






First confirmed record of the LaVal's Disk-winged Bat, *Thyroptera lavalii* Pine, 1993 (Chiroptera, Thyropteridae), from Colombia

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Abstract

We document the first record of Laval's Disk-winged Bat, *Thyroptera lavalii* Pine, 1993, from the Amazon region of Colombia. This record increases to four the number of *Thyroptera* species in the country and extends the known range of *T. lavalii* 428 km east and 338 km north from the nearest previous localities. The distribution of this species now comprises 11 localities from six ecoregions and five countries: Brazil, Colombia, Ecuador, Peru, and Venezuela. We highlight the paucity of knowledge on bat species in the Colombian Amazon.

Keywords

Amazon, distribution, Mammalia, Noctilionoidea, uncommon species

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Introduction

The Neotropical bats of the genus *Thyroptera* Spix, 1823 are commonly known as disk-winged bats owing to the presence of suction disks located at the wrists and ankles which enable these bats to adhere to foliage (Wilson 2008; Velazco et al. 2014; García et al. 2019). The genus includes five described species (Lee 2019): *T. tricolor* Spix, 1823, *T. discifera* (Lichtenstein & Peters, 1854), *T. devivoi* Gregorin, Gonçalves, Lim & Engstrom, 2006,

T. lavalii Pine, 1993, and *T. wynneae* Velazco, Gregorin, Voss & Simmons, 2014.

The known distribution of the genus ranges from southern Mexico, extending through Central America and northern South America, to southeastern Brazil (Wilson 2008). *Thyroptera* species inhabit lowland, moist, Neotropical forests, including primary and secondary forests and riparian forests in savanna ecosystems

(Velazco et al. 2014; Rodríguez-Posada et al. 2017; Lee 2019). In Colombia, three species have been recorded: *T. tricolor*, *T. discifera*, and *T. devivoi* (Rodríguez-Posada et al. 2017).

Thyroptera lavalii is an uncommon species, known by few specimens collected from few localities in north-eastern Venezuela, eastern Ecuador, and the Amazon basin of Brazil and Peru (Lee 2019). Previously, *T. lavalii* was reported in the Colombian Andes (Solari et al. 2013; Reyes-Amaya et al. 2016), but Rodríguez-Posada et al. (2017) discussed these records and concluded that all correspond to *T. tricolor*. Although *T. lavalii* has not been recorded in Colombia, the distributional gap among Venezuelan and the western Amazonian localities in Ecuador and Peru (Lee 2019) suggests the presence of this species in the Colombian Amazon. Herein, we present the first confirmed record of *T. lavalii* in Colombia based on morphological and molecular data.

Methods

During a rapid assessment of mammals carried out in 2019 in La Chorrera, in the Amazonas Department, DMM mist-netted one disk-winged bat in the understory of a *Mauritia flexuosa* L.f. palm swamp which had been cleared for local fishing. The specimen was fixed in 10% formalin, and the skull was extracted and cleaned by dermestid beetles. Tissue samples were taken and preserved in 96% ethanol for later molecular analyses. The specimen was deposited in the “Alberto Cadena García” Collection of Mammals, Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN). The tissue sample was deposited in the “Banco de ADN y Tejidos de la Biodiversidad” (BATB), Instituto de Genética, Universidad Nacional de Colombia (IGUN-BATB). In the field, captured bats were handled following the animal care and guidelines of the American Society of Mammalogists (Sikes et al. 2016), and the specimens were collected under the Institutional collection permits of Instituto Amazónico de Investigaciones Científicas SINCHI.

To conduct the morphological identification, we reviewed specimens of *T. discifera*, *T. tricolor*, and *T. devivoi* deposited in the ICN collection. Additionally, we examined two Peruvian specimens of *T. lavalii* housed at the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM 13966, 19803).

We took external and skull measurements according to Velazco et al. (2014): total length (TL), length of tail (LT), hindfoot length (HF), ear length (Ear), free tail length (FTL), forearm length (FA), greatest length of skull (GLS), condyloincisive length (CIL), braincase breadth (BB), rostral length (ROL), zygomatic breadth (ZB), postorbital breadth (PB), maxillary toothrow length (MTRL), width at M3 (M3–M3), length of mandible (LMA), and mandibular toothrow length (MANDL).

