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Source: American Museum Novitates, 2008(3635) : 1-16

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/464.1

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3635, 16 pp., 6 figures, 2 tables December 31, 2008

A new species of *Lonchophylla* (Chiroptera: Phyllostomidae) from the eastern Andes of northwestern South America

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ABSTRACT

Since 2004 five new species have been described in the nectar-feeding phyllostomid bat genus *Lonchophylla*. All the new species are endemic to one Neotropical ecoregion, suggesting that more species remain to be discovered among collected specimens currently referred to several widespread taxa. Herein we describe a new species, *Lonchophylla orienticollina*, endemic to the middle elevations of the eastern Andes of Venezuela, Colombia, and Ecuador. The new species superficially resembles its sympatric congener *L. robusta*, but its cranial morphology and combination of measurements are distinctive. Throughout its range, *L. orienticollina* is sympatric with *L. robusta*, and it also overlaps with *L. handleyi* in the Cordillera Oriental of Ecuador. The evolutionary processes leading to the divergence among *Lonchophylla* species, as well as the ecological mechanisms that enable multiple, subtly different species to coexist will remain obscure without new field and phylogenetic studies.

INTRODUCTION

Four lonchophylline genera—*Lonchophylla*, *Platalina*, *Lionycteris*, and *Xeronycteris*—form a clade of nectar-feeding phyllostomids distributed from southern Nicaragua to southeastern Brazil and, west of the Andes, to northern Chile (Galaz et al., 1999; Gregorin and Ditchfield, 2005; Koopman, 1994). Analyses of morphological (Carstens et al., 2002; Gregorin and Ditchfield, 2005; Wetterer et al., 2000; Woodman, 2007; Woodman and Timm, 2006) and molecular data (Dávalos and Jansa, 2004) strongly support the monophyly of the tribe, but relationships among the included genera are less certain. Although the

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 ISSN 0003-0082

four genera are morphologically distinct (Woodman and Timm, 2006), both morphological and molecular data have failed to recover a monophyletic genus *Lonchophylla*, see Woodman (2007), Gregorin and Ditchfield (2005), and Dávalos and Jansa (2004).

Growing interest in the systematics of the Lonchophyllini has uncovered greater species diversity than previously suspected. Since the publication of the latest comprehensive taxonomic treatment of Chiroptera by Simmons in 2005, six species in two genera have been described and one subspecies has been elevated to species status (Albuja V. and Gardner, 2005; Dávalos, 2004; Gregorin and Ditchfield, 2005; Woodman, 2007; Woodman and Timm, 2006). The recently described species appear to be narrowly endemic, often known from fewer than five localities e.g., Albuja V. and Gardner (2005), Gregorin and Ditchfield (2006), and Woodman and Timm (2006). The rapid rate of species discovery and narrow endemicity of the taxa in question suggests that the diversity of this clade is still underestimated (Reeder et al., 2007).

While investigating variation within and among lonchophylline species to describe *Lonchophylla chocoana* (Dávalos, 2004), we found distinctive specimens from the foothills of the Cordillera de Mérida of Venezuela, the Serranía del Perijá of Venezuela, the Cordillera Oriental and the Serranía de la Macarena of Colombia, and the Cordillera Oriental of Ecuador. These specimens represent an unrecognized *Lonchophylla* externally similar to *L. robusta* (Miller, 1912), but differing from that species, and from other congeners, by a unique combination of traits. In this article, we describe this new species, its diagnostic morphological attributes, and present a summary of available observations on its distribution and natural history.

MATERIALS AND METHODS

Measurements

Most measurements follow those of Woodman and Timm (2006), who described and illustrated skull dimensions relevant to lonchophyllines, with additional measurements as described for *chocoana* (Dávalos, 2004). Thumbs, tibias, and skulls were measured to the nearest 0.1 mm using manual calipers. External measurements are those recorded by the original collectors, with the exceptions of length of thumb and length of tibia. All measurements reported here are from adult individuals with closed epiphyses. Linear measurements of external and craniodental dimensions are reported in millimeters mm; weights are reported in grams (g).

Measurements are described below:

Total length	Distance from the tip of the snout to the tip of the last caudal vertebra
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 oleocranon process to the wrist including the carpals, measured with the wing partially folded
Tibia length	From the proximal end of the tibia to the posterior base of the calcar
Thumb length	From the metacarpal-phalangeal joint to the tip of the claw of the thumb
Greatest length of skull	From the posteriormost point on the occiput to the anteriormost point on the premaxillae, including the incisors
Condylo-incisive length	From the posteriormost point on the occipital condyles to the anteriormost point on the upper incisors
Condylo-canine length	From the posteriormost point on the occipital condyles to the anteriormost point on the upper canines
Maxillary toothrow length	From the anteriormost edge of the canine crown to the posteriormost edge of the crown of M3
Maxillary breadth	Dorsal breadth of the maxillary bone at M2
Breadth across molars	Greatest breadth across the outer edges of the crowns of the upper molars
Mastoid breadth	Greatest cranial breadth across the mastoid region, excluding the mastoid processes

Zygomatic breadth	Greatest breadth of the posterior zygomatic processes
Postorbital breadth	Least breadth across frontals posterior to the postorbital bulges
Braincase breadth	Greatest breadth of the globular part of the braincase
Palatal length	From the anteriormost point behind the incisors to the edge of the bony palation
Mandibular length	From the anteriormost edge of the mandible to the posteriormost edge of the mandibular ramus
Mandibular toothrow length	From the anteriormost edge of the canine crown to the posteriormost edge of the crown of m3
Height of the coronoid process	From the lowermost edge of the mandible to the uppermost edge of the coronoid process

To identify the specimens from Venezuela, Colombia, and Ecuador, we compared these with original descriptions, notes on distribution, and series of specimens from throughout the range of *Lonchophylla* in southeastern Central America and northwestern South America (appendix). We examined specimens from the following collections: AMNH, American Museum of Natural History (New York); IAvH, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (Villa de Leyva); ICN, Instituto de Ciencias Naturales (Bogotá); MHN, Museo de Historia Natural (Popayán); NHM, Natural History Museum (London); ROM, Royal Ontario Museum (Toronto); USNM, United States National Museum (Washington, DC).

Quantitative Analyses of Morphology

The new species described here is most similar in size (table 1) and morphology to *Lonchophylla robusta* Miller (1912). To compare the new species with *L. robusta* in a quantitative framework, we extracted principal components (PC) from the correlation matrix of six measurements most clearly linked to qualitative differences between the taxa, and plotted the resulting factor scores. The variables selected for principal components analyses using SPSS 16.0 for Mac were: thumb length, greatest length of skull, palatal length, maxillary breadth, breadth across molars, and mandibular length. Because there are no estimates of significance associated with PC analyses, we used these same measurements to generate a discriminant function with species identity as the dependent variable. This allowed us to evaluate both the significance of the assignment function and the accuracy of classification based on these measurements only. Variables for both analyses were measured from 23 individuals of the new species from Venezuela, Colombia, and Ecuador; and 34 *L. robusta* from Costa Rica, Panama, Colombia, Venezuela, and Ecuador.

Distributional Modeling

To estimate the potential range of the new species based on climatic variables, we generated an environmental niche model based on the locality data associated with the specimens examined. Nineteen unique localities for the new species were used to infer the environmental niche. Environmental niche models (ENMs) are grounded on the relationship between a species' ecological requirements and the environmental characteristics of its distribution (Graham et al., 2004). ENMs integrate known records with environmental data (e.g., seasonality in temperature), and the resulting statistical models can then be projected across spatial layers of environmental variables to infer the suitability of the environment beyond the known distribution, e.g., Jarvis et al. (2003).

