



A NEW SPECIES OF WREN (TROGLODYTIDAE: *THRYOPHILUS*) FROM THE DRY CAUCA RIVER CANYON, NORTHWESTERN COLOMBIA

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ABSTRACT.—We describe a new species of wren in the genus *Thryophilus* (Troglodytidae) based on analysis of morphological, vocal, and genetic variation. Individuals of the new species are readily separated in the field or the museum from those of any other wren species, including its closest relatives *T. rufalbus* and *T. nicefori*, by a combination of traits including, but not limited to, plumage coloration of the upperparts, the pattern of barring on the wings and tail, overall smaller body size, a richer repertoire of syllable types, shorter trills, and distinctive terminal syllables. The new species is allopatrically distributed in relation to its congeners, being restricted to the dry Cauca River Canyon, a narrow inter-Andean valley enclosed by the Nechí Refuge rainforests and the northern sectors of the Western and Central Andes of Colombia. Individuals or pairs have been found only in remnant patches of dry forest and scrub at 250–850 m elevation. This newly discovered species is uncommon and threatened because of ongoing transformation of natural habitats in the Cauca River Canyon, and especially because of the planned construction of a major dam in the region; immediate conservation actions are thus imperative. Received 21 February 2012, accepted 19 May 2012.

Key words: Antioquia, duet, inter-Andean valley, Niceforo's Wren, Rufous-and-white Wren, systematics, *Thryothorus*, tropical dry forest.

Una Nueva Especie de Cucarachero (Troglodytidae) del Cañón del Río Cauca, Noroeste de Colombia

RESUMEN.—Describimos una nueva especie de cucarachero del género *Thryophilus* (Troglodytidae) con base en análisis de la variación morfológica, vocal y genética. Los individuos de esta especie nueva son diferenciables tanto en el campo como en el museo de cualquier otra especie de troglodítido, incluyendo sus parientes más cercanos *T. rufalbus* y *T. nicefori*, por una combinación de características que incluyen, pero no se limitan a: la coloración dorsal del plumaje, el patrón de barrado de las alas y la cola, un tamaño más pequeño, un repertorio más rico de sílabas, trinos más cortos, y sílabas terminales distintas. La nueva especie está distribuida alopatricamente en relación con sus congeneres; está restringida al cañón del río Cauca, un valle interandino angosto y seco encerrado por las selvas húmedas del refugio de Nechí y por el norte de las cordilleras Occidental y Central de Colombia. Algunos individuos o parejas han sido encontrados en los remanentes de bosque y matorrales secos entre 250 y 850 m de elevación. La nueva especie no es común y está amenazada de extinción debido a la pérdida creciente de los hábitats naturales en el cañón del Cauca y especialmente debido a la inundación planeada por la construcción de una gran represa hidroeléctrica. Por lo tanto, es indispensable emprender acciones de conservación de inmediato.



This article contains sound files that may be accessed by reading the full-text version of this article online at dx.doi.org/10.1525/auk.2012.12028.

World, and it reaches its highest species diversity in Central America and northwestern South America (Barker 2004, Kroodsma and

WITH ABOUT 85 species, Troglodytidae is the largest family of the avian clade Passerida living in the New

Brewer 2005, Johansson et al. 2008). *Thryothorus* used to be the largest genus in the family, with 27 species (Dickinson 2003, Kroodsma and Brewer 2005), but molecular phylogenetic studies revealed that it represented a polyphyletic assemblage of at least four independent clades now recognized at the genus level (Barker 2004, Mann et al. 2006, Remsen et al. 2012). The relatively conserved overall shape, coloration, and plumage patterns of "*Thryothorus*" wrens not only hampered the recognition of their phylogenetic diversity (Barker 2004, Mann et al. 2006), but also suggests that cryptic species of wrens in this group

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might be uncovered with field and museum work, and with the advent of integrative studies of species limits. However, disentangling cryptic diversity in wrens is complicated by their elaborate, rich, and culturally transmitted vocal repertoires.

Thryophilus (Baird 1874) is one of the genera resurrected to solve the four-fold polyphyly of “*Thryothorus*” (Mann et al. 2006, Remsen et al. 2012). *Thryophilus* currently consists of four species of medium-sized wrens with white supercilia, rufous or grayish-brown backs, and whitish underparts. Two species of *Thryophilus* (total three taxa) occur in northern South America: *T. rufalbus* (Rufous-and-white Wren) in the Caribbean lowlands (*T. r. cumanensis*) and east of the Andes (*T. r. minlosi*), and *T. nicefori* (Niceforo’s Wren) in the dry Chicamocha Valley of the Eastern Andes of Colombia (Kroodsma and Brewer 2005, Valderrama et al. 2007). For four decades, *T. nicefori* was known only from a handful of specimens from a single locality (Meyer de Schauensee 1946, López-Lanús and Cadena 2002), and despite its phenotypic distinctiveness, an unvouchered verbal description of its song rendered doubts about its species rank by claiming it was identical to that of *T. rufalbus* (Collar et al. 1992). Detailed studies have subsequently demonstrated that *T. nicefori* is distinct from any subspecies of *T. rufalbus* in vocalizations and morphology (Valderrama et al. 2007, C. D. Cadena et al. unpubl. data). No *Thryophilus* species is known to occur in Colombia outside the described ranges of *T. rufalbus* and *T. nicefori*.

On 26 February 2010, C. E. Lara discovered a *Thryothorus*-like wren in the Cauca River Canyon in Antioquia, northwestern Colombia. Since then, we have discovered pairs of the same wren in several locations along this narrow stretch of the northern portion of the Cauca Valley, where, to the best of our knowledge, no specimens, sound recordings, or observations of any *Thryothorus*-like wren had been reported (Haffer 1967b, Hilty and Brown 1986, Kroodsma and Brewer 2005). Our field observations,

photographs, and recently collected specimens indicate that this newly discovered wren is similar in plumage pattern and coloration to *Thryophilus nicefori* and to *T. rufalbus*. A study of data on natural history, distribution, vocalizations, morphology, and genetic variation led us to conclude that the wren from Antioquia indeed belongs to the genus *Thryophilus* and that it is readily separated from any other wren, including *T. rufalbus* and *T. nicefori*. Thus, we propose to name this recently discovered population as a new species:

***Thryophilus sernai*, sp. nov.**

Antioquia Wren

Cucarachero Paísa (Spanish)

Holotype.—Adult male deposited at the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN) number 37848; from vereda El Espinal, ~3.2 km SSW Santa Fé de Antioquia, west bank of the Cauca River, Department of Antioquia, Colombia (6°31′55″N, 75°49′54″W; 515 m elevation); collected by C. E. Lara on 15 March 2010 and prepared by W. A. Múnera. Standard morphometric measurements are shown in Table 1. Hologenotype (Chakrabarty 2010) sequences of the mitochondrial gene cytochrome-*b* (*cyt-b*) deposited in GenBank (accession no. JX013498). Sound recordings of the song of the holotype were recorded by C. E. Lara and deposited in the Banco de Sonidos Animales, Instituto Alexander von Humboldt (BSA 22001–22002).

Diagnosis: Morphology.—A typical medium-sized wren, assignable to the genus *Thryophilus* by overall appearance, size, and coloration (see Fig. 1), and by its nostrils lacking opercula and being relatively small, oval, and nonperforate (vs. elongated and operculate in *Pheugopedius*; Baird 1874, Ridgway 1904). Sexes are similar in plumage. Specimens of *T. sernai* are readily separated from other

TABLE 1. Mean (\pm SE) morphometric measurements (mm) and body mass (g) of *Thryophilus sernai* sp. nov., *T. nicefori*, and different subspecies of *T. rufalbus*. Sample sizes are indicated in parentheses.

Taxa	Mass (g)	Wing ^a	Tail	Tarsus	Culmen ^b	Bill length ^c	Bill height ^d	Bill width ^d
Males								
<i>T. sernai</i> sp. nov. (holotype)	21.9	62.2	53.7	24.5	20	12.4	4.3	3.7
<i>T. sernai</i> sp. nov. (paratype)	21.4	62.6	55.2	24	20	11.8	4.2	3.4
<i>T. sernai</i> sp. nov. (2)	21.7 \pm 0.3	62.4 \pm 0.2	54.4 \pm 0.8	24.3 \pm 0.3	20.0 \pm 0.0	12.1 \pm 0.3	4.3 \pm 0.0	3.6 \pm 0.2
<i>T. nicefori</i> (3)	27.4 \pm 0.2	69.4 \pm 0.5	55.1 \pm 0.5	24.7 \pm 0.1	23.4 \pm 0.2	14.1 \pm 0.1	4.6 \pm 0.1	3.7 \pm 0.1
<i>T. rufalbus cumanensis</i> (7)	24.9 \pm 0.5	69.0 \pm 1.3	52.2 \pm 0.6	24.8 \pm 0.3	20.7 \pm 0.5	12.5 \pm 0.3	4.7 \pm 0.1	3.7 \pm 0.1
<i>T. r. minlosi</i> (9)	24.6 \pm 0.3 (4)	67.9 \pm 0.4	49.4 \pm 0.6	24.4 \pm 0.1	20.7 \pm 0.4	12.4 \pm 0.2	4.5 \pm 0.1	3.5 \pm 0.1
<i>T. r. castanonotus</i> (6)	26.9 \pm 0.6	71.0 \pm 0.9	50.9 \pm 1.9 (5)	24.4 \pm 0.4	22.3 \pm 0.3	13.1 \pm 0.2	4.5 \pm 0.1	3.7 \pm 0.1
<i>T. rufalbus</i> (Panama) (2)	27.8 \pm 0.3	70.3 \pm 0.8	49.2 \pm 1.0	24.8 \pm 1.2	22.1 \pm 0.2	13.3 \pm 0.0	4.2 \pm 0.0	3.7 \pm 0.1
<i>T. r. transfinis</i> (1)	—	70	55.7	23.2	21.3	11.8	4.3	3.7
Females								
<i>T. sernai</i> sp. nov. (paratype)	22.9	58.9	48.9	22.9	19.6	11.3	4	3.4
<i>T. nicefori</i> (1)	26	65.3	53.4	23.8	22.7	13.7	4.1	3.5
<i>T. r. cumanensis</i> (2)	24 (1)	63.2 \pm 1.3	44.9 \pm 1.6	23.6 \pm 0.9	21.1 \pm 1.5	12.7 \pm 0.6	4.8 \pm 0.4	3.6 \pm 0.3
<i>T. r. minlosi</i> (9)	23.3 \pm 1.6 (5)	61.4 \pm 0.6	45.2 \pm 0.7	23.6 \pm 0.4	20.1 \pm 0.2	12.1 \pm 0.3	4.3 \pm 0.1	3.5 \pm 0.1
<i>T. r. castanonotus</i> (9)	24.7 \pm 0.6 (7)	66.2 \pm 0.9	47.4 \pm 1.9 (8)	23.3 \pm 0.4	21.8 \pm 0.3 (8)	12.5 \pm 0.2 (8)	4.31 \pm 0.1	3.5 \pm 0.1
<i>T. rufalbus</i> (Panama) (1)	23.2	65	46.2	23.1	20.2	12.3	4.4	3.7
<i>T. r. transfinis</i> (2)	—	67.8 \pm 1.3	53.6 \pm 0.9	22.5 \pm 0.3	21.5 \pm 0.1	12.4 \pm 0.4	4.3 \pm 0.1	3.6 \pm 0.1