To corroborate the identification of our specimen, we performed a molecular characterization based on

the cytochrome c oxidase subunit I (COI) mitochondrial gene. We extracted genomic DNA using the phenol-chloroform method (Sambrook et al. 1989) from a fresh sample of muscle tissue preserved in 96% ethanol. We amplified a fragment of 641 base pairs (bp) of the COI mitochondrial DNA (mtDNA) using a polymerase chain reaction (PCR) with the primers dgLCO and dgHCO (Folmer et al. 1994). The PCR was carried out in a total volume of 30 µl with approximately 2 µl of DNA, 1× buffer (with 2.0 mm of MgCl₂), 0.6 mm of deoxyribonucleotide triphosphates (dNTPs), 1.5 µm of each primer, and 0.2 U/µl of Taq DNA Polymerase (Thermo Scientific, Waltham, MA, USA). The program consisted of an initial denaturing step at 95 °C for 5 minutes followed by 35 cycles of denaturation at 95 °C for 45 seconds, annealing at 52 °C for 45 seconds and extension at 72 °C for 1 minute, and a final extension step at 72 °C for 10 minutes. We carried out purification and sequencing with the amplification primer on an ABI 3500 sequencer (Applied Biosystems, Waltham, MA, USA). Finally, we submitted it to GenBank under the accession number MW173609.

We analyzed the sequence of our specimen in a phylogenetic framework to assess its affinities with other *Thyroptera* species. For this purpose, additional sequences of COI of *T. tricolor* and *T. lavalii* from Costa Rica, Guyana, Suriname, and Ecuador were downloaded from GenBank to obtain a final dataset of 30 sequences (Appendix Table A1). We performed a sequence alignment using the Clustal W algorithm in BioEdit v. 7.2.6 software (Hall 1999). We assessed the optimal partitioning scheme and the best-fit evolutionary model using PartitionFinder v. 2 based on the Akaike Information Criterion (Lanfear et al. 2012) and selected the 1st + 2nd codon and 3rd partitioning scheme. We applied the following resulting model in a Bayesian analysis (BA) using MrBayes v. 3.2.1 (Ronquist et al. 2012) implemented with Geneious Prime software (Biomatters Limited, Auckland, New Zealand): COI 1st and 2nd codon GTR+I, 3rd codon TRN+I. Those models were incorporated into a single tree search. To ensure convergence, we ran two independent replicates using four Markov chains, run for 10 million generations, sampling every 1000 generations. We discarded 25% of the resulting trees as burn-in, and 85% of the trees were used for generating a 50% majority-rule consensus. We assessed an acceptable level of the MCMC chains and estimated the effective sample sizes for all parameters with Geneious Prime software (Biomatters Limited, Auckland, New Zealand). Also, we performed phylogenetic analysis using the Maximum Likelihood algorithm implemented in RAxML v. 1.5 beta software (Stamatakis 2006). The default GTR+G model was set across all partitions. To assess the branch support, 1000 non-parametric thorough bootstrap values were computed and plotted against the best tree. For all phylogenetic analyses, homologous sequences of *Furipterus horrens* (Cuvier, 1828) and *Micronycteris megalotis* (Gray, 1842) were used as outgroups (Appendix Table A1). Additionally, we calculate average uncorrected *p*-distances and

model-corrected Kimura 2-parameter (K2P) distances in the COI matrix using MEGA X (Kumar et al. 2018).

We described the distribution of *T. lavalii* considering all records with confirmed taxonomical identification in literature (Bernard and Fenton 2002; García et al. 2019) and according to the terrestrial ecoregions of the world proposed by Olson et al. (2001).

Results

Order Chiroptera

Family Thyropteridae

Thyroptera lavalii Pine, 1993

LaVal's Disk-winged Bat

New records. COLOMBIA • Amazonas Department, La Chorrera no municipalized area, Cabildo Okaina, Puerto Oriente community; 01°31'43.9"S, 072°40'38.6"W (Fig. 1); 108 m a.s.l.; 6 Oct. 2019; Darwin Morales Martínez leg; mist netting at 19:00 h in an open *Mauritia flexuosa* palm swamp cleared for fishing in the middle of the indigenous community; 1 ♂, adult; ICN 25000, IGUN-BATB 10175; GenBank MW173609.

