. In particular, specimens of *L. handleyi* reported from the western slopes of the Cordillera Occidental of Departamentos of Valle and Nariño, Colombia, and specimens of *Lonchophylla* sp. from the Pacific lowlands of Ecuador (Alberico and Orejuela, 1982; Alberico, 1987; Albuja, 1999) deserve investigation.

ETYMOLOGY: For the Chocó, an area of endemism comprising tropical and subtropical humid forests west of the Andes from western Panama through Colombia to northern Ecuador.

DIAGNOSIS: A large-sized species of *Lonchophylla* (forearm 45–48 mm; weight 19–23 g) with chocolate-brown to chestnut-colored dorsal fur and brown ventral fur; dorsal and ventral hairs bicolored (the former more distinctly banded than the latter), 7–8 mm long in shoulder region; pinnae short with rounded tips; thumb large (7.5–8.3 mm); fringe of the uropatagium sparse; calcar shorter than foot; palate long; with postpalatine torus; right and left upper I1 meet at distal third of the crown; large gap present between I1 and I2, and smaller gap between I2 and C; outer upper incisors (I2) pointed ventrally more than ventromedially; upper canines large; height of P3 slightly less than P4; gap present between C and P3; smaller gap present between P3 and P4; P4 with small but well-developed lingual cusp; M1 and M2 roughly the same width; lower incisors small and trilobed, with crown height approximately equal to crown width.

Of the characters listed above, five are particularly useful for field identification of *Lonchophylla chocoana*: size (forearm 44–48 mm; weight 19–23 g); thumb length (7.5–8.3 mm); dorsal fur color; ventral fur bicolored;

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Fig. 2. Dorsal (A), ventral (B), and lateral (C) views of the skull of the holotype of *Lonchophylla chocoana* (ROM 105768). Scale bar = 5 mm.

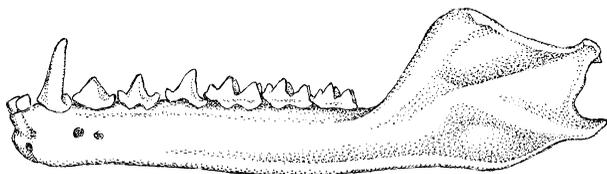
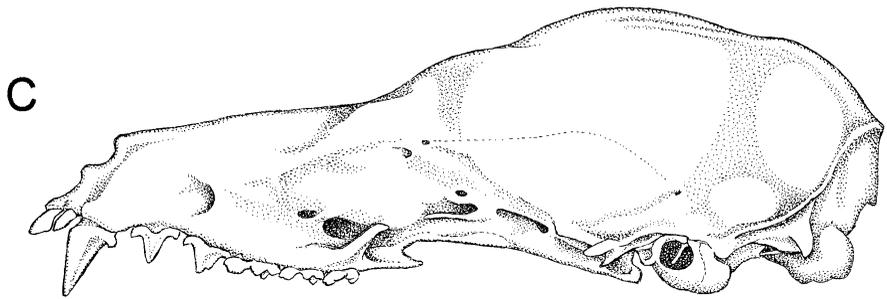
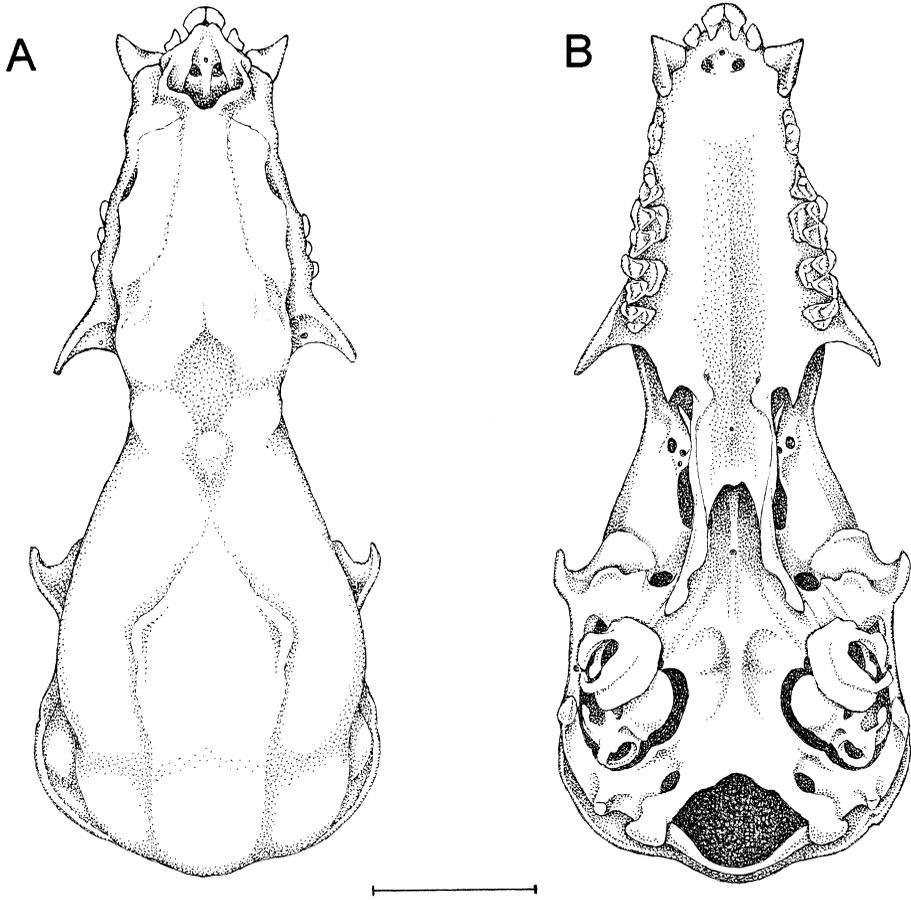


