

ISSN 0103-5657

Revista Brasileira de Ornitologia

www.ararajuba.org.br/sbo/ararajuba/revbrasorn

Volume 18
Número 2
Junho 2010



Publicada pela
Sociedade Brasileira de Ornitologia
São Paulo - SP

Scytalopus petrophilus (Rock Tapaculo): a new species from Minas Gerais, Brazil

Bret M. Whitney^{1,4}, Marcelo Ferreira de Vasconcelos², Luís Fábio Silveira^{3,4}, and José Fernando Pacheco⁴

¹ Museum of Natural Science, 119 Foster Hall, Louisiana State University, Baton Rouge, Louisiana 70803 USA. E-mail: ictinia@earthlink.net.

² Pós-graduação em Zoologia de Vertebrados, Pontifícia Universidade Católica de Minas Gerais. Avenida Dom José Gaspar, 500, Prédio 41, Coração Eucarístico, 30535-610, Belo Horizonte, MG, Brasil. E-mail: mfvasconcelos@pucminas.br.

³ Departamento de Zoologia, Universidade de São Paulo. Caixa Postal 11.461, 05422-970, and Curador associado das coleções ornitológicas, Museu de Zoologia da Universidade de São Paulo, Caixa Postal 42.494, 04218-970, São Paulo, SP, Brasil. E-mail: lfsilvei@usp.br.

⁴ CBRO – Comitê Brasileiro de Registros Ornitológicos (www.cbro.org.br). E-mail: jfpacheco@terra.com.br.

Recebido em: 18/12/2009. Aceito em: 25/06/2010.

Special Editor: Dr. Alexandre Aleixo, Museu Paraense Emílio Goeldi.

RESUMO: Uma nova espécie de *Scytalopus* do Estado de Minas Gerais, Brasil. É descrita uma nova espécie de *Scytalopus* da porção meridional da Cadeia do Espinhaço e de outros pontos do estado de Minas Gerais, Brasil. *Scytalopus petrophilus* sp. nov. (tapaculo-serrano) ocupa uma ampla variedade de habitats entre cerca de 900 e 2.100 m de altitude, variando desde áreas abertas nos altos das serras, em formações arbustivas sobre afloramentos rochosos (campos rupestres) a florestas mais altas em vales encaixados e capoeiras de florestas semidecíduas. Sua morfologia, vocalizações e uma filogenia molecular mostram consistentemente que esta espécie se encaixa no clado formado por *S. novacapitalis* (tapaculo-de-brasília), *S. pachecoi* (tapaculo-ferreirinho) e *S. diamantinensis* (tapaculo-da-chapada-diamantina). Fenotipicamente, *S. petrophilus* é diagnosticado de suas aloespécies por combinações de caracteres morfológicos e vocais.

PALAVRAS-CHAVE: *Scytalopus*, tapaculo, nova espécie, holótipo, localidade tipo, nomenclatura, sinonímia, Espinhaço.

ABSTRACT: We describe a new species of *Scytalopus* tapaculo from the southern section of the Espinhaço Range and other points in Minas Gerais, Brazil. *Scytalopus petrophilus* sp. nov., Rock Tapaculo, occupies a variety of habitats between about 900 and 2,100 m elevation, from open, rocky shrub associations (*campos rupestres*) high in the mountains to taller forest in steep-walled valleys to second-growth of semi-deciduous woodland. Its morphology, vocalizations, and preliminary genetic profile place it solidly within the *S. novacapitalis* (Brasília Tapaculo) complex, joining that species, *S. pachecoi* (Planalto Tapaculo), and the newly described *S. diamantinensis* (Diamantina Tapaculo). *S. petrophilus* is phenotypically diagnosed from its allospecies by combinations of morphological and vocal characters.

KEY-WORDS: *Scytalopus*, tapaculo, new species, holotype, type-locality, nomenclature, synonymy, Espinhaço.

Diversification in the genus *Scytalopus* in eastern Brazil has received heightened attention from ornithologists over the past several years, with four new species recently described (Bornschein *et al.* 1998, Maurício 2005, Raposo *et al.* 2006, Bornschein *et al.* 2007, Raposo and Kirwan 2008). Several other populations that appear to warrant recognition as distinct species are currently under study (Parrini *et al.* 1999, Vasconcelos 2001, Silveira *et al.* 2005, Mata *et al.* 2009, pers. obs.). The first of these unnamed forms to be identified as such was discovered in the rocky uplands of the Espinhaço Range of Minas Gerais in 1989 and has sometimes been attributed to *S. novacapitalis* (Brasília Tapaculo) due to its plumage similarity and general confusion among ornithologists (*see* Collar *et al.* 1992) but most recently has been explicitly recognized at the species level based on both phenotypic characters (plumage and voice; Bornschein *et al.* 2007) and its preliminary

genetic profile (Mata *et al.* 2009). Raposo *et al.* (2006), followed by Raposo and Kirwan (2008), identified this form as *S. speluncae* (Mouse-colored Tapaculo) but Maurício *et al.* (2010), in a different interpretation of the same objective pieces of evidence, showed that the new species cannot be assigned to *Scytalopus speluncae* (Ménétrières). Furthermore, Mata *et al.* (2009) showed that *S. speluncae* and the unnamed taxon are not even sisters. The purpose of this paper is the formal designation of this taxon as:

***Scytalopus petrophilus* sp. nov.**
Rock Tapaculo
Tapaculo-serrano

Holotype – Museu de Zoologia da Universidade de São Paulo [MZUSP] 78822; adult male (skull 15%)

pneumatized; testes 8.2×4 mm) from Serra da Piedade, Caeté, Minas Gerais, Brazil ($19^{\circ}49'S$, $43^{\circ}40'W$), at 1,720 m; collected and prepared by MFV on 17 September 2004; tissue sample and carcass preserved.

Paratypes – Departamento de Zoologia da Universidade Federal de Minas Gerais [DZUFMG] 5333; sub-adult female (skull 15% pneumatized; ovary 4×2 mm; ova 0.3 mm) from Serra da Piedade at 1,700 m; collected and prepared by MFV on 7 January 2004; tissue sample and carcass preserved. DZUFMG 5334; adult male (skull 15% pneumatized; testes 8.4×3.4 mm) from Serrinha, Lavras, Minas Gerais, Brazil ($21^{\circ}19'S$, $44^{\circ}59'W$), at 1,150 m; collected by MFV and S. D'Angelo-Neto on 5 December 2003; tissue sample and carcass preserved; tape-recorded and prepared by MFV, voice deposited at Arquivo Sonoro Elias Coelho (ASEC). MZUSP 78821; adult male (skull 25% pneumatized; testes 6.3×3.4 mm) from Sítio Ponte Velha, São João del-Rei, Minas Gerais, Brazil ($21^{\circ}04'S$, $44^{\circ}20'W$); collected and tape-recorded by MFV and V. T. Lombardi on 15 January 2005; prepared by MFV; tissue sample and carcass preserved; voices deposited at ASEC. MZUSP 78812; adult male (skull partially pneumatized; small testes) from Pico do Inficionado, Serra do Caraça, Catas Altas, Minas Gerais, Brazil ($20^{\circ}08'S$, $43^{\circ}27'W$), at 1,850 m; collected by LFS and MFV on 23 December 1999; prepared by LFS; tissue sample and carcass preserved. Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre [MCP] 1560; adult male (skull partially pneumatized; small testes) from Pico do Inficionado, Serra do Caraça, at 2,020 m; collected by LFS and MFV on 23 December 1999; prepared by LFS; tissue sample and carcass preserved. MCP 1561; adult male (skull partially pneumatized; small testes) from Pico do Inficionado, Serra do Caraça, at 2,040 m; collected by LFS and MFV on 23 December 1999; prepared by LFS; tissue sample and carcass preserved. MZUSP 78811; adult male (skull partially pneumatized; small testes) from Pico do Inficionado, Serra do Caraça, at 2,020 m; collected by LFS and MFV on 23 December 1999; tape-recorded and prepared by LFS; tissue sample and carcass preserved, voices deposited at ASEC. MZUSP 78813; adult male (skull partially pneumatized; testes 3×2 mm) from Pico do Inficionado, Serra do Caraça, at 1,920 m; collected by LFS and MFV on 23 December 1999; prepared by LFS; tissue sample and carcass preserved. MZUSP 78815; juvenile female (skull not pneumatized; ovary 5×3 mm; ova 1.5 mm) from Gruta de Lourdes, Serra do Caraça, Catas Altas, Minas Gerais, Brazil ($20^{\circ}06'S$, $43^{\circ}27'W$), at 1,580 m; collected by MFV and M. M. Coelho on 14 November 2000; prepared by MFV; carcass preserved; tape-recorded by M. M. Coelho. MZUSP 78814; immature female (skull not pneumatized; ovary 4×1.5 mm) from Pico do Inficionado, Serra do Caraça, at 2,050 m; collected by MFV and G. N. Maurício on 4 February 2003; prepared

by MFV; tissue sample and carcass preserved. MZUSP 78816; subadult male (skull not fully pneumatized; testes 2×1 mm) from Pico do Inficionado, Serra do Caraça, at 2,050 m; collected by MFV and G. N. Maurício on 4 February 2003; prepared by MFV; tissue sample and carcass preserved; tape-recorded by G. N. Maurício. MZUSP 78817; adult male (skull not fully pneumatized; testes 2×1 mm) from Pico do Inficionado, Serra do Caraça, at 2,040 m; collected by MFV and G. N. Maurício on 4 February 2003; prepared by MFV; tissue sample and carcass preserved. DZUFMG 4169; unsexed adult (skull not fully pneumatized; gonads destroyed by shot) from Pico do Inficionado, Serra do Caraça, at 2,050 m; collected by MFV and G. N. Maurício on 5 February 2003; prepared by MFV; tissue sample and carcass preserved. MCP 1562; adult male (skull not fully pneumatized; testes 2×1 mm) from trail to Pico do Inficionado, Serra do Caraça, at 1,750 m; collected by MFV and G. N. Maurício on 6 February 2003; prepared by MFV; tissue sample and carcass preserved. MZUSP 78818; unsexed adult (skull and gonads destroyed by shot) from trail to Pico do Inficionado, Serra do Caraça, at 1,840 m; collected and prepared by MFV on 20 November 2004; tissue sample and carcass preserved. DZUFMG 5335; subadult male (skull destroyed by shot; testes 6.6×3.4 mm) from Pico do Inficionado, Serra do Caraça, at 2,050 m; collected and prepared by MFV on 20 November 2004; tissue sample and carcass preserved. MZUSP 78823; adult male (skull 10% pneumatized; testes 3×1.3 mm) from Brumas do Espinhaço, Lapinha de Cima, Santana do Riacho, Minas Gerais, Brazil ($19^{\circ}02'S$, $43^{\circ}42'W$), at 1,300 m; collected and prepared by MFV on 1 February 2004; tissue sample and carcass preserved. MZUSP 78824; adult male (skull 10% pneumatized; testes 3×1.5 mm) from Brumas do Espinhaço, at 1,400 m; collected and prepared by MFV on 2 February 2004; tissue sample and carcass preserved. DZUFMG 5336; adult male (skull 15% pneumatized; testes 7×3 mm) from Brumas do Espinhaço, at 1,350 m; collected and prepared by MFV on 10 January 2005; tissue sample and carcass preserved. DZUFMG 4167; adult male (skull 10% pneumatized; testes 2×1 mm) from Pico Dois Irmãos, Parque Estadual do Rio Preto, São Gonçalo do Rio Preto, Minas Gerais, Brazil ($18^{\circ}24'S$, $43^{\circ}21'W$), at 1,780 m; collected by MFV, M. R. Bornschein, and R. B.-Lopes on 17 May 2004; prepared by MFV; tissue sample and carcass preserved. DZUFMG 4168; adult female (skull 10% pneumatized; ovary 4×2.5 mm; ova 1 mm) from Pico Dois Irmãos, at 1,710 m; collected by MFV, M. R. Bornschein, and R. B.-Lopes on 17 May 2004; prepared by MFV; tissue sample and carcass preserved. MZUSP 78825; adult female (skull 10% pneumatized; ovary 4.5×3 mm; ova 1 mm) from Pico Dois Irmãos, at 1,710 m; collected by MFV, M. R. Bornschein, and R. B.-Lopes on 17 May 2004; prepared by MFV; tissue sample and carcass preserved.

