



First record of the De Vivo's Disk-winged Bat, *Thyroptera devivoi* Gregorin, Gonçalves, Lim & Engstrom, 2006 (Chiroptera, Thyropteridae), from Colombia, with comments about the record of *Thyroptera lavalii* Pine, 1993 from the country

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Abstract

We report the first record of *Thyroptera devivoi* from Colombia in a palm swamp of *Mauritia flexuosa* in an aeolian seasonally flooded savanna ecosystem. This record is the seventh specimen and the fifth locality known for *T. devivoi* and extends the known distribution of the species 1250 km northwest from nearest locality in Guyana. We revised the specimen that was previously reported as voucher material of *Thyroptera lavalii* from Colombia, but it matches in all characters with *Thyroptera tricolor*. We considered the presence of *T. lavalii* in Colombia uncertain.

Key words

Neotropical flooded savannas, gallery forest, geographic distribution, range extension.

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Introduction

The genus *Thyroptera* Spix, 1823 is a group of Neotropical insectivorous foliage-roosting bats characterized by the presence of adhesive disks in the base of the thumbs and the soles of their feet. The genus is distributed from southern Mexico across Central America and northern South America to southern Brazil. Currently, 5 species of *Thyroptera* are recognized (Wilson 2008, Velazco et al. 2014).

Three species of *Thyroptera* have been recorded in Colombia: *T. tricolor* Spix, 1823 has a spread distribution

in the country; *T. discifera* (Lichtenstein & Peters, 1854) is known from Andean foothills, Caribbean and Pacific regions; and *T. lavalii* Pine, 1993 has been reported from one locality from the Andean region (Solari et al. 2013, Reyes-Amaya et al. 2016). Additionally, fragmented fossils from middle Miocene from La Venta (Huila department) have been reported as *T. lavalii* (Czaplewski 1996, 1997). However, the taxonomic assignment of these fossils is considered uncertain (Velazco et al. 2014).

Thyroptera devivoi is a rare species that inhabits gallery forest in savanna formations. It is known by only 6 specimens from 4 localities (1 from southwestern Guy-



Figure 1. Panoramic view of the Palm swamp of *Mauritia flexuosa* (locally known as Morichales) associated to a strip of gallery forest where the specimen ICN 21985 of *Thyroptera devivoi* was captured. Photography credit: María C. Calderón-Capote.

ana and 3 from northeastern Brazil). However, the great distance between these localities suggest that the species can be widely distributed (Gregorin et al. 2006, Wilson 2008, Santos et al. 2013, Velazco et al. 2014).

In this report, we present the first record of *T. devivoi* for Colombia. Additionally, we discuss the previous report of *T. lavalii* from the Andean region of the country.

Methods

The specimen reported here was mist netted in the understory of a palm swamp of *Mauritia flexuosa* (locally known as “morichales”, Fig. 1) at Laguna Encantada in the Hato Viejo farm, vereda Varsovia, Municipality of Paz de Ariporo, Department of Casanare (06°02'15" N, 070°12'43" W; 111 m above sea level [a.s.l.]) (Fig. 2). The capture took place on 9 April 2015 under the research permit 500-41-15.07209 of CORPORINO-QUIA. This place is in an aeolian seasonally flooded savanna ecosystem, dominated by grasslands, strips of gallery forest, and palm swamps associated to rivers and wetlands (Sarmiento 1983, Romero-Ruiz et al. 2010). The specimen was captured during the beginning of the rainfall season that extends from April to November in Colombian Llanos (Romero-Ruiz et al. 2010).

The specimen (ICN 21985) is an adult male with scrotal testis preserved in ethanol (96%) with the skull removed and cleaned and deposited in the mammalian collection “Alberto Cadena García” of Instituto de Ciencias Naturales of the Universidad Nacional de Colombia (ICN).

To confirm the taxonomic identification of our specimen and compare with other species of *Thyroptera* reported for Colombia, we examined the specimens of the genus deposited in ICN and the mammalian collection of the Museo Javeriano de Historia Natural Lorenzo Uribe (MPUJ-MAMM; MPUJ-MAMM 648; 1216). We reviewed all identifications based on characters by Pine

(1993), Solari et al. (2004), Gregorin et al. (2006), Wilson (2008) and Velazco et al. (2014). The measurements reported here follow Gregorin et al. (2006) and Velazco et al. (2014). These were measured with a digital caliper to the nearest 0.1 mm. The external measurements were taken from the specimen’s tags.