^aFlattened wing chord.

^bTotal culmen from base of bill at skull to bill tip.

^cLength from anterior edge of nares to bill tip.

^dTaken at anterior edge of nares.



FIG. 1. Wrens in the genus *Thryophilus* from northwestern South America, and a detail of their tail pattern. (Top) Rufous-and-white Wren (*T. rufalbus*); center: Niceforo's Wren (*T. nicefori*); (bottom) the newly discovered Antioquia Wren (*T. sernai* sp. nov.). Original watercolor by Daniel F. Lane.



FIG. 2. (A) *Thryophilus sernai* sp. nov. from Santa Fé de Antioquia (type locality), Antioquia, Colombia. (B) Dorsal view and (C) lateral view (left to right) of *T. rufalbus minlosi* (ICN 37667), *T. r. cumanensis* (ICN 34936), *T. sernai* sp. nov. (male paratype, Andes-O 667), and *T. nicefori* (ICN 36026). Photographs by C. E. Lara.

Thryophilus taxa by plumage coloration and morphometrics. In coloration and pattern, *T. sernai* is similar to *T. rufalbus*, but (1) upperparts are paler, more cinnamon-brown rather than bright or dark rufous; (2) the blackish barring of the wings and tail is decidedly much finer, tending to break up into spots on the rectrices; (3) the white superciliary is narrower; (4) the dark streaking on the cheeks is brownish and blurry rather than blackish and distinct; and (5) the underparts are more extensively tinged with pale brownish, the flanks in particular duller brown, without rufous tones. *Thryophilus sernai* is also similar to *T. nicefori*, which differs in (1) being decidedly darker, colder brown above; (2) with faint black barring on the dorsum and uppertail coverts; (3) barring of the wings and tail much heavier and blacker; and (4) sides and flanks more grayish-brown than in the new species (Fig. 2). Morphometric and body-mass data of the new species and other *Thryophilus* taxa are presented in Table 1. *Thryophilus sernai* is smaller in body mass and wing length than both *T. rufalbus* and *T. nicefori*. The new species has a smaller bill than *T. nicefori*, and it tends to have a longer tail than most subspecies of *T. rufalbus* (Table 2).

Diagnosis: Vocalizations.—Male and female *T. sernai* sing melodious flute-like songs consisting of varied introductory syllables followed by repeated trilled syllables and a terminal frequency-modulated syllable. Overall, the vocalizations of the new species are structurally similar to those of *T. rufalbus* and *T. nicefori* (Mennill and Vehrencamp 2005, Valderrama et al. 2007, Mann et al. 2009); however, the songs of *T. sernai* are distinctive in nine acoustic variables (Table 3). In particular, the songs of *T. sernai* have a richer repertoire of syllable types, shorter trills, lower number of trill syllables, a distinctive terminal syllable with more modulations, and higher spectral frequencies than other taxa in *Thryophilus* (for details, see below).

Description of holotype.—A wren in the genus *Thryophilus*, with pileum dull brown (near Cinnamon Brown 33; capitalized colors follow Smithe 1975); nape slightly paler, shading to a paler, brighter hue (near Mikado Brown 121C) over most of the back, and to a brighter color (Cinnamon 123A) on the posterior rump and upper tail-coverts. The outer webs of the remiges, and the entire feathers of the innermost secondaries, similar or slightly paler (between Cinnamon 123A and Sayal Brown 223C) and evenly and lightly barred with blackish. Rectrices Cinnamon (123A) to Clay Color (26), barred and spotted with black (the black bars much narrower than the brown areas and about 1–1.5 mm thick). Throat, breast, and median abdomen white, tinged with buffy brown; sides pale dull brown (near Light Drab 119C but less grayish); flanks brighter, darker brown (closer to Sayal Brown 223C); and undertail coverts white, sparsely and broadly barred

TABLE 2. Results of *t*-tests comparing the means of five morphological variables between *Thryophilus sernai* sp. nov. and other four taxa of *Thryophilus* from northern South America and southern Central America. Asterisks indicate statistically significant differences at the 95% confidence level (degrees of freedom are shown in parentheses).

<i>T. sernai</i> comparison	Mass	Wing	Tail	Tarsus	Culmen
vs. <i>T. nicefori</i> (6)	–8.65*	–4.43*	–1.21	–1.37	–11.78*
vs. <i>T. rufalbus</i>					
<i>cumanensis</i> (11)	–3.27* (10)	–2.65*	–0.84	–1.16	–1.13
vs. <i>T. r. minlosi</i> (20)	–1.16 (11)	–1.56	–2.93*	–0.35	–0.97
vs. <i>T. r. castanonotus</i>					
(15)	–2.97*	–3.19* (17)	1.73	–0.21 (17)	–4.53*

TABLE 3. Comparative song structure of *Thryophilus sernai* sp. nov., *T. nicefori*, and *T. rufalbus*. Values are means \pm SE. All Kruskal-Wallis (KW) tests were statistically significant ($P < 0.0001$).

Acoustic variable	<i>T. sernai</i>	<i>T. nicefori</i>	<i>T. rufalbus</i>	KW χ^2
Number of frequency modulations of terminal syllable	2.8 \pm 0.1	1.8 \pm 0.1	0.3 \pm 0.1	108.4
Number of syllables	7.9 \pm 0.4	9.9 \pm 0.5	17.1 \pm 0.7	187.5
Number of syllable types	5.1 \pm 0.2	3.6 \pm 0.1	4.1 \pm 0.1	53.1
Song length (s)	2.28 \pm 0.06	1.91 \pm 0.03	2.52 \pm 0.04	95.6
Trill length (s)	0.44 \pm 0.03	0.69 \pm 0.02	1.16 \pm 0.04	187.5
Number of trill syllables	3.1 \pm 0.3	7.1 \pm 0.4	12.7 \pm 0.7	133.6
Bandwidth of terminal syllable (kHz)	2.01 \pm 0.09	0.74 \pm 0.05	0.24 \pm 0.03	167.4
Trill frequency of maximum amplitude (kHz)	1.16 \pm 0.02	1.04 \pm 0.01	0.94 \pm 0.01	228.6
Frequency at maximum amplitude of terminal syllable (kHz)	2.37 \pm 0.09	1.94 \pm 0.05	1.58 \pm 0.04	86.8

blackish-brown (Raw Umber 223). Iris brown, eye ring pale yellow, maxilla blackish with whitish tomium, mandible grayish-white, legs and feet gray with paler gray soles. Mass 21.9 g, skull fully ossified, light fat, testes 2.4 \times 1.6 (left) and 2.0 \times 1.6 mm (right); in fresh plumage overall, no molt on wings or body, the pair of central rectrices molting symmetrically, sheathed, 50% grown.

Designation of paratypes.—Two specimens at the ornithological collection of Museo de Historia Natural, Universidad de los Andes, Bogotá (ANDES-O), numbers 667 (adult male) and 668 (adult female), taken by C. E. Lara and prepared by W. A. Múnera on 18 August 2010 at vereda Tefetanes, ~4.2 km northwest of San Jerónimo, east bank of the Cauca River, Department of Antioquia, Colombia (6°27'50"N, 75°45'48"W; 550 m elevation). Both specimens are in worn plumage with no molt, skulls fully ossified, and very light fat. The male paratype had enlarged testes (left 8.3 \times 4.5 mm, right 5.7 \times 3.6 mm) and weighed 21.4 g; it is slightly darker and duller brown above than the holotype; the remiges are paler (near Sayal Brown 223C) with the dark bars more brownish (near Raw Umber 123); below much more heavily suffused with pale, dull brownish with the sides and flanks darker and duller. The female paratype is like the holotype in color, except that the median abdomen is tinged with pale, buffy-brown; it weighed 22.9 g and its ovary was enlarged (37 \times 11 mm).

Etymology.—The epithet honors the late Marco Antonio Serna Díaz (1936–1991), a Colombian naturalist from San Vicente Ferrer, Antioquia. Serna was an avid ornithologist and curator of birds, amphibians, and reptiles at the Museo San José de la Salle, and a professor of ornithology at Universidad de Antioquia. He was founder and president of the Sociedad Antioqueña de Ornitología. Serna's often underappreciated legacy has been foundational for the ongoing rise of ornithological and herpetological research in Antioquia, the department to which the new species is endemic.

