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SCYTALOPUS STILESI, A NEW SPECIES OF TAPACULO (RHINOCRYPTIDAE) FROM THE CORDILLERA CENTRAL OF COLOMBIA

Andrés M. Cuervo,[1,5] Carlos Daniel Cadena,[2] Niels Krabbe,[3] and Luis Miguel Renjifo[2,4]

[1]*Instituto de Biología, Universidad de Antioquia, A.A. 1226, Medellín, Colombia;*
[2]*Department of Biology and International Center for Tropical Ecology, University of Missouri-St. Louis, 8001 Natural Bridge Road, St. Louis, Missouri 63121, USA;*
[3]*Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark; and*
[4]*Departamento de Ecología y Territorio, Facultad de Estudios Ambientales y Rurales, Pontificia Universidad Javeriana, Transversal 4 No. 42-00 Piso 8, Bogotá, Colombia*

Abstract.—We describe *Scytalopus stilesi*, an overlooked species of tapaculo endemic to Colombia, on the basis of a series of eight specimens taken in 2002 and comparative analyses of its vocalizations, mitochondrial DNA sequences, and distribution. The new species ranges in the northern half of the Cordillera Central of the Colombian Andes in the Departments of Antioquia, Caldas, and Risaralda, in cloud forests between 1,420 and 2,130 m above sea level. The song, calls, and female song of the new species differ distinctly from those of all other known *Scytalopus* taxa. Phylogenetic analyses based on sequences of the cytochrome-*b* gene strongly suggest affinities with *S. robbinsi* of southwestern Ecuador and with two as-yet-undescribed tapaculos from the Colombian Andes. *Scytalopus stilesi* coexists locally with, though it is ecologically segregated from, *S. atratus, S. latrans,* and *S. spillmanni*. The mid-elevation premontane wet forests to which the new species is restricted have been subject to severe deforestation and fragmentation. The species is, however, relatively common in continuous mature-forest remnants, large primary-forest fragments, riparian forests, and tall secondary-forest patches. We employed a geographic information system (GIS) approach to model the potential distribution of the new species and assess its conservation status under the International Union for the Conservation of Nature (IUCN) criteria. *Scytalopus stilesi* does not qualify as threatened according to those criteria, but it should be regarded as near threatened. The new species coexists with numerous threatened bird species that are in need of more effective conservation. *Received 25 April 2004, accepted 18 November 2004.*

Key words: Andes, cytochrome *b*, new species, *Scytalopus*, suboscines, systematics.

Scytalopus stilesi, una Nueva Especie de Tapaculo (Rhinocryptidae) de la Cordillera Central de Colombia

Resumen.—Describimos a *Scytalopus stilesi*, una nueva especie de tapaculo endémica de Colombia, con base en una serie de ocho especímenes colectados en 2002 y en análisis comparativos de sus vocalizaciones, secuencias de ADN mitocondrial y distribución. La nueva especie se distribuye en la mitad norte de la Cordillera Central de los Andes colombianos en los departamentos de Antioquia, Caldas y

[5]Present address: Department of Biology, University of Puerto Rico, P.O. Box 23360, San Juan, Puerto Rico 00931. E-mail: wa022129@cnnet.upr.edu

Risaralda, en bosques de niebla entre 1,420 y 2,130 m de elevación. El canto, los reclamos y el canto de la hembra de la nueva especie difieren distintivamente de los de todos los taxa conocidos del género *Scytalopus.* Los análisis filogenéticos basados en secuencias del gen mitocondrial citocromo *b* sugieren fuertemente afinidades con *S. robbinsi* del suroccidente de Ecuador y con dos especies aún no descritas de los Andes colombianos. *Scytalopus stilesi* coexiste localmente con *S. atratus, S. latrans* y *S. spillmanni*, aunque se segrega ecológicamente de ellos por uso de hábitat. Los bosques premontanos húmedos de elevaciones medias a los cuales está restringida la nueva especie han sido objeto de una severa deforestación y fragmentación. Sin embargo, la especie es relativamente común en remanentes de bosques maduros continuos, fragmentos de bosque primario, bosques riparios y parches de bosque secundario avanzado. Empleamos un análisis basado en sistemas de información geográfica para modelar la distribución potencial de la nueva especie y evaluar su estado de conservación bajo los criterios de la IUCN. *S. stilesi* no califica como amenazada de acuerdo con estos criterios, pero debe ser considerada como casi amenazada. La nueva especie coexiste con numerosas especies de aves amenazadas que requieren un nivel de conservación más efectivo.

Species limits in the suboscine genus *Scytalopus* (Rhinocryptidae) have been exceedingly difficult to resolve, leading ornithologists to consider its taxonomy "unusually difficult" (Zimmer 1939) and "the most complicated of all Neotropical bird genera" (Ridgely and Tudor 1994). The difficulty results from subtle variation in plumage and morphology among species, coupled with substantial age-related and individual variation within species; the birds' skulking behavior in low and dense understory, which makes them difficult to observe and collect; lack of specimens with reliable data from many areas; "foxing" of old skin specimens, including types; and insufficient study of their vocalizations (Zimmer 1939; Whitney 1994; Krabbe and Schulenberg 1997, 2003).

Increased fieldwork in South America over recent years has confirmed that plumage is not a good indicator of species limits in *Scytalopus,* casting doubt on the reliability of traditional, museum-based taxonomic treatments of the group (e.g. Zimmer 1939) and spurring development of new studies that draw on other types of data to delimit species (Whitney 1994, Krabbe and Schulenberg 1997, Coopmans et al. 2001). As in other tracheophone suboscines, vocalizations in *Scytalopus* are believed to be innate and highly stereotyped within populations (Fjeldså and Krabbe 1990; Vielliard 1990; Krabbe and Schulenberg 1997, 2003) and appear to characterize genetically distinct units (Arctander and Fjeldså 1994). Moreover, *Scytalopus* distributions are characterized by sharp replacements of species along altitudinal gradients, and sympatric taxa are often segregated by habitat (Whitney 1994, Krabbe and Schulenberg 2003). Thus, it is now evident that resolving the classification of *Scytalopus* requires comprehensive assessments of populations in terms of vocalizations, elevational distribution, and habitat, ideally in combination with genetic analyses.

Extensive new data on vocalizations and distribution have revealed that the number of *Scytalopus* species occurring in the northern Andes was grossly underestimated by traditional taxonomy and have led to the description of three new species from Ecuador and the elevation of several previously named forms to species rank (Krabbe and Schulenberg 1997). Although Krabbe and Schulenberg (1997) included some taxa whose ranges extend into Colombia, our understanding of *Scytalopus* taxonomy and distribution in this country remains especially complicated (e.g. Krabbe and Schulenberg 2003). As with Ecuadorian taxa, the number of species occurring in Colombia has clearly been underestimated, yet no detailed taxonomic studies of Colombian *Scytalopus* have been undertaken. Currently, some new species remain undescribed because of insufficient comparative material (e.g. Krabbe and Schulenberg 1997, Cuervo et al. 2003), and others may have been overlooked in spite of ornithological fieldwork. By integrating data on vocalizations, distribution, ecology, and mitochondrial DNA variation, we have started to re-address the species-level taxonomy of

Colombian *Scytalopus*. The present study is the first in a series that, we expect, will ultimately result in a substantially better understanding of the diversity and distribution patterns of this genus in Colombia.

Over the past ten years, A.M.C., C.D.C., L.M.R., and others (see Acknowledgments) have repeatedly observed and tape-recorded vocalizations of a *Scytalopus* tapaculo in mid-elevation humid forests of the Cordillera Central of the Andes in the Departments of Antioquia, Caldas, and Risaralda (Colombia). Upon examining its vocalizations, N.K. suspected that this tapaculo was a new species. Recent fieldwork by A.M.C. in northern Antioquia resulted in collection of eight specimens with associated tissue samples, in addition to numerous recordings of calls and songs of this taxon. Vocal, morphological, ecological, and genetic comparative analyses of the available material confirm that this Central Andean *Scytalopus* indeed represents a heretofore undescribed species, which we propose to name:

Scytalopus stilesi, sp. nov.
Stiles's Tapaculo
Tapaculo de Stiles

Holotype.—Instituto de Ciencias Naturales (ICN) at Universidad Nacional de Colombia no. 34569; adult male (testes: 8.6 × 5.8 mm left, 7.5 × 5.0 mm right) from Finca Canales, Vereda Cajamarca, Municipality of Amalfi, Department of Antioquia, Colombia (6°49′25.2″N, 75°05′37.8″W, ~1,845 m above sea level). Collected by A.M.C. (field number AMC 104) on 5 January 2002. Tissue samples deposited in the tissue bank of Instituto Alexander von Humboldt, Colombia (IAvH-BT, no. 2093); recordings of voice to be archived in the Macaulay Library of Natural Sounds (MLNS), Cornell Laboratory of Ornithology, Ithaca, New York. DNA sequence of a fragment of the cytochrome-*b* mitochondrial gene deposited in GenBank (accession no. AY755652).

