

Taxonomy of southern populations in the *Scytalopus speluncae* group, with description of a new species and remarks on the systematics and biogeography of the complex (Passeriformes: Rhinocryptidae)

Giovanni Nachtigall Maurício^{1, 2, 3}

¹ Programa de Pós-graduação em Biociências – Zoologia, PUCRS. Laboratório de Ornitologia, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul. Av. Ipiranga, 6681, C. P. 1429, Porto Alegre, RS, Brazil

² Grupo Especial de Estudo e Proteção do Ambiente Aquático do Rio Grande do Sul – GEEPAA-RS, Rua Tiradentes, 2247, CEP 96010-160, Pelotas, RS, Brazil. E-mail: gnmauricio@wnet.com.br

³ CBRO – Comitê Brasileiro de Registros Ornitológicos

Recebido em 25 de março de 2004; aceito em 27 de abril de 2005

RESUMO. Taxonomia de populações meridionais no grupo *Scytalopus speluncae*, com descrição de uma nova espécie e comentários sobre sistemática e biogeografia do complexo (Passeriformes: Rhinocryptidae). – Pesquisas em campo e em museus revelaram que populações tradicionalmente identificadas como *Scytalopus speluncae* no sul do Brasil e na província de Misiones, Argentina, representam uma espécie não descrita, que é aqui nomeada e caracterizada. Essa nova espécie difere de *S. speluncae*, quanto à plumagem do macho, pela presença constante – em qualquer idade – de ampla área acanelada nos flancos marcada por conspícuo barramento negro (vs. flancos uniformemente cinzas em machos adultos de *S. speluncae*) e pelo cinza mais claro das partes inferiores. Ademais, difere de *S. speluncae* por emitir as notas do canto em andamento mais lento (2,01-3,36 notas/s vs. 4,56-5,86 notas/s), por emitir gritos distintos quanto a estrutura geral e forma das notas e por ter em seu repertório vocal um tipo de canto quase único, cuja parte final é notavelmente acelerada até tornar-se semelhante a um trinado (vs. ausência em *S. speluncae*). A nova espécie também difere consistentemente quanto a caracteres vocais e de plumagem das outras duas espécies nomeadas do grupo *S. speluncae*, a saber, *S. iraiensis* e *S. novacapitalis*. A nova espécie ocorre em três áreas distintas: Serra do Sudeste (sul do Rio Grande do Sul), Província argentina de Misiones e áreas adjacentes do Brasil e partes mais altas do Planalto do nordeste do Rio Grande do Sul e sudeste de Santa Catarina. A análise aqui desenvolvida indicou, adicionalmente, que o “tradicional” *S. speluncae* provavelmente compreende um outro táxon não descrito, o qual estaria distribuído ao sul da área do verdadeiro *S. speluncae* (de São Paulo até o Rio Grande do Sul). Verificou-se que a nova espécie compartilha com *S. novacapitalis* e populações possivelmente não nomeadas de Minas Gerais o tipo de canto com aceleração final mencionado acima, o qual parece ser único na família, sugerindo que esses táxons são estreitamente relacionados. Salienta-se que a pesquisa taxonômica sobre o grupo em questão ainda é incipiente; populações recentemente encontradas nos estados de Minas Gerais e Bahia podem representar espécies adicionais ainda não nomeadas. Entretanto, análises baseadas em séries pequenas e não vinculadas a um tipo vocal são desencorajadas. Adicionalmente, hipóteses biogeográficas alternativas para explicar a origem e a diversificação do grupo *S. speluncae* são apresentadas e discutidas. Palavras-chave: *Scytalopus*, nova espécie, *S. speluncae*, *S. iraiensis*, *S. novacapitalis*, biogeografia, sul do Brasil.

ABSTRACT. Some populations traditionally identified as *Scytalopus speluncae* populations in southern Brazil and Misiones, Argentina, actually represent an unnamed species, which is described in this paper. Field and museum studies showed that male plumage differs from traditional *S. speluncae* by the presence of black and buff barring over the flanks in all ages (absent in the adult male plumage of *S. speluncae*) and by having paler gray underparts. Also, this new species differs from *S. speluncae* by its slower paced song (2.01-3.36 notes/s vs. 4.56-5.86 notes/s), by having two types of calls that differ in general structure and note shape from the calls of *S. speluncae* and by having an almost unique song type marked by the ending, in which it rapidly accelerates the pace into a trill (trill absent in *S. speluncae*). The new species also differs consistently in plumage and vocal characters from the other described taxa in the *S. speluncae* group, namely *S. iraiensis* and *S. novacapitalis*. The distribution of the new species encompasses three distinct areas: Serra do Sudeste (southern Rio Grande do Sul), the Argentinian Province of Misiones and adjacent areas of Brazil and the highest areas of the plateau (Planalto) of northeastern Rio Grande do Sul and southeastern Santa Catarina. Also, the data suggest that the “traditional” *S. speluncae* probably comprises other undescribed species, whose range would encompass the southern areas of the range admitted for *S. speluncae* (from São Paulo to Rio Grande do Sul). The new species shares the accelerating song type mentioned above, which is apparently unique in the genus, with *S. novacapitalis* and populations in Minas Gerais (also possibly new species), suggesting that these species are more closely related to each other than to any other species in the genus. Taxonomic research on the group is still incipient and populations recently discovered in Minas Gerais and Bahia may be additional, unnamed species. However, analyses based upon few museum specimens and without vocal data are discouraged. Additionally, alternative biogeographic hypotheses to explain the origins and the diversification of the *S. speluncae* group are presented. Key words: *Scytalopus*, new species, *S. speluncae*, *S. iraiensis*, *S. novacapitalis*, biogeography, southern Brazil.

The rhinocryptid genus *Scytalopus* is one of the most speciose groups of Neotropical birds. At least 37 species are presently recognized, the great majority being confined to the Andes and related orographic systems while some others are endemic to southeastern Brazil and adjacent Argentina (Fjeldså and Krabbe 1990, Krabbe and Schulenberg 1997, 2003, Sick 1997). Whereas the Andean counterpart of the genus includes several major groups, some of which containing a large

number of species, the Brazilian one comprises only two discrete complexes, namely the *S. indigoticus* and the *S. speluncae* species groups, comprising two and three named taxa, respectively (Vielliard 1990, Bornschein *et al.* 1998, Krabbe and Schulenberg 1997, 2003).

The systematics and taxonomy of the genus *Scytalopus* has a long and puzzling history. The relative uniformity of morphology throughout the genus and high intraspecific, age-

related variation pose several limitations to recognizing component taxa (Whitney 1994, Krabbe and Schulenberg 1997). Even after a meticulous revisional study, involving primarily Andean taxa, Zimmer (1939) was not satisfied with his own results: "(...) there are some confusing portions of the picture that more material will be needed to clarify" and "The group is an unusually difficult one and although there are a number of species that must be recognized, there is such similarity of pattern and color, all in browns and grays without striking differences, that exact definitions are not easy". Such a confusing scenario, which has begun to improve only recently through the use of vocalizations to recognize species limits (Whitney 1994, Krabbe and Schulenberg 1997, Coopmans *et al.* 2001), has also been verified among the Brazilian counterparts. For instance, Sick (1958) had doubts to which species – *S. indigoticus* or *S. speluncae* – he would allocate his new subspecies *novacapitalis*; although first allocated to the former, it was later (Sick 1960) recognized as a full species, forming a superspecies with *S. speluncae* (Vielliard 1990). More recently, other problems concerning the taxonomy of Brazilian *Scytalopus* have arisen: there have been doubts about the validity of *S. psychopompus* (Gonzaga *et al.* 1995, Krabbe and Schulenberg 1997) and the applicability of the name *S. speluncae* (J. F. Pacheco in BirdLife International 2000). In the Espinhaço Range, eastern Minas Gerais State, an apparently undescribed species, morphologically similar to *S. novacapitalis* but vocally nearest to *S. speluncae*, has been found (Collar *et al.* 1992, Melo-Júnior *et al.* 2001), while marsh-dwelling populations in the state of Paraná have proved to represent a new species, *S. iraiensis* (Bornschein *et al.* 1998).

However, a less obvious but equally important taxonomic problem among the southeastern *Scytalopus* – involving populations attributed to *S. speluncae* – remains largely overlooked. Reference catalogues (e.g. Sclater 1890, Cory and Hellmayr 1924), the original description (Ménétrières 1835), and some recent field guides and manuals (e.g. Meyer de Schauensee 1982, Sick 1985, Ridgely and Tudor 1994, Krabbe and Schulenberg 2003) describe the adult male of this species as a uniformly slate gray bird, while other works (e.g. Gai 1951, Olrog 1984, Narosky and Yzurieta 1987, de la Peña and Rumboll 1998) describe it as a gray bird with paler gray underparts and rufous, dark-banded flanks and crissum. This latter morphotype, which has been attributed to the superficially similar immature plumage of typical *S. speluncae* (Naumburg 1937), is the only plumage pattern known for the birds occupying Misiones Province, Argentina (see descriptions in Naumburg [1937], Gai [1951] and Narosky and Yzurieta [1987]). There, among other names, these birds have been called "churrín de vientre rayado" (bar-bellied tapaculo) by some authors (e.g. Navas and Bo 1977, Straneck 1990), which further suggests a constancy in the barring pattern over the posterior underparts in that population. Recently, in the Serra do Sudeste region, southern Rio Grande do Sul State, Brazil, the author and Rafael A. Dias found a population that matched the description of the Misiones birds and noticed that this population had a slower-paced song (i.e. 2-3 vs. 5 notes/s) compared to the song of *S. speluncae* occurring elsewhere in the Atlantic forest region. Additionally, J. F. Pacheco and P. S. M. da

Fonseca (unpublished report) found that birds in northernmost Rio Grande do Sul (contiguous with the Misiones forest) and in the highlands of southeastern Santa Catarina State (Planalto) have similar, slow-paced songs. However, such differences in song pace have been attributed to individual variation within populations of *S. speluncae*, including in Rio Grande do Sul (Belton 1985, Ridgely and Tudor 1994). This scenario clearly indicated that at least the southern populations traditionally ascribed to *S. speluncae* needed a taxonomic revision. In this paper, the plumage and vocal patterns of some *Scytalopus* populations traditionally identified as *S. speluncae* are analyzed and, as a result, a new species is herein proposed. Furthermore, remarks on the taxonomy, systematics and biogeography of the entire *S. speluncae* complex are advanced.

METHODS

Some plumage patterns within *Scytalopus*, such as the barring on the flanks, are present in younger birds (juveniles, immatures, and subadults) of virtually all members of the genus, disappearing in full adults of several species, but being present in all ages of others (Fjeldså and Krabbe 1990, Whitney 1994, Krabbe and Schulenberg 1997). Barring over the flanks should be regarded as a constant (diagnostic) character of a given species only if found consistently in full adults; given the large proportion of immature and subadult birds in at least some populations (Krabbe and Schulenberg 1997; pers. obs.), exhaustive sampling of specimens and/or adequate field observations are of crucial importance to ensure that adults in definitive plumage are represented in the analysis. In consideration of the above premises, the constancy of plumage and vocal patterns presumably characterizing *Scytalopus* populations occupying the three regions mentioned above was tested through extensive collecting of specimens, direct field observations, and thorough sampling of vocalizations. Data collection was conducted initially in the southern hills of Rio Grande do Sul (Serra do Sudeste) and, subsequently, in the other two regions (Misiones and Planalto highlands of southeastern Santa Catarina and adjacent Rio Grande do Sul). Although field work specifically oriented to study these populations began only in early 2001, data collection dates from early March 1994, when the population of southern Rio Grande do Sul was discovered. Since this latter date, all types of vocalizations uttered by each individual detected in the field and the plumage characteristics of birds carefully observed have been recorded. As a result, about 580 individual records (i.e. different individuals detected per field trip) were accumulated up to 2004. Opportunistically in 1998/1999 and systematically since 2001, specimens and vocalizations of tapaculos having a "typical" *S. speluncae* song (i.e. fast-paced series with about 5 notes/s) were sampled at the Serra Geral, Serra do Mar and Serra da Mantiqueira ranges in the states of Rio Grande do Sul, Santa Catarina, Paraná, São Paulo, Rio de Janeiro and Minas Gerais. In addition, comparative material of other presumably related species was gathered in the field for this study. Specimens and tape-recordings representing *S. novacapitalis* and a probably undescribed form were taken, respectively, at

Brasília (Distrito Federal) and in the Espinhaço Range (eastern Minas Gerais) in 2003/2004. *Scytalopus iraiensis* was sampled along coastal Rio Grande do Sul mainly in 2001-2003, with previous field work between 1998 and 2000.

Specimens were collected with carbines and, after body mass and total length had been taken, were prepared as skins and deposited at the ornithological collection of the Museu de Ciências e Tecnologia of the Pontifícia Universidade Católica do Rio Grande do Sul, Brazil (MCP). Vocalizations were recorded in the field with a Sony TCM 5000EV tape-recorder and a Sennheiser ME 66 microphone. Tape-recordings will be deposited at the Arquivo Sonoro Prof. Elias Coelho, Universidade Federal do Rio de Janeiro (UFRJ). In addition to the 46 specimens collected during this study, 68 skins representing populations attributed to the *S. speluncae* group deposited at other Brazilian institutions were examined: Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP), Museu Nacional, Rio de Janeiro (MNRJ), Departamento de Zoologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro (DZUFRJ), Museu de História Natural de Taubaté, Taubaté (MHNT), Coleção Ornitológica Marcelo Bagno, Universidade de Brasília, Brasília (COMB), Museu de História Natural Capão da Imbuia, Curitiba (MHNCI) and Museu de Ciências Naturais of the Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (MCN). These specimens are listed in the Results. Furthermore, digital images of the type-specimen of *S. speluncae* (housed at the Academy of Sciences of St-Petersburg, Russian Federation), provided by L. F. Silveira, and a color plate from the original description provided by M. L. Isler (*per* J. F. Pacheco), were analyzed. Specimens were measured with a caliper to the nearest 0.1 mm. The following morphometric data were taken: bill length (from anterior edge of the operculum to the bill tip), length of the exposed culmen, bill depth (taken at the posterior edge of the nares), wing length (chord), tail length (from the insertion of the central rectrices to their tip) and tarsus length. Measures of unsexed specimens were excluded from the analysis. Statistical testes (*t*-test of Student, 95% significance level) were conducted to evaluate the existence of significant differences in morphometrics between the taxa with better sample sizes (i.e. 10 or more specimens).

Tape-recordings were digitized at 44.1 kHz, 16-bit and were analyzed using the programs Cool Edit 2000 and Cool Edit 96 (Syntrillium Software Corporation). Spectrograms were produced in a personal computer with Cool Edit 96, with a resolution of 256 bands. The following vocal variables were analyzed from the tape-recordings: pace (from songs and alarm calls), total duration (from songs only), frequency (from song and alarm call notes), and length, shape and structure of notes (from songs and alarm and contact calls). Pace is defined as the number of notes delivered per second, and was calculated by dividing the number of counted notes per the time interval (in seconds) comprised between the beginning of the first counted note and the beginning of the last one. The songs which showed distinct change in pace through time (accelerating songs) were divided into three sections for calculations of pace: the slow-paced section, the trilled final section and the transition between these two sections (i.e. when the inter-note intervals become increasingly shorter before stabilizing in the accelerated end). For measurements

of pace, the notes of the beginning of songs, which may be delivered in a distinct pace, were not considered. Song duration was measured from the beginning of the first recorded note to the end of the last one. Frequency measures were taken from the top of the fundamental of individual notes through visual inspection in the spectrograms. Note length (or duration) was measured from the beginning to the end of the fundamental of individual notes. Measures of frequency and note length of normal songs were taken from 15 notes of the central section of each song; in accelerating songs these measures were taken from five notes of the trilled section; for alarm calls, these measures were taken from one note in the middle of the calls. As the number of alarm calls tape-recorded per individual was highly variable, a mean for each individual was calculated first; then, the mean value obtained for each bird was the basis for the general mean and standard deviation calculations. As unsolicited songs are given at long and unpredictable intervals, most recordings were obtained after playback (see Vocalizations).

It has been documented that vocal differences are positively correlated with genetic distinctions in *Scytalopus* (Arctander and Fjeldså 1994, Krabbe and Schulenberg 1997). For this study, it is assumed that vocalizations are entirely inherited in this genus, and as such, provide potentially highly informative characters for systematic and taxonomic study.

