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Phylogeny and phylogenetic classification of the tyrant flycatchers, cotingas, manakins, and their allies (Aves: Tyrannides)

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Abstract

Phylogenetic relationships among the Tyrannides were assessed using over 4000 base pairs of nuclear recombination activating 1 (RAG-1) and 2 (RAG-2) DNA sequence data from about 93% of all described genera, which represents the most complete assessment of relationships for this diverse New World radiation to date. With this sampling we propose a significantly expanded interpretation of higher-level relationships within the group. The Tyrannides are shown to be comprised of six major lineages, all of which represent traditional family-level taxa (*sensu* Fitzpatrick, 2004a and Snow, 2004a,b; del Hoyo et al., 2004): (i) manakins (Pipridae); (ii) cotingas (Cotingidae); (iii) the sharpbill (*Oxyruncus*) + onychorhynchine flycatchers (Onychorhynchini); (iv) tityrines (Tityridae); (v) rhynchocycline flycatchers (Rhynchocyclidae); and (vi) the tyrant flycatchers (Tyrannidae). In addition, the RAG data recovered isolated lineages with uncertain relationships, including *Neopipo*, *Platyrinchus*, *Piprites*, and *Tachuris*. The Pipridae are the sister-group to all the other Tyrannides. Within the latter, the clade ((Oxyruncidae + Tityridae) + Cotingidae) is the sister-group of the Tyrannoidea. Within the Tyrannoidea, the Rhynchocyclidae and their allies are sisters to *Neopipo* + Tyrannidae. Using our phylogenetic hypothesis, we propose the first comprehensive phylogenetic classification that attempts to achieve isometry between the tree and a classification scheme using subordination and phyletic sequencing. This study thus provides a phylogenetic framework for understanding the evolution of this diverse New World assemblage, and identifies many avenues for further systematic study.

The Tyrannides (= Tyrannoidea of Sibley and Ahlquist, 1985, 1990) are one of two major clades of suboscine passerines restricted to the New World (Barker et al., 2004; Chesser, 2004; Ericson et al., 2006). Together, the Furnariides (Moyle et al., 2009) and the Tyrannides constitute a substantial fraction of the Neotropical avifauna (Stotz et al., 1996). The Tyrannides contain approximately 150 genera and 557 species arranged in three traditional families: Tyrannidae (tyrant flycatchers), Cotingidae (cotingas), and Pipridae (manakins) (Fitzpatrick, 2004a; Snow, 2004a,b). With the exclusion of *Sapayoa*, which is more closely related to Old World suboscines (Warter, 1965; Fjeldså et al., 2003; Chesser, 2004; Moyle et al., 2006), monophyly of the Tyrannides is supported by morphology (Warter, 1965; Ames, 1971; Raikow, 1987), DNA–DNA hybridization (Sibley and Ahlquist, 1985, 1990), and DNA sequencing (Irestedt et al., 2001; Johansson et al., 2002; Barker et al., 2004; Chesser, 2004; Ericson et al., 2006).

The limits of these traditional families have been problematic because of the uncertain taxonomic affinities of several taxa, and the inflation of taxonomic ranks due to the practices of evolutionary taxonomists. Within the traditional Tyrannidae, the mourner *Laniocera* and the "typical" tityrine flycatchers—*Tityra*, *Pachyramphus*, and *Xenopsaris*—have been united into a major clade, the Tityrinae, along with the cotingas *Iodopleura* and *Laniisoma* and the manakin *Schiffornis* (Sibley and Ahlquist, 1985, 1990; Prum and Lanyon, 1989; Prum et al., 2000; Johansson et al., 2002; Chesser, 2004; Ericson et al., 2006; Ohlson et al., 2007, 2008).

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However, none of these studies included all the taxa simultaneously in their taxon sampling. Moreover, the phylogenetic position of the Tityrinae has been uncertain. DNA–DNA hybridization grouped this clade with certain tyrant flycatchers (Sibley and Ahlquist, 1985, 1990), and DNA sequencing data suggested either a close relationship with the cotingids (Prum et al., 2000; Johansson et al., 2002), with the piprids (Chesser, 2004), or more recently with *Oxyruncus* plus the tyrannids (Ericson et al., 2006; Ohlson et al., 2008). The latter authors found *Oxyruncus* to be the sister-group of the Tityrinae, and suggested it should be placed in the same family, which they called Tityridae. Another tyrannid, the antpipit genus *Corythopis*, was formerly included in the Conopophagidae until Ames et al. (1968) argued that syringeal morphology placed the genus in the Tyrannidae. Subsequent work has consistently confirmed this result (Meyer de Schauensee, 1970; Ames, 1971; Traylor, 1977, 1979; Sibley and Ahlquist, 1985, 1990; Johansson et al., 2002; Chesser, 2004; Tello and Bates, 2007; Ohlson et al., 2008). The two morphologically distinctive genera *Phytotoma* and *Oxyruncus* have long been treated taxonomically as belonging to their own monotypic families, Phytotomidae and Oxyruncidae (Sclater, 1888; Ridgway, 1907; Hellmayr, 1929; Wetmore, 1960; Ames, 1971; Snow, 1979). Other studies have shown that *Phytotoma* belongs to the Cotingidae (Küchler, 1936; Lanyon, 1985a,b; Lanyon and Lanyon, 1989; Sibley and Ahlquist, 1990; Prum et al., 2000; Johansson et al., 2002; Chesser, 2004; Ericson et al., 2006; Ohlson et al., 2007), but the position of *Oxyruncus* has been uncertain (Sibley et al., 1984; Lanyon, 1985a,b; Sibley and Ahlquist, 1985, 1990; Prum, 1990a; Prum et al., 2000; Johansson et al., 2002; Chesser, 2004), until the work of Ericson et al. (2006) (see above). In the Pipridae, the genus *Neopipo* has been shown recently to belong in the Tyrannidae on the basis of morphology and nest structure (Mobley and Prum, 1995) and molecular data (Ohlson et al., 2008; Rheindt et al., 2008); and the genus *Piprites* has been suggested to be outside the Pipridae and closer to the Tityrinae and *Oxyruncus* because of its tyrannid-like internal syringeal cartilages (Prum and Lanyon, 1989; Prum, 1990a). More recently, *Piprites* has been found to be sister to the tyrannids, and even suggested to be part of this family (Ericson et al., 2006; but see Ohlson et al., 2008).

Basal relationships within the Tyrannides are also poorly resolved (Fig. 1). Prum's (1990a) morphological analysis did not find sufficient informative characters to resolve basal nodes (Fig. 1a). DNA–DNA hybridization (Sibley and Ahlquist, 1985, 1990) suggested that tyrannids were polyphyletic, and a group of them, which they called Pipromorphinae, was found to be basal to all remaining taxa (Fig. 1b). Dendrograms derived from Sibley and Ahlquist's DNA hybridization distances do not include measures of nodal support that can be compared with other studies. Two subsequent DNA-sequencing studies supported the monophyly of the tyrannids, including Pipromorphinae, but did not resolve basal relationships within the Tyrannides (Johansson et al., 2002; Chesser, 2004; Fig. 1c). A more recent study of relationships within the Tyrannides (Ericson et al., 2006) expanded on the work of Johansson et al. (2002) by adding a few more taxa and molecular markers. They found support for some basal nodes, except for the node joining the piprids and cotingids, which received low posterior probability (Fig. 1d). All these molecular and morphological studies have suggested conflicting relationships and changes in the content of traditional groups within the Tyrannides, but a combination of limited character and taxon sampling has precluded full phylogenetic resolution of the group as a whole.

In this study, we assess phylogenetic relationships of the Tyrannides using nuclear RAG-1 and RAG-2 gene sequence data from about 93% of the described genera. Phylogenetic relationships inferred from this data set were used to examine the monophyly and relationships of traditional and nontraditional groups within the Tyrannides, as well as relationships of taxa having uncertain affinities. With this large taxon sampling we obtained strong support for significantly new interpretations of higher-level relationships within this major Neotropical radiation.

Materials and methods

Taxon sampling and data acquisition

We sampled 179 individuals representing 141 of 151 genera (93%) of currently recognized tyrannoid genera (see Appendix 1; generic and specific names follow the most recent classification of Fitzpatrick, 2004a; Snow, 2004a,b). When possible, for some genera we included samples from multiple species if their monophyly had previously been questioned. Tissue samples from 10 genera were either unavailable (*Calyptura*, *Deltarhynchus*, *Muscipipra*, *Nesotriccus*, *Phelpsia*, *Phibalura*, *Tijuca*, and *Xenotriccus*), or we had difficulties obtaining sequences (*Heteroxolmis*, *Conopias*, *Aphanotriccus*, and *Tyrannulus*). Five taxa were used as outgroups for the phylogenetic analyses (GenBank numbers in brackets): Blue Jay (*Cyanocitta cristata* [AY443280, AY443137], Corvidae), African Broadbill (*Smithornis capensis* [FJ501593, FJ501773], Eurylaimidae), Rusty-napped Pitta (*Pitta oatesi* [DQ320612, DQ320576], Pittidae), Plain Xenops (*Xenops minutus* [FJ461153, FJ461055], Furnariidae), and Collared Crescent-chest (*Melanopareia torquata* [FJ461228, FJ461002], Rhinocryptidae).

Total DNA was extracted from a small (*ca.* 0.05 g wet weight) portion of tissue using the DNeasy tissue

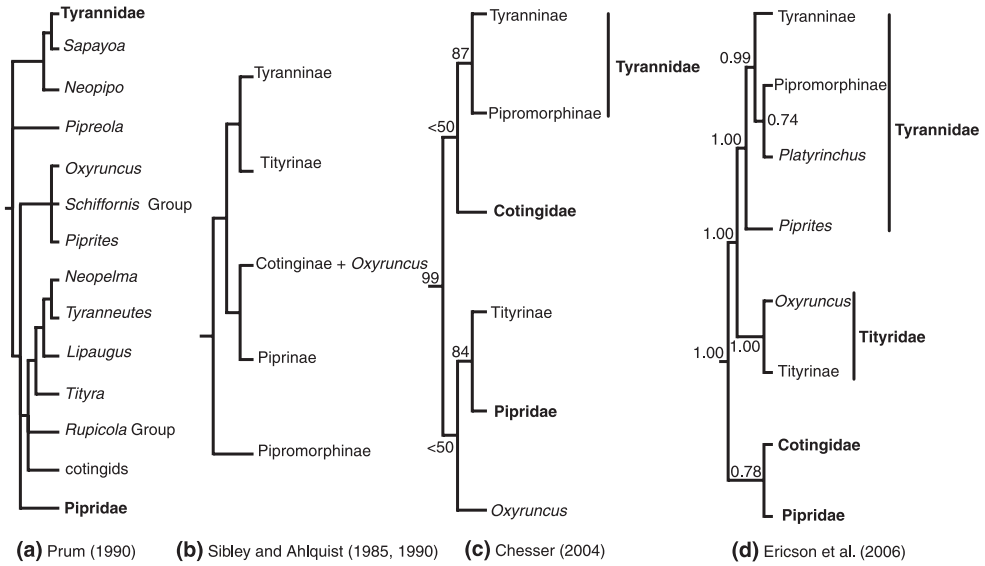

Fig. 1 Hypotheses of relationships for the Tyrannides: (a) Prum's (1990a) relationships based on morphological characters; (b) Sibley and Ahlquist's (1985, 1990) relationships based on DNA–DNA hybridization data; (c) Chesser's (2004) relationships based on ND3 and B-Fibrinogen intron 7; (d) Ericson et al.'s (2006) relationships based on *c-myc*, RAG-1, myoglobin, G3PDH, ODC, and cyt-*b* data.

extraction kit following the manufacturer's directions (Qiagen, MD). The final pellet was resuspended in 200 μL of Qiagen DNA hydration solution. PCR primers designed for two nuclear gene regions, recombination activating 1 (RAG-1) and 2 (RAG-2) were used in this study RAG-1: 13c-16, 25b-18b, 17-20, 19-22, 21-24, 23-2i; RAG-2: 1-22, 6-11, 16-31 (Barker et al., 2002, 2004; Groth and Barrowclough, 1999; and other unpublished primers from Jeff Groth).

The general PCR profile included an initial cycle of 15 min at 94°C, followed by 40 cycles of 30 s at 94°C, 30 s at 54°C, and 30 s at 72°C, with a final extension of 15 min at 72°C. For certain taxa and primer pairs, it was necessary to vary the annealing temperature and number of cycles to optimize PCR amplification. PCR bands were visualized in 1% low melting-point agar gels, and PCR products were purified with QIAquick PCR purification kits (Qiagen). DNA sequencing was done using the ABI Big Dyes ver. 3.1 cycle sequencing kit (Perkin Elmer, Foster City, CA) for dye-terminator chemistry following the manufacturer's instructions. Cycle-sequencing reactions were precipitated in 75% solution of ethanol following the ABI protocol. Dried cycle-sequencing reactions were resuspended and electrophoresed on an ABI 3100 Genetic Analyzer (Perkin Elmer). Both strands were sequenced to verify accuracy of the sequences.

Sequences were aligned across taxa using Sequencher (ver. 4.5; Genecodes, Ann Arbor, MI) and checked by eye to identify gap locations. Sequences have been deposited in GenBank (accession numbers FJ501594–FJ501952).

Phylogenetic analyses

Prior to undertaking phylogenetic analysis, we used the incongruence length difference (ILD) test (Farris et al., 1995a,b) and an assessment of topological conflicts (Mason-Gamer and Kellog, 1996; Miadlikowska and Lutzoni, 2000; Kauff and Lutzoni, 2002a) to search for conflicting phylogenetic signals between the two RAG gene data sets.

Phylogenetic analyses were conducted using Bayesian inference (BI), maximum likelihood (ML), and maximum parsimony (MP), as implemented in MrBayes ver. 3.1.1 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003), PHYML ver. 2.4.4 (Guindon and Gascuel, 2003), PAUP* (Swofford, 2002), and TNT ver. 1.0 (Goloboff et al., 2003). Prior to model-based analyses, we used Modeltest 3.7 (Posada and Crandall, 1998) to choose the most appropriate model of DNA evolution as determined by the Akaike information criterion (Posada and Buckley, 2004). This was done for the combined data set and for 11 different partitions of the data. Saturation was not expected to be a concern due to the relatively low rates of nucleotide substitutions present in these markers (Groth and Barrowclough, 1999).

For the Bayesian analyses, we performed several short runs (2 million generations) for parameter tuning and model selection, and two simultaneous long runs (10 million generations each) for final estimation of the tree topology. For the long runs, posterior probabilities (Rannala and Yang, 1996; Yang and Rannala, 1997) were estimated by Metropolis-coupled Markov chain

Monte Carlo (MCMCMC) with four incrementally heated chains that were simultaneously run for 10 million generations using the default priors (except for the branch-length prior, see further explanation below) as starting values for the model parameters. A temperature value of 0.04 (determined by running several short runs using different temperature settings) was used to allow acceptance rates and chain-swapping percentages to be between 10 and 70%, as suggested by Ronquist et al. (2005). For the long run, two simultaneous, independent analyses of 10 million generations, each starting from different random trees, were performed to check for potentially poor mixing of MCMCMC sampling using the default option in MrBayes 3.1.1. This version of the program automatically compares tree samples of the two runs and calculates various run diagnostics. Bayesian posterior probabilities were obtained from the 50% majority rule consensus of all trees retained after discarding those trees representing a ''burn-in'' period, which was determined graphically. Nodes with posterior probability values of 0.95 or greater were considered to receive ''high support''. For data sets with short internal branch lengths, it has been suggested that an initial flat branch-length prior can overestimate node support (Suchard et al., 2001; Zwickl and Holder, 2004; Yang and Rannala, 2005). Thus, before performing the long-run analysis, we examined the effects of branch-length prior settings on node support by running three short runs with branch-length prior means of 1 (less informative), 0.1, and 0.01 (more informative), none of which changed the support for clades with short internodes. In general, a more informative prior may prevent overestimation of node support, thus we used the average internal branch length of the data (0.00233) to set the prior mean (Lewis et al., 2005). Bayesian model selection was undertaken by comparing the results of short runs using four data partition settings: (i) one containing a single data partition; (ii) a second containing a partition for each gene; (iii) a third containing three partitions using nucleotide positions of the two genes; and (iv) a fourth containing six partitions using nucleotide positions from each gene independently. For the latter three analyses, all parameters were partitioned by a rate multiplier (using the unlink command in MrBayes; Ronquist and Huelsenbeck, 2003; Nylander et al., 2004). Differences in the log-likelihood values of the trees obtained from the Bayesian analyses were assessed visually and the values were compared using Bayes factors (Kass and Raftery, 1995; Nylander et al., 2004). The Bayes factor favouring one model over another was calculated as the ratio of the model log-likelihoods, and the results were interpreted following Kass and Raftery (1995). The harmonic mean of the log-likelihood values sampled from the stationary phase of the Bayesian run was used as an estimator of the model likelihood (Newton and Raftery, 1994). This procedure permitted assessment of the effects of data partition settings on the fit of the model used in the analyses.

Maximum likelihood searches were performed in PHYML and PAUP* using the best model of evolution and parameters (base frequencies, matrix of substitution types, proportion of invariant sites, and shape of gamma distribution) suggested by Modeltest. PHYML implements a hill-climbing algorithm that adjusts tree topology and branch length simultaneously, which permits analysis of large data sets in a comparatively short period (Guindon and Gascuel, 2003). Due to the large number of taxa involved, it was logistically impractical to run a PAUP ML analysis until termination. We followed a procedure suggested by Voelker and Edwards (1998) to estimate the ML tree. First, we started with a PAUP search employing heuristic methods using tree bisection–reconnection (TBR, Swofford and Olsen, 1990) branch-swapping, and starting from a neighbour-joining tree. This search was stopped after 5000 rearrangements were performed, and it was noted that the log-likelihood value had not decreased for over 3000 rearrangements. Then we used the resulting tree as the starting tree of a new heuristic search, and repeated this process for a third time. On the final analysis, over 25 000 rearrangements were performed; again the log-likelihood value did not change after the first few thousand rearrangements, and the tree topology had not changed from the previous heuristic search. This procedure potentially helps to avoid the possibility of achieving only local optima in the first incomplete PAUP search (Voelker, 1999). Node support for the ML trees was determined by the 500 replicates of nonparametric bootstrap performed with PHYML. Parameters for each of the two genes and the combined data set were estimated from the ML tree using PHYML.

For the MP analyses, all characters were weighted equally and treated as unordered (nonadditive). Parsimony searches were implemented using heuristic unconstrained searches of optimal trees using TBR branch-swapping within each of 1000 replicates of random taxon-addition sequences and keeping up to five trees per replication. To increase the chances of finding the shortest length topology, we also performed parsimony ratchet searches (Nixon, 1999) and tree fusion (Goloboff, 1999) as implemented in TNT. Twenty iterations of parsimony ratchet were performed for each 5000 random addition sequence (totaling 1000 000 ratchet iterations). This was followed by three rounds of unidirectional tree fusion conducted on ratchet trees. In this analysis, half the runs used 1 as random seed and the other runs used 2. Node support under parsimony was calculated using both bootstrap indices (5000 replicates) and absolute Bremer support. To prevent overestimation of Bremer support values, we implemented the strategy suggested by Bertelli and

Giannini (2005) and obtained suboptimal trees in 15 successive stages, saving up to 2000 suboptimals in each stage. This procedure consisted of searching suboptimal trees 1 step longer that the optimals, next saving suboptimals up to 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14 and 15 steps longer than the optimals.

Finally, graphic comparisons of posterior probability, bootstrap, and decay values between BI, ML, and MP trees of the combined analyses were performed to assess the congruence of node supports among these three methods.

Results: data, tree topologies, branch support

Data characteristics

The length of the RAG-1 sequences varied from 2866 to 2872 bp, with most taxa having either 2869 or 2872 bp. In RAG-1, five indel regions inferred from aligned sequences varied from 1 to 3 bp. The length of the RAG-2 sequences varied from 1149 to 1152 bp, with most taxa having 1152 bp. In RAG-*2*, three indel regions inferred from aligned sequences were 3 bp in length. No regions of ambiguous alignment were identified. The final alignment of the combined genes included a total of 4024 bp.

RAG-2 had a higher proportion of variable and parsimony informative sites than RAG-1 (Table 1), and RAG-2 showed a relatively higher TS/TV ratio as well as a higher among-site rate heterogeneity, as indicated by a lower value of the alpha shape parameter (Yang, 1996; Table 1). Both genes were relatively A + T-rich, but the χ^2 tests for base-composition heterogeneity across taxa did not show significant biases overall or when partitioned by position (not shown). Transitions and transversions increase linearly with percentage sequence divergence, thus showing no evidence of saturation (data not shown; see Groth and Barrowclough, 1999). Average pairwise sequence divergences of RAG-1 varied from 1.9% (between *Platyrinchus* and *Neopipo*) and 3.3% (between *Oxyruncus* and Tyrannidae), while divergences at RAG-2 varied from 1.9% (between *Neopipo* and *Platyrinchus*) and 4.9% (between *Piprites* and Onychorhynchini). Comparison of pairwise divergences among the two genes indicates that RAG-2 evolves *ca.* 1.1 times faster than RAG-1 (Fig. 2).

The ILD test implemented in PAUP* (called the partition homogeneity test), using each gene as a partition, returned a significant value ($P = 0.01$), indicating that the two genes may contain conflicting phylogenetic signals. The characteristics of these two genes do not exhibit the attributes known to bias the ILD test, such as a disparate level of homoplasy (Dolphin et al., 2000), extreme differences in rate heterogeneity (Barker and Lutzoni, 2002; Darlu and Lecointre, 2002), or uncertain sequence alignments (Messenger and McGuire, 1998). However, it is possible that rejection of the hypothesis of phylogenetic congruence by the ILD test was still caused by differences in rate heterogeneity and sequence size (Barker and Lutzoni, 2002; Darlu and Lecointre, 2002; Dowton and Austin, 2002). RAG-1 has a site-specific substitution rate approximately 1.6 times more homogeneous than RAG-2 and is approximately 2.5 times larger (Table 1). These differences may affect the ILD test result through their effect on the amount of phylogenetic structure in the data (Barker and Lutzoni, 2002). Furthermore, the appropriate level of significance for *P* values in ILD tests has been questioned (Sullivan, 1996; Cunningham, 1997a,b), suggesting the possibility that the test is a fundamentally flawed estimator of data combinability (Yoder et al., 2001). All of this cast further doubt on the direct interpretation of ILD *P* scores.

We decided to investigate further the nature of the "incongruence" between RAG genes by looking for topological conflicts (Mason-Gamer and Kellog, 1996; Miadlikowska and Lutzoni, 2000; Kauff and Lutzoni, 2002a). A conflict was assumed to be significant if different relationships for the same set of taxa (monophyly versus nonmonophyly) were observed on consensus trees for the two genes under the criteria of posterior probabilities ≥ 0.99, bootstraps ≥ 70%, and Bremer scores ≥ 3. The program Compat.py (Kauff and Lutzoni, 2002b) was used to detect topological conflict among supported clades of the two RAG trees from the BI analyses (not shown). Then we compared support values of nodes on the trees of the ML and MP analyses. We also used the topology of the combined analyses (Fig. 3) to explore further the nature of the conflict of alternative topologies suggested by the separate

Table 1
Properties of two nuclear genes sequenced for 179 samples of taxa in the Tyrannides and five outgroups (Appendix 1)

Data partitions	Total sites (bp)	Variable sites (%)	PI* sites (%)	CI	Tree length	MP trees	A+T (%)	Base comp. bias	TS/TV	P_i	α
RAG-1	2872	1231 (42.9)	846 (29.5)	0.39	3502	995	0.59	NS	6.153	0.419	1.237
RAG-2	1152	562 (48.8)	383 (33.2)	0.34	1803	35	0.60	NS	7.010	0.347	0.782
Combined	4024	1793 (44.6)	1229 (30.5)	0.37	5376	960	0.59	NS	6.444	0.401	1.054

*PI = parsimony informative; CI = consistency index excluding uninformative sites; MP = maximum parsimony; TS = transitions; TV = transversions; P_i = proportion of invariant sites; α = alpha-shape parameter of the gamma distribution.

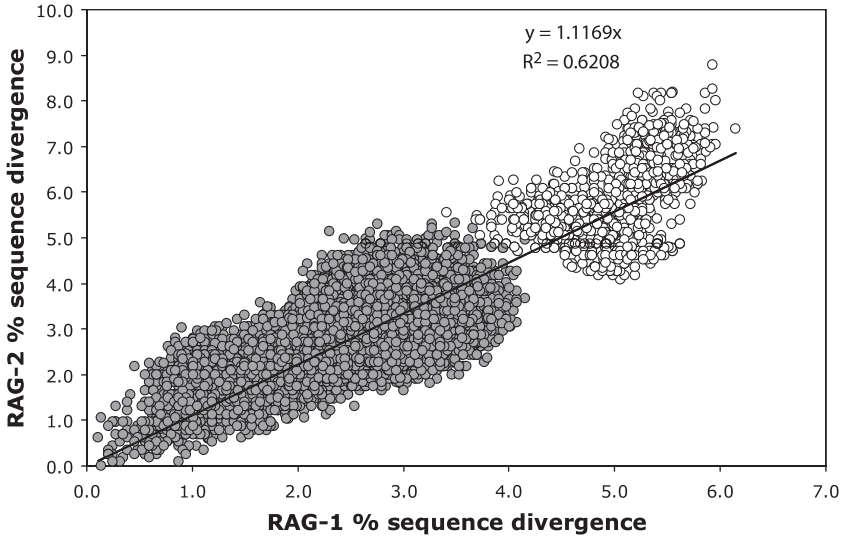

Fig. 2. Comparison of uncorrected percentage sequence divergence between RAG-1 and RAG-2. The slope is represented by its regression equation. Grey circles represent ingroup comparisons; white circles represent ingroup–outgroup and outgroup comparisons.

analyses. In the combined tree, a potentially "spurious" conflicting node that is identified in a single analysis might be expected either not to be recovered, or to receive low support. Thus recovering one of the alternative topologies with high support may indicate that the conflict is artefactual. The majority-rule consensus of the trees sampled in the BI analyses for the RAG-1 and RAG-2 data sets, respectively, exhibited some differences, although they were extremely similar in their overall topology. Four of the different relationships revealed in the separate analyses had conflicting posterior probabilities ≥ 0.99, bootstraps ≥ 70%, and decay support ≥ 3 (not shown), which involved taxa from nodes A, B, C, and D (Fig. 3). The combined tree recovered the RAG-2 topology in two of those cases (nodes B and C; Fig. 3a) and the RAG-1 topology in the other two (nodes A and D; Figs 3a,d, respectively). Nodes B and C were more basal than A and D. In nodes B and C, the alternative RAG-1 topology (*Iodopleura* sister to *Oxyruncus*) is not supported by other studies, due to the well supported membership of *Iodopleura* in the Tityridae (Prum and Lanyon, 1989; Ericson et al., 2006; Barber and Rice, 2007). In nodes A and D, few characters supported the RAG-2 topology such that its high posterior probability may due to short branches separating these nodes (Suchard et al., 2001; Zwickl and Holder, 2004; Yang and Rannala, 2005). Seven nodes (A–F) were identified as conflicting when 0.95 or greater posterior probability was used as the cut-off, including the four discussed above. Of the other three conflicts, two were terminal and involved rearrangements among five closely related taxa in the *Xolmis* group (node E; Fig. 3b); the other conflict was located in the middle of the tree and involved rearrangements among members of the tyrannine radiation, which received low support in the combined analysis (node F, Fig. 3b). In both cases, the combined topology (Fig. 3b) recovered the RAG-1 tree, and the nodes separating relationships among taxa in these two groups were short, which may explain the reason for the conflict in the RAG-2.

Comparison of tree topologies

In the BI analyses, visual comparisons of tree log-likelihoods (not shown) and Bayes factors of the Bayesian short runs of different data partition models found that the six-partition model (using each gene nucleotide codon positions as independent partitions: 1st RAG-1 [GTR + I + G], 2nd RAG-1 [GTR + G], 3rd RAG-1 [GTR + I + G], 1st RAG-2 [GTR + I + G], 2nd RAG-2 [TVM + I + G], and 3rd RAG-2 [TrN + G]) had the best fit to the data (Table 2). A three-partition model setting performed significantly better than a two-partition model, but was outperformed by a six-partition model (Table 2). Thus the long-run analysis was undertaken using the six-partition model setting. The BI majority rule tree ($-\ln L = 40562.38$) recovered 175 nodes, with 80% having ≥ 0.95% posterior probability support (Fig. 3).

Five independent searches in PHYML produced a single topology (see Fig. S1) with a likelihood score of $-\ln L = 40\,223.2$, GTR + I + G. The heuristic search in PAUP* using TBR branch swapping and the parameter estimates from Modeltest produced a final topology ($-\ln L = 40\,199.4$, GTR + I + G) that was virtually identical to the PHYML tree. The difference in likelihood scores may be due in part to differences in the way the

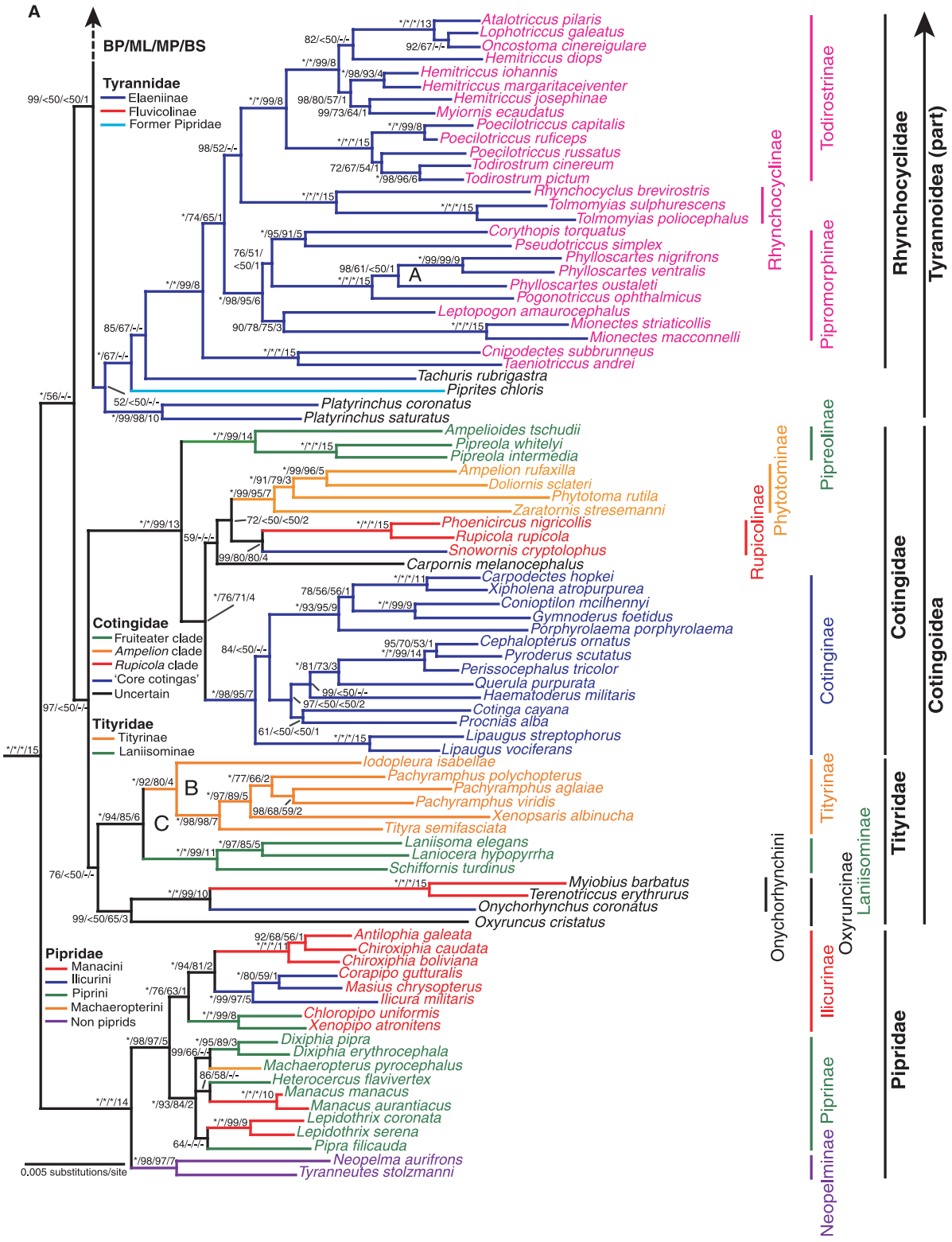

Fig. 3. Phylogenetic analyses of the Tyrannides: tree represents the majority-rule consensus obtained from Bayesian analysis of the combined RAG-1 and RAG-2 data using a complex partitioned model setting containing six partitions (see text). Numbers above branches indicate values of support: (i) posterior probabilities; (ii) maximum likelihood bootstraps; (iii) maximum parsimony bootstraps; (iv) Bremer decay indexes. Nodes that received 100% posterior probability or bootstrap support are represented by an asterisk. Nodes that were not recovered by a particular method are represented by "–". Colored taxa names and lines represent previous taxonomic placement based on Fitzpatrick, 2004a (Tyrannidae); Ohlson et al., 2007 (Cotingidae); Barber and Rice, 2007 (Tityridae); Prum, 1992 (Pipridae). Letters represent relevant nodes discussed in the text.

Fig. 3. (*Continued*)

Table 2
Summary of Bayes factors tests showing the effects of different data partitions on model likelihood

Model* (number of partitions)	1	2	3	4
1: RAG-1–RAG-2 (1)	0	–1022.8†	–96.8	1084.4
2: RAG-1, RAG-2 (2)		0	926.0	2107.2
3: 1st, 2nd, 3rd (3)			0	1181.2
4: 1st RAG-1, 2nd RAG-1, 3rd RAG-1, 1st RAG-2, 2nd RAG-2, 3rd RAG-2 (6)				0

Row models are labelled M_0; positive values in cells indicate support for the column model, M_1.

*For the models, dashes indicate linked topology parameters among data partitions; commas indicate unlinked parameters among partitions.

†Values are twice the log of the Bayes factors in the comparison between models M_1 and M_0 ($2\log B_{10}$).

two programs handle missing data. The ML tree had 98.3% similarity in nodal congruence to the BI tree. The ML tree recovered 173 nodes (excluding outgroup taxa) with 63.6% of them having ≥ 70% bootstrap support. Differences with the BI tree were due to three poorly supported nodes (BP < 95; here and elsewhere Bayesian posterior probabilities are expressed as whole numbers) on the Bayesian tree that were not found on the ML tree, and one poorly supported node (< 70%) on the ML tree not found on the BI tree.

The MP analysis resulted in 960 most parsimonious trees with a consistency index (CI, excluding uninformative character) of 0.37 and a tree length of 5373 steps; 30.5% of the characters were parsimony-informative. The strict consensus (Fig. S2) of those 960 trees was 82.3% similar to the Bayesian tree. The MP tree recovered 144 nodes, with 68.8% of them having ≥ 70% bootstrap and ≥ 2 Bremer support. Differences with the Bayesian tree were due to 10 poorly supported nodes on the Bayesian tree not found on the MP tree. The MP tree did not recover several of the basal lineages that were resolved and supported by both BI and ML analyses (Fig. 3).

Because only four instances occurred of well supported conflict between the genes (discussed above), the systematic and taxonomic discussion below is based on the Bayesian tree with branch lengths that shows the topological congruence that emerged across the three methods (Fig. 3). However, potential incongruence does exist when branch support is poor or ambiguous. Hence branch support values are reported as (BP/ML bootstrap/MP bootstrap/Bremer support); a dash (–) indicates cases in which a Bayesian node, generally having low BP, was also not recovered by either ML or MP, or when Bremer support was zero. In most cases these nodes are effectively best interpreted as polytomies. The MP and ML trees are shown in Figures S1 and S2.

Comparison of branch support across methods

The major conclusion from the preceding results is that all three methods recovered essentially the same set of relationships, and differences can be attributed to poor branch support for a small number of nodes in one or more of the branch support measures we used. Because the interpretation of various levels of branch support is of interest to systematists, we made a closer comparison of the nodal support values on our tree (Fig. 3). The key finding of this comparison is that the systematist would be well served by examining branch support using multiple methods, especially if one is assuming *a priori* that Bayesian posterior probabilities, by themselves, will provide an accurate assessment of support. We stress that the observations below are based on inspection of our data.

We discovered several simple relationships when Bayesian posterior probabilities (BP) were compared with ML and MP bootstrap and Bremer support values (Fig. 4). First, when ML or MP bootstraps were > 80%, or Bremer values were ≥ 3, then BP was at, or very near, 100%. Second, when ML or MP bootstraps were < 70%, or Bremer values were < 3, values of BP were frequently seen as being "significant" (≥ 95%), hence the high correlation among support values broke down. Values of ML and MP bootstraps were correlated, but ML values were consistently higher. When Bremer support values reached 5 or 6, both ML and MP bootstraps were high (> 85%). Below a Bremer support value of 5, both bootstrap values were highly variable.

Not unexpectedly, the occurrence of high BP, on the one hand, and low MP and ML bootstrap and low Bremer support (< 3), on the other, were associated with short internodes across the tree. This suggests either that BP is far more sensitive in finding true support when other measures cannot, or that BP is more apt to find false support when other measures are indeed telling us that little exists.

Previous work has suggested that posterior probabilities and bootstrap proportions are difficult to compare directly (Douady et al., 2003), thus interpreting observed differences is difficult. Some studies have concluded that posterior probabilities provide better estimates of node support than nonparametric bootstraps (Wilcox et al., 2002; Alfaro et al., 2003), especially when the "correct" model is chosen (Erixon et al., 2003). This is said to be particularly important in phylogenetic studies in which insufficient taxon sampling may result in substantial variation in branch length that can potentially affect the results of non-model-based methods such as maximum parsimony (Holder and Lewis, 2003). However, others propose that posterior probabilities may be excessively high and thus less conservative than bootstraps (or jackknifes), which

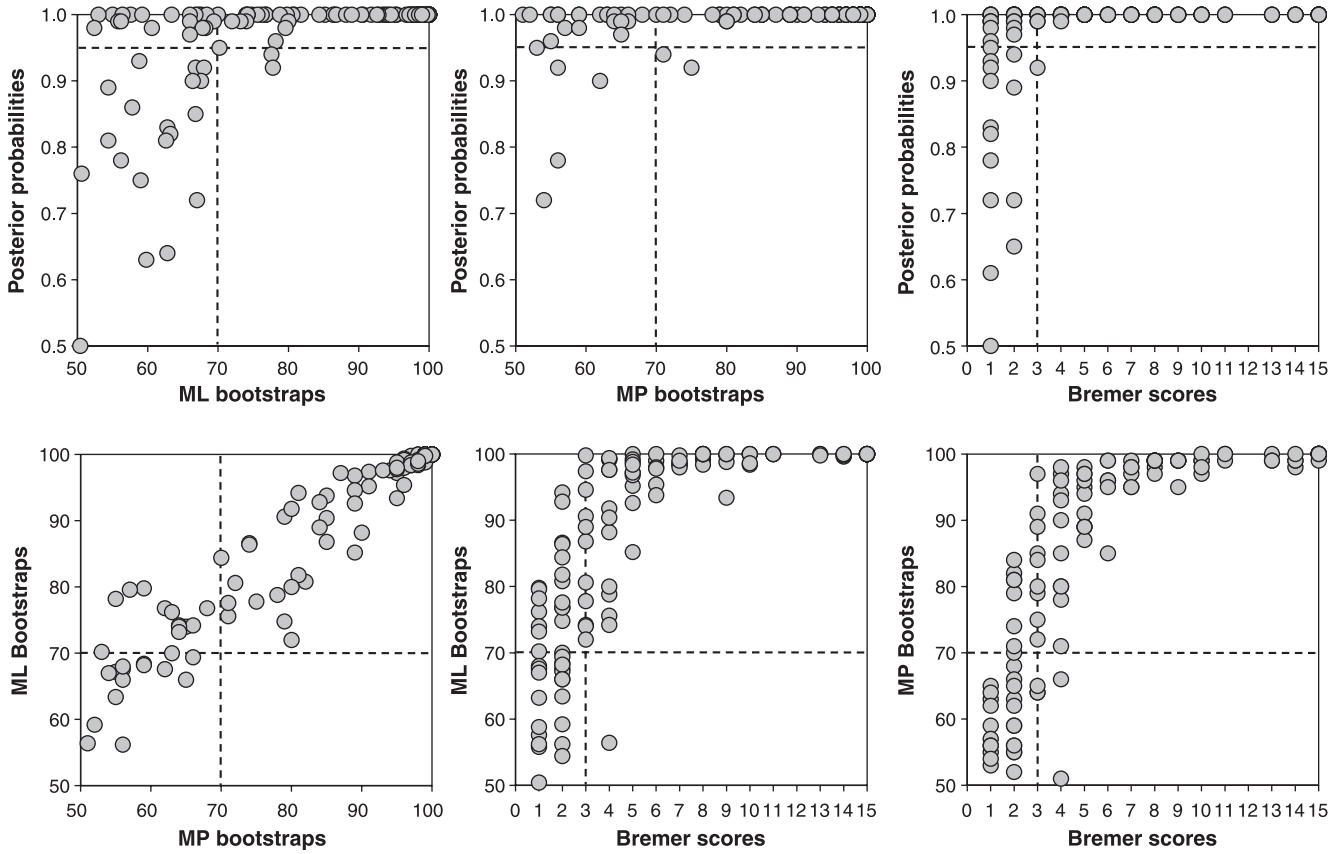

Fig. 4. Comparison of Bayesian posterior probability, maximum likelihood bootstrap, maximum parsimony bootstrap, and Bremer decay index support. Each dot represents pairwise values on the branches of BI, ML and MP topologies. The horizontal dashed lines are the 95% posterior probability of Bayesian support and the 70% value of bootstrap support, respectively; vertical dashed lines are the 70% value of bootstrap support and a Bremer decay index of 3, respectively.

can make the former more prone to support an equivocal phylogenetic hypothesis (Suzuki et al., 2002; Cummings et al., 2003; Simmons et al., 2004).

Given the ambiguity in assessing the meaning of comparisons among support values, we take away from this exercise that the use of multiple measures of support helps identify problematic, as well as moderately to well supported, nodes. Such nuance is impossible to determine in studies in which only one measure of support is reported. This becomes especially important in those studies that rely on Bayesian posterior probabilities alone.

Basal relationships within the Tyrannides

Our analyses recovered a monophyletic Tyrannides with very strong support (100/100/100/15; Fig. 3a). The RAG data also recovered most of the traditionally accepted "higher" taxa (families, subfamilies, and tribes), but revealed many novel relationships among these groups or to isolated genera or groups of genera (Fig. 3a and b). Thus, for example, we resolved the (i) manakins (Pipridae; 100/100/100/14), (ii) cotingas (Cotingidae; (100/100/99/13); (iii) tityrines (Tityrinae + Laniisominae; 100/94/85/6); (iv) a lineage of flycatchers (here, Rhynchocyclidae) that formed Sibley and Ahlquist's Mionectidae (1985) plus their allies (100/100/99/8); and (v) a lineage comprised of the core of the Tyrannidae (100/100/100/15).

Support for most of the basal nodes was equivocal, inasmuch as many of these relationships were supported only by Bayesian posterior probabilities (Fig. 3). The RAG data resolved the Pipridae as the sister-group to all the other Tyrannides, but this node was not strongly supported except by BP (100/56/–/–). A major clade formed by the Tyrannidae, Rhynchocyclidae, and closely allied genera was also weakly supported (99/<50/<50/1), as was its sister-group, the Cotingoidea (97/<50/–/–).

Within the large flycatcher clade, basal relationships involving *Platyrinchus*, *Piprites*, and *Tachuris* (Fig. 3a) and *Neopipo* (Fig.3b) are all uncertain. Within the Cotingoidea, the tityrines (Tityrinae + Laniisominae) were sister to an expanded Oxyruncinae (99/<50/65/3), but with low support (76/<50/–/–).

Our hypothesis for the placement of the Pipridae (Fig. 3a) differs from that of Ericson et al. (2006). They found the piprids to be sister to the Cotingidae (although nodal support for this relationship was low). More recently, Ohlson et al. (2008) found the piprids to be sister to the Tityridae + Tyrannidae, but this relationship was also poorly supported. Given the relative lack of support (except in Bayesian BP) that was found across these nodes, and those at the base of the flycatcher lineage, it is difficult to defend any hypothesis over another.

Family Pipridae

The Pipridae, excluding *Schiffornis* and *Piprites*, were strongly monophyletic (Fig. 3a; 100/100/100/14). In addition, the RAG data recovered three well supported clades within the family and numerous resolved intergeneric relationships. As a consequence, our data provide the most comprehensive hypothesis yet for this group, and on the basis of these results we propose to erect additional higher taxa to reflect phylogenetic patterns within the group.

Subfamily Neopelminae, ***new taxon*** *(type genus:* Neopelma *Sclater 1860)*

Diagnosis. The most inclusive crown clade that contains *Neopelma aurifrons* and *Tyranneutes stolzmanni* but not *Chiroxiphia caudata* or *Pipra filicauda*. The Neopelminae are very strongly supported by molecular data (100/98/97/7; Fig. 3a), derived characters of the syrinx (narrow, elongated, and curved [subtle S-shape] internal cartilage; Prum, 1990a), and by three protein electrophoretic loci (Lanyon, 1985a,b).

The phylogenetic placement of this lineage within the Pipridae has been uncertain. Lanyon (1985a,b) found that the *Tyranneutes–Neopelma* clade belonged to a group that includes all manakins, but relationships within that group were not fully resolved. Prum (1990a) did not place *Tyranneutes* and *Neopelma* in his restricted Pipridae, but suggested instead that they were related to a group of problematic taxa having ambiguous relationships to both cotingids and piprids. Our study reveals that *Neopelma* and *Tyranneutes* are the sister-group of all other piprids, with strong support.

Subfamily Piprinae, ***new rank*** *(type genus:* Pipra *Linnaeus 1764)*

Diagnosis. The most inclusive crown clade that contains *Pipra filicauda*, *Manacus manacus*, and *Dixiphia pipra* but not *Chiroxiphia caudata* or *Neopelma aurifrons*. No morphological synapomorphies are known, but S. Lanyon (1985a,b) found two synapomorphic electrophoretic loci changes for the three genera he sampled.

The Piprinae as here circumscribed are quite strongly supported by the RAG data (100/93/84/2; Fig. 3a). It is now recognized that traditional "*Pipra*" is not monophyletic (Prum, 1992; Rêgo et al., 2007). The type of the genus, *P. aureola*, was not sampled in our study, but *P. filicauda* and *P. fascilicauda* are close relatives of *P. aureola* (Prum, 1992; Rêgo et al., 2007).

We also sampled two other "*Pipra*" species, *P. erythrocephala* and *Dixiphia pipra*, which formed a very well supported group (100/95/89/3). *Pipra erythrocephala* belongs to a larger clade that also includes *P. mentalis*, *P. rubrocapilla*, *P. chloromeros*, and *P. cornuta* (Prum, 1992), and *Machaeropterus* as well (Rêgo et al., 2007; our results). Prum (1992) suggested the subgeneric name *Ceratopipra* to differentiate this clade from the remainder of the species in his reduced *Pipra*, thus this name is available. Alternatively, the members of the *P. erythrocephala* clade could be subsumed within the genus *Dixiphia* (Reichenbach, 1850), which has priority over *Ceratopipra*. We opted for the latter option.

Within piprinae, we found slight support for a group formed by *Dixiphia erythrocephala* + *D. pipra* and *Machaeropterus* (99/66/–/–). Two other clades that were recovered within Piprinae received essentially no support: one was *Lepidothrix* + *Pipra filicauda* (64/–/–/–), and the other *Heterocercus* + *Manacus* (86/58/–/–).

Our results thus confirm that traditional "*Pipra*" is not monophyletic. Our tree, however, conflicts with Prum's (1990b, 1992) results using behavioural and morphological data. He found that the two *Pipra* clades we sampled, *filicauda* (presumably close to *P. aureola*) and *erythrocephala*, were close relatives. Our results, on the other hand, are consistent with the mtDNA findings of Rêgo et al. (2007). Prum (1992) introduced the name Piprini, but his concept of included genera and that advanced here are substantially different.

Subfamily Ilicurinae, ***new rank*** *(type genus:* Ilicura *Reichenbach 1850)*

Diagnosis. The most inclusive crown clade that contains *Chiroxiphia caudata*, *Ilicura militaris*, and *Xenopipo atronitens* but not *Neopelma aurifrons* or *Pipra filicauda*. No synapomorphies have been proposed, but the clade is well supported by molecular sequence data (100/76/63/1). Scott Lanyon (1985a,b) also found synapomorphic electrophoretic change at two loci for four genera included in this subfamily (he did not sample three others). Inasmuch as Lanyon's sampling did cover the three core lineages of the subfamily, the electrophoretic characters are potential synapomorphies for the group as a whole. Prum (1992) proposed the name Ilicurini for *Ilicura*, *Masius*, and *Corapipo*. His tribe is equivalent to our *Ilicura* group, and we expand the family-group name to include four additional genera.

We uncovered three core groups within the Ilicurinae (Fig. 3a): (a) *Xenopipo* group (100/100/99/8): *Chloropipo* + *Xenopipo*; (b) *Ilicura* group (100/99/97/5): *Corapipo*, *Masius*, *Ilicura*; and (c) *Antilophia* group (100/100/100/11): *Antilophia* + *Chiroxiphia*. The *Xenopipo* group was sister to all other ilicurines. Within the *Xenopipo* group, an analysis of syringeal characters showed that the monotypic *Xenopipo* was embedded in *Chloropipo* (Prum, 1992), which led Prum to suggest the two genera should be merged. Our study did not address this suggestion because we only included one representative of *Chloropipo*. Within the *Ilicura* group, *Ilicura* was sister to a clade formed by *Corapipo* and *Masius* (100/80/59/1). These relationships have been suggested previously on the basis of shared behavioural (Prum and Johnson, 1987; Prum, 1990b) and syringeal characters (Prum, 1992), and the "*Ilicura* group" corresponds to the Ilicurini of Prum (1992). Within the *Antilophia* group, *Antilophia* was found embedded within *Chiroxiphia*, but support for the nonmonophyly of *Chiroxiphia* was low (92/68/56/1). Species of these two genera are genetically close to each other, as shown by the low levels of differentiation in the RAG genes (0.50% *C. caudata* versus *C. boliviana*; 0.46% *Chiroxiphia* versus *Antilophia*) and by the occurrence of hybridization (Sick, 1979; Pacheco and Parrini, 1995). The monophyly of *Chiroxiphia* is supported by one derived syringeal character (longer cartilaginous A1–B1 bridge with square craniolateral projection) and overall plumage coloration (Prum, 1992), thus suggesting that the node joining *Antilophia* and *C. caudata* may be an artefact of the few changes occurring in RAG genes at terminal nodes.

General comments on the Pipridae

As noted above, the Neopelminae were sister to the more "typical" manakins (Piprinae + Ilicurinae), with the latter receiving very high support in all analyses (100/98/97/5). These three main lineages recovered by the RAG data are consistent with electrophoretic data (Lanyon, 1985a,b), but not with behavioural (Prum, 1990b) or morphological (Prum, 1992) evidence. The electrophoretic data (Lanyon, 1985a,b) discovered similar groups to our study, but differed in the relationships among these groups. Prum (1992) erected four new tribes (not families as in Bock, 1994, p. 149): Ilicurini, Manacini, and Piprini, and a monotypic Machaeropterini. With the exception of his Ilicurini (*Ilicura*, *Masius*, and *Corapipo*), *Antilophia* + *Chiroxiphia*, and *Chloropipo* + *Xenopipo*, there is no congruence with our results.

Superfamily Cotingoidea, new rank (type genus: *Cotinga* Brisson 1760)

Diagnosis. The most inclusive crown clade that contains *Cotinga cayana*, *Tityra semifasciata*, *Onychorhynchus coronatus*, and *Oxyruncus cristatus* but not *Tyrannus savanna* or *Pipra filicauda*. No synapomorphies have been proposed, but the clade is supported by molecular data (97/<50/–/–), albeit not compellingly.

To our knowledge Cotingoidea is a new taxonomic concept. Additional data will be required to test the validity of this taxon.

Family Tityridae

The Tityridae as recognized here include 11 genera distributed in three major lineages (Fig. 3a): (i) Oxyruncinae (*Oxyruncus*, *Onychorhynchus*, *Myiobius*, *Terenotriccus*); (ii) Laniisominae (*Schiffornis*, *Laniisoma*, *Laniocera*); and (iii) Tityrinae (*Iodopleura*, *Tityra*, *Xenopsaris*, *Pachyramphus*). The genera in this family were formerly placed in three traditional families within the Tyrannides: *Oxyruncus*, *Onychorhynchus*, *Myiobius*, *Terenotriccus*, *Tityra*, *Xenopsaris*, *Pachyramphus*, and *Laniocera* in the Tyrannidae; *Oxyruncus*, *Iodopleura*, and *Laniisoma* in the Cotingidae; and *Schiffornis* in the Pipridae. Uncertainty over the relationships of these taxa resulted from the difficulty in identifying diagnostic morphological characters that could place them in one of the traditional tyrannine families (McKitrick, 1985; Prum and Lanyon, 1989; Prum, 1990a; Prum et al., 2000; Ericson et al., 2006).

Based on DNA–DNA hybridization, Sibley and Ahlquist (1985, 1990) placed *Schiffornis* as sister to *Tityra* + *Pachyramphus*, which together formed their subfamily Tityrinae. The latter was considered to be sister to their core Tyranninae (see Fig. 1b). Sibley and Ahlquist's Tityrinae was later supported by electrophoretic (Lanyon, 1985a) and DNA sequence data (Johansson et al., 2002; Chesser, 2004; Ericson et al., 2006; Barber and Rice, 2007). Prum et al.'s (2000) phylogeny of the Cotingidae using partial cyt-*b* sequences showed that the *Schiffornis* group plus *Tityra* constituted a monophyletic group, which they called Tityrinae, within their Cotingidae. The small set of molecular characters used to reconstruct the phylogeny (375 bp) limited resolution and support for the internal nodes within the Tityrinae, and the inclusion of the Tityrinae in the Cotingidae was an artefact of their limited sampling. With more character sampling, Johansson et al. (2002), Chesser (2004), Ericson et al. (2006), and Ohlson et al. (2008) rejected the inclusion of the Tityrinae in the Cotingidae. Furthermore, Ericson et al. (2006) and Ohlson et al. (2008) proposed recognition of the family Tityridae, which included all tityrines and the sharpbill *Oxyruncus*. Our study agrees with the latter results, and we expand the family limits to include the *Onychorhynchus* clade (*Onychorhynchus*, *Myiobius*, and *Terenotriccus*), which is sister to *Oxyruncus*. With nearly complete

sampling of genera, we resolved all internal relationships.

Several terminal relationships within the typical tityrines (Laniisominae + Tityrinae) are also supported by morphological data (Fig. 5 in Prum and Lanyon, 1989), but basal nodes were less well resolved. The two major tityrine clades have very distinctive breeding and mating systems (Barber and Rice, 2007): monogamy in the Laniisominae; and polygamy in the Tityrinae.

Subfamily Oxyruncinae

Over the years, the relationships of the Sharpbill (*Oxyruncus cristatus*) have consistently stirred controversy. Often it has simply been placed in its own monotypic family (e.g. Ridgway, 1906; Wetmore, 1960; Warter, 1965; Ames, 1971; Traylor, 1979). Mayr and Amadon (1951) placed *Oxyruncus* within the Tyrannidae, based on putative morphological similarities, whereas molecular data have suggested that *Oxyruncus* is close to the Cotingidae (Sibley et al., 1984; Sibley and Ahlquist, 1985, 1990), the Tityrinae (= Tityridae, Ericson et al., 2006; Ohlson et al., 2008), a Tityrinae + Tyrannidae clade (Lanyon, 1985a,b), or simply *incertae sedis* (e.g. Johansson et al., 2002; Chesser, 2004). Because of dense taxon sampling, our results offer a new hypothesis altogether: *Oxyruncus* is the sister-group (99/<50/65/3) to a clade formed by *Onychorhynchus*, *Myiobius*, and *Terenotriccus*. The latter, well supported clade (100/100/99/10) now deserves formal taxonomic recognition.

Tribe Onychorhynchini, ***new taxon*** *(type genus:* Onychorhynchus *Fischer von Waldheim 1810)*

Diagnosis. The most inclusive crown clade, including *Onychorhynchus coronatus*, *Myiobius barbatus*, and *Terenotriccus erythrurus* but not *Oxyruncus cristatus*, *Laniisoma elegans*, *Tityra semifasciata*, or *Cotinga cayana*. The clade is supported by molecular data and two morphological characters (presence of at least two double, complete, ossified syringeal A elements; and an ossified interorbital septum), which are hypothesized to be derived (Birdsley, 2002). The close relationship of these three genera is also said to be supported by the presence of long rictal bristles (Birdsley, 2002), as well as by their behaviour of building long pendant nests (Traylor and Fitzpatrick, 1982; Fitzpatrick, 2004a).

Onychorhynchus, *Myiobius*, and *Terenotriccus* were formerly included within the Tyrannidae, but our data place them outside of that group. Onychorhynchines lack the intrinsic syringeal muscle M. obliquus ventralis, which is found in almost all tyrannids and appears to constitute the least ambiguous morphological synapomorphy for that family (Prum, 1990a; Birdsley, 2002; Ericson et al., 2006). A clade formed by *Onychorhynchus*, *Myiobius*, and *Terenotriccus* has previously been recovered by Birdsley's (2002) phylogenetic assessment of tyrannid relationships using morphological and behavioural characters, as well as by Tello and Bates (2007) molecular study using mitochondrial and nuclear intron data. More recently, Ohlson et al. (2008) recovered the *Onychorhynchus* clade, which they found to be outside the traditional Tyrannidae and close to the tityrids, in agreement with our results.

A relationship of the Onychorhynchini to *Oxyruncus* is moderately supported (99/<50/65/3; Fig. 3a). Ericson et al. (2006) found that *Oxyruncus* was sister to the tityrines with strong support, although that study did not sample the Onychorhynchini. In a subsequent study (Ohlson et al., 2008), additional taxon sampling, including the Onychorhynchini, recovered the relationships (Onycorhynchini + (*Oxyruncus* + tityrines)), but branch support among the three was low.

One issue is how our results might be treated taxonomically. We propose applying the name Oxyruncinae to the clade *Oxyruncus* + Onychorhynchini. To our knowledge, the first use of the name Oxyruncinae was by Mayr and Amadon (1951), who included *Oxyruncus* in their Tyrannidae. As previously noted, *Oxyruncus* has often been included in its own monotypic family, Oxyruncidae Ridgway, 1906 based on *Oxyruncus* Temminck 1820. *Onychorhynchus* Fischer von Waldheim 1810 is the older generic name, but to our knowledge it has not been used for a family-group name.

Subfamily Laniisominae

The Laniisominae (erected by Barber and Rice, 2007) was strongly monophyletic (100/100/99/11) and comprised *Schiffornis* (*Laniisoma* + *Laniocera*), with the later sister-pair being well supported (100/97/85/5).

Subfamily Tityrinae

The Tityrinae (100/92/80/4) included *Iodopleura* as the sister-group to *Tityra* (*Pachyramphus* + *Xenopsaris*). Barber and Rice (2007) had the latter three genera in a trichotomy based on ND2 sequences, but the RAG data resolved a *Pachyramphus* + *Xenopsaris* relationship with high support (100/97/89/5).

One unsampled genus, *Calyptura*, has been thought to be closely related to *Iodopleura* (Snow, 1973, 1982) and therefore may belong in the Tityridae.

Family Cotingidae

Our analysis provides a substantially expanded assessment of the content and interrelationships of this clade compared with previous studies (Prum et al., 2000;

Ohlson et al., 2007). The Cotingidae, as recognized here, excludes *Iodopleura*, *Laniisoma*, and *Oxyruncus* and was strongly monophyletic (100/100/99/13; Fig. 3a). This concept of the group matches that of Ohlson et al. (2007) but not that of Prum et al. (2000). The RAG data revealed a number of strongly supported lineages, and these results necessitate a revised taxonomy for the group.

Subfamily Pipreolinae, ***new taxon*** *(type genus:* Pipreola *Swainson 1837)*

Diagnosis. The most inclusive crown clade that contains *Pipreola whitelyi* and *Ampelioides tschudii* but not *Phytotoma rutila*, *Rupicola rupicola*, *Carpornis melanocephalus*, or *Cotinga cayana*. No morphological synapomorphies have been proposed, but the clade is supported by RAG molecular data and by a 2-bp deletion event in the G3PDH intron (Ohlson et al., 2007).

The monophyly of the Pipreolinae is very strongly supported (100/100/99/14), as it was also in the Ohlson et al. (2007) study. Prum et al. (2000) placed *Oxyruncus* with *Pipreola* and *Ampelioides*, but *Oxyruncus* lies well outside cotingids (Ohlson et al., 2007; this study). Importantly, we also found that pipriolines were the sister-group of all other cotingid lineages with good support (100/76/71/4; Ohlson et al., 2007 also found this relationship, but it had poor support).

Subfamily Cotinginae

Within the remaining cotingids, the RAG data identified four primary lineages, each with high support, but whose interrelationships were ambiguous. One of these lineages is the genus *Carpornis*. The second, and largest, subclade of cotingids is the Cotinginae. Sibley and Monroe (1990) clustered all the cotingas in a subfamily within their greatly enlarged Tyrannidae, but here we follow a taxonomic conception for the Cotinginae similar to Prum et al. (2000) and Ohlson et al. (2007; less *Snowornis* discussed below). We found the Cotinginae to be very highly supported (100/98/95/7), and within this subfamily multiple clades could be recognized (Fig. 3a). A number of nodes toward the base of the group, however, are poorly supported or ambiguous, thus we refrain from proposing formal names until additional data resolve some of these relationships. We instead recognize several generic groups.

The monophyly of the *Gymnoderus* group is strongly supported (100/93/95/9). There are five genera in the group, with *Porphyrolaema* being the sister-group of the remaining four. The latter can be divided into *Gymnoderus* + *Conioptilon* (100/100/99/9) and *Xipholena* + *Carpodectes* (100/100/100/11).

A second well supported clade (100/81/73/3)—fruitcrows of the *Cephalopterus* group—includes four genera, and probably a fifth. At the core are (*Querula* (*Perissocephalus* (*Pyroderus* + *Cephalopterus*))), with all nodes well supported. Their sister-group is apparently *Haematoderus*, but this hypothesis has ambiguous support (99/<50/–/–). A similar resolution for this clade was found by Ohlson et al. (2007), except that instead they found *Cephalopterus* + *Perissocephalus*.

Three other genera were included in the Cotinginae. Our data resolved a relationship between *Cotinga* and *Procnias*, but with no support (61/<50/<50/1). That they might be the sister-clade of the *Cephalopterus* group was slightly better supported (97/<50/<50/2), but we judge these two relationships to be ambiguous and in need of much further analysis. *Cotinga* and *Procnias* were united in Prum et al.'s (2000) analysis but with no strong support, but they were far apart in Ohlson et al.'s (2007) study. The position of *Procnias* has been difficult to assess, mainly due to his highly derived syrinx which gives no clue about its relationships (Ames, 1971; Snow, 1973; Prum, 1990a). Finally, our data shows *Lipaugus* as the sister-group of all remaining Cotinginae, but that has no support on our tree (84/<50/–/–). *Lipaugus* has a similarly basal position on the Prum et al. (2000) tree but with little support, whereas in Ohlson et al.'s (2007) analysis it is sister to the *Gymnoderus* group with no support. In summary, interrelationships within the Cotinginae deserve much more study.

On our tree (Fig. 3a), three lineages cluster as the sister-group of the Cotinginae, but the joint monophyly of these three has no support (59/–/–/–). The three lineages, however, are supported. One is the genus *Carpornis* with two species. The other two, resolved as sister-taxa with little support (72/<50/<50/2), are two monophyletic groups that have received previous taxonomic recognition.

Subfamily Rupicolinae (type genus: Rupicola *Brisson 1760)*

Diagnosis. The most inclusive crown clade that contains *Rupicola rupicola*, *Phoenicircus nigricollis*, and *Snowornis cryptolophus* but not *Phytotoma rutila*, *Cotinga cayana*, or *Pipreola whitelyi*. The clade is strongly supported by molecular data (99/80/80/4). We diagnose the group more formally, inasmuch as the names "Rupicolidae" or "Rupicolinae" have almost always referred only to *Rupicola*, but see Prum et al. (2000).

Within the Rupicolinae, *Snowornis* was sister to the well supported *Rupicola* + *Phoenicircus* clade (100/100/100/15). Ohlson et al. (2007) placed *Snowornis* at the base of their "core cotinga" clade, and they found strong BP support (100) for this. Although a *Snowornis* + Cotinginae node appeared on two of the three genes they examined, only cytochrome *b* had a

"significant" BP (98). The RAG data would appear to be the strongest signal at this time for the placement of *Snowornis*.

Subfamily Phytotominae (type genus Phytotoma *Molina 1782)*

Diagnosis. The most inclusive crown clade containing *Zaratornis stresemanni*, *Phytotoma rutila*, and *Ampelion rufaxilla* but not *Rupicola rupicola*, *Cotinga cayana*, or *Pipreola whitelyi*. The clade is strongly supported by RAG (100/99/95/7), electrophoretic (Lanyon, 1985a) and syringeal morphology data (Lanyon and Lanyon, 1989; see Prum in litt., cited in Robbins et al., 1994).

Phytotoma has frequently been placed in its own family, but molecular data now place this genus decisively within cotingids. The branching pattern revealed in this study matches the results of Lanyon and Lanyon (1989) and Ohlson et al. (2007). Thus *Phytotoma* is the sister-group of *Ampelion* + *Doliornis*, and *Zaratornis* is then sister to those three. The RAG data provide much stronger support for these nodes (Fig. 3a) than in previous studies. To our knowledge, Prum et al. (2000) were the first to use the subfamily name Phytotominae.

General comments on the Cotingidae

The Cotinginae are composed of the *Cephalopterus* group, the *Gymnoderus* group, and *Lipaugus*, but the relationships among these three are not resolved with the RAG data. Likewise, although the Cotinginae are well supported, relationships among *Carpornis*, the Rupicolinae, and the Phytotominae are effectively unresolved. Our results suggest the latter two taxa are sister-groups, but the support is very low (72/< 50/<50/2). Consequently, there is a real possibility that one or more of these lineages could be more closely related to the Cotinginae than to each other as resolved on our tree.

We did not sample three genera (*Phibalura*, *Tijuca*, and *Calyptura*). The relationships of *Phibalura* are uncertain. The lack of anatomical or tissue specimens in collections has prevented a rigorous assessment of its phylogenetic relationships (Prum and Lanyon, 1989; Prum, 1990a). In some external characters, primarily in their black or blackish crowns with erectile nuchal crests of much the same red colour, *Phibalura* resembles *Ampelion*, which has been proposed to be its closest relative (Snow, 1973, 1982). In contrast to other cotingas, *Phibalura* also eats mistletoe fruits and, like *Ampelion*, hawks for flying insects (Snow, 1982).

The genus *Tijuca* has been found to be close to *Lipaugus* by Ohlson et al. (2007). In their study, they found *T. atra* to be embedded within an unresolved clade that also included *L. unirufus* and *L. fuscocinereus*. Snow (1982) reported that feather protein analyses showed greater electrophoretic similarity values between *T. condita* and *L. vociferans* than between *T. condita* and *T. atra*, which agrees with the overall vocal similarity between *T. condita* and *L. vociferans*. These findings, combined with the general resemblance in structure and female plumage of *Tijuca* spp., support the close relationship to *Lipaugus*, and even suggest the possibility of merging these two genera in *Lipaugus*, the oldest name.

The relationships of the monotypic genus *Calyptura* are also uncertain. It was placed in the Cotingidae based on its tarsal scutellation and foot structure (Snow, 1973, 1982), but its overall shape and size resemble a manakin or tyrant flycatcher. The genus has often been associated with *Iodopleura* because of their size and frugivorous behaviour (Sclater, 1888; Ridgway, 1907; Cory and Hellmayr, 1927, 1929; Snow, 1973, 1979, 1982), however no characters linking this genus to *Iodopleura* or any other tyrannidan have been identified. *Calyptura cristata* was considered extinct until its rediscovery in 1996 (Pacheco and Fonseca, 2001), thus it is considered critically endangered. Knowledge of its phylogenetic relationships will require the use of DNA isolated from museum skins.

Superfamily Tyrannoidea

Diagnosis. The most inclusive crown clade, including *Platyrinchus coronatus*, *Mionectes striaticollis*, *Neopipo cinnamomea*, and *Tyrannus savanna* but not *Cotinga cayana*, *Tityra semifasciata*, *Onychorhynchus coronatus*, *Oxyruncus cristatus*, or *Pipra filicauda*. The clade is supported by molecular data (99/<50/<50/1; see also Ohlson et al., 2008).

The taxonomic concept Tyrannoidea has traditionally been applied to the clade we call the Tyrannides, that is, all the ingroup taxa considered in this paper (Traylor, 1979; Lanyon, 1985a,b; Johansson et al., 2002). However, because of our increasing knowledge of the interrelationships of these taxa (Johansson et al., 2002; Ericson et al., 2006; Ohlson et al., 2008; this paper), there is a need to recognize this new understanding in an expanded and more detailed taxonomic hierarchy. Accordingly, here we use the concept Tyrannoidea to apply to those taxonomic entities often included under the name Tyrannidae (e.g. Traylor, 1979; Fitzpatrick et al., 2004; see Fig. 5). The problem, as we describe below, is that the "Tyrannoidea" may not be monophyletic, but it is comprised of a number of well supported subgroups, two of which are our Rhynchocyclidae and Tyrannidae. We have chosen to apply the name "Tyrannidae" to a large, well supported clade rather than to a still larger, possibly nonmonophyletic group. This will "fix" the family-level name much more firmly to a monophyletic group, in contrast to most

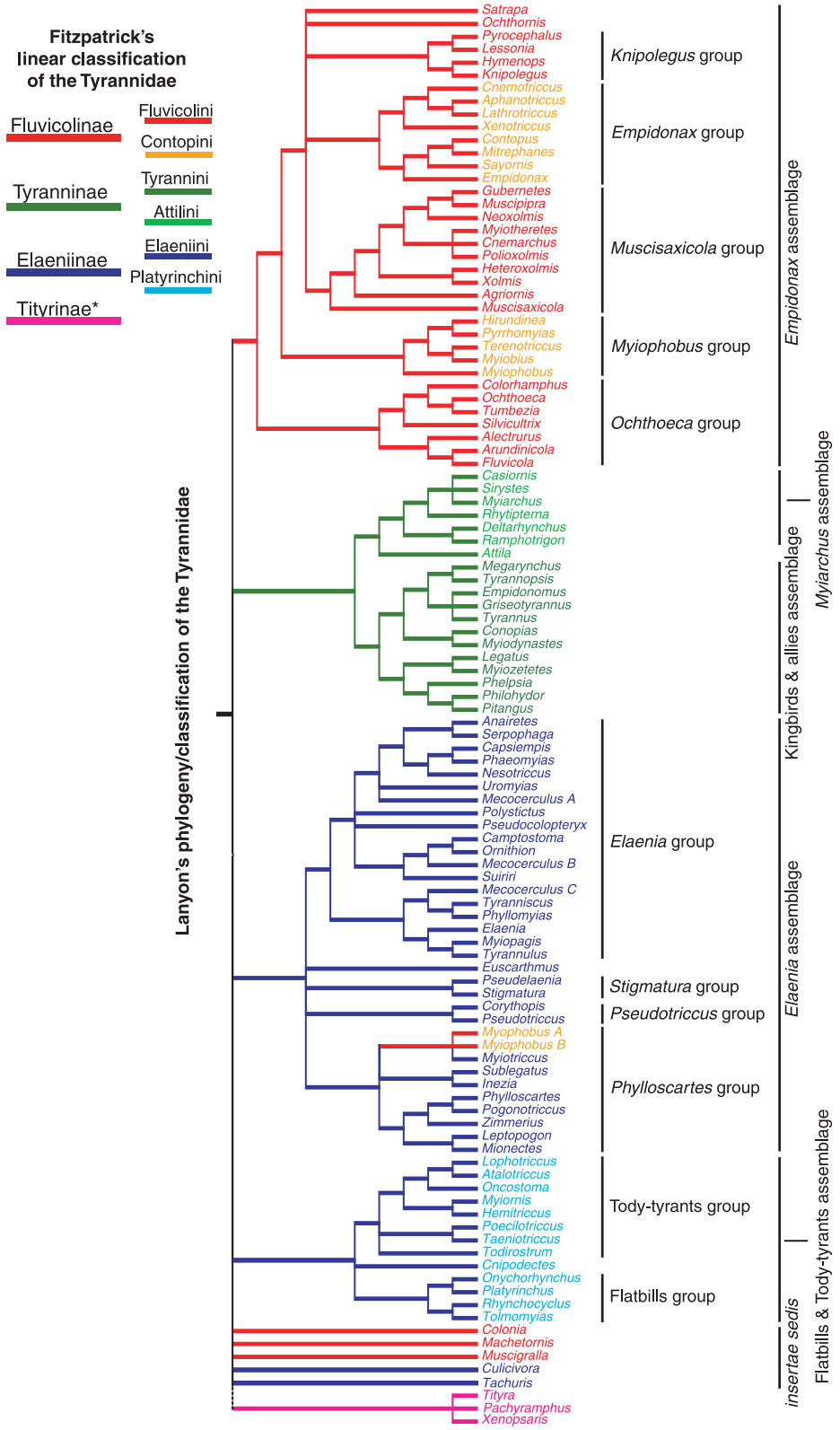

Fig. 5. Hypothesis of relationships for the Tyrannidae based on Lanyon's (1984, 1985b, 1986, 1988a,b,c). Colours represent Fitzpatrick's (2004) more recent linear classification of the Tyrannidae. * Fitzpatrick tentatively placed the Tityrinae at the end of his classification due to similarities with the tyrannids in cranial morphology.

previous studies in which the name "Tyrannidae" was applied to a (now) demonstrably nonmonophyletic taxon. The membership of the "Tyrannoidea" can be adjusted if future work shows that it is not monophyletic or if an outside clade is found to be a close relative.

Historical background

Early character-based systematic work discussing relationships among tyrannoids was based on analyses of cranial osteology (Warter, 1965) and syringeal morphology (Ames, 1971). Traylor (1977, 1979) incorporated information from these studies, in addition to behavioural and ecological data, to revise tyrannid classification in which he recognized three core taxa ranked as subfamilies: the Elaeniinae, Fluvicolinae, and Tyranninae. *Tityra* and *Pachyramphus* were tentatively allied with the Tyrannidae by Traylor, and placed at the end of the family in his linear classification. *Xenopsaris* was considered *insertae sedis* in the Tyrannidae (Traylor, 1977, 1979). We have already shown that these three genera are part of an enlarged Tityridae (Fig. 3a).

Other morphological comparisons have played a role in the dialogue about tyrannoid relationships. By re-examining traditional morphological characters, McKitrick (1985) found no support for the monophyly of the Tyrannidae as delineated by Traylor (1977, 1979). Instead, she suggested that, with the exception of some parallel losses, the possession of internal syringeal cartilages and the intrinsic muscle M. obliquus ventralis supported a slightly larger clade formed by the tyrannids plus the genera *Oxyruncus*, *Iodopleura*, *Pachyramphus*, *Schiffornis*, and *Piprites*. Prum (1990a, 1992; Fig. 1a) disagreed, and thought that the condition of the M. obliquus ventralis in *Iodopleura* and *Oxyruncus* was not homologous with that of the tyrant flycatchers, suggesting that the character is a synapomorphy of the tyrannids *sensu stricto*. Prum's interpretation was subsequently corroborated by a recent molecular study (Ericson et al., 2006).

In a series of important papers on tyrannid morphology and classification, Wesley Lanyon (1984, 1985a,b, 1986, 1988a,b,c) built on Warter's (1965) and Ames's (1971) work and undertook an extensive morphological revision using primarily cranial and syringeal morphology that resulted in the recognition of five major assemblages—kingbirds, *Myiarchus*, *Empidonax*, *Elaenia*, and the flatbills and tody-tyrants—which together constituted the bulk of the traditional Tyrannidae (Fig. 5). Lanyon's studies were restricted to these primary assemblages, and he did not investigate relationships across tyrannids as a whole, or with explicit outgroups. Birdsley (2002) used Lanyon's morphological and behavioural data, as well as others', to investigate phylogenetic relationships within the Tyrannidae. He found that monophyly of the family was ambiguously supported; an equally most-parsimonious hypothesis suggested that the flatbill/tody-tyrant assemblage was more distantly related to other tyrannids than were cotingids and piprids. Birdsley's results supported Lanyon's kingbird, a portion of his *Empidonax*, and *Myiarchus* assemblages, and several other lower-level groupings, but the monophyly of the *Elaenia* and the flatbill/tody-tyrant assemblages was not supported.

The early morphological studies were soon followed by a series of analyses using molecular data. Based on DNA–DNA hybridization distances, Sibley and Ahlquist (1985, 1990) proposed that the Tyrannidae *sensu stricto* were not monophyletic (Fig. 1b). They recognized an expanded "Tyrannidae" in which the rhynchocycline (= mionectine) flycatchers (Mionectidae, Sibley and Ahlquist, 1985; our Rhynchocyclidae, Fig. 3a) were sister to all other Tyrannides ((Cotinginae + Piprinae) + (Tityrinae + Tyranninae)). This concept of the Tyrannides was depicted on their "Tapestry" tree (Sibley and Ahlquist, 1990, figs 372–373) that was hand-drawn from hybridization distances. In contrast, their tree derived from a matrix of distances using the FITCH algorithm (Sibley and Ahlquist, 1990, fig. 345) showed the Tyrannidae as monophyletic, which suggests that the "Tapestry" topology may have resulted from the lack of an objective method of tree-building.

Subsequent DNA-sequencing studies using mitochondrial and nuclear data found support for the monophyly of Tyrannidae *sensu stricto* (Johansson et al., 2002; Chesser, 2004; Ericson et al., 2006; Fig. 1c, d). Taxon sampling was limited in these studies, thus monophyly and relationships within the group could not be assessed in detail. In a more recent study using nuclear intron data, Ohlson et al. (2008) found that traditional Tyrannidae were not monophyletic in that *Onychorhynchus* and its allies as well as *Piprites* were outside that group. Their Tyrannidae, instead, included *Platyrinchus*, *Neopipo*, *Tachuris*, the pipromorphines, and the remainder of the typical tyrant flycatchers.

The most current treatment of tyrannid classification is that of Fitzpatrick (2004a), which takes a very conservative approach, and recognizes subfamilies and tribes based on Traylor and Lanyon's suggestions (Fig. 5) and some proposals by Warter (1965). Following Traylor, Fitzpatrick tentatively placed the Tityrinae at the end of his linear classification due to similarities with the tyrannids in cranial morphology. Fitzpatrick (2004b) also described a new tribe within the Fluvicolinae, the Contopini. The remainder of the fluvicolines were placed in the tribe Fluvicolini. Some tribal names (Tyrannini and Attilini) were proposed by Fitzpatrick (2004a) for the first time without providing formal diagnosis.

Results from RAG-1 and RAG-2

We found that the Tyrannidae as circumscribed by Fitzpatrick (2004a; Fig. 5) are not strictly monophyletic (Fig. 3). As discussed in previous sections, a number of genera traditionally placed in the Tyrannidae are more properly members of the tityrine and oxyruncine clades, and are apparently distant relatives of core tyrannids (Fig. 3a). Second, the enigmatic manakin-like genera, *Piprites* and *Neopipo*, are not piprids but were found to be inside the Tyrannoidea (Fig. 3a,b). The Tyrannoidea are characterized by a high Bayesian posterior probability, but other measures of support are weak or nonexistent (99/<50/<50/1; Fig. 3a).

The RAG data reveal two strongly supported major clades plus several basal genera with uncertain affinities. The rhynchocycline flycatchers form one of these lineages (100/100/99/8) and we recognize it as part of the Rhynchocyclidae (Fig. 3a; see below). Likewise, the RAG data confirm a large clade of traditional tyrant flycatchers, for which we here use the name Tyrannidae (Fig. 3b). This clade also has extremely strong branch support (100/100/100/15). Four genera (*Tachuris*, *Piprites*, *Platyrinchus*, and *Neopipo*) have weak support at the base of the tyrannoids, and their relationships remain uncertain at this time. Three of these genera—*Tachuris*, *Piprites*, and *Platyrinchus*—may be related to the rhynchocyclines (Fig. 3a). *Tachuris* and *Piprites* are linked to the rhynchocyclines with ambiguous branch support (100/67/–/–); *Platyrinchus* essentially has no support. The fourth genus, *Neopipo*, is resolved as the sister-group to the tyrannids (Fig. 3b) but also with no support (55/–/–/–). In the sections that follow we discuss tyrannoid relationships and our data in more detail.

Unnamed higher taxon Platyrinchus, Piprites, Tachuris*, and Rhynchocyclidae*

Our data reveal a clade comprised of *Platyrinchus*, *Piprites*, *Tachuris*, and the Rhynchocyclidae (Fig. 3a). Because the basal nodes of this clade are ambiguously supported, we refrain from naming the entire group. If these relationships are corroborated with additional data, these taxa could be united with the Rhynchocyclidae.

Platyrinchus, Piprites, *and* Tachuris.

The relationships of *Platyrinchus* are uncertain, although most studies generally place them near the base of the pipromorphines (= rhynchocyclines), albeit with little or no support (e.g. Tello and Bates, 2007; Ohlson et al., 2008). Our results are similar, and more data are clearly needed to confirm their systematic position.

Piprites was formerly placed in the Pipridae and later suggested to be outside this family because it possesses tyrannid-like internal syringeal cartilages (Prum and Lanyon, 1989; Prum, 1990a). Recent studies using molecular data corroborated this suggestion and placed it next to the tyrannids (Ericson et al., 2006; Ohlson et al., 2008). Our data point to a rhynchocycline relationship, and although the Bayesian PP is high (100), both ML bootstrap is low (67%), and MP bootstrap is low or nonexistent.

The monotypic *Tachuris* is one of the most bizarre and most specialized of all tyrant flycatchers, and its evolutionary relationships have remained mysterious (Fitzpatrick, 2004a). The genus was postulated as belonging in the Elaeniinae on the basis of cranial morphology (Warter, 1965), and the only other proposal has been that it might be related to *Pseudocolopteryx* because of shared marsh-living habits (Traylor, 1977; Fitzpatrick, 2004a). Our data indicate affinities with the rhynchocyclines.

Family Rhynchocyclidae, new rank (type genus: *Rhynchocyclus* Cabanis and Heine, 1859–1860)

Diagnosis. The most inclusive crown clade that contains *Todirostrum cinereum*, *Rhynchocyclus brevirostris*, *Mionectes striaticollis*, and *Cnipodectes subbrunneus*, but not *Tyrannus tyrannus*, *Cotinga cayana*, *Tityra semifasciata*, *Oxyruncus cristatus*, or *Dixiphia pipra*.

For reasons explained below, we apply the name Rhynchocyclidae to the group that includes four well supported clades (the *Cnipodectes* group, Pipromorphinae, Rhynchocyclinae, and Todirostrinae; Fig. 3a). The family includes genera formerly placed in the Mionectidae/Pipromorphinae of Sibley and Ahlquist (1985, 1990), Pipromorphinae of Sibley and Monroe (1990), Lanyon's (1988a) "tody-tyrant and flat-bill assemblage" (Tello and Bates, 2007), and Fitzpatrick's (2004a) Platyrinchini and some of his Elaeniini. The monophyly of the family as we circumscribe it is strongly supported (100/100/99/8; Fig. 3a), and there are other studies that provide support for this clade (Tello and Bates, 2007; Ohlson et al., 2008). Within the Rhynchocyclidae, we found that *Cnipodectes* + *Taeniotriccus* (our *Cnipodectes* group) are sister to a major clade formed by the Pipromorphinae, which itself is sister to the Rhynchocyclinae (flatbills) + Todirostrinae (tody-tyrants).

The sister relationship between the flatbills and tody-tyrants uncovered by the RAG data is ambiguously supported (98/52/–/–). Other investigators have also found these two groups to be sister clades (Tello and Bates, 2007; Rheindt et al., 2008; but nearly all the key sequences in the latter study are from Tello and Bates, 2007). In both of these studies support was likewise ambiguous, and *Cnipodectes* was associated with the flatbills (again because of Tello and Bates' data). In contrast, Ohlson et al. (2008) found *Cnipodectes* to be

associated with the tody-tyrants with high Bayesian support. Lanyon (1988a) proposed three synapomorphies for a flatbill + tody-tyrant clade, but he also included several genera (*Platyrinchus*, *Onycorhynchus*) that we found to lie well outside this group. Birdsley (2002), in his cladistic reanalysis of data from all of W. Lanyon's tyrannid studies, was unable to recover this clade. Interestingly, however, of Lanyon's (1988a) three synapomorphic characters for the flatbill + tody-tyrant clade, one was absent from *Onychorhynchus*, and one from *Platyrinchus*. Taken together, the available data indicate that flatbills and tody-tyrants are sisters, but this relationship needs to be tested further.

Comments on nomenclature

The nomenclatural history of the family-group name for taxa in this clade is somewhat tortuous (see Todd, 1921). The group name Pipromorphinae was proposed by Bonaparte (1853, p. 645) without mention of a type genus or species. The genus-group name *Pipromorpha* was first cited in a taxonomic list by Bonaparte (1854, p. 134) as "Pipromorpha, Schiff" but with no mention of a type species. As noted by Todd (1921, p. 174), *Pipromorpha* Bonaparte, 1854 is a *nomen nudum*. Because *Pipromorpha* was not formerly established until Gray designated *Muscicapa oleagina* Lichtenstein as its type (Gray, 1855, p. 146), the family-group name Pipromorphinae Bonaparte, 1853 is thus itself a *nomen nudum* (see also Olson, 1995, p. 546). Parallel to the case of *Pipromorpha*, Bonaparte (1854) erected many new generic names with the authorship assigned to "Schiff", the name undoubtedly referring to the great physiologist Moritz Schiff. Apparently, Schiff was working on collections at the Senckenberg Museum around 1854, and according to Schäfer (1967), p. 304; from Gerald Mayr, personal communication) Schiff presumably sent a manuscript to *Compte Rendu*. At that time, Schiff was sending frequent notes to *Compte Rendu*, but they were all on physiological topics, and no paper of his pertaining to avian systematics was published in that journal. We conjecture instead that Schiff sent this manuscript to Bonaparte, who, one might surmise, was in the process of writing his 1854 paper, and he incorporated Schiff's new generic names. In that paper each was a *nomen nudum* until Gray (1855).

The next family-group name proposed for taxa in this clade was Cychlorhyncheae (Bonaparte, 1854, p. 134), a tribe-level group within his Tyranninae. The Cychlorhyncheae included *Pipromorpha* (see above), *Myiocapta* (a *nomen nudem*, also ascribed to "Schiff" but apparently never formally published, see Richmond Index at http://www.zoonomen.net/cit/RI/Genera/RI-GenM.html), *Myiobius*, *Megalophus* (= *Onychorhynchus*), *Onychorhynchus*, and *Cychlorhynchus*. Traylor (1979, p. 98) declared the latter genus a *nomen oblitum* and placed it as a synonym of *Rhynchocyclus*. Under Article 40 of the Code (International Commission of Zoological Nomenclature, 1999), the family-group name Cychlorhynaceae remains available, but just as the genus name is a *nomen oblitum*, the family-group name can be interpreted similarly since, to our knowledge, it has not been used since it was created.

In his 1854 paper, Bonaparte created many taxa at the tribe level with *-eae* endings. All these were based on included genera, thus these names can be interpreted as valid family-group names. He did not specify the rank, but identified them as subdivisions of subfamilies: "Je donne donc une nouvelle édition de ma classification, et j'en profite pour y ajouter l'énumération de tous les genres sous chaque sous-division de sous-famille ou série subordonnée. Au besoin, à cette énumération se trouveront jointes des notes explicatives" (1854, pp. 107–108). The *-eae* suffix was common at that time, persisting today as the suffix for tribe names in botany, and it was recognized as being part of the historical nomenclatural landscape of the time by the American Ornithologists' Union (1886, p. 25).

After the 1850s, some of the genera we include here in the Rhynchocyclidae were placed in the subfamily Elaeiinae (Cabanis and Heine, 1859–60), which over the years became a repository for many genera not assigned to the Tyranninae. As far as we can determine, the name Pipromorphinae lapsed into disuse until it resurfaced in Wolters (1977, p. 192) and Sibley and Ahlquist (1990).

Sibley and Ahlquist (1985) were the first to recognize the distinctiveness of a basal clade that was sister to their "Tyrannidae", which included flycatchers and tityrines as well as, incorrectly, manakins and cotingas. They proposed the family-group name Mionectidae for it (not "Mionectinae Sibley and Ahlquist, 1985; " as synonymized in Bock, 1994, p. 148), presumably because *Mionectes* Cabanis 1844 is the oldest genus-group name. In their 1988 classification of birds, they changed the rank and name of this taxon to Corythopinae within their Tyrannidae (Sibley et al., 1988). Two years later, they again changed the name to Pipromorphinae (Sibley and Ahlquist, 1990; Sibley and Monroe, 1990), citing the name Pipromorphinae Bonaparte, 1853 as the reason (Sibley and Ahlquist, 1990, p. 595). The latter two citations have been misinterpreted and misquoted on several occasions, which has increased confusion over the history of the name for this clade. Remarking on the results of Sibley and Ahlquist, for example, Fitzpatrick (2004a, p. 171) noted: "DNA–DNA hybridization evidence was interpreted as revealing such a deep split within the 'true' tyrant-flycatchers that is was deemed necessary to erect a new subfamily, Pipromorphinae, later changed to Mionectinae, in order to recognize a previously unsuspected assemblage that included the genera *Mionectes* and *Todirostrum* and relatives." Unfortunately, the history of the names is backwards.

Bock (1994, pp. 148, 198) added to the confusion over the name and rank associated with this group by his statement (p. 198) that "Mionectinae Sibley and Ahlquist, 1985 takes precedence from 1985 and lacks priority with respect to Pipromorphinae G.R. Gray, 1885 [*sic*] as recognized by Sibley and Monroe (1990:334) who use Mionectinae for this subfamily." The confusion arises because, in his list of synonymies, Bock repeatedly changed the original rank of taxa that he synonymized, thus obscuring the first and subsequent use of specific names and their ranks. To clarify, Sibley and Ahlquist (1985) used "Mionectidae", and Sibley and Monroe (1990, p. 334) used "Pipromorphinae", and not "Mionectinae". We surmise that the above statement of Fitzpatrick (2004a) stems from this error by Bock because we know of no other use of the name "Mionectinae" in the literature. Tello and Bates (2007) and Ohlson et al. (2008) used the name Pipromorphinae, as did Rheindt et al. (2008), but the latter authors confused the history of these names again: "…they [Sibley and Ahlquist, 1985, 1990;] singled out certain genera (Fig. 1) into a new family Pipromorphidae (= Mionectidae) and placed it basal to all Tyranni…" This lapse may be the first use of the name "Pipromorphidae".

Given the preceding morass, the question is what is the valid family-group name for the clade we have identified? Berlepsch (1907, p. 482) erected a new subfamily, Rhynchocyclinae, for *Cnipodectes*, *Craspedoprion* (= *Rhynchocyclus*), *Rhynchocyclus*, and *Ramphotrigon*. We propose that this is the oldest valid family-group name for the clade we have identified (Fig. 3a) that has not been designated a *nomen nudum* or *nomen oblitum*. We therefore erect a new family-rank name, Rhynchocyclidae, based on Berlepsch (1907), and we use Pipromorphinae as a subfamily within this clade based on Wolters, 1977, who to our knowledge used this family-group name properly for the first time.

In our effort to construct a phylogenetic classificatory framework with some long-term stability, we are eliminating the traditional, expanded concept of the Tyrannidae because nodes along the spine of that clade are nearly all ambiguously supported, including the basal node. In contrast, our concepts of Tyrannidae and Rhynchocyclidae are strongly monophyletic and thus likely to provide long-term stability for their names. We note, however, that if *Platyrhynchus* is confirmed to be the sister to the rhynchocyclines, then the family-group name would revert to Platyrhynchidae. That group name is not attributable to Horsfield 1821–24 (in Bock, 1994), as Olson (1995) has observed. The earliest valid use we could find is Platyrhyncheae, a tribe-level taxon erected by Bonaparte (1854, p. 133; see discussion above about Bonaparte's *-eae* endings). The first use of a subfamily rank suffix, Platyrhynchinae, was apparently in Olph-Gaillard (1857, p. 170), who listed it as "Trib. 5. Platyrhynchinae" under his Family Tyrannidae. Olph-Gaillard used the word tribe for all names ending in *-inae*. Sclater (1862, p. 206) used Platyrhynchinae, and then Gray (1869, p. 347) also used the name, incorrectly ascribing authorship to Sclater (1862). We propose the tribe-group name stems from Bonaparte (1854).

Cnipodectes *group*

The clustering of *Cnipodectes* and *Taeniotriccus* was unexpected, but this node is extremely well supported (100/100/100/15). Moreover, we found these two genera to be the sister-group of all the pipromorphine clades just discussed above (Fig. 3a). *Cnipodectes* was previously resolved, using nuclear intron data, as belonging to the flatbills (Tello and Bates, 2007) or being sister to the tody-tyrants (Ohlson et al., 2008; although these authors did not include *Taeniotriccus*), whereas *Taeniotriccus* had been suggested as being congeneric with *Poecilotriccus* on the basis of internal morphology (Traylor, 1977, 1979; Lanyon, 1988a). Differences in external morphology and vocalizations between *Taeniotriccus* and *Poecilotriccus*, however, led to the interpretation that the former should stay in its own genus (Fitzpatrick et al., 2004; Zimmer and Whittaker, 2004) and even created doubts about its prior inclusion in the tody-tyrants. Moderate support for several nodes on the RAG tree (Fig. 3a) is inconsistent with these previous hypotheses and excludes *Cnipodectes* and *Taeniotriccus* from the tody-tyrants and flatbills. This conflict among data sets will have to be resolved with combined analyses and additional character evidence.

Subfamily Pipromorphinae Wolters, 1977 (type genus: Pipromorpha *G.R. Gray, 1855)*

Diagnosis. The most inclusive crown clade that contains *Corythopis torquatus* and *Mionectes macconnelli*, but not *Todirostrum cinereum* or *Rhynchocyclus brevirostris*. This clade (Fig. 3a) is well supported by RAG (100/98/95/6) and nuclear intron data (Ohlson et al., 2008).

Within our Pipromorphinae, three clades can be recognized, with relationships among the three being essentially unresolved: (i) *Mionectes* (including *Pipromorpha*) + *Leptopogon* (90/78/75/3); (ii) *Corythopis* + *Pseudotriccus* (100/95/91/5); and (iii) *Phylloscartes* + *Pogonotriccus* (100/100/100/15). A sister relationship between *Mionectes* and *Leptopogon* has previously been suggested by syringeal morphology (Lanyon, 1988b), DNA–DNA hybridization (Sibley and Ahlquist, 1985, 1990), and mitochondrial and nuclear DNA (Chesser, 2004; Tello and Bates, 2007; Ohlson et al., 2008). These two genera were supported as sisters on our tree by ML and MP bootstraps, but not by BP. A sister relationship between *Pseudotriccus* and

Corythopis is also supported by cranial and syringeal characters, as well as other molecular markers (Lanyon, 1988b; Tello and Bates, 2007; Ohlson et al., 2008). It has been proposed previously (Traylor, 1977) that *Pogonotriccus* should be merged with *Phylloscartes*, and our results are not inconsistent with that view. The species included in *Mionectes* and *Pipromorpha* are indeed extremely closely related, but seem to sort into these two names on the basis of mtDNA (Rheindt et al., 2008), although this will need further sampling. They have repeatedly been combined under the name *Mionectes* for well over 100 years (for a counter-argument against this merger, see http://www.museum.lsu.edu/~remsen/SACCprop202.html).

Subfamily Rhynchocyclinae von Berlepsch, 1907

Diagnosis. The most inclusive crown clade that contains *Rhynchocyclus brevirostris* and *Tolmomyias poliocephalus*, but not *Todirostrum cinereum*, *Atalotriccus pilaris*, *Mionectes striaticollis*, or *Cnipodectes subbrunneus*. The clade is supported by RAG, nuclear introns, and mtDNA characters (Tello and Bates, 2007; Ohlson et al., 2008) as well as external and syringeal morphology and nest structure (Cory and Hellmayr, 1927; Traylor, 1977; Lanyon, 1988a).

Subfamily Todirostrinae ***new taxon*** *(type genus:* Todirostrum *Lesson 1831)*

Diagnosis. The most inclusive crown clade that contains *Todirostrum cinereum*, *Myiornis ecaudatus*, and *Atalotriccus pilaris*, but not *Rhynchocyclus brevirostris*, *Mionectes striaticollis* or *Cnipodectes subbrunneus*. The clade is supported by molecular data (RAG, nuclear introns, and mtDNA sequences, see Tello and Bates, 2007 and Ohlson et al., 2008) and two syringeal characters (a horseshoe-shaped, cartilaginous bronchial plate; and delicate, rod-like internal cartilages located near the caudal ends of the horseshoe), which are hypothesized to be derived (Lanyon, 1988a; Birdsley, 2002).

This new subfamily is well supported (100/100/99/8). Within the Todirostrinae we recovered several sub-clades. *Poecilotriccus* formed a clade with *Todirostrum* that is sister to all other Todirostrinae. *Atalotriccus* (*Lophotriccus* + *Oncostoma*) formed one lineage; their putative sister-group is *Hemitriccus diops* but this relationship has no branch support. Related to them, with moderate to strong support (98/80/57/1), is a clade comprised of three species of *Hemitriccus* and *Myiornis*. In our analyses, neither *Hemitriccus* nor *Poecilotriccus* is monophyletic (see also Tello and Bates, 2007). Using mitochondrial and nuclear intron data, Tello and Bates (2007) also found evidence supporting the nonmonophyly of *Hemitriccus* (see also Ohlson et al., 2008), but relationships of these species to the other genera just discussed were inconsistent across markers. Species-level sampling of *Hemitriccus* in Tello and Bates (2007) and in this study have major gaps, thus additional data will be needed to resolve interrelationships among these apparently closely related taxa. Given that *H. diops* is the type species, it is likely that taxonomic changes will have to be made to accommodate the other species.

Likewise, *Poecilotriccus ruficeps* (the type species) and *P. capitalis* are strongly united and separate from *P. russatus*, which is poorly supported as the sister-group to *Todirostrum*. Tello and Bates (2007) did not sample these species, but did find two other species of *Poecilotriccus* as sister to *Todirostrum*. Solving this problem will require additional taxon and character sampling.

Neopipo

Our results suggest that *Neopipo* occupies a basal position within the Tyrannoidea (Fig. 3b), but given the lack of branch support along the spine of the group, its exact position is uncertain with our data. Previous work by Mobley and Prum (1995) suggested that *Neopipo* belongs in Lanyon's (1986, 1988c) *Myiophobus* group (*Myiophobus*, *Myiobius*, *Terenotriccus*, *Pyrrhomyias*, and *Hirundinea*), a hypothesis that is not supported by our study. Ohlson et al. (2008), and later Rheindt et al. (2008), found strong support for a sister relationship between *Platyrinchus* and *Neopipo* (the latter was not sampled by Tello and Bates, 2007). Thus *Neopipo* may belong in the Rhynchocyclidae as well.

Family Tyrannidae

Diagnosis. The most inclusive crown clade that contains *Tyrannus savana*, *Hirundinea ferruginea*, and *Elaenia albiceps* but not *Mionectes striaticollis*, *Cotinga cayana*, *Tityra semifasciata*, or *Dixiphia pipra*. With this diagnosis we restrict Tyrannidae to a strongly supported monophyletic group based on RAG (100/100/100/15) and nuclear intron data (Ohlson et al., 2008).

Within this newly circumscribed Tyrannidae (Fig. 3b), our analyses revealed five lineages with various levels of branch support that include the cores of some of the currently recognized subfamilies and tribes of traditional Tyrannidae (Fitzpatrick, 2004a; Fig. 5). These groups are (Fig. 3b): (i) Fluvicolinae (98/68/–/–); (ii) Tyranninae (89/54/50/1); (iii) the monotypic genus *Muscigralla*; (iv) Elaeniinae (100/100/99/13); and (v) a newly discovered lineage of basal flycatchers consisting of *Hirundinea* and allies (96/78/55/1). Relationships among these lineages received varying support depending on the analytical approach. The Fluvicolinae + Tyranninae + *Muscigralla* were strongly supported as a monophyletic group (100/89/84/3), with fluvicolines and tyrannines being

each other's closest relatives with strong support (100/74/64/3). These three lineages were, in turn, sister to the Elaeniinae + *Hirundinea* group, but the latter pairing had virtually no support (55/< 50/–/–). Ohlson et al. (2008) found the *Hirundinea* clade to be sister to a major clade formed by the tyrannines + fluvicolines + *Muscigralla*, but support for this relationship was very weak. Thus the base of the strongly monophyletic tyrannids is essentially a trichotomy. We now discuss these five lineages in turn.

Subfamily Hirundineinae, **new taxon** (type genus: Hirundinea d'Orbigny and Lafresnaye 1837)

Diagnosis. The most inclusive crown clade that contains *Hirundinea ferruginea* and *Myiotriccus ornatus*, but not *Elaenia albiceps*, *Muscigralla brevicauda*, or *Tyrannus savana*. No morphological synapomorphies are known, but the clade is supported by molecular characters (this study and Ohlson et al., 2008).

We recovered a lineage (96/78/55/1; Fig. 3b) formed by *Hirundinea*, *Pyrrhomyias*, and *Myiophobus ochraceiventris* from Fitzpatrick's (2004a,b) Fluvicolinae tribe, Contopini, plus the addition of *Myiotriccus* from his Elaeniinae tribe, Elaeniini. *Hirundinea* and *Pyrrhomyias* are strongly supported as sister-groups (100/99/98/7), as are *Myiotriccus* and "*Myiophobus*" *ochraceiventris* (100/100/98/8). Ohlson et al. (2008) recovered the Hirundineinae using nuclear intron data, but their internal relationships differed from ours in that "*Myiophobus*" (*ochraceiventris*, *lintoni*, and *pulcher*) was found to be sister to *Hirundinea* + *Pyrrhomyias* with high BP support.

A sister relationship between *Hirundinea* and *Pyrrhomyias* was suggested by Lanyon (1986, 1988c) based on syringeal similarities (narrow strand of cartilage located ventrally within internal tympaniform membrane, between ventral ends of B2 and B3) and on nesting habits (nests built in niches or crevices). He placed these two genera together with *Myiobius* (including *Terenotriccus*) and some species of *Myiophobus* (*fasciatus*, *flavicans*, *inornatus*, and perhaps *cryptoxanthus*) into the *Myiophobus* group of his *Empidonax* assemblage (Lanyon, 1986, 1988b,c). The other species of "*Myiophobus*" were placed in two different groups (one formed by *ochraceiventris*, *lintoni* and *pulcher*; the second formed by *roraimae* and *phoenicomitra*), which, together with *Myiotriccus*, were suggested to belong to the *Phylloscartes* group in the *Elaenia* assemblage (Lanyon, 1988b). The latter clade was supported solely on the presence of the concealed crown patch (Lanyon, 1988b).

Our results add clarity to the systematic position of these flycatchers, but there are still unresolved problems. The clade discussed here is moderately supported but its relationships to the Elaeniinae and Tyranninae + Fluvicolinae are unresolved. We have confirmed the nonmonophyly of "*Myiophobus*", but it will take future species-level analyses to fully resolve which species are near *Hirundinea* and *Pyrrhomyias* and which are in the Fluvicolinae. We also confirmed Lanyon's (1988c) observation of a close relationship between *Myiobius* and *Terenotriccus*, but these two genera are instead related to *Onychorhynchus* (see above), not to the present group.

Subfamily Elaeniinae

This strongly supported lineage (100/100/99/13; Fig. 3b) includes the core of Fitzpatrick's (2004a, see Fig. 5) Elaeniini, with the exclusion of *Myiotriccus*, *Pseudotriccus*, *Corythopis*, *Phylloscartes*, *Pogonotriccus*, *Leptopogon*, *Mionectes*, and *Tachuris*, all of which except *Tachuris* we found to belong in the Rhynchocyclidae (see below). Within the subfamily, we find two well supported clades, recognized here as the tribes Euscarthmini and Elaeniini.

Tribe Euscarthmini, ***new rank*** *(type genus* Euscarthmus *Wied 1831)*

Diagnosis. The most inclusive crown clade that contains *Tyranniscus burmeisteri*, *Euscarthmus rufomarginatus*, *Stigmatura budytoides*, and *Zimmerius viridiflavus* but not *Elaenia albiceps* or *Culicivora caudacuta*. No morphological synapomorphies have been proposed, but the clade is strongly supported by molecular data.

The family-group name Euscarthminae was first used by von Ihering (1904). To our knowledge, this name has not been applied at a tribal rank, and as our arrangement within the Elaeniinae departs from previous authors, we provide a diagnosis. The Euscarthmini is a strongly supported clade on the basis of RAG sequences (100/90/85/4) and more recently supported by nuclear intron data (Ohlson et al., 2008). Three lineages can be recognized within this tribe: (i) *Zimmerius*; (ii) *Stigmatura* as sister to *Euscarthmus* + *Inezia* (65/<50/<50/2); and (iii) *Tyranniscus* (*uropygialis* and *burmeisteri*) as sister to *Camptostoma* + *Ornithion* (100/99/96/6).

The genus *Zimmerius* was proposed by Traylor (1977) to include five distinctive species formerly placed in *Tyranniscus* (the two genera were placed next to each other in his linear classification). Traylor (1977) supported the creation of *Zimmerius* on the basis of differences in external (Zimmer, 1955), cranial (Warter, 1965), and syringeal (Ames, 1971) morphology. This was later corroborated by a more detailed assessment of the Elaeniinae (Lanyon, 1988b). In that study, Lanyon found that *Zimmerius* possessed a trabecular plate within the septum lacking an "anterior notch", the cranial diagnostic character of his *Elaenia* assemblage. Within this assemblage, he found that similarities in

syringeal morphology suggested *Zimmerius* to be sister to *Phylloscartes* of his *Phylloscartes* group (Lanyon, 1988b). We found that all members of Lanyon's *Phylloscartes* group, with the exception of *Zimmerius*, fall outside the Elaeniinae.

The taxonomic position of *Stigmatura* has also been uncertain. Its external morphology led some to suggest its placement within the thamnophilid antbirds (Ridgway, 1907; Wetmore, 1926), until Cory and Hellmayr (1927) showed it was a tyrannid and placed it in his Serpophaginae, next to *Serpophaga*, a decision endorsed by Smith (1971). Traylor (1977) acknowledged a close resemblance between *Inezia* and *Stigmatura*, and placed both genera between *Serpophaga* and *Anairetes*. Surprisingly, Ames (1971) remarked that the syrinx of *Stigmatura* is unlike any of the genera from Hellmayr's Serpophaginae; and Warter (1965) pointed out that the nasal septum of the specimen he examined lacked the trabecular plate, unlike the other members of *Serpophaga*. Later, Lanyon (1988b) demonstrated that the apparent lack of trabecular plate in *Stigmatura* was an artefact of the preservation of the specimen used by Warter, and he placed *Stigmatura* in his *Elaenia* assemblage.

A relationship between *Euscarthmus* and *Inezia* has only been recently suggested (Ohlson et al., 2008). *Euscarthmus* has represented another long-standing enigma (Lanyon, 1988b). *Euscarthmus* was at one time excluded from the Tyrannidae on the basis of its taxaspidean tarsi, and was suggested to belong in the thamnophilid antbirds (Wetmore, 1926). The presence of internal syringeal cartilages supported its inclusion within the Tyrannidae, but did not provide any clues about its phylogenetic position within the family (Ames, 1971; Lanyon, 1988b). However, its nasal septum has the key characters that diagnose Lanyon's (1988b) *Elaenia* assemblage (being fully ossified with large trabecular plate, located within the septum and laterally deflected), but he did not present information on its phylogenetic position within this assemblage (nasal septa as in *Euscarthmus* are also found in *Inezia*, *Polystictus*, and *Serpophaga*). Lanyon (1988b) also placed *Inezia* in his *Elaenia* assemblage because it shared the derived syringeal characters that characterized this assemblage (see above; Fig. 5), but he excluded it from his *Elaenia* group because it lacked the fused A-elements into a "drum", a feature present in members of his *Elaenia* group. He placed it in his *Phylloscartes* group as sister to *Sublegatus*; we now know this is not a natural group.

A sister relationship of *Camptostoma* and *Ornithion* has been suggested on the basis of similar syringeal morphology (ventral extension from distal half of internal cartilage poorly staining and amorphous; and broad dorsal ends of the A1 elements; Lanyon, 1988b). Lanyon also suggested that some species of "*Mecocerculus*" (*stictopterus*, *poecilocercus*, and *hellmayri*) were sister to *Camptostoma* + *Ornithion* on the basis of having similar internal cartilages (straight and broad with a ventral extension from its distal half). We found instead that two species of *Tyranniscus* (previously placed in *Phyllomyias* by Traylor, 1979; see below) were the sister-group of *Camptostoma* + *Ornithion* (see remarks below).

Tribe Elaeniini

Diagnosis. The most inclusive crown clade that contains *Myiopagis viridicata*, *Elaenia albiceps*, and *Culicivora caudacuta* but not *Euscarthmus rufomarginatus*.

The clade Elaeniini is well supported by the RAG data (100/79/78/4; Fig. 3b). Our tree shows two basal sister-groups, one of which has little support. The latter lineage includes the genera *Elaenia*, *Myiopagis*, and *Suiriri*. *Elaenia* is characterized by its remarkable uniformity in external, syringeal, and cranial morphology, as well as in nest structure and egg colour (see references in Lanyon, 1988b), and is resolved as the sister-group to *Myiopagis* + *Suiriri* but essentially with no support (50/50/<50/1). *Myiopagis* has been previously suggested to be sister to *Tyrannulus* on the basis of sharing similar syringeal (internal cartilages conspicuously attached to dorsal end of A2 elements as well as to the drum, and with amorphous segment projecting ventrally from their posterior third) and cranial (nasal capsule more fully ossified, including alinasal walls and turbinals) morphology (Lanyon, 1988b). However, Birdsley (2002) did not recover *Myiopagis* + *Tyrannulus*; instead, the two genera were part of an unresolved clade that also included *Elaenia*. Although we did not include a specimen of *Tyrannulus* in this analysis, subsequent preliminary work suggests that *Tyrannulus* is a close relative of *Myiopagis* (Tello et al., unpublished data; see also Rheindt et al., 2008). *Suiriri* traditionally has been allied to *Elaenia* and its closest relatives (Berlepsch, 1907; Cory and Hellmayr, 1927; Traylor, 1977), but syringeal morphology suggested to Lanyon (1988b) that *Suiriri* was more closely related to a clade that included *Ornithion*, *Camptostoma*, "*Mecocerculus*" (*stictopterus*, *poecilocercus*, *hellmayri*), than to *Elaenia*. Our data, instead, strongly indicate that *Suiriri* is close to *Myiopagis* (99/74/64/3), and therefore to *Tyrannulus*.

The second basal clade of the Elaeniini is well supported (100/74/66/4; Fig. 3b) and contains four lineages: (i) the *Capsiempis* group (100/98/97/10) that contains the genera *Capsiempis*, *Phaeomyias*, and *Phyllomyias* (*griseiceps*); (ii) *Pseudelaenia*; (iii) *Mecocerculus*; and (iv) the *Culicivora* group (100/96/94/5) with *Anairetes*, *Uromyias*, *Culicivora*, *Polystictus*, *Pseudocolopteryx*, and *Serpophaga*.

Within the *Capsiempis* group, *Capsiempis flaveola* was sister to the monotypic *Phaeomyias* and to *Phyllomyias griseiceps*. Previously, *Capsiempis* was merged with *Phylloscartes* on the basis of mensural similarities (Traylor, 1977), but these genera are very distantly related on our tree. Later, Lanyon (1988b) grouped *Capsiempis* with *Phaeomyias* and with *Nesotriccus*, which we were unable to sample. Our results are therefore not inconsistent with Lanyon's suggestion (see also Fitzpatrick, 2004a). Traylor (1977) proposed an expanded *Phyllomyias* that included species of the genera *Phyllomyias sensu stricto* (*fasciatus*, *griseiceps*, *griseocapilla*), *Tyranniscus* (*nigrocapillus*, *uropygialis*, *cinereiceps*), *Acrochordopus* (*burmeisteri*), *Xanthomyias* (*sclateri* and *virescens*), and *Oreotriccus* (*plumbeiceps*). Lanyon (1988b) found that cranial and syringeal morphology supported the merger of these taxa, with the exception of the three species of *Phyllomyias sensu stricto*. In the latter group, he also found that the syringes were very different from each other (Lanyon, 1988b), thus suggesting to him that *Phyllomyias sensu* Traylor (1977) was polyphyletic. Our results confirm this: *Phyllomyias griseiceps* was found to be sister to *Phaeomyias murina*, but "*Phyllomyias*" *uropygialis* and *burmeisteri* formed a clade that was distantly related to *P. griseiceps*. Although the type of *Phyllomyias*, *P. fasciatus*, was unavailable for our study, Rheindt et al. (2008) and Ohlson et al. (2008) found *P. fasciatus* to be sister to *P. griseiceps*, thus both should maintain the name *Phyllomyias*. Lanyon (1988b) placed *Phyllomyias uropygialis* in *Tyranniscus* and *Phyllomyias burmeisteri* in *Acrochordopus*. Our results indicate the necessity of resurrecting the genus *Tyranniscus* (Cabanis and Heine, 1859–1860), which would have priority over *Acrochordopus* (Berlepsch and Hellmayr, 1905), and we have placed *uropygialis* and *burmeisteri* in the former. Ohlson et al. (2008) also included a sample of *Phyllomyias virescens* (formerly in *Xanthomyias*) and found it to be sister to a clade formed by two species of "*Mecocerculus*" (*calopterus* and *poecilocercus*). They showed that the latter genus was not monophyletic. The name *Xanthomyias* is available for this new clade, but further inclusion of unsampled *Phyllomyias* will be required to clarify its limits.

Within the *Culicivora* group we found *Anairetes* and *Uromyias* to be sister-taxa. *Anairetes* and *Uromyias* share similar external and syringeal morphologies (Cory and Hellmayr, 1927; Lanyon, 1988b), and some have suggested they are congeneric (Smith, 1971; Traylor, 1977). Lanyon (1988b), on the other hand, proposed that *Anairetes* was sister to *Serpophaga* on the basis of cranial and plumage similarities. We, instead, found *Serpophaga* to be the sister of *Pseudocolopteryx* (100/84/70/2), two taxa that were widely separated in Lanyon's analysis. These two genera are then related to *Polystictus*, *Culicivora*, and *Anairetes* + *Uromyias*. *Pseudocolopteryx*, *Culicivora*, and *Polystictus*, together with *Euscarthmus*, were placed at the end of Cory and Hellmayr's (1927) Euscarthminae, and Traylor (1977) pointed out similarities between species in the first three genera and those in *Serpophaga* in that they shared whitish and streaked crests, weak rectal bristles, and cup-shaped nests. Lanyon (1988b) placed *Pseudocolopteryx* and *Polystictus* in a major tyrannulet clade within his *Elaenia* group, but neither cranial nor syringeal morphology resolved their relationships to each other, or to the other genera included in that group. Lanyon (1988b) did not examine the skull of *Culicivora* because it was unavailable, and syringeal morphology did not provide any clues about its relationships of this taxon. Our results (Fig. 3b) clarify the relationships of these genera, but some internal nodes are still poorly supported.

Two genera seemingly have relationships to the *Culicivora* group. One is *Pseudelaenia leucospodia*, which has had a chequered taxonomic history (Lanyon, 1988b). It was originally assigned to *Elaenia* (Taczanowski, 1877; Sclater, 1888; Cory and Hellmayr, 1927), then *Phaeomyias* (Zimmer, 1941), and *Myiopagis* (Traylor, 1977), until Lanyon (1988b) showed it to belong in its own monotypic genus, *Pseudelaenia*, within his *Elaenia* assemblage. Lanyon (1988b) suggested that *Pseudelaenia* was sister to *Stigmatura* on the basis of sharing similar cranial and syringeal morphology. Our results support *Pseudelaenia* as an independent lineage with uncertain relationships to the *Culicivora* group.

The second is *Mecocerculus*, and we examined the type, *M. leucophrys*. Lanyon (1988b) suggested that *Mecocerculus* was polyphyletic, but our sampling did not permit an examination of this hypothesis. However, Ohlson et al. (2008) confirmed Lanyon's suggestion by finding that *Mecocerculus* is composed of two unrelated clades: (i) one formed by the type species, *M. leucophrys*, which was recovered at a similar phylogenetic position as in this study; and (ii) a second clade formed by *M. calopterus* and *M. poecilocercus* that were sister to "*Phyllomyias*" *virescens*. Both clades received high BP support. The other unsampled "*Mecocerculus*" species (*minor*, *stictopterus*, and *hellmayri*) have been suggested to be closely related to *calopterus* (including *minor*) and *poecilocercus* (including *stictopterus*, and *hellmayri*), thus we expect them to belong to the second *Mecocerculus* clade. This clade would require a new generic name.

Muscigralla

Our data provide moderately strong support for the monotypic genus *Muscigralla* forming an ancient taxon that is the sister-group of the fluvicolines + tyrannines (Fig. 3b). The phylogenetic position of *Muscigralla* has been enigmatic (Lanyon, 1986)—even its placement

within the Tyrannidae has been questioned (Ridgway, 1907; Cory and Hellmayr, 1927)—and it was not until the work of Warter (1965) and Ames (1971) that its placement inside the Tyrannidae was fully accepted. Similarities in external morphology and behaviour have led others to suggest a close relationship to *Muscisaxicola* (Smith and Vuilleumier, 1971; Traylor and Fitzpatrick, 1982), which was questioned by Lanyon (1986) on the basis of *Muscigralla* having a very distinctive nasal septum with respect to that of the *Empidonax* assemblage (= the Fluvicoline of Fitzpatrick, 2004a). Ohlson et al. (2008) found *Muscigralla* as sister of the fluvicolines, but support for this relationship was low/nonexistent.

Subfamily Tyranninae

This lineage includes most genera from Fitzpatrick's (2004a) Tyranninae except for *Laniocera*, and with the addition of *Machetornis*, which was previously placed in the Fluvicolinae. Although support for the Tyranninae was low (89/54/50/1), this major lineage was recovered by all three phylogenetic methods (Fig. 3b). We recovered the two traditional groups: (i) the Myiarchini (*Casiornis*, *Rhytipterna*, *Sirystes*, and *Myiarchus*), which were well supported (100/87/74/2), and (ii) the Tyrannini (*Empidonomus*, *Griseotyrannus*, *Tyrannus*, *Myiozetetes*, *Megarynchus*, *Tyranopsis*, *Myiodynastes*, *Philohydor*, *Pitangus*, and *Machetornis*, which were well supported only in the Bayesian analysis (99/<50/<50/2). Three genera formed separate lineages at the base of the Tyranninae. The genus *Attila* was resolved as the sister-group of all other taxa in the subfamily. Ascending the clade, *Attila* was followed by *Legatus*, and then by *Rhamphotrigon*, which was sister to Myiarchini + Tyrannini. All of these internodes were strongly supported by Bayesian analysis, but essentially lacked support with MP and ML bootstrap resampling, thus additional data are needed to confirm this branching sequence. Ohlson et al. (2008) did not recover the Tyranninae as circumscribed here, but instead found a poorly supported clade formed by the tyrannines + myiarchines + *Legatus* + *Attila*. *Ramphotrigon* was found to be outside this clade and, together with *Deltarhynchus*, to be closely related to *Muscigralla* + fluvicolines.

Three genera of the Tyranninae were unsampled. Lanyon (1985a,b) thought that *Deltarhynchus* must be closely related to *Ramphotrigon* (which is near the base of the subfamily) because of their remarkable similarities in syringeal morphology and nest structure (both nest in cavities and build their nest without using a lining of hair and feathers). This suggestion was corroborated by Ohlson et al. (2008), who found *Deltarhynchus* embedded within *Ramphotrigon* with high Bayesian support. Two other unsampled genera, *Phelpsia* and *Conopias*, have also been suggested as belonging within this major lineage (Lanyon, 1984; Mobley, 2002), but this needs to be confirmed.

Tribe Myiarchini

Diagnosis. The most inclusive crown clade that contains *Myiarchus tyrannulus and Casiornis rufus* but not *Tyrannus savana*, *Attila spadiceus*, or *Colonia colonus*. This clade is strongly supported by morphological and molecular data.

The Myiarchini are supported by similarities in syringeal morphology (large J- or L-shaped dorsal internal cartilages attached to ventral tracheo-bronchial junction; Lanyon, 1985a,b; Birdsley, 2002), nuclear intron data (Ohlson et al., 2008), as well as behaviour (Fitzpatrick, 1985, 2004a). Within this clade, shared structure of holaspidean tarsi (Traylor, 1977) supports a group formed by *Syristes*, *Casiornis*, and *Rhytipterna*, and in our data *Casiornis* and *Rhytipterna* are sisters. Our results do not support Lanyon (1985a,b) suggestion that *Syristes* and *Casiornis* should be merged in *Myiarchus* unless that expanded genus also included *Rhytipterna*.

Tribe Tyrannini

The Tyrannini include all members of Lanyon's kingbird assemblage (Lanyon, 1984) plus *Machetornis*. The monophyly of kingbirds *sensu* Lanyon is also supported by cranial, syringeal, and plumage characters (Lanyon, 1984; Birdsley, 2002), but the inclusion of *Machetornis* in this group has been controversial (Lanyon, 1984; Fitzpatrick, 1985). Fitzpatrick (1985) argued that *Machetornis* should be placed in the kingbird group on the basis of striking similarities in plumage, voice, display, and attenuated primaries, but Lanyon (1984) placed this genus in his Fluvicolinae based on their similar nasal septum. At the same time, he also acknowledged that one skull character—a conspicuous medial ridge on the frontal region of the skull that is a synapomorphy of all other kingbirds—although interpretably present in *Machetornis*, is still much less ridge-like (Lanyon, 1984). Lanyon (1984) gave more weight to differences in cranial (nasal septum with a well developed transverse trabecular plate located along the ventral edge of the septum) and syringeal morphology (calcified supporting elements of the bronchia reduced to a single complete ring formed by the fusion of the A1 and A2 elements and lack of intrinsic syringeal muscles) to exclude *Machetornis* from his kingbird assemblage. Sibley and Ahlquist (1990) also found *Machetornis* within a group that included several fluvicolines.

Within the Tyrannini, *Pitangus* and *Philohydor* formed a poorly supported group (75/59/–/–) that was sister to all other kingbird genera, followed by *Machetornis*, and then a group formed by all the other

kingbirds (although support for the latter group was quite low: 83/63/–/–). Ohlson et al. (2008) found a well supported clade formed by *Pitangus* and *Machetornis*, and although they did not include *Philohydor*, their results are not inconsistent with our findings. Similarities in syringeal morphology supported the sister-relationships of *Pitangus* and *Philohydor* (A2 and A3 elements form complete and independent rings around each bronchus; Lanyon, 1984; Birdsley, 2002) and of *Tyrannopsis–Megarynchus* (syringeal cartilages are robust and bent in a J or L shape; Lanyon, 1984; Birdsley, 2002); and the group formed by *Tyrannus*, *Griseotyrannus*, and *Empidonomus* is supported by their having their outer primaries conspicuously notched (Lanyon, 1984; Birdsley, 2002). Our results agree with a previous mtDNA phylogeny of the kingbirds (Mobley, 2002) in three places: (i) the *Tyrannus–Griseotyrannus–Empidonomus* clade; (ii) the sister-relationship of *Griseotyrannus* and *Empidonomus*; (iii) and the relationship of *Tyrannopsis* and *Megarynchus*.

Subfamily Fluvicolinae

Our results show significant differences in generic composition from Fitzpatrick's (2004a,b) concept of the Fluvicolinae. Excluded are *Machetornis*, *Muscigralla*, *Pyrrhomyias*, *Hirundinea*, *Myiophobus ochraceiventris*, *Myiobius*, *Terenotriccus*, and *Neopipo*, and included is *Sublegatus*, which was in his Elaeniinae. The monophyly of this newly circumscribed Fluvicolinae is ambiguously supported (98/68/–/–; Fig. 3b), but it has been supported by nuclear intron data (Ohlson et al., 2008). Our analysis revealed four main groups within the subfamily: the xolmiine flycatchers, the contopines, fluvicolines, and isolated by itself, the genus *Colonia*. Many nodes along the base of this subfamily and within these four groups are not well supported, hence the relationships derived from the RAG data need to be further tested.

The phylogenetic placement of *Colonia* within the Fluvicolinae is uncertain (Fig. 3b). Traylor (1977) followed Warter (1965) in allocating *Colonia* to the fluvicolines on the basis of similarities in the nasal septa. Lanyon (1986) questioned Warter's (1965) assessment of that similarity and suggested that the nasal septum of *Colonia* was sufficiently different from typical fluvicolines and thus the genus should be placed outside this subfamily as *insertae sedis*. Fitzpatrick (2004a) followed Traylor's (1977) suggestion and left *Colonia* as part of the Fluvicolini. Our results support the inclusion of *Colonia* in the broader Fluvicolinae, but do not provide information on its phylogenetic placement within this major lineage. More recently, Ohlson et al. (2008) have found *Colonia* within a well supported clade formed by *Alectrurus*, *Gubernetes*, *Arundinicola*, *Fluvicola*, *Pyrocephalus* (clade F2 in fig. 1 of Ohlson et al., 2008).

Tribe Fluvicolini

The tribe Fluvicolini is only modestly supported by the RAG data (100/59/52/2). Within this clade, we uncovered four lineages: one formed by *Colorhamphus* and *Silvicultrix* (97/66/65/2); a second by *Ochthoeca* and *Tumbezia* (100/100/97/3); a third by *Myiophobus roraimae*; and a fourth that included *Sublegatus*, *Pyrocephalus*, *Fluvicola*, *Arundinicola*, *Gubernetes*, and *Alectrurus* (100/63/55/2). A sister-relationship between *Colorhamphus* and *Silvicultrix* has not previously been suggested. Our results are slightly ambiguous: although Bayesian support is 97%, the node is poorly supported by ML and MP analyses. The clade does, however, appear in the MP and ML trees. Within the second group, *Tumbezia* was embedded within *Ochthoeca* as sister to *O. oenanthoides*, but with poor support. *Tumbezia salvini* was originally described in *Ochthoeca* (Taczanowski, 1877), and it was Chapman (1925) who established the new genus. The consistency of the characters used to diagnose this genus was questioned by Lanyon (1986), who suggested that *T. salvini* is congeneric with *Ochthoeca* based on similarities in syringeal morphology. A previous mitochondrial study of the relationships in these chat-tyrants (Garcia-Moreno and Arctander, 1998) also failed to find sufficient variation to solve species relationships, and they did not recommend the inclusion of *Tumbezia* in *Ochthoeca*. Given the well supported relationship between the two genera, however, there is logic in combining them.

Using cranial and syringeal characters, Lanyon (1986, 1988b) proposed that *Myiophobus* was not monophyletic. Lanyon (1988b) suggested that *M. roraimae* and *M. phoenicomitra* formed a group together with *M. ochraceiventris*, *M. lintoni* and *M. pulcher*, as well as with *Myiotriccus*, all of which were placed in his *Phylloscartes* group of the *Elaenia* assemblage. Our study does not support this specific hypothesis, even as we support nonmonophyly. Instead, we found that *M. ochraceiventris* belongs in a newly discovered clade that also includes *Hirundinea*, *Pyrrhomyias*, and *Myiotriccus* (see below); this clade is phylogenetically distant from *M. roraimae*, which we found to be referable to the Fluvicolini. Ohlson et al. (2008) found that species taxa formerly placed in *Myiophobus* belonged to three unrelated clades that were well supported (see their fig. 1): (i) *fasciatus* + *cryptoxanthus*; (ii) *phoenicomitra* + *flavicans* + *roraimae*; and (iii) *pulcher* + *lintoni* + *ochraceiventris*. Ohlson et al. (2008) did not include *Myiophobus inornatus*, but this taxon previously has been suggested to belong in the second clade (Fitzpatrick et al., 2004). Based on these findings, the name *Myiophobus* should be restricted to the species in the first clade that includes the type species *fasciatus*. Ohlson et al. (2008) found that *Myiophobus sensu stricto* was

sister to *Ochthoeca* within a major group that includes taxa from our Contopini. Although we did not sample *M. fasciatus*, we include samples of their other two clades, which will require new generic names because none is currently available.

We also found another clade within the Fluvicolini that included the genera *Alectrurus*, *Gubernetes*, *Arundinicola*, *Fluvicola*, *Pyrocephalus*, and *Sublegatus*. Lanyon (1986) previously suggested a clade containing *Arundinicola*, *Fluvicola*, and *Alectrurus*, but *Gubernetes* and *Pyrocephalus* were united with genera now making up our Xolmiini, and *Sublegatus* was placed in his Elaeniinae *Phylloscartes* group. In agreement with our data, analyses of DNA–DNA hybridization (Sibley and Ahlquist, 1990) and nuclear intron data (Ohlson et al., 2008) found *Sublegatus* to be with fluvicoline genera.

Unnamed higher taxon: Contopini + Xolmiini

The Contopini and Xolmiini are sister-groups on our tree, but they have ambiguous support in that the clade has a high Bayesian posterior probability of 100 but lacks MP and ML support (100/53/–/–). We therefore refrain from introducing a formal name in our classification (below) until the relationship can be tested with additional data.

Tribe Contopini

The Contopini are not well supported, despite having high Bayesian posterior probability (100/<50/–/–). However, a similar group has been also recovered by Ohlson et al. (2008). These authors also included two species of *Myiophobus* (*fasciatus* and *cryptoxanthus*) that were found to be sister to all the other contopines. Within this tribe, we recovered two groups, one formed by *Ochthornis*, *Cnemotriccus*, and *Lathrotriccus* (100/55/–/–), and a second by *Mitrephanes*, *Sayornis*, *Empidonax*, and *Contopus* (100/100/99/9). All these genera except *Ochthornis* were members of Lanyon's *Empidonax* group (Lanyon, 1986).

In the first group, *Ochthornis* was sister to a *Cnemotriccus + Lathrotriccus* clade (100/55/–/–). The relationship between the latter two genera is also supported by syringeal morphology (calcified nodule of lateral surface of A1 and A2 elements, with cartilaginous connection between them; Lanyon, 1986), allozyme patterns (Lanyon and Lanyon, 1986), and mitochondrial data (Cicero and Johnson, 2002). In previous studies, however, the position of *Ochthornis* was uncertain. Lanyon (1986) placed it within his *Empidonax* assemblage based on similarities in the nasal septum, but he could not find syringeal characters that would corroborate this. In the second group, *Mitrephanes* was sister to a clade formed by *Sayornis* + (*Empidonax + Contopus*). These four taxa previously have been grouped together on the basis of syringeal anatomy (cartilaginous segments of A2s modified into broad, transverse cartilages at oblique angle to, and barely if at all connected with, dorsal end of calcified A2s; Lanyon, 1986), allozyme (Lanyon and Lanyon, 1986), mitochondrial (Cicero and Johnson, 2002) and nuclear intron data (Ohlson et al., 2008). The sister-relationship between *Empidonax* and *Contopus* is also supported by allozyme, mitochondrial, and nuclear intron data (Lanyon and Lanyon, 1986; Cicero and Johnson, 2002; Ohlson et al., 2008), but the positions of *Sayornis* and *Mitrephanes* have been more problematic. Our study discovered that *Sayornis* was sister to *Empidonax + Contopus* but with poor support, whereas other studies proposed that either *Mitrephanes* is the sister of the latter two genera (Lanyon and Lanyon, 1986; Cicero and Johnson, 2002) or shares a sister-taxon relationship with *Sayornis* (Ohlson et al., 2008).

Tribe Xolmiini, ***new taxon*** *(type genus:* Xolmis *Boie 1826)*

Diagnosis. The most inclusive crown clade that includes *Agriornis micropterus* and *Lessonia rufa* but not *Contopus fumigatus* or *Fluvicola pica*. No morphological synapomorphies have been proposed, but the clade is moderately supported by molecular data.

Although this new tribe has support (100/66/56/2), we have purposely left its diagnosis somewhat ambiguous with respect to excluded taxa, as it is possible that with more data some of the latter will be shown to have closer relationships to xolmiines than to their putative relatives, as shown in Fig. 3b. On the other hand, a recent study using nuclear intron data uncovered a similarly well supported group (Ohlson et al., 2008). Within the Xolmiini, we recovered two groups (Fig. 3b), neither of which is particularly well supported): (i) one formed by *Hymenops*, *Knipolegus*, and *Lessonia* (96/56/<50/1), and (ii) the other by *Agriornis*, *Neoxolmis*, *Myiotheretes*, *Xolmis*, *Cnemarchus*, *Polioxolmis*, *Muscisaxicola*, and *Satrapa* (92/<50/–/–).

All members of the first group correspond to Lanyon's *Knipolegus* group (Lanyon, 1986). We found that *Hymenops* was embedded within *Knipolegus* (*signatus* and *poecilurus*; 94/78/71/2), thereby rendering *Knipolegus* paraphyletic. *Lessonia* was sister to these three species. Despite its morphological differences from the two species of *Knipolegus* (Lanyon, 1986), *Hymenops perspicillatus* must now be included in the former genus. In contrast to our results, Ohlson et al. (2008) found *Lessonia* to belong in our first subgroup.

All members of the second group correspond to W. Lanyon's *Muscisaxicola* group (here called the *Xolmis* group) except for the enigmatic *Satrapa*. Lanyon (1986) suggested that the latter genus belonged in

his *Empidonax* assemblage (= our Contopini) on the basis of sharing a similar nasal septum, but he was not sure about its phylogenetic placement within that group. *Satrapa* shares the pale outer webs of the outer rectrices that are characteristic of Lanyon's *Muscisaxicola* group, but its syrinx and nesting behaviour (cup nest) do not provide any clues that might link this genus to any of the major groups in the *Empidonax* assemblage.

Missing fluvicoline genera.

Four genera of probable fluvicolines were not sampled. *Heteroxolmis dominicanus* was formerly placed in the genus *Xolmis* (Traylor, 1979), until Lanyon (1986) placed it in its own genus. Lanyon (1986) diagnosed *Heteroxolmis* based on its unique syrinx (greatly swollen and slightly J-shaped internal cartilages, a difference that is remarkable due to the homogeneity of the syrinx of *Muscisaxicola*, *Agriornis*, *Xolmis*, and *Myiotheretes*) as well as its cranial morphology (fully ossified nasal capsule, including the alinasal walls and turbinals, and extremely narrow trabecular plate). Lanyon (1986) suggested a sister relationship with *Xolmis*, which was supported by similar external morphology, especially their white-patterned remiges. We expect *Heteroxolmis* will be shown to belong in the Fluvicolinae and probably the Xolmiini.

Xenotriccus was postulated by Lanyon (1986) as being related to *Cnemotriccus*, *Aphanotriccus*, and *Lathrotriccus* because of similarities in syringeal morphology (cartilaginous segments of A2 enlarged caudally but continuous with calcified A2s). Within this group, Lanyon proposed that *Aphanotriccus* was sister to *Lathrotriccus* based on the presence of a calcified nodule on the lateral surface of the A1 and A2 elements, a relationship that has also been supported by allozyme data (Lanyon, 1985a). Thus *Aphanotriccus* and *Xenotriccus* almost certainly belong within the Fluvicolinae and probably the Contopini.

Finally, the features of the nasal septum and the syrinx led Lanyon (1986) to conclude that *Muscipipra* was a member of his *Muscisaxicola* group, thus it is likely this genus is also a fluvicoline.

Discussion

Toward a phylogenetic classification of the Tyrannides: general comments

Classification has been of importance to phylogenetics from the very inception of cladistic thinking (Hennig, 1950, 1966; also Crowson, 1965). Thus the implications of tree-thinking—in terms of representing phylogenetic relationships in a hierarchical classification—have been there from the beginning. Indeed, much of the controversy over cladistics during the 1960s–1980s largely revolved around classification theory, with cladists supporting an isometry between clades on a tree and groups in a classification, whereas opponents typically argued for maintaining the status quo of evolutionary classification, or for arrangements based on phenetics.

Cladists have long recognized the difficulty of achieving an isometry between the large numbers of taxa on trees and the relatively small number of ranks that characterizes hierarchical Linnean classifications. As a consequence, long before the current debate over phylogenetic nomenclature (as proposed in the *Phylocode*; Cantino and de Queiroz, 2007) cladists were discussing ways in which classifications might reflect phylogenetic relationships in the context of adjustments to traditional Linnean hierarchies (Hennig, 1966; Cracraft, 1970, 1974; Crowson, 1970; Nelson, 1970, 1971, 1972, 1973; Griffiths, 1973; Wiley, 1975, 1979, 1981; Patterson and Rosen, 1977; Eldredge and Cracraft, 1980; Nelson and Platnick, 1981). Yet it was clear from the outset, and widely remarked, that as the Tree of Life was built it would become increasingly difficult to represent all nodes—even those having strong support—in terms of a classification based on a hierarchy of Linnean ranks: there simply were not enough ranks. At the same time, it was widely appreciated that a particular rank assigned to a clade is largely subjective, and that supraspecific taxa of the same rank are not comparable phylogenetically or biologically (see citations above; for a contemporary view see Bertrand et al., 2006; there are many who have made these points).

From the early 1980s to the beginning of the debate over phylogenetic nomenclature, systematists largely ignored classification and directed their energies to discovering phylogenetic relationships. With the *Phylocode* debate, however, classification has regained attention within the community, so much so that if one wants to express relationships in a classification, then there is some obligation to address the framework for classificatory decisions (an extensive bibliography of the recent literature for and against the *Phylocode* can be found at http://www.ohiou.edu/phylocode/documents.html).

The key intellectual concept behind phylogenetic classification has always been to reflect phylogenetic relationships in terms of a hierarchical information system. And, given a phylogenetic classification, it should be possible to "retrieve" the phylogenetic relationships from it. This implies that any classification claiming to be phylogenetic must be based on some phylogenetic hypothesis or a consensus of a set of hypotheses.

In general, we share much of the philosophy and approach of Frost et al. (2006) in their amphibian classification. Thus the goal of phylogenetic classification is

largely achievable, given the scope of most contemporary studies. This results from the manageable size of most studies (such as this one, although taxon sampling is increasing rapidly) as well as because those adhering to phylogenetic classification would not claim that we must name, and therefore rank, all nodes on a tree. Of course, supporters of phylogenetic nomenclature also do not claim we must name all nodes. The major shortcoming of the current state of phylogenetic nomenclature is that classifications are in danger of losing the informatic/hierarchical isometry between a phylogenetic hypothesis and its implied classification. Presently, phylogenetic nomenclature is focused on naming clades (the best example so far may be Cantino et al., 2007), but the important point is that unless those names are expressed hierarchically in some manner, names by themselves hardly constitute classifications that can serve a broader user-community, most of whom want and need classifications that reflect relationships. Linear lists of names, unless memorized for their cladistic content, or translated by an algorithm into a hierarchy on a computer screen, are poor vehicles for phyloinformatics. Some of the proposals for phylogenetic nomenclature seemed designed to confound communication and understanding. Thus many biologists understand the notion of subordination of ranks and the hierarchy that implies, namely that "-inae" names are subordinate to "-idae" names, but in phylogenetic nomenclature it is possible to have, for example, the Apiidae within the Campanulidae, which are in the Gentianidae, which are in the Asteridae, which are in the Gunneridae (Cantino et al., 2007).

One of the reasons why Linnean taxonomy is viewed as being too unstable to continue using is that taxonomic informatics systems are inadequate for mapping the groups and their names in one classification against those in another. The same state of affairs is true for the *Phylocode*. With respect to the later, an algorithm/database will eventually be required to take these names and their "definitions" and convert them into a hierarchical representation of relationships that end-users can understand. Maybe, in time, people will come to learn the taxonomic content of these new *Phylocode* names, much as they have the name "Mammalia", but at the rate these names are being generated, it may take a while. The plant example above illustrates perhaps the need to legislate less and think more about how classifications might better facilitate communication with the user communities.

At the same time, it is true that some of these problems may be unavoidable for phylogenetic classifications as well, because as the Tree of Life is resolved, more and more well supported groups, worthy of being named, will be discovered. Nevertheless, subordination of ranks and phyletic sequencing together offer many options for creating phylogenetic classifications of large taxonomic groups. They will entail, as does the one proposed below, some ways of thinking that are unfamiliar to the majority of biologists, as well as to quite a few systematists.

Classificatory guidelines and conventions

We present here a phylogenetic classification of the Tyrannides based on Fig. 3. The system of ranks is placed in the context of the entire suboscine clade. Our purpose is not only to explore how a phylogenetic classification might be constructed for a clade this size, but also to propose an approach that might begin to stabilize the use of names within the group. For many ornithologists, the classification may appear to be unconventional in reflecting relationships across the entire clade in question, rather than taking a more traditional approach in which there is a mixture of hierarchy and linear lists, the latter of which do not imply a particular cladistic structure (the classification of Sibley et al., 1988; and later Sibley and Monroe, 1990, took an approach similar to ours in using both subordination and sequencing).

In this study, new formal names are applied to clades only when they have moderate-to-strong branch support, or when there are additional studies using other data that are congruent with our results. We recognize that the monophyly of many genera needs further testing by increased species sampling. This is also true for some groups of related genera, which we choose not to name formally (usually because of their relatively small content). These informal "generic groups" are named for the oldest named genus. We have tried to use pre-existing family-group names whenever possible, although the ranks of those names may have changed. Generic names with quotation marks signify taxa for which there is good evidence for nonmonophyly.

The classification uses a sequencing convention throughout (Nelson, 1972, 1973; Cracraft, 1974, in which the convention was termed phyletic sequencing; see also Wiley, 1979). Thus, in a list of taxa at a given level of subordination—*signified by the relative level of indentation*—the first-named taxon is the sister-group of all those taxa listed below it; the second taxon at that level is the sister-group of those below it, and so on. In any given list, therefore, we do not imply that all aligned taxa are each being "ranked" at a similar level. Thus the Family Pipridae is the sister-group of the superfamilies Cotingoidea + Tyrannoidea, and a monotypic genus, *Muscigralla*, is the sister-group of a series of higher-ranked taxa listed below it. This subordination and sequencing approach to classification (Nelson, 1973) has the beneficial effect of not creating unnecessary higher taxa for single genera or for those of uncertain status or

placement. The only exceptions to this sequencing convention are the five instances in which our tree shows a trichotomy. We have marked each of the three taxa in those instances with asterisks (*) to indicate that phyletic sequencing is not implied.

Using this scheme, many different classifications might be constructed, each maintaining a one-to-one reflection of the phylogenetic hypothesis (Nelson, 1973; Cracraft, 1974; Wiley, 1979). The rank names only serve to impart hierarchical information to the user, and the ranks of taxa have no intrinsic significance or meaning as a given rank (in some sense, then, this is a ''rank-free'' Linnean classification). Nevertheless, we strive to maintain a ranking system that will be familiar to most avian systematists as well as to the user community of avian classifications. Our starting point for this effort was the extensive series of names and ranks proposed by Sibley et al. (1988) and Sibley and Monroe (1990), based on DNA-hybridization distances. Although the relationships depicted in those works differ in a number of ways from those discovered by subsequent DNA-sequence analysis, the names and ranks have been widely applied—but sometimes modified, when new evidence calls for it—in a number of contemporary studies (e.g. Ericson et al., 2003; Ericson and Johansson, 2003; Barker et al., 2002, 2004; Cracraft and Barker, 2009; among others). Finally, to facilitate standardization of taxon names we generally follow Sibley et al. (1988) and Sibley and Monroe's (1990) suffixes for taxon names assigned to particular suprageneric ranks. The names of most of their ranks were traditional, even though two remain generally unfamiliar: Parvclass, standing between Infraclass and Superorder; and Parvorder, standing between Infraorder and Superfamily. As far as we can ascertain, the rank Parvclass was first used by Sibley et al. (1988), whereas the rank Parvorder was introduced by McKenna (1975).

A preliminary phylogenetic classification of the Tyrannides

The higher taxa of the Order Passeriformes can be arranged as follows:

Order Passeriformes
- Suborder Acanthisitti
- Suborder Passeri (oscine passeriforms)
- Suborder Tyranni (suboscine passeriforms)
  - Infraorder Eurylaimides (Old World suboscines)
  - Infraorder Tyrannides (New World suboscines)
    - Parvorder Tyrannida
  - Infraorder Furnariides (New World suboscines)
    - Parvorder Thamnophilida
    - Parvorder Furnariida

The Infraorder Tyrannides can be classified as follows:

INFRAORDER Tyrannides
- PARVORDER Tyrannida
  - FAMILY Pipridae
    - SUBFAMILY **Neopelminae, new taxon** (type genus: *Neopelma* Sclater 1860)
      - *Neopelma*, *Tyranneutes*
    - SUBFAMILY Piprinae
      - **Pipra* group: *Pipra*, *Lepidothrix*
      - **Manacus* group: *Manacus*, *Heterocercus*
      - **Dixiphia* group: *Machaeropterus*, *Dixiphia*
    - SUBFAMILY **Ilicurinae, new rank** (type genus: *Ilicura* Reichenbach 1850)
      - *Xenopipo* group: *Xenopipo*, *Chloropipo*
      - *Ilicura* group: *Ilicura*
        Masius, *Corapipo*
      - *Antilophia* group: *Chiroxiphia*, *Antilophia*
  - SUPERFAMILY Cotingoidea
    - FAMILY Tityridae
      - SUBFAMILY Oxyruncinae
        - *Oxyruncus*
        - TRIBE **Onychorhynchini, new taxon** (type genus: *Onychorhynchus* Fischer von Waldheim 1810)
          - *Onychorhynchus*
          - *Terenotriccus*, *Myiobius*
      - SUBFAMILY Laniisominae
        - *Schiffornis*
        - *Laniocera*, *Laniisoma*
      - SUBFAMILY Tityrinae
        - *Iodopleura*

Tityra
Xenopsaris, *Pachyramphus*
FAMILY Cotingidae
SUBFAMILY **Pipreolinae, new taxon** (type genus: *Pipreola* Swainson 1837)
Pipreola, *Ampelioides*
SUBFAMILY Cotinginae
Lipaugus [*Tijuca*]
Gymnoderus group: *Porphyrolaema*
Gymnoderus, *Conioptilon*
Xipholena, *Carpodectes*
Procnias, *Cotinga*
Haematoderus
Cephalopterus group: *Querula*
Perissocephalus
Pyroderus, *Cephalopterus*
Carpornis
SUBFAMILY Rupicolinae
Snowornis
Rupicola, *Phoenicircus*
SUBFAMILY Phytotominae
Zaratornis
Phytotoma
Doliornis, *Ampelion*
SUPERFAMILY Tyrannoidea
UNNAMED HIGHER TAXON: *Platyrinchus*, *Piprites*, *Tachuris*, and Rhynchocyclidae
Platyrinchus
Piprites
Tachuris
FAMILY Rhynchocyclidae
Cnipodectes group: *Taeniotriccus*, *Cnipodectes*
SUBFAMILY Pipromorphinae
Mionectes group: *Mionectes*, *Leptopogon*
Corythopis group: *Corythopis*, *Pseudotriccus*,
Phylloscartes group: *Pogonotriccus*, *Phylloscartes*
SUBFAMILY Rhynchocyclinae
Rhynchocyclus, *Tolmomyias*
SUBFAMILY **Todirostrinae, new taxon** (type genus: *Todirostrum* Lesson 1831)
Todirostrum group: *Todirostrum*, *''Poecilotriccus''*
Myiornis group: *Myiornis*, *''Hemitriccus''*
Hemitriccus
Oncostoma group: *Atalotriccus*
Lophotriccus, *Oncostoma*
Neopipo
FAMILY Tyrannidae
UNNAMED HIGHER TAXON: Hirundineinae + Elaeniinae
SUBFAMILY **Hirundineinae, new taxon** (type genus: *Hirundinea* d'Orbigny & Lafresnaye 1837)
Hirundinea, *Pyrrhomyias*
''Myiophobus'' ochraceiventris, *Myiotriccus*
SUBFAMILY Elaeniinae
TRIBE **Euscarthmini, new rank** (type genus: *Euscarthmus* Wied 1831)
**Zimmerius*
**Euscarthmus* group: *Stigmatura*
Inezia, *Euscarthmus*
**Ornithion* group: *Tyranniscus*
Ornithion, *Camptostoma*
TRIBE Elaeniini
Elaenia group: *Elaenia*
Suiriri
Myiopagis, [*Tyrannulus*]
Capsiempis group: *Capsiempis*
Phaeomyias, *Phyllomyias*
Pseudelaenia
Mecocerculus
Culicivora group: *Anairetes*, *Uromyias*
**Culicivora*
**Polystictus*

Pseudocolopteryx, *Serpophaga*
Muscigralla
SUBFAMILY Tyranninae
Attila
Legatus
Rhamphotrigon
TRIBE **Myiarchini, new rank** (type genus: *Myiarchus* Cabanis 1844)
Myiarchus
Sirystes
Rhytipterna, *Casiornis*
TRIBE Tyrannini
Pitangus, *Philohydor*
Machetornis
Megarhynchus group: *Myiodynastes*
Tyrannopsis, *Megarynchus*
Tyrannus group: *Myiozetetes*
Tyrannus
Griseotyrannus, *Empidonomus*
SUBFAMILY Fluvicolinae
**Colonia*
*TRIBE Fluvicolini
Colorhamphus group: *Silvicultrix*, *Colorhamphus*
**Ochthoeca* