Three new species of tapaculo (*Scytalopus*): Chusquea Tapaculo (*S. parkeri*), female upper left, male upper right; Ecuadorian Tapaculo (*S. robbinsi*), male bottom left; Chocó Tapaculo (*S. chocoensis*), bottom right (male above, female below). From a watercolor painting by Jon Fjeldså.

Ornithological Monographs
Volume 48 (1997), pp. 47–88

SPECIES LIMITS AND NATURAL HISTORY OF *SCYTALOPUS* TAPACULOS (RHINOCRYPTIDAE), WITH DESCRIPTIONS OF THE ECUADORIAN TAXA, INCLUDING THREE NEW SPECIES

NIELS KRABBE[1,2] AND THOMAS S. SCHULENBERG[3,4]

[1]*Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100, Copenhagen, Denmark;*

[2] *present address: Casilla 17-21-791, Quito, Ecuador;*

[3]*Committee on Evolutionary Biology, University of Chicago, Chicago Illinois 60637 and Department of Zoology, Field Museum of Natural History, Chicago, Illinois 60605, USA;*

[4]*present address: Environmental and Conservation Programs, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605, USA, and Conservation International, 2501 M Street NW, Suite 200, Washington, D.C. 20037, USA*

ABSTRACT.—The taxonomy of the genus *Scytalopus* (Aves; Rhinocryptidae) is revised. Full descriptions of the 10 Ecuadorian taxa are given, with some indication of their annual cycle, and details of their vocalizations, habitats, and geographical distribution. Notes are given on all extralimital forms, and a new taxonomy based on vocal data, and often supported by new distributional and genetic data, is proposed. The number of species in the genus rises from 11 to 37, two or three of which remain unnamed. Two additional populations are identified as being distinct, but their geographical distributions have not been satisfactorily delimited. Sonagrams of most taxa are presented.

Three new species are named and described. Full species status is proposed for most taxa ranked as subspecies by Zimmer (1939) and Peters (1951). Several of these species have sympatric distributions, and others have different songs. Allopatric taxa with the same body mass and elevational distributions, and with relatively similar, but yet distinctive songs are united into superspecies.

RESUMEN.—Se revisa la taxonomía del género *Scytalopus* (Aves; Rhinocryptidae), uno de los géneros más problemáticos del mundo. Se dan descripciones completas de los 10 taxa ecuatorianos, con algunas indicaciones sobre su ciclo anual, y detalles de sus vocalizaciones, habitats, y distribución geográfica. También se dan notas sobre todas las formas extralimitales, y se propone una nueva taxonomía basada en datos de vocalizaciones, en muchos casos respaldados por nuevos registros geográficos y análisis genéticos. El número de especies en este género sube de 11 hasta 37, dos o tres de ellas permanecen innominanadas. Adicionalmente dos poblaciones han sido claramenete identificadas, pero su distribución geográfica todavía no está satisfactoriamente delimitada. Sonogramas de las vocalizaciones conocidas para casi todas las especies se presentan.

Tres especies nuevas han sido nominadas y descritas. Se propone el status de especie para la mayoría de los taxa ubicados como subespecie por Zimmer (1939) y Peters (1951). Algunas de estas especies tienen distribuciones simpátricas, otras tienen cantos diferentes. Taxa allopátricos con el mismo peso corporal y la misma distribución altitudinal, y con cantos relativamente similares pero aún distintos, se agrupan en superespecies.

Taxonomically *Scytalopus* is one of the most complicated of all bird genera. Even the diagnosis of taxa has been problematic, and only recently has headway been made in the study of the relationships among taxa.

The taxonomy of *Scytalopus* long was based on the analysis of Zimmer (1939), which entailed, among other revisions, the description of no fewer than nine new taxa. Even so, Zimmer, working entirely from museum material, was not satisfied with his own results. Little further progress was made until recent years, when museum ornithologists became familiar with these birds in

the field. Beginning in the late 1970s, our own experiences with the genus quickly convinced us that the taxonomy of the genus was confused. Working at first independently, and then for many years in collaboration, we have studied these birds in the field and museum, solicited information from other field workers, and attempted to apply our expanding knowledge to the classification of the group. During the course of our work on the genus in the last decade, it has become clear that the traditional morphological approach is not at all sufficient to delimit species in this genus. Allopatric forms inhabiting the same ecological zone are not necessarily conspecific, and genetic data (Arctander and Fjeldså 1994) show that such taxa are often not each other's closest relatives. Species of *Scytalopus* are extremely similar by plumage characters and structure, and differ from each other primarily in vocalizations, in body mass, and in elevational distribution, although some have diagnostic plumage patterns. Many individual specimens cannot be unequivocally assigned to a species because plumage differences often become apparent only when comparing large series of specimens collected within the same decade. The collecting and weighing of specimens of known song types at known elevations, and comparison of material collected in the same decade, has made it possible to clarify some of the confusion.

Our preliminary results have formed the basis for several recent, somewhat differing classifications of the genus (Fjeldså and Krabbe 1990; Ridgely and Tudor 1994; Parker et al. 1996), and have helped inspire independent studies as well (Whitney 1994). To date, however, most of the underlying documentation for our classification has not been published. This paper, then, represents an overdue "progress report" for our ongoing studies of *Scytalopus*. It treats in depth only the taxa occurring in Ecuador. We also include new distributional and vocal data on a number of extralimital forms, and point out additional taxonomic problems. We compare the traditional taxonomy (i.e., that of Peters 1951 and of the describers of new taxa published later) with one that we suggest. We are well aware that we have not "solved" all taxonomic problems in *Scytalopus*, and we regard our classification as provisional on certain points. We outline remaining problems or areas of uncertainty, and encourage additional studies of these poorly known, but fascinating birds.

GENERAL DESCRIPTION OF THE GENUS

Tapaculos of the genus *Scytalopus* (Gould 1837) are small (13 to 43 g), usually dark gray birds. Almost exclusively montane, and primarily Andean, they are found from Costa Rica to Panama, and through the Andes from Colombia and Venezuela to Cape Horn. They also are found in the coastal mountains of Venezuela, and from eastern and southeastern Brazil into adjacent Misiones, Argentina (Peters 1951). A possible *Scytalopus* has been found in Quaternary deposits on Cuba (Olson and Kurochkin 1987).

The foraging behavior described for an individual of *Scytalopus schulenbergi* (Whitney 1994) agrees with our 20 or 30 observations of forest species, and is probably typical for the genus. None was ever seen reaching up, and none gleaned green foliage with leaves more than a few millimeters in size. We can add several observations of birds using tunnels through piles of rocks, tussocks of grass, moss-covered roots, or root tangles on banks or steep slopes while foraging. We have seen *S. unicolor latrans* spend up to an hour in the same thicket and sit on the same perch for up to 30 s, but most foraging birds observed were active and moved along persistently, covering up to 75 m in 20 min. They feed almost entirely on arthropods, usually tiny insect imagos, mostly gleaned from mosses, dead twigs, or grass (pers. obs. both authors; Whitney 1994). One adult among 15 *S. vicinior* had eaten a 4 to 5-cm grasshopper, one a 2-cm imago scarab beetle. Only 4 of over 300 stomachs we examined contained vegetable matter: a single juvenile among 36 *S. canus opacus* had eaten a berry, and three among four *S.* [*superciliaris*] *zimmeri* had their stomachs crammed with tiny seeds. Thus there is little evidence of trophic segregation of the species. Up to 60 individual arthropods were present in some stomachs.

Scytalopus tapaculos typically inhabit dense forest understory, shrubbery, or dense bunch grass or moss. They often seem reluctant to fly, and usually do so for only short distances. We have not seen birds naturally fly more than 3 m and consider them nearly flightless. The longest flight we have witnessed, and which was heavily labored, was of a bird that escaped handling at chest level and flew ca. 20 m across a creek. When they escape handling, they usually flutter to the ground and dart into cover without flying. They could be described as "agoraphobic."

These tapaculos sing and respond to playback of song mainly for two or three hours after dawn and for an hour before dark, but occasionally at other times, if the sky is overcast (pers. obs.). They often are shy of humans. After playback of their voice, they usually approach through dense thickets, crossing small open spaces with great speed, but occasionally (males only) an

immediate, direct attack on the tape-recorder takes place; during attacks or when fleeing, they are exceptionally rapid (pers. obs.).

They often occur in high densities, as judged from numbers of birds vocalizing and the rapidity with which collected birds are replaced (pers. obs. N.K.). The aversion of most taxa to open habitats and their weak flying abilities render them poor dispersers. Their narrow elevational montane distributions, which are subject to fragmentation by geological and climatic changes, give them unusual opportunities to differentiate in isolation.

Owing to the dense habitat in which they are found and their active foraging mode, their life history is difficult to study, but apparently they stay in close pairs during breeding. The few known nests (Johnson 1967; Skutch 1972; Rosenberg 1986; Sick 1993; and two nests of *Scytalopus affinis* found by N.K.) were globular structures of grass, moss, and roots, one also with some feathers, with a side entrance, hidden near or just under the ground under cover of moss or bunch grass. As far as is known, clutch size is two, and eggs are white. Eggs of *S. indigoticus* took 15 days to hatch (Sick 1993). A brood patch has so far been noted only in females (pers. obs. N.K.). Males defend their territory vigorously during breeding. They may respond to the songs of other *Scytalopus* species, but do so much more consistently to voices of their own species.

As in several rhynocryptid genera the feathers of the lores and forehead are more or less erect.

Unusual (and possibly unique) among passerine birds is the complete lack of skull ossification in the genus. In many other suboscine passerines the skull apparently only ossifies partly (see Miller 1963; Winkler 1979), but during our own collecting of over 300 specimens of 22 of the taxa that we include in *Scytalopus,* we have never seen signs of even an incipient ossification. We therefore consider reports of specimens with partly or completely ossified skulls in error.

Few plumage features serve to distinguish the taxa. Sexual dimorphism is also weak. Females are usually somewhat smaller and paler than males, and have more brown in their plumage. A large percentage of the individuals have one or two albino feathers in their plumage. Albinism usually occurs on different feathers of different individuals, but occasionally it is inbred. Most of a *Scytalopus* population may show identical partial albinism, but in one sex only. For example, in a series of 15 specimens of *S. canus opacus* from Cordillera las Lagunillas, southern Loja, Ecuador, seven of eight males (and three more seen), but none of four females, have a prominent white patch on the wing-coverts, whereas in a series of *S. parvirostris* from Cordillera Colán, depto. Amazonas, Peru, a similar spot is present in four out of six females, but in none of the six males.

The plumage sequence is not well known, but more or less asymmetrical molt is the rule rather than the exception. Birds generally molt into plumages with less brown. We therefore consider only the grayest birds true adults. The very large proportion of immatures and subadults to adults in series of specimens, despite that mainly territory-holding birds are collected, and the very gradual transformation in each molt, suggest that several molts are needed to attain full adult plumage. Generally the brown, juvenal plumage is more or less barred with dusky or black (the amount of barring being extremely variable even within one population: see under *S. canus opacus* and *S. unicolor subcinereus*). Subadults often have silvery feather-tips on the belly and have variable amounts of brown in the plumage. Adult plumages are predominantly gray or black. In many species the adults have brown-barred flanks; in some, the vent and rump also are barred. Other plumage variations, which may be more or less developed, are: brownish tail, whitish belly, whitish throat, whitish supercilium, silvery fore-crown, a white central crown-patch, and straight bars versus scallops on the flanks. The iris is dark brown. The bill is dark gray to blackish in Andean forms. The feet in all Ecuadorian forms are gray-brown to blackish brown on the frontal and lateral surfaces, light gray-brown to gray-brown on the medial surfaces, generally lightest in *S. parkeri* and *S. robbinsi* (described below, p. 81 and 78). A reversal of the pigmentation of the feet (yellowish or dull reddish, and palest on the frontal and lateral surfaces) is found in a few non-Ecuadorian forms (*S. zimmeri*, *S. superciliaris*, and *S. indigoticus*).

The plumage colors in *Scytalopus* change ("fox") quickly in dried museum skins (pers. obs. both authors; Whitney 1994). Gray pigments become considerably paler over just a few years and may eventually take on a brownish tone; brown pigments become more reddish but change at a slower rate. This makes it difficult to compare old and recent material. The descriptions in this paper, therefore, are restricted to recent material except when otherwise noted.

TAXONOMY

The morphological similarity of many *Scytalopus* taxa gives few clues about the relationships of allopatric forms. Variation in characters is often subtle, overlapping, and, especially in the case of plumage characters, difficult to quantify. Many taxa merely show lack of any distinctive characters. We also are reluctant to unite taxa on the basis of what few plumage characters as do exist, because we fear that some such characters may be homoplastic. We only feel confident in using plumage characters to unite taxa in cases in which such an interpretation is supported by additional evidence (e.g., similarities in elevational distribution among different taxa).

Although many individual specimens cannot be assigned to a given species by plumage alone, certain plumage differences do become apparent on larger series of recent specimens of known song-type. Each song-type is associated with a distinctive elevational distribution (as was reported for Bolivia by Whitney [1994]). Specimens of birds belonging to a given song-type are of the same size (primarily as indexed by body mass). Measurements of wing, tail, tarsus, and bill (Table 1) also differ among the taxa, but with more overlap than body masses. The number of rectrices ranges from eight to 14, but may vary within at least six taxa (Table 2). No differences in wing formula, tarsal scutellation, feather-shape and rigidity, or microscopic location of feather pigmentation could be discerned. Apparently voice is the major factor in species recognition.

We generally treat as species the allopatric taxa that differ in territorial songs. We are aware of some cases (e.g., between the northern and southern populations of *S. canus opacus*) in which call notes vary between populations that have similar or identical songs. Such variation in vocalizations presumably reflects underlying genetic variation as well, but we are reluctant to recognize populations of taxa purely on the variation in calls. This reluctance stems in part from an assumption, admittedly untested, that the song is more important in species-recognition and pair-formation than is a call. Although we strongly doubt it, the different calls might not be homologous.

Our treatment gives species rank to the majority of the vocally known taxa previously treated as subspecies. We do not change the taxonomic status of vocally unknown taxa. We unite into superspecies the morphologically distinguishable taxa that show some vocal similarities, and that occupy similar habitats at similar elevations.

This approach is based partly on the positive correlation between vocal and genetic differences found in the genus by Arctander and Fjeldså (1994); on the assumption that vocal characters are as important as, or more important than, morphological characters; and on the assumption that vocal characters are entirely inherited in *Scytalopus*. Although the latter assumption has not been demonstrated specifically for tapaculos, it may be true of all sub-oscines (Kroodsma 1982, 1984).

A comparison of the traditional taxonomy and the one that we propose is presented in Table 4.

METHODS

During the last decade we have tape-recorded several hundred individual birds of the genus *Scytalopus* at a number of sites in Ecuador; these data form the core of the distribution sections of the species accounts below. More than 200 individual tapaculos (Appendix), representing all the call-/and song-types heard, were called in with voice playback and then shot or netted, with a blood-sample extracted for DNA-sequencing, and the number of rectrices counted. All specimens were weighed and sexed by gonad inspection. Elevation, locality, and stomach contents were also recorded on the specimen labels. These series of specimens of known song-type form the basis of the descriptions below. We also examined the *Scytalopus* specimens in all major museum collections, to check the previously published distributions of morphologically identifiable species.

Capitalized color names in the descriptions refer to Ridgway (1912).

Only juveniles and females with active gonads (largest ovum over 2 mm and oviduct greatly thickened and curled) or a brood patch have been used to assess timing of breeding. The material is limited, but apart from single August juveniles of *Scytalopus chocoensis* (described below, p. 75) and *S. spillmanni*, there is no sign of breeding of any species in Ecuador between late May and late September, i.e., during the dry season in the highlands and on the Pacific slope. If data of males with enlarged gonads are included, breeding birds have been found throughout the year except in May ($n = 4$) on the east slope, and in August ($n = 14$) (no May and June specimens) on the west slope.

Acronyms of museums and acoustic libraries cited in the text are: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences of Philadelphia, Philadel-

phia, Pennsylvania (ANSP); British Museum (Natural History), Tring, U.K. (BMNH); Bioakustisk Laboratorium, Aarhus, Denmark (BLA); British Library of Wildlife Sounds, London (BLOWS); Colección Boliviana de Fauna, Museo de Historia Natural, La Paz, Bolivia (CBF); Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (CM); Escuela Politécnica Nacional, Quito, Ecuador (EPN); Fundación Miguel Lillo, Tucumán, Argentina (FML); Field Museum of Natural History, Chicago, Illinois (FMNH); Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia (ICN); Los Angeles County Museum, Los Angeles, California (LACM); Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York (LNS); Louisiana State University Museum of Natural Science, Baton Rouge, Louisiana (LSUMZ); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador (MECN); Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MHN); Musée d'Histoire Naturelle, Neuchâtel, Switzerland (MHNN); Museu Nacional, Rio de Janeiro, Brazil (MNRJ); Museu de Zoologia da Universidade de São Paulo, Brazil (MZUSP); Naturhistoriske Riksmuseet, Stockholm (NRS); Phelps Collection, Caracas, Venezuela (PCC); National Museum of Natural History, Washington, D.C. (USNM); Western Foundation of Vertebrate Zoology, Camarillo, California (WFVZ); Zoological Museum, University of Copenhagen, Copenhagen (ZMUC).

VOCALIZATIONS

Sonagrams of most non-Brazilian taxa are shown in Figures 1 to 85. Earlier discussions of *Scytalopus* vocalizations documented by sonagrams are found in Vieillard (1990) (most Brazilian taxa), Fjeldså and Krabbe (1990) (most Andean taxa), and Whitney (1994) (some Bolivian and Peruvian taxa).

Over 600 tape-recordings, representing 35 of the roughly 42 taxa in the genus, were available for this study. Some 350 of our own recordings are from Ecuador, and sonagrams of these recordings form the basis for the descriptions in the following section. Descriptions of pitch (frequency) of vocalizations are complicated by the usual presence of genuine overtones (harmonics). The first overtone (second harmonic) is usually the loudest, but this may vary among species, or even individually (see under vocalizations of *S. unicolor latrans*). The pitch and shape of individual notes, and the rate of delivery are generally distinctive for each taxon. They may vary in one individual in different states of excitement (compare Figs. 11 and 12), but as is typical of most suboscine passerines (see Ridgely and Tudor 1994), vocalizations generally show lack of plasticity over geographic distance. A study of syringeal morphology in *Scytalopus* might reveal variations comparable to those found in some other suboscines (see Prum 1992).

Most *Scytalopus* vocalizations are repetitions of a single note, given from 1 to 34 per second. In some taxa the song consists of a rapid trill. Analyses of mitochondrial DNA sequences suggest that these trilled songs have developed independently several times in the genus. For example, *S. schulenbergi* has a rapid trilled song (Fig. 8) that resembles that of *S. parvirostris* (Fig. 6). The closest known relative of *S. schulenbergi* (J. C. da Silva, pers. comm.), however, is an unnamed taxon from depto. Apurímac, Peru, with a very different song (Fig. 35).

Functions of the different vocalizations are not always easy to infer. We assume that songs are homologous across taxa, but it is possible that there is more than one kind of song. For example, the song of the male *S. parkeri* during duets (pair-formation?) is different from its territorial song (Figs. 82 and 79). Some vocalizations appear to be contact calls (Fig. 3), others distress calls (Fig. 4), and others might serve both as territorial patrol calls and contact calls (Fig. 48).

We have some evidence for seasonal variation in the repertoire of some taxa. For example, only male songs and female (contact?) calls of *Scytalopus robbinsi* were heard in El Oro in September, whereas at the same site in November only high-pitched, descending series from females were heard.

Territorial advertising songs of most species are given only at large intervals (one to three times) during the morning and evening. During sunny days birds normally do not respond to playback of their song between 0800 and 1700 hr. During territorial disputes song may be given nearly continuously for up to 30 min. Male songs during territorial disputes sometimes differ from the usual advertising song (compare Fig. 79 with 80 and 61 with 62). As pointed out by Whitney (1994) scolds (alarms) are often relatively similar in different species, but the territorial songs of *Scytalopus caracae* (Fig. 77) and *S. a. atratus* (Fig. 14) sound much like scolds of other species. Some species appear to have fewer kinds of vocalizations than others. High-pitched descending series of notes by females sometimes initiate duets with males (Figs. 81 and

TABLE 1

MEASUREMENTS OF BODY MASS AND LENGTH OF WING, TAIL, TARSUS, AND BILL OF ECUADORIAN *Scytalopus* TAPACULOS. TAXA ARRANGED BY INCREASING MEAN VALUES FOR MALES

	Males			Females		
	N	Mean	Range	N	Mean	Range
Body mass (g):						
opacus (north)	23	16.2	13.9–17.9	7	14.8	13.4–15.5
opacus (south)	9	16.5	15.0–17.8	3	15.7	15.0–16.0
latrans (west)	15	18.2	16.8–20.9	14	16.9	15.5–18.0
subcinereus	4	18.8	15.9–20.0	7	16.7	14.2–19.1
latrans (east)	8	18.8	17.5–19.6	5	17.5	15.8–20.0
robbinsi	8	19.6	18.1–21.0	3	19.1	18.7–19.5
chocoensis	17	21.0	19.0–22.5	5	19.0	17.0–20.1
parkeri	13	22.5	21.0–24.4	4	20.1	18.8–22.3
vicinior	14	22.5	20.5–24.6	2	23.6	22.9–24.2
spillmanni	36	25.2	21.0–30.0	5	24.1	20.0–29.5
atratus	7	26.2	24.6–32.5	1	25.3	—
micropterus	9	29.7	27.0–32.5	—	—	—
Wing (flat) (mm):						
robbinsi	8	53.9	52.0–55.0	3	56.5	52.0–59.0
latrans (east)	6	54.7	53.0–56.0	2	58.5	57.0–60.0
chocoensis	20	55.3	52.0–60.0	8	52.6	47.6–58.0
subcinereus	4	56.2	54.0–59.0	7	52.6	49.0–59.0
opacus (north)	22	57.2	52.0–63.0	4	55.3	54.0–56.0
vicinior	13	57.3	55.0–60.0	3	58.5	57.0–60.0
latrans (west)	20	57.5	53.0–63.0	19	56.2	49.0–63.0
opacus (south)	8	57.8	55.0–59.0	1	56.0	—
atratus	8	60.1	55.0–65.0	2	60.5	59.0–62.0
micropterus	15	61.4	59.9–64.0	1	64.0	—
spillmanni	38	61.9	56.0–67.0	7	58.4	56.0–62.0
parkeri	14	62.9	59.0–66.0	5	61.4	58.0–65.0
Tail (mm):						
robbinsi	8	36.0	34.0–39.2	3	37.2	35.7–39.0
chocoensis	19	38.7	33.8–40.7	9	36.9	34.0–38.5
latrans (east)	6	39.3	37.0–41.0	2	40.0	37.0–43.0
latrans (west)	18	39.8	36.0–45.0	18	37.4	34.0–40.1
subcinereus	5	40.4	39.0–42.0	7	37.2	34.0–42.3
opacus (north)	19	42.8	35.4–46.7	4	39.8	39.0–42.0
opacus (south)	8	43.4	39.0–47.0	1	41.7	—
parkeri	13	44.5	42.3–50.0	5	44.3	42.0–48.0
spillmanni	35	45.3	39.0–54.0	7	41.7	38.0–45.0
atratus	8	47.2	44.0–52.0	2	44.7	42.4–47.0
vicinior	11	48.1	46.0–52.0	1	43.5	—
micropterus	12	53.5	48.0–59.0	1	58.0	—
Tarsus (mm):						
latrans (east)	5	21.9	21.0–23.1	2	21.4	21.2–21.6
robbinsi	4	22.2	22.2–22.3	3	21.6	21.2–22.0
chocoensis	8	22.2	21.2–25.0	2	21.4	21.1–21.7
opacus	27	22.5	20.8–24.2	8	20.8	19.8–22.0
latrans (west)	12	22.6	20.5–24.0	12	21.6	20.0–23.1
subcinereus	3	22.9	22.2–23.4	6	21.2	20.6–21.7
vicinior	9	23.5	22.8–24.3	2	23.5	22.8–24.1
spillmanni	18	24.5	22.2–26.0	5	24.0	23.5–24.2
parkeri	14	24.6	23.8–25.3	3	22.0	21.0–23.0
micropterus	6	24.9	24.3–25.4	1	26.0	—
atratus	6	25.5	24.7–26.2	1	22.6	—

TABLE 1
CONTINUED

	Males			Females		
	N	Mean	Range	N	Mean	Range
Bill from fore edge of operculum to tip (mm):						
opacus	19	5.5	5.0–6.1	1	5.1	—
parkeri	8	6.4	6.1–7.0	—	—	—
latrans (west)	10	6.4	5.6–7.0	3	5.7	5.3–6.2
subcinereus	2	6.5	5.8–7.1	—	—	—
latrans (east)	2	6.7	6.3–7.0	2	6.6	6.5–6.6
robbinsi	5	6.9	6.6–7.2	—	—	—
spillmanni	14	7.0	6.1–7.6	2	6.8	6.4–7.1
vicinior	9	7.4	6.6–8.3	—	—	—
atratus	3	7.4	7.3–7.7	—	—	—
chocoensis	7	7.7	7.5–8.1	2	6.6	6.5–6.6
micropterus	4	7.8	7.5–8.2	—	—	—

82), but are sometimes given alone, in which case the function is less clear. Both males and females are often attracted to playback of their various vocalizations, but strong responses usually are elicited only by playback of male territorial song.

DESCRIPTIONS OF ECUADORIAN TAXA WITH NOTES ON EXTRALIMITAL FORMS

In the following section we give accounts of the *Scytalopus* species that are found in Ecuador, presenting for each taxon a brief diagnosis (generally valid only for Ecuador), and detailed data on plumage, voice, habitat, elevational, and geographic distribution in Ecuador. In addition, we briefly discuss extra-limital taxa that have been regarded as conspecific with taxa found in Ecuador, and we provide comments on taxonomy. Measurements of Ecuadorian taxa are given in Table 1. Comparisons of elevational ranges are given in Table 3. A comparison of different classifications of the genus is given in Table 4. Geographical distributions in Ecuador are shown in Figure 86. Elevational distributions in Ecuador are shown in Figures 87 and 88.