TABLE 1: Summary of measurements (mean \pm SD) for members of the *Scytalopus novacapitalis* and *S. speluncae* complexes. For all variables, measurements of males are shown in the first row, females in the second except for *S. novacapitalis* and *Scytalopus* sp. from S Bahia, for which only males were available. All measurements are in millimeters. Sample sizes are in parentheses.

Taxon/Variable	Exposed culmen	Wing (chord)	Tail	Tarsus
<i>Scytalopus petrophilus</i>	11,83 \pm 0,5 (30)	50,8 \pm 1,57 (31)	45,67 \pm 3,05 (23)	20,09 \pm 0,54 (30)
	11,8 \pm 0,28 (2)	49,7 \pm 0,28 (2)	46,55 \pm 0,28 (2)	19,05 \pm 0,63 (2)
Range	10,6 – 12,4	48,6 – 53,4	42 – 50,1	18,6 – 21
<i>Scytalopus speluncae</i>	11,17 \pm 0,47 (43)	48,49 \pm 2,35 (43)	43,06 \pm 3,6 (38)	19,59 \pm 0,82 (43)
	11 \pm 0,51 (19)	47,68 \pm 2,39 (21)	41,48 \pm 2,96 (16)	19,33 \pm 0,8 (20)
Range	10,1 – 10,4	43,3 – 53,5	36,2 – 48,8	17,2 – 20,8
<i>Scytalopus diamantinensis</i>	12,26 \pm 0,37 (6)	53,2 \pm 2,08 (6)	44,88 \pm 3,07 (5)	20,35 \pm 0,65 (6)
	11,45 \pm 0,2 (2)	50,23 \pm 0,68 (3)	41,73 \pm 2,41 (3)	20,3 \pm 0,36 (3)
Range	11,3 – 12,6	49,7 – 55,3	39 – 45,1	19,5 – 21,1
<i>Scytalopus pachecoi</i>	11 \pm 0,42 (26)	49,17 \pm 1,48 (26)	41,52 \pm 2,09 (24)	19,14 \pm 0,45 (26)
	10,91 \pm 0,43 (6)	45,55 \pm 1,66 (6)	39,9 \pm 2,8 (3)	18,4 \pm 0,63 (6)
Range	10,1 – 11,5	46 – 51,6	38 – 44,8	17,9 – 20,1
<i>Scytalopus</i> sp. Bahia	12,15 \pm 0,48 (8)	49,7 \pm 1,18 (8)	37,55 \pm 0,79 (6)	19,42 \pm 0,3 (8)
	Range	11,5 – 12,8	47,5 – 51,8	35,7 – 39,1
<i>Scytalopus novacapitalis</i>	12,27 \pm 0,32 (4)	52,89 \pm 2,12 (5)	46,51 \pm 1,74 (5)	20,25 \pm 0,24 (5)
	Range	11,6 – 12,64	50,3 – 55,7	45 – 48,5

Diagnosis – Morphology: Alphanumeric color designations determined through direct comparison with Munsell soil color charts (1994). Among members of the *Scytalopus novacapitalis* clade (Mata *et al.* 2009), *S. petrophilus* (n = 21) is distinguished from *S. novacapitalis* (n = 5) by its darker chin, throat, and breast. However, one male of *S. novacapitalis* (MCP 1481) is darker in coloration, approaching specimens of *S. petrophilus* having the palest throat and breast. *Scytalopus petrophilus* is distinguished from *S. pachecoi* (n = 32) in showing notably more contrast between the whitish abdomen and the gray chin, throat, and breast; contrast is inconspicuous or lacking in *S. pachecoi*. Additionally, the crissum and center of the lower abdomen are less densely barred than in *S. pachecoi*, although a single *S. petrophilus* (MZUSP 78816) showed a pattern similar to *S. pachecoi*. Diagnosability of adult *S. petrophilus* from *S. diamantinensis* (n = 9) appears to be restricted to the color/contrast of the belly region of adult males, being paler and more whitish, thus with more contrast, than the more uniformly gray underparts of *S. diamantinensis*.

Full adults of *Scytalopus petrophilus* are readily separated from those of *S. speluncae* (*sensu* Maurício *et al.* 2010) by the barred flanks; the flanks are unmarked in full adult *S. speluncae* (e.g. MZUSP 36347 and MZUSP 82618). In adults and subadults of *S. petrophilus* (Gley chart 1: between close to 8/N and 5/N) the chin, throat and breast are lighter than those of *S. speluncae* (Gley chart 1: between 4/N and close to 2.5/N). Furthermore, in adults of *S. petrophilus* the abdomen is distinctly paler, more whitish than the chin, throat, and breast whereas adults of *S. speluncae* lack notable contrast in the underparts.

Measurements (exposed culmen, wing [chord], tail, and tarsus) were taken from all specimens and analyzed with analytic and descriptive statistics (parametric and non-parametric ANOVA, mean and standard deviation). Notwithstanding the small sample of females, there appear to be no significant differences between the sexes of *S. petrophilus*. Compared to members of the *Scytalopus novacapitalis* and *S. speluncae* complexes, *S. petrophilus* shows significant differences for all characters only with respect to *S. pachecoi* and *S. speluncae* (Table 1).

Diagnosis – Voice: *Scytalopus petrophilus* possesses at least four distinct types of vocalizations which, within the *S. novacapitalis* clade (*sensu* Mata *et al.* 2009), show greatest similarity to *S. pachecoi* and *S. diamantinensis* and little or no overlap with *S. novacapitalis* (Bornschein *et al.* 2007). Most importantly, *S. petrophilus* delivers a strongly modulated *pzeen* call (Figure 1A), absent in *S. diamantinensis* and *S. novacapitalis* (although calls of the latter, other than the multi-note alarm, are unknown, which we suspect reflects a lack of attention to recording the species' vocalizations in the field). This “contact call” is both shorter and more down-slurred than a similar call of *S. pachecoi* (Figure 1B) and has a tonality audibly distinct from that species; it is the only vocalization that appears to be diagnostic of *S. petrophilus*. The most diagnostic vocalization of *S. diamantinensis*, a single *tcheep* call (Figure 1C) that may be followed by one or two lower, sharper notes, is absent from the repertoire of *S. petrophilus* and those of both *S. pachecoi* and *S. novacapitalis*. We make no assumption of homology of *tcheep* and *pzeen* calls, although we suspect that they are homologous;

behavioral contexts have not been sufficiently documented. The salient observation is that these short, frequently delivered calls are diagnostic of some populations and can be applied in concert with other phenotypic characters to distinguish taxa (Table 2). Bornschein *et al.* (2007) suggested that a type of multi-note call (other than the alarm call) heard from two individuals of *S. diamantinensis* on a single day, and partially recorded once, “could be

seen as another diagnostic vocal character” between that species and *S. petrophilus* (see their figure 9D). Similarly, we have a single, poor-quality recording of *S. petrophilus* delivering a distinctive song-variant comprising a series of evenly paced, bisyllabic notes that is unknown from other taxa. Whitney (1994) reported that certain vocal variants among a set of recordings of *S. schulenbergi* (Diademed Tapaculo) appeared to be given only by juvenile/subadult birds (vocalizing birds recorded and collected), and it is possible that these two rarely heard vocalizations of *S. petrophilus* were delivered by young birds, perhaps as an age signature or as part of the inevitable process of perfecting adult vocal types. Until such anomalous vocalizations are studied much more thoroughly, the safest practice is to exclude them from species-level diagnoses.

Description of holotype – Lores, chin, auriculars, and throat gray (Gley chart 1: 6/N). Breast blended with two tones of gray (between Gley chart 1: 5/N and 6/N). Abdomen light-gray (Gley chart 1: 7/N), washed with white (Gley chart 1: 8/N). Crown, nape, mantle, scapulars, remiges, and tail dark-gray (Gley chart 1: 3/N). Flanks, uppertail and undertail coverts varying between yellowish brown (10YR 5/8) and brownish yellow (10YR 6/8) barred with black (7.5YR 2.5/1). Soft parts colors: bill black with gray tip; tarsus and feet brownish-cream; iris dark brown. Tail with 12 rectrices.

Measurements of holotype – Total length of fresh, unskinned specimen 132.0 mm; bill, from anterior edge of operculum to tip, 6.1 mm; exposed culmen, 11.1 mm; bill depth at the base (posterior edge of nares), 4.3 mm; wing (chord), 52.7 mm; tail, from the insertion of the central rectrices to the tip, 44.2 mm; tarsus, 20.5 mm; body mass 15.0 g.

REMARKS

Variation in the type series – See color frontispiece, based on DZUFMG 5335, a specimen substantially like the holotype. There appears to be no clear sexual dichromatism in plumage among adult specimens of *Scytalopus petrophilus*, but the amount and extent of whitish or grayish feathers in the abdomen varies from white (Gley chart 1: 8/N) and light gray (Gley chart 1: 7/N) to gray (Gley chart 1: 5/N) without regard to locality. Among a series of 21 specimens displaying adult plumage through the underparts, only one (MZUSP 78817) has a gray abdomen lacking the typical breast/belly contrast. This pattern also does not appear to be related to the sex or the age of birds, because the abdomen of adults of both sexes from a single locality can also show different amounts of white or gray. For example, among our largest series of definitive adult males from a single locality (n = 7 from Pico do

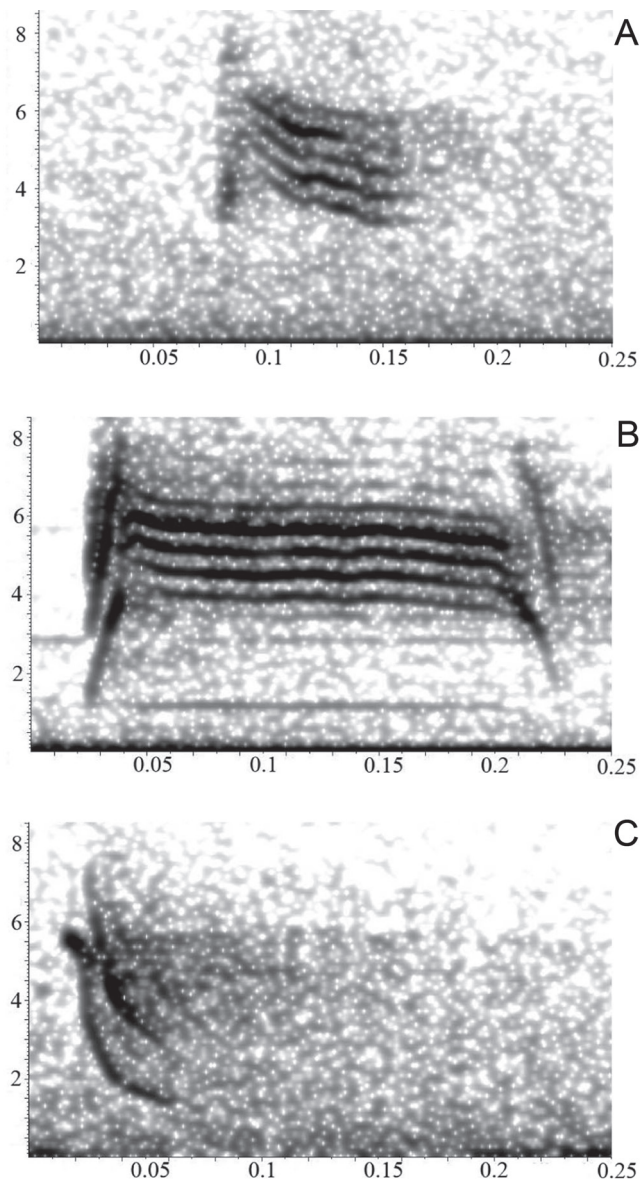


FIGURE 1: Spectrograms of monosyllabic “contact” calls of three members of the *Scytalopus novacapitalis* clade (*sensu* Mata *et al.* 2009). A: *S. petrophilus* sp. nov., short, downslurred *pzeen* call (Sítio Ponte Velha, right bank of Rio das Mortes, municipality of São João del Rei, Minas Gerais, 26 May 2005 (recorded by V. Torga); B: *S. pachecoi*, longer, steadier-frequency *pzeen* call (Cerro das Almas, municipality of Capão do Leão, Rio Grande do Sul, 14 September 2002 (recorded by G. N. Maurício); C: *S. diamantinensis*, short, sharp *tcheep* call, Morros de Ouro, municipality of Barra da Estiva, Bahia, 26 August 2006 (recorded by R. Belmonte-Lopes). Homology of these vocalizations has not been determined, but we strongly suspect that they are homologous. No similar monosyllabic vocalization has yet been identified for *S. novacapitalis*.

TABLE 2: Pairwise diagnostic phenotypic comparisons among adults of the four species in the *Scytalopus novacapitalis* clade assembled largely from Bornschein *et al.* (2007) and (for *S. pachecoi*) from Maurício (2005). Sample sizes in parentheses. S is the regular song, AS the accelerating song divided into “initial” and “trilled” sections with a separately analyzed “transition” between them. Descriptions are of species in the left column vs. their counterparts across the top row.

Taxon	<i>S. novacapitalis</i> (5)	<i>S. diamantinensis</i> (9)	<i>S. pachecoi</i> (32)
<i>S. petrophilus</i> (27)	Throat and breast almost always ^a notably darker gray; S pace faster and note length shorter; AS initial faster; <i>pzeen</i> call present	Center belly whitish (not distinctly grayish); AS initial slower, transition pace faster and duration shorter, notes of trilled section longer; <i>pzeen</i> call present, <i>tcheep</i> call absent and alarm call with distinct note-shape	Crissum and center of lower abdomen almost always ^b less densely barred. <i>pzeen</i> call shorter, more downslurred and with distinct tonality
<i>S. novacapitalis</i>		Belly whitish (not gray). S pace slower and note length longer; AS initial slower; <i>tcheep</i> call absent ^c	Chin and throat pale (not medium) gray, center belly whitish (not gray). S pace slower with longer and lower-frequency notes, alarm call pace faster and higher frequency; <i>pzeen</i> call absent ^c
<i>S. diamantinensis</i>			Adult plumage not diagnosable, immatures have distinct patterns of barring on upperwing coverts. Male bill deeper, culmen longer and female larger in all standard measurements except tail length; AS transition pace slower; <i>tcheep</i> call present and alarm with distinct note-shape

^a One specimen of *S. novacapitalis* (MCP 1481) was nearly as dark as the palest examples of *S. petrophilus*.

^b A single *S. petrophilus* (MZUSP 78816) is indistinguishable from *S. pachecoi*.

^c No monosyllabic “contact” call has yet been identified for *S. novacapitalis*.

Inficionado, Serra do Caraça), two males have pure-white abdomens (MCP 1560, MZUSP 78812) and the above-mentioned specimen has a pure-gray abdomen (MZUSP 78817); the remaining four (MCP 1561, 1562, MZUSP 78813, 78811) exhibit varying intermediate amounts of white and gray. We initially suspected that birds with paler abdomens might be younger than those with grayish ones, but it appears that this is not the case in *S. petrophilus*, because a male from Pico do Inficionado (MZUSP 78816) with complete adult plumage except for some retained juvenal remiges has less white in the abdomen than other specimens in definitive adult plumage from that locality (MCP 1560, MZUSP 78812, 78811).

Three specimens (MZUSP 78811, 78825, DZUFMG 4168,) have chins and throats between white (Gley chart 1: 8/N) and light-gray (Gley chart 1: 7/N), thus slightly paler than that described for the holotype. Three specimens (MZUSP 78813, MZUSP 78817, MZUSP 78818) have chins and throats slightly darker than that of the holotype (gray – Gley chart 1: 5/N). This, too, is best explained by individual variation, because MZUSP 78811, an adult male with pale chin and throat, was taken at the same locality (Pico do Inficionado) as the three above-mentioned specimens (two males and one unsexed) with darker chins and throats.

The amount of yellowish-brown or brownish-yellow feathers with black bars on the flanks, uppertail coverts, and undertail coverts also varies across the type series. It appears to be unrelated to sex, because adult males and females can exhibit differing quantities of these feathers. This character may well be related to age, however,

because juveniles and subadults show a much higher proportion of brownish, barred feathers (*see below*).

Soft parts in the type series accord well with those of the holotype. Of 16 specimens with complete tails, 15 had 12 rectrices and one had 10 rectrices (MZUSP 78811).

Geographical distribution – Patchily distributed along the Espinhaço Range from central Minas Gerais (Pico Dois Irmãos) to the south of this mountain chain (Brumas do Espinhaço, Serra do Cipó, Serra da Piedade, Serra do Caraça, Serra do Batatal, and Pico do Itacolomi) and southern Minas Gerais (Lavras, Ijaci, São João del-Rei, Bocaina de Minas, Camanducaia). Bocaina de Minas and Camanducaia are in the Mantiqueira Range, close to the border of the states of Rio de Janeiro and São Paulo, respectively (Figure 2). Thus, the species might be found in these states also. Occurs mostly between 900 and 2,100 m elevation in the mountains and foothills.

Additional specimens examined – DZUFMG 5322; sub-adult female from Pedra de São Domingos, Gonçalves, Minas Gerais, Brazil (22°41’S, 45°57’W), at 1,990 m; collected and prepared by MFV on 27 March 2007; tissue sample and carcass preserved. DZUFMG 5719; adult male from base of Serra do Juncal, Camanducaia, Minas Gerais, Brazil (22°44’S, 45°56’W), at 1,450 m; collected and prepared by MFV on 11 January 2008; tissue sample and carcass preserved; tape-recorded by MFV. DZUFMG 6016; adult male from Serra da Gandarela, Rio Acima, Minas Gerais, Brazil (20°06’S, 43°39’W), at 1,610 m; collected and prepared by MFV on 25 September 2008;

tissue sample and carcass preserved. MCP 1509; sub-adult male from Serra do Palmital, Bocaina de Minas, Minas Gerais, Brazil (22°12'S, 44°27'W) at 1,330 m; collected by M. R. Bornschein, G. N. Maurício, and C. Gatto on 2 December 2004; prepared by M. R. Bornschein; tissue sample and carcass preserved; tape-recorded by G. N. Maurício. MCP 1510; adult male from Serra do Palmital at 1,330 m; collected by M. R. Bornschein, G. N. Maurício, and C. Gatto on 2 December 2004; prepared by M. R. Bornschein; tissue sample and carcass preserved; tape-recorded by G. N. Maurício. MZUSP 78819; adult female (skull not ossified) from Serra do Caraça, collected by JFP and BMW on 4 March 1997; prepared by L. P. Gonzaga. MZUSP 78820; juvenile female (skull not ossified), from Serra do Caraça, collected by JFP and BMW on 4 March 1997; prepared by L. P. Gonzaga. MZUSP 83542, adult male, from Poços de Caldas, Minas Gerais, Brazil (21°47'S, 46°30'W), collected by G. R. Rocha Brito on 16 July 2008; prepared by E. Boaventura. MZUSP 83543, adult male, from Poços de Caldas, Minas Gerais, Brazil, same data as MZUSP 83542. See also Appendix 1 and 2.

Ontogenetic variation – In *S. petrophilus*, juveniles have more barred and brownish plumage than adults, as appears typical in the genus (Fjeldså and Krabbe 1990, Whitney 1994, Krabbe and Schulenberg 1997); a juvenile female (MZUSP 78814) is here described. Chin and throat pale-yellow (2.5Y 7/4) with fine, inconspicuous black bars (7.5YR 2.5/1). Breast brownish-yellow (between 10YR 6/6 and 10YR 6/8) finely barred with black (7.5YR 2.5/1). Center of abdomen brownish-yellow (between 10YR 6/6 and 10YR 6/8) washed with pale-yellow (2.5Y 7/4). Flanks, uppertail coverts and undertail coverts yellowish-brown (10YR 5/6) barred black (7.5YR 2.5/1). Lores pale-yellow (2.5Y 7/4) blended with strong brown (7.5YR 5/8) and finely barred black (7.5YR 2.5/1). Auriculars pale-yellow (2.5Y 7/4) blended with strong brown (7.5YR 5/8). Sides of neck deep-brown (7.5YR 5/8) finely barred black (7.5YR 2.5/1). Crown, nape, and mantle dark-yellowish-brown (10YR 3/4) finely barred black (7.5YR 2.5/1). Rump dark-yellowish-brown (between 10YR 3/4 and 10YR 3/6) with more densely and well marked black (7.5YR 2.5/1) bars. Lesser upperwing coverts dark-yellowish-brown (10YR 3/4) with a black (7.5YR 2.5/1) bar and a deep-brown (7.5YR 5/6) apical spot. Greater upperwing coverts dark-yellowish-brown (10YR 3/4) barred black (7.5YR 2.5/1) with a yellowish-brown (10YR 5/6) apical spot. Remiges dark-gray or blackish (10YR 3/1) fringed with black (7.5YR 2.5/1), dark-yellowish-brown (10YR 3/6) in the outer webs. Rectrices dark-grayish-brown (10YR 3/2) with inconspicuous yellowish-brown (10YR 5/6) fringes.