Climatic data including temperature, precipitation, and their extremes and variability were obtained from published high-resolution ~1 km climate layers compiled from ground stations from 1950–2000 (Hijmans et al., 2005). The maximum entropy algorithm implemented in maxent v. 3.2.1 (Phillips and Dudík, 2008) was applied to obtain the function relating occurrence points to local climate. The function maximizes the entropy of the predicted habitat suitability and is constrained so that the expected value of each climate variable (or its transform) in the distribution equals its empirical mean (Phillips et al., 2006). This ENM allowed us to quantify climate suitability the new species across northwestern South America.

TABLE 1
Summary of measurements of specimens of similarly sized *Lonchophylla* from northwestern South America

	Lonchophylla orienticollina		*Lonchophylla handleyi*		*Lonchophylla chocoana*	*Lonchophylla robusta*	
Measurement	19 males	16 females	5 males	4 females	7 females	26 males	33 females
Total length	76.53 (67.5–81) 18	72.24 (55–80) 9	72.67 (66–80) 3	84 1	78.79 (70–84.5) 7	73.80 (60–86) 22	76.19 (58–96) 26
Tail length	8.78 (6.5–10) 17	9.25 (7–11.3) 8	6.00 (5–7) 2	6 1	9.07 (7–11) 7	9.30 (7–11) 20	8.92 (7–12) 24
Hindfoot length	14.44 (10–35) 18	16.47 (11.5–29) 9	11.67 (10–14) 3	14 1	12.75 (10–15) 7	13.19 (10–28) 22	13.90 (10–29) 26
Ear length	15.50 (11–18) 18	16.52 (15–17.3) 9	17.00 (17) 3	17 1	16.00 (14–17) 7	15.65 (9–19) 21	16.01 (14–19) 25
Forearm length	43.57 (40–47) 10	43.57 (43–44) 3	45.93 (45–46.8) 3	47.7 1	44.33 (42–48) 6	44.10 (43–46) 12	43.87 (41–46.2) 17
Weight	13.58 (11–15.9) 17	13.85 (12.9–16) 6	16.50 (12–21) 2	16 1	20.50 (19–23) 3	14.29 (11–17.9) 16	14.95 (12.5–20) 15
Tibia length	15.28 (14.5–16.6) 18	14.67 (14.3–16.2) 9	16.85 (16.4–17.3) 2	16.8 1	17.35 (16.5–18.2) 6	15.08 (12.8–16.7) 19	15.14 (12.6–16.6) 25
Thumb length	6.52 (5.8–7.3) 18	6.21 (5.2–6.8) 9	6.16 (5.3–6.9) 3	5.8 1	7.21 (6.1–8.3) 7	5.78 (4.9–6.8) 19	6.08 (5.0–7.4) 24
Greatest length of skull	25.64 (24.7–26.7) 17	25.72 (24.8–26.9) 15	28.90 (28.9–28.9) 1	27.97 (27.4–28.7) 3	26.00 (25.7–26.3) 2	26.92 (25.8–27.9) 21	26.44 (25.5–27.4) 26
Condylo–incisive length	24.38 (23.4–25.4) 18	24.36 (23.3–25.4) 15	26.95 (26.3–27.9) 5	27.08 (26.6–27.8) 4	25.74 (24.35–27.4) 7	25.77 (24.7–27.6) 22	25.26 (24.1–26.0) 31
Condylo–canine length	23.12 (21.8–24.3) 17	23.33 (22.1–24.4) 15	26.7 1	25.87 (25.5–26.2) 3	21.00 (18.3–23.7) 2	24.48 (23.6–25.5) 21	24.02 (23.0–24.65) 25
Maxillary toothrow length	9.09 (8.5–9.7) 19	9.14 (8.6–9.4) 15	10.24 (9.9–10.7) 5	10.07 (9.88–10.2) 4	9.67 (8.89–11.7) 7	9.67 (9.3–10.1) 21	9.46 (8.9–9.9) 32
Maxillary breadth	6.38 (5.9–6.8) 19	6.34 (5.9–6.5) 15	6.79 (6.3–7.3) 5	6.75 (6.6–6.8) 4	6.95 (6.5–7.2) 7	6.59 (6.1–7.0) 23	6.44 (6.05–6.85) 32
Breadth across molars	6.39 (5.9–6.7) 18	6.28 (5.7–6.6) 15	6.60 (6.4–6.8) 5	6.62 (6.4–6.8) 4	7.04 (6.7–7.3) 7	6.59 (6.15–7) 22	6.47 (6.15–6.8) 32
Mastoid breadth	10.58 (10.0–11.0) 17	10.40 (9.8–11.0) 15	11.3 1	11.00 (10.6–11.5) 3	10.80 (10.6–11) 2	10.85 (10.3–11.2) 22	10.59 (10.2–11.1) 26
Zygomatic breadth	10.79 (10.1–11.4) 17	10.65 (10.3–11.0) 14	11.1 1	10.97 (10.9–11) 3	11.3 1	11.01 (10.4–11.5) 21	10.70 (10.2–11.3) 24
Postorbital breadth	5.09 (4.7–5.4) 18	5.12 (4.9–5.4) 15	5.07 (4.96–5.3) 5	5.15 (5–5.29) 4	5.21 (5.1–5.4) 7	5.03 (4.7–5.4) 23	5.13 (4.8–5.5) 32
Braincase breadth	10.18 (9.6–10.8) 18	10.02 (9.5–10.5) 15	10.12 (9.8–10.3) 5	10.30 (10.2–10.4) 4	10.28 (10.1–10.5) 7	10.30 (9.9–10.6) 23	10.06 (9.6–10.5) 32
Palatal length	13.54 (12.2–14.9) 18	13.60 (12.7–14.4) 15	16.00 (15.5–17.1) 5	16.21 (15.8–16.6) 4	14.69 (13.36–15.8) 7	14.29 (13.4–15.7) 22	14.24 (13.4–15.1) 31
Mandibular length	17.28 (16.3–18.0) 17	17.24 (16.2–18.5) 14	20.3 1	19.40 (19.1–20) 3	17.65 (17.3–18) 2	18.32 (17.2–19.4) 22	18.00 (17.2–18.8) 26
Mandibular toothrow length	9.26 (8.8–10.0) 16	9.29 (9.0–9.8) 15	10.8 1	10.33 (10.3–10.4) 3	9.20 (9.2–9.2) 2	9.70 (8.8–10.6) 22	9.56 (9–10.3) 26
Height of coronoid process	5.08 (4.5–5.5) 17	4.75 (4.2–5.3) 15	5.5 1	5.03 (4.9–5.2) 3	4.90 (4.9–4.9) 2	5.39 (4.9–6.1) 22	4.83 (4.2–5.3) 26

RESULTS

SYSTEMATICS

FAMILY PHYLLOSTOMIDAE GRAY, 1825

SUBFAMILY GLOSSOPHAGINAE BONAPARTE, 1845

GENUS *LONCHOPHYLLA* THOMAS, 1903

Lonchophylla orienticollina, new species

Eastern Cordilleran Nectar Bat

Figures 1, 2

Lonchophylla robusta: Handley 1976: 21 part, not *Lonchophylla robusta* Miller, 1912.
Lonchophylla robusta: Alberico, Cadena, Hernández-Camacho, and Muñoz-Saba 2000: 153 part, not *Lonchophylla robusta* Miller, 1912.
Lonchophylla robusta: Dávalos 2004: 14 part, not *Lonchophylla robusta* Miller, 1912.
Lonchophylla robusta: Woodman and Timm 2006: 476 part, not *Lonchophylla robusta* Miller, 1912.
Lonchophylla robusta: Woodman 2006: 356 part, not *Lonchophylla robusta* Miller, 1912.