Results

Most of the measures of the specimen ICN 21985 (Tables 1, 2) coincide with the ranges of measurements previously reported for *T. devivoi* (Gregorin et al. 2006, Velazco et al. 2014). Only the length of tail, the condyloincisive length measured to the incisors tips (sensu Gregorin et al. 2006), and zygomatic breadth are slightly bigger in our specimen (11.3 mm, 0.3 mm, 0.1 mm, respectively), but it does not represent a great variation more than individual. Regarding other species of the genus, *T. devivoi* overlapped in most measurements with *T. tricolor*, but is slightly greater than *T. discifera* and *T. wynneae* Velazco, Gregorin, Voss & Simmons, 2014; and smaller than *T. lavalii* (Gregorin et al. 2006; Velazco et al. 2014; Tables 1, 2).

The specimen ICN 21985 has all diagnostic characters recognized for *T. devivoi* (Gregorin et al. 2006, Velazco et al. 2014): Externally, it has the ventral hair with 2 bands; the basal band is brown and the distal band is grayish brown, giving a frosted appearance. The adhesive disks of the wings are oblong, and the calcar has no lappets. The other 2 species of *Thyroptera* confirmed from Colombia, *T. discifera* and *T. tricolor* (see below), are easily differentiated externally from *T. devivoi* because they have unicolored ventral hair. *T. discifera* has light color dorsum and *T. tricolor* has whitish ventral hairs. Additionally, both have 2 lappets in the calcar and the adhesive disks are circular (Fig. 3). Cranially, *T. devivoi* has the rostrum subequal to the braincase, the foramen oval is large (small in *T. discifera*), and the mesopterygoid fossa is divided in 2 cavities by a midventral blade crest



Figure 2. Localities of *Thyroptera devivoi*. Circles correspond to localities previously reported: 1. Brazil: Maranhão, Barreirinhas (03°00' S, 043°06' W; Santos et al. 2013). 2. Brazil: Piauí; Estação Ecológica Uruçuí-Una, Bom Jesus (08°52' S, 044°57' W; Gregorin et al. 2006). 3. Brazil: Tocantins; Estação Ecológica Serra Geral do Tocantins (Jalapão) (10°33' S, 046°45' W Gregorin et al. 2006). 4. Guyana: Upper Takutu-Upper Essequibo; Tamton (02°21' N, 059°42' W; Gregorin et al. 2006). Star corresponds to the locality reported in this work: Colombia, Paz de Ariporo: Laguna Encantada in Hato Viejo farm (06°2'15" N, 070°12'43" W). Areas in light green correspond to Neotropical savanna formations after biome map layer from WWF (Olson et al. 2001). The locality 1 is in Cerrado formation, see Santos et al. (2013).

(undivided in *T. discifera*) (Fig 4). In dental characters, *T. devivoi* differs because the cusps of the I2 are perpendicularly arranged relative to the long axis of the toothrow, whereas the cusps of I2 are positioned obliquely in *T. tricolor* and *T. discifera* (Figs 4, 5). In the lower teeth, *T. devivoi* has the i3 taller and faintly tricuspid than i1

and i2, while in *T. tricolor* and *T. discifera* the i3 is less developed.

The other 2 species of *Thyroptera*, *T. lavalii* and *T. wynneae*, are not present in Colombia. Both have oblong adhesive disks in the wings as *T. devivoi*, but they are easily differentiated. *T. lavalii* differs from *T. devivoi* by

Table 1. Range of external and skull measurements (mm) and body mass (g) of *Thyroptera devivoi* based on all previous records summarized by Gregorin et al. (2006). †To the most anterior point of premaxilla. ‡To the incisors tips.

Measurements	Gregorin et al. (2006)				This study
	MZUSP 30073	MZUSP 32345	ROM 35588	ROM 35589	ICN 21985
Sex	Male	Male	Male	Female	Male
FA	35.7	36.0	37.7	38.0	37.6
Third metacarpal length (MET III)	35.6	35.2	36.3	36.1	36.2
First phalanx of 3rd digit (1P3)	15.5	16.0	16.6	17.4	15.5
Second phalanx of 3rd digit (2P3)	10.0	10.9	10.3	11.4	10.3
Fourth metacarpal length (METIV)	35.5	35.8	36.2	36.7	35.7
First phalanx of 4th digit (1P4)	10.2	9.8	10.3	11.0	10.2
Fifth metacarpal length (METV)	31.8	36.1	33.2	33.5	32.4
First phalanx of 5th digit (1P5)	8.5	10.2	9.6	9.8	9.0
Tail free	5.5	5.1	3.8	3.0	—
Greatest length of skull (GLS) †	14.9	15.1	15.1	15.3	15.3
Condylolncisive length (CIL) ‡	13.8	13.9	14	13.9	14.2

Table 2. Range of external and skull measurements (mm) of *Thyroptera devivoi* based on previous records summarized by Gregorin et al. (2006) and not included by Velazco et al. (2014).