RESULTS

All birds with slow-paced songs from the three populations under study – Misiones, Planalto and Serra do Sudeste – collected ($n = 25$; 23 males, two females) or observed in the field ($n = 77$; 61 presumed males, 16 females) had relatively pale gray (except younger females) underparts and buff or rufous flanks conspicuously barred black or blackish. Besides these characters, these three populations shared a peculiar song type and a distinctive contact call not found among birds with fast-paced songs. Unless they were females, immatures or subadults (see below for aging criteria), all these birds with fast-paced songs ($n = 11$ collected, plus 10 observed) were plain or nearly plain-gray, including the flanks. Additionally, most museum specimens representing presumed adult males from the range of the fast-paced song populations (13 out of 16) were also plain-gray. Therefore, it is apparent that these two vocal and morphological types represent distinct species, one of which (that with slow-paced songs and permanently-bared flanks) is described below. Furthermore, analyses of the vocal repertoires and morphometric data strongly suggested that the birds with rapid-paced songs encompass more than one species, for which reason these are treated separately in the present study (see below).

Scytalopus pachecoi sp. nov.

Tapaculo-ferreirinho (Portuguese name)

Planalto Tapaculo (English name)

Holotype – MCP no. 1179; adult male, Cerro das Almas (31°46'S, 52°35'W), approximately 180 m elevation, municipality of Capão do Leão, Rio Grande do Sul State,

Brazil. Collected and tape-recorded by the author on 8 January 2003 and prepared as a skin by Cristian Marcelo Joenck.

Paratypes – MCP no. 962, adult male, Arroio Andrade headwaters (31°27'S, 52°28'W), Pelotas / Arroio do Padre municipalities, 27 October 2001; MZUSP no. 75761, subadult male, same locality as the holotype, 14 October 2001; MZUSP no. 75762, subadult male, same locality as the holotype, 14 October 2001; MCP no. 959, subadult male, Arroio Cadeia (31°35'S, 52°33'W), municipality of Morro Redondo, 26 October 2001; MCP no. 960, subadult male, Morro da Antena (31°36'S, 52°31'W), municipality of Pelotas, 26 October 2001; MCP no. 961, subadult male, upper Arroio Moinho (31°19'S, 52°30'W), municipality of Canguçu, 27 October 2001; MZUSP no. 75763, subadult male, Santo Amor (31°40'S, 52°35'W), municipality of Morro Redondo, 3 December 2001; MCP no. 977, subadult male, same locality and date as MZUSP no. 75763; MCP no. 1009, subadult male, Harmonia (31°18'S, 52°25'W), municipality of São Lourenço do Sul, 6 February 2002; MZUSP no. 75764, adult male, Colônia Solidez (31°18'S,

52°32'W), municipality of Canguçu, 6 April 2002; MCP no. 1082, subadult male, same locality as the holotype, 14 September 2002; MCP no. 1022, subadult female, Monte Bonito (31°39'S, 52°27'W), municipality of Pelotas, 3 April 2002. The type series is restricted to the above thirteen specimens and, therefore, excludes material collected in other than the Serra do Sudeste region, southern Rio Grande do Sul.

Diagnosis – Morphology and Plumage: The presence of a mobile nasal operculum and four notches in the sternum immediately places *S. pachecoi* within the family Rhinocryptidae (see Plótnick 1958, Krabbe and Schulenberg 2003). The allocation of the new species in the genus *Scytalopus* (*sensu* Krabbe and Schulenberg 1997) is rather arbitrary, since no objective characterization or synapomorphy has been proposed. However, the combination of small size (total length about 120 mm; body mass c. 15 g), predominantly gray coloration, relatively short tail (shorter than wing) and the comparatively less elevated base of the bill places the new species within *Scytalopus*, the type of which is *S. magellanicus*.



Figure 1. Ventral view of adult males of taxa in the *Scytalopus speluncae* group. From left to right: *S. novacapitalis* (MCP no. 1481), *S. pachecoi* (MCP no. 962), *S. iraiensis* (MCP no. 957), southern *S. speluncae* (MCP no. 988) and northern *S. speluncae* (MCP no. 1172). This picture illustrates differences in plumage color tonality between *S. pachecoi* and the other taxa: *S. pachecoi* is conspicuously darker than *S. novacapitalis*, somewhat lighter on belly and darker on throat and breast than *S. iraiensis* (though *S. pachecoi* may have lighter throat and breast) and is much lighter than both southern and northern *S. speluncae*. Note the barred flanks of *S. novacapitalis* and *S. pachecoi*.

The new species differs consistently in plumage characters, as well as in vocalizations (see below), from all other named taxa in the *S. speluncae* group – *S. novacapitalis*, *S. iraiensis* and *S. speluncae* (see below for a brief tentative characterization of the group; see figure 1). All males of *S. pachecoi* examined ($n = 23$, including adults and subadults) differed immediately from birds judged to be adult males of *S. speluncae* (those with plain or nearly plain-colored wings, without obvious light marks; $n = 24$) by having buff or ferruginous flanks conspicuously barred black or blackish, vs. flank feathers uniformly gray or with only vestigial barring (see cover). Exceptions are two *S. speluncae* at MZUSP (Nos. 6121 and 34804) and one at MHNCI (No. 5491) which have almost unmarked wing feathers but have obvious barring on the flanks, though all of them have darker gray underparts and duskier background color on the flanks than in *S. pachecoi*. On the other hand, a specimen of *S. speluncae* at MZUSP (No. 36347), despite having some light marks on the tertials, has nearly unbarred flanks. Younger males of *S. speluncae* – those with conspicuous light marks or bars on the wing feathers and sometimes brownish wash on the lower back ($n = 10$) – were most similar to *S. pachecoi* in having barred flanks (which

also may be a sign of immaturity), though they have, as the adult males, darker gray underparts, except on one specimen (MCP no. 1076), which has the belly and breast as light-gray as some specimens of *S. pachecoi*. It is important to note that the specimens MZUSP nos. 6121 and 34804, MHNCI no. 5491 and MCP no. 1076 come from areas where *S. speluncae* is the only representative of the group; additionally, MCP no. 1076 had a typical *S. speluncae* song (i.e. fast-paced series of notes; pers. obs.). Females of *S. pachecoi* ($n = 2$) and *S. speluncae* ($n = 15$) are apparently indistinguishable by plumage. *Scytalopus pachecoi* also has significantly greater wing length and body mass than the southern populations (eastern São Paulo southward) of *S. speluncae* (hereafter southern *S. speluncae*) which, in turn, may represent an additional undescribed species (see below); the body mass of northern populations of *S. speluncae* (hereafter northern *S. speluncae*) and *S. pachecoi* are similar, but those populations have significantly greater culmen, tail and tarsus lengths than *S. pachecoi* (table 1). From *S. iraiensis* the new tapaculo can be reliably distinguished by its buff flanks conspicuously barred blackish, instead of dark gray flanks with ($n = 3$ males, 1 female) or no ($n = 1$ male) weak irregular bars, by its dark

Table 1. Measurements (mm) of taxa in the *Scytalopus speluncae* group (males first). The values shown are: range, sample size (in parentheses), and mean \pm standard deviation. *Scytalopus pachecoi* have significantly (t -test) greater wing length ($P < 0.001$) and weight ($P < 0.001$) than southern *S. speluncae* and significantly smaller culmen ($P < 0.01$), tail ($P < 0.001$), and tarsus length ($P < 0.001$) than northern *S. speluncae*. Southern *S. speluncae* have significantly smaller culmen ($P < 0.01$), wing ($P < 0.001$), tail ($P < 0.001$) and tarsus ($P < 0.001$) than northern *S. speluncae* (see text).

Species / Characters	<i>S. pachecoi</i>	southern <i>S. speluncae</i>	northern <i>S. speluncae</i>	<i>S. iraiensis</i>	<i>S. novacapitalis</i>
Bill	5.0-6.0 (23) 5.5 \pm 0.27	5.1-5.8 (17) 5.4 \pm 0.21	5.1-6.5 (16) 5.4 \pm 0.38	5.1-5.7 (4) 5.4 \pm 0.25	6.4 (1)
♀♀	5.0, 5.6 (2)	4.8-5.5 (4) 5.2 \pm 0.34	4.8-5.8 (10) 5.3 \pm 0.34	5.0, 5.2 (2)	6.0 (1)
Bill depth	3.6-4.2 (22) 3.9 \pm 0.19	3.5-4.1 (13) 3.8 \pm 0.21	3.3-4.7 (15) 3.8 \pm 0.3	4.0-4.4 (3) 4.3 \pm 0.23	4.3, 4.7 (2)
♀♀	3.2, 3.8 (2)	3.4-3.7 (3) 3.6 \pm 0.15	3.5-4.0 (7) 3.7 \pm 0.17	4.2 (1)	4.3 (1)
Culmen	10.1-11.5 (23) 10.9 \pm 0.38	10.0-11.8 (17) 10.9 \pm 0.4	10.8-12.0 (16) 11.2 \pm 0.5	11.2-11.7 (3) 11.5 \pm 0.25	12.0 (1)
♀♀	10.3, 10.7 (2)	10.4-11.3 (4) 10.8 \pm 0.39	10.1-12.0 (9) 10.9 \pm 0.64	10.6 (1)	11.6 (1)
Wing (chord)	46.0-51.6 (23) 49.4 \pm 1.36	43.6-50.7 (17) 46.8 \pm 2.0	48.0-53.5 (17) 50.0 \pm 2.15	44.5-49.4 (5) 47.0 \pm 2.01	50.1, 53.8 (2)
♀♀	45.2, 48.4 (2)	43.3-49.0 (4) 45.9 \pm 2.34	44.8-49.5 (10) 47.7 \pm 1.35	43.3, 45.6 (2)	51.7 (1)
Tail	38.0-44.8 (21) 41.7 \pm 2.07	36.6-44.1 (14) 39.9 \pm 1.98	43.5-48.8 (16) 45.9 \pm 2.8	38.4-41.0 (4) 39.6 \pm 1.32	45.0, 48.2 (2)
♀♀	42.8 (1)	36.2-39.2 (3) 37.5 \pm 1.54	38.3-44.4 (10) 41.5 \pm 1.83	37.7, 38.2 (2)	45.2 (1)
Tarsus	18.3-20.1 (23) 19.1 \pm 0.46	18.0-19.8 (16) 18.8 \pm 0.46	19.1-21.3 (17) 20.2 \pm 0.72	17.7-19.6 (5) 18.7 \pm 0.86	19.9, 20.4 (2)
♀♀	17.9, 18.1 (2)	17.2-20.2 (4) 18.8 \pm 1.42	18.5-20.6 (10) 19.5 \pm 0.6	18.3, 18.5 (2)	19.2 (1)
Weight (g)	13.2-17.0 (23) 15.1 \pm 0.99	11.2-14.9 (13) 12.9 \pm 1.1	13.3-16.0 (6) 14.9 \pm 0.8	12.8-15 (5) 14.0 \pm 1.04	19.2 (2)
♀♀	13.0, 13.6 (2)	12.3-15.0 (3) 13.8 \pm 1.36	14.1-15.8 (4) 14.8 \pm 0.73	12.4, 12.4 (2)	18.6

gray instead of blackish upperparts and by its narrower tail. From *S. novacapitalis* (n = 2 males, 1 female and 3 unsexed), which may be its closest named relative (see below), *S. pachecoi* is diagnosed by having medium gray chin and throat, instead of pale gray, and by having the center of belly medium gray (n = 10 males) or variably lighter gray (n = 13 males, 1 female), rather than whitish. The available data suggest that these two species also differ in measurements and body mass, but note that the sample size for *S. novacapitalis* is very small (only characters showing no overlap in range are mentioned; valid for both sexes): *S. pachecoi* has a less elevated base of the bill, a somewhat shorter tail and is lighter-bodied. For descriptive statistics and sample sizes see table 1.

Diagnosis – Voice: *S. pachecoi* may be diagnosed in comparison to all other members of the genus by having in its vocal repertory a peculiar song type (apparently shared only with *S. novacapitalis* and a possibly undescribed form) whose final part is greatly accelerated into a trill-like end. Furthermore, it differs from all members of the *S. speluncae* group by having a very distinctive, semi-metallic contact call, which is monosyllabic and has several closely spaced harmonics (n = 9 individuals and 151 calls); both southern and northern *S. speluncae* have a short call which, perhaps, also function as a contact call, but it is clearly bisyllabic and has fewer and widely spaced overtones (n = 2 individuals and 60 calls for southern *S. speluncae*; n = 1 individual and 4 calls for northern *S. speluncae*). The alarm call of *S. pachecoi* also differs appreciably in note shape from the alarm calls of *S. novacapitalis* and southern and northern *S. speluncae*, each note showing a clear up-downward frequency modulation. From *S. novacapitalis* it further differs by its faster paced song, slower paced alarm call, higher pitched song notes, lower pitched alarm call notes and by having shorter song notes. From southern *S. speluncae*, *S. pachecoi* further differs by having a slower paced song and lower pitched alarm call notes. From northern *S. speluncae*, it is further distinguished by its slower paced song and shorter alarm call notes. From *S. iraiensis*, *S. pachecoi* also differs by having a slower paced song and higher pitched song notes; in addition, *S. iraiensis* has a short, mono- or bisyllabic call (thought to be an alarm call) which is very distinct from any call of *S. pachecoi* in note shape and structure (see spectrogram in Bornschein *et al.* 1998). See table 2 for a descriptive statistics of the diagnostic measures mentioned above and sample sizes; see spectrograms in figures 2-4.

Description of holotype. Possibly a very old bird, displaying the least amount of brown and barring in the plumage compared to the paratypes and to all other individuals of the new species collected. Plumage moderately worn, especially on the tail and tertial feathers. The gray hues mentioned below, corresponding to alphanumeric designations, were determined through comparisons with the Chart 1 for Gley of Munsell soil color charts (1994); capitalized color names (remaining colors) are according to Smithe (1975). Feathers surrounding base of maxilla dark gray (3/N) with a very narrow and inconspicuous blackish subterminal band. These feathers are somewhat stiffened and narrowed distally. Entire crown (including sides), nape, dorsal surface of neck, scapulars and upper back dark gray (near 3/N). The feathers of the forehead, like those surrounding the base of the maxilla, have indistinct subterminal blackish

bands. Lower back similar in color to the upper back but having a faint brownish cast posteriorly. Rump grayish brown with a slight wash of Cinnamon Brown (color # 33), especially on the feather tips. Upper tail coverts and rectrices Sepia (color # 219). Remiges and greater upper wing coverts Sepia (color # 219), lesser wing coverts dark gray (near 3/N). Loral feathers pale to medium gray (near 6/N), conspicuously stiffened and with darker tips. Auriculars, malar region and sides of body medium gray (between 4/N and 5/N). Sides of neck dark gray (near 3/N). Flank feathers Buff (color # 124) or slightly more rufescent, with well marked black or blackish transverse bars 1.7–2.9 mm in width. This barring pattern, roughly corresponding to six interposing bands of black and buff, extends over some 2 cm on the flanks. Chin, throat, upper and lower breast, belly and crissum medium gray (between 5/N and 4/N). Under tail coverts Buff (color # 124) with some dark bars which are narrower than in the flanks. Tibial feathers medium gray with a faint brownish suffusion. Under wing coverts medium gray (near 5/N). Soft parts colors: iris dark brown; bill blackish with pale brown to buff on the mandibular rami, sides of the genys and on a narrow fringe in the tomia; claws Sepia (color # 219); acrotarsus Raw Umber (color # 123); plantar surface of the tarsus Hair Brown (color # 119^A). Tail with eleven rectrices, the outermost on the left side anomalous, greatly narrowed and shorter than its equivalent of the right side.

Measurements of holotype. Bill, 5.8 mm; exposed culmen, 10.9 mm; bill depth at the base (slightly posterior to the nares), 3.8 mm; wing (chord), 49.1 mm; tail, from the insertion of the central rectrices to their tips, 38.0 mm; tarsus, 19.4 mm; mass, 14.8 g.

Variation in the type series. Besides the holotype, only two other specimens within the type series were regarded to be full adult males (MCP no. 962 and MZUSP no. 75764). These birds are similar to the holotype, except for the following features: one is much larger (mass 16.3 g, wing chord 51.4 mm, tail 44.8 mm) while the other is the smallest specimen of the entire series (mass 13.2 g, wing chord 48.2 mm, tail 38.1); the two have a more pronounced brownish wash on the rump, which posteriorly have some dark bars; the gray tonality of the underparts in the smaller bird is slightly lighter (nearly approaches 5/N) and some feather margins on the belly are pale gray; they have tiny indistinct darker/lighter marks to the tips of two outermost tertials and on some upper-tail coverts; and they have more extensive barring on the flanks (2.5-2.7 cm) and on the under-tail coverts.