REMARKS

Morphology.—We examined museum specimens of the other four described *Thryophilus* species and compared the external morphology of 55 specimens of *T. rufalbus*, *T. nicefori*, and *T. sernai* (see Appendix and Table 1) using univariate statistical tests of five traits (body mass, total culmen, wing chord, tail, and tarsus). Species of *Thryophilus* exhibit sexual dimorphism in size, with females being slightly smaller than males (Table 1). Because the same conclusions were obtained with and without separating the data by sex, and given the small number of museum specimens for some taxa, we combined

specimens of both sexes for comparisons. *Thryophilus sernai* has a smaller body mass, shorter bill, and shorter wings than *T. nicefori* and differs significantly from various subspecies of *T. rufalbus* in traits including body size, total culmen, and wing length (Table 2). Overall, measure by measure, *T. sernai* is morphometrically closest to *T. rufalbus minlosi* but differs significantly in tail length.

Vocalizations.—Both males and females of the new species produce similar songs, which can be emitted either as solos or as duets (Fig. 3). Male songs consist of 3–19 syllables, including 1–13 trill syllables, and 2–8 syllable types combined in a song of 2.21 s, on average (sound file 1). Female songs average 1.87 s, and consist of 4–11 syllables, 2–5 trill syllables and 3–6 syllable types. Female songs of *T. sernai* are similar to those of *T. nicefori* and *T. rufalbus* (Mennill and Vehrencamp 2005, Valderrama et al. 2007). Female songs have a higher mean (\pm SE) trill peak frequency (2,208.7 \pm 493.9 Hz) and terminal syllable peak frequency (3,281.6 \pm 733.8 Hz), compared with male songs (Table 3); females sing slightly longer trills (0.64 \pm 0.14 s) than males (0.44 \pm 0.03 s).

Pairs of *T. sernai* sing in duets by alternating or overlapping their songs. We recorded 86 duets, typically including one or two contributions from each individual in the sequences FM, FME, MFM, MFF, or MFFM (where M represents one song by a male and F represents one song by a female; Fig. 4). More rarely, individuals contributed more than two songs (e.g. FFMFM; Fig. 3). In 74.4% of duets ($n = 86$), the female initiated singing and was followed by the male to form the duet; in the remaining 25.6%, the male initiated singing and was followed by the female.

Males and females produce five types of calls, including two similar to calls produced by *T. nicefori* and *T. rufalbus* (i.e., “reow” and “click” calls) (sound file 2). We found five calls that, as with “reow” calls, are used for contact between pair members, whereas “clicks” are used as alarm calls (Fig. 5).

We conducted a multivariate statistical analysis of 54 songs of *T. sernai*, 175 songs of *T. nicefori*, and 240 songs of *T. rufalbus* from across its range. To quantify the distinctiveness in songs of *T. sernai* in relation to *T. rufalbus* and *T. nicefori*, we conducted a discriminant analysis (DA), extending a vocal data set from a previous study (Valderrama et al. 2007). We randomly selected a balanced subset of five songs from each of four individuals per species, and one song from each of five subspecies of *T. rufalbus* and from the species *T. nicefori* and *T. sernai*. We subsequently cross-validated the analysis by verifying the assignment to the correct species for the remaining 393 songs from all three species. The songs of the new species clustered in the multivariate vocal space and

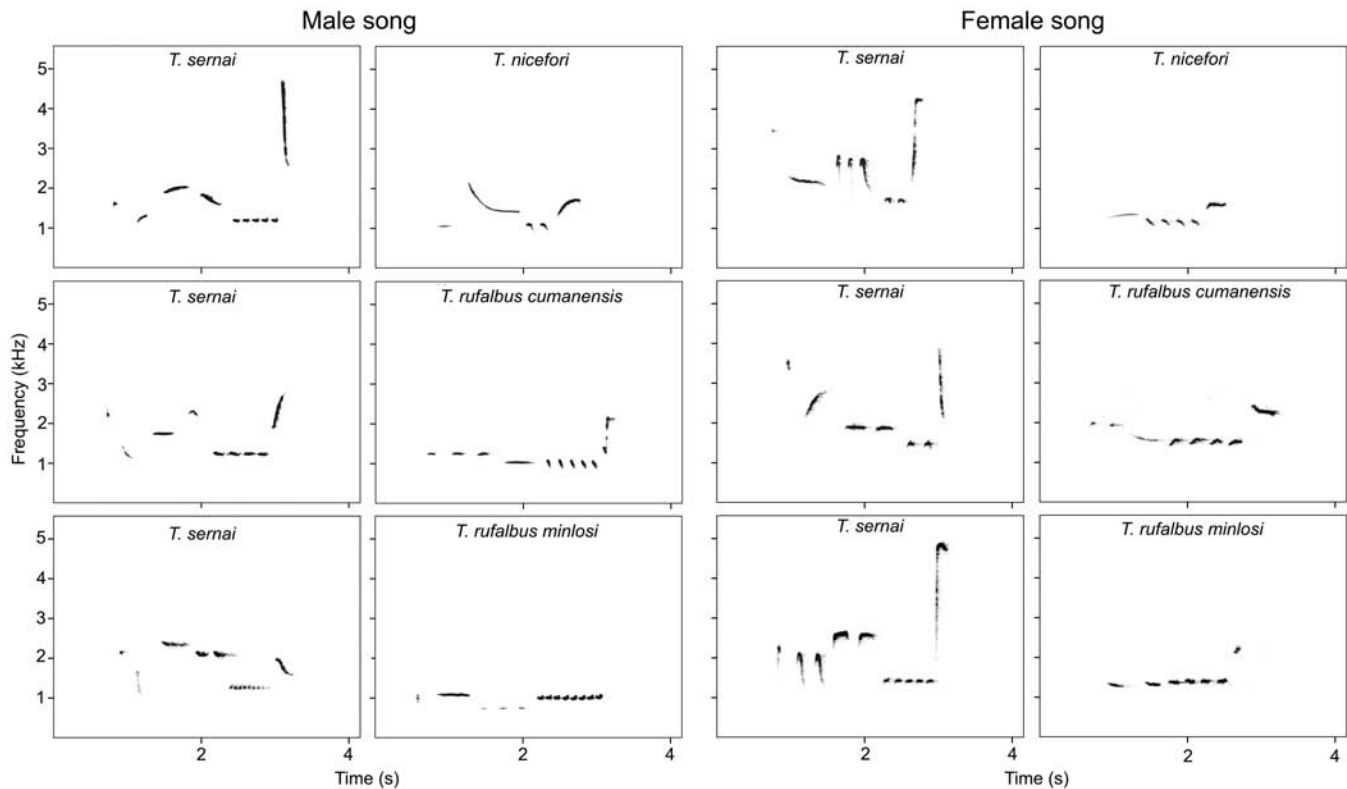


FIG. 3. Three examples of songs of males (left) and females (right) of *Thyrophilus sernai* sp. nov. in comparison to the songs of *T. nicefori*, *T. rufalbus cumanensis*, and *T. rufalbus minlosi*. Song of the holotype of *T. sernai* is available for listening (sound file 1; listen to audio file by reading the full-text version of this article online at [dx.doi.org/10.1525/auk.2012.12028](https://doi.org/10.1525/auk.2012.12028)).

could be discriminated from the songs of *T. nicefori* and *T. rufalbus* (Wilks's $\lambda = 0.05$, $F = 26.02$, $P < 0.0001$; Fig. 6A). Overall, the analysis assigned songs to the correct species with 83.7% accuracy. Songs of *T. sernai* were classified with 93.1% accuracy, whereas songs of *T. nicefori* and *T. rufalbus* were classified with 87.4% and 80.0% accuracy, respectively. The DA was mainly influenced by trill length, the number of syllables, and syllable types (Table 4).

We also conducted a separate DA including only taxa distributed in northern South America because they are most closely related (see below). We analyzed a balanced subset of 80 songs from *T. sernai*, *T. nicefori*, *T. r. cumanensis*, and *T. r. minlosi*, with five songs from each of four individuals per taxon. Our results support the distinction of the new species because it was acoustically separated from its closest relatives (Wilks's $\lambda = 0.01$, $F = 22.53$, $P < 0.001$; Fig. 6B). The DA was mainly influenced by the number of syllables, trill length, and number of trill syllables (Table 4). We cross-validated the analysis by verifying the assignment for the remaining 250 songs from these taxa; 91.2% of the songs of *T. sernai* were accurately assigned to this species, with the remaining 8.8% of songs incorrectly assigned to *T. nicefori*.

Systematics.—We examined the phylogenetic placement of the new species in the Troglodytidae and its evolutionary differentiation in relation to other *Thyrophilus* taxa by sequencing a segment of the mitochondrial gene *cyt-b* (1,041 base pairs) for *T. nicefori*, *T. rufalbus*, and the three specimens of the type series of *T. sernai*. DNA sequences were obtained for a larger study on

the evolutionary differentiation of *Thyrophilus* wrens (C. D. Cadena et al. unpubl. data), and complemented with data from previous studies to increase taxon sampling (Barker 2004, 2007; Mann et al. 2006; Burney and Brumfield 2009). Outgroup taxa were selected to include major groups in the Troglodytidae (Mann et al. 2006) and to encompass the four lineages formerly included in “*Thryothorus*” (i.e., strict-sense *Thryothorus*, *Cantorchilus*, *Pheugopedius*, and *Thyrophilus*). For polymerase chain reaction and sequencing, we used primers L14990 and H16065 (Kocher et al. 1989, Helm-Bychowski and Cracraft 1993) and generally followed protocols described by Barker (2004). New sequences were deposited in GenBank (accession nos. JX013495–JX013500). Maximum likelihood (ML) in RAXML, version 7.2.6 (Stamatakis 2006), and Bayesian inference (BI) in MRBAYES, version 3.1.2 (Huelsenbeck and Ronquist 2001), were used to estimate phylogenetic relationships via the CIPRES Science Gateway 3.1 portal (Miller et al. 2010). RAXML implemented the GTR+G model and used the automatic rapid-bootstrapping option (-# autoMRE) to assess nodal support. The BI analysis consisted of four runs (four MCMC chains, 20 million generations, of which 50% was discarded as burn-in) using default settings for priors. For this analysis, the GTR+I+G substitution model was selected on the basis of Akaike's information criterion using MRMODELTEST, version 2.3 (Nylander 2004). An earlier phylogenetic study recommended resurrecting the genus *Thyrophilus* Baird, 1874, for members of a clade formed by *T. sinaloa*, *T. pleurostictus*, and *T. rufalbus* (Mann et al. 2006). That study did