Diagnosis.—A typical rhinocryptid (see cover plate and Fig. 1), assignable to the genus *Scytalopus* by the combination of a fairly sharp and laterally compressed bill with high culmen; nares covered by a conspicuous operculum; short and somewhat erect feathers in lores; soft, short, very concave, and very rounded wings, with 10 primaries; relatively short and graduated tail with the outermost rectrices shorter than the rest; tail much shorter than wing; large and strong feet, with distinct taxaspidean tarsal scutellation; hind claw strongly curved and shorter than the digit; overall dark and soft plumage, with little sexual dimorphism and substantial individual variation in plumage related to age (Ridgway 1911, Krabbe and Schulenberg 2003).

The new species is most readily diagnosed by its vocalizations, the song being a long series of short churrs, the three-note call and female advertising song differing distinctly from voices of all other known *Scytalopus* taxa (see below). *Scytalopus stilesi* can also be reliably diagnosed genetically, on the basis of DNA sequences of the cytochrome-*b* mitochondrial gene (see below).

Morphologically, the new species may not be reliably distinguishable from most other *Scytalopus* taxa. However, *S. stilesi* is likely to co-occur only with *S. atratus*, *S. latrans*, *S. spillmanni*, and possibly *S. vicinior* (see below). *Scytalopus stilesi* can be distinguished from *S. latrans* on the basis of its larger size, less blackish appearance, and brown wash and barring on the plumage; from *S. atratus* on the basis of its smaller body size and lack of white crown spot; and from *S. spillmanni* by its generally smaller size and longer bill (see Table 1 and Krabbe and Schulenberg 1997, 2003). *Scytalopus stilesi* is less dark than some specimens of *S. vicinior* (e.g. ICN 31207 and 31208 from Risaralda), but not than others (e.g. ICN 34840 from Valle del Cauca), and has a shorter tail (apparently no overlap; Krabbe and Schulenberg 1997).

Fig. 1. Adult *Scytalopus stilesi* at Otún-Quimbaya Fauna and Flora Sanctuary, Risaralda. (Photo courtesy of Gustavo Londoño.)

TABLE 1. Body mass (g) and selected morphological measurements (mm) of *S. stilesi* specimens. Juvenile male ICN 34584 not included. Measurements are omitted in cases in which they could not be taken accurately.

ICN number	Body mass	Wing (flat)	Tail	Tarsus	Bill length[a]	Bill height[b]	Bill width[b]
			Males				
34569	24.5	64.5	43.3	23.0	7.5	4.0	3.5
34609	21.5	63.0	42.0	22.9	8.1	4.1	3.6
$x \pm$ SD	23.0 ± 2.1	63.75 ± 1.1	42.65 ± 0.9	22.95 ± 0.1	7.8 ± 0.4	4.05 ± 0.1	3.55 ± 0.1
			Females				
34420	20.0	58.0	40.0	21.8	7.0	3.8	3.6
34505	20.5	60.0	40.6	22.0	7.0	3.9	3.4
34512	21.5	61.0	41.1	22.9	7.8	3.8	3.5
34610	22.0	58.0	39.8	21.5	7.2	–	3.5
34615	22.0	59.0	42.3	21.6	–	–	–
$x \pm$ SD	21.2 ± 0.9	59.2 ± 1.3	40.8 ± 1.0	22.0 ± 0.6	7.25 ± 0.4	3.8 ± 0.1	3.5 ± 0.1

[a] From fore edge of operculum to tip.
[b] At fore edge of operculum.

Juveniles of *S. stilesi* are probably not diagnosable morphologically from those of similar species (for comparative morphometrics see Table 1 and Krabbe and Schulenberg 1997).

Description of holotype.—A medium-sized tapaculo with forecrown, lores, ear coverts, and upper parts—including crown, mantle, scapulars, and back—uniformly Blackish Neutral Gray 82 (capitalized color names and numbers follow Smithe 1975). Underparts paler in the chin and throat, between Medium Neutral Gray 84 and Light Neutral Gray 85, becoming darker toward chest, sides, and upper belly (between Blackish Neutral Gray and Dark Neutral Gray 83). Lower belly, flanks, and thighs bright brown (closest to Mikado Brown 121C), with dark gray (Blackish Neutral Gray) barring. Rump somewhat darker brown (between Mikado Brown and Brussels Brown 121B) and much less barred than the underparts. Tail and wings (including wing coverts) Black Neutral Gray. Irides dark brown, bill black with base of the mandible horn, feet and toes grayish brown, and claws pale horn. Stomach contents: small insect fragments; relatively abundant subcutaneous fat. Body mass 24.5 g; bill (from fore edge of the operculum) 7.5 mm; bill height 4.0 mm; bill width 3.5 mm; tarsus 23.0 mm; tail 43.3 mm; wing (flattened) 64.5 mm; 11 rectrices.

Designation of paratypes.—A total of seven specimens from Antioquia, prepared as conventional study skins deposited at the ICN, with tissue samples deposited at the IAvH-BT, as follows: adult male: ICN 34609, IAvH-BT 2227; adult female: ICN 34505, IAvH-BT 2231; adult female: ICN 34610, IAvH-BT 2119; juvenile male: ICN 34584, IAvH-BT 2229; subadult female: ICN 34420, IAvH-BT 2230; adult female: ICN 34615, IAvH-BT 2127; immature female: ICN 34512, IAvH-BT 2228.

Etymology.—We take great pleasure in naming this species after F. Gary Stiles, in recognition of his outstanding career and the many substantial contributions he has made to Neotropical ornithology over the past three decades. Gary has admirably combined the traditions of museum and field ornithology while based in Neotropical countries (Costa Rica and Colombia), where he has forged his seminal studies on the ecology and taxonomy of birds, most notably hummingbirds. Since his arrival in Colombia in 1988, he has deeply influenced the development of ornithology as a science in the country through his research and teaching, and through his pivotal role in the establishment and growth of the Asociación Bogotana de Ornitología and, more recently, the Asociación Colombiana de Ornitología.

REMARKS

Variation within the type series.—Considerable variation exists in the type series, largely reflecting variation related to age. Adult male ICN 34609 resembles the holotype closely, but is generally slightly paler, with subtle brownish tinges in the crown and wing (on tertials and upper coverts); also, the rump is more conspicuously barred and darker brown (closest to Brussels Brown), and the brown extends higher into the lower back than in the type. Juvenile male ICN 34584 is similar to juveniles of other *Scytalopus* species: completely lightly barred brown and gray; head, back, and wings (Brussels Brown) darker than throat, chest, and lower belly (closest to Mikado Brown). That specimen had presumably fledged recently, because it had no rectrices and had only a few growing wing feathers, of less than one-quarter of their expected full size. Females tend to be paler ventrally, closer to Medium Neutral Gray than to the Dark Neutral Gray of males. Most female specimens have brown secondaries and wing coverts; the latter often show brown margins and a dark subterminal half moon. Immature female ICN 34420 (see cover) shows paler grays and redder browns overall: throat and chest between Light Neutral Gray (85) and Pale Neutral Gray (86); feathers on sides of head, lores, and malars tinged brown; the brown in lower abdomen is paler than in other specimens (closest to Tawny 223D). Most of that specimen's plumage shows some barring, which is especially pronounced dorsally, where it is fine in the head and becomes thicker in the back; the specimen has an overall scaled appearance. Like male ICN 34609, all the females show tinges of brown to varying degrees in the back and head, mostly in the crown. The extent of barring in the rump and upper tail coverts is variable: in some specimens (e.g. female ICN 34505), it is very pronounced; whereas in others (e.g. female ICN 34512), it is faint. Although sample sizes are limited, males and females do not appear to differ in morphometrics or in body mass, yet males tend to have longer wings (Table 1). Number of rectrices seems to vary among specimens (range 10–12). In general, no molt was observed on the type series, but female ICN 34615 had a single remix and some wing coverts growing.