Scytalopus unicolor, sensu Zimmer 1939

Zimmer (1939) described three new taxa, *subcinereus*, *intermedius*, and *parvirostris*, which he united, together with *latrans*, as subspecies of *S. unicolor*. That at least two species were included in Zimmer's *S. unicolor* became evident when we by 1983 had learned that the vocalizations of *parvirostris* and *latrans*, as detailed below, are entirely different. Furthermore, the distribution of *parvirostris* may overlap with that of *intermedius* in north-central Peru. Series of

TABLE 2
RECTRIX NUMBER IN ECUADORIAN *Scytalopus* TAPACULOS. ENTRIES IN EACH COLUMN SHOW THE NUMBER OF INDIVIDUAL SPECIMENS PER TAXON THAT POSSESS THE INDICATED NUMBER OF RECTRICES

	Number of rectrices					
Taxon	8	10	11	12	13	14
opacus	3	29				
latrans (west)		12	2	6		
latrans (east)	1	3				
subcinereus	1	8		1		
spillmanni				14	1	2
parkeri				16		
vicinior		2		11		
chocoensis		11				
robbinsi		8				
atratus		2		4		
micropterus				4		

TABLE 3

ELEVATIONAL DISTRIBUTION OF *Scytalopus* IN ECUADOR. TAXA ARE ARRANGED BY INCREASING MEAN ELEVATION (M)

	Mean	Range
Generalized characterization of elevational distribution in Ecuador:		
chocoensis	700	350–1,065[a]
robbinsi	975	700–1,250[b]
atratus	1,250	850–1,650
micropterus	1,725	1,250–2,100
vicinior	1,800	1,250–2,350
parkeri	2,700	2,250–3,150
spillmanni	2,700	1,900–3,500
subcinereus	2,750	1,500–4,000
latrans	2,990	1,975–4,000
opacus	3,465	3,050–3,980
Pacific slope in provs. Carchi and Esmeraldas:		
chocoensis	700	350–1,065[a]
vicinior	2,000	1,650–2,350[c]
spillmanni	2,775	2,350–3,200
latrans	3,225	3,100–3,350
opacus	3,690	3,400–3,980
Pacific slope in prov. Pichincha:		
vicinior	1,675	1,450–1,900[c]
spillmanni	2,625	1,900–3,350
latrans	3,285	2,700–3,870[d]
Pacific slope in prov. Azuay:		
robbinsi	1,070	890–1,250[b,e]
subcinereus	2,750	1,500–4,000
Amazonian slope in prov. Napo:		
atratus	1,275	1,200–1,350[f]
micropterus	1,675	1,250–2,100
latrans	2,225	2,000–2,450[g]
spillmanni	2,800	2,100–3,500
opacus	3,650	3,350–3,950
Amazonian slope in prov. Zamora-Chinchipe:		
atratus	1,150	1,050–1,250[f]
micropterus	1,700	1,400–2,000[h]
latrans	2,200	2,100–2,300
parkeri	2,825	2,300–3,350
opacus	3,350	3,050–3,650

[a] Might range higher and lower. In Colombia known down to 250 m, in Panama up to 1,465 m.
[b] May formerly have ranged lower.
[c] Probably ranges lower. In prov. Cotopaxi known down to 1,250 m.
[d] Might range higher and lower. On Pasochoa, prov. Pichincha, known up to 4,000 m, in prov. Cotopaxi down to 2,300 m along clearings.
[e] Probably ranges lower.
[f] Might range higher and lower. In prov. Zamora-Chinchipe known down to 1,050 m, in prov. Morona-Santiago up to 1,650 m and possibly down to 850 m. In prov. Napo reportedly up to 1,950 m at Cosanga (P. Greenfield, M. Lysinger, both, pers. comm. to N.K.).
[g] Might range higher and lower in disturbed areas. There are old prov. Napo specimens labelled "Baeza, 1830 m" and "Papallacta, 3100".
[h] Might range slightly higher and lower.

two taxa, consistent in morphology with *parvirostris* and *intermedius*, were collected in sympatry on Cordillera Colán, depto. Amazonas (LSUMZ). There also exists a single tape-recording (B. Whitney) of a bird (not collected) with a *parvirostris*-like song, obtained within the range of *intermedius*. Unfortunately vocal and genetic data are lacking for *intermedius*, but we presume that this *parvirostris*-like recording corresponds to the birds with *parvirostris*-like morphology collected nearby, strongly suggesting local sympatry of these taxa.

Likewise, we have no knowledge of the voice of nominate *unicolor*, which, like *intermedius*, has only a small distribution in northern Peru. Consequently, although there is evidence for more than one species within the taxa in Zimmer's polytypic *S. unicolor*, we are not certain of the relationships of nominate *unicolor* to other taxa, and the taxonomy of all these forms cannot be

TABLE 4

PROVISIONAL TAXONOMY OF *Scytalopus* TAPACULOS. THE LINEAR SEQUENCE IS ARBITRARY

Zimmer 1939; Peters 1951	Krabbe and Schulenberg 1997	Comments[a]
Scytalopus unicolor unicolor	*Scytalopus unicolor unicolor*	a
Scytalopus unicolor subcinereus	*Scytalopus unicolor subcinereus*	
Scytalopus unicolor intermedius	*Scytalopus unicolor intermedius*	a
Scytalopus unicolor latrans	*Scytalopus unicolor latrans*	b
Scytalopus unicolor parvirostris	*Scytalopus parvirostris*	b
Scytalopus speluncae	*Scytalopus speluncae*	
Scytalopus macropus	*Scytalopus macropus*	
	Scytalopus [*femoralis*]:	
Scytalopus femoralis femoralis	*Scytalopus femoralis*	
Scytalopus femoralis micropterus	*Scytalopus micropterus*	
	Scytalopus [*bolivianus*]:	
Scytalopus femoralis bolivianus	*Scytalopus bolivianus*	
Scytalopus femoralis atratus	*Scytalopus atratus atratus*	b, d, f
Scytalopus femoralis confusus	*Scytalopus atratus confusus*	c, f
Scytalopus femoralis nigricans	*Scytalopus atratus nigricans*	f
Scytalopus femoralis sanctaemartae	*Scytalopus sanctaemartae*	e
Scytalopus argentifrons	*Scytalopus argentifrons argentifrons*	
Scytalopus chiriquensis	*Scytalopus argentifrons chiriquensis*	c
	Scytalopus [*panamensis*]:	
Scytalopus panamensis panamensis	*Scytalopus panamensis*	
Scytalopus panamensis vicinior (in part)	*Scytalopus chocoensis*	
	Scytalopus robbinsi	
Scytalopus panamensis vicinior (in part)	*Scytalopus vicinior*	e
	Scytalopus [*latebricola*]	
Scytalopus latebricola latebricola	*Scytalopus latebricola*	
Scytalopus latebricola meridanus (in part)	*Scytalopus meridanus*	b
Scytalopus latebricola meridanus (in part)	*Scytalopus infasciatus* (?) (unnamed ?)	
Scytalopus latebricola caracae	*Scytalopus caracae*	e
Scytalopus latebricola spillmanni	*Scytalopus spillmanni*	
	Scytalopus parkeri	
	Scytalopus [*indigoticus*]:	
Scytalopus indigoticus	*Scytalopus indigoticus*	
	Scytalopus psychopompus	a, c
	Scytalopus novacapitalis	
Scytalopus magellanicus magellanicus	*Scytalopus magellanicus*	e
Scytalopus magellanicus superciliaris	*Scytalopus superciliaris superciliaris*	g
	Scytalopus superciliaris santabarbarae	a, c, g
Scytalopus magellanicus zimmeri	*Scytalopus zimmeri*	g
Scytalopus magellanicus simonsi	*Scytalopus simonsi*	g
Scytalopus magellanicus urubambae	*Scytalopus urubambae*	g
	Scytalopus unnamed species	
	Scytalopus unnamed species	
Scytalopus magellanicus altirostris	*Scytalopus altirostris*	g
Scytalopus magellanicus affinis	*Scytalopus affinis*	g
Scytalopus magellanicus opacus	*Scytalopus canus opacus*	g
Scytalopus magellanicus canus	*Scytalopus canus canus*	a, g
Scytalopus magellanicus griseicollis	*Scytalopus griseicollis griseicollis*	
Scytalopus magellanicus fuscicauda	*Scytalopus griseicollis fuscicauda*	a, g
Scytalopus magellanicus fuscus	*Scytalopus fuscus*	b, e
Scytalopus magellanicus acutirostris	*Scytalopus acutirostris*	
	Scytalopus schulenbergi	

[a] a = voice unknown; b = two or more species may be involved; c = doubtfully valid; d = population south of the Río Marañón vocally distinct and perhaps closer to *Scytalopus nigricans*. Treatment by Ridgely and Tudor (1994) when differing from traditional taxonomy: e = distinct species; f = subspecies of *S. bolivianus*; g = subspecies of *S. griseicollis*.

FIGS. 1–85. Sonagrams of most non-Brazilian taxa of *Scytalopus* tapaculos. Except when otherwise noted recordings are from Ecuador. Last locality modifier is province (Chile, Argentina, Ecuador), department (Bolivia, Peru, Colombia), or state (Venezuela). Dates are denoted day/month/year. PB = after playback, i.e., recorded in response to a tape-recording of the individual's or the species' voice. NV = natural vocalization, i.e., recorded without the stimulus of tape playback. Roman numerals refer to the original N.K. tapes (available from N.K. upon request), following numerals to counter of tape-recorder used.

→

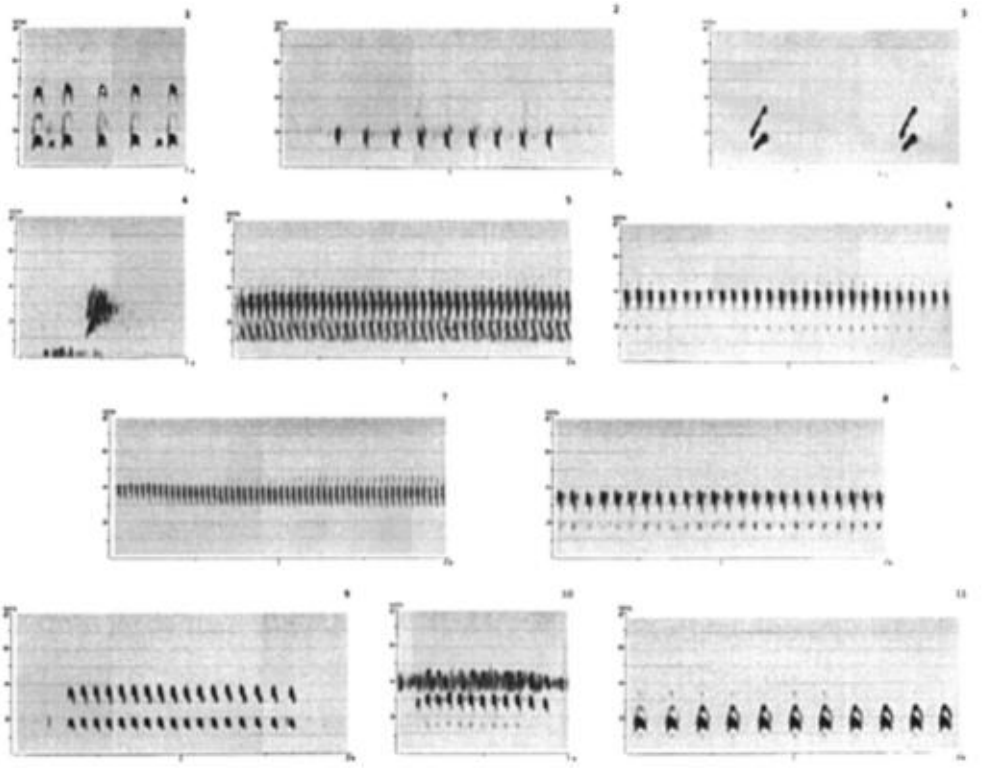
satisfactorily resolved on present knowledge. In their uniform plumage, for what it is worth, *unicolor* and *intermedius* appear more similar to the northern taxa (*latrans* and *subcinereus*) than to *parvirostris*.

We suggest that the best taxonomic solution at the moment is to unite the northern forms into one polytypic species, *S. unicolor* (including *subcinereus*, *intermedius*, *unicolor*, and *latrans*), and to regard *S. parvirostris* as an independent species. This approach is conservative because it masks subtle, but consistent, vocal differences between *subcinereus* and *latrans*, and even between populations of *latrans* east and west of the Andes, as detailed below. We suspect that our *S. unicolor*, like Zimmer's before us, will prove to include more than one species. We continue to investigate this complex, but, because vocal and genetic data are lacking or are incomplete for two of these taxa, we are reluctant to introduce further taxonomic changes, until new information becomes available.

UNICOLORED TAPACULO *Scytalopus unicolor latrans*
(Hellmayr 1924; type in FMNH)

Brief diagnosis.—Relatively small. Depicted in Fjeldså and Krabbe (1990, pl. XLI 3a). The only Ecuadorian tapaculo (except *subcinereus* male) that may lack brown in the plumage. Even when some brown is present, the brown is usually unbarred and less extensive than in congeners, but a few individuals cannot, unless they weight more than 18 g, be separated from dark and fully adult males of *S. canus opacus*.

Plumage.—Adult male (n = 19): Fourteen western birds uniform: Chaetura Drab, Dark Mouse Gray, Chaetura Black, or Blackish Mouse Gray. Five eastern birds uniform black and may represent a different subspecies (see voice). *Adult female* (n = 14): Twelve western birds between Hair Brown and Chaetura Drab, Chaetura Drab, or Chaetura Black. Ten uniform, two with an almost indiscernible wash of Dresden Brown to Olive Brown on the tips of some flank feathers. One of two eastern birds similar, the other darker (Blackish Mouse Gray), about as dark as western males. *Immature/subadult male* (n = 2): Two western birds. One Fuscous Black with a faint wash of Dresden Brown to Olive Brown on thighs. One Dark Mouse Gray, with a wash of Dresden Brown to Mummy Brown on flanks, thighs, tertials, and edges of remiges, and with traces of Mouse Gray barring on flanks, thighs, and tertials; two primaries and a tertial in the left wing fresh or growing, uniform Blackish Mouse Gray. *Immature/subadult female* (n = 3): Two western, one eastern bird. One molting from juvenal into fairly uniform plumage, Dark Mouse Gray above, Light Mouse Gray below, distinctly lighter than its fresh-plumaged presumed mother, which is uniform Chaetura Black. One has 5 mm broad Cinnamon tips to the feathers of lowermost belly and vent, and has traces of this color as faint bars on the flanks and undertail coverts. The eastern bird similar to the latter but with even less brown, despite exhibiting juvenal primary-coverts, alula, and flight feathers except tertials. *Juvenal female* (n = 2): One western bird, molting. Crown and side of head between Ochraceous-Tawny and Cinnamon-Brown, mantle between Cinnamon-Brown and Brussels Brown, throat between Clay Color and Tawny-Olive, lower belly Cinnamon-Buff. Flanks obscurely barred gray and Tawny-Olive. Axillars Cinnamon-Buff. Wing-coverts and inner tertial Cinnamon-Brown with dusky bases and subterminal bar, remiges Dark Mouse Gray narrowly edged Cinnamon-Brown, inner remiges with narrow Cinnamon-Brown tips and faint indications of a presubterminal bar. One eastern bird (ANSP 176878) similar, but lores and feathering along the mandibular rami near Clay Color, contrasting somewhat with adjacent areas; feathers of lores also narrowly fringed black. Throat near Light Ochraceous-Buff. Rectrices unmarked, dark gray. *Juvenal male* (n = 1): One western bird, aberrant (ZMUC 80073). This schizochroic specimen had pinkish bill and feet, and the gray colors replaced with pallid gray, and appears uniform pale brown at a distance. We have seen several old museum specimens (NRS, BMNH) that we believe also represent the juvenal plumage of *latrans*. They all have less barring on the underparts than juvenals of other Ecuadorian species.



FIGS. 1–11. *Scytalopus unicolor latrans*: 1. Excited song by pair, female fast, male slow. PB. Lloa, Pichincha, 2,700 m, 21/7/84. Both collected. N.K. 2. Song on east slope. PB. Cutucú, Morona-Santiago, 1,525 m, 1/7/84. T.S.S. 3. Call. NV. Yanacocha, Pichincha, 3,400 m, 30/9/83. N.K. 4. "*Brzk*", presumably by a female or young. PB of female. Yanayacu, Pichincha, 3,700 m. 7/3/92. XLVIIA 410–417. N.K. *Scytalopus parvirostris*: 5. Male song. PB. Playa Pampa, Pasco, Peru, 2,325 m, 24/6/85. Collected. T.S.S. 6. Song. PB. Machu Picchu, Cuzco, Peru, 2,600 m, 13/7/83. N.K. 7. Song. PB. Siberia cloud forest, Santa Cruz, Bolivia, October 1983. T. A. Parker. *Scytalopus schulenbergi*: 8. End of male song. NV. Below Abra Malaga, Cuzco, Peru, 3,000 m, 4/12/83. Collected. N.K. 9. Call. PB. Below Abra Malaga, Cuzco, Peru, 3,350 m, 21/7/85. T.S.S. 10. Call. NV. Above Sandia, Puno, Peru, 2,800 m, 25/12/83. N.K. *Scytalopus unicolor subcinereus*: 11. Excited male song. PB. Sural, Azuay, 2,650 m, 4/3/91. Collected. XXIIA 381–385. N.K.

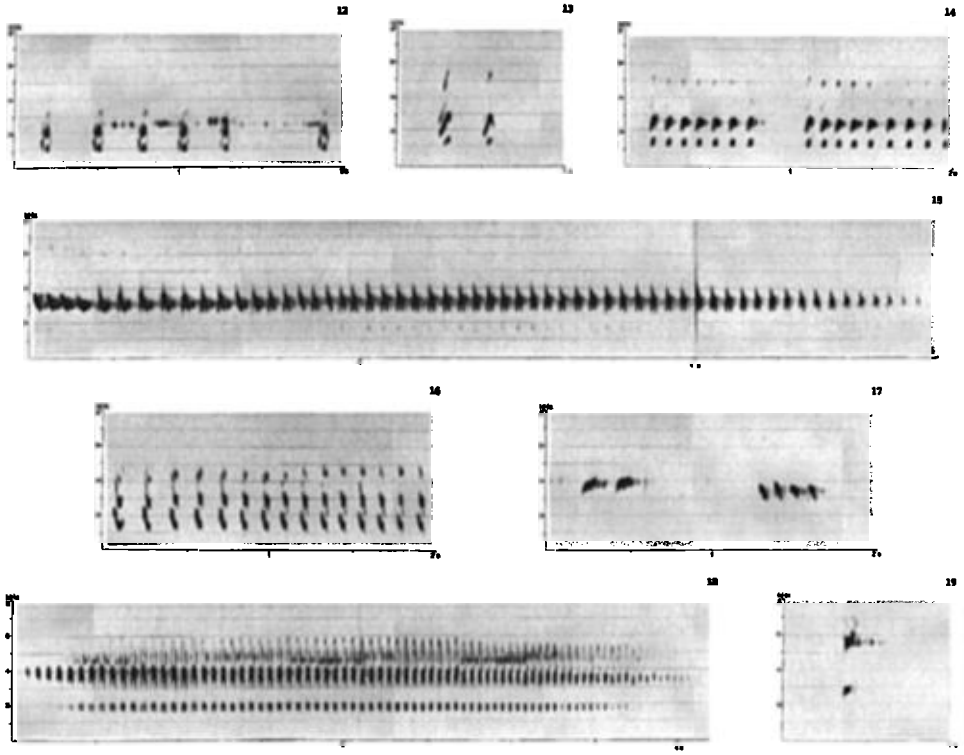
Annual cycle in Ecuador (*n* = 13).—*Juvenals*: 7, 7 October; 7, 19, 20 March; 27 April; 2, 10 May (all prov. Pichincha); 11 July (prov. Morona-Santiago). *Brood patch:* 5 January (female) (west prov. Cotopaxi). *Active ovary:* 7 March (prov. Pichincha); 15 March (southeast prov. Carchi). *Nest:* 8 October (near Baños, prov. Tungurahua) (Skutch 1972).

Vocalizations in Ecuador.—Song a repeated note 2–8 times/s (fastest at high excitement, such as countersinging birds). The song also may be given by both sexes in duet, with the song of the female slightly higher-pitched than that of the male (Fig. 1) (also Fjeldså and Krabbe [1990, p. 425 sonagram 2]). Song on most of the east slope (Papallacta, prov. Napo southwards; Fig. 2) averages faster than in remainder of Ecuadorian range, the notes are sharper, and the song is more frequently rhythmic, reminiscent of that of *subcinereus*. A song often begins with a "stutter," in which notes may be given singly, less often in doublets or triplets. In the song, the fundamental note is frequently loudest, 1.2–1.4 kHz, but first and second overtones almost equally as loud, and occasionally the first overtone is louder than the fundamental. Each note is about 0.06 s long, the pitch rising in the beginning, and then descending smoothly to the end.

The call of both sexes is a single note that resembles song notes in pitch and overtones, but is given singly or in a series of two or three at irregular intervals. Each note is distinctly rising throughout (Fig. 3). Commonly heard in the west, rarely in the east.

An excited "*brzk*" (Fig. 4) is only heard infrequently. On two occasions it was found to be given either by a female or its young, and was interpreted as a distress call.

Habitat in Ecuador.—Humid forest undergrowth, *Chusquea* bamboo or *Neurolepis* cane, hu-



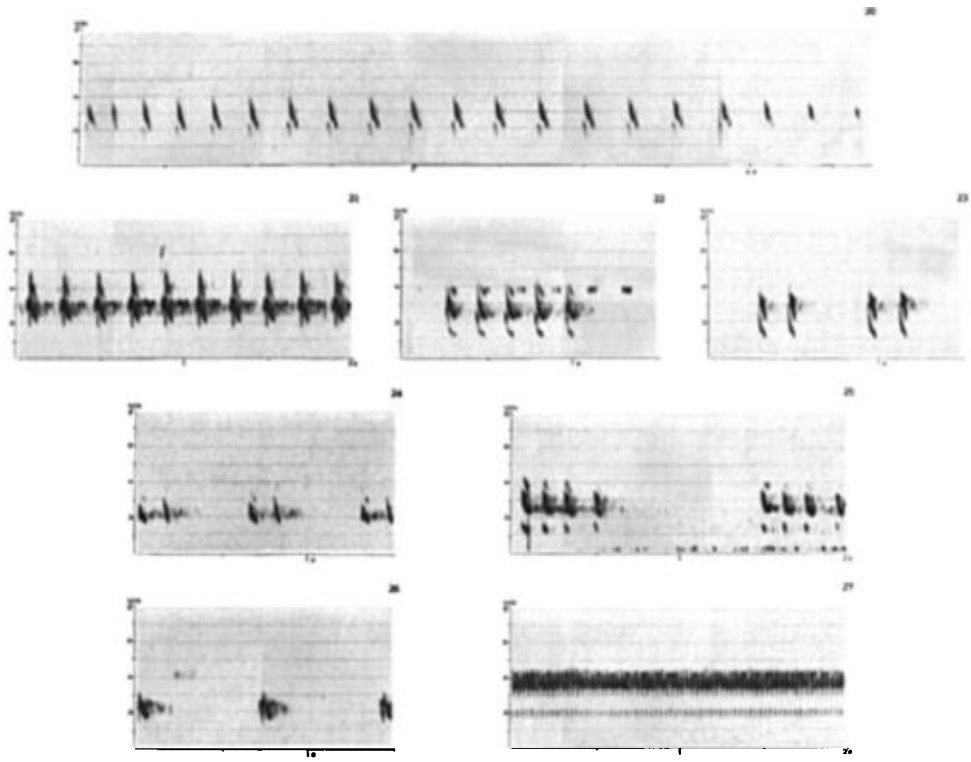
FIGS 12–19. *Scytalopus unicolor subcinereus*: 12. Normal male song, each note with a double quality. NV. Same bird as previous. XXIIA 386–395. N.K. 13. Call of female with young. PB. Sural, Azuay, 2,650 m, 4/3/91. Both collected. XXIIA 306–324. N.K. *Scytalopus atratus atratus*: 14. Male song. PB. Hollín road, Napo, 1,350 m, 11/10/92. Collected. LIXB 216–224. N.K. *Scytalopus bolivianus*: 15. Song. PB. Calabatea, La Paz, Bolivia, 1,400 m, October 1983. T. A. Parker. 16. Song. PB. Chapare road below Miguelito, Cochabamba, Bolivia, 1,800 m, 30/10/83. R. A. Rowlett. 17. Call. PB. Calabatea, La Paz, Bolivia, 1,400 m, October 1983. T. A. Parker. *Scytalopus sanctaemartae*: 18. Song. NV. Below Cincinnati, above Campana, nw-slope of Santa Marta mountains, Colombia, 1,480 m, 6/2/84. S. Hilty. 19. "*Brzk*". PB. Santa Marta mountains, Colombia, 1,700 m, early January 1994. P. Coopmans.

mid *Polylepis* scrub, shrubbery, swampy areas, along ditches. Opportunistic and often numerous in second growth, entering relatively dry regions through riparian shrubbery. Where in contact with *S. canus opacus, S. u. latrans* haunts more humid and broad-leaved shrubbery or bamboo rather than ericaceous scrub. Where syntopic with *S. spillmanni, S. u. latrans* may be found slightly more at edge and in open or drier understory.

Distribution in Ecuador.—Two nearly isolated populations, differing somewhat vocally and in color, but not notably in measurements. One at 1,975–4,000 m on the Pacific watershed south to northern prov. Cañar, just "spilling over" and down to 2,750 m on the east slope along the Colombian border in the Sucumbíos region, and to 3,000 m in Napo at Oycacachi. Another locally at 1,975–2,450 m on the east slope from Papallacta, prov. Napo, southwards; known also from the outlying ridges of Sumaco (prov. Napo), Cutucú (prov. Morona-Santiago), and the highest parts of Cordillera del Cóndor (prov. Zamora-Chinchipe) (EPN). Birds recorded at 2,600 m on Volcán Tungurahua, prov. Tungurahua, may also belong here. The eastern form may deserve taxonomic recognition. It meets *subcinereus* along the right bank of the Río Paute, prov. Azuay, where N.K. recorded both song-types, but their voices, and the plumage of subadult female (one such collected), are so similar that intermediates are difficult to identify on this basis.