Measurements	Gregorin et al. 2006; Velazco et al. (2014)	ICN 21985
	males	
Total length (TL)	—	78
Length of tail (LT)	20.4, 21.7	33
Hind foot length (HF)	—	7
Ear length (EAR)	—	13
Free tail length (FTL)	4.8 (3.8–5.5) 3	?
Forearm length (FA)	36.5 (35.7–37.7) 3	37.6
Greatest length of the skull (GLS) †	14.9 (14.7–15.1) 3	15.0
Condyloincisive length (CIL) †	13.8 (13.7–13.9) 3	14.2
Braincase breadth (BBC)	7.0 (6.7–7.2) 3	7.1
Rostral length (ROL)	5.8	4.2
Zygomatic breadth (ZB)	7.5 (7.4–7.7) 3	7.8
Postorbital breadth (PB)	2.7 (2.5–2.8) 3	2.7
Maxillary tooththrow length (MTRL)	6.0 (5.7–6.1) 3	6.1
Width at M3 (M3-M3)	5.4 (5.3–5.5) 3	5.5
Length of mandible (LMA)	10.9 (10.6–11.3) 3	?
Mandibular tooththrow length (MANDL)	6.1 (5.8–6.3) 3	6.3
Weight	—	5

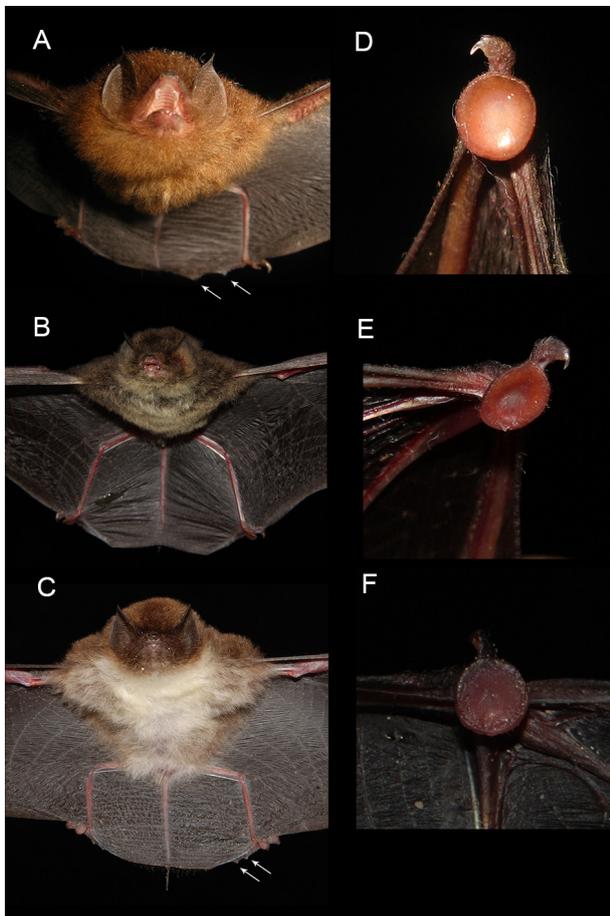
† Incisors included.

‡ To the anterior surface of the incisors.

not having frosted ventral hair, only 1 lappet in the calcar, and poorly defined cusps of i3 (not tricuspoid). *T. wynneae* differs from *T. devivoi* by having tricolored ventral hair, densely haired forearm, 2 lappets in the calcar, and shorter rostrum than the braincase (Gregorin et al. 2006, Velazco et al. 2014).

