

Extraordinary Local Diversity of Disk-Winged Bats (Thyropteridae: Thyroptera) in Northeastern Peru, with the Description of a New Species and Comments on Roosting Behavior

Authors: Velazco, Paúl M., Gregorin, Renato, Voss, Robert S., and Simmons, Nancy B.

Source: American Museum Novitates, 2014(3795) : 1-28

Published By: American Museum of Natural History

URL: <https://doi.org/10.1206/3795.1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Extraordinary Local Diversity of Disk-winged Bats (Thyropteridae: *Thyroptera*) in Northeastern Peru, with the Description of a New Species and Comments on Roosting Behavior

PAÚL M. VELAZCO,¹ RENATO GREGORIN,² ROBERT S. VOSS,¹
AND NANCY B. SIMMONS¹

ABSTRACT

Species of *Thyroptera* are insectivorous foliage-roosting bats that inhabit lowland moist forests (including gallery formations in savanna landscapes) from Mexico to southeastern Brazil. Although four species are currently recognized, only one or two species were previously known to occur at most localities. Recent inventory work in northeastern Peru has documented the local cooccurrence of four species of *Thyroptera*, one of which is here described as new. The new species (*T. wynneae*), which also occurs in Brazil, can easily be recognized by a combination of diagnostic morphological traits. The latter include small size, tricolored ventral pelage, long and woolly hairs between the shoulders, a uropatagium with the proximal half densely covered by long hairs, wing tips sparsely covered by long hairs, a calcar with two lappets and five tiny skin projections between the foot disk and the proximal lappet, a rostrum considerably shorter than the braincase, third lower incisors that are subequal in height to the first and second lower incisors, and third lower incisors with two well-developed accessory cusps. We illustrate the crania of all five known species of *Thyroptera* and provide a key based on craniodental and external characters. Unexpectedly high local diversity of these elusive bats poses a challenge for future

¹ Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History.

² Departamento de Biologia, Universidade Federal de Lavras, Lavras, Minas Gerais, Brazil.

inventory research and raises interesting questions about ecological-niche partitioning in Neotropical bat communities and the evolutionary history of thyropterids.

INTRODUCTION

Disk-winged bats (Thyropteridae: *Thyroptera*) comprise a group of foliage-roosting, insectivorous species that occur in lowland moist forests from southern Mexico to southeastern Brazil (Wilson, 2008). Thyropterids are easily distinguished from all other Neotropical bats by the presence of a circular adhesive disk on the sole of the foot, an oval or circular disk attached by a short pedicle to the base of the thumb, and by fusion of the soft tissues of digits III and IV of the hind foot (Simmons, 1998). In the possession of adhesive disks thyropterids resemble Old World sucker-footed bats of the family Myzopodidae, but anatomical and evolutionary analyses concur that the adhesive disks in these two groups evolved convergently (Schliemann, 1970, 1971; Simmons, 1998). Thyropterids are additionally characterized by their small size (forearm length = 31–41 mm); an elongate, slender muzzle; circular and well-separated nares; and funnel-shaped ears. The tail extends one to a few millimeters beyond the distal margin of the long interfemoral membrane. The toes have only two phalanges and, as noted above, the third and fourth toes (including claws) are fused. Wing digit II is reduced to an incomplete metacarpal, and the third phalanx of digit III is ossified. The manubrium of the sternum is small and keeled, and its width is about one-half the combined length of the manubrium and mesosternum. The mesosternum is broad, flat, and lacks a keel. The first and second thoracic vertebrae are fused. The trochiter of the humerus is larger than the trochin and articulates with the scapula. The skull has a rounded braincase elevated above the slender rostrum, and has complete premaxillae, but lacks postorbital processes (Wilson, 2008).

Four species of living thyropterids are currently recognized. *Thyroptera discifera* (Lichtenstein and Peters, 1854) is known from Nicaragua, northeastern Costa Rica, and central Panama in Central America, and from northern South America (Colombia, northern Venezuela, and the Guianas) to northwestern Ecuador, eastern Peru, northern Bolivia, and southeastern Brazil (Gregorin et al., 2006: fig. 5). *Thyroptera tricolor* Spix, 1823, is patchily distributed in Central America from southern Mexico (Veracruz) to Panama (it has not been recorded in El Salvador or Nicaragua); in South America it has a similar distribution to that of *T. discifera*, but it seems to be more widely distributed in southeastern Brazil (Wilson, 2008: map 222). *Thyroptera lavalii* Pine, 1993, is known from eastern Ecuador and Peru to northeastern Venezuela and the central Brazilian Amazon (Solari et al., 2004). *Thyroptera devivoi* Gregorin et al., 2006, is only known from southwestern Guyana and northeastern Brazil, but the considerable distance (ca. 2000 km) spanning documented collection localities (Gregorin et al., 2006: fig. 5) suggests that the species is widely distributed.

Recent inventory work in the Peruvian Amazon and southeastern Brazil has resulted in the collection of three specimens of *Thyroptera* that do not fit the diagnosis of any previously described species in the genus. In this report we describe these specimens as a new species, and we discuss the remarkably high local diversity of disc-winged bats in northeastern Peru, where four species are now known to occur between the Yavarí and Ucayali rivers.

METHODS

The external and osteological characters we examined include (but are not limited to) those defined by Gregorin et al. (2006) and Solari et al. (2004). Premolar nomenclature follows O'Leary et al. (2013) and Dávalos et al. (in press): the three upper premolars are P1, P4, and P5, and the three lower premolars are p1, p4, and p5. We examined 80 specimens of adult *Thyroptera* (36 males and 44 females; appendix 1) for comparative purposes. All measurements reported herein are from adult individuals with closed epiphyses. The first four measurements listed below were taken from skin tags or other records made by the original collector; all other measurements were taken by us using digital calipers and were recorded to the nearest 0.01 mm. Linear measurements are given in millimeters (mm), and weights are reported in grams (g). Descriptive statistics (mean and observed range) were calculated for all samples. Measurements are defined as follows:

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

Length of tail (LT): Measured from the point of dorsal flexure of the tail with the sacrum to the tip of the last caudal vertebra.

Hind foot length (HF): Measured from the anterior edge of the base of the calcar to the tip of the claw of the longest toe.

Ear length (Ear): Measured from the ear notch to the fleshy tip of the pinna.

Free tail length (FTL): Length of the free portion of the tail, measured from the tip of the last caudal vertebra to the distal border of the interfemoral membrane (uropatagium).

Forearm length (FA): Distance from the elbow (tip of the olecranon process) to the wrist (including the carpals). This measurement is made with the wing at least partially folded.

Greatest length of skull (GLS): Distance from the posteriormost point on the occiput to the anteriormost point on the premaxilla (excluding the incisors).

Condylolincisive length (CIL): Distance between the anteriormost point on the upper incisor and a line connecting the posteriormost margins of the occipital condyles.

Braincase breadth (BB): Greatest breadth of the globular part of the braincase, excluding mastoid and paraoccipital processes.

Rostral length (ROL): Distance from the alveolar process of the premaxilla above the first upper incisor to the ipsilateral postorbital constriction.

Zygomatic breadth (ZB): Greatest breadth across the zygomatic arches.

Postorbital breadth (PB): Least breadth at the postorbital constriction.

Maxillary toothrow length (MTRL): Distance from the anteriormost surface of the upper canine to the posteriormost surface of the crown of M3.

Width at M3 (M3–M3): Greatest width of palate across labial margins of the M3s.

Length of mandible (LMA): Distance from the anteriormost point on the first lower incisor to the posteriormost point on the ipsilateral coronoid process.

Mandibular toothrow length (MANDL): Distance from the anteriormost surface of the lower canine to the posteriormost surface of m3.

Eight craniodental measurements (GLS, CIL, BB, PB, MTRL, M3–M3, LMA, and MANDL) and one external measurement (FA) of male specimens were log-transformed for multivariate statistical analysis, and we used principal components analysis to assess species differences in these data. A few measurements (TL, LT, HF, Ear, FTL, ROL, and ZB) were omitted because they were unavailable from more than a few specimens. Principal components were extracted from the variance-covariance matrix using the program PAST (Hammer et al., 2001). A dichotomous identification key for all the species of *Thyroptera* was constructed based on morphological traits identified during the course of the study.

The specimens discussed in this report belong to the following collections:

AMNH	American Museum of Natural History, New York.
CEBIOMAS	Centro de Ecología y Biodiversidad, Lima, Peru.
CMUFLA	Coleção de Mamíferos da Universidade Federal de Lavras, Lavras, Minas Gerais, Brazil.
FMNH	Field Museum of Natural History, Chicago, Illinois.
MUSM	Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru.
MZUSP	Museo de Zoologia da Universidade de São Paulo, São Paulo, Brazil.
ROM	Royal Ontario Museum, Toronto, Ontario, Canada.

SYSTEMATICS

Family Thyropteridae Miller, 1907

Genus *Thyroptera* Spix, 1823

Thyroptera wynneae, new species

Patricia's Disk-winged Bat

HOLOTYPE: The holotype (CEBIOMAS 237; figs. 1, 2, 4E, 5E, 6E), an adult male specimen preserved in alcohol with the skull removed and cleaned, was collected by Robert S. Voss and subsequently prepared by Paúl M. Velazco (original number: PMV 2469) on 29 January 2012 at the Centro de Investigaciones Jenaro Herrera (45°05'S, 73°40'W), a forestry research station located about 2.5 km inland from the right bank of Río Ucayali in the Peruvian department of Loreto (fig. 3, locality 27). Frozen tissues are deposited at the American Museum of Natural History (AMNH 278486).

PARATYPES: Two additional specimens (CMUFLA 694 and CMUFLA 1160), both adult males preserved in alcohol with the skulls removed and cleaned, were collected at a site called Campolina (ca. 19°42'S, 42°30'W; fig. 3), about 25 km E of Marliéria in the Parque Estadual do Rio Doce, Minas Gerais, Brazil. Campolina is shown on a map of bat sampling localities by Tavares et al. (2007: fig. 1), who also worked at this locality. One paratype (CMUFLA 1160) was collected by Renato Gregorin on 11 January 2013 and the other (CMUFLA 694) was collected by Karina Lobão Vasconcellos and Bruno Bret Gil (original field number: PERD 310).

on 11 March 2013. CMUFLA 694 has a damaged skull (the braincase is broken in the parietal region and the left auditory bulla is missing), but the other specimen is in good condition.

DISTRIBUTION: *Thyroptera wynneae* is currently known only from the type locality in north-eastern Peru and from the Parque Estadual do Rio Doce in southeastern Brazil (fig. 3; appendix 1).

DIAGNOSIS AND DESCRIPTION: *Thyroptera wynneae* is a small thyropterid with a short, slender rostrum and a globular braincase (figs. 1–2, 4–6). The dorsal fur is light brown with a slightly grayish overtone. Dorsal hairs are unicolored for most of their length, but a tiny basal portion of each hair is lighter than the rest of the shaft (fig. 1A, 2A). Ventral hairs are tricolored with the basal third of each hair whitish in color, the middle segment light brown, and the tip darker. The fur is long and woolly, approximately 11 mm long between the shoulders and 7 mm on the chest. The proximal portion of the forearm (roughly 12 mm of the shaft just distal to the elbow) is densely furred with long hairs. Most of the dorsal surface of the pinna is densely covered with long hairs, but the distal portion is naked (fig. 1A).