Since the *Scytalopus* species generally molt into plumages with less amount of brown (the grayest birds are the oldest; cf. Naumburg 1937, Krabbe and Schulenberg 1997), birds with more brown in their plumage were considered to be subadults, though some of them (those with “wing bars”) may represent immatures. The remaining nine males in the type series have the lower back conspicuously washed brownish and their tail more dusky-brown; their tertials also have a conspicuous subterminal black spot/bar and a terminal light mark on the outer web, while the greater wing coverts (in some cases also the lesser) are variably suffused with brownish. Thus, these were judged to be subadults. Six specimens (MCP nos. 960, 961, 977, 1009 and 1082, MZUSP no. 75763) have a somewhat lighter gray center of belly merging into the buff of the crissum, which has a variable amount of barring. Four

Table 2. Measures of selected variables of songs and calls of taxa in the *S. speluncae* group: pace (notes per second), song duration (in seconds), frequency (in kHz) and note length (in seconds). Frequency values refers to the top of the fundamental of individual notes. Values shown are range and mean \pm standard deviation. Fully diagnostic measures (i.e. without overlap in range) distinguishing *S. pachecoi* from one or more taxa are as follows: pace of the song (from all taxa); frequency of the fundamental of song notes (from *S. iraiensis* and *S. novacapitalis*); length of the song note (from *S. novacapitalis*); pace of alarm call (from *S. novacapitalis*); frequency of the fundamental of alarm call notes (from southern *S. speluncae* and *S. novacapitalis*); and length of the alarm call notes (from northern *S. speluncae*). Furthermore, *S. pachecoi* differs from all taxa but *S. novacapitalis* by having in its vocal repertory a peculiar, acceletaring song; note that the pace of the slow section of this song type differs between these two species, as is the case of normal songs.

Species / Characters	<i>S. pachecoi</i>	southern <i>S. speluncae</i>	northern <i>S. speluncae</i>	<i>S. iraiensis</i>	<i>S. novacapitalis</i>
Song ¹	n = 95 indiv. and 98 songs	n = 41 indiv. and 43 songs	n = 5 indiv. and 5 songs	n = 6 indiv. and 8 songs	n = 6 indiv. and 8 songs
Pace	2.01-3.36 (2.7 \pm 0.27)	4.56-5.86 (5.06 \pm 0.31)	5.17-5.74 (5.44 \pm 0.26)	4.05-5.8 (4.82 \pm 0.61)	1.03-1.19 (1.1 \pm 0.063)
Duration	32-300 (102.8 \pm 55.31)	26-165 (86.5 \pm 42.72)	-	54-298 (167.2 \pm 98.7)	194-743 (361.5 \pm 215.2)
Frequency	4.1-6.4 (4.93 \pm 0.4)	3.7-5.5 (4.62 \pm 0.4)	2.3-5.1 (3.83 \pm 1.24)	2.3-3.4 (2.87 \pm 0.35)	2.7-3.5 (3.14 \pm 0.22)
Note length	0.032-0.062 (0.048 \pm 0.005)	0.029-0.056 (0.047 \pm 0.006)	0.052-0.072 (0.064 \pm 0.007)	0.024-0.044 (0.032 \pm 0.006)	0.076-0.102 (0.09 \pm 0.006)
Accelerating song ²	n = 10 indiv. and 12 songs	-	-	-	n = 1-2 indiv. and 3 songs
Pace of the slow section	2.64-3.17 (2.89 \pm 0.2)	-	-	-	1.0-1.2 (1.12 \pm 0.12)
Pace of the transition	3.51-6.71 (4.93 \pm 1.1)	-	-	-	2.45-3.6 (2.86 \pm 0.64)
Pace of the trilled section	6.03-10.1 (8.49 \pm 1.42)	-	-	-	7.03-9.66 (8.73 \pm 1.47)
Duration of the entire song	12.5-23.0 (18.86 \pm 3.53)	-	-	-	31.1-54.5 (40.67 \pm 12.28)
Duration of the transition	1.1-4.83 (2.87 \pm 1.28)	-	-	-	2.22-7.76 (4.76 \pm 2.79)
Duration of the trilled section	0.65-7.26 (3.3 \pm 1.89)	-	-	-	2.73-4.55 (3.6 \pm 0.91)
Frequency	4.6-5.8 (5.31 \pm 0.3)	-	-	-	4.4-4.7 (4.49 \pm 0.09)
Note length	0.028-0.039 (0.034 \pm 0.003)	-	-	-	0.029-0.034 (0.031 \pm 0.001)
Alarm call ³	n = 8 indiv. and 154 calls	n = 7 indiv. and 110 calls	n = 2 indiv. and 11 calls	-	n = 2 indiv. and 41 calls
Pace	6.13-9.8 (7.86 \pm 0.94)	6.38-10.43 (8.55 \pm 1.07)	2.65-6.69 2.98, 6.44	-	12.9-15.6 13.64, 14.71
Frequency	1.8-2.3 (2.09 \pm 0.14)	3.6-4.6 (3.93 \pm 0.27)	1.8-2.0 1.8, 2.0	-	3.1-3.7 3.3, 3.58
Note length	0.031-0.047 (0.039 \pm 0.004)	0.041-0.069 (0.053 \pm 0.008)	0.072-0.096 0.073, 0.094	-	0.023-0.036 0.024, 0.034

¹ Number of recordings adequate for measurements of song duration (complete and nearly complete recorded series of notes) were as follows: 63 for *S. pachecoi*, 27 for southern *S. speluncae*, none for northern *S. speluncae*, 8 for *S. iraiensis* and 6 for *S. novacapitalis*. Frequency and note length measurements were not possible for 7 songs of *S. pachecoi* and one of southern *S. speluncae*.

² This song type is absent from the vocal repertory of both southern and northern *S. speluncae* and from that of *S. iraiensis*. Pace measurements are given separately for each of the three distinct sections of this song type: slow-paced section (main part of the song); transition (i.e. when inter-note intervals become increasingly shorter before the pace stabilize into the final section); and trilled section (accelerated final section of the song). Two recordings were too incomplete for measurements of the total duration of this song type. The values of frequency and note length presented for this song refers only to the trilled section; for *S. pachecoi* measurements of these variables were not possible in four songs.

³ For northern *S. speluncae* and *S. novacapitalis* the values shown below range are the mean of the measures obtained for each of the two individuals whose calls were available. The number of alarm call notes was variable: *S. pachecoi* = 3-7, most often 4; southern *S. speluncae* = 3-9, most often 5; northern *S. speluncae* = 1-4, most often 2-3; *S. novacapitalis* = 6-12, most often 9.

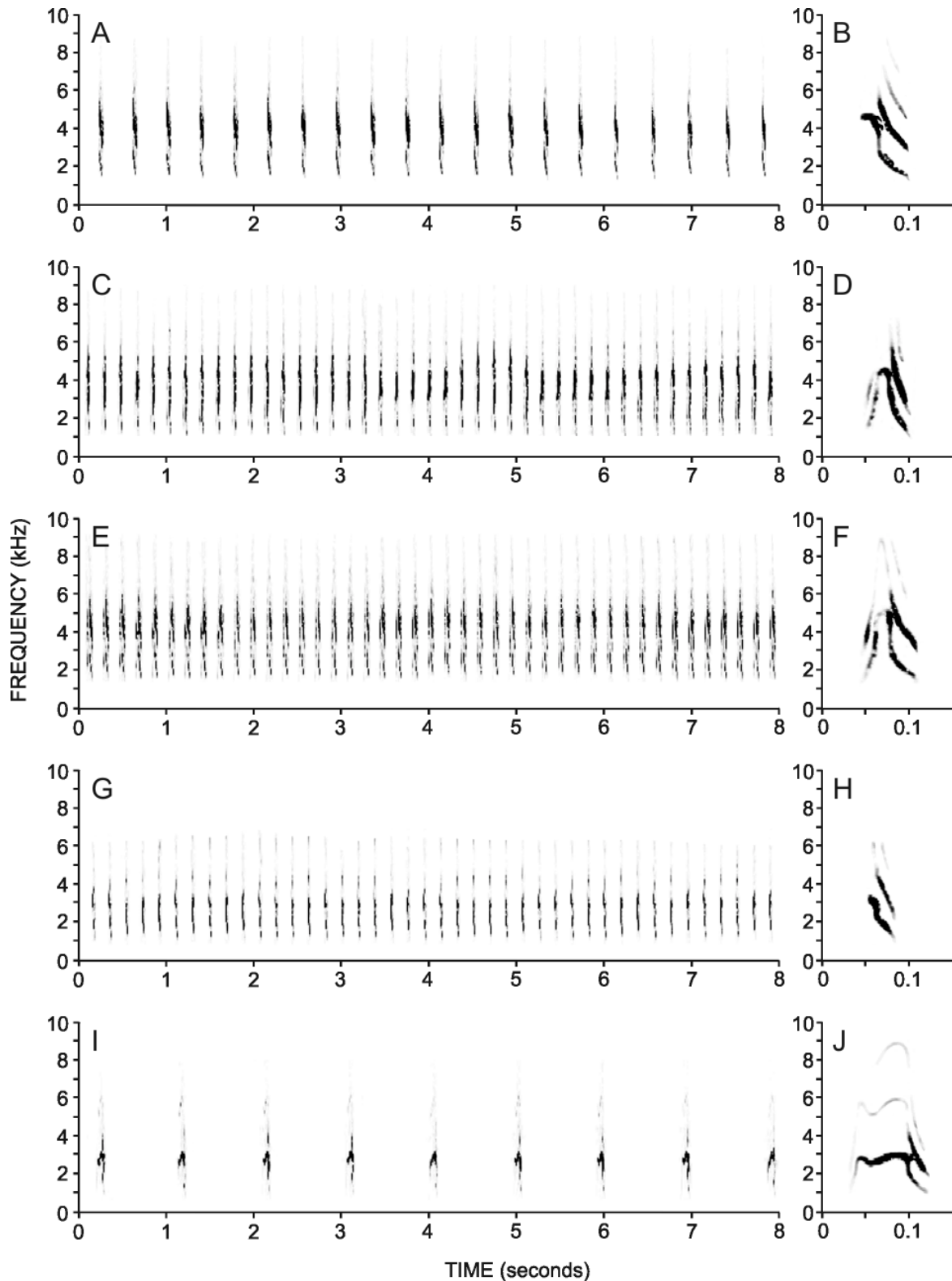


Figure 2. Spectrograms of songs of taxa in the *Scytalopus speluncae* group. (A) *S. pachecoi*; Cerro das Almas, Capão do Leão, Rio Grande do Sul, 8 January 2003 (after playback); adult male, holotype (MCP no. 1179). (B) Song note of *S. pachecoi* in detail. (C) Southern *S. speluncae*; Serra do Umbu, Maquiné, Rio Grande do Sul, 16 December 2001 (after playback); adult male (MCP no. 988). (D) Song note of southern *S. speluncae* in detail. (E) Northern *S. speluncae*; Pico dos Marins, Piquete, São Paulo, 12 October 2002 (after playback); adult male (MCP no. 1177). (F) Song note of northern *S. speluncae* in detail. (G) *S. iraiensis*; Banhado do Maçarico, Rio Grande, Rio Grande do Sul, 1 December 2000 (unsolicited song; after playback, the pace was essentially the same); adult male (MCP no. 958). (H) Song note of *S. iraiensis* in detail. (I) *S. novacapitalis*; Ribeirão do Gama, Brasília, Distrito Federal, 17 July 2004 (after playback); adult male (MCP no. 1481). (J) Song note of *S. novacapitalis* in detail. Spectrograms in B, D, F, H and J represent an enlargement of 10 times in the time scale of A, C, E, G and I. Spectrograms in A, C, E, G and I illustrate the differences in song pace between *S. pachecoi* and the other taxa (the measures for each individual refer to the pace of the entire sequence, of which only an eight seconds section is shown): *S. pachecoi*, c. 2.6 notes/s; southern *S. speluncae*, c. 5.3 notes/s; northern *S. speluncae*, c. 5.7 notes/s; *S. iraiensis*, c. 5.1 notes/s; *S. novacapitalis*, c. 1.1 notes/s. All recordings by the author.

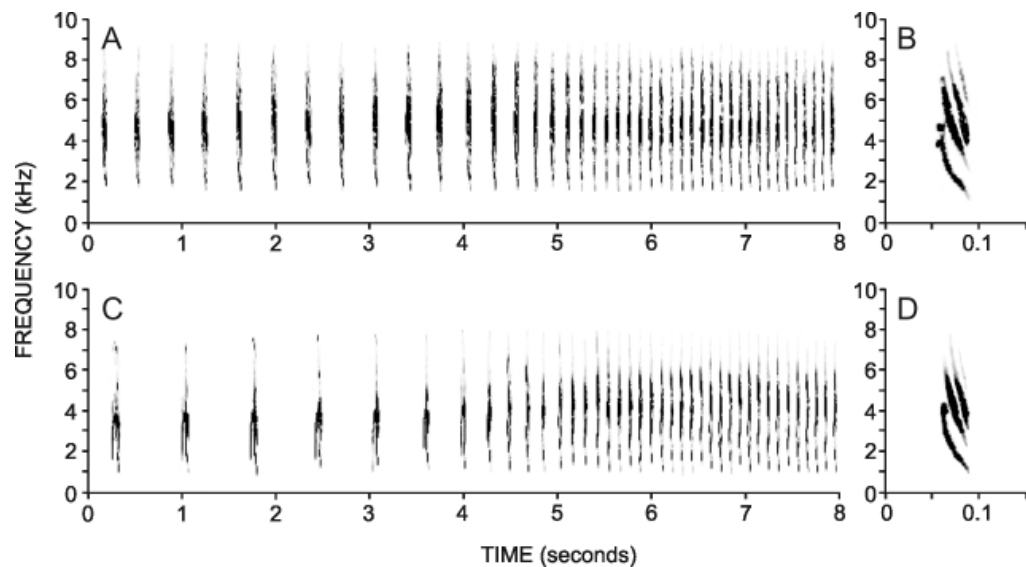


Figure 3. Spectrograms of accelerating songs of two species in the *Scytalopus speluncae* group. (A) *S. pachecoi*; Cerro das Almas, Capão do Leão, Rio Grande do Sul, 29 December 2001 (after playback); presumed adult female (identified by plumage). (B) Note of the accelerated section of the song of *S. pachecoi* in detail. (C) *S. novacapitalis*; Reserva Ecológica do IBGE, Brasília, Distrito Federal, 24 September 1981 (after playback); tape-recorded by J. Vielliard. (D) Note of the accelerated section of the song of *S. novacapitalis* in detail. Only the final section of each song is illustrated (some final notes of both songs are not shown). Spectrograms in B and D represents an enlargement of 10 times in the time scale of A and C. Note the similar pace of the accelerated section of the two sequences, in both cases with about 10 notes/s. This song type is very unusual within Rhinocryptidae, and possibly represents a synapomorphy for these two taxa (see text). Tape-recordings of spectrograms A and B by the author.

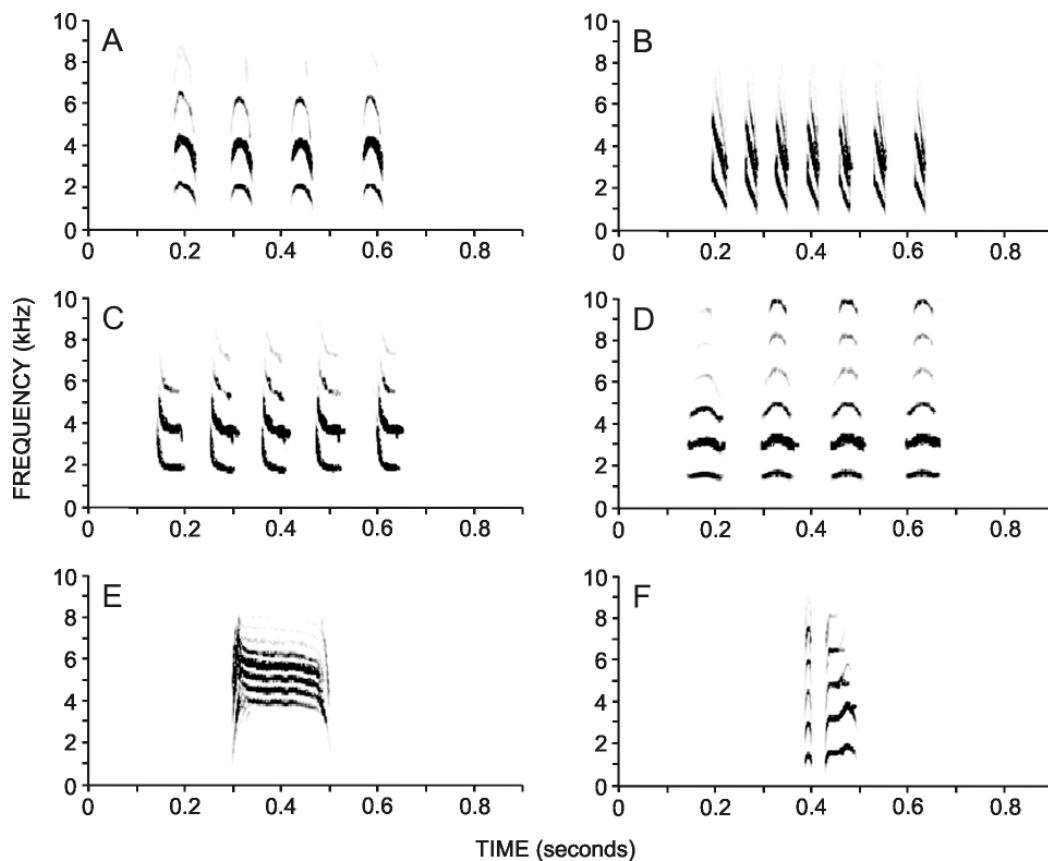


Figure 4. Spectrograms of calls of taxa in the *Scytalopus speluncae* group. (A) *S. pachecoi*; alarm call, Serra das Asprezas, Piratini, Rio Grande do Sul, 18 June 2004 (unsolicited). (B) *S. novacapitalis*; alarm call, Reserva Ecológica do IBGE, Brasília, Distrito Federal, 24 September 1981 (unsolicited?); tape-recorded by J. Vielliard. (C) Southern *S. speluncae*; alarm call, Serra do Umbu, Maquiné, Rio Grande do Sul, 16 December 2001 (unsolicited); adult female (MCP no. 987). (D) Northern *S. speluncae*; alarm call, Serra do Bananal, Bananal, São Paulo, 20 March 1995 (unsolicited); tape-recorded by D. R. C. Buzzetti. (E) *S. pachecoi*; contact call (“pzeen”), Cerro das Almas, Capão do Leão, Rio Grande do Sul, 14 September 2002 (unsolicited); subadult or immature male, paratype (MCP no. 1082). (F) Southern *S. speluncae*; bisyllabic call, Josafaz, São Francisco de Paula, Rio Grande do Sul, 3 September 2002 (unsolicited). Notice that the alarm calls of the taxa differ from one another in note shape. All recordings by the author, except when otherwise noted.

specimens (MCP nos. 959, 961 and 1082, MZUSP no. 75761) have a brownish suffusion over the mantle on a variable degree of intensity, in one case extending to the nape, and have a “wing bar” formed by subterminal blackish spots and terminal buff-cinnamon marks on the outer web of the greater wing coverts. These four individuals also have more extensive barring over the flanks (3-3.4 cm), which may have a darker back-ground color, toward cinnamon or rufous, extending variably over the rump and sides of body. The only female in the type series (MCP no. 1022) is very different from all males collected. This specimen has the entire underparts buff to ochraceous-tawny (with some grayish feathers), widely barred flanks, and entirely brown upperparts.