An immature female (MZUSP 78815) shows plumage features intermediate between adults and the juvenile

described above. Its crown, lores, auriculars, chin, throat, and breast are similar to those of adults, whereas the remiges, flanks, tail coverts, and tail are apparently juvenal. The upperparts are a blend of dark-grey (10YR 3/1) and dark-grayish-brown (10YR 3/2), with less barring than MZUSP 78815. The center of abdomen is between pale-yellow (2.5Y 8/4) and yellow (10YR 7/6).

Three specimens (MZUSP 78816, DZUFMG 5333, 5335) in nearly definitive adult plumage retain some brownish tones with faint blackish bars on the wings or a brownish tail, typical features of subadult birds.

Breeding and molt – Specimens collected between September and early December had well-developed gonads; most birds taken between the end of December and May apparently were not in reproductive condition. This observation together with the fact that juveniles were collected in February and March suggests that *S. petrophilus* breeds during the spring, mostly September–November. Furthermore, specimens showing heavy molt in the body, wings, and tail were collected in February; specimens showing no evidence of molt were taken in May (perhaps 5–7 months post-breeding) and between September and January.

Voice specimens examined – *Scytalopus petrophilus* was an integral component of a diagnosis-oriented vocal analysis of the *S. novacapitalis* clade (*sensu* Mata *et al.* 2009) of four species that share an accelerating song variant (Bornschein *et al.* 2007 who called it “*Scytalopus* sp. nov.”). Bornschein *et al.* (2007, their Table 2) presented ranges and means of multiple measurements, with spectrograms of typical vocalizations (their figures 4–7 and 9) of the most frequently recorded vocalizations of all four members of the group. We invoked the sample and analysis of vocalizations presented by Bornschein *et al.* (2007) and interpreted it in the context of diagnosing vocal characters of *S. petrophilus* relative to the other three members of the *S. novacapitalis* clade (*see Diagnosis* above and Table 2). The most pertinent of their figures, illustrating “contact” calls, are reproduced in Figure 1.

Etymology – The name *petrophilus* is Greek for “rock-loving”, which is quite appropriate for the new species although it also inhabits forest understory not far from more open, rocky places. The English name is a simplified version of the Greek, and the Portuguese name recognizes that the distribution of this tapaculo is essentially restricted to serras, at present only in the state of Minas Gerais.

Vocalizations – The song and alarm calls (*sensu* Bornschein *et al.* 2007) of *S. petrophilus* show varying degrees of overlap in all characters with at least one other member of the group, but on average and considered in

combination with contact calls, vocal repertoires of all species are diagnostic (Table 2). The short, sharp *pzeen* call appears to be diagnostic of *S. petrophilus* (Bornschein *et al.* 2007, pers. obs.). Removing any assumptions concerning the importance of one kind of vocalization over another in maintaining species integrity (*e.g.* songs were arbitrarily considered more important than calls by Krabbe and Schulenberg 1997) because the functions of discreet vocalization types in a species' repertoire are usually not known (as is the case with most vocalizations of *Scytalopus* tapaculos), "contact calls" may be more operational in communicating species identities within some complexes, or between some species-pairs, than are, for example, "territorial songs". Such was recently shown to be the case with two syntopic *Hypocnemis* antbirds inhabiting dense understory of lowland Amazonian forest where visual cues almost certainly take a secondary role to auditory communication of identities: "contact calls" have apparently evolved the seminal role of maintaining the identities of these two biological species of thamnophilid antbirds with essentially indistinguishable songs (Isler *et al.* 2007). Within Brazilian *Scytalopus*, most taxa of which are allopatric, Bornschein *et al.* (2007) noted, "...in two species so highly distinct ecologically, genetically and, to a lesser degree, morphologically, as *S. iraiensis* and *S. speluncae*, the differences between their songs are minimal... while they differ notably from one another in calls." Thus, it is appropriate to recognize that contact calls may reflect as much or more information on the diagnosability of populations as songs.

Natural History – *Scytalopus petrophilus* lives in a wide variety of habitats, from open formations on mountaintops to forested areas in the foothills. In the Espinhaço Range it is common in a rugged, rocky association of low trees, shrubs and grasses called *campo rupestre*, here typified by a high level of endemism. Characteristic genera of this flora are: *Aechmea*, *Baccharis*, *Chusquea*, *Hololepis*, *Huperzia*, *Laelia*, *Lychnophora*, *Nematanthus*, *Paepalanthus*, *Sinningia*, *Stachytarpheta*, *Vellozia*, and *Zygopetalum*. *Scytalopus petrophilus* shares the *campo rupestre* of the south-central Espinhaço Range with several other endemic or highly range-restricted montane birds, such as Hyacinth Visorbearer (*Augastes scutatus*), Cipo Canastero (*Asthenes luizae*), Itatiaia Spinetail (*Oreophylax moreirae*), Gray-backed Tachuri (*Polystictus superciliaris*), and Pale-throated Serra-Finch (*Embernagra longicauda*) (Vasconcelos 2008). Downslope, *S. petrophilus* occupies the elfin forests and cloud forests in canyons and steep valleys with or without streams, where plants of the following genera abound: *Begonia*, *Drymis*, *Eremanthus*, *Ilex*, *Miconia*, *Neoregelia*, *Nidularium*, *Podocarpus*, *Schefflera*, *Sophronites*, *Tibouchina*, *Tillandsia*, and *Vriesea*. In these habitats, *S. petrophilus* occurs alongside (among many others) Variable Antshrike (*Thamnophilus caerulescens*),

Ochre-rumped Antbird (*Drymophila ochropyga*), White-breasted Tapaculo (*Eleoscytalopus indigoticus*), Mottle-checked Tyrannulet (*Phylloscartes ventralis*), Rufous-bellied Thrush (*Turdus rufiventris*), Rufous-browed Peppershrike (*Cyclarhis gujanensis*), and Brassy-breasted Tanager (*Tangara desmaresti*). It also persists in partially deforested and burnt areas in the mountains where many invasive plants occur, especially the fern *Pteridium aquilinum* which provides dense cover. *Scytalopus petrophilus* has even been recorded in high-elevation marshes with thick growth of *Chusquea attenuata*, *Chusquea pinifolia*, *Cortaderia* sp., and *Tibouchina* sp. In southern Minas Gerais (Lavras and São João del-Rei regions), *S. petrophilus* has been taken in second-growth semideciduous woodland. Typical tree species there include *Alchornea triplinervia*, *Amaioua guianensis*, *Casearia arborea*, *Copaifera langsdorffii*, *Croton verrucosus*, *Miconia argyrophylla*, *M. trianae*, *Myrcia rostrata*, *Ocotea corymbosa*, *O. odorifera*, *Pera glabrata*, *Persea pyrifolia*, *Sclerolobium rugosum*, *Siphoneugena densiflora*, *Tapirira obtusa*, and *Vochysia magnifica* (Oliveira-Filho and Machado 1993, Oliveira-Filho *et al.* 1994, Gavilanes *et al.* 1995, Dalanesi *et al.* 2004).

Scytalopus petrophilus forages mostly on the ground, alone or in pairs. It hops slowly among or scuttles quickly over rocks and crevices in the dense vegetation of *campos rupestres*, and in the tangled understory of cloud forests. In the drier woodlands of south-central Minas Gerais, birds forage with brief picks and probes in the leaf litter. Stomachs of five specimens contained only insect fragments. Singing is most frequent about August through October. Males sing from atop rocks within concealing vegetation or from other low perches within forest, mostly from shortly after sunrise until about 08:00, then occasionally through the remainder of the day, especially on cloudy days, with another peak around dusk, especially on clear days. After playback of conspecific vocalizations, birds occasionally climb in rocks or vegetation to about 2.5 m above ground. Singing birds hold the neck slightly stretched upwards, the bill above horizontal, and the tail angled downward at about 45 degrees. The bill opens slightly as the throat pulsates and tail vibrates with each note in the song; the head is constantly but irregularly moved side-to-side to broadcast the song in various directions as the eyes are irregularly opened and closed. With a good view (best accomplished when a male is singing in good light), the legs appear distinctly yellowish or pinkish.

Systematic relationships and biogeography – Maurício (2005) hypothesized that the four species of light-gray *Scytalopus* in Brazil sharing accelerating songs in their vocal repertoires (*S. novacapitalis*, *S. pachecoi*, and, at that time, both *S. diamantinensis* and *S. petrophilus* as *species novae*) form a monophyletic group, which was

well-corroborated by part of a broader phylogenetic study of Brazilian *Scytalopus* although relationships within this *S. novacapitalis* clade were not well resolved (Mata *et al.* 2009). We strongly suspect, however, that *S. petrophilus* is sister to the recently described *S. diamantinensis*. *S. petrophilus* almost certainly evolved in the Espinhaço Range of Minas Gerais, in agreement with the theory of Mata *et al.* (2009) that the *S. novacapitalis* clade arose through a late-Pliocene (~2.4-1.8 Mya) radiation “burst” driven by fragmentation of populations into “islands of suitable habitats... that would have persisted in places subjected to orographic rain where long-term stability could be maintained”. It probably subsequently expanded its distribution into formerly inhospitable, lower-elevation

regions west and south of the Espinhaço free of close relatives and ecological competitors (*see below*); these areas became increasingly humid into the late Pliocene (Lara and Patton 2000, Grazziotin *et al.* 2006). *S. diamantinensis* occupies the disjunct, northern section of the Espinhaço Range, specifically the Chapada Diamantina geomorphological unit, entirely within Bahia (Figure 2). That pattern is mirrored by the sister-species of *Augastes* hummingbirds, with *A. scutatus* (Hyacinth Visorbearer) endemic to the Espinhaço of Minas Gerais and *A. luma-chella* (Hooded Visorbearer) inhabiting the Espinhaço and associated chapadas in Bahia. Based on several avi-faunal surveys conducted by MFV in the mountains of extreme northern Minas Gerais and southern Bahia (the