One of the specimens examined for comparisons,

MPUJ-MAMM 1216, has been reported as evidence of the presence of *T. lavalii* in Colombian Andes (Reyes-Amaya et al. 2016). However, different traits of this specimen support its identification as *T. tricolor* (Solari et al. 2004, Velazco et al. 2014). We considered that the external measurements from the label were taken using a distinct protocol than that used by us. All skull measurements of the specimen MPUJ-MAMM 1216 (Table 3), except for condyloincisive length (CIL), coincide with the previously reported for *T. tricolor* (Velazco et al. 2014). The greatest value of CIL in the specimen could represent intraspecific variation, considering the specimen has all morphological diagnostic characters of *T. tricolor*: externally, the specimen has white ventral pelage, circular suction disk of the wing, and 2 lappets in the calcar (Fig. 6). The skull has the rostrum tilted up and the mesopterygoid fossa is divided in 2 cavities by a midventral blade crest. Dental characters included a cusp in the second upper incisor obliquely arranged relative to the long axis of the tooththrow (Velazco et al. 2014).



◀ **Figure 3.** Comparative figure of *Thyroptera discifera*, *Thyroptera devivoi*, and *Thyroptera tricolor*. These individuals were included in the specimens reviewed for comparisons. **A.** *T. discifera*, (ICN 21207). **B.** *T. devivoi*, (ICN 21985). **C.** *T. tricolor* (ICN temp D3M 400). **D.** Adhesive disk of wings in *T. discifera*. **E.** Adhesive disk of wings in *T. devivoi*. **F.** Adhesive disk of wings in *T. tricolor*. *T. devivoi* has the ventral hair bicolored with frosted appearance (B) while *T. discifera* is unicolored with the light color of dorsum (A) and *T. tricolor* is unicolored with the ventral hairs whitish (C). *T. devivoi* does not have lappets in the calcar (E) while *T. discifera* and *T. tricolor* have two lappets in the calcar (A and C, see white arrows). *T. devivoi* has adhesive disks of wings oblong (E), while these are circular in *T. discifera* and *T. tricolor* (D and F). Photography credit: *T. discifera* (A and D) Miguel E. Rodríguez-Posada, *T. devivoi* (B and E) María C. Calderón-Capote, and *T. tricolor* (C and F) Darwin M. Morales-Martínez.