The wing membranes of *Thyroptera wynneae* are dark brown. The plagiopatagium and uropatagium (fig. 1C, 2A) are marked by transverse lines of elastine fibers punctuated by regularly spaced wartlike somatosensory domes (sensu Zook, 2007). The dorsal surface of the uropatagium is densely covered with long hairs proximally, and sparsely covered with long hairs distally. The tip of the wing is also sparsely covered with long hairs, and the uropatagium, plagiopatagium, and dactilopatagium have hairs distributed sparsely along their edges. The adhesive disks of the thumb and foot are oblong (fig. 1B, 1C). The thumb disks vary somewhat in size among individuals, ranging from 2.7–4.0 mm in length and 1.8–3.1 mm in width (length being measured along the longest axis of the disk). Similarly, foot disks range from 1.6–2.5 mm in length and 1.4–2.2 mm in width. Some of this variation, however, might be due to differences in preservation. The calcar is long (8.5–12.0 mm) and has two lappets (small cartilaginous flanges) that project posterolaterally from the shaft of the calcar. In addition to these skeletal processes, five tiny skin projections are also present between the foot disk and the proximal lappet (fig. 1C).

The skull of *Thyroptera wynneae* has a smoothly rounded braincase that lacks a sagittal crest (figs. 4E, 6E). The angle between the rostrum and braincase is approximately 130° (fig. 6E) and the rostrum is considerably shorter than the braincase (table 1). There is a large foramen ovale which is 0.5 mm in length. A transverse ridge is present between the right and left hamular processes of the pterygoid. This ridge is intersected anteriorly by a midventral blade-like crest, dividing the mesopterygoid fossa into two separate concavities (fig. 5E; Gregorin et al., 2006, fig. 2A).

Like all other thyropterids, *Thyroptera wynneae* has a dental formula of I2/3, C1/1, P3/3. M3/3 = 38 teeth. The upper incisors are bicuspidate. The second upper incisor (I2) has a mesial cusp that is larger than the distal cusp. Both cusps on I2 are perpendicularly arranged relative to the long axis of the toothrow. The first and second upper incisors are in contact with one other and are separated from the canine by a small diastema. P1 is rounded in occlusal view. Anteroposterior length of P1 is less than that of P4, and crown height of P1 is slightly less than that of P4. P1 and P4 both have narrow lingual and labial cingula. P4 and P5 are subequal in

TABLE 1. Measurements (mm) and Weights (g) of the Type Series of *Thyroptera wynneae*.

	CEBIOMAS 237♂ ^a	CMUFLA 694♂ ^b	CMUFLA 1160♂ ^b
TL	68.0	64.4	65.9
LT	26.0	26.4	26.7
HF	4.0	4.4	3.9
Ear	11.0	12.5	12.7
FTL	4.0	3.1	3.2
FA	33.0	34.2	34.0
GLS	13.2	13.8	12.9
CIL	12.5	13.2	13.6
BB	6.7	6.5	6.9
ROL	4.9	5.0	5.0
ZB	6.8	7.2	7.1
PB	2.6	2.5	2.5
MTRL	5.3	5.6	5.5
M3–M3	4.8	5.0	4.8
LMA	9.9	10.6	10.2
MANDL	5.5	6.2	5.7
Weight	3.5	3.8	2.6

^a Holotype.^b Paratype.

anteroposterior length but crown height of P4 is slightly less than that of P5. P5 has a narrow labial cingulum and a very large lingual cingulum that forms a distinct lobe, the latter extending as far lingually as the protocone of M1. A well-developed anterolingual cusp is present on the labial cingulum of P5. M1 and M2 are subequal in size. A parastyle is present and the protocone is well developed on all upper molars including M3. A metastyle is present and the paracone and metacone are subequal in size on M1 and M2. In contrast, a metastyle is absent and the paracone is taller than the metacone on M3. Lingual cingula are present on all three upper molars. The preparacrista is shorter than the postparacrista on M1 and M2, but the preparacrista is longer than the postparacrista on M3. The premetacrista is shorter than the postmetacrista on M1 and M2, but the postmetacrista is absent on M3.

The first and second lower incisors (i1 and i2) are tricuspidate. The third lower incisor (i3) has two small accessory cusps on each side (mesostyles and distostyles). The i3 is subequal in height to i1 and i2, and is 1.5 times the buccolingual width of i1 and i2. The p1 is triangular in occlusal view. The p4 and p5 are buccally flattened and ovate in occlusal view. All three lower premolars are subequal in height. The lower molars are similar in shape. The m3 is slightly shorter in anteroposterior length than m1 and m2. The protoconids are taller than the hypoconids on all three lower molars. All of the cristids on all lower molars are clearly notched.

COMPARISONS: External and craniodental measurements for *Thyroptera wynneae* and its congeners are provided in tables 1 and 2. *T. wynneae* can be easily distinguished from *T. devi-*

TABLE 2. Measurements (mm) and Weights (g) of Four Species of *Thyroptera*.

	<i>T. devivui</i>		<i>T. discifera</i>		<i>T. lavali</i>		<i>T. tricolor</i>		
	Males ^a	Females ^b	Males ^c	Females ^d	Males ^e	Females ^f	Males ^g	Females ^h	
TL	--	74, 75	74, 76	83.0 (78-87)	4	74, --	72.9 (68-79)	16	71.9 (67-77)
LT	20.4, 21.7	27, 30	33, 35	30.5 (30-31)	4	23, --	27.3 (25-30)	18	28.6 (25-30)
HF	--	6	5.5, 7.0	6.3 (4-7)	4	6, --	5.7 (4-6)	18	5.9 (4-7)
Ear	--	--	13.5, 14.0	9.0 (8-12)	4	8, --	12.3 (11-13)	8	12.4 (11-13)
FTL	4.8 (3.8-5.5)	1.4, 1.7	--	4.0	--	--	7.0 (5.0-9.0)	14	6.0 (4.4-7.3)
FA	36.5 (35.7-37.7)	33.6 (33.0-34.2)	32.8 (32.2-33.4)	39.8 (37.3-41.0)	4	39.0, 39.0	37.1 (35-39)	27	36.7 (33.5-40.0)
GLS	14.9 (14.7-15.1)	14.9 (14.4-15.5)	14.1 (13.5-14.5)	15.6 (15.4-15.8)	4	15.5, 15.2	14.6 (13.6-15.5)	24	14.3 (13.8-15.7)
CIL	13.8 (13.7-13.9)	13.4 (13.1-13.6)	13.7, 13.7	14.9 (14.9-14.9)	4	14.6, 15.0	13.7 (12.9-14.3)	24	13.5 (12.9-14.4)
BB	7.0 (6.7-7.2)	6.8 (6.4-6.9)	6.9 (6.6-7.0)	7.2 (7.1-7.4)	4	7.3, 7.2	7.3 (6.7-7.6)	24	7.3 (6.9-7.5)
ROL	5.8	5.4, 5.9	--	6.5	--	--	5.3, 5.5	--	--
ZB	7.5 (7.4-7.7)	7.1 (6.8-7.3)	7.1 (6.9-7.4)	8.0, 8.0	--	8.1, --	7.5 (6.9-7.7)	13	7.4 (7.1-7.7)
PB	2.7 (2.5-2.8)	2.5 (2.5-2.7)	2.6 (2.6-2.7)	2.8 (2.7-2.9)	4	2.8, 2.8	2.7 (2.5-2.8)	25	2.7 (2.6-2.8)
MTRL	6.0 (5.7-6.1)	5.8 (5.7-5.9)	5.7 (5.5-5.8)	6.5 (6.5-6.5)	4	6.2, 6.3	5.9 (5.5-6.2)	25	5.9 (5.6-6.3)
M3-M3	5.4 (5.3-5.5)	4.9 (4.8-5.2)	5.0 (4.8-5.1)	5.8 (5.7-5.8)	4	5.6, 5.5	5.2 (4.8-5.5)	25	5.2 (5.0-5.5)
LMA	10.9 (10.6-11.3)	10.7 (10.4-10.8)	10.4 (10.0-10.6)	11.6 (11.5-11.7)	3	11.3, --	10.6 (9.7-11.3)	23	10.4 (9.6-10.7)
MANDL	6.1 (5.8-6.3)	6.1 (6.0-6.2)	6.0 (5.9-6.1)	6.6 (6.5-6.6)	3	6.3	6.2 (5.7-6.5)	25	6.1 (5.8-6.3)
Weight	--	--	--	6	--	--, 4	4.5 (3.5-5.1)	12	4.4 (3.4-5.1)

^a Summary statistics (mean, observed range in parentheses, and sample size) for measurements of MZUSP 30073 (holotype), 32345; ROM 35588.

^b Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 16686, 94549; FMNH 140791; MZUSP 16395, 16396.

^c Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 46687; FMNH 46160, 69509; MZUSP 5628.

^d Summary statistics (mean, observed range in parentheses, and sample size) for measurements of FMNH 89119, 89120, 89121 (holotype); ROM 104026, 105215.

^e Measurements of FMNH 89118 and MZUSP 5944.

^f Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 74024, 74025, 77558, 97129, 97130, 97132-97134, 97136, 97137, 183860, 185342, 239077, 239080, 239085, 239088, 267216, 267217, 272761, 273155, 273156, 273160; FMNH 89117, 203644; MZUSP 13263, 15278, 15282; MZUSP 6585, 8583-8586, 14181, 16393.

^g Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 29693, 67592, 74022, 77556, 94550, 97131, 239078, 239081, 239084, 239086, 266353, 273157, 273161; FMNH 43980, 53054, 180726; MZUSP 13262, 15279-15281, 21332; MZUSP 5702, 14180.

voi, *T. lavalii*, and *T. tricolor* by its shorter forearm and smaller greatest length of skull (tables 1–2). *T. wynneae* and *T. discifera* overlap somewhat in size (tables 1–2) but can be unambiguously distinguished based on pelage characteristics.

Externally, *Thyroptera wynneae* can be distinguished from all the other species in the genus by its tricolored ventral pelage, which contrasts with the unicolored ventral pelage of *T. discifera* and *T. tricolor*, and with the bicolored ventral pelage of *T. devivoi* and *T. lavalii*. The overall appearance of the ventral pelage is light brown in *T. wynneae*, whereas it is grayish brown in *T. devivoi*, yellowish brown in *T. discifera*, medium brown in *T. lavalii*, and white or whitish in *T. tricolor*. Dorsally the hairs between the shoulders are long (11 mm) and woolly in *T. wynneae* (fig. 2A) while they are long (8.0–12.0 mm) and not woolly in *T. discifera* and *T. tricolor*, and short (3.5–6.0 mm) and woolly in *T. devivoi* and *T. lavalii*. The proximal portion of the forearm is well furred in *T. wynneae* and *T. discifera*, whereas it is only sparsely haired in *T. devivoi*, *T. lavalii*, and *T. tricolor*.

The dorsal surface of the uropatagium is densely covered with long hairs proximally, and sparsely covered distally, in *T. wynneae* and *T. discifera*. In contrast, the entire dorsal surface of the uropatagium is sparsely covered with short hairs in *T. lavalii* and *T. tricolor*. The tip of the wing is covered sparsely by long hairs (> 1.8 mm) in *T. wynneae* and *T. tricolor*, whereas these hairs are short (< 1.2 mm) in *T. discifera* and *T. lavalii* (we were not able to examine *T. devivoi* for this characteristic). The adhesive disks of the thumb are oblong in *T. wynneae* (fig. 1B), *T. devivoi*, and *T. lavalii*, whereas they are circular in *T. discifera* and *T. tricolor*. The calcar has two lappets that project posterolaterally from the shaft of the calcar in *T. wynneae* (fig. 1C) and *T. tricolor*. In contrast, they are absent or only one faintly developed lappet is present in *T. devivoi*, and only a single lappet is present in *T. discifera* and *T. lavalii*. Five tiny skin projections are present between the foot disk and the proximal lappet in *T. wynneae* (fig. 1C) and *T. tricolor*, whereas these structures are entirely absent in *T. devivoi*, *T. discifera*, and *T. lavalii*.