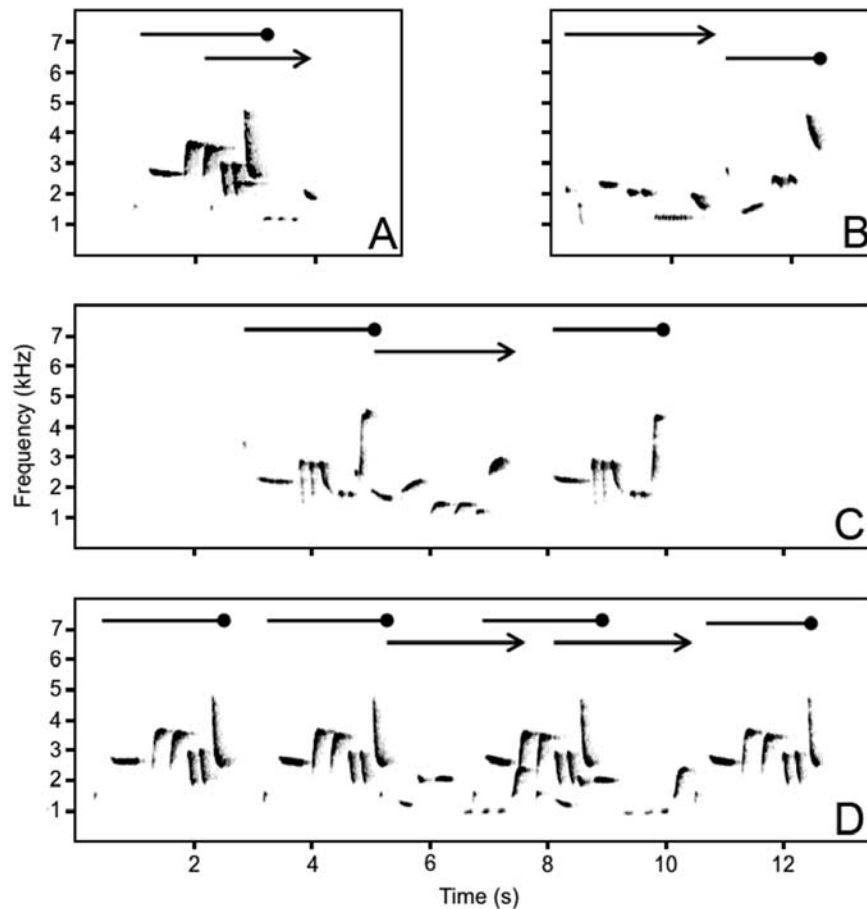


FIG. 4. Four duet sequences by male and female of *Thryophilus sernai* sp. nov. (A, B) Simple duets with one contribution from male and female. (C) More complex duets with at least two songs from one individual. (D) More than two songs from both male and female. Male and female songs are indicated with arrows and bold circles, respectively.

not consider samples of *T. nicefori*, but this species was predicted to belong to the genus *Thryophilus* on the basis of its morphological similarity to *T. rufalbus* as well as song style (Mann et al. 2009). Our phylogenetic analyses confirmed that *T. nicefori* belongs in *Thryophilus* and further indicated that *T. sernai* is a distinct lineage within this clade. Moreover, *T. sernai* was phylogenetically nested within a paraphyletic *T. rufalbus*, which also included the distinct species *T. nicefori* (Fig. 7). The specific affinities of *T. sernai* in relation to *T. nicefori* and to some populations of *T. rufalbus* could not be resolved because of the lack of statistical support, presumably owing to rapid differentiation (Fig. 7). The maximum sequence divergence observed between *T. sernai* and subspecies of *T. rufalbus* was 6.3% (with nominate *rufalbus* from Guatemala), whereas the minimum divergence was 2.7% (with *cumanensis* of northern Colombia). Sequence divergence with *T. nicefori* and *T. r. minlosi* was 3.8% and 3.6%, respectively (Table 5).

Evidence for species rank.—The proposed new species is a diagnosable lineage with respect to other wrens, including *T. nicefori* and populations of *T. rufalbus*, on the basis of joint evidence from plumage pattern, morphometrics, vocalizations, and genetic variation, coupled with its unique geographic distribution. To achieve its degree of phenotypic differentiation and monophyly, *T. sernai* has likely been isolated from *T. nicefori* and *T. rufalbus*

for a considerable period. Indeed, our results suggest that *T. sernai* has been evolving from its closest relatives for 1.4–2 million years, assuming a 2% rate of nucleotide substitution per million years for avian *cyt-b* (Weir and Schluter 2008). Thus, *T. sernai* is an independent evolutionary unit that represents a segment of a population lineage, which validates its species rank under the general or unified species concept (de Queiroz 1998, 2005).

Because *T. sernai* is a diagnosable taxon, it is also clearly a valid species under the phylogenetic species concept (Cracraft 1983) and, minimally, a subspecies under the biological species concept (BSC; Remsen 2010). A more problematic task is assessing the taxonomic status of *T. sernai* under the BSC (Mayr 1963, Johnson et al. 1999), which emphasizes the existence of reproductive isolation between populations. Because *T. sernai* is truly allopatric with respect to *T. nicefori* and *T. rufalbus* (see below; Fig. 8), we cannot ascertain that the lines of evidence that define the new taxon reflect the existence of reproductive isolating mechanisms, because they may simply be the result of geographic isolation. Nonetheless, we note that the distinct traits of *T. sernai*, including plumage and song, may be involved in territory defense, courtship, and mating, and that differences in plumage and song are known to function as isolating mechanisms in birds (Baptista and Kroodsma 2001, Remsen 2005, Price 2008). Thus, it is likely that *T. sernai* has differentiated from *T. nicefori* and

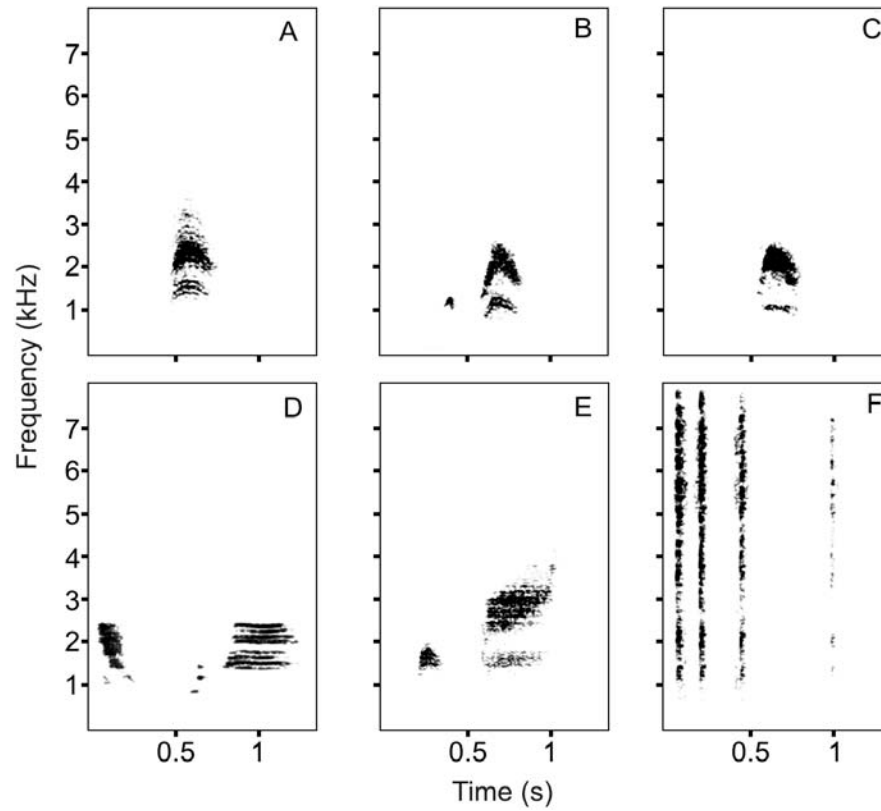


FIG. 5. Calls of *Thryophilus sernai* sp. nov. Examples of (A–E) “reow” calls and (F) stereotyped “click” calls. The latter call is available for listening (sound file 2; listen to audio file by reading the full-text version of this article online at dx.doi.org/10.1525/auk.2012.12028).

T. rufalbus to the point that they would behave as reproductively isolated units should they come into contact. In comparison to the differences in plumage and song existing between the two *Thryophilus* species pairs known to be sympatric (*pleurostictus-sinaloa* and *pleurostictus-rufalbus*), *T. sernai* is arguably less different from *T. nicefori* and *T. rufalbus*. However, greater divergence is expected between sympatric pairs of species than between allopatric pairs (Price 2008). Furthermore, in the context of currently accepted species limits among members of the *T. rufalbus* complex (Valderrama et al. 2007, Remsen et al. 2012), *T. sernai* appears to be just as divergent (or more so) from *T. rufalbus* and *T. nicefori* as these two good species are divergent from each other. Therefore, the weight of evidence indicates that *T. sernai*, *T. nicefori*, and *T. rufalbus* have diverged to the point associated with reproductive isolation in the group, which is consistent with comparative frameworks (see Isler et al. 1998, Helbig et al. 2002, Remsen 2010). Thus, we also recommend recognizing *T. sernai* as a species-level taxon under the BSC.

