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Systematic relationships and biogeography of the tracheophone suboscines (Aves: Passeriformes)

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Abstract

Based on their highly specialized "tracheophone" syrinx, the avian families Furnariidae (ovenbirds), Dendrocolaptidae (woodcreepers), Formicariidae (ground antbirds), Thamnophilidae (typical antbirds), Rhinocryptidae (tapaculos), and Conopophagidae (gnateaters) have long been recognized to constitute a monophyletic group of suboscine passerines. However, the monophyly of these families have been contested and their interrelationships are poorly understood, and this constrains the possibilities for interpreting adaptive tendencies in this very diverse group. In this study we present a higher-level phylogeny and classification for the tracheophone birds based on phylogenetic analyses of sequence data obtained from 32 ingroup taxa. Both mitochondrial (cytochrome *b*) and nuclear genes (c-*myc*, RAG-1, and myoglobin) have been sequenced, and more than 3000 bp were subjected to parsimony and maximum-likelihood analyses. The phylogenetic signals in the mitochondrial and nuclear genes were compared and found to be very similar. The results from the analysis of the combined dataset (all genes, but with transitions at third codon positions in the cytochrome *b* excluded) partly corroborate previous phylogenetic hypotheses, but several novel arrangements were also suggested. Especially interesting is the result that the genus *Melanopareia* represents a basal branch within the tracheophone group, positioned in the phylogenetic tree well away from the typical tapaculos with which it has been supposed to group. Other novel results include the observation that the ground antbirds are paraphyletic and that *Sclerurus* is the sister taxon to an ovenbird–woodcreeper clade. Patterns of generic richness within each clade suggest that the early differentiation of feeble-winged forest groups took place south of the Amazon Basin, while the more recent diversification was near the equator and (in tapaculos and ovenbirds) in the south of the continent.

1. Introduction

The tracheophone suboscines (Furnarioidea *sensu* Wetmore, 1960) include ovenbirds (Furnariidae), woodcreepers (Dendrocolaptidae), ground antbirds (Formicariidae *sensu* Sibley and Ahlquist, 1990), typical antbirds (Thamnophilidae), tapaculos (Rhinocryptidae), and gnateaters (Conopophagidae). Endemic to the Neotropics, this group contains 560 of the known 5712 passerine species (*sensu* Sibley and Monroe, 1990).

The tracheophone group is extraordinarily diverse in its ecological specialization, and it has been suggested that the ovenbird family (Furnariidae) in particular is the most diverse of all bird families in terms of natural history and habitat utilization (Leisler, 1977). This makes the tracheophone suboscines well suited to the study of ecological adaptations and biogeography. It is regrettable, however, that the phylogenetic relationships of major lineages of the group are poorly resolved and that the position of some terminal taxa is questionable. The arrangement of species in families, tribes, and genera, from external morphology, nest types, etc. (e.g., Vaurie, 1971, 1980), is not based on phylogenetic analysis, and the few cladistic studies all concern intrafamily relationships (Raikow, 1994; Rice, 2000; Rudge and Raikow, 1992; Zyskowski and Prum, 1999) or have a limited taxon sample (Irestedt et al., 2001).

The monophyly of this group, as suggested by their common possession of the so-called tracheophone

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syrinx morphology (Ames, 1971; Müller, 1847, 1878; Ridgway, 1911), is supported by molecular data, which also supports a sister group relationship with a clade consisting of all other suboscines in the New World (Irestedt et al., 2001; Johansson et al., in press; Sibley and Ahlquist, 1985, 1990). While a few character states uniquely define particular families or subfamilies, other characters are primitive (e.g., the syrinx) or apparently homoplastic (e.g., the shape of metasternum) (cf. Ames, 1971; Ames et al., 1968; Heimerdinger and Ames, 1967) and therefore poorly suited for resolving the deeper phylogenetic branching. Only the monophyly of an ovenbird–woodcreeper clade is well supported by the presence of two intrinsic muscles in the tracheophone syrinx (Ames, 1971; Ridgway, 1911), DNA–DNA hybridization (Sibley and Ahlquist, 1990), and DNA sequence data (Irestedt et al., 2001). Most authors consider ovenbirds and woodcreepers to constitute monophyletic groups, although the value of the single synapomorphy proposed for the ovenbirds, the pseudoschizorhinal condition of the nasal bone (Garrod, 1873, 1877), has been questioned (Feduccia, 1973; von Ihering, 1915). Feduccia (1973), based on a phenetic analysis of several anatomical and biochemical characters, suggested that the woodcreepers form a highly specialized lineage nested within the Furnariidae and that certain woodcreeper genera could even be more closely related to the so-called philydorine ovenbirds than to the other woodcreepers. However, several morphological synapomorphies support the monophyly of woodcreepers (Ames, 1971; Clench, 1995; Raikow, 1994) and DNA–DNA hybridization data (Sibley and Ahlquist, 1990) suggest that ovenbirds and woodcreepers are sister taxa.

The division of the Formicariidae (*sensu* Wetmore, 1960) into two, possibly unrelated groups of typical antbirds and ground antbirds (including antpittas and antthrushes) is supported by morphology (Ames, 1971; Ames et al., 1968; Heimerdinger and Ames, 1967) in addition to molecular data (Sibley and Ahlquist, 1990). Based on morphology, a close relationship was also suggested between gnateaters and ground antbirds (Ames, 1971; Ames et al., 1968) and between ground antbirds and tapaculos (Feduccia and Olson, 1982; Heimerdinger and Ames, 1967; Rice, 2000). Furthermore, the tapaculos have been found to bear a morphological resemblance to the Australian lyrebirds (*Menura*) and scrubbirds (*Atrichornis*) in the oscine group Menurae (Feduccia and Olson, 1982). Feduccia and Olson also found the enigmatic tapaculo genus *Melanopareia* to be unique within the suboscine assemblage in possessing stapes (ear ossicles) of the oscine type. Thus they suggested "that the Menurae and the Rhinocryptidae are almost certainly the most primitive of the Passeriformes and are representative of the ancestral stock that gave rise to the remainder of the passerines" (Feduccia and Olson, 1982, p. ii). They further suggested that in a linear classification the tracheophone taxa should begin with the most primitive group, the tapaculos, followed by ground antbirds and ending with ovenbirds and woodcreepers. However, undue emphasis may be placed on overall similarities or symplesiomorphies rather than grouping by synapomorphies.

DNA–DNA hybridization data (Sibley and Ahlquist, 1990) indicated a basal dichotomy between typical antbirds and other tracheophone groups and that the latter group in turn is divided into a woodcreeper–ovenbird lineage and a "ground antbird–gnateater–tapaculo" lineage. DNA sequence data (Irestedt et al., 2001) are generally congruent with this, although they suggest that gnateaters may be closer to the typical antbirds than to ground antbirds and tapaculos.

It is the aim of the present study to provide a robust phylogeny for the major groups of tracheophone birds and thereby create a framework for more detailed evolutionary and biogeographic analyses. To achieve this we use DNA sequences obtained from molecular markers with different properties and rates of base substitution. The analysis is based on nucleotide sequences obtained from two protein-coding nuclear genes (c-*myc*, RAG-1), one mitochondrial protein-coding gene (cytochrome *b*), and one nuclear intron (the second in the myoglobin gene). More than 3000 bp have been sequenced for 32 tracheophone taxa.

2. Materials and methods

2.1. Examined taxa and choice of outgroups

Considering the extraordinary diversity of the tracheophone group, we had to select a manageable sample of species, which can represent all traditionally recognized families and groupings suggested by the DNA–DNA hybridization data (Sibley and Ahlquist, 1985, 1990).

The classification used herein is from Wetmore's (1960) with slight modifications: *Corythopis* is excluded from the Conopophagidae, as morphological (Ames et al., 1968) and molecular (Johansson et al., in press; Sibley and Ahlquist, 1985, 1990) data prove that it belongs to the Tyrannoidea. Furthermore, the Formicariidae is divided into ground antbirds (Formicariidae) and typical antbirds (Thamnophilidae) following Sibley and Ahlquist (1985, 1990).

The phylogenetic trees were rooted using the outgroup comparison (Farris, 1972; cf. Nixon and Carpenter, 1993), with four representatives of Tyrannoidea (*Corythopis*, *Elaenia*, *Pipra*, and *Pyroderus*) and three Old World suboscines (*Pitta*, *Philepitta*, and *Smithornis*), based on the current understanding of suboscine

Table 1
Samples used in the study

Species	Family	Voucher No.	c-*myc*	RAG-1	Myoglobin	Cytochrome *b*
Chamaeza meruloides	Formicariidae	ZMCU S2053	AY065691	AY065747	AY065776	AY065718
Formicarius nigricapillus	Formicariidae	ZMCU S1436	AY065692	AY065748	AY065777	AY065719
Grallaria squamigera	Formicariidae	ZMCU S78	AY065693	AY065749	AY065778	AY065720
Hylopezus fulviventris	Formicariidae	ZMCU S1427	AY065694	AY065750	AY065779	AY065721
Cercomacra melanaria	Thamnophilidae	NRM 947099	AY065696	AY065752	AY065781	AY065723
Drymophila squamata	Thamnophilidae	ZMCU S2199	AY065695	AY065751	AY065780	AY065722
Pyriglena leuconota	Thamnophilidae	ZMCU S2007	AY065697	AY065753	AY065782	AY065724
Thamnophilus caerulescens	Thamnophilidae	NRM 967007	AF295180 (Ref. 1)	AF295201 (Ref. 1)	AY065783	AY078176 (Ref. 2)
Melanopareia maximiliani	Rhinocryptidae	ZMCU S494	AY065698	AY065754	AY065785	AY065725
Pteroptochos tarnii	Rhinocryptidae	AMNH RTC467	AY065690	AY065746	AY065774	AY065717
Rhinocrypta lanceolata	Rhinocryptidae	NRM 966793	AF295178 (Ref. 1)	AF295199 (Ref. 1)	AY065775	AY078174 (Ref. 2)
Scytalopus spillmanni	Rhinocryptidae	ZMCU S540	AY065689	AY065745	AY065773	AY065716
Conopophaga aurita	Conopophagidae	ZMCU S 1245			AY065784	
Conopophaga lineata	Conopophagidae	NRM 956653	AF295163 (Ref. 1)	AF295185 (Ref. 1)		AY078173 (Ref. 2)
Dendrocincla fuliginosa	Furnariidae: Dendrocolaptinae	NRM 976662	AY065686	AY065742	AY065770	AY065713
Drymornis bridgesii	Furnariidae: Dendrocolaptinae	NRM 966930	AY065684	AY065740	AY065768	AY065711
Lepidocolaptes angustirostris	Furnariidae: Dendrocolaptinae	NRM 9371 84	AF295168 (Ref. 1)	AF295190 (Ref. 1)	AY065767	AY078175 (Ref. 2)
Sittasomus griseicapillus	Furnariidae: Dendrocolaptinae	NRM 967031	AY065687	AY065743	AY065771	AY065714
Xiphocolaptes major	Furnariidae: Dendrocolaptinae	NRM 966847	AY065685	AY065741	AY065769	AY065712
Anumbius annumbi	Furnariidae: Furnariinae	NRM 966903	AY065682	AY065738	AY065765	AY065709
Asthenes cactorum	Furnariidae: Furnariinae	ZMCUS150	AY065678	AY065734	AY065761	AY065705
Coryphistera alaudina	Furnariidae: Furnariinae	NRM 966910	AY065683	AY065739	AY065766	AY065710
Cranioleuca pyrrhophia	Furnariidae: Furnariinae	NRM 966821	AY065681	AY065736	AY065764	AY065708
Furnarius chstatus	Furnariidae: Furnariinae	NRM 966772	AF295165 (Ref. 1)	AF295187 (Ref. 1)	AY064255 (Ref. 3)	AY064279 (Ref. 3)
Lochmias nematura	Furnariidae: Furnariinae	ZMCU S2577	AY065672	AY065728	AY065755	AY065699
Margarornis squamiger	Furnariidae: Furnariinae	ZMCU S1112	AY065676	AY065732	AY065759	AY065703
Philydor atricapillus	Furnariidae: Furnariinae	NRM 937334	AY065675	AY065731	AY065758	AY065702
Pseudoseisura lophotes	Furnariidae: Furnariinae	NRM 976799	AY065679	AY065735	AY065762	AY065706
Pygarrhichas albogularis	Furnariidae: Furnariinae	AMNH PRS1128	AY065677	AY065733	AY065760	AY065704
Sclerurus scansor	Furnariidae: Furnariinae	NRM 937258	AY065688	AY065744	AY065772	AY065715
Synallaxis ruficapilla	Furnariidae: Furnariinae	NRM 956643	AY065680	AY065737	AY065763	AY065707
Thripadectes flammulatus	Furnariidae: Furnariinae	ZMCU S428	AY065674	AY065730	AY065757	AY065701
Upucerthia jelskii	Furnariidae: Furnariinae	ZMCU S439	AY065673	AY065729	AY065756	AY065700
Philepitta castanea	Philepittidae	ZMCU S458	AF295172 (Ref. 1)	AF295193 (Ref. 1)	AY065790	AY065726
Pitta baudii	Pittidae	ANSP 1224	AF295177 (Ref. 1)	AF295198 (Ref. 1)	AY064762	AY064280 (Ref. 3)
Smithornis rufolateralis	Eurylaimidae	FMNH 391675	AF295179 (Ref. 1)	AF245200 (Ref. 1)	AY065789	AY065727
Pyroderus scutatus	Cotinginae	NRM 967030	AF453789 (Ref. 2)	AF453803 (Ref. 2)	AY065786	AF453820 (Ref. 2)
Pipra fasdicauda	Piprinae	NRM 947271	AF295175 (Ref. 1)	AF295196 (Ref. 1)	AY065787	AF153817 (Ref. 2)
Corythopsis delalandi	Pipromorphinae	NRM 937282	AF453779 (Ref. 2)	AF453792 (Ref. 2)	AY065788	AF453805 (Ref. 2)
Elaenia flavogaster	Tyranninae	NRM 966970	AF377279	AF453794 (Ref. 2)	AY064254 (Ref. 3)	AF453807 (Ref. 2)

Note. Family and subfamily names follow the classification of Sibley and Monroe (1990). Dendrocolaptinae and Furnariinae are subfamilies of the Furnaridae in that classification, while Cotinginae, Piprinae, Pipromorphinae, and Tyranninae all are placed in the Tyrannidae. Abbreviations: AHMN, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; FMNH, Field Museum of Natural History, Chicago; NRM, Swedish Museum of Natural History; ZMCU, Zoological Museum of the University of Copenhagen. References: (1) Irestedt et al. (2001); (2) Johansson et al. (in press); (3) Ericson et al. (in press).

relationships (Ames, 1971; Ericson et al., 2002; Irestedt et al., 2001; Sibley and Ahlquist, 1990). Sample identifications and GenBank accession numbers are given in Table 1.

2.2. Extraction, amplification, and sequencing

Extraction, amplification, and sequencing procedures for c-*myc* and RAG-1 follow those described by Groth and Barrowclough (1999), Ericson et al. (2000), Irestedt et al. (2001), and Johansson et al. (2001). A similar protocol was also followed for the amplification and sequencing of the cytochrome *b* gene. Initially, approximately 1000 bp of this gene were amplified as a single fragment with either of the primer pairs L14841 (Kocher et al., 1989) and H15915 (Edwards and Wilson, 1990) or L14841 and Thr 1 (5′-TCT TTG GCT TAC AAG ACC AA-3′). The thermocycling conditions included an initial denaturation at 94 °C for 5 min, followed by 40 cycles of 94 °C for 40 s, 49 °C for 40 s, and 72 °C for 1 min and was completed with a final extension at 72 °C for 5 min. For the sequencing reactions the following primers were used: L14841, P5L (5′-CCT TCC TCC ACG AAA CAG GCT CAA ACA ACC C-3′), H658 (5′-TCT TTG ATG GAG TAG TAG GGG TGG AAT GG-3′), and H15915 or Thr 1, with P5L and H658 as internal primers on the light and heavy strands, respectively.

The myoglobin intron 2 was amplified with the primer pairs Myo 2 and Myo 3f (Heslewood et al., 1998; Slade et al., 1993) positioned in exons two and three, respectively. The thermocycling conditions in these amplifications were a hot start at 94 °C for 5 min, followed by 40 cycles of 94 °C for 40 s, 55 °C for 40 s, and 72 °C for 1 min and was completed with a final extension at 72 °C for 5 min. For the sequence reactions the following primers were used: Myo 2, Myo 3f, Myoint.c (5′-AGC CCT GGA GGA TCC ATT GG-3′), Myoint.nc (5′-CCA ATG GAT CCT CCA GGG CT-3′), Myoint.H1 (5′-TGA CAG GTC TTA TGT AAT ATA G-3′), Myoint.H2 (5′-TCT AAA CTT GGA TAT TCA CAT-3′), and Myoint.L1 (5′-CTA TAT TAC ATA AGA CCT GTC A-3′).

The sequencing procedures for the myoglobin intron and cytochrome *b* were similar to those used for c-*myc* and RAG-1.

2.3. Alignment and sequence properties

For each gene and taxon, multiple sequence fragments were obtained by sequencing with different primers. They were assembled to complete sequences with SeqManII (DNASTAR). Positions where the nucleotide could not be determined with certainty were coded with the appropriate IUPAC code. No insertions or deletions or start, stop, or nonsense codons were observed in any of the protein-coding genes.

The lengths of the combined sequences varied between 3083 and 3393 bp. We obtained 477 bp from exon 3 of the c-*myc* gene (corresponding to positions 759–1235 in the published chicken sequence, Watson et al., 1983) and 930 bp from RAG-1 (corresponding to positions 1054–1983 in the chicken sequence, Carlson et al., 1991). From the mitochondrial cytochrome *b* gene, 999 bp were used in the analyses (corresponding to positions 15,037–16,035 in the chicken mitochondrial genome sequence, Desjardins and Morais, 1990). The entire intron 2 (of varying length) of the nuclear myoglobin gene corresponding to the region between positions 303 (exon 2) and 400 (exon 3) of the humans was sequenced (GenBank Accession No. XM009949).

The combined sequences were aligned by eye in MegAlign (DNASTAR). Also the sequences from the noncoding myoglobin intron could be aligned easily thanks to the rather low number of insertions and deletions. In a few regions, where the homology of positions in the myoglobin intron could not be fully determined, alignments slightly different from that preferred in the analysis could be produced. Different myoglobin alignments were tried to estimate their influence upon the phylogenetic results. The preferred alignment of the myoglobin intron 2 sequences is deposited in GenBank.

Statistics for nucleotide variation were computed with Mega 1.0 (Kumar et al., 1993).

2.4. Phylogenetic analyses and weighting of characters

Parsimony and maximum-likelihood analyses were performed using Paup* 4.0b8 (Swofford, 1998). Searches for the most parsimonious trees were performed under the heuristic search option with all characters coded as unordered. To reduce the risk of finding local optima only, all analyses were performed with 10 random additions of taxa. The phylogenetic hypotheses are presented by a strict consensus tree (calculated from all the most parsimonious trees obtained) with bootstrap support values exceeding 50% indicated on the nodes, along with decay values (Bremer, 1988, 1994) computed with TreeRot v.2 (Sorenson, 1999). The bootstrap support values were calculated from 1000 replicates.

It has been shown that the regions of the c-*myc* and RAG-1 genes analyzed herein are not saturated at the levels of sequence divergence observed in the present dataset (Irestedt et al., 2001). The degree of saturation in the cytochrome *b* dataset was investigated by plotting the number of transition and transversion substitutions against pairwise genetic distances calculated for the combined c-*myc* and RAG-1 sequences. The analysis showed a nonlinear correlation between the axes for the third codon positions, indicating that the cytochrome *b* genes are saturated for the most distantly related taxa (Fig. 1). The cytochrome *b* dataset was included in the

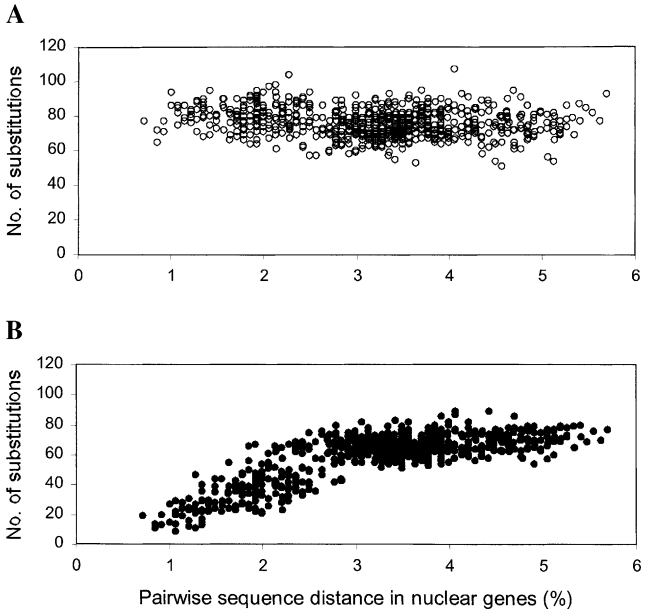

Fig. 1. The observed number of transitions (A) and transversions (B) at third codon positions in the cytochrome *b* gene, plotted against the pairwise sequence divergences calculated for the combined c-*myc* and RAG-1 genes. The observation that the number of substitutions seems to be uncorrelated with pairwise sequence distances suggests saturation of third position transitions.

parsimony analyses both with all codon positions weighted equally (called the "unweighted" dataset) and with transitions at third codon positions excluded ("weighted"). The rationale is the observation of an increased phylogenetic signal to "noise" (i.e., homoplasy) ratio after the removal of the saturated portions of some datasets (e.g., Groth, 1998; but see Källersjö et al., 1999 for another opinion).

Parsimony analyses were performed for all genes separately, for a dataset consisting of all nuclear genes (c-*myc*, RAG-1, and myoglobin), and for a dataset with all four genes included (but with transitions at third codon positions in the cytochrome *b* gene excluded). All positions of the myoglobin intron 2 alignment, including indels, were thus used in the phylogenetic analyses, with gaps treated as missing values. To investigate the influence of indels upon the phylogenetic results, tests were also made by replacing each indel with one extra character in the parsimony analyses.

The maximum-likelihood analysis of the combined dataset was performed with the general time-reversal model (GTR). The general time-reversal model was selected with the likelihood-ratio test implemented in MODELTEST 3.06 (Posada and Crandall, 1998). A discrete gamma model (four rate categories) was used where the gamma parameters were initially estimated from a neighbor-joining tree. These estimates were then used with the empirical base frequencies in a heuristic search with TBR branch-swapping. From the resulting tree, the gamma parameters, proportion of invariable sites, and substitution rate parameters were again estimated and a new heuristic search with TBR branch-swapping was performed. A final estimate of the parameters was done and used in a final heuristic search.

3. Results

3.1. Alignments, indels, and their influence upon the phylogenetic results

Several indels were found in the noncoding myoglobin intron 2. In all taxa, except *Hylopezus* (987 bp) and *Corythopis* (753 bp), the myoglobin intron 2 length range between 677 and 722 bp. The considerably longer sequence of *Hylopezus* is due primarily to the occurrence of a single, autapomorphic insertion of more than 250 bp.

Analyses of alternative alignments of the myoglobin intron 2 did not result in different tree topologies. The discussion of indels observed in the myoglobin sequences thus refer to the alignment chosen for the analysis (see Section 2). Most indels in this alignment are autapomorphies. Of the phylogenetically informative indels, the majority are shared between taxa that are monophyletic according to our phylogenetic analysis. For example, all woodcreepers share a deletion of 12 bp, and the woodcreeper–ovenbird clade (including *Sclerurus*) shares a deletion of approximately 29 bp. However, some indels are also shared by taxa that are not closely related according to our results, e.g., *Melanopareia* and *Pitta* (a deletion of 11 bp) and *Sclerurus* and *Rhinocrypta* (a deletion of 4 bp).

All gaps in the sequences were treated as missing data by the phylogenetic analyses, and the indels thus had no influence upon the results. As an alternative strategy, the indels were replaced with an extra, single character each in the analyses. This did not alter the topologies of the phylogenetic trees obtained and it affected nodal support values only marginally.

3.2. Phylogenetic analysis

The parsimony analyses of the individual genes resulted in phylogenetic trees that differ considerably in their resolution and number of supported nodes. The largest number of supported nodes were obtained in the analysis of the myoglobin dataset and that of the weighted cytochrome *b* dataset. Largely unresolved trees were obtained in the individual analyses of the genes RAG-1, c-*myc*, and cytochrome *b* (unweighted). The latter dataset also produced some unexpected topologies of the deeper nodes, e.g., a 55% bootstrap support for combining the tracheophones with the Old World suboscines. For comparison, the analysis of the weighted cytochrome *b* dataset resulted in a tree topology almost

congruent with that obtained in the analysis of all nuclear genes combined (Fig. 2). No nodes in the weighted cytochrome *b* tree with a bootstrap support higher than 50% are in conflict with the topology of the tree based on all nuclear genes.

We focus here on the results from the analysis of the combined dataset with transitions at third codon positions of the cytochrome *b* excluded due to saturation. The parsimony analysis resulted in five most parsimonious trees (length = 2872 steps, CI = 0.45, RI = 0.54), from which a strict consensus tree (Fig. 3) was calculated.

Monophyly of the ingroup is strongly supported by the bootstrap analysis (98%), but only low boostrap values are obtained for the basalmost divergencies: the

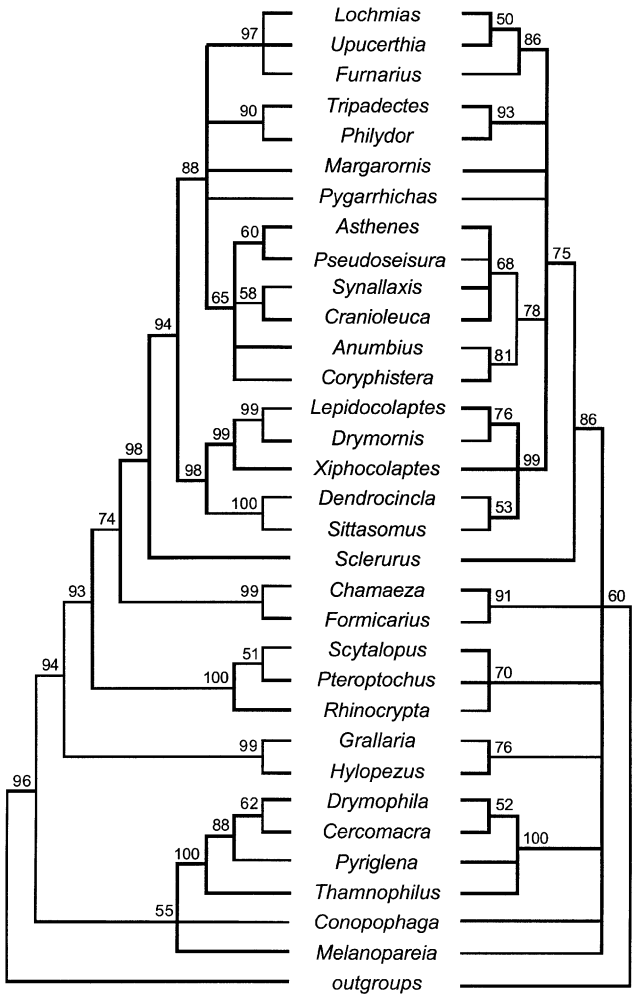

Fig. 2. Strict consensus trees. The nuclear tree (left), based on aligned sequences from RAG-1, c-*myc*, and myoglobin intron 2, is calculated from the 52 most parsimonious trees (length = 1337 steps, CI = 0.646, RI = 0.668). The mitochondrial tree (right) is based on aligned cytochrome *b* sequences with transition at third codon positions excluded. It is calculated from one most parsimonious tree (length = 1531 steps, CI = 0.274, RI = 0.447). At the nodes in both trees, bootstrap supports above 50% are indicated.

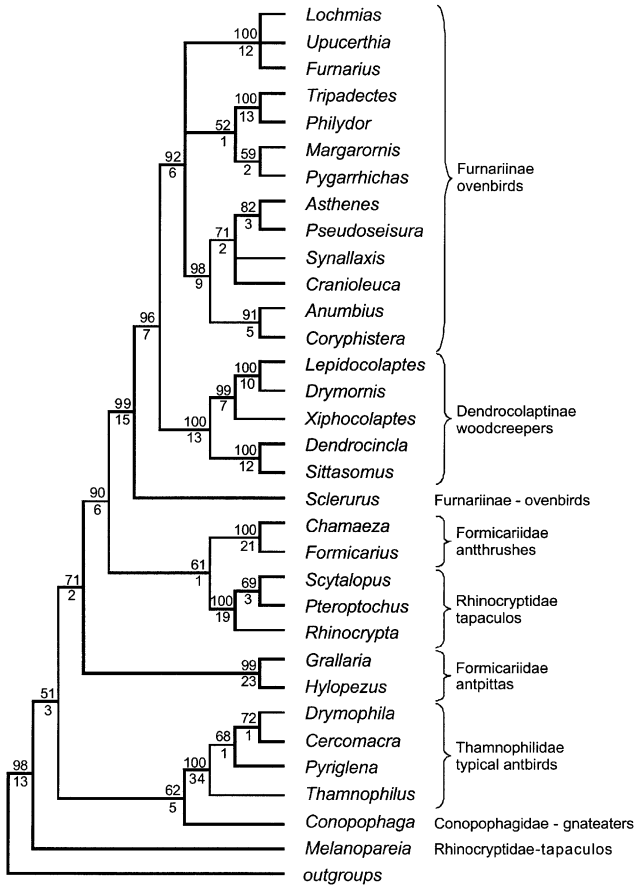

Fig. 3. Strict consensus tree calculated from the five most parsimonious trees (length = 2872 steps, CI = 0.45, RI = 0.54) obtained from the analyses of the weighted combined dataset (RAG-1, c-*myc*, myoglobin intron 2, and cytochrome *b*) with transitions at third codon positions in cytochrome *b* excluded. Bootstrap support values (if more than 50%) are indicated above the nodes, with decay values below. Family and subfamily names follow Sibley and Monroe (1990).

sister group relationship between *Melanopareia* and all other tracheophone birds receives only a 51% support. The separation of *Melanopareia* and other tapaculos is prominent, however. Other results, which differ significantly from traditional taxonomy, are the position of the gnateater genus *Conopophaga* near the typical antbirds, albeit with only 62% bootstrap support, a strong support for separating antpittas (*Grallaria*, *Hylopezus*) and antthrushes (*Chamaeza*, *Formicarius*), and a basal position of *Sclerurus* in relation to the ovenbird and woodcreeper lineages.

The monophyly of the tracheophones (98%) and a woodcreeper–ovenbird clade, including *Sclerurus* (99%), are strongly supported by bootstrap values. Strong supports are also given for a woodcreeper–ovenbird lineage, excluding *Sclerurus* (96%), and, within this clade, for both the ovenbirds (92%) and the woodcreepers (100%).

The ovenbird clade is partly unresolved, consisting of a trichotomy of three major clades. The first clade in-

cludes *Margarornis*, *Pygarrhichas*, *Thripadectes*, and *Philydor* (52% bootstrap support), and, within this clade, sister taxon relationships between *Philydor* and *Thripadectes* (100%) and between *Margarornis* and *Pygarrhichas* (59%) are suggested. A second major ovenbird lineage includes *Lochmias*, *Upucerthia*, and *Furnarius* (100%), although the relationships among these taxa are unresolved. The third clade (receiving 98% bootstrap support) includes two lineages that both receive bootstrap support: *Anumbius* and *Coryphistera* (91%), and *Asthenes*, *Pseudoseisura*, *Cranioleuca*, and *Synallaxis* (71%). A sister relationship between *Asthenes*, and *Pseudoseisura* (82%) is recognized within this latter lineage. The woodcreeper lineage includes two major clades. The first includes *Dendrocincla* as sister to *Sittasomus* (100%), and the other includes *Lepidocolaptes* sister to *Drymornis* (99%) and *Xiphocolaptes* forming the sister taxon (100%).

The parsimony analysis of the weighted, combined dataset further suggests that the tapaculos (*Pteroptochos*, *Rhinocrypta*, and *Scytalopus*) are the sister taxon to the antthrushes (*Chamaeza* and *Formicarius*; 61%) and form the sister group to the ovenbird–woodcreeper clade (90%). Monophyly of both antthrushes and tapaculos is also confirmed (100% in both cases). Within the tapaculo lineage, *Scytalopus* and *Pteroptochos* are most closely related (69%). It is further suggested that the antpittas (*Grallaria* and *Hylopezus*, 99%) are the sister group to the ovenbird–woodcreeper–tapaculo–antthrush lineage (71%). Monophyly of the typical antbirds is strongly supported (100%). Within this lineage, *Drymophila* and *Cercomacra* are suggested to be sister taxa (72%), with *Pyriglena* as their closest relative (68%). The gnateater genus, *Conopophaga*, forms the sister lineage to the typical antbirds included in this analysis.

The maximum-likelihood tree calculated from the combined dataset is essentially congruent with that obtained from the parsimony analysis (Fig. 3). However, the maximum-likelihood tree differs from this (and agrees with the parsimony analysis of the combined nuclear dataset) in the recognition of antthrushes and tapaculos as separate lineages within the ovenbird–woodcreeper–tapaculo–antthrush lineage. It also differs in the generic topology within the typical antbirds by placing *Drymophila* as sister to *Pyriglena* and *Cercomacra*. All other supported nodes in the parsimony analysis of the weighted, combined dataset are also recognized by the maximum-likelihood analysis.

4. Discussion

Overall, our analysis results in well-resolved phylogenies, with very similar topologies according to parsimony and maximum-likelihood analyses. We will discuss here the discrepancies with other phylogenetic hypothesis and their underlying characters and thereafter some biogeographic implications of this phylogeny. Finally, a classification which reflects the phylogenetic relationships will be presented.

4.1. Phylogenetic relationships: deeper branches

Our phylogeny resembles that from DNA–DNA hybridization data (Sibley and Ahlquist, 1985, 1990) in many respects, with a basal position for typical antbirds (Sibley and Ahlquist, op. cit., did not include *Melanopareia*). The subsequent deep nodes, with ground antbirds (including antpittas and antthrushes), tapaculos, gnateaters, and ovenbirds/woodcreepers, are not congruent with ours, but they are densely packed ($T_{50}H$ 10.7–13.8). In a reanalysis (Harshman, 1994), these nodes have been shown to be unresolvable using the DNA–DNA hybridization data. Also, the depths of the nodes between the two antthrush genera (*Chamaeza* and *Formicarius*; $T_{50}H$ 9.9) and between the tapaculos (*Pteroptochos* and *Scytalopus*/*Liosceli*s; $T_{50}H$ 9.6) are in agreement with an explosive mid-Tertiary radiation with densely packed nodes. Our generally high bootstrap values suggest that a robust resolution has nevertheless been achieved for most parts of the tree.

Melanopareia represents a very deep branch, which may be basal to all other tracheophones. However, the bootstrap support is not strong, and some of the partial datasets result in unresolved trees or a basal position near typical antbirds and gnateaters. *Melanopareia* was placed with the tapaculos by Wetmore (1926), but the evidence that he provided is indeed weak, and it differs from other tapaculos in its straight humerus, rather long tail, pterylography, and boldly patterned plumage, with white interscapular patch, shared with some typical antbirds.

A basal position for *Melanopareia* was suggested already by Feduccia and Olson (1982), based first of all on its oscine-like stapes (Ames et al., 1968; Feduccia, 1974). However, as they assumed Melanopareia to be a tapaculo, the discussion became confused by the demonstration of numerous other similarities between tapaculos and Australian scrub-birds and lyrebirds, which could be specialized traits associated with a similar (near-flightless) life in dense vegetation cover (Bock and Clench, 1985). According to Fig. 3, the "true" tapaculos are far from basal in the Furnarioidea, but Ericson et al. (2002) provides molecular evidence for a basal position of the Menurae among oscines. While we support that *Melanopareia* is basal—within the tracheophones—we do not think that a specific phylogenetic branching sequence can be deduced from shared primitive characters.

Based on bioaccoustic data (Ridgely and Tudor, 1994; N. Krabbe unpublished sonograms) and mor-

phology, we also suggest that the monotypic genus *Teledromas* (not included in our analysis) represents a robust, pale, and desert-adapted relative of *Melanopareia*. The two are similar in general shape and differ from other tapaculos in shape, details of the nasal operculum and tarsal scutellation, pterylography, and shape of the humerus (X-ray photos of study skins). Unfortunately the condition of the stapes could not be assessed from the only spirit specimen of *Teledromas* that exists (S.L. Olson, pers. comm.).

In Fig. 3, gnateaters (*Conopophaga* and *Pittasoma*, according to Rice (2000)) are placed as a sister group to typical antbirds. The buffy and diffusely spotted eggs in gnateaters and typical antbirds (and *Melanopareia*) (Schönwetter, 1979) may be an indication of their close relationship. Variably spotted eggs are also seen in the antpitta genus *Grallaricula*, while other antpittas mostly have uniform blue-green eggs, and antthrushes and tapaculos have white eggs, like ovenbirds (Schönwetter, 1979). On the other hand, the proximity of gnateaters and typical antbirds disagrees with earlier interpretations of syrinx muscles and the four-notched condition of the sternum, which place gnateaters with the ground antbirds and tapaculos, including *Melanopareia* (Ames et al., 1968; Ames, 1971). The sternum morphology may not, however, be a particularly reliable systematic character within this group, as many ground antbirds (*Chamaeza*, most *Formicarius*, and most *Grallaria* spp.) have a two-notched sternum (Heimerdinger and Ames, 1967).

According to Fig. 3, antshrikes (exemplified in our analysis by *Thamnophilus*) are basal to the other typical antbirds included in our analysis. However, a good understanding of phylogenetic branching among the smaller antbirds (bare-eyes, antwrens, etc.) requires a much broader taxonomic sampling.

We found good support for separating antpittas from antthrushes. Instead antthrushes–tapaculos are associated with ovenbirds–woodcreepers, as also suggested by Rice (2000). Morphological differences between antpittas and antthrushes are poorly known and a closer analysis is clearly needed. However, the separation makes sense if we consider locomotion (antpittas/gnateaters jumping and using similar jerking movements; antthrushes and tapaculos running, with horizontal body and often cocking their tail). Garrod (1877) mentions that the syrinx of the antthrush *Chamaeza* is very similar to that of the tapaculo *Pteroptochos*. Partial phylogenies of antpittas (with *Hylopezus*, *Myrmothera*, and *Grallaricula* being sister to the large and heterogeneous genus *Grallaria*) are published by Krabbe et al. (1999) and Rice (2000).

Among the tapaculos, the large *Rhinocrypta* is basal to the large *Pteroptochos* and the small *Scytalopus*. Sibley and Ahlquist (1985, 1990) had the medium-sized *Lioscelis* between *Pteroptochos* and two *Scytalopus* spp.; so there is good evidence for regarding the large (austral) tapaculos as basal to the radiation of small sooty-gray forms (*Merulaxis*, *Eugralla*, *Myiornis* and *Scytalopus*). *Psiloramphus* is highly aberrant, but several morphological details suggests that it is a tapaculo (Plótnick, 1958; S.L. Olson, pers. comm.).

4.2. Phylogenetic relationships of ovenbirds and woodcreepers

The phylogeny robustly places *Sclerurus* basally within the Furnariidae, below the split between woodcreepers and remaining ovenbirds. Sibley and Ahlquist (1985, 1990) found a sister group relationship between woodcreepers and ovenbirds but placed *Sclerurus* basally among ovenbirds. While a unique pterylographic character (Clench, 1995) can define woodcreepers, the characters defining ovenbirds may be primitive (lack of horns on *processi vocales* and pseudoschizorhinal skull) and none are shared by all furnarids (Ames, 1971; Feduccia, 1973). *Sclerurus* has traditionally been placed near *Automolus* (and *Lochmias*) among the philydorine ovenbirds, and it is pseudoschizorhinal, but it also has an almost four-notched sternum and pale and flabby breast muscles (S.L. Olson, pers. comm.), like more basal tracheophones. Although they forage as terrestrial "leaftossers", these birds have stiff and very sharp tail tips, which provide support when they briefly cling to tree trunks when alarmed (Skutch, 1969). Since projecting stiff tail tips are shared by *Sclerurus*, woodcreepers, and various taxa in all main clades of ovenbirds, we suggest that this represents a derived character for the family, which was modified—or lost—in a number of terminal branches and strongly developed for support during climbing only in woodcreepers and *Pygarrhicas*.

The phylogeny of woodcreepers is in good agreement with the DNA–DNA hybridization data (Sibley and Ahlquist, 1990) and with the interpretation of Feduccia (1973), but diverges strongly from a phylogeny based on musculature of the hind limb and bill morphology (Raikow, 1993, 1994). We suggest that the great variability in substrates used by these scansorial birds leads to accumulation of selectively neutral alleles that cause great variability in development expression and great plasticity (Bledsoe et al., 1997), making it difficult to use morphological characters associated with feeding and climbing for phylogenetic analysis.

The phylogeny of true ovenbirds (Furnariinae excl. *Sclerurus*) is not completely resolved, as the three main groups form a trichotomy, with a rather low support to the philydorine branch (represented by *Tripadectes*, *Philydor*, *Margarornis*, and *Pygarrhichas* in the analyses). However, the tree provides clear answers to some of the controversies in the literature and identifies several misjudgments in the classification by Vaurie (1971, 1980).

Lochmias clearly is related to *Upucerthia* (and therefore also to *Cinclodes*, which was not included in our dataset). Like *Lochmias*, *Cinclodes* often lives along streams. A placement near *Furnarius*—in the same tribe—was suggested by Sclater (1890), but Hellmayr (1925) moved it to the Sclerurinae, and it remained near *Sclerurus* in Vaurie's (1971, 1980) Philydorinae, based on general similarity, "pearly" pattern on the breast, tail spines, and nest structure. However, very uniform dark colors, indications of scaled pectoral pattern, and tail spines are variously expressed also in *Cinclodes*. Thus, the Furnariini should be expanded (from Vaurie, 1980) to include *Lochmias* (and *Eremobius*; Fjeldså and Krabbe, 1990; Ridgely and Tudor, 1994).

The phylogeny robustly places *Pseudoseisura* among the Synallaxini, near *Asthenes* (and therefore also *Tripophaga* and *Phacellodomus*, which were not included in our dataset). These large, noisy savanna birds of somewhat jay-like appearance have been difficult to place. According to Vaurie (1971, 1980) they "seem to belong to the Philydorinae," but their huge stick nests resemble those of *Asthenes* and *Phacellodomus*. Apart from the transfer of this genus, the synallaxines can probably be maintained as in Vaurie's classification. The terrestrial *Anumbius* and *Coryphistera* are basal within the group, but more detailed data are needed to work out the further branching pattern to delimit large genera such as *Synallaxis* and *Cranioleuca* and to precisely place aberrant forms (*Acrobatornis*, *Limnornis*, *Metopothrix*, *Phleocryptes*, *Spartonoica*, *Sylviorthorhynchus*, *Tripophaga*, and *Xenerpestes*).

More detailed data are needed to fully resolve the relationship of the Philydorini and its internal branches. *Pygarrhichas*, a distinctive scansorial bird of the Patagonian forests, had no clear relatives according to Vaurie (1971, 1980), as the woodcreeper-like spike-like tail tips and pseudoschizorhinal condition provide conflicting evidence. Our analysis confidently places it with *Margarornis*, another genus previously associated with woodcreepers, and our data provide some bootstrap support to Vaurie's decision to place it (and the genera *Premnornis*, *Premnoplex*, and *Roraimia*) in the Philydorini. However, judging from the bootstrap values and the maximum-likelihood tree, the *Pygarrhichas–Margarornis* line may represent a very early lineage among ovenbirds. The core group of philydorines comprises *Philydor–Anabacerthia–Automolus–Hylocryptes*, probably with *Pseudocolaptes* and *Berlepschia*, and *Thripadectes*. Our data do not permit us to place *Xenops* and *Megaxenops*.

Our ovenbird phylogeny is only partly congruent with trees based on nest architecture characters (Zyskowski and Prum, 1999), although it holds true that complex domed vegetative structures characterize the synallaxines and the *Margarornis* group. The nest type variation may depend very much on the availability of sites for cavity nesting (probably the primitive condition) and material available in each particular habitat. Nest characters are also subject to interpretations. For instance, Zyskowski and Prum (1999) grouped the globular nest of *Lochmias*, placed in a tunnel in a bank, with the globular nests of some Synallaxini rather than with the cup-shaped nests placed in tunnels and other cavities in Furnariini.

4.3. Biogeography

Emerging patterns of early passerine evolution suggest a southern (Gondwanan) origin (Boles, 1995, 1997; Raikow and Bledsoe, 2000). Ericson et al. (2002) provides molecular evidence for an early separation of east Gondwanan oscines (with an early radiation in Australia) and west Gondwanan suboscines, the latter dividing into pittas, broadbills, and asities in Africa and southeast Asia, and Tyrannides (Tyrannoidea and Furnarioidea) in the Neotropics. This means that the South American groups could well have originated in the far south of that continent, or even on Antarctica, which had a pleasant climate up until the early Miocene (Kennett, 1995).

Today, tracheophones and tyrannoids both show an overwhelming dominance near the equator, in the upper and central Amazon basin (Fig. 4B), which gives rise to two diverging interpretations: (1) these groups originated in the south but gradually became concentrated in the intertropical convergence zone as environmental conditions changed, leaving only some relict forms in the forests of Patagonia, or (2) early specializations to the dark under story of humid forest restricted them to tropical environments at an early stage of diversification, while adaptations to the harsh conditions in the far south took place later and in some lineages only.

It is not a trivial matter to analyze this problem. Despite advances in analytic biogeography, the information that can be derived from studying area relationships is often blurred by the large amount of ecological disturbance and the dynamic nature of distributions. In view of the drastic changes in the global climate (e.g., Kennett, 1995), the complex processes of mountain building in the Andes region (and consequent aridification of Patagonia east of the Andes), and the extensive marine incursions in the lowlands (e.g., Räsänen et al., 1995; Uliana and Biddle, 1988) there was ample opportunity for adaptive redistribution since the early diversification of tracheophone lineages. Thus, the combined species richness pattern (Fig. 4B) is extremely similar to that for all South American nonmarine birds, which can to a large extent be explained from contemporary climate and coarse-scale topographic heterogeneity (Rahbek and Graves, 2001) and which may also be constrained by the geometry of the continent (cf. Jetz and Rahbek, 2001). Current ecology and topography will, together with the mid-domain effect, cause waxing

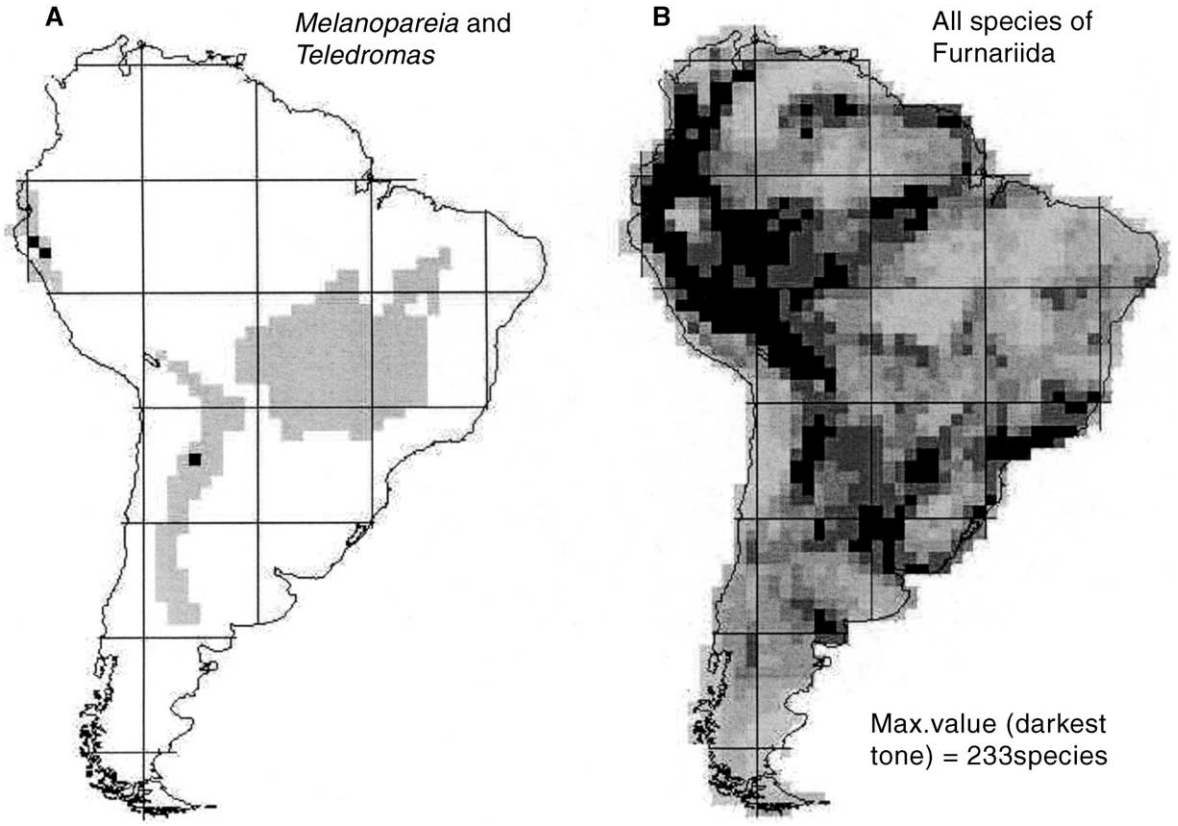

Fig. 4. Species richness patterns of tracheophone suboscines, from databases of South American bird distributions (see Fjeldså and Rahbek, 1997 and Rahbek and Graves, 2001 for details). (A) Assumed deep branch: *Melanopareia* and *Teledromas*; (B) species richness for all Furnariida (*sensu* the present study). This pattern is almost identical to the pattern for all resident South American land birds (Rahbek and Graves, 2001) except for slightly higher species richness in the zones of geological uplift in the Inambari and Napó areas of the western Amazon basin and in northern Argentina.

of species richness near the equator and waning in the southern cone of the continent, irrespective of where the different groups originated.

Melanopareia–Teledromas (Fig. 4A) inhabits bushy semidesert and savanna-like habitats along an eastern Brazilian–Andean track (da Silva, 1995) south to Río Negro in Patagonia. Being absent from the arid zones north of the equator, it could well be austral by origin. However, all other groups overlap broadly in the tropical and subtropical forest biomes and therefore do not provide much historical information. In general, these birds are feeble-winged inhabitants of the interior of dense evergreen vegetation, so it is possible that the early stages of diversification involved birds already adapted to vegetation types that exist only on low latitudes. Only tapaculos and furnarines (which have relatively terminal positions in Figs. 2 and 3) are present in the south of the continent.

The question of where these groups originated could possibly be illuminated by examining patterns of generic distributions. Generic maps were therefore assembled from a database of species distributions in South America (Fjeldså and Rahbek, 1997). This information is presented in a simplified form in Table 2.

The antshrikes, which represent the deepest branch among typical antbirds (Fig. 3), are most diverse and unique (with three endemic genera, *Biatas*, *Mackenziana*, and *Hypodaleus*) in the Brazilian Atlantic forest, while the smaller (advanced) antbirds are much more Amazon-centered (Table 2). The distribution of the gnateaters falls inside areas with many antshrike genera. Antpitta (*Grallaria* and *Hylopezus* in Fig. 3) diversity and uniqueness (with four endemic species groups) peak in the humid tropical Andes region (Table 2). This could indicate that the early differentiation of forest-adapted tracheophones happened south of the Amazon Basin, in the Brazilian Atlantic forests, humid Chaco, and the mountain ranges that built up from the mid-Tertiary along the eastern edge of the Altiplano.

The tapaculos diverged after colonization of the Patagonian part of the Andes. We suggest that this dispersal and isolation of the large austral tapaculos was followed by northward dispersal—and proliferation—of small sooty-gray forms along the eastern Brazilian Andean track (*Eugralla*, *Scytalopus*, *Myiornis*, *Merulaxis*, and possibly also *Psilorhamphus*). Such small forms even reached Central America and, across the Proto-Antillean plate (once an extensive land area, separated by the

Table 2
Number of genera represented in different biogeographic regions (endemic genera in parentheses)

	Melanopareia and *Teledromas*	Gnatcatchers	Antshrikes	Other antbirds	Antpittas	Tapaculos	Antthrushes and *Sclerurus*	Wood creepers	Ovenbirds
Chocó–Central America		1	1 (1)	16 (1)	1	1	2	9	13
Savannas and dry forests in the North			3	9			2	8	5
Amazonia: Inambari to Guiana			7 (1)	24 (2)	3 (1)	1 (1)	3	12	15 (2)
Amazonia: Rondo–Para–Belem			7	23 (1)	2		2	11	12
Tropical Andes	1	1	5	12	6 (4)	3 (1)	3	8	28 (5)
Brazilian Atlantic forest	[b]	1[a]	7 (3)	10 (1)	2	3 (2)	3	8	24 (5)
Cerrado and humid chaco	1	1	4	5	1	2	1	8 (1)	24 (4)
Southern Cone	2 (1)					5 (3)		[b]	18 (5)

Note. For the antpittas, generic rank was used for five species groups of *Grallaria*, two of *Hylopezus*, and two of *Grallaricula* (Ridgely and Tudor, 1994). The Amazon Basin is much larger than the other regions and was therefore divided into two parts (the western/northern Inambari–Napó–Imeri–Guiana region and the southeastern Rondonia–Pará–Belém region) according to biogeographic subdivision that is supported by most studies of area relationships in the region (Bates et al., 1998).

[a] *Conopophaga melanops*, sympatics with *C. lineata*, is very different and somewhat *Pittasoma*-like.

[b] Enters zone marginally.

narrow Cayman Trench from the Greater Antilles; see Taylor, 1995), it reached Cuba (Olson and Kurochkin, 1987; S.L. Olson, pers. comm.).

Antthrushes (*Chamaeza*, *Formicarius*), *Sclerurus*, and woodcreepers (including the four "primitive" genera *Dendrocincla*, *Sittasomus*, *Glyphorynchus*, and *Deconychura*) are very uniformly distributed across the tropical and subtropical forest biomes of the Neotropics. The antthrush genus *Chamaeza* mainly follows the Circum-Amazonian Track, with a very complex diversification pattern, and woodcreepers are relatively better represented than the other groups in the Meridional deciduous forests.

True ovenbirds have a high generic richness along the Andes and in the humid chaco in the southern part of the eastern Brazilian region and may have successfully proliferated in the southern cone of the continent. The generic richness actually peaks in the tropical Andes region, but since only two lineages (represented by *Margarornis* and *Cranioleuca* in the phylogeny) have endemic tropical Andean genera, it seems that overall this family radiated in the Meridional region and southern Andes and dispersed north along the mountain range. This follows Chapman's (1926) interpretation of the origin of the páramo avifauna. It should be noted that the deepest synallaxine branch, with *Anumbius* and *Coryphistera*, is Meridional (humid chaco to northern Patagonia). Only the philydorines successfully colonized the Amazon rainforest, and a few synallaxine lines (*Cranioleuca* and *Synallaxis* s.l.) have colonized second growth, marsh, and riverine vegetation in the tropical lowlands.

These patterns suggest that, despite the enormous species richness of tracheophones in the upper Amazon Basin, the early diversification of feeble-winged forest groups took place further south, probably in the Meridional or eastern Brazilian regions (viz., in the relatively species rich parts of northern Argentina and southern Brazil in Fig. 4B). The Amazonian proliferations therefore came later, as did the evolution of tapaculos (dispersal from the Patagonian Andes) and the large Meridional/Andean proliferation of ovenbirds. The lack of representatives of deep tracheophone lineages in the Patagonian forests is strange, considering the dominance by Gondwanan plant families. Either the tracheophone lineage was initially specialized to steppe-like vegetation, and did not adapt to humid forest—and proliferate—before the group had invaded the southern tropics, or they died out in the south. It is worth noting that South America was positioned further south than today and that the western (humid) part of Patagonia was, for part of the Tertiary, isolated from the Patagonian mainland by marine ingressions.

4.4. Classification of tracheophone suboscines

Our phylogenetic analysis demonstrates that the current classification (Ridgely and Tudor, 1994; Sibley and Monroe, 1990) does not correctly reflect natural groupings of the tracheophone suboscines. First, we cannot support keeping *Melanopareia* (and *Teledromas*) with tapaculos, so a new family name is needed. Second, we cannot support keeping *Sclerurus* with the philydorine ovenbirds, so Sclater's (1888) subfamily Sclerurinae

needs to be resurrected. It is also necessary to separate antpittas from antthrushes and to emphasize the strong support for uniting antthrushes and tapaculos with ovenbirds and woodcreepers. Sclater's (1888) group names are not suitable for defining this subdivision. For higher category names we selected Thamnophiloidea and Furnarioidea. The first group is numerically dominated by typical antbirds and the second by ovenbirds (for a higher taxon name, patronymi is irrelevant and would even be confusing in this case).

We propose the following classification of the tracheophone suboscines:

Furnariida (ovenbirds, woodcreepers, tapaculos, gnateaters, antbirds, and allies)
Incertae sedis
Melanopareiidae (new family, incl. *Melanopareia* and *Teledromas*)
Thamnophiloidea
Thamnophilidae
Conopophagidae
Furnarioidea
Grallariidae (with *Grallaria*, *Hylopezus*, *Myrmothera*, and *Grallaricula*)
Rhinocryptidae (tapaculos excl. *Melanopareia* and *Teledromas*)
Formicariidae (with *Formicarius* and *Chamaeza*)
Furnariidae
Sclerurinae (with *Sclerurus*)
Dendrocolaptinae
Furnariinae (ovenbirds excl. *Sclerurus*)

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