Cranially, *Thyroptera wynneae* can be distinguished from all other species of *Thyroptera* by having a rostrum that is considerably shorter than the braincase. The rostrum is of equal length or longer than the braincase in *T. devivoi*, *T. discifera*, *T. lavalii*, and *T. tricolor*. The foramen ovale is large (0.50–0.65 mm) in *T. wynneae*, *T. devivoi*, *T. lavalii*, and *T. tricolor*, whereas it is smaller (< 0.45 mm) in *T. discifera*. The transverse ridge present between the hamular processes of the pterygoid is anteriorly intersected by a midventral bladeliike crest, dividing the mesopterygoid fossa in two separate concavities in *T. wynneae*, *T. devivoi*, *T. lavalii*, and *T. tricolor*. The midventral bladeliike crest does not reach the transverse ridge in *T. discifera* (fig. 5).

Dental characters can also be used to distinguish species of *Thyroptera*. The mesial cusp is larger than the distal cusp on I2 in *T. wynneae*, *T. discifera*, and *T. tricolor*, whereas these cusps are subequal in *T. devivoi* and *T. lavalii*. Both cusps on I2 are perpendicularly arranged relative to the long axis of the toothrow in *T. wynneae*, *T. devivoi*, and *T. lavalii*, whereas they are obliquely arranged in *T. discifera* and *T. tricolor*. The first and second upper incisors are in contact with each other in *T. wynneae*, *T. devivoi*, *T. lavalii*, and *T. tricolor* but are separated by a small diastema in *T. discifera*. P1 is rounded in occlusal view in *T. wynneae*, *T. devivoi*, *T. lavalii*, and *T. tricolor*, whereas it is elongated in *T. discifera*. All three lower incisors are

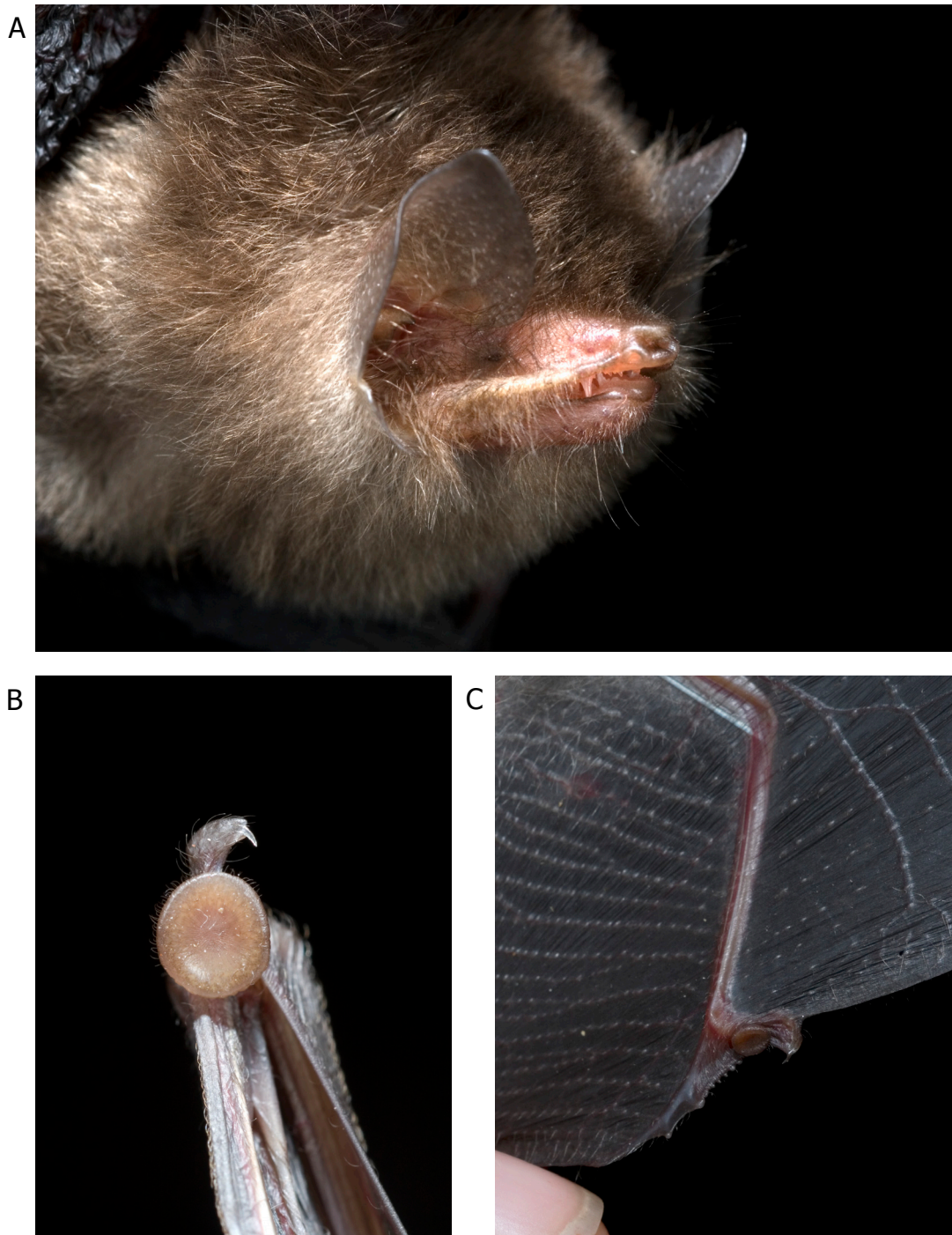


FIG. 1. Right oblique view of the head (A), right wrist with adhesive disk (B), and left hind limb (C) of the holotype of *Thyroptera wynneae* (CEBIOMAS 237). Note that due to the angle from which image (B) was taken, the adhesive disk on the thumb looks circular, but it is in fact oblong vertically. Photos: Burton Lim.

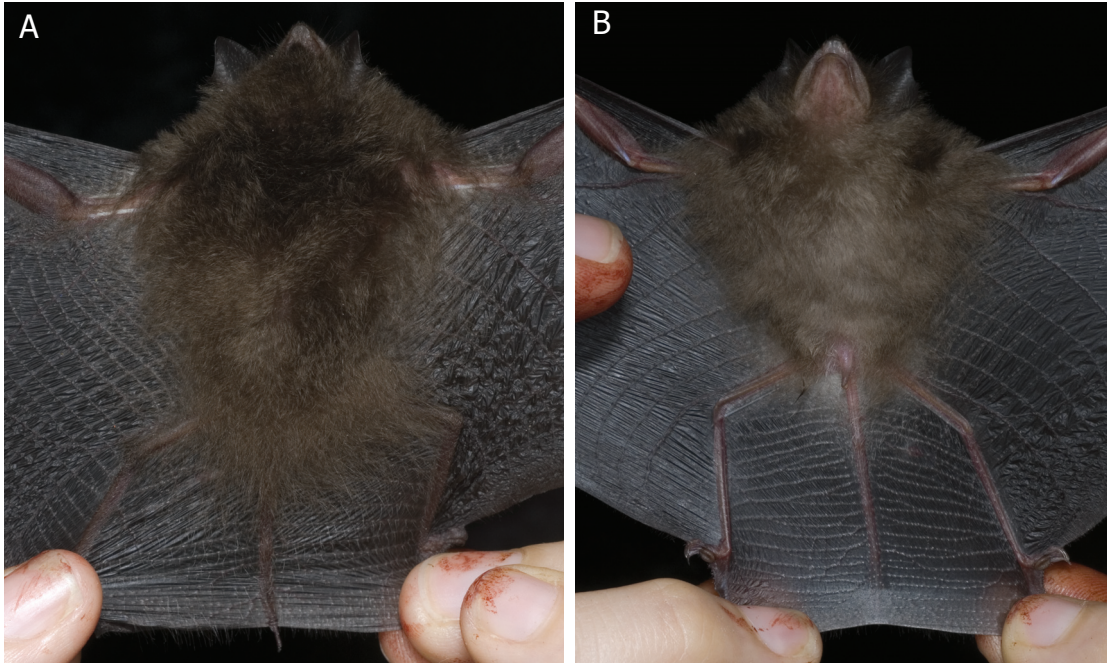


FIG. 2. Dorsal (A) and ventral (B) views of the holotype of *Thyroptera wynneae* (CEBIOMAS 237). Photos: Burton Lim.

subequal in height in *T. wynneae*, whereas the i_3 is taller than i_1 and i_2 in *T. devivoi*, *T. discifera*, *T. lavalii*, and *T. tricolor*. The third lower incisor has two small accessory cusps on each side (mesostyle and distostyle) in *T. wynneae* and *T. discifera*, but these accessory cusps are only faintly developed in *T. devivoi* and *T. tricolor* and are either faintly developed or entirely absent in *T. lavalii*. The i_3 is 1.5 times the buccolingual width of i_1 and i_2 in *T. wynneae*, *T. discifera*, and *T. tricolor*, whereas the i_3 is twice the buccolingual width of i_1 and i_2 in *T. devivoi* and *T. lavalii*. The p_4 and p_5 are buccally flattened and ovate in occlusal view in *T. wynneae*, *T. discifera*, whereas they are flattened and squarish in *T. tricolor*, and wide and squarish in *T. devivoi* and *T. lavalii*.

MULTIVARIATE ANALYSIS: Our multivariate statistical analysis included only male specimens because females are unknown for *Thyroptera wynneae*. We conducted a principal component analysis of measurements of 21 specimens of *Thyroptera*, including 3 each of *T. wynneae*, *T. devivoi*, and *T. discifera*, 2 of *T. lavalii*, and 10 of *T. tricolor* (appendix 1). The first three principal components accounted for 88.5% of the total variance in the log-transformed measurements of this material (table 3). PC 1 accounted for the highest percentage (70.1%), and this vector has uniformly positive loadings, suggesting that it is a size factor (with a notably high loading for forearm length). Correspondingly, specimens of small-bodied species (*T. wynneae* and *T. discifera*) have lower scores along this axis, large-bodied *T. lavalii* has high scores, and medium-sized species (*T. tricolor* and *T. devivoi*) have intermediate values (fig. 7). Although *T. wynneae* and *T. discifera* have overlapping scores on PC2 (fig. 7A), these species are resolved as distinct clusters on PC3 (fig. 7B). Factor loadings on PC3 suggest that this separation is primarily attributable to taxonomic differences in forearm length and width at M3.