Identification. Our specimen (ICN 25000) coincides in all characteristics with previous descriptions of *T. lavalii* (Pine 1998; Solari et al. 2004; Wilson 2008; Velazco et al. 2014; Lee 2019): large size—the largest for the genus (FA = 37.3–41.0 mm; GLS = 15.4–15.8 mm; ICN 25000 FA = 38 mm, GLS = 15.61 mm)—dorsal fur short, dense and unicolored cinnamon-brown; ventral fur bicolored, brown and yellowish; suction disks on wrists oblong; interfemoral membrane naked, with a fringe of hairs on its external edge; calcar with a single, well-developed lap-pet (Fig. 2); skull with the rostrum larger than, and forming an obtuse angle with, the braincase; mesopterygoid fossa divided into two separate concavities by a longitudinal ridge (Fig. 3); cusps on the second upper incisors (12) subequal and arranged perpendicular to the long axis of the toothrow; and third lower incisor with faintly developed or absent cusps. All external and skull measurements are within or near to the known range (Table 1). Other *Thyroptera* species, including *T. discifera*, *T. tricolor*, and *T. wynneae*, can be differentiated from *T. lavalii* based on the shape of the wrist suction disks: circular in the first group and oblong in *T. lavalii* and *T. devivoi*. Additionally, *T. lavalii* and *T. devivoi* have bicolored



Figure 1. Geographic distribution of *Thyroptera lavalii*. The yellow star represents the first confirmed record from Colombia, and the yellow triangles represent previous localities known for the species (Table 2).

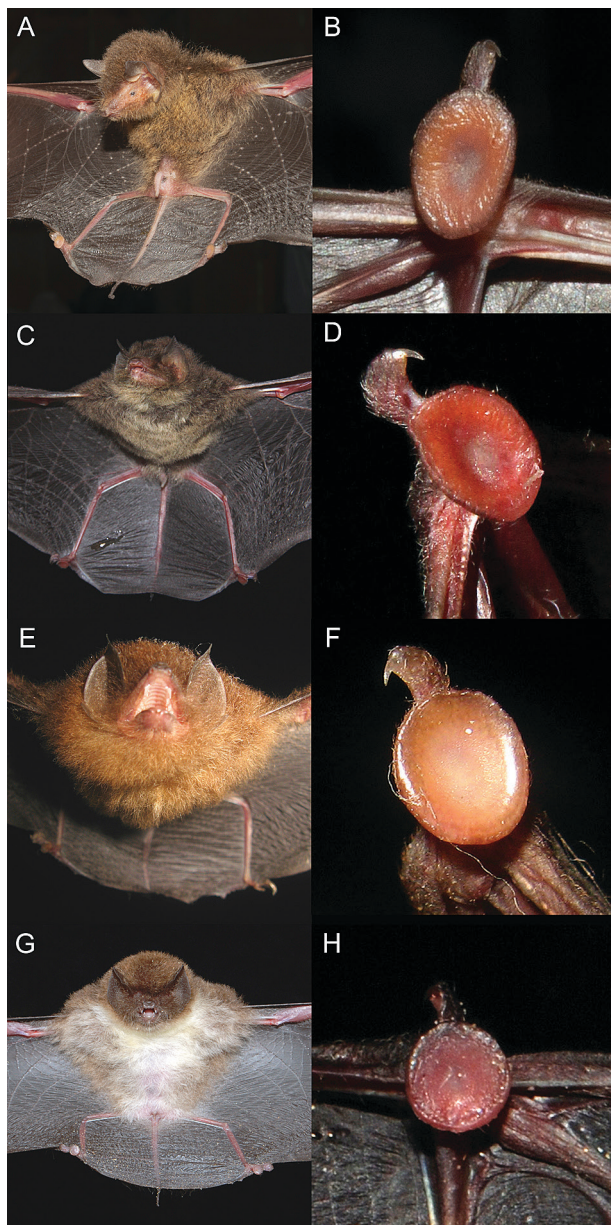


Figure 2. Comparative external morphology of four *Thyroptera* species recorded from Colombia. **A.** *Thyroptera lavalii* head and body ventral view (ICN 25000). **B.** *T. lavalii* wrist suction disk. **C.** *Thyroptera devivoi* head and body ventral view (ICN 21985). **D.** *T. devivoi* wrist suction disk. **E.** *Thyroptera discifera* head and body ventral view (ICN 21207). **F.** *T. discifera* wrist suction disk. **G.** *Thyroptera tricolor* head and body ventral view (ICN temp D3M 400). **H.** *T. tricolor* wrist suction disk.

ventral fur, whereas in *T. discifera* and *T. tricolor* this fur is unicolored, and in *T. wynneae* it is tricolored. Morphologically, *T. devivoi* is the most similar species to *T. lavalii*, but they can be externally differentiated because the former is externally (forearm) and cranially smaller (Fig. 3), has frosted ventral fur, and poorly developed lappets on the calcar (Fig. 2). Dentally, *T. devivoi* has two conspicuous accessory cups on the third lower incisors, whereas *T. lavalii* lacks such cusps.