The number of rectrices was variable within the type-series, with four birds presenting 12, four others having 11 and two having 10 rectrices. Similar variation is found in the other populations of the new species and also in *S. speluncae*, *S. novacapitalis* and in several Andean forms (Krabbe and Schulenberg 1997, Bornschein *et al.* 1998).

Interpopulational variation within S. pachecoi. Besides the external variation observed within the type series (intrapopulational), some interpopulational differences also occur in the new species. The large proportion (75%) of male paratypes with a conspicuous amount of brown on their upperparts, including on the upper wing coverts, contrasts with the generally grayer birds obtained from the Planalto population. As shown above, small buffish marks or blotches bordered by black spots/bars were also variably present in the tertials, upper wing coverts and on the upper tail coverts of that paratypes which, therefore, were judged to be subadults. All nine male specimens from the Planalto population showed their upper wing coverts uniformly gray, and six showed little or almost no brown on their upperparts and inconspicuous or no spots on the tertials, being most similar to the holotype. The other three birds, the brownest males of the Planalto population, showed a more pronounced amount of brown in the lower back and rump, and a faint brownish tinge over the tertials and tail while the wing marks, when present, were only incipient and mainly restricted to the tertials. The two specimens from northern Rio Grande do Sul (Misiones population) are similar in plumage to the birds from Planalto. The three brownest individuals of the Planalto population and one from northern Rio Grande do Sul were tentatively regarded as subadults.

Geographical distribution. Three populations of the new species, occupying distinct regions of southern Brazil and adjacent northeastern Argentina, were found (figure 5). One of these populations occupies the Serra do Sudeste of southern Rio Grande do Sul (“southeastern hills” of Belton 1984, 1985). At Serra do Sudeste, *S. pachecoi* occurs between 30°50' and 31°47' of south latitude and between 52°18' and 53°15' of west longitude. In this region the species inhabits primarily the forests on the eastern slopes of the Serra, but also ranges upstream along the Rio Camaquã valley to at least 53°W. To a much lesser extent the species occupies lowland areas where some forested connection exists between the slope forests to the west and the coastal plain to the east. The species' altitudinal range verified in this region extends from about 10 to 400 m a.s.l., though the center of distribution seems to be 100-350 m a.s.l. All published records from this general area under the name *S. speluncae* (Belton 1985,

Maurício and Dias 1998, 2001) are referable to *S. pachecoi*.

Since 1919, *S. pachecoi* has been found in Misiones Province, Argentina, though it has been confused with *S. speluncae* by all authors (e.g. Bertoni 1919, Naumburg 1937, Gai 1951, Partridge 1954). *Scytalopus pachecoi* apparently ranges widely in the northern and eastern half of Misiones, reaching the adjacent northern sector of Rio Grande do Sul. In Brazil, this population was sampled in the Parque Estadual do Turvo (27°14'S, 53°57'W) and at the indigenous settlements of Nonoai / Rio da Várzea (27°21'S, 52°57'W) and Guaritas (27°27'S, 53°37'W), all sites in Rio Grande do Sul. The new species was also observed and tape-recorded at San Pedro, eastern Misiones Province, Argentina, near the Río Peperi-Guazu, at 26°36'S, 53°43'W. Photographs and detailed descriptions of 18 specimens from Arroyo Uruguayí and other areas in north-central Misiones (housed at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” and at the American Museum of Natural History), provided by J. Mazar-Barnett and L. F. Silveira, confirm that the records mentioned by Gai (1951) and Partridge (1954) represent *S. pachecoi*. Additionally, a sound recording from this same general area presented in a commercially available cassette (Straneck 1990) represents a typical song of *S. pachecoi*. The altitudinal range occupied in this region is from about 120 to 600 m a.s.l. The new species probably also occurs in the adjacent sectors of western Paraná and Santa Catarina states, although surveys conducted in these regions by the author and M. R. Bornschein failed to locate it.

Birds identified as *S. speluncae* in Depto. Caazapá, eastern Paraguay (Brooks *et al.* 1995), could well represent *S. pachecoi*. However, Hayes (1995) regarded the species' presence in Paraguay as “hypothetical” due to the complete lack of documentation and Bertoni (1919) stated that the species does not cross the Rio Paraná from Misiones into the Paraguayan territory. These Paraguayan records are, therefore, best regarded as doubtful.

Another population of *S. pachecoi* is found on the higher sectors of the Planalto Meridional (here called simply Planalto) above the Serra Geral escarpment in northeastern Rio Grande do Sul and adjacent southeastern Santa Catarina. In this region, in part also known as “Campos de Cima da Serra”, the species occupies forested valleys in the upper reaches of Rio Pelotas and Rio das Antas basins, at least between 28°18'S and 29°09'S. This population appears locally confined to the araucaria forests (characterized by the presence of the Parana Pine *Araucaria angustifolia*) at altitudes ranging from 980 to 1,500 m a.s.l., and is apparently absent downstream in these river basins. Intensive searches for *S. pachecoi* in areas only about 30 km downstream from confirmed recording sites revealed the exclusive presence of the southern *S. speluncae*, which ranges upstream and occurs syntopically with *S. pachecoi* in a few places (see below). The new species also occurs very locally at the Planalto edge near the escarpment, as confirmed by a specimen collected and tape-recorded near Serra do Rio do Rastro, Bom Jardim da Serra municipality (Santa Catarina), and by birds heard at the edge of Itaimbezinho Canyon in the Aparados da Serra National Park. At several other sites in the Planalto edge only southern *S. speluncae* was found.

The three populations of *S. pachecoi* appears to be isolated from each other, since extensive field work by Belton

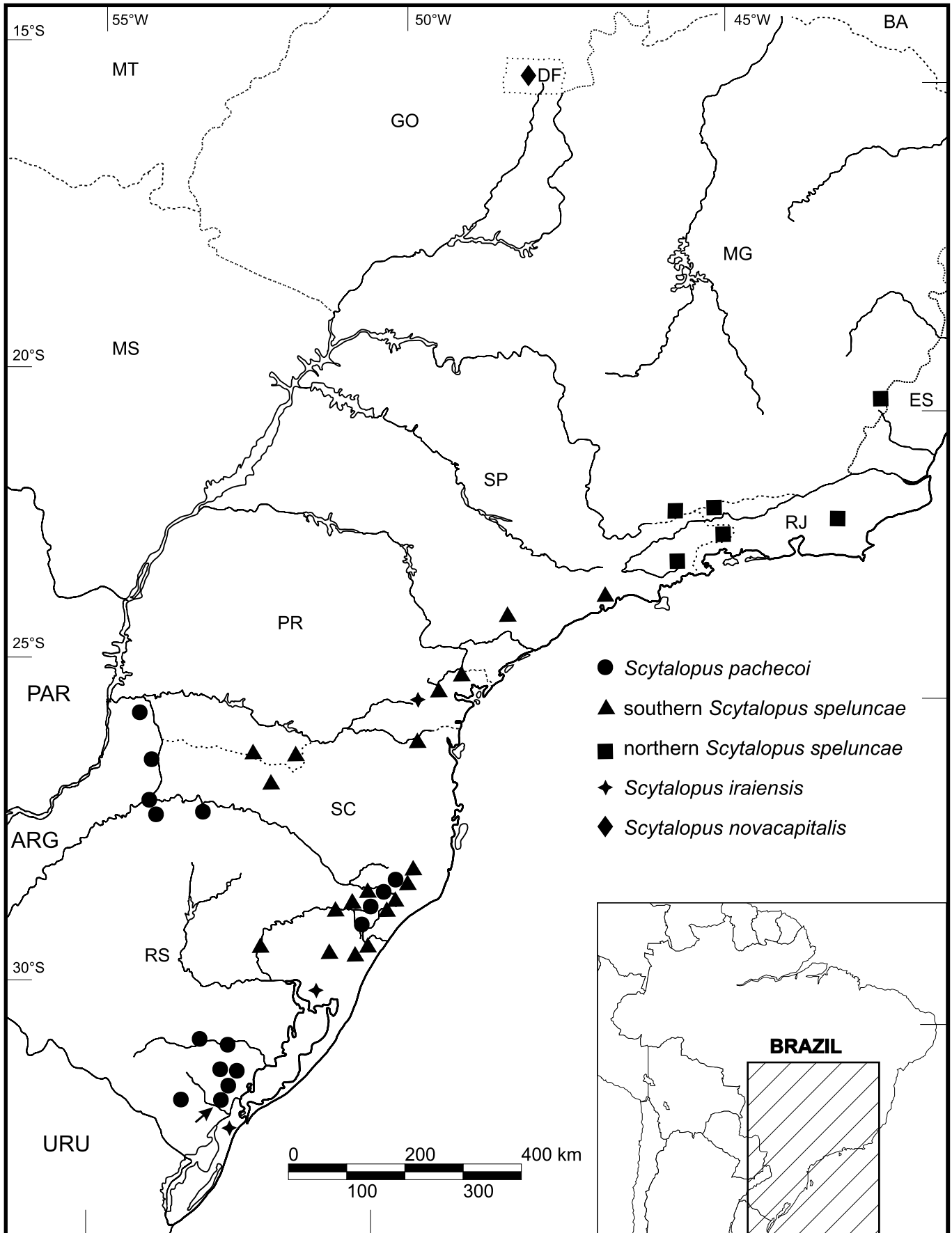


Figure 5. Distribution of taxa in the *Scytalopus speluncae* group, as confirmed by examination of specimens and tape-recordings. Note that *S. pachecoi* occurs disjunctly in three areas of southern Brazil and adjacent Argentina. Also note that *S. pachecoi* and southern *S. speluncae* are sympatric in northeastern Rio Grande do Sul and southeastern Santa Catarina. Populations of the *S. speluncae* group occupying the central-eastern and western sectors of Minas Gerais as well as central and southern Bahia are not mapped (see text). An arrow indicates the type-locality of *S. pachecoi*. Some symbols represents more than one locality. PAR = Paraguay; ARG = Argentina; URU = Uruguay.

(1984, 1985) and others (e.g. Bencke 1996) at several localities along the gaps did not find any *Scytalopus* species or revealed only the presence of southern *S. speluncae* (G. A. Bencke, pers. comm.). However, there is a report of *S. speluncae* for a locality in the upper Rio Uruguay (Albuquerque 1983), half way between Misiones and the Planalto highlands; this record may represent *S. pachecoi*, but it appears to be undocumented and intensive searches by the author and G. A. Bencke in 2000/2001 failed to find any *Scytalopus* species in the same area.

Non-type specimens examined. The following list complements the material of *S. pachecoi* gathered for this study. Rio Grande do Sul: MCP no. 1040, adult male, upper Rio das Antas (28°47'S, 49°58'W), São José dos Ausentes municipality, 6 May 2002; MCP no. 1015, adult male, same locality as the latter, 20 March 2002; MCP no. 1016, upper reaches of das Contas creek, same municipality as before, 21 March 2002; MCP no. 1043, subadult male, São Gonçalo creek (28°53'S, 50°01'W), municipality of Cambará do Sul, 6 May 2002; MCP no. 1075, subadult male, from the northern edge of Cambará do Sul town (29°02'S, 50°08'W), 25 August 2002; MCP no. 1039, adult female, upper Rio das Antas, municipality of São José dos Ausentes, 6 May 2002; MCP no. 994, adult male, Parque Estadual do Turvo (27°14'S, 53°57'W), municipality of Derrubadas, 17 January 2002; MCP no. 1174, subadult male, near Terra Indígena de Nonoai / Rio da Várzea (27°21'S, 52°57'W), municipality of Nonoai, 21 December 2002. Santa Catarina: MCP no. 1188, adult male, edge of Bom Jardim da Serra town (28°20'S, 49°37'W), 21 November 2002; MCP no. 1190, adult male, same locality and date as the latter; MCP no. 1183, subadult male, Fazenda Rocinha (28°18'S, 49°35'W), municipality of Bom Jardim da Serra, 22 November 2002; MCP no. 1189, adult male, Serra do Rio do Rastro, at the Planalto edge, Bom Jardim da Serra / Lauro Müller border (28°23'S, 49°32'W), 23 November 2002

Additional specimens examined – presumably related species. Specimens of three other recognized species and of presumably undescribed taxa were examined for this study, all of which have been attributed to the *S. speluncae* group. For each specimen, locality (when available) and municipality of origin (when possible), the number of specimens, institution, label number and sex are mentioned (m = male; f = female; ? = sex unknown).

Scytalopus sp. – Bahia: Ibicoara (2) (MN nos. 42741 [m] and 42472 [f]); Bonito (2) (MN nos. 43053 [m], 43054 [f]). Additionally, 13 uncatalogued specimens (eight males, three females and two unsexed birds) from the Serra do Caraça, on the Espinhaço Range of Minas Gerais, were examined; these specimens are housed at MZUSP, MCP and DZUFRJ.

Scytalopus speluncae (southern populations). – São Paulo: Alto da Serra (1) (MZUSP no. 4836 [f]). Paraná: Fazenda Tunas, Clevelândia (MHNCI no. 5491 [m]); Corvo, Quaro Barras (1) (MHNCI no. 3193 [f]); Mananciais da Serra, Piraquara (1) (MN no. 38757 [m]); Morro Anhangava, Quatro Barras (1) (MN no. 38751 [f]); General Carneiro (1) (MCP no. 01106 [m]); Coqueiro, Campina Grande do Sul (2) (MCP nos. 01175 [m], 01176 [m]). Santa Catarina: Limoeiro, Água Doce (1) (MHNCI no. 3452 [m]); Fazenda Naderer, São Bento (1) (MN no. 13400 [?]). Rio Grande do Sul: Santo Antônio, São Francisco de Paula (3) (MCP nos. 983 [m], 984 [m], 985 [m]); Serra do Umbu, Maquiné (2) (MCP nos. 987

[f], 988 [m]); Colinas de São Francisco, São Francisco de Paula (1) (MCP no. 1169 [m]); Passo do Meio, São Francisco de Paula (1) (MCP no. 1213 [m]); Passo do Meio, Bom Jesus (1) (MCP no. 1083 [m]); Josafaz, São Francisco de Paula (1) (MCP no. 1076 [m]); Serra da Boa União, Três Forquilhas / São Francisco de Paula (1) (MCP no. 1170 [m]); Morro Pelado, Canela (1) (MCN/FZB no. 1413 [m]); Lajeadozinho, São José dos Ausentes (1) (MNC/FZB no. 2082 [m]); Farroupilha (2) (MCN/FZB nos. 2093 [m], 2112 [m]); ? (MCN/FZB no. 2535 [?]).