HOLOTYPE: Skin and skull of a female specimen ICN 10280 collected by M.P. Rivas (original number RST409) on 9 July 1988 at the intersection of caño Guamalito and caño la Curía, northern part of the Serranía de la Macarena, San Juan de Arama, 500 m elevation, Departamento del Meta, Colombia.

REFERRED SPECIMENS: (16) One male (ICN 10278) and one female (ICN 10279) collected by María del Pilar Rivas (original numbers RST041 and RST076) on 23 and 26 April 1988 at caño la Curía, northern part of the Serranía de la Macarena, San Juan de Arama, 500 m elevation, Departamento del Meta, Colombia. One female (ICN 9702) collected by the students of Alberto Cadena (original number ACG1747) on 5 December 1985 at Colegio Departamental Agropecuario, vereda San José, Acacías, 625 m elevation, Departamento del Meta, Colombia. One female (ICN 10114) collected by Alberto Cadena (original number ACG2405) on 5 May 1988 at bocatoma Caney Alto, Restrepo, Departamento del Meta, Colombia. One female (ICN 13839) collected by A. Cadena (original number ACG2784) on 24 September 1995 at the forest, vereda Brisas del Guayuriba, Acacías, 480 m elevation, Departamento del Meta, Colombia. One male (ICN 13839) collected by Alberto Cadena (original number ACG2782) on 26 September 1995 at the forest surrounding the Guayuriba river, vereda Brisas del Guayuriba, Acacías, 480 m elevation, Departamento del Meta, Colombia. Two males (ICN 14399 and 14400) collected by students of group 5 of the Introducción Sistemática Animal course (original numbers 11 and 15) on 5 June 1996 at finca La Estrella, vereda El Vergel, Cubarral, 750 m elevation, Departamento del Meta, Colombia. One male (IAvH 6679) collected by Yaneth Muñoz Saba (original number YMS702) on 23 September 1999 at P.N.N. Tamá, Finca "San Isidro" de Pablo Contreras (07°07′22″N 72°14′42″W), 1000 m elevation, Rio Negro, Mpio. Toledo, Norte de Santander, Colombia. One male and one female (USNM 419409 and 419410) collected by Norman E. Peterson, Fred P. Brown, John O. Matson, and C. E. Yunker (original numbers 22129 and 22600) on 17 April 1968 at Kasmera 9°59′N 72°43′W, 21 Km SW of Machiques, Zulia, Venezuela. One male and one female (USNM 419425 and 419426) collected by Arden L. Tuttle, Benjamin Inquilla, and Ernest L. Stromeyer (original numbers 34095, and 34274) in January 1968 at Altamira (8°50′N 70°30′W), Barinas, Venezuela. Three females (BM-NH 78-1354, 78-1356, and 78-1359) collected by Liam Hutson and R.E. Stebbins on 30 July 1976 at Yaupi (2°93′S 77°54′W), Morona Santiago, Ecuador.

DISTRIBUTION: Currently known from the southeastern versant of the Cordillera de Mérida, the eastern versant of the Serranía del Perijá in Venezuela, the eastern and western versants of Cordillera Oriental and the northern portion of the Serranía de la Macarena of Colombia, and the eastern versant of the Cordillera Oriental of Ecuador (fig. 3).

ETYMOLOGY: From the Latin *oriens* ("eastern") and *collis* ("hill"), to summarize the known distribution of the species in northwestern South America.

DIAGNOSIS: A medium-sized species of *Lonchophylla* (forearm 40–47 mm; weight 11–16 g) with dorsal fur ranging from intense ochraceous orange to buckthorn brown to snuff brown and light tawny olive ventral fur

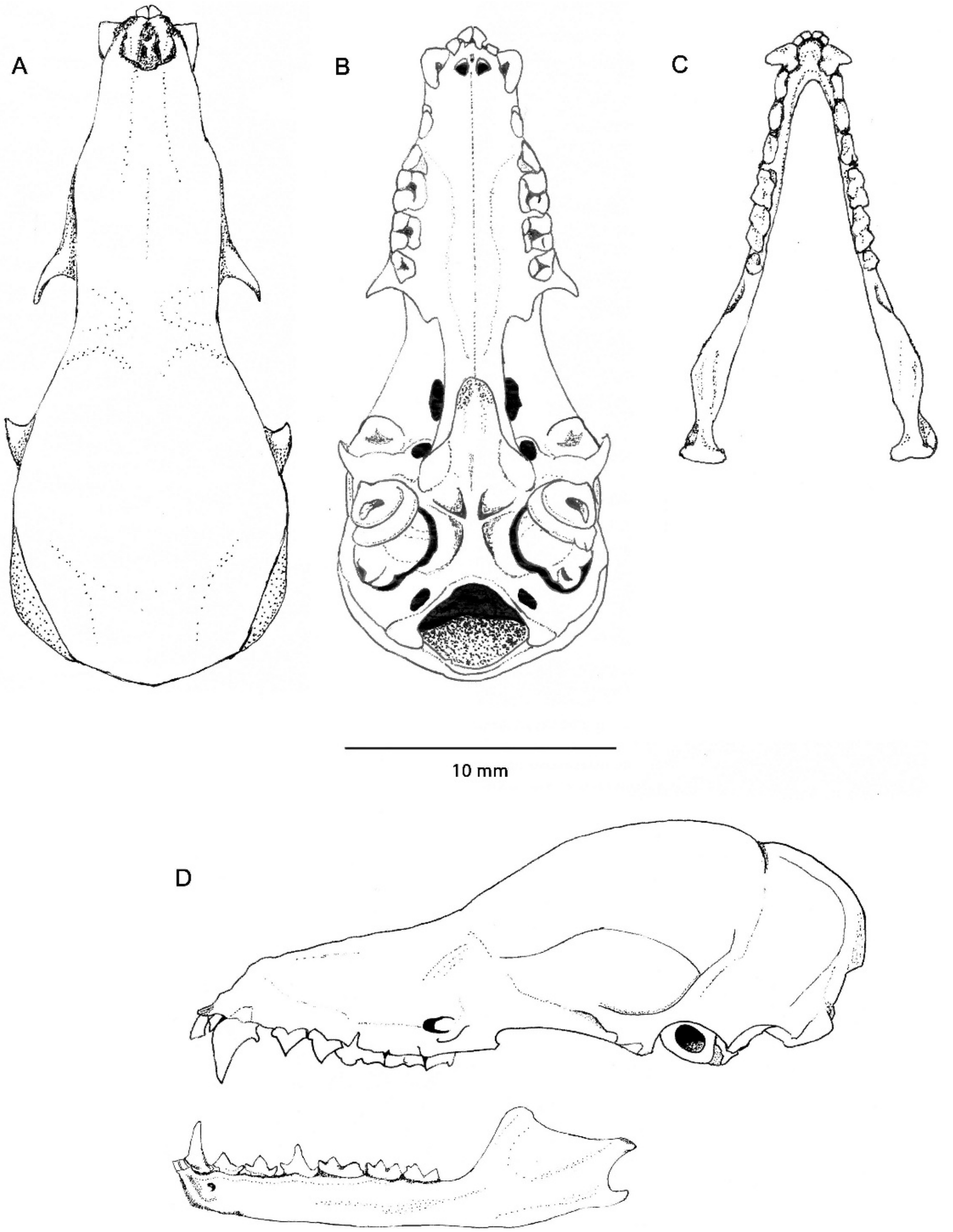

Fig. 1. Dorsal (A) and ventral (B) views of the skull, dorsal (C) view of the mandible, and lateral (D) view of the skull and mandible of the holotype of *Lonchophylla orienticollina* (ICN 10280).