TABLE 1
Measurements of the Specimens of
Lonchophylla chocoana

	Holotype ROM 105786	Paratype ICN 13649
Sex	Female	Female
Weight	23.0	19.0
Total length	78.0	84.5
Tail length	7.0	10.5
Hind foot length	15.0	13.2
Ear length	17.0	14.0
Forearm length	48.0	45.0
Thumb length	7.5	8.3
Tibia length	16.5	18.2
Greatest length of skull	27.7	28.3
Palatal length	7.0	6.9
Condylolincisive length	26.9	27.4
Postorbital breadth	5.3	5.3
Braincase breadth	10.2	10.5
Mastoid breadth	6.9	7.0
Maxillary toothrow length	9.8	11.7
Breadth across molars	7.3	7.3
Height of upper canine	2.6	2.7
Breadth at base of upper canine	1.7	1.7

and trilobed lower incisors. Within the genus *Lonchophylla* this combination of traits is unique to *L. chocoana*. Appendix 1 summarizes the molecular data that prompted the investigation of morphological differentiation in *L. chocoana*. The average uncorrected pairwise sequence divergence of the mitochondrial cytochrome *b* gene of *L. chocoana* with respect to *L. robusta* from Colombia is 11.6%, to *L. robusta* from Panama is 12.3%, and to *L. handleyi* is 11.6%. These genetic distances are indicative of species-level differentiation, according to one recently proposed criterion (Bradley and Baker, 2001).

MEASUREMENTS: Dimensions of both specimens of *Lonchophylla chocoana* are provided in table 1, and metrical comparisons with representative series of other large congeners within its range are summarized in table 2.

DESCRIPTION AND COMPARISON: *Lonchophylla chocoana* is the largest member of the genus, as large or slightly larger than *handleyi*, and larger than *robusta*, *hesperia*, and *bokermanni* (tables 1–3; Taddei et al., 1983). Females are generally larger than males in *robusta* and *handleyi* (table 2), and the two *chocoana* females (table 1) are therefore

probably larger than their male conspecifics. Although this might produce some overlap in measurements between female *robusta* and male *chocoana*, other nonmetric characters remain diagnostic.