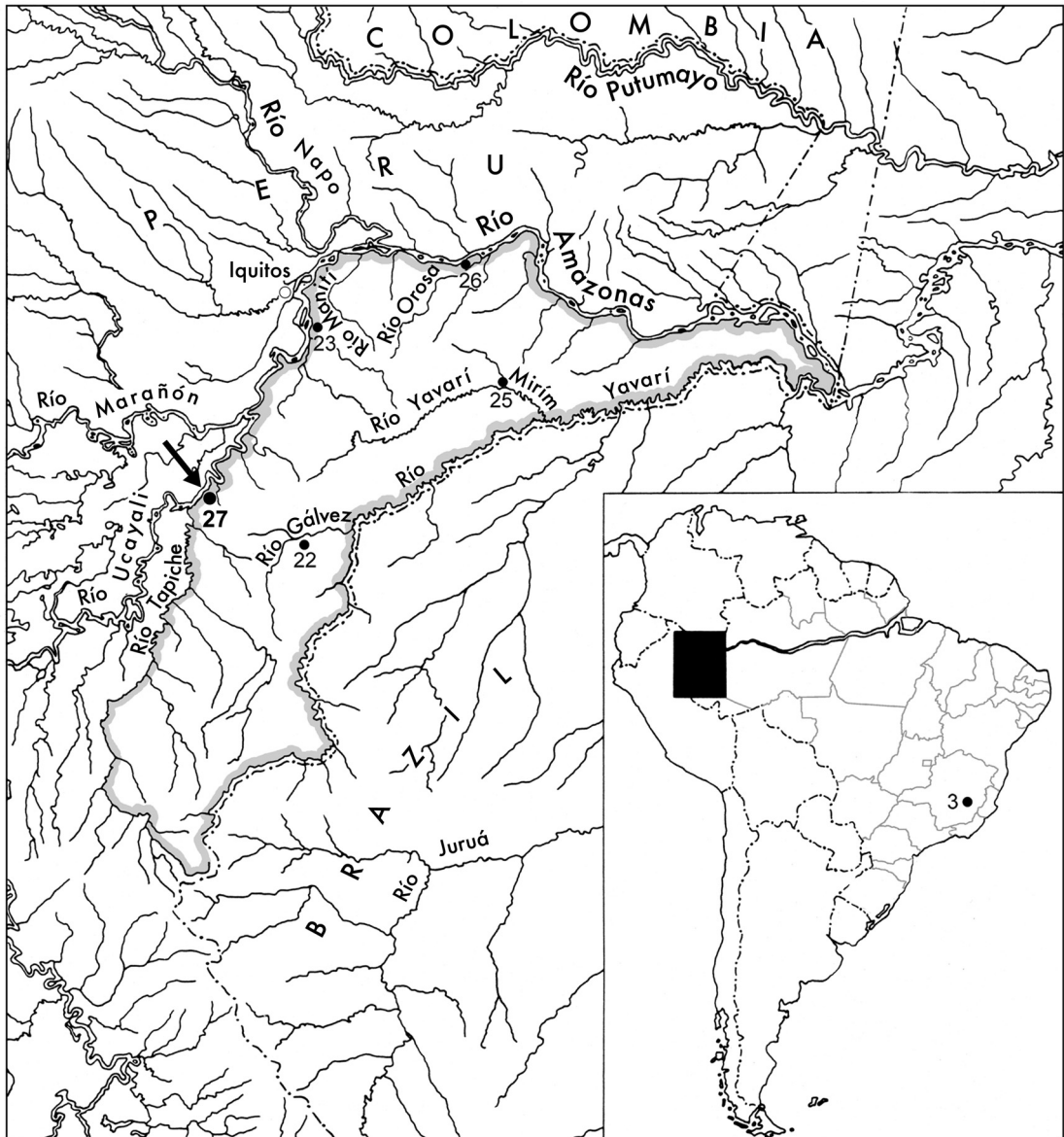


FIG. 3. The Yavari-Ucayali interfluvial region (boundaries highlighted in grey) showing the type locality of *Thyroptera wynneae* (arrow) and adjacent localities where other thyropterid species have been collected. The inset shows where the paratypes were collected in southeastern Brazil. Numbers are keyed to entries in the gazetteer (appendix 2).

NATURAL HISTORY: The Centro de Investigaciones Jenaro Herrera is a forestry research station located about 2.5 km inland from the right bank of the Río Ucayali in the Peruvian department of Loreto. The station is on a terrace above the river floodplain and is not subject to annual flooding by river water. The local vegetation consists of primary and secondary lowland rainforest (“high terrace forest” sensu López-Parodi and Freitas, 1990) on well-drained soils, but a distinctive riparian formation (“creek forest” sensu López-Parodi and Freitas, 1990;

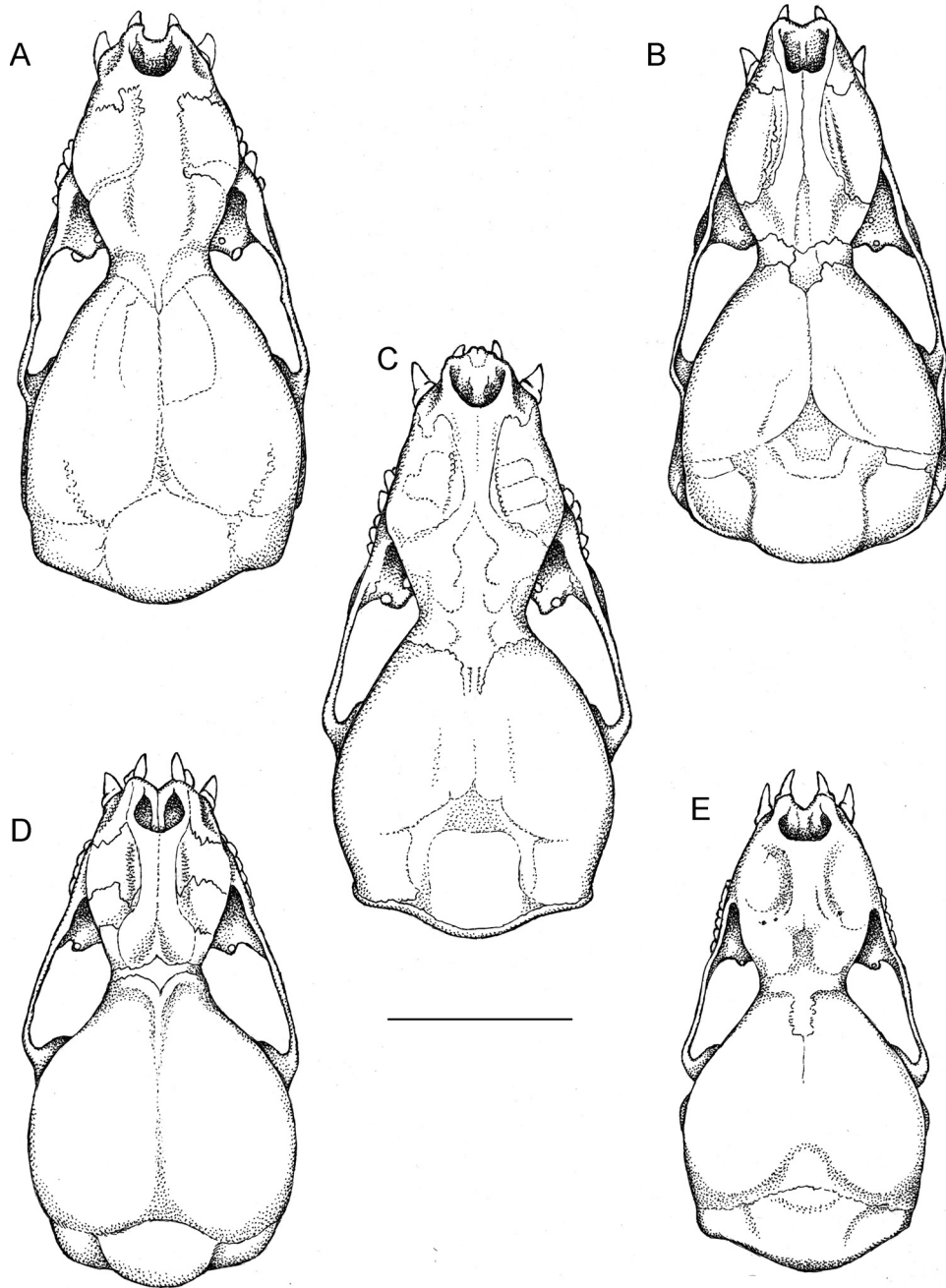


FIG. 4. Dorsal views of the skulls of **A**, *Thyroptera devivoi* (ROM 35588 ♂); **B**, *Thyroptera discifera* (AMNH 16686 ♀); **C**, *Thyroptera lavalii* (ROM 104026 ♀); **D**, *Thyroptera tricolor* (AMNH 273160 ♀); **E**, *Thyroptera wynneae* (CEBIOMAS 237 ♂, holotype). Scale bar = 5 mm.

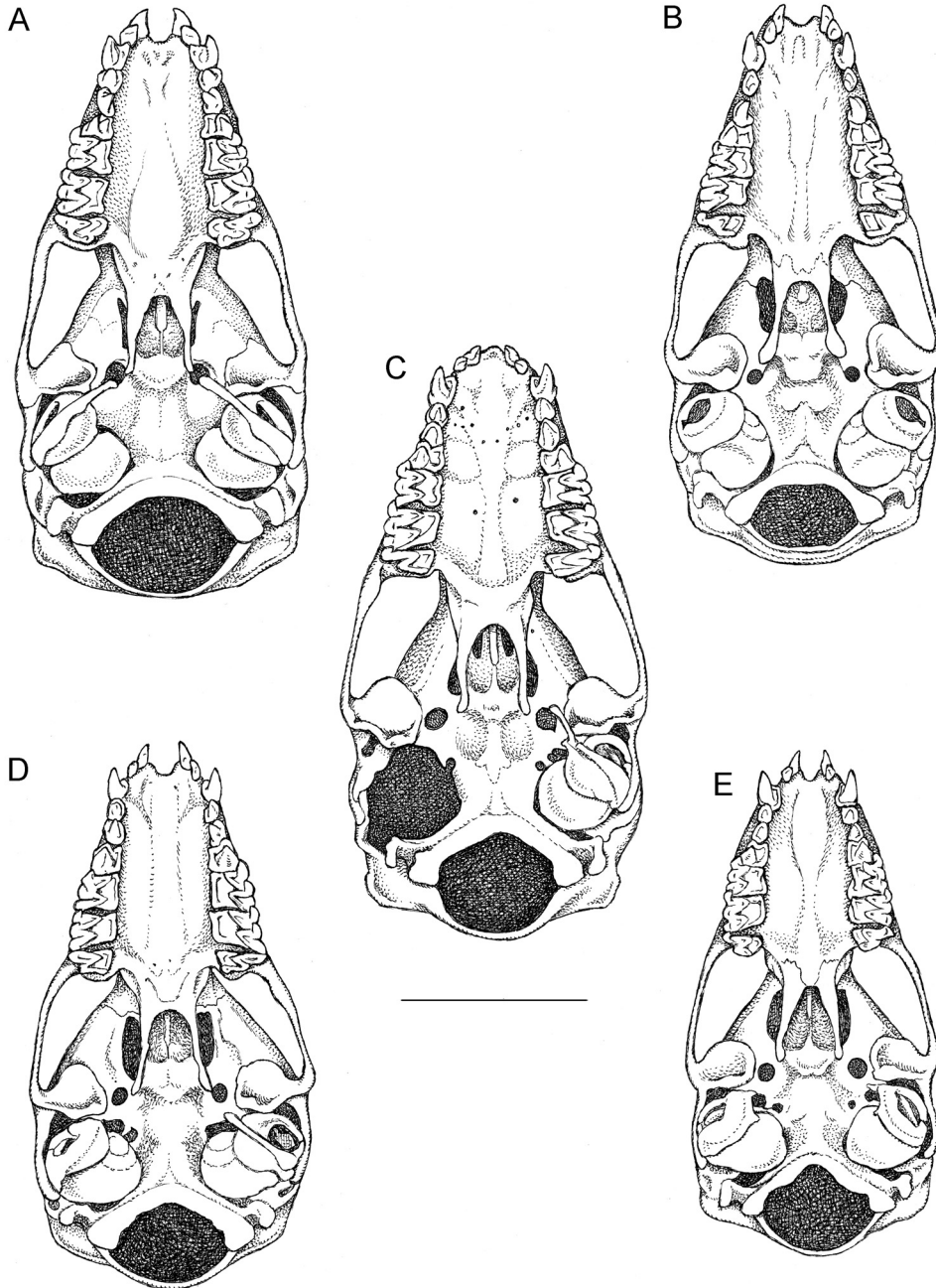


FIG. 5. Ventral views of the skulls of **A**, *Thyroptera devivoi* (ROM 35588 ♂); **B**, *Thyroptera discifera* (AMNH 16686 ♀); **C**, *Thyroptera lavalii* (ROM 104026 ♀); **D**, *Thyroptera tricolor* (AMNH 273160 ♀); **E**, *Thyroptera wynneae* (CEBIOMAS 237 ♂, holotype). Scale bar = 5 mm.