UNICOLORED TAPACULO *Scytalopus unicolor subcinereus*
(Zimmer 1939; type in AMNH)

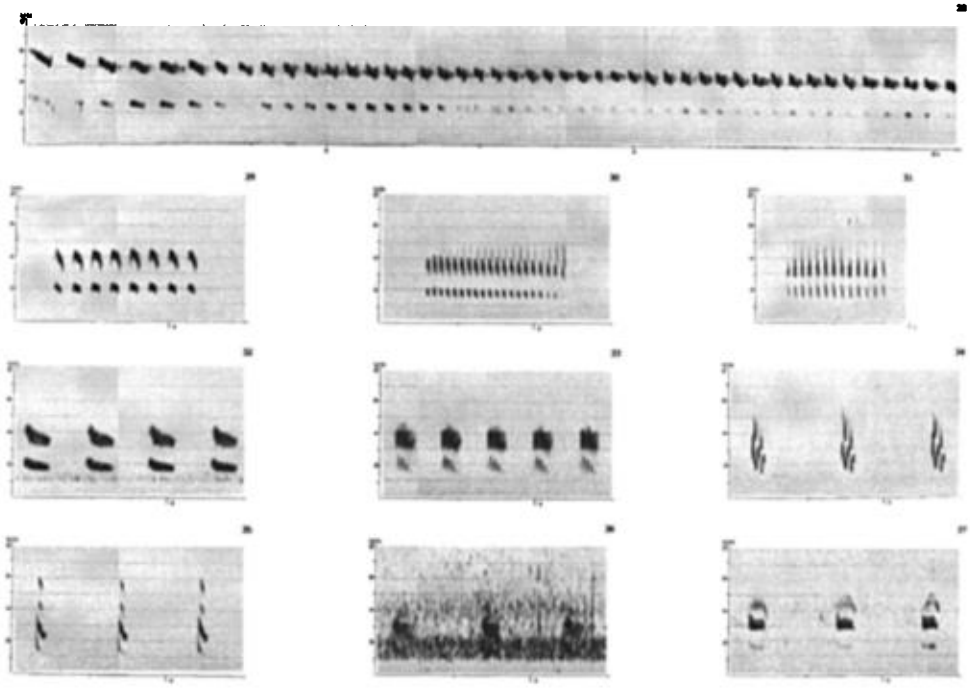
Brief diagnosis.—Relatively small. Adult males uniform blackish like *intermedius* and east Ecuadorian *latrans*. Adult females considerably paler and with extensively brown flanks that are



FIGS. 20–27. *Scytalopus atratus nigricans*: 20. Song. NV. Cerro El Teteo, Táchira, Venezuela, 1,050 m. P. Schwartz. *Scytalopus* new species?: 21. Song. PB. Finca Merenberg, Huila, Colombia, 2,200 m, 18/10/86. B. Whitney. *Scytalopus atratus "atratus"*: 22. Part of song. NV. Jirillo, San Martín, Peru, 1,350 m, 26/7/86. T.S.S. 23. Part of song. NV. Jirillo, San Martín, Peru, 1,350 m, 27/7/86. T.S.S. *Scytalopus micropterus*: 24. Song. NV. Cutucú, Morona-Santiago, 1,750 m, 24/6/84. T.S.S. 25. Call/alarm, possibly female. NV. Guacamayos, Napo, 2,035 m, 23/8/91. XXVIIIA 231–232. N.K. *Scytalopus femoralis*: 26. Song. PB. Abra Patricia, Amazonas, Peru, 2,250 m, 7/9/83. N.K. *Scytalopus canus opacus*: 27. Male song. PB. Limón road, Azuay, 3,400 m, 13/12/91. Collected. XLA 12–22. N.K.

uniform or obscurely and faintly barred; paler than female *intermedius*, but usually darker than female *unicolor*. Wings and tail distinctly shorter than in *S. parkeri*. Flanks not distinctly barred as in *S. robbinsi*. Subadult male with barred flanks much paler than *S. robbinsi*. Juveniles variably barred or uniform below, but much paler than *latrans*.

Plumage.—Adult male (n = 2): Uniform black, morphologically indistinguishable from males of east Ecuadorian "*latrans*". *Adult female* (n = 5): Deep Mouse Gray, Dark Mouse Gray, or Blackish Mouse Gray. Flanks, under-tail coverts, and in all but one, also the lower belly Tawny-Olive; usually rump and sometimes upper-tail coverts and lower sides also more or less washed with this color; either uniform or with faint and obscure blackish barring on the flanks. Axillars rather light, between Pinkish-Buff and Cinnamon-Buff. One specimen has nape, back, wings, and upper-tail coverts faintly washed with brown, and has Pallid Gray edges to the feathers of the throat and belly, giving a slightly streaked effect. *Immature/subadult male* (n = 2): Both molting from juvenal plumage, one with large bursa, slightly enlarged testes and singing; the other without bursa and with small testes. Wings, upper-tail coverts, most of tail, lower sides and flanks Tawny Olive, barred dusky on wing-coverts, tertials, upper-tail coverts and flanks. Some rectrices brown and dark-barred at their tip, others uniform, dark gray. Lower belly Pinkish-Buff. No older subadults from Ecuador were available, but two males from Porculla, depto. Lambayeque, Peru (ANSP), and Cruz Blanca, depto. Piura, Peru (LSUMZ), have some dull brown mixed into the flanks; the first is paler gray than adults. *Juvenal male* (n = 1): Crown, side of head, mantle, and back between Dresden Brown and Mummy Brown, feathers narrowly tipped blackish, wing-coverts Dresden Brown, each with blackish tip and central bar. Remiges Chaetura Drab, narrowly edged Mummy Brown. Inner tertial much like wing-coverts, next two



FIGS. 28–37. *Scytalopus canus opacus*: 28. Female part of duet, probably pair-formation. PB. Near Papallacta, Napo, 3,900 m, 14/10/83. N.K. 29. Male call. PB. Cerro Mongus, Carchi, 3,600 m, 22/3/92. Collected. XLVIIIA 61–65. N.K. 30. Call. PB. Cerro Chinguela, Piura, Peru, 1980. T. A. Parker. *Scytalopus affinis*: 31. Female alarm near nest (male collected). NV. Quebrada Pucavado, Ancash, Peru, 4,100 m, 16/2/87. N.K. 32. Male song. PB. Chinancocha, Quebrada Llanganuco, Ancash, Peru, 9/2/86. T.S.S. *Scytalopus altirostris*: 33. Song (?). Not seen. PB. Bosque Unchog, Huánuco, Peru, 3,500 m, 15/11/83. N.K. *Scytalopus* unnamed species: 34. Song. NV. Millpo, Pasco, Peru, 3,650 m, 8/7/85. T.S.S. *Scytalopus* unnamed species: 35. Male song. PB. Nevado Ampay, Apurimac, Peru, 3,500 m, 17/3/87. Collected. N.K. 36. Call. NV. Nevado Ampay, Apurimac, Peru, 3,500 m, 18/3/87. N.K. *Scytalopus urubambae*: 37. Song. NV. Near Totora, Río Ucumare, Santa Teresa valley, Cuzco, Peru, 3,700 m, December 1990. G. Engblom.

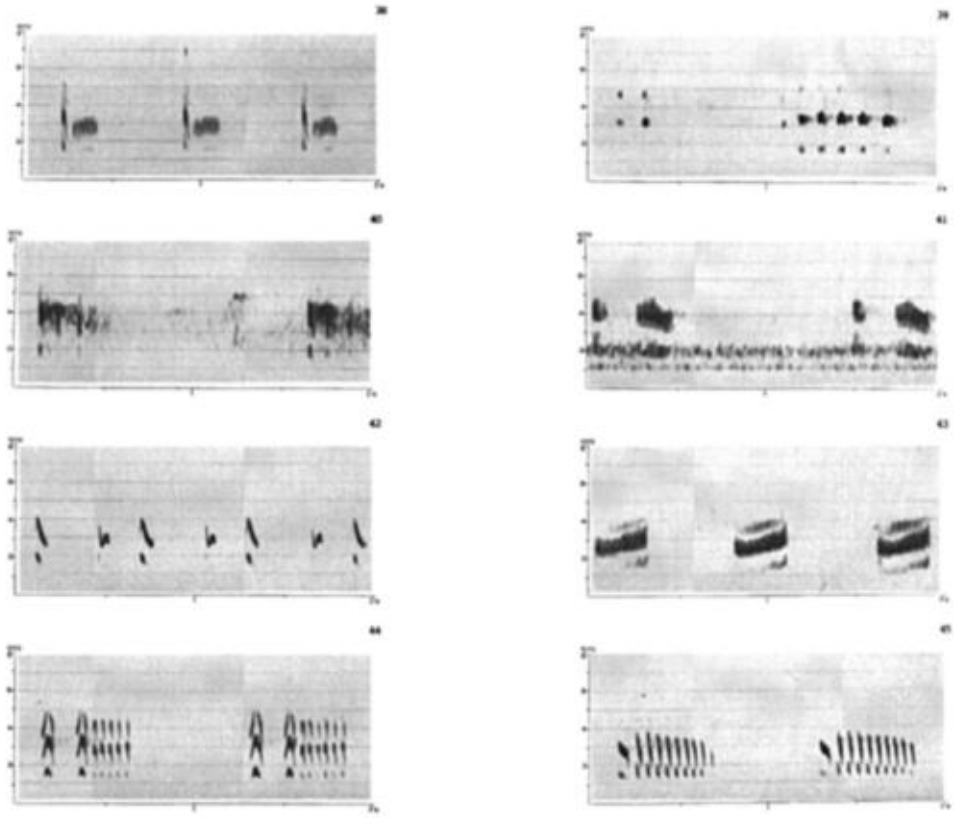
like remiges, but with a narrow Dresden Brown subterminal bar. Rump and upper-tail coverts barred blackish and Antique Brown. Chin and throat Cinnamon-Buff, grading to Clay Color on rest of underparts, feathers of the entire underparts narrowly tipped dusky, those of belly, flanks and under-tail coverts also with a presubterminal dusky bar. Rectrices Chaetura Drab, central pair uniform, remainder with faint barring of Dresden Brown. Two birds described by Zimmer (1939) also have barred underparts. *Juvenal female:* Five were described by Zimmer (1939), four nearly uniform ochraceous or dull ochraceous below, one completely barred below. Three of these were re-examined and found to have more or less uniform brown backs. One from Canchaque, depto. Piura, Peru (LSUMZ), similar, but with light-brown feathers of nape scalloped with blackish. Below all with pale ochraceous breasts and bellies, the relatively bright, buffy, lower bellies barred.

Annual cycle in Ecuador (n = 4).—*Juvenal:* 4 March. *Active ovary:* 6 February; 5 March; 12 April.

Vocalizations in Ecuador.—The normal song (Fig. 12) is sharper than that of *latrans*, and each note has a double quality, the first part sharp (0.013 s long). The excited song (Fig. 11) is very much like that of *latrans*, but with a different spectrum of harmonics, and of a somewhat sharper quality, as seen by all notes being slightly peaked, rather than most notes smooth and rounded as in latrans (Fig. 1).

The song is also more rhythmic than *latrans*, with a short pause after the slightly lower first note followed by a varied number of 2–5 or more similar notes (Fig. 12); pauses between phrases usually 0.2–1.0 s, excited song continuous (Fig. 11).

The first overtone is loudest, 1.6–2.2 kHz. In low-pitched notes the second overtone is relatively loud, the fundamental and third overtones are barely audible, in higher-pitched notes the



FIGS. 38–45. *Scytalopus simonsi*: 38. Male song. NV. 70 road km west of Cochabamba on Oruro road, Cochabamba, Bolivia, 3,850 m, 14/4/87. N.K. 39. Female call. PB. Above Cuyocuyo, Puno, Peru, 3,600 m, 22/12/83. Collected. N.K. *Scytalopus zimmeri*: 40. Song. NV. Cerro Campamiento (20°48'S, 64°30'W), Chuquisaca, Bolivia, 2,700 m, 23/9/91. J. Fjeldså. *Scytalopus superciliaris superciliaris*: 41. Song. PB. Above Tafi del Valle, Tucumán, Argentina, 2,400 m, ca. 1989. R. S. Ridgely. *Scytalopus magellanicus*: 42. Song. NV. Parque Nacional Nahuelbuto, Malleco, Chile, 1,300 m, 25/8/85. B. M. Whitney. *Scytalopus fuscus*: 43. Song. PB. Parque Nacional Campana, Santiago, Chile, 450 m, 6/12/87. B. Whitney. *Scytalopus acutirostris*: 44. Male song. NV. Carpish tunnel, Huánuco, Peru, 2,760 m, 9/2/87. Collected. N.K. 45. Male song. PB. Same bird as previous cut. N.K.

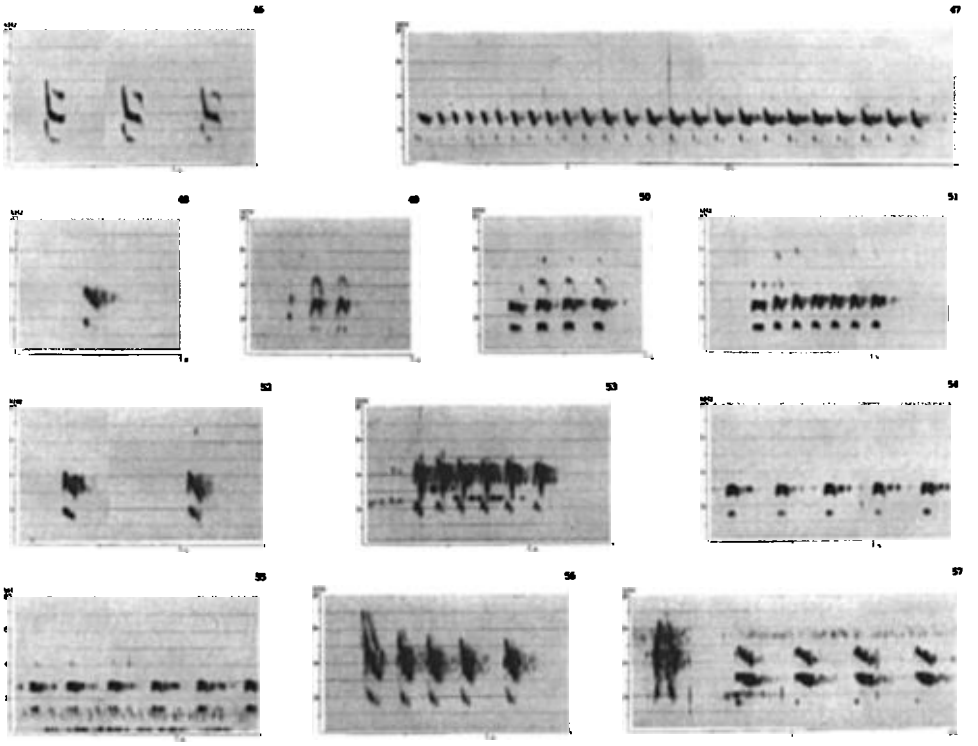
fundamental is almost as loud as the first overtone, and the second overtone barely audible; apparently any sound between 0.9 and 2.6 kHz is loud irrespective of whether it is an overtone or a fundamental.

Call (Fig. 13; also Fjeldså and Krabbe [1990, p. 425, sonagram 1]) given by both sexes is similar to that of *latrans*, sometimes with a harsher quality, and often given in slow series of 1–3 notes.

As in *latrans* a rarely heard, excited "*brzk*" is given, presumably by the female or young, during distress.

Habitat in Ecuador.—Humid and semi-humid forest undergrowth and shrubbery, including small and secondary patches along streams and ditches into the arid zones. Also mixed *Polylepis-Gynoxys* woodland. Tolerates drier conditions than congeners, but invades humid forest in absence of competitors. Where syntopic with *S. parkeri, S. u. subcinereus* avoids stands of bamboo.

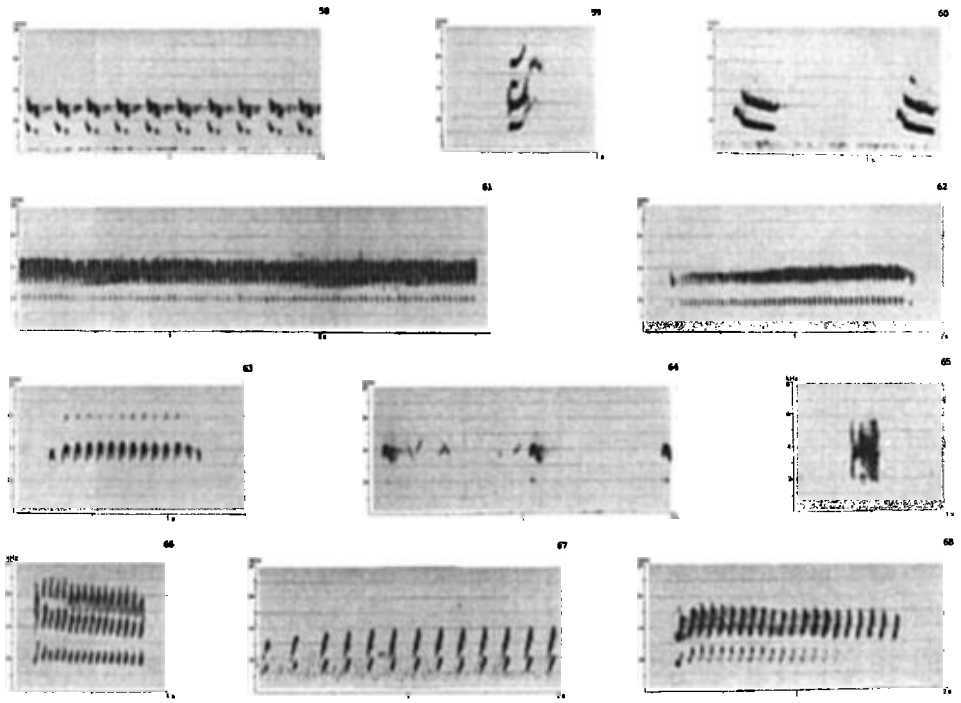
Distribution in Ecuador.—1,500–4,000 m. Southwestern Ecuador from the Pacific slope in prov. Azuay, the Cajas plateau, and the inter-Andean slopes of Cuenca valley south and west on the inter-Andean and Pacific slopes, including all the more-or-less isolated mountains over 2,000 m. Along the right bank of Río Paute, it meets east slope *latrans* near Amaluza, where both song-types can be heard. Here its range also overlaps with that of *S. spillmanni*. Elsewhere on the west slope of the Eastern Andes *subcinereus* is replaced above by *S. canus opacus* with no overlap. On the Páramos de Matanga both occur right to the crest, *S. canus opacus* on the eastern



FIGS. 46–57. *Scytalopus acutirostris*: 46. Male call. NV. Same bird as previous cuts. N.K. *Scytalopus vicinior*: 47. Song. NV. La Planada, Nariño, Colombia, 1,800 m, January 1989. F. Lambert. 48. Call. NV. Parque Nacional Farallones, Valle del Cauca, Colombia, 1,950 m. 13/1/83. B. Whitney. 49. Call. NV. Parque Nacional Farallones, Valle del Cauca, Colombia, 1,950 m. 3/1/83. B. Whitney. 50. Female call. PB. Mindo, Pichincha, 1,700 m, 15/11/92. Collected. XLIIIA 340–345. N.K. 51. Female call. PB. Maquipucuna, Pichincha, 1,775 m, 31/3/93. Collected. LXVIIIA 339–343. N.K. 52. Female end of very high-pitched descending series. Mindo, Pichincha, 1,700 m, 2/11/91. XXXVIB 121–122. N.K. *Scytalopus panamensis*: 53. Alarm? Headwaters of Río Tigre, Cerro Tacarcuna, Chocó, Colombia, 1,150 m, October 1990. M. Pearman. *Scytalopus chocoensis*: 54. Song. PB. El Placer, Esmeraldas, 670 m, 13/8/87. T.S.S. Collected. 55. Male song. PB. El Placer, Esmeraldas, 670 m, August 1987. T.S.S. 56. Female call. PB. Alto Tambo, Esmeraldas, 550 m, 16/2/92. Collected. XLVB 201–209. N.K. 57. "*Brzk*" and beginning of song. "*Brzk*" presumably given by a female. NV. El Placer, Esmeraldas, 670 m, 5/7/84. N.K.

slope, *subcinereus* on the western. Near the top they occur in similar habitat within 20 m of one another but on their respective slopes. On the Pacific slope in prov. Azuay, *subcinereus* is replaced below by *S. robbinsi* with little or no overlap.

Distribution beyond Ecuador of S. [unicolor].—In Venezuela *S. unicolor latrans* is known from the Andes of edos. Mérida and Táchira at 1,800–2,200 m (AMNH, Berlin Museum; see also Meyer de Schauensee and Phelps [1978]). In Colombia it is known from all slopes of the three main Andean chains, ranging from 1,800 to 3,800 m (AMNH, BMNH, FMNH, LACM, NRS, USNM, WFVZ). Three recently collected specimens, two from the east slope and one from the west slope of the Eastern Andes in depto. Cundinamarca (ICN) show the same black color found in eastern Ecuadorian birds. Birds from depto. Antioquia in the Central Andes sound closest to the west Ecuadorian birds (tape-recordings by N.K.). In Peru birds singing like those in east Ecuador occur east of the Huancabamba valley in northern depto. Cajamarca (Cerro Chinguela, 2,000 m [Parker et al. 1985; T. A. Parker tape-recordings in LNS]). Others collected in Peru without vocal data, but taken nearby at Chaupe, depto. Cajamarca, northeast of Huancabamba, 1860 m [AMNH]; and at Lomo Santo above Jaen, depto. Cajamarca, 1,525 m [AMNH], undoubtedly also belong here. *S. unicolor intermedius* (Zimmer 1939; type in AMNH) occurs in depto. Amazonas in the northern end of the Central Andes, Peru (AMNH, ANSP, BMNH, LSUMZ), and similar specimens have been taken further south in depto. San Martín (Puerto del Monte, 3200 m [LSUMZ]). A male from Chira, 2,290 m (ANSP) was referred to

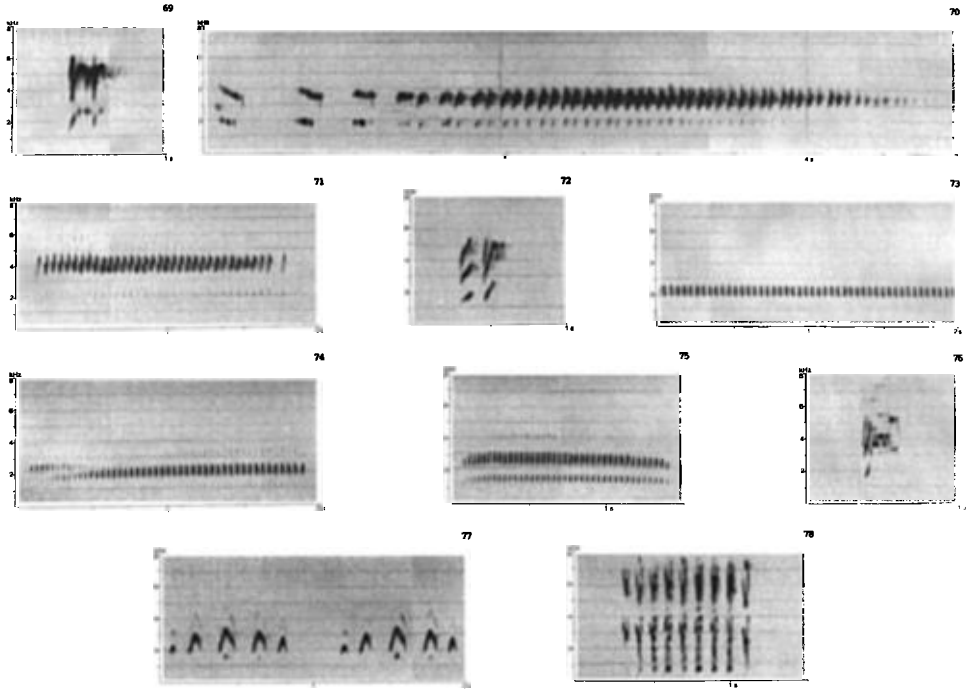


FIGS. 58–68. *Scytalopus robbinsi*: 58. Song. NV. Piñas, El Oro, 900 m, 12/6/85. M. B. Robbins. 59. Female single-note call. NV. Piñas, El Oro, 900 m, 26/9/90. VIIB 221–230. N.K. 60. Female descending series. PB. Piñas, El Oro, 900 m, 16/11/91. Collected. XXXVIIA 45–78. N.K. *Scytalopus spillmanni*: 61. Song. PB. Above Tandayapa, Pichincha, 2,300 m, 29/7/84. T.S.S. 62. Male excited (short rising trills). PB. Maldonado road, Carchi, 2500 m, 20/11/90. Collected. XIIB 195–200. N.K. 63. Alarm. PB. Above Tandayapa, Pichincha, 2,300 m, 29/7/84. T.S.S. 64. Female long, slowly descending series as also given in duet. PB. Apuela road, Imbabura, 2,300 m, 12/6/87. Collected. VIIB 272–274. N.K. 65. "*Brzk*" presumably given by a female. NV. Llanganates, Napo, 3,300 m, 27/5/92. XLIXB 217–219. N.K. *Scytalopus latebricola*: 66. Call. PB. Santa Marta mountains, Colombia, 2,350 m, January 1994. P. Coopmans. *Scytalopus meridanus*: 67. NV. Los Frailes Hotel, Mérida. Venezuela. P. Coopmans. 68. Alarm. NV. Universidad Los Andes (ULA) forest, Mérida, Venezuela, 2,200 m, 18/1/94. G. Engblom.

latrans by Zimmer (1939), who believed the locality to be north or west of Río Marañón. As far as it is now known, however, Chira is south and east of the river, so the specimen is presumably referable to *intermedius*.