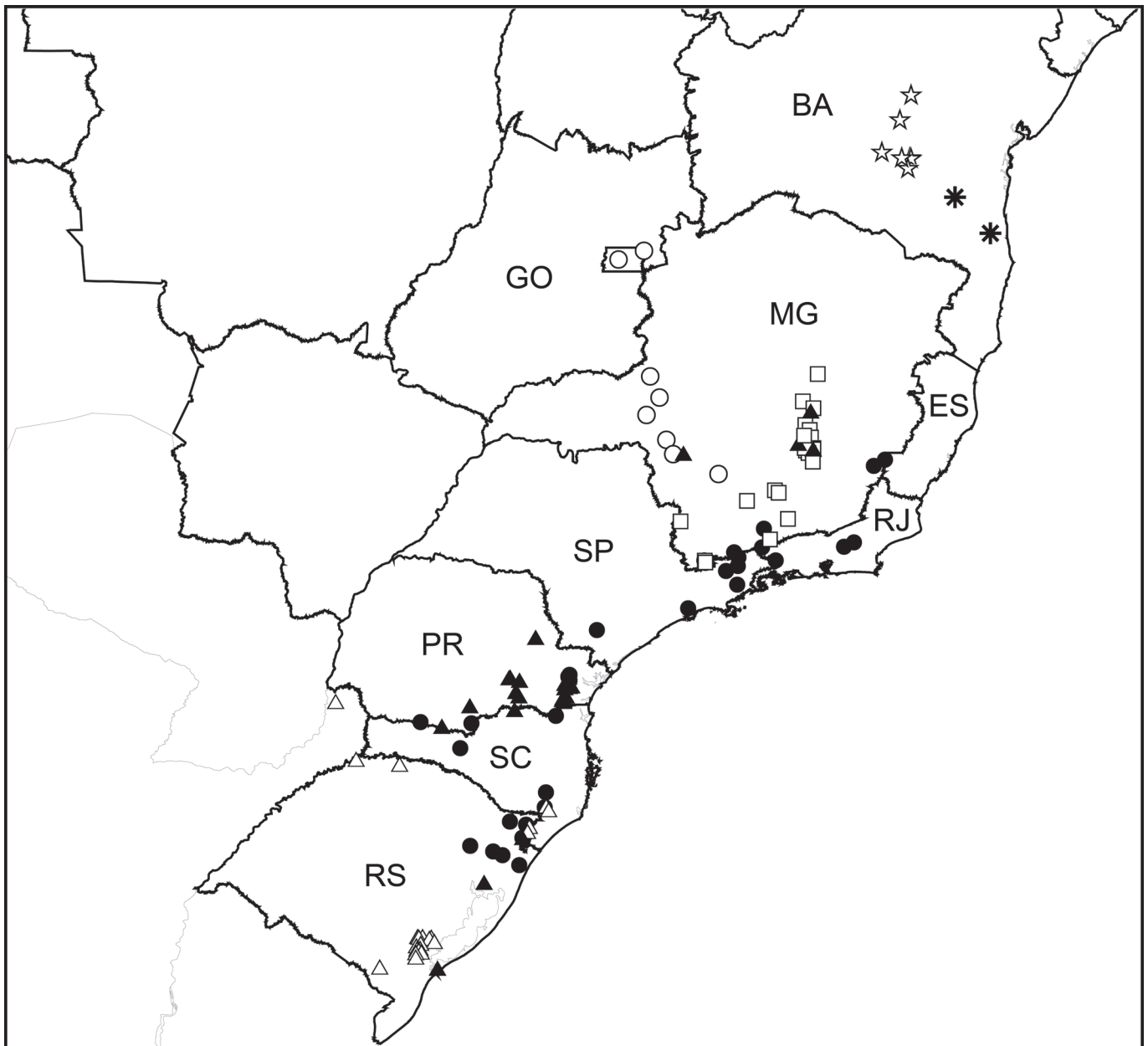


FIGURE 2: Distribution of the *Scytalopus novacapitalis* (open symbols) and *S. speluncae* (black symbols) complexes in eastern Brazil. Open circles: *S. novacapitalis*; open squares: *S. petrophilus*; open stars: *S. diamantinensis*; open triangles: *S. pachecoii*; black circles: *S. speluncae*; black triangles: *S. iraiensis*; black asterisks: *Scytalopus* sp. nov. in southeastern Bahia. Capital letters refer to Brazilian states.

“Campos Geraes” of Wied), where no tapaculo species has been found, the geographical barriers that probably led to speciation in both groups are: 1) the absence of cloud forests and more mesic habitats; contemporary vegetation on the rocky outcrops of these mountains is quite xeric, with several Cactaceae and spiny Bromeliaceae or, in the Espinhaço Range of southern Bahia (Caetitê region), the plateau is covered mainly by *cerrado*, a fire-adapted phytogeographic association apparently never colonized by *Scytalopus*; and 2) low elevations recently covered by *caatinga* vegetation between the ridge that comes across northern Minas Gerais/southern Bahia and Chapada Diamantina, in Bahia (Brumado region). Geographical separation and, almost certainly, sexual selection in *Augastes* has led to significant plumage divergence in that species-pair relative to the minor plumage difference between *Scytalopus diamantinensis* and *S. petrophilus*, which is in accordance with the minimal morphological divergences observed between many closely related species

in the genus (Whitney 1994, Krabbe and Schulenberg 1997, Mata *et al.* 2009).

Sympatry/parapatry with other species of *Scytalopus* –

S. petrophilus occurs from the Espinhaço Range west and south to southern Minas Gerais at Poços de Caldas, São João del Rei, Lavras, Lima Duarte, Gonçalves, Camanducaia, and Bocaina de Minas. At Lima Duarte (Ibitipoca area), *S. petrophilus* is sympatric with *S. speluncae* (Pacheco *et al.* 2008). At Gonçalves and Camanducaia specimens of *S. petrophilus* (DZUFMG 5322 and 5719) were shot only 80-100 m distant from specimens of *S. speluncae* (DZUFMG 5321 and 5718) in elfin forest and along a marsh/forest ecotone, respectively (Vasconcelos and D’Angelo-Neto 2009). Thus, part of the Mantiqueira of Minas Gerais appears to be a narrow zone of secondary contact between the *S. novacapitalis* and *S. speluncae* complexes. In the Serra do Caraça region, *S. petrophilus* is in contact with *S. iraiensis*; both have been recorded in

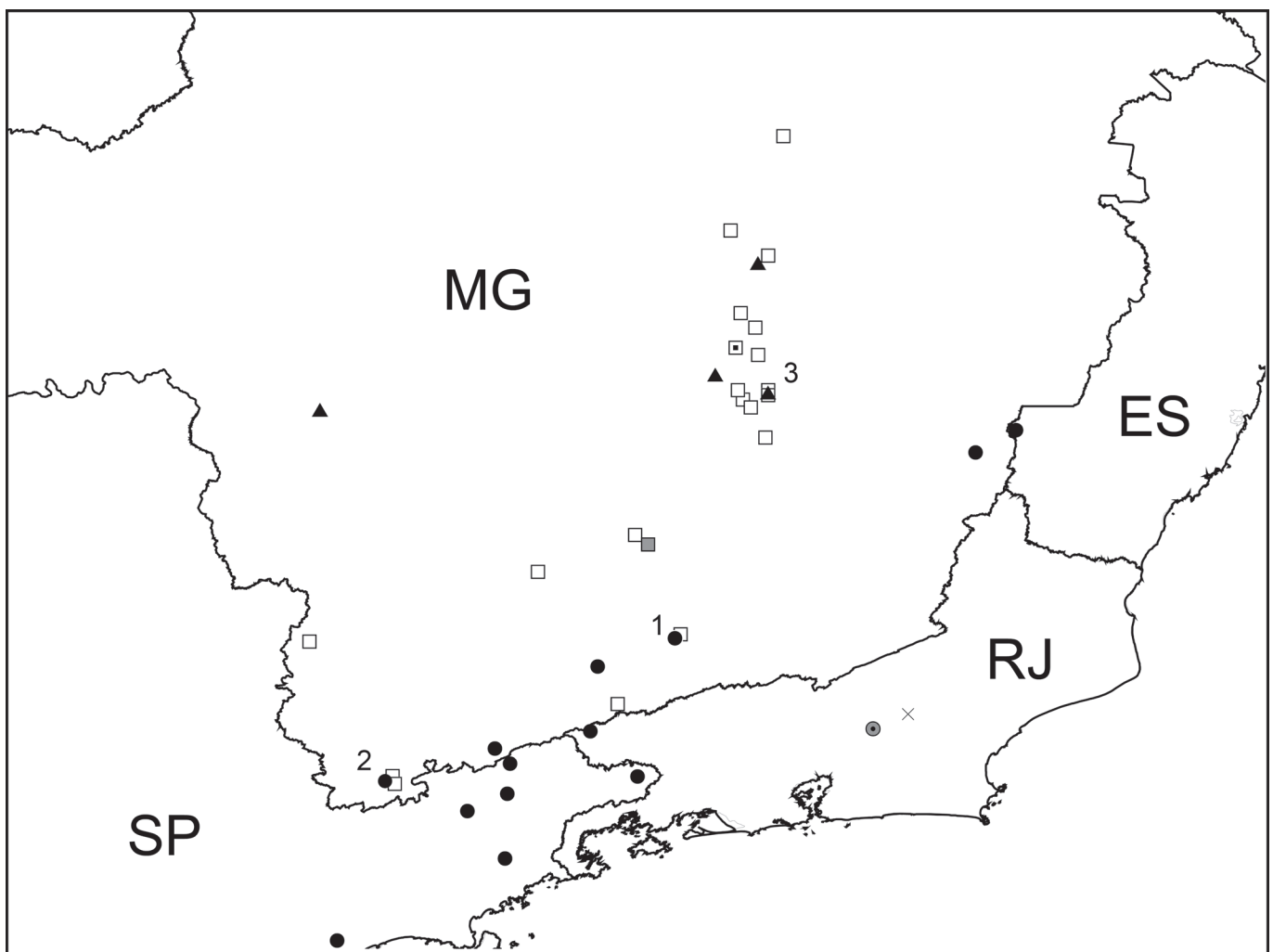


FIGURE 3: Distributions of *Scytalopus petrophilus*, *S. speluncae* (partial), and *S. iraiensis* (partial) based on specimens examined to highlight area of parapatry/sympatry and allow more detail of species-overlaps in Minas Gerais. Open squares: *S. petrophilus*; open square with dot: type-locality of *S. petrophilus*. Black circles: *S. speluncae*; gray circle with dot: Serra dos Órgãos, type locality of *S. speluncae*; X: Nova Friburgo, type-locality of *S. notorius*; gray square: São João del Rei. Black triangles: *S. iraiensis*. Numbers are: 1) Lima Duarte; 2) Camanducaia and Gonçalves; 3) Pico do Inficionado in the Serra do Caraça, all documented localities of contact of *S. petrophilus* with *S. speluncae* (1, 2) and *S. iraiensis* (3).

the same high-elevation marsh (Vasconcelos *et al.* 2008). Populations in south-central Minas Gerais (Poços de Caldas, Lavras, and São João del Rei) are close to populations of *S. novacapitalis* (Serra da Canastra and Capitólio) and *S. iraiensis* (Serra da Canastra), but sympatry among these has not yet been documented (Figures 2 and 3). It seems likely that *S. petrophilus* will eventually be found in São Paulo state, and possibly even into the Mantiqueira of Rio de Janeiro.

