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Molecular systematics of New World suboscine birds

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Abstract

Phylogenetic relationships among New World suboscine birds were studied using nuclear and mitochondrial DNA sequences. New World suboscines were shown to constitute two distinct lineages, one apparently consisting of the single species *Sapayoa aenigma*, the other made up of the remaining 1000+ species of New World suboscines. With the exception of *Sapayoa*, monophyly of New World suboscines was strongly corroborated, and monophyly within New World suboscines of a tyrannoid clade and a furnarioid clade was likewise strongly supported. Relationships among families and subfamilies within these clades, however, differed in several respects from current classifications of suboscines. Noteworthy results included: (1) monophyly of the tyrant-flycatchers (traditional family Tyrannidae), but only if the tityrines (see below) are excluded; (2) monophyly of the pipromorphine flycatchers (Pipromorphinae of Sibley and Ahlquist, 1990) as one of two primary divisions of a monophyletic restricted Tyrannidae; (3) monophyly of the tityrines, consisting of the genus *Tityra* plus all sampled species of the *Schiffornis* group (Prum and Lanyon, 1989), as sister group to the manakins (traditional family Pipridae); (4) paraphyly of the ovenbirds (traditional family Furnariidae), if woodcreepers (traditional family Dendrocolaptidae) are excluded; and (5) polyphyly of the antbirds (traditional family Formicariidae) and paraphyly of the ground antbirds (Formicariidae sensu stricto). Genus *Melanopareia* (the crescent-chests), although clearly furnarioid, was found to be distant from other furnarioids and of uncertain affinities within the Furnarii. Likewise, the species *Oxyruncus cristatus* (the Sharpbill), although clearly tyrannoid, was distantly related to other tyrannoids and of uncertain affinities within the Tyranni. Results of this study provide support for some of the more novel features of the suboscine phylogeny of Sibley and Ahlquist (1985, 1990), but also reveal key differences, especially regarding relationships among suboscine families and subfamilies. The results of this study have potentially important implications for the reconstruction of character evolution in the suboscines, especially because the behavioral evolution of many suboscine groups (e.g., Furnariidae) is of great interest.
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1. Introduction

Suboscine, or non-oscine, birds are one of two major components of the large avian order Passeriformes (passerines) and consist of roughly 1150 species, or about one-eighth of extant birds. Found throughout the Americas, they account for more than 30% of the world's richest avifauna, that of the Neotropics, where they have undergone a remarkable large-scale radiation. Suboscines are predominantly a New World group, but the 51 species of the families Eurylaimidae (broadbills), Philepittidae (asities), and Pittidae (pittas) occur exclu-

sively in the tropics of the Old World, where they appear to be relictually distributed (Mayr and Amadon, 1951).

Although suboscines were defined in part based on lack of a character—they are passerine birds that lack the oscine, or songbird, syrinx—and have been referred to as "this by no means natural group" (Stresemann, 1934, translated in Sibley, 1970), the modern view is that suboscines are monophyletic relative to other passerines and that they consist of two monophyletic groups divisible along geographical lines: the New World suboscines and the Old World suboscines (Irestedt et al., 2001; Raikow, 1987; Raikow and Bledsoe, 2000; Sibley and Ahlquist, 1990).

New World suboscines are likewise generally considered to consist of two monophyletic groups, one ("Tyranni" in Ames, 1971 and Raikow, 1987, "Tyrannida" in Sibley and Ahlquist, 1990) consisting of the

tyrant-flycatchers and relatives, the other ("Furnarii" in Ames, 1971 and Raikow, 1987, "Furnariida" and "Thamnophilida" in Sibley and Ahlquist, 1990) consisting of the ovenbirds, antbirds, and related taxa. The Tyranni contain many taxa of uncertain familial affinities, variously placed in the traditional families Tyrannidae (tyrant-flycatchers), Pipridae (manakins), or Cotingidae (cotingas), including members of the *Schiffornis* group (Prum and Lanyon, 1989) and the Sharpbill *Oxyruncus cristatus*. Species composition of families in the Furnarii (sensu Ames, 1971 and Raikow, 1987), in contrast, has with few exceptions been well defined, but the monophyly and relationships of specific families have been a matter of debate.

Although most previous systematic work on suboscines has been based on morphology, Sibley and Ahlquist (1985, 1990) produced a detailed phylogenetic hypothesis of New World suboscines based on DNA–DNA hybridization data (Fig. 1). This phylogeny was consistent in some ways with traditional classifications, but it contained several striking features, including polyphyly of the traditional family Tyrannidae (species included in the Tyranninae and Pipromorphinae of Sibley and Ahlquist) and polyphyly of the traditional family Formicariidae (species included in the Formicariidae and Thamnophilidae of Sibley and Ahlquist). Polyphyly of the traditional Formicariidae has also been supported by a recent study using DNA sequence data (Irestedt et al., 2002).

Below I provide a phylogenetic hypothesis for New World suboscines based on DNA sequence data, and use this hypothesis to address: (1) the monophyly of New World suboscines, (2) the monophyly and relationships of traditional and non-traditional groups of New World suboscines, and (3) the relationships of suboscine taxa of uncertain affinities.

2. Materials and methods

Fifty-three taxa were sampled (Table 1), including one non-passerine (the woodpecker *Campethera nivosa*), four oscine passerines (two representatives of each oscine parvorder in Sibley and Ahlquist, 1990), one passerine of uncertain affinities (the New Zealand wren *Acanthisitta chloris*), three Old World suboscines (one representative from each family), and 44 New World suboscines. Taxon sampling among New World suboscines was guided largely by the phylogeny of Sibley and Ahlquist (1985, 1990) and the classification of Sibley and Monroe (1990), and was designed to establish relationships among major groups, to provide simple tests of the monophyly of major groups, and to indicate relationships of problematical taxa. The following were considered major groups for sampling purposes, using the nomenclature of Sibley and Monroe (1990), with number of taxa sampled in parentheses: Pipromorphinae (5), Tyranninae (4), Tityrinae (3), Cotinginae (5), Piprinae (3), Furnariinae (6), Dendrocolaptinae (3), Thamnophilidae (4), Formicariidae (4), Conopophagidae (2), and Rhinocryptidae (4). The Broad-billed Sapayoa, *Sapayoa aenigma*, a New World suboscine of uncertain affinities, was also sampled. Larger numbers of taxa were sampled for groups with relatively large numbers of species (e.g., Furnariidae) or for more controversial groups (e.g., Pipromorphinae), and smaller numbers for relatively small groups (e.g., Conopophagidae). Taxa within major groups were chosen to be as divergent as possible, to strengthen tests of monophyly and to break up long branches for phylogenetic analysis.

Intron 7 of the nuclear gene β-fibrinogen and the complete mitochondrial genes *ND3* and *COII* were sequenced for all taxa, with two exceptions. Complete mitochondrial but only partial β-fibrinogen sequence was obtained for *Melanopareia torquata*, and complete β-fibrinogen but no mitochondrial sequence was obtained for *A. chloris*. Tissue samples were collected during fieldwork in South America and from the Department of Ornithology, American Museum of Natural History, New York, NY; the Genetic Resources Collection, Louisiana State University Museum of Natural Science, Baton Rouge, LA; the Division of Birds, Field Museum of Natural History, Chicago, IL; the Royal Ontario Museum, Toronto, Ont.; the Marjorie Barrick Museum, University of Nevada Las Vegas, Las Vegas, NV; and the University of Arizona Bird Collection, Tucson, AZ. Sequences were obtained using DNA extracted from tissue by means of a 5% Chelex solution (Walsh et al., 1991). Primers used for initial PCR amplification of intron 7 were FIBI7U and FIBI7L, both
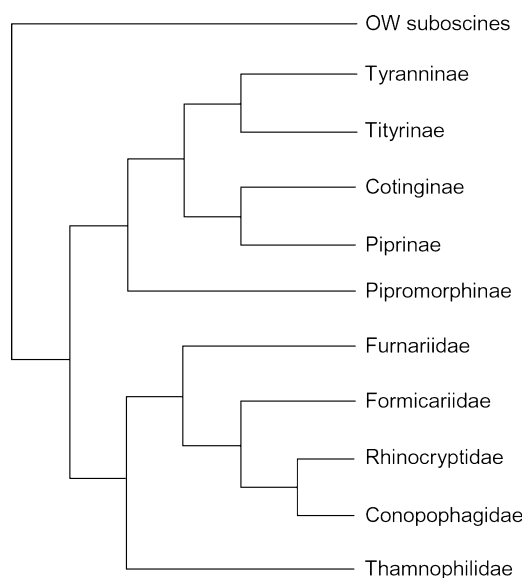

Fig. 1. Phylogenetic hypothesis of suboscine birds based on DNA–DNA hybridization data (Sibley and Ahlquist, 1985, 1990). This is Sibley and Ahlquist's preferred tree, obtained using UPGMA analysis.

Table 1
List of species name, tissue reference number, and putative taxonomic affinities of sequenced individuals

Species	Tissue number	Higher group	Family (prior to Sibley and Monroe)	Family/Subfamily (Sibley and Monroe)
Mionectes oleaginea	AMNH GFB 2231	Tyranni	Tyrannidae	Pipromorphinae
Leptopogon amaurocephalus	AMNH RTC 312	Tyranni	Tyrannidae	Pipromorphinae
Hemitriccus margaritaceiventer	MBM GAV 1001	Tyranni	Tyrannidae	Pipromorphinae
Todirostrum cinereum	AMNH PEP 2051	Tyranni	Tyrannidae	Pipromorphinae
Corythopis torquata	AMNH PEP 2014	Tyranni	Tyrann./Conopo.	Pipromorphinae
Muscisaxicola capistrata	AMNH RTC 377	Tyranni	Tyrannidae	Tyranninae
Elaenia albiceps	AMNH PRS 1136	Tyranni	Tyrannidae	Tyranninae
Tyrannus melancholicus	AMNH PRS 1090	Tyranni	Tyrannidae	Tyranninae
Laniocera hypopyrra	AMNH GFB 1401	Tyranni	Piprid./Cot./Tyrann.	Tyranninae
Tityra semifasciata	AMNH GFB 1035	Tyranni	Coting./Tyrann.	Tityrinae
Pachyramphus marginatus	AMNH GFB 1407	Tyranni	Coting./Tyrann.	Tityrinae
Schiffornis turdinus	AMNH GFB 2223	Tyranni	Piprid./Cot./Tyrann.	Tityrinae
Iodopleura isabellae	LSU B-4184	Tyranni	Coting./Tyrann.	Cotinginae
Procnias alba	AMNH ROP 309	Tyranni	Cotingidae	Cotinginae
Rupicola rupicola	AMNH PEP 1962	Tyranni	Cotingidae	Cotinginae
Phytotoma rutila	AMNH PRS 1153	Tyranni	Phytotom./Coting.	Cotinginae
Oxyruncus cristata	LSU B-2186	Tyranni	Oxyrun./Tyrann./Cot.	Cotinginae
Pipra pipra	AMNH GFB 2080	Tyranni	Pipridae	Piprinae
Machaeropterus deliciosus	FMNH 11761	Tyranni	Pipridae	Piprinae
Tyranneutes stolzmanni	AMNH CJW 104	Tyranni	Pipridae	Piprinae
Sapayoa aenigma	LSU B-2330	Tyranni	Piprid./Tyrann.	(*incertae sedis*)
Geositta cunicularia	AMNH APC 3280	Furnarii	Furnariidae	Furnariinae
Margarornis rubiginosus	AMNH GFB 1024	Furnarii	Furnariidae	Furnariinae
Furnarius rufus	AMNH RTC 389	Furnarii	Furnariidae	Furnariinae
Synallaxis cinerascens	AMNH RTC 326	Furnarii	Furnariidae	Furnariinae
Automolus rufipileatus	AMNH GFB 2079	Furnarii	Furnariidae	Furnariinae
Sclerurus mexicanus	AMNH ROP 108	Furnarii	Furnariidae	Furnariinae
Lepidocolaptes fuscus	AMNH APC 96-11	Furnarii	Dendrocolaptidae	Dendrocolaptinae
Dendrocincla fuliginosa	AMNH SC 771	Furnarii	Dendrocolaptidae	Dendrocolaptinae
Drymornis bridgesii	LSU B-25799	Furnarii	Dendrocolaptidae	Dendrocolaptinae
Frederickena viridis	AMNH ROP 281	Furnarii	Formicariidae	Thamnophilidae
Myrmotherula haematonota	AMNH GFB 2189	Furnarii	Formicariidae	Thamnophilidae
Pithys albifrons	AMNH GFB 2078	Furnarii	Formicariidae	Thamnophilidae
Pyriglena leucoptera	AMNH RTC 317	Furnarii	Formicariidae	Thamnophilidae
Formicarius colma	AMNH SC 721	Furnarii	Formicariidae	Formicariidae
Grallaria ruficapilla	AMNH GFB 3159	Furnarii	Formicariidae	Formicariidae
Grallaricula nana	AMNH ROP 362	Furnarii	Formicariidae	Formicariidae
Myrmothera simplex	AMNH GFB 2136	Furnarii	Formicariidae	Formicariidae
Conopophaga lineata	AMNH APC 96-3	Furnarii	Conopophagidae	Conopophagidae
Conopophaga aurita	LSU B-4685	Furnarii	Conopophagidae	Conopophagidae
Rhinocrypta lanceolata	AMNH PRS 1152	Furnarii	Rhinocryptidae	Rhinocryptidae
Scytalopus magellanicus	LSU B-8348	Furnarii	Rhinocryptidae	Rhinocryptidae
Pteroptochos castaneus	AMNH RTC 471	Furnarii	Rhinocryptidae	Rhinocryptidae
Melanopareia torquata	LSU B-14572	Furnarii	Rhinocryptidae	Rhinocryptidae
Smithornis rufolateralis	AMNH MKW 448	Pitti	Eurylaimidae	Eurylaimidae
Neodrepanis coruscans	FMNH 8049	Pitti	Philepittidae	Philepittidae
Pitta guajana	AMNH PRS 732	Pitti	Pittidae	Pittidae
Myzomela cardinalis	AMNH MKL 33	Passeres	Meliphagidae	Meliphagidae
Corvus brachyrhynchus	AMNH PRS 1180	Passeres	Corvidae	Corvidae
Sylvia nana	AMNH LMC 95-13	Passeres	Sylviidae	Sylviidae
Aimophila botterii	UABC TRH 3572	Passeres	Emberizidae	Fringillidae
Acanthisitta chloris	ROM RIF002	*incert. sedis*	Acanthisittidae	Acanthisittidae
Campethera nivosa	AMNH PRS 2012	Piciformes	Picidae	Picidae

Higher-level group names, except for Piciformes, were taken from Raikow (1987): the Tyranni and Furnarii are the two groups of New World suboscines, the Pitti are the Old World suboscines, and the Passeres are the oscine passerines. Family groupings prior to Sibley and Monroe (1990) are a composite of major sources. Abbreviations: Tyrann., Tyrannidae; Conopo., Conopophagidae; Piprid., Pipridae; Cot., Coting., Cotingidae; Phytotom., Phytotomidae; and Oxyrun., Oxyruncidae.

from Prychitko and Moore (1997). Primers used for re-amplifications, in addition to FIBI7U and FIBI7L, were FIBI7-397U (5′-AGTAACATATAATGGTTCCTGA A-3′), FIBI7-413U (3′-TCCTGAAGAAAGAGACAG GTAGCAT-3′), FIBI7-439L (5′-CAACTGAGCTCC TGTCTTCTGAGTAGG-3′), and FIBI7-453L (5′-GTA CTTTACAACTGAGCTCCT-3′). Primers used for the mitochondrial genes *ND3* and *COII* were those detailed previously (Chesser, 1999, 2000). Sequencing was conducted using an ABI 377 automated sequencer (Applied Biotechnologies). Mitochondrial sequences were aligned using Sequencher 4.1 (GeneCodes Corp, 2000), and nuclear sequences were aligned using ClustalX 1.8 (Thompson et al., 1997) with obvious errors corrected by eye. Apparent heterozygosities were coded using the IUPAC ambiguity codes. All sequences used in this study have been deposited in GenBank (Accession Nos. AY489408–AY489556).

Data analysis was performed using the computer programs PAUP* 4.0b8a (Swofford, 2001) and MacClade 4.0 (Maddison and Maddison, 2000). Data were analyzed using maximum parsimony and maximum likelihood approaches, with *C. nivosa* designated the outgroup in all analyses. Parsimony analyses were conducted using heuristic searches, with equal character weighting and 100 random addition replicates. Nuclear and mitochondrial data were analyzed separately and combined (total evidence). Nucleotide gaps were treated as missing data, but nucleotide gaps of two or more bases were subsequently mapped onto the nuclear and combined phylogenetic trees. Due to the relatively high levels of homoplasy and character saturation in the mitochondrial dataset, mitochondrial analyses were also conducted using various character weighting schemes, including 2:1 transversion–transition weighting and downweighting of characters at third positions by factors of 2, 5, and 10. Character support for parsimony-based phylogenies was assessed via bootstrapping (Felsenstein, 1985), using 100 heuristic searches with 10 random addition replicates each, and branch support (Bremer, 1988, 1994), which was computed using the computer program TreeRot, version 2 (Sorensen, 1999).

Maximum likelihood analyses were performed on the separate and combined data using heuristic searches with 10 random addition replicates. The program MODELTEST (Posada and Crandall, 1998) was used to evaluate a variety of models of sequence evolution for maximum likelihood analysis. Using likelihood ratio tests, MODELTEST determines the model of sequence evolution that most efficiently maximizes likelihood, while minimizing the number of model parameters. For the nuclear data, the HKY85 + G model (Hasegawa–Kishino–Yano + Gamma; Hasegawa et al., 1985; Yang, 1994) was most efficient and the following settings, derived from MODELTEST, were used in the likelihood analysis: TI/TV (transition/transversion) ratio = 2.027;

freq. [A] = 0.2883, freq. [C] = 0.1889, freq. [G] = 0.2095, freq. [T] = 0.3133; and shape parameter = 4.0335. For the mitochondrial data, the GTR + G + I model (General Time Reversible + Gamma + Proportion Invariant; Swofford et al., 1996) was most efficient and the following settings were used: prob. [A–C] = 0.6009, prob. [A–G] = 14.2877, prob. [A–T] = 2.8370, prob. [C–G] = 0.7893, prob. [C–T] = 28.6713, prob. [[G–T]] = 1.0000; freq. [A] = 0.3750, freq. [C] = 0.3696, freq. [G] = 0.0608, freq. [T] = 0.1946; shape parameter = 0.4087; and proportion of invariant sites = 0.3639. For the combined data, the GTR + G + I model was again most efficient and the following settings were used: prob. [A–C] = 0.7673, prob. [A–G] = 3.3216, prob. [A–T] = 1.0182, prob. [C–G] = 0.4112, prob. [C–T] = 6.8899, prob. [[G–T]] = 1.0000; freq. [A] = 0.3354, freq. [C] = 0.3030, freq. [G] = 0.1368, freq. [T] = 0.2248; shape parameter = 0.4461; and prop. invar. sites = 0.0978. Character support for maximum likelihood phylogenies was assessed via bootstrapping (Felsenstein, 1985) using 100 heuristic pseudoreplicates with single random addition replicates.

3. Results

The aligned nuclear dataset consisted of 1013 characters; individual intron 7 sequences ranged in length from 831 to 897 bases. There were 746 variable characters, 489 of which were potentially phylogenetically informative. Uncorrected pairwise divergence ranged from 1.0% between the two species of *Conopophaga* to 24.3% between the woodpecker *C. nivosa* and *S. aenigma*. Uncorrected pairwise divergence within New World suboscines was as high as 14.8% (between *Schiffornis turdinus* and *Synallaxis cinerascens*). The transition–transversion ratio for the dataset, calculated from the most parsimonious trees, was 1.98, and average GC content of the sequences was 34.9%. The nuclear dataset contained 13 potentially phylogenetically informative insertion/deletion events of two or more base pairs.

The aligned mitochondrial dataset consisted of 1036 characters. Although the *COII* sequences contained no indels, the *ND3* sequence of *C. nivosa* contained a single base insertion following position 173; this insertion is typical of a variety of non-passerine taxa (Mindell et al., 1998). Of the 1036 mitochondrial characters, 563 were variable and 495 potentially parsimony informative. Uncorrected pairwise divergence ranged from 8.6% between the two species of *Conopophaga* to 26.1% between the passerine *Sylvia nana* and the Old World suboscine *Neodrepanis coruscans*. Uncorrected pairwise divergence within New World suboscines was as high as 21.5% (between *Tyranneutes stolzmanni* and *Melanopareia torquatus*). The transition–transversion ratio for the dataset, calculated from the most parsimonious tree,

was 2.36. Base composition was biased towards A, T, and C (base frequencies of 27–31%), with average frequency for G of only 13.2%.

3.1. Phylogenetic analyses—nuclear

Parsimony analysis of the nuclear data yielded 168 most parsimonious trees of 1932 steps (CI = 0.60, CI excluding uninformative characters = 0.51, RI = 0.64); mean number of changes per variable character on the most parsimonious trees was 2.6. The bootstrap consensus tree (Fig. 2) indicated that the New Zealand wren *A. chloris*, member of a group sometimes considered suboscine, was sister to all other passerines, consistent with previous studies using sequence data (Barker et al., 2002; Ericson et al., 2002). Within the remainder of the passerines, the suboscines and oscines formed monophyletic groups. Two well-supported clades were also present within the suboscines; however, these differed from the accepted biogeographic division between Old World and New World suboscines (Irestedt et al., 2001; Raikow, 1987; Raikow and Bledsoe, 2000; Sibley and

Ahlquist, 1990). The Broad-billed Sapayoa *S. aenigma*, resident of a narrow zone of rainforest from Panama to Ecuador, received strong support (100% bootstrap) as an Old World suboscine.

Monophyly of New World suboscines, excluding *S. aenigma*, was strongly corroborated by the bootstrap consensus tree (Fig. 2), with a bootstrap value of 96%. The primary split within suboscines resulted in a tyrannoid clade (Tyranni), consisting of all representatives of the Tyranninae, Tityrinae, Pipromorphinae, Cotinginae, and Piprinae; and a second clade consisting of furnarioid taxa (Furnarii), including all representatives of the Furnariinae, Dendrocolaptinae, Thamnophilidae, Formicariidae, Conopophagidae, and Rhinocryptidae (usage of family/subfamily names following Sibley and Ahlquist, 1990). These results also received strong bootstrap support (100 and 96%, respectively).

Within the Tyranni, the bootstrap tree (Fig. 2) revealed three clades, which diverged in a polytomy. The first consisted of the Tyranninae and the Pipromorphinae, which were monophyletic sister groups, and the single taxon *O. cristatus*, which was sister to these; the second
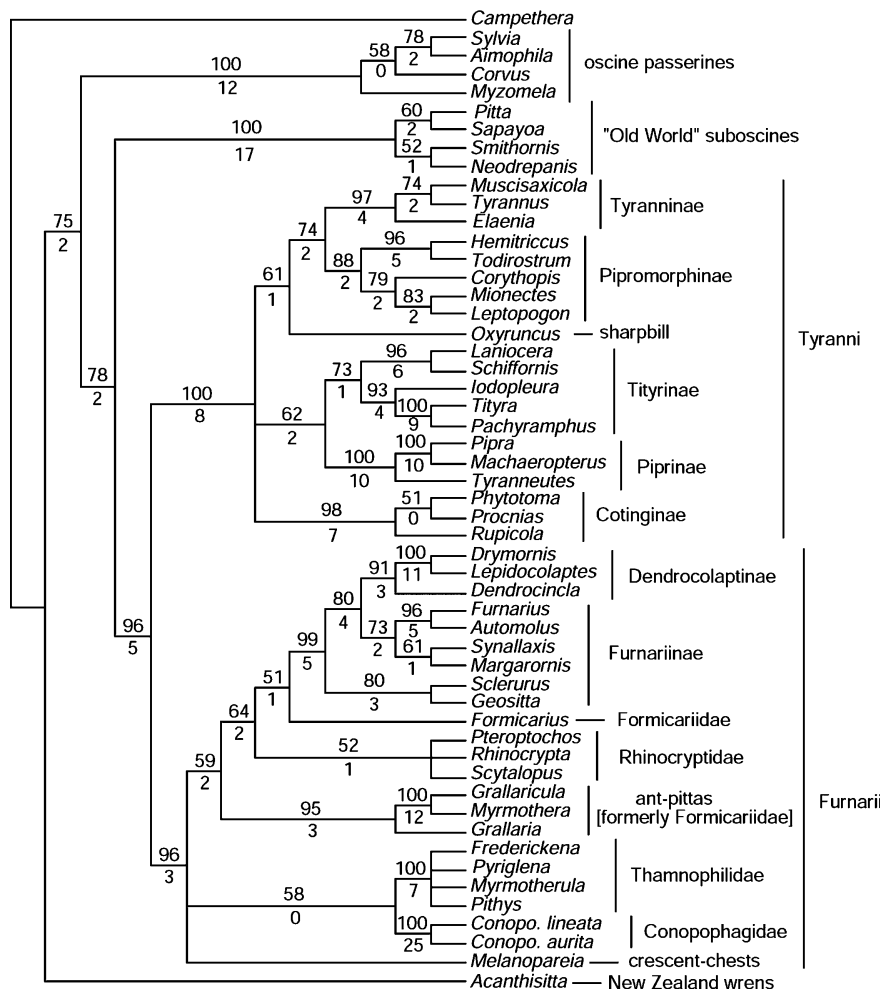

Fig. 2. Phylogenetic relationships among suboscine birds based on maximum parsimony analyses of the nuclear sequence data. Trees shown are bootstrap consensus trees; numbers above branches are bootstrap values and numbers below are decay indices.

consisted of the Tityrinae (*Schiffornis, Laniocera, Iodo-pleura, Pachyramphus,* and *Tityra*) and Piprinae (including *Tyranneutes*); and the third of the Cotinginae (including *Phytotoma*). Within the Furnarii, three clades also diverged in a polytomy. The first was a large clade containing the Dendrocolaptinae/Furnariinae, a paraphyletic Formicariidae (sensu stricto), and most of the Rhinocryptidae (excluding *Melanopareia*). Within this clade, *Formicarius* was sister to the dendrocolaptines/furnariines. The Dendrocolaptinae, although monophyletic, grouped within the Furnariinae; the furnariines *Geositta* and *Sclerurus* were sister to the rest of the Dendrocolaptinae/Furnariinae. The rhinocryptids were sister to the dendrocolaptine/furnariine/*Formicarius* clade, and the rest of the Formicariidae (*Grallaria, Myrmothera,* and *Grallaricula*) was sister to this large grouping. The second major clade within the Furnarii consisted of the Thamnophilidae and Conopophagidae, and the third consisted of the single taxon *M. torquata.*

Strong support was present for most subfamily and family groupings of Sibley and Ahlquist also identified here as clades; bootstrap values ranged from 88% for Pipromorphinae to 100% for Piprinae, Thamnophilidae, and Conopophagidae, with the exception of 73% for the modified Tityrinae and 52% for the modified Rhinocryptidae (Fig. 2). Support for relationships *among* these groups was lower and, with the exception of 99% support for the clade uniting the Dendrocolaptinae with a paraphyletic Furnariinae, ranged from <50% for any sister group relationship involving the Cotinginae or *M. torquatus,* to 74% for a sister group relationship between the Tyranninae and the Pipromorphinae (Fig. 2).

Mapping of insertion/deletion events onto the nuclear consensus tree revealed that one indel was a synapomorphy for all suboscines and three others were synapomorphies uniting *S. aenigma* with the Old World suboscines. Indels also supported the monophyly of the Tyranni, the Tityrinae, and the Rhinocryptidae (excluding *Melanopareia*). Other indels occurred only among specific taxa within the Pipromorphinae, the Cotinginae, the Dendrocolaptinae/Furnariinae, and the Formicariidae. A partially homoplasious indel was found in the oscine passerines, two dendrocolaptines (*Lepidocolaptes* and *Drymornis*) and one rhinocryptid (*Pteroptochos*), and another occurred only in two tityrines (*Schiffornis* and *Laniocera*), one furnariine (*Furnarius*), and one rhinocryptid (*Rhinocrypta*).

Results of the nuclear maximum likelihood analysis (Fig. 3) revealed two most likely trees (score−Ln = 11451.343) and supported all major findings of the parsimony analyses, including the New Zealand wren as sister to all other passerines (although with weak support), monophyly of the *Sapayoa*-Old World suboscine clade, monophyly of the New World suboscines if *Sapayoa* is excluded, and monophyly of the Tyranni (excluding *Sapayoa*) and the Furnarii, and was virtually identical to

the nuclear parsimony tree. Noteworthy differences between parsimony and likelihood trees involved the relationships of the sharpbill *Oxyruncus*, which was sister to the Piprinae/Tityrinae in the likelihood analysis but sister to the Tyranninae/Pipromorphinae in the parsimony analysis, and relationships of the family Cotinginae, which was sister to the Tyranninae/Pipromorphinae in the likelihood analysis but was unresolved in the parsimony analysis. However, as with the parsimony analysis, neither likelihood result was strongly supported (bootstrap values <50%).

All major family and subfamily-level results found in the nuclear parsimony tree were also recovered in the likelihood analyses. However, bootstrap support (Fig. 3) for the likelihood results was generally higher than in the parsimony analysis. For example, support for monophyly of the Tyranninae/Pipromorphinae clade (87%), of the Piprinae/Tityrinae clade (84%), of the *Formicarius*/Dendrocolaptinae/Furnariinae clade (65%), and of the Thamnophilidae/Conopophagidae clade (78%) were all noticeably higher than in the parsimony tree, as was support for monophyly of suboscines as a group (97%).

3.2. Phylogenetic analyses—mitochondrial and combined

Parsimony analysis of the mitochondrial data, using equal weighting of characters, resulted in two most parsimonious trees (not shown) of 5133 steps (CI = 0.19, CI excluding uninformative characters = 0.18, RI = 0.32); mean number of changes per variable character on the most parsimonious mitochondrial tree was 9.1. Despite extremely high levels of homoplasy in this dataset, the most parsimonious trees under the various weighting regimes shared a number of features with the nuclear trees, including monophyly of New World suboscines (excluding *S. aenigma*), monophyly of the Tyranninae/Pipromorphinae clade, monophyly of the Tityrinae/Piprinae clade, monophyly of the Cotinginae, Piprinae, Dendrocolaptinae, and Conopophagidae, polyphyly of the traditional Formicariidae, and paraphyly of the traditional Furnariidae. As in the nuclear trees, *Geositta* and *Sclerurus* were sister to a clade consisting of the other dendrocolaptines and furnariines. The bootstrap consensus trees of the mitochondrial data were largely unresolved, although monophyly of the Tyranninae, Dendrocolaptinae, Thamnophilidae, and Conopophagidae received strong support.

The combined nuclear and mitochondrial parsimony analysis resulted in three most parsimonious trees (not shown) of 7113 steps (CI = 0.30, CI excluding uninformative characters = 0.26, RI = 0.40); mean number of changes per variable character on the combined trees was 5.4. The combined bootstrap consensus tree was entirely consistent with the nuclear bootstrap tree, although resolution at medium depths was reduced. There was strong support for monophyly of New World suboscines,
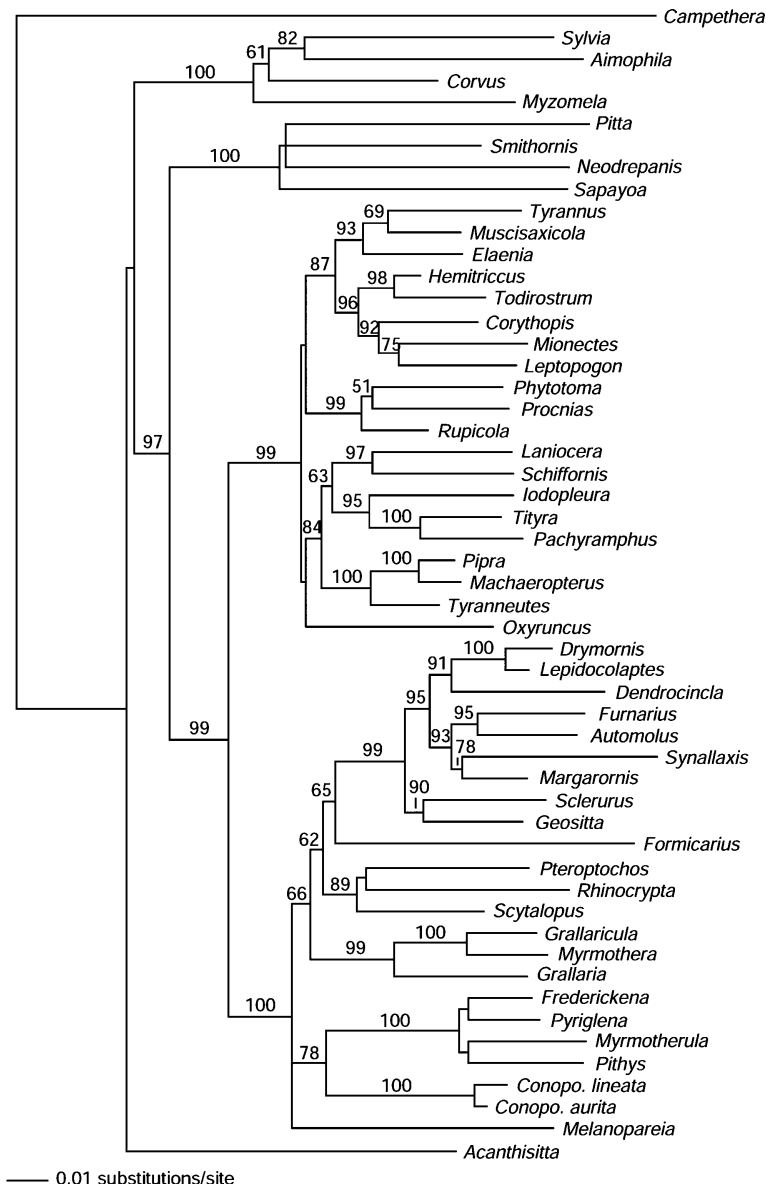
Fig. 3. Phylogram showing relationships among suboscine birds based on maximum likelihood analysis of sequence data from intron 7 of the nuclear gene β-fibrinogen.

Tyranni, and Furnarii (bootstrap support from 86 to 99%), and for all major family and subfamily groupings except Tityrinae. Indeed, the combined results revealed improved support for several family/subfamily groups (Tyranninae, Dendrocolaptinae, and Rhinocryptidae), but relationships *among* family/subfamily groups were largely unresolved, especially within the Furnarii. Likewise, the positions of *Oxyruncus* and *Melanopareia* within the Tyranni and Furnarii, respectively, were unresolved.

Likelihood analysis of the mitochondrial data revealed a most likely tree (score −Ln = 19691.279; not shown) virtually identical to the mitochondrial parsimony tree, containing all major features described for the most parsimonious mitochondrial tree.

Likelihood analysis of the combined tree yielded a most likely tree (score −Ln = 32377.321; not shown)

very similar to the likelihood tree based on the nuclear data (Fig. 3). Distinctive features of the combined likelihood tree were the position of the Cotinginae as sister to the remainder of the Tyranni and the position of *Melanopareia* as sister to the Thamnophilidae/Conopophagidae clade within the Furnarii.

4. Discussion

4.1. Higher-level systematics

This study indicates polyphyly of New World suboscines and possible paraphyly of Old World suboscines, due to the phylogenetic position of the appropriately named *S. aenigma*. The affinities of this species with Old

World suboscines mean that suboscines resident in the New World constitute two distinct lineages, one apparently consisting of a single species, the other apparently made up of the remaining 1000+ species of New World suboscines. Whether *Sapayoa* was always the only New World representative of the "Old World" suboscine lineage, or whether it is the sole surviving species from a New World radiation of this lineage, is unknown; nevertheless, this remarkable result provides the only known instance of pantropical distribution among the large avian order Passeriformes, and in fact echoes results from other research. Lanyon (1985), for example, in an electrophoretic study of the Tyrannoidea, found *Sapayoa* to be only distantly related to the other taxa studied, and suggested that its true affinities may be outside the tyrannoids. Likewise, Sibley and Ahlquist (1990) included *Sapayoa* in their DNA–DNA hybridization studies, where their melting curves indicated its possible relationship with Old World suboscines. However, they were evidently uncertain of these data and excluded *Sapayoa* from their phylogenetic analyses.

With the exception of *S. aenigma*, the data presented above corroborate the monophyly of New World suboscines and support the basic biogeographical dichotomy between New World and Old World suboscines. Traditional classifications, such as those of Mayr and Amadon (1951) and Wetmore (1960), had placed most suboscines, including the Old World pittas, asities, and New Zealand wrens (then considered suboscines) and all the New World taxa, in a suborder separate from that of the Old World broadbills (Eurylaimi), and included the pittas and asities with the New World tyrannids, cotingas, plantcutters, manakins, and sharpbill in the superfamily Tyrannoidea. Suggested rearrangements such as that of Olson (1971) also involved an admixture of Old World and New World groups, although Ames (1971) suggested that the suborder Tyranni, previously consisting of all suboscines other than the Eurylaimi, be restricted to the New World members of the superfamily Tyrannoidea (Tyrannidae, Cotingidae, Phytotomidae, Pipridae, and Oxyruncidae). The modern view of the basic biogeographical division between Old World and New World suboscines, enunciated by Sibley and Ahlquist (1985, 1990; Fig. 1) and Raikow (1987), is strongly supported by the DNA sequence data presented above (again, with the exception of *Sapayoa*). Likewise, the sequence data support the division of New World suboscines into a tyrannid-related clade and a furnariid-related clade. This was also the traditional view, except that the Old World pittas, asities, and New Zealand wrens, as stated above, were typically included in the tyrannid-related clade.

4.2. Tyranni

The tyrannoid suboscines have long been a confusing group, due in large part to the variety of taxa of un-

certain affinities within the group (Table 1). These have included the genera *Oxyruncus, Phytotoma, Corythopis, Schiffornis, Tityra, Pachyramphus, Iodopleura, Laniocera*, and *Tyranneutes*, among others. Based on morphological data, *O. cristatus* has been alternately placed in its own family (e.g., Ames, 1971; Traylor, 1979; Wetmore, 1960) or merged into the Tyrannidae (Mayr and Amadon, 1951). More recently, the molecular data of Sibley et al. (1984), Sibley and Ahlquist (1985, 1990), and Prum et al. (2000) placed *Oxyruncus* well within the Cotingidae. The genus *Phytotoma* was traditionally placed in its own family, although much recent evidence (Johansson et al., 2002; Lanyon, 1985; Lanyon and Lanyon, 1989; Prum et al., 2000; Sibley and Ahlquist, 1990) indicates that the plantcutters are cotingas. *Corythopis torquatus* was traditionally included in the Conopophagidae (in the Furnarii), but more recently has been consistently placed in the Tyrannidae (Ames, 1971; Ames et al., 1968; Meyer de Schauensee, 1970; Sibley and Ahlquist, 1985, 1990; Traylor, 1977, 1979; but see Johansson et al., 2002). *S. turdinus* generally has been proposed as a member of the Pipridae, but has also been considered part of the Cotingidae (Wetmore, 1972) or Tyrannidae (Ames, 1971), or even as evidence that the "traditional division of the manakin–cotinga–flycatcher complex into three families cannot be maintained" (Snow, 1973). Sibley and Ahlquist included *Schiffornis* in their Tityrinae, whereas Prum and Lanyon (1989) included it in their eponymous *Schiffornis* group. Traditional morphological studies have placed the genera *Tityra, Pachyramphus, Iodopleura*, and *Laniocera* alternately in the Cotingidae or the Tyrannidae (summarized in Prum and Lanyon, 1989). Sibley and Ahlquist (1985, 1990) placed *Tityra* and *Pachyramphus* in their subfamily Tityrinae; their studies did not include *Iodopleura* or *Laniocera*, but Sibley and Monroe (1990) placed these genera in the Cotinginae and Tyranninae, respectively. *Pachyramphus, Iodopleura*, and *Laniocera* formed part of the *Schiffornis* group of Prum and Lanyon (1989), but *Tityra* was specifically excluded from this group. The genus *Tyranneutes* has been typically placed in the family Pipridae, although Prum (1990a) determined that it was not a manakin, but one of a group of non-piprid tyrannoids erroneously placed in the family.

Relationships *within* tyrannoid groups, especially within the traditional family Tyrannidae, have also been a subject of controversy. Traylor (1977, 1979) used cranial (Warter, 1965) and other morphological, behavioral, and ecological data to extensively revise the classification of the family, and recognized three core groups: Elaeniinae, Fluvicolinae, and Tyranninae. Traylor (1979) also tentatively included the genera *Tityra* and *Pachyramphus* with the tyrannids, but primarily as taxa not easily placed elsewhere. Sibley and Ahlquist (1985, 1990) and Sibley and Monroe (1990), in

contrast, split Traylor's core Tyrannidae into two quite different groups: Tyranninae, which included all the Tyranninae and Fluvicolinae and part of the Elaeniinae of Traylor (1977, 1979), and thus constituted the bulk of the family; and Pipromorphinae (called Mionectidae in 1985), which consisted of the other genera in Traylor's Elaeniinae, including *Mionectes/Pipromorpha, Leptopogon, Pseudotriccus, Poecilotriccus, Taeniotriccus, Hemitriccus/Idioptilon, Todirostrum*, and *Corythopis* (Sibley and Ahlquist, 1990; Sibley and Monroe, 1990). Most surprisingly, the Tyranninae and Pipromorphinae were not sister groups in Sibley and Ahlquist's (1985, 1990) phylogeny; rather, the Pipromorphinae were sister to all other tyrannoid groups (Cotinginae, Piprinae, Tityrinae, Tyranninae). Thus, Sibley and Ahlquist found the traditional family Tyrannidae to be polyphyletic.

The DNA sequence data clearly support the inclusion of *Phytotoma* in the Cotinginae and *Hemitriccus, Todirostrum, Corythopis, Mionectes*, and *Leptopogon* in the Pipromorphinae. While these results are congruent with those of Sibley and Ahlquist (1985, 1990) and Johansson et al. (2002), the pipromorphine results contrast with a variety of previous studies of tyrant-flycatchers. Monophyly of the Pipromorphinae, for example, was supported by neither protein electrophoresis (Lanyon, 1985) nor syringeal morphology (Lanyon, 1988a,b), nor does such a group appear in traditional classifications, although Wolters (1977; after Bonaparte, 1853), used the same name to refer to a subfamily consisting solely of the genera *Mionectes* and *Pipromorpha*.

The sequence data also support a monophyletic Tityrinae; however, this group consists of an amalgamation of the *Schiffornis* group (Prum and Lanyon, 1989) with Sibley's Tityrinae (cf. Johansson et al., 2002). The *Schiffornis* group consisted of the six genera *Schiffornis, Laniisoma, Iodopleura, Laniocera, Xenopsaris*, and *Pachyramphus*. Sibley and Ahlquist, as noted above, restricted their Tityrinae to *Tityra, Pachyramphus*, and *Schiffornis*. The sequence data identified *Schiffornis, Laniocera, Iodopleura, Pachyramphus*, and *Tityra* as a reasonably well-supported clade, with strong support for internal groupings of *Laniocera* and *Schiffornis*, and *Tityra, Pachyramphus*, and *Iodopleura*, respectively. *Laniisoma* and *Xenopsaris* were not sequenced for this study, although the mitochondrial data of Prum et al. (2000) supported inclusion of *Laniisoma* in a group containing *Schiffornis, Iodopleura, Pachyramphus*, and *Tityra*. Despite the suggestion of Prum et al. (2000) that both the *Schiffornis* group and Sibley's Tityrinae may be valid higher-level taxa, both groups are demonstrably paraphyletic in the phylogenetic trees presented above.

Although the Tyranninae, Tityrinae (as modified above), and Pipromorphinae all form well-supported clades in the analyses presented here, relationships among these groups differed considerably from those presented by Sibley and Ahlquist (1985, 1990). The se-

quence data recognize the Tyranninae and Pipromorphinae as sister groups, as did the results of Johansson et al. (2002), supporting monophyly of Traylor's (1977, 1979) core group of tyrant-flycatchers. This arrangement was also present in an alternate FITCH tree (Fig. 4) presented by Sibley and Ahlquist (1990, their Fig. 345). The Tityrinae were distant from these groups and were the sister group to the manakins (Piprinae), a clade that included *Tyranneutes* as sister to the "true manakins" *Pipra* and *Machaeropterus*, as in Lanyon (1985). The sister relationship between tityrines and manakins was also partially consistent with Lanyon's (1985) electrophoretic results.

Consistent with the difficulties morphologists have encountered in their attempts to classify it, the position of the sharpbill *O. cristatus* within the Tyranni was not well resolved (see also Johansson et al., 2002). In analyses of the sequence data, *Oxyruncus* appears variously as sister to the Tyranninae/Pipromophinae, sister to the Piprinae/Tityrinae, or sister to the Cotinginae. This result contrasts markedly with those of Sibley and Ahlquist (1985, 1990) and Prum et al. (2000), who concluded that *Oxyruncus* is nested deep within the cotingas. However, the cytochrome *b* sequence used by Prum et al. (2000) was recently proposed to have been erroneous (Johansson et al., 2002). Furthermore, the electrophoretic study of Lanyon (1985), despite extensive sampling of cotingas, also failed to place *Oxyruncus* in the Cotinginae; rather, it appeared to be more closely related to members of the Tyranninae or Tityrinae.
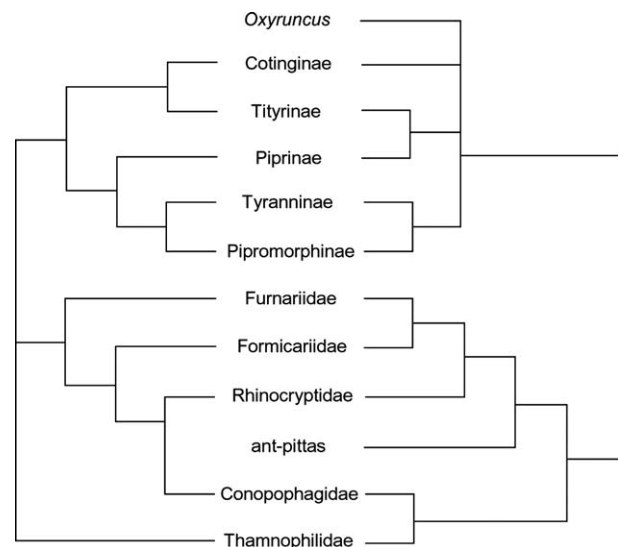

Fig. 4. Evolutionary relationships among major groupings of suboscine birds. Phylogeny on the left side is based on an alternate (FITCH) analysis of the DNA–DNA hybridization data of Sibley and Ahlquist (1990, their Fig. 345). Phylogeny on the right is simplified from the DNA sequence results presented above. Note that *Oxyruncus cristatus* (the Sharpbill) is included within the Cotinginae and that the antpittas are included in the Formicariidae in Sibley and Ahlquist's tree.

4.3. Furnarii

The furnarioids have historically been characterized by relatively well-defined families with few problematical taxa, but relationships among families have remained obscure. Relationships within the large traditional families Furnariidae and Formicariidae have likewise been subject to debate. There has long been discussion, for example, of whether the Dendrocolaptidae are separable as a family from the closely related Furnariidae (summarized in Feduccia, 1973). This discussion has typically focused on the degree of morphological difference between the two groups, rather than questions of monophyly. However, Feduccia's "hypothetical phylogeny" (Fig. 20 in Feduccia, 1973) clearly illustrates a paraphyletic Furnariidae if dendrocolaptids are excluded from the family (the synallaxine furnariids are sister to the remaining furnariids and dendrocolaptids), and Ihering (1915) proposed an apparently paraphyletic Furnariidae, with woodcreepers having twice arisen from within the Philydorinae. Although the Formicariidae traditionally was considered a cohesive family, Ames (1971) found two distinct syringeal forms within the family, one in the "ground antbirds" and the other in the "typical antbirds," a division presaged by Heimerdinger and Ames' (1967) study of sternal notches of suboscines.

The DNA hybridization data (Sibley and Ahlquist, 1985, 1990; Figs. 1 and 4) showed that although the Furnariinae and Dendrocolaptinae were monophyletic sister groups, the ground antbirds and typical antbirds were not: the typical antbirds (Thamnophilidae) were the sister group to rest of the Furnarii, and placed in Sibley and Ahlquist's classification into a distinct parvorder, whereas the ground antbirds (Formicariidae) were sister to a clade consisting of the Rhinocryptidae and the Conopophagidae. This three-family clade was in turn sister to the Furnariinae/Dendrocolaptinae clade.

The DNA sequence data of Irestedt et al. (2002) indicated that the traditional family Furnariidae is paraphyletic if the dendrocolaptids are excluded; *Sclerurus* was found to be sister to the remainder of the furnariid/dendrocolaptid clade. Sibley and Ahlquist had previously shown that *Sclerurus* is a genetically atypical furnariid genus, but in their phylogeny it was sister to all other furnariids rather than to a furnariid/dendrocolaptid clade. Irestedt et al. (2002) also found the traditional family Formicariidae to be paraphyletic and Sibley and Ahlquist's restricted Formicariidae to be paraphyletic, as well, with the antpittas separated from the antthrushes (see also Rice, 2000).

The sequence data presented here also show the Furnariidae to be paraphyletic if the dendrocolaptids are excluded. However, these data indicate that the genus *Geositta*, in addition to *Sclerurus*, lies outside the clade consisting of the rest of the furnariids and den-

drocolaptids. Interestingly, Ames (1971) concluded that *Geositta* was the only furnariid genus to possess horns in the syrinx, a trait he found in all dendrocolaptids, suggesting that *Geositta* is a morphologically atypical furnariid genus. Ames examined the species *Geositta cunicularia* in his study, the same species sequenced here. These findings contrast markedly with the DNA hybridization results of Sibley and Ahlquist (1985, 1990), who found *Geositta* to nest deep within the Furnariidae. It is unclear which species of *Geositta* was included in Sibley's hybridization experiments, however, and it is possible that this discrepancy is due to sampling different branches of a polyphyletic genus.

The data presented here also support the separation of the "ground antbirds" and "typical antbirds" or Formicariidae and Thamnophilidae (Sibley and Ahlquist, 1985, 1990), as well as the paraphyly of the ground antbirds (Formicariidae sensu stricto). The antthrush *Formicarius* was not sister to the antpittas *Grallaria, Myrmothera*, and *Grallaricula*, consistent with other sequencing results (Irestedt et al., 2002; Rice, 2000). Furthermore, a sister relationship between the Thamnophilidae and the remainder of the Furnarii, as proposed by Sibley and Ahlquist (1985, 1990), is inconsistent with the sequence results above (see also Irestedt et al., 2002), in which the Thamnophilidae are sister to the Conopophagidae; this clade is then sister to the remainder of the Furnarii (Fig. 4).

Finally, the sequence data were unable to resolve the position of the genus *Melanopareia. Melanopareia* has generally been considered part of the furnarioid family Rhinocryptidae, although Ridgely and Tudor (1994) suggested that it is not rhinocryptid. The genus was not included in the studies of Sibley and Ahlquist (1985, 1990). The trees of Irestedt et al. (2002) placed it in a polytomy that also included the Thamnophilidae and the Conopophagidae, or as sister to the rest of the Furnarii, although support for these results was weak. The sequence data presented here clearly place *Melanopareia* in the Furnarii, but it appears to be distantly related to other furnarioids and its affinities within the group remain uncertain.

4.4. Comparing relationships among groups with results of the DNA hybridization studies

Although family and subfamily groups identified as monophyletic generally received strong support in the analyses presented here, relationships *among* groups were typically less well supported, and in some cases were unresolved (Figs. 2 and 3).

Comparison of relationships among families and subfamilies in the DNA sequence results with those of Sibley and Ahlquist (Figs. 1 and 4) revealed little congruence. The proposed sister relationship between the Pipromorphinae and the rest of the tyrannoids (Sibley

and Ahlquist, 1990) was contradicted by the sequence data, as was the proposed sister relationship between the Thamnophilidae and the rest of the furnarioids. Indeed, *no sister group relationship within the tyrannoids or the furnarioids was present in both the preferred (UPGMA) phylogeny of Sibley and Ahlquist (Fig. 1) and the DNA sequence trees presented above*.

Critics have noted that many internal branches in Sibley and Ahlquist's (1985, 1990) phylogeny are unstable and not robust to different types of analysis (e.g., Cracraft, 1987; Harshman, 1994; Lanyon, 1985). For example, the alternate FITCH tree (Fig. 4, left), presented but only briefly discussed by Sibley and Ahlquist (1990, their Fig. 345), depicted several relationships not present in their preferred phylogeny (their UPGMA tree), especially among the tyrannoids. Noteworthy among these was a sister relationship between the Tyranninae and the Pipromorphinae, as reported in this study and in Johansson et al. (2002), supporting monophyly of the tyrant-flycatchers if the tityrines are excluded. Also notable was the absence of a sister group relationship between the Piprinae and the Cotinginae, a result that contradicts most traditional views but is consistent with the sequence results presented above.

Harshman (1994) re-analyzed the data of Sibley and Ahlquist (1990), introducing random ordering of taxa, the use of additional tree-building algorithms, and single-taxon jackknifing procedures, then constructed a jackknife consensus tree of all the best-fit trees. Although 56% of the interior branches included in Sibley and Ahlquist (1990)'s FITCH trees remained intact in re-analyses of their data for all birds, interior branches within the tyrannoid and furnarioid New World suboscines became near-complete polytomies (Harshman, 1994). Within the Tyranni, the Tyranninae, Piprinae, Cotinginae, Tityrinae, and Pipromorphinae all collapsed into a polytomy; and within the Furnarii, the Thamnophilidae were sister to a polytomy consisting of the Dendrocolaptinae, the Furnariinae, the Conopophagidae, the Rhinocryptidae, and the Formicariidae. Even this single internal branch, as noted above, is not supported by the DNA sequence results.

4.5. Implications for character evolution

Suboscines are the most species-rich constituent of the world's most species-rich avifauna, that of the Neotropics, and their morphological, behavioral, and ecological diversity is equally impressive. Studies of behavioral evolution in particular families have been especially prominent (e.g., Fitzpatrick, 1985; Prum, 1990b, 1994; Skutch, 1996; Snow, 1976; Zyskowski and Prum, 1999), due to the variety of mating systems, displays, nest types, foraging behavior, diet, and other characters exhibited by suboscine birds. The DNA sequence results

presented here may bear directly on previous work concerning the evolution of morphology, ecology, or behavior, despite the focus of this study on higher-level relationships and the necessarily limited intrafamilial sampling.

Syringeal characters have played a prominent role in suboscine systematics as far back as the landmark works of Müller (1847) and Garrod (1876). A key character within the tyrannoids has been the presence of internal syringeal cartilages, proposed by Ames (1971) as a synapomorphy for the tyrant-flycatchers (traditional family Tyrannidae). However, several other tyrannoids were discovered to share this character (Lanyon, 1984; Prum, 1990a; Prum and Lanyon, 1989), and the homology of many of these structures has been questioned (Prum, 1990a; Prum and Lanyon, 1989). Sibley and Ahlquist's hypothesis that the traditional family Tyrannidae is polyphyletic, and that part of the tyrannids form a sister group to a clade consisting of the cotingas, manakins, tityrines, and remaining tyrant-flycatchers, suggested that internal syringeal cartilages evolved independently in the pipromorphines and the tyrannines and were not homologous. This hypothesis was met with skepticism by at least one syringeal morphologist (Lanyon, 1988a). The sequence data presented above support monophyly of a tyrannine/pipromorphine clade relative to tyrannoids that lack internal syringeal cartilages (most Piprinae and Cotinginae) and other tyrannoids that possess these cartilages, including the tityrines, *Oxyruncus, Tyranneutes* and several other piprid-like taxa, and the cotingid genus *Lipaugus* (McKitrick, 1985; Prum, 1990a; Prum and Lanyon, 1989). Thus, at a minimum, homology of the internal cartilages of the Tyranninae and the Pipromorphinae is supported by the sequence data. Internal syringeal cartilages among a wider group of tyrannoids may also be homologous, depending on resolution of the polytomies within the Tyranni.

Nest placement and nest structure in the traditional Furnariidae are among the most diverse of any bird family, and the evolution of nest-building in this group is of great behavioral interest. Zyskowski and Prum (1999) recently provided a phylogenetic analysis of the furnariines based on careful examination of nests and nesting behavior. They concluded that "comparisons with outgroups demonstrate that cavity nesting is plesiomorphic to the family," based on the phylogeny of Sibley and Ahlquist, in which the Dendrocolaptidae and their Formicaroidea (Formicariidae, Conopophagidae, and Rhinocryptidae) were successive outgroups to the Furnariidae. Although cavity nesting is characteristic of the dendrocolaptids, it is only one of several nesting types found in the Formicaroidea and the Furnariidae, and it seems unclear without detailed within-group phylogenetic analysis whether cavity nesting is actually the ancestral form of furnariid nest. The DNA sequence data, however, despite the merging of the Dendrocolaptinae

into the Furnariinae, considerably strengthen the case that cavity nesting is the ancestral state of furnariids. *Formicarius* and other antthrushes, sister to the furnariid clade (consisting of all furnariines and dendrocolaptines), are obligate cavity nesters. Within the Furnariidae, *Geositta* and *Sclerurus*, sisters to the rest of the group, are both obligate cavity nesting genera. The remainder of the group consists of two clades, one of which (the dendrocolaptines) is an obligate cavity nesting group, the other of which (the rest of the furnariines) contains cavity nesting along with a variety of other nesting types. Thus, under the first doublet rule (Maddison et al., 1984), the unequivocal most parsimonious character state of the ancestors both of the Furnariidae as a whole and of the Furnariidae excluding *Geositta* and *Sclerurus*, is cavity nesting.

The evolution of other behavioral characters likely bears re-evaluation in light of the phylogenetic data presented above. For example, the evolution of mating systems and display behavior among manakins (Piprinae) and other tyrannoids has been traditionally interpreted in the context of a sister group relationship between the manakins and the cotingas. However, the DNA sequence data indicate that the Piprinae are the sister group to the Tityrinae. Prum and Lanyon (1989), in their discussion of the *Schiffornis* group, suggested that *Schiffornis* and *Laniocera* may be dispersed lekking genera and that *Pachyramphus* and *Iodopleura* are monogamous genera. They indicated that the sister group of the *Schiffornis* group was unknown, but suggested that these species are probably not closely related to the true lekking lineages of the Tyranni, and that monogamy was the likely ancestral breeding system in the group. A sister group relationship between the Piprinae and the Tityrinae suggests that the lekking behavior exhibited by such genera as *Schiffornis* may not represent an independent development to that in the Piprinae. Although the ancestral character state cannot be thoroughly evaluated without a much more complete phylogeny, it appears at the very least that the evolution of breeding systems within the Tityrinae/Piprinae, and perhaps elsewhere within the Tyranni, should be re-examined.

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