Scytalopus speluncae (northern populations). – Minas Gerais: Serra do Caparaó (5) (MN nos. 26267 [m], 27035 [m], 27036 [m], 26281 [m], 14202 [m]); Delfim Moreira (2) (MCP nos. 01172 [m], 01173 [f]). Rio de Janeiro: Fazenda Toledo, Nova Friburgo (4) (MN nos. 36652 [m], 36655 [f], 36653 [f], 36656 [f]). Serra do Itatiaia (10) (MZUSP nos. 34804 [m], 36347 [m], 6121 [m], 34381 [m], 34807 [f], 34805 [f], 36349 [f], 34806 [?]; MN nos. 14206 [?], 14205 [?]). São Paulo: Catuçaba, São Luiz do Paraitinga (4) (MHNT nos. 3057 [m], 3732 [m], 3529 [m], 3733 [m]); Pico dos Marins, Piquete (4) (MHNT nos. 4268 [m], 4330 [f], 4327 [?]; MCP no. 1177 [m]); Guaratinguetá (1) (MHNT no. 3036 [f]); Pindamonhangaba (1) (MHNT no. 4356 [f]); Serra de Bananal (1) (MN no. 25845 [m]). Additionally, an uncatalogued specimen (male) from Boa Nova, Bahia, was examined at DZUFRJ; it apparently represent a distinct taxon, presently included in *S. speluncae* (see Krabbe and Schulenberg 2003).

Scytalopus iraiensis. – Paraná: rio Iraí, Quatro Barras (3) (MN nos. 43378 holotype [f], 43379 paratype [m], 43380 paratype [m]); two additional paratypes, now housed at the Museu Paraense Emílio Goeldi, Belém do Pará (nos. 52945 [m] and 52944 [f]), were examined before deposition at that institution. Rio Grande do Sul: Banhado do Maçarico, Rio Grande (2) (MCP nos. 957 [m], 958 [m]).

Scytalopus novacapitalis. – Distrito Federal: Brasília (3) (MN nos. 27906, holotype [m], 27905, paratype [?]; also an unsexed paratype in alcohol); Reserva Ecológica do IBGE, Brasília (1) (MZUSP no. 71007 [f]); Fazenda Água Limpa, Brasília (1) (COMB no. 2628 [?]); Ribeirão do Gama, near the village of Vargem Bonita, Brasília (1) (MCP no. 1481 [m]).

Voice specimens examined. Unless otherwise stated, tape-recordings listed here were obtained by the author and are not yet deposited at sound archives. When recordings are associated with collected specimens the latter's label number is given in brackets. For each set of recordings general localities are followed by the names of municipalities.

Scytalopus pachecoi. – **“Serra do Sudeste population”.** Brazil: Rio Grande do Sul: Cerro das Almas, Capão do Leão, song (n = 20, representing at least 19 individuals [including MCP nos. 1082 and 1179, MZUSP no. 75762]), “accelerating” song (n = 7, representing 6 individuals), contact call (n = 116, from three individuals [including MCP no. 1082]) and alarm call (n = 20, from the same bird); Santo Amor, Morro Redondo, song (n = 4, representing four individuals [including MCP no. 977 and MZUSP no. 75763]) and “accelerating” song (n = 1); Serra das Asperezas, Piratini, contact call (n = 26, from the same individual) and alarm call (n = 29, from three birds); Arroio Santa Bárbara, Pelotas, song (n = 2, from the same individual) and contact call (n = 2, from two individuals); Monte Bonito, at highway BR 392, Pelotas, song (n = 1) and “accelerating” song (n = 1 [MCP no. 1022]);

Morro da Antena, Pelotas, song (n = 2, from the same individual [MCP no. 960]) and contact call (n = 2, from two individuals); Arroio do Ouro, Morro Redondo, song (n = 1); Arroio Cadeia, Morro Redondo, song (n = 1 [MCP no. 959]); upper Arroio Cadeia, Morro Redondo, song (n = 1); Santa Eulália, Morro Redondo, song (n = 1); Arroio Andrade headwaters, Pelotas / Arroio do Padre border, song (n = 1 [MCP no. 962]); first District (a municipality subdivision) of Canguçu, Canguçu, song (n = 2, from different birds); Colônia Cerrito Alegre, Arroio do Padre, song (n = 2, from two birds); upper Arroio Moinho, Canguçu, song (n = 1 [MCP no. 961]); Harmonia, São Lourenço do Sul, song (n = 1 [MCP no. 1009]) and “accelerating” song (n = 1); Colônia Solidez, Canguçu, song (n = 1 [MZUSP no. 75764]); Paredão, Encruzilhada do Sul, song (n = 1). **“Planalto population”**. Brazil: Rio Grande do Sul: upper Rio das Antas, São José dos Ausentes, song (n = 8, from eight different individuals [including MCP nos. 1015, 1040 and 1039]) and alarm call (n = 61, from two birds); Arroio das Contas, São José dos Ausentes, song (n = 2, from two birds [including MCP no. 1016]); Arroio Santa Rosa, São José dos Ausentes, song (n = 2, from two birds) and contact call (n = 4, from two birds); upper Rio Camisas, Cambará do Sul, alarm call (n = 1); periphery of Cambará do Sul town, song (n = 3, from three individuals [including MCP no. 1075]) and contact call (n = 2, from two birds); Ouro Verde, Cambará do Sul, song (n = 2, from different birds); Arroio São Gonçalves, Cambará do Sul, song (n = 3, from three birds). Santa Catarina: border of Bom Jardim da Serra town, song (n = 6, from six individuals [including MCP nos. 1188 and 1190]); Fazenda da Rocinha, Bom Jardim da Serra, song (n = 5, from five individuals [including MCP no. 1183]) and “accelerating” song (n = 1); 7 km east of Bom Jardim da Serra town, song (n = 2, from two individuals); Serra do Rio do Rastro (at the Planalto edge), on the Bom Jardim da Serra / Lauro Müller border, song (n = 2, from the same individual [MCP no. 1189]). **“Misiones population”**. Brazil: Rio Grande do Sul: Parque Estadual do Turvo, Derrubadas, song (n = 14, representing at least 12 individuals) and alarm call (n = 43, from the same individual); Terra Indígena de Guarita, Erval Seco, song (n = 2, from two birds). Argentina: Misiones: Ruta Provincial 20, at the Río Peperi-Guazu valley (near Brazilian border), San Pedro, song (n = 1); Parque Provincial islas Malvinas (now included in the Parque Provincial Arroyo Urugua-í), “accelerating” song (n = 1, from Straneck 1990).

Scytalopus speluncae (northern populations). – Brazil: Minas Gerais: road to Marmelópolis, Delfim Moreira, song (n = 3, from three birds). Rio de Janeiro: Parque Nacional da Serra dos Órgãos, Teresópolis, alarm call (n = 3, apparently from the same individual) and bisyllabic call (n = 4, apparently from the same individual), L. P. Gonzaga (from Gonzaga and Castiglioni 2001). São Paulo: Pico dos Marins, Piquete, song (n = 1 [MCP no. 1177]); Serra do Bananal (Serra da Bocaina region), Bananal, song (n = 1) and alarm call (n = 8, from the same individual; D. R. C. Buzzetti).

Scytalopus speluncae (southern populations). – Brazil: Rio Grande do Sul: Santo Antônio, São Francisco de Paula, song (n = 4, from three individuals [MCP nos. 983, 984 and 985]); Serra do Umbu, Maquiné, song (n = 1 [MCP no. 988]) and alarm call (n = 18, from two birds [including MCP no. 987]); Arroio Barreiro, Bom Jesus, alarm call (n = 47, from the same bird); Matemático, Bom Jesus, song (n = 3, from

three individuals); Monte Negro, São José dos Ausentes, song (n = 1); Colinas de São Francisco, São Francisco de Paula, song (n = 4, from different individuals [including MCP no. 1169]); Passo do Meio, São Francisco de Paula, song (n = 1 [MCP no. 1213]); Passo do Meio, Bom Jesus, song (n = 3, from two individuals [including MCP no. 1083]) and bisyllabic call (n = 15, from the same individual); Capão Alto, São Francisco de Paula, song (n = 2, from two birds) and alarm call (n = 4, from the same bird); Arroio São Gonçalves, Cambará do Sul, song (n = 5, representing four individuals); Josafaz, São Francisco de Paula, song (n = 10, from ten individuals [including MCP nos. 1076 and 1170]), bisyllabic call (n = 45, from the same individual), and alarm call (n = 21, from the same individual); Hotel Veraneio Hampel, São Francisco de Paula, song (n = 2, from two birds) and alarm call (n = 16, from the same bird); right bank of Rio da Prata, Linha Flores, song (n = 2, from the same individual). Santa Catarina: Campina da Alegria, Água Doce, song (n = 1); Morro da Igreja, Urubici (within the Parque Nacional de São Joaquim), song (n = 1); Fazenda da Rocinha, Bom Jardim da Serra, song (n = 1); Serra do Rio do Rastro (at the Planalto edge top), on the Bom Jardim da Serra / Lauro Müller border, song (n = 2, from two birds). Paraná: Corvo, Quatro Barras, song (n = 1); Coqueiro, Campina Grande do Sul, song (n = 2, from two individuals [MCP nos. 1176 and 1175]); highway BR 153, General Carneiro, song (n = 1 [MCP no. 1106]). São Paulo: Parque Estadual Intervales, alarm call (n = 4, from the same individual), E. Endrigo.

Scytalopus iraiensis. – Brazil: Rio Grande do Sul: Banhado do Maçarico, Rio Grande, song (n = 6, representing four individuals [including MCP no. 958]), and call (several samples from the same individual); Banhado dos Pachecos, Viamão, song (n = 2, from two birds).

Scytalopus novacapitalis. – Brazil: Distrito Federal: “Reserva Ecológica do IBGE” (actually Reserva Ecológica do Roncador), Brasília, song (n = 7, representing five individuals; two recordings by J. Vielliard, five by the author), “accelerating” song (n = 3, representing one or two individuals; J. Vielliard) and alarm call (n = 41, representing two individuals; one recording by J. Vielliard, another one by the author); Ribeirão do Gama, near the village of Vargem Bonita, Brasília, song (n = 1 [MCP no. 1481]).

Scytalopus sp. – Brazil: Minas Gerais (Espinhaço Range): Serra do Caraça, Catas Altas, song (n = 4, representing three individuals [two of them collected]), and “accelerating” song (n = 2, from the same bird); Serra da Piedade, Caeté, song (n = 2, from two birds).

Etymology. The author is pleased to name this new species of *Scytalopus* after José Fernando Pacheco, whose close cooperation and interest on the group under study made this work possible. Furthermore, J. F. Pacheco has made some of the major contributions to Brazilian ornithology in the past decade, including research on the taxonomy of *Scytalopus* tapaculos. The portuguese name “tapaculo-ferreirinho” (“ferreiro” = ironworker; “inho” is diminutive) refers to the contact call frequently delivered by *S. pachecoi*, which sounds like a weak metallic beat.

Vocalizations. Several hundred hours of field work revealed that the vocal repertory of all three populations of *S. pachecoi* is composed of the normal song, a variant of the song and by two types of calls. The song consists of a lengthy

repetition of a single, 0.032-0.062 s note (“*tcheep..tcheep..*”) in series varying from a few seconds to three min or more (see figure 2A). Song notes always showed an audible fundamental which reached maximum frequencies from 4.1 to 6.4 kHz and an equally loud first overtone (figure 2B). The pace in which song notes were delivered was relatively slow, varying from 2.01 to 3.36 notes per second. The first two seconds of the song had a faster pace, about 4.2 notes/s, and the notes had a lower pitched fundamental and first overtone, sounding somewhat nasal; in the next 4-5 s the pace slowed gradually and the notes attained higher frequency. There were some tendential differences in the song pace between the three disjunct populations of *S. pachecoi*. Birds from the Planalto highlands tended to have faster songs (average pace 2.85 notes/s, range 2.4-3.36, SD \pm 0.23; n = 37) than those from the Misiones region (mean pace 2.56 notes/s, range 2.16-3.3, SD \pm 0.29; n = 17) and from the Serra do Sudeste area (mean pace 2.63 notes/s, range 2.01-3.1, SD \pm 0.25; n = 46). In all but one case, there were no perceptible differences in pace between natural and solicited songs. The song pace of a bird collected in the Planalto averaged about 2.86 notes/s before and 2.99 notes/s after a playback. The song was delivered throughout the year and, as in other passerine species, most often early in the morning and about two hours before sunset, though after tape-recording playback or imitation of the song birds often responded immediately at any period of the day. The song was by far the commonest voice detected, being heard in 415 out of 582 individual records and in 170 out of 197 field trips in which the species was detected.

Scytalopus pachecoi also delivers a peculiar variant of the song which is very similar to the normal song, with the pace tending to be slightly faster; its final section, however, is greatly accelerated, sounding like a trill (figure 3A). This accelerating song was generally shorter than the normal songs, ranging from 12.5 to 23 s, although much longer sequences were occasionally heard. The duration of the accelerated section was short (0.7-7.2 s). The pace of the first two-thirds of this song type varied from 2.64 to 3.17 notes/s while the accelerated section varied from 6.1 to 10.1 notes/s. The accelerated section represented an increase of about 188% in the overall song pace compared to the slow-paced (earlier) section of the song (range 94.2-251%, SD \pm 0.47; n = 11). The transition between these two parts (i.e. when the inter-note intervals become increasingly shorter before stabilizing in the accelerated trilled end) was brief (1.1-4.8 s). There is strong evidence that this type of song is uttered more frequently by females. Four birds which accelerated the final section of their songs were paired with collected males and the only individual collected while accelerating the song pace was a female. Furthermore, birds properly observed in the field accelerating songs (n = 10, including the birds paired with collected males) were all in brownish, typical female plumage. None of 23 males collected uttered other than the normal song, although both individuals of a pair studied for about four months (presumably male and female) uttered accelerating songs. Therefore, it is possible that males only exceptionally give this song type, perhaps in response to their mates during the breeding period. This peculiar song was heard in all months of the year (on a total of 53 field trips) and on at least 73 individual encounters. In about half of these occasions two birds sang together, interposing their song notes (duet?), and

subsequently one of them (presumably the female) accelerated the pace into the final trill; in most cases the other member of the pair remained uttering its normal song for a long time.

The species also has two very different types of vocalizations, which presumably function as contact and alarm calls. A very distinctive, harmonic-rich monosyllabic call interpreted as “*pzeen*” greatly resembled a semi-metallic sound (figure 4E). Its duration varied from 0.109 to 0.232 s, and had a mean length of 0.159 s (SD \pm 0.02; n = 9 individuals and 151 calls). This voice was recorded on 121 individual encounters, and in 80 field trips covering all months. On at least eight occasions, members of five pairs studied in the Serra do Sudeste and at the Planalto responded to each other several times with this call, both at close and long distances. Since these birds were apparently not perturbed and the voice in question elicited reciprocal responses, it is inferred that, among other possible functions, it represents a contact call. This vocalization was also heard on at least 70 occasions from presumably solitary individuals which, in some cases, apparently were on territorial patrol, uttering innumerable individual notes. In such situations, the contact call could be used to elicit response from a conspecific (possibly intruder) which, once detected, would be driven away. On three occasions birds delivered this note after playback of the song, while on two other occasions an individual delivered it after being startled (in one case during a short flight). The other type of call is a series of generally four, less often three or five (rarely six or seven) “*te*” notes delivered in a pace of 6.13-9.8 notes/s (figure 4A). The fundamental was low pitched (1.8-2.3 kHz) and each note varied in length from 0.031 to 0.047 s. This call was heard on at least 118 encounters (and during 83 field trips), about half of these when an observer entered the area covered by a territorial bird. In some of these instances, an individual started to give several of these series just after a strong sound was produced nearby; it then approached and, after visual contact, became silent. On some other occasions, birds uttering this call moved nervously on a perch or on the ground while in visual contact with an observer. On eight other opportunities a bird delivered the call after playback, in some cases keeping the observer under visual contact. It appears that this relatively loud voice represents a scold or alarm call, which would include an alert message to call attention of other birds (conspecific or not) toward the presence of a potential threat. Similarly patterned vocalizations identified as scolds/ alarm calls have been described for several Andean *Scytalopus* (Whitney 1994, Krabbe and Schulenberg 1997, Mayer 2000). See table 2 for a more complete descriptive statistics of the measures mentioned here.

