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RESEARCH ARTICLE

A new species of tapaculo (Rhinocryptidae: *Scytalopus*) from the Western Andes of Colombia

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ABSTRACT

We describe *Scytalopus alvarezlopezi* from the Western Andes of Colombia. The new species forms part of a distinctive clade of *Scytalopus* tapaculos (Rhinocryptidae) that also includes *S. robbinsi* from Ecuador and *S. stilesi* and *S. rodriguezi*, which occur on the Central and Eastern Andes of Colombia. *S. alvarezlopezi* is easily diagnosable from its near relatives by its song and mitochondrial DNA; differences in plumage exist but are more subtle. The species inhabits dense understory vegetation on the floors and lower slopes of ravines in cloud forest at elevations of 1,300 to 2,100 m. On the Pacific slope, its altitudinal distribution is sandwiched between those of *S. chocoensis* (below) and *S. vicinior* (above); the latter in turn is replaced higher up by *S. spillmanni* and *S. latrans,* but *S. alvarezlopezi* also occurs at ~2,000–2,100 m on eastern slopes just below the low ridgeline. All of the latter species are distinguished by vocal and plumage characters. Marked sexual differences in plumage exist in *stilesi*, but females have yet to be collected for *alvarezlopezi* and *rodriguezi*. We consider that *S. alvarezlopezi* is not threatened at present, but could be potentially vulnerable due to its restricted distribution; it is endemic to Colombia.

Keywords: Colombia, endemic species, new species, ecology, vocalizations

Una nueva especie de tapaculo (Rhinocryptidae: *Scytalopus*) de la Cordillera Occidental de Colombia

RESUMEN

Describimos *Scytalopus alvarezlopezi* de la cordillera Occidental de los Andes colombianos. Esta nueva especie forma parte de un clado bien definido de tapaculos del género *Scytalopus* (Rhinocryptidae) que también incluye a *S. robbinsi* de Ecuador y *S. stilesi* y *S. rodriguezi*, las cuales están presentes en las cordilleras Central y Oriental de los Andes colombianos. *S. alvarezlopezi* es fácilmente diagnosticable en comparación con sus parientes por sus vocalizaciones y ADN mitocontrial; también hay diferencias en plumaje pero son más sutiles. La especie habita en el sotobosque denso de los fondos y lados de barrancos en bosque nuboso entre elevaciones de 1,300 y 2,100 m. Sobre la vertiente del Pacífico, la distribución altitudinal de *alvarezlopezi* está entre las de *chocoensis* (hacia abajo) y *vicinior* (hacia arriba); más arriba, *vicinior* es reemplazado por *spillmanni* y *S. latrans*; sin embargo, *alvarezlopezi* alcanza localmente elevaciones de 2,100 m o más sobre la vertiente oriental de algunos filos bajos justo por debajo de la cima. Todas estas especies se distinguen por vocalizaciones y plumaje. Existen differencias en plumaje entre los sexos de *stilesi*, pero aun falta recolectar hembras de *rodriguezi* y *alvarezlopezi*. Consideramos que actualmente *S. alvarezlopezi* no está amenazado, pero debido a su distribución restringida, potencialmente podría considerarse vulnerable; es una especie endémica a Colombia.

Palabras clave: Colombia, ecología, especie endémica, nueva especie, vocalizaciones

INTRODUCTION

On a collecting trip to the Alto de Pisones on the mule trail from Geguadas to Puerto de Oro in northwestern Risaralda department, Colombia, in early June 1992, F. Gary Stiles (FGS) repeatedly heard churring trills emanating from the thick understory of the slopes above the campsite at an elevation of 1,530 m, and ascribed them to some sort of frog. While sitting quietly higher on this slope, he was surprised to find a presumed pair of *Scytalopus* tapaculos walking and hopping toward him, one of which gave the churring call. The birds approached him to within ~3 m, then at some slight movement hurriedly moved away and disappeared in the morass of low vegetation; some 2 min later he heard several longer churrs from the direction in which they had disappeared. Now realizing that the sound was that of a tapaculo, FGS attempted on

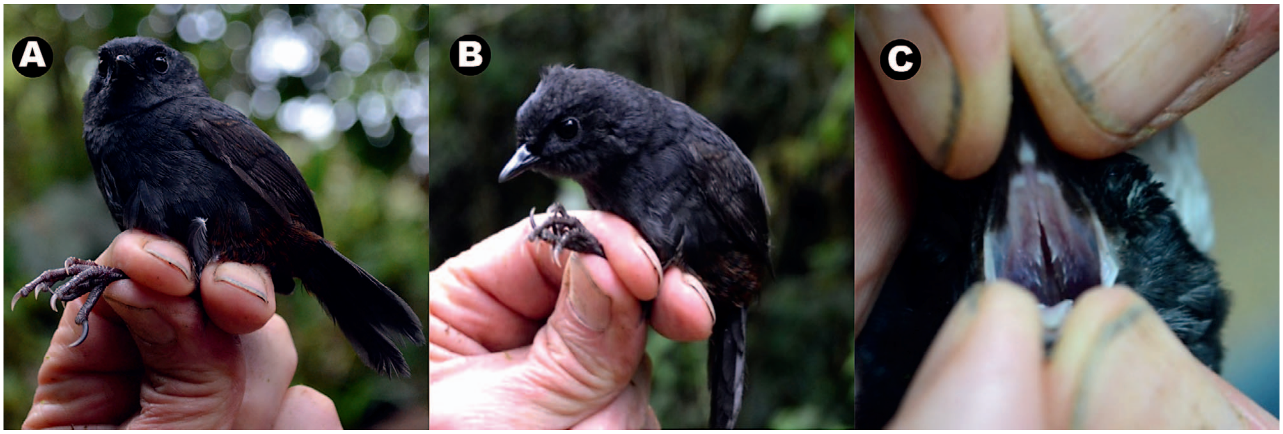

FIGURE 1. (**A**, **B**) Two views of the paratype of *Scytalopus alvarezlopezi* upon capture at Cerro Montezuma, Mpo. Pueblo Rico, Dpto. Risaralda, Colombia, April 2, 2015. Note the overall dark coloration with blurry, dark rufous barring on the flanks and crissum. (**C**) The striking pattern of the mouth lining of the paratype. The tongue, commissure, and center of the mandible are white, the lateral portions of the mandible are black. The mouth lining has not been described for any other tapaculo, but might provide a useful character for distinguishing species. Photos by J. Heavyside.

succeeding days to record and collect a specimen, which he did on June 6. Upon his return to Bogotá, FGS found that the specimen, an adult male, did not match any *Scytalopus* specimen in the collection of the Instituto de Ciencias Naturales (ICN); based on its voice and morphology it was later recognized that this specimen most likely represented an undescribed species (Cuervo et al. 2003). When Carlos Daniel Cadena (CDC) took a toepad from the specimen for DNA analysis in 2004, he found that the specimen was not related to any other Colombian tapaculo then known and that its closest relatives were *S. robbinsi* of Ecuador, and the then-undescribed Colombian endemics *S. stilesi* and *S. rodriguezi* (Cuervo et al. 2005, Krabbe et al. 2005). This confirmed that the Alto de Pisones specimen probably represented an undescribed species.

Species Description

Upon collecting the Pisones bird, FGS decided to await the collection of at least one more specimen before describing this taxon, and there followed more than 20 years of frustration: various people recorded and sometimes saw the "Pisones tapaculo" at several mid-elevation localities in the Western Andes (e.g., see http://www.xeno-canto.org/species/Scytalopus-sp.nov.Alto_Pisones), but all efforts to collect a specimen (including at least 2 attempts each by FGS, Oscar Laverde-R., and CDC) were unsuccessful. Finally, on a trip to the Reserva Cerro Montezuma in April 2015, some 15 km SSW of Pisones, FGS and Julian Heavyside succeeded in netting and collecting a second adult male specimen (Figure 1). With the collection of the paratype of the Pisones bird and confirmation of its identity with the holotype by CDC, we can finally describe this species as:

Scytalopus alvarezlopezi, sp. nov.
Tatamá Tapaculo

Holotype. ICN 31209, adult male, collected June 6, 1992, by F. G. Stiles (original no. FGS 2893).

Type locality. Colombia, department of Risaralda, municipality of Mistrató, Alto de Pisones, 8 km northeast of Geguadas, elevation 1,710 m, shallow ravine in cloud forest; coordinates 5°25′N, 76°02′W.