Our phylogenetic analysis of the COI gene confirms that the sequence of ICN 25000 is nested within sequences of *T. lavalii* reported from Ecuador (PP = 0.98;

Table 1. External and craniodental measurements of the first record of *Thyroptera lavalii* from Colombia (ICN 25000), and those previously reported by Velazco et al. (2014). Summary statistics mean, observed range, and sample size. Weight is given in grams; all other measurements are recorded in millimeters. See Methods section for abbreviations.

	ICN 25000		Velazco et al. (2014)	
Sex	Male	Females	Males	
TL	79	83.0 (78–87) 4	74, –	
LT	32	30.5 (30–31) 4	23, –	
HF	5	6.3 (4–7) 4	6, –	
Ear	12	9.0 (8–12) 4	8, –	
FTL	—	4.0	—	
FA	38	39.8 (37.3–41.0) 4	39.0, 39.0	
GLS	15.61	15.6 (15.4–15.8) 4	15.5, 15.2	
CIL	14.89	14.9 (14.9–14.9) 4	14.6, 15.0	
BB	7.42	7.2 (7.1–7.4) 4	7.3, 7.2	
ROL	6.02	6.5	—	
ZB	8.03	8.0, 8.0	8.1, –	
PB	2.86	2.8 (2.7–2.9) 4	2.8, 2.8	
MTRL	6.31	6.5 (6.5–6.5) 4	6.2, 6.3	
M3–M3	6.06	5.8 (5.7–5.8) 4	5.6, 5.5	
LMA	—	11.6 (11.5–11.7) 3	11.3, –	
MANDL	—	6.6 (6.5–6.6) 3	6.3	
Weight	4.75	6	–, 4	

Bootstrap = 73). This close relationship confirms the taxonomic identity of ICN 25000 as *T. lavalii*. The genetic distance between ICN 25000 haplotype and other available haplotypes of *T. lavalii* is between 0.47% (K2P) or 0.62% (*p*-distance), and 1.10% (K2P and *p*-distance), whereas the percentages between the ICN 25000 and the remaining *T. tricolor* haplotypes are between 12.00% and 13.60% (considering both *p*-distances and K2P).

Our record extends the known range of *T. lavalii* 428 km to the east and 338 km to the north from the nearest previously known localities from Ecuador and Peru, respectively. The distribution of *T. lavalii* comprises 11 confirmed records, including our new record (Table 2). Those localities coincide with Lee's (2019) records with the exception of a record from the Brazilian Amazon, which lacks geographic reference and voucher specimen, and thus was excluded from our results. The distribution of *T. lavalii* comprises six Neotropical ecoregions, including the Southwest Amazon Moist Forests (Peru), the Madeira-Tapajós Moist Forests (Brazil), the Solimões-Japurá moist forests (Colombia), the Napo moist forests (Ecuador), the Iquitos varzea (Peru), and the Llanos (Venezuela).

Discussion

Our record confirms the presence of *T. lavalii* in Colombia and increases to four the number of *Thyroptera* species in the country (Rodríguez-Posada et al. 2017). Additionally, our record partially fills a large gap between Venezuelan, Peruvian, and Ecuadorean *T. lavalii* records (Lee 2019) and confirms the species occurrence in the Colombian Amazon. However, known gaps between Amazonian localities and published records in the Venezuelan Lower