S. unicolor subcinereus occurs in northern Peru at 1,220–3,200 m on the Pacific slope of Western Andes in depto. Piura (Palambla, 1,220 m [AMNH, ANSP]; El Tambo, 2,800 m [ANSP, MHN]; Cruz Blanca, 1,700–3,200 m [Parker et al. 1985, tape-recordings by T. A. Parker in LNS]), depto. Lambayeque (Porculla, 1,830 m [ANSP]), and depto. Cajamarca (vicinity of Cascabamba, 2,400–2,900 m [MHN and tape-recordings by N.K.]; Hda. Taulis, 1,700–2,700 m [AMNH, MHN]; Nancho and [=] Montaña de Nancho, 2,350 m [MHN, Warsaw Museum]). It seems possible that *subcinereus* crosses over to the east slope of West Andes in depto. Cajamarca. A male and a female from Cutervo, depto. Cajamarca, 3,000 m (BMNH, Warsaw Museum), were ascribed to *S. magellanicus* by Taczanowski (1884), then to *latrans* by Hellmayr (Cory and Hellmayr [1924]). Zimmer (1939) discussed them and left them in *latrans*, although the description of a dark male and a pale (molting) female with a nearly uniform juvenal tail suggests they belong with *subcinereus*, as might a specimen from Tambillo [1,770–2,440 m] (MHN).

The pale *Scytalopus unicolor unicolor* (Salvin 1895; type in BMNH) is definitely known from farther south on the eastern slope of the Western Andes, Peru, in southern depto. Cajamarca (Cajabamba, 2,750 m [AMNH, BMNH]) and depto. La Libertad (Huamachuco, 3,170 m [AMNH]; Succha [AMNH]; Soquián, 2,000 m [ANSP]), and has been recorded also from the Pacific slope in depto. Cajamarca (Chugur [AMNH]; Sunchubamba, 2,650 m [MHN]) (Koepcke 1961). Chugur is north of the southernmost locality known for *subcinereus*. Zimmer (1939) pointed out that two males from Chugur are no darker than some topotypical specimens of



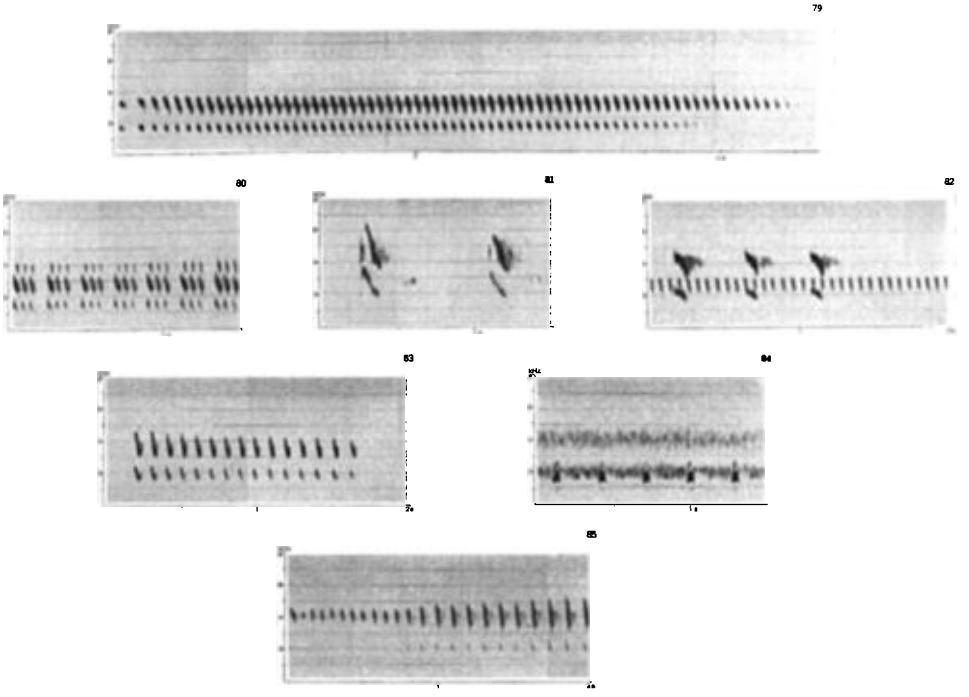
FIGS. 69–78. *Scytalopus meridanus*: 69. "*Bzrk*". NV. ULA forest, Mérida, Venezuela, 2,200 m, 18/1/94. G. Engblom. 70. Song. NV. ULA forest, Mérida, Venezuela, 2,200 m, 18/1/94. G. Engblom. 71. Alarm. NV. Near Lagrita, east Táchira, Venezuela, 2,680 m, 21/10/88. B. Whitney. 72. Call. NV. Near Lagrita, east Táchira, Venezuela, 2,680 m, 21/10/88. B. Whitney. *Scytalopus "meridanus"* (= *S. infasciatus*?): 73. Song. NV. Parque Nacional Chingaza, Cundinamarca, Colombia, in tall mossy forest, 3,100 m, February 1989. F. Lambert. 74. Short rising trills. Same bird as in Fig. 73. NV. F. Lambert. 75. Alarm. East of Bogotá, Cundinamarca, Colombia. P. Coopmans. *Scytalopus caracae*: 76. "*Brzk*". NV. Near Colonia Tovar, coastal mts, Aragua, Venezuela, 1985. J. P. O'Neill. 77. Song of same individual as in Fig. 76. PB. J. P. O'Neill. 78. Alarm. PB. Near Colonia Tovar, coastal mts, Aragua, Venezuela, 26/2/91. D. Fischer.

unicolor. The morphological differences between *unicolor* and *subcinereus* are not great. In view of this similarity, and the geographic proximity of these taxa, it is possible that they intergrade. Such intergrades would be difficult or impossible to detect morphologically, however. Again, we can only lament the paucity of information on nominate *unicolor*.

Populations that currently we treat as *Scytalopus parvirostris* (Zimmer 1939; type in AMNH; the type from La Paz, Bolivia, and a molting juvenal from Machu Picchu, Peru, depicted in Fjeldså and Krabbe [1990, pl. XLI 4c and 4b]), occur in central Peru from Cordillera Colán, depto. Amazonas (LSUMZ; no vocal data but the series is consistent in morphology with *S. parvirostris*) and Florida, depto. Amazonas (one tape-recording by B. M. Whitney), south at least to Machu Picchu, depto. Cuzco, Peru. *Scytalopus parvirostris* is also found from depto. La Paz south to depto. Santa Cruz, Bolivia, in which area it occurs up to 3,200 m (AMNH, ANSP, FMNH, LSUMZ, NRS, ZMUC).

The rate of delivery (notes/s) of the song of *Scytalopus parvirostris* varies from 21 (depto. Pasco, central Peru) (Fig. 5) to 14 (Machu Picchu, depto. Cuzco) (Fig. 6), to 20–28 in deptos. Cochabamba and Santa Cruz, Bolivia (Fig. 7). Also, the elevational distribution of birds that we assign to *S. parvirostris* varies latitudinally. In central Peru (depto. Pasco) they range from 1,800 to ca. 2,400 m, whereas in Bolivia the elevational range is ca. 2,000–3,200 m (Whitney 1994), and the elevation for the type locality of *S. parvirostris* was reported to be 3300 m (Zimmer 1939). As also noted by Whitney (1994), further work might show that more than one species is involved in what we here call *S. parvirostris* (the name *sylvestris* Taczanowski, 1874 may be available for the central Peruvian population).

Some puzzling recordings from the Amazonian slope in depto. Cuzco (below Abra Málaga, 3,000 m, subad. male [ZMUC 80007] tape-recorded by N.K. [Fig. 8] and 3,350 m, tape-recorded by T.S.S. [Fig. 9]), and in depto. Puno (above Sandia, 2,800 m [tape-recording by N.K.; Fig.



FIGS. 79–85. *Scytalopus parkeri*: 79. Male song. NV. Cord. del Cóndor, Zamora-Chinchipe, 2,100 m, July 1993. T. A. Parker. 80. Male excited song. PB. Limón road, Morona-Santiago, 3,100 m, 9/6/84. Collected. N.K. 81. Beginning in duet, female highest pitched. NV. Limón road, Morona-Santiago, 2,280 m, 18/6/84. Female collected. N.K. 82. Later in same duet as Fig. 81. N.K. 83. Call (typical of male). NV. Acanamá, Loja, 3,100 m, 13/2/91. XXIA 335–367. N.K. *Scytalopus macropus*: 84. Song. NV. Bosque Unchog, Huánuco, Peru, 3,500 m, 17/11/83. N.K. *Scytalopus argentifrons argentifrons*: 85. Song. PB. Parque Nacional Monteverde, Costa Rica, 24/5/79. O. Jakobsen.

10]) referred to under *parvirostris* in Fjeldså and Krabbe (1990) appear to be representatives of a recently discovered species. This species, *Scytalopus schulenbergi*, which is found above *parvirostris,* was described from deptos. Puno, Peru, and La Paz and Cochabamba, Bolivia, by Whitney (1994). Two individuals tape-recorded (and one of them collected) at Abra Málaga sang like Bolivian birds. Scolds recorded at both Abra Málaga and in depto. Puno are slightly softer than scolds of Bolivian birds.

We do not know where to place two specimens with relatively pale gray chests and bright brown, unbarred flanks from depto. Ayacucho (NE Tambo, 2,600 and 3,390 m [LSUMZ]). They might represent an undescribed taxon.

Scytalopus femoralis, sensu Zimmer 1939

Zimmer considered the forms *bolivianus* (Allen 1889; type in AMNH), *femoralis* (Tschudi 1844; type in MNN), *micropterus* (Sclater 1858; type in BMNH), *confusus* (Zimmer 1939; type in AMNH), *atratus* (Hellmayr 1922; type in CM), and *sanctaemartae* (Chapman 1915; type in AMNH) as subspecies of *S. femoralis*. Zimmer noted that some specimens that he included in this polytypic species exhibited a white spot on the forecrown, but evidently considered the presence or absence of this white crown spot to be an individually variable character. Later *nigricans* (Phelps and Phelps 1953; type on deposit to AMNH) also was described as a subspecies of Zimmer's *S. femoralis*.

T.S.S. and others found that in Peru and Ecuador Zimmer's *Scytalopus femoralis* encompassed two sympatric species. Birds with a white crown spot differ from birds without it in vocalizations and by being darker, smaller, relatively shorter-tailed, by often having white tips to the belly feathers, and also by generally occurring at lower elevations, at ca. 1,070–2,030 m, whereas dark-crowned birds occur at ca. 1,300–2,300 m. Specimens (LSUMZ) documenting the co-occurrence of both types along the same elevational transects in Peru were collected on the Cor-

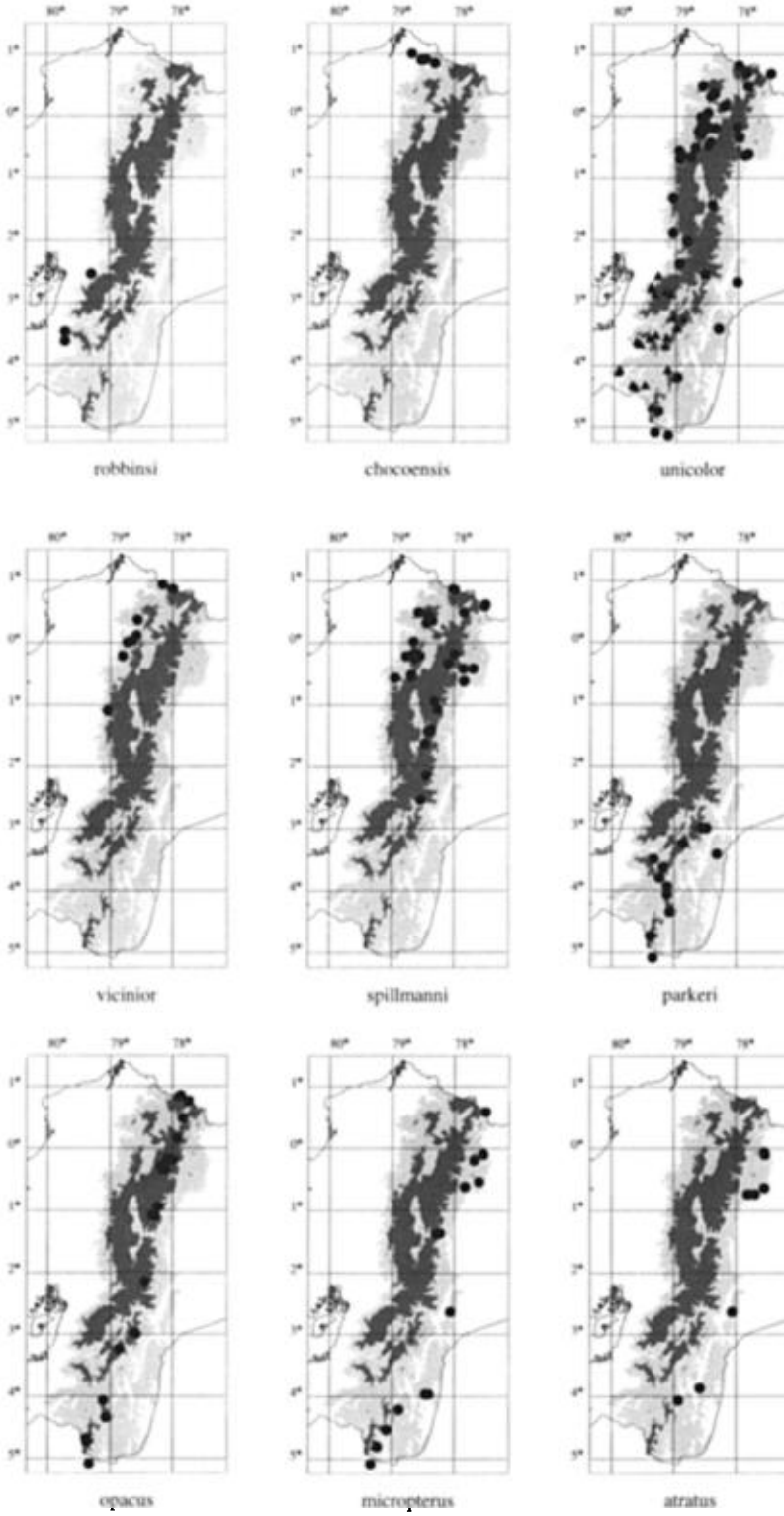
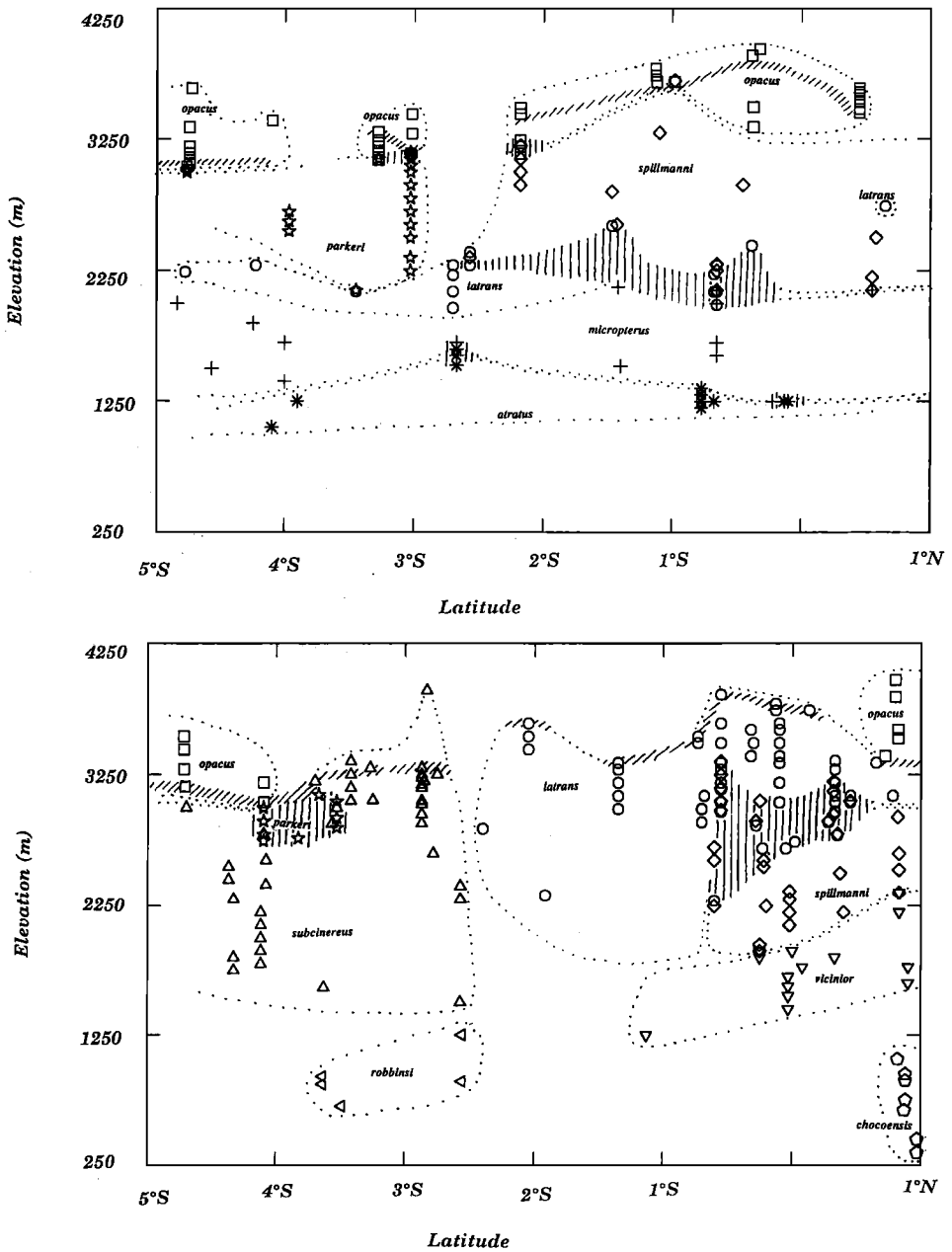


FIG. 86. Geographical distribution of *Scytalopus* tapaculos in Ecuador. Light gray shading indicates areas between 1,200 and 3,000 m elevation, dark gray shading for areas above 3,000 m. For *Scytalopus unicolor*, circles represent the subspecies *latrans*, and triangles represent the subspecies *subcinereus*.



FIGS. 87 and 88. Elevational distribution of *Scytalopus* taxa in Ecuador. X-axis is latitude in degrees, y-axis is elevation (m). Fig. 87. Amazonian slope including Cordillera de Cutucú and Cordillera del Cóndor. Fig. 88. Pacific slope, in the south including the western slope of eastern Andes. Square *Scytalopus canus opacus*, star *S. parkeri*, diamond *S. spillmanni*, circle *S. unicolor latrans*, triangle pointing up *S. unicolor subcinereus*, plus *S. micropterus*, asterisk *S. atratus*, triangle pointing down *S. vicinior*, triangle pointing left *S. robbinsi*, pentangle *S. chocoensis*. Vertical hatching known areas of overlapping ranges, slanting hatching treeline.

dillera Colán, depto. Amazonas; along the trail from Cumpang to Utcubamba, depto. La Libertad; and in the Carpish Mountains, depto. Huánuco. This same pattern was discovered in 1984 in Ecuador in Cordillera de Cutucú, prov. Morona-Santiago, later also in provs. Napo and Zamora-Chinchipe (ANSP, MECN, ZMUC).

Clearly Zimmer's *Scytalopus femoralis* is in need of revision. The nomenclature of the dark-crowned birds is relatively straightforward. Birds along the eastern slope of the Andes from southern Colombia (where crossing over to the head of Magdalena valley) south to northern Peru north of the Río Marañón, are the large, very long-tailed *micropterus*. Those populations from northern Peru, just south and east of the Río Marañón south to central Peru, are what historically have been referred to nominate *femoralis* (but see below). Thus these taxa are allopatric, and under the biological species concept, their taxonomy is another question. The songs of *femoralis* and *micropterus* (Figs. 24 and 26) are similar, but consistently different. Furthermore, there are two fixed allelic differences between these two taxa (T.S.S., unpublished), suggesting long-standing genetic isolation. For these reasons we recommend that *S. femoralis* and *S. micropterus* be treated as allospecies in a *S.* [*femoralis*] superspecies.

The remaining forms in Zimmer's *Scytalopus femoralis* all have a white crown spot, which we consider to be a possible synapomorphy, but *sanctaemartae* is unlike the others in its pale color and entirely different song (Fig. 18). It is isolated in the Santa Marta mountains, Colombia, at elevations from 900 to 1,700 m or slightly higher (ANSP, AMNH, ICN). The other taxa with a white crown spot (*bolivianus*, *atratus*, *confusus*, and *nigricans*) all appear morphologically very alike, but most differ somewhat vocally (Figs. 14, 15, 16, 17, 20, 22, and 23) and we treat them as allospecies in a *S.* [*bolivianus*] superspecies.

The nomenclature of the white-crowned birds is particularly problematic. The oldest available name is *bolivianus*, the type of which is from depto. La Paz, Bolivia, and is a small, dark specimen with a well-developed crown spot. Birds assigned to this taxon are found from depto. Chuquisaca, Bolivia (Fjeldså and Mayer 1996;, pers. obs. T.S.S.), north to deptos. of Santa Cruz (tape-recording by T. A. Parker in LNS), Cochabamba (NRS) and La Paz (AMNH, ANSP, LSUMZ), Bolivia, and depto. Puno, Peru (AMNH, ANSP, LSUMZ), at elevations ranging from 1,000 to 2,300 m (and possibly to 2,850 m [Whitney 1994]). Tape-recordings of *bolivianus* show an unusually wide range of variation (Figs. 15, 16, and 17), but all vocalizations are fairly different from the known voices of other white-crowned birds farther north in Peru. Hence, we recommend that *S. bolivianus* be regarded as a separate species, but emphasize that more needs to be learned about its morphological variation and distributional limits. Among the unresolved questions surrounding this treatment are birds from depto. Cuzco, Peru, with a *bolivianus*-like song, but without a white crown spot; and the possibility that the type of *femoralis*, which is very dark and has very little barring on the flanks, may represent the central Peruvian species that usually has a white crown spot.

On the basis of current knowledge, then, available names for the white-crowned birds from central Peru north are *atratus, confusus,* and *nigricans*. All three holotypes are dark specimens with well-developed crown spots. The pale throat on the female and on one of the two males in the type series of *atratus* are matched in the female and (in part) by the male in the type series of *nigricans*, in a female specimen from Ecuador (ZMUC 80142), and is suggested as well by prominent white scalloping on the throat of a male from Ecuador (ANSP 176885); these markings, although distinctive, probably reflect nothing more than individual, or, perhaps, ontogenetic variation.

There is no information on the vocalizations of topotypical populations of either *atratus* (the type of which is from the east slope of Eastern Andes of Colombia) or of *confusus* (type locality in the upper Cauca valley, Colombia). Recent recordings of a white-crowned bird (not collected) from the west slope of the Eastern Andes of Colombia in depto. Cundinamarca (P. Coopmans) are similar to our recordings of white-crowned birds from the east slope of the Andes in Ecuador. Consequently, we provisionally use the name *atratus* for the birds of the east slope of the Andes in Colombia, Ecuador, and Peru. We restrict the name *confusus* to the birds of the Central and Western Andes of Colombia, and, in the absence of firm knowledge of the vocalizations of *confusus*, we provisionally regard this taxon as a subspecies of *atratus*. Clearly, judicious field work, including the collecting of specimens and the preservation of tissue or blood samples, in the Andes of Colombia will be necessary to resolve these nomenclatural issues. Yet another problem is posed by an apparent pattern of geographic variation in the songs of white-crowned birds. Songs recorded in Peru (Figs. 22 and 23) and Venezuela (Fig. 20) are very similar, yet these populations are separated by the different-sounding birds (Fig. 14) of eastern Ecuador and, apparently, Colombia. We can think of several possible explanations for this peculiar situation.

Most likely may be that the white-crowned populations in eastern Peru are a species different from those in Ecuador, either conspecific with, or closely related to, *nigricans* of Venezuela. In view of the surprising biogeographic picture that this paints, and of the already convoluted nomenclatural problems posed by this group, we refrain at this time from naming new taxa, but recommend further studies of these white-crowned populations throughout the Andes.

NORTHERN WHITE-CROWNED TAPACULO *Scytalopus atratus atratus*
(Hellmayr 1922; type in CM)

Brief diagnosis.—Relatively large. Male blackish, with white crown spot and distinct, brown bars on the flanks (Fjeldså and Krabbe [1990, pl. XLI 9 as *confusus*]). Female, at least when immature or subadult, slightly paler, washed with brown on most of the upperparts, with a smaller crown spot and a whitish throat. Both sexes may have whitish tips on the belly feathers.

Plumage.—Male (n = 9): All Blackish Mouse Gray, forecrown with a snow white central spot (very small in two), flanks barred Ochraceous Tawny. Two specimens are washed with dark brown and have faint, dark bars on rump and upper-tail coverts; one is also washed with dark brown on terminal half of tertials. Belly variable (age-related ?). Pale, broad tips or subtips to feathers of upper belly silvery white and conspicuous in two specimens, gray and inconspicuous in one, faintly indicated on a few feathers in one, absent in others. One appears uniform blackish on the belly, the others have slight Ochraceous-Orange to Ochraceous-Tawny or more olivaceous barring on the lower belly and under-tail coverts. One has feathers of a restricted area on upper belly with grayish white, subterminal bars, appearing scaled. Axillars gray with a slight olivaceous wash. *Female* (n = 1): White crown spot very small, white feathers broadly dark-tipped. Rest of forecrown dark gray, remainder of upperparts between Argus Brown and Brussels Brown, of a very dark shade; rump and upper-tail coverts barred blackish, tertials with 1–2 dark bars near tips and edges. Greater wing-coverts with subterminal Ochraceous bar, bordered with blackish. Throat whitish. Rest of underparts Deep Mouse Gray, 2 mm wide terminal or subterminal bars on upper belly whitish. Lower belly, lower sides, flanks and under-tail coverts Ochraceous-Tawny barred blackish. Axillars Olivaceous. *Juvenal female:* An old specimen (BMNH) taken at an elevation of 850 m in prov. Morona-Santiago, probably of this taxon, shows no trace of a pale crown-spot (the spot is found in juveniles from Peru [LSUMZ]).

Annual cycle in Ecuador (n = 1).—*Juvenile:* 6 January (prov. Morona-Santiago).