NOMENCLATURE

Over the years following the discovery of *Scytalopus petrophilus* in the Serra do Caraça in Minas Gerais and other localities in the state outside the Espinhaço Range, it became apparent that it would be necessary to compare our specimens with Ménétriès's type of *Malacorhynchus speluncae*, from "São João del Rei, Minas Gerais, Brazil" (Peters, 1951) held at the Zoological Institute, Russian Academy of Sciences (ZISP), St. Petersburg. São João del Rei lies in interior Minas Gerais, definitely within the range and habitat of *S. petrophilus* and only about 70 km from the Serra da Mantiqueira, a known locality for *S. speluncae*. Habitat there is much more humid forest than the semi-deciduous woodland around the purported type locality. In 1997, JFP wrote to ZISP personnel, enclosing color transparencies of two *Scytalopus* specimens (dorsal and ventral views of each) for comparison with Ménétriès's type, ZISP 145251. Specimen #1 was an adult *S. petrophilus* from the Serra do Caraça (MZUSP 78819) and #2 an adult *S. speluncae* from Parque Nacional do Itatiaia; identities and localities of the specimens were not provided. Vladimir Loskot, Curator of Ornithology at ZISP, replied to JFP in a letter dated 3 February 1998, "Our specimen is more similar to your bird labelled 1: it is noticeably lighter than your specimen 2, both in the ventral and dorsal surfaces. Apparently the type specimen is young, 1-st year bird in summer rather worn plumage".

JFP received no photos of the type specimen from ZISP, and we were left especially perplexed by Loskot's diagnosis of the type being immature, as this did not accord well with either Ménétriès's type description or the accompanying color illustration of the type, both of which described a bird in adult plumage with plain-gray flanks – thus quite different from JFP's #1, which clearly showed brown flanks with numerous dark bars, conspicuous features Loskot did not mention. That the type specimen would appear notably paler than JFP's #2 was expected due to inevitable foxing/fading of the 180-year-old specimen. We resolved to collect further specimens from the vicinity of São João del Rei, and perhaps attempt to obtain photographs of Ménétriès's type specimen or even visit the ZISP in St. Petersburg. Avifaunal surveys conducted by MFV and LFS in semideciduous

forests of the São João del Rei and Lavras region (south-central Minas Gerais), involving more than 80 days of intensive fieldwork during 2001-2005, produced only *S. petrophilus*. Two specimens were collected (MZUSP 78821, DZUFMG 5334) and several were tape-recorded. Most recently, independent researchers have introduced excellent evidence and well-presented arguments that permit us to resolve proper application of the name *Scytalopus speluncae* (Ménétriès 1835) under the rules of the International Code of Zoological Nomenclature (ICZN 1999, fourth edition) and also to address Ménétriès's (1835) designation of São João del Rei as the type locality.

Raposo *et al.* (2006) and Raposo and Kirwan (2008) attributed the name *S. speluncae* to the population that we have in this paper described as *S. petrophilus*, arguing that the type specimen (ZISP 145251), an adult male from "near São João del Rei" (Ménétriès 1835), matched two specimens they collected near São João del Rei in 2005. Most recently, however, Maurício *et al.* (2010) showed that their formal descriptions of these "topotypes" do not agree with the type specimen or Ménétriès's (1835) description of it, and do not approximate the excellent color illustration (pl. 13, fig. 1) that accompanied and is perfectly consistent with the description. We further concur with Maurício *et al.* (2010) that Ménétriès almost certainly obtained the type specimen of *S. speluncae* in the mountains of central Rio de Janeiro state. Their redesignation of the type locality as "Serra dos Órgãos" should stand until, perhaps one day, a molecular analysis of Ménétriès's type – one free of conflict of interest – might allow us to establish a more precise provenance.

The name of Mouse-colored Tapaculo must remain *Scytalopus speluncae* (Ménétriès 1835) with *S. notorius* Raposo, Stopiglia, Loskot, and Kirwan 2006 as a junior synonym. We note, however, that the specimen these authors selected as the holotype, from Parque Estadual Três Picos, Nova Friburgo, Rio de Janeiro is especially dark relative to all other available specimens from the Serra do Mar, including others from Nova Friburgo. Regrettably, none of the recordings in the small sample of vocalizations presented in the description of *S. notorius* was recorded at Três Picos or Nova Friburgo. Thus, the analyses of specimens and vocalizations presented by Raposo *et al.* (2006) are not linked, a situation that only lends further confusion to an already complicated taxonomic problem. Further study of the northern *S. speluncae* group (*sensu* Maurício 2005, Bornschein *et al.* 2007, this study) is encouraged: variably isolated serras, particularly in the states of Rio de Janeiro, Espírito Santo, and Bahia may harbor additional populations on independent evolutionary trajectories, and *S. notorius* could conceivably be resurrected at some level.

The case of *Scytalopus speluncae* (Ménétriès 1835) presents a prime example of the critical importance of

appropriate examination of type specimens and all associated information (description, illustrations, collector's diaries and catalogs, etc.) in the process of naming novel taxa or proposing taxonomic changes, as emphasized recently by Whitney *et al.* (2000). The several high-quality photographs of the type specimen presented by Raposo *et al.* (2006) and Raposo and Kirwan (2008) served to illustrate the type specimen of *Malacorhynchus speluncae* Ménétrières in detail for both their analysis and arguments, and those of Maurício *et al.* (2010).

CONCLUDING REMARKS

The Serra do Mar and other ancient, uplifted areas in eastern Brazil comprise a paleohistorically and topographically complex region of South America. Recent ornithological investigation, especially studies focused on the correlation of vocalizations and biogeography with molecular analysis, has revealed that several avian groups have undergone significantly greater diversification than previously estimated. It is apparent that the genus *Scytalopus* is a leading example of this new wave of "discovery", one that promises to highlight both the tremendous biodiversity of Brazil and the urgent need for the Brazilian government to enforce existing measures to preserve it.

ACKNOWLEDGMENTS

MFV is deeply grateful to the Brehm Foundation ("Brehm Fonds Mata Atlântica Brasilienprojekt") for financial support for fieldwork, to the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for a master and a doctoral fellowship, and the American Museum of Natural History (AMNH) for a Collection Study Grant to work on eastern Brazilian birds. The Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) and the Instituto Estadual de Florestas de Minas Gerais (IEF-MG) supplied authorizations to collect bird specimens. We are also grateful to the following colleagues that accompanied us during fieldwork: Giovanni N. Maurício, Marcos R. Bornschein, Cassiano Gatto, Marcos Maldonado Coelho, Ricardo Belmonte-Lopes, Santos D'Angelo-Neto, Vitor Torga Lombardi, Claudia Bauer, and John L. Rowlett. Luiz Antônio Pedreira Gonzaga (UFRJ) prepared some of the first specimens of *S. petrophilus* from the Serra do Caraça. Érika Machado, Gláucia del Rio and Thyago Santos (MZUSP) helped in the gazetteer. Vítor Piacentini helped with the final version of the maps. Vladimir Loskot (ZISP), Joel Cracraft, Paul Sweet, and Peg Hart (AMNH), Pedro Scherer-Neto (MHNCI), Marcos A. Raposo (MNRJ), Carla S. Fontana (PUCRS), and Luiz Antônio Pedreira Gonzaga (ASEC) for providing access to the specimens and voice samples under their care, and Vladimir Loskot kindly responded in writing to Pacheco's inquiries concerning the holotype of *Malacorhynchus speluncae*. The Fundação de Amparo à Pesquisa no Estado de São Paulo (FAPESP) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) provided financial support to LFS. M. R. Bornschein, J. V. Remsen, Jr., and an anonymous reviewer provided helpful comments on the manuscript, and Bornschein also allowed us to reproduce some of the spectrogram figures from Bornschein *et al.* (2007).

REFERENCES

- Bornschein, M. R.; Reinert, B. L. and Pichorim, M. (1998). Descrição, ecologia e conservação de um novo *Scytalopus* (Rhinocryptidae) do sul do Brasil, com comentários sobre a morfologia da família. *Ararajuba*, 6(1):3-36.
- Bornschein, M. R.; Maurício, G. N.; Belmonte-Lopes, R.; Mata, H. and Bonatto, S. L. (2007). Diamantina Tapaculo, a new *Scytalopus* endemic to the Chapada Diamantina, northeastern Brazil (Passeriformes: Rhinocryptidae). *Revista Brasileira de Ornitologia*, 15(2):151-174.
- Collar, N.; Gonzaga, L. P.; Krabbe, N.; Madroño Nieto, A.; Naranjo, L. G.; Parker III, T. A. and Wege, D. C. (1992). *Threatened Birds of the Americas*. Cambridge: International Council for Bird Preservation.
- Dalanesi, P. E.; Oliveira Filho, A. T. and Fontes, M. A. L. (2004). Flora e estrutura do componente arbóreo da floresta do Parque Ecológico Quedas do Rio Bonito, Lavras, MG e correlações entre a distribuição das espécies e variáveis ambientais. *Acta Botanica Brasilica*, 18(4):737-757.
- Fjeldså, J. and Krabbe, N. (1990). *Birds of the High Andes*. Svendborg: Zoological Museum, University of Copenhagen and Apollo Books.
- Gavilanes, M. L.; Carvalho, D. A.; Oliveira Filho, A. T. and Vilela, E. A. (1995). Flora arbustivo-arbórea de uma floresta ripária no Alto Rio Grande em Bom Sucesso, MG. *Acta Botanica Brasilica*, 9(2):231-245.
- Graziotin, F. G.; Monzel, M.; Echeverrigaray, S. and Bonatto, S. L. (2006). Phylogeography of the *Bothrops jararaca* complex (Serpentes: Viperidae): past fragmentation and island colonization in the Brazilian Atlantic Forest. *Molecular Ecology*, 15:3969-3982.
- Isler, M. L.; Isler, P. R. and Whitney, B. M. (2007). Species limits in Antbirds: The Warbling Antbird (*Hypocnemis cantator*) complex. *Auk*, 124(1):11-28.
- Krabbe, N. and Schulenberg, T. S. (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).
- Lara, M. C. and Patton, J. L. (2000). Evolutionary diversification of spiny rats (genus *Trinomys*, Rodentia: Echymidae) in the Atlantic Forest of Brazil. *Zoological Journal of the Linnean Society*, 130(4):661-686.
- Mata, H.; Fontana, C. S.; Maurício, G. N.; Bornschein, M. R.; Vasconcelos, M. F. and Bonatto, S. L. (2009). Molecular phylogeny and biogeography of the eastern tapaculos (Aves: Rhinocryptidae: *Scytalopus*, *Eleoscytalopus*): cryptic diversification in Brazilian Atlantic Forest. *Molecular Phylogenetics and Evolution*, 53(2):450-462.
- Maurício, G. N. (2005). 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). *Ararajuba*, 13(1):7-28.
- Maurício, G. N.; Bornschein, M. R.; Vasconcelos, M. F.; Whitney, B. M.; Pacheco, J. F. and Silveira, L. F. (2010). Taxonomy of "Mouse-colored Tapaculos". I. On the application of the name *Malacorhynchus speluncae* Ménétrières, 1835 (Aves: Passeriformes: Rhinocryptidae) *Zootaxa*, 2518:32-48.
- Ménétrières, E. (1835). Monographie de la famille des Myiotherinae. *Mem. Acad. Imp. Sci. St. Pétersbourg*, 6th ser. III, part 2: 443-543.
- Munsell. (1994). *Soil color charts, revised edition*. Macbeth Division of Kollmorgan Instruments Corporation. New York: New Windsor.
- Oliveira Filho, A. T. and Machado, J. N. M. (1993). Composição florística de uma floresta semidecídua montana, na serra de São José, Tiradentes, Minas Gerais. *Acta Botanica Brasilica*, 7(2):71-88