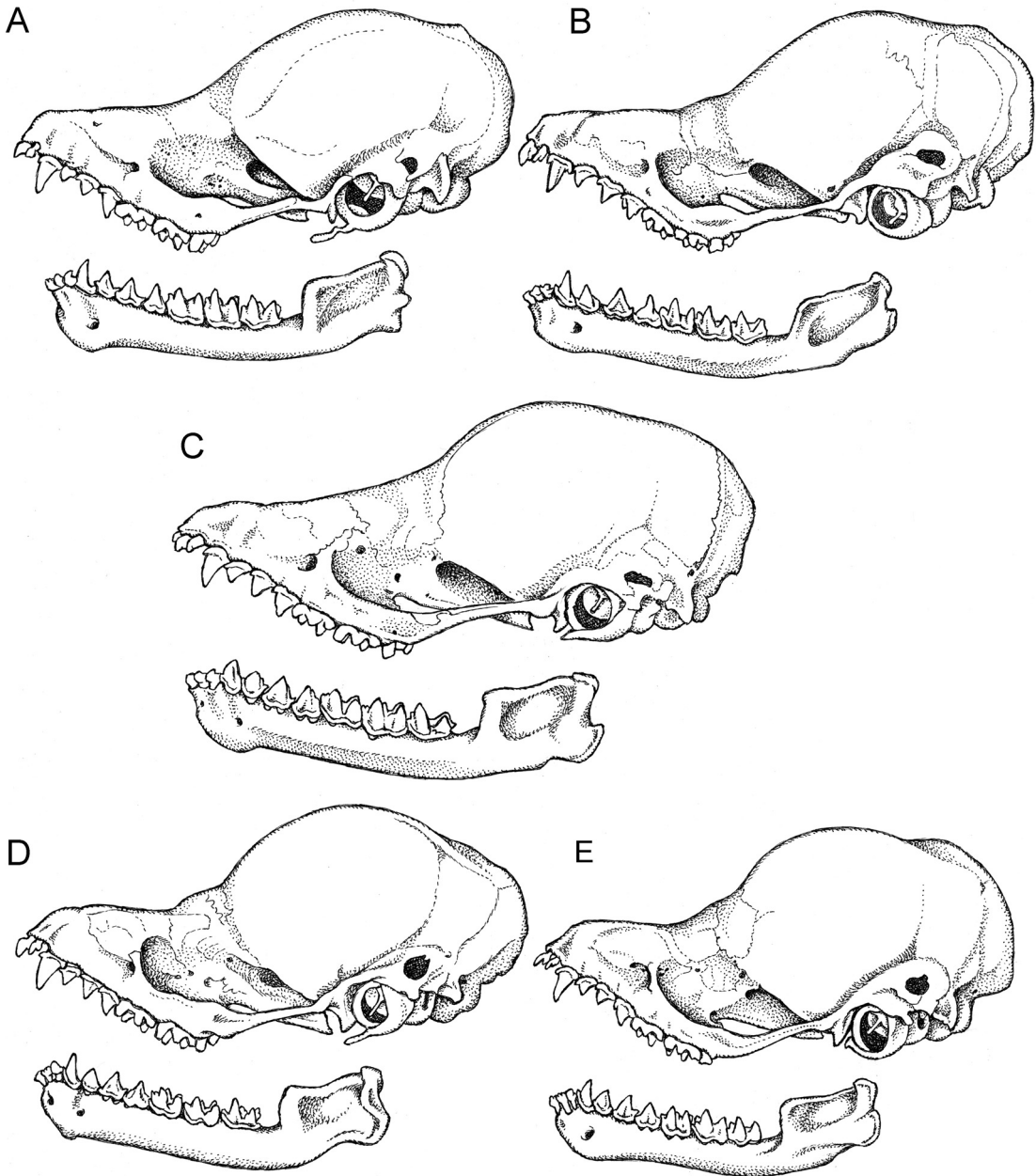


FIG. 6. Lateral views of the skulls and lower jaw of **A**, *Thyroptera devivoi* (ROM 35588 ♂); **B**, *Thyroptera discifera* (AMNH 16686 ♀); **C**, *Thyroptera lavalii* (ROM 104026 ♀); **D**, *Thyroptera tricolor* (AMNH 273160 ♀); **E**, *Thyroptera wynneae* (CEBIOMAS 237 ♂, holotype). Scale bar = 5 mm.

“bosque de quebrada” sensu Kahn and Mejia, 1990) occurs along streams, and palm swamps dominated by *Mauritia flexuosa* (locally known as “aguajales”) occupy depressions with permanently waterlogged soils. Small plantations (of yuca, pineapple, etc.) are also scattered

TABLE 3. Factor Loadings for the First Three Factors Extracted from a Principal Component (PC) Analysis of Nine Variables for All Species of *Thyroptera*.

Measurements	PC 1	PC 2	PC 3
FA	0.476	-0.421	0.482
GLS	0.377	0.345	-0.031
CIL	0.265	0.247	-0.295
BB	0.237	-0.509	-0.046
PB	0.235	-0.401	-0.618
MTRL	0.384	0.048	-0.123
M3-M3	0.382	0.162	0.433
LMA	0.283	0.435	-0.068
MANDL	0.275	0.062	-0.299
Proportion of variation	70.1%	13.0%	5.4%

throughout the area. The holotype of *Thyroptera wynneae* was found roosting with another individual (which escaped capture) in the late morning (about 11:00 hrs). Both bats were concealed within a dead *Cecropia* leaf that was hanging from understory vegetation by its petiole about 2 m above the ground in secondary forest next to a trail about 50 m from the main buildings of the biological station (fig. 8).

The Parque Estadual do Rio Doce protects some 36,000 hectares of semideciduous forest, most of which is thought to be secondary growth (Lopes et al., 2002). The park includes hills and low mountains (Stallings, 1988; Lopes et al., 2002), but Campolina is located in primary forest with tall (20–30 m) trees and a relatively open understory on level terrain. Both paratypes were captured in ground-level mist nets.

ETYMOLOGY: We are pleased to name this species in honor of Patricia J. Wynne (fig. 9), longtime artist-in-residence in the AMNH Department of Mammalogy, who has drawn mammals for scientific and educational publications for over 40 years. Exceptional for clarity, elegant rendering, and meticulous attention to relevant detail, Patricia's work is immediately recognizable and inimitable (e.g., figs. 3–6).

DISCUSSION

The discovery of a new species of *Thyroptera* at Jenaro Herrera was unexpected because two congeners (*T. discifera* and *T. lavalis*; Solari et al., 2004) were already known to occur there. Furthermore this locality had previously been sampled intensively for bats by Ascorra et al. (1993), who recorded almost 2500 captures in the course of their multiyear inventory study. Additionally, Jenaro Herrera (fig. 3: locality 27) lies within the Yavarí-Ucayali interfluvium, where a fourth species (*T. tricolor*) has been collected at Nuevo San Juan (fig. 3: locality 22). Although Jenaro Herrera and Nuevo San Juan are almost 70 km apart, they are otherwise separated only by the Río Gálvez, a small river that dwindles to a narrow stream in its adjacent headwater region (<300 m above sea level) and is unlikely to be an effective faunal barrier. Therefore, it seems plausible that as many as four species of *Thyroptera* might be sympatric at some sites within this interfluvial region.

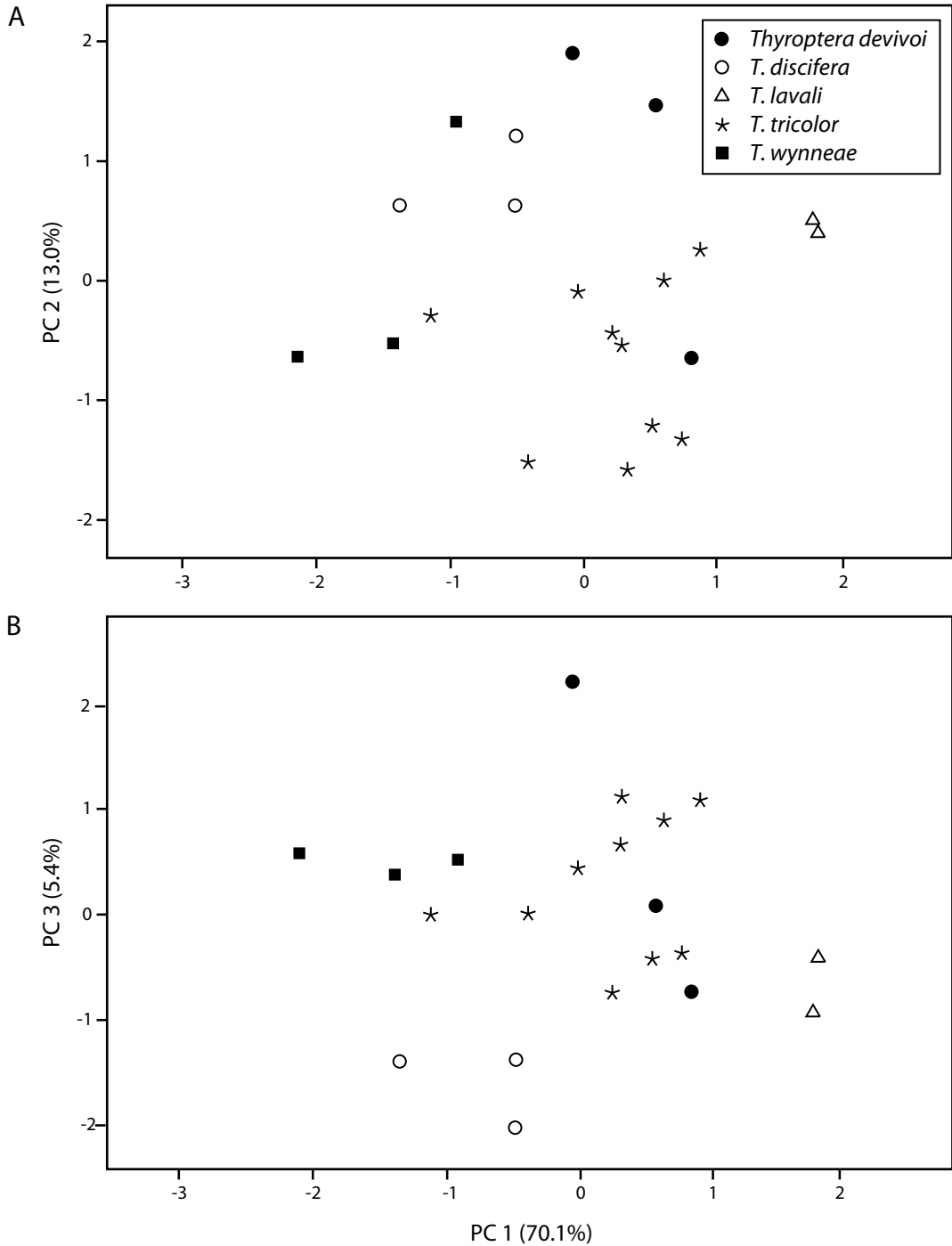


FIG. 7. Results of principal components analysis, illustrating the dispersion of specimen scores for male *Thyroptera devivoi* (filled circles), *Thyroptera discifera* (open circles), *Thyroptera lavalii* (open triangles), *Thyroptera tricolor* (asterisk), and *Thyroptera wynneae* (filled squares). See text for explanation and table 3 for factor loadings and other results.

