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Hidden generic diversity in Neotropical birds: Molecular and anatomical data support a new genus for the "*Scytalopus*" *indigoticus* species-group (Aves: Rhinocryptidae)

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ABSTRACT

The genus *Scytalopus* is a species-rich and taxonomically complicated component of the Neotropical avian family Rhinocryptidae. Probably because *Scytalopus* is a superficially uniform assemblage, its monophyly has not been seriously questioned. We investigated phylogenetic relationships of a representative set of species in the genus using nuclear and mitochondrial DNA sequences as well as anatomical data, and provided the first test of its presumed monophyly by including in the analyses its hypothesized closest relatives (the genera *Myornis*, *Eugralla*, and *Merulaxis*) as well as most rhinocryptid genera. We found strong support for the paraphyly of the genus *Scytalopus*, with the *Scytalopus indigoticus* species-group forming a clade with *Merulaxis*. A well-supported clade including the genera *Eugralla*, *Myornis*, and the remaining *Scytalopus* was also recovered. Because these results were recovered independently and with strong support using mitochondrial and nuclear data, and were entirely consistent with anatomical data, we erect a new genus for the *S. indigoticus* species-group. These findings illustrate the importance of formally testing hypotheses of monophyly even for well-accepted groups of Neotropical birds.

1. Introduction

The Neotropical family Rhinocryptidae, as presently defined (Remsen et al., 2008), includes 11 genera of forest and non-forest birds with mainly terrestrial habits (Ridgely and Tudor, 1994; Krabbe and Schulenberg, 2003). It comprises a somewhat heterogeneous assemblage of species of medium to fairly large body size (19–24 cm of total length) in the genera *Pteroptochos*, *Scelorchilus*, *Acropternis*, *Rhinocrypta*, *Teledromas*, *Liosceles*, and *Merulaxis*, as well as a more uniform component which includes small (10–14 cm of total length), wren-like, gray or mainly gray taxa placed in the genera *Scytalopus*, *Eugralla*, and *Myornis*. The more divergent, small (c.13 cm), and rather slender *Psilorhamphus guttatus* was long placed in two diverse families, but is now accepted as a rhinocryptid (Plótnick, 1958; Krabbe and Schulenberg, 2003). *Pteroptochos*, *Scelorchilus*, *Eugralla*, *Acropternis*, and *Myornis* are confined to the Andes, *Rhinocrypta* and *Teledromas* inhabit central South American lowlands and foothills, *Liosceles* is restricted to the southwestern Amazonian basin, and *Psilorhamphus* and *Merulaxis* are endemic to the Atlantic forest of eastern South America. *Scytalopus* is by far the most widespread genus of all rhinocryptids, as it ranges along the entire Andean chain (and contiguous mountain systems) and, rather disjunctly, throughout eastern Brazil, and adjacent northeastern Argentina.

Whereas the other rhinocryptid genera include only one to three species, *Scytalopus* is among the most speciose genera of Neotropical birds, and has a growing number of recognized species, now reaching 40 (Krabbe and Schulenberg, 1997, 2003; Remsen et al., 2008). The limits of species and species-groups in *Scytalopus* have been traditionally difficult to establish, and although numerous taxonomic revisions have been published recently (e.g., Whitney, 1994; Krabbe and Schulenberg, 1997, 2003; Bornschein et al., 1998, 2007; Cuervo et al., 2005; Krabbe et al., 2005; Maurício, 2005; Raposo et al., 2006), further taxonomic investigations are still pending and several new species are likely to be discovered.

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On the basis of general observations on morphology, plumage coloration, and vocalizations, it has been suggested that the closest relatives of *Scytalopus* are the genera *Myornis*, *Eugralla*, and *Merulaxis* (Krabbe and Schulenberg, 1997, 2003). Except for the merger of *Myornis* into *Scytalopus* by Hilty and Brown (1986), a treatment that was firmly rejected subsequently (Fjeldså and Krabbe, 1990; Ridgely and Tudor, 1994; Krabbe and Schulenberg, 1997, 2003), the monophyly of *Scytalopus* has not been seriously questioned by any author, probably as a result of the uniformity in external morphology of all the members of the group. However, based on molecular phylogenetic analyses we have found that members of the genus *Scytalopus* are not as closely related as traditionally thought, a hypothesis we have further corroborated based on analyses of the internal anatomy of a variety of taxa. Here, we present molecular (nuclear and mitochondrial) and anatomical (syringeal and skeletal) data that strongly suggest that *Scytalopus*, as currently defined, is actually a paraphyletic group; two clades currently subsumed in *Scytalopus* are best considered separate genera, one of which we describe as new. These novel findings lead to a reinterpretation of morphological diversification in the Rhinocryptidae and illustrate the importance of formally testing hypotheses of monophyly even for well-accepted groups of Neotropical birds.

2. Materials and methods

2.1. Taxonomic sampling

The Andean component of the genus *Scytalopus* comprises a large number of species that may be clustered into several groups, whereas the Brazilian one comprises only seven named taxa that are distributed into two discrete complexes, namely the *S. indigoticus* and the *S. speluncae* species-groups (Bornschein et al., 1998, 2007; Krabbe and Schulenberg, 1997, 2003; Maurício, 2005). We included representatives of the Andean component and of both Brazilian species-groups in addition to several outgroups in analyses aimed at assessing the deep phylogenetic relationships within *Scytalopus* and between *Scytalopus* and related genera. Tissue samples of *Merulaxis ater*, *Psilorhamphus guttatus*, and all named species in the *S. indigoticus* (*S. indigoticus* and *S. psychopompus*) and the *S. speluncae* (*S. pachecoi*, *S. novacapitalis*, *S. iraiensis*, and *S. speluncae*, but not the recently described *S. diamantinensis*) species-groups were obtained during field work throughout eastern Brazil. A representative set of the Andean *Scytalopus* (*S. magellanicus*, *S. canus*, *S. stilesi*, and *S. vicinior*) as well as the closely related taxa *Myornis senilis* and *Eugralla paradoxa*, in addition to *Scelorchilus rubecula*, were included in the analyses based on results from a comprehensive molecular phylogeny of the genus that is in preparation by Cadena and collaborators. A representative of the Grallariidae (*Hylopezus ochroleucus*), a family closely related to Rhinocryptidae (Irestedt et al., 2002; Chesser, 2004), was sampled as an outgroup. Sequences of different genes from the taxa mentioned above composed our main data set (Table 1). In addition, we used sequences of different loci obtained from GenBank for *Pteroptochos castaneus*, *P. tarnii*, *Liosceles thoracicus*, *Rhinocrypta lanceolata*, and *Scytalopus spillmanni* (Rhinocryptidae), and *Grallaria ruficapilla* (Grallariidae), in different analyses (Table 1; see below).

2.2. DNA extraction, amplification, and sequencing

Genomic DNA was extracted from tissue samples using either the Chelex 100 method (Karp et al., 1998) or a QIAamp DNA Mini Kit (Qiagen). Based on these extracts, we amplified and sequenced fragments of three mitochondrial protein-coding genes and two nuclear introns for different subsets of species and individuals (Table 1) following standard PCR protocols (see Cadena et al., 2007). The mitochondrial NADH-subunit 2 (ND2) was amplified for 22 individuals of 15 different species using the primers L5216 and H6313 (Sorenson et al., 1999), and sequenced with these two primers or with the internal primers L5758 and H5766 (Sorenson et al., 1999). For a total of nine individuals of nine species, we also amplified and sequenced a fragment spanning part of the cytochrome *b* and NADH-subunit five mitochondrial genes (cyt *b*-ND5) using primers L14764 and H15295 (Sorenson et al., 1999). For 22 individuals of 16 species, we amplified, and sequenced the nuclear β-fibrinogen intron 7 (FIB7) with primers FIB-BI7L and FIB-BI7U (Prychitko and Moore, 1997). Finally, we obtained sequences of the nuclear glyceraldehyde-3-phosphate dehydrogenase intron 11 (G3PDH) for nine individuals of nine species using primers G3PDH11F and G3PDH11R (Fjeldså et al., 2003). PCR products were purified with ExoSap-It (Amersham Biosciences), sequenced with DYEnamic ET Dye Terminator Cycle Sequencing Kit (Amersham Biosciences), and read on a MegaBACE 1000 automated sequencer (Amersham Biosciences) following the manufacturer's protocols.

2.3. Phylogenetic analyses

Sequence traces were checked by eye, edited manually using Bioedit 6.0.7 (Hall, 1999), and aligned using Clustal X 1.83 (Thompson et al., 1997). A partition homogeneity test (ILD, Farris et al., 1995) as implemented in PAUP*4.0b10 (Swofford, 2002) using 1000 random replications was undertaken to assess congruence in the phylogenetic signal between mitochondrial and nuclear genes. Saturation in the DNA sequences was examined by plotting the number of transition and transversion substitutions against *p*-distances for each pairwise comparison using the program Dambe (Xia and Xie, 2001).

We implemented different strategies to reconstruct phylogenies, using both independent and combined data sets. First, we maximized the number of species, and genera by analyzing a data set consisting of 15 taxa (21 individuals) and 1814 bp (930 bp of ND2 and 884 bp of FIB7), of which 661 were variable and 428 were parsimony-informative. Second, we maximized the number of molecular characters, with a data set that included nine taxa (nine sequences) and 2647 bp (930 bp of ND2, 462 of cyt *b*-ND5 and their intergenic spacer, 884 bp of FIB7, and 371 bp of G3PDH); 824 of these were variable and 420 were parsimony-informative. Note that in this data set, the representative of *S. iraiensis* was a composite sample, consisting of nuclear sequences of specimen MCP 957 and mitochondrial sequences of specimen MPEG 52945. We also analyzed a third set consisting only of FIB7 sequences, with 19 taxa (25 individuals) and 884 bp, of which 289 were variable and 136 were parsimony-informative (see Table 1 for the taxa included in each data set). Finally, we conducted additional analyses including only sequences of other genes (e.g., ND2), but because results were similar to those obtained with other, more comprehensive data sets, they are not reported here.

Phylogenies were estimated using maximum parsimony (MP) and maximum likelihood (ML) methods in PAUP* 4.0b10 and Bayesian analysis in MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001). Maximum parsimony analyses were conducted based on heuristic searches using the TBR branch swapping algorithm with no upper limit set for the maximum number of trees saved. Gaps were treated as missing data. Branch support was evaluated using 1000 bootstrap replicates (Felsenstein, 1985). For the maximum likelihood analyses, we used the best-fit substitution models selected based on the Akaike Information Criterion (AIC) in ModelTest 3.7 (Posada and Crandall, 1998), as follows: FIB7 + ND2: TIM + I + G, ND2 + cyt *b*-ND5 + FIB7 + G3PDH: GTR + G, FIB7:

Table 1
Samples included in the molecular phylogenetic analyses, with museum or collector reference numbers, geographic origin (when known), and GenBank Accession Numbers for the different loci whenever sequences were available

Species	Catalogue No.[a]	Locality	ND2 (930 bp)	cyt *b*-ND5 (462 bp)	FIB7 (884 bp)	G3PDH (371 bp)	Source
Grallariidae							
Grallaria ruficapilla	AMNH GFB 3159	Venezuela	—	—	AY489453	—	Chesser (2004)
Hylopezus ochroleucus	MCP 2036	Brazil: state of Minas Gerais	EU479686	EU479695	EU479654	EU479664	This study
Rhinocryptidae							
Pteroptochos castaneus	AMNH RTC 471	Chile: Región VIII	—	—	AY489456	—	Chesser (2004)
Pteroptochos tarnii	AMNH RTC 467	—	—	—	—	AY590096	Fjeldså et al. (2005)
Scelorchilus rubecula	CC 130	Chile: Región X	—	—	EU479655	—	This study
Rhinocrypta lanceolata	AMNH PRS 1152	—	—	—	AY489457	—	Chesser (2004)
Rhinocrypta lanceolata	NRM 966793	—	—	—	—	DQ438953	Ericson et al. (2006)
Liosceles thoracicus	FMNH 4545	—	AY370595	—	—	—	Rice (2005)
Psilorhamphus guttatus	MCP 1720*	Brazil: state of São Paulo	EU479676	EU479693	EU479645	EU479661	This study
Merulaxis ater	MCP 1740*	Brazil: state of Paraná	EU479678	EU479694	EU479647	EU479663	This study
Eugralla paradoxa	AMNH RTC 463	Chile: Región IX	EU479683	—	EU479651	—	This study
Myornis senilis	IAvH 11866	Colombia: Depto. Caldas	EU479684	—	EU479652	—	This study
Scytalopus speluncae	MCP 988*	Brazil: state of Rio Grande do Sul	EU479667	—	EU479636	—	This study
Scytalopus speluncae	MCP 1736*	Brazil: state of Paraná	EU479675	EU479692	EU479644	EU479660	This study
Scytalopus pachecoi	MCP 976*	Brazil: state of Rio Grande do Sul	EU479666	EU479687	EU479635	EU479657	This study
Scytalopus pachecoi	MCP 1082*	Brazil: state of Rio Grande do Sul	EU479668	—	EU479637	—	This study
Scytalopus iraiensis	MCP 957*	Brazil: state of Rio Grande do Sul	EU479665	—	EU479634	EU479656	This study
Scytalopus iraiensis	MCP 2046	Brazil: state of Minas Gerais	EU479677	—	EU479646	—	This study
Scytalopus iraiensis	MPEG 52945	Brazil: state of Paraná	EU479685	EU479691	—	—	This study
Scytalopus stilesi	ICN 34569	Colombia: Depto. Antioquia	EU479682	—	EU479650	—	This study
Scytalopus vicinior	ICN 34840	Colombia: Depto. Valle del Cauca	EU479681	—	EU479653	—	This study
Scytalopus spillmanni	ZMUC S540	Ecuador	—	—	—	AY590097	Fjeldså et al. (2005)
Scytalopus novacapitalis	MCP 1481*	Brazil: Distrito Federal	EU479669	—	EU479638	—	This study
Scytalopus novacapitalis	MCP 1865	Brazil: state of Minas Gerais	EU479674	EU479690	EU479643	EU479659	This study
Scytalopus indigoticus	MCP 1721*	Brazil: state of Rio de Janeiro	EU479670	—	EU479639	—	This study
Scytalopus indigoticus	MCP 1730*	Brazil: state of Bahia	EU479671	EU479688	EU479640	EU479658	This study
Scytalopus psychopompus	MCP 1722*	Brazil: state of Bahia	EU479672	—	EU479641	—	This study
Scytalopus psychopompus	MCP 1734*	Brazil: state of Bahia	EU479673	EU479689	EU479642	EU479662	This study
Scytalopus magellanicus	AMNH RTC 449	Chile: Región VII	EU479679	—	EU479649	—	This study
Scytalopus canus	ZMUC 134903	Colombia: Depto. Antioquia	EU479680	—	EU479648	—	This study

For each locus, the total length of the alignment on which analyses were based is shown in parentheses. Taxonomic sequence follows Remsen et al. (2008).

[a] Institutions or collector acronyms—AMNH: American Museum of Natural History; CC, Cintia Cornelius, unvouchered blood sample; IAvH, Instituto Alexander von Humboldt, Colombia; FMNH, Field Museum of Natural History; ICN, Instituto de Ciencias Naturales, Universidad Nacional de Colombia; MPEG, Museu Paraense Emílio Goeldi; MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul; NRM, Swedish Museum of Natural History; ZMUC, Zoological Museum, University of Copenhagen. Numbers followed by an asterisk indicate that the corresponding voucher skin specimen (under the same catalogue number) was also examined for morphological analyses.

GTR + G. ML analyses used a neighbor-joining starting tree, and heuristic searches with simple taxon addition and the TBR branch swapping algorithm; branch support was evaluated using 200 bootstrap replicates. For Bayesian inference, we selected substitution models according to the AIC using MrModeltest (Nylander, 2002). The GTR + I + G model was used for the mitochondrial genes, and the GTR + G model for the nuclear genes, which were specified as separate partitions in combined analyses. Each Bayesian analysis involved two independent runs, each consisting of five million generations of Metropolis-coupled Markov Chain Monte Carlo (MCMC) sampling with one cold and three heated chains; samples were taken every 100 generations, and we discarded trees from the first 1.25 million generations as burn-in. Plots of likelihood scores against generation number indicated that analyses reached stationary distributions, and convergence diagnostics implemented in MrBayes indicated that the independent runs converged on the same posterior distribution. Based on the post burn-in samples of trees, we calculated majority-rule consensus trees for each data set, and assessed branch support based on posterior probability values.

We estimated divergence times between a selected set of taxa for which sequences of both mitochondrial fragments were available (i.e., cyt *b*-ND5 and ND2; Table 1) using the uncorrelated log-normal relaxed molecular clock model implemented in the program BEAST 1.4.6 (Drummond et al., 2006; Drummond and Rambaut, 2007). We employed the DNA substitution model selected by Modeltest as described above and a Yule tree prior in MCMC analyses that were run for 20^7 generations, with parameters sampled every 10^3 generations; the first 20^3 were discarded as burn-in. The program Tracer 1.4 (Available from http://tree.bio.ed.ac.uk/software/tracer/) was used to calculate the mean and 95% highest posterior density interval (HPD) for selected divergence times. Considering the absence of a reasonable calibration point in Rhinocryptidae, we based our node age estimates on a 1.6% rate of sequence divergence per million years estimated for passerine cyt *b* (Fleischer et al., 1998); using a 2% rate (Weir and Schluter, 2008) would not substantially change the general patterns we describe. A comparison of pairwise distances between individuals calculated for the cyt *b*-ND5 sequences and the ND2 sequences revealed these were very similar (overall means of 0.16 and 0.17, respectively), which justifies the application of the 1.6% rate to the combined data.

2.4. Anatomical data

We examined specimens deposited at the ornithological collections of the following Brazilian institutions: Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul (MCP), Porto Alegre; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo; Museu de História Natural de Taubaté (MHNT), Taubaté; Museu de Zoologia João Moojen de Oliveira, Universidade Federal de Viçosa (MZUFV), Viçosa; and Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus. Additionally, we examined high-resolution photographs of skeletal specimens housed at the American Museum of Natural History (AMNH), New York, and the Louisiana State University Museum of Natural Science (LSUMZ), Baton Rouge, USA. Most specimens used for the anatomical analyses were collected by M.R.B. and G.N.M., and the corresponding voucher skins are housed at MCP. See the appendices for a complete list of species and specimens we examined for this study.

We examined syringeal specimens of 12 species in four rhinocryptid genera (*Liosceles*, *Psilorhamphus*, *Scytalopus* and *Merulaxis*) and the descriptions of the syrinx of five additional genera (*Pteroptochos*, *Scelorchilus*, *Rhinocrypta*, *Teledromas*, and *Eugralla*; Ames, 1971) for discrete (i.e., discontinuous) characters. In addition, syringeal specimens of 35 species in 32 genera representing all remaining tracheophone suboscine families presently recognized (Irestedt et al., 2002; Remsen et al., 2008) have been analyzed for comparative purposes, as part of an ongoing study aimed at producing a genus-level, morphology-based cladistic analysis of the Rhinocryptidae (Maurício et al., unpublished). Syringeal specimens were fixed in 10% formalin for several days before the staining process. For calcium staining, syringeal specimens were immersed in a solution of Alizarin Red S and ethyl alcohol (at 75%) for 24–72 h (Springer and Johnson, 2000). A solution of glacial acetic acid and Alcian Blue was used for cartilage staining (Taylor and Van Dyke, 1985), with immersion for periods of 24–96 h. Immersion in iodine for short periods was used for muscle staining (Cannell, 1988). The terminology used for syringeal morphology follows Ames (1971).

In addition to analyzing syringeal structure, we checked the condition of the clavicles, a trait that is important in tapaculo systematics (Feduccia and Olson, 1982). The terminology of clavicle morphology follows Baumel and Witmer (1993). We also made cursory inspections of plumage coloration on museum specimens.

3. Results

3.1. Molecular phylogenetics

No stop codons or unusual substitution patterns were observed in mtDNA sequences, suggesting they were indeed of mitochondrial origin and did not correspond to nuclear pseudogenes (Sorenson and Quinn, 1998). The incongruence length difference test (ILD) did not reveal significant incongruence in phylogenetic signal between nuclear and mitochondrial genes ($P > 0.05$). Plots of pairwise divergence did not show evidence of saturation, except in the cyt *b*-ND5 fragment, which exhibited saturation of substitutions at the third positions of codons due to the presence of the very divergent *Hylopezus ochroleucus* sequence in the data set. However, results of parsimony analyses in which *H. ochroleucus* was excluded were very similar to those in which this taxon was included, indicating that saturation did compromise phylogenetic analyses.

Phylogenetic trees obtained using different data sets and estimated by different methods were very similar topologically, but differed somewhat in branch support values (Figs. 1–3). A salient feature of all trees was the strong support for the paraphyly of the genus *Scytalopus*: *S. indigoticus* and *S. psychopompus* consistently formed a clade that was independent from a clade (hereafter called the true *Scytalopus*; Figs. 1–3) formed by all other representatives of the genus, including both all the Andean species sampled and the remaining Brazilian taxa. The clade formed by *S. indigoticus* and *S. psychopompus* always grouped with *Merulaxis ater*, a relationship that was consistently supported by high bootstrap and posterior probability values. In all analyses where sequences of *Myornis* and *Eugralla* were included, they grouped with moderate to high support with a clade composed by all sampled true *Scytalopus* taxa (including the type species of the genus, *S. magellanicus*), exclusive of the *S. indigoticus* species-group. The sister-taxon relationship between the *S. indigoticus* species-group and the genus *Merulaxis* was also recovered when we used other partial data sets whose results are not shown here, such as an G3PDH intron 11 data set (376 bp) in which were added *Rhinocrypta lanceolata*, *Pteroptochos tarnii*, and *Scytalopus spillmanni*, and an ND2 data set that included a 492 bp sequence of *Liosceles thoracicus*.

The two nuclear introns exhibited informative indels in our alignments that provided additional support for some nodes in the phylogeny (Fig. 3). For example, a deletion of four base pairs

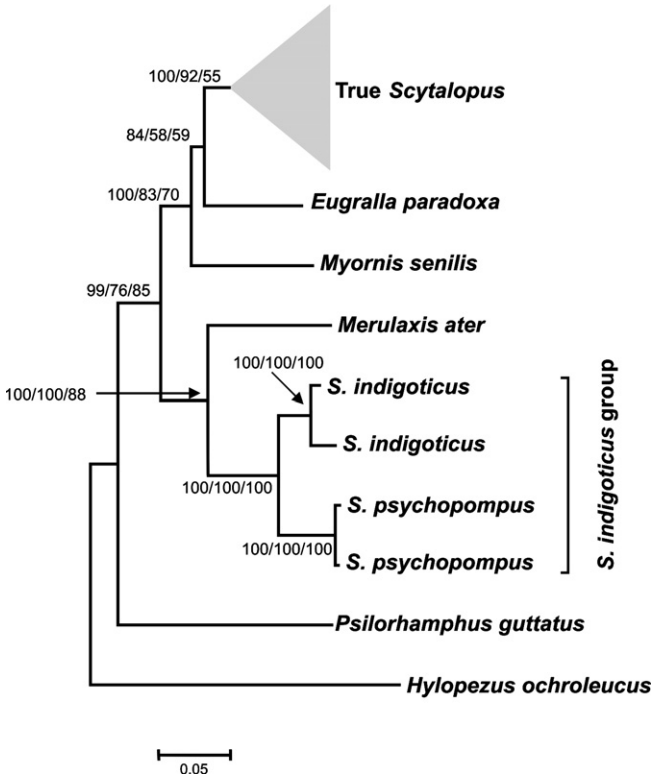

Fig. 1. Phylogenetic relationships among species of *Scytalopus* and related genera based on the ND2 + FIB7 combined data set (1814 bp). The topology shown is the result of the Bayesian analysis. Support values shown along each branch are Bayesian posterior probabilities, and maximum-likelihood and maximum parsimony bootstrap values, respectively. Species of true *Scytalopus* included in this data set are *S. speluncae*, *S. pachecoi*, *S. iraiensis*, *S. stilesi*, *S. vicinior*, *S. novacapitalis*, *S. magellanicus*, and *S. canus*.

at positions 206–209 in FIB7 is synapomorphic for a clade composed by *Merulaxis* and the *S. indigoticus* species-group, and a deletion of 24 bp at positions 418–442 is synapomorphic for the clade formed by the true *Scytalopus*, *Myornis*, and *Eugralla*. Additionally, a single nucleotide insertion at position 812 and deletions of three base pairs at positions 495–497 and of one nucleotide at position 701 are synapomorphic for the *S. indigoticus* species-group. For G3PDH, an insertion at position 213 is synapomorphic for the clade formed by *Merulaxis* and the *S. indigoticus* species-group, and an insertion at position 331 is synapomorphic for the latter group.

The relaxed molecular clock analysis based on mitochondrial data assuming a 1.6% divergence per million years suggests that the clade formed by the *S. indigoticus* species-group and *Merulaxis* diverged from the true *Scytalopus* approximately 19 million years ago (m.a.), with a Bayesian confidence interval (95% highest posterior density) of 18–26 m.a. These estimates place the divergence between these two lineages in the Early to Middle Miocene. Likewise, the divergence between the *S. indigoticus* species-group and *Merulaxis* also appears to have occurred in the Middle Miocene, with an approximate divergence time of 15 m.a. (95% HPD 13.3–20.5 m.a). Divergence times between members of the *S. indigoticus* species-group will be described and discussed in detail in a forthcoming publication.

3.2. Anatomical data

Anatomical data are fully congruent with the molecular phylogenies. The sister-taxon relationship between *Merulaxis* and the *S. indigoticus* species-group is supported by two likely syringeal synapomorphies: (1) a reduction or absence of A-3, A-4 and A-5 elements in the dorsal surface of the syrinx, forming an incomplete (i.e., although present, the three elements are dorsolaterally reduced, never reaching the Processus vocalis) or complete (i.e., at least one element is totally absent) "window" in the caudal half of Membrana trachealis (Fig. 4A and B); and (2) the possession of a Processus vocalis ending cranially as a very soft, thin and hyaline surface to which the Musculus tracheolateralis is caudally inserted (Fig. 5A and B). The dorsal window, although present in all individuals of *Merulaxis* and the *S. indigoticus* species-group examined, is variable across taxa. In *M. stresemanni* ($n = 1$) all three elements are absent dorsally; in *M. ater* A-3 may be absent ($n = 1$) or present as a dorsolaterally very reduced, vestigial medial bar ($n = 3$),

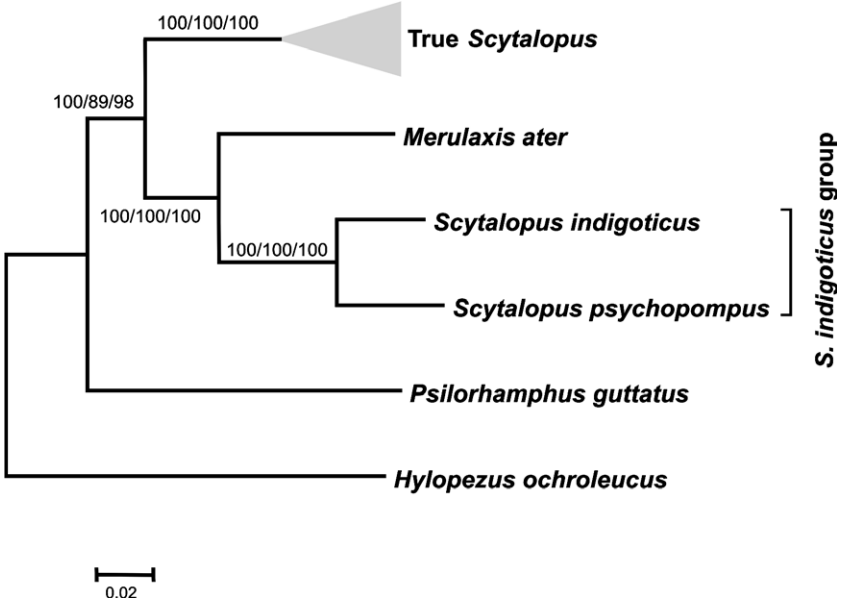

Fig. 2. Phylogenetic relationships among species of *Scytalopus* and related genera based on the ND2 + cyt *b*-ND5 + FIB7 + G3PDH combined data set (2647 bp). The topology shown is the result of the Bayesian analysis. Support values shown along each branch are Bayesian posterior probabilities, and maximum-likelihood and maximum parsimony bootstrap values, respectively. Species of true *Scytalopus* included in this data set are *S. speluncae*, *S. pachecoi*, *S. iraiensis*, and *S. novacapitalis*.

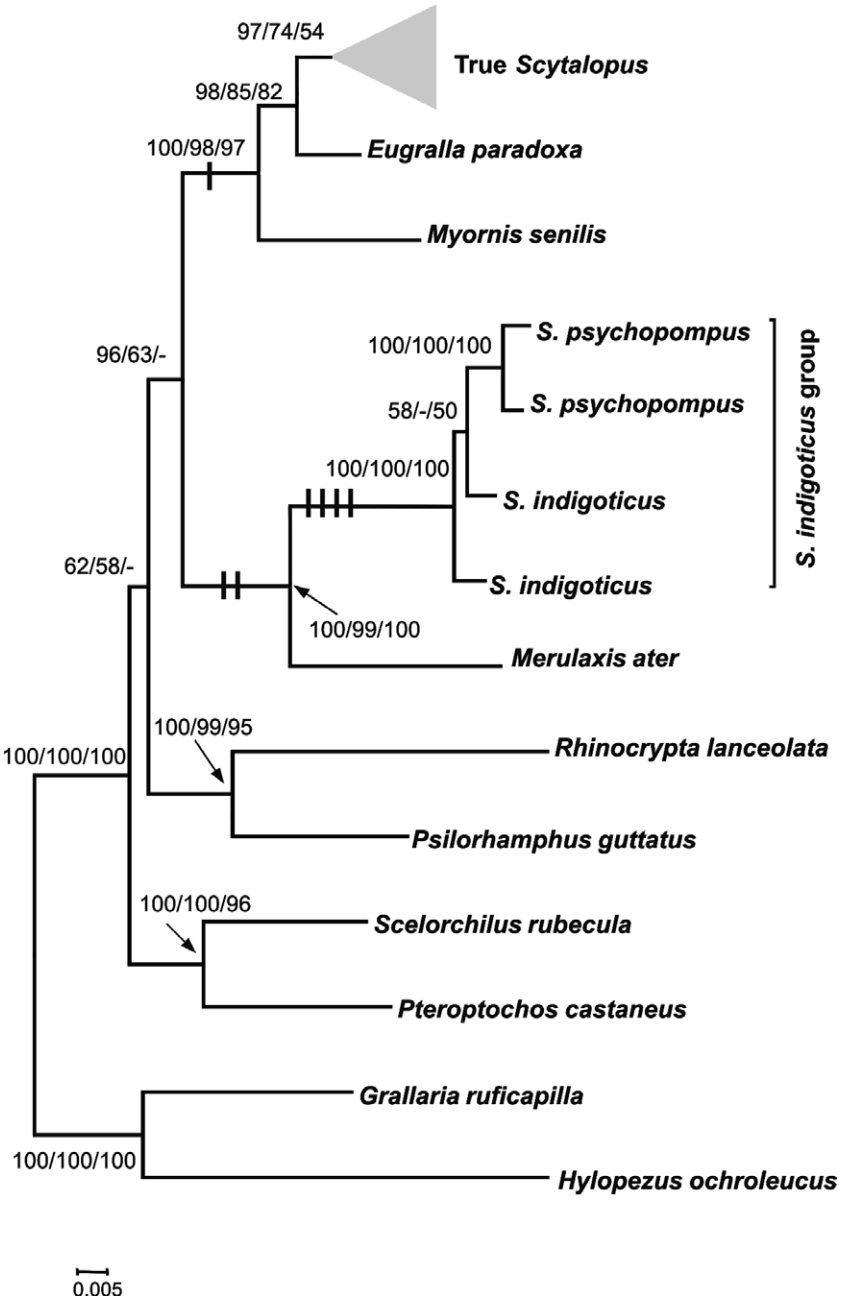

Fig. 3. Phylogenetic relationships among species of *Scytalopus* and related genera based on nuclear FIB7 sequences (884 bp). The topology shown is the result of the Bayesian analysis. Support values shown along each branch are Bayesian posterior probabilities, and maximum-likelihood and maximum parsimony bootstrap values, respectively (–indicates values <50%). Black bars indicate synapomorphic indels mentioned in the text. Species of true *Scytalopus* included in this data set are *S. speluncae*, *S. pachecoi*, *S. iraiensis*, *S. stilesi*, *S. vicinior*, *S. novacapitalis*, *S. magellanicus*, and *S. canus*.

whereas A-4 and A-5 are lacking, although in one case A-5 was present. In *S. indigoticus*, A-3 and A-4 may be dorsally vestigial (i.e., narrow and very reduced dorsolaterally, appearing only as short medial segments, $n = 6$; see Bornschein et al., 1998) or more conspicuous (i.e., less reduced dorsolaterally, $n = 9$) medial bars, whereas A-5 is always comparatively less reduced; in *S. psychopompus* ($n = 2$), dorsally the three elements are as in the less reduced examples of *S. indigoticus*.

Syringeal data also supported the monophyly of a clade formed by *S. indigoticus* and *S. psychopompus*, as they have a nearly rectangular, calcified or partially calcified plate (as indicaded by a intense impregnation of Alizarin Red S stain) in the cranial half of the Processus vocalis (Fig. 5B). On the other hand, both species of *Merulaxis* exhibit a unique cartilaginous protuberance in the midline of the ventral Membrana trachealis between elements A-2 and A-5 and a rigid cartilaginous extension in the ventral edge of the Processus vocalis; these characters support the monophyly of the genus.

The characteristics described above were not observed in any of the other eight rhinocryptid genera whose syringes are known (the syringes of *Myornis* and *Acropternis* have not been described), nor in any other Furnarii examined by us or reported in the literature (Ames, 1971; see Section 4). Additionally, we did not find any syringeal characters suggesting alternative relationships to those supported by the distribution of character states described above. Although we have directly analyzed the syringes of only four recognized rhinocryptid genera, the descriptions or illustrations given

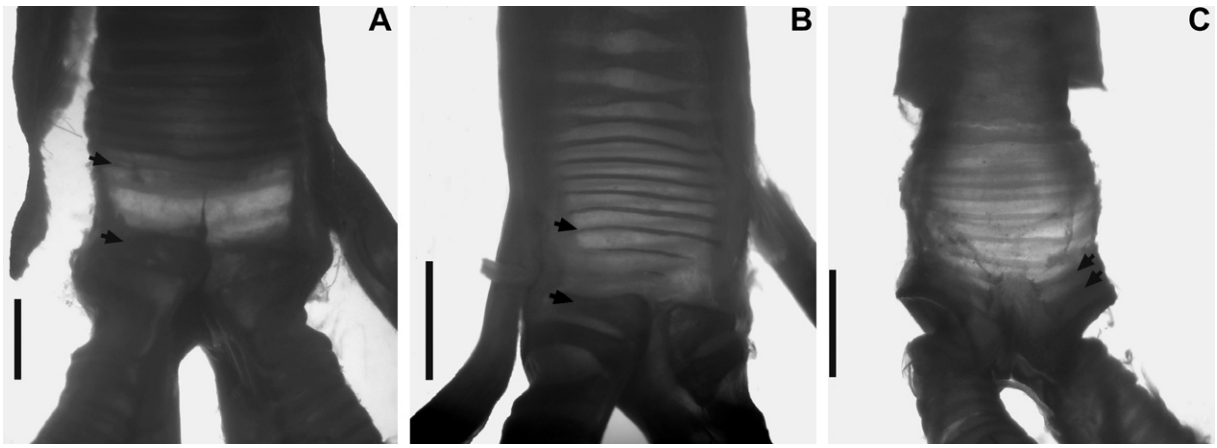

Fig. 4. Dorsal view of the syringes of (A) *Merulaxis stresemanni*, (B) *Scytalopus indigoticus* and (C) *Scytalopus pachecoi*. The arrows in A and B indicate A-2 (below) and A-6 (above) elements, those in C A-2 (below) and A-3 (above) elements. The dorsal reduction or absence of A-3–A-5 elements, seen in A and B, forms a "window" in the Membrana trachealis, a feature not seen in C, in which A-2, A-3 and subsequent A elements are dorsally complete (see text). Scale bars 1 mm.

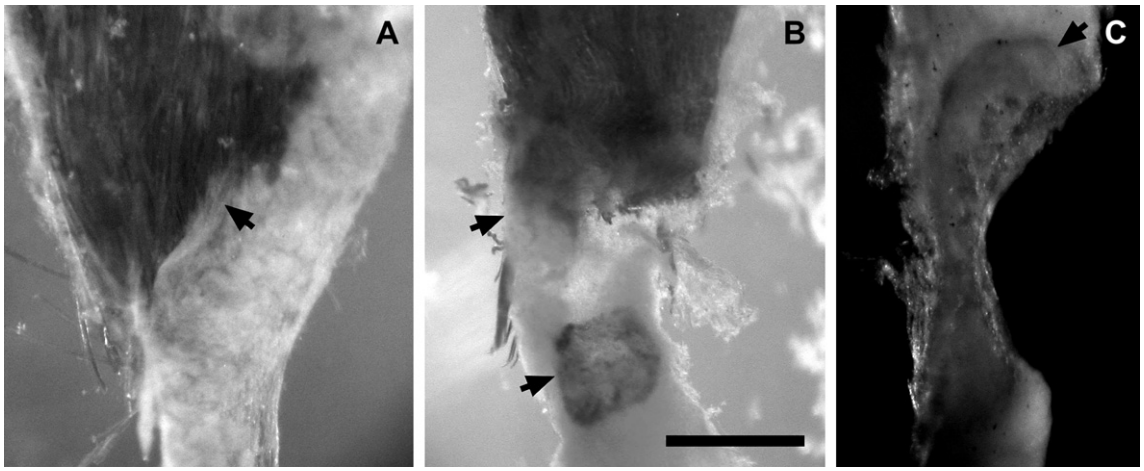

Fig. 5. Medial view of the Processus vocalis of (A) *Merulaxis stresemanni*, (B) *Scytalopus indigoticus* and (C) *Scytalopus pachecoi*. The arrows indicate the cranial end of the Processus vocalis (top arrow in B), which is very soft and thin in A and B (as indicated by the light shading) and firm, calcified and thicker in C (as indicated by the darker shading). The bottom arrow in B highlights the calcified plate uniquely found in the *S. indigoticus* species-group. Shown are the left Processus in A and C, and the right one in B, with the caudal end of Musculus tracheolateralis inserted on its cranial portion. Scale bar 0.5 mm (all pictures are in the same scale).

by Ames (1971) for *Pteroptochos*, *Scelorchilus*, *Rhinocrypta*, *Teledromas*, and *Eugralla* (and also the type species of *Scytalopus*, *S. magellanicus*) are detailed enough to allow a number of direct comparisons with our data. However, the syringes of *Merulaxis* and the *S. indigoticus* species-group share other similarities (e.g., the cranial margin of element A-2 in both groups is approximately horizontal, instead of inclined) that were not observed in the other genera we examined, but whose conditions in other taxa could not be assessed based on the information provided by Ames (1971).

A close relationship between *Merulaxis* and the *S. indigoticus* species-group is also suggested by plumage coloration. Both have slate blue upperparts and sides of body (*Merulaxis* also on the underparts), except on the posterior flanks and lower back; no other rhinocryptid has a blue plumage.

The clavicles of virtually all the Furnarii (as in most birds) show a similar morphology, with a wide and triangular Extremitas omalis (Epicleideum), and a medially fused Extremitas sternalis that forms a deep "U"-shaped furcula, with a strong and flat apophysis (Hypocleideum). In the Rhinocryptidae, we observed this same structure in *Liosceles*, *Acropternis*, *Merulaxis stresemanni*, *M. ater*, *Scytalopus indigoticus*, *S. psychopompus*, and *Psilorhamphus* (Fig. 6A). This condition is also found in *Pteroptochos*, *Scelorchilus*, *Rhinocrypta* and *Teledromas* (Feduccia and Olson, 1982). In contrast, in *Eugralla*, *Myornis*, and the true *Scytalopus*, the clavicles show atrophy of the Extremitas sternalis and, because these are very thin and unfused, they do not form a furcula (Fig. 6B; see also Feduccia and Olson, 1982). Only in one species, *Scytalopus argentifrons* (specimen LSUMZ 135542), we observed a particular condition where the Extremitas sternalis of the clavicles are very thin and exhibit a tenuous medial join, but no Hypocleideum. In sum, members of the clade formed by *Eugralla*, *Myornis*, and the true *Scytalopus* possess an apomorphic conditon of the clavicles, with atrophy of the Extremitas sternalis and the loss of the furcula.

4. Discussion

4.1. Taxonomic implications

Our molecular and anatomical data demonstrate conclusively that the genus *Scytalopus* as currently defined is not monophyletic. To correct this, there are two plausible alternatives concerning the placement of the *S. indigoticus* species-group: (1) merge it into the genus *Merulaxis* or (2) erect a new genus for it. The first alternative would result in a rather heterogeneous genus composed by two *Scytalopus*-like (small sized and short tailed) taxa and two large sized, long tailed species (*Merulaxis*); such heterogeneity would

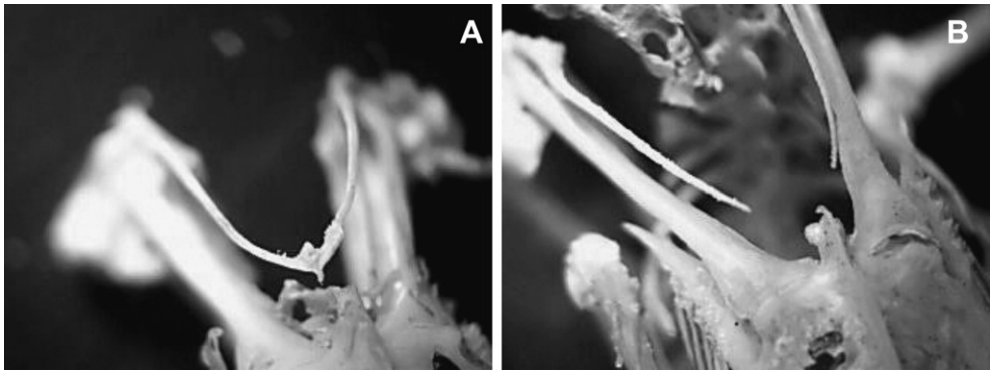

Fig. 6. Clavicles of (A) *Scytalopus indigoticus* and (B) *Scytalopus* sp. nov., an undescribed species of the *S. speluncae* species-group. The furcula (with Hypocleideum) is present in A but is absent in B.

be inconsistent with the current genus-level classification of the Rhinocryptidae (Remsen et al., 2008). Furthermore, *Merulaxis* and the *S. indigoticus* species-group are monophyletic lineages, each being characterized by putative anatomical synapomorphies; the monophyly of the latter is also supported by multiple molecular synapomorphies, including indels. Therefore, we believe that these clades are better treated as two separate genera. Accordingly, here we propose a new genus for the "*Scytalopus*" *indigoticus* species-group:

Eleoscytalopus gen. nov.

Type-species: *Myiothera indigotica* Wied, 1831 [=*Scytalopus indigoticus* (Wied); the syntypes, which are housed at the American Museum of Natural History (AMNH 5416 and 5417), New York, USA (LeCroy and Sloss, 2000), were examined through recent photographs.].

4.1.1. Diagnosis

Eleoscytalopus is a member of the suborder Furnarii, having a typical tracheophone syrinx with Membrana trachealis and Processus vocalis, two derived characters not found elsewhere in Passeriformes (Ames, 1971; Raikow and Bledsoe, 2000). The new genus presents the Pteryla ventralis undivided in the flank margin, a hypothesized synapomorphy for the family Rhinocryptidae (Krabbe and Schulenberg, 2003; Rice, 2005; see also Ames et al., 1968; Bornschein et al., 1998). Other characters useful to diagnose the family members, but that are shared with some other Furnarii families, are present in the members of the new genus: a mobile nasal operculum (shared with Melanopareiidae) and four notches in the sternum (a state found also in Melanopareiidae, Conopophagidae, and in some Grallariidae).

Eleoscytalopus is diagnosed from all tapaculo genera whose syringes are known by the presence of a nearly rectangular plate (calcified or partially calcified) in the cranial half of the Processus vocalis (Fig. 5B). This chararacter represents a putative synapomorphy for the new genus. The presence of a dorsal window in the caudal half of the Membrana trachealis and the possession of a cranially very soft Processus vocalis are nearly unique to the new genus, being shared only with *Merulaxis*. In having perfectly fused clavicles with a distinct Hypocleideum (therefore forming a furcula), a condition found in most rhinocryptid genera and related families, *Eleoscytalopus* differs distinctly from *Myornis*, *Eugralla*, and *Scytalopus*, which have unfused clavicles and always lack a Hypocleideum. The new genus further differs from at least *Scytalopus* and *Eugralla* by having the Membranae tracheales without finite anterior limits (i.e., the "long type" sensu Ames, 1971), instead of having both membranes sharply and shortly limited anteriorly (see Bornschein et al., 1998).

It is noteworthy that in its small size (less than 15 cm of total length), relatively short tail (shorter than wings), bill with a base that is laterally compressed but not strongly elevated, and in generally wren-like appearance, *Eleoscytalopus* closely matches the current definition of *Scytalopus* (e.g., Fjeldså and Krabbe, 1990; Ridgely and Tudor, 1994; Krabbe and Schulenberg, 1997, 2003), where its constituent species have been placed for more than 150 years (see Cory and Hellmayr, 1924). However, *in addition to the* distinct syringeal morphology and the condition of the clavicles described above, *Eleoscytalopus* can be further diagnosed with respect to *Scytalopus* and other rhinocryptid genera by the combination of extensive pure-white central underparts (from the chin and throat to the lower belly) and slate-blue anterior upperparts (head, neck, and mantle) and sides of body (except the posterior flanks).

Included taxa: *Eleoscytalopus indigoticus* (Wied) comb. nov.; *E. psychopompus* (Teixeira and Carnevalli) comb. nov.

Etymology. *Eleos*, from the Greek *heleos*, meaning swamp, refers to swampy forests, the preferred habitat of *E. indigoticus* and *E. psychopompus*; *Scytalopus* refers to the genus in which these two species were long included. Gender masculine.

Specimens examined: see Appendix A.

4.2. Hidden generic diversity within Furnarii

Much of avian classification at the genus and species levels is still based on traditional studies that emphasized the overall external appearence of taxa, an approach which frequently created excessively inclusive groupings (e.g., Vaurie, 1980) lacking unambiguous diagnoses. Recognition of non-monophyletic groups is an expected outcome of this approach. Not surprisingly, therefore, recent molecular phylogenetic analyses have revealed that several traditional genera of tracheophone suboscines are non-monophyletic assemblages of species (Aleixo, 2002; Irestedt et al., 2004, 2006; Chesser et al., 2007; Fjeldså et al., 2007; Brumfield et al., 2007; Brumfield and Edwards, 2007). Consequently, new generic names have been proposed or revalidated (e.g., Isler et al., 2006; Chesser and Brumfield, 2007; Aleixo et al., 2007) and others need to be erected or recognized, especially to accomodate taxa in highly polyphyletic genera (see Irestedt et al., 2004; Chesser et al., 2007; Fjeldså et al., 2007; Brumfield et al., 2007). We think that this "splitting" approach is preferable to the recognition of highly inclusive and confusingly heterogeneous genera in the sense that it more accurately reflects the complex evolutionary pathways of relatively old lineages of Neotropical birds.

As reported here for *Eleoscytalopus*, and related tapaculos, the importance of anatomical investigation in the age of molecular phylogenetics should not be underestimated. We suggest that, as with *Scytalopus*, *Eleoscytalopus* and their closest relatives, careful inspections of morphology are likely to reveal the existence of diagnostic and phylogenetically informative phenotypic features in other groups of Neotropical birds that may help to better uncover other instances of "hidden generic diversity". Thus,

although thorough morphological analyses are often hampered by insufficient anatomical collections (Livezey, 2003; Causey and Trimble, 2005), completing morphology-based phylogenies of tracheophone families (e.g., Claramunt and Rinderknecht, 2005) would be highly desirable whenever the relevant material is available.

The superficial similarity between taxa that led former avian systematists to recognize polyphyletic genera within Furnarii may be explained by the convergence of some character suites (e.g., color patterns, size and general body proportions) resulting from adaptations to similar life styles (Fjeldså et al., 2007; see also Chesser et al., 2007). However, the close external similarity between *Scytalopus* (and also *Myornis* and *Eugralla*) and *Eleoscytalopus* may instead represent a case of evolutionary conservatism rather than convergent evolution of some general features (e.g., size and proportions) that characterize all taxa within these genera. Regardless of whether paraphyly has resulted from traditional taxonomists being misled by conservativeness in some lineages or by convergence, our results illustrate the importance of formally testing previous (and generally only implicit) hypotheses of monophyly of genera in studies concerned mostly with the reconstruction of intrageneric relationships, even in cases in which generic limits have not been disputed.

4.3. Morphologial evolution in Rhinocryptidae

No morphology-based phylogenetic analysis of a tracheophone group published to date has included syringeal data. However, our results demonstrate that syringeal variation is phylogenetically informative within Rhinocryptidae. At least two syringeal characters were uniquely found in *Eleoscytalopus* and *Merulaxis* (the dorsal window in the caudal half of the Membrana trachealis and the soft cranial portion of the Processus vocalis), whereas additional characters were found to be exclusive to each of these genera. The presence of windows (reduction or absence of A elements) in the Membrana trachealis is also known for some Furnariidae genera (e.g., *Synallaxis*, *Schoeniophylax*, *Limnoctites*, and *Cranioleuca*; pers. obs.; see also Ames, 1971), but the condition of the furnariid window is very distinct from that of *Eleoscytalopus* and *Merulaxis*, being more cranial in position (spanning from A-5 to A-9 or A-10) and being present both ventrally and dorsally. Thus, we hypothesize that these two types of windows are not homologous. The widespread and presumably ancestral condition within Furnarii is the absence of any type of window, as exemplified here with a typical *Scytalopus* (Fig. 4C), in which A-2/A-3 and subsequent elements are dorsally complete. A relatively soft Processus vocalis is found in some Thamnophilidae genera (Ames, 1971), notably in *Herpsilochmus* and *Formicivora* (pers. obs.), but the cranial end of the Processus in these taxa was found to be a more consistent cartilage, with conspicuous calcification on the edge. The widespread condition within Furnarii, a firm and generally well-calcified cranial portion of the Processus vocalis, is illustrated here with a member of *Scytalopus* (Fig. 5C).

Because Ames (1971) described intrinsic syringeal musculature for all the tapaculo genera he examined, except *Teledromas*, it is noteworthy that no intrinsic syringeal muscles were found in the five tapaculo genera (including *Scytalopus*) we examined (see also Bornschein et al., 1998). The possession of a dorsally originating intrinsic muscle with a ventral insertion, tentatively named Musculus vocalis dorsalis by Ames (1971), was hypothesized to be a synapomorphy for the Rhinocryptidae (Rice, 2005). However, owing to the absence of intrinsic muscles in at least five of a total of ten tapaculo genera whose syringes are known (including *Eleoscytalopus*), that hypothesis is not corroborated in the light of the new information. Furthermore, the particular condition of the "intrinsic muscle" found in the only specimen of *Scytalopus* examined by Ames (1971), a narrow lateral band of fibers nearly covered by the Musculus tracheolateralis, might simply be the result of a discontinuity in the fibers of this extrinsic muscle.

4.4. Biogeography of the "small" tapaculos

Unlike true *Scytalopus*, members of *Eleoscytalopus* are not truly montane taxa. Although in the northen part of its distribution (between the states of Rio de Janeiro and Bahia, in Brazil) *E. indigoticus* is found only above 600 m elevation, in the southern half of its range (between the states of Rio Grande do Sul and São Paulo) it ranges from sea level to about 1100 m, being apparently most common in swampy forests in the lowlands; *E. psychopompus* is restricted to swampy forests of coastal Bahia from sea level to about 150 m elevation (Ridgely and Tudor, 1994; Bornschein and Maurício, unpublished). The two species of *Merulaxis* show a similar distributional pattern (though they do not inhabit swampy forests), with *M. ater* occurring from sea level to about 1600 m between the states of Santa Catarina and Espírito Santo, and *M. stresemanni* occupying lowland forests of coastal Bahia and, locally, montane forests in the border with the state of Minas Gerais (Ridgely and Tudor, 1994; Bencke et al., 2006).

The estimated split between the *Eleoscytalopus–Merulaxis* clade and the *true Scytalopus* (i.e., the *Myornis–Eugralla–Scytalopus* lineage) at c. 19 million years before present in the Early to Middle Miocene, supports the existence of an old phylogenetic break between eastern and western South America. The Brazilian shield was being subducted beneath the central Andes during this period (Gregory-Wodzicki, 2000), and such a geological episode and the environmental changes it triggered may have caused the disruption of a formerly continuous biota distributed from the paleo-Andean Cordillera to the Atlantic coast. Alternatively, such a biotic disruption and the consequent first split within the small tapaculos may have been related to a drying and cooling event of global climate in the Middle Miocene (Gregory-Wodzicki, 2000), independently of, or in conjunction with, subsidence episodes.

The evolutionary history of the Brazilian *Scytalopus* has been the subject of some scrutiny in the ornithological literature (Sick, 1985; Vielliard, 1990; Maurício, 2005). Vielliard (1990) pointed out to two main alternative hypotheses regarding their origins: (1) they would form a monophyletic group, implying a single colonization event from the Andes, or (2) *S. indigoticus* (i.e., *Eleoscytalopus*) and *S. speluncae*/*S. novacapitalis* (i.e., the *S. speluncae* species-group) would be derived independently from distinct Andean ancestors, implying two colonization events. In the light of the results present here, the first alternative can be firmly rejected, whereas the second is partially supported, since the Brazilian taxa formerly or presently placed in *Scytalopus* fall into distinct, distantly related lineages. However, the question about their biogeographic origins cannot be answered at this moment, since the hypothesis that the ancestor of the clade formed by *Eleoscytalopus* and *Merulaxis* colonized eastern South America from the Andes is not more parsimonious than the one in which the ancestor of the clade formed by *Myornis*, *Scytalopus*, and *Eugralla* colonized the Andes from eastern Brazil. These hypotheses could be distinguished with a more complete phylogenetic analysis of *Scytalopus* and related genera. We note, however, that the derived position of *Scytalopus* within its primarily Andean clade (with the exception of the *S. speluncae* species-group, all other taxa are restricted to the Andes or contiguous mountain chains) tends to support the Andean origin for the genus, with a subsequent colonization of eastern Brazil.

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racicus housed at Coleção de Aves, Instituto Nacional de Pesquisas da Amazônia (INPA). Marcelo F. de Vasconcelos also provided several anatomical specimens of tapaculos. Rômulo Ribon kindly sent in loan to the Museu de Ciências e Tecnologia (MCP) a specimen of *Merulaxis stresemanni*. Luís Fábio Silveira and Marina Openheimer kindly provided access to the bird collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP). Paul Sweet and Margaret Hart of the American Museum of Natural History (AMNH), and Santiago Claramunt and J.V. Remsen from the Louisiana State University Museum of Natural Science (LSUMZ) provided digital images of skeletons housed at their institutions. Carla S. Fontana (Laboratório de Ornitologia), and Tiago Carvalho and Roberto E. Reis (Laboratório de Ictiologia) provided access to facilities at MCP. Morevy M. Cheffe, José Fernando Pacheco and Ubirajara R. Martins helped us with nomenclatural or grammatical issues. We are grateful to the following institutions and individuals for loans of tissue samples: AMNH (Paul Sweet and Joel Cracraft), Instituto Alexander von Humboldt (Juan Diego Palacio), Instituto de Ciencias Naturales—Universidad Nacional de Colombia (F. Gary Stiles), and Zoological Museum, University of Copenhagen (Niels Krabbe and Jon Fjeldså). Cintia Cornelius provided a blood sample of *Scelorchilus rubecula.* G.N.M. is supported by a doctoral fellowship (process number 141149/2006-0) from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). Molecular work was supported by a CNPq grant to S.L.B. and by grants from the Chapman Memorial Fund of the AMNH and Facultad de Ciencias, Universidad de los Andes, to C.D.C. Field work by M.R.B. and G.N.M. was partially supported by SAVE Brasil/BirdLife International and the Fundação O Boticário de Proteção à Natureza. The Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) sent collecting permits to G.N.M. and M.R.B. (031/2006 – COFAN).

Appendix A. Anatomical specimens examined

The anatomical parts examined from each specimen are indicated within parentheses (S = syrinx, C = clavicles). See Section 2 for the explanation of institution accronyms. Brazilian state names are abbreviated as follows: Amazonas, AM; Distrito Federal, DF; Bahia, BA; Minas Gerais, MG; Rio de Janeiro, RJ; São Paulo, SP; Paraná, PR; Santa Catarina, SC; Rio Grande do Sul, RS. An asterisk denote that the corresponding voucher skin specimen (under the same catalogue number) was also examined.

RHINOCRYPTIDAE: *Liosceles thoracicus*—Brazil: AM: INPA 879 (S, C) (sent in loan to MCP); Brazil: MHNT 4493 (C). *Psilorhamphus guttatus*—Brazil: SP: MCP 1720* (S, C), MHNT 4812 (C); PR: MCP 2045* (S) and uncat. (S, C). *Acropternis orthonyx*—Peru: Dpto. Amazonas: LSUMZ 88163 (C). *Merulaxis ater*—Brazil: SP: MCP 2001* (S), 2002* (S) and 1864 (S, C), MHNT 160 (C), 625 (C) and 1409 (C); PR: MCP 1740* (S, C). *Merulaxis stresemanni*—Brazil: BA/MG: MZUFV 1408* (S, C) (sent in loan to MCP). *Eleoscytalopus indigoticus*—Brazil: BA: MCP 1728* (S) and 1730* (S); MG: MCP 1859 (S, C), 1860 (S, C), 1861 (S, C), 1862 (S) and 1863 (S), MHNT 1891 (C) and 4826* (C); RJ: MCP 1721* (S); SP: MCP 2044* (S); PR: MCP 1731* (S), 2198 (S), 2199 (S), 2200 (S), 2201 (S), and 2202 (S). *Eleoscytalopus psychopompus*—Brazil: BA: MCP 1722* (S, C) and 1734* (S, C). *Scytalopus speluncae*—Brazil: MG: MCP 1172* (S); SP: MHNT 4356 (C); PR: MCP 1175* (S), 1176* (S), MCP 2039* (S) and 2042* (S); RS: MCP 1169* (S) and 987* (S). *Scytalopus iraiensis*—Brazil: RS: MCP 958* (S). *Scytalopus pachecoi*—Brazil: SC: MCP 1183* (S); RS: MCP 949* (S), 959* (S), 976* (S), 1174* (S) and 1039* (S). *Scytalopus novacapitalis*—Brazil: DF: MCP 1481* (S, C); MG: MCP 1865 (S, C). *Scytalopus diamantinensis*—Brazil: BA: MCP 1896* (S), 1900* (S), 1897* (S) and 1898* (S). *Scytalopus* sp. nov.—Brazil: MG: MCP uncat. 1 (S), uncat. 2 (S), uncat. 3 (S), uncat. 4 (S), MHNT 1883 (C) and 1886 (C). *Scytalopus argentifrons*—Costa Rica: Prov. San José: LSUMZ 135542 (C). *Scytalopus* sp., *magellanicus* species-group—Peru: Dpto. Amazonas: LSUMZ 89971 (C). *Myornis senilis*—Peru: Dpto. Amazonas: LSUMZ 88108 (C) and 84015 (C). *Eugralla paradoxa*—Chile: Región IX: AMNH 24358 (C). GRALLARIIDAE: *Hylopezus ochroleucus*—Brazil: MG: MCP 2036 (S, C). *Hylopezus nattereri*—Brazil: MHNT 1320 (C), 1366 (C) and 1564 (C). CONOPOPHAGIDAE: *Conopophaga lineata*—Brazil: PR: MCP uncat. (S, C); RS: MCP 1521* (S); Brazil: MHNT 1077 (C). *Conopophaga melanops*—Brazil: MHNT 159 (C). FORMICARIIDAE: *Chamaeza campanisona*—Brazil: PR: MCP uncat. (S, C); RS: MCP 175* (S, C). MELANOPAREIIDAE: *Melanopareia torquata*—Brazil: BA: MCP uncat.* (S, C); MG: MCP uncat. (S). THAMNOPHILIDAE: *Taraba major*—Brazil: PR: MCP uncat. (S, C). *Hypoedaleus guttatus*—Brazil: PR: MCP uncat. (S, C). *Thamnophilus ruficapillus*—Brazil: RS: MCP 557* (S). *Thamnophilus caerulescens*—Brazil: PR: MCP uncat. (S); RS: MCP 1820* (S, C). *Mackenziaena leachii*—Brazil: PR: MCP uncat. (S); RS: MCP 028* (S, C). *Sakesphorus cristatus*—Brazil: MG: MCP uncat. (S, C). *Dysithamnus mentalis*—Brazil: PR: MCP uncat. (S, C). *Myrmorchilus strigilatus*—Brazil: MG: MCP uncat. (S, C). *Pyriglena leucoptera*—Brazil: PR: MCP uncat. (S, C). *Drymophila malura*—Brazil: PR: MCP uncat. (S). *Myrmotherula unicolor*—Brazil: PR: MCP uncat. (S, C). *Formicivora rufa*—Brazil: MCP uncat. (S). *Formicivora melanogaster*—Brazil: MG: MCP uncat. (S, C). *Stymphalornis acutirostris*—Brazil: PR: MCP uncat. (S, C). *Herpsilochmus sellowi*—Brazil: MG: MCP uncat. (S, C). *Myrmeciza squamosa*—Brazil: PR: MCP uncat. (S, C). FURNARIIDAE: (SCLERURINAE): *Geositta cunicularia*—Brazil: RS: MCP 1873* (S, C). (FURNARIINAE): *Furnarius rufus*—Brazil: RS: MCP 1058 (S), 1054 (S), 1803 (C) and 708 (C). *Lochmias nematura*—Brazil: RS: MCP 986* (S, C). *Phleocryptes melanops*—Brazil: RS: MCP 1696* (S, C). *Limnornis curvirostris*—Brazil: RS: MCP 1233* (S) and 1594* (C). *Limnoctites rectirostris*—Brazil: RS: MCP 870* (S, C). *Cranioleuca sulphurifera*—Brazil: RS: MCP 775* (S) and 1874 (C). *Cranioleuca* cf. *pyrrhophia*—Brazil: RS: MCP 995* (S, C) and 996* (S). *Synallaxis spixi*—Brazil: RS: MCP 1879* (S). *Schoeniophylax phryganophilus*—Brazil: RS: MCP 1950 (S, C). *Philydor rufum*—Brazil: RS: MCP 1832* (S). *Syndactyla rufosuperciliata*—Brazil: RS: MCP 596* (S, C) and 1385* (S, C). *Xenops rutilans*—Brazil: SC: MCP 1938* (S, C). (DENDROCOLAPTINAE): *Sittasomus griseicapillus*—Brazil: RS: MCP 1949 (S, C). *Lepidocolaptes falcinellus*—Brazil: RS: MCP 1948 (S, C).

Appendix B. Additional skin specimens examined (Rhinocryptidae only)

See Section 2 for the explanation of institution accronyms.

Pteroptochos megapodius—Chile: MZUSP 3807. *Scelorchilus albicollis*—Chile: MZUSP 2075 and 3786. *Scelorchilus rubecula*—Chile: MZUSP 3785. *Rhinocrypta lanceolata*—Argentina: São Luiz: MZUSP 3976. *Eugralla paradoxa*—Chile: MZUSP 3814. *Acropternis orthonyx*—Ecuador: MZUSP 1336 and 62447. *Liosceles thoracicus*—Brazil: MZUSP 61728, 18064 and 18065.

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