Scytalopus alvarezlopezi posseses all of the characteristics that diagnose the genus *Scytalopus* (Ridgway 1911, Krabbe & Schulenberg 1997). It is a medium-sized, blackish tapaculo; males are black above, the rump slightly tinged dark brown; dark grayish-black below; the posterior flanks, extreme lower abdomen, and crissum are broadly and slightly indistinctly barred black and dark rufous; the primaries and tail are dark brownish-black (Figure 1). Female and juvenile plumages are presently unrecorded, but the 2 members of the presumed pair seen at close range by FGS did not differ appreciably.

Diagnosis. Four other *Scytalopus* species have been recorded on the Pacific slope of Colombia: *S. chocoensis*, *vicinior*, *spillmanni*, and *latrans* (Figure 2). From *chocoensis*, *alvarezlopezi* differs in plumage in being more uniform blackish below, the median abdomen not paler gray; the barring of the flanks and crissum is much finer in *chocoensis* and the brown of the rump is paler and extends forward to the midback; *alvarezlopezi* is also heavier, with longer wings and tarsi and a thicker bill, and it occurs at higher elevations. From *vicinior*, *alvarezlopezi* is distinguished by its darker and more uniform blackish underparts; at least the abdomen of *vicinior* is gray and the pattern on the flanks and crissum is more finely scalloped with paler rufous, not broadly barred with dark

FIGURE 2. *Scytalopus alvarezlopezi* and the other species of *Scytalopus* tapaculos occurring with it on the Pacific slope of the Western Andes, in the elevational sequence (left to right): *S. chocoensis*, *S. alvarezlopezi* (holotype), *S. vicinior*, *S. spillmanni*, and *S. latrans*. (Above) ventral views; (below) dorsal views.

rufous; *alvarezlopezi* also has a longer, thicker bill but shorter wings, tail, and tarsi, and occupies lower elevations. *S. spillmanni* is gray below, often with whitish spotting on the median abdomen and with narrower barring of black and paler rufous on the flanks and crissum, has much longer wings, tail, and tarsi, and occurs at much higher elevations. The Western Andes subspecies of *S. latrans* is much more uniform blackish, lacking rufous barring on the flanks and crissum and brown on the back (although certain other subspecies of the eastern slope of the Andes do show some rufous barring on the flanks); *alvarezlopezi* is much heavier and has a longer, thicker bill, longer wings and tail, and occurs at lower elevations (Table 1).

The differences in plumage between *S. alvarezlopezi* and males of its 2 Colombian relatives, *stilesi* and *rodriguezi*, are more subtle, such that based solely on specimens, a museum taxonomist might consider them all conspecific (Figure 3). All 3 are blackish above with at most a trace of dark brown on the lower back; however, the rufous barring on the flanks, crissum, and lower abdomen is slightly paler, narrower, and tending more toward scalloping in both *stilesi* and *rodriguezi*. In both, the underparts may be nearly as blackish as in *alvarezlopezi* or slightly but distinctly paler gray. Only for *stilesi* is the female plumage known, and in this species, females are decidedly paler gray below with brighter and more extensive rufous barring or scalloping on the flanks, lower abdomen, and crissum. In measurements, the feature best distinguishing *S. alvarezlopezi* from its 2 relatives appears to be its larger bill (Table 1). However, all 3 differ strongly in their songs, mitochondrial DNA sequences, and distributions: *stilesi* occurs in the Central Andes and *rodriguezi* in the Central and Eastern Andes, while *alvarezlopezi* is the only species in the clade occurring in the Western Andes (see below).

Description of holotype. Color nomenclature and numbers follow Smithe (1975, 1981). Upperparts uniform black, slightly tinged brownish (near 21, Fuscous) on rump and wings; tail near 19, Dusky Brown but darker; chin between 82, Dark Neutral Gray and 83, Blackish Neutral Gray, passing to Blackish Neutral Gray on the remaining underparts. Posterior flanks, lower abdomen and crissum broadly barred dark rufous (darker than 36, Amber) and black. Ten rectrices. Iris dark brown, bill black, commisure pale flesh-white, legs and feet dark brown, soles dark grayish-brown, claws horn color. Body mass: 25.4 g; measurements in Table 1; skull 15% ossified, trace of fat; left testis: 9.0 $\times$ 5.0 mm; stomach contents: insect fragments.

Paratype. ICN 39110, adult male, collected April 2, 2015, by F. G. Stiles and J. Heavyside (original number FGS 4512). Risaralda, municipality of Pueblo Rico, Reserva Natural Cerro Montezuma, ~15 km northeast of Pueblo Rico, elevation 1,640 m, on the steep slope above the floor of a deep ravine in cloud forest; coordinates 5°15′N, 76°06′W. Body mass: 24.0 g; measurements in Table 1; skull 10% ossified, very light fat; left testis: 10.0 $\times$ 4.5 mm, right testis: 8.5 $\times$ 5.0 mm; stomach contents: arthropod fragments including 2 small beetles, one small spider. In color and pattern very similar to the holotype but the area of paler feathers of the chin is much reduced and the rufous barring on the posterior underparts is slightly darker and less extensive (Figure 4). A feature not noticed in the holotype is the strikingly bicolored mouth lining, pale pinkish-white medially, the tongue and commissure white, the inside of the bill black laterally and terminally (Figure 1C).

Etymology. We take pleasure in naming this species in honor of Humberto Álvarez-López, the "dean of Colombian ornithology," for his many contributions to the knowledge and study of this country's birds over nearly half a century. Humberto was professor of ornithology at the Universidad del Valle for nearly 4 decades and helped train several of Colombia's foremost ornithologists and conservationists; in 1979 he founded in Cali the first local ornithological society in Colombia, an example soon followed by other cities in the country, and long edited and wrote for its journal. His book *Introducción a las Aves de Colombia*, published in 1979, was instrumental in making the observation of birds accessible to students and the public at large in Colombia, and arguably spearheaded the development of field ornithology in the country. In 1987 Humberto was president of the third Neotropical Ornithological Congress, the only one to be held in Colombia. He painstakingly translated Hilty's monumental *Guide to the Birds of Colombia* into Spanish and was a founding member of the Asociación Colombiana de Ornitología, serving for more than 10 years as president and member of its governing body, where his sage advice on difficult matters often has been decisive. ¡Muchas gracias, "Maestro"!

We suggest the English name of Tatamá Tapaculo for *S. alvarezlopezi* because the majority of localities for this species are in the middle sector of the Western Andes near the border between Risaralda and Chocó Departments, in which the most prominent and best-known mountain is Cerro Tatamá, the center of Tatamá National Park; Cerro Montezuma is in the park's buffer zone, Pisones is also within ~7 km of the park boundary, and CDC and OLR have found this species in several sites within the park itself.

Genetic Analyses

For an ongoing study on the phylogeny and diversification of *Scytalopus*, CDC and several collaborators have obtained DNA sequences of mitochondrial and nuclear genes for more than 230 specimens, sampling nearly all named species and subspecies in the genus, in addition to several unnamed taxa and multiple populations of

TABLE 1. Measurements of several species of *Scytalopus* tapaculos from Colombia. Abbreviations: Cordilleras are: W = Western Andes; C = Central Andes; E = Eastern Andes; Elev. = elevation in m of collection locality; Mass = body mass in g; Tot. Cul. = total culmen (mm); W. Com. = width of commissure (mm); Ht. Bill = height of bill at midpoint of operculum (mm); W. Ch. = chord of folded wing (mm); L. Tail = length of tail (mm); L. Tars. = length of tarsus (mm); H. Cl. = chord of hallux claw (mm). An asterisk on the species number indicates the holotype of the species.