- Oliveira Filho, A. T.; Scolforo, J. R. S. and Mello, J. M. (1994).** Composição florística e estrutura comunitária de um remanescente de floresta semidecídua montana em Lavras, MG. *Revista Brasileira de Botânica*, 17(2):167-182.
- Pacheco, J. F.; Parrini, R.; Lopes, L. E. and Vasconcelos, M. F. (2008).** A avifauna do Parque Estadual do Ibitipoca e áreas adjacentes, Minas Gerais, Brasil, com uma revisão crítica dos registros prévios e comentários sobre biogeografia e conservação. *Cotinga*, 30:16-32.
- Parrini, R.; Raposo, M. A.; Pacheco, J. F.; Carvalhães, A. M. P.; Melo Jr., T. A.; Fonseca, P. S. M. and Minns, J. C. (1999).** Birds of the Chapada Diamantina, Bahia, Brazil. *Cotinga*, 11:86-95.
- Peters, J. L. (1951).** *Check-list of birds of the world*, volume 7. Museum of Comparative Zoology, Cambridge, Massachusetts, USA.
- Raposo, M. A.; Stopiglia, R.; Loskot, V. and Kirwan, G. M. (2006).** The correct use of the name *Scytalopus speluncae* (Ménétriés, 1835), and the description of a new species of Brazilian tapaculo (Aves: Passeriformes: Rhinocryptidae). *Zootaxa*, 1271:37-56.
- Raposo, M. A. and Kirwan, G. M. (2008).** The Brazilian species complex *Scytalopus speluncae*: how many times can a holotype be overlooked? *Revista Brasileira de Ornitologia*, 16(1):78-81.
- Silveira, L. F.; Develey, P. F.; Pacheco, J. F. and Whitney, B. M. (2005).** Avifauna of the Serra das Lontras-Javi mountain complex, Bahia, Brazil. *Cotinga*, 24:45-54.
- Vasconcelos, M. F. (2001).** *Estudo biogeográfico da avifauna campestre dos topos de montanha do Sudeste do Brasil*. M. Sc. Thesis. Belo Horizonte: Universidade Federal de Minas Gerais.
- Vasconcelos, M. F. (2008).** Mountaintop endemism in eastern Brazil: why some bird species from campos rupestres of the Espinhaço Range are not endemic to the Cerrado region? *Revista Brasileira de Ornitologia*, 16(4):348-362.
- Vasconcelos, M. F.; Maurício, G. N.; Kirwan, G. M. and Silveira, L. F. (2008).** Range extension for Marsh Tapaculo *Scytalopus iraiensis* to the highlands of Minas Gerais, Brazil, with an overview of the species' distribution. *Bulletin of the British Ornithologist's Club*, 128(2):101-106.
- Vasconcelos, M. F. and D'Angelo-Neto, S. (2009).** First assessment of the avifauna of *Araucaria* forests and other habitats from extreme southern Minas Gerais, Serra da Mantiqueira, Brazil, with notes on biogeography and conservation. *Papéis Avulsos de Zoologia*, 49(3):49-71.
- 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 Bulletin*, 106(4):585-614.
- Whitney, B. M.; Pacheco, J. F.; Buzzetti, D. R. C. and Parrini, R. (2000).** Systematic revision and biogeography of the *Herpsilochmus pileatus* complex, with description of a new species from northeastern Brazil. *Auk*, 117(4):869-891.

APPENDIX 1

Specimens examined

Scytalopus novacapitalis: MZUSP 71007, f, Reserva Ecológica do IBGE, DF, 21.vii.1979; MZUSP 78806, m, Chapadãozinho, São José do Barreiro, MG, 22.i.2000; MZUSP 78807, f, Chapadãozinho, São José do Barreiro, MG, 09.vi.2004; MZUSP 78808, m, Chapadãozinho, São José do Barreiro, MG, 09.vi.2004; MZUSP 78826, m, Chapada na margem direita do Rio Turvo, Capitólio, MG, 01.x.2004; MCP 1481, m, Ribeirão do Gama, near the village of Vargem Bonita, Brasília, DF.

Scytalopus petrophilus: MZUSP 78811, m, Pico do Inficionado, Serra do Caraça, Catas Altas, MG, 23.xii.1999; MZUSP 78812, m, Pico do Inficionado, Serra do Caraça, Catas Altas, MG, 23.xii.1999; MZUSP 78813, m, Pico do Inficionado, Serra do Caraça, Catas Altas, MG, 23.xii.1999; MZUSP 78814, f, Pico do Inficionado, Serra do Caraça, Catas Altas, MG, 04.ii.2003; MZUSP 78815, f, Gruta de Lourdes, Serra da Caraça, Catas Altas, MG, 14.xi.2000; MZUSP 78816, m, Pico do Inficionado, Serra da Caraça, Catas Altas, MG, 04.ii.2003; MZUSP 78817, m, Pico do Inficionado, Serra do Caraça, Catas Altas, MG, 04.ii.2003; MZUSP 78818, ind, trail to Pico do Inficionado, Serra do Caraça, Catas Altas, MG, 20.xi.2004; MZUSP 78819, f, MG, Santa Bárbara, Serra do Caraça, 04.iii.1997; MZUSP 78820, f, MG, Santa Bárbara, Serra do Caraça, 04.iii.1997; MZUSP 78821, m, Sítio Ponte Velha, São João del Rei, MG, 15.i.2005; MZUSP 78822, m, Serra da Piedade, Caeté, MG, 17.ix.2004; MZUSP 78823, m, Brumas do Espinhaço, Lapinha de Cima, Santana do Riacho, MG, 01.ii.2004; MZUSP 78824, m, Brumas do Espinhaço, Lapinha de Cima, Santana do Riacho, MG, 02.ii.2004; MZUSP 78825, f, Pico Dois Irmãos, Parque Estadual do Rio Preto, São Gonçalo do Rio Preto, MG, 17.v.2004; DZUFMG 5333, f, Serra da Piedade, Caeté, MG, 07.i.2004; DZUFMG 5334, m, Serrinha, Lavras, MG, 05.xii.2003; MCP 1560, m, Pico do Inficionado, Serra do Caraça, Catas Altas, MG, 23.xii.1999; MCP 1561, m, Pico do Inficionado, Serra do Caraça, Catas Altas, MG, 23.xii.1999; DZUFMG 4169, ind, Pico do Inficionado, Serra do Caraça, Catas Altas, 05.ii.2003; MCP 1562, m, trail to Pico do Inficionado, Serra do Caraça, Catas Altas, MG, 06.ii.2003; DZUFMG 5335, m, Pico do Inficionado, Serra do Caraça, Catas Altas, MG, 20.xi.2004; DZUFMG 5336, m, Brumas do Espinhaço, Lapinha de Cima, Santana do Riacho, MG, 10.i.2005; DZUFMG 4167, m, Pico Dois Irmãos, Parque Estadual do Rio Preto, São Gonçalo do Rio Preto, MG, 17.v.2004; DZUFMG 4168, f, Pico Dois Irmãos, Parque Estadual do Rio Preto, São Gonçalo do Rio Preto, MG, 17.v.2004; DZUFMG 5322, f, Pedra de São Domingos, Gonçalves, MG, 27.iii.2007; DZUFMG 5719, m, Serra do Juncal, Camanducaia, MG, 11.i.2008; DZUFMG 6016, m, Serra da Gandarela, Rio Acima, MG, 25.ix.2008; MCP 1509, m, Serra do Palmital, Bocaina de Minas, MG, 02.xii.2004; MCP 1510, m, Serra do Palmital, Bocaina de Minas, MG, 02.xii.2004; MZUSP 83542, m, Parque Ambiental Alcoa, Poços de Caldas, MG, 16.vii.2008; MZUSP 83543, m, Parque Ambiental Alcoa, Poços de Caldas, MG, 16.vii.2008.

Scytalopus sp. nov.: MZUSP 78809, m, Serra das Lontras, BA, 06.xi.1999; MZUSP 78810, m, Boa Nova, BA, 26.viii.1993.

Scytalopus speluncae: MZUSP 4836, f, Alto da Serra, SP, viii-1904; MZUSP 6121, m, Campos Itatiaya, RJ, 03.v.1906; MZUSP 6123, f, Campos Itatiaya, RJ, 05.v.1906; MZUSP 34380, f, Maromba, km 7, PN do Itatiaia, RJ, 01.viii.1950; MZUSP 34381, m, Maromba, km 4, PN do Itatiaia, RJ, 14.viii.1950; MZUSP 34804, m, Planalto Várzea dos Lírrios, PN do Itatiaia, RJ, 21.v.1951; MZUSP 34805, f, Macieiras, PN do Itatiaia, RJ, 28.v.1951; MZUSP 34806, m? Macieiras, PN do Itatiaia, RJ, 30.v.1951; MZUSP 34807, f, Macieiras, PN do Itatiaia, RJ, 01.vi.1951; MZUSP 34808, f, Maromba, km 6, PN do Itatiaia, RJ, 07.vi.1951; MZUSP 36347, m, km 12, PN do Itatiaia, RJ, 28.i.1958; MZUSP 36348, f, km 11, PN do Itatiaia, RJ, 22.i.1954; MZUSP 36349, f, km 11, PN do Itatiaia, 26.i.1954; MZUSP 82618, m, Resende, RJ, 12.x.2008; DZUFMG 4924, m, Serra da Vargem Grande, Divino, MG, 22.iii.2006; DZUFMG 4925, m, Serra da Vargem Grande, Divino, MG, 23.iii.2006; DZUFMG 5321, m, Pedra de São Domingos, Gonçalves, MG, m, 27.iii.2007; DZUFMG 5718, m, base of Serra do Juncal, Camanducaia, MG, 11.i.2008; AMNH 492362, m, Campos do Itatiaya, MG/RJ, 23.iv.1906; AMNH 188960, m, Alto Itatiaya, MG/RJ, 02.iii.1922; AMNH 188961, m, Alto Itatiaya, MG/RJ, 03.iii.1922; AMNH 188962, f, Alto Itatiaya, MG/RJ, 14.iii.1922; AMNH 188964, m, Alto Itatiaya, MG/RJ, 15.ii.1922; AMNH 188965, f, Alto Itatiaya, MG/RJ, 15.ii.1922; AMNH 188966, f, Alto Itatiaya, MG/RJ, 18.ii.1922; AMNH 188967, m, Alto Itatiaya, MG/RJ, 20.ii.1922; AMNH 188968, m, Alto Itatiaya, MG/RJ, 04.iii.1922; AMNH 188969, f, Macieiras, Serra do Itatiaya, RJ, 02.iv.1922; AMNH 188970, f, Macieiras, Serra do Itatiaya, RJ, 04.iv.1922; AMNH 785876, m, Serra do Caparaó, MG, 27.iii.1941; AMNH 785877, m, Serra do Caparaó, MG, 14.iv.1941.

Scytalopus pachei: Brazil: MZUSP 75761, m, Serro das Almas, Capão do Leão, RS, 14.x.2001; MZUSP 75762, m, Serro das Almas, Capão do Leão, RS, 14.x.2001; MZUSP 75763, m, Santo Amor, Morro Redondo, RS, 03.xii.2001; MZUSP

75764, m, Colônia, Solidez, Canguçu, RS, 05.iv.2002. Argentina: AMNH 771238, m, Arroyo Urugua-i, km 30, Misiones, 20.ix.1957; AMNH 771239, f, Arroyo Urugua-i, km 30, Misiones, 24.i.1958; AMNH 771241, f, Arroyo Urugua-i, km 30, Misiones, 17.ix.1957; AMNH 771242, f, Arroyo Urugua-i, km 30, Misiones, 02.xii.1957; AMNH 795289, m, Arroyo Urugua-i, km 30, Misiones, 27.x.1960; AMNH 771240, f, Arroyo Urugua-i, km 10, Misiones, 27.v.1958; AMNH 795288, m, Arroyo Urugua-i, km 10, Misiones, 20.vi.1960.

Scytalopus diamantinensis: MZUSP 77827, f, Serra do Ribeirão, Lençóis, BA, 23.viii.2006.

APPENDIX 2

Gazetteer of *Scytalopus speluncae* complex

Scytalopus diamantinensis: Parque Nacional da Chapada Diamantina, BA, 12°33'S, 41°28'W; Rodovia Bonito-Utinga, BA, 12°11'S, 59°41'W; Serra do Ribeirão, Lençóis, BA, 12°34'S, 41°25'W; Sítio Santa Teresinha, Abaíra, BA, 13°18'S, 41°53'W; Campo Redondo, Ibicoara, BA, 13°24'S, 41°14'W; Serra do Sincorá, Near Ibicoara, BA, 13°26'S, 41°14'W; Bonfim, Iramaia, BA, 13°27'S, 41°13'W; Morros de Ouro, Barra da Estiva, BA, 13°40'S, 41°17'W; Capão do Vale, Ibicoara, BA, 13°26'S, 41°23'W (type).

Scytalopus iraiensis: Banhado do Maçarico, RS, 32°02'S, 52°05'W; Banhado dos Pachecos, Viamão, RS, 30°04'S, 51°01'W; Fazenda Bocaina, MG, 20°00'S, 43°48'W; Serra do Caraça, MG, 20°07'S, 43°27'W; Serra da Canastra, MG, 20°14'S, 45°58'W; Serra do Cipó, Santana do Riacho, MG, 19°15'S, 43°31'W; Santa Bárbara, MG, 20°00'S, 43°28'W; Rio das Almas, Teixeira Soares, PR, 25°22'S, 50°27'W; Alto Rio Iguaçu, PR, 25°36'S, 54°36'W; Cruz Machado, PR, 26°01'S, 51°20'W; São João do Triunfo/Lapa, PR, 25°40'S, 50°17'W; Rio Várzeas, Tijucas do Sul, PR, 25°55'S, 49°11'W; Parque Nacional Aparados da Serra, RS, 29°09'S, 50°05'W; Right bank of Iraí River, near to Iraí Dam, PR, 25°21'S, 49°04'W (type).

Scytalopus sp. nov.: Bonito, BA, 11°57'S, 41°16'W; Serra das Lontras, BA, 15°11'S, 39°23'W; Boa Nova, BA, 14°21'S, 40°12'W; Ibicoara, BA, 13°24'S, 41°17'W.

Scytalopus novacapitalis: Tapira, MG, 19°55'S, 46°49'W; Parque Nacional da Serra da Canastra, MG, 20°15'S, 46°40'W; Reserva Ecológica do IBGE, Brasília, DF, 15°56'S, 47°53'W; Fazenda Água Limpa, Brasília, DF, 15°30'S, 47°25'W; Ribeirão do Gama, near the village of Vargem Bonita, Brasília, DF, 15°55'S, 47°56'W; Brasília, DF, 15°47'S, 47°55'W (type).

Scytalopus pachecoi: Arroio Uruguay-i Misiones, AR, 25°55'S, 54°25'W; San Pedro, Rio Peperi-Guazu, AR, 26°36'S, 53°43'W; Parque Estadual do Turvo, RS, 27°14'S, 53°57'W; Nonoai, RS, 27°21'S, 52°57'W; Guaritas, RS, 27°27'S, 56°37'W; Terra Indígena de Guarita, Erval Seco, RS, 27°32'S, 53°30'W; Bom Jardim da Serra, SC, 28°20'S, 49°37'W; Fazenda da Rocinha, Bom Jardim da Serra, SC, 28°18'S, 49°35'W; Serra do Rio do Rastro, Bom Jardim da Serra, SC, 28°23'S, 49°32'W; Rio das Antas, São José dos Ausentes, RS, 28°47'S, 49°58'W; São Gonçalo, Cambará do Sul, RS, 28°53'S, 50°01'W; limite norte de Cambará do Sul, RS, 29°02'S, 50°11'W; Harmonia, São Lourenço do Sul, RS, 31°18'S, 52°25'W; Colônia Solidez, Canguçu, RS, 31°18'S, 52°32'W; Arroio Moinho, Canguçu, RS, 31°19'S, 52°30'W; Arroio Andrade, Pelotas/Arroio do Padre, RS, 31°27'S, 52°28'W; Arroio Cadeia, Morro Redondo, RS, 31°35'S, 52°33'W; Morro da Antena, Pelotas, RS, 31°36'S, 52°31'W; Monte Bonito, Pelotas, RS, 31°39'S, 52°27'W; Santo Amor, Morro Redondo, RS, 31°40'S, 52°35'W; Serra das Asperezas, Piratini, RS, 31°26'S, 53°06'W; Paredão, Encruzilhada do Sul, RS, 30°32'S, 52°31'W; Cerro das Almas, Capão do Leão, RS, 31°46'S, 52°35'W (type).

Scytalopus petrophilus: Pico dois Irmãos, Rio Preto, MG, 18°24'S, 43°21'W; Brumas do Espinheiro, Santana do Riacho, MG, 19°02'S, 43°42'W; Gruta de Lourdes, Caraça, MG, 20°06'S, 43°27'W; Inficionado, Caraça, MG, 20°08'S, 43°27'W; Serrinha, Lavras, MG, 21°19'S, 44°59'W; Sítio Ponte Velha, São João del Rei, MG, 21°04'S, 44°20'W; Serra do Palmital, Bocaina de Minas, MG, 22°12'S, 44°27'W; Pedra de São Domingos, MG, 22°41'S, 45°57'W; Serra do Juncal, MG, 22°44'S, 45°56'W; Poços de Caldas, MG, 21°47'S, 46°30'W; Serra da Gandarela, Rio Acima, MG, 20°06'S, 43°39'W; Lima Duarte, MG, 21°51'S, 43°48'W; Pedra de São Domingos, Gonçalves, MG, 22°40'S, 45°51'W; Serra do Caraça, MG, 20°08'S, 43°30'W; Serra da Piedade, Caeté, MG, 19°49'S, 43°40'W (type).

Scytalopus speluncae: Serra Vargem Grande, Divino, MG, 20°31'S, 42°04'W; Delfim Moreira, MG, 22°30'S, 45°16'W; Parque Nacional do Caparaó, ES, 20°22'S, 41°48'W; Parque Nacional do Itatiaia, RJ, 22°23'S, 44°38'W; Catuçaba, São Luiz do Paraitinga, SP, 23°14'S, 45°12'W; Pico dos Marins, Piquete, SP, 22°36'S, 45°10'W; Guaratinguetá, SP, 22°48'S, 45°11'W; Pindamonhangaba, SP, 22°55'S, 45°27'W; Bananal, SP, 22°41'S, 44°19'W; Alto da Serra, SP, 23°47'S, 46°19'W; Parque Estadual Intervales, SP, 24°17'S, 48°25'W; Fazenda Tumas, Clevelândia, PR, 26°23'S, 52°28'W; Corvo, Quatro Barras, PR, 25°21'S, 49°04'W; Mananciais da Serra, Piraquara, PR, 25°26'S, 49°03'W; Morro Anhangava, Quatro Barras, PR, 25°21'S, 49°04'W; General Carneiro, PR, 26°25'S, 51°18'W; Coqueiro, Campina Grande do Sul, PR, 25°18'S, 49°03'W; Limoeiro/Campina da Alegria, Água Doce, SC, 26°59'S, 51°33'W; São Bento, SC, 26°15'S, 49°22'W; Parque Nacional de São Joaquim, Morro da Igreja, Urubici, SC, 28°00'S, 49°35'W; Fazenda da Rocinha, Bom Jardim da Serra, SC, 28°18'S, 49°35'W; Serra do Rio do Rastro, Bom Jardim da Serra, SC, 28°23'S, 49°32'W; Santo Antônio, São

Francisco de Paula, RS, 29°26'S, 50°35'W; Serra do Umbú, Maquiné, RS, 29°40'S, 50°12'W; Colinas de São Francisco/Josafaz, São Francisco de Paula, RS, 29°26'S, 50°35'W; Passo do Meio, São Francisco de Paula, RS, 29°26'S, 50°35'W; Passo do Meio, Bom Jesus, RS, 28°40'S, 50°25'W; Serra da Boa União, São Francisco de Paula, RS, 29°26'S, 50°35'W; São Gonçalo, Cambará do Sul, RS, 28°53'S, 50°01'W; Morro Pelado, Canela, RS, 29°21'S, 50°48'W; Lajeadozinho, São José dos Ausentes, RS, 28°44'S, 50°03'W; Farroupilha, RS, 29°13'S, 51°20'W; Serra da Boa União, Três Forquilhas, RS, 29°32'S, 50°03'W; Pedra de São Domingos, MG, 22°41'S, 45°57'W; Serra do Juncal, MG, 22°44'S, 45°56'W; Serra do Papagaio, MG, 21°57'S, 44°35'W; São João del Rei, MG, 21°08'S, 44°15'W; Fazenda Toledo, Nova Friburgo, RJ, 22°16'S, 42°31'W; Lima Duarte, MG, 21°51'S, 43°48'W; Serra dos Órgãos, Teresópolis, RJ, 22°22'S, 42°45'W (type).