Vocalizations.—We analyzed natural (unprovoked) songs recorded from ≥24 different individuals from various localities encompassing most of the range of *S. stilesi*. Bouts of song consisted of up to 35 or more monotonous *churrs*, the first often longest, ranging from 3 to 5 s and occasionally up to 15 s long, the following one or two transitional, all the rest constant, 1–2 s long, typically with pauses 0.5–1.0 s between them (Fig. 2). Each *churr* was composed of a single note repeated regularly at a pace of 23–30 s^{-1} (Fig. 3A). As in most congeners, the first overtone in a song note of *S. stilesi* was normally the loudest. The fundamental note was usually weaker, and the second overtone barely audible; but in one recording, the fundamental was loudest. The first overtone ranged in frequency between 1.8 and 2.2 kHz. Within each *churr*, the volume increased gradually over the first 0.3–0.5 s and then remained constant, to fade and fall slightly on the last one or two notes, which were also slightly lower-pitched than the rest. No geographic variation in the song or calls of the new species was observed.

In comparison with the song of the closely related *S. robbinsi* (see below), the song of *S. stilesi* is considerably faster and lower-pitched and composed of *churrs* rather than being a continuous series, and the individual song notes are single and mainly upstrokes, instead of the usually double strokes and mainly downstrokes of *S. robbinsi* (Fig. 3B). Song of *S. stilesi* also differs distinctly from song of *S. atratus confusus* (Fig. 3C), *S. spillmanni* (Fig. 3D), and *S. latrans* (Fig. 3E), three taxa whose ranges locally overlap with or border the range of *S. stilesi*.

Calls of *S. stilesi* were recorded from at least eight different individuals. Calls were repeated at irregular intervals and were a two-note or, more commonly, three-note *cu-wi?*, *cu-cui-wi?*, or *cu-wi-wi?*, first note at 2.1–2.2 kHz, last note distinctly rising at 2.3–2.5 kHz, and middle note variably like the first or the last note or intermediate (Fig. 4A–C). The calls were lower-pitched than the single-note, slowly rising calls of *S. robbinsi* (Fig. 4D–F) and also unlike the calls of any other known *Scytalopus*.

The single female advertising song recorded was given in duet with male song (Fig. 5A). It was ~13 s long; a series of ~10 sharp downstroke

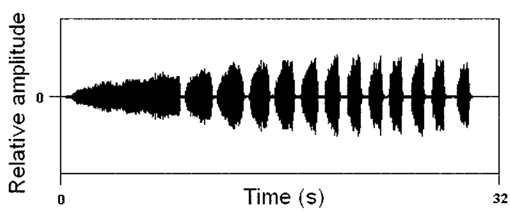

Fig. 2. Song bout of 13 *churrs* by *S. stilesi*. Aranzazu, Caldas, Colombia, 27 August 2003 (P. Caycedo).

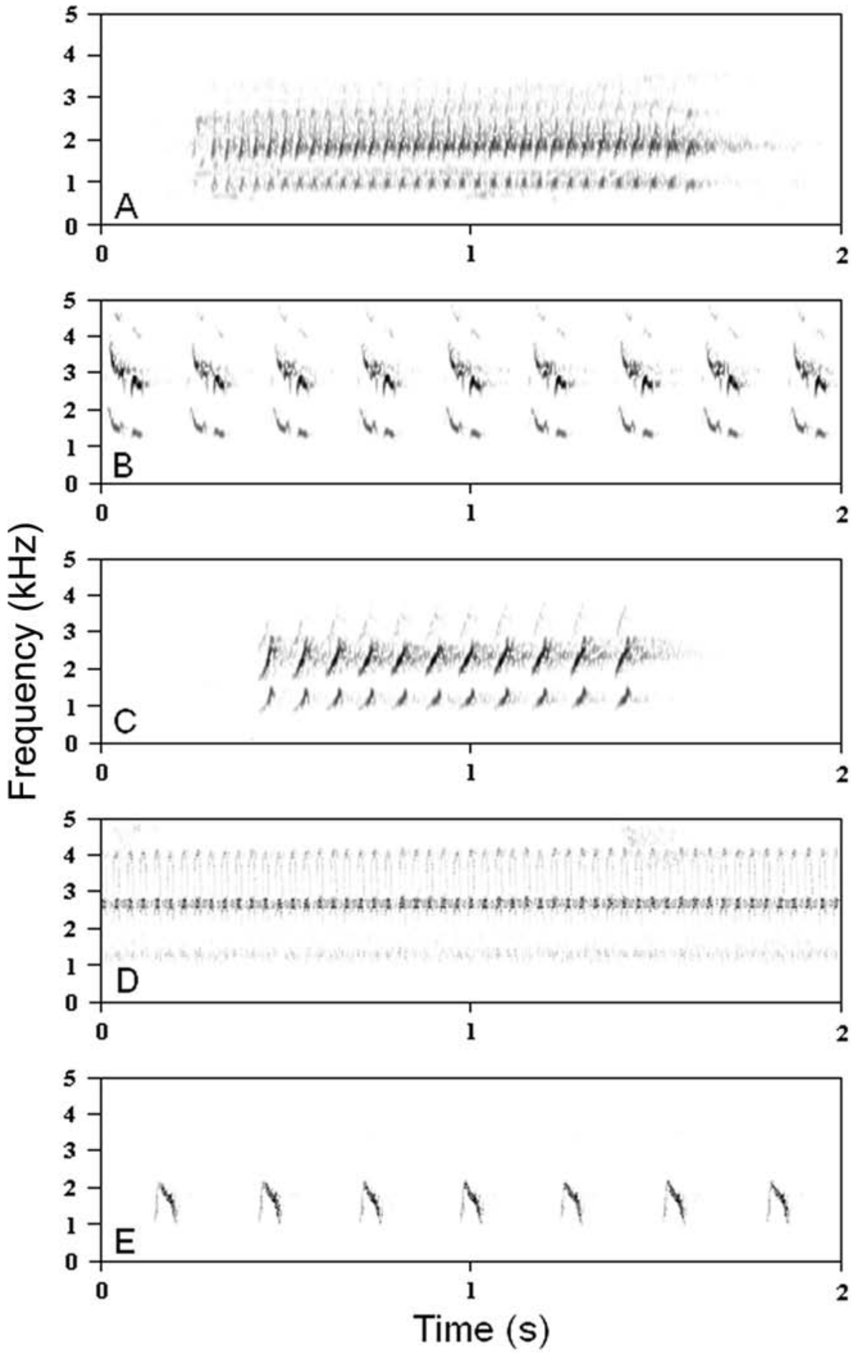

FIG. 3. Songs of males of various *Scytalopus* spp. (A) Single *churr* by *S. stilesi*, Otún-Quimbaya, Risaralda, Colombia, 2 November 1996 (L.M.R.); (B) part of song by *S. robbinsi*, Buenaventura, El Oro, Ecuador, 15 April 1991 (N.K.); (C) one song phrase by *S. atratus confusus*, Mampuestos, Antioquia, Colombia, 30 March 2002 (A.M.C.); (D) part of song by *S. spillmanni*, Ucumarí, Risaralda, Colombia, 17 July 2001 (C.D.C.); (E) part of song by *S. latrans*, Alto El Gallinazo, Antioquia, Colombia, 12 June 1994 (N.K.).