TABLE 4. Records of Sympatry among Species of *Thyroptera*.

	<i>devivoi</i>	<i>discifera</i>	<i>lavori</i>	<i>tricolor</i>	<i>wynneae</i>
<i>devivoi</i>	—				
<i>discifera</i>	?	—			
<i>lavori</i>	?	sympatric ^a	—		
<i>tricolor</i>	sympatric ^b	sympatric ^c	sympatric ^d	—	
<i>wynneae</i>	?	sympatric ^c	sympatric ^e	?	—

^a At Jenaro Herrera, Loreto, Peru (Solari et al., 2004).

^b In the Kanuku Mountain region of southwestern Guyana (Parker et al., 1993). The two specimens of *T. discifera* originally reported from this area by Parker et al. (1993) were reidentified as *T. devivoi* by Gregorin et al. (2006).

^c At La Selva, Costa Rica (Tschapka et al., 2000); Barro Colorado Island, Panama (Voss and Emmons, 1996); near Manaus, Brazil (Sampaio et al., 2003); and three other sites listed by Pine (1993).

^d At four sites in Ecuador, Peru, and Brazil (Solari et al., 2004).

^e At Jenaro Herrera, Loreto, Peru (this report).

Such diversity poses a challenge for bat inventory research, because disk-winged bats are hard to capture in mist nets, even where they are known to be locally common (Vonhof and Fenton, 2004). For example, Simmons and Voss (1998) captured 37 specimens of *T. tricolor* by searching for roosts, but the same researchers captured only four individuals of this species in 112 nights of mist-netting at their French Guianan study site. If other congeneric species usually roost in less accessible situations than *T. tricolor* (e.g., in the canopy or subcanopy; Pine, 1993), then it may seldom be possible to know whether local thyropterid diversity has been completely inventoried. The recent discovery of *T. discifera* at La Selva, Costa Rica (Tschapka et al., 2000), one of the most thoroughly inventoried rainforest sites anywhere in the New World tropics (Voss and Emmons, 1996: appendix 2) underscores the elusive nature of these bats.

Given the broadly overlapping geographic distributions of thyropterids, four or more species might be sympatric throughout much of cis-Andean South America, despite the fact that only one or two are known to cooccur at sites other than Jenaro Herrera. To date, sympatry has been documented for six of the 10 possible pairwise combinations of *Thyroptera* species (table 4). The obvious ecological outlier in this context is *T. devivoi*, which occupies edaphically moist gallery formations in savanna landscapes (Gregorin et al., 2006). Among the four species known to inhabit continuous tracts of climatically moist (evergreen or semideciduous) forest, five of the six possible combinations of pairwise sympatry have been observed. What ecological differences among these species might facilitate such coexistence? Divergent roosting behavior is one possibility.

Well-developed adhesive disks on the wing and foot occur in only two families of bats: the Neotropical family Thyropteridae and the Old World family Myzopodidae, which is endemic to Madagascar (Goodman et al., 2007; Wilson, 2008).³ Such disks allow these bats to adhere to smooth surfaces when roosting, and their occurrence in two distantly related families is thought to represent an extraordinary example of convergent evolution (Eisenberg, 1981; Riskin and Racey, 2010; Schliemann and Goodman, 2011; Schliemann and Maas, 1978). However, the

³ Certain other foliage-roosting bats have adhesive pads rather than well-developed disks (Thewissen and Etnier, 1995).



FIG. 8. Roost of *Thyroptera wynneae* in secondary growth at the Centro de Investigaciones Jenaro Herrera, Loreto, Peru. Two bats occupied the dark interior of this dead *Cecropia* leaf (arrows), which was hanging in understory vegetation by its petiole about 2 m above the ground. One specimen was captured in a butterfly net placed underneath the leaf, but the other bat escaped. *Cecropia* (Cecropiaceae) is a speciose genus of trees commonly found in secondary vegetation throughout the Neotropics, where hanging dead leaves like this one are abundant in the subcanopy and understory.

mechanisms of substrate-disk adhesion used in each case are different: whereas thyropterid disks use suction to adhere to surfaces, myzopodid disks operate by wet adhesion (Goodman et al., 2007; Riskin and Fenton, 2001; Riskin and Racey, 2010; Schliemann and Goodman, 2011). Although bats in both families are said to use large, furled leaves for roost sites (Kunz and Lumsden, 2003), most of what is actually known about thyropterid roosts is derived from observations of a single species, *Thyroptera tricolor*.

By far the most commonly collected thyropterid, *Thyroptera tricolor* has often been reported as roosting in the half-unrolled new leaves of large understory monocots such as *Heliconia* (Heliconiaceae), *Musa* (Musaceae), *Calathea* (Marantaceae), and *Phenakospermum* (Strelitziaceae). In general, leaves used as roosts by *T. tricolor* form upright, tubular (or conical) shelters with openings 40–100 mm in diameter; they are located <4 m above the ground; and they are not in direct contact with other vegetation (Goodwin and Greenhall, 1961; Wimsatt and Villar., 1970; Findley and Wilson, 1974; Simmons and Voss, 1998; Vonhof and Fenton, 2004). Recently, Chaverri and Gillam (2013) reported that besides shelter, *T. tricolor* uses the furled leaves as acoustic horns that amplify incoming and outgoing social calls among group members. Such shelters are ephemeral because unfurling new leaves soon lose the small-diameter



FIG. 9. Patricia J. Wynne at her microscope in the AMNH Department of Mammalogy. Patricia's first mammalogical illustration appeared almost 40 years ago (in Hooper, 1975), and she has lost track of how many she has drawn since then. In addition to her technical work for museum researchers, Patricia has illustrated museum exhibition labels, numerous educational publications, and dozens of popular science books. She is now busier than ever in semiretirement. Photo: Denis Finnin.

tubular/conical form preferred by bats; therefore, colonies of *T. tricolor* must change roosts every night and seem to favor habitats with dense concentrations of suitable host plants (Findley and Wilson, 1974; Vonhof and Fenton, 2004; Chaverri and Kunz, 2011). Because the ventral surfaces of roosting bats are pressed against the roosting substrate, and because young leaves are paler green than mature leaves (fig. 10), the whitish ventral coloration of *T. tricolor* might be an adaptation for roosting in translucent shelters, where dark ventral fur might often betray the presence of resident bats to visually oriented predators.

To the best of our knowledge, no other *Thyroptera* species has ever been collected in shelters similar to those normally occupied by *T. tricolor*, and from this fact alone it may be supposed that they use different diurnal refugia. Apparently, only three day roosts of *T. discifera* have been described, all of them under (Robinson and Lyon, 1901) or inside (Torres et al., 1988) dead banana leaves. Dead banana leaves are brown, opaque, and hang suspended from collapsed petioles, so dead-leaf roosts are dark and open downward, quite unlike the shelters normally occupied by *T. tricolor*. The only described roost of *T. devivoi* was characterized by



FIG. 10. Roost of *Thyroptera tricolor* in the half-unrolled new leaf of a small *Heliconia* in primary forest at Paracou, French Guiana. The adhesive disks of the roosting bats are visible as dark spots through the translucent tissue of the leaf. The bats themselves (an adult male and three adult females) form a dark mass within their tubular shelter (arrow).

the collector as “under an eaté palm leaf” (Gregorin et al., 2006: 239),⁴ and one specimen of *T. lavalii* is also thought to have also been collected from a palm (Solari et al., 1999). Apparently, these five observations, together with our discovery of *T. wynneae* roosting in a dead *Cecropia* leaf, comprise all that is known of the roosting habits of other species of *Thyroptera*.

If populations of disk-winged bats are limited by roost availability (Findley and Wilson, 1974; but see Vonhof and Fenton, 2004), then there may have been strong selection for divergent roosting habits in the course of thyropterid phylogeny, possibly resulting in species that routinely occupy dead leaves or palm fronds.⁵ Morphological products of such selection might include taxonomic differences in size, ventral pelage coloration, and disk morphology. Smaller bats, for example, can probably occupy smaller shelters (e.g., *Cecropia* leaves) than larger bats, bats with dark ventral fur might inhabit darker refugia (e.g., dead or opaque-green leaves) than pale-ventered bats, and bats with oval adhesive disks might be better equipped to roost in leaves (such as palm fronds) with vanes divided by well-developed ribs than bats with rounded disks (if these routinely use smoother leaves as shelters). In the current absence of reliable information about the roosting habits of most *Thyroptera* species, these are mere conjectures, but they could be tested by actively searching for different kinds of roosts in areas where multiple species could be expected to occur.

Interestingly, not all of the diurnal shelters known to be used by *Thyroptera* afford substrates suitable for disk adhesion. In particular, the finely corrugated surface of dried *Cecropia* leaves seem unsuitable for suction-based attachment. Instead, bats inhabiting these (and perhaps other) rough-surfaced shelters may use their claws instead (Riskin and Fenton, 2001), and in downward-opening roosts it is possible that they hang head-down (like other bats), rather than the heads-up posture normally observed in *T. tricolor*.

Reconstructing the evolutionary history of roosting habits among disk-winged bats will obviously require much more information about the behavior of extant species, as well as knowledge about their phylogenetic relationships. In particular, dated phylogenies will be crucial for correlating relevant character transformations with historical events in the evolution of Neotropical plant communities, and the thyropterid fossil record is obviously important in this context. Although fossil thyropterids are known from the Miocene of South America, they are poorly preserved and taxonomically problematic. Czaplewski (1997) described fossils from the Miocene La Venta deposits in Colombia as a new species, *Thyroptera robusta*, but he subsequently synonymized *robusta* with *lavalii* (Czaplewski, 1996; Czaplewski et al., 2003).⁶ The La Venta material currently referred to *T. lavalii* consists only of isolated fragments: a broken dentary with m1 and m2; another dentary fragment preserving only the talonid of m3; two

⁴ The collector was probably referring to the swamp palm *Mauritia flexuosa*, locally known (in Guyana) as *ité* (Henderson et al., 1995).

⁵ Interestingly, although *Thyroptera tricolor* usually occupies upright-tubular or -conical living leaves, roosts of this species are occasionally found elsewhere. For example, colonies of *T. tricolor* have sometimes been reported roosting in pendant dead leaves of *Heliconia* (Goodwin and Greenhall, 1961) and *Phenakospermum* (Simmons and Voss, 1998), and individual bats are sometimes found roosting on the underside of unfurled leaves (Vonhof and Fenton, 2004). Such behavioral variability within species, if heritable, might have facilitated the evolution of taxonomic differences in roosting habits.