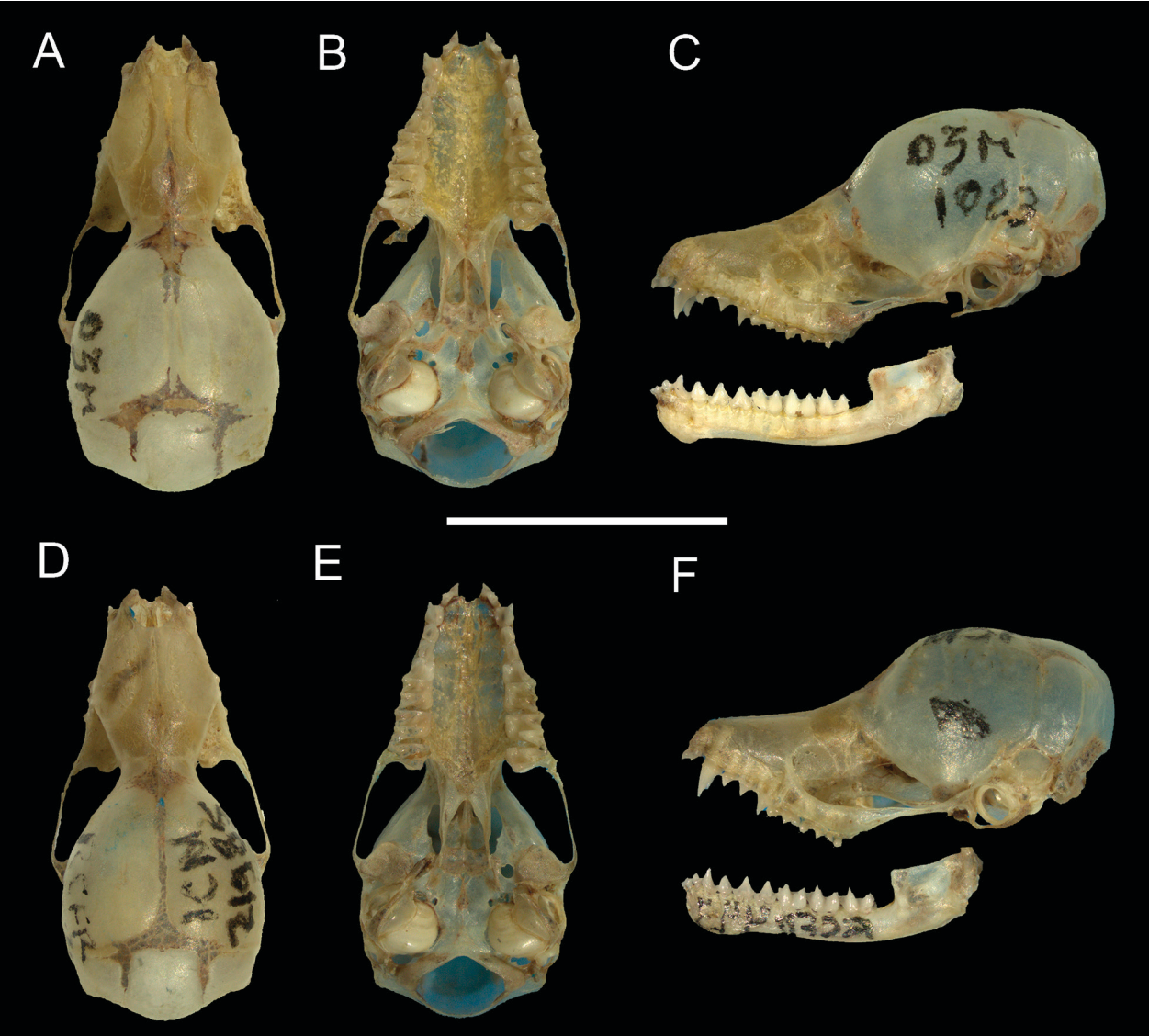


Figure 3. Comparative skull morphology between *Thyroptera lavalii* and *T. devioi*. **A.** *T. lavalii* dorsal view of the skull (ICN 25000). **B.** *T. lavalii* ventral view of the skull (ICN 25000). **C.** *T. lavalii* lateral view of skull and mandible (ICN 25000). **D.** *T. devioi* dorsal view of the skull (ICN 21985). **E.** *T. devioi* ventral view of the skull (ICN 21985). **F.** *T. lavalii* lateral view of skull and mandible (ICN 21985). Scale bar = 10 mm.

Table 2. Localities with supported records of *Thyroptera lavalii*. Numbers and star coincide with numbers on the map (Fig. 1).