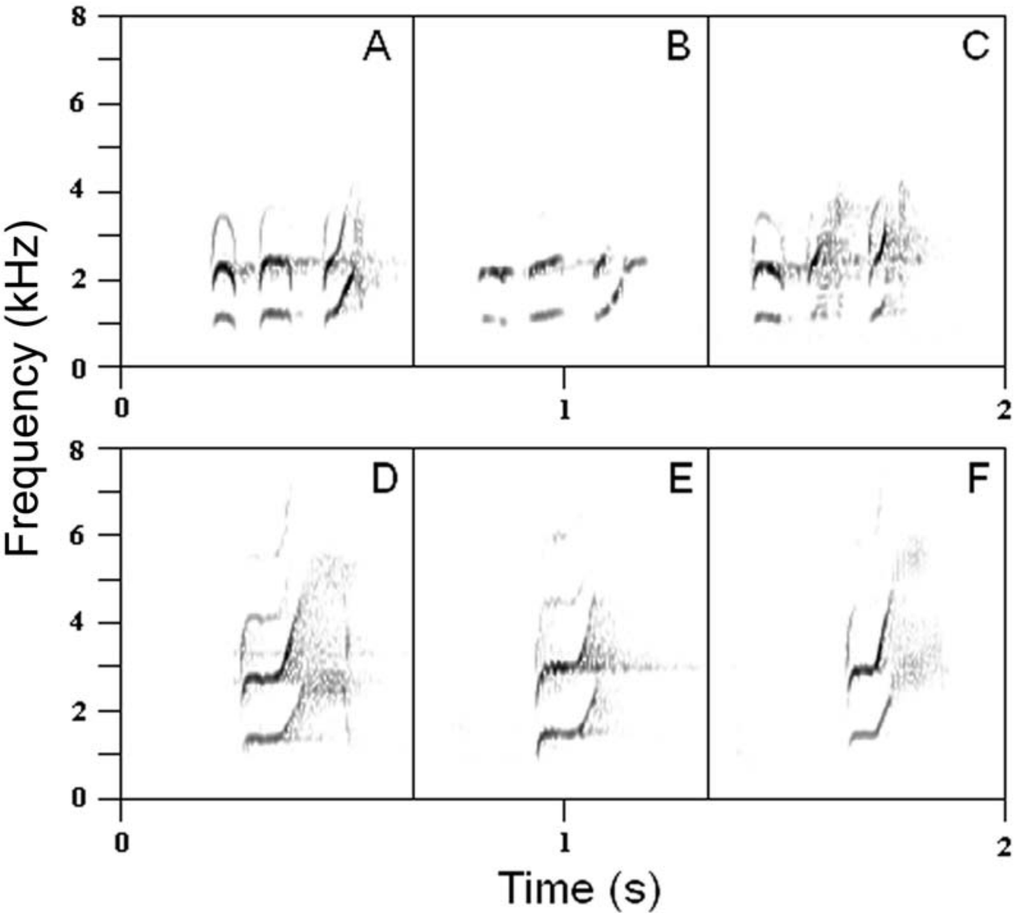

Fig. 4. Calls of two closely related *Scytalopus* tapaculos. *Scytalopus stilesi*: (A) Carolina, Antioquia, Colombia, April 1985 (T. Cuadros); (B) Otún-Quimbaya, Risaralda, Colombia, 22 April 1999 (C.D.C.); (C) Cajamarca, Amalfi, Antioquia, Colombia, 9 January 2002 (A.M.C.). *Scytalopus robbinsi*: (D–F) recorded at Buenaventura, El Oro, Ecuador by N.K.: (D) 16 April 1991; (E) 16 November 1991; (F) 26 September 1990.

notes; notes first single, later double and triple; gradually descending in pitch from 3.0 to 2.5 kHz. Notes were given at intervals of 1.2–1.4 s, with the first interval a little longer (1.7 s). The female advertising song of *S. robbinsi* is higher-pitched and composed only of single notes of different quality (Fig. 5B). Female advertising songs of *S. vicinior*, *S. spillmanni*, *S. parkeri,* and *S. canus opacus* are both higher-pitched and faster than that of *S. stilesi* (Fig. 5C–F).

Distribution.—*Scytalopus stilesi* is known from 21 localities on both slopes of the northern half of the Cordillera Central of Colombia (Fig. 6 and Appendix). On the western slope, records range from southern Risaralda north to western Antioquia. On the eastern slope, records are from the northernmost part of Antioquia (Fig. 6 and Appendix). The southernmost locality known is Otún-Quimbaya Fauna and Flora Sanctuary in the Municipality of Pereira, Risaralda; the northernmost is Santa Gertrudis in the Municipality of Anorí, Antioquia (Fig. 6 and Appendix); those two localities are separated by a linear distance of ~280 km. Although we have no records of *S. stilesi* from the eastern slope of the Cordillera Central south of northern Antioquia, we believe that the species is likely distributed continuously in wet premontane forest along both slopes of the northern half of

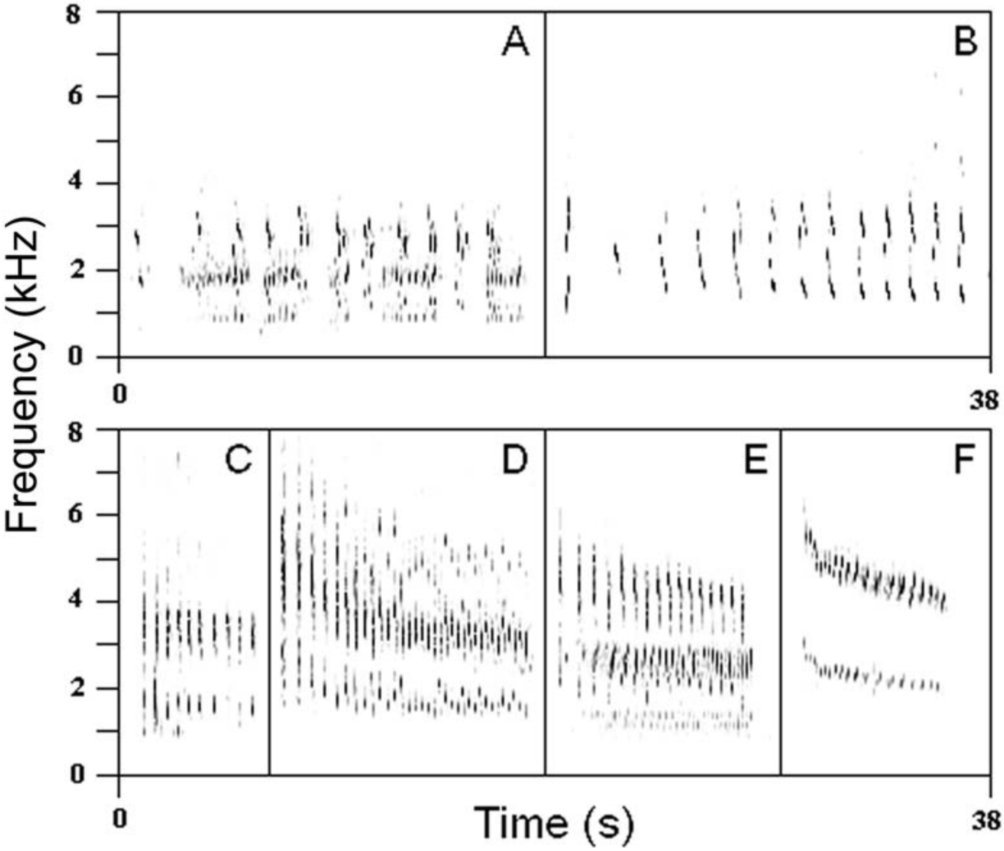

FIG. 5. Female advertising songs. (A) *Scytalopus stilesi* (in duet with male), Otún-Quimbaya, Risaralda, Colombia, 2 November 1996 (L.M.R.); (B) *Scytalopus robbinsi*, Buenaventura, El Oro, Ecuador, 16 November 1991 (N.K.); (C) *Scytalopus vicinior*, Mindo, Pichincha, Ecuador, 27 April 1991 (N.K.); (D) *Scytalopus spillmanni*, Ucumarí, Risaralda, Colombia, 17 July 2001 (C.D.C.); (E) *Scytalopus parkeri* (in duet with male), Gualaceo-Limón road, Morona-Santiago, Ecuador, 18 June 1984 (N.K.); (F) *Scytalopus canus opacus*, Papallacta Pass, Pichincha-Napo border, Ecuador, 14 October 1983 (N.K.).

that mountain range. Before extensive deforestation took place, the wet premontane forests that *S. stilesi* inhabits extended continuously along both slopes of the cordillera, from its northern extreme to dryer forest enclaves farther south. On the western slope, those wet premontane forests range from central Antioquia south through Caldas, Risaralda, and Quindío just into Valle del Cauca (Fig. 7); on the eastern slope, they extend from the northernmost part of the cordillera in Antioquia south through Caldas and Tolima to its border with Huila (Fig. 7). Thus, the distribution of *S. stilesi* may correspond to the distribution of wet premontane forests in the northern sector of the Cordillera Central, its limits imposed by marked habitat discontinuities. In addition, considering that parapatric distributions along the Andes are common in the genus, the range of *S. stilesi* may abut that of another *Scytalopus* at its southern extreme. In fact, an unnamed species occurs at similar elevations farther south in the Cordillera Central at the head of the Magdalena Valley in Huila and Cauca (Krabbe and Schulenberg 1997).