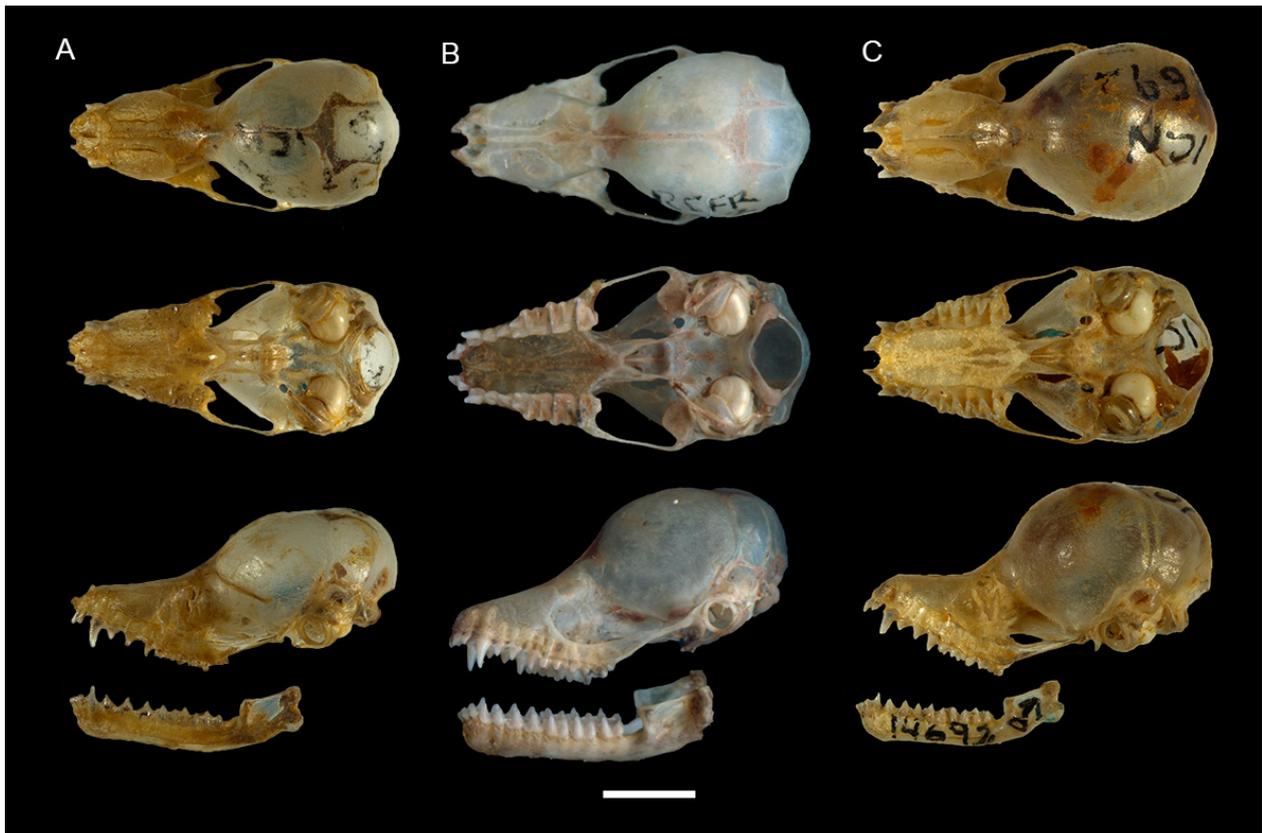


Figure 4. Comparative figure of the skulls of *Thyroptera discifera*, *T. devivoi*, and *T. tricolor*. These individuals were included in the specimens reviewed for comparisons. Dorsal (upper), ventral (middle) and lateral (lower) views of the skulls and lateral views of the mandibles of: **A.** *T. discifera*, (ICN 21207). **B.** *T. devivoi*, (ICN 21985). **C.** *T. tricolor* (ICN 14692). Scale bar = 5 mm.

Table 3. Range of external and skull measurements (mm) and body mass (g) of *Thyroptera tricolor* based on all previous records summarized by Velazco et al. (2014).

Measurements	Velazco et al. (2014) males	Velazco et al. (2014) females	MPUJ-MAMM 1216 female
Total length (TL)	71.9 (67–77) 12	72.9 (68–79) 16	62.1
Length of tail (LT)	28.6 (25–30) 12	27.3 (25–30) 18	21.8
Hind foot length (HF)	5.9 (4–7) 10	5.7 (4–6) 18	—
Ear length (EAR)	12.4 (11–13) 7	12.3 (11–13) 8	11.6
Free tail length (FTL)	6.0 (4.4–7.3) 7	7.0 (5.0–9.0) 14	—
Forearm length (FA)	36.7 (33.5–40.0) 18	37.1 (35–39) 27	38.6
Greatest length of the skull (GLS)	14.3 (13.8–15.7) 18	14.6 (13.6–15.5) 24	15.4
Condyloincisive length (CIL)	13.5 (12.9–14.4) 18	13.7 (12.9–14.3) 24	14.8
Braincase breadth (BBC)	7.3 (6.9–7.5) 17	7.3 (6.7–7.6) 24	7.5
Rostral length (ROL)	—	5.3, 5.5	5.8
Zygomatic breadth (ZB)	7.4 (7.1–7.7) 10	7.5 (6.9–7.7) 13	—
Postorbital breadth (PB)	2.7 (2.6–2.8) 17	2.7 (2.5–2.8) 25	2.5
Maxillary tooththrow length (MTRL)	5.9 (5.6–6.3) 18	5.9 (5.5–6.2) 25	6.3
Width at M3 (M3–M3)	5.2 (5.0–5.5) 18	5.2 (4.8–5.5) 25	5.4
Length of mandible (LMA)	10.4 (9.6–10.7) 15	10.6 (9.7–11.3) 23	?
Mandibular tooththrow length (MANDL)	6.1 (5.8–6.3) 15	6.2 (5.7–6.5) 25	6.6
Weight	4.4 (3.4–5.1) 11	4.5 (3.5–5.1) 12	5.8

Discussion

The new record of *T. devivoi* in Colombian Llanos extends the distribution of the species approximately 1250 km northwest from the nearest locality in Guyana, and west to the Orinoco river. This wider distribution of the species has been inferred by the long distance between localities (Gregorin et al. 2006, Velazco et al.