ICN no.	Species	Cordillera	Elev.	Sex	Mass	Tot. Cul.	W. Com.	Ht. Bill	W. Ch.	L. Tail	L. Tars.	Hal. Cl.
31209*	*S. alvarezlopezi*	W	1,710	M	25.4	15.9	8.7	4.6	54.6	39.6	22.6	7.5
39110	*S. alvarezlopezi*	W	1,640	M	24.0	15.6	8.1	4.5	53.9	38.9	22.2	5.8
	Mean		**1,675.0**		**24.70**	**15.75**	**8.40**	**4.55**	**54.35**	**39.35**	**22.40**	**6.65**
	SD		**49.5**		**0.99**	**0.21**	**0.42**	**0.07**	**0.49**	**0.49**	**0.28**	**1.20**
31208	*S. vicinior*	W	1,750	M	23.5	13.3	8.2	4.2	58.2	46.4	23.5	8.2
31207	*S. vicinior*	W	1,780	F	23.1	14.7	8.8	4.4	56.5	41.6	23.1	7.8
37463	*S. vicinior*	W	1,950	F	22.3	15.1	8.4	3.6	58.1	42.3	22.3	7.6
34840	*S. vicinior*	W	2,100	F	22.8	14.8	7.7	4.1	56.8	45.2	23.8	8.1
	Mean		**1,895.0**		**22.93**	**14.48**	**8.28**	**4.05**	**57.40**	**43.88**	**23.18**	**7.93**
	SD		**162.6**		**0.51**	**0.80**	**0.46**	**0.32**	**0.88**	**2.29**	**0.65**	**0.28**
37480	*S. chocoensis*	W	1,100	M	20.7	15.5	7.6	4.2	53.1	40.0	21.7	7.4
39595	*S. chocoensis*	W	1,050	M	17.8	15.3	7.4	4.2	54.1	40.2	21.8	6.6
	Mean		**1,075.0**		**19.50**	**15.40**	**7.50**	**4.20**	**53.60**	**40.10**	**21.75**	**7.00**
	SD		**35.4**		**2.05**	**0.14**	**0.14**	**0.00**	**0.71**	**0.14**	**0.14**	**0.57**
33166	*S. spillmanni*	W	2,450	M	27.0	15.8	8.9	4.2	60.5	44.2	24.1	8.0
35032	*S. spillmanni*	W	2,300	M	23.0	15.9	8.6	4.1	58.5	46.4	25.3	8.1
35033	*S. spillmanni*	W	2,300	M	24.0	14.6	9.6	3.9	57.0	44.3	23.8	7.4
35034	*S. spillmanni*	W	2,200	M	26.8	16.3	9.0	4.5	60.4	47.1	23.9	7.6
35201	*S. spillmanni*	W	2,400	M		15.3	8.8	4.3	56.9	43.5	23.6	8.3
35209	*S. spillmanni*	W	2,600	F	22.0	15.3	9.2	3.9	56.3	41.8	23.9	7.5
	Mean		**2,375.0**		**24.56**	**15.53**	**9.02**	**4.15**	**58.27**	**44.55**	**24.10**	**7.82**
	SD		**140.5**		**2.25**	**0.60**	**0.35**	**0.23**	**1.84**	**1.94**	**0.61**	**0.37**
25906	*S. latrans*	W	2,620	M		11.8	7.3	3.3	51.7	34.8	22.5	6.6
26048	*S. latrans*	W	2,650	M		11.5	6.7	3.4	53.1	36.7	22.7	6.8
35211	*S. latrans*	W	2,250	M	15.0	11.3	6.5	3.6	50.5	35.1	21.9	6.6
35000	*S. latrans*	W	2,400	M	15.9	11.8	7.1	3.8	53.3	38.9	20.9	6.4
35210	*S. latrans*	W	2,200	F	15.0	11.3	6.5	3.6	50.6	35.0	21.9	6.4
	Mean		**2,424.0**		**15.30**	**11.54**	**6.82**	**3.54**	**51.84**	**36.10**	**21.98**	**6.56**
	SD		**206.5**		**0.52**	**0.25**	**0.36**	**0.19**	**1.33**	**1.74**	**0.70**	**0.17**
35234	*S. r. rodriguezi*	C	2,100	M	21.6	12.6	7.1	3.7	54.4	42.8	22.8	6.4
34845	*S. r. rodriguezi*	C	2,235	M	21.4	13.3	7.6	3.7	53.4	42.6	22.5	6.1
35844*	*S. r. rodriguezi*	C	2,235	M	22.7	12.7	7.5	3.6	54.2	42.4	22.6	6.4
	Mean		**2,190.0**		**21.90**	**12.87**	**7.40**	**3.67**	**54.00**	**42.60**	**22.63**	**6.30**
	SD		**77.9**		**0.70**	**0.38**	**0.26**	**0.06**	**0.53**	**0.20**	**0.15**	**0.17**
36178*	*S. r. yariguiorum*	E (Y)	2,000	M	18.0	13.3	7.5	3.8	54.0	39.4	21.0	6.0
36179	*S. r. yariguiorum*	E (Y)	2,000	M	17.5	13.7	7.5	3.6	53.1	38.6	21.3	6.0
35821	*S. r. yariguiorum*	E (Y)	2,100	F	16.8	13.8	7.3	3.8	52.2	35.3	20.9	6.2
	Mean		**2,033.3**		**17.43**	**13.60**	**7.43**	**3.73**	**53.10**	**37.77**	**21.07**	**6.07**
	SD		**57.7**		**0.60**	**0.26**	**0.12**	**0.12**	**0.90**	**2.17**	**0.21**	**0.12**
34609	*S. stilesi*	C	1,560	M	21.5	14.6	7.6	4.2	57.7	44.4	23.1	7.3
35708	*S. stilesi*	C	1,665	M	20.0	15.0	7.9	4.2	58.5	45.1	23.0	6.7
36315	*S. stilesi*	C	1,530	M	22.5	15.4	8.0	4.4	58.0	42.1	23.7	7.1
34569*	*S. stilesi*	C		M	24.5	15.2	7.5	4.5	59.8	43.5	23.4	7.2
34610	*S. stilesi*	C		F	22.0	14.1	7.5	4.5	55.2	39.3	23.1	7.5
34615	*S. stilesi*	C		F	21.5		7.7		58.4	43.8	22.9	6.7
34512	*S. stilesi*	C		F	21.5	15.3	7.6	4.3	55.1	42.6	24.3	7.0
36316	*S. stilesi*	C	1,535	F		14.8	7.6	4.6	55.3	42.3	23.6	6.2
35759	*S. stilesi*	C	1,530	F	21.0	13.8	7.4	3.7	54.5	37.5	24.0	7.4
35758	*S. stilesi*	C	1,530	F	20.5	14.6	7.5	4.0	56.5	41.5	23.0	6.5
34505	*S. stilesi*	C	1,660	F	20.5	14.4	7.2	4.2	56.9	43.4	22.8	6.6
	Mean		**1,572.9**		**21.55**	**14.72**	**7.59**	**4.26**	**56.90**	**42.32**	**23.35**	**6.93**
	SD		**62.2**		**1.28**	**0.52**	**0.22**	**0.27**	**1.72**	**2.24**	**0.49**	**0.41**

FIGURE 3. *Scytalopus alvarezlopezi* and its 2 closest relatives in Colombia. Left: ventral views, right: dorsal views. From left to right in each: *S. r. rodriguezi*, *S. stilesi*, and *S. alvarezlopezi*. We chose the darkest examples of the first 2 for comparison; most examples are somewhat paler gray below; even so, the darker color of *S. alvarezlopezi* is evident, as is the difference in the rufous barring on the flanks and abdomen (see text).

widespread species. Phylogenetic analyses of the complete data set have confirmed earlier results reported in Cuervo et al. (2005) indicating that *S. alvarezlopezi* forms a clade with *S. stilesi*, *S. robbinsi*, and *S. rodriguezi*. Based on these data, we selected a set of specimens to be included in analyses aimed at assessing the systematic position of *S. alvarezlopezi* and at estimating its genetic distinctiveness relative to its closest relatives. The data set consisted of sequences of the ND2 mitochondrial gene (1,041 base pairs) obtained for the 2 type specimens of *S. alvarezlopezi*, one specimen of *S. robbinsi*, 4 specimens of *S. stilesi*, and 3 specimens of *S. rodriguezi* (one nominate, two of subspecies *yariguiorum*). In addition, we included sequences of other species occurring in the Western Andes of Colombia approaching the distribution range of *alvarelopezi*, namely *S. chocoensis*, *S. vicinior*, *S. spillmanni*, and *S. latrans*; for the latter 2 species, which have ranges extending to other cordilleras, we selected specimens from the Western Andes. We estimated ND2 gene trees using maximum-likelihood and Bayesian inference analyses following methods described in Avendaño et al. (2015); *S. latrans* was designated as the outgroup in phylogenetic analyses because this is the only species from the Western Andes not being a member of a clade including members of the *latebricola* group as defined by Zimmer (1932) plus other recently described taxa (CDC personal observation).

Our phylogenetic analyses based on ND2 sequences consistently suggested that *S. alvarezlopezi* is sister to *S. robbinsi* (Figure 6), but support for this relationship was not very strong (74% maximum-likelihood bootstrap, 0.87 Bayesian posterior probability). In both analyses, the clade formed by *S. alvarezlopezi* and *S. robbinsi* was sister to *S. stilesi*, but this result was not strongly supported in any analysis. Irrespective of the lack of definite resolution of the systematic position of *S. alvarezlopezi*, genetic distances suggest that the new species is well differentiated from other *Scytalopus* closely allied to it or occurring in the Western Andes, indicating long-term evolutionary isolation (Table 2).

Vocalizations

We examined good-quality tapaculo recordings deposited in the Macaulay Library of Natural Sounds (MLS), Xeno-

FIGURE 4. The holotype (left) and paratype (right) of *Scytalopus alvarezlopezi*, ventral (left) and dorsal (right) views. The paratype is very slightly darker than the holotype, especially on the barring of the flanks and thighs.