We have recorded *S. stilesi* in wet forests from 1,420 to 2,130 m in elevation. Because we have not sampled forests at lower elevations thoroughly, we have not documented the lower elevational limit for the species, but we expect that it is not found below 1,200 m. Below that elevation, the premontane wet forest shifts into a transitional life-zone with lowland rainforests, where no *Scytalopus* species occur. The upper elevational limit is not well established either, because we

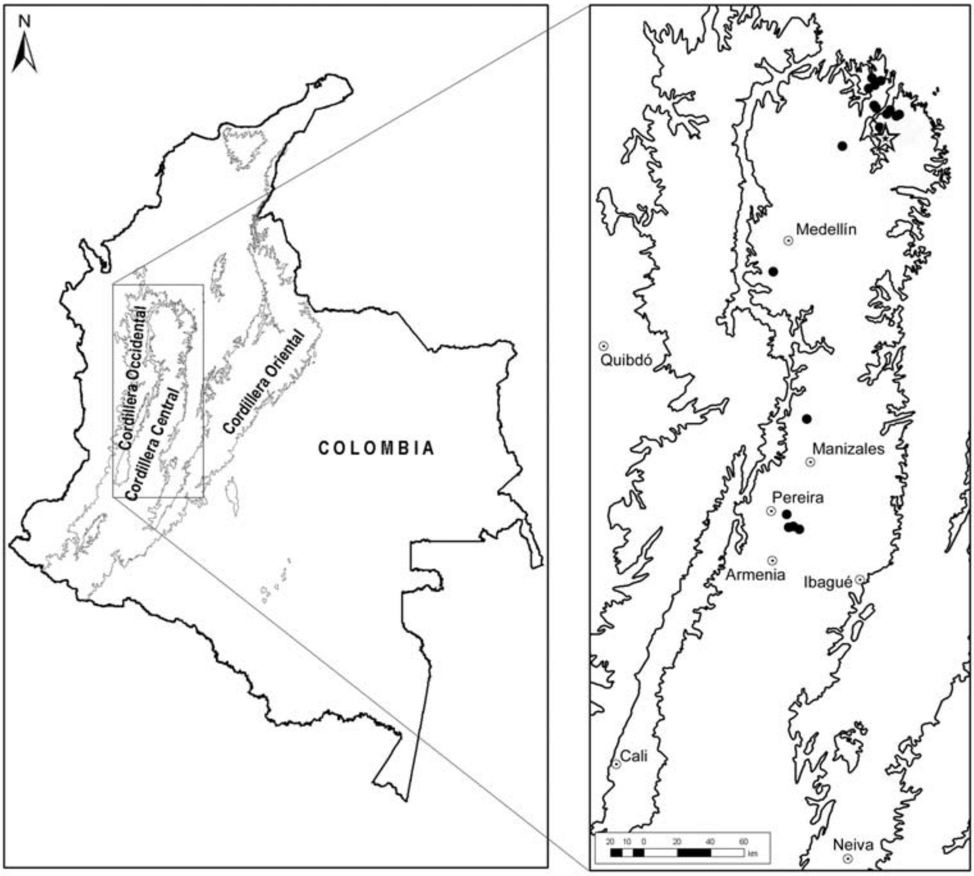

Fig. 6. Map of western Colombia showing major cities and principal mountain ranges in the country, which are depicted by a contour line at 1,000 m elevation. Black dots along Cordillera Central represent the localities of *Scytalopus stilesi,* and the star indicates the type locality at Cajamarca, Amalfi (Deptartment of Antioquia).

have not surveyed locations between 2,200 and 2,400 m extensively. However, within the Otún river watershed in Risaralda, we have noted that *S. stilesi* is absent from forests at 2,430 m at Parque Regional Ucumarí (La Pastora), but the species is common up to 2,110 m in the Otún-Quimbaya Fauna and Flora Sanctuary, just a few kilometers down-slope. At least in this region, *S. stilesi* is replaced altitudinally by *S. spillmanni*, which is common there at elevations of 2,040 to >2,800 m.

Systematics and Biogeography

Systematic affinities.—We assessed the systematic position and genetic distinctiveness of *S. stilesi* as part of an ongoing study on the phylogeny of the genus *Scytalopus* based on mitochondrial DNA sequence data. Phylogenetic trees and detailed descriptions of methods and analyses will be published elsewhere (C. D. Cadena et al. unpubl. data); here, we summarize preliminary results relevant to the affinities of *S. stilesi*. We focus on analyses based on 284–315 base pairs of sequence from the cytochrome-*b* gene generated for four *S. stilesi* individuals from different localities and for multiple additional *Scytalopus* and outgroup taxa (Table 2). Sequences taken from the literature vary in length because they were generated for different studies that did not target exactly the same DNA regions. Although this data set consists of an admittedly small number of characters, it is taxonomically comprehensive, including 21 of the 37 species of *Scytalopus*

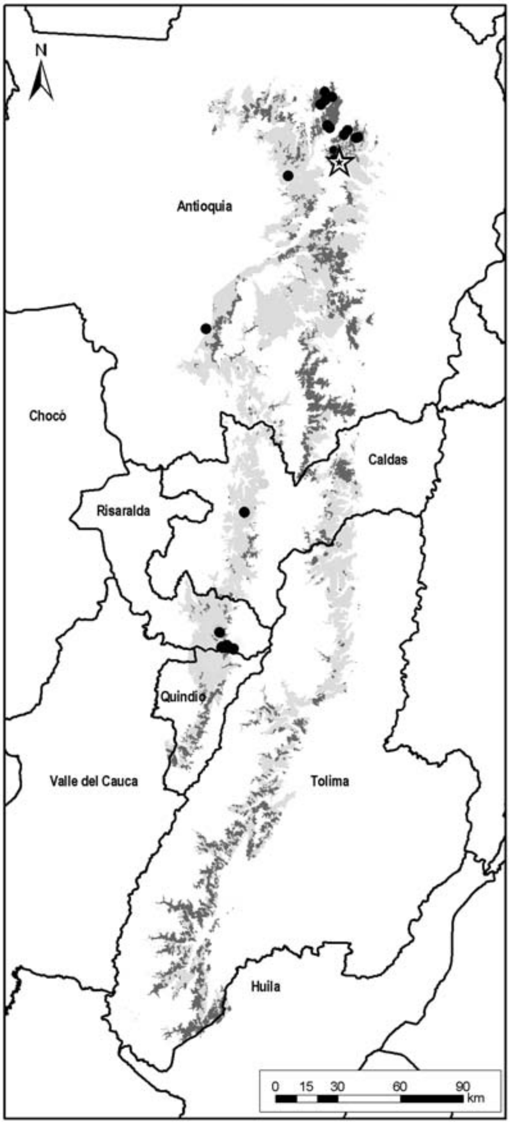

FIG. 7. Map of the distribution of *Scytalopus stilesi* in the Cordillera Central modeled by GIS analyses (see text). Forest clearance is depicted in light gray, and remnants of premontane wet forests in dark gray. Most of the suitable habitat for the species is located in Antioquia, and remarkably along the eastern slope in Caldas and southern Tolima, where confirmed records are still lacking.

currently recognized (Krabbe and Schulenberg 2003), in addition to several vocally or morphologically distinct populations, including a few as-yet-undescribed species-level taxa. With the exception of *S. sanctaemartae* and *S. latebricola*, both endemic to the Sierra Nevada de Santa Marta, all the species of *Scytalopus* known to occur in Colombia and Ecuador are represented in the data set.

A variety of parsimony- and model-based (i.e. maximum likelihood, Bayesian inference) phylogenetic analyses consistently recovered a monophyletic group formed by *S. stilesi*, *S. robbinsi* (a species endemic to the Pacific slope of the Andes of southwestern Ecuador), and two undescribed *Scytalopus* species from the Colombian Andes: one from Alto de Pisones, Pacific slope of the Cordillera Occidental, Risaralda (see Cuervo et al. 2003); the other from Finca Merenberg, head of the Magdalena Valley, Huila (see Krabbe and Schulenberg 1997). The clade formed by those four species was well supported in all analyses, with parsimony bootstrap values >90% and a Bayesian posterior probability of 1.0. The four species are very distinct genetically from all other *Scytalopus*, which indicates that they have been isolated for a substantial time; the minimum sequence divergence (uncorrected *P* distance) observed with other *Scytalopus* was ~9.5%. Because of the short length of the sequences available, relationships among the four taxa could not be established clearly, and the specific position of *S. stilesi* was unresolved or lacked support. In any case, it is noteworthy that all the members of this highly distinctive clade were recently discovered (*S. robbinsi* was described in 1997), highlighting the general lack of understanding of the diversity of *Scytalopus* in the northern Andes, especially in Colombia.