Vocalizations in Ecuador.—Song (Fig. 14) by both sexes, a series of 5–8 similar notes lasting 0.6–0.7 s, and repeated about once/s. First overtone loudest, 2.5 kHz, the fundamental weaker. Although resembling the scold of some other species, we have never heard other vocalizations from this species that could be interpreted as song. Some high-pitched squeaks have been noted from males after playback of song.

Habitat in Ecuador.—Humid, primary forest undergrowth, at edge and in second growth. In broader-leaved vegetation than *S. micropterus* in the zone of overlap.

Distribution in Ecuador.—850–1,650 m, along the entire east slope of Eastern Andes and on the outlying ridges (Volcán Sumaco-Pan de Azúcar, prov. Napo; Cordillera de Cutucú, prov. Morona-Santiago; Cordillera del Cóndor, prov. Zamora-Chinchipe). Replaced above by *S. micropterus*, but with considerable elevational overlap.

EQUATORIAL RUFOUS-VENTED TAPACULO *Scytalopus micropterus*
(Sclater 1858; type in BMNH)

Brief diagnosis.—Large and heavy, dark gray with long blackish tail composed of 12 rectrices. Flanks always barred. Bill relatively stout. No white crown spot.

Plumage.—Adult male (n = 7): Blackish Mouse Gray to Dark Mouse Gray, lower back and rump between Mars Brown and Argus Brown with or without dark bars. In three birds brown also found on the nape (two birds), wing-coverts, edges of remiges, and on upper-tail coverts; one also has tips of innermost remiges with a subterminal light brown bar bordered blackish. Tail blackish. Below Deep Mouse Gray to Dark Mouse Gray; the two birds brownest above with Light Mouse Gray tips to feathers of upper belly. Lower sides, flanks, lower belly and under-tail coverts between Amber Brown, Sudan Brown, Ochraceous-Tawny and Cinnamon-Brown, distinctly barred blackish. Axillars Sayal Brown. *Adult female:* Zimmer (1939) described 14 birds as being duller than males, with a slight tinge of drab in gray of back and anterior underparts, but flanks sometimes more contrastingly barred.

Annual cycle in Ecuador.—Unknown.

Vocalizations in Ecuador.—Song (Fig. 24; also Fjeldså and Krabbe [1990:430, sonagram 2])

given by male consists of two resonant notes 0.2 s apart, second note shortest. Some birds may start with a single note, sometimes with a slight double quality, and later change to the typical double-noted song (occasionally and irregularly triple-noted) "*cu-ock*" at 2.0–2.2 kHz and repeated endlessly at 0.3–0.7 s intervals. An alarm-type call (Fig. 25), and a single "*kick*" note may be given by the female.

Habitat in Ecuador.—Humid shrubbery at forest edge and along streams, frequently in second growth. In the zones of overlap found in more microphyllous vegetation than *S. atratus*. The replacements above by *S. spillmanni* and *S. parkeri* appear to be very abrupt.

Distribution in Ecuador.—1,250–2,100 m along the entire east slope of Eastern Andes and on the outlying ridges (Volcán Sumaco - Pan de Azúcar, prov. Napo; Cordillera de Cutucú, prov. Morona-Santiago; Cordillera del Cóndor, prov. Zamora-Chinchipe; Cordillera de Tzunantza).

Distribution beyond Ecuador of species.—In Colombia *S. micropterus* has been tape-recorded on the west slope of Eastern Andes at the head of Magdalena Valley (Cueva de Los Guácharos; B. M. Whitney recording), and a specimen from the east slope of Central Andes in depto. Huila (La Palma, 1,525 m [BMNH]) appears to be of this form (wing 59.5, tail 50, tarsus 24.5 mm, coloration and bill like *S. micropterus*). Some specimens from the Amazonian slope in southern Colombia, at Llorente, depto. Nariño, 1,800 (?) m (FMNH 292139, female), at Cerro Pax (ANSP), and at 30 km E Cerro Pax (ANSP), all in depto. Nariño, also seem to belong here, but apparently the species does not range further north. In Peru, it occurs north of Río Marañón in depto. Cajamarca (Cerro Chinguela, 1,700–1,950 m [Parker et al. 1985, tape-recordings by T. A. Parker in LNS]; Chaupe, 1,830 m [AMNH, ANSP]; Lomo Santo [ANSP]).

South and east of the Río Marañón in Peru the very similar, but slightly shorter-tailed *S. femoralis* (Tschudi 1844; type in MNN) is widespread, but its exact southern limit (in southern Peru) has not yet been located (see also notes under *S. atratus*).

Scytalopus magellanicus, sensu Zimmer 1939

All forms referred to *Scytalopus magellanicus* by Zimmer (1939) are small and are found near or above treeline. In life all have a relatively flat crown that at certain angles appears to have a silvery sheen, forming a contrast with the exposed, dark bases of the feathers of the loral and ocular region. These characteristics could be plesiomorphies, the small size possibly even an adaptation to the dense treeline scrub and tussock grass. The songs of most forms (all but *canus*, *fuscicauda*, and *santabarbarae*) are now known, and they are all different (compare Figs. 27 through 43). Furthermore, there are three cases of elevational parapatry between two forms.

In 1983, N.K. found that birds assigned to *Scytalopus magellanicus* from the Carpish mountains, depto. Huánuco, central Peru were different in plumage, song, and habitat, from birds, also assigned to *S. magellanicus*, occurring at treeline in deptos. Apurímac and Cuzco, south-central Peru. A Louisiana State University expedition (T. J. Davis and G. and K. Rosenberg) independently found two sympatric species in depto. Pasco, central Peru, and later also in the Carpish mountains. A dark species was found in the upper reaches of forest, whereas a more or less white-superciliaried species was at and above treeline. The dark, forest populations in Huánuco and Pasco were morphologically similar to each other, and had similar vocalizations. For reasons outlined below, we apply the name *acutirostris* (Tschudi 1844, type in MHNN) to these birds.

The treeline populations in Huánuco and Pasco, however, differed from each other in vocalizations. The Huánuco treeline form is referable to *altirostris* (Zimmer 1939), whereas the Pasco population remains undescribed (K. Rosenberg and T. Davis, in prep.; specimens LSUMZ). Whitney (1994) reported a parallel situation in south-eastern Peru and northern Bolivia, in which a white-diademed bird was found in the upper reaches of forest (*S. schulenbergi*), and a white-superciliaried bird at and above treeline (*simonsi*).

Farther south, local sympatry has been reported in Chile between two other taxa, *fuscus* and *magellanicus* (Johnson 1969, Riveros and Villegas 1994).

Evidently Zimmer's "*Scytalopus magellanicus*" must be subdivided into several component species. Based on vocalizations, Whitney (1994) proposed to split Zimmer's "*S. magellanicus*" into two groups, *S. griseicollis* and *S. magellanicus*, found north and south of "the North Peruvian Low," respectively, whereas Ridgely and Tudor (1994), also based on vocalizations, treated *fuscus* and *magellanicus* as distinct species and grouped all other taxa as members of a polytypic *S. griseicollis*. Because of their different songs (and the above-mentioned cases of elevational parapatry) we feel obliged to treat all the vocally known forms in *S. magellanicus*, *sensu* Zimmer (1939), as distinct species. Biogeographically and morphologically, *canus* appears

to be closest to *opacus*, which we therefore treat as a subspecies of *S. canus*. We treat *fuscicauda* as a subspecies of its nearest neighbor, *S. griseicollis*. Although they appear to be widely separated geographically and could be unrelated, they are very similar in morphology. The newly described *santabarbarae* appears to be a recent isolate of *S. superciliaris*, and we leave it as a subspecies of that species.

PARAMO TAPACULO *Scytalopus canus opacus*
(Zimmer 1939, 1941, type in AMNH)

Brief diagnosis.—Very small. Adult male (depicted in Fjeldså and Krabbe [1990, pl. XLI 1 d]) varies from light to deep gray; usually lighter-colored and with more distinct barring than brown-flanked individuals of *S. unicolor latrans* and *S. unicolor subcinereus*, but old museum specimens not always identifiable. Females and subadults on the other hand, are easily separated by being considerably browner above. Healthy-looking birds (breast muscle bulging above sternum) weighing less than 15.5 g immediately after capture, safely referable to *S. canus opacus*.

Plumage.—Adult male (n = 21): Above Deep to Dark Mouse Gray, below from between Light Mouse Gray and Mouse Gray to Deep Mouse Gray, belly palest. Birds from prov. Morona-Santiago average lightest. Flanks, under-tail coverts, and sometimes vent Ochraceous-Tawny to Cinnamon-Brown, relatively narrowly and densely barred blackish. One very dark with faint bars on flanks. Crown feathers minutely tipped with Light Mouse Gray and with a darker subterminal band, and in certain lights all show a silvery sheen on the crown, contrasting with the darker loral and ocular region. Axillars gray like rest of underwing. Birds from prov. Zamora-Chinchipe have faint brown and dark bars on tips of tertials. *Adult female* (n = 5): Four are Mouse Gray on crown; between Dresden Brown and Sepia on nape, mantle and back; feathers with minute Dark Mouse Gray tips except on back. Rump between Dresden Brown and Sudan Brown, faintly barred dusky; tail Cinnamon-Brown with faint barring at edges and tip. Wings Brussels Brown, inner five remiges with Sudan Brown subterminal band bordered with blackish. Below Mouse Gray, in one grading to Light Mouse Gray on the apical 2–3 mm. Central lower belly Pinkish Buff. Flanks and under-tail coverts like rump or slightly brighter. One much darker and more uniform, like ad. male except for a faint wash of dark brown above. *Immature/subadult male* (n = 5): One has crown Deep Mouse Gray; nape, mantle, and wash on central crown between Brussels Brown and Raw Umber, feathers of these parts indistinctly tipped dusky. Back, wing-coverts, and edges of remiges Brussels Brown; wing-coverts and back-feathers with subbasal and subterminal black bar; tertials with subbasal, presubterminal, and narrow, terminal, black bar, and like the inner remiges with narrow Snuff Brown subterminal bar, that is lighter, forming a spot near the shaft on the outer web. Rump like mantle, feathers with narrow subbasal and subterminal black bar. Tail above with regular, 2 mm wide between Brussels Brown and Sudan Brown, and 1 mm wide blackish bars. Sides of head and neck like crown, grading into Mouse Gray of throat and breast. Most of belly Warm Buff to light Buff, almost uniform. Feathers of extreme lower belly with subterminal blackish bar. Sides, flanks, and under-tail coverts between Ochraceous Tawny and Tawny Olive, regularly barred blackish like the upperside of the tail. Underwing dull Light Mouse Gray, greater coverts and axillars with spot-like silvery-white streak along shaft. Underside of tail blackish. Another much like it, but brown colors more olive, belly-feathers broadly tipped whitish rather than Light Buff. One molting into adult plumage still brown on nape, upper mantle, some feathers on central back, some wing-coverts, and edges of the remiges. Tertials and edge of rectrices vermiculated brown and black, rump and upper-tail coverts barred brown and blackish. Two like adults, but one with faint wash of brown on back, wing-coverts, tips of inner remiges, and on tail, one with light brown dots on tips of greater wing-coverts, and with brown vermiculations on tail and tips of inner remiges. *Immature/subadult female* (n = 2): Entire upperparts between Dresden Brown and Sepia, greater wing-coverts and tertials blackish subapically and with Ochraceous Buff tips. Lower rump and upper-tail coverts barred, edge of rectrices barred or vermiculated, with blackish. Side of head, throat, and breast Mouse Gray washed with brown, entire belly uniform Ochraceous Buff. Lower sides, flanks, and under-tail coverts Cinnamon to Cinnamon Buff and barred blackish. They thus mainly differ from subadult male by their uniform bright ocher bellies. *Juvenal male* (n = 2): One with upperparts including wing-coverts and tail Cinnamon Brown barred blackish, dark bars inconspicuous on crown and sides of head. Edges of remiges Cinnamon Brown, tertials and wing-coverts more evenly barred than in most congeners. Below Tawny Olive, palest on belly, throat and most of breast uniform. Blackish subterminal markings appear as spots on lower breast and widen to become regular bars on lower underparts. Axillars Tawny Olive. One much

like it, but darker brown above, more uniform below, spots confined to sides of breast, and bars to sides, flanks and under-tail coverts; belly whitish. *Juvenal female* (n = 3): One with upperparts much like the first-mentioned juvenal male, but brown brighter, near Sudan Brown. Underparts also similar, but brighter, near Yellow Ocher, and regular barring confined to sides, flanks, and under-tail coverts. Spots on lower breast continue onto the almost uniform central belly as scattered streaks and spots. One similar above, but unmarked below except for dark bars on flanks and under-tail coverts, and feathers of cheeks, lower throat and breast with extensive, ill-defined, Mouse Gray bases and minute tips, this area from most angles appearing as a gray that grades into the Yellow Ocher chin and belly. One somewhat brighter brown above, and with more conspicuous bars on crown, cheeks, nape, and back. Underparts Yellow Ocher with dark bars, nearly spot-like on throat and breast. All with axillars between Yellow Ocher and Tawny Olive.

Annual cycle in Ecuador (n = 8).—*Juveniles:* 16, 20 March (se prov. Carchi); 6, 11, 22 May (prov. Napo); 8 November (prov. Zamora-Chinchipe). *Brood patch:* 9, 14 November (females) (provs. Loja and Morona-Santiago).

Vocalizations in Ecuador.—Song by male (Fig. 11; also Fjeldså and Krabbe [1990:442, sonagram 2]) is a fast, long trill of ca. 34 notes/s, the loudest, first overtone at 3.8 kHz. The beginning of the song is a distinctive "stuttering," usually of 1–3, rarely up to 5, somewhat lower-pitched, slower notes. Simultaneously with the male song the female may break into a usually high-pitched, descending (5.7–4.2 kHz) series of 15–20 notes, 5–8/s (Fig. 28). Call in most of range consists of 5–9 "*kee*" notes, 4.0 kHz in male (Fig. 29), 4.5 kHz in female, lasts ca. 1 s, and is repeated at 2–6 s intervals. In southernmost Ecuador (Cordillera Las Lagunillas) and immediately adjacent Peru (Cerro Chinguela, depto. Piura) the call by both sexes is very different (Fig. 30), and resembles a short burst of male song. It should be noted that calls are given rather frequently, i.e., the noted differences are between homologous calls.

Habitat in Ecuador.—0.2–2.0 m tall, dense, humid to fairly dry shrubbery at treeline, notably *Escallonia myrtilloides* and ericaceous scrub. Locally the upper parts of taller humid forest, mainly in *Chusquea* bamboo. The replacement below by *S. unicolor latrans* and *S. unicolor subcinereus* is everywhere very sharp. There are small zones of overlap with *S. spillmanni* and *S. parkeri* in humid forest, but those species never enter *Escallonia* and ericaceous scrub, even where *S. canus opacus* is absent.

Distribution in Ecuador.—3,050–3,980 m at treeline, lowest in the south. On Páramo El Angel, depto. Carchi, in the northwest, and along the entire Eastern Andes, where the rivers Pastaza, Paute, and Zamora, and the low ridge between Yangana (prov. Loja) and Valladolid (prov. Zamora-Chinchipe) divide it into four populations. Birds of the southernmost population may be subspecifically distinct on basis of their distinctive call-note, and the presence of a white wing spot in most males. Reports from the eastern edge of the Cajas plateau in western prov. Azuay (King 1989) are in error, caused by confusion with the female of *S. unicolor subcinereus*, the only tapaculo inhabiting the plateau and its temperate slopes.

Distribution beyond Ecuador of Zimmer's Scytalopus magellanicus.—In Colombia *S. canus opacus* occurs in depto. Nariño at Puerres (Denumbo), 2,820 (?) m (ANSP), and on the Colombian side of the border at Aguas Hediondas, Páramo El Angel ([tape-recordings by N.K.]). Tape-recordings by F. Lambert and B. M. Whitney from the southern end of Central Andes in depto. Cauca (Volcán Puracé, 3,300–3,400 m) prove indistinguishable from Ecuadorian birds. In Peru *S. canus opacus* is found in northernmost depto. Cajamarca on the border to depto. Piura (Cerro Chinguela, 2,600–3,500 m [Parker et al. 1985; specimen from 3,100 m in LSUMZ; tape-recording by T. Parker in LNS]).

The Colombian form *S. canus canus* (Chapman 1915; type in AMNH; type depicted in Fjeldså and Krabbe [1990, pl. XLI 1a]) occurs in the northern end of Western Andes in depto. Antioquia (Paramillo [type-locality], 3810 m [AMNH, BMNH]; Páramo Frontino [Hilty and Brown 1986]). Birds from Central Andes in depto. Caldas (La Leonera east of Manizales, 3,600 m) were included in this taxon by Peters (1951), but there are no tape-recordings from either region.

Scytalopus griseicollis griseicollis (Lafresnaye 1840; type presumably in Paris Museum, once on loan to MCZ; depicted in Fjeldså and Krabbe [1990, pl. XLI 1c]) is found at 2,600–3,900 m in low, often fairly dry scrub ("mattoral") in, around, and east of Bogotá, depto. Cundinamarca and in depto. Boyacá, in the Eastern Andes, Colombia (ICN, AMNH, ANSP, BMNH). Although its bright, unbarred flanks are matched by south Peruvian *urubambae*, its whitish abdomen differs from any adults of the forms to the west or south of it. Its vocalizations differ distinctly from those of *S. canus opacus* (F. G. Stiles, pers. comm.), and consequently we regard *opacus* and *griseicollis* as separate species.

Scytalopus griseicollis fuscicauda (Hellmayr 1922; type in CM; depicted in Fjeldså and Krab-

be [1990, pl. LXIV 31]) occurs at 2,500–3,200 m in south edo. Lara and edo. Trujillo, Venezuela (CM). It resembles *griseicollis* so much that, at least until its voice is known, we treat it as a subspecies of that form.

Scytalopus affinis (Zimmer 1939; type in ANSP; an unusually dark specimen depicted in Fjeldså and Krabbe [1990, pl. XLI 1e, sonagram 1 p. 442]) occurs in the northern Andes of Peru in depto. Cajamarca (Colmena, 2,835 m: LSUMZ; Chota [LSUMZ]) and depto. Ancash (Cordillera Blanca, 3,050–4,100 m [ANSP, LSUMZ, MHN, ZMUC]). It is very pale and lacks a silvery supercilium. It has a rather peculiar call (Fig. 31), and a distinctive song (Fig. 32) with a rapid delivery of three bursts per second, and an equally loud fundamental and first overtone.

Scytalopus altirostris (Zimmer 1939; type in ANSP; imm. female depicted in Fjeldså and Krabbe [1990, pl. XLI 1f, sonagram 2 p. 441]) occurs in deptos. San Martín (Puerto del Monte, 3250 m [MHN]), Amazonas (Atuén [type-locality; ANSP]), La Libertad (Patas [ANSP]), and Huánuco (Bosque Unchog, 3450 m [LSUMZ and tape-recordings by N.K.]), Peru. We only have a single recording of its presumed song (Fig. 33). This song is distinctive, given with the same rapid delivery as the song of *S. affinis*, but rougher, with a broader frequency amplitude, and with a different relative volume of the fundamental and the first overtone.

In depto. Pasco, central Peru (Chipa [AMNH]; near Millpo, 3,450–3,650 m [LSUMZ, MHN]) a rather brownish, yet unnamed form is found (see above). Its song (Fig. 34) is distinctive. Bouts are given at ca. 2 per second, and are composed of a high-pitched, rough, fundamental with a wide frequency amplitude, and an equally loud first overtone.

In Apurímac, south-central Peru (Nevado Ampay, 3,000–4,000 m [ZMUC and tape-recordings by N.K.]; Cerro Queñua Khasa, 4,000–4,600 m [ZMUC]) another, yet unnamed form is found (depicted in Fjeldså and Krabbe [1990, pl. XLI 1h, sonagram p. 440]). It has a distinctive song (Fig. 35), consisting of a single note given twice per second. The fundamental is low-pitched, the first overtone loudest, and both second and third overtone clearly audible. A rarely given vocalization, only documented by a poor recording (Fig. 36), shows some resemblance to the song of *urubambae*.

In the southern Cordillera Vilcabamba, depto. Cuzco, Peru, the enigmatic *Scytalopus urubambae* (Zimmer 1939; type in AMNH) is found at treeline at 3,660–4,170 m. Superficially it resembles *S. griseicollis* of Colombia and differs from adjacent forms by lacking a supercilium and by having no bars on its fairly orange flanks. Hence we doubted its correct systematic position as well as the labelling of the types. However, in 1990 and 1991 G. Engblom (in litt.) obtained photographs, several tape-recordings, and a juvenile specimen near the type locality. The photographs are unmistakably of birds resembling the type of *urubambae*. Its song (Fig. 37) is distinctive. Bouts are given twice per second, and are of a fairly narrow frequency amplitude, in roughness finer than *S. altirostris*, slightly rougher than *S. affinis*, much like *S. superciliaris*. The first overtone is loudest, the second overtone and the fundamental audible.

We refer all (usually white-browed) birds with similar voices (Figs. 38 and 39) at and above treeline from Vilcanota mountains, depto. Cuzco, south through depto. Puno, Peru, and to deptos. La Paz and Cochabamba, Bolivia (specimens in AMNH, ANSP, BMNH, LSUMZ, NRS, ZMUC; tape-recordings by N.K.), to a single form, *S. simonsi* (Chubb 1917; type in BMNH; depicted in Fjeldså and Krabbe [1990, pl. XLI 1i, sonagram p. 439]). Bouts of song are given once to twice per second. Each bout has two components, a single note followed by a short "*churr*", which is about as rough as the "*churr*" of *S. altirostris*.

In deptos Chuquisaca and Tarija, Bolivia, *Scytalopus zimmeri* (Bond and Meyer de Schauensee 1942; type in ANSP; depicted in Fjeldså and Krabbe [1990, pl. XLI 1j]) is found. Its plumage is intermediate between *S. simonsi* and *S. superciliaris* but closest to the latter. Adult males may have yellow feet, which we have not seen in *simonsi*, but which is suggested in dry museum skins of *superciliaris*. The 3-syllabled song of *zimmeri* is distinctive (Fig. 42, clearer recordings by N.K. were obtained too late for inclusion in this paper). Records are from 25 km E Padilla, 2,500 m (ANSP); and Monte Chapeados, 2,500–3,000 m (CBF, ZMUC; tape-recordings by J. Fjeldså and N.K.), both depto. Chuquisaca, and from numerous sites in depto. Tarija (Fjeldså and Mayer 1996).

A few apparent hybrids or intergrades between *simonsi* and *zimmeri* have been reported (Whitney 1994). Although suggestive, these hybrids have not been corroborated by genetic data. One of the putatuve hybrids (ZMUC 80031) gave a typical *simonsi* song, and was collected along steep stream banks in open grassland at 3,600 m. Records of *zimmeri* with the 3-syllabled song are from *Alnus* and *Podocarpus* forest below 3,000 m on the easternmost slopes of the Andes in deptos. Chuquisaca and Tarija. We are not sure at present where *zimmeri* would come into

contact with *simonsi*. The two may be separated by the dry valley of the Río Grande and the extensive dry regions in western and central depto. Chuquisaca.

Scytalopus superciliaris (Cabanis 1883; type in Berlin Museum; depicted in Fjeldså and Krabbe [1990, pl. XLI 1k]) (Fig. 41, see also sonagram by Whitney [1994, Fig. 4 C]) is found at 1,500–3,350 m in northwest Argentina in provs. Jujuy, Salta, Tucumán, and Catamarca (specimens in AMNH, Berlin Museum, FML, FMNH, NRS; tape-recordings by R. S. Ridgely and N. Gardner).

The recently described *Scytalopus superciliaris santabarbarae* (Nores 1986; type in FML) from Santa Barbara in prov. Jujuy, Argentina, is similar to, but slightly darker than *S. superciliaris* (specimen in AMNH examined). We do not know of any recordings of its song.

Apparently there is a large distributional gap from prov. Tucumán to prov. Mendoza in north-central Argentina where no *Scytalopus* is found. Farther south nominate *S. magellanicus* (Linnaeus 1789, p. 979; type lost; depicted in Fjeldså and Krabbe [1990, pl. XLI1, sonagram p. 437]) occurs from prov. Río Negro, Argentina, and prov. Valdivia, Chile, south to Cape Horn (AMNH, ANSP, Buenos Aires Museum, BMNH, FMNH, LACM, NRS, WFVZ; tape-recordings by B. M. Whitney). It lacks the brown back and white throat and supercilium of *S. superciliaris*, and has a silvery fore-crown in adult males. Its song (Fig. 42) is distinctive, with bouts consisting of two different single notes given about twice per second.

In central Chile *Scytalopus fuscus* is found (Gould 1837; type lost; depicted in Fjeldså and Krabbe [1990, pl. XLI 1m, sonagram p. 438]). It occurs from sea level to 2,900 m from prov. Coquimbo to the Río Bío Bío (AMNH, Berlin Museum, BMNH, FMNH, LACM, NRS, MCZ, Paris Museum; tape-recordings by B. M. Whitney). Two birds from prov. Mendoza, Argentina (Berlin Museum, BMNH), one taken as high as 3,500 m, might also belong to this taxon. Morphologically *fuscus* differs from *magellanicus* by its larger size, and its uniform black plumage is matched by only some individuals of *magellanicus* (Riveros and Villegas 1994). Its song (Fig. 43) is also very different from that of *magellanicus*. The two occur sympatrically from Valdivia to Río Bío Bío (Johnson 1969; Ridgely and Tudor 1994).

The possible presence of a third taxon (in part "*albifrons*" of Landbeck 1857) resembling *S. fuscus* in large size and blackish coloration, but with a white forecrown in both sexes (specimens from Colchagua in Berlin Museum and BMNH) may have caused some of the earlier confusion in the identification of central Chilean specimens.

As mentioned above, we use the name *Scytalopus acutirostris* (Tschudi 1844; type in MHNN) for the dark-bodied taxon that occurs in central Peru in forest below the treeline taxa. This name has been used by most authors (Hellmayr 1924; Zimmer 1939; Peters 1951; Whitney 1994) for populations of the former polytypic "*magellanicus*" from central Peru, or from there south to western Bolivia.