⁶ See Wilson (2008: 395) for relevant comments on publication dates.

upper canines, one lacking enamel; an upper M1 and M2; and fragments of an upper and lower molar (Czaplewski, 1996, 1997; Czaplewski et al., 2003). Although we agree that these fossil fragments may not be distinguishable from recent material of *T. lavalii*, in our opinion they simply indicate that a *lavalii*-sized thyropterid existed in the Miocene. Czaplewski (1997: 420) also described from La Venta a series of isolated teeth, probably from one skull, that he referred to “*Thyroptera* cf. *T. tricolor*.” Noting that differences between these teeth and those of *tricolor* were minor and might not exceed the expected limits of individual variation in *tricolor*, Czaplewski (1997: 422) concluded:

Although with more and better specimens it may eventually be determined that these teeth represent an undescribed species of *Thyroptera*, I cannot find sufficient reason to name a new species based on the fossils, despite the fact that they are separated by some 12.5 million years from their living relatives. These specimens indicate a significant period of evolutionary stasis for disk-winged bats consistent with their present lack of diversity.

Two additional extant species of *Thyroptera* have since been discovered, and our review indicates that few dental characters distinguish the five living species from one another. We suggest that the Miocene fossils described by Czaplewski (1996, 1997) and Czaplewski et al. (2003) probably represent taxa related to, but not conspecific with, extant species. More complete fossils and more comprehensive analyses will be needed before the relationships of Miocene thyropterids to extant lineages can be determined. Rather than providing evidence that *T. lavalii* and *T. tricolor* diverged from *T. discifera* at least 12 Mya (as suggested by Solari et al., 2004), we would argue that the most we can say based on the fossil record is that the genus *Thyroptera* was clearly distinct by about 12.5 Mya.

Molecular-clock dating and biogeographic analyses indicate that the lineage leading to *Thyroptera* diverged from that of other noctilionoids approximately 36–45 Mya, and that this divergence occurred in the Neotropics (Miller-Butterworth et al., 2007). Therefore, thyropterids were probably present in South America for approximately 23 to 33 million years before the La Venta fauna existed. Given that we do not know the relationships of these Miocene fossils to extant species, it is premature to speculate about the timing of the origin of the unique anatomical specializations and unusual roosting habits seen in modern members of this group.

KEY TO THE SPECIES OF *THYROPTERA*

1. Disk at base of thumb clearly oval in outline (not round); ventral pelage bicolored or tricolored; both cusps of the second upper incisor perpendicularly arranged relative to the long axis of the toothrow.....2
- 1'. Disk at base of thumb nearly circular in outline; ventral pelage unicolored; both cusps on the second upper incisor obliquely arranged relative to the long axis of the tooth row.....4

2. Forearm ≥ 35.0 mm; GLS ≥ 14.0 mm; ventral pelage bicolored; proximal portion of forearm sparsely haired; rostrum of equal length or longer than the braincase; accessory cusps on the third lower incisor absent or only faintly developed.....3
- 2'. Forearm ≤ 34.5 mm; GLS ≤ 13.5 mm; ventral pelage tricolored; proximal portion of the forearm densely haired; rostrum considerably shorter than the braincase; accessory cusps well developed on the third lower incisor.....*Thyroptera wynneae*
3. Ventral pelage distinctly frosted, individual hairs dark brown to blackish at the base with grayish-brown to whitish tips; calcar lacks lappets or only one faintly developed lappet is present; GLS ≤ 15.1 mm and ZB ≤ 7.7 mm.....*Thyroptera devivoi*
- 3'. Ventral pelage bicolored, not distinctly frosted; calcar has one well-developed lappet that project posterolaterally from the shaft of the calcar; GLS ≥ 15.2 mm and ZB ≥ 8.0 mm...
.....*Thyroptera lavalii*
4. Ventral pelage unicolored white or pale gray; proximal portion of forearm sparsely haired; large foramen ovale (0.50–0.65 mm).....*Thyroptera tricolor*
- 4'. Ventral pelage unicolored yellowish-brown (not white); proximal portion of forearm densely haired; small foramen ovale (< 0.45 mm).....*Thyroptera discifera*

ACKNOWLEDGMENTS

We thank all the participants of the “International Bat Course 2012” organized by CEBIO (Centro de Ecología y Biodiversidad) for their camaraderie at Jenaro Herrera, and we thank course organizer Erika Paliza for inviting P.M.V. to attend this event and for obtaining the necessary permits that enabled P.M.V. and R.S.V. to collect bats there after the course ended. The following curators and collection staff graciously provided access to specimens under their care: Erika Paliza (Centro de Ecología y Biodiversidad, Lima), Bruce D. Patterson and John Phelps (Field Museum of Natural History, Chicago), Víctor Pacheco (Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima), and Burton Lim (Royal Ontario Museum, Toronto). We are also grateful to Burton Lim for his live photographs of *Thyroptera wynneae* and to Wendy Calderón for assistance in the field. Brock Fenton and Burton Lim provided helpful comments on the submitted draft of this manuscript. Partial funding for R.G.’s fieldwork in Brazil was provided by the Fundação de Amparo à Pesquisa do Estado de Minas Gerais.

REFERENCES

- Ascorra, C.F., D.L. Gorchov, and F. Cornejo. 1993. The bats from Jenaro Herrera, Loreto, Peru. *Mammalia* 57: 533–552.
- Chaverri, G., and E.H. Gillam. 2013. Sound amplification by means of a horn-like roosting structure in Spix’s disc-winged bat. *Proceedings of the Royal Society of London Series B* 280: 20132362.
- Chaverri, G., and T.H. Kunz. 2011. Response of a specialist bat to the loss of a critical resource. *PLoS ONE* 6 (12): e28821. [doi:10.1371/journal.pone.0028821]
- Czaplewski, N.J. 1996. *Thyroptera robusta* Czaplewski, 1996, is a junior synonym of *Thyroptera lavalii* Pine, 1993 (Mammalia: Chiroptera). *Mammalia* 60: 153–156.

- Czaplewski, N.J. 1997. Chiroptera. In R.F. Kay, R.H. Madden, R.L. Cifelli, and J.J. Flynn (editors), Vertebrate paleontology in the Neotropics: The Miocene fauna of La Venta, Colombia, 410–430. Washington D.C.: Smithsonian Institution Press.
- Czaplewski, N.J., M. Takai, T. Naeher, N. Shigehara, and T. Setoguchi. 2003. Additional bats from the middle Miocene La Venta fauna of Colombia. *Revista de la Academia Colombiana de Ciencias* 27: 263–282.
- Dávalos, L.M., P.M. Velazco, O.M. Warsi, P.D. Smits, and N.B. Simmons. In press. Integrating incomplete fossils by isolating conflictive signal in saturated and non-independent morphological characters. *Systematic Biology*.
- Eisenberg, J.F. 1981. The mammalian radiations: an analysis of trends in evolution, adaptation, and behavior. Chicago: University of Chicago Press.
- Findley, J.S., and D.E. Wilson. 1974. Observations on the Neotropical disk-winged bat, *Thyroptera tricolor* Spix. *Journal of Mammalogy* 55: 562–571.
- Goodman, S.M., F. Rakotondraparany, and A. Kofoky. 2007. The description of a new species of *Myzopoda* (Myzopodidae: Chiroptera) from western Madagascar. *Mammalian Biology* 72: 65–81.
- Goodwin, G., and A.M. Greenhall. 1961. A review of the bats of Trinidad and Tobago: descriptions, rabies infection, and ecology. *Bulletin of the American Museum of Natural History* 122: 187–302.
- Gregorin, R., E. Gonçalves, B.K. Lim, and M.D. Engstrom. 2006. New species of disk-winged bat *Thyroptera* and range extension for *T. discifera*. *Journal of Mammalogy* 87: 238–246.
- Hammer, Ø., D.A.T. Harper, and P.D. Ryan. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4: 1–9.
- Henderson, A., G. Galeano, and R. Bernal. 1995. Field guide to the palms of the Americas. Princeton, NJ: Princeton University Press.
- Hooper, E.T. 1975. Orbital region and size of eye in species of *Scotinomys* (Rodentia). *Journal of Mammalogy* 56: 667–671.
- Kahn, F., and K. Mejia. 1990. Palm communities in wetland forest ecosystems of Peruvian Amazonia. *Forest Ecology and Management* 33/44: 169–179.
- Kunz, T.H., and L.F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. In T.H. Kunz and M.B. Fenton (editors), *Bat Ecology*: 3–89. Chicago: University of Chicago Press.
- Lopes, W.P., A.F. da Silva, A.L. de Souza, and J.A.A.M. Neto. 2002. Estrutura fitossociológica de um trecho de vegetação arbórea no Parque Estadual do Rio Doce, Minas Gerais, Brasil. *Acta Botanica Brasílica* 16: 443–456.
- López-Parodi, J., and D. Freitas. 1990. Geographical aspects of forested wetlands in the lower Ucayali, Peruvian Amazon. *Forest Ecology and Management* 33/34: 157–168.
- Miller-Butterworth, C.M., et al. 2007. A family matter: conclusive resolution of the taxonomic position of the long-fingered bats, *Miniapterus*. *Molecular Biology and Evolution* 24: 1553–1561.
- O’Leary, M.A., et al. 2013. The placental mammal ancestor and the Post-K-Pg radiation of placentals. *Science* 339: 662–668.
- Parker, T.A., et al. 1993. A biological assessment of the Kanuku Mountain region of southwestern Guyana (RAP Working Papers 5). Washington, DC: Conservation International.
- Pine, R.H. 1993. A new species of *Thyroptera* Spix (Mammalia: Chiroptera: Thyropteridae) from the Amazon Basin of northeastern Perú. *Mammalia* 57: 213–225.
- Riskin, D.K., and M.B. Fenton. 2001. Sticking ability in Spix’s disk-winged bat, *Thyroptera tricolor* (Microchiroptera: Thyropteridae). *Canadian Journal of Zoology* 79: 2261–2267.
- Riskin, D.K., and P.A. Racey. 2010. How do sucker-footed bats hold on, and why do they roost head-up? *Biological Journal of the Linnean Society* 99: 233–240.