From all other large *Lonchophylla*, *chocoana* can be unambiguously distinguished on the basis of fur coloration, forearm length, greatest length of skull, and palatal length. Additionally, *chocoana* can be distinguished from *robusta* on the basis of size of the thumb, greatest length of skull, palatal length, orientation and size of the outer upper incisors, and the relative size of gaps between I1, I2 and C, which are roughly equal in *robusta*. *L. chocoana* can be distinguished from *handleyi* on the basis of the furry fringe along the uropatagium, size of the thumb, the relative size of the upper canines, presence of a ridge along the posterior edge of the palate (postpalatine torus), and the well-developed lingual cusp on P4. *Lonchophylla chocoana* is larger than all remaining congeners in most anatomical dimensions. *L. hesperia* and *bokermanni* may reach similar length of skull, but they have greater skull length-to-width ratios and are absent from the known range of *chocoana* (see measurements in Taddei et al., 1983).

As with *robusta* and *handleyi*, the dorsal pelage of *chocoana* is composed of bicolored hairs with cream-white bases and brown tips. The length of the dorsal fur along the upper back in *chocoana* is approximately 7–8 mm, slightly longer than in *handleyi* and *robusta* (4.0–7.5 mm). The ventral pelage of *chocoana* contrasts with both *handleyi* and *robusta* in being bicolored from neck to genital region, whereas in *handleyi* the ventral fur is exclusively beige-brown unicolored, while some *robusta* individuals (particularly females) show bicolored hairs around the neck but never in the abdominal region.

The cranial morphology of *chocoana* is similar to that of other members of the genus. *L. chocoana* has a relatively long rostrum, a small but noticeable anteorbital inflation, and a large braincase. Zygomatic arches are absent as in all other lonchophyllines, and the palate is the longest of any congener. Like all *Lonchophylla*, *L. chocoana* has a dental formula I2/2, C1/1, P2/3, M3/3 × 2 = 34. The inner upper incisors are large compared

TABLE 3
 Summary of Principal Diagnostic Characters for Field Identification of Large Species of
Lonchophylla from Northwestern South America

	<i>L. robusta</i>	<i>L. handleyi</i>	<i>L. choacoana</i>
Weight (g)	11.0–20.0	16.0–21.0	19.0–23.0
Forearm length (mm)	41.0–46.2	45.0–46.8	45.0–48.0
Thumb length (mm)	5.2–6.9	5.4–6.3	7.5–8.3
Dorsal fur	Light chestnut to orange yellow	Light chestnut	Dark chestnut to chocolate brown
Ventral fur	Uniform beige-brown or slightly bicolored only in the neck and thoracic region	Uniform beige-brown	Bicolored from neck to genital region
Lower outer incisors	Not trilobed or slightly trilobed	Bilobed	Always trilobed or bilobed

to the outer incisors and are separated by a gap from each other and from the canine. In the latter respect *choacoana* also resembles all other species of *Lonchophylla*.

Differences in the dentition are subtle, but they provide the means to distinguish species of *Lonchophylla* (see Hill, 1980). In *choacoana* the inner upper incisors have a small triangular gap between them, meeting at the distal third of the crown. This is unlike *robusta*, *handleyi*, *mordax*, and *thomasi*, all of which show a taller gap between the inner upper incisors, meeting at the distal quarter of the crown. The upper canines of *choacoana* are relatively and absolutely larger than those of *robusta* and *handleyi*. The posterior cusp of the upper canines of *choacoana* is blunt, similar to that of *handleyi*, while the posterior cusp is sharp in *robusta*, *thomasi*, and

mordax (the latter shows variation between the two disjunct subspecific populations).