The type of *acutirostris* was collected by Tschudi at an unspecified locality in central Peru; Hellmayr (1924) restricted the type locality to Maraynioc, depto. Junín, in central Peru, which is where Tschudi made his collection (Tschudi 1844). The type is unsexed, and the tail is missing. Recent field work by T. J. Davis, G. H. Rosenberg, K. V. Rosenberg, G. Engblom, and ourselves has shown that, except for *urubambae*, birds found above treeline in the range ascribed to *acutirostris* by Hellmayr (1924) and Zimmer (1939) are: very small; more or less silvery-/or white-browed in adult males; the rump and flanks are densely barred, the bars forming more or less straight lines; and with a dark mask when viewed at certain angles. Such birds do not agree well with the type of *acutirostris*. The type is washed with brown above, and so is presumably a female or an immature/subadult. The following description is by N.K., based upon his examination of this specimen in 1987. The description of the type by Berlepsch and Hellmayr (1905) is consistent with N.K.'s, but is less detailed: Crown and mantle Dark Mouse Gray with a single white feather over the right eye. Rump Argus Brown very faintly dark-barred. Wings dark with faint wash of Argus Brown, most conspicuous on primaries and tertials, which have a slightly lighter (between Argus and Amber Brown), inconspicuous, subterminal bar. Lores Light to Pale Mouse Gray tipped Dark Mouse Gray. Sides of head and entire throat and breast Mouse Gray, central belly similar, but feathers with 2 mm or longer, relatively well-defined Pale Mouse Gray tips. Flanks Amber Brown with curved, dark bars. Lower central belly to vent Sudan Brown to Ochraceous Tawny with irregular, dark, curved bars. Wing (both) 56 mm, tarsus 21.6 mm, the middle toe with claw 21.5 mm.

The lack of distinct barring on the rump of such a brown individual, the lack of a dark mask, the rather acute bill shape, and the curved bars on the flanks convinces N.K. that the type of *acutirostris* does not represent any of the central Peruvian taxa found above treeline.

So what population, then, does the type of *acutirostris* represent? In the 1980s we indepen-

dently discovered that two vocally distinct species replace each other elevationally in humid forest of the upper subtropical and temperate zone of Central Peru. One occurs at 1,850–2,500 m, sings much like *S. parvirostris* from Bolivia (as described above), and often has silvery tips to the belly-feathers. Another is found at 2,675–3,500 m from eastern depto. La Libertad (tape-recordings by T. A. Parker, LNS 17224 and LNS 17254) south to deptos. Huánuco (ZMUC, LSUMZ), Pasco (LSUMZ), and apparently Junín (MHNN, Warsaw Museum). This species differs from *S. parvirostris* in that the adult males are darker and more uniform with no pale sheen on the belly, and the vocalizations (Figs. 44, 45 and 46) differ greatly from sympatric forms of *S. parvirostris*, *S. altirostris* and the unnamed, superciliaried form at and above treeline in depto. Pasco. This taxon was referred to as "*Scytalopus* unnamed species" by Fjeldså and Krabbe (1990:427–428). Provisionally we use the name *acutirostris* for this second taxon, because its morphology is consistent with the type of *acutirostris*, and because this taxon otherwise has no name. At the present time we can not rule out the possibility that the name *acutirostris* refers to the populations from central Peru that we are calling *parvirostris*; there is an additional complication, as noted above, that these populations are distinct from typical *parvirostris* from Bolivia, in which case the determination of the identity of this type will become even more important. Or, perhaps, if the type of *acutirostris* can not be identified with certainty, it may become necessary to declare it a *nomen dubium*, and designate a fresh type specimen for this taxon or to rename the population to which we have applied this name.

Scytalopus panamensis, *sensu* Zimmer 1939

Zimmer (1939) described a new taxon, *vicinior*, as a subspecies of *Scytalopus panamensis*. In the 1980s we discovered that *vicinior* encompassed two sympatric species that replace each other elevationally. They differ in vocalizations, and recognizably in morphometrics. Tape-recordings from the type-locality of *vicinior* (D. Willis and F. Lambert) and the information that only one species of *Scytalopus* occurs there showed that the high-elevation species represents *vicinior*. The low-elevation species thus lacks a name. The call of the low-elevational species (Fig. 56) shows some resemblance to that of *S. panamensis* (Fig. 53) as noted by Pearman (1993). We thus treat the two as allospecies. We see no particular similarity, either in plumage or in voice, between true *S. vicinior* and *S. panamensis*, and recommend that they are treated as genuinely independent species. We propose to describe the new low-elevation form as:

Scytalopus chocoensis sp. nov.
Chocó Tapaculo

Type: ANSP 180144; adult male from El Placer, ca. 670 m, prov. Esmeraldas, Ecuador, 00°52′N, 78°33′W; collected 14 August 1987 by T. S. Schulenberg, original field number 4577; copies of tape-recordings of this individual deposited at LNS, recording LNS 40016.

Paratype: ZMUC 80094; adult male from 18 km north-northwest of Alto Tambo, ca. 450 m, prov. Esmeraldas, Ecuador, ca. 00°58′N, 78°43′W; collected 18 February 1992 by N. Krabbe, blood sample N.K. 29-18.2.92. Copy of a tape-recording of this individual deposited at LNS, recording LNS 65993.

Paratype: MECN 6362; adult male from ca. 10 km west of Lita, ca. 900 m, prov. Esmeraldas, Ecuador, ca. 00°48′N, 78°28′W; collected 23 November 1991 by N. Krabbe, blood-sample no. 2-23.11.91.

Description of type.—Forehead, crown, sides of nape, and feathers around eye near Dark Mouse Gray; feathers narrowly tipped blackish, creating a slightly scaled appearance. Nape and center of upper back between Argus Brown and Brussels Brown, but very dark (in the rest of the descriptions of this species this color is referred to as very dark brown); feathers of these parts tipped blackish. Proximal scapulars and sides of back near Dark Mouse Gray, the (generally concealed) feather-centers very dark brown, tips narrowly blackish. Distal scapulars and lower back very dark brown, feathers narrowly tipped blackish. Lower rump brighter, near Amber Brown, feathers with one or two blackish subterminal bars. Upper-tail coverts very dark brown. Rectrices blackish-gray. Wing-coverts dull brownish-gray, amount of brown increasing medially such that innermost coverts are largely very dark brown, with narrow blackish tips. Primaries brownish-gray. Outermost secondaries brownish-gray with a narrow, very dark brown fringe on outer web, broadening into a narrow subterminal band at tip of feather. Amount of brown in secondaries increases medially, such that innermost secondaries are almost entirely brown, with a small subterminal Amber Brown spot at tip of outer web. Lores near Pale Mouse Gray with darker tips. Chin and throat near Light Mouse Gray, shading darker, near Mouse Gray, on breast and belly. Feathers of central lower belly with broad whitish gray tips, forming an irregular, pale

belly patch. Flanks and under-tail coverts Amber Brown, feathers with two or three narrow, blackish bars. Body mass 21.5 g, wing (chord) 53.5 mm, tail 39.8 mm, tarsus 21.3 mm. Iris brown, bill black, feet gray-brown.

Description of paratypes.—Both with 10 rectrices. Coloration of soft parts and plumage like the type, but center of upper back Dark Mouse Gray, nape with only a faint wash of very dark brown, and innermost secondaries without a small, pale spot at tip of outer web. ZMUC specimen: body mass 21.7 g, wing (flat) 55 mm, tail 36.2 mm, tarsus 21.4 mm. MECN specimen: body mass 21.0 g, wing 57 mm, tail 37.0 mm, tarsus 25 mm.

Etymology.—The name refers to the distribution of the taxon, which is restricted to the Chocó region, an important center of endemism, from Cerro Pirre, easternmost Panama, south through western Colombia to extreme north-western Ecuador.

Brief diagnosis.—Small, with 10 rectrices. Wings and tail shorter, underparts paler and more extensively gray, and flanks darker than in *S. vicinior*, which usually has 12 rectrices. Virtually indistinguishable from an allopatric population (p. 78), but *S. chocoensis* averages heavier, the gray of plumage is slightly more towards Neutral Gray and paler below, male has broader silvery feather-tips on the belly when fresh, female distinctly paler throat, brown of plumage is slightly darker, and feet in dried specimens are darker. Lacks the broad silvery supercilium of *S. panamensis*.

Plumage.—Adult male (n = 7): Includes the paratypes but not the type. Crown, nape and mantle Dark Mouse Gray, feathers narrowly tipped black, feathers of mantle basally Blackish Mouse Gray. Wings Blackish Mouse Gray with faint wash of a very dark brown on edge of remiges and on the entire outer half or third of each of the three tertials, that in three specimens have a subterminal pale dot or bar on the outer web. Back, most of rump, and upper-tail coverts the same very dark brown, grading to Amber Brown on lower rump, feathers narrowly tipped, those of rump barred, with blackish. Tail blackish. Side of head like crown, grading to Mouse Gray on throat, breast and belly. Four specimens have the gray feathers below tipped with Pale Mouse Gray, minutely on the throat and breast, 2 mm wide on the belly. Three others have Light Mouse Gray feather-tips on the belly. Extreme lower belly Ochraceous Tawny barred black. Lower sides, flanks and under-tail coverts Amber Brown with black bars, barring scaly on lower sides and upper flanks. Axillars Ochraceous Tawny. *Adult female* (n = 3): Much like male, but brown above extended to nape, mantle and wing-coverts, and more extensive on the remiges. Wing-coverts sometimes with black presubterminal and terminal bar. The tertials may have a small, light spot near tip of outer web, Amber Brown, and encircled with black. Edge of tail with slight, dark brown wash. Below also like male, but throat distinctly paler (Pale Mouse Gray), breast also paler, and entire lower belly Ochraceous Tawny, barred black. All brown colors in plumage slightly brighter than in male. *Subadult/immature male* (n = 1): Indistinguishable from adult males with pale feathertips on the belly, but with a bursa. *Juvenal male* (n = 1): Above more or less uniform, drab brown, feathers narrowly tipped blackish. Rump and upper-tail coverts as in adult. Rectrices and remiges as in adult, although the primary coverts differ by being broadly edged with dark brown on the outer web and tip of inner web. This brown edging on the outer, middle primary-coverts is paler, brighter brown (near Yellow Ocher) than the brown of the other feathers. Feathers of chin and throat basally light gray, those of breast and belly blackish, all with a paler subterminal band and a narrow, blackish tip, the entire underparts thus appearing barred. The pale, subterminal band is very pale, drab brown on the throat but shades to a deeper brown caudally (to near Tawny Olive). Flanks and under-tail coverts as in adult.

Annual cycle in Ecuador (n = 1).—*Juvenile:* 3 August (prov. Esmeraldas). *Active ovary:* 16 February (prov. Esmeraldas).

Vocalizations in Ecuador.—Song by male (Fig. 54) a 5–60 s or longer (longest at high excitement) series of 0.09–0.11 s long notes delivered at 2.6–3.6/s, first overtone loudest, 3 kHz, beginning of each note rising. Frequently, a song begins with two or more slightly faster and lower-pitched notes, and the last note may be given after a short pause. There is some variation in the shape of the notes between different individuals (Fig. 55). Call (Fig. 56) by both sexes a rapid series of 3–8 short, sharp notes, lasting 0.4–1.0 s, and repeated every 3–4 s, first overtone loudest, 2.5 kHz. As pointed out by Pearman (1993), there is some similarity between this call and one given by *S. panamensis* (compare Figs. 53 and 56). Also given, at least by the female *S. chocoensis*, is a sharp, explosive, buzzy "*brzk*" (Fig. 57), with equally loud fundamental and first overtone. The vocalizations of *S. chocoensis* were described by Robbins et al. (1985) under *S. vicinior* and by Hilty and Brown (1986) under *S. femoralis*.

Habitat in Ecuador.—Dense undergrowth of wet, mainly primary forest.

Distribution in Ecuador.—Pacific lowlands north of Río Guayllabamba in prov. Esmeraldas

and immediately adjacent prov. Imbabura. Known from along the Ibarra-San Lorenzo railroad and the nearby parallel road, between 350 and 950 m. A specimen from prov. Imbabura (Paramba, 1065 m [AMNH]) is probably also referable to this taxon. The species is replaced at higher elevations by *S. vicinior*, but the extent of overlap or existence of a gap between them still needs to be determined.

Distribution beyond Ecuador.—Cerro Pirre, Panama, where known at 1,340–1,465 m (ANSP; also tape-recordings by T. A. Parker in LNS), south along the Pacific slope of Colombia, where it occurs at elevations between 250 and 1,250 m in deptos. Antioquia (Alto Bonito, 450 m [AMNH]), Valle de Cauca (Río Anchicayá, 700–1,050 m [AMNH]; also tape-recordings by S. Hilty), and Nariño (La Guayacana, 250 m [FMNH, LACM]; below El Diviso, 600 m [tape-recordings by P. Coopmans]; Ricaurte, 1,200 m, [LACM]; Río Nambi, 1,250 m [heard by P. Coopmans]).

NARIÑO TAPACULO *Scytalopus vicinior*
(Zimmer 1939; type in AMNH)

Brief diagnosis.—Medium-sized and long-tailed. Lower belly in both sexes more extensively brown and with feathers more distinctly dark-tipped than in *S. spillmanni*. Individual specimens of the two rarely identifiable with certainty. Longer-tailed than *S. chocoensis*, and usually with 12 instead of 10 rectrices, and without the pale throat of female *S. chocoensis*.

Plumage.—Adult male (n = 12): Crown Deep Mouse Gray, feathers narrowly tipped blackish. Nape, (mantle), back, upper-tail coverts, wing-coverts and edges of remiges very dark Brussels Brown, feathers of nape, mantle, and back tipped blackish. Seven specimens have some or most of feathers of mantle Dark Mouse Gray, either uniform, with narrow, blackish feather-tips, or with subterminal brown area and blackish tips. Central rump Cinnamon Brown faintly barred dusky, tail blackish. Breast Hair Brown to Deep Mouse Gray, throat only slightly paler except for one bird, which has Light Mouse Gray throat grading to a Mouse Gray breast. Upper or most of belly Light Mouse Gray, feathers very narrowly tipped dusky. Lower belly from between Ochraceous Orange and Cinnamon to between Mars Yellow and Sudan Brown, feathers very narrowly, but invariably tipped dusky. Flanks and under-tail coverts Amber Brown, distinctly barred blackish. Axillars Cinnamon Brown. *Adult female* (n = 2): One has crown Deep to Blackish Mouse Gray, feathers tipped blackish. Nape, mantle, back, most of rump, and wings Blackish Mouse Gray very faintly washed with blackish Brussels Brown on edge of remiges, on wing-coverts and broadly subterminally on feathers of nape, mantle, back, and rump; lower rump barred blackish and Brussels Brown, brightest on lowermost rump. Upper-tail coverts and tail blackish. Chin and throat Mouse Gray grading to Deep Mouse Gray on breast, upper sides and upper belly. Feathers of upper and mid belly with 2–3 mm wide Light Mouse Gray terminal or subterminal area, those of mid belly with very narrow, blackish tips. Lower belly between Ochraceous Tawny and Ochraceous Orange, feathers very narrowly tipped blackish. Lower sides and flanks Antique Brown with scaly, black barring; lower flanks brighter, Ochraceous Orange with straighter black bars. Axillars Cinnamon Brown. Another is like it, but with slightly paler throat, heavy Ochraceous-Buff wash on central belly, and with indistinct and smaller dusky markings on rump and flanks, forming mottles rather than bars. *Immature/subadult male* (n = 1): Molting from juvenal plumage (only fresh feathers described). Crown Deep Mouse Gray, feathers tipped blackish. Nape, mantle, back, most of rump, and wings Blackish Mouse Gray washed with blackish Brussels Brown on edge of remiges and on wing-coverts. Inner wing-coverts also with this wash subbasally, and broadly subterminally on feathers of nape, mantle, back, and upper rump, feathers of lower rump barred blackish and Brussels Brown. Upper-tail coverts and tail blackish. Chin and throat Light Mouse Gray to Mouse Gray, grading to Deep Mouse Gray on breast, upper sides, and upper belly. Feathers of breast and upper belly with pale shafts basally until 2–3 mm from tips. Feathers of upper and mid belly with 2–3 mm wide Light Mouse Gray terminal or subterminal area. Narrow tips blackish on mid belly and on the Ochraceous Tawny lower belly. Lower sides and flanks as in the first described adult female. Axillars Tawny Olive. *Immature/subadult female* (n = 1): Only the type. Type-description by Zimmer (1939): "Upper parts very dark reddish brown with the uropygium brighter (light Auburn) and banded with blackish; forehead and superciliary region slightly tinged with grayish; lores, auriculars, chin, throat and breast light Neutral Gray in strong contrast to the dark brown lower parts; flanks, femoral areas and under-tail coverts deep Argus Brown barred with blackish; middle of belly paler, near Pinkish Cinnamon. Tail and wings like the back, with a slight, pale spot and dusky bar at the tip of the shortest tertial." *Juvenal male* (n = 1): In molt (only juvenal

feathers described). Feathers of sides of throat, throat, breast and belly with a 1.0–1.5 mm wide Tawny Olive subterminal bar and subbasal area around the shaft, with blackish narrow tip and 1.5–2.0 mm wide presubterminal area, and with gray extreme base.

Three juveniles from southwestern Colombia at Ricaurte, depto. Nariño, 1,200 m (LACM 30865), Ricaurte, depto. Nariño, 2,500 m (LACM 37071), and Cerro Munchique, depto. Cauca, 2,500 m (FMNH 249752) are worth mentioning. They are quite alike, but on distributional grounds the latter two probably belong with *S. spillmanni*, whereas the first may represent the lowest known elevation for *S. vicinior*. They differ from a juvenal *S. chocoensis* in the following features: barring of ventral surface broader on throat; brown subterminal bars of underparts brighter, closer to Yellow Ocher, deepening only slightly or not at all from throat to belly; bases of feathers of forehead brown, not gray as in *S. chocoensis*; barred pattern of underparts extends farther onto sides of throat; a superciliary is present, feathers with the same barred pattern as the underparts.

Annual cycle in Ecuador (*n* = 2).—*Juvenile:* 6 November (prov. Pichincha; advanced molt). *Active ovary:* 15 November (prov. Pichincha).

Vocalizations in Ecuador.—Song by male (Fig. 47) a 2.5–20 s long (longest at high excitement), decelerating series of notes given at 13–7/s, and increasing in amplitude (also Fjeldså and Krabbe [1990:432, sonagram 1]). The first few notes are a bit slower and sometimes higher-pitched than the following. Loudest first overtone 3.2 kHz in the first few notes, 2.8 kHz in the following ones. Call by male (Fig. 48) a 3.5 kHz descending "*ki*" given every 6–7 s. Alarms by female and apparently also male include a higher-pitched "*ke ki ki*" (Fig. 49), "*kekikiki*" (Fig. 50), and "*kekikikikikike*" (Fig. 51); the first note is slightly higher-/or lower-pitched than the following, which is at 2.8 kHz (3.6 kHz through most of the corresponding call of *S. spillmanni*). Also given by female *S. vicinior* is a 5 s-long series of roughly 10 notes at 3.3 kHz, and a 10 to 15 s-long, descending series of roughly 9 high-pitched, explosive notes (Fig. 52).

Habitat in Ecuador.—Humid forest undergrowth. Sometimes in ferns and broader-leaved, more primary vegetation than *S. spillmanni*.

Distribution in Ecuador.—1,250–2,000 m, locally (prov. Carchi) to 2,350 m. Range abuts that of *S. spillmanni* above, contact with *S. chocoensis* not yet demonstrated. Pacific slope from the Colombian border south at least to southernmost prov. Cotopaxi. A specimen from prov. Chimborazo (Chaguarpata, 1,740 m [Warsaw Museum]) may belong here. P. Coopmans (pers. comm.) was the first to point out the presence of *S. vicinior* in Ecuador, in 1990.

Distribution beyond Ecuador.—1,400–1,950 m, probably both higher and lower, on the Pacific slope of Colombia, where known from depto. Risaralda (Alto de Pisonas, 1,750 m [ICN, specimens and tape-recordings collected by F. G. Stiles]), depto. Valle del Cauca (Las Lomitas, 1,400 and 1,525 m [AMNH, no vocal material]; Parque Nacional Farallones, 1950 m [tape-recording by B. Whitney]) and depto. Nariño (Mayasquer, 1,465 m [ANSP, no vocal material]; Ricaurte, 1500–1,800 m, type-locality, also tape-recordings by F. Lambert, D. Willis and F. G. Stiles). Some subspecific differentiation may have occurred in Colombia, because the two Risaralda specimens are exceptionally dark and heavy (male 24.5 g, female 26.7 g).

Ecuadorian Tapaculo new species

During field work by ANSP in south-west Ecuador a tapaculo was collected that was thought to represent a southern population of the morphologically similar *Scytalopus chocoensis*. However, N.K. found the southern population to differ in all vocalizations, and it is also genetically distinct (Arctander and Fjeldså 1994, T.S.S. unpub.). We therefore treat it as an independent species, which we propose to name:

Scytalopus robbinsi sp. nov.

Holotype: ZMUC 80102; adult male from 9.5 km west of Piñas, 870 m, prov. El Oro, Ecuador, at 03°40′S, 79°44′W, collected 25 September 1990 by N. Krabbe; blood sample N.K.2–25.9.90. Copy of a tape-recording of this individual deposited at LNS, recording LNS 65994.

Description of type.—10 rectrices. Above Dark Mouse Gray, feathers faintly tipped blackish, notably on crown. Rump, upper-tail coverts and faint wash on nape, lower back, and inner remiges Prout's Brown. Tail blackish. Underparts between Mouse Gray and Deep Mouse Gray, belly with ill-defined, 2 mm wide silvery gray feather-tips. Lower sides, flanks, extreme lower belly, and under-tail coverts Cinnamon Brown barred blackish. Axillars Tawny Olive. Body mass 18.4 g. Wing (flat) 55 mm, tail 36 mm, tarsus 21.5 mm. Iris dark brown, bill blackish, feet gray-brown.

Etymology.—We take the pleasure of naming this bird after Mark B. Robbins, who was the first to tape-record and collect it (recordings in LNS; specimen in ANSP); his tape-recordings greatly facilitated the collecting of further specimens and sound material. We also take the opportunity to acknowledge his substantial contribution to Neotropical ornithology.

Brief diagnosis.—Small. Told from dark females of *S. unicolor subcinereus* by having distinctly barred flanks. For differences from the allopatric *S. chocoensis* see under that species.

Plumage.—Adult male (n = 7): Includes the type. Above Dark Mouse Gray, feathers tipped blackish. Nape, lower back, upper-tail coverts, sometimes rump, and usually inner remiges Prout's Brown, rump otherwise like flanks. Tail blackish. Below between Mouse Gray and Deep Mouse Gray, belly sometimes with broad and indistinct silvery gray feather-tips. Lower sides, flanks, extreme lower belly, and undertail coverts Cinnamon Brown barred blackish. Axillars Tawny Olive, usually with faint, dusky barring. *Adult female* (n = 3): Like male, but brown of nape reaching onto upper mantle; wing-coverts brown with black subterminal dot or bar, tertials with pale, Warm Buff spot at tip of outer web. Entire lower belly Cinnamon Brown barred blackish in two, only extreme lower belly in one. Most of belly in the latter specimen with distinctive whitish feather-tips. *Juvenal:* Unknown.

Annual cycle in Ecuador.—High song activity was noted 25–26 September 1990 and 1 February 1991, only females vocalized 15 November 1991, low or no song activity 9 December 1991, 14–16 April 1991 and 17–19 April 1993.

Vocalizations.—Song by male (Fig. 58) and possibly also female somewhat reminiscent of that of *S. chocoensis*, but considerably faster, 4.4 to 5.3 notes/s, and each note with two distinct components, the latter part lower-pitched than the first, the first overtone loudest, at first 2.7–3.0 kHz, then 2.6–2.8 kHz. The beginning of each note is descending (rising in *S. chocoensis*). Call of female (Fig. 59) an 0.11 s-long single note rising at both beginning and end, centered at 1.4 kHz. The loudest is variably the fundamental, first or second overtone, third overtone sometimes as loud as some of the others. Other female calls include an often slowly descending, 15 to 20 s-long series of some 10 to 20 high-pitched notes, that after the first, somewhat faster 10 notes are given at 1/s (Fig. 60), each note about 0.77 s-long and descending; only the first and the louder second overtones at 3.8–2.4 and 5.7–3.6 kHz are audible.

Habitat.—Undergrowth of wet forest.

Distribution.—Ecuador, where known at 700–1,250 m. Restricted to the Pacific slope in provs. Azuay and El Oro. In prov. Azuay it is replaced at higher elevations by *S. unicolor subcinereus* with little or no overlap.

Discussion.—This species appears to be a southern isolate of *Scytalopus chocoensis*, on the basis of its similar morphology, and geographical and elevational distribution. Our decision not to place them in the same species is based in part on the contrast between the uniformity of the voice of *S. chocoensis* from Panama south to northern Ecuador, and the different vocalizations of *S. robbinsi*. Furthermore T.S.S. (unpubl. data) found several apparently fixed allelic differences between *S. robbinsi* and *S. chocoensis*. The distribution of *S. robbinsi* is similar to that of the recently described parakeet *Pyrrhura orcesi* (Ridgely and Robbins 1988). Both species occupy restricted geographic ranges, within which their habitat is now largely destroyed, and the remnants highly fragmented (Ridgely and Robbins 1988; Collar et al. 1992). Long-term survival of these species, and of the many endemic bird species of the adjacent Tumbesian center of endemism, will depend upon effective measures to maintain these last forests (see Best and Kessler 1995).

Scytalopus latebricola, sensu Zimmer 1939

Zimmer united the forms *caracae*, *meridanus*, *latebricola*, and *spillmanni* in a polytypic *S. latebricola*. These forms, however, share only a lack of diagnostic features. Three of them have different vocalizations. The fourth, nominate *latebricola*, is not well known vocally. The alarm call of a bird presumed to represent it bears some resemblance to the alarm call of *meridanus*. These calls are not entirely alike, however, and as the two are geographically isolated, with *latebricola* found in the upper reaches of the Santa Marta massif, which is known for its many endemic species, we recommend that they are best treated as allospecies of a *S.* [*latebricola*] superspecies.