Canto (XC), and the Banco de Sonidos Animales of the Instituto Alexander von Humboldt (BSA); see Appendix 1. We analyzed 3 recordings of songs of *S. rodriguezi*, 7 of *S. stilesi*, 3 of *S. alvarezlopezi*, and 5 of *S. robbinsi*. We selected between one and nine songs on each recording depending on the quality of recordings. A song was defined as a cluster of single vocal units separated from other clusters by a longer time span than that between any intra-unit time interval (Thompson et al. 1994). Songs were analyzed with the RAVEN bioacoustics program ver. 1.4 (Cornell Lab of Ornithology, Ithaca, New York, USA) using these settings: FFT window = 512, overlap = 50%, window method = hann. Song structure was quantified on sonograms using on-screen cursors to measure time and frequency characteristics. Lowest and highest frequencies were measured using a threshold set at −20 dB from the maximum amplitude of peak frequency. For each song selected we measured 8 parameters: song length, number of notes, pace, highest frequency, lowest frequency, peak frequency, bandwidth, and average entropy, which measures the dispersion of frequencies (Charif et al. 2010).

Vocalizations of *S. alvarezlopezi* are distinctive and may be used to diagnose it from its congeners. Sonograms of 10-second selections (Figure 6) illustrate overall song syntax and pace, clearly demonstrating striking differences between the songs of *S. alvarezlopezi* and the other species of the Western Andes (Figure 6) and between this species and its close relatives (Figure 7). In the Western Andes of Colombia the only tapaculo to produce a long series of short trills is *S. alvarezlopezi*. The song of *S. stilesi* is also a series of distinct phrases, but these are longer with many more notes repeated much more rapidly, producing a more buzzy effect. *S. chocoensis*, *S. vicinior*, and *S. latrans* produce long songs consisting of the slow repetition of a single note. *S. spillmani* emits very fast-paced songs, but not in short phrases as do *S. alvarezlopezi* and *stilesi*.

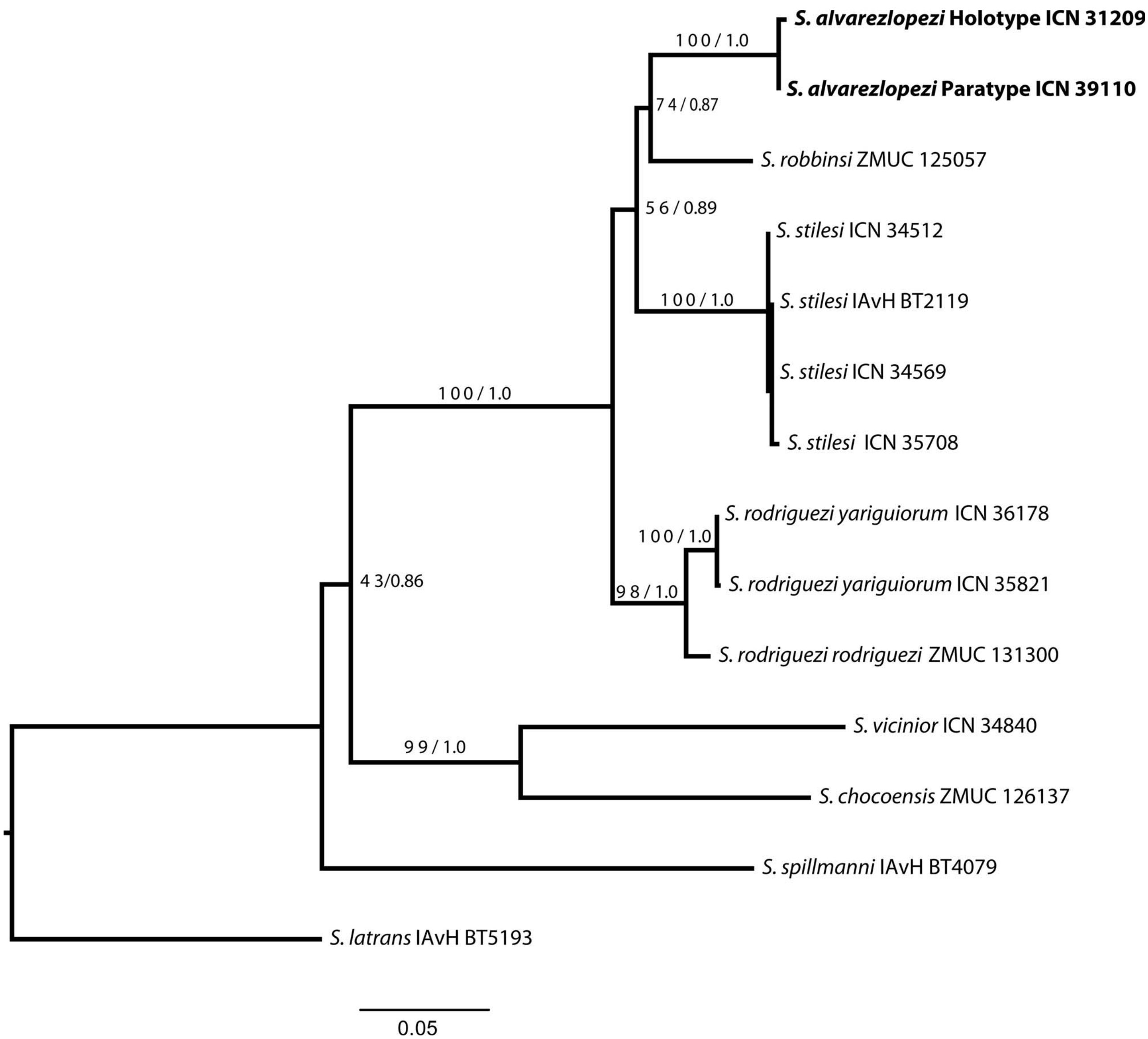

FIGURE 5. Phylogenetic position of *S. alvarezlopezi* sp. nov. relative to other tropical montane *Scytalopus* from northern South America based on 1,041 base pairs of the ND2 mitochondrial gene. The sampling included species identified as closely allied to the new species based on a comprehensive phylogeny of the genus (*S. robbinsi*, *S. rodriguezi*, *S. stilesi*), plus species occurring in the same general area of the Cordillera Occidental (*S. vicinior*, *S. chocoensis*, *S. latrans*). The phylogeny shown is the maximum-likelihood tree estimated using RAxML; numbers on nodes are maximum-likelihood bootstrap values and Bayesian posterior probabilities obtained in MrBayes.

In sum, the song of *S. alvarezlopezi* is unmistakable: a seemingly endless, machine-like series of short phrases of ~7–9 nearly identical notes. The song may be very long (most recordings show only a segment). The song of the holotype (XC-148624) was an 86 s series of trills (*churrs*), which at the beginning of the song are very short (0.83 ± 0.05 s) with a very long trill (12 s) after the first 10 phrases; then around the middle of the song the trills (*churrs*) become shorter (0.51 ± 0.27 s), louder, and more spaced until the end of the song. This song is not modulated in frequency. Vocalizations in tapaculos usually are characterized by harmonics (Figures 6, 7, 8). In *S. alvarezlopezi* the first overtone or second harmonic is usually the loudest with a peak frequency of 1.97 ± 0.09 kHz, a lower frequency of 1.67 ± 0.13 kHz and a higher frequency of 2.20 ± 0.12 kHz, and a very narrow frequency bandwidth of 0.52 ± 0.13 kHz (Table 3).

To quantify the differences in songs of *S. alvarezlopezi* and those of its near relatives (*S. robbinsi*, *S. stilesi*, and *S. rodriguezi*) by temporal and spectral parameters, we made

TABLE 2. Genetic distances calculated using sequences of the ND2 mitochondrial gene showing differentiation between *S. alvarezlopezi* (in bold) and other taxa included in phylogenetic analyses. Values above the diagonal are net distances correcting for intraspecific diversity and values below are uncorrected p-distances. The new species is most similar to, but still markedly different from, *S. rodriguezi* and *S. robbinsi*.