ID	Country	Locality	Latitude	Longitude	Source
★	Colombia	Amazonas, Área no municipalizada de la Chorrera, Cabildo Okaina, Comunidad de Puerto Oriente	01°31'43.9"S	072°40'38.6"W	This study
1	Brazil	Pará, Alter do Chão, rio Tapajós	02°30'00"S	054°57'00"W	Bernard and Fenton 2011
2	Ecuador	Napo, Parque Nacional Yasuni, 42 km S, 1 km E of Pompeya Sur	00°40'58.8"S	076°25'58.8"W	ROM 104026; 105215 (GBIF)
3	Peru	Cuzco, Camisea, Cashiriari-3	00°40'58.8"S	072°39'00.0"W	Solari et al. 2004
4	Peru	Loreto, río Yavari Mirim, quebrada Esperanza	04°27'00"S	071°47'00"W	FMNH 89118; 89120; 89121 (GBIF); Velazco et al. 2014
5	Peru	Madre de Dios, 13.4 km NNW Atalaya, left bank of río Alto	12°46'18.12"S	071°23'07.80"W	FMNH 174916 (GBIF); Velazco et al. 2014
6	Peru	Ucayali, Padre Abad, Bosque Nacional Alexander von Humboldt, 86 kmW Pucallpa	08°46'58.80"S	075°07'58.80"W	MUSM 8643 Solari et al. 2004
7	Venezuela	Anzoátegui, Paso bajito, río Moquete, Sur de El Tigre	08°36'16.92"N	064°13'6.96"W	MBUCV-I 3477; 4736; García et al. 2019
8	Venezuela	Bolívar, Cedeño, Hato Caurama	07°27'15.80"N	065°09'22.68"W	MHNS 12768; García et al. 2019
9	Venezuela	Bolívar, Cedeño, Maripa, between Caura and Sipao rivers	07°30'00"N	065°16'59.90"W	EBRG 17411; García et al. 2019
10	Venezuela	Monagas, Morichal Largo	09°19'00"N	062°56'00"W	MHNS-5391; García et al. 2019

Orinoco Basin suggests that *T. lavalii* could occur across the Colombian Amazonian and Orinoco regions, as is illustrated by Wilson (2008). Furthermore, the occurrence of *T. wynneae* in Colombia is highly probable, as

the nearest locality for this species is 283 km from the Colombian border (Velazco et al. 2014).

The presence of *T. lavalii* in Colombia has been controversial. The first mention of the species was a fossil