Natural History. *Scytalopus pachecoi* inhabits both primary and secondary forests, including their edges. At Serra do Sudeste it occupies humid semideciduous forests on slopes, valleys and plateaus and, to a lesser extent, riverine woods. In tall primary forests it favors small stream valleys or slopes densely covered by undergrowth bushes (generally with large stones), and frequently wanders on exposed rocks and near (1-2 m high) or on the ground within more open forest undergrowth. In denser secondary woods and disturbed primary forests it is more widespread and numerous, especially along edges. For example, inside a sector of c. 100 ha of continuous pristine forest (15-25 m tall) at the type-

locality only three pairs and two apparently unpaired individuals were found during exhaustive surveys, whereas in smaller, disturbed sections at the same locality (partially opened by mining and road construction), up to six pairs plus four lone individuals were detected. In small, naturally isolated forest patches to the west of the formerly continuous forests of the coastal slopes, it was found exclusively within sectors where the terrestrial bromeliad *Bromelia antiacantha* forms large stands and dominates the forest undergrowth. In the Misiones region (including northern Rio Grande do Sul) the species has been found in humid deciduous forests and adjacent araucaria forests on ridge tops, along creeks and streams in the bottom of valleys and near larger rivers. There it thrives in dense tangles with *Chusquea* sp. bamboo or other plants that grow along roads and also in stands of *Merostachys* sp. bamboo (especially along streams, but also on hill tops). In riverine areas it was found in relatively open to moderately dense undergrowth. In the highland araucaria forests of the Planalto the new species is fairly common in recent second-growth and disturbed woodlots with a semi-open canopy, generally with the undergrowth dominated by dense clumps of a giant *Chusquea* sp. bamboo and small bushes. *Scytalopus pachecoi* was recorded at three of the few sites with tall, less disturbed forests found in this region; in these cases, the forest undergrowth was relatively open, with small bushes and scattered patches of *Merostachys* sp. bamboo.

In the few places in the Planalto highlands where *S. pachecoi* and southern *S. speluncae* were found together, there appeared to be strong interspecific segregation. In the upper reaches of the Rio das Antas (between Cambará do Sul and São José dos Ausentes municipalities, Rio Grande do Sul), all five territories of *S. speluncae* found in two localities during five expeditions were confined to a small and contiguous sector 100-200m across in the valley slopes, whereas vast areas surrounding them were occupied exclusively and continuously by pairs or lone individuals of *S. pachecoi*. On at least three opportunities, two individuals of the latter species sang in response to the song of the former, which was 40-50m away. At five other localities in this region only *S. pachecoi* was found. In the upper reaches of the Rio Pelotas, between the northern half of São José dos Ausentes and Bom Jardim da Serra (this latter lying in Santa Catarina State), where *S. pachecoi* has been found at eight localities, the two species were found together in two additional places, though detailed observations of interactions between them could not be conducted, except for one brief opportunity, in the latter municipality. On this occasion, a pair of each species was very close to each other (10-20 m apart or less), apparently maintaining contiguous territories, *S. pachecoi* on the nearly flat hill top and *S. speluncae* on the adjacent steep slope. They showed no particular interest in the songs of one another, and after several tape playbacks of their songs, each species responded exclusively to its own specific song. Further data on the natural history of *S. pachecoi*, especially on breeding and behavior, will be published elsewhere.

Although having a relatively small and disjunct distribution, *S. pachecoi* is not facing any risk of extinction, since it tolerates well – and is apparently more numerous in – second-growth and disturbed forests, habitats that are still common in the three regions where it occurs.

Remarks on plumage, vocal and morphometric variation

in the *S. speluncae* group. The plumage of the taxa in the *S. speluncae* group is essentially gray (though *S. pachecoi* and *S. novacapitalis* have buff, dark barred flanks), with underparts varying from pale gray (with whitish center of belly) in *S. novacapitalis* to medium gray in *S. pachecoi* (which generally has variably lighter gray belly) and *S. iraiensis* and to dark gray in southern and northern *S. speluncae* (see figure 1); the upperparts varies from dark gray in *S. pachecoi* and *S. novacapitalis* to a very dark gray in both southern and northern *S. speluncae* and to blackish in *S. iraiensis*. These taxa share a song type which is a lengthy repetition (sometimes exceeding five minutes) of a single simple note delivered in a pace between one and five per second (table 2). Song notes are relatively similar in shape and structure among taxa, showing a clear downward frequency modulation in the final part of each note and a well-marked first overtone (see spectrograms in figure 2). An initial upward frequency modulation, seen in the spectrograms of song notes of both southern and northern *S. speluncae* and *S. novacapitalis*, was not found in the available recordings of *S. iraiensis*; although most tape-recordings of *S. pachecoi* lacked the upward frequency modulation, as illustrated in the spectrogram, the songs of some individuals showed clearly this feature. There are important differences in frequency and duration of song notes between taxa; for instance, *S. novacapitalis* has longer song notes than in the other taxa in the group, and this species and *S. iraiensis* have lower pitched notes than in *S. pachecoi* and southern *S. speluncae*; northern *S. speluncae* has longer song notes than in southern *S. speluncae*, though with some overlap in range (see table 2). All taxa, except *S. iraiensis*, have a multisyllabic alarm call whose notes show considerable interespecific variation in shape, each taxon being unambiguously diagnosed in comparison to the others in this character, including southern vs. northern *S. speluncae* (see figure 4A-D). Other features of the alarm call differ appreciably within the group; for example, the pace of northern *S. speluncae* call is slower than in the other taxa, but there is some overlap in range with *S. pachecoi* and southern *S. speluncae*, while *S. novacapitalis* has a much faster paced alarm call compared to the others; *S. pachecoi* and northern *S. speluncae* have lower pitched call notes than in southern *S. speluncae* and *S. novacapitalis*; northern *S. speluncae* has longer call notes than in the other taxa (see table 2). Birds almost always deliver the alarm call repeatedly for several seconds, generally after an intruder had entered an area covered by a territorial bird (D. R. C. Buzzetti, pers. comm.; pers. obs.). *Scytalopus iraiensis* has a mono- or bisyllabic call which is very distinct from the calls of the other members of the *S. speluncae* group (see spectrogram in Bornschein *et al.* 1998). Although it appears to function as an alarm call (Bornschein *et al.* 1998; pers. obs.), its distinct shape and temporal organization (it is delivered almost always isolately and at unpredictable intervals) do not permit establish its homologous condition to the multisyllabic alarm call of the other species. The short, semi-metallic call of *S. pachecoi* has no clear parallel in the vocal repertory of the other species in the group. Superficially it resembles the bisyllabic calls known for southern and northern *S. speluncae* (compare figure 4E with 4F), but more field observations are required to determine accurately the nature of these bisyllabic calls.

Among the described taxa in the family Rhinocryptidae

the accelerating song of *S. pachecoi* is matched only by the same song type of *S. novacapitalis* (compare figure 3A with 3C). In this latter species this song has a slower pace, about 1.12 notes/s, but the accelerated final section has a very similar pace to the same section of the equivalent song of *S. pachecoi*, about 8.5 notes/s (table 2). Although in the main part of the song length and frequency of notes differ between these two species (the notes of *S. novacapitalis* song being longer and lower pitched) these parameters are most similar in the accelerated section of the song, whose notes have two well-marked, closely spaced overtones (see figures 3B and 3D). In both species this song may be delivered together with the normal song of another, presumably paired bird (duet?). Other species in the genus may change the pace of their songs (e.g. the Andean *S. schulenbergi*, cf. Whitney 1994) but these changes (accelerations or decelerations) occurs in the first half or in the middle of the sequence, with the pace tending to stabilize throughout the series just after the increase in the song pace (see also Krabbe and Schulenberg 1997, Mayer 2000). *Scytalopus indigoticus* of southeastern Brazil also has an accelerating vocalization, but the pace of this voice accelerates progressively and gradually as a whole instead of abruptly at the end of the sequence as in *S. pachecoi* and *S. novacapitalis*. Furthermore, this voice has been regarded a contact call, being very different from the true song (see figure 3C in Vielliard 1990).

As previously shown, most specimens (75%) of *S. pachecoi* from the Serra do Sudeste differ from the series obtained in the Planalto and Misiones regions in having more brown in their plumages, including on the upper wing coverts, which were plain gray in the individuals from the last named regions. One hypothesis to explain the observed differences between these populations is that individuals from the Serra do Sudeste require more molts to attain the definitive main gray plumage, thus retaining juvenile characters (e.g. brown feathers and wing marks) for a longer period. Because populational differences are restricted to only part of the series, the three disjunct populations are judged to represent the same species. Furthermore, these populations share exactly the same vocal repertory, and minor average differences in song pace between birds of the Planalto highlands vs. the other two areas are broadly overlapping (see Vocalizations). However, as stated by Cracraft (1992), the understanding of the limits of terminal taxa will be refined as the groups are studied more thoroughly; apparent differences between these populations, even if restricted to individuals of a certain age, may diagnose additional taxa as more material confirms the consistency of the pattern. It is emphasized here that more studies – including molecular-based ones – are needed to test if additional diagnosable units are involved within this population assemblage.

The analysis performed here showed that besides the species described in this paper the traditional *S. speluncae* probably involves one more species, which is here called southern *S. speluncae*. It appears to be represented by populations from eastern São Paulo state south to the Planalto escarpment in central Rio Grande do Sul. These birds have significantly (*t*-test; $P < 0.001$) smaller wing, tail and tarsus lengths (see table 1) than *S. speluncae* specimens coming from areas north of São Paulo city, though they were similar in plumage coloration. The available data indicated that the

southern *S. speluncae* is constant in its higher pitched, “L” shaped notes of the alarm call at least from southeastern São Paulo (Parque Estadual Intervales) and eastern Paraná (see Bornschein *et al.* 1998) southward. The notes of its song are shorter than that of the northern *S. speluncae* (with a slight overlap in range), a feature verified from Paranapiacaba (southeast of the São Paulo city) to Rio Grande do Sul, as firstly shown by Vielliard (1990). The only museum specimen from Alto da Serra (= Paranapiacaba; cf. Paynter and Traylor 1991) is a female whose tarsus, wing and tail measurements were even shorter than those of the remaining three females from southern localities; this bird was judged to represent the putative southern *S. speluncae*. Adult males from the Serra do Mar at São Luiz do Paraitinga, east-northeast of Paranapiacaba, have wing, tail and tarsus lengths well above the range verified for the southern birds; tape-recordings from Serra da Bocaina, further east, showed relatively long song notes and alarm calls with notes shaped like those of calls recorded in the Serra dos Órgãos region by Gonzaga and Castiglioni (2001; pers. obs.) and Vielliard (1990, figure 2k) (see figure 4D). Birds from the Mantiqueira range to the north agree at least in size and in the length of song notes. These data suggest that indeed there is a distinct entity occupying the southern part of the Atlantic forest (eastern São Paulo to the south). The existence of a biogeographic discontinuity, with related taxa replacing each other over northeastern São Paulo, has long been recognized. Pinto (1941) noticed that the populations of *Cichlocolaptes leucophrus* found from eastern São Paulo state south to Santa Catarina differed markedly in size and coloration from birds of São Paulo/Rio de Janeiro boundary northeastward; he named southern birds *C. l. holti*, whose type-locality is Alto da Serra (Paranapiacaba). There are other closely related taxa that replace each other between eastern São Paulo and adjacent sectors of Rio de Janeiro state: *Lepidocolaptes falcinellus* / *L. squamatus* and *Heliobletus contaminatus camargoi* / *H. c. contaminatus* (Silva and Stotz 1992, Silva and Straube 1996).

The consistency of the observed differences between southern and northern *S. speluncae* must be tested through the analysis of additional material, especially from coastal São Paulo, from where very few vocal and museum specimens are available. If further studies prove that they are consistently distinct, the southern entity will lack a name. According to Chrostowski (1921), the type specimen of *S. speluncae*, said to have come from São João del Rey, southern Minas Gerais (Ménétrières 1835; but see Pacheco [2004] for a discussion of problems surrounding the origins of Ménétrières’ type specimens), has wing, tail and tarsus measuring 51.0, 45.8 and 20.5 mm, respectively. Therefore, it quite probably represents the northern populations, as these measurements are above the range verified for southern birds (see table 1). Examination of two photographs of the type, which depict a uniformly dark gray bird, indicates that it was an adult male. The original description and the color plate accompanying it (Ménétrières 1835) also refer to an unbarred, adult bird, although it shows a pallid gray throat not apparent in the photographs. Chrostowski (1921), who carefully examined the type, added only that the rump feathers had a very narrow reddish fringe, a detail not mentioned in the original description and not perceptible in the available photographs.

The taxonomy of the group is in further progress. Material

recently obtained in Bahia and Minas Gerais apparently represents additional taxa in this group; these populations, which are under study by some colleagues (see Parrini *et al.* 1999, Vasconcelos 2001, and below), appear to differ both in plumage and vocalizations from all described forms (and also from the species described here) in this group (see also Krabbe and Schulenberg 2003).

DISCUSSION

Systematic relationships. Systematic arrangement within *Scytalopus* has long been based solely on Zimmer's (1939) conclusions, later adopted by Peters (1951). Recent efforts to establish hypotheses of phylogenetic relationships within the Andean members of the genus have appeared, and are based primarily on DNA sequence data and, to a lesser extent, on external morphology and vocalizations (Arctander and Fjeldså 1994, Whitney 1994, Krabbe and Schulenberg 1997). These studies proposed that the Andean counterpart of the genus includes several major groups, some of which containing a large number of species.

In contrast to the Andean scenario, the much less diverse *Scytalopus* radiation in southeastern Brazil falls into two groups: (1) *S. indigoticus* and *S. psychopompus*; and, (2) *S. speluncae*, *S. iraiensis*, *S. pachecoi*, and *S. novacapitalis*. The first group, the *S. indigoticus* group, can be unambiguously diagnosed from the other *Scytalopus* species by having extensive pure-white underparts (though with rufous, barred or unbarred flanks) and blue-gray upperparts and sides of body (see Vielliard 1990, Bornschein *et al.* 1998, Krabbe and Schulenberg 2003). On the basis of its distinctive, short trilled song and some anatomical data, *S. indigoticus* (no vocal or anatomical material of *S. psychopompus* seems to be available) has been regarded as not closely related to the second group, in spite of the fact that no phylogenetic analysis has been conducted nor a tentative sister taxon relationship has been suggested (Vielliard 1990, Bornschein *et al.* 1998). The species in the second group, here called *S. speluncae* group, shares an essentially gray plumage (see above). However, a generally gray plumage also characterizes most Andean *Scytalopus* and, therefore, no external characters diagnoses unambiguously the putative *S. speluncae* group. Vocal characters, on the other hand, have been regarded most useful in characterizing the group. Based on a bioacoustic study on Brazilian *Scytalopus*, Vielliard (1990) proposed to unite *S. speluncae* and *S. novacapitalis* in a superspecies, most recently referred to as the *S. speluncae* / *novacapitalis* group (see Parrini *et al.* 1999, Vasconcelos 2001). *Scytalopus iraiensis*, a recently described species, was regarded phylogenetically close to *S. speluncae* due to the great similarities of their songs and syringeal morphology (Bornschein *et al.* 1998). In fact, these three species (and also *S. pachecoi*) share similarly patterned songs and similarly shaped song notes (Vielliard 1990, Bornschein *et al.* 1998; this study). Nevertheless, despite being a possible indicative of an immediate common ancestry of these species, as postulated by Vielliard (1990) for *S. speluncae* and *S. novacapitalis*, these shared song characters have an uncertain systematic value, since similarly patterned songs are also found in some Andean taxa and no phylogenetic analysis has been conducted (Fjeldså and Krabbe 1990, Krabbe and Schulenberg 1997,

Coopmans *et al.* 2001). Therefore, the putative *S. speluncae* group, as here tentatively characterized, lacks unambiguous support (e.g. proposed synapomorphies), making its recognition rather a poorly substantiated decision, with the most sound justification for its maintenance being the fact that *S. pachecoi* represents a clear link in both vocal (song pace) and plumage (tonality of the gray) characters between *S. novacapitalis* and *S. speluncae* / *S. iraiensis*. Notwithstanding, there is unambiguous evidence for a more restricted grouping within this assemblage; given its uniqueness, the accelerating song type described above (see figure 3) represents a likely synapomorphy for a clade containing *S. pachecoi* and *S. novacapitalis* plus one possibly undescribed form from the Espinhaço Range (see below). If this hypothesis is true, it implies that *S. speluncae*, as traditionally defined, comprises a paraphyletic assemblage of species.

Scytalopus pachecoi and *S. novacapitalis* also share the buff and black barring on the flanks, which are plumage characters not found in full adult males of *S. speluncae* and *S. iraiensis*. These characters, however, at a first glance appear to be plesiomorphic, since they are found in most rhinocryptid genera and in young birds of virtually all members of the genus (Fjeldså and Krabbe 1990, Krabbe and Schulenberg 2003). Thus, the absence of buff and black barring in definitive male plumage could be viewed as a derived character, which is shared by all populations of *S. speluncae* and *S. iraiensis*, and also by several Andean taxa.