Affinities of *S. stilesi* to species that occur in different regions and not to those co-occurring with it on the same mountain slopes (i.e. *S. atratus*, *S. latrans*, and *S. spillmanni*) support the scenario of allopatric speciation proposed for the genus by Arctander and Fjeldså (1994), which seems to be predominant in Andean birds (García-Moreno and Fjeldså 2000). The close relationship of *S. stilesi* to species occurring on the Andean Pacific slope suggests a biogeographic connection between the Chocó area and the Cordillera Central of Colombia. That connection is also suggested by several species whose distributions are concentrated in the Pacific slope of the Andes and have been found to occur in the northern Cordillera Central (A. M. Cuervo et al. unpubl. data). This may be

Table 2. Specimens of *Scytalopus* and rhinocryptid outgroups used for molecular analyses, with GenBank accession numbers of their cytochrome-*b* sequences. Unless otherwise noted, specimens are referable to the corresponding nominate subspecies. Nomenclature follows Krabbe and Schulenberg (2003).

Taxon	Voucher(s)	GenBank number	Locality
S. aff. *bolivianus*	FMNH 390674	AY755631[a]	Perú, Junín, Cordillera Vilcabamba, Río Poyeni
S. atratus	ZMUC 80145	U06168[b]	Ecuador, Napo, Guacamayos Mountains
S. a. confusus	ICN 34387	AY755632[a]	Colombia, Antioquia, Anorí, Mampuestos
S. femoralis	LSUMZ 106110	U06159[b]	Perú, Pasco, Santa Cruz, 9 km south-southeast of Oxapampa
S. micropterus 1	MECN 5798	U06160[b]	Ecuador, Morona-Santiago, Cutucú, Yapitya
S. micropterus 2	IAvH 12377	AY755633[a]	Colombia, Huila, Cueva de los Guácharos
S. vicinior 1	ZMUC 125176	AY755634[a]	Ecuador, Pichincha, Obelisque near Mindo
S. vicinior 2	ICN 34840	AY755635[a]	Colombia, Valle del Cauca, La Cumbre
S. robbinsi	ZMUC 80100	U06176[b]	Ecuador, El Oro, 9 km west of Piñas
S. chocoensis	ANSP 180149	U06158[b]	Ecuador, Esmeraldas, El Placer
S. argentifrons	LSUMZ 135542	AY755636[d]	Costa Rica, km 120 San José–San Isidro road
S. spillmanni 1	ZMUC 80012	U06171[b]	Ecuador, Sucumbíos, 10 km east of Santa Bárbara
S. spillmanni 2	ZMUC 80014	U06173[b]	Ecuador, Imbabura, 15 km southeast of Apuela, Las Delicias
S. parkeri 1	ZMUC 80054	U06178[b]	Ecuador, Morona-Santiago, Zapote-Najda mountains
S. parkeri 2	ZMUC 80055	U06169[b]	Ecuador, Morona-Santiago, Zapote-Najda mountains
S. parvirostris 1	LSUMZ 128572	U06161[b]	Perú, Pasco, Playa Pampa, 8 km northwest of Cushi
S. parvirostris 2	CBF 2368	U35080[c]	Bolivia, La Paz, Nor Yungas
S. griseicollis 1	IAvH 12586	AY755637[a]	Colombia, Boyacá, Villa de Leyva
S. griseicollis 2	IAvH 12701	AY755638[a]	Colombia, Cundinamarca, Guasca
S. canus opacus	ZMUC 125688	AY755639[a]	Ecuador, Loja, Jimbura
S. affinis	ZMUC 125154	AY755640[a]	Perú, Ancash, Quebrada Pucuvado
S. schulenbergi 1	CBF 2640	U35081[c]	Bolivia, La Paz, Franz Tamayo, 5 km east of Pelechuco
S. schulenbergi 2	CBF 2636	U35082[c]	Bolivia, La Paz, Nor Yungas, 4 km west-northwest of Chuspipata
S. simonsi 1	ZMUC 80031	U35083[c]	Bolivia, Cochabamba, Khasa Punta Pampa
S. simonsi 2	ZMUC 80029	U35085[c]	Perú, Cusco, north of Urubamba below Chainapuerto
S. zimmeri	ZMUC 126277	AY755641[a]	Bolivia, Potosí, Portillo
S. magellanicus 1	AMNH RTC 449	AY755642[a]	Chile, Región VII, Termas de Chillán
S. magellanicus 2	AMNH RTC 451	AY755643[a]	Chile, Región VII, Ralco
S. fuscus 1	AMNH RTC 392	AY755644[a]	Chile, Región Metropolitana, Cerro El Roble
S. fuscus 2	AMNH RTC 497	AY755645[a]	Chile, Región Metropolitana, Cerro El Roble

Table 2. Continued.

Taxon	Voucher(s)	GenBank number	Locality
S. latrans 1	ZMUC 80042	U06170[b]	Ecuador, Sucumbíos, between Santa Bárbara and Guanderal
S. latrans 2	IAvH 11682	AY755646[a]	Colombia, Cundinamarca, Bojacá
S. l. subcinereus 1	ZMUC 125127	AY755647[a]	Ecuador, Loja, Utuana
S. l. subcinereus 2	ZMUC 125122	AY755648[a]	Ecuador, Azuay, Molleturo
S. latrans (unnamed E race)	ZMUC 125112	AY755649[a]	Ecuador, Napo, Guacamayos Mountains
S. superciliaris 1	MBM 8242	AY755650[a]	Argentina, Tucumán, Tafí del Valle
S. superciliaris 2	MBM 8487	AY755651[a]	Argentina, Tucumán, Tafí del Valle
S. stilesi 1 (holotype)	ICN 34569	AY755652[a]	Colombia, Antioquia, Amalfi, Cajamarca
S. stilesi 2	ICN 34609	AY755653[a]	Colombia, Antioquia, Amalfi, Escuela Las Ánimas
S. stilesi 3	ICN 34512	AY755654[a]	Colombia, Antioquia, Amalfi, Bodega Vieja
S. stilesi 4	ICN 34584	AY755655[a]	Colombia, Antioquia, Amalfi, La Secreta
Unnamed species Alto de Pisones	ICN 31209	AY755656[a]	Colombia, Risaralda, Mistrató, Pisones
Unnamed species Finca Merenberg	ICN 34841	AY755657[a]	Colombia, Huila, Finca Merenberg
Unnamed species Millpo	LSUMZ 128624	X60945[e]	Perú, Pasco, Millpo, Abra Portachuela, east of Tambo de Vacas
Unnamed species Ampay	ZMUC 80025	U35084[b]	Perú, Apurímac, north side of Nevado Ampay
Myornis senilis 1	ZMUC 80061	U35087[c]	Ecuador, Loja, Parque Nacional Podocarpus
M. senilis 2	IAvH 11866	AY755658[a]	Colombia, Caldas, Aranzazu, El Laurel
Pteroptochos tarnii	AMNH RTC 467	AY065717[f]	Chile, Región IX, Provincia Cantín, Chacamo
Rhinocrypta lanceolata	NRM 966793	AY078174[g]	Paraguay, Dept. Boquerón, 7 km west of Dr. P. Peña

[a] Present study
[b] Arctander and Fjeldså 1994
[c] Arctander 1995
[d] J. M. C. Silva unpubl. data
[e] Edwards et al. 1991
[f] Irestedt et al. 2002
[g] Johansson et al. 2002

Museum acronyms: AMNH (American Museum of Natural History, New York); ANSP (Academy of Natural Sciences of Philadelphia, Philadelphia); CBF (Colección Boliviana de Fauna, La Paz); FMNH (Field Museum of Natural History, Chicago); IAvH (Instituto Alexander von Humboldt, Villa de Leyva); ICN (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá); LSUMZ (Louisiana State University Museum of Natural Science, Baton Rouge); MBM (Marjorie Barrick Museum, University of Nevada, Las Vegas); NRM (Swedish Museum of Natural History, Stockholm); ZMUC (Zoological Museum, University of Copenhagen, Copenhagen).

a general pattern that was not previously appreciated because of inadequate sampling of montane birds in this sector of the Cordillera Central (e.g. Cuervo et al. 2001). In fact, a similar pattern is well documented for low-elevation birds, many of which are distributed throughout the rainforests of the Chocó and extend eastward along the northern lower foothills of the Andes into the Nechí center of endemism (Cracraft 1985) and into the mid-Magdalena valley (i.e. the Chocó–Magdalena biogeographic province; Hernández-Camacho et al. 1992). Moreover, close relationships between pairs of taxa occurring in the Cordillera Central and Cordillera

Occidental have been reported for murid rodents (Voss et al. 2002) and leptodactylid frogs (Lynch 1999).