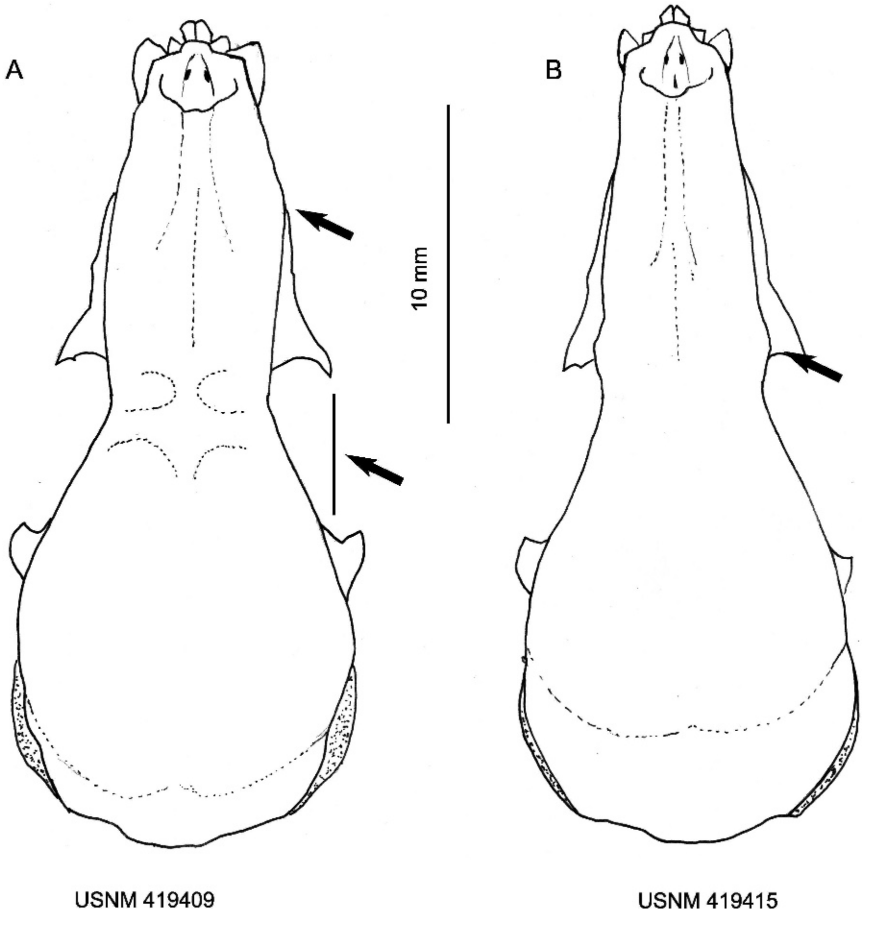

Fig. 2. Dorsal view of *Lonchophylla orienticollina* USNM 419409♀ (A), and dorsal view of *Lonchophylla robusta* USNM 419415♀ (B). Arrows indicate fixed differences helpful in distinguishing these species.

(Ridgway, 1912); ventral hairs sometimes bicolored, the banding is almost imperceptible and disappears towards the abdomen; pinnae short with rounded tips; no furry fringe along uropatagium; calcar shorter than foot; and long feet and thumbs relative to body size. The shape of the skull is distinctive: the braincase is tall; the rostrum is inflated and short, appearing thick in profile; the palate is wide, with postpalatine torus. The height of the braincase makes the slope to the rostrum have a relatively high angle, visible in profile. The spatial arrangement of teeth in the palate is diagnostic: P4 is angled outward about 15° with respect to P3, making the palate appear wide and almost round. There are narrow gaps between I1 and I2, outer upper incisors I2 point ventromedially; wide gaps are present between C and P3; narrower to no gaps between P3 and P4; height of P3 less than P4; lingual cusp on P4 well defined; M1 longer (anteroposterior axis) than M2; M3 is the smallest of the molars. Lower incisors are small, with crowns taller than they are wide, bilobed or trilobed.

Cleaned skulls are necessary to diagnose this species from its sympatric congeners *robusta* and *handleyi*. Five characters are particularly useful in this regard: in dorsal view the rostrum appears short and wide, inflated at the center; in profile the rostrum appears thick, particularly in the postorbital region; the braincase appears tall and forms a marked angle with respect to the rostrum; in ventral view P4 is at about a 15° angle outward from P3; and this considerable

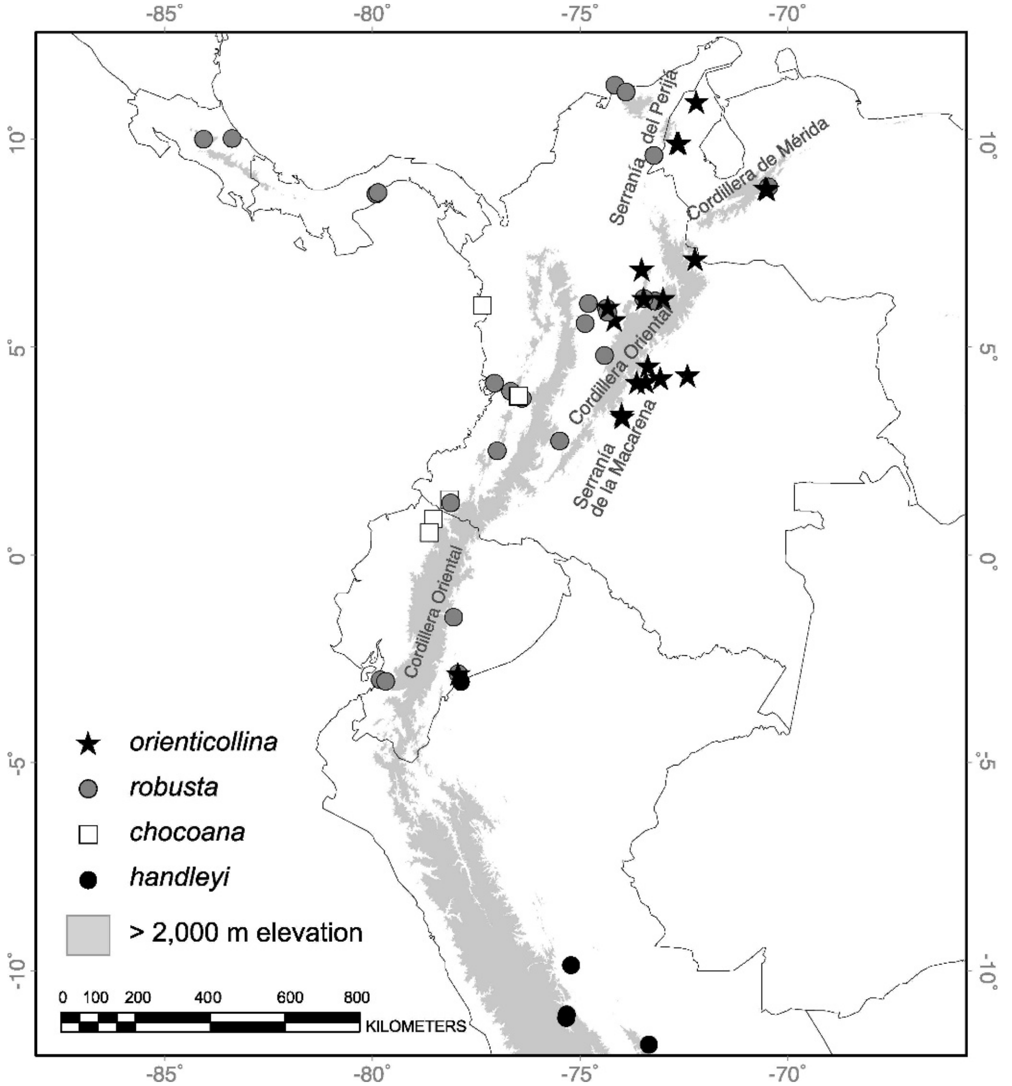

Fig. 3. Map of southern Central America and northwestern South America illustrating localities for specimens of sympatric *Lonchophylla* of similar size. *L. handleyi* is included because it has been found in sympatry with *orienticollina* at Yaupi, Morona Santiago, Ecuador.

widening makes the palate seem wide and almost round. *Lonchophylla orienticollina* is the only species of its size in the genus to display this combination of traits.