Ideally, any assumption of relationship should be tested through a detailed phylogenetic analysis including a thorough taxon sampling and as many characters as possible. Unfortunately, the external morphology and coloration in *Scytalopus* offer a limiting factor to this task, since these features are relatively uniform throughout the genus, with most species being uniformly gray or variously barred posteriorly (Fjeldså and Krabbe 1990, Whitney 1994, Krabbe and Schulenberg 1997). Voice, a greatly variable feature within *Scytalopus*, appears to be an important source of phylogenetically informative characters, although it has been suggested, on the basis of DNA sequence data, that birds with dramatically different song types are each other's closest relatives and that trilled songs evolved independently several times in the genus (Krabbe and Schulenberg 1997, 2003). In any event, the investigation of additional sources of characters would be an important follow up; the study of syringeal morphology of only three Brazilian taxa, namely *S. speluncae*, *S. iraiensis* and *S. indigoticus*, revealed important character variation that may retain much phylogenetic information (see Bornschein *et al.* 1998). Therefore, the field is ripe for investigation. It is emphasized here that the research on taxonomy and systematics of the southeastern South American *Scytalopus* is very incipient; apparently several species remain to be properly recognized while available hypotheses of relationships to extralimital forms (e.g., Willis 1992a) are based only on general extrapolations. Furthermore, adequate material, such as good museum series associated with tape-recordings is scarce. The knowledge of the vocal repertory and external variation of each population, undoubtedly of great importance for the taxonomy of the group, should be improved so that the real diversity of the genus *Scytalopus* in southeastern South America can be recognized and understood.

Biogeography. The origins and the identity of the Brazilian *Scytalopus* have been subject of some debate. Early in the twentieth century, Miranda-Ribeiro (1906) identified two *S. speluncae* from the Itatiaia massif as *S. sylvestris*, a name erected by Taczanowski for a bird from the Peruvian Andes, later synonymized with *S. femoralis* (Cory and Hellmayr 1924). Miranda-Ribeiro (1923, 1928), who recognized the great Andean affinity in the Brazilian highlands' fauna, later considered *S. speluncae* (together with *S. sylvestris*) the same species as *S. magellanicus*, and subsequently suggested (Miranda-Ribeiro 1930) that other Andean *Scytalopus* might be present in the southeastern Brazilian mountains. Taxonomic identity apart (no recent author has questioned the distinction between Andean and southeastern species), the main question regarding the origins of Brazilian *Scytalopus* concerns the routes through which they colonized southeastern South America (see Vielliard 1990, Willis 1992a). Sick (1985) pointed to a route through northern Argentina (Chaco region), accepting the assumption of a former floristic connection between the Andes and southern Brazilian highlands in that area (around 27°S latitude). Sick (1985, 1997) assumed that the ancestors of some montane Brazilian birds (including *Scytalopus*) crossed this gap during the Pleistocene, thus in a time when the Chaco lowlands were already formed (Lundberg *et al.* 1998). Consequently, it would be necessary to assume that montane taxa such as *Scytalopus* had established populations over a general landscape of arid/semi-arid flat terrain (including large flood-plains eastwards) to reach southeastern South America. However, given the fact that aridity and xeromorphic vegetation have been established throughout the Chaco and adjacent regions apparently since the late Oligocene (Spichiger *et al.* 1995, Maury *et al.* 1996) and that *Scytalopus* species currently inhabiting the nearest Andean slopes and southern Brazil occupy montane habitats (as low as 1,500 m in the Andes; Fjeldså and Krabbe 1990) and / or subtropical / temperate moist forests, a crossing through this general area seems unlikely. Furthermore, this region was low-lying, and at times also invaded by marine waters ("Paranan Sea"), over most of the Tertiary (Lundberg *et al.* 1998) and, therefore, probably never supported physiographic conditions appropriate for maintenance of a biota that had evolved under the cooler and moister climates of montane areas (see Silva [1994] for additional arguments against a crossing through the Chaco from Andean slopes to southeast Brazil by forest birds). It seems most likely that a faunal connection between the Andes and eastern South America, at least for true montane taxa, might have taken place through central Brazil and adjacent Bolivia, a more elevated and moister "route" (in part mountainous) first suggested by Vielliard (1990). This connection would have been established since the late Oligocene–early Miocene, after a phase of significant uplift and eastward propagation of the central Bolivian Andes, which produced the contact ("Chapare Buttress") with the subsurface edge of the Brazilian Shield and formed a new structural divide between the Amazonas and Paraná basin-systems (Lundberg *et al.* 1998: 33, figures 16-18). This drainage divide represents the narrowest point between the Andes and the Brazilian Shield (Lundberg *et al.* 1998) – the two geologic units to which the entire genus *Scytalopus* is virtually restricted. Subsequent rupture in the connection for montane

taxa might have occurred after a new tectonic episode in the central Andes of Bolivia, which produced flexural subsidence in the foreland basin (enhanced by erosion) during Late Miocene (Lundberg *et al.* 1998: 36-37; see also Gregory-Wodzicki 2000). As a result, populations of montane taxa occupying the subsided area would have become extinct, allowing populations distributed beyond that area to evolve independently. The location of this putative, ancient connection, nearly corresponds to the "center-south route" of Willis (1992a: 6, figure 3) who, however, found "little evidence of passage" for birds and argued for a more southern route, through the Chaco of northern Argentina and Paraguay. Nevertheless, several montane Andean taxa presumably or certainly closely related to southeastern forms (e.g. taxa in *Schizoeaca*, *Chamaeza*, *Laniisoma*, *Phibalura* and *Pyroderus*, and the genera *Schistes*, *Myornis* and *Ampelion*; Snow 1982, Willis 1992b, Silva 1995, Krabbe and Schulenberg 1997, Sick 1997) occur only from northern Bolivia or Peru northward along the Andes, pointing to a central connection, though a southern, chaquenian route probably operated in some cases (e.g. *Amazona tucumana* / *A. pretrei*, which are "travel-prone" taxa; see Nores 1992). Indeed, based upon the pattern shown by the two *Augastes* species of the Espinhaço Range and their putative sister taxon – the genus *Schistes* of northern Andes –, Silva (1995) postulated the occurrence of an ancient vicariant event between the eastern Brazilian highlands and the Andean region, followed by extinction of lineages that inhabited the areas between these two orographic systems.

For floristic elements, it has been hypothesized that the Andean / southeastern Brazil corridor functioned at a number of times in both early and late Cenozoic, and that its probable location can be discerned by referring to modern distribution patterns (Safford 1999). Despite southern connections, e.g. through eastern Argentina, Uruguay and southernmost Brazil, are most likely for many Austral-Andean taxa occurring in southeastern South America (e.g. *Araucaria*, whose connection was disrupted in the Oligocene; cf. Spichiger *et al.* 1995), the disjunct occurrence of several high-altitude plant species and species groups in the Itatiaia massif and in the northern Andes, in conjunction with the strong general floristic similarities between the páramo formation of equatorial Andes and the *campos de altitude* of southeastern mountains (Serra da Mantiqueira and Serra do Mar), points to a biotic connection between these orographic systems through the central Brazilian highlands (see Brade 1956, Safford 1999). Since this hypothesized interchange involves multiple ecological groups, such as subtropical and temperate forest taxa as well as non-forest ones, the connections would have occurred under diverse climatic conditions in distinct epochs within Miocene. Palinological and floristic data from western Minas Gerais showed that mesophytic and floodplain forests, open grasslands / savanna and *Araucaria* forests alternated their occurrence over the last 30,000 years, indicating that warm / moist, warm / dry, cool / moist and cool / dry climates operated in the central Brazilian Plateau during the Quaternary (Ledru 1993). However, there appear to be no lines of evidence to support the conclusion that a similar interpolation of climatic conditions occurred during Miocene. In any event, the subsidence of the western corner of the Brazilian Shield, including the former Amazonas / Paraná drainage divide in Bolivia (Chapare Buttress), in the late Miocene, produced

profound environmental changes (e.g. subsequent capture of headwaters of the Paraná system by the Amazonas system; Lundberg *et al.* 1998), presumably enough to disrupt an ancient, putative connection for montane elements, although taxa not strictly montane and more vagile may have been less affected by this event. If so, it could be expected to find more direct evidence of the central connection in the present-day distribution of some taxa. *Platyrinchus mystaceus*, a small understory tyrannid with montane forms in the northern Andes (and in other northern mountains) and others in the central and eastern parts of the Brazilian Shield (both in highlands and lowlands), appears to show such a connection. Recently, Remsen *et al.* (1991) reported on the first lowland populations of *P. mystaceus* discovered in Bolivia, filling the gap between montane and eastern forms; they found phenotypic evidence of gene flow between Andean (*P. m. partridgei*) and west Brazilian (*P. m. bifasciatus*, of both highland plateaus and adjacent lowlands to the south) populations through the center-north of the country. Remsen *et al.* (1991) termed this type of distribution the “circum-Amazonian distribution pattern”, in which sister taxa are found in montane forested areas of the humid Andes (and, in several cases, also in the Tepui region) and in forested areas south and east of the lowland forests of Amazonia. These authors pointed out that several species or species groups share this pattern (though not necessarily with present-day contact between Andean and eastern taxa), notably some thamnophilids (e.g. *Dysithamnus mentalis*), tyrannids (e.g. *Phyllomyias burmeisteri*), some tanagers (e.g. *Chlorophonia cyanea*) and the genus *Scytalopus*. *Lochmias nematura*, a stream-side montane furnariid, also matches closely this pattern, reaching the westernmost plateaus of central Brazil, near the Bolivian border (Fjeldså and Krabbe 1990, Ridgely and Tudor 1994). Within the framework of this proposed pattern, the occurrence of a population (differentiated or not) in central Brazil may be interpreted as the product of an expansion from the Atlantic forest or as a relict of a formerly continuous range between the Andes and southeastern Brazil (Silva 1996). In the case of *S. novacapitalis*, at least, a restricted occurrence in central Brazil is most parsimoniously explained as a relictual presence in suitable areas of a formerly more widespread population (which would include the ancestors of *S. pachecoi* and other populations; see below), now extremely fragmented and somewhat diversified. The proposed expansion of *S. novacapitalis* from the coastal Atlantic forest through a direct derivation from *S. speluncae* (Sick 1985, 1997) does not make sense in light of the rationale exposed here, though it appears more plausible under Sick’s hypothesis of a colonization of southeastern Brazil by the genus *Scytalopus* through an austral connection.

The Tertiary orogeny may have had additional implications for the diversification of the genus in southeastern South America. The significant phase of uplift of the Serra do Mar and Serra da Mantiqueira between the Miocene and the Pliocene (Almeida 1976, Petri and Fúlfaro 1983) may help explain the origins of *S. speluncae*, which is restricted to these orographic systems (except in the south, where the southern populations penetrate inland into the Planalto). The formation of the Rio Paraíba do Sul valley, whose subsidence was associated with the uplift of the referred mountain systems, has been suggested as being responsible for the split of some

closely related forest birds (e.g. *Lepidocolaptes falcinellus* / *L. squamatus*, *Cichlocolaptes l. leucophrus* / *C. l. holti*; Silva and Straube 1996). However, these taxa meet or replace each other along the Serra do Mar chain, not across the gap formed by the valley, which implies that the valley’s formation does not fully explain the replacement (see map in Silva and Straube 1996). Rather, this replacement seems to coincide with the location of a large geologic fault, which touches the northern border of the São Paulo Basin, where the city of the same name is located; this basin, where the upper reaches of the Rio Tietê lay, was formed by tectonic movements associated to the fault, having an uncertain age, perhaps dating from the Pliocene (Almeida 1976). Interestingly, the birds attributed to the northern and southern *S. speluncae* (see above) come, respectively, from areas to the north and south of the fault’s location. On the other hand, these geological events do not seem to be directly related to the range disjunction (see map in figure 5) and differentiation between the putatively related *S. pachecoi* and *S. novacapitalis*, since the eastern edge of the Paraná Basin – which corresponds to most of the distributional gap – does not show any sign of Late Tertiary tectonic activities, even though this area spans alongside the uplifted Serra do Mar and Serra da Mantiqueira (Petri and Fúlfaro 1983; see below).

The age of these geological events and the presumably correlated taxa’s origin conform well to the proposed ages for some montane avian taxa based on molecular data. Evidence coming from mtDNA sequences suggests that the split between some clades within the Andean genera *Ochthoeca* and *Hemispingus* predates the Pleistocene, probably having taken place during the Miocene / Pliocene transition, and that speciation events leading to the terminal taxa in different lineages would have occurred in the Pliocene and Early-Pleistocene (García-Moreno *et al.* 1998, 2001).

Under the hypothesis of close relationship (see above) of *S. pachecoi* and *S. novacapitalis*, the latter a central-Brazilian endemic, an interesting biogeographic scenario arises, where two possible sister taxa are separated by a very large (more than 1,300 km) distributional gap. However, the highlands of south-central Minas Gerais state (mainly the Espinhaço range, above about 1,000 m a.s.l.) are occupied by *Scytalopus* populations that share with the above-named taxa the accelerating song type previously described. This apparently unnamed taxon has the coloration of the underparts relatively similar to that of *S. novacapitalis*, although vocally it is most similar to *S. pachecoi*. These populations, which were already identified as *S. novacapitalis* (e.g. Willis and Oniki 1991), are currently under study by M. F. de Vasconcelos, L. F. Silveira, B. M. Whitney and J. F. Pacheco (see Collar *et al.* 1992, Vasconcelos *et al.* 1999, 2002, Vasconcelos 2001, Vasconcelos and Melo-Júnior 2001, BirdLife International 2000, Melo-Júnior *et al.* 2001). Additionally, birds identified as *S. novacapitalis* have been reported from the Serra da Canastra, southwestern Minas Gerais, as well as from other parts of this state (Sick 1997, Silveira 1998). Nevertheless, the distributional gap between the northernmost sector of the range of *S. pachecoi* (northern Misiones Province, Argentina) and the nearest population of its supposed closest relatives spans at least 900-1,000 km, thus contrasting with the northern and southern *S. speluncae*, whose populations form a nearly-continuum from Rio Grande do Sul to Espírito Santo (the

taxonomic status of a population assigned to *S. speluncae* in south-central Bahia [Gonzaga *et al.* 1995] requires further study; see also Krabbe and Schulenberg 2003). The areas occupied by those allopatric forms (plateaus and interior escarpments) lay to the west of the coastal mountain chains (Serra do Mar and adjacent systems) which are inhabited by *S. speluncae*, the exception being the seaward slopes of Serra do Sudeste, where *S. pachecoi* is the only representative of the genus (see figure 5). It seems that the birds with slow-paced songs tend to favor cooler climates, which occurs in the southern plateaus and in the highland areas northward (plateaus and western escarpments above 1,000 m a.s.l.). This could help explain why this group has such a fragmented range. Northern Paraná and almost all inland areas of the São Paulo state (west of Serra do Mar) are well below 800 m a.s.l. and have a relatively warm climate. It seems plausible to suppose that a former (ancestral) population may have had an essentially continuous distribution over the presently observed gap during past cooler periods. Assuming that the process under which populations became isolated was range fragmentation (which was followed by differentiation) caused by climatic changes, the age of events remains to be determined. Sick (1997) also suggested that the fragmented distribution of some *Scytalopus* was caused by drastic climatic and floristic changes in the past. He also added that the almost flightless *Scytalopus* species would be unable to colonize a mountain range under present-day climatic conditions and concluded that the presently isolated montane biomes were once connected.

Evidently, much more research on this subject is needed, although details about past geological / paleoclimatic history of southeastern Brazil are scanty (Almeida 1976) or unknown to ornithologists.

ACKNOWLEDGEMENTS

The author is deeply indebted to several friends for their help in the field: Aline M. da Silveira, Marcos R. Bornschein, Carla S. Fontana, Glayson A. Bencke, Cristian Marcelo Joenck, Luciano R. Matheus, Herculano Alvarenga, Rafael A. Dias, Rogério S. Ferrer, Enrique A. Salazar, Alceu Martinoto, Paulo Peroba, Jan K. Mähler Jr., Marcelo F. de Vasconcelos, Mauro Pichorim, Bianca L. Reinert, Luís Fábio Silveira, Márcio Repenning, Dante R. C. Buzzetti, Marcelo Burns, José Milton Schlee Jr., Cristiano Sousa, Morevy Moreira Cheffe, Franck L. da Silveira, Roberto K. Baltar, Marcelo M. Dutra, Leomar S. Rosa, João Nelci Brandalise, Fábio Mazim and Carla Rodeghiero. Roberto E. Reis and C. S. Fontana provided important support at the Pontifícia Universidade Católica do Rio Grande do Sul, making this work possible. The manuscript was greatly improved with comments and suggestions by Bret M. Whitney, G. A. Bencke, L. F. Silveira, R. A. Dias, M. R. Bornschein, M. F. de Vasconcelos, José Fernando Pacheco, R. E. Reis and an anonymous referee. Luiz Antônio Pedreira Gonzaga, Mario Cohn Haft and Gervásio Carvalho commented on a preliminary version of the manuscript. Ricardo Lima, Rafael K. Arnoni and Márcio Repenning helped with preparation of the figures. Helena Mata, Paulo Sérgio M. da Fonseca, Marcos Raposo, J. F. Pacheco, M. R. Bornschein and M. F. de Vasconcelos provided some important references. Jacques Viellard

(Arquivo Sonoro Neotropical), D. R. C. Buzzetti and Edson Endrigo kindly shared with the author some of their own tape-recordings of *Scytalopus tapaculos*. M. A. Raposo and Jorge B. Nacinovic (MNRJ), L. A. P. Gonzaga (DZUFRJ), H. Alvarenga (MHNT), L. F. Silveira (MZUSP), Miguel Â. Marini (COMB/UnB), Pedro Scherer-Neto (MHNCI) and G. A. Bencke (MCN) kindly allowed examination of specimens in the collections under their care. Juan Mazar Barnett provided data on Argentinian specimens housed at Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". This paper represents the author's M.Sc. thesis, which was presented to the Programa de Pós-graduação em Biociências – Zoologia at the Pontifícia Universidade Católica do Rio Grande do Sul. Between March 2001 and February 2003 the author received a fellowship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). Special thanks to Rafael A. Dias, who kindly painted the tapaculos for the cover plate.