In *choacoana* P4 is longer than P3 (anteroposterior dimension), as it is in *robusta*, *handleyi*, *mordax*, and *thomasi*. The height (dorsoventral dimension) of P3 is either equal to or very slightly less than P4. Both *robusta* and *handleyi* have shorter (dorsoventral dimension) P3 than P4, while *mordax* and *thomasi* show upper premolars that are subequal in height. The basal lingual cusp on P4 is present and well developed in *choacoana*, *robusta*, and *thomasi*, less developed in *mordax*, and poorly developed or absent in *handleyi*. The first molar of *choacoana* is comparatively wide, and it is larger (both in anteroposterior and lateral dimensions) than M2, which in turn is larger than M3. Both *robusta* and *handleyi* have similar widths of

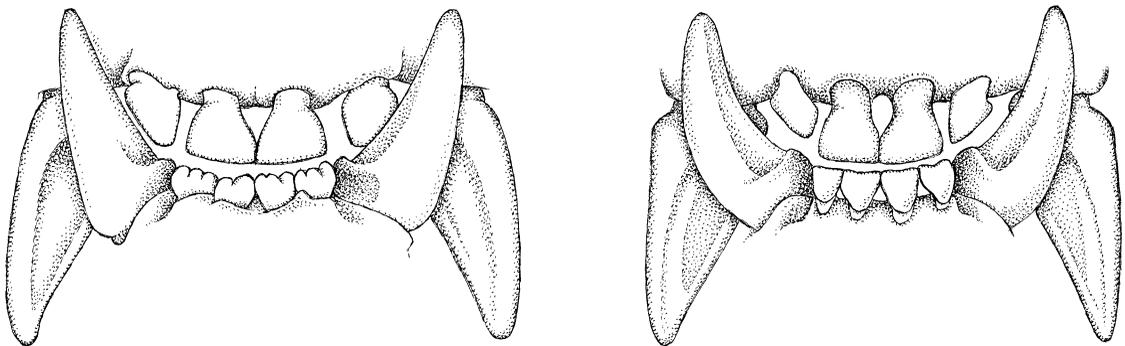


Fig. 3. Anterior views of the lower dentition of *Lonchophylla choacoana* (left, ROM 105786) and *L. robusta* (right, ICN 13648, male). Note the shape and height of the gap between inner upper incisors and the trilobed lower incisors in *choacoana*. These morphological traits can be used in conjunction with size and other characters for field identification.

M1 and M2, although M1 is longer (anteroposterior dimension) than M2, with overall smaller M3. The first two molars of *thomasi* and *mordax* are similar in length and height.

The lower outer incisors of *chocoana* are trilobed, as they are in *thomasi*. Lower incisors are rarely trilobed in *robusta*; *m. mordax* has trilobed incisors, but *m. concava* does not; and incisors are bilobed in *handleyi*. The height of the lower incisors is roughly the same as the width of these teeth in all species of *Lonchophylla*. The lower premolar dentition of *chocoana* resembles that of *handleyi*. In *robusta* the maximum height (dorsoventral dimension) of the series corresponds to p3, and the maximum length (anteroposterior dimension) corresponds to p4. In *handleyi*, p4 is the highest and longest tooth of the series, and in comparison the p4 of *chocoana* is narrow (lateral dimension). In contrast, the longest lower premolar of *thomasi* and *mordax* is p2. The height of the premolars in *thomasi* is roughly the same throughout the premolar series, whereas in *mordax* p4 is the highest premolar (dorsoventral dimension). The first molar of *chocoana* is the widest and longest of the molar series. This is the same condition as in *handleyi*, although m1 of *handleyi* is slender in comparison. In *robusta* the m1 is slightly wider (lateral dimension) than m2, which in turn is wider than m3. In *robusta* m1 is the longest molar (anteroposterior dimension). The differences among the molars are less marked in *mordax* and *thomasi*, particularly the latter. Although m1 is the longest molar (anteroposterior dimension) in both species, height and width vary only slightly along the series.