		1	2	3	4	5	6	7	8
1	*latrans*	–	0.116	0.118	0.110	0.113	0.125	0.118	**0.118**
2	*vicinior*	0.116	–	0.107	0.101	0.109	0.108	0.111	**0.108**
3	*spillmanni*	0.118	0.107	–	0.101	0.105	0.115	0.108	**0.101**
4	*rodriguezi rodriguezi*	0.110	0.101	0.101	–	0.013	0.048	0.047	**0.044**
5	*rodriguezi yariguiorum*	0.114	0.110	0.106	0.013	–	0.051	0.049	**0.051**
6	*stilesi*	0.125	0.108	0.115	0.049	0.052	–	0.048	**0.052**
7	*robbinsi*	0.118	0.111	0.108	0.047	0.050	0.049	–	**0.044**
8	***alvarezlopezi***	**0.112**	**0.109**	**0.102**	**0.045**	**0.052**	**0.053**	**0.045**	–

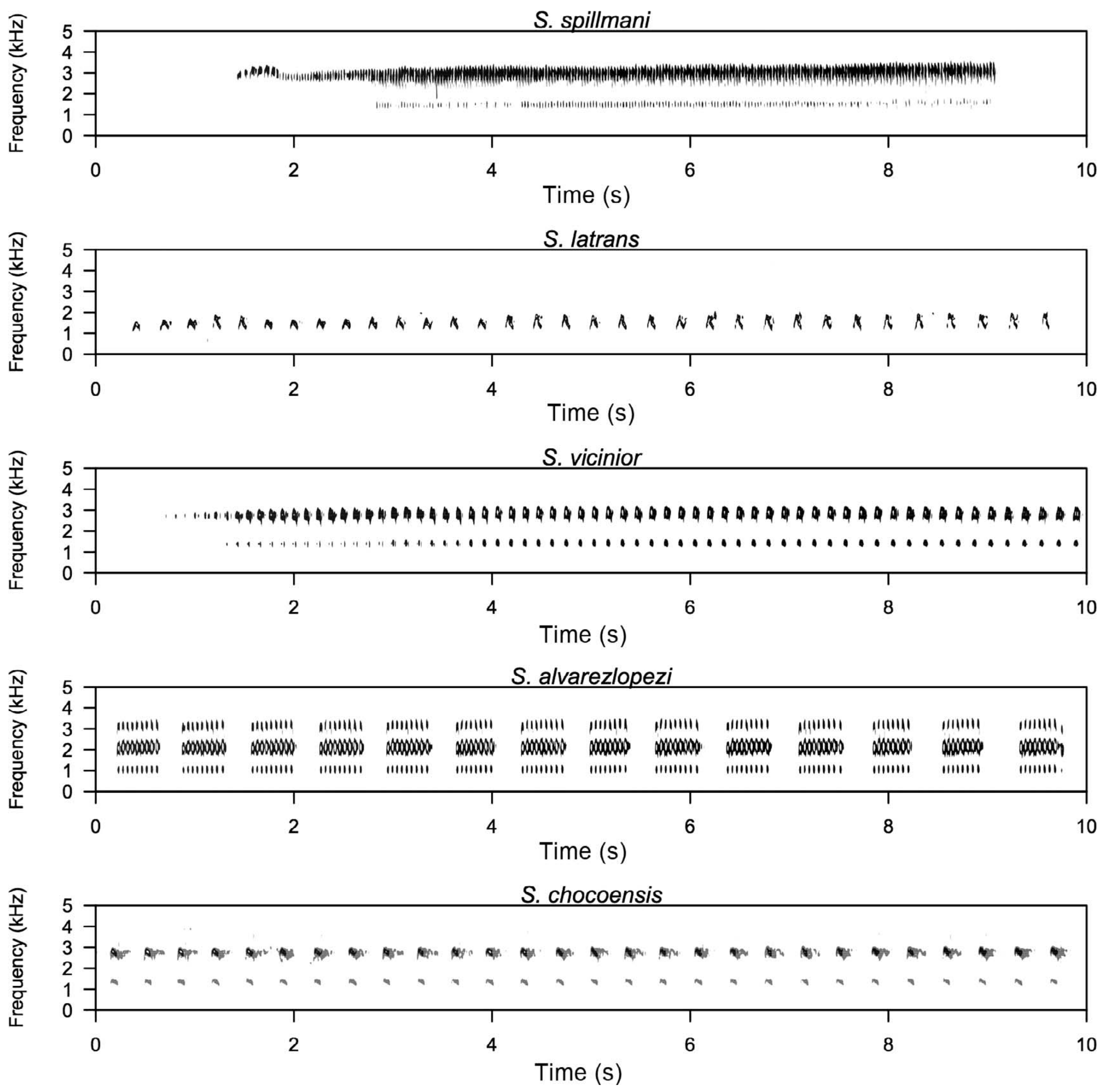

FIGURE 6. Ten-second sequences of sonograms of *Scytalopus alvarezlopezi* and the 4 species occurring with it on the Pacific slope of the Western Andes. Note that among these species, the song of *S. alvarezlopezi* is unique in being broken into numerous short phrases; that of *S. stilesi* consists of long phrases repeated at longer intervals, while the other species repeat long series of single notes differing among themselves in structure and tempo.

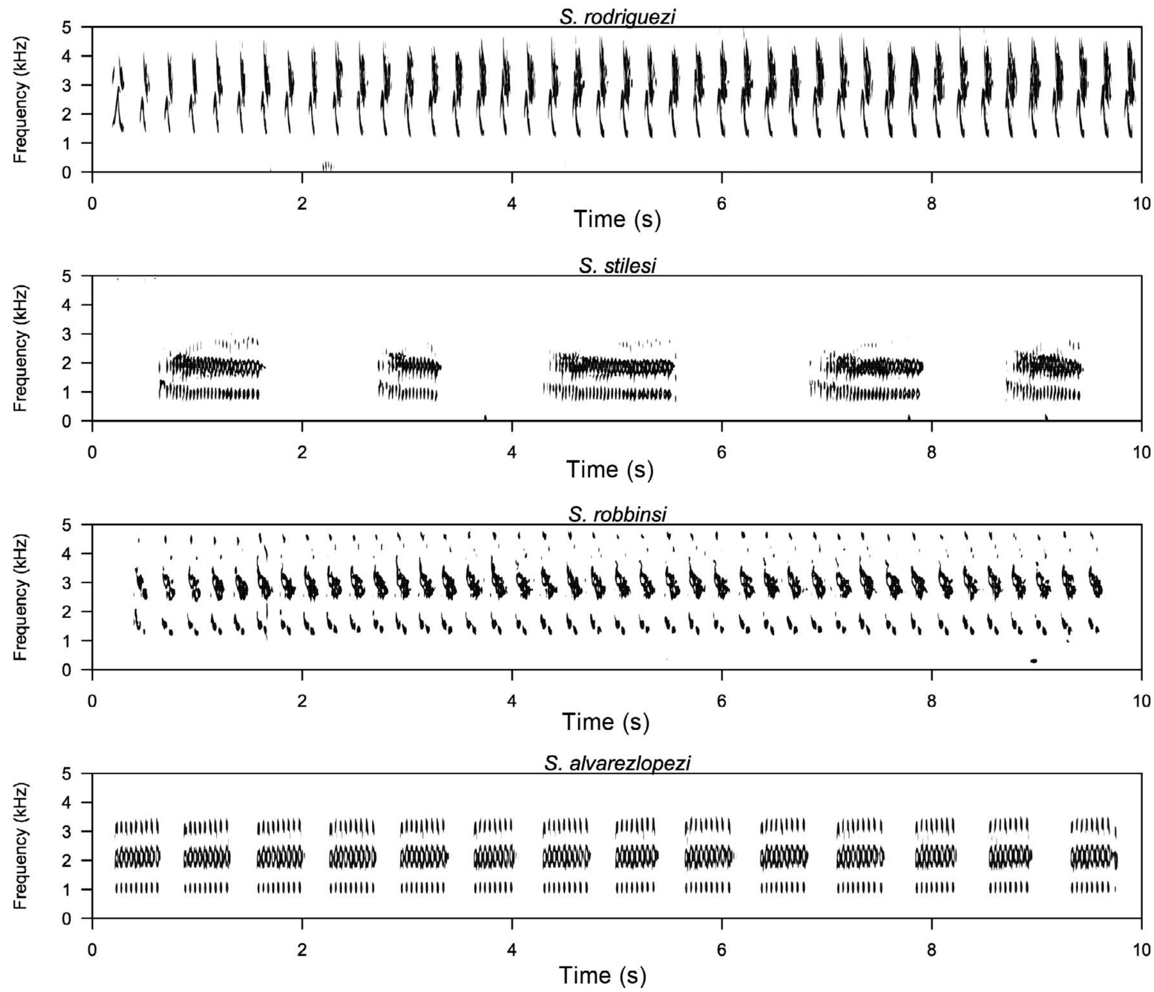

FIGURE 7. Ten-second sequences of sonograms of the songs of the members of the clade that includes *Scytalopus alvarezlopezi*, to demonstrate the overall structure (syntax) of the songs. Note that the songs of *S. robbinsi* and *S. rodriguezi* comprise repetitions of a single note type, whereas those of *S. stilesi* and *S. alvarezlopezi* are broken into shorter phrases.