MEASUREMENTS: A summary of all known specimens of *Lonchophylla orienticollina* is provided in table 1. Comparisons with a representative series of other similarly sized congeners are also compiled in table 1.

DESCRIPTION AND COMPARISONS: *Lonchophylla orienticollina* is a medium-sized member of the genus, larger than *mordax*, *concava*, *fornicata*, *thomasi*, *pattoni*, *cadenai*, and *dekeyseri*, and smaller than *handleyi*, *chocoana*, *orcesi* and most, but not all, *robusta*; see table 1 (Albuja V. and Gardner, 2005; Dávalos, 2004; Taddei et al., 1983; Woodman, 2007; Woodman and Timm, 2006). *Lonchophylla orienticollina* can be unambiguously distinguished from the smaller *Lonchophylla* species on the basis of forearm length (> 40 mm) and greatest length of skull

(> 24.5 mm). Additionally, *orienticollina* can be distinguished from *mordax* and *thomasi* based on dorsal fur coloration. The latter are dark brown bister or sepia of Ridgway (1914), whereas *orienticollina* exhibits the orange-brown dorsal fur coloration common in *robusta*.

There is overlap in measurements between *orienticollina* specimens and smaller *robusta* individuals (table 1). Qualitative characters are diagnostic for this comparison. In dorsal view the skull of *orienticollina* appears blunter and shorter, with all features shortened when compared to *robusta* of similar size; the rostrum clearly inflated above P4 (fig. 2). In profile, the blunt and shortened appearance persists, with the braincase taller and the rostrum shorter and thicker than in *robusta*; the braincase slopes at a higher angle from the horizontal plane than in *robusta*, and in *robusta* the postorbital area appears inflated relative to *orienticollina*. In ventral view, the palate of *orienticollina* is wide, appearing shorter than that of *robusta* of similar size although palatal length is not diagnostic; P4 forms an angle about 15° with respect to P3, widening the palate and making it look almost round compared to the rectangular appearance of the palate of *robusta*.

Lonchophylla orienticollina is smaller than all remaining congeners in cranial dimensions. *Lonchophylla hesperia* and *L. bokermanni* are absent from the range of *orienticollina*, have longer skulls, with greater skull length-to-width ratios, and have shorter forearms (Taddei et al., 1983). *Lonchophylla orienticollina* is smaller than *chocoana* and *orcesi* in most dimensions (Albuja V. and Gardner, 2005; Dávalos, 2004), and their distributional ranges do not overlap. *Lonchophylla orienticollina* can be distinguished from its sympatric congener *handleyi* on the basis of size, the furry fringe along the uropatagium, the definition and size of lingual cusp on P4, presence of a ridge along the posterior edge of the palate postpalatine torus, and the shape of the palate, which is long and pointed at the incisors in *handleyi*.

As with *robusta*, *handleyi*, and *chocoana*, the dorsal pelage of *orienticollina* is composed of bicolored hairs with cream-white bases and ochraceous orange to brown tips. The length of the dorsal fur along the upper back in *chocoana* is approximately 7–9 mm, slightly longer than in *robusta*, *handleyi*, and *orienticollina* 4–8 mm. The ventral pelage of *orienticollina*, as in *robusta*, sometimes shows bicolored hairs around the neck and in the abdominal region.

The cranial morphology of *orienticollina* is similar to that of other members of the genus. *L. orienticollina* has long rostrum relative to non–nectar-feeding phyllostomids, a small but noticeable anteorbital inflation, and a large, relatively tall braincase (see Woodman and Timm, 2006, for diagnosis of the genus). Zygomatic arches are almost never preserved after preparation, as in all other lonchophyllines. As all *Lonchophylla*, *orienticollina* has a dental formula I2/2, C1/1, P2/3, M3/3 × 2 = 34. As found in smaller members of the genus (Woodman and Timm, 2006), *L. orienticollina* may have supernumerary premolars. The inner upper incisors are large compared to the outer incisors and are separated by a gap from each other and from the canine. In this *orienticollina* resembles all other species of *Lonchophylla*.

The dentition of *orienticollina* resembles that of *robusta*, even in close detail. Both *orienticollina* and *robusta* show a tall gap between the inner upper incisors, meeting at the distal quarter of the crown. The upper canines of *orienticollina* are similar in absolute size to those of *handleyi*, *robusta*, and *thomasi* whose canines are large for their body size, larger than those of *mordax* and *concava*, and smaller than those of *chocoana*, which are exceptionally large. The posterior cusp of the upper canines *orienticollina* is sharp, similar to that of *robusta*, *thomasi*, and *mordax*. In *orienticollina* P4 is slightly longer than P3 anteroposterior dimension, as it is in *chocoana*, *robusta*, *handleyi*, *mordax*, and *thomasi*. P3 is shorter than P4 dorsoventral dimension in *orienticollina*, as it is in *robusta*, *handleyi*, and less so in *chocoana*. In *mordax*, *concava* and *thomasi* P3 is taller than P4.

Beginning with the description of *Lonchophylla handleyi* (Hill, 1980), the degree of development of the basal lingual cusp of P4 has been used as a character to distinguish among species in this genus. After close examination of a large series of *robusta*, *orienticollina*, and specimens of *chocoana*, *handleyi*, *mordax*, *concava* and *thomasi*; differences in this character deserve further comment. The basal lingual cusp on P4 can be seen as a small protuberance in *mordax*, and it has been described as "well developed" (Taddei et al., 1983: 629). This cusp is absent or imperceptible in *concava*. In *handleyi* this cusp has been described as "small and undeveloped, occasionally very small and insignificant" (Hill, 1981: 235), and in *chocoana* as "well developed" (Dávalos, 2004: 8). All the *handleyi* and *chocoana* specimens examined here had a basal lingual protuberance on P4, but the degree of development varied from a fully formed cusp projecting upward (fig. 4B), to a small shapeless knob (fig. 4D). In both *robusta* and *orienticollina* the basal lingual cusp is invariably visible and distinct. There are individual differences in the sharpness and height of the cusp, probably related to dental wear. A few *robusta* individuals had rounded cusps, comparable to those of some *chocoana* and *handleyi* specimens, though never as blunt or small (fig. 4). Individual variation might thus confound some pairwise comparisons aimed at identifying large *Lonchophylla* congeners based on this character alone. In addition to the features of P4, other characters, e.g., fringe of the uropatagium, size of canines, or length and shape of the palate should be used for species identification.

As in *robusta* and *handleyi*, the M1 and M2 of *orienticollina* have similar widths (lateral dimension), with M1 longer (anteroposterior dimension) than M2, and an overall smaller M3. In contrast, in *thomasi*, *mordax*, and *concava* the first two molars are similar in length and height.