The four individuals of *S. stilesi* examined had identical haplotypes in the cytochrome-*b* region assayed. The mean sequence divergence (*P* distance) in cytochrome *b* between *S. stilesi* and the other members of its clade is 5.4% (range: 3.9–6.7%; Table 3). Assuming a sequence substitution rate of 1.6–2.0% divergence per million years estimated for that gene (Fleischer et al. 1998, Lovette 2004), the separation of *S. stilesi* from its closest relatives appears to have been an ancient event, likely taking place in the late Pliocene, more than ~2 million years ago. During the late Pliocene, the northern Andes were in an active geological period of major uplift (Gregory-Wodzicki 2000), which presumably created opportunities for allopatric differentiation through formation of biogeographic barriers that fragmented previously continuous populations. We must caution, however, that this temporal scenario should be considered tentative, because a molecular clock has not been calibrated specifically for *Scytalopus* and rates of cytochrome-*b* evolution >2% per million years have been estimated for some passerine taxa (e.g. Warren et al. 2003). Thus, it is conceivable that the split of *S. stilesi* may have taken place more recently, possibly in the Pleistocene.

Criteria for recognition as a new species.—Vocalizations in suboscine birds are innate. Given the slight variation in plumage in *Scytalopus*, vocalizations very likely function as the principal species-recognition signal and reproductive isolating mechanism in the group. Indeed, songs and scolds in *Scytalopus* populations are highly stereotypical and appear to be reliable indicators of species limits in the genus, with vocal differentiation being concordant with genetic differentiation (Arctander and Fjeldså 1994; Krabbe and Schulenberg 1997, 2003). *Scytalopus stilesi* has distinctive vocalizations, which differ from the vocalizations of other *Scytalopus* species about as much as those species' vocalizations differ from one another; it is genetically distinct; and it retains its integrity throughout a wide expanse of the Cordillera Central of the Colombian Andes, where it occupies a unique habitat and elevational range. In sum, *S. stilesi* is a segment of an evolutionary lineage than can be considered a species under the general lineage concept of species (De Queiroz 1998). In addition, this taxon is fully diagnosable and reproductively isolated from other *Scytalopus*, thus meeting the criteria to be considered a new species under the phylogenetic and biological species concepts (Cracraft 1989, Johnson et al. 1999).

Potential additional specimens.—Given that *S. stilesi* is relatively widespread and common within its distribution range, the species could have been collected and misidentified in the past. Thus, we reviewed the catalogues or examined specimens of several major museum collections housing Colombian birds. The only *Scytalopus* specimens from the distribution and elevational range of *S. stilesi* that we found corresponded to *S. atratus* (morphologically distinctive from *S. stilesi*) and *S. vicinior* (very difficult to distinguish from *S. stilesi*). Considering the lack of well-substantiated records (i.e. specimens linked to recordings of vocalizations) of *S. vicinior* from the Cordillera Central, it is conceivable that at least some specimens referred to that species—taken on both slopes in Quindío, Tolima, and Caldas (1,500–2,600 m) and housed at the American Museum of Natural History and the Carnegie Museum—are, in fact, *S. stilesi*. However, because plumage

Table 3. Pairwise mitochondrial DNA sequence-divergence among *Scytalopus stilesi* and its three closest relatives. Numbers below the diagonal are uncorrected *P* distances; those above are numbers of transition/transversion substitutions. Comparisons are based on a 284-base-pair region of the cytochrome-*b* gene for which sequences were available for all four taxa. Four *S. stilesi* individuals were sequenced and had identical haplotypes.

Taxon	(1)	(2)	(3)	(4)
(1) *Scytalopus stilesi*	–	11/0	18/1	15/1
(2) Unnamed *Scytalopus*, Alto de Pisones	0.0389	–	13/1	8/1
(3) Unnamed *Scytalopus*, Finca Merenberg	0.0671	0.0495	–	15/2
(4) *S. robbinsi*	0.0565	0.0318	0.0601	–

and overall morphology are not diagnostic, the identity of those specimens cannot, at present, be established reliably. *Scytalopus stilesi* and *S. vicinior* are quite distinct in mitochondrial DNA sequences (i.e. 11% cytochrome-*b* divergence; C. D. Cadena et al. unpubl. data), so analyses of "ancient DNA" extracted from the specimens would probably enable identification. In any case, field surveys involving collection of specimens and voice recordings should be conducted in Quindío, Tolima, and Caldas to identify confidently the *Scytalopus* species that occur there. We did not find any additional specimens that could potentially correspond to *S. stilesi*, and there are no type specimens of *Scytalopus* from the northern sector of the Cordillera Central.

Ecology and Conservation

Habitat.—*Scytalopus stilesi* is restricted to mid-elevation montane forests (between 1,420 and 2,130 m) classified as "premontane wet forest" (*sensu* Holdridge 1967) or as "subandean forest" (*sensu* Cuatrecasas 1958). The forests have mild mean temperatures year-round (17.0–22.0°C). Rainfall pattern is bimodal, with drier periods toward the beginning and middle of the year (Witte 1995); total annual rainfall varies regionally from 2,500 to 4,500 mm. These mid-elevation forests are characterized by outstanding tree and epiphyte diversity. The most abundant tree families are Lauraceae, Moraceae, Clusiaceae, and Myristicaceae. Although there are no dominant tree genera, palms such as *Dyctiocarium lamarckianum, Wettinia* spp., and *Geonoma* spp., as well as tree ferns (Cyatheaceae), are characteristic floristic components at some sites. Shrubs in the Melastomataceae and Rubiaceae and vascular epiphytes (especially aroids) are abundant in the understory. Terrestrial bromeliads are locally common, and *Chusquea* bamboo is locally abundant on ridges, disturbed patches, gaps, and forest edges. In Antioquia, canopy height ranges from 6 to 7 m on ridges, 15 to 17 m on slopes, and 22 to 24 m along stream valleys, with scattered emergent trees of up to 30–32 m (Cuervo et al. 2001). In Risaralda, canopy height at study sites was 21 m, on average, with emergent trees ≤45 m (Renjifo 1999, 2001).

Ecology.—*Scytalopus stilesi* is a common species throughout its known range. At Represa Miraflores, Antioquia, it was the fourth most abundant understory bird in a 6-ha plot (listed as "*S. femoralis*" in Cuadros 1988). Throughout a year of study, its relative abundance within continuous forest sites in Risaralda was 0.47 individuals per count during 15-min point-counts. In addition, during ~200 days of fieldwork in Antioquia, *S. stilesi* was recorded almost daily in 14 localities.

Scytalopus stilesi is strongly dependent on forests, occurring in continuous forests (>1,000 ha), mature-forest fragments (2.8–500 ha), tall secondary forests, riparian forests, and forest edges along roads. In contrast, despite intensive sampling, we did not detect *S. stilesi* in other habitats, such as pine, eucalyptus, or shade coffee plantations; young second growth; or open areas. However, one individual seemed to hold a territory in a live fence composed of a single row of trees with no understory, where it has been repeatedly observed and tape-recorded (P. Caycedo pers. comm.). Although *S. stilesi* occurs mostly in understory, below closed canopy-cover, it can also be found in forest gaps and in a variety of environmental conditions within forest. We did not find any significant effect of mean canopy height, terrain slope, elevation (range: 1,860–2,065 m), density of stems in understory, or basal area of trees (ANOVAs, $P > 0.05$, $n = 8$ sites) on the abundance of *S. stilesi* estimated during point-counts.

The new species' distribution partly overlaps those of *S. atratus confusus*, *S. latrans latrans*, and *S. spillmanni*. With *S. a. confusus* it co-occurred in six localities in Anorí and Amalfi (Antioquia) between 1,420 and 1,735 m; with *S. l. latrans* in Vía Parque Angelópolis (Antioquia) between 1,950 and 2,050 m; and with *S. spillmanni* in Ucumarí Regional Park and Otún-Quimbaya Fauna and Flora Sanctuary (Risaralda) between 2,040 and 2,110 m. In other localities, *S. stilesi* was the only *Scytalopus* present. When *S. stilesi* co-occurred with other tapaculo, they were markedly segregated by habitat. For instance, *S. a. confusus* occupied forest edges, young gaps, steep slopes along streams, shrubby stands where *Chusquea* bamboo thickets were dominant, and nearby secondary vegetation; whereas *S. stilesi* occupied less-disturbed areas, typically the understory of tall, closed-canopy forest.