2014). Previous known localities for the species are in areas dominated by savanna formations, and the capture sites were associated with humid forest and palm swamps along rivers and streams (Gregorin et al. 2006). Likewise, other species of *Thyroptera* have been sampled adjacent to palm swamps of *Mauritia* in different types of lowland ecosystems as tropical wet forest (Velazco et al. 2014). These formations can be very important habitats for the

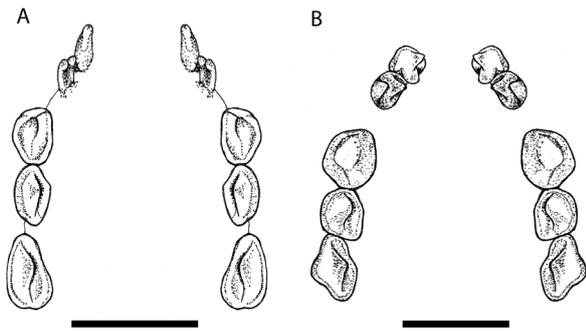


Figure 5. Occlusal views of the upper dentition. **A.** *Thyroptera devivoi* (ICN 21985; male). **B.** *Thyroptera discifera* (ICN 21207; male). The cusps of I2 in *T. devivoi* are perpendicularly arranged relative to the long axis of the tooththrow, whereas, in *T. discifera* and *T. tricolor* (no drawing) the cusps of I2 are positioned obliquely to the long axis of the tooththrow. Scale bars = 2 mm. Illustration by Valentina Nieto Fernández.

conservation of the thyropterid bats.

The distribution of *T. devivoi* is wide and disjunctive, includes 3 ecosystems of savanna bioma: the Cerrado, the Rupunini savannas, and the aeolian seasonally flooded savannas of the Orinoco river basin, all separated by a gap of wet forest. Yet, the species is scarcely represented in biological collections possibly due to the elusive nature of the thyropterid bats (Velazco et al. 2014).

Two species of Thyropterid bats have been reported for the Orinoco river basin, *T. lavalii* and *T. tricolor* (Ferrer Pérez et al. 2009). For the Llanos region, only *T. lavalii* was recorded, but we do not know the voucher

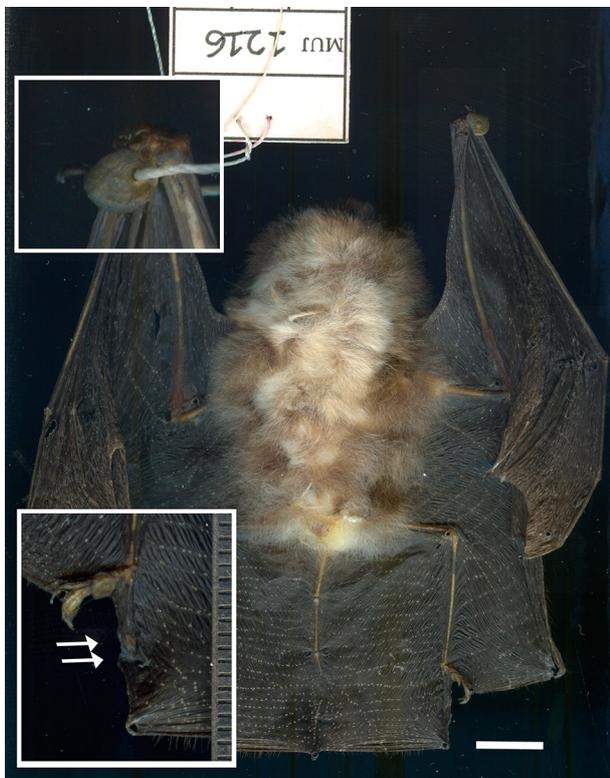


Figure 6. Ventral view of the specimen MPUJ-MAMM 1216 shown the external characters for *Thyroptera tricolor*: Ventral hairs are unicolored with whitish coloration. Adhesive disks of wing are circular (upper box). Calcar has 2 lappets (white arrows in the lower box).

specimens for these records and the specimen from the supporting reference is not available for revision. In our knowledge, no Colombian specimens exist of this species from the Llanos. On the other hand, Linares and Rivas (2003) reported *T. lavalii* for the Orinoco Delta region well before the description of *T. devivoi*; as these 2 species may be externally confused, a proper examination of this material is ideal to clarify their occurrence. Hence, we consider the distribution of *T. lavalii* uncertain for the llanos of the Orinoco river basin and possibly the only species of *Thyroptera* in this region is *T. devivoi*.

Finally, we discard the presence of *T. lavalii* in Colombian Andes and we agree with Velazco et al. (2014) about the uncertainty identity of the *Thyroptera* fossils from La Venta. Any of the morphological diagnostic characters for the actual 5 species of *Thyroptera* are distinguishable in the fossil material of La Venta (Czaplewski 1996, 1997); therefore, the actual species assignments of this material is not possible. We recommend the use of *T. robusta* Czaplewski, 1996 for this material because it is the name under which this fossil taxon was described. Therefore, we considered the presence of *T. lavalii* in Colombia uncertain.