The coronoid process in *Lonchophylla chocoana* is high and oriented at an angle of about 110° with respect to the toothrow, as in *robusta*. In *handleyi* the coronoid process projects at an angle of around 130°. Both *thomasi* and *mordax* show even greater angles, as well as a longish (anteroposterior dimension) coronoid process in comparison to their larger congeners.

NATURAL HISTORY

Both known specimens of *Lonchophylla chocoana* were captured in ground-level mist nets. The notes on the specimen from Alto

Tambo indicate that it was captured along with other glossophagines (*Anoura* spp.) in a disturbed secondary forest in nets left open overnight due to continuous rain (Burton Lim, personal commun.). The specimen from La Guarapería was also captured in secondary forest, between dusk and 2200 hours, along with *Anoura caudifera*, *A. cultrata*, and *A. geoffroyi* (Cadena et al., 1998). The survey in Nariño additionally captured *Lonchophylla robusta* and *L. mordax* within the same general region at the Altaquer locality. Both specimens were captured in early March: at Alto Tambo on 3 March 1996, and at La Guarapería on 12 March 1995.

Although these data are scant, some aspects are noteworthy. First, *L. chocoana* currently seems rare in its range; one specimen from Alto Tambo prompted this investigation, and the search for conspecifics only found 1 more among 11 specimens of large-bodied *Lonchophylla* from west of the Cordillera Occidental of Colombia. As noted above, a few large *Lonchophylla* from western Colombia and Ecuador reported in the literature might correspond to *chocoana*. Only further sampling can document the complete range and the rarity of *chocoana*. Second, as with other *Lonchophylla*, *chocoana* can be captured using ground-level mist netting. At Paracou, French Guiana, and in southern Venezuela, most *L. thomasi* were captured using ground-level mistnets (Handley, 1976; Simmons and Voss, 1998), as were all *L. robusta* individuals of the Smithsonian Venezuelan Project (Handley, 1976) and all *L. robusta* from Tambito, Colombia (Dávalos and Guerrero, 1999). Third, the habitat associated with the capture of *L. chocoana* has been characterized as disturbed, and the simultaneous capture of other glossophagines probably indicates the presence of local food resources, regardless of the habitat condition.

Little is known about the ecological niche of species in this genus, but observed diversity in body size and habitat choice (from dry scrub to lowland rainforest) indicates that there is some sort of partitioning in feeding and roosting ecology. These ecological characteristics become more intriguing now that three species of *Lonchophylla* have been found in similar habitats, as they were in the

western slopes of the Cordillera Occidental of Nariño, Colombia (Cadena et al., 1998).

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Note added in proof: After this paper was in press, Dr. Luis Albuja kindly agreed to let me examine one additional *Lonchophylla choacoana* specimen. One female, USNM 575171, was collected at Los Pambiles, Provincia Esmeraldas, Ecuador on 24 July 1985 by P. Mena V. and J. Regalado B. It corresponds to *Lonchophylla* sp. A of Albuja (1999: 96). The measurements are all in mm: $70 \times 9 \times 10 \times 15 = 19.5$ g. Thumb = 8.0, greatest length of skull = 27.7, palatal length = 15.1, condyloincisive length = 26.7, postorbital breadth = 5.4, braincase breadth = 10.5, mastoid breadth = 7.2, maxillary toothrow length = 10.2, breadth across molars = 7.1, height of upper canine = 2.7, and breadth at the base of upper canine = 1.7.

APPENDIX 1

VARIABLE SITES OF CYTOCHROME B IN LARGE NORTHERN SOUTH AMERICAN SPECIES OF *LONCHOPHYLLA*

L. robusta Panama = ROM 104268; *L. robusta* Colombia 1 = MHN 512-514; *L. robusta* Colombia 2 = MHN 515; *L. handleyi* Peru 1 = AMNH 230214; *L. handleyi* Peru 2 = TTU 46164; and *L. choacoana* Ecuador = ROM 105786.

Molecular sequences generated as part of the lonchphylline study have been deposited with GenBank under accession numbers AF423079-AF423101. — = same base as the one immediately above.