Like other *Scytalopus*, *S. stilesi* is much more often heard than seen; the species is very difficult to observe as it forages rapidly on or close to the forest floor, in root tunnels, and in tangles of vegetation. Stomach contents invariably included small fragments of arthropods and no plant material. Breeding and reproduction may take place during the first half of the year, as with most passerine birds in the northern sector of the Cordillera Central (Cuadros 1988, Cuervo et al. 2001). Adult males ICN 34569 and 34609 were in breeding condition on 5 January and 14 February, respectively. Females ICN 34610 (14 February), 34615 (17 February), and 34505 (20 February) were reproductively active, as suggested by the condition of their gonads (e.g. the largest ovum of the former measured 2.7 mm). The last two females also had brood patches, an indication of active nesting. An adult was observed feeding a fledgling on 20 July 1985 at Represa Miraflores (Cuadros 1988), and in August 2002 at Otún-Quimbaya (G. Londoño pers. comm.), and a recently fledged juvenile male (ICN 34584) was collected on 9 June 2002. Although songs and calls are heard year-round, some variation in vocal activity has been noted by Cuadros (1988), who observed a peak of activity from August to December at Represa Miraflores.

Conservation.—The subtropical premontane wet forests of the Cordillera Central have been significantly deforested and fragmented since pre-Columbian times, especially during the 19th and 20th centuries (Santa 1993, Etter and van Wyngaarden 2000). The Cordillera Central is currently the most deforested Andean range in Colombia; for the most part, its mid-elevation landscapes are dominated by urban settlements, pastures, coffee plantations, and other types of production systems, and much of the remaining forests are highly fragmented (Etter 1998).

To evaluate the conservation status of *S. stilesi* according to the criteria of the International Union for Conservation of Nature (IUCN), we used the method developed by Renjifo et al. (2002). A geographic information system (GIS) was used to model the distribution of the species on the basis of four geographic layers: a general ecosystem map of Colombia (1: 1500000; Etter 1998), an ecosystem map of the Andean region of Colombia for the year 2000 (1: 1000000; IAvH 2004), a digital elevation model (90 × 90 m; Shuttle Radar Topography Mission 2000; see Acknowledgments), and the localities' geographic coordinates. We generated a potential distribution map for the species based on these layers, using habitat continuity and elevation range to define distribution limits (Fig. 7). The first step was to delimit a minimum convex polygon that included all known localities for the species. That polygon was extended to include entirely continuous blocks of forest types where the species was recorded, until a clear habitat discontinuity was located (i.e. a dryer forest type or elevations above or below known range). Working with that new polygon, we measured extent of occurrence and potential area of occupancy based on suitable habitat, following IUCN (2001) guidelines. Finally, we measured the extent of habitat loss as the amount of formerly suitable forests that have been replaced by agroecosystems. We estimated population size on the basis of extent of suitable habitat to make comparisons with each of the IUCN thresholds that define levels of threat (IUCN 2001; Fig. 7).

We estimated that *S. stilesi* has lost 63% of its original habitat. That habitat loss has taken place over centuries, and we believe it is unlikely that ≥30% of the remaining habitat will be lost within the next 10 years. Moreover, the species is not subject to any known selective pressure. For those reasons, the species does not qualify as threatened according to IUCN criterion A. In addition, its extent of occurrence is 38,800 km^2 and potential area of occupancy 4,030 km^2; therefore, the species does not meet the thresholds of IUCN criterion B to be considered threatened because of a small, fragmented, and declining distribution (20,000 km^2 extent of occurrence or 2,000 km^2 area of occupancy). Further, the species has high population densities. For instance, two pairs had permanent territories in a 2.8-ha forest fragment, which is roughly equivalent to 140 mature individuals per square kilometer. In Risaralda, the species was found in three forest fragments of 7.3 ± 6.2 ha. Assuming there was only one pair per fragment, that would be roughly equivalent to 30 mature individuals per square kilometer. These estimates should not be considered accurate, but they are useful for making an educated guess of overall population size. The figures are quite high for most Neotropical birds (e.g. Cresswell et al. 1999, Robinson et al. 2000), but some small insectivores attain high population densities; for instance, *Hylophylax naevioides* has densities of 40 mature individuals per square kilometer in lowland Panamá (Willis 1974). If we multiply these estimates for *S. stilesi* by the extent of suitable habitat (i.e. 4,030 km^2), projected population size exceeds the threshold of 10,000 mature individuals (IUCN criterion C) by more than one order of magnitude. As a result, even if only 10% of the suitable habitat were occupied, the species would not qualify as threatened under criterion C. Further, the species does not qualify as threatened under criterion D, because it largely exceeds the thresholds for being considered vulnerable because of a very small (1,000 mature individuals) or restricted population (<20 km^2, or less than five localities). In conclusion, despite its small distribution and significant habitat loss, *S. stilesi* does not qualify as a threatened species under IUCN criteria. Notwithstanding, the species does approach the thresholds for criterion B, and current habitat loss and fragmentation are likely to continue. Therefore, *S. stilesi* is likely to become threatened in the future, and should be regarded as near threatened. On the other hand, the species is clearly range-restricted and should be considered for site protection by conservation initiatives, such as Important Bird Areas.

Several populations of *S. stilesi* occur within nationally and regionally protected areas. Those include Otún-Quimbaya Fauna and Flora Sanctuary, Ucumarí Regional Park, and Campoalegre Municipal Park in Risaralda; and Vía Parque Angelópolis, La Forzosa, and La Serrana Nature Reserves in Antioquia. However, some of the largest populations are found in still unprotected forests in Anorí and Amalfi (Antioquia), where many other species of special conservation concern occur (e.g. *Lipaugus weberi, Bangsia melanochlamys, Hypopyrrhus pyrohypogaster*). The concentration of all those rare, range-restricted, and threatened species and the general healthy state of the forests in the region suggest that they should be seriously considered for establishment of new protected areas. Other large forest tracts, especially on the eastern slope of the Cordillera Central in Antioquia, Caldas, and Tolima, should be surveyed, because they are likely to harbor additional populations of *S. stilesi* and may have strong potential for establishment of new protected areas. Description of various species new to science from the Cordillera Central in recent years (e.g. *Doliornis remseni, Cercomacra parkeri, Lipaugus weberi, Scytalopus stilesi*) highlights the necessity for extensive fieldwork in every elevational zone in this apparently well-known mountain range, and the need for additional protected areas.

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Appendix

List of localities of *Scytalopus stilesi* (geographical coordinates and elevation above sea level). Antioquia: Municipality of Amalfi: Cajamarca (6°49′25.2″N, 75°05′37.8″W) 1,810–1,880 m; La Secreta (6°49′44.1″N, 75°06′31.1″W) 1,820–1,900 m; Guayabito Forest (6°52′18.6″N, 75°06′18.6″W), 1,700–1,815 m; Las Ánimas (6°56′05.7″N, 75°01′13.2″W), 1,510–1,545 m; Escuela Las Ánimas (6°56′15.7″N, 75°00′38.2″W), 1,535–1,610 m; Bodega Vieja (6°58′04.7″N, 75°03′23.0″W), 1,505–1,530 m; Santa Catalina (6°58′N, 75°03′W), 1,500–1,540 m. Municipality of Anorí: El Chaquiral (6°58′46.0″N, 75°08′02.7″W), 1,650–1,735 m; Mampuestos (7°04′51.8″N, 75°10′25.3″W), 1,445–1,495 m; La Forzosa Natural Reserve (6°59′15.8″N, 75°08′34.6″W), 1,675–1,740 m; Santa Gertrudis (7°08′07.6″N, 75°09′19.0″W), 1,420–1,470 m, La Serrana Municipal Reserve (7°06′02.2″N, 75°08′21.7″W), 1,630–1,690 m; La Condena (7°06′N, 75°06′W), 1,600–1,750 m. Municipality of Carolina del Príncipe: Represa Miraflores (6°45′N, 75°20′W), 2,130 m. Municipality of Angelópolis: Vía Parque (6°06′N, 75°40′W), 1,805–2,050 m. Caldas: Municipality of Aranzazu, vereda El Laurel (5°16′N, 75°29′W), 1,830 m. Risaralda: Municipality of Pereira, Otún-Quimbaya Fauna and Flora Sanctuary (4°43′N, 75°33′W), 1,860–2,110 m; El Líbano (4°43′24″N, 75°36′34″W), 2,040 m; Municipality of Santa Rosa de Cabal, Ucumarí Regional Park (4°44′25″N, 75°34′52″W), 1,980 m; La Selva (4°46′48″N, 75°36′12″W), 1,870–1,990 m; Campoalegre Municipal Reserve (4°51′N, 75°32′W), 1,900–2,100 m.