2-second sonograms and oscillograms of each species (examples in Figure 8). Although *S. alvarezlopezi* songs differ from those of the other members of its clade, its songs are more similar to *S. stilesi* in some of the parameters measured; these are the only species whose songs consist of repeated short phrases rather than repetitions of a single note type. The song pace in *S. alvarezlopezi* is faster (21.53 $\pm$ 0.27 notes s^{-1}) than the pace of *S. rodriguezi* (5.27 $\pm$ 0.81 notes s^{-1}) and *S. robbinsi* (4.73 $\pm$ 0.25 notes s^{-1}) songs, but slower than the song of *S. stilesi* (28.27 $\pm$ 1.59 notes s^{-1}). The song bouts in *S. robbinsi* are very long compared to the other members of the clade. The peak frequency (PF) of songs of *S. alvarezlopezi* is similar to that of *S. stilesi*, but lower than PF values for *S. rodriguezi* and *S. robbinsi* (Table 3, Figures 7 and 8). Regarding bandwidth, the songs of *S. alvarezlopezi* are narrower (0.52 $\pm$ 0.13 kHz) compared to *S. stilesi* (0.87 $\pm$ 0.14 kHz), *S. rodriguezi* (1.8 $\pm$ 0.13 kHz), and *S. robbinsi* (1.11 $\pm$ 0.08 kHz).

We explored whether these 4 taxa were vocally distinguishable in a linear multivariate space using discriminant analyses based on the above acoustic variables (Figure 9). Discriminant analysis based on average values demonstrated that *S. alvarezlopezi*, *S. rodriguezi*, *S. robbinsi*, and *S. stilesi* are clearly distinguishable in multivariate space in primary songs (Wilks's $\lambda = 0.0002$, $F = 16.48$, $P > 0.0001$, $n = 20$ individuals): all vocalizations were assigned properly to their corresponding species (Figure 9). Songs were best discriminated by the discriminant function 1, which was associated with pace (number of notes per second). Discriminant function 2 was associated with bandwidth (Table 4).

Ecology and Behavior

S. alvarezlopezi favors dense understory vegetation in cloud forest ravines (Figure 10) and slopes between ~1,300–1,400 and 1,750 m on the Pacific slope of the

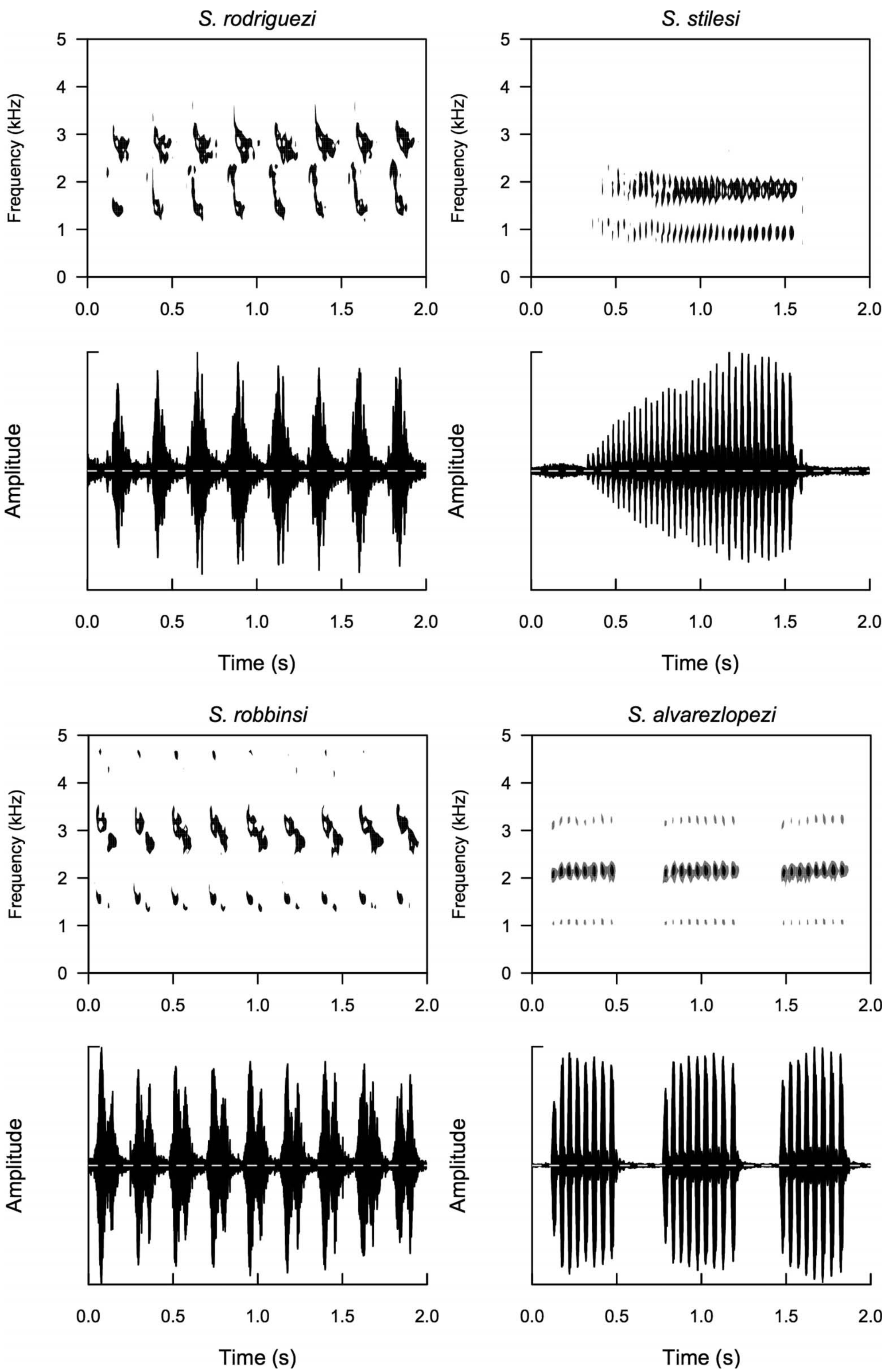

FIGURE 8. Representative two-second segments of sonograms and oscillograms of the songs of *Scytalopus alverezlopezi* and the other members of its clade, as used to quantify differences in frequency and other song parameters (see text and Table 3). Note that amplitude modulation is pronounced in *S. stilesi* but barely detectable in *S. alvarezlopezi*; frequency modulation is essentially absent in both; the dominant frequencies of *S. rodriguezi* and *S. robbinsi* are ~1 kHz higher than in *S. stilesi* and *S. alvarezlopezi*.

TABLE 3. Vocal characters of songs of *S. alvarezlopezi* and their relatives. Numbers correspond to the average and standard deviation. Lower frequency, higher frequency, and bandwidth were measured using a threshold set at −20 dB from the maximum amplitude of peak frequency. Peak frequency was defined as the frequency at which most energy in the note selected is found (Charif et al. 2010). Average entropy describes the amount of disorder for a selected spectrum; high values correspond to sounds with greater disorder whereas zero entropy corresponded to a pure tone with energy in only one frequency bin (Charif et al. 2010).

	S. rodriguezi ($n = 3$)	*S. stilesi* ($n = 7$)	*S. robbinsi* ($n = 3$)	*S. alvarezlopezi* ($n = 6$)
Lower frequency (kHz)	2.19 ± 0.06	1.51 ± 0.16	2.33 ± 0.11	1.67 ± 0.13
Higher frequency (kHz)	3.81 ± 0.61	2.37 ± 0.11	3.44 ± 0.13	2.20 ± 0.12
Bandwidth (kHz)	1.81 ± 0.35	0.87 ± 0.14	1.11 ± 0.08	0.52 ± 0.13
Peak frequency (kHz)	2.83 ± 0.46	1.98 ± 0.08	2.85 ± 0.14	1.97 ± 0.09
Song length (s)	8.43 ± 7.36	1.71 ± 0.93	34.15 ± 40.94	0.53 ± 0.25
Number of notes	40.25 ± 29.08	48.13 ± 26.1	167.88 ± 205.65	11.45 ± 6.19
Pace (number of notes s^{-1})	5.27 ± 0.81	28.27 ± 1.59	4.73 ± 0.25	21.53 ± 2.13
Average entropy	3.04 ± 0.38	2.22 ± 0.15	2.44 ± 0.1	1.61 ± 0.41

Western Andes. At least at Cerro Montezuma, its range of elevations is sandwiched between those of *S. vicinior* (above) and *S. chocoensis* (below). Here, 4 species replace each other with little overlap on this slope: *S. chocoensis* up to ∼1,250–1,300 m, *alvarezlopezi* between ∼1,300 and 1,750–1,800 m, *vicinior* from ∼1,750–1,800 to ∼2,100 m, and *spillmanni* from ∼2,100 up to at least 2,600 m (the highest elevation of Cerro Montezuma), based on voice records. *S. latrans* also has been found at the highest part of Cerro Montezuma but differs in habitat, being found more in subparamo matorral, whereas the preceding species occur more in forest (G. Londoño, personal communication). *S. spillmanni* and *S. latrans* doubtless occur higher on nearby Cerro Tatamá itself, where forest extends to well over 3,000 m, with subpáramo and páramo at the highest elevations above 4,000 m where one might expect to find *S. opacus*. Where its altitudinal range meets that of *vicinior, alvarezlopezi* occurs on the floor and lower slopes of ravines, *vicinior* on the upper slopes and ridgetops, both at Cerro Montezuma and Pisones.