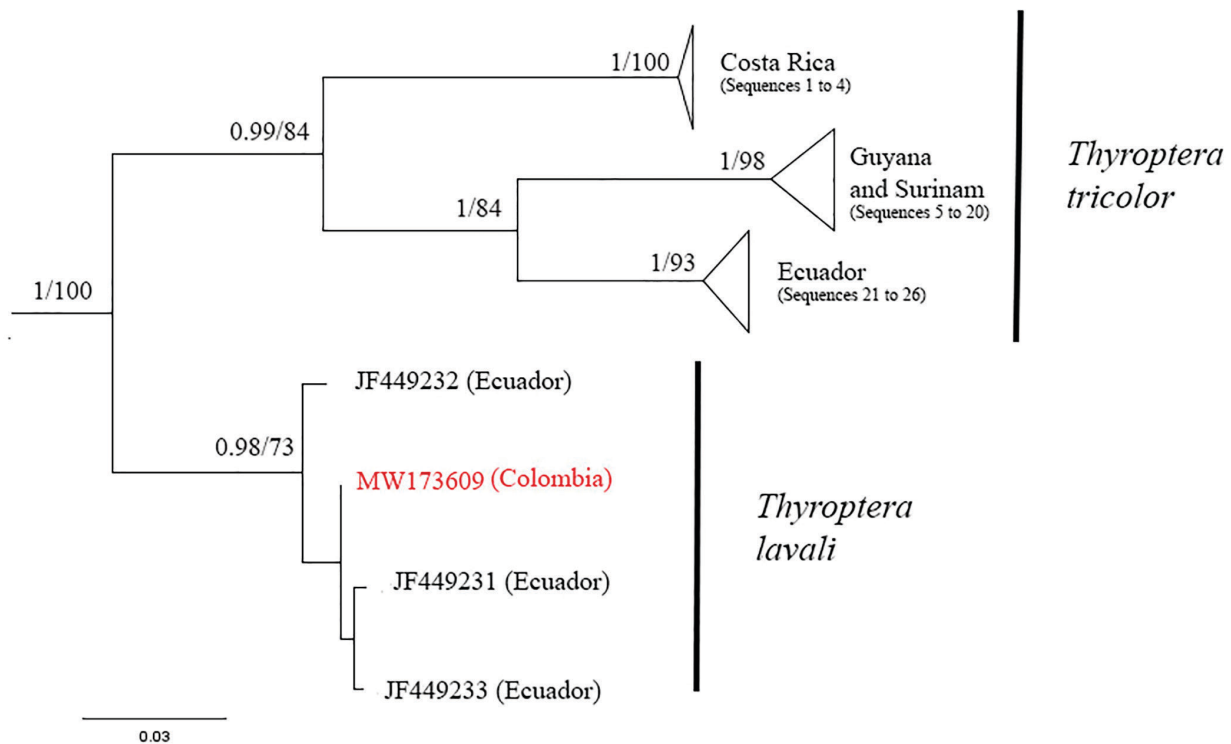


Figure 4. Phylogram of COI gene showing the nesting of specimen ICN 25000 from Colombia (red letter) within the clade of *Thyroptera lavalii* from Ecuador. Numbers above clades indicate the support of each clade, the first number shows Bayesian Posterior Probabilities (PP), and the second number shows the Bootstrap values in the Maximum likelihood analysis. The numbers of sequences of *T. tricolor* are shown in Appendix Table A1.

from La Venta (Czaplewski 1996; Czaplewski et al. 2003) which was described as *T. robusta* (Czaplewski 1997). However, Velazco et al. (2014) noted that the type material consists only of isolated fragments and suggested that a *lavalii*-sized thyropterid existed in the Miocene, but certainly not *T. lavalii*. Therefore, the taxonomic assignment of these fossils is still unresolved (Velazco et al. 2014). We searched for the specimens which were said by Czaplewski et al. (2003) to have been deposited in the INGEOMINAS Paleontological Museum, but these specimens were not deposited there. Therefore, we follow Velazco et al.'s (2014) recommendation and recognize the La Venta fossils as *T. robusta*. Finally, the specimen mentioned by Reyes-Amaya et al. (2016) for the Andean region housed in the Museo Javeriano de Historia Natural "Lorezo Uribe, S.J.", Bogotá, Colombia (MPUJ-MAMM 1216), was reidentified as *T. tricolor* (Rodríguez-Posada et al. 2017). Thus, within Colombia, *T. lavalii* is known to occur only in the Amazon region.

Recently, Rosa et al. (2020) described the echolocation calls and shelters of *T. devivoi*. However, we think that the bat showed by Rosa et al. (2020: fig. 3), may be *T. lavalii*. We base our hypothesis on the ventral coloration, which is bicolored brown to yellowish and without a frosted appearance, as diagnostic for *T. lavalii*; the ventral pelage in *T. devivoi* is also bicolored, but frosted (Gregorin et al. 2006; Velazco et al. 2014). Additionally, the skull and mandible presented in Rosa et al.'s (2020) figure 3 correspond to a bat of the genus *Myotis*. The key character to assign this skull to the genus *Myotis* is the

presence of an emargination in the anterior edge of the palatal. In vespertilionid species, the premaxillaries lack palatal branches and are separated from one another, whereas *Thyroptera* bats have the nasal and palatal rami of the premaxillaries well developed (Koopman 1994). Also, the second and third upper premolars are minute in *Myotis* (Koopman 1994); although in *Thyroptera* these premolars are smaller than the fourth upper molar, they are not minute, and they are easily visible in lateral view without magnification.

Although *T. lavalii* has a wide distribution, including recent records in the Guianan Shield (García et al. 2019), and occurs in various ecosystems such as forests and savannas, it is still an uncommon species known only by scattered localities. In most of the localities, *T. lavalii* is associated with swamp-forest habitats with high, *Mauritia flexuosa* palms (Pine 1993; Solari et al. 2004). We captured *T. lavalii* in a similar habitat, although at our site the original vegetation was severely disturbed, with the forest cover—excepting for some *Mauritia* palms—removed. The surrounding vegetation was mainly composed of secondary forest. This could suggest that the species maintains a strong relationship with *Mauritia* palms but tolerates high human impact (Lee 2019).

Knowledge of the bat diversity in the Colombian Amazon is very poor. In a region of over 477,000 km², only five inventories of bats have been published. These inventories include the Sierra de la Macarena (Sánchez-Palomino et al. 1993), Serranía de Chiribiquete (Montengro and Romero-Ruiz 1999; Mantilla-Meluk et al. 2017),

Parque Nacional Natural La Paya (Polanco-Ochoa et al. 1999), and Serranía de la Lindosa (Morales-Martínez et al. 2020). This noticeable knowledge gap should be of great concern, especially if we consider the ongoing deforestation, biodiversity loss, and climate change. It is crucial to expand studies focussing on the biodiversity of the Colombian Amazon region and use their results in conservation actions, such as the recent expansion of Chiribiquete National Park, the largest protected area in the region (FCDS 2019).

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Authors' Contributions

All authors contributed to writing the paper. DMM collected the specimen took its images. MRP revised *Thyroptera lavalii* from Peru. MRP and SGA measured the specimens. SGA made the map. AMS generated the COI sequence and performed molecular analyses. DMM, SGA, and AMS edited manuscript figures.

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Appendix

Table A1. GenBank accession numbers of COI sequences used in the phylogenetic analyses.

Sequence number	Species	Accession numbers	Voucher Code	Source
1	<i>Thyroptera tricolor</i>	JF446603	ROM 108311	Clare et al. 2011
2	<i>Thyroptera tricolor</i>	JF446604	ROM 108312	Clare et al. 2011
3	<i>Thyroptera tricolor</i>	JF446605	ROM 108313	Clare et al. 2011
4	<i>Thyroptera tricolor</i>	JF446606	ROM F44044	Clare et al. 2011
5	<i>Thyroptera tricolor</i>	EF080732	ROM 101079	Clare et al. 2007
6	<i>Thyroptera tricolor</i>	EF080733	ROM 108524	Clare et al. 2007
7	<i>Thyroptera tricolor</i>	JF455953	ROM 101129	Clare et al. 2011
8	<i>Thyroptera tricolor</i>	JF455954	ROM 98200	Clare et al. 2011
9	<i>Thyroptera tricolor</i>	JF455955	ROM 98201	Clare et al. 2011
10	<i>Thyroptera tricolor</i>	JF455956	ROM 98203	Clare et al. 2011
11	<i>Thyroptera tricolor</i>	JF455957	ROM 98199	Clare et al. 2011
12	<i>Thyroptera tricolor</i>	JF448139	ROM 113925	Clare et al. 2011
13	<i>Thyroptera tricolor</i>	JF447741	ROM 113952	Clare et al. 2011
14	<i>Thyroptera tricolor</i>	JF447742	ROM 113951	Clare et al. 2011
15	<i>Thyroptera tricolor</i>	EU097046	ROM 117616	Borisenko et al. 2008
16	<i>Thyroptera tricolor</i>	EU097047	ROM 117569	Borisenko et al. 2008
17	<i>Thyroptera tricolor</i>	EU097048	ROM 117568	Borisenko et al. 2008
18	<i>Thyroptera tricolor</i>	EU097049	ROM 117636	Borisenko et al. 2008
19	<i>Thyroptera tricolor</i>	JF447743	ROM 113953	Clare et al. 2011
20	<i>Thyroptera tricolor</i>	JF448138	ROM 113956	Clare et al. 2011
21	<i>Thyroptera tricolor</i>	JF449236	ROM 10447	Clare et al. 2011
22	<i>Thyroptera tricolor</i>	JF449237	ROM 106160	Clare et al. 2011
23	<i>Thyroptera tricolor</i>	JF449238	ROM 118834	Clare et al. 2011
24	<i>Thyroptera tricolor</i>	JF449239	ROM 118836	Clare et al. 2011
25	<i>Thyroptera tricolor</i>	JF449234	ROM 105609	Clare et al. 2011
26	<i>Thyroptera tricolor</i>	JF449235	ROM 106318	Clare et al. 2011
27	<i>Thyroptera lavalii</i>	JF449231	ROM 105215	Clare et al. 2011
28	<i>Thyroptera lavalii</i>	JF449233	ROM 105667	Clare et al. 2011
29	<i>Thyroptera lavalii</i>	JF449232	ROM 104026	Clare et al. 2011
30	<i>Thyroptera lavalii</i>	MW173609	ICN 25000	This study
Outgroup	<i>Furipterus horrens</i>	EF080358	ROM 100202	Clare et al. 2007
Outgroup	<i>Micronycteris megalotis</i>	EU096780	ROM 117357	Borisenko et al. 2008