The two remaining forms are vocally so distinctive that they are best treated as genuinely independent species: *Scytalopus caracae* and *S. spillmanni*. Birds from the Eastern Andes of Colombia were included in *meridanus* with some reservation by Zimmer. Vocally they appear to be a genuinely independent species, which might be represented by *S. infasciatus* (Chapman 1915), but a comparison of adequate material with the type (in AMNH) has not taken place.

SPILLMANN'S TAPACULO *Scytalopus spillmanni*
(Stresemann 1937; type in Berlin Museum)

Brief diagnosis.—Relatively large (depicted in Fjeldså and Krabbe [1990, pl. XLI 6 as unnamed species]). Tail shorter than in the even heavier *S. micropterus*. Heavier, shorter-tailed, and belly less extensively brown and less dark-scaled, in female also slightly brighter than in *S. vicinior*, but the two not always separable. Female virtually indistinguishable from some specimens of the allopatric *S. parkeri*, but usually heavier.

Plumage.—Adult male (*n* = 25): Above Blackish Mouse Gray, feathers indistinctly tipped blackish. Edges of inner remiges, lower back, rump, upper-tail coverts, usually edges of retrices, and faint wash on nape Prout's Brown to Brussels Brown. Rump sometimes barred blackish and then lighter (Cinnamon Brown). Below Deep Mouse Gray, belly sometimes with silvery-gray feather-tips. Extreme lower belly Pinkish Cinnamon to Cinnamon Buff. Flanks and under-tail coverts Ochracous Tawny to Cinnamon Brown, barred blackish. Axillars Cinnamon Buff to Ochraceous Tawny. *Adult female* (*n* = 3): Includes the type. Above much like male but more extensively brown and with somewhat more distinctive dusky feather-tips. Below lighter than male (Mouse Gray), and lower belly extensively Ochraceous Orange to Cinnamon Buff. Lower sides, flanks, and under-tail coverts also lighter than in male (Sudan Brown), barred blackish. *Juvenal female* (*n* = 1): Fore-crown Ochraceous Tawny grading to Brussels Brown on rest of upperparts, and barred blackish throughout. Tail blackish. Primary coverts with Pale Orange-Yellow subterminal bar and blackish vermiculations. Below Pale Pinkish Buff barred blackish, throat almost without bars. Axillars Clay Color. *Juvenal male* (*n* = 1): Similar to juvenal female, but somewhat darker, Pinkish Buff rather than Pale Pinkish Buff below.

Annual cycle in Ecuador (*n* = 2).—*Juveniles:* 5, 6 January (prov. Napo).

Vocalizations in Ecuador.—Song by male (Fig. 61) (also Fjeldså and Krabbe [1990:432, sonagram 2 as "*vicinior*" Pichincha]) a 10 to 20 (rarely 60 or more) s-long, very fast series of notes (25–35/s). Rate of delivery steady at the beginning, the pitch often slightly rising towards the end (whereas the very similar song of *S. canus opacus* begins with a "stutter," never rises, and stops abruptly). First overtone loudest, 4 kHz. At high excitement (Fig. 62) such as after playback of song, during encounters with other males, or in the presence of a female, the male may repeat every 2 s an 0.5 to 1.0 s-long, distinctly rising series of notes delivered at 26–30/s. First overtone loudest, rising from 2.8 to 3.4 kHz (Fjeldså and Krabbe [1990:432, sonagram 3 as "*vicinior*" Pichincha]). A call (Fig. 63), perhaps of an alarm type, is a roughly 1 s long series of 11 to 15 notes, first overtone loudest, 3.6 kHz, first note lower (3.1 kHz), last one or two slightly lower (3.2–3.3 kHz); compare with corresponding, but lower-pitched call of *S. vicinior* (Fig. 51). The female may utter various high-pitched notes, sometimes in a descending series of 5 to 6 such notes (Fig. 64) and at high excitement initiated with a sharp and high-pitched "*brzk*" (Fig. 65). This descending series often triggers male song.

Habitat in Ecuador.—Humid forest undergrowth including *Chusquea* bamboo.

Distribution in Ecuador.—1,900–3,200 m, locally (prov. Napo) to 3,500 m. On the east slope of Eastern Andes from the Colombian border south, only just crossing to the right bank of Río Paute. Not found in Cordillera de Cutucú, prov. Morona-Santiago, or Cordillera del Cóndor, prov. Zamora-Chinchipe, but specimens from Pan de Azúcar (prov. Napo: 00°27'S, 77°43'W, 2,900 m [MECN, WFVZ]) undoubtedly referable here. On the western slope of Western Andes from the Colombian border south at least to west of Sigchos in western prov. Cotopaxi (N.K. tape-recordings). A specimen from Hacienda Porvenir, ca. 2,500 m, prov. Bolívar (BMNH) may be this taxon. Also locally on the upper slopes of the inter-Andean valleys (southeast prov. Carchi, Volcán Tungurahua). Only after obtaining females of the present form in 1990 and after delimitating the ranges of the two species and collecting near the type locality, did we realize that the type of *spillmanni*, which is a female taken on Volcán Iliniza in northwestern Ecuador, represents it and not the morphologically similar *S. parkeri*; hence their distributions were confused in Fjeldså and Krabbe (1990). The elevational ranges of *S. spillmanni*, *S. micropterus*, *S. vicinior*, and *S. canus opacus* barely overlap where they meet. In the lower part of its elevational range on the east slope, *S. spillmanni* co-occurs with *S. unicolor latrans* in the zone where *S. micropterus* replaces *S. spillmanni*.

Distribution beyond Ecuador.—In Colombia *S. spillmanni* is known from the Central Andes in deptos. Antioquia (3 km southeast of the town of Caldas, 2,530–2,650 m [tape-recordings by N.K.]), Cauca (Volcán Puracé [heard by P. Coopmans]), and the eastern slope of Eastern Andes in depto. Nariño (La Victoria, 2,700 m [FMNH]). Undoubtedly also occurs on the Pacific slope in Nariño, whence come a number of specimens (Mayasquer, 2,375 m [ANSP]; Piqualé, [WFVZ,

LSUMZ]; Ricaurte, 2,000 and 2,500 m [LACM]), but a lack of vocal data makes distinction from *S. vicinior* uncertain.

Scytalopus latebricola (Bangs 1899; type in MCZ; depicted in Fjeldså and Krabbe [1990, pl. LXIII 30]) is restricted to the Santa Marta Mountains in northernmost Colombia, where it apparently occurs at 2,000 m (ICN; tape-recordings by P. Coopmans; Fig. 66) and at 3,660 m (AMNH, type in MCZ). There are no known tape-recordings from the elevation where the type was collected, but we consider it likely that the birds at 2000 m represent the same form as the type.

Scytalopus meridanus (Hellmayr 1922; type in AMNH; depicted in Fjeldså and Krabbe [1990, pl. XLI 2a, sonagram p. 434]) was based on a specimen from 4000 m in the Andes of edo. Mérida, Venezuela. Other specimens from the same mountains and edo. Táchira at elevations ranging down to 1980 m (AMNH, ANSP, BMNH, FMNH, PCC) have been referred to this taxon (Hellmayr 1922, 1924; Peters 1951; Phelps and Meyer de Schauensee 1978), as have some from the Central and Eastern Andes of Colombia; also in Fjeldså and Krabbe (1990:434, sonagrams 1 and 2). Zimmer (1939) questioned the allocation of Colombian specimens to *meridanus* and noted that more material was needed to clarify the relationships. Recently *S. spillmanni* was found in the Central Andes of Colombia (tape-recordings by N.K.). Birds from the Eastern Andes of Colombia are vocally distinct (Figs. 73–75) from birds from the upper subtropical zone of Mérida and Táchira (Figs. 67–72). Vocal material from the elevation in Mérida where the type of *meridanus* was collected, and a comparison of material from the Eastern Andes of Colombia with the type of *infasciatus* (Chapman 1915; type in AMNH from Páramo de Beltrán, 2,970 m) is needed before the taxonomy and nomenclature of these forms can be further addressed.

The coastal mountains of Venezuela are inhabited by *S. caracae* (Hellmayr 1922; type in AMNH). Its voice (Figs. 76–78) and plumage differs strongly from those of any other tapaculo.

Chusquea Tapaculo new species

Field work by N.K. has shown that a population at 2,250–3,150 m in south-east Ecuador differs from *S. spillmanni* in voice and habitat, and to some degree in morphology. It also differs genetically (Arctander and Fjeldså 1994). We propose to name this population:

Scytalopus parkeri sp. nov.

Holotype.—ZMUC 80173; subadult male from ca. 20 km south-southwest of San Lucas, 2,770 m, prov. Loja, Ecuador, at 03°50′S, 79°16′W, collected 7 March 1991 by N. Krabbe; blood sample N.K.1–7.3.91. Copy of a tape-recording of this individual deposited at LNS, recording LNS 65995.

Description of type.—12 rectrices. Crown, mantle, upper back, and wings Dark Mouse Gray, feathers narrowly and indistinctly tipped blackish, most conspicuous on crown. Nape, lower back, rump, upper-tail coverts, edge of rectrices, and a faint wash on the wing-coverts and edges of remiges between Dresden Brown and Snuff Brown; tertials wholly this color but for a buff, subterminal bar bordered blackish. Rump and upper-tail coverts faintly barred blackish, most conspicuous on tips of upper-tail coverts. Below Mouse Gray, central belly with 3 mm wide, silvery feather-tips, appearing uniform silvery. Lower belly bright, uniform Ochraceous Buff. Lower sides, flanks, and under-tail coverts between Ochraceous Tawny and Cinnamon Brown barred blackish. Barring distinct on lower sides, otherwise faint. Axillars between Tawny Olive and Cinnamon Buff. Body mass 24.4 g. Wing (flat) 61 mm, tail 43 mm, tarsus 24.5 mm. Iris dark brown, bill blackish, feet light brown.

Etymology.—We take pleasure in naming this species after the late Theodore. A. Parker III (who was the first to tape-record and collect it), in recognition of his emphasis of the importance of field study and the role of vocalizations in bird systematics, and in honor of his vast knowledge and generous heart, which led to outstanding contributions to our knowledge of Neotropical birds.

Brief diagnosis.—12 rectrices. Not identifiable with certainty from female *S. spillmanni*. Medium-sized and long-winged, tail brown or broadly brown-edged (depicted in Fjeldså and Krabbe [1990, pl. XLI 2b as *spillmanni*]). Central belly often silvery white (presumably younger birds) and lower belly then brighter and lighter brown than in the black-tailed *S. micropterus*, and unbarred. Older birds are easily told from adult *S. micropterus* by their virtually unbarred rump, flanks, and lower belly, and from female *S. unicolor subcinereus* by their much longer wings and longer tail, and by 12 rather than usually 10 rectrices. In dry specimens the feet average

slightly paler than in Ecuadorian congeners. Largely confined to dense stands of *Chusquea* bamboo.

Plumage.—Adult male (*n* = 14): Above Dark Mouse Gray, feathers almost always narrowly, and usually indistinctly, tipped blackish. Nape, lower back, rump, upper-tail coverts, tail, and usually inner (sometimes all) remiges between Dresden Brown and Snuff Brown, lower rump slightly brighter. Upper-tail coverts usually barred blackish. Below Mouse Gray, belly sometimes with 1–3 mm wide, silvery feather-tips. Lower or extreme lower belly from Ochraceous Tawny to Ochraceous Buff. Flanks and under-tail coverts between Ochraceous Tawny and Cinnamon Brown, more or less barred blackish, sometimes (older birds?) virtually unbarred. Axillars Cinnamon to Tawny Olive. *Adult female* (*n* = 3): Similar to male, and like it may lack silvery feather-tips on the belly and have unbarred flanks. *Immature/subadult male* (*n* = 1): The type, described above. *Juvenal male* (*n* = 2): One molting. Feathers of crown and side of head Dark Mouse Gray with (sub)terminal Amber Brown bar and with a narrow, black tip that may wear off. Mantle, wing-coverts, and remiges Argus Brown, feathers vermiculated with black and Cinnamon to Pinkish Buff at their tips. Lower back, rump, upper-tail coverts, and tail Argus Brown barred blackish, tail darkest and only indistinctly barred. Underparts Mouse Gray to blackish, evenly and narrowly barred Pinkish Buff (thus appearing dark with pale bars rather than the opposite as in most or all congeners). Flanks broadly barred Prout's Brown and blackish, under-tail coverts somewhat lighter. Axillars between Tawny Olive and Cinnamon Buff. Bill almost as dark as in adult, feet wholly so.

Annual cycle in Ecuador (*n* = 1).—*Juvenile:* 13 December (prov. Morona-Santiago).

Vocalizations.—Song given by male (Fig. 79) a 1 to 9 s long (up to 15 s or more after playback) series, of initially descending notes delivered at 10 to 12/s and repeated at 1 to 8 s intervals. First overtone loudest, 3.4 to 3.6 kHz (Fjeldså and Krabbe [1990:436, sonagram 2 as *spillmanni*-group]). Each note is relatively short (0.03–0.04 s) with a distinctly descending beginning and a less pronounced, rising end. At excitement (Fig. 80) the delivery of notes may rise up to 19/s, each note may lack the rising end, and each series may be shorter (down to 3 notes: Fjeldså and Krabbe [1990:436, sonagram 3] as *spillmanni*-group) and repeated with hardly any interval; the notes are then lower-pitched, 2.7 kHz. During duets, possibly given at pair-formation (Figs. 81 and 82; also Fjeldså and Krabbe [1990:436, sonagram 1] as *spillmanni*-group) male sustains an even series of 2.8 kHz notes delivered at 19/s, while the female simultaneously gives a long, descending series of 2 notes/s (sometimes faster), the first two or three notes explosive and high-pitched (up to 7 kHz), the following falling from 5 to 4 kHz (first overtone). Call (Fig. 83) much like song, but sharper and composed of only 9 to 12 notes. It lasts ca. 1 s and is repeated every 4 to 7 s. Some of the species's vocalizations were described by Parker et al. (1985) under *S. latebricola.*

Habitat in Ecuador.—Dense stands of *Chusquea* bamboo and adjacent humid forest undergrowth.

Distribution in Ecuador.—2,250–3,350 m. Found south of Río Paute on the east slope of the Eastern Andes and in the highest parts of Cordillera del Cóndor, prov. Zamora-Chinchipe, and from the eastern Chilla mountains south along the west slope of Eastern Andes to the headwaters of Río Catamayo. Does not occur on the Pacific slope of prov. Azuay, in the Celica mountains, or on the eastern rim of the Cajas plateau, and has so far not been found on the west slope of Cordillera de Sabanilla (Río Calvas drainage). The recent discovery of *S. spillmanni* south of the Río Paute, within 50 km of the northernmost specimens of *S. parkeri*, and with no apparent habitat break between them, suggests that the two may be genuinely sympatric, separated by habitat and voice only. Where *S. parkeri* co-occurs with *S. unicolor subcinereus*, *subcinereus* is restricted to drier and more secondary vegetation.

Distribution beyond Ecuador.—Peru in northern depto. Cajamarca and immediately adjacent depto. Piura on Cerro Chinguela, 2,590–2,900 m (LSUMZ and tape-recordings by T. A. Parker in LNS).

NON-ECUADORIAN SPECIES

For completeness we will briefly mention the six known species not discussed above (see also Table 1):

The huge (32–43 g: LSUMZ), dark *Scytalopus macropus* (Berlepsch and Stolzmann 1896; type in Warsaw Museum or lost; species depicted in Fjeldså and Krabbe [1990, pl. XLI 10a,b, sonagram p. 429]) (Fig. 84) is endemic to the Central Andes of Peru, at 2,590–3,500 m from depto. Amazonas south to depto. Junín (ANSP, FMNH, MHN, LSUMZ).

Three forms with white or pale superciliaries are confined to Central America: *Scytalopus argentifrons argentifrons* (Ridgway 1891; type in USNM; tape-recording by O. Jakobsen in BLA; Fig. 85) in Costa Rica and Volcán de Chiriqui in western Panama (AMNH, BMNH, USNM, WFVZ); the closely related (Wetmore 1972) *S. argentifrons chiriquensis* (Griscom 1924; type in AMNH; vocalizations similar to those of nominate *argentifrons* [B. M. Whitney, pers. comm.]) to eastern provs. Chiriqui and Veraguas, western Panama (AMNH, BMNH); and the more distantly related *S. panamensis* (Chapman 1915; type in AMNH) to Cerro Malí (Ridgely 1976) and Cerro Tacarcuna in easternmost Panama (AMNH, BMNH) and immediately adjacent Colombia (tape-recording by M. Pearman in BLOWS; Fig. 53).

Three species are confined to eastern Brazil: *Scytalopus indigoticus* (Neuwied 1831; types in AMNH), *S. speluncae* (Ménétriès 1835; type in St. Petersburg Museum), and *S. novacapitalis* (Sick 1958; type in MHNRJ). Sonagrams of most of their vocalizations were published by Vielliard (1990). Systematics and biology of all the Brazilian rhinocryptids were discussed by Sick (1960). The recently described taxon *S. psychopompus* (Teixeira and Carnevalli 1989; type in MHNRJ; no vocal data available) inhabits a small area in coastal Bahía, Brazil (MHNRJ, MZUSP). Despite close resemblance to *S. indigoticus* (differing only in unbarred flanks and bluish slate thighs), it was given full species status by its describers. This treatment was followed with some reservation by Ridgely and Tudor (1994). We consider the arguments for granting species rank to this taxon to be weak, and its taxonomic status was also doubted by Gonzaga et al. (1995). However, without vocal or genetic data, we are in no position to suggest changes in its taxonomic status.

We have no doubts that further research in the Andes, in particular Peru and Colombia (see e.g., Fig. 21), will reveal the presence of yet undescribed species of *Scytalopus* and will shed further light on the taxonomy on some of the taxa that are now scarcely known in life.

Related genera: Three other rhinocryptid genera seem to be the closest relatives of *Scytalopus*:

The monotypic *Eugralla paradoxa* (Ochre-flanked Tapaculo) of Valdivian forest in Chile and immediately adjacent Argentina is very similar to *Scytalopus* both morphologically and vocally. It mainly differs by its more elevated base of the bill.

The monotypic *Myornis senilis* (Ash-colored Tapaculo) inhabits thickets of *Chusquea* bamboo in the northern half of the Andes. It was considered to be a member of *Scytalopus* by Hilty and Brown (1986), a view with which we disagree. It is relatively light (21 g) and differs from *Scytalopus* by its more slender shape, much longer tail (*Myornis*: tail 58–68, tail/body mass ratio 3.0–3.8 mm/g; *Scytalopus* tail 35.1–57.2 mm, tail/body mass ratio 1.7–2.6 mm/g), more rounded wings and slightly more elevated base of the bill. Its song (described by Fjeldså and Krabbe [1990]) is structured differently from that of any *Scytalopus*.

Merulaxis ater (Slaty Bristlefront) and the similar, but larger *Merulaxis stresemanni* (known from two specimens) inhabit the Atlantic forests of eastern Brazil. They are shaped like *Myornis*, have narrow, pointed, stiffer and longer, erect feathers of the loral region than *Scytalopus* and *Myornis*, and are sexually dimorphic, males being gray, females rather uniform brown, resembling the juvenal of *Myornis*. As pointed out to us by the late T. A. Parker III, the similarity of the songs of *Merulaxis* and *Myornis*, minute-long repetitions of a single note terminating with one or more descending series of "hysterical laughter," suggests that they are each others closest relatives.

ACKNOWLEDGMENTS

Our field work in Ecuador was made possible by the collaboration of the MECN, Quito. The Ministerio de Agricultura, Quito, kindly issued the necessary permits. N. K. acknowledges the support of his field work by ZMUC, and field work by T.S.S. was supported by LSUMZ and ANSP. We would like to thank the following museum curators for loans and for letting us examine the collections: M. LeCroy, L. L. Short, and F. Vuilleumier, AMNH; F. B. Gill, ANSP; P. Colston, BMNH; K. C. Parkes and D. S. Wood, CM; R. Mena, EPN; J. W. Fitzpatrick, S. M. Lanyon, and D. E. Willard, FMNH; F. G. Stiles, ICN; K. Garrett, LACM; J. V. Remsen and S. W. Cardiff, LSUMZ; M. Moreno, MECN; I. Franke, MHN; F. Gehringer, MHNN; G. R. Graves and R. L. Zusi, USNM; O. Grönwall, NRS; and L. Kiff, WFVZ. We would like to thank P. Hansen, BLA, for use of their sonagraph and for help with the time-consuming preparation of the sonagrams; LNS and R. Ranft, BLOWS for use of vocal material from these libraries, and the individual recordists: A. van den Berg, B. Best, C. Carter, C. Clarke, P. Coopmans, G. Engblom, D. Fischer, J. Fjeldså, N. Gardner, P. Greenfield, S. Hilty, O. Jakobsen, F. Lambert, D. McDonald, J. P. O'Neill, T. A. Parker, R. S. Ridgely, R. A. Rowlett, M. Pearman, M. B. Robbins,

F. G. Stiles, R. Templeton, B. M. Whitney, and D. Willis. The field work and museum visits of N.K. were generously funded by H.R.H. Crownprince of Denmarks Foundation, Dr. Bøje Benzons Foundation, Gads Foundation, and a collection study grant from the Chapman Fund (AMNH). J. M. Carrión translated the abstract into Spanish. Bent Otto Paulsen provided needed measurement data on short notice, for which we most grateful. The manuscript greatly benefitted from the criticism of J. Fjeldså, C. Marantz, J. V. Remsen, J. M. C. da Silva, B. M. Whitney, and F. Vuilleumier.

LITERATURE CITED

ALLEN, J. A. 1889. List of birds collected in Bolivia by Dr. H. H. Rusby, with field notes by the collector. Bull. Amer. Mus. Nat. Hist. 2:77–112.

ARCTANDER, P., AND J. FJELDSÅ. 1994. Andean tapaculos of the genus *Scytalopus* (Aves, Rhinocryptidae): a study of modes of differentiation, using DNA sequence data. Pp. 205–225 in Conservation Genetics (V. Loeschcke, J. Tomiuk, and S. K. Jain, Eds.). Birkhauser Verlag, Basel, Switzerland.

BANGS, O. 1899. On some new or rare birds from the Sierra Nevada de Santa Marta, Colombia. Proc. Biol. Soc. Washington 13:91–108.

BEST, B. J., AND M. KESSLER. 1995. Biodiversity and Conservation in Tumbesian Ecuador and Peru. Birdlife International, Cambridge, U.K.

BLOCH, H., M. K. POULSEN, C. RAHBEK, AND J. F. RASMUSSEN. 1991. A survey of the montane forest avifauna of the Loja province, southern Ecuador. International Council for Bird Preservation Study Report No. 49.

BOND, J., AND R. MEYER DE SCHAUENSEE. 1942. The birds of Bolivia. Part 1. Proc. Acad. Nat. Sci. Philadelphia 94:307–391.

CABANIS, J. 1883. Bericht über die December-Sitzung. J. Ornithol. 31:104–106.

CHAPMAN, F. M. 1915. The more northern species of the genus *Scytalopus* Gould. Auk 32:406–423.

CHUBB, C. 1917. *Scytalopus simonsi*; sp. nov. Bull. Brit. Ornithol. Club 38:17.

COLLAR, N., L. P. GONZAGA, N. KRABBE, A. MADROÑO NIETO, L. G. NARANJO, T. A. PARKER III, AND D. C. WEGE. 1992. Threatened Birds of the Americas. International Council for Bird Preservation, Cambridge, U.K.

CORY, C. B., AND C. E. HELLMAYR. 1924. Catalogue of birds of the Americas. Field Mus. Nat. Hist., Zool. series 13, part 3.

DE LAFRESNAYE, F. 1840. Oiseaux noveaux. Rev. Zool. 3:101–106.

FJELDSÅ, J., AND N. KRABBE. 1990. Birds of the High Andes. Zoological Museum, University of Copenhagen, Denmark.

FJELDSÅ, J., AND S. MAYER. 1996. Recent ornithological surveys in the "Valles" region of southern Bolivia and the possible role of Valles for the evolution of the Andean avifauna. Danish Environmental Research (DIVA) Technical Report No. 1.

GONZAGA, L. P., J. F. PACHECO, C. BAUER, AND G. D. A. CASTIGLIONI. 1995. An avifaunal survey of the vanishing montane Atlantic forest of southern Bahia, Brazil. Bird Conserv. International 5:279–290.

GOULD, J. 1837. Exhibition of birds allied to the European Wren, with characters of new species. Proc. Zool. Soc. London Part 4:88–90.

GRISCOM, L. 1924. Descriptions of new birds from Panama and Costa Rica. Amer. Mus. Novitates No. 141.

HELLMAYR, C. E. 1922. Neue Formen der Gattung *Scytalopus*. Ornithol. Monatsber. 30:54–59.

HILTY, S., AND W. L. BROWN. 1986. Birds of Colombia. Princeton University Press, Princeton, New Jersey.

JOHNSON, A. W. 1967. The Birds of Chile and Adjacent Regions of Argentina, Bolivia and Peru. Vol. II. Platt Establecimientos Gráficos, Buenos Aires.

KING, J. R. 1989. Notes on the birds of the Rio Mazan valley, Azuay Province, Ecuador, with special reference to *Leptopsittaca branickii, Hapalopsittaca amazonina pyrrhops* and *Metallura baroni*. Bull. Brit. Ornithol. Club 109:140–147.

KOEPCKE, M. 1961. Birds of the western slope of the Andes of Peru. Amer. Mus. Novitates No. 2028.

KROODSMA, D. E. 1982. Learning and the ontogeny of sound signals in birds. Pp. 1–23 *in* Acoustic Communication in Birds, vol. 2 (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.

KROODSMA, D. E. 1984. Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate. Auk 101:13–24.

LANDBECK, L. 1857. *Pteroptochos albifrons* n. sp. Arch. Naturg. 23:273–275.

MÉNÉTRIÈS, E. 1835. Monographie de la famille des Myiotherinae où sont décrites les espèces qui ornent le Musée de l'Académie Impériale des Sciences. St. Pétersb. Acad. Sci. Mém., (6th ser.) 3, part 2 (Sci. Nat.):443–544.

MEYER DE SCHAUENSEE, R. 1970. A Guide to the Birds of South America. Livingston Pub. Co., Narberth, Pennsylvania.