The 2 birds observed at close range by FGS were walking and hopping along the ground, scratching in the leaf litter, and hopping and fluttering briefly up to ∼50 cm to glean arthropod prey from the understory foliage and keeping within 1–2 m of each other. Within its restricted range of elevations, *S. alvarezlopezi* is at least locally very common in intact forest; neither at Cerro Montezuma nor at Pisones does it appear to range into second-growth to any extent. It is, if anything, even more terrestrial and reluctant to fly than other *Scytalopus*. During the attempt to capture a second specimen of *alvarezlopezi* in a steep-sided ravine with a deep gully at the base, FGS noted that as a bird approached the tape recorder, it chose to cross by running along the only fallen branch to bridge the gully rather than flying the 1 m or so to the other side; perhaps because of this, this species has been extraordinarily difficult to capture in a mist net. J. Heavyside and FGS set nets in (supposedly) strategic places in several ravines and repeatedly tried to lure a bird into them with tape recordings, only to find that it apparently approached the recording site by a circuitous route and arrived and sang from a few meters behind us, a frustration also shared by CDC and OLR. Only after several attempts with different

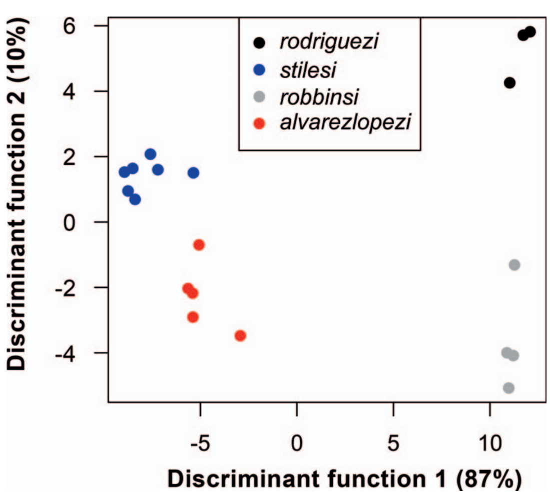

FIGURE 9. Results of the discriminant analysis of 8 song parameters of the 4 species of the clade that includes *Scytalopus alvarezlopezi*. Note that this analysis gives a clear separation of the songs of these species.

TABLE 4. Results of discriminant analysis based on 8 acoustic measurements of songs of *S. rodriguezi*, *S. stilesi*, *S. robbinsi*, and *S. alvarezlopezi*. Bold numbers highlight the most important variables in the discriminant functions.

	DF 1	DF 2
Lower frequency (kHz)	0.287	0.127
Higher frequency (kHz)	0.284	0.215
Bandwidth (kHz)	0.210	**0.508**
Peak frequency (kHz)	0.248	0.030
Song length (s)	0.064	0.108
Number of notes	0.044	0.088
Pace (number of notes s^{-1})	**−0.765**	0.202
Average entropy	0.135	0.350
Variance explained	88.42%	10.24%

FIGURE 10. Typical dark, dense vegetation of ravine floors preferred by *Scytalopus alvarezlopezi* at Cerro Montezuma, Risaralda, Colombia. Photo by T. Forrester.

individuals were we able to capture the paratype, which walked along the net and only entered it when JH lay flat on the ground and played several notes of the song from just behind it. Both of the individuals collected had enlarged gonads and were not molting, suggesting that the breeding season falls mainly in the middle months of the year, which include the months of lowest rainfall on the western slope of the Western Andes. The nest remains unrecorded.

Distribution and Biogeography

So far, records of *S. alvarezlopezi* (based on its distinctive song, see above) range from western Chocó (El Carmen, Chocó, XC 116858) and northwestern Antioquia (Parque Nacional Natural Las Orquídeas) to southwestern Valle del Cauca (Parque Nacional Farallones de Cali), mostly on the Pacific slope at ~1,350–1,800 m, but this species also is found locally on the east-facing slopes of some ridges at 2,000–2,200 m where the ridge line does not exceed 2,200–2,300 m. The definite records all fall between ~6°35′ and 3°N in the Western Andes (Figure 11). The lack of voice records (despite playback attempts) indicates that *alvarezlopezi* evidently does not occur farther south at the appropriate elevations and habitats in the Parque Nacional Natural Cerro Munchique (~2°30′N) in Cauca or in the Reserva Ñambí in Nariño (~1°20′N), so it is clearly a restricted-range Colombian endemic (Figure 11).

Records of *S. stilesi*, a species closely related to *S. alvarezlopezi,* are from between 1,400 and 2,000 m in the Central Andes, between ~5° to 3°N on the western slope (western Antioquia to Risaralda) and 8° south to at least to 4°45′N on the eastern slope (northern Antioquia to southern Caldas). At its southernmost extreme on the eastern slope, the range of *stilesi* could approach that of nominate *rodriguezi*, currently known in this cordillera only from a restricted area at ~2°N at the head of the Magdalena valley on the eastern slope of the Central Andes. All confirmed records of *vicinior* are from the Western Andes; several old specimen records from the Central Andes (not accompanied by voice records) might be better ascribed to *S. stilesi* (Cuervo et al. 2005), which is very similar in plumage (Figures 2 and 3). *S. robbinsi* occurs on the Pacific slope of southwestern Ecuador at somewhat lower elevations (700–1,250 m). It is interesting that its closest relative, *S. alvarezlopezi*, is the only other member of the clade with a Pacific-slope distribution (Figure 11). The distributions of the 2 subspecies of *S. rodriguezi* are widely disjunct; they differ subtly in vocalizations and slightly in morphology but show only weak genetic differentiation (Figure 5, Table 2); this species should be sought along the eastern side of the Eastern Andes, although deforestation on this slope is very extensive. All 4 species of the clade inhabit intact wet middle-elevation forests, a notable example of niche conservatism.

Conservation

At present, we would consider *S. alvarezlopezi* to be Near-threatened or at most, Vulnerable, because of its limited distribution (it is clearly a restricted-range species) and restriction to intact forest, but because its habitat—at least in the Tatamá region—is fairly continuous and for the most part not threatened, and because it is locally common to abundant, we see no reason to raise any higher red flags. However, because of the potential effects of climate change, its abundance and elevation range should be monitored into the future, especially in conjunction with those of the other tapaculos sharing the Pacific slope of the Western Andes, since we know nothing about the relative vulnerabilities of any of them and their respective abilities to track potential changes in climate and vegetation. Cerro Montezuma seems the ideal place to initiate such a monitoring program.

DISCUSSION

The diversity of many genera of tracheophone suboscines had long been greatly underestimated because many species differ only subtly in plumage, rendering their recognition by traditional museum studies based solely on specimens extremely problematic. Over the last 2 decades, this situation has changed dramatically. The first indication of the heretofore underestimated diversity of many genera was the recognition that many populations differed strikingly in their vocalizations, which are genetically determined in these suboscines. Studies of DNA indicated that vocal and genetic differences were strongly correlated (Arctander and Fjeldså 1994), justifying the descriptions of numerous new species. For no group has the change been so striking as in the genus *Scytalopus*, long recognized as a particularly refractory genus due to extremely subtle differences in plumage and morphology over its wide