Acknowledgements

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Authors' Contributions

All authors contributed to the identification of the specimen, recorded all morphological data, and wrote the paper. MCC, RCFR collected the specimen. DMM made the map, took the specimens images, and edited all manuscript figures. MRP coordinated the researchers' work.

References

- Czaplewski NJ (1996) *Thyroptera robusta* Czaplewski, 1996, is a junior synonym of *Thyroptera lavalii* Pine, 1993 (Mammalia: Chiroptera). *Mammalia* 60: 153–156. <https://doi.org/10.1515/mamm.1996.60.1.141>
- Czaplewski NJ (1997) Chiroptera. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ (Eds) *Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington DC, 410–430.
- Ferrer Pérez A, Beltrán M, Díaz-Pulido AP, Trujillo F, Mantilla-Meluk H, Herrera O, Alfonso AF, Payán E (2009) Lista de los mamíferos

- de la cuenca del río Orinoco. *Biota Colombiana* 10: 179–207.
- Gregorin R, Gonçalves E, Lim BK, Engstrom MD (2006) New species of disk-winged bat *Thyroptera* and range extension for *T. discifera*. *Journal of Mammalogy* 87: 238–246. <https://doi.org/10.1644/05-MAMM-A-125R1R1.1>
- Linares OJ, Rivas BA (2004) Mamíferos del Sistema Deltaico (delta del Orinoco-golfo de Paria), Venezuela. *Memoria de la Fundación La Salle de Ciencias Naturales* 159–160: 27–104.
- Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wetzel WW, Hedao P, Kassem KR (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience* 51: 933–938. <http://doi.org/c635xt>
- Pine RH (1993) A new species of *Thyroptera* Spix (Mammalia: Chiroptera: Thyropteridae) from the Amazon basin of north-eastern Perú. *Mammalia* 57: 213–225. <https://doi.org/10.1515/mamm.1993.57.2.213>
- Reyes-Amaya N, Lozano-Flórez J, Flores D, Solari S (2016) Distribution of Spix's Disk-Winged Bat, *Thyroptera tricolor* SPIX, 1823 (Chiroptera: Thyropteridae) in Colombia, with first records for the middle Magdalena Valley. *Mastozoología Neotropical* 23: 127–137.
- Romero-Ruiz M, Etter A, Sarmiento A, Tansey K (2010) Spatial and temporal variability of fires in relation to ecosystems, land tenure and rainfall in savannas of northern South America. *Global Change Biology* 16: 2013–2023. <https://doi.org/1.1111/j.1365-2486.2009.02081.x>
- Santos CLC, Pereira ACN, Bastos VJC, Gracioli G, Rebêlo JMM (2013) Parasitism of ectoparasitic flies on bats in the northern Brazilian cerrado. *Acta Parasitologica* 58: 207–214. <https://doi.org/10.2478/s11686-013-0135-9>
- Sarmiento G (1983) The savannas of tropical America. In: Bourliere F (Ed.) *Ecosystems of the World XIII, Tropical Savannas*. Elsevier, Amsterdam, 245–288.
- Solari S, Van Den Bussche RA, Hofer SR, Patterson BD (2004) Geographic distribution, ecology, and phylogenetic affinities of *Thyroptera lavalii* Pine 1993. *Acta Chiropterologica* 6: 293–302. <https://doi.org/10.3161/001.006.0207>
- Solari S, Muñoz-Saba Y, Rodríguez-Mahecha JV, Defler TR, Ramírez-Chaves HE, Trujillo F (2013) Riqueza, endemismo y conservación de los mamíferos de Colombia. *Mastozoología Neotropical* 20: 301–365.
- Velazco PM, Gregorin R, Voss RS, Simmons NB (2014) Extraordinary local diversity of Disk-winged Bats (Thyropteridae: *Thyroptera*) in northeastern Peru, with description of a new species and comments on roosting behavior. *American Museum Novitates* 3795: 1–28.
- Wilson DE (2008) Family Thyropteridae. In: Gardner AL (Ed.) *Mammals of South America. Volume 1. Marsupials, Xenarthrans, Shrews, and Bats*. University of Chicago Press, Chicago, 392–396.