- Robinson, W., and M.W. Lyon. 1901. An annotated list of mammals collected in the vicinity of La Guaira, Venezuela. *Proceedings of the United States National Museum* 24: 135–162.
- Sampaio, E.M., E.K.V. Kalko, E. Bernard, B. Rodríguez-Herrera, and C.O. Handley, Jr. 2003. A biodiversity assessment of bats (Chiroptera) in a tropical lowland rainforest of central Amazonia, including methodological and conservation considerations. *Studies on Neotropical Fauna and Environment* 38: 17–31.
- Schliemann, H. 1970. Bau und Funktion der Haftorgane von *Thyroptera* und *Myzopoda* (Vespertilionoidea, Microchiroptera, Mammalia). *Zeitschrift für wissenschaftliche Zoologie* 181: 353–400.
- Schliemann, H. 1971. Die Haftorgane von *Thyroptera* und *Myzopoda* (Microchiroptera, Mammalia)—Gedanken zu ihrer Entstehung als Parallelbildungen. *Journal of Zoological Systematics and Evolutionary Research* 9: 61–80.
- Schliemann, H., and S.M. Goodman. 2011. A new study on the structure and function of the adhesive organs of the Old World sucker-footed bat (*Myzopoda*: Myzopodidae) of Madagascar. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg N.F.* 46: 313–330.
- Schliemann, H., and B. Maas. 1978. *Myzopoda aurita*. *Mammalian Species* 116: 1–2.
- Simmons, N.B. 1998. A reappraisal of interfamilial relationships of bats. In T.H. Kunz and P.A. Racey (editors), *Bat biology and conservation*: 3–26. Washington, DC: Smithsonian Institution Press.
- Simmons, N.B., and R.S. Voss. 1998. The mammals of Paracou, French Guiana: a Neotropical lowland rainforest fauna. Part 1. Bats. *Bulletin of the American Museum of Natural History* 237: 1–219.
- Solari, S., V. Pacheco, and E. Vivar. 1999. Nuevos registros distribucionales de murciélagos peruanos. *Revista Peruana de Biología* 6: 152–159.
- Solari, S., R.A. Van Den Bussche, S.R. Hooper, and B.D. Patterson. 2004. Geographic distribution, ecology, and phylogenetic affinities of *Thyroptera lavalii* Pine 1993. *Acta Chiropterologica* 6: 293–302.
- Stallings, J.R. 1988. Small mammal inventories in an eastern Brazilian park. *Bulletin of the Florida State Museum (Biological Sciences)* 34: 159–200.
- Tavares, V.C., F.A. Perini, and J.A. Lombardi. 2007. The bat communities (Chiroptera) of the Parque Estadual do Rio Doce, a large remnant of Atlantic Forest in southeastern Brazil. *Lundiana* 8: 35–47.
- Thewissen, J.G.M., and S.A. Etnier. 1995. Adhesive devices on the thumb of vespertilionoid bats (Chiroptera). *Journal of Mammalogy* 76: 925–936.
- Torres, M.P., T. Rosas, and S.I. Tiranti. 1988. *Thyroptera discifera* (Chiroptera: Thyropteridae) in Bolivia. *Journal of Mammalogy* 69: 434–435.
- Tschapka, M., A.P. Brooke, and L.T. Wasserthal. 2000. *Thyroptera discifera* (Chiroptera: Thyropteridae): a new record for Costa Rica and observations on echolocation. *Zeitschrift für Säugetierkunde* 65: 193–198.
- Vonhof, M.J., and M.B. Fenton. 2004. Roost availability and population size of *Thyroptera tricolor*, a leaf-roosting bat, in north-eastern Costa Rica. *Journal of Tropical Ecology* 20: 291–305.
- Voss, R.S., and L.H. Emmons. 1996. Mammalian diversity in Neotropical lowland rainforests: a preliminary assessment. *Bulletin of the American Museum of Natural History* 230: 1–115.
- Wilson, D.E. 2008 [“2007”]. Family Thyropteridae Miller 1907. In A.L. Gardner (editor), *Mammals of South America*, vol. 1: marsupials, xenarthrans, shrews, and bats: 392–396. Chicago: University of Chicago Press.
- Wimsatt, W.A., and B. Villa-R. 1970. Locomotor adaptations in the disc-winged bat *Thyroptera tricolor*. I. Functional organization of the adhesive discs. *American Journal of Anatomy* 129: 89–119.
- Zook, J.M. 2007. Somatosensory adaptations of flying mammals. In J.H. Kaas and L. Krubitzer (editors), *Evolution of nervous systems: a comprehensive reference*. Vol. 3, mammals: 215–226. Boston: Elsevier Academic Press.

APPENDIX 1

SPECIMENS EXAMINED

The following list includes all the specimens used in this study, with their respective localities. See Material and Methods for abbreviations. Coordinates are provided in appendix 2. Specimens used in the morphometric analyses are marked with an asterisk.

Thyoptera devivoi ($N = 3$). BRAZIL—*Piauí*: Estação Ecológica Uruçuí-Una, Bom Jesus (MZUSP 30073*). *Tocantins*: Estação Ecológica Serra Geral do Tocantins (Jalapão) (MZUSP 32345*). GUYANA—*Upper Takutu-Upper Essequibo*: Tamton (ROM 35588*).

Thyoptera discifera ($N = 10$). BRAZIL—*Bahia*: probably near Salvador (MZUSP 16395, 16396). *Pará*: Caxiricatuba (MZUSP 5628); Santarém, Tapajós River, Tauari (AMNH 94549). COLOMBIA—*Córdoba*: Socorré, Upper Río Sinú (FMNH 69509*). *Valle del Cauca*: La Costa, El Tambo (FMNH 140791). ECUADOR—*Pichincha* (AMNH 46687). PERU—*Loreto*: Requena, Jenaro Herrera, Centro de Investigaciones Jenaro Herrera (MUSM 5546*). *Ucayali*: Atalaya, Cumarí (FMNH 46160*). VENEZUELA—*Distrito Federal*: La Guaira, San Julián (AMNH 16686).

Thyoptera laveli ($N = 7$). ECUADOR—*Napo*: Yasuní National Park, 42 km S, 1 km E Pompeya Sur (ROM 104026, 105215). PERU—*Loreto*: Mariscal Ramón Castilla, Río Yavarí Mirím, Quebrada Esperanza (FMNH 89118*, 89120, 89121); Requena, Jenaro Herrera, Centro de Investigaciones Jenaro Herrera (MUSM 5944*).

Thyoptera tricolor ($N = 57$). BRAZIL—*Amapá*: Rio Amapari (MZUSP 16393). *Pará*: Santarém, Tapajós River, Piquiatuba (AMNH 94550*); Abaetetuba (MZUSP 8583–8586); Rio Tocantins, Ihla do Taiuna (AMNH 97129, 97130, 97131*, 97132–97134, 97136, 97137). *Rio de Janeiro*: Angra dos Reis (MZUSP 6585). *São Paulo*: Iguape (MZUSP 5702). COLOMBIA—*Valle del Cauca*: Anchicaya river (AMNH 239084–239086, 239088); Dagua, Cali-Buenaventura highway, near Dagua River (AMNH 239077, 239078*, 239080, 239081*). COSTA RICA—*Puntarenas*: Esparza (FMNH 43980*); Parque Nacional Carara (FMNH 180726). ECUADOR—*Tungurahua*: Palmira (AMNH 67592*). FRENCH GUIANA—*Paracou*, near Sinnamary (AMNH 267216, 267217, 266353*). PERU—*Loreto*: Alto Amazonas, Nuevo San Juan, Gálvez River (AMNH 272761, 273155, 273156, 273157*, 273160, 273161*; MUSM 13262, 13263, 15278–15282); Estación Biológica Isla Muyuy (MUSM 21332); Estirón, Río Ampiyacu (MZUSP 14180, 14181); Mariscal Ramón Castilla, Río Yavarí Mirím, Quebrada Esperanza (FMNH 89117); Maynas, Orosa, Amazon River (AMNH 74022, 74024, 74025). *San Martín*: Moyobamba, Tingana (FMNH 203644). TRINIDAD AND TOBAGO—*Trinidad*: (FMNH 53054); Saint Andrew, Sangre Grande (AMNH 185342); Saint George, Heights of Aripo, Cerro Aripo (AMNH 29693); Saint George, Port of Spain (AMNH 183860). VENEZUELA—*Amazonas*: Río Negro, Muyrapinimo (AMNH 77556*, 77558).

Thyoptera wynneae ($N = 3$). BRAZIL—*Minas Gerais*: Campolina, about 25 km E Marliéria, Parque Estadual do Rio Doce (CMUFLA 694*, 1160*). PERU—*Loreto*: Requena, Jenaro Herrera, Centro de Investigaciones Jenaro Herrera (CEBIOMAS 237*).

APPENDIX 2

GAZETTEER OF COLLECTING LOCALITIES

Below we list all localities from which we personally examined specimens of *Thyroptera*. Names of the largest administrative unit (department, state, etc.) within each country are italicized, and geographic coordinates are provided.

BRAZIL

1. *Amapá*, Rio Amapari (2°00'N, 52°30'W).
2. *Bahia*, probably near Salvador (12°58'S, 38°30'W). See Gregorin et al. (2006) for a discussion of this problematic locality.
3. *Minas Gerais*: Parque Estadual do Rio Doce, Campolina (19°42'S, 42°30'W), about 25 km E Marliéria, Parque Estadual do Rio Doce.
4. *Pará*, Abaetetuba (1°43'S, 48°52'W).
5. *Pará*, Caxiricatuba (2°45'S, 55°02'W).
6. *Pará*, Rio Tocantins, Iha do Taiuna (2°15'S, 49°29'W).
7. *Pará*, Santarém, Tapajós River, Tauari (3°05'S, 55°06'W).
8. *Pará*, Santarém, Tapajós River, Piquiatuba (2°34'S, 54°42'W).
9. *Piauí*, Estação Ecológica Uruçuí-Una, Bom Jesus (8°52'S, 44°57'W).
10. *Rio de Janeiro*, Angra dos Reis (23°00'S, 44°19'W).
11. *São Paulo*, Iguape (24°42'S, 47°33'W).
12. *Tocantins*, Estação Ecológica Serra Geral do Tocantins (Jalapão) (10°33'S, 46°45'W).

COLOMBIA

13. *Córdoba*, Socorré, Upper Río Sinú (7°51'N, 76°17'W).
14. *Valle del Cauca*, Anchicaya river (3°39'N, 76°56'W).
15. *Valle del Cauca*, La Costa, El Tambo (2°36'N, 77°44'W).
16. *Valle del Cauca*, Dagua, Cali-Buenaventura highway, near Dagua River (3°40'N, 76°42'W).

COSTA RICA

17. *Puntarenas*, Esparza (9°59'N, 84°40'W).
18. *Puntarenas*, Parque Nacional Carara (9°47'N, 84°33'W).

ECUADOR

19. *Napo*, Yasuní National Park, 42 km S, 1 km E Pompeya Sur (0°41'S, 76°26'W).
- . “*Pichincha*” (precise locality unknown).
- . *Tungurahua*, Palmira (coordinates unknown).

FRENCH GUIANA

20. Paracou, near Sinnamary (5°17'N, 52°55'W).

GUYANA

21. *Upper Takutu–Upper Essequibo*, Tamton (2°21'N, 59°42'W).

PERU

22. *Loreto*, Alto Amazonas, Nuevo San Juan, Gálvez River (5°15'S, 73°10'W).
23. *Loreto*, Estación Biológica Isla Muyuy (3°58'S, 73°04'W).

24. *Loreto*, Estirón, Río Ampiyacu (3°19'S, 71°51'W).
25. *Loreto*, Mariscal Ramón Castilla, Río Yavari Mirím, Quebrada Esperanza (4°20'S, 71°55'W).
26. *Loreto*, Maynas, Orosa, Amazon River (3°32'S, 72°11'W).
27. *Loreto*, Requena, Jenaro Herrera, Centro de Investigaciones Jenaro Herrera (4°55'S, 73°40'W).
28. *San Martín*, Moyobamba, Tingana (5°54'S, 77°06'W).
29. *Ucayali*, Atalaya, Cumarí (9°51'S, 74°01'W).

TRINIDAD AND TOBAGO

30. *Trinidad*, Saint Andrew, Sangre Grande (10°35'N, 61°07'W).
31. *Trinidad*, Saint George, Heights of Aripo, Cerro Aripo (10°43'N, 61°15'W).
32. *Trinidad*, Saint George, Port of Spain (10°39'N, 61°31'W).

VENEZUELA

- . *Amazonas*, Río Negro, Muyrapinimo (coordinates unknown).
33. *Distrito Federal*, La Guaira, San Julián (10°37'N, 66°50'W).

Complete lists of all issues of *Novitates* and *Bulletin* are available on the web (<http://digitallibrary.amnh.org/dspace>). Order printed copies on the web from <http://www.amnhshop.com> or via standard mail from:

American Museum of Natural History—Scientific Publications
Central Park West at 79th Street
New York, NY 10024

Ⓒ This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).