MEYER DE SCHAUENSEE, R., AND W. H. PHELPS, JR. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, New Jersey.

MILLER, A. H. 1963. Seasonal activity and ecology of the avifauna of an American equatorial cloud forest. Univ. Calif. Publ. Zool. 66:1–74.

NORES, M. 1986. Diez nuevas subespecies de aves provenientes de islas ecologicas argentinas. Hornero 12: 262–273.

OLSON, S. L., AND E. N. KUROCHKIN. 1987. Fossil evidence of a tapaculo in the Quarternary of Cuba (Aves: Passeriformes: Scytalopodidae). Proc. Biol. Soc. Washington 100:353–357.

PARKER, T. A. III, T. S. SCHULENBERG, G. R. GRAVES, AND M. J. BRAUN. 1985. The avifauna of the Huancabamba region, northern Peru. Pp. 169–197 *in* Neotropical Ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). Ornithol. Monogr. No. 36.

PARKER, T. A. III, D. F. STOTZ, AND J. W. FITZPATRICK. 1996. Ecological and distributional databases for Neotropical birds. Pp. 118–436 *in* Neotropical Birds: Ecology and Conservation (D. F. Stotz, J. W. Fitzpatrick, T. A. Parker III, and D. K. Moskovits, Eds.). University of Chicago Press, Chicago.

PEARMAN, M. 1993. Some range extensions and five new species to Colombia, with notes on some scarce or little known species. Bull. Brit. Ornithol. Club 113:66–75.

PETERS, J. L. 1951. Check-List of Birds of the World, Vol. 7. Museum of Comparative Zoology, Cambridge, Massachusetts.

PHELPS, W. H., AND W. H. PHELPS, JR. 1953. Eight new subspecies of birds from the Perijá Mountains, Venezuela. Proc. Biol. Soc. Washington 66:1–12.

PRUM, R. O. 1992. Syringeal morphology, phylogeny and evolution of the Neotropical manakins (Aves: Pipridae). Amer. Mus. Novitates No. 3043.

RIDGELY, R. S. 1976. A Guide to the Birds of Panama. Princeton University Press, Princeton, New Jersey.

RIDGELY, R. S., AND M. B. ROBBINS. 1988. *Pyrrhura orcesi*, a new parakeet from southwestern Ecuador, with systematic notes on the *P. melanura* complex. Wilson Bull. 100:173–182.

RIDGELY, R. S., AND G. TUDOR. 1994. The Birds of South America, vol 2. University of Texas Press, Austin, Texas.

RIDGWAY, R. 1891. Notes on some Costa Rican birds. Proc. U.S. Nat. Mus. 14:473–478.

RIDGWAY, R. 1912. Color Standards and Color Nomenclature. Published by the author. Washington, D.C.

RIVEROS, G., AND N. VILLEGAS R. 1994. Análisis taxonómico de las subespecies chilenas de *Scytalopus magellanicus* (Fam. Rhinocryptidae, Aves) a través de sus cantos. An. Mus. Hist. Nat. Valparaíso 22: 91–101.

ROBBINS, M. B., T. A. PARKER III, AND S. E. ALLEN. 1985. The avifauna of Cerro Pirre, Darién, Eastern Panama. Pp. 198–207 *in* Neotropical Ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). Ornithol. Monogr. No. 36.

ROSENBERG, G. H. 1986. The nest of the Rusty-belted Tapaculo (*Liosceles thoracicus*). Condor 88:98.

SALVIN, O. 1895. On birds collected in Peru by Mr. O.T. Baron. Nov. Zool. 2:1–20.

SCLATER, P. L. 1858. Notes on a collection of birds received by M. Verreaux of Paris from the Río Napo. Proc. Zool. Soc. London Part 26:59–77.

SIBLEY, C. G. AND B. L. MONROE. 1990. Distribution and Taxonomy of Birds of the World. Yale University Press, New Haven.

SICK, H. 1958. Resultados de uma excursão ornitológica do Museu Nacional a Brasília, novo Distrito Federal, Goiás, com a descrição de um novo representante de *Scytalopus* (Rhinocryptidae, Aves). Bol. Mus. Nac., nova série, Zool. 185:1–20.

SICK, H. 1960. Zur Systematik und Biologie der Bürzelstelzer (Rhinocryptidae), speziell Brasiliens. J. Ornithol. 101:141–174.

SICK, H. 1993. Birds in Brazil. Princeton University Press, Princeton, New Jersey.

SKUTCH, A. F. 1972. Studies of tropical American birds. Publ. Nuttall Ornithol. Club No. 10.

STRESEMANN, E. 1937. Vögel vom Monte Illiniza (Central-Ecuador). Ornithol. Monatsber. 45, 3:75–77.

TACZANOWSKI, L. 1874. Liste des oiseaux recueillis par M. Constantin Jelski dans la partie centrale du Pérou occidental. Proc. Zool. Soc. London 1874:501–565.

TACZANOWSKI, L. 1884. Ornithologie du Pérou, vol. 1. Oberthur, Paris.

TEIXEIRA, D. M., AND N. CARNEVALLI. 1989. Nova espêcie de *Scytalopus* Gould 1837, do nordeste do Brasil (Passeriformes, Rhinocryptidae). Bol. Mus. Nac., nova série, Río de Janeiro, 331.

VIELLIARD, J. M. E. 1990. Estudio bioacústico das aves do Brasil: o gênero *Scytalopus*. Ararajuba 1:5–18.

VON BERLEPSCH, H. G., AND C. E. HELLMAYR. 1905. Studien über wenig bekannte Typen neotropischer Vögel. J. Ornithol. 53:18–19.

VON BERLEPSCH, H. G., AND M. J. STOLZMANN. 1896. On the ornithological researches of M. Jean Kalinowski in central Peru. Proc. Zool. Soc. London 1896:322–388.

VON LINNAEUS, C. 1789. *In* Caroli Linnaei Systema naturae sive regna tria naturae systematice proposita per classes, ordines, genera et species. 13 edition: 1 (2) (J. F. Gmelin, Ed.). Leipzig.

VON NEUWIED, M., PRINZ. 1831. Beitrage zur Naturgeschichte von Brasilien. 3 (2). J. B. Delamolliere, Weimar.

VON TSCHUDI, J. J. 1844–1846. Untersuchungen über die Fauna Peruana. Ornithologie. Scheitlin und Zollekofer, St. Gallen, Switzerland.

WETMORE, A. 1972. The Birds of the Republic of Panama. Smiths. Misc. Coll. Vol. 150, part 3.

WHITNEY, B. M. 1994. A new *Scytalopus* tapaculo (Rhinocrytidae) from Bolivia, with notes on other Bolivian members of the genus and the *magellanicus* complex. Wilson Bull. 106:585–614.

WINKLER, R. 1979. Zur Pneumatisation des Schädeldachs der Vögel. Ornithol. Beob. 76:49–118.

ZIMMER, J. T. 1939. Studies of Peruvian birds. No. 32. Amer. Mus. Novitates No. 1044.

ZIMMER, J. T. 1941. Studies of Peruvian birds. No. 38. Amer. Mus. Novitates No. 1126.

APPENDIX

Ecuadorian localities and specimens. Unless otherwise noted the specimens are deposited in ZMUC. Province, coordinates, and elevations are given in parentheses.

Scytalopus canus opacus.—Birds with one call type: 6 ad. males: Páramo El Angel (w. Carchi: 00°43–49′N, 77°47–56′W, 3,400–3,980 m); 4 ad. males (1 in ANSP), 1 subad. male, 1 imm. female, 1 imm. unsexed., 1 juv. female: Cerro Mongus (se. Carchi: 00°27′N, 77°52′W, 3,460–3,650 m); tape-recordings (N.K.; no specimens): Laguna San Marcos (Pichincha: 00°07′N, 77°58′W, 3400 m); 4 ad. males (2 in ANSP), 1 subad. male: Papallacta (Pichincha/Napo: 00°19–23′S, 78°09–13′W, 3,350–3,950 m); 1 male (tape-recording and blood sample only): Río Anatenorio (Napo: 00°59′S, 78°17′W, 3,350–3,700 m); tape-recordings (N.K.; no specimens): around Oyacachi (Napo: 00°11–13′S, 78°03–08′W, 3,400–3,600); 2 ad. males, 2 subad. males, 1 imm. male, 2 juv. females: Cordillera de Los Llanganates (Tungurahua/Napo: 01°07–08′S, 78°19–22′W, 3,700–3,800 m); male type and female topotype (AMNH): "Tambillo, 2440 m" [cf = Tambo de Ashilán, 3,200 m]; tape-recordings and sightings by N.K.: Tambo de Ashilán (Chimborazo: 02°11′S, 78°29′W, 3,150–3,500 m); 2 ad. males (1 in MECN), 1 female: Cordillera Zapote-Najda (Azuay/Morona-Santiago: 03°01–02′S, 78°38–39′W, 3,150–3,450 m); 2 ad. females: Páramos de Matanga (Azuay/Morona-Santiago: 03°17′S, 78°54′W, 3,100–3,350 m).

Birds with another call type: heard by Bloch et al. (1991) and N.K.: Cajanuma (Loja/Zamora-Chinchipe: 04°06′S, 79°09′W, 3050–3400 m); 1 ad. male (MECN) and tape-recordings by N.K.: Cerro Toledo (Zamora-Chinchipe: 04°23′S, 79°07′W, 3150–3350 m); 7 ad. males (1 in ANSP), 3 ad. females (2 in ANSP), 1 juv. male: Cordillera Las Lagunillas (Loja/Zamora-Chinchipe: 04°43–46′S, 79°25–26′W, 3,050–3,650 m).

Scytalopus unicolor latrans.—Dark gray birds with one song type: 1 male (MECN): Pacific slope of Páramo El Angel (Carchi: 00°47′N, 78°01′W, 3,100 m); 1 male: interandean slope of Páramo El Angel (Carchi: 00°39′N, 77°54′W, 3,350 m); 2 males (1 in MECN): near Santa Barbara (Sucumbíos: 00°39′N, 77°30′W, 2,750 m); 1 male, 3 females (1 in ANSP): Cerro Mongus (Carchi: 00°27′N, 77°52′W, 3,220–3,300 m); 1 male: Cordillera de Toisán (w. Imbabura: 00°27′N, 78°36′W, 3,100 m, tape-recordings by N.K. down to 3,050 m); 1 male, 1 female (LSUMZ): Apuela road (w. Imbabura: 00°21′N, 78°26′W, 2,800 m); tape-recordings by N.K.: Apuela road (w. Imbabura: 00°20′N, 78°24–25′W, 2,980–3,365 m); tape-recording by N.K.: Loma Taminanga (Imbabura: 00°17′N, 78°28′W, 2,900 m); tape-recording by N.K.: Lag. Negra, Mojanda Mts. (Imbabura/Pichincha: 00°08′N, 78°15′W, 3,750 m); 5 males, 5 females (1 in MECN), 1 juv. male: Volcán Pichincha (Pichincha: 00°03–15′S, 78°30–38′W, 2,700–3,750 m); heard by N.K.: Mt Ilalo (Pichincha: 00°14′S, 78°24′W, 2,400 m); 2 unsexed (ANSP): Chiriboga road (Pichincha: 00°17–18′S, 78°37–40′W, 2,875–3,500 m); tape-recordings by N.K.: w. slope V. Atacazo (Pichincha: 00°19′S, 78°37′W, 3,400–3,600 m); tape-recordings by N.K.: Pasochoa (Pichincha: 00°27–28′S, 78°29′W, 2,700–4,000 m); tape-recording by O. Jakobsen: 1 km NE Machachi (Pichincha: 00°31′S, 78°31′W, 3,000 m); tape-recordings by N.K.: Corazon (Pichincha: 00°33′S, 78°43′W, 2,980–3,870 m); 3 females: Volcán Iliniza (w. Cotopaxi: 00°42′S, 78°47–48′W, 2,900–3,000 m); 2 males, 1 female: tape-recordings by N.K.: Río Rayo (Cotopaxi: 00°36′S, 78°59′W, 2,250–2,300 m); tape-recordings by N.K.: 2 km SSE Quillotuna (Cotopaxi: 00°41′S, 78°57′W, 3,100 m); 2 males, 1 female: Cerro Parcato (w. Cotopaxi: 00°44′S, 78°58′W, 3,500–3,550 m); tape-recordings by N.K. and blood sample: 10 km NW Salinas (Bolívar: 01°21′S, 79°05′W, 3,000–3,350 m); tape-recording by N.K.: 3.5 km NW Chillanes (Bolívar: 01°55′S, 79°05′W, 2,340 m); heard by N.K.: Loma Totol (Chimborazo: 02°03′S, 78°51′W, 3,450–3,650 m); 1 male: 11 km N Zhud (Cañar: 02°24′S, 78°58–59′W, 2,850 m). Black birds with another song type: 1 imm. female: above Cuyuja (Napo: 00°23′S, 78°01′W, 2,450 m); 3 males (1 in MECN): Cordillera de Guacamayos (Napo: 00°39′S, 77°52′W, 2,000–2,300 m); heard by N.K.: Hacienda Aragón (Napo: 00°40′S, 77°55′W, 2,100–2,235 m); heard by N.K.: east of Oyacachi (Napo: 00°13′S, 78°03′W, 3,020 m); tape-recording by N.K. (calls, song-type?): nw. slope of Volcán Tungurahua (Tungurahua: 01°28′S, 78°27′W, 2,600 m); 6 males (5 in ANSP, 1 in MECN), 1 female (ANSP), 1 juv. female (ANSP): Cordillera de Cutucú (Morona-Santiago: 02°42′S, 78°03′W, 1,975–2,300 m); 1 female and tape-recordings by N.K.: Arenales, right bank of Río Paute (Azuay: 02°34′S, 78°34′W, 2,300–2,400 m); 1 male (EPN) and tape-recordings by T. A. Parker III: Cordillera del Cóndor (Morona-Santiago: 03°27′S, 78°21′W, 2,100 m); tape-recording by N. Flanagan: Cordillera de Tzunantza, Romerillos-San Luis trail (Zamora-Chinchipe: ca. 04°14′S, 79°01′W, 2,300 m); 1 male (ANSP) and tape-recordings by M. B. Robbins: Río Isimanchi (Zamora-Chinchipe: 04°47′S, 79°20′W, 2,250 m).

Two males (BMNH, no vocal data) labeled "Papallacta, 3,100 m" (Napo: ca. 00°22′S, 78°08′W) and "Baeza, 1830 m" (Napo: 00°27′S, 77°53′W) undoubtfully also belong here.

Scytalopus unicolor subcinereus: tape-recordings by N.K.: Arenales, right bank of Río Paute (Azuay: 02°34′S, 78°34′W, 2,300–2,400 m); heard by N.K.: Molleturo road (Azuay: 02°34′S, 79°20′W, 1,500 m); tape-recordings by N.K.: Cerro Paredones (Azuay: 02°45′S, 79°26–27′W, 3250 m); 2 males, 2 females, 1 juv. female: Sural (w. Azuay: 02°47′S, 79°26′W, 2,650 m); 1 female and tape-recordings by N.K.: above Chaucha (Azuay: 02°52′S, 79°23′W, 2,880–3,300 m); tape-recordings by N.K.: Laguna Illincocha (Azuay: 02°50′S, 79°13′W, 3,890 m); tape-recordings by N.K.: Laguna Llaviuco (Azuay: 02°51′S, 79°08′W, 3,200 m); 1 imm. male and tape-recordings by N.K.: Río Mazan (Azuay: 02°52′S, 79°07′W, 2,950–3,300 m); tape-recordings by N.K.: Guagualoma (Azuay: 03°15′S, 79°05′W, 3,055 m); 1 subad. male: Páramos de Matanga (Azuay/Morona-Santiago: ca. 03°16′S, 78°56′W, 3,300 m); old specimen (AMNH) and tape-recordings by

N.K.: Bestión (Azuay: 03°25′S, 79°01′W, 3,050–3,350 m); heard (Bloch et al. 1991): between Selva Alegre and Manu (Loja: 03°32′S, 79°22′W, 2,850–2,950 m); 1 female (MECN): near San Antonio de Cumbe (Loja: 03°34′S, 79°12′W, 2,875 m); tape-recordings by N.K.: Acanamá (Loja: 03°42′S, 79°13′W, 3,200 m); 1 female and tape-recordings by N.K.: Celica Mts. (Loja: 04°05–07′S, 79°57–59′W, 1,800–2,410 m); tape-recordings by N.K.: Cajanuma (Loja: 04°05′S, 79°11′W, 2,600 m); heard (Bloch et al. 1991): Uritusinga (Loja: 04°06′S, 79°09′W, 2,800–2,950 m); tape-recordings by N.K.: 2 km S Cariamanga (Loja: 04°20′S, 79°33′W, 2,300 m); 1 female and tape-recordings by N.K.: Utuana, Sozoranga Mts. (Loja: 04°20–22′S, 79°42–45′W, 1,750–2,550 m); tape-recordings by N.K.: above Jimbura (Loja: 04°42′S, 79°27′W, 3,000 m). AMNH specimens from Taraguacocha (5 males) (El Oro: ca. 03°35′S 79°28′W ?), El Chiral (2 males) (El Oro: ca. 03°38′S, 79°41′W, 1,615 m), Zaruma (3 males) (El Oro: 03°41′S, 79°37′W), and above Zaruma (1 female) (El Oro: ca. 03°40′S, 79°39′W) first mentioned by Chapman (1926) were referred here by Zimmer (1939).

Scytalopus spillmanni.—3 males: Laurel (w. Carchi: 00°49–50′N, 78°01–03′W, 2,350–2,930 m); 1 male: Cordillera de Toisán (w. Imbabura: 00°27′N, 78°36′W, 3,050 m); 4 males: Apuela road (w. Imbabura: 00°19–24′N, 78°23–27′W, 2,200–3,200 m); 3 males, 1 female: Loma Taminanga (w. Imbabura: 00°17′N, 78°28′W, 2,900 m); 11 males (2 in MECN, 7 in ANSP), 1 female (ANSP), 2 unsexed (1 in MECN), 1 imm. male (ANSP), 1 imm. female (ANSP): Volcán Pichincha (Pichincha: 00°01–15′S, 78°35–41′W, 2,100–3,050 m); tape-recordings and heard by N.K.: Chiriboga road (Pichincha: 00°15–17′S, 78°40–48′W, 1,900–2,900 m); tape-recordings by N.K.: Corazón (Pichincha: 00°33′S, 78°43′W, 2,980–3,350 m); 1 female (the type in Berlin Museum): Volcán Iliniza (Cotopaxi/Pichincha: ca. 00°35′S, 78°43′W); tape-recordings by N.K.: Río Rayo (Cotopaxi: 00°36′S, 78°59′W, 2,250, 2,500, and 2,700 m); 3 males: near Santa Barbara (Sucumbíos: 00°33–35′N, 77°31–32′W, 2,100–2,500 m); tape-recording by G. Rosenberg: Cerro Mongus (Carchi: 00°27′N, 77°52′W, 3,200 m); 4 males: Cordillera de Guacamayos (Napo: 00°39′S, 77°52′W, 2,100–2,300 m); 1 male, 1 female, 1 juv. male, 1 juv. female: Río Anatenorio (Napo: 00°59′S, 78°21′W, 3,000–3,500 m); tape-recordings by N.K.: Cordillera de Los Llanganates (Napo: 01°06′S, 78°18′W, 3,300 m); 2 males: Volcán Tungurahua (Tungurahua: 01°22–28′S, 78°24–29′W, 2,600–2,850 m); tape-recordings by N.K.: Orregán, w. slope Volcán El Altar (Chimborazo: 01°39–40′S, 78°30′W, 3,100–3,300 m); old specimen (AMNH) and tape-recordings by N.K.: upper Río Upano, "Tambillo" [cf. = Tambo de Ashilán] (Chimborazo: 02°11′S, 78°29′W, 2,440–3,200 m); 1 male: Arenales, right bank of Río Paute (Azuay: 02°34′S, 78°34′W, 2,300–2,400 m).

A male (MECN, more specimens in WFVZ) from 2 km south of Pan de Azúcar, 15 km east-southeast of Borja: (Napo: 00°27′S, 77°43′W, 2,900 m), a male (MECN) from Papallacta (Napo: ca. 00°22′S, 78°08′W), and a female (AMNH) from above Baeza (Napo: ca. 00°27′S, 77°53′W) look similar and should undoubtedly be referred here.

Scytalopus parkeri.—5 male, 5 females, 2 unsexed, 1 imm. male, 1 imm. unsexed, 1 juv. male: Cordillera Zapote Najda (Morona-Santiago: ca. 03°02′S, 78°31–36′W, 2,250–3,150 m); tape-recordings by N.K.: Páramos de Matanga (Azuay: 03°17′S, 78°54′W, 3,000–3,250 m); tape-recordings by T. A. Parker III: Cordillera del Cóndor (Morona-Santiago: ca. 03°27′S, 78°21′W, ca. 2,300 m); heard (Bloch et al. 1991): between Selva Alegre and Manu (Loja: 03°32′S, 79°22′W, 2,850–2,950 m); 2 males: 7 km NE San Lucas (Loja: 03°40′S, 79°13′W, 3,100 m); 1 subad. male (type): ca. 20 km SSW San Lucas (Loja: 03°50′S, 79°16′W, 2,770 m); heard and blood sample (Bloch et al. 1991): ca. 10 km ENE Loja (Loja: 03°58′S, 79°09′W, 2,550–2,700 m); 2 males (1 in ANSP): Cajanuma (Loja: 04°06′S, 79°09′W, 2,750–2,900 m); tape-recording by M.K. Poulsen: Uritusinga (Loja: 04°06′S, 79°09′W, 2,800–3,000 m); 1 male (MECN), 1 female (ANSP): Río Isimanchi (Zamora-Chinchipe: 04°46′S, 79°25′W, 3,000–3,350 m); tape-recordings by N.K.: Cerro Toledo (Zamora-Chinchipe: 04°23′S, 79°07′W, 3,000–3,275 m).

Scytalopus vicinior.—4 males (1 in ANSP, 1 in MECN): Maldonado road (w. Carchi: 00°50–54′N, 78°03–12′W, 1,650–2,350 m); tape-recordings by N.K.: Cordillera de Toisán (Imbabura: 00°20′N, 78°36′W, 1,850 m); 1 female: Maquipucuna (Pichincha: 00°05′N, 78°37′W, 1,775 m); tape-recordings by N.K.: 1 km above Tandayapa (Pichincha: 00°00′, 78°41′W, 1,900 m); 9 males, 1 female, 1 imm. male: near Mindo (Pichincha: 00°02′S, 78°45–46′W, 1,700 m, heard by N.K. down to 1,450 m); tape-recording by N.K.: Chiriboga road (Pichincha: 00°15′S, 78°50′W, 1,850–1,900 m); heard by N.K.: El Corazón (Cotopaxi: 01°08′S, 79°05′W, 1,250 m).

Scytalopus chocoensis.—17 males (9 including the type in ANSP, 1 in MECN), 5 females (2 in ANSP), 1 juv. male (ANSP): near Ibarra-San Lorenzo railroad (Imbabura and Esmeraldas: 00°52–58′N, 78°30–43′W, 350–950 m). A male (AMNH) from Paramba (Imbabura: 00°49′S, 78°21′W, 1,065 m) undoubtedly also belongs here.

Scytalopus robbinsi.—3 males (1 in ANSP): Molleturo road (w. Azuay: ca. 02°34′S, 79°20′W, 890 m, heard by N.K. to 1,250 m); tape-recording by N.K.: Daucay (El Oro: 03°30′S, 79°45′W, 700 m); 5 males including type (1 in ANSP, 1 in MECN), 3 females (1 in ANSP): 9 km W Piñas (El Oro: 03°39′S, 79°45′W, 870–930 m).

Scytalopus atratus: heard by P. Coopmans: Coca Falls (Napo: 00°06′S, 77°35′W, 1,250 m); 1 male: n-slope of Pan de Azúcar (Napo: ca. 00°08′S, 77°34′W, 1,250 m); 5 males (1 in EPN, 2 MECN), 1 female: Rio Hollín road (Napo: 00°40–46′S, 77°35–51′W, 1,200–1,350 m); 3 males (ANSP): w. slope of Cordillera de Cutucú (Morona-Santiago: ca. 02°40′S, 78°06′W, 1,525–1,650 m); tape-recordings by N.K.: w. slope of Cord. del Cóndor, S Paquisha (Zamora-Chinchipe: ca. 03°58′S, 78°37′W, 1,250 m); tape-recording by N.K.: Río Bombuscaro (Zamora-Chinchipe: 04°06′S, 78°58′W, 1,050 m).

Scytalopus micropterus.—heard by N.K.: La Bonita road (Sucumbíos: 00°33′N, 77°32′W, 2,100 m); 3 males: Pan de Azúcar (Napo: ca. 00°08′S, 77°34′W, 1,250 m); tape-recording by O. Jakobsen: El Salado

(Napo: 00°13′S, 77°43′W, 1,250 m); 11 males, 10 females (AMNH, no vocal data): lower Volcán Sumaco (Napo: ca. 00°34′S, 77°38′W, subtropical); tape-recordings by N.K.: Cordillera de Guacamayos (Napo: 00°39′S, 77°52′W, 1,600–2,100 m); 5 males (1 in MECN, 4 in ANSP), 1 female (BMNH, no vocal data): w. slope of Cordillera de Cutucú (Morona-Santiago: ca. 02°40′S, 78°06′W, 1,700 m); 2 males: w. slope of Cordillera del Cóndor (Zamora-Chinchipe: 04°00′S, 78°27–30′W, 1,400–1,700 m); 1 male (ANSP): Quebrada Avioneta, Cordillera de Tzunantza (Zamora-Chinchipe: 04°15′S, 78°55–56′W, 1850 m); tape-recording by P. Coopmans: near (S) Valladolid (Zamora-Chinchipe: 04°34′S, 79°08′W, 1,500 m); heard by F. Sornoza: San Andrés (Zamora-Chinchipe: 04°50′S, 79°17′W, ca. 2,000 m).

2 old specimens (Warsaw Museum, no vocal data): Mapoto and Machay, Volcán Tungurahua (Tungurahua: 01°24–25′S, 78°16–20′W, 1,521–2,125 m) probably belong here.