	Base on cytochrome <i>b</i>																			
	12	15	21	24	27	30	36	42	45	54	60	61	62	66	67	69	77	84	87	
<i>L. robusta</i> Panama	C	G	C	T	T	C	A	T	C	C	T	C	T	C	G	C	A	A	T	
<i>L. robusta</i> Colombia 1	—	—	—	—	—	—	—	—	T	—	—	—	—	—	—	—	—	—	C	
<i>L. robusta</i> Colombia 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	A	—	—	—	—	
<i>L. handleyi</i> Peru 1	T	—	T	C	C	—	—	—	C	T	C	—	—	—	G	T	—	—	—	
<i>L. handleyi</i> Peru 2	—	—	—	—	—	—	—	—	—	—	—	T	C	—	—	—	—	—	—	
<i>L. choacoana</i> Ecuador	—	A	C	T	—	T	G	C	T	C	T	C	T	T	A	—	G	C	—	
	93	96	99	105	109	138	144	147	156	159	165	174	180	189	190	195	198	199	204	
<i>L. robusta</i> Panama	A	T	T	T	T	G	C	C	T	A	C	T	A	T	A	C	C	A	T	
<i>L. robusta</i> Colombia 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	G	—	
<i>L. robusta</i> Colombia 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>L. handleyi</i> Peru 1	G	C	—	—	—	A	A	—	C	—	T	C	—	—	G	—	—	A	—	
<i>L. handleyi</i> Peru 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>L. choacoana</i> Ecuador	A	T	C	C	C	—	—	T	—	G	C	T	T	C	—	T	T	—	C	
	207	213	228	231	232	234	237	243	244	255	258	273	282	285	288	291	294	297	303	
<i>L. robusta</i> Panama	C	A	A	G	C	C	C	T	C	C	A	C	A	C	T	C	A	A	G	
<i>L. robusta</i> Colombia 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	A	
<i>L. robusta</i> Colombia 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>L. handleyi</i> Peru 1	—	—	G	A	—	G	T	—	—	T	—	T	G	—	—	—	G	C	—	
<i>L. handleyi</i> Peru 2	T	—	—	—	—	—	—	—	—	—	G	—	—	—	—	—	—	—	—	
<i>L. choacoana</i> Ecuador	—	G	A	—	G	C	C	C	A	C	A	C	A	T	C	T	A	C	—	
	309	315	321	326	330	330	336	339	343	345	351	354	357	364	369	375	378	384	393	
<i>L. robusta</i> Panama	C	T	C	A	A	A	A	A	G	A	C	C	C	A	G	C	T	C	C	
<i>L. robusta</i> Colombia 1	—	—	T	—	G	G	—	—	—	—	T	—	—	—	—	—	—	—	—	
<i>L. robusta</i> Colombia 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>L. handleyi</i> Peru 1	—	—	C	T	—	—	—	G	—	C	—	—	—	—	—	—	—	—	T	
<i>L. handleyi</i> Peru 2	—	C	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>L. choacoana</i> Ecuador	T	T	T	A	A	A	T	A	A	—	—	T	T	G	A	A	C	T	C	
	397	399	408	411	414	417	423	438	462	471	483	489	498	501	510	513	519	534	538	
<i>L. robusta</i> Panama	T	G	G	G	A	G	A	C	T	G	C	A	C	C	A	T	T	C	A	
<i>L. robusta</i> Colombia 1	—	—	—	—	—	A	—	—	—	—	—	—	—	—	—	C	—	—	—	
<i>L. robusta</i> Colombia 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>L. handleyi</i> Peru 1	—	A	A	A	—	C	G	—	—	C	—	—	G	—	G	—	—	T	—	
<i>L. handleyi</i> Peru 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>L. choacoana</i> Ecuador	C	G	—	—	G	A	A	T	C	T	T	G	C	T	A	—	C	C	G	

APPENDIX 1
(Continued)