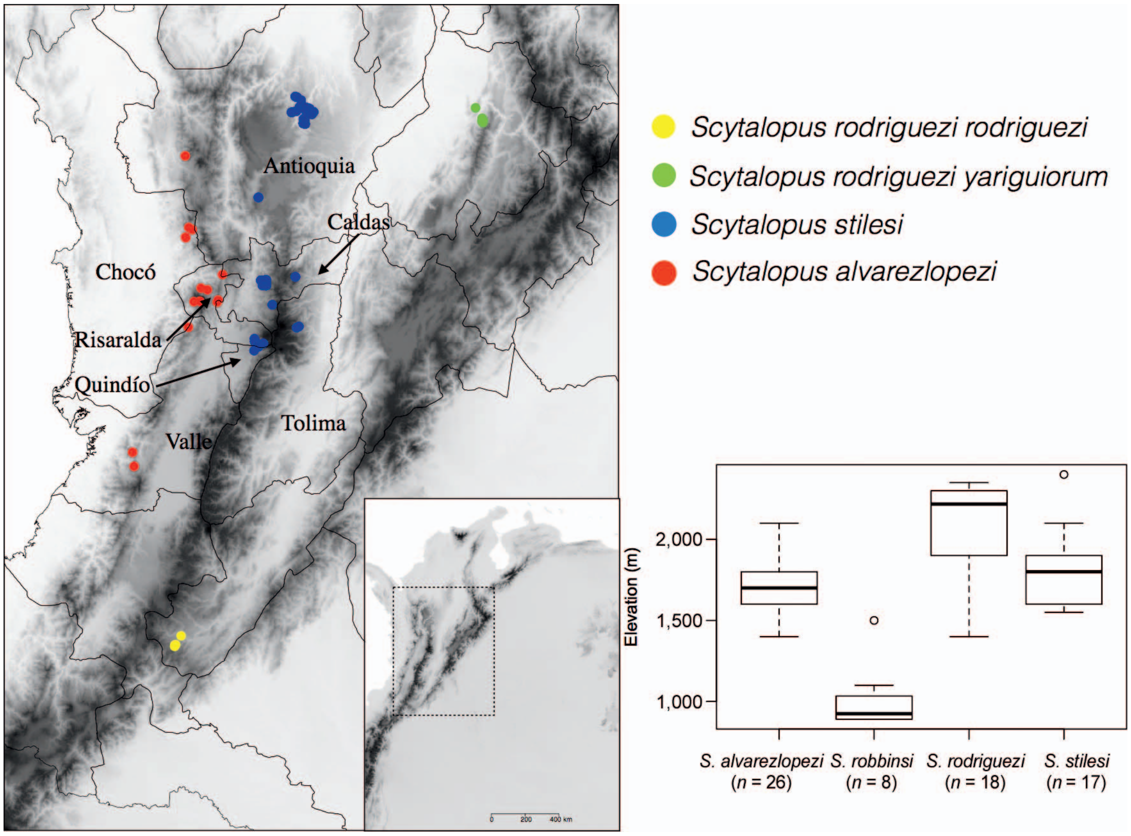

FIGURE 11. Distributions of *Scytalopus alvarezlopezi* and its close relatives in Colombia, and the elevational distributions of all 4 members of its clade. Note the similar altitudinal distributions of *S. stilesi* and *S. alvarezlopezi* in different mountain ranges, the great disjunction between the 2 subspecies of S. *rodriguezi*, and the different elevational range of *S. robbinsi* in southwestern Ecuador.

geographical distribution from Costa Rica through southern South America (Zimmer 1932, Krabbe and Schulenberg 2003, Remsen et al. 2015). Beginning with the seminal study of Krabbe and Schulenberg (1997), the number of recognized species has increased fourfold. The number of species known from Colombia alone has increased from 6 (Hilty and Brown 1986) to 14 (Krabbe and Schulenberg 1997, 2003, Cuervo et al. 2005, Krabbe et al. 2005, Avendaño et al. 2015, present study), as well as recognition of considerable subspecific variation (e.g., Donegan and Avendaño 2008, Donegan et al. 2013, Avendaño and Donegan 2015), all of which have permitted deciphering the subtle morphological differences between many taxa. *Scytalopus* has proven to be a striking example of the influences of geographic variation and isolation in speciation, leading to a better understanding of its biogeography in relation to the complexities of the uplifting of the Andes in particular. The present study fills a nomenclatural and distributional gap for the Western Andes, and ongoing studies may well result in the description of new taxa in hitherto unstudied regions of the other ranges in Colombia. All of this has added greatly to our knowledge of the conservation status of many taxa, several of which are under threat (notably *S. rodriguezi* in Colombia), setting priorities for the declaration of new conservation areas.

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Ethics statement: This research was conducted in compliance with the Guidelines to the Use of Wild Birds in Research. Specimen collecting was authorized by the Colombian Autoridad Nacional de Licencias Ambientales ANLA (Resolution 0255 from 2014).

Author contributions: F.G.S. and C.D.C. conceived the study. F.G.S., O.A.L, and C.D.C. performed the fieldwork. F.G.S., O.A.L, and C.D.C. analyzed the data. F.G.S., O.A.L,. and C.D.C. wrote the paper.

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APPENDIX 1. Recordings used to calculate song parameters for Table 3 and Figure 9 for *Scytalopus alvarezlopezi* and related species. BSA = Banco de Sonidos Animales, Instituto Alexander von Humboldt; MLS = Macaulay Library of Natural Sounds; XC = xeno-canto.

Species	*n*	dt	notes	avg. ent.	lf	hf	pf	df	pace	Source	Recordist	Location
S. alvarezlopezi	6	0.34	7.33	1.48	1623.25	2042.42	1866.20	419.20	21.50	BSA 24413	Oscar Laverde	Colombia, Risaralda, Pueblo Rico, Cerro Montezuma
S. alvarezlopezi	3	0.89	21.67	2.21	1561.57	2295.53	1981.10	733.97	24.35	BSA 24741	Oscar Laverde	Colombia, Risaralda, Pueblo Rico, Cerro Montezuma
S. alvarezlopezi	6	0.69	12.83	1.61	1681.78	2185.60	1981.03	503.85	18.53	XC 273907	Peter Boesman	Colombia, Risaralda, Pueblo Rico, Cerro Montezuma
S. alvarezlopezi	3	0.30	6.67	1.66	1597.30	2128.10	1923.63	530.83	22.42	XC 51261	David Geale	Colombia, Risaralda, Pueblo Rico, Cerro Montezuma
S. alvarezlopezi	4	0.42	8.75	1.08	1900.63	2335.70	2110.28	435.08	20.88	XC 82000	Andrew Spencer	Colombia, Chocó, El Carmen, Las Tangaras Natural Reserve
S. robbinsi	1	95.24	475.00	2.48	2221.80	3374.90	2756.20	1153.00	4.99	MLS 43467	Mark B. Robbins	Ecuador, El Oro
S. robbinsi	2	18.38	86.50	2.30	2456.55	3487.45	3057.70	1030.90	4.59	XC 192699	Niels Krabbe	Ecuador, El Oro
S. robbinsi	1	8.20	40.00	2.54	2251.60	3300.10	2756.20	1048.60	4.88	XC 192671	Niels Krabbe	Ecuador, Guayas
S. robbinsi	3	14.78	70.00	2.44	2390.07	3586.77	2813.67	1196.70	4.46	XC 192680	Niels Krabbe	Ecuador, El Oro
S. rodriguezi	3	5.50	30.33	2.65	2188.07	3234.97	2555.30	1576.80	5.61	XC 143848	Diego Calderón-F.	Colombia, Santander, San Vicente
S. rodriguezi	7	2.98	17.43	3.07	2132.33	3754.96	2584.00	1622.63	5.87	XC 143850	Diego Calderón-F.	Colombia, Santander, San Vicente
S. rodriguezi	1	16.80	73.00	3.40	2248.50	4446.30	3359.20	2197.70	4.35	XC 27394	Niels Krabbe	Colombia, Huila, Finca Meremberg
S. stilesi	5	1.19	36.20	2.04	1737.34	2412.56	2067.20	675.22	30.40	BSA 19080	Andrés Cuervo	Colombia, Antioquia, Amalfi
S. stilesi	6	2.01	53.00	2.28	1402.12	2375.90	1968.80	973.80	26.42	BSA 19353	Andrés Cuervo	Colombia, Antioquia, Amalfi
S. stilesi	6	3.43	97.00	2.52	1354.30	2445.38	1968.80	1091.07	28.32	BSA 19354	Andrés Cuervo	Colombia, Antioquia, Amalfi
S. stilesi	7	2.29	65.57	2.22	1395.49	2301.50	1982.19	905.99	28.68	BSA 19355	Andrés Cuervo	Colombia, Antioquia, Amalfi
S. stilesi	6	1.13	33.33	2.16	1479.60	2278.85	1923.65	799.23	29.53	MLS 165765	Matthew J. Sarver	Colombia, Antioquia, Anorí, El Arrierito Natural Reserve
S. stilesi	5	0.87	22.60	2.19	1739.62	2566.88	2084.42	827.26	25.97	XC 273463	Peter Boesman	Colombia, Antioquia, Medellín
S. stilesi	5	1.02	29.20	2.15	1443.06	2241.98	1860.46	798.92	28.55	XC 75363	Fabrice Schmitt	Colombia, Antioquia, Anorí