The recognition of *T. sernai* based on the discussion above implies that *T. rufalbus* may be a paraphyletic species because the *cyt-b* haplotypes of the new species are well nested within a clade formed by haplotypes that correspond to populations of *T. rufalbus*. Instead of invalidating the treatment of *T. sernai* (and of *T. nicefori*, which is also nested within *T. rufalbus*) as a species, the inferred paraphyletic pattern in the *cyt-b* genealogy suggests that *T. rufalbus* as currently defined might comprise multiple species, which highlights the need for a species delimitation analysis and comprehensive analyses of vocal and

morphological differentiation across the complex. For example, the forms *T. r. minlosi* and *T. r. cumanensis* exhibit some differences in vocalizations (Valderrama et al. 2007) and may come into contact near low passes in northern Venezuela and in the northern Eastern Andes of Colombia, where they may be behaving as separate species. In addition, the existence of highly divergent phylogroups in Central America (present study, C. D. Cadena et al. unpubl. data), which are also phenotypically distinct from other populations, suggests that more than one species might be involved. However, we note that the paraphyly of species is an expected outcome of speciation processes in which differentiation occurs in peripheral populations (i.e., peripatric speciation; Mayr 1963), and thus the recognition of paraphyletic species is not at odds with the species concepts mentioned above (Funk and Omland 2003). Indeed, the scenario of speciation by geographic isolation at the periphery of the distribution range of a formerly widespread taxon might account for the evolution of the range-restricted species *T. sernai* and *T. nicefori*, two of the southernmost members of the complex. In sum, we believe that our data are consistent with the consideration of *T. sernai* as a valid species under various species concepts, and that attention should now be turned to assessing whether disjunct populations of *T. rufalbus* are sufficiently differentiated to be treated as distinct species. We emphasize, however, that the paraphyly of *T. rufalbus* in the *cyt-b* gene tree is not conclusive evidence of species paraphyly because the *cyt-b* genealogy may be potentially in conflict with the true species tree; species-tree

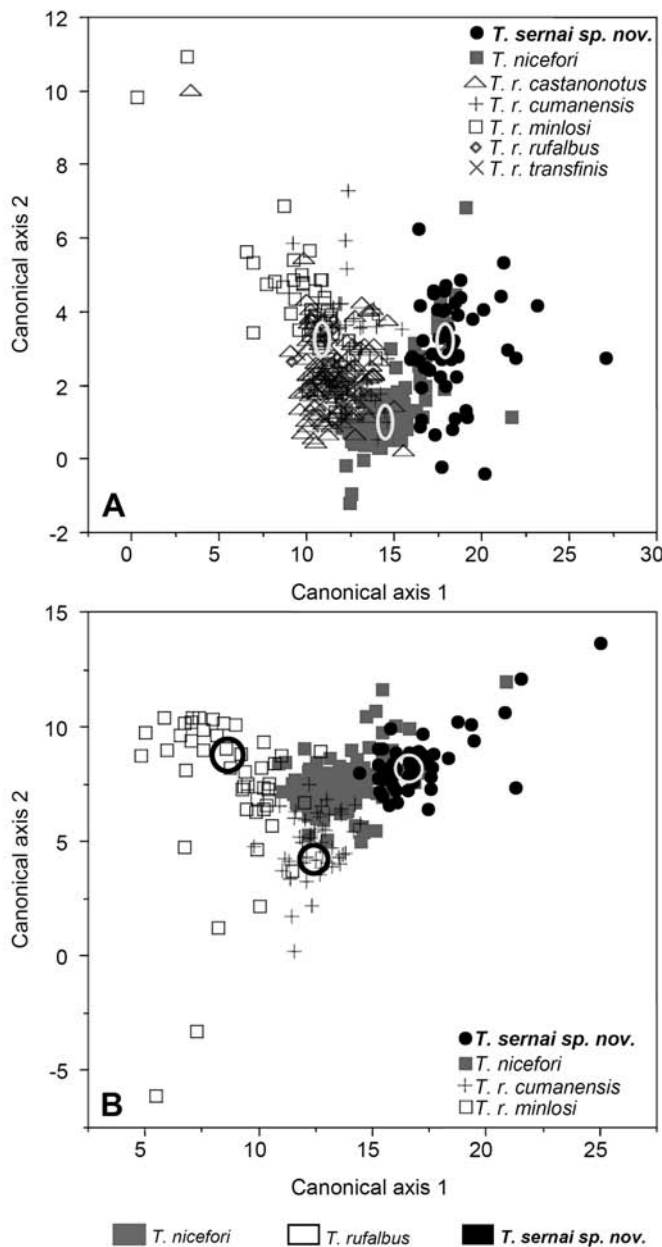


FIG. 6. Multivariate vocal space of wrens in the genus *Thryophilus* from two discriminant analyses (DA) based on nine song traits. (A) Scatter plot of the first two canonical functions that discriminated songs of *T. sernai* sp. nov., *T. nicefori*, and five subspecies of *T. rufalbus*. (B) Scatter plot from a similar DA, but including only the two South American subspecies of *T. rufalbus*: *cumanensis* and *minlosi*.

analysis of additional loci and samples are necessary to address this possibility.

Distribution.—*Thryophilus sernai* is known from six localities from both banks of the Cauca River Canyon, which separates the northern ends of the Western and Central Andes and is entirely confined to the Department of Antioquia (Fig. 8). The known records extend for ~150 km along this narrow valley from Ituango in the north to the border between Concordia and Salgar in the south,

TABLE 4. Results of two discriminant analyses of songs of wrens in the genus *Thryophilus*, based on nine acoustic variables. The first discriminant analysis included recordings of *T. sernai* sp. nov., *T. nicefori*, and the five subspecies of *T. rufalbus* with available sound recordings (Complete), whereas the second analysis (Subset) was focused on the four *Thryophilus* taxa from northern South America: *T. sernai*, *T. nicefori*, *T. r. cumanensis*, and *T. r. minlosi*. In bold are the values of acoustic variables that contributed to each discriminant analysis, with the highest loadings for the discrimination between groups in the first two canonical functions (CF).

Acoustic variable	Complete		Subset	
	CF1	CF2	CF1	CF2
Number of frequency modulations of terminal syllable	0.46	-0.39	0.28	-0.27
Number of syllables	-0.60	0.40	-0.28	-0.68
Number of syllable types	0.70	-0.03	0.43	0.53
Song length	0.27	0.46	0.51	-0.14
Trill length	-0.92	0.88	-1.25	-0.35
Number of trill syllables	0.54	-0.42	0.21	-0.74
Terminal syllable bandwidth	0.00	0.00	0.00	0.00
Trill frequency of maximum amplitude	0.01	0.00	0.00	0.01
Frequency at maximum amplitude of terminal syllable	0.00	0.00	0.00	0.00
Eigenvalue	8.70	1.18	8.06	3.09
Percentage of variance explained	88.01	11.99	66.07	25.34

at elevations of 250–850 m at localities within 7 km from the Cauca River. The new species is most likely restricted to the remnant dry-forest habitats (sensu Espinal 1992) found along this narrow stretch of the Cauca River and adjacent small tributaries. Therefore, its distribution may extend slightly farther north of Ituango and south to La Pintada according to the geographic limits of the Cauca River Canyon and the extent of appropriate habitat in the region. Medium-sized river gorges within this region with good stands of dry to semideciduous forests, such as the San Juan, Sinifaná, and Tonusco rivers, may harbor populations of *T. sernai*. Although we have not surveyed slopes above 850 m systematically, the upper elevational limit of *T. sernai* likely does not extend much beyond that elevation, which corresponds to a transitional zone from the dry forest zone to the humid premontane zone in the region (Espinal 1992).

Thryophilus species in northern South America occupy separate areas of tropical dry forest that are highly disjunct because of physical and ecological discontinuities (Haffer 1967b, Pennington et al. 2009). Dry inter-Andean valleys like the Cauca River Canyon are bounded by adjacent mountains and intervening lowlands receiving much higher rainfall (Pennington et al. 2010). *Thryophilus sernai* is separated from *T. rufalbus cumanensis* of the Caribbean plains of northern Colombia by the continuous lowland rainforests of the lower Cauca, Nechí, and middle Magdalena river basins (i.e., Nechí Refuge; Haffer 1967a), which surround the northern ends of the Western and Central cordilleras and enclose the Cauca River Canyon (Fig. 8). No wren in the genus *Thryophilus* has ever been found in the better-explored lowland rainforests of the Nechí Refuge (Haffer 1967a, Cracraft 1985). The range of *T. sernai* is further separated from that of *T. nicefori* and *T. rufalbus minlosi* by successive intervening discontinuities. Thus, the range of *T. sernai* is truly allopatric from that of congeners, and there are no possible areas of intergradation.