		Base on cytochrome <i>b</i>																		
		543	552	553	564	568	579	582	585	588	594	597	600	606	609	615	618	621	624	627
<i>L. robusta</i>	Panama	T	G	T	C	G	A	T	C	C	G	T	A	G	C	C	C	T	C	A
<i>L. robusta</i>	Colombia 1	-	-	-	-	-	-	-	-	A	-	-	-	-	-	T	-	-	-	-
<i>L. robusta</i>	Colombia 2	-	-	C	-	-	-	-	-	-	-	-	-	-	-	C	-	-	-	-
<i>L. handleyi</i>	Peru 1	C	A	T	-	A	-	A	-	T	-	C	G	A	T	-	-	C	-	G
<i>L. handleyi</i>	Peru 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. chocoana</i>	Ecuador	-	-	C	T	-	G	G	T	C	-	-	A	-	C	T	T	-	A	A
		636	642	645	654	657	660	666	669	675	678	681	687	688	690	702	705	708	711	717
<i>L. robusta</i>	Panama	C	C	A	T	T	C	C	T	C	C	A	C	C	C	T	G	T	C	C
<i>L. robusta</i>	Colombia 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-
<i>L. robusta</i>	Colombia 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. handleyi</i>	Peru 1	A	T	G	C	C	T	-	C	T	-	-	T	T	A	T	-	C	-	-
<i>L. handleyi</i>	Peru 2	G	-	-	-	-	T	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. chocoana</i>	Ecuador	A	C	A	-	A	C	-	-	-	T	G	C	C	-	C	-	T	T	T
		724	729	730	732	738	753	771	774	786	789	795	798	801	804	807	813	816	819	822
<i>L. robusta</i>	Panama	T	C	T	G	A	A	C	A	T	T	C	A	T	C	G	G	A	C	C
<i>L. robusta</i>	Colombia 1	C	-	C	-	G	-	-	-	-	-	-	G	-	-	-	-	G	T	-
<i>L. robusta</i>	Colombia 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. handleyi</i>	Peru 1	-	T	-	A	A	G	-	G	-	C	T	A	-	T	A	A	A	C	-
<i>L. handleyi</i>	Peru 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. chocoana</i>	Ecuador	-	C	-	G	-	A	A	A	C	T	-	-	C	-	-	-	-	-	T
		828	852	858	864	876	880	885	891	894	898	903	909	915	916	918	921	954	975	978
<i>L. robusta</i>	Panama	C	C	T	G	A	T	G	C	T	G	A	C	C	A	T	C	T	C	A
<i>L. robusta</i>	Colombia 1	T	T	-	-	G	-	-	-	-	A	-	-	-	-	-	-	-	T	-
<i>L. robusta</i>	Colombia 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. handleyi</i>	Peru 1	C	C	C	-	-	C	A	C	C	-	G	-	T	-	C	-	C	-	-
<i>L. handleyi</i>	Peru 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. chocoana</i>	Ecuador	T	C	T	A	A	-	-	-	-	G	A	T	-	G	-	A	-	-	G
		981	984	987	991	992	993	999	1014	1017	1020	1023	1026	1033	1035	1038	1041	1047	1050	1056
<i>L. robusta</i>	Panama	G	G	G	G	T	T	C	C	A	A	A	A	T	C	C	C	T	T	G
<i>L. robusta</i>	Colombia 1	-	A	A	-	-	C	-	-	-	G	-	-	C	-	-	-	C	-	A
<i>L. robusta</i>	Colombia 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. handleyi</i>	Peru 1	A	-	-	-	-	-	T	-	G	A	-	C	T	-	A	T	-	C	-
<i>L. handleyi</i>	Peru 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. chocoana</i>	Ecuador	-	-	-	A	C	-	-	T	-	-	G	A	-	T	-	C	-	-	-
		1059	1069	1071	1086	1090	1092	1069	1108	1113	1114	1129	1140							
<i>L. robusta</i>	Panama	G	C	C	C	A	C	C	A	C	A	C	A							
<i>L. robusta</i>	Colombia 1	A	-	G	-	-	-	T	-	-	-	-	-							
<i>L. robusta</i>	Colombia 2	-	-	-	-	-	-	-	-	-	-	-	-							
<i>L. handleyi</i>	Peru 1	-	-	A	-	G	-	C	G	T	G	T	-							
<i>L. handleyi</i>	Peru 2	-	-	-	-	-	-	-	-	-	-	-	-							
<i>L. chocoana</i>	Ecuador	-	T	-	T	-	T	-	A	-	-	C	G							

