



Phylogeny and classification of the New World suboscines (Aves, Passeriformes)

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Abstract

Here we present a phylogenetic hypothesis for the New World suboscine radiation, based on a dataset comprising of 219 terminal taxa and five nuclear molecular markers (ca. 6300 bp). We also estimate ages of the main clades in this radiation. This study corroborates many of the recent insights into the phylogenetic relationships of New World suboscines. It further clarifies a number of cases for which previous studies have been inconclusive, such as the relationships of Conopophagidae, Melanopareiidae and Tityridae. We find a remarkable difference in age of the initial divergence events in Furnariida and Tyrannida. The deepest branches in Furnariida are of Eocene age, whereas the extant lineages of Tyrannida have their origin in the Oligocene. Approximately half of the New World suboscine species are harboured in 5 large clades that started to diversify around the Mid Miocene Climatic Optimum (16–12 Mya). Based on our phylogenetic results we propose a revised classification of the New World suboscines. We also erect new family or subfamily level taxa for four small and isolated clades: Berlepschiinae, Pipritidae, Tachurididae and Muscigrallinae.

Key words: Furnariida, Tyrannida, phylogeny, classification

Introduction

With more than 1200 extant species, the New World suboscines (NWS) are one of the largest endemic vertebrate radiations on the South American continent. Phylogenetic relationships are comparatively well studied. The studies with the most comprehensive taxon sampling have either relied on the RAG1 and RAG-2 protein coding regions (Moyle *et al.* 2009; Tello *et al.* 2009) or nuclear introns, primarily myoglobin intron 1, G3PDH intron 11 and ODC introns 6 and 7 (e.g. Irestedt *et al.* 2009; Ohlson *et al.* 2008), in some cases complemented by mitochondrial DNA. These two sets of molecular markers have yielded phylogenetic hypotheses that are generally congruent but also differ at several points. Partially conflicting tree topologies have previously been observed between the RAG genes and nuclear introns (Irestedt & Ohlson 2008) or between RAG genes and other nuclear protein-coding markers (e.g. ZENK, Treplin *et al.* 2008).

The last decade has seen a drastic overturning of the traditional view of systematic relationships in nearly every larger group of passerines. However, adjustments in classification often lag, creating a discrepancy between classification and current hypotheses of phylogenetic relationships. Moyle *et al.* (2009) and Tello *et al.* (2009) proposed several changes to the classification of Furnariida and Tyrannida respectively, whereas the studies by Irestedt *et al.* (2009) and Ohlson *et al.* (2008) have not been synthesized into a comprehensive proposal for a new classification. At this point we have a sufficiently clear picture of the NWS radiation to propose a consensus classification that reflects the results of these combined analyses. The NWS are among the most comprehensively sampled bird radiations and there are no taxa left unstudied that are likely to have any impact on classification at the subfamily level. A few taxa of uncertain affinities at the generic level still remain to be included in molecular studies and a few large radiations of rather recent origin remain to be disentangled to settle generic limits.

In this study we aim to explore the effects of increased data on the topology of the NWS tree. We compare the phylogenies obtained using RAG-1 and RAG-2 with those obtained from intron data (G3PDH intron 11,

Myoglobin intron 2 and ODC introns 6 and 7) and we analyse a combined dataset of these five markers for 219 species of NWS from a number of studies by our own research group and others. Through this enlarged dataset we aim to clarify uncertain phylogenetic relationships and propose a new classification that reflects these relationships. This is the first study to cover a broad taxon sampling across the entire New World suboscine radiation, including roughly 70 % of the genera, following the Gill & Donsker (2012).

Another important aim of this paper is to explore the temporal frames of diversification within the NWS. Age estimates of divergences have been made in a number of studies (e.g. Brumfield *et al.* 2007; Ohlson *et al.* 2008; Irestedt *et al.* 2009; Derryberry *et al.* 2011). However, as the focus of these studies has been on smaller clades within the suboscine radiation, these estimates have never been synthesized to present an overview of the chronology of New World suboscine diversification. Here we put stronger focus on this issue by estimating divergence ages across the entire New World suboscine radiation.

Material and methods

Phylogenetic analyses. Together with co-workers we have generated phylogenetic hypotheses of NWS over several years, using nuclear intron markers (e.g. Ericson *et al.* 2006; Ohlson *et al.* 2007; 2008; Irestedt *et al.* 2002, 2004, 2006, 2009). Other research groups have suggested phylogenetic hypotheses with somewhat different tree topologies based on nuclear protein coding genes (Moyle *et al.* 2009; Tello *et al.* 2009). To achieve higher confidence we therefore analysed a new dataset with sequence data for three nuclear introns (G3P intron 11, Myoglobin intron 2 and ODC introns 6 and 7) together with the nuclear protein coding RAG-1 and RAG-2 genes for representatives of all major radiations in the NWS, including representatives of ca. 70 % of all recognised genera. By using sequence data downloaded from Genbank and some complementary sequencing we produced a data set of 219 NWS species with complete sequence data for all five markers. In a few cases we used sequence data from two closely related species. For computational efficiency, we excluded a few long, autapomorphic insertions in the nuclear introns to produce an aligned dataset of ca 6300 bp, of which ca. 2300 are nuclear intron data. Relationships within large and recently radiated clades, such as the Thamnophilidae, Synallaxinae and Fluvicolinae, were not the prime focus of this study and these clades have not been exhaustively sampled in relation to their species number.

We analysed the data under Maximum Likelihood (ML) and Bayesian Inference (BI) criteria using the RAxML (Stamatakis *et al.* 2008) and MrBayes 3.1.1 (Ronquist & Huelsenbeck 2003) programs, respectively. We used the AIC criterion in MrModeltest 2 (Nylander *et al.* 2004) in conjunction with PAUP* to select substitution models for each partition. For the partition by gene these were GTR+G for Myoglobin and G3PDH and GTR+G+I for ODC, RAG-1 and RAG-2. When partitioning the two RAG genes by codon, GTR+G+I was selected for 1st and 2nd positions and GTR+G for 3rd positions.

The ML analyses were conducted in RAxML v7.2.6 (Stamatakis 2006), as implemented in RAXMLGUI v0.93 (Silvestro & Michalak 2010). We performed three ML analyses with ML search and thorough bootstrap for 1 run and 1000 replicates under a GTR+G model. The dataset was partitioned by gene and branch lengths were calculated independently for each partition.

Bayesian Inference analyses were run on the University of Oslo Bioportal (www.bioportal.uio.no). Individual introns were treated as separate partitions in all analyses, but we tested different partition schemes for the RAG data by partitioning either by gene (5 partitions), by codon positions (6 partitions) or by both gene and codon position (9 partitions). We analysed the combined data set and also performed separate analyses on each gene individually and on the RAG and nuclear intron data respectively. Several preliminary analyses were performed to explore the effect of chain temperature on the mixing behaviour of the chains. We found that lowering the temperature to 0.05 resulted in better mixing of the chains than the default value of 0.2. Partitions were unlinked to allow independent parameter estimation for each one. Analyses were run for 50 M generations with 4 incrementally heated chains and trees sampled every 1000th generation. Trees saved before the target distribution had been reached (the burn-in phase) were discarded and the final phylogenetic tree was estimated from 40000 trees from each run.

Divergence date estimates. Divergence dates were estimated in BEAST v1.5.3. No topological constraints were enforced, each marker was treated as a separate partition, and substitution and clock models were unlinked

between partitions, but tree models were kept linked. We used the same substitution models for each partition as in the 5 partition Bayesian analysis (see above). An uncorrelated lognormal distribution was assumed for the molecular clock model and a Yule process was assumed for the tree prior. As a calibration point we used the split of *Acanthisitta* Lafresnaye from the rest of the Passeriformes, as this has been linked to the geographical separation of New Zealand from the remainder of Gondwanaland (Barker *et al.* 2002; Ericson *et al.* 2002). New Zealand is estimated to have become isolated from mainland Gondwanaland at 85–65 Mya (Ladiges & Cantrill 2007). To account for the uncertainty in age estimates we set the age of the split between *Acanthisitta* and the rest of Passeriformes as a normally distributed prior with the median at 76 Mya, and a standard deviation of 8 Ma (quartiles 2.5% = 60.3 Mya, 5% = 62.8 Mya, 95% = 89.2 Mya, 97.5% = 91.7 Mya. All other priors were kept at default values.

Results

Phylogenetic results

The Bayesian analyses of the concatenated dataset produced a well resolved tree with strong support for most nodes (Fig. 1). We count a Bayesian posterior probability (PP) of 0.97 and above and a Maximum Likelihood bootstrap value (ML) of 90 and above as strong support. Regarding the RAG and nuclear intron partition trees, the RAG tree (Fig. 2) is nearly identical to the ones presented in Moyle *et al.* (2009) and Tello *et al.* (2009) and the nuclear intron tree (Fig. 3) is largely congruent with previously published trees based on these nuclear introns (e.g. Irestedt *et al.* 2002, 2004, 2009; Ohlson *et al.* 2007, 2008). Instances of conflicting signal between the nuclear introns were few and without exception associated with short internodes. The Maximum Likelihood analyses of the concatenated dataset produced a tree that was nearly identical to the Bayesian tree, but there are two instances in which well supported relationships in the BI analyses are not found in the ML tree. First, the basal divergences in Rhynchocyclidae differ between the BI and the ML trees. The sister relationship of *Cnipodectes* P. L. Sclater & Salvin and *Taeniotriccus* Berlepsch & Hartert to Todiostroinae is not recovered in the ML tree, but *Cnipodectes*/*Taeniotriccus* is instead recovered as the sister clade to the remainder of Rhynchocyclidae, although with very low support. Second, basal relationships in Tyranninae are slightly different in the ML tree, where *Ramphotrigon* G. R. Gray is the sister to Myiarchini and *Legatus* P. L. Sclater sister to Tyrannini, with *Attila* Lesson placed as the sister to the remainder of Tyranninae. ML support values are not very strong in this part of the tree.

A combination of RAG and nuclear intron data yielded stronger support for some relationships that were unresolved by one or both of these datasets on their own. Among the more notable are the following: 1) Conopophagidae and Melanopareiidae group with Thamnophilidae; 2) Grallariidae and Rhinocryptidae are sequential sister groups to the remainder of Furnarioidea; 3) basal relationships within Furnariidae are generally better resolved; 4) *Platyrinchus* Desmarest and *Neopipo* P. L. Sclater & Salvin form a strongly supported clade, Platyrinchidae (also including *Calyptura*, see Ohlson *et al.* 2012) but still occupy an unresolved position at the base of the Tyrant Flycatcher clade.

Poorly resolved nodes in the combined tree are mostly the result of low support in both partitions. In the current study the following relationships are unresolved due to low support throughout: 1) between Melanopareiidae, Conopophagidae and Thamnophilidae; 2) between Euchrepomidinae (previously *Terenura*; see Bravo *et al.* 2012), Myrmornithinae and Thamnophilinae; 3) between Furnariinae, Philydorinae and Synallaxinae; 4) between Oxyruncidae, Onychorhynchidae (Onychorhynchini in Tello *et al.* 2009) and Tityridae, and 5) between Hirundineinae, Elaeniinae and the remainder of Tyrannidae. Some unresolved nodes in the combined tree are caused by conflicts between strongly supported topologies (i.e. with a PP of 0.97 or higher) in the RAG and nuclear intron datasets. In the combined tree these signals cancel each other out, resulting in unresolved relationships. At higher taxonomic levels this affects three regions of the NWS tree: 1) the position of *Xenops* Illiger in relation to Dendrocolaptidae and Furnariidae; 2) the position of Cotingidae in relation to Pipridae and Tyrannoidea; 3) the position of *Piprites* Cabanis, Platyrinchidae and *Tachuris* Lafresnaye in relation to Rhynchocyclidae and Tyrannidae. These unresolved relationships are all located in regions of the tree with short internodes, especially the ones in Tyrannida.

Divergence dates. In Fig. 4 we present a simplified chronogram for the NWS. The split between Furnariida

and Tyrannida took place in the Early Eocene (55,5±8 Mya). The timing of subsequent divergence events proceeded quite differently in the two clades. In Furnariida, the initial divergences took place in the middle and late Eocene (44–37 Mya), with the extant families emerging in rapid succession. In Tyrannida, on the other hand, the extant clades trace their origin back to the Oligocene (32–25 Mya). Subsequent diversification events show common patterns with a number of small clades that date back to the early period, while five species-rich clades began to diversify around or just after the mid-Miocene climatic optimum (16–12 Mya).

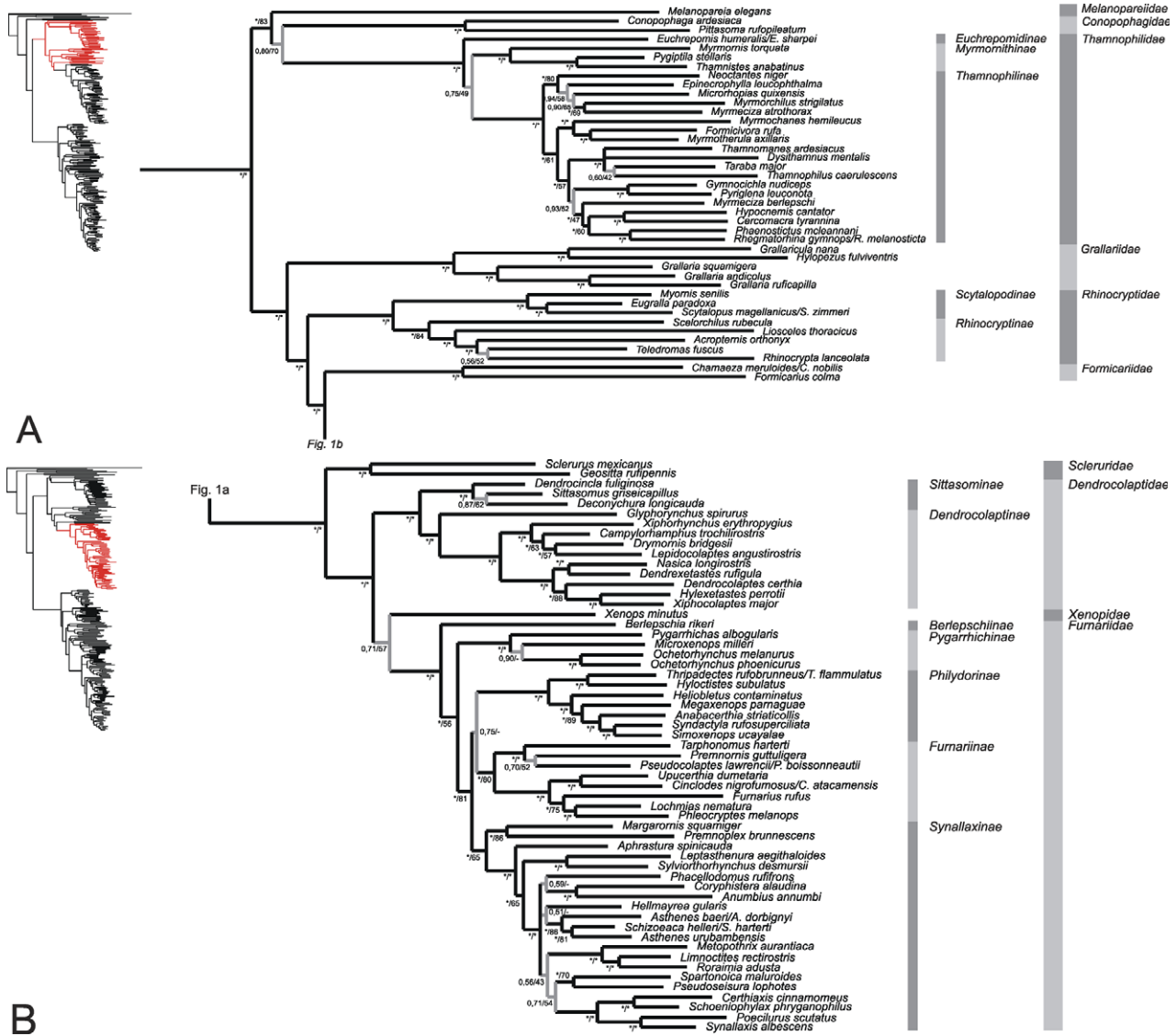


FIGURE 1A–B. Bayesian consensus tree of the New World Suboscines based on the 5-marker analysis of 219 ingroup taxa. A) Furnariida: Thamnophiloidea through Formicariidae, B) Furnariida: Scleruridae through Furnariidae. Branch support values are presented as Bayesian posterior probabilities (PP) and Maximum Likelihood (ML) bootstrap support values at each node (PP/ML). An asterisk (*) denotes a PP value of 0,98 or higher and a ML value at 90 or higher. Families and subfamilies as in Table 2.

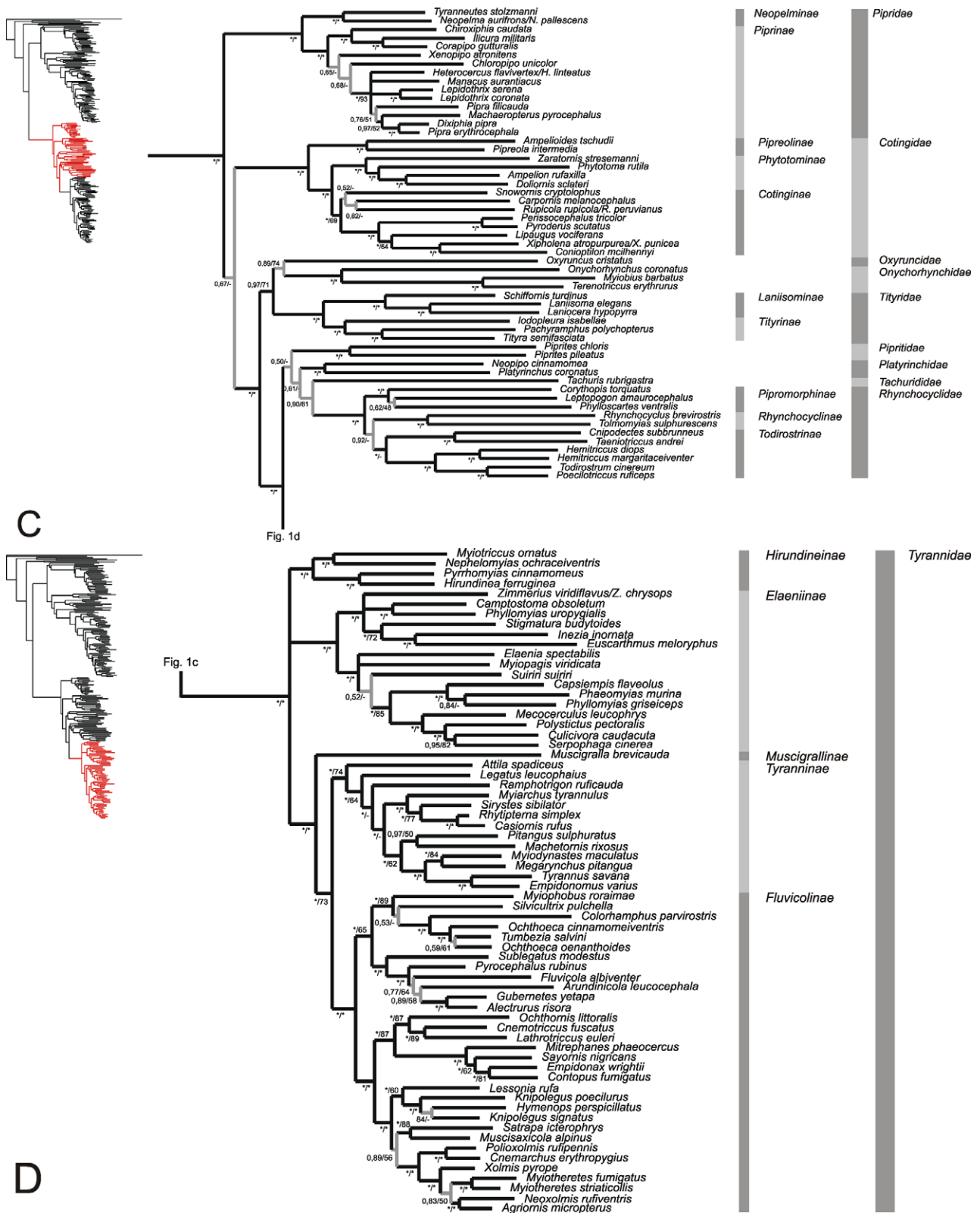


FIGURE 1C–D. Bayesian consensus tree of the New World Suboscines based on the 5-marker analysis of 219 ingroup taxa. C) Tyrannida: Pipridae, Cotingidae and Oxyruncidae through Rhynchocyclidae, D) Tyrannida: Tyrannidae. Branch support values are presented as Bayesian posterior probabilities (PP) and Maximum Likelihood (ML) bootstrap support values at each node (PP/ML). An asterisk (*) denotes a PP value of 0,98 or higher and a ML value at 90 or higher. Families and subfamilies as in Table 2.



FIGURE 2. Consensus tree for the Bayesian analyses of the RAG-1 and RAG-2 data set. Nodes with PP support below 0,97 are in grey.

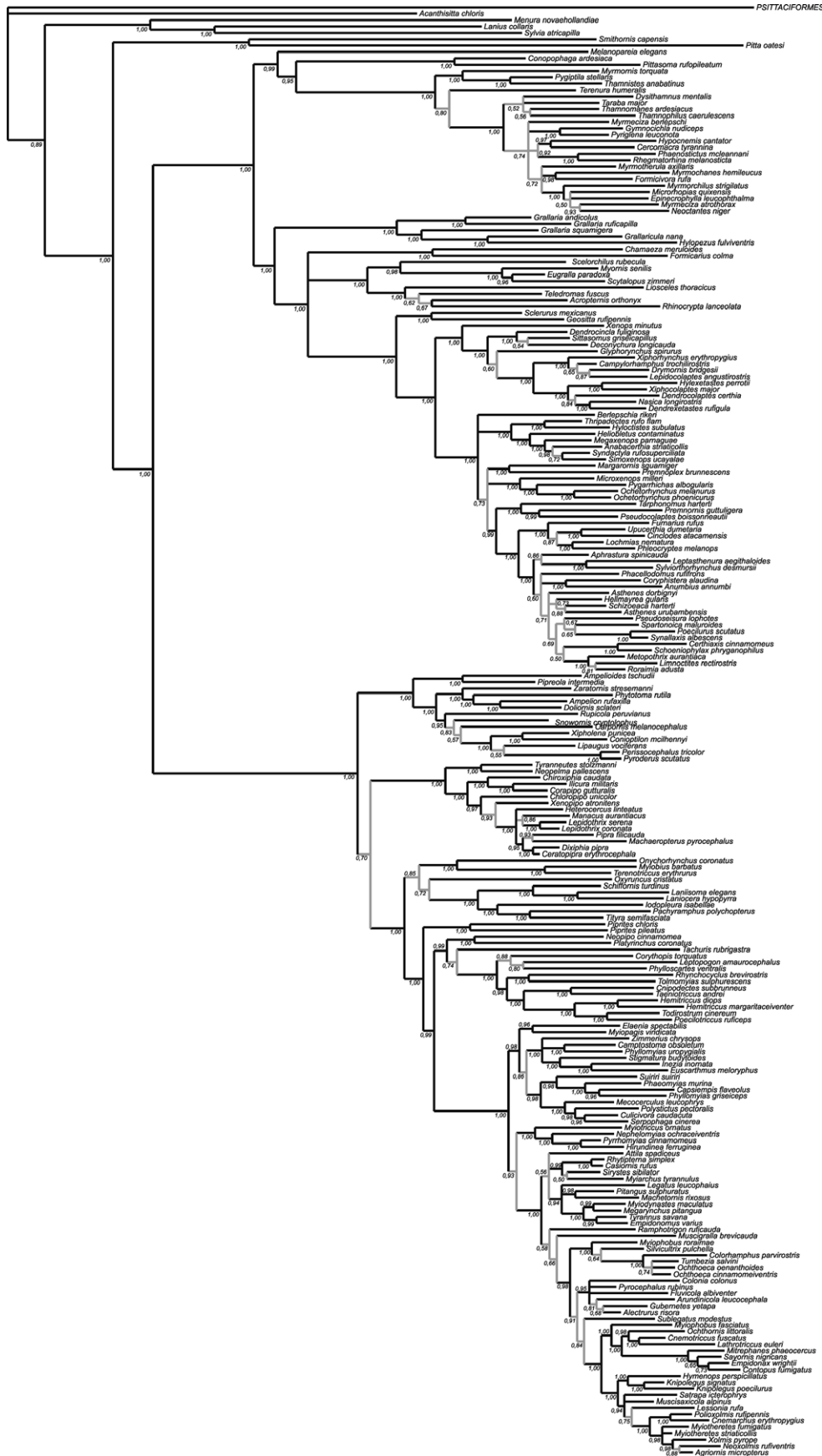


FIGURE 3. Consensus tree for the Bayesian analyses of the nuclear intron data set. Nodes with PP support below 0,97 are in grey.

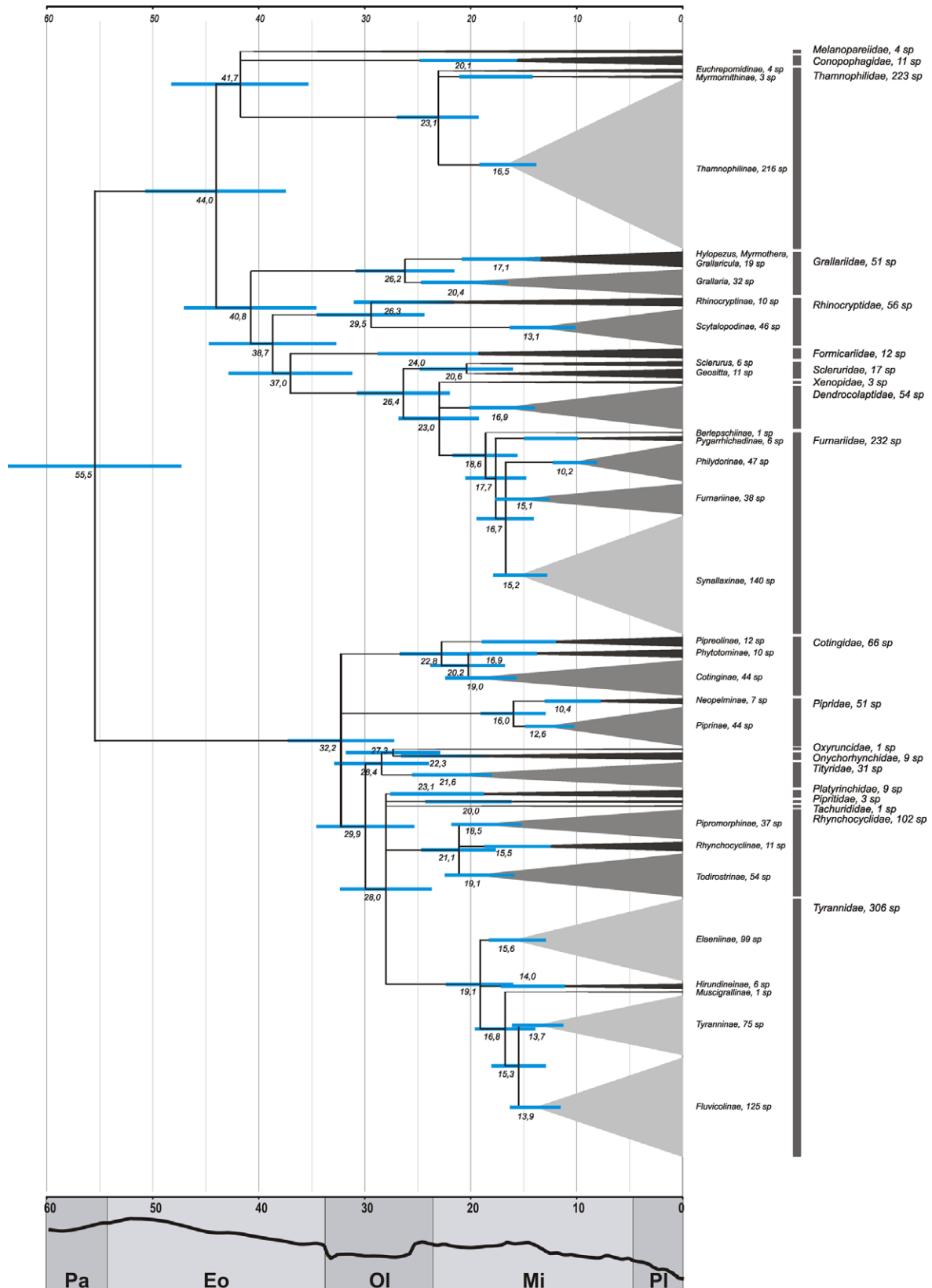


FIGURE 4. simplified chronogram from the BEAST analyses, illustrating the crown age and number of extant species for most clades recognized as family level taxa in our proposed classification. Unresolved nodes are collapsed and species richness of each terminal clade is illustrated by its height. Clades are coloured in accordance with their species number: black: ≤ 19 species; medium grey: 31–54 species, light grey: ≥ 75 species. Blue bars show the 95% confidence interval of the age estimates. The curve at the bottom of the chronogram is a simplified version of the δO^{18} curve of Zachos *et al.* (2001), serving as a proxy for global temperature.

TABLE 1. List of taxa, with Genbank accession numbers, included in this study. Sample identification is included only for samples for which new sequence data were generated for this study.

Scientific name	Sample id	RAG-1	RAG-2	g3p	myo	odc
Melanoparceidae						
<i>Melanoparceia elegans</i>	ZMUC 125046	FJ461227	FJ461001	KC157400	KC157441	KC157480
Conopophagidae						
<i>Conopophaga ardesiaca</i>	ZMUC 137055	AY443271	AY443125	KC157401	KC157442	KC157481
<i>Pittasoma rufipileatum</i>	ZMUC 125667	FJ461218	FJ460992	KC157402	KC157443	KC157482
Thamnophilidae						
<i>Cercomacra tyrannina</i>	ZMUC 126119	FJ461191	FJ461081	KC157403	KC157444	KC157483
<i>Dysithamnus mentalis</i>		FJ461181	FJ461071	AY677042	AY676995	GQ925877
<i>Epinecrophylla leucophthalma</i>	ZMUC S1306	KC157543	KC157551	AY677046	AY676999	KC157484
<i>Euchrepomis humeralis</i>		--	--	AY677051	AY677004	GQ925878
<i>Euchrepomis sharpei</i>		FJ461190	FJ461080	--	--	--
<i>Formicivora rufa</i>	NRM 947236	FJ461188	FJ461078	AY677053	AY677005	KC157485
<i>Gymnocichla nudiceps</i>	ZMUC S2732	FJ461197	FJ461087	AY677071	AY677021	KC157486
<i>Hypocnemis cantator</i>	ZMUC S1300	FJ461194	FJ461084	AY677061	AY677011	KC157487
<i>Microhospias quixensis</i>	FMNH 321993	FJ461187	FJ461077	AY677044	AY676997	KC157488
<i>Myrmeciza atrothorax</i>	ZMUC 128283	FJ461202	FJ461092	KC157404	KC157445	KC157489
<i>Myrmeciza berlepschi</i>	ZMUC 126182	FJ461203	FJ461093	AY677070	AY677020	KC157490
<i>Myrmochanes hemileucus</i>	LSUMZ B-7245	FJ461196	FJ461086	AY677062	AY677012	KC157491
<i>Myrmorchilus strigilatus</i>	NRM 956742	FJ461185	FJ461075	AY677054	AY677006	KC157492
<i>Myrmornis torquata</i>	LSUMZ B-3228	FJ461205	FJ461095	AY677072	AY677022	KC157493
<i>Myrmotherula axillaris</i>	ZMUC 126870	FJ461183	FJ461073	AY677048	AY677001	KC157494
<i>Neotantes niger</i>	FMNH 321806	FJ461178	FJ461068	AY677057	AY677007	KC157495
<i>Phaenostictus mcleannani</i>	ZMUC S1647	FJ461210	FJ461100	AY677077	AY677027	KC157496
<i>Pygiptila stellaris</i>	LSUMZ B-9703	FJ461177	FJ461067	AY677039	AY676992	KC157497
<i>Pyrgilena leuconota</i>	ZMUC S2007	FJ461192	FJ461082	AY677056	AY065782	KC157498
<i>Rhegatorhina gymnops</i>		FJ461208	FJ461098	--	--	--
<i>Rhegatorhina melanosticta</i>	ZMUC S1825	--	--	AY677075	AY677025	KC157499
<i>Taraba major</i>	NRM 956694	FJ461174	FJ461064	AY677032	AY676985	KC157500
<i>Thamnistes anabatinus</i>	ZMUC S1607	FJ461180	FJ461070	AY677040	AY676993	KC157501
<i>Thamnomanes ardesiacus</i>	ZMUC 126489	FJ461182	FJ461072	KC157405	KC157446	KC157502
<i>Thamnophilus caeruleus</i>		FJ461176	FJ461066	AY336587	AY065783	DQ435504

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TABLE 1. (continued)

Scientific name	Sample id	RAG-1	RAG-2	g3p	myo	odc
Grallariidae						
<i>Grallaria andicola</i>	ZMUC 124615	FJ461214	FJ460988	KC157406	KC157447	KC157503
<i>Grallaria ruficapilla</i>	ZMUC 138196	FJ461215	FJ460989	KC157407	KC157448	KC157504
<i>Grallaria squamigera</i>	ZMUC 124629	KC157544	KC157552	AY677078	AY065778	GQ140073
<i>Grallaricula nana</i>	ZMUC 138203	FJ461217	FJ460991	KC157408	KC157449	KC157505
<i>Itylopezus fuviventris</i>	ZMUC S1427	KC157545	KC157553	KC157409	AY065779	KC157506
Rhinocryptidae						
<i>Acropternis orthonyx</i>		FJ461224	FJ460998	GQ925879	GQ925894	GQ925860
<i>Engralla paradoxa</i>		FJ461225	FJ460999	GQ925888	GQ925903	GQ925871
<i>Liosceles thoracicus</i>		FJ461223	FJ460997	GQ925890	GQ925905	GQ925873
<i>Myornis senilis</i>		FJ461226	FJ461000	GQ925883	GQ925898	GQ925865
<i>Rhinocrypta lanceolata</i>		FJ461221	FJ460995	DQ438953	AY065775	DQ435499
<i>Scelorchilus rubecula</i>		FJ461220	FJ460994	GQ925889	GQ925904	GQ925872
<i>Scytalopus magellanicus</i>		AY443331	AY443226	--	--	--
<i>Scytalopus zimmeri</i>		--	--	GQ925886	GQ925901	GQ925869
<i>Teledromas fuscus</i>		FJ461222	FJ460996	GQ925881	GQ925896	GQ925863
Formicariidae						
<i>Chantaeza meruloides</i>		--	--	AY590095	AY065776	GQ140072
<i>Chantaeza nobilis</i>		FJ461211	FJ460985	--	--	--
<i>Formicarius colma</i>	ZMUC 137095	AY056993	AY443147	KC157410	KC157450	KC157507
Scleruridae						
<i>Geositta rufipennis</i>	ZMUC S290	KC157546	KC157554	AY590062	AY590052	GQ140039
<i>Sclerurus mexicanus</i>		FJ461150	FJ461052	AY590079	AY590059	GQ140043
Xenopidae						
<i>Xenops mimutus</i>		FJ461153	FJ461055	AY590082	AY590060	EF212127
Dendrocolaptidae						
<i>Campylorhynchus trochilirostris</i>		AY443264	AY443112	AY590085	AY442961	EF212093
<i>Decorychura longicauda</i>		FJ461158	FJ460974	AY590086	AY442963	EF212097
<i>Dendrocyastes rufigula</i>		FJ461163	FJ460979	GQ140174	AY442973	GQ140020
<i>Dendrocincla fuliginosa</i>		FJ461157	FJ460973	GQ140175	AY065770	GQ140021
<i>Dendrocolaptes certhia</i>		FJ461166	FJ460982	GQ140177	EU739955	GQ140023
<i>Drymornis bridgesii</i>		FJ461161	FJ460977	AY590088	AY065768	GQ140025
<i>Glyphorhynchus spirurus</i>		FJ461160	FJ460976	AY590089	AY442966	GQ140026

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TABLE 1. (continued)

Scientific name	Sample id	RAG-1	RAG-2	g3p	myo	odc
<i>Hylexetastes perrotii</i>		FJ461164	FJ460980	GQ140179	AY442974	GQ140027
<i>Lepidocolaptes angustirostris</i>		FJ461168	FJ460984	AY336576	AY065767	DQ435486
<i>Nasica longirostris</i>		FJ461162	FJ460978	AY590091	AY442969	GQ140030
<i>Sittasomus griseicapillus</i>		FJ461159	FJ460975	AY590092	AY065771	GQ140031
<i>Xiphocolaptes major</i>		FJ461165	FJ460981	AY590093	AY065769	EF212129
<i>Xiphorhynchus erythropygius</i>	ZMUC S1616	KC157547	KC157555	AY590094	AY442971	EF212130
Furnariidae						
<i>Anabacerthia striaticollis</i>		FJ461141	FJ461043	AY998219	AY998237	GQ140040
<i>Anumbius annumbi</i>		FJ461128	FJ461030	AY590072	AY065765	EF212088
<i>Aphrastura spinicauda</i>		FJ461110	FJ461012	AY998206	AY998225	GQ140048
<i>Asthenes baeri</i>		FJ461125	FJ461027	--	--	--
<i>Asthenes dorbignyi</i>		--	--	GQ140194	GQ140216	GQ140049
<i>Asthenes urubambensis</i>		FJ461124	FJ461026	AY998214	AY998232	EF212090
<i>Berlepschia rikeri</i>		FJ461140	FJ461042	AY590075	AY590057	EF212092
<i>Certhiaxis cinnamomeus</i>		FJ461122	FJ461024	AY998213	AY998231	GQ140055
<i>Cinclodes atacamensis</i>		--	--	GQ140188	GQ140210	GQ140038
<i>Cinclodes nigrofumosus</i>		FJ461107	FJ461009	--	--	--
<i>Coryphistera alaudina</i>		FJ461129	FJ461031	AY590073	AY065766	EF212095
<i>Furnarius rufus</i>	NRM 976711	AY056995	AY443149	KC157411	KC157451	KC157508
<i>Heliobletus contaminatus</i>		FJ461152	FJ461054	AY998222	AY998240	EF212102
<i>Hellmayrea gularis</i>		FJ461120	FJ461022	AY998211	AY998230	GQ140059
<i>Hylocistetes subulatus</i>		FJ461145	FJ461047	GQ140189	GQ140211	GQ140041
<i>Leptasthenura aegithaloides</i>	ZMUC 126280	FJ461111	FJ461013	KC157412	FU054009	KC157509
<i>Linnocittes rectirostris</i>		FJ461108	FJ461010	AY996358	AY996347	GQ140061
<i>Lochmias nematura</i>		FJ461151	FJ461053	AY590081	AY065755	EF212106
<i>Margarornis squamiger</i>	ZMUC S1112	KC157548	KC157556	AY590074	AY065759	EF212107
<i>Megaxenops parnaguae</i>		FJ461155	FJ461057	AY998223	AY998241	EF212108
<i>Metopothrix aurantiaca</i>		FJ461131	FJ461033	AY998224	GQ140224	GQ140062
<i>Microxenops milleri</i>		FJ461154	FJ461056	GQ140193	GQ140215	GQ140047
<i>Ochetorhynchus melanurus</i>		FJ461106	FJ461008	EF212144	EF212135	EF212094
<i>Ochetorhynchus phoenicurus</i>		FJ461105	FJ461007	EF212145	EF212136	EF212099
<i>Phacellodomus rufifrons</i>		FJ461127	FJ461029	GQ140203	GQ140226	GQ140065
<i>Phleocryptes melanops</i>		FJ461109	FJ461011	AY996360	AY996348	GQ140066

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TABLE 1. (continued)

Scientific name	Sample id	RAG-1	RAG-2	g3p	myo	odc
<i>Poecilurus scitatus</i>		FJ461117	FJ461019	AY998210	AY998229	EF212120
<i>Prennoplex brunnescens</i>		FJ461135	FJ461037	AY998216	AY998234	EF212111
<i>Prennornis guttuligera</i>		FJ461134	FJ461036	AY998215	AY998233	EF212112
<i>Pseudocolaptes boissonneaui</i>		--	--	AY998217	AY998235	EF212113
<i>Pseudocolaptes lawrencii</i>		FJ461139	FJ461041	--	--	--
<i>Pseudoisoura lophotes</i>	NRM 976799	FJ461138	KC157557	AY998218	AY998236	EF212114
<i>Pygarrhichas albogularis</i>		FJ461156	FJ461058	AY590084	AY065760	EF212115
<i>Roraimia adusta</i>		FJ461136	FJ461038	GQ140190	GQ140212	GQ140042
<i>Schizoeaca harterti</i>		--	--	AY998207	AY998226	EF212116
<i>Schizoeaca helleri</i>		FJ461114	FJ461016	--	--	--
<i>Schoenophylax phryganophilus</i>		FJ461115	FJ461017	AY998209	AY998228	EF212117
<i>Simoxenops ucayalae</i>		FJ461143	FJ461045	GQ140191	GQ140213	GQ140044
<i>Spartanoica maluroides</i>		FJ461112	FJ461014	GQ140206	GQ140229	GQ140069
<i>Sylviorhynchus desmursii</i>		FJ461113	FJ461015	GQ140207	GQ140230	GQ140070
<i>Synallaxis albescens</i>	NRM 956720	FJ461118	FJ461020	KC157413	KC157452	KC157510
<i>Syndactyla rufosuperciliata</i>		FJ461142	FJ461044	AY998220	AY998238	EF212121
<i>Tarphonomus harterti</i>		FJ461104	FJ461006	EF212147	EF212138	EF212123
<i>Thripadectes flammulatus</i>		--	--	AY590077	AY065757	GQ140045
<i>Thripadectes rufobrunneus</i>		FJ461148	FJ461050	--	--	--
<i>Upucerthia dumetaria</i>		FJ461103	FJ461005	EF212151	EF212142	EF212132
Pipridae						
<i>Chiroxiphia caudata</i>		FJ501612	FJ501792	DQ435462	DQ435516	DQ435477
<i>Chloropipo unicolor</i>	ZMUC 125221	KC157549	KC157558	KC157414	KC157453	KC157511
<i>Corapipo gutturalis</i>	USNMB10631	FJ501621	FJ501801	KC157415	KC157454	KC157512
<i>Dixiphia pipra</i>	ZMUC 126081	FJ501625	FJ501805	KC157416	KC157455	KC157513
<i>Heterocercus flavivertex</i>		FJ501642	FJ501822	--	--	--
<i>Heterocercus limteatus</i>	NRM 569488	--	--	KC157417	KC157456	KC157514
<i>Ilicura militaris</i>	NRM 569489	FJ501645	FJ501825	KC157418	KC157457	KC157515
<i>Lepidothrix coronata</i>		FJ501655	FJ501835	EU231647	EU231745	EU231846
<i>Lepidothrix serena</i>	USNMB10572	FJ501656	FJ501836	KC157419	KC157458	KC157516
<i>Machaeropterus pyrocephalus</i>	NRM 569490	FJ501662	FJ501842	KC157420	KC157459	KC157517
<i>Manacus aurantiacus</i>	USNMB02315	FJ501665	FJ501845	KC157421	KC157460	KC157518
<i>Neopelma aurifrons</i>		FJ501689	FJ501869	--	--	--

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TABLE 1. (continued)

Scientific name	Sample id	RAG-1	RAG-2	g3p	myo	odc
<i>Neopelma pallescens</i>		--	--	EU231646	EU231744	EU231845
<i>Pipra erythrocephala</i>	ZMUC 126397	FJ501713	FJ501893	KC157422	KC157461	KC157519
<i>Pipra flicauda</i>	ZMUC 126686	FJ501714	FJ501894	KC157423	KC157462	KC157520
<i>Tyrannetes stolzmanni</i>		FJ501760	FJ501940	EU231645	EU231743	EU231844
<i>Xenopipo atronitens</i>	ZMUC 128321	FJ501766	FJ501946	KC157424	KC157463	KC157521
Cotingidae						
<i>Amphispiza bilineata</i>		FJ501597	FJ501777	DQ470516	DQ470543	EU231841
<i>Amphispiza rufaxilla</i>	ZMUC 121450	FJ501598	FJ501778	KC157425	KC157464	KC157522
<i>Carpornis melanocephalus</i>	ZMUC 81356	FJ501608	FJ501788	KC157426	KC157465	KC157523
<i>Coniptionil mcilhennyi</i>	KU B-1416	FJ501619	FJ501799	DQ470520	DQ470546	KC157524
<i>Doliornis sclateri</i>	ZMUC 91610	FJ501626	FJ501806	DQ470523	DQ470550	KC157525
<i>Lipaugus vociferans</i>	ZMUC 128387	FJ501660	FJ501840	KC157427	KC157466	KC157526
<i>Perissocephalus tricolor</i>	AMNH uncat.	FJ501702	FJ501882	DQ470531	DQ470557	KC157527
<i>Phytotoma rutila</i>		FJ501712	FJ501892	AY336581	AY338743	DQ435494
<i>Pipreola intermedia</i>	ZMUC 126043	FJ501716	FJ501896	KC157428	KC157467	KC157528
<i>Pyroderus scutatus</i>		FJ501734	FJ501914	AY336582	AY065786	DQ435498
<i>Rupicola peruvianus</i>		--	--	DQ435474	DQ435526	DQ435500
<i>Rupicola rupicola</i>		FJ501740	FJ501920	--	--	--
<i>Snowornis cryptolophus</i>	ZMUC 126004	FJ501747	FJ501927	DQ470538	DQ470565	KC157529
<i>Xipholena atropurpurea</i>		FJ501768	FJ501948	--	--	--
<i>Xipholena punicea</i>	ZMUC 130641	--	--	DQ470541	DQ470568	KC157530
<i>Zaratornis stresemanni</i>		FJ501770	FJ501950	DQ470542	DQ470569	EU231842
Oxyruncidae						
<i>Oxyruncus cristatus</i>		FJ501698	FJ501878	AY336572	AY338745	DQ435492
Onychorhynchidae						
<i>Myiobius barbatus</i>		FJ501675	FJ501855	JF970145	JF970156	JF970167
<i>Onychorhynchus coronatus</i>		FJ501696	FJ501876	--	--	--
<i>Onychorhynchus occidentalis</i>		--	--	EU231653	EU231751	EU231853
<i>Terenotriccus erythrus</i>		FJ501753	FJ501933	EU231655	EU231753	EU231855
Tityridae						
<i>Iodopleura isabellae</i>		FJ501648	FJ501828	DQ435467	DQ435519	DQ435485
<i>Laniisoma elegans</i>		FJ501651	FJ501831	EU231649	EU231747	EU231848
<i>Laniocera hypopyrra</i>		FJ501652	FJ501832	DQ470527	DQ470554	EU231849

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TABLE 1. (continued)

Scientific name	Sample id	RAG-1	RAG-2	g3p	myo	odc
<i>Pachyrhamphus polychopterus</i>		FJ501699	FJ501879	AY336573	AY338747	DQ435493
<i>Schiffornis turdina</i>		FJ501743	FJ501923	EU231648	EU231746	EU231847
<i>Tityra semifasciata</i>		FJ501754	FJ501934	JF970144	JF970155	JF970166
Pipritidae NEW TAXON						
<i>Piprites chloris</i>		FJ501717	FJ501897	EU231656	EU231754	EU231856
<i>Piprites pileatus</i>	ZMUC 128817	JF970177	KC157559	DQ435472	DQ435524	DQ435496
Platyrrhinidae						
<i>Neopipo cinnamomea</i>		FJ501690	FJ501870	EU231658	EU231756	EU231858
<i>Platyrrhinus coronatus</i>		FJ501720	FJ501900	JF970147	JF970158	JF970169
Tachuritidae NEW TAXON						
<i>Tachuris rubrigastra</i>		FJ501751	FJ501931	EU231657	EU231755	EU231857
Rhynchocyclidae						
<i>Cnipodectes subbrunneus</i>		FJ501616	FJ501796	EU231663	EU231761	EU231863
<i>Corythopsis torquatus</i>		FJ501622	FJ501802	JF970148	JF970159	JF970170
<i>Hemitriccus diops</i>		FJ501638	FJ501818	EU231668	EU231766	EU231868
<i>Hemitriccus margaritaceiventer</i>		FJ501641	FJ501821	EU231669	EU231767	EU231869
<i>Leptopogon amaurocephalus</i>		FJ501657	FJ501837	DQ435468	DQ435520	DQ435487
<i>Phylloscartes ventralis</i>		FJ501711	FJ501891	EU231659	EU231757	EU231859
<i>Poecilotriccus ruficeps</i>		FJ501723	FJ501903	EU231666	EU231764	EU231866
<i>Rhynchocyclus brevirostris</i>		FJ501738	FJ501918	JF970149	JF970160	JF970171
<i>Taeniotriccus andrei</i>	USNM B06904	FJ501752	FJ501932	KC157429	KC157468	KC157531
<i>Todirostrum cinereum</i>		FJ501755	FJ501935	AY336575	AY338740	DQ435506
<i>Tolmomyias sulphureus</i>		FJ501757	FJ501937	JF970150	JF970161	JF970172
Tyrannidae						
<i>Agrionis micropterus</i>		FJ501594	FJ501774	JF970154	JF970165	JF970176
<i>Alectrurus risora</i>		FJ501595	FJ501775	EU231722	EU231820	EU231923
<i>Arundinicola leucocephala</i>		FJ501601	FJ501781	EU231721	EU231819	EU231922
<i>Attila spadiceus</i>		FJ501603	FJ501783	EU231697	EU231795	EU231898
<i>Camptostoma obsoletum</i>		FJ501605	FJ501785	EU231689	EU231787	EU231890
<i>Capsiempis flaveola</i>		FJ501606	FJ501786	EU231672	EU231770	EU231873
<i>Casiornis rufus</i>		FJ501609	FJ501789	EU231703	EU231801	EU231904
<i>Chenarnichus erythropygius</i>		FJ501614	FJ501794	EU231742	EU231840	EU231943
<i>Chenotriccus fuscatus</i>		FJ501615	FJ501795	EU231727	EU231825	EU231928

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TABLE 1. (continued)

Scientific name	Sample id	RAG-1	RAG-2	g3p	myo	odc
<i>Colorhamphus parvirostris</i>	NRM 570023	FJ501618	FJ501798	KC157430	KC157469	KC157532
<i>Contopus fumigatus</i>	ZMUC 128832	FJ501620	FJ501800	KC157431	KC157470	KC157533
<i>Culicivora canadacuta</i>		FJ501624	FJ501804	EU231680	EU231778	EU231881
<i>Elaenia spectabilis</i>		FJ501628	FJ501808	JF970151	JF970162	JF970173
<i>Empidonax wrightii</i>	UWBM 66178	FJ501629	FJ501809	KC157432	KC157471	KC157534
<i>Empidonomus varius</i>		FJ501630	FJ501810	EU231711	EU231809	EU231912
<i>Euscarthmus meloryphus</i>		FJ501631	FJ501811	EU231684	EU231782	EU231885
<i>Fluvicola albiventer</i>		FJ501633	FJ501813	DQ435465	DQ435517	DQ435481
<i>Gubernetes yetapa</i>		FJ501635	FJ501815	AY336578	AY338739	DQ435483
<i>Hirundinea ferruginea</i>		FJ501643	FJ501823	EU231692	EU231790	EU231893
<i>Hymenops perspicillatus</i>		FJ501644	FJ501824	EU231732	EU231830	EU231933
<i>Inezia inornata</i>		FJ501646	FJ501826	DQ435466	DQ435518	DQ435484
<i>Knipolegus poecilurus</i>	ZMUC 126362	FJ501649	FJ501829	KC157433	KC157472	KC157535
<i>Knipolegus signatus</i>	ZMUC 126257	FJ501650	FJ501830	KC157434	KC157473	KC157536
<i>Lathrotriccus euleri</i>		FJ501653	FJ501833	EU231726	EU231824	EU231927
<i>Legatus leucophaius</i>		FJ501654	FJ501834	EU231705	EU231803	EU231906
<i>Lessonia rufa</i>		FJ501658	FJ501838	EU231733	EU231831	EU231934
<i>Machetornis rixosus</i>		FJ501663	FJ501843	EU231706	EU231804	EU231907
<i>Mecocerculus leucophrys</i>		FJ501667	FJ501847	EU231676	EU231774	EU231877
<i>Megarynchus pitangua</i>		FJ501668	FJ501848	EU231709	EU231807	EU231910
<i>Mitrephanes phaeocercus</i>		FJ501670	FJ501850	EU231729	EU231827	EU231930
<i>Muscigralla brevicauda</i>		FJ501671	FJ501851	EU231712	EU231810	EU231913
<i>Muscisaxicola alpinus</i>	ZMUC 125219	KC157550	KC157560	EU231735	EU231833	EU231936
<i>Myiarchus tyrannulus</i>		FJ501674	FJ501854	DQ435469	DQ435521	DQ435489
<i>Myiodynastes maculatus</i>		FJ501676	FJ501856	EU231710	EU231808	EU231911
<i>Myiopagis viridicata</i>		FJ501680	FJ501860	DQ435470	DQ435522	DQ435490
<i>Myiophobus roraimae</i>	ZMUC 128167	FJ501682	FJ501862	KC157435	KC157474	KC157537
<i>Myiotheretes fumigatus</i>		FJ501684	FJ501864	EU231737	EU231835	EU231938
<i>Myiotheretes striaticollis</i>	UWBM 77238	FJ501685	FJ501865	KC157436	KC157475	KC157538
<i>Myiothricus ornatus</i>		FJ501686	FJ501866	EU231691	EU231789	EU231892
<i>Neoxolmis rufiventris</i>		FJ501691	FJ501871	EU231739	EU231837	EU231940
<i>Nephelomyias ochraceiventris</i>		FJ501681	FJ501861	EU231696	EU231794	EU231897
<i>Ochthoeca cinnamomeiventris</i>	ZMUC 134976	FJ501692	FJ501872	KC157437	KC157476	KC157539

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TABLE 1. (continued)

Scientific name	Sample id	RAG-1	RAG-2	g3p	myo	odc
<i>Ochthoeca oenanthoides</i>		FJ501693	FJ501873	JF970152	JF970163	JF970174
<i>Ochthornis littoralis</i>		FJ501694	FJ501874	JF970153	JF970164	JF970175
<i>Phaeomyias murina</i>		FJ501703	FJ501883	EU231673	EU231771	EU231874
<i>Phyllomyias griseiceps</i>		FJ501708	FJ501888	EU231675	EU231773	EU231876
<i>Phyllomyias uropygialis</i>		FJ501706	FJ501886	EU231685	EU231783	EU231886
<i>Pitangus sulphuratus</i>		FJ501719	FJ501899	EU231707	EU231805	EU231908
<i>Polioptilnis rufipennis</i>		FJ501726	FJ501906	EU231741	EU231839	EU231942
<i>Polystictus pectoralis</i>		FJ501727	FJ501907	EU231679	EU231777	EU231880
<i>Pyrocephalus rubinus</i>		FJ501733	FJ501913	EU231720	EU231818	EU231921
<i>Pyrrhomyias cinnamomeus</i>		FJ501735	FJ501915	EU231693	EU231791	EU231894
<i>Ramphotrigon ruficauda</i>		FJ501737	FJ501917	EU231701	EU231799	EU231902
<i>Rhytipterna simplex</i>		FJ501739	FJ501919	EU231704	EU231802	EU231905
<i>Satrapa icterophrys</i>		FJ501741	FJ501921	EU231734	EU231832	EU231935
<i>Sayornis nigricans</i>		FJ501742	FJ501922	EU231728	EU231826	EU231929
<i>Serpophaga cinerea</i>	ZMUC 125539	FJ501744	FJ501924	KC157438	KC157477	KC157540
<i>Silvicultrix pulchella</i>	ZMUC 132224	FJ501745	FJ501925	KC157439	KC157478	KC157541
<i>Sirystes sibilator</i>		FJ501746	FJ501926	EU231702	EU231800	EU231903
<i>Stigmatura budytoides</i>		FJ501748	FJ501928	DQ435476	DQ435528	DQ435503
<i>Sublegatus modestus</i>		FJ501749	FJ501929	EU231723	EU231821	EU231924
<i>Suiriri suiriri</i>		FJ501750	FJ501930	EU231671	EU231769	EU231872
<i>Tumbezia salvini</i>		FJ501759	FJ501939	EU231718	EU231816	EU231919
<i>Tyrannus savana</i>		FJ501763	FJ501943	AY336579	AY165826	DQ435507
<i>Xolmis pyrope</i>	NRM 570015	FJ501769	FJ501949	KC157440	KC157479	KC157542
<i>Zimmerius chrysops</i>		--	--	EU231683	EU231781	EU231884
<i>Zimmerius viridiflavus</i>		FJ501771	FJ501951	--	--	--

Discussion

Phylogeny and divergence dates

The chronology of the New World suboscine radiation. Furnariida and Tyrannida diverged from each other during the warm Paleogene “greenhouse” period, when most of the South American continent experienced a warm and equable climate allowing highly diverse forest floras with tropical plants to reach mid-latitudes in Patagonia (Wilf *et al.* 2003). The estimated divergence date (Fig. 4) closely matches the Paleocene-Eocene transition (55.5 Mya) when the Earth experienced a brief “heat shock” driven by major methane emissions released by volcanism (Svensen *et al.* 2004), which was followed by additional hyperthermal periods in the early Eocene until the global temperature peaked around 50 Mya (Zachos *et al.* 2001).

The most striking feature emerging from our chronogram is the more than 10 Ma difference in initial divergence dates between the extant Furnariida and Tyrannida clades. Divergence events leading to the extant families are thus much more densely packed in Tyrannida, as also reflected by the poorer resolution in the deeper regions of the Tyrannida tree. According to our chronogram, whereas the Furnariida began diversifying already in the Middle Eocene (ca. 44 Mya), the early diversification of extant Tyrannida lineages started a few million years after the abrupt global cooling and onset of the first Antarctic chill at the Eocene-Oligocene transition (32.2 Mya) (Zachos *et al.* 2001). This event triggered the expansion of savannah and desert habitats and a regression of tropical deciduous forests to near the equator (Jacobs *et al.* 1999), and was followed, on all continents, by a high biotic turnover. Although the phylogenetic relationships of extant groups cannot explain the early diversification history, it is tempting to assume that the presumably forest-adapted and frugivorous Tyrannida stem group was more seriously weeded by the extinction crises at the Eocene-Oligocene transition than the more terrestrial and insectivorous Furnariida.

The five most species-rich radiations (Thamnophilinae, Synallaxinae, Elaeniinae, Tyranninae and Fluvicolinae) all originated in the period around the mid-Miocene climate optimum (16–12 Ma). With the exception of Thamnophilinae, these clades clearly diversified in connection with the expansion of open savannah habitats that developed south of the tropical rainforest biome (Jacobs *et al.* 1999). These clades also rapidly proceeded into riparian habitats in the tropical lowlands as well as in more open habitats in the south of the continent and then north into the tropical Andes region (Ohlson *et al.* 2008; Rheindt *et al.* 2008a; Fjeldså & Irestedt 2009). Thamnophilinae represent a different diversification pattern, maintaining a high diversification rate in the tropical rainforest biome. This pattern is also found in several other clades, e.g. Dendrocolaptinae, Philydorinae, Piprinae and one clade of the Cotinginae. These clades are all most diverse in humid forest and, with the exception of Cotingidae, mostly restricted to forest understory. Their common diversification patterns likely reflect a response to the landscape dynamics in the Amazon Basin (e.g., Aleixo & Rossetti 2007; Hoorn & Wesselingh 2010).

Tree topology and definition of monophyletic clades. The current study corroborates much of the general picture of New World suboscine relationships that has been retrieved from earlier studies, chiefly the broad studies of Furnariida (Moyle *et al.* 2009) and Tyrannida (Tello *et al.* 2009), but also studies of various family-level clades, such as Irestedt *et al.* (2004, 2009), Brumfield *et al.* (2007), Ohlson *et al.* (2008), and Derryberry *et al.* (2011). In the following, we summarize the phylogenetic results from the current study, highlighting instances in which previously unresolved relationships have been clarified. Tribal level names in the following sections refer to the classification proposed by Moyle *et al.* (2009) and Tello *et al.* (2009).

Furnariida. In the combined tree, we found Melanopareidae and Conopophagidae to group with strong support with the Thamnophilidae, in line with the topology found in the nuclear intron tree. Their positions in the RAG tree were unresolved, in accordance with Moyle *et al.* (2009).

Thamnophilidae. There is still no strong evidence in favour of any of the alternative hypotheses on the initial splits in Thamnophilidae, between Euchrepomidinae, Myrmornithinae and Thamnophilinae. RAG data favour a placement of Euchrepomidinae as the sister to the remainder of Thamnophilidae, whereas the nuclear intron data show a poorly supported sister relationship between Euchrepomidinae and Thamnophilinae to the exclusion of Myrmornithinae. In the combined tree, Euchrepomidinae comes out as the sister to the remainder of Thamnophilidae, but with only low support. Irestedt *et al.* (2004b) places Euchrepomidinae as the sister to Myrmornithinae, whereas Brumfield *et al.* (2007), Moyle *et al.* (2009) and Bravo *et al.* (2012) placed it as the most basal offshoot in the Thamnophilidae.

Relationships within Thamnophilinae have proven rather difficult to establish, as the basal nodes are densely packed with little internal structure. Further, differences in both marker and taxon sampling in different studies have hampered a straightforward comparison of topologies. With the combined RAG and nuclear intron data we find an expanded Microrhopiini, as the sister group to the remaining Thamnophilinae. Microrhopiini also includes *Neotantes* P. L. Sclater, which was unresolved in Moyle *et al.* (2009), and *Epinecrophylla* M. L. Isler & Brumfield, which was not sampled in that study. This clade is also found in the nuclear intron tree.

Formicivorini is the sister to a clade consisting of Thamnophilini, Pyriglenini and Pithyini. This relationship is well supported in the combined tree, but not recovered with any support in the RAG or nuclear intron trees, nor in Moyle *et al.* (2009). A sister relationship between Formicivorini and the Thamnophilini/Pyriglenini/Pithyini complex is also well supported in Brumfield *et al.* (2007), where ca. 2300 bp of mitochondrial data and denser taxon sampling were applied to resolve internal relationships.

The relationships within the Thamnophilini/Pyriglenini/Pithyini complex are not consistently recovered in the different studies, nor in our combined tree. There are differences between our RAG and nuclear intron trees and even between our RAG tree and that of Moyle *et al.* (2009). The best overall resolution is presented in Brumfield *et al.* (2007), where good support is found for a sister relationship between Pyriglenini and Pithyini, with Thamnophilini as their sister. In that study, the *Sclateria* group (represented in our dataset by *Myrmeciza berlepschi* Hartert) is found as the most basal offshoot in Pyriglenini, contrary to our combined tree. On the other hand, the support for Thamnophilini is surprisingly low in Brumfield *et al.* (2007).

Overall, the diversification in Thamnophilinae is comparatively recent, and the combination of densely packed nodes and a large number of species makes it important to employ exhaustive taxon sampling and a large amount of molecular data to gain stability and high topological resolution. Denser taxon sampling and the inclusion of more sequence data is necessary to resolve the relationships in Thamnophilidae, as can be seen in this study, where already a modest increase in the amount of data from comparatively slowly evolving markers, results in a better internal resolution. Much remains to be sorted out in terms of intergeneric relationships, and many genera are known to be non-monophyletic (e. g. *Myrmeciza* G. R. Gray, *Myrmotherula* P. L. Sclater, *Cercomacra* P. L. Sclater, *Pernostola* Cabanis & Heine).

Furnarioidea. Small basal families. Grallariidae, Rhinocryptidae and Formicariidae form the most basal lineages within the Furnarioidea. The phylogeny of Formicariidae is uncontroversial at the genus level, but for the other two families there are some points of disagreement. We find Grallariidae and Rhinocryptidae to be the consecutive sister groups to the remainder of Furnarioidea. This differs from the relationships indicated by the RAG data (this study, Moyle *et al.* 2009) where a sister relationship between the two receives moderate support. The only published molecular phylogeny of Grallariidae (Rice 2005) is based on two mitochondrial markers for 16 ingroup taxa, and our results do not disagree with that one in any respect. However, a comprehensive multi-locus phylogeny is needed in order to understand both generic boundaries and diversification patterns in the family.

In Rhinocryptidae, nuclear intron data and RAG data yield conflicting results concerning the placement of *Scelorchilus* Oberholser. Nuclear intron data (this study, Fig. 3; Ericson *et al.* 2010) place them with Scytalopodinae, while RAG data place them with Rhinocryptidae. Both relationships receive strong support and in the combined dataset, the result is driven by the signal in the RAG data, placing *Scelorchilus* as the sister to the remainder of Rhinocryptinae. The RAG topology, with the small and near-flightless species together in one group that mainly radiated along the Andes, might be more compatible with biogeography and gross morphology.

Scleruridae, Dendrocolaptidae and Furnariidae. Several studies have established that *Geositta* Swainson and *Sclerurus* Swainson form a clade that is the sister to the rest of Furnariidae and Dendrocolaptidae (Irestedt *et al.* 2002; Chesser *et al.* 2004; Moyle *et al.* 2009; Derryberry *et al.* 2011). *Geositta* and *Sclerurus* are terrestrial feeders, like the basal Furnarioidea groups, while Dendrocolaptidae and Furnariidae are primarily scansorial and arboreal (Fjeldså *et al.* 2005). The intergeneric division of Scleruridae is uncontroversial and the split between the two genera is very old. The estimates differ between 20.6 Mya (Irestedt *et al.* 2009) and herein, and ca. 26 Mya (Derryberry *et al.* 2011).

A major point of controversy concerning the deeper phylogenetic relationships in this clade is the position of *Xenops* relative to Dendrocolaptidae and Furnariidae. Nuclear intron data favour a position of *Xenops* as the sister to Dendrocolaptidae, while RAG data place it as the sister to Furnariidae. In the combined tree, its position is unresolved in relation to the other two clades. When scrutinizing the gene trees in Irestedt *et al.* (2009) *Xenops* associates with Dendrocolaptidae in the myoglobin and G3PDH trees, but not in the ODC, beta-Fibrinogen intron 5 or cytochrome b trees.

The densely sampled phylogeny by Derryberry *et al.* (2011) suggests a continuously high rate of speciation, as the group diversified into new niche space that emerged as a consequence of the South American landscape dynamics (Fjeldså & Irestedt 2009). However, as in other New World suboscine groups, there is a marked imbalance between species-poor and species-rich clades, as several lineages that originated during the early or mid-Miocene apparently did not undergo such marked (net) radiation: *Xenops*, Sittasominae, *Berlepschia* Ridgway, Pygarrhichinae, *Margarornis* Reichenbach and *Aphrastura* Oberholser.

Except for the placement of *Glyphorhynchus* Wied-Neuwied in Irestedt *et al.* (2004a, 2009), there is a general agreement on the relationships within Dendrocolaptidae between those studies, Moyle *et al.* (2009), Derryberry *et al.* (2011) and the current study. The position of *Glyphorhynchus* as the sister to the remainder of Dendrocolaptidae is found only in the cytochrome b results of Irestedt *et al.* (2004a, 2009). Within Dendrocolaptinae, there is some uncertainty as to the position of *Dendroplex* Swainson, as its placement in the *Xiphorhynchus* group is supported by Moyle *et al.* (2009) but not by Derryberry *et al.* (2011). As in many other groups we find a marked imbalance in species number between the two main clades, with Sittasominae counting only nine species and Dendrocolaptinae 44. These two clades also exhibit some differences in habitat utilization, with Sittasominae more restricted to forest interior, while many members of Dendrocolaptinae occur in forest exterior and semi-open habitats, a pattern that is recurrent in many clades in the New World suboscines.

For Furnariidae, the combined dataset of RAG and nuclear introns yields a tree with a mostly well supported but short backbone nodes. In the trees based on individual datasets, the backbone topology for Furnariidae is characterized by many short internodes and a high instance of low or moderate statistical support. Comparison with other studies reveals that at least some of these topological differences depend on the choice of markers, but this mostly involve short internodes and often rather recent (<15 MA) divergences that are sparsely sampled in our study.

There are a number of differences between the RAG tree and the nuclear intron tree. In the combined tree, RAG data generally appear to have a stronger influence on the topology than do the nuclear intron data. As in Moyle *et al.* (2009) and Derryberry *et al.* (2011), but contrary to Irestedt *et al.* (2009), *Berlepschia* is placed as the sister to the remainder of Furnariidae. Likewise, in accordance with Moyle and Derryberry, Pygarrhichinae is the sister group to a large clade consisting of the subfamilies Furnariinae, Philydorinae and Synallaxinae. The sister relationship between Philydorinae and Furnariinae, recovered by Derryberry *et al.* (2011), was not recovered with significant support by Moyle *et al.* (2009) or in the present study. We found Furnariinae and Philydorinae to form an unresolved polytomy with the large Synallaxinae radiation, although a sister relationship between the two is weakly supported in the combined tree. Terminal relationships in Furnariinae, Philydorinae and Synallaxinae are more thoroughly clarified in Derryberry *et al.* (2011), which is based on mitochondrial and nuclear data and a near-complete sampling of the species taxa.

The relative positions of *Berlepschia*, Margarornithini and Pygarrhichinae differ between Moyle *et al.* (2009) and Derryberry *et al.* (2011) on one side and Irestedt *et al.* (2009) on the other. The most deviant tree is that from Irestedt *et al.* (2009) in which *Margarornis* and *Premnoplex* Cherrie were not found to be the sister to the rest of Synallaxinae, but are instead part of a basal polytomy with *Berlepschia*, Philydorinae and Pygarrhichinae. Secondly, Furnariinae was not found to be monophyletic by Irestedt *et al.* (2009) as instead the *Pseudocolaptes* group was sister to the *Furnarius* group plus Synallaxinae (except Margarornithini). Much of the uncertainty may stem from the generally short internodes separating these groups.

Tyrannida. The interrelationships between Pipridae, Cotingidae and Tyrannoidea were not recovered with confidence in this study. This has been a recurring feature in Tyrannida systematics (e.g. Ericson *et al.* 2006; Tello *et al.* 2009), suggesting that these nodes will be very difficult to tease apart, despite increased amounts of data. Furthermore, the Cotingoidea clade suggested by the RAG data in Tello *et al.* (2009), comprised of Cotingidae and an enlarged Tityridae, was not recovered with significant support by our RAG data. On the contrary, with the addition of nuclear intron data we yield strong support for including Tityridae, *Oxyruncus* and Onychorhynchini as members of the Tyrannoidea.

Pipridae. As has been demonstrated previously (Tello *et al.* 2009; McKay *et al.* 2010) we found that Pipridae is divided into two clades, Neopelminae, consisting of *Neopelma* P. L. Sclater and *Tyranneutes* P. L. Sclater & Salvin, and the “typical manakins”. Also in agreement with those studies, we show that the “typical manakins” in turn consists of two strongly supported clades. The smaller of these two consists of *Chiroxiphia* Cabanis, *Antilophia* Reichenbach, *Ilicura* Reichenbach, *Corapipo* Bonaparte and *Masius* Bonaparte and is largely

distributed outside of the Amazon Basin. The other clade consists of *Heterocercus* P. L. Sclater, *Manacus* Brisson, *Lepidothrix* Bonaparte, *Pipra* Linnaeus, *Dixiphia* Reichenbach and *Machaeropterus* Bonaparte and has its distributional centre in the Amazon basin. These two clades were ranked as the subfamilies Ilicurinae and Piprinae respectively by Tello *et al.* (2009). However, in view of the relatively recent divergence (at ca 12.5 Mya, Fig 4) we prefer to keep the entire “typical manakin” clade as one subfamily (Piprinae). *Xenopipo atronitens* Cabanis and *Chloropipo unicolor* Taczanowski are placed in unresolved positions alongside these two clades. These results further suggest that *Chloropipo* and *Xenopipo* do not form a clade. *Chloropipo uniformis* has been shown to be the sister species to *Xenopipo atronitens* (Tello *et al.* 2009), but *Chloropipo unicolor*, used in the present study, does not group with *Xenopipo* in any analysis. This strongly suggests that *Chloropipo* is not monophyletic, but a complete taxonomic sampling of *Chloropipo* is needed before the position of the remaining species can be determined. The uncertainty of the position of *Xenopipo* and *Chloropipo* within Piprinae stems from conflicting topologies in the RAG and nuclear intron datasets, and there is also a conflict between mitochondrial and nuclear intron data regarding the position of *Chloropipo unicolor* in McKay *et al.* (2010). Resolution within Piprinae is generally poor in all studies, especially in the deeper parts of Piprinae and among members of the genera *Pipra*, *Machaeropterus* and *Dixiphia*, and a comprehensively sampled phylogeny is sorely needed for this group.

Cotingidae. The subdivision of Cotingidae into Pipreolinae and Phytotominae of the Andean and Austral regions and the Cotinginae of the tropical rainforests is unambiguous, while relationships within the large Cotinginae are less clear (cf. Ohlson *et al.* 2007; Tello *et al.* 2009 and Fig. 1 herein). This uncertainty involves the relationships of the genera *Rupicola* Brisson, *Phoenicircus* Swainson, *Carpornis* G. R. Gray and *Snowornis* Prum to the remaining Cotinginae. Their positions are unresolved in Tello *et al.* (2009), and in Ohlson *et al.* (2007) *Snowornis* form part of Cotinginae whereas the placements of *Rupicola* and *Phoenicircus* are unresolved. Secondly, the relationships of the genera *Cotinga* Brisson, *Procnias* Illiger, *Lipaugus* Boie and *Tijuca* Ferussac to the well supported *Cephalopterus* and *Gymnoderus* groups also differs between Ohlson *et al.* (2007), Tello *et al.* (2009) and our study and may in part depend on choice of molecular markers and rather sparse taxon sampling.

Tityridae, Oxyruncus and Onychorhynchidae. The monophyly of a clade comprising *Oxyruncus*, Onychorhynchidae and Tityridae has been suggested previously (e.g. Ohlson *et al.* 2008; Tello *et al.* 2009), but never with strong support. Here we receive a PP=97 for this clade in the combined tree, but only PP=85 in the nuclear intron tree, and an unsupported association with Cotingidae in the RAG tree, as was also found by Tello *et al.* (2009). In the nuclear intron data set, Onychorhynchidae forms a clade with *Oxyruncus* as a sister to Tityridae, but with low support for relationships between these three groups. In the RAG dataset there is no resolution between these three and Cotingidae. According to our chronogram, Tityridae, *Oxyruncus* and Onychorhynchidae diverged already during the Oligocene (Fig. 2). In Tityridae we further find a deep split (ca. 22 Mya) between Schiffornithinae, which is mainly restricted to forest interior, and Tityrinae, whose broader habitat spectrum is largely centered on forest exterior and semi-open habitats. This split is consistently recovered in all studies, regardless of markers used (e.g. Barber & Rice 2007; Ohlson *et al.* 2008; Tello *et al.* 2009).

Piprites, Platyrinchidae and Tachuris. The relationships of Platyrinchidae, *Tachuris* and *Piprites* could not be clarified with the increased amount of data herein. *Tachuris* is placed as the sister to Rhynchocyclidae in both the RAG and the nuclear intron datasets, but not with statistically significant support. Platyrinchidae (including *Calypturna* Swainson, see Ohlson *et al.* 2012) is placed with *Tachuris* and Rhynchocyclidae in the nuclear intron dataset, while it is placed as the sister group of Tyrannidae in the RAG tree, likewise with strong support. *Piprites* is placed basally in a clade with *Tachuris* and Rhynchocyclidae in the RAG dataset, whereas the nuclear intron data place *Piprites* as the sister to the entire clade of *Platyrinchus*, *Neopipo*, *Tachuris*, Rhynchocyclidae and Tyrannidae. The conflicting signals from the two datasets are borne out in the combined tree (Fig. 1) as unresolved position of all three groups alongside Rhynchocyclidae and Tyrannidae.

Rhynchocyclidae. Rhynchocyclidae has been found to consist of three well supported clades, Pipromorphinae, Rhynchocyclinae and Todiostroinae, but the relationships between these are not clear from the combined tree. However, in both the RAG tree and the intron tree Rhynchocyclinae and Todiostroinae are sister groups, a result that receives strong support. The poor resolution in the combined tree stems from the radically different placement of the *Cnipodectes* group in the RAG and intron trees. In the RAG tree they are sister to the rest of Rhynchocyclidae, while nuclear intron data place them as sister to Todiostroinae. In Tello & Bates (2007) *Cnipodectes* was placed as the sister of Rhynchocyclinae by both mitochondrial data and the nuclear intron beta-fibrinogen 5, but support was inconclusive. Apart from this, our results are consistent with those in Tello & Bates

(2007) and Tello *et al.* (2009), lending strong support to the three subfamilies, although some uncertainty remains regarding their interrelationships. Most likely, Rhynchocyclinae and Todiostroinae are sister clades, but this and the position of *Cnipodectes* and *Taeniotriccus* needs to be investigated more exhaustively.

Tyrannidae. As in all recent studies, we find a basal polytomy with Hirundineinae, Elaeniinae and a clade consisting of *Muscigralla* Orbigny & Lafresnaye, Tyranninae and Fluvicolinae. We also find some incongruence between RAG and nuclear intron datasets regarding the positions of *Muscigralla*, *Attila*, *Ramphotrigon* and *Legatus*.

Elaeniinae. Elaeniinae consists of two main clades and the relationships agree with the results of Rheindt *et al.* (2008b) and Tello *et al.* (2009), with two clades corresponding to Euscarthmini and Elaeniini in Tello *et al.* (2009). The tree in Ohlson *et al.* (2008) differs in placing the *Culicivora* group, represented here by *Serpophaga* Gould, *Culicivora* Swainson, *Polystictus* Reichenbach and *Mecocerculus leucophrys* Orbigny & Lafresnaye, and also including *Anairetes* Reichenbach and *Pseudocolopteryx* Lillo (Ohlson *et al.* 2008, Tello *et al.* 2009), as an additional clade in a basal polytomy. Here, they are instead nested in the Elaeniini, as the sister group to a clade consisting of *Capsiempis* Cabanis & Heine, *Phaeomyias* Berlepsch and *Phyllomyias* Cabanis & Heine. Basal divergences are poorly resolved in both the principal clades.

Tyranninae. Myiarchini and Tyrannini are both recovered with good support, with *Attila*, *Legatus* and *Ramphotrigon* in basal positions. The placement of *Legatus* outside of Tyrannini is rather unexpected, and is apparently driven by the signal in the RAG data. In the nuclear intron tree, *Attila* and *Ramphotrigon* are placed with Fluvicolinae, although with low support. The placement of *Attila* and *Ramphotrigon* in basal positions in Tyranninae are in line with morphological as well as behavioural evidence (Ohlson *et al.* 2008). The placement of *Ramphotrigon* at the base of Fluvicolinae in the nuclear intron data is poorly supported (see also Ohlson *et al.* 2008), as is the placement of *Attila* at the base of Fluvicolinae in the RAG tree.

Fluvicolinae. The relationships in Fluvicolinae are nearly identical to the ones recovered by Tello *et al.* (2009). They differ from the results in Ohlson *et al.* (2008) in the positions of the *Ochthoeca* and *Fluvicola* clades. In Ohlson *et al.* (2008) and in the nuclear intron tree in this study, *Ochthoeca* clade is sister to the remainder of Fluvicolinae, although with only moderate support, whereas in the RAG tree the *Fluvicola* clade is nested within the *Ochthoeca* clade, as in the combined tree and the tree in Tello *et al.* (2009). A sister relationship between Contopini and Xolmiini is strongly supported (Fig. 1) and we find strong support for this relationship in both the RAG and the nuclear intron trees. Deeper nodes in Fluvicolinae are generally short and a more comprehensive study is needed.

Classification. Based on the phylogenetic results in this study and in a number of other studies, primarily Moyle *et al.* (2009), Tello *et al.* (2009), Irestedt *et al.* (2004), Brumfield *et al.* (2007), Ericson *et al.* (2010), Irestedt *et al.* (2009), Derryberry *et al.* (2011), Ohlson *et al.* (2007) and Ohlson *et al.* (2008), we recommend the taxonomic arrangement for the New World suboscines presented in Table 2. Below are some principal views about the need for proposing new taxa, followed by formal descriptions of new family- and subfamily level taxa.

We largely follow Moyle *et al.* (2009) and Tello *et al.* (2009), which are the only previous attempts to synthesize new findings regarding NWS phylogeny into a new classification. The inclusion of sequence data from three nuclear introns results in different topologies in the deep phylogeny of Furnariida and Tyrannida and in these cases we propose modifications from the classifications put forward by Moyle *et al.* (2009) for Furnariida and Tello *et al.* (2009) for Tyrannida. First, we find strong support for Melanopareiidae and Conopophagidae being most closely related to Thamnophilidae, although the split between them is very deep. In accordance with this, we refer Melanopareiidae and Conopophagidae to the superfamily Thamnophiloidea. Second, the superfamily Grallarioidea of Moyle *et al.* (2009), consisting of Grallariidae and Rhinocryptidae, is not recovered in our combined tree. In fact the support was weak in the tree of Moyle *et al.* (2009) and the relationship is unsupported in our RAG tree. In the nuclear intron tree, Grallariidae is the sister of the remainder of the Furnarioidea, and this is also the topology in our combined tree. Thus, we refer Grallariidae and Rhinocryptidae to the superfamily Furnarioidea. Third, we do not recover the Cotingoidea of Tello *et al.* (2009), consisting of Cotingidae and an expanded Tityridae. The support for that constellation is rather weak in the RAG trees, whereas the intron data strongly favour a placement of *Oxyruncus*, Onychorhynchidae and Tityridae as the sister clade to the clade consisting of Tyrannidae, Rhynchocyclidae and allies. We prefer to treat these clades as separate families, Oxyruncidae, Onychorhynchidae and Tityridae, and we refer them to the superfamily Tyrannoidea.

The last decades has seen a drastic overturning of the conventional view of avian systematic relationships,

making it ever harder to adhere to a “traditional view” in classification. There has been a general tendency in the past to merge small and aberrant taxa into larger families, both as a means of maintaining a simple classification, and because of a lack of a strict phylogenetic approach and data that could guide the taxonomic decisions in a transparent way. Even with a more well founded phylogenetic basis there has often been a reluctance to erect new family-level taxa, especially for small clades of “problematic” affinities. This has left a number of distinctive and comparatively old clades hanging in a taxonomic limbo, awaiting additional data that would allow inclusion in a well-established family. It has also led to a neglect of patterns that might determine the fate of clades, whether they fail to diversify, become relictual or undergo great phylogenetic expansion. Treating these small clades as family level taxa highlights their distinctiveness, deep evolutionary history and their hitherto unresolved relationships.

The phylogenetic tree of the NWS, like that of almost every other large radiation, contains lineages of widely different species richness and several taxa whose systematic positions have been contentious. Large amounts of data have been employed to clarify the phylogenetic positions of various debated taxa of NWS. We argue that the failure so far in associating these taxa, such as *Platyrrhinidae*, *Oxyruncus* and *Xenops* unambiguously with any larger clades cannot be explained solely by insufficient data. Instead, these taxa stand out as isolated clades that were part of rapid successions of divergence events along with clades that today are rich in species (Fig. 4). These small clades are distinctive and internally coherent in terms of ecology and morphology and they have independent evolutionary histories that are likely to span at least 20 million years. Keeping these taxa in taxonomic limbo (i.e. as *incertae sedis*) becomes harder to justify and here we opt to highlight their isolation, distinctiveness and old age by treating them as family level taxa. Looking at avian systematics as a whole, there are many small families that most ornithologists would never consider subsuming into more inclusive taxonomic entities, even if their sister relationships are unambiguous (consider merging the Shoebill into *Pelecanidae*, for example). Concerning the New World suboscines, we would in several cases argue in favour of recognizing these clades as family level taxa, despite the “relatively little content” of monotypic families (Tello *et al.* 2009). These taxa are all “isolated” early offshoots from the larger radiations, and they are in most cases ecologically and morphologically distinctive from their closest living relatives. In our view, a treatment as family level taxa is more informative about the nature and phylogenetic position of taxa like *Oxyruncus*, *Xenops*, *Tachuris* and *Platyrrhinus* compared to subsuming them into the larger groups from which they diverged early in their histories.

TABLE 2. Proposed new classification of the New World suboscines. Genera denoted “*sedis mutabilis*” are of slightly unclear relationships within their nearest higher taxonomic rank due to inconclusive results in this and other molecular phylogenetic studies. Genera denoted “(provisional)” are assumed to belong in the proposed taxonomic group although there are no molecular data published. Genera denoted “*incerta sedis*” have not yet been included in any molecular phylogenetic study and are of uncertain affinities within the nearest above taxonomic rank. Several genera are known to be non-monophyletic, but no names have been proposed for the constituent groups. These groups are detailed as far as possible in this classification

The higher order of taxa in Passeriformes can be arranged as follows

ORDER Passeriformes

SUBORDER Acanthisitti

SUBORDER Tyranni (suboscines)

INFRAORDER Eurylaimides (Old World suboscines)

INFRAORDER Tyrannides (New World suboscines)

PARVORDER Furnariida

SUPERFAMILY Thamnophiloidea

SUPERFAMILY Furnarioidea

PARVORDER Tyrannida

FAMILY Pipridae

FAMILY Cotingidae

SUPERFAMILY Tyrannoidea

SUBORDER Passeri (oscines)

The Infraorder Tyrannides can be arranged as follows

ORDER Passeriformes

SUBORDER Tyranni (suboscines)

INFRAORDER Tyrannides (New World suboscines)

PARVORDER Furnariida

SUPERFAMILY Thamnophiloidea

FAMILY Melanopareiidae Ericson, Olson, Irestedt, Alvarenga & Fjeldså, 2010

Melanopareia

FAMILY Conopophagidae P. L. Sclater & Salvin, 1873

Pittasoma

Conopophaga

FAMILY Thamnophilidae Swainson, 1824

SUBFAMILY Euchrepomidae Bravo, Remsen, Whitney & Brumfield, 2012

Euchrepomis

SUBFAMILY Myrmornithinae Sundevall, 1872

Myrmornis

Pygiptila

Thamnistes

SUBFAMILY Thamnophilinae Swainson, 1824

Tribe Microrhopiini Moyle, Chesser, Brumfield, Tello, Marchese & Cracraft, 2009

Myrmorchilus

Myrmeciza atrothorax group (*M. atrothorax*, *M. pelzelni*)

Microrhopias

Neotantes

Epinecrophylla

Clytoctantes (provisional)

Tribe Formicivorini Bonaparte, 1854

Formicivora

Myrmochanes

Terenura

Myrmotherula

Tribe Thamnophilini Swainson, 1824

Dichrozona

Rhopias

Isleria

Thamnomanes

Megastictus

Dysithamnus

Herpsilochmus

Cymbilaimus

Taraba

Hypoedaleus

Batara

Mackenziaena

Frederickena

Sakesphorus

Thamnophilus

Biatas (provisional)

Xenornis (provisional)

Tribe Pyriglenini Moyle, Chesser, Brumfield, Tello, Marchese & Cracraft, 2009

Sclateria

Myrmeciza hyperythra

Schistocichla

Hypocnemoides

Hylophylax

Myrmeciza berlepschi group (*M. berlepschi*, *M. exsul*)

Myrmeciza laemosticta group (*M. griseiceps*, *M. laemosticta*, *M. nigricauda*)

Myrmoborus

Percnostola lophotes

Pyriglena

Gymnocichla

Percnostola rufifrons

Myrmeciza fortis group (*M. fortis*, *M. goeldii*, *M. immaculata*, *M. melanoceps*)

Myrmeciza loricata group (*M. loricata*, *M. ruficauda*, *M. squamosa*)

Myrmeciza hemimelaena group (*M. castanea*, *M. hemimelaena*)

Tribe Pithyini Ridgway 1911

Cercomacra

Dryophila

Hypocnemis

Willisornis

Pithys

Phaenostictus

Phlegopsis

Skutchia

Gymnopithys

Rhegmatorhina

Incerta sedis within Thamnophilinae

Myrmeciza disjuncta

Myrmeciza ferruginea

Rhopornis

Myrmeciza s.str.(M. longipes)

SUPERFAMILY Furnarioidea

FAMILY Grallariidae P. L. Sclater & Salvin, 1873

Grallaricula

Myrmothera

Hylopezus

Grallaria

FAMILY Rhinocryptidae Wetmore, 1930 (1837)

SUBFAMILY Rhinocryptinae Wetmore, 1930 (1837)

Pterotochos

Scelorchilus

Liosceles

Psilorhamphus

Acropternis

Rhinocrypta

Teledromas

SUBFAMILY Scytalopodinae J. Müller, 1846

Eleoscytalopus

Merulaxis

Myornis

Eugralla

Scytalopus

FAMILY Formicariidae G. R. Gray, 1840

Formicarius

Chamaeza

FAMILY Scleruridae Swainson, 1827

Sclerurus

Geositta

FAMILY Dendrocolaptidae G. R. Gray, 1840

SUBFAMILY Sittasominae Ridgway, 1911

Certhiasomus

Deconychura

Sittasomus

Dendrocincla

SUBFAMILY Dendrocolaptinae G. R. Gray, 1840

Glyphorynchus

Dendrexetastes

Nasica

Hylexetastes

Xiphocolaptes

Dendrocolaptes

Dendroplex

Campylorhamphus

Drymornis

Drymotoxeres

Lepidocolaptes

Xiphorhynchus

FAMILY Xenopidae Bonaparte, 1854

Xenops

FAMILY Furnariidae G. R. Gray, 1840

SUBFAMILY Berlepschiinae NEW TAXON Ohlson, Irestedt, Ericson & Fjeldså

Berlepschia

SUBFAMILY Pygarrhichinae Wolters, 1977

Microxenops

Pygarrhichas

Ochetorhynchus

SUBFAMILY Philydorinae P. L. Sclater & Salvin, 1873

Anabazenops

Megaxenops

Philydor erythrocerum group (*P. erythrocerum*, *P. fuscipenne*)

Cichlocolaptes

Heliobletus

Philydor s.str. (*P. atricapillus*, *P. novaesi*, *P. pyrrhodes*)

Anabacerthia

Syndactyla

Ancistrops

Philydor rufum group (*P. erythropterum*, *P. rufum*)

Hylocryptus (incl. *Automolus rubiginosus*, *A. rufipectus*, *Clibanornis*)

Thripadectes

Automolus melanopezus group (*A. melanopezus*, *A. rufipileatus*)

Hyloctistes

Automolus s. str.

SUBFAMILY Furnariinae G. R. Gray, 1840

Pseudocolaptes

Premnornis

Tarphonimus

Furnarius

Lochmias

Phleocryptes

Limnornis

Geocerthia

Upucerthia

Cinclodes

SUBFAMILY Synallaxinae de Selys-Longchamps, 1839

Margarornis

Premnoplex

Aphrastura

Leptasthenura

Sylviorthorhynchus

Phacellodomus

Hellmayrea

Anumbius

Coryphistera

Asthenes

Tribe Synallaxini de Selys-Longchamps, 1839

Pseudasthenes

Spartonoica

Pseudoseisura

Synallaxis propinqua

Schoeniophylax

Certhiaxis

Synallaxis

Tribe Thripophagini Moyle, Chesser, Brumfield, Tello, Marchese & Cracraft, 2009

Acrobatornis

Metopothrix

Xenerpestes

Siptornis

Roraimia

Thripophaga

Limnoctites

Cranioleuca

PARVORDER Tyrannida

FAMILY Pipridae Rafinesque, 1815

SUBFAMILY Neopelminae Tello, Moyle, Marchese & Cracraft, 2009

Tyranneutes

Neopelma

SUBFAMILY Piprinae Rafinesque, 1815

Chloropipo sedis mutabilis

Xenopipo sedis mutabilis

Ilicura

Masius

Corapipo

Antilophia

Chiroxiphia

Lepidothrix

Heterocercus

Manacus

Pipra

Machaeropterus

Dixiphia

Ceratopipra

FAMILY Cotingidae Bonaparte, 1849

SUBFAMILY Pipreolinae Tello, Moyle, Marchese & Cracraft, 2009

Ampelioides

Pipreola

SUBFAMILY Phytotominae Swainson, 1837

Zaratornis

Phytotoma

Doliornis

Ampelion

Phibalura (provisional)

SUBFAMILY Cotinginae Bonaparte, 1849

Snowornis

Carpornis

Phoenicircus

Rupicola

Cotinga

Tijuca

Lipaugus

Procnias

Haematoderus

Querula

Perissocephalus

Pyroderus

Porphyrolaema

Gymnoderus

Conioptilon

Carpodectes

Xipholena

SUPERFAMILY Tyrannoidea

FAMILY Oxyruncidae Ridgway, 1906

Oxyruncus

FAMILY Onychorhynchidae Tello, Moyle, Marchese & Cracraft, 2009

Onychorhynchus

Terenotriccus

Myiobius

FAMILY Tityridae G. R. Gray 1840

SUBFAMILY Schiffornithinae Sibley & Ahlquist, 1985

Schiffornis

Laniocera

Laniisoma

SUBFAMILY Tityrinae G. R. Gray, 1840

Iodopleura

Tityra

Xenopsaris

Pachyramphus

FAMILY Pipritidae NEW TAXON Ohlson, Irestedt, Ericson & Fjeldså

Piprites

FAMILY Platyrinchidae Bonaparte 1854

Calyptura

Platyrinchus

Neopipo

FAMILY Tachurididae NEW TAXON Ohlson, Irestedt, Ericson & Fjeldså

Tachuris

FAMILY Rhynchocyclidae Berlepsch, 1907

SUBFAMILY Pipromorphinae Wolters, 1977

Mionectes

Leptopogon

Pseudotriccus

Corythopsis

Phylloscartes

Pogonotriccus

SUBFAMILY Rhynchocyclinae Berlepsch, 1907

Rhynchocyclus

Tolmomyias

SUBFAMILY Todirostrinae Tello, Moyle, Marchese & Cracraft, 2009

Taeniotriccus sedis mutabilis

Cnipodectes sedis mutabilis

Todirostrum

Poecilotriccus

Myiornis

Hemitriccus

Atalotriccus

Lophotriccus

Oncostoma

FAMILY Tyrannidae Vigors, 1825

SUBFAMILY Hirundineinae Tello, Moyle, Marchese & Cracraft, 2009

Myiobicca

Nepelomyias

Pyrrhomyias

Hirundinea

SUBFAMILY Elaeniinae Cabanis & Heine, 1859–60

Tribe Euscarthmini von Ihering 1904

Zimmerius

Stigmatura

Inezia

Euscarthmus

Ornithion

Camptostoma

Tyranniscus (part of *Phyllomyias*)

Acrochordopus (part of *Phyllomyias*)

Xanthomyias (part of *Phyllomyias*)

Mecocerculus poecilocercus group (all sp. except *M. leucophrys*)

Tribe Elaeniini Cabanis & Heine, 1859–60

Elaenia

Tyrannulus

Myiopagis

Suiriri

Capsiempis

Phyllomyias s. str. (*P. fasciatus*, *P. griseiceps*, *P. weedeni*)

Phaeomyias

Nesotriccus (provisional)

Pseudelaenia

Mecocerculus s. str. (*M. leucophrys*)

Anairetes

Polystictus

Culicivora

Pseudocolopteryx

Serpophaga

SUBFAMILY Muscigrallinae NEW TAXON Ohlson, Irestedt, Ericson & Fjeldså

Muscigralla

SUBFAMILY Tyranninae Vigors, 1825

Attila

Legatus

Rhamphotricon

Deltarhynchus

Tribe Myiarchini Hellmayr 1927

Rhytipterna

Casiornis

Sirystes

Myiarchus

Tribe Tyrannini Vigors, 1825

Pitangus

Philohydor

Machetornis

Tyrannopsis

Megarynchus

Myiodynastes

Myiozetetes

Conopias (provisional)

Phelpsia (provisional)

Empidonomus

Griseotyrannus

Tyrannus

SUBFAMILY Fluvicolinae Swainson, 1832–33

Colonia, *sedis mutabilis*

Myiophobus s. str., *sedis mutabilis* (*M. cryptoxanthus*, *M. fasciatus*)

Tribe Fluvicolini Swainson 1832–33

Myiophobus roraimae group (*M. flavicans*, *M. inornatus*, *M. phoenicomitra*, *M. roraimae*)

Silvicultrix

Colorhamphus

Ochthoeca

Sublegatus

Pyrocephalus

Fluvicola

Arundinicola

Gubernetes

Alectrurus

Muscipipra (provisional)

Tribe Contopini Fitzpatrick 2004

Ochthornis

Cnemotriccus

Aphanotriccus

Lathrotriccus

Mitrephanes

Sayornis

Empidonax

Contopus

Xenotriccus (provisional)

Tribe Xolmiini Tello, Moyle, Marchese & Cracraft, 2009

Lessonia

Hymenops

Knipolegus

Satrapa

Muscisaxicola

Cnemarchus

Polioxolmis

Xolmis

Agriornis

Neoxolmis

Myiotheretes

New taxa

SUBFAMILY Berlepschiinae, new subfamily level taxon, (type genus: *Berlepschia* Ridgway, 1887)

Diagnosis. Molecular studies have demonstrated this genus to be an isolated lineage within Furnariidae, although its position differs depending on molecular marker choice. It is, however, always a deep and isolated clade; age estimates vary between 18 and 22 Mya. Morphologically and behaviourally it is one of the most distinctive members of the family. A large (ca. 20 cm), slender furnariid with a long and straight bill and longish tail with protruding shafts. It has a striking pattern of black and white striping and barring on head and underparts and bright rufous upperparts. It is completely restricted to *Mauritia* palm swamps, where it forages by climbing among palm fronds, probing and gleaning for arthropod prey.

Included species: The genus *Berlepschia*, with a single species, *B. rikeri* Ridgway.

FAMILY Pipritidae, new family level taxon (type genus *Piprites* Cabanis, 1847)

Diagnosis. Molecular studies have repeatedly shown this genus to be an isolated old lineage related to Rhynchocyclidae and Tyrannidae. Dating estimates, although inconclusive due to poor resolution, point to an age between 25 and 28 Mya. Small (12–14 cm) stocky tyrannids with large head, and stubby, laterally compressed bill. Intricately patterned in green, yellow and grey, or black, yellow and chestnut. Unique among Tyrannida in having digits 1 and 2 of the foot fused. Possesses internal cartilages in the syrinx, a feature shared with the rest of Tyrannoidea, but lacks the *Musculus obliquus ventralis*, which is present in almost all members of Rhynchocyclidae and Tyrannidae, and also in Platyrinchidae and *Tachuris* (Ericson *et al.* 2006). Largely arboreal, mostly feeding on arthropods and small fruit. Forages by perch-gleaning and short sallies and often joins mixed flocks.

Included species: The three species traditionally included in the genus *Piprites*: *P. pileata* Temminck, *P. chloris* Temminck and *P. griseiceps* Salvin. Although the divergence between *P. pileatus* and *P. chloris* is very deep (ca 19 Mya) there is no reason to believe that the genus is not monophyletic.

FAMILY Tachurididae, new family level taxon (type genus *Tachuris* Lafresnaye, 1836)

Diagnosis. Molecular studies have consistently shown that this genus is an old and isolated lineage related to Rhynchocyclidae and Tyrannidae, but not unambiguously associated with any of them. Age estimates, although inconclusive due to poor resolution, point to an age between 25 and 28 Mya. In morphology and behaviour *Tachuris* is one of the most distinctive members of Tyrannida. Tiny (11–11.5 cm), slender, vaguely “warbler-like” tyrannid with long and slender tarsi and an extremely narrow and pointed bill. Colourful and uniquely patterned

among Tyrannida, with a distinctive juvenile plumage. An ecological specialist, confined to reed-beds, where it forages for small arthropods by perch-gleaning and short sallies.

Included species: The genus *Tachuris*, with a single species, *T. rubrigastra* Vieillot.

SUBFAMILY Muscigrallinae, new subfamily level taxon (type genus *Muscigralla* Orbigny & Lafresnaye, 1837)

Diagnosis. Molecular studies have consistently placed this genus as an old and isolated lineage in Tyrannidae, although the exact position varies slightly between studies. The current study strongly favours a sister relationship with Tyranninae+Fluvicolinae and dating estimates point to an age of ca. 17 Mya. Small (11–11.5 cm), long-legged, and extremely short-tailed tyrant flycatcher, brownish grey above and whitish below, with contrasting loreal marks and wing bars. Upper tail coverts and tip of tail contrasting orange buff. Unique among suboscines in having the lower tibiotarsus unfeathered. Terrestrial in arid habitats along the Pacific coast of South America, where it forages by pursuing prey by running and sallying.

Included species: The genus *Muscigralla*, with a single species, *M. brevicauda* Orbigny & Lafresnaye.

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References

- Aleixo, A. & Rossetti, D.F. (2007) Avian gene trees, landscape evolution, and geology: towards a modern synthesis of Amazonian historical biogeography? *Journal of Ornithology*, 148, 443–453. <http://dx.doi.org/10.1007/s10336-007-0168-7>
- Barker, F.K., Barrowclough, G. & Groth, J.G. (2002) A phylogenetic hypothesis for passerine birds: taxonomic and biogeographical implications of an analysis of nuclear DNA sequence data. *Proceeding of the Royal Society of London, Series B*, 269, 295–308. <http://dx.doi.org/10.1098/rspb.2001.1883>
- Barber, B.R. & Rice, N.H. (2007) Systematics and evolution in the Tityrinae (Passeriformes: Tyrannoidea). *Auk*, 124, 1317–1329. [http://dx.doi.org/10.1642/0004-8038\(2007\)124\[1317:SAEITT\]2.0.CO;2](http://dx.doi.org/10.1642/0004-8038(2007)124[1317:SAEITT]2.0.CO;2)
- Bravo, G.A., Remsen, J.V. Jr., Whitney, B.M. & Brumfield, R.T. (2012). DNA sequence data reveal a subfamily-level divergence within Thamnophilidae (Aves: Passeriformes). *Molecular Phylogenetics and Evolution*, 65, 287–293. <http://dx.doi.org/10.1016/j.ympev.2012.06.016>
- Brumfield, R.T., Tello, J.G., Cheviron, Z.A., Carling, M.D., Crochet, N. & Rosenberg, K.V. (2007) Phylogenetic conservatism and antiquity of a tropical specialization: Army-ant-following in the typical antbirds (Thamnophilidae). *Molecular Phylogenetics and Evolution*, 45, 1–13. <http://dx.doi.org/10.1016/j.ympev.2007.07.019>
- Chesser, R.T. (2004) Molecular systematics of New World Suboscines. *Molecular Phylogenetics and Evolution*, 32, 11–24. <http://dx.doi.org/10.1016/j.ympev.2003.11.015>
- Derryberry, E.P., Claramunt, S., Derryberry, G., Chesser, R.T., Cracraft, J., Aleixo, A., Pérez-Emán, J., Remsen, J.V.Jr. & Brumfield, R.T. (2011) Lineage diversification and morphological evolution in a large-scale continental radiation: the Neotropical ovenbirds and woodcreepers (Aves: Furnariidae). *Evolution*, 65, 2973–2986. <http://dx.doi.org/10.1111/j.1558-5646.2011.01374.x>
- Ericson, P.G.P., Christidis, L., Cooper, A., Irestedt, M., Jackson, J., Johansson, U.S. & Norman, J.A. (2002) A Gondwanan origin of passerine birds supported by DNA sequences of the endemic New Zealand wrens. *Proceeding of the Royal Society of London, Series B*, 269, 235–241. <http://dx.doi.org/10.1098/rspb.2001.1877>
- Ericson, P.G.P., Zuccon, D., Ohlson, J.I., Johansson, U.S., Alvarenga, H. & Prum, R.O. (2006) Higher-level phylogeny and morphological evolution of tyrant flycatchers, cotingas, manakins and their allies (Aves: Tyrannida). *Molecular Phylogenetics and Evolution*, 40, 471–483. <http://dx.doi.org/10.1016/j.ympev.2006.03.031>
- Ericson, P.G.P., Olson, S.L., Irestedt, M., Alvarenga, H. & Fjeldså, J. (2010) Circumscription of a monophyletic family for the tapaculos (Aves: Rhinocryptidae): *Psiloramphus* in and *Melanopareia* out. *Journal of Ornithology*, 151, 337–345. <http://dx.doi.org/10.1007/s10336-009-0460-9>
- Fjeldså, J., Irestedt, M. & Ericson, P.G.P. (2005) Molecular data reveal some major adaptational shifts in the early evolution of the most diverse avian family, the Furnariidae. *Journal of Ornithology*, 146, 1–13. <http://dx.doi.org/10.1007/s10336-004-0054-5>
- Fjeldså, J. & Irestedt, M. (2009) Diversification of the South American avifauna: patterns and implications for conservation in

- the Andes. *Annals of the Missouri Botanical Garden*, 96, 398–409. <http://dx.doi.org/10.3417/2007148>
- Gill, F & Donsker, D. (2012) IOC World Bird Names (v 2.11). Available from <http://www.worldbirdnames.org/> [Accessed 2012-04-16].
- Hoorn, C. & Wesselingh, F.P. (2010) *Amazonia: Landscape and Species Evolution. A Look into the Past*. Wiley Blackwell. 482 pp.
- Irestedt, M., Fjelds , J., Johansson, U.S. & Ericson, P.G.P. (2002) Systematic relationships and biogeography of the tracheophone suboscines (Aves: Passeriformes). *Molecular Phylogenetics and Evolution*, 23, 499–512. [http://dx.doi.org/10.1016/S1055-7903\(02\)00034-9](http://dx.doi.org/10.1016/S1055-7903(02)00034-9)
- Irestedt, M., Fjelds , J. & Ericson, P.G.P. (2004a). Phylogenetic relationships of woodcreepers (Aves: Dendrocolaptinae) - incongruence between molecular and morphological data. *Journal of Avian Biology*, 35, 280–288. <http://dx.doi.org/10.1111/j.0908-8857.2004.03234.x>
- Irestedt, M., Fjelds , J., Nylander, J.A.A. & Ericson, P.G.P. (2004b) Phylogenetic relationships of typical antbirds (Thamnophilidae) and test of incongruence based on Bayes factors. *BMC Evolutionary Biology*, 4, 23. <http://dx.doi.org/10.1186/1471-2148-4-23>
- Irestedt, M., Fjelds , J. & Ericson, P.G.P. (2006) Evolution of the ovenbird-woodcreeper assemblage (Aves: Furnariidae) – major shifts in nest architecture and adaptive radiation. *Journal of Avian Biology*, 37, 260–272. <http://dx.doi.org/10.1111/j.2006.0908-8857.03612.x>
- Irestedt, M., Fjelds , J., Dal n, L. & Ericson, P.G.P. (2009) Convergent evolution, habitat shifts and variable diversification rates in the ovenbird-woodcreeper family (Furnariidae). *BMC Evolutionary Biology*, 9, 268. <http://dx.doi.org/10.1186/1471-2148-9-268>
- Irestedt, M. & Ohlson, J.I. (2008). The division of the major songbird radiation into Passerida and “core Corvoidea” (Aves: Passeriformes) - the species tree versus gene trees. *Zoologica Scripta*, 37, 305–313. <http://dx.doi.org/10.1111/j.1463-6409.2007.00321.x>
- Jacobs, B.F., Kingston, J.D. & Jacobs, L.L. (1999) The origin of grass-dominated ecosystems. *Annals of the Missouri Botanical Garden*, 86, 590–643. <http://dx.doi.org/10.2307/2666186>
- Ladiges, P.Y. & Cantrill, D. (2007) New Caledonian-Australian connection: biogeographic patterns and geology. *Australian Systematic Botany*, 20, 383–389. <http://dx.doi.org/10.1071/SB07018>
- McKay, B.D., Barker, F.K., Mays, H.L.Jr., Doucet, S.M. & Hill, G.E. (2010) A molecular phylogenetic hypothesis for the manakins (Aves: Pipridae). *Molecular Phylogenetics and Evolution*, 55, 733–737. <http://dx.doi.org/10.1016/j.ympev.2010.02.024>
- Moyle, R.G., Chesser, R.T., Brumfield, R.T., Tello, J.G., Marchese, D.J. & Cracraft, J. (2009) Phylogeny and phylogenetic classification of the antbirds, ovenbirds, woodcreepers and allies (Aves: Passeriformes: infraorder Furnariides). *Cladistics*, 25, 386–405. <http://dx.doi.org/10.1111/j.1096-0031.2009.00259.x>
- Nylander, J.A.A. (2004) *MrModeltest v.2.2*. Evolutionary Biology Center, Uppsala University. Uppsala, Sweden. Available from: <http://www.abc.se/~nylander/>
- Ohlson, J.I., Prum, R.O. & Ericson, P.G.P. (2007) A molecular phylogeny of the cotingas, (Aves: Cotingidae). *Molecular Phylogenetics and Evolution*, 42, 25–37. <http://dx.doi.org/10.1016/j.ympev.2006.05.041>
- Ohlson, J.I., Fjelds , J. & Ericson, P.G.P. (2008) Tyrant flycatchers coming out in the open: phylogeny and ecological radiation of Tyrannidae (Aves: Passeriformes). *Zoologica Scripta*, 37, 315–335. <http://dx.doi.org/10.1111/j.1463-6409.2008.00325.x>
- Ohlson, J.I., Irestedt, M., Fjelds , J. & Ericson, P.G.P. (2012) Nuclear DNA from a 180 years old museum skin reveals the relationships of the Kinglet *Calyptura Calyptura cristata* (Passeriformes, Tyrannides). *Ibis*, 154, 533–541. <http://dx.doi.org/10.1111/j.1474-919X.2012.01243.x>
- Rheindt, F.E., Christidis, L. & Norman, J.A. (2008a). Habitat shifts in the evolutionary history of a Neotropical flycatcher lineage from forest and open landscapes. *BMC Evolutionary Biology*, 8, 193. <http://dx.doi.org/10.1186/1471-2148-8-193>
- Rheindt, F.E., Norman, J.A. & Christidis, L. (2008b) Phylogenetic relationships of tyrant-flycatchers (Aves: Tyrannidae), with an emphasis on the elaeiniine assemblage. *Molecular Phylogenetics and Evolution*, 46, 88–101. <http://dx.doi.org/10.1016/j.ympev.2007.09.011>
- Rice, N.H. (2005) Phylogenetic relationships of antpitta genera (Passeriformes: Formicariidae). *Auk*, 122, 673–683. [http://dx.doi.org/10.1642/0004-8038\(2005\)122\[0673:PROAGP\]2.0.CO;2](http://dx.doi.org/10.1642/0004-8038(2005)122[0673:PROAGP]2.0.CO;2)
- Ronquist, F. & Huelsenbeck, J.P. (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574. <http://dx.doi.org/10.1093/bioinformatics/btg180>
- Silvestro, D. & Michalak, I. (2010) *RAXMLGUI: a graphical front-end for RAXML*. Available from <http://sourceforge.net/projects/raxmlgui/>.
- Stamatakis, A. (2006) RAXML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690. <http://dx.doi.org/10.1093/bioinformatics/btl446>
- Svensen, H., Planke, S., Malthe-S rensen, A., Jamtveit, B., Myklebust, R., Eidem, T. & Rey, S.S. (2004) Release of methane from a volcanic basin as a mechanism for initial Eocene global warming. *Nature*, 429, 542–545. <http://dx.doi.org/10.1038/nature02566>
- Tello, J.G. & Bates, J.M. (2007) Molecular phylogenetics of the tody-tyrant and flatbill assemblage of tyrant flycatchers (Tyrannidae). *Auk*, 124, 134–154. [http://dx.doi.org/10.1642/0004-8038\(2007\)124\[134:MPOTTA\]2.0.CO;2](http://dx.doi.org/10.1642/0004-8038(2007)124[134:MPOTTA]2.0.CO;2)

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- Tello, J.G., Moyle, R.G., Marchese, D.J. & Cracraft, J. (2009) Phylogeny and phylogenetic classification of the tyrant flycatchers, cotingas, manakins and their allies (Aves: Tyrannides). *Cladistics*, 25, 429–467. <http://dx.doi.org/10.1111/j.1096-0031.2009.00254.x>
- Treplin, S., Siegert, R., Bleidorn, C., Thompson, H.S., Fotsó, R. & Tiedemann, R. (2008) Molecular phylogeny of songbirds (Aves: Passeriformes) and the relative utility of common nuclear marker loci. *Cladistics*, 24, 328–349. <http://dx.doi.org/10.1111/j.1096-0031.2007.00178.x>
- Wilf, P., Cúneo, N.R., Johnson, K.R., Hicks, J.F., Wing, S.L. & Obradovich, J.D. (2003) High plant diversity in Eocene South America: Evidence from Patagonia. *Science*, 300, 122–125. <http://dx.doi.org/10.1126/science.1080475>
- Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, 292, 686–693. <http://dx.doi.org/10.1126/science.1059412>