REFERENCES

- Albuquerque, E. P. de (1983) Lista preliminar das aves observadas no Parque Florestal Estadual de Espigão Alto, Barracão, Rio Grande do Sul, Brasil. *Roessleria* 5: 371-378.
- Almeida, F. F. M. de (1976) The system of continental rifts bordering the Santos Basin, Brazil. *An. Acad. Bras. Ciênc.* 48 (Supplement): 15-26.
- Arctander, P. and J. Fjeldså (1994) Andean tapaculos of the genus *Scytalopus* (Aves, Rhinocryptidae): a study of speciation using DNA sequence data, p. 205-225. In: V. Loeschcke, J. Tomiuk and S. K. Jain (eds.) *Conservation Genetics*. Birkhäuser Verlag Basel / Switzerland.
- Belton, W. (1984) Birds of Rio Grande do Sul, Brazil. Part 1. Rheidae through Furnariidae. *Bull. Amer. Mus. Nat. Hist.* 178: 369-636.
- _____ (1985) Birds of Rio Grande do Sul, Brazil. Part 2. Formicariidae through Corvidae. *Bull. Amer. Mus. Nat. Hist.* 180: 1-242.
- Bencke, G. A. (1996) Annotated list of birds of Monte Alverne, central Rio Grande do Sul. *Acta Biol. Leopold.* 18: 17-42.
- Bertoni, A. W. (1919) Especies de aves nuevas para el Paraguay. *Hornero* 1: 255-258.
- BirdLife International (2000) *Threatened Birds of the World*. Barcelona and Cambridge: Lynx Edicions and BirdLife International.
- Bornschein, M. R., B. L. Reinert and M. Pichorim (1998) Descrição, ecologia e conservação de um novo *Scytalopus* (Rhinocryptidae) do sul do Brasil, com comentários sobre a morfologia da família. *Ararajuba* 6: 3-36.
- Brade, A. C. (1956) A flora do Parque Nacional do Itatiaia. *Boletim do Parque Nacional do Itatiaia* (no. 5).
- Brooks, T. M., R. P. Clay, J. C. Lowen, S. H. M. Butchart, R. Barnes, E. Z. Esquivel, N. I. Etcheverry and J. P. Vincent (1995) New information on nine birds from Paraguay. *Orn. Neotrop.* 6: 129-134.
- Chrostowski, T. (1921) Sur les types d'oiseaux néotropicaux du Musée Zoologique de l'Académie des Sciences de Pétrougrade. *Annales Zoologici Musei Polonici, Historiae Naturalis* 1(1): 9-30.
- Collar, N., L. P. Gonzaga, N. Krabbe, A. Madronõ Nieto, L. G. Naranjo, T. A. Parker III and D. C. Wege (1992) *Threatened Birds of the Americas*. Cambridge: International Council for Bird Preservation.
- Coopmans, P., N. Krabbe and T. S. Schulenberg (2001) Vocal

- evidence of species rank for nominate Unicolored Tapaculo *Scytalopus unicolor*. *Bull. Brit. Orn. Cl.* 121: 208-213.
- Cory, C. B. and C. E. Hellmayr. (1924) Catalogue of birds of the Americas and the adjacent islands. *Field Mus. Nat. Hist. Zool. Series* 13, Part 3: 1-369.
- Cracraft, J. (1992) The species of the birds-of-paradise (Paradisaeidae): applying the phylogenetic species concept to a complex pattern of diversification. *Cladistics* 8: 1-43.
- Fjeldsã, J. and N. Krabbe (1990) *Birds of the High Andes*. Svendborg: Zoological Museum, University of Copenhagen and Apollo Books.
- García-Moreno, J., P. Arctander and J. Fjeldsã (1998) Pre-Pleistocene differentiation among Chat-Tyrants. *Condor* 100: 629-640.
- _____, J. Ohlson and J. Fjeldsã (2001) MtDNA sequences support monophyly of *Hemispingus* tanagers. *Mol. Phylogenet. Evol.* 21: 424-435.
- Giai, A. G. (1951) Notas sobre la avifauna de Salta y Misiones. *Hornero* 9: 247-276.
- Gonzaga, L. P., and G. Castiglioni (2001) *Aves das montanhas do sudeste do Brasil*. CD. Rio de Janeiro: Arquivo Sonoro Prof. Elias Coelho, Universidade Federal do Rio de Janeiro – UFRJ.
- _____, 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. Intern.* 5: 279-290.
- Gregory-Wodzicki, K. M. (2000) Uplift history of the Central and Northern Andes: a review. *GSA Bulletin* 112: 1091-1105.
- Hayes, F. E. (1995) *Status, distribution and biogeography of the birds of Paraguay*. American Birding Association (Monographs in Field Ornithology No. 1).
- Krabbe, N. and T. S. Schulenberg (1997) Species limits and natural history of *Scytalopus* tapaculos (Rhinocryptidae), with descriptions of the Ecuadorian taxa, including three new species, p. 47-88. In: J. V. Remsen, Jr. (ed.) *Studies in Neotropical Ornithology honoring Ted Parker*. Washington: The American Ornithologist's Union (Ornithological Monographs 48).
- _____, and _____ (2003) Family Rhinocryptidae (Tapaculos), p. 748-787. In: J. del Hoyo, A. Elliott and D. A. Christie (eds.) *Handbook of the birds of the world. Volume 8: Broodbirds to tapaculos*. Barcelona: Lynx Edicions.
- Ledru, M-P (1993) Late Quaternary environmental and climatic changes in central Brazil. *Quarter. Res.* 39: 90-98.
- Lundberg, J. G., L. G. Marshall, J. Guerrero, B. Horton, M. C. S. L. Malabarba and F. Wesselingh (1998) The stage for Neotropical fish diversification: a history of tropical South American rivers, p. 13-48. In: L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. S. Lucena and C. A. S. Lucena (eds) *Phylogeny and classification of Neotropical fishes*. Porto Alegre: Edipucrs.
- Maurício, G. N. and R. A. Dias (1998) Range extensions and new records for forest birds in southern Rio Grande do Sul, Brazil. *Bull. Brit. Orn. Cl.* 118: 14-25.
- _____, and _____ (2001) Distribuição e conservação da avifauna florestal na Serra dos Tapes, Rio Grande do Sul, Brasil, p. 137-158. In: J. L. B. Albuquerque, J. F. Cândido Jr., F. C. Straube and A. L. Roos (eds.) *Ornitologia e Conservação: da ciência às estratégias*. Tubarão: Editora Unisul.
- Maury, E. A., R. Pinto da Rocha and J. J. Morrone (1996) Distribution of *Acropsopilio chilensis* Silvestri, 1904 in southern South America (Opiliones, Palpatores, Caddidae). *Biogeographica* 72: 127-132.
- Mayer, S. (2000) *Birds of Bolivia 2.0*. CD-ROM. Westernland: Bird Songs International B. V.
- Melo-Júnior, T. A., M. F. de Vasconcelos, G. W. Fernandes and M. A. Marini (2001) Bird species distribution and conservation in Serra do Cipó, Minas Gerais, Brazil. *Bird Conserv. Intern.* 11: 189-204.
- Ménétrières, E. (1835) Monographie de la famille des Myiotherinae. *Mem. Acad. Imp. Sci. St. Pétersbourg*, 6th ser. III, part 2: 443-543.
- Meyer de Schauensee, R. 1982. *A guide to the birds of South America*. Philadelphia: Academy of Natural Sciences of Philadelphia.
- Miranda-Ribeiro, A. de (1906) Vertebrados do Itatiaya (Peixes, Serpentes, Saurios, Aves e Mammiferos). *Arch. Mus. Nac.* 13: 163-190.
- _____, (1923) Nota crítica sobre a ornis do Itatiaya. *Arch. Mus. Nac.* 24: 238-255.
- _____, (1928) A survey of Dr. Holt's survey of the serra do Itatiaya, Brasil. *Bol. Mus. Nac.* 4: 55-61.
- _____, (1930) Notas Ornithologicas X. Ainda *Scytalopus speluncae*. *Bol. Mus. Nac.* 6: 11-15.
- Munsell (1994) *Soil color charts, revised edition*. Macbeth Division of Koll Morgan Instruments Corporation. New York: New Windsor.
- Narosky, T., and D. Yzurieta (1987) *Guia para la identificación de las aves de la Argentina y Uruguay*. Buenos Aires: Vazques Mazzini.
- Naumburg, E. M. B. (1937) Studies of birds from eastern Brazil and Paraguay, based on a collection made by Emil Kaempfer. Conopophagidae, Rhinocryptidae, Formicariidae (part). *Bull. Amer. Mus. Nat. Hist.* 74: 139-205.
- Navas, J. R., and N. A. Bo. (1977) Ensayo de tipificación de nombres comunes de las aves argentinas. *Rev. Mus. Arg. Cienc. Nat. "Bernardino Rivadavia" y Inst. Nac. Invest. Cienc. Nat., Zool.* 12.
- Nores, M. (1992) Bird speciation in subtropical South America in relation to forest expansion and retraction. *Auk* 109: 346-357.
- Olrog, C. C. (1984) *Las aves argentinas. Una nueva guía de campo*. Buenos Aires: Administración de Parques Nacionales.
- Pacheco, J. F. (2004) Pílulas Históricas VI. Sabará ou Cuiabá? O problema das localidades de Ménétrières. *Atualidades Orn.* 117: 4-5.
- Parrini, R., M. A. Raposo, J. F. Pacheco, A. M. P. Carvalhães, T. A., Jr. Melo, P. S. M. Fonseca and J. C. Minns. (1999) Birds of the Chapada Diamantina, Bahia, Brazil. *Cotinga* 11: 86-95.
- Partridge, W. H. (1954) Estudio preliminar sobre una coleccion de aves de Misiones. *Rev. Inst. Nac. Invest. Cienc. Nat. y Mus. Arg. Cienc. Nat. "Bernardino Rivadavia"* 3: 87-153.
- Paynter, R. and M. A. Traylor (1991) *Ornithological gazetteer of Brazil*. 2 vols. Cambridge: Museum of Comparative Zoology.
- Peña, M. R. de la and M. Rumboll (1998) *Birds of Southern South America and Antarctica*. London: Harper Collins.
- Peters, J. L. (1951) *Check-List of birds of the world. Vol. 7*. Cambridge: Museum of Comparative Zoology.
- Petri, S. and V. J. Fúlfaro (1983) *Geologia do Brasil*. São Paulo: T. A. Queiroz and Ed. da Universidade de São paulo.
- Pinto, O. (1941) Sobre a variação geográfica das populações de *Cichlocolaptes leucophrus* (Jard. & Selby), com a descrição de uma raça nova. *Rev. Arg. Zoogeogr.* 1: 165-171.
- Pinto, O. M. de O. (1978) *Novo catálogo das aves do Brasil*. São Paulo: Empresa Gráfica da Revista dos Tribunais.
- Plótnick, R. (1958) Posición sistemática del género "Psilorhamphus" (Rhinocryptidae, Passeriformes). *Physis* 21: 130-136.
- Remsen, J. V., Jr., O. Rocha O., C. G. Schmitt and D. C. Schmitt (1991) Zoogeography and geographic variation of *Platyrinchus mystaceus* in Boliva and Peru, and the circum-Amazonian distribution pattern. *Orn. Neotrop.* 2: 77-83.
- Ridgely, R. S. and G. Tudor (1994) *The birds of South America, vol. 2*. Austin: University of Texas Press.
- Safford, H. D. (1999) Brazilian Páramos I. An introduction to the physical environment and vegetation of the *campos de altitude*. *J. Biogeogr.* 26: 693-712.

- Sclater, P. L. (1890) *Catalogue of the birds in the British Museum*. Vol. 15. London: British Museum.
- Sick, H. (1958) Resultados de uma excursão ornitológica do Museu Nacional a Brasília, novo Distrito Federal, Gioás, com a descrição de um novo representante de *Scytalopus* (Rhinocryptidae, Aves). *Bol. Mus. Nac.*, N. Sér., Zool. 185: 1-20.
- _____ (1960) Zur systematik und biologie der Bürzelstelzer (Rhinocryptidae), speziell Brasiliens. *J. Orn.* 101: 141-174.
- _____ (1985) Observations on the Andean-Patagonian component of southeastern Brazil's avifauna, p. 233-237. In: P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely and F. G. Buckley (eds.) *Neotropical Ornithology* (Ornithological Monographs 36).
- _____ (1997) *Ornitologia Brasileira*. Edição revista e ampliada por José Fernando Pacheco. Rio de Janeiro: Editora Nova Fronteira.
- Silva, J. M. C. da (1994) Can avian distribution patterns in northern Argentina be related to gallery-forest expansion – retraction caused by Quaternary climatic changes? *Auk* 111: 495-499.
- _____ (1995) Biogeographic analysis of the South American Cerrado avifauna. *Steenstrupia* 21: 49-67.
- _____ (1996) Distribution of amazonian and atlantic birds in gallery forests of the Cerrado Region, South America. *Orn. Neotrop.* 7: 1-18.
- _____ and D. F. Stotz (1992) Geographic variation in the Sharp-billed Treehunter *Heliobletus contaminatus*. *Bull. Brit. Orn. Cl.* 112: 98-101.
- _____ and F. C. Straube (1996) Systematics and biogeography of Scaled Woodcreepers (Aves: Dendrocolaptidae). *Stud. Neotrop. Fauna and Environm.* 31: 3-10.
- Silveira, L. F. (1998) The birds of Serra da Canastra National Park and adjacent areas, Minas Gerais, Brazil. *Cotinga* 10: 55-63.
- Smithe, F. B. (1975) *Naturalist's color guide*. New York: American Museum of Natural History.
- Snow, D. W. (1982) *The Cotingas*. Ithaca: Cornell Univ. Press and British Museum (Natural History).
- Spichiger, R., R. Palese, A. Chautems and L. Ramella (1995) Origin, affinities and diversity hot spots of the Paraguayan dendrofloras. *Candollea* 50: 515-537.
- Straneck, R. (1990) *Canto de las aves de Misiones. II*. Buenos Aires: L.O.L.A. (Literature of Latin America).
- Vasconcelos, M. F. de (2001) *Estudo biogeográfico da avifauna campestre dos topos de montanha do Sudeste do Brasil*. M. Sc. Thesis. Belo Horizonte: Universidade Federal de Minas Gerais.
- _____, M. Maldonado-Coelho and R. Durães (1999) Notas sobre algumas espécies de aves ameaçadas e pouco conhecidas da porção meridional da Cadeia do Espinhaço, Minas Gerais. *Melopsittacus* 2: 44-50.
- _____ and T. A. de Melo Júnior (2001) An ornithological survey of Serra do Caraça, Minas Gerais, Brazil. *Cotinga* 15: 21-31.
- _____, S. D'Angelo Neto, L. F. S. Brand, N. Venturin, A. T. de Oliveira-Filho and F. A. F. Costa (2002) Avifauna de Lavras e municípios adjacentes, sul de Minas Gerais, e comentários sobre sua conservação. *Unimontes Científica* 4: 153-165.
- Vielliard, J. M. E. (1990) Estudo bioacústico das aves do Brasil: o gênero *Scytalopus*. *Ararajuba* 1: 5-18.
- Whitney, B. M. (1994) A new *Scytalopus* tapaculo (Rhinocryptidae) from Bolivia, with notes on other Bolivian members of the genus and the *magellanicus* complex. *Wilson Bull.* 106: 585-614.
- Willis, E. O. (1992a) Zoogeographical origins of eastern Brazilian birds. *Orn. Neotrop.* 3: 1-15.
- _____ (1992b) Three *Chamaeza* antthrushes in eastern Brazil (Formicariidae). *Condor* 94: 110-116.
- _____ and Y. Oniki (1991) Avifaunal transects across the open zones of northern Minas Gerais, Brazil. *Ararajuba* 2: 41-58.
- Zimmer, J. T. (1939) Studies of Peruvian birds. No. XXXII. The genus *Scytalopus*. *Amer. Mus. Novitates*. 1044.