APPENDIX 2
SPECIMENS EXAMINED

The following list summarizes the taxa and specimens examined for this article. Specimens measured for tables 1–3 are indicated with asterisks.

Lonchophylla chocoana—**Colombia**: Nariño, Barbacoas, Junín, sitio La Guarapería (ICN *13649). Ecuador: Esmeraldas, 2 km south of Alto Tambo (ROM *105786).

Lonchophylla handleyi—**Peru**: Junín, Tarma, 2 km northwest of San Ramón (AMNH *230214); Junín, 3.2 km north of Vitoc, Rio Tulumayo (USNM *507172); Pasco, Oxapampa, San Juan (USNM *364347). Huanuco, Leoncia Prado, 6 km north of Tingo Maria (TTU46164).

Lonchophylla mordax—**Colombia**: Nariño, Barbacoas, Altaquer (ICN 13647); Valle del Cauca, Carretera vieja al mar, ca. 10 km west of Bajo Anchicayá (ICN 5983, 5986). **Brazil**: Bahia, Barra (AMNH 235608).

Lonchophylla robusta—**Colombia**: Nariño, Barbacoas, Altaquer (ICN *13648); Cauca, El Tambo, Sector 20 de Julio, Tambito (MHN *512, *513, *514, *515); Valle del Cauca, Calima, Rio Azul, left margin of the Calima river (ICN *8895); Valle del Cauca, Rio Calima, 20 km northeast of Buenaventura (ICN *4390), Valle del Cauca, Calima, Rio Azul, Rio Azul (ICN *9166); Valle del Cauca, Rio Zabaletas, 22 km east of Buenaventura (ICN *4395, *4396); Antioquia, San Luis, El Prodigio,

El Tigre, Finca Cobidal (ICN *13320); Caldas, Samaná, Norcasia, around the CHEC camp (ICN *10810); Cundinamarca, Medina, Choupal, Rio Gazagüan (ICN *10848); Cundinamarca, Melgar (AMNH 207820); Tolima, Cunday, Hacienda Camelia, Cueva El Edén (ICN *5610); Boyacá, Puerto Boyacá, Puerto Romero, La Fiebre, Quebrada La Fiebre (ICN *14852); Magdalena, Santa Marta, Alto de Mira, 3 km west of Rio Buritaca (ICN *13020); Santander, Suaita, San José de Suaita, en route to La Cascada (ICN *15294); Santander, Suaita, San José de Suaita, San Cipriano, Quebrada La Cascada (ICN *15401); Meta, Cubarral, El Vergel, Finca La Estrella (ICN *14399); Meta, Acacías, San José, Colegio Departamental Agropecuario (ICN *9702). **Panama**: Panamá, Cerro Campana (ROM *99938); Panamá, Parque Nacional Altos de Campana (ROM *104268). **Costa Rica**: Limón, foothills Talamanca mountains, near Rio Barbilla (ROM *94194, *94199, *94215, *94215, *94245).

Lonchophylla thomasi—**French Guiana**: Paracou, near Sinnamary (AMNH 267940). **Colombia**: Risaralda, Pueblo Rico, Santa Cecilia, left margin of Rio San Juan (ICN 12210). **Brazil**: Rio Tocantins, Mocajuba (AMNH 97272). **Peru**: Pasco, Oxapampa, San Pablo (AMNH 230284). **Bolivia**: Beni, 1.5 km below Costa Marques, Brazil (AMNH 209358).

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