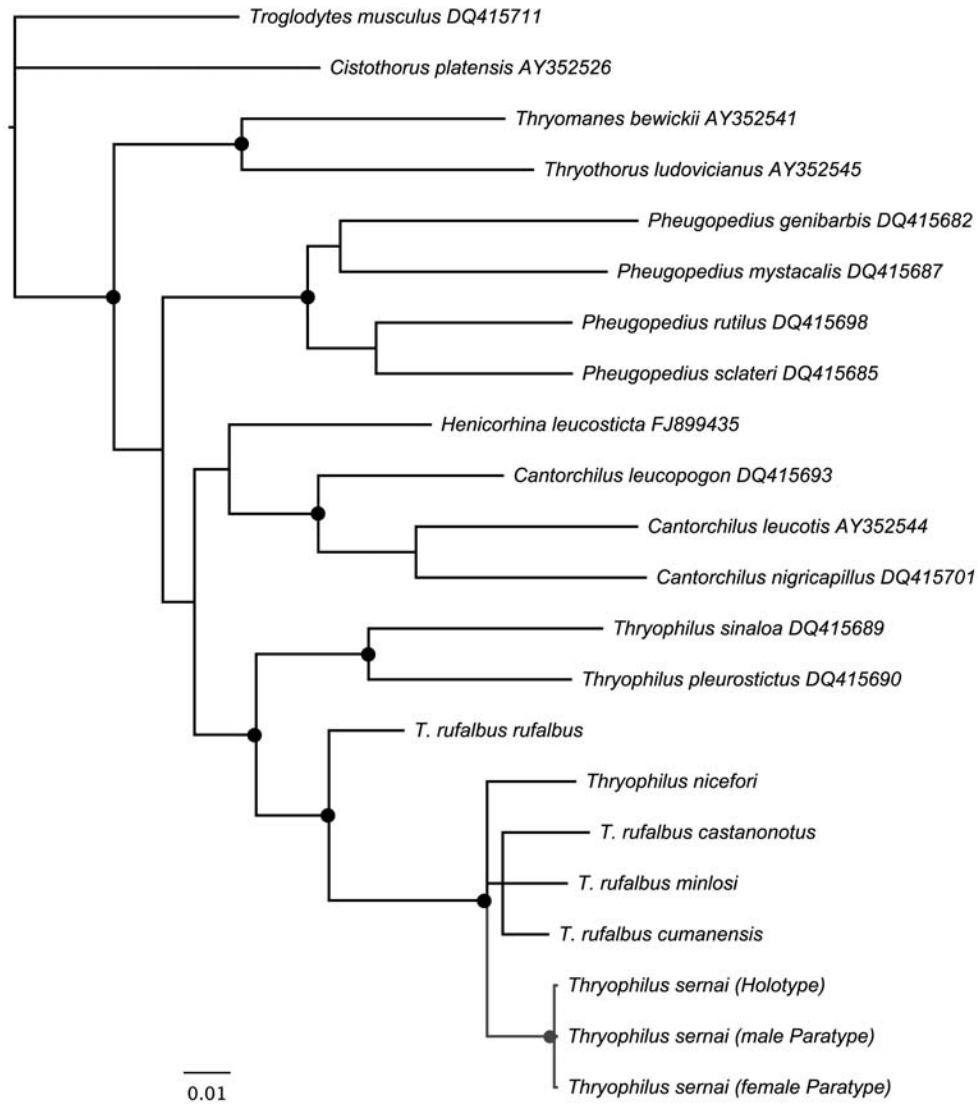


FIG. 7. Phylogenetic position of the new species in the genus *Thryophilus* based on cytochrome-*b* sequences. The tree is a 50% majority-rule consensus tree from the Bayesian analysis. Black dots on nodes indicate strong statistical support in Bayesian and maximum-likelihood analyses (>0.99 posterior probability and >95% bootstrap support, respectively).

TABLE 5. Pairwise sequence divergence among wrens in the genus *Thryophilus*. Numbers above the diagonal are model-corrected distances (GTR+I+ Γ , shape = 1.6067, pinvar = 0.6065), and those below the diagonal are uncorrected *p*-distances.

<i>Thryophilus</i> taxon	1	2	3	4	5	6	7	8
1. <i>sinaloa</i>	—	0.106	0.111	0.145	0.131	0.133	0.138	0.126
2. <i>pleurostictus</i>	0.083	—	0.101	0.124	0.125	0.118	0.130	0.119
3. <i>rufalbus rufalbus</i>	0.087	0.080	—	0.068	0.067	0.065	0.075	0.063
4. <i>r. castanonotus</i>	0.105	0.093	0.059	—	0.040	0.031	0.044	0.041
5. <i>r. minlosi</i>	0.097	0.094	0.058	0.037	—	0.027	0.042	0.036
6. <i>r. cumanensis</i>	0.098	0.090	0.056	0.029	0.025	—	0.035	0.027
7. <i>nicefori</i>	0.100	0.095	0.062	0.039	0.038	0.032	—	0.038
8. <i>sernai</i> sp. nov.	0.094	0.090	0.055	0.038	0.033	0.025	0.035	—

ECOLOGY AND CONSERVATION

Habitat.—The dry to semi-humid habitats of the Cauca River Canyon in Antioquia (Fig. 9) between 250 and 1,000 m are classified as tropical dry forest (sensu Holdridge 1967, Espinal 1992) or as seasonally dry tropical forest (Pennington et al. 2009). Mean annual temperature is 24°C, and maximum temperature can reach 38°C. Total annual rainfall ranges from 700 to 2,000 mm, typically with one or two strong drought periods during the year (Espinal 1992, IAvH 1998). *Thryophilus sernai* has only been found in patches of semideciduous forest and dry scrub (Fig. 9), and more frequently in vegetation along watercourses. Overall, the forest patches where the species has been found are characterized by an open understory not exceeding 8 m in height, and by a canopy averaging 20 m tall (Espinal 1992). Dry forest patches are dominated by secondary growth; vegetation with thorns, smooth flat bark, and composite leaves; and locally by some succulent plants (IAvH 1998). Some of the most locally abundant plants in the habitat of *T. sernai* belong to the families Bombacaceae, Euphorbiaceae, Meliaceae, Moraceae, Caesalpiniaceae, Mimosaceae, and Fabaceae (IAvH 1998). Individuals of the new species have also been observed using live fences located in the open and dense patches of scrub near busy roads.

Ecology.—*Thryophilus sernai* is uncommon in its range, but no study on the population ecology of this species has been conducted.

As with most “*Thryothorus*” wrens (Kroodsmas and Brewer 2005, Mann et al. 2009), individuals of the new species are vocally very active, producing highly coordinated duets. Overall, *T. sernai* is more readily detected by sound but also by sight once territories or vocalizing individuals are located. Individuals forage actively by searching hanging dead leaves (as is typical for many members of broadly defined *Thryothorus*; Remsen and Parker 1984) and in vine-tangles and dead branches in the lower and middle strata of vegetation. The species is most often found in pairs, defending territories and foraging from above the ground to the subcanopy. Stomach contents of the holotype included remains of insects in four orders: Orthoptera was the most abundant (mouthparts, femurs, and shinbones of the family Acrididae), followed by Coleoptera (elytra and mouthparts of Tenebrionidae and Buprestidae) and Hemiptera (heads and limbs of Alydidae), whereas Lepidoptera was the least abundant (scales). Information on breeding is limited; the female paratype had an active ovary, the male paratype had enlarged testes in August, and an inactive nest was found in December (C. E. Lara unpubl. data).

Conservation.—For several decades, the Cauca River Canyon has been subject to continued transformation from an originally heterogeneous landscape with dry forest patches into mining and agricultural fields, pastures for cattle ranching, and urban areas. This dry and narrow valley is the most developed area for tourism in Antioquia; most localities where the new species exists are found

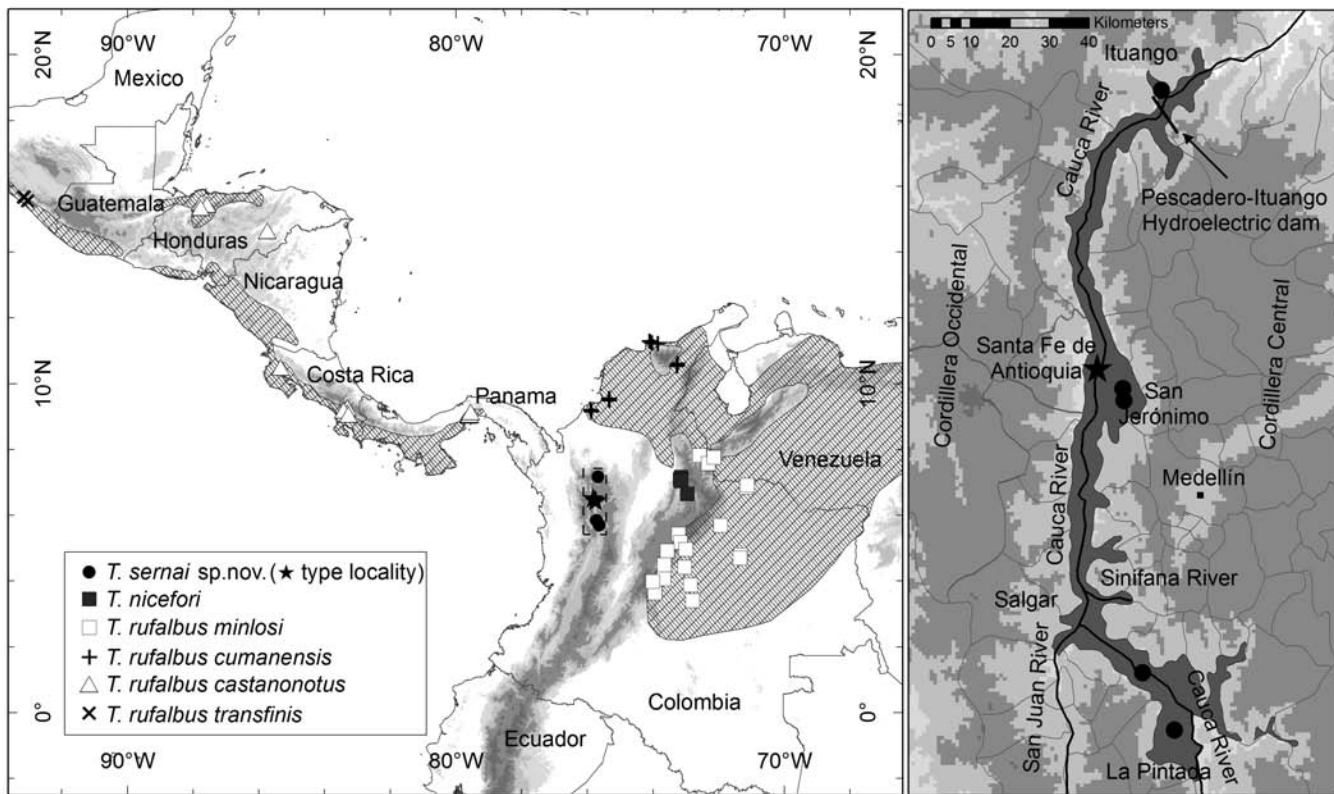


FIG. 8. Distribution of wrens in the genus *Thryophilus* and localities of examined specimens in northern South America and southern Central America: *T. sernai* sp. nov., *T. nicefori*, and *T. rufalbus* (shaded area). Inset map of Antioquia depicts the approximate distribution of *T. sernai* between La Pintada and Ituango in the Cauca River Canyon, based on elevation (<850 m) and the potential extent of its habitat in this valley. The star represents the type locality near Santa Fé de Antioquia.

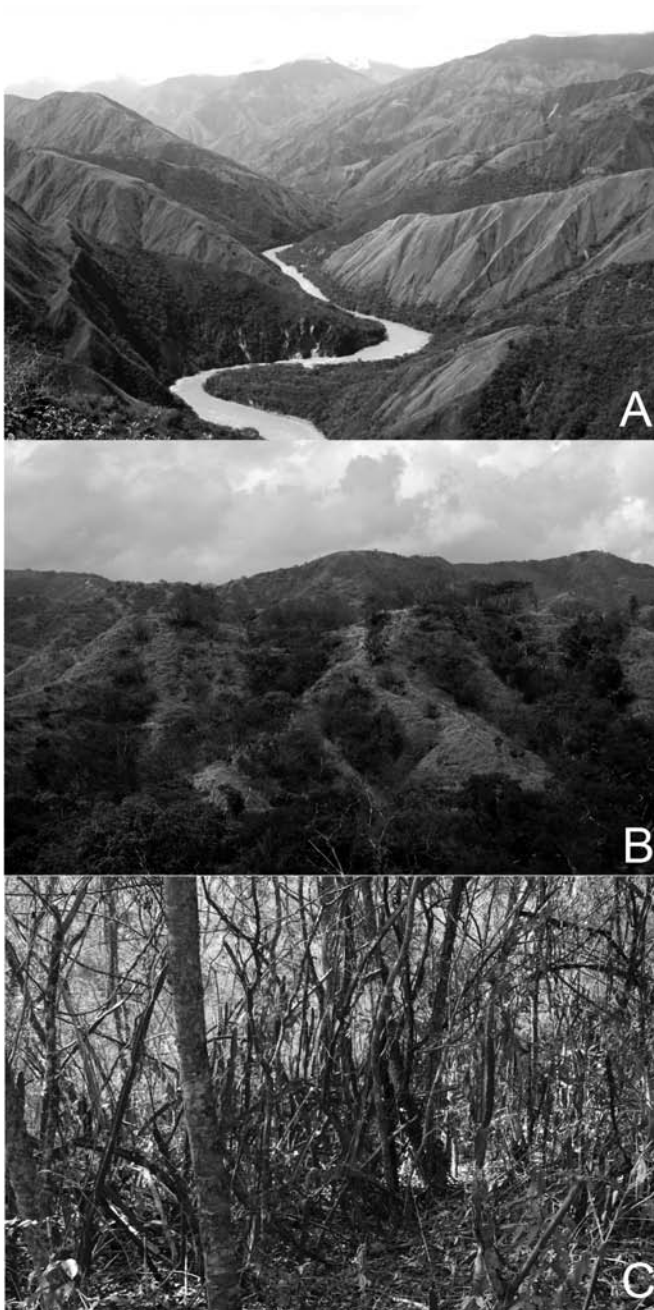


FIG. 9. Landscape view of the Cauca River Canyon and habitat of *Thryophilus sernai* sp. nov. (A) Dry forest stands along the Cauca River in Ituango where *T. sernai* is found and that are expected to be flooded by the Pescadero-Ituango dam. (B) View of the dry forest patches. (C) Interior of a dry scrub patch, habitat type in the territories of the new species. Photographs by C. E. Lara.

near recreational resorts and farms characterized by open pastures with no habitat for the species. The historical and current factors contributing to the ongoing dramatic loss of dry forest habitats in the Cauca River Canyon pose important threats for the conservation of the new species, especially considering that no formally protected areas are established within its distribution range. However,

the lack of ornithological work in much of the Cauca River Canyon (see Haffer 1967b), and the fact that we detected populations in various locations after target searches guided by its unique vocalizations, indicates the ability of populations of *T. sernai* to persist in the heavily transformed landscape of the region. This new wren is presently known from six localities within an estimated total area of ~1,700 km², and the extent and quality of its habitat are expected to decline. Thus, the species would be classified as “vulnerable” under IUCN Red List Criteria (B1a+b(iii); IUCN 2001). However, the remnant tracts of dry forest in the northern end of the new species range are planned to be flooded in the next few years, owing to the construction of the Pescadero-Ituango hydroelectric dam. Such flooding would lead to the loss of an important area for the conservation of *T. sernai*, precisely in the sector with the least-disturbed dry forests of the region and where other bird species of conservation concern occur (e.g., *Ara militaris* and *Clytoctantes alixii*; Colorado 2008). We urge that a rigorous evaluation of the population viability and distributional range of *T. sernai* be conducted, and that conservation measures be established in the near future. *Thryophilus sernai* adds to the growing number of recent discoveries of range-restricted species in northwestern South America (Cuervo et al. 2005, Cortés-Diago et al. 2007, Carantón-Ayala and Certuche-Cubillos 2010), which highlight the need for continued field and museum research to strengthen the baseline knowledge for biodiversity science and effective conservation.

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LITERATURE CITED

- BAIRD, S. F. 1874. Review of American birds in the Museum of the Smithsonian Institution. Part 1. Smithsonian Miscellaneous Collections 181. Smithsonian Institution, Washington, D.C.
- BAPTISTA, L. F., AND D. E. KROODSMA. 2001. Avian bioacoustics: A tribute to Luis Baptista. Pages 11–52 in *Handbook of the Birds of the World*, vol. 6: Mousebirds to Hornbills (J. del Hoyo, A. Elliott, and J. Sargatal, Eds.). Lynx Edicions, Barcelona, Spain.
- BARKER, F. K. 2004. Monophyly and relationships of wrens (Aves: Troglodytidae): A congruence analysis of heterogeneous mitochondrial and nuclear DNA sequence data. *Molecular Phylogenetics and Evolution* 31:486–504.
- BARKER, F. K. 2007. Avifaunal interchange across the Panamanian isthmus: Insights from *Campylorhynchus* wrens. *Biological Journal of the Linnean Society* 90:687–702.
- BURNEY, C. W., AND R. T. BRUMFIELD. 2009. Ecology predicts levels of genetic differentiation in Neotropical birds. *American Naturalist* 174:358–368.
- CARANTÓN-AYALA, D., AND K. CERTUCHE-CUBILLOS. 2010. A new species of antpitta (Grallariidae: *Grallaria*) from the northern sector of the Western Andes of Colombia. *Ornitología Colombiana* 9:56–70.
- CHAKRABARTY, P. 2010. Genotypes: A concept to help integrate molecular phylogenetics and taxonomy. *Zootaxa* 2632:67–68.
- COLLAR, N. J., L. P. GONZAGA, N. KRABBE, A. MADROÑO-NIETO, L. G. NARANJO, T. A. PARKER, AND D. C. WEGE. 1992. Threatened birds of the Americas: The ICBP/IUCN Red Data Book. International Council for Bird Preservation, Cambridge, United Kingdom.
- COLORADO, G. J. 2008. Rediscovery of the Recurve-billed Bushbird for the Cordillera Central of Colombia. *Ornitología Neotropical* 19:467–471.
- CORTÉS-DIAGO, A., L. A. ORTEGA, L. MAZARIEGOS-HURTADO, AND A.-A. WELLER. 2007. A new species of *Eriocnemis* (Trochilidae) from southwest Colombia. *Ornitología Neotropical* 18:161–170.
- CRACRAFT, J. 1983. Cladistic analysis and vicariance biogeography. *American Scientist* 71:273–281.
- CRACRAFT, J. 1985. Historical biogeography and patterns of differentiation within the South American avifauna: Areas of endemism. Pages 49–84 in *Neotropical Ornithology* (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). *Ornithological Monographs*, no. 36.
- CUERVO, A. M., C. D. CADENA, N. KRABBE, AND L. M. RENJIFO. 2005. *Scytalopus stilesi*, a new species of tapaculo (Rhinocryptidae) from the Cordillera Central of Colombia. *Auk* 122:445–463.
- DE QUEIROZ, K. 1998. The general lineage concept of species, species criteria, and the process of speciation. Pages 57–75 in *Endless Forms: Species and Speciation* (D. J. Howard and S. H. Berlocher, Eds.). Oxford University Press, New York.
- DE QUEIROZ, K. 2005. A unified concept of species and its consequences for the future of taxonomy. *Proceedings of the California Academy of Sciences* 56 (Supplement 1):196–215.
- DICKINSON, E. C., ED. 2003. *The Howard and Moore Complete Checklist of the Birds of the World*, 3rd ed. Princeton University Press, Princeton, New Jersey.
- ESPINAL, L. S. 1992. *Geografía Ecológica de Antioquia: Zonas de Vida*. Editorial Lealon. Facultad de Ciencias, Universidad Nacional de Colombia, Medellín, Colombia.
- FUNK, D. J., AND K. E. OMLAND. 2003. Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology and Systematics* 34:397–423.
- HAFFER, J. 1967a. Speciation in Colombian forest birds west of the Andes. *American Museum Novitates* 2294:1–57.
- HAFFER, J. 1967b. Zoogeographical notes on the “nonforest” lowland bird faunas of northwestern South America. *Hornero* 10:315–333.
- HELBIG, A. J., A. G. KNOX, D. T. PARKIN, G. SANGSTER, AND M. COLLINSON. 2002. Guidelines for assigning species rank. *Ibis* 144:518–525.
- HELM-BYCHOWSKI, K., AND J. CRACRAFT. 1993. Recovering phylogenetic signal from DNA sequences: Relationships within the corvine assemblage (class Aves) as inferred from complete sequences of the mitochondrial DNA cytochrome-*b* gene. *Molecular Biology and Evolution* 10:1196–1214.
- HILTY, S. L., AND W. L. BROWN. 1986. *A Guide to the Birds of Colombia*. Princeton University Press, Princeton, New Jersey.
- HOLDRIDGE, L. R. 1967. *Life Zone Ecology*. Tropical Science Center, San José, Costa Rica.
- HUELSENBECK, J. P., AND F. RONQUIST. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17:754–755.
- IAVH. 1998. El Bosque Seco Tropical (Bs-T) en Colombia. Programa de Inventario de la Biodiversidad. Instituto Alexander von Humboldt, Bogotá, Colombia.
- ISLER, M. L., P. R. ISLER, AND B. M. WHITNEY. 1998. Use of vocalizations to establish species limits in antbirds (Passeriformes: Thamnophilidae). *Auk* 115:577–590.
- IUCN. 2001. IUCN Red List Categories and Criteria: v3.1. IUCN species survival commission [Online.] Available at www.iucnredlist.org/.
- JOHANSSON, U. S., J. FJELDSÅ, AND R. C. K. BOWIE. 2008. Phylogenetic relationships within Passerida (Aves: Passeriformes): A review and a new molecular phylogeny based on three nuclear intron markers. *Molecular Phylogenetics and Evolution* 48:858–876.
- JOHNSON, N. K., J. V. REMSEN, JR., AND C. CICERO. 1999. Resolution of the debate over species concepts in ornithology: A new comprehensive biologic species concept. Pages 1470–1482 in *Proceedings 22nd International Ornithological Congress* (N. J. Adams and R. H. Slotow, Eds.). BirdLife South Africa, Johannesburg.
- KOCHER, T. D., W. K. THOMAS, A. MEYER, S. V. EDWARDS, S. PÄÄBO, F. X. VILLABLANCA, AND A. C. WILSON. 1989. Dynamics of mitochondrial DNA evolution in animals: Amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences USA* 86:6196–6200.
- KROODSMA, D. E., AND D. BREWER. 2005. Family Troglodytidae (Wrens) in *Handbook of the Birds of the World*, vol. 10: Cuckoos to Thrushes (J. del Hoyo, A. Elliott, and D. A. Christie, Eds.). Lynx Edicions, Barcelona, Spain.
- LÓPEZ-LANÚS, B., AND C. D. CADENA. 2002. *Thryothorus nicefori*. Pages 375–378 in *Libro Rojo de Aves de Colombia* (L. M. Renjifo, A. M. Franco, J. D. Amaya, G. H. Kattan, and B. López-Lanús, Eds.). Instituto Alexander von Humboldt, Ministerio del Medio Ambiente, Bogotá, Colombia.
- MANN, N. I., F. K. BARKER, J. A. GRAVES, K. A. DINGESS-MANN, AND P. J. B. SLATER. 2006. Molecular data delineate four genera of “*Thryothorus*” wrens. *Molecular Phylogenetics and Evolution* 40:750–759.

- MANN, N. I., K. A. DINGESS, F. K. BARKER, J. A. GRAVES, AND P. J. B. SLATER. 2009. A comparative study of song form and duetting in Neotropical *Thryothorus* wrens. *Behaviour* 146:1–43.
- MAYR, E. 1963. *Animal Species and Evolution*. Harvard University Press, Cambridge, Massachusetts.
- MENNILL, D. J., AND S. L. VEHCAMP. 2005. Sex differences in singing and duetting behavior of Neotropical Rufous-and-white Wrens (*Thryothorus rufalbus*). *Auk* 122:175–186.
- MEYER DE SCHAUENSEE, R. 1946. A new species of wren from Colombia. *Notulae Naturae*, no. 182.
- MILLER, M. A., W. PFEIFFER, AND T. SCHWARTZ. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pages 1–8 in *Proceedings of the Gateway Computing Environments Workshop (GCE 2010)*. Institute of Electrical and Electronics Engineers, Piscataway Township, New Jersey.
- NYLANDER, J. A. A. 2004. MrModeltest, version 2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.
- PENNINGTON, R. T., M. LAVIN, AND A. OLIVEIRA-FILHO. 2009. Woody plant diversity, evolution, and ecology in the tropics: Perspectives from seasonally dry tropical forests. *Annual Review of Ecology, Evolution, and Systematics* 40:437–457.
- PENNINGTON, R. T., M. LAVIN, T. SÄRKINEN, G. P. LEWIS, B. B. KLITGAARD, AND C. E. HUGHES. 2010. Contrasting plant diversification histories within the Andean biodiversity hotspot. *Proceedings of the National Academy of Sciences USA* 107:13783–13787.
- PRICE, T. 2008. *Speciation in Birds*. Roberts, Greenwood Village, Colorado.
- REMSEN, J. V., JR. 2005. Pattern, process, and rigor meet classification. *Auk* 122:403–413.
- REMSEN, J. V., JR. 2010. Subspecies as a meaningful taxonomic rank in avian classification. Pages 62–78 in *Avian Subspecies* (K. Winker and S. M. Haig, Eds.). Ornithological Monographs, no. 67.
- REMSEN, J. V., JR., C. D. CADENA, A. JARAMILLO, M. NORES, J. F. PACHECO, J. PÉREZ-EMÁN, M. B. ROBBINS, F. G. STILES, D. F. STOTZ, AND K. J. ZIMMER. 2012. A classification of the bird species of South America. Version 7 May 2012. American Ornithologists' Union. [Online.] Available at www.museum.lsu.edu/~Remsen/SACCBaseline.html.
- REMSEN, J. V., JR., AND T. A. PARKER III. 1984. Arboreal dead-leaf-searching birds of the Neotropics. *Condor* 86:36–41.
- RIDGWAY, R. 1904. *The Birds of North and Middle America*, part 3. *Bulletin of the U.S. National Museum* No. 50.
- SMITHE, F. B. 1975. *Naturalist's Color Guide*. American Museum of Natural History, New York.
- STAMATAKIS, A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22:2688–2690.
- VALDERRAMA, S. V., J. E. PARRA, AND D. J. MENNILL. 2007. Species differences in the songs of the critically endangered Niceforo's Wren and the related Rufous-and-white Wren. *Condor* 109:870–877.
- WEIR, J. T., AND D. SCHLUTER. 2008. Calibrating the avian molecular clock. *Molecular Ecology* 17:2321–2328.

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APPENDIX

Specimens of *Thryophilus sernai*, *T. nicefori*, and *T. rufalbus* examined at Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN); Universidad de La Salle, Bogotá (MLS); Instituto Alexander von Humboldt, Colombia (IAvH); Universidad de Los Andes, Colombia (ANDES-O); Louisiana State University, Museum of Natural Science (LSUMZ), Colección Ornitológica Phelps, Venezuela (COP), Marjorie Barrick Museum, University of Las Vegas-Nevada (MBM-JK). Sequenced individuals are indicated by an asterisk.

Thryophilus sernai sp. nov. Colombia: ICN 37848* (holotype), Santa Fé de Antioquia, Antioquia; ANDES-O 667* (male paratype), San Jerónimo, Antioquia; ANDES-O 668* (female paratype), San Jerónimo, Antioquia. *Thryophilus nicefori*. Colombia: MLS 5-361, San Gil, Santander; MLS 5-362, San Gil, Santander; MLS 5-363, San Gil, Santander; ICN 36026, Florida Blanca, Santander; ICN 36027, Florida Blanca, Santander; ICN 36028*, Florida Blanca, Santander; ANDES-O 442, Curití, Santander. *Thryophilus rufalbus cumanensis*. Colombia: ICN 24136, Santa Marta, Magdalena; ICN 34936, Loricá, Córdoba; ICN 34937*, Loricá, Córdoba; ANDES 440, Valledupar, Cesar; ANDES 441, Valledupar, Cesar; IAvH 0954, Santa Marta, Magdalena; IAvH 0983, Santa Marta, Magdalena; IAvH 15046, Colosó, Sucre; IAvH 15097, Colosó, Sucre. *Thryophilus rufalbus minlosi*. Colombia: ICN 3444, Miraflores, Boyacá; ICN 11864, San Carlos de Guevara; ICN 11865, San Carlos de Guevara; ICN 13430, Miraflores, Boyacá; ICN 13963, Corregimiento Páez, Boyacá; ICN 18869, Villavicencio, Meta; ICN 18870, Villavicencio, Meta; ICN 20125, Guamal, Meta; ICN 30646, Restrepo, Meta; ICN 32728, Cubaral, Meta; ICN 34828, Villavicencio, Meta; ICN 35943, Labala, Cundinamarca; ICN 37667, San Cayetano, Norte de Santander; IAvH 1810, Carimagua, Meta; IAvH 1826, Carimagua, Meta; IAvH 14172, Pore, Casanare; IAvH 14719, Arauquita, Arauca; IAvH 14730, Arauquita, Arauca. Venezuela: COP-JPL304*, Chorro El Indio, Táchira; COP-KCC202, Río Chiquito, Táchira. *Thryophilus rufalbus rufalbus*. Guatemala: MBM JK02027*, Quetzaltenango. *Thryophilus rufalbus transfinis*. Mexico: LSUMZ 46641, Tonalá, Chiapas; LSUMZ 46642, Tonalá, Chiapas; LSUMZ 46643, Pijijiapan, Chiapas. *Thryophilus rufalbus castanonotus*. Honduras: LSUMZ 27100, Río Petaste, Olancho; LSUMZ 29848, Finca Fé, Cortés; LSUMZ 29850, Finca Fé, Cortés; LSUMZ 29868, Finca Fé, Cortés. Costa Rica: LSUMZ 30685, Monte Verde, Puntarenas; LSUMZ 33918, Monte Verde, Puntarenas; LSUMZ 48368, Playón de Aguirre, Puntarenas; LSUMZ 48369, Playón de Aguirre, Puntarenas; LSUMZ 48370, Playón de Aguirre, Puntarenas; LSUMZ 48371, Playón de Aguirre, Puntarenas; LSUMZ 48372, Paso Real, Puntarenas; LSUMZ 48373, Paso Real, Puntarenas; LSUMZ 48374, Paso Real, Puntarenas; LSUMZ 48375, Tilarán, Guanacaste; LSUMZ 140192, Esparta, Puntarenas. Panama: LSUMZ 163701, Paraíso, Panamá; LSUMZ 163702, Paraíso, Panamá; LSUMZ 1643293, Río Farfán, Panamá.