Lower incisors may be trilobed or bilobed in *orienticollina*, as in *robusta*. In *handleyi*, incisors are variably trilobed, bilobed, or neither, while both *mordax* and *concava* have trilobed incisors, though this can be difficult to detect in the latter. The height of the lower incisors is greater than the width of these teeth in *orienticollina*, and sometimes in *robusta*. Height and width of the crown of the lower incisors are roughly the same in other *Lonchophylla* examined. The lower premolar dentition of *orienticollina* resembles that of *robusta*. The posterior cusp of p2 is distinct

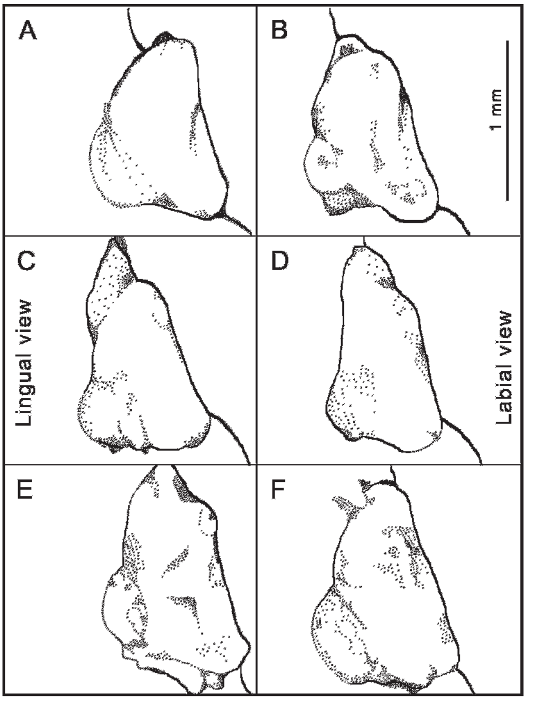

Fig. 4. Ventral view of P4 of *Lonchophylla handleyi*: (A) USNM 588021, (B) AMNH 230215; *L. chocoana*: (C) ROM 105798, (D) ICN 4395; *L. robusta*: (E) ICN 13648; *L. orienticollina*: (F) ICN 10114. Note the differences in size, degree of development, and bluntness across species and individuals. A and C each have a cusp, but it is blunt compared to that of E or F. B has a small cusp, while D has an indistinct protuberance in place of a cusp.

and hooklike in *robusta*, *thomasi*, *handleyi*, *chocoana*, and *orienticollina*, with some individual variation in sharpness probably caused by wear. In *mordax* this cusp, if present, is not clearly distinct or hooklike. In *orienticollina* p4 is taller (dorsoventral dimension) and longer (anteroposterior dimension) than p3; p3 was erroneously reported to be taller than p4 in *robusta* (Dávalos 2004: 9). As in *robusta*, the first molar of *orienticollina* is the widest (lateral dimension), tallest, and longest of the molar series, followed by m2, which is in turn wider and slightly longer than m3. The molar series varies in width and length more than in height. As in *robusta*, the coronoid process in *orienticollina* is high and oriented at an angle of about 110° with respect to the tooth row.

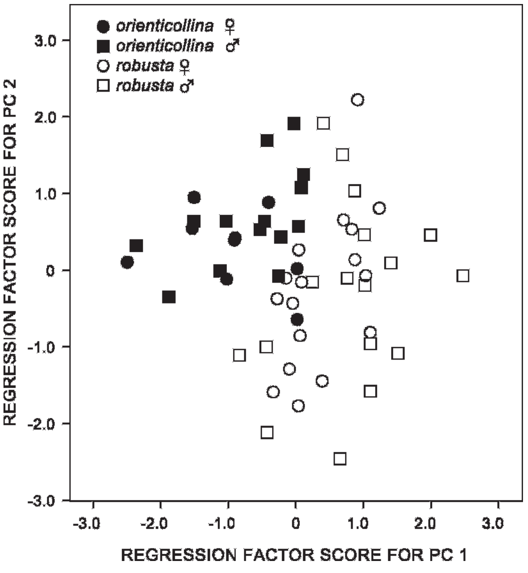

Fig. 5. Plot of regression factor scores on the first and second axes from principal component analyses of eight variables measured from 34 *Lonchophylla robusta*, and 23 *L. orienticollina*. Factor loadings for cranial dimensions on PC 1 are positive (table 2), so the largest individuals have the highest scores on that axis.

Multivariate Analyses of Morphology

A plot of factor scores from a principal components analysis comparing *orienticollina* to *robusta* shows *orienticollina* at the low end of PC 1 (fig. 5), which comprises mostly cranial size, and reflects its shorter skull (table 2). In contrast, *orienticollina* falls at the high end of PC 2, resulting from the longer thumb relative to *robusta*. The sexes of each species do not separate along either axis, despite the longer, wider skulls of male *robusta* (table 1). Specimens of *orienticollina* had a narrower size distribution than the sample of *robusta*, perhaps reflecting the narrower geographic range of the former. The two species overlapped considerably along each axis, but *orienticollina* spans a combination of measures distinct from that of *robusta* (fig. 5).

A discriminant function fitted to the variables used to generate the PC factors was highly significant < 0.0001, with a canonical correlation R* between the species assignment and the function generated of 0.78 (where R* ranges from 0, indicating no correlation, to 1, indicating perfect correlation). Skull and palatal length were the variables most relevant to the discriminant function coefficients (table 2). The resulting discriminant function based on only six metric variables successfully predicted species assignments for 21 of 23 *orienticollina* (91.3%) and 30 of 34 *robusta* (88.2%), in either case much better than at random (50%).

Climate-Based Distributional Modeling

Distributional modeling using the maxent algorithm found two variables, seasonality of rainfall and the mean of monthly temperature range, as the most important determinants of presence of *Lonchophylla orienticollina*. Together, these climate variables explained 63% of the variation in inferred suitability. High seasonality in precipitation characterizes the eastern slopes of the east Andes of Venezuela and Colombia, where a marked

TABLE 2

Results of principal components and discriminant function analyses

Factor loadings for the first two axes of regression factors extracted from the correlation matrix of selected metric variables, and coefficients of the discriminant function fitted to those same variables.

Measurement	Principal component 1	Principal component 2	Coefficients obtained in discriminant function
Thumb length	−0.302	0.815	−0.402
Greatest length of skull	0.938	−0.118	0.427
Palatal length	0.828	−0.146	0.441
Mandibular length	0.841	−0.187	0.349
Breadth across molars	0.820	0.335	−0.254
Maxillary breadth	0.691	0.522	−0.054
Eigenvalues	3.52	1.12	Not applicable
Proportion of variation	58.59%	18.65%	Not applicable

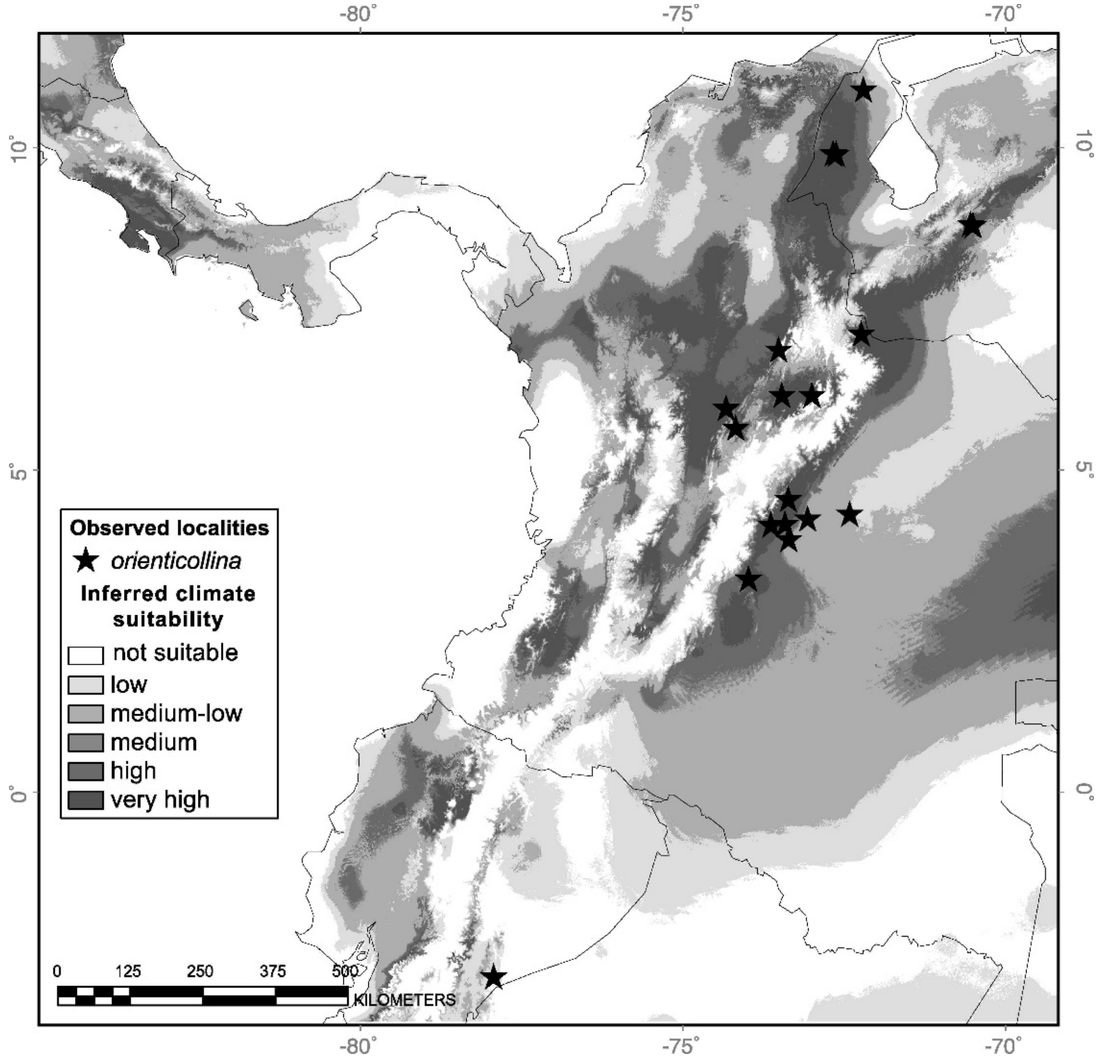

Fig. 6. Environmental niche model (ENM) of *Lonchophylla orienticollina* based on 19 unique localities. All known localities were used to generate the model, and 10,000 random points from the background were used as pseudo-absences. The degree of suitability was based on the least restrictive, second most restrictive, etc., of the non-fixed thresholds provided by maxent.

dry season extends from December to March (Marston, 1948). The known localities for *orienticollina* suggest a continuous distribution northward from the eastern versant of the Andes in Ecuador, widening in northern Colombia and northwestern Venezuela (fig. 3). In contrast, the model inferred relatively low suitability for the northwestern versant of the Cordillera de Mérida, and most of the eastern slopes of the Cordillera Oriental in Ecuador (fig. 6), resulting in a more complex distributional pattern than expected from elevation and land cover alone. High Andean elevations, the Colombian Choco, and the Isthmus of Panama were all found to be unsuitable for *orienticollina*.

The modeled distribution inferred high suitability in regions beyond the known species distribution in central Colombia and western Ecuador. The lack of records from these areas could be explained by historical events such as orogeny, failure to disperse, or ecological interactions such as competitive exclusion by a close relative (Anderson et al., 2002), leading to a narrower range than expected from climate alone. Alternatively, poor sampling (Voss and Emmons, 1996) or failure to include one or several critical environmental variables might account for these distributional over-predictions. Only additional sampling through targeted field surveys in the relatively undersampled mid-elevations of the northeastern Andes has the potential to further refine our understanding of the environmental requirements of this species, and its ecological interactions.

NATURAL HISTORY

Lonchophylla orienticollina has been captured in both old growth and fragmented habitats ranging from the grounds of an agrotechnical high school in Acacías (Meta, Colombia), to the relatively remote and forested biological station of Kasmera (Zulia, Venezuela). Known localities encompass a broad altitudinal range, from 75 m elevation at Hacienda Platanal (Zulia, Venezuela) to 2013 m elevation at finca El Aserradero (Santander, Colombia), with most captures occurring between 600 and 1070 m elevation. This altitudinal band is much narrower along the Andes than even the highest suitability modeled (fig. 6), but broadens around the Serranía de la Macarena in Colombia. Suggestively, more specimens of *orienticollina* have been captured during or around the dry season (seven in December, five in January, and six in April) than in any other period, but this might reflect collecting biases toward sampling during vacations and holidays, as June also records five captures. Most *orienticollina* specimens were captured using mist nets, as part of field surveys (the method of capture of the Ecuadorian specimens is unknown).

The relatively broad range of habitats encompassed by the known *orienticollina* localities suggests broad tolerance to fragmentation, but too little is known about the ecology of this species to fully assess its independence from old growth habitats. Other species in the genus, such as *robusta*, *chocoana*, and *thomasi* have also been found in both closed forests and secondary growth (Cadena et al., 1998; Handley, 1976; Sazima et al., 1978). In contrast, *cadenai*, *pattoni* and *orcesi*, appear to be confined to old growth forests (Albuja V. and Gardner, 2005; Woodman, 2007; Woodman and Timm, 2006). *Lonchophylla orienticollina* has been found in at least two protected areas: Parque Nacional Natural (PNN) Tamá and PNN La Macarena, both in Colombia. This does not automatically ensure the conservation of old growth habitats locally, as La Macarena is currently undergoing large-scale fragmentation associated with coca cultivation (Dávalos and Bejarano, 2008).

Throughout its range, *Lonchophylla orienticollina* is sympatric with *L. robusta*, and both have been captured at Altamira, Venezuela, San Jose de Suaita, Colombia, and Yaupi, Ecuador. The slopes of the Cordillera Oriental and Serranía de la Macarena in Meta, Colombia, might be an exception to this distributional overlap, as no *robusta* specimens were found in collections. Extensive fieldwork is needed to uncover the ecological mechanisms that enable these close relatives to coexist, or the possibility of competitive exclusion in parts of their range. Other nectar-feeding bats captured at *L. orienticollina* localities include *Glossophaga soricina*, *Anoura caudifer*, *A. geoffroyi*, and *A. latidens* (Handley, 1976; Handley, 1984). The presence of these other nectar-feeding species suggests these habitats support a variety of local food resources, and highlights the need for future ecological investigation.

Recent morphological studies, which could not resolve evolutionary relationships among lonchophyllines (Woodman, 2007; Woodman and Timm, 2006), underscored the need to increase sampling of characters and species. Both molecular and morphological data will likely be required to confidently estimate the lonchophylline phylogeny, and thus begin to elucidate the evolutionary processes leading to diversification in this clade.

ACKNOWLEDGMENTS

For acquiring the specimens to enable this description we thank the Smithsonian Venezuela Project, the Instituto de Ciencias

Naturales of Universidad Nacional (Colombia), and Expedición Los Tayos. We thank the curators and curatorial staff who provided access to specimens under their care: N.B. Simmons at the American Museum of Natural History; A. Cadena and Y. Muñoz at the Instituto de Ciencias Naturales; J. Maldonado at Instituto de Investigación de Recursos Biológicos Alexander von Humboldt; M.P. Rivas and J. Guerrero at Museo de Historia Natural; P. Jenkins, R. Sabin, and L. Tomsett at the Natural History Museum; M. Engstrom and B. Lim at the Royal Ontario Museum; M. Carleton, A. Gardner, L. Gordon, K. Helgen, and H. Kafka at the United States National Museum. M. Gómez Laverde, H. Ramírez, L. Raz, and J. Berrío provided logistical support at the Instituto de Ciencias Naturales. J. Schipper and D. Tirira, through an invitation of the IUCN, provided the means to visit Instituto Humboldt. H. Ramírez made available pictures of specimens from Instituto Humboldt and Instituto de Ciencias Naturales. Y. Muñoz and L. Raz at Instituto de Ciencias Naturales provided much-needed, last minute data, as did H. Kafka at the United States National Museum. L. M. Alvaré provided logistical support in Washington, DC. T. Donegan and B. Huertas provided logistical support in London. N.B. Simmons provided invaluable advice during the course of this study. LMD thanks Patricia J. Wynne for her excellent illustrations for the *chocoana* description.

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APPENDIX

Specimens Examined

The following list summarizes the taxa and specimens examined for this study. Specimens measured for table 1 are indicated with asterisks.

Lonchophylla chocoana—**Colombia**: Chocó, P.N.N. Utria, La ensenada de Utria (IAvH 6944); Nariño, Barbacoas, Junín, sitio La Guarapería (ICN *13649); Valle del Cauca, Río Zabaletas, 22 km E de Buenaventura (ICN *4395, *4399); Valle del Cauca, Río Zabaleta, 29 km SE de Buenaventura (USNM *483361, *483362). **Ecuador**: Esmeraldas, 2 km south of Alto Tambo (ROM *105786); Esmeraldas, Los Pambiles (USNM 575171).

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

Lonchophylla handleyi—**Ecuador**: Morona Santiago, Yaupi, Expedicion Los Tayos 3°07′S 78°12′W (BM-NH *78-1363, *78-1368, *78-1369); Morona Santiago, Yaupi, Expedicion Los Tayos 2°93′S 77°54′W (BM-NH *78-1378). **Peru**: Cuzco, Provincia la Convención, CN Tangoshiari, Ridge Camp (USNM *588021); Junín, Tarma, 2 km northwest of San Ramón (AMNH *230214); Junín, Tarma, 13 mi. north of La Merced (AMNH *230215); Junín, 3.2 km north of Vitoc, Rio Tulumayo (USNM *507172); Pasco, Oxapampa, San Juan (USNM *364347).

Lonchophylla mordax—**Brazil**: Bahia, Barra AMNH 235608.

Lonchophylla orienticollina—**Colombia**: Boyacá, Otanche, Vereda La Y, Escuela La Y, 1000 m elevation (ICN *16238); Boyacá, Santa Maria, Caño Negro, Camino entre las fincas Santa Rosita y El Tesoro, ruta a Palo Negro (ICN *17130); Cundinamarca, Medina, vereda Choupal, Rio Gazagüan (ICN *10848); Meta, Acacías, vereda San José, Colegio Departamental Agropecuario, 625 m elevation (ICN *9702); Meta, Acacías, vereda Brisas del Guayuriba, en bosque aledaño al rio Guayuriba, 480 m elevation (ICN *13839); Meta, Cubarral, vereda El Vergel, finca La Estrella, 750 m elevation (ICN *14399, *14400); Meta, Restrepo, vereda Caney Alto, bocatoma (ICN *10114); Meta, San Juan de Arama, parte norte Serranía de la Macarena, caño la Curía, 500 m elevation (ICN *10278, *10279); Meta, San Juan de Arama, Serranía de la Macarena, intersección caño Guamalito y caño la Curía (ICN *10280); Meta, Villavicencio (ICN *12968); Norte de Santander, Toledo, Rio Negro, Finca San Isidro de Pablo Contreras, P.N.N. Tamá (IAvH *6679, 6695, 6718, *6732, 6757, 6763); Santander, Suaita, San Jose de Suaita, via a la Cascada (ICN *15294); Santander, Cordillera de La Paz, hacienda El Trianon, carretera entre San Vicente de Chucuri y Barrancabermeja (ICN *847); Santander, Encino, Vereda Río Negro, sitio Las Tapias, finca El Aserradero, 2013 m elevation (ICN *17534). **Ecuador**: Morona Santiago, Yaupi, Expedicion Los Tayos 2°93′S 77°54′W (BM-NH *78-1354, *78-1356, *78-1359). **Venezuela**: Barinas, 2 km SW of Altamira, La Vega del Río Sto. Domingo (USNM *419418, *419419, *419420, *419422, *419425); Barinas, 2 km SW Altamira USNM *415386; Barinas, Altamira (USNM *419413, *419426, *419427, *419428); Zulia, 10 km +18 km W of Machiques, Kasmera, 270 m elevation (USNM *419409, *419410); Zulia, 31 km + 19 km W of Machiques, Novito, 1135 m (USNM *419412); Zulia, 18 km +49 km W of Maracaibo, Hacienda Platanal, 75 m elevation (USNM *456535).

Lonchophylla robusta—**Costa Rica**: Heredia, Parque Nacional Braulio, Carrillo, 1 Km S, 11.5 Km E San Miguel, 700 m elevation (USNM *562767, *562768, *562769, *562770, *56271, *56272, *56273); Limón, foothills Talamanca mountains, near Rio Barbilla (ROM *94194, *94199, *94215, *94215, *94245). **Panama**: Panamá, Cerro Campana ROM *99938; Panamá, Parque Nacional Altos de Campana (ROM *104268). **Colombia**: Antioquia, San Luis, El Prodigio, El Tigre, Finca Cobidal (ICN *13320); Boyacá, Puerto Boyacá, vereda La Esmeralda, quebrada La Fiebre, a 1 Km. al NE Campamento Techint (ICN *14807); Boyacá, Puerto Boyacá, Inspección de Policia Puerto Romero, vereda La Fiebre, Quebrada La Fiebre (ICN *14852); Caldas, Samaná, Norcasia, around the CHEC camp (ICN *10810, *10811); Cauca, El Tambo, Sector 20 de Julio, Tambito (MHN *512, *513, *514, *515); Cesar, Serranía de Perijá, Zumbador (ICN *18499); Cundinamarca, Yacopi, Guadualito, vereda la Laguna, finca La Planada, 1320 m elevation (ICN *13792); Huila, Yaguará, vereda Upar, 850 m elevation (ICN *17760); Magdalena, Santa Marta, Parque Nacional Natural Tayrona, Arrecifes (ICN *7854, *7983); Magdalena, Santa Marta, Alto de Mira, 3 km west of Rio Buritaca, Sierra Nevada de Santa Marta, 1050 m elevation (ICN *13020); Nariño, Barbacoas, Altaquer (ICN *13648); Santander, Charala, Virolin, El Reloj, margen derecha rio Oibita, 1740 m elevation (ICN *6612); Santander, Suaita, San José de Suaita, San Cipriano, Quebrada La Cascada (ICN *15401); Valle del Cauca, Rio Calima, 20 km northeast of Buenaventura (ICN *4390); Valle del Cauca, Rio Zabaletas, 22 Km. E de Buenaventura (ICN *4394, *4396, *4397); Valle del Cauca, Calima, Rio Azul, left margin of the Calima river (ICN *8895); Valle del Cauca, Calima, Rio Azul, Rio Azul, 500 m elevation (ICN *9166); Valle del Cauca, Calima, Rio Azul, Campamento CVC, 500 m elevation (ICN *9167, *9168). **Ecuador**: Guayas, Huerta Negra/Tenguel, 20 Km ESE Balao (USNM *498830, *498831, *522157, *534298); Guayas, Huerta Negra/Tenguel (USNM *534299, *534300); Guayas, San Rafael, 7 Km S Balao (USNM *498827, *498828, *498829); Mera, Pastaza (USNM *548069); Morona Santiago, Yaupi, Expedicion Los Tayos 2°93′S 77°54′W (BM-NH *78-1355, *78-1357, *78-1358, *78-1360, *78-1361, *78-1362); Ecuador (USNM *522156). **Venezuela**: Barinas, 7 km NNE of Altamira, Agua Fría (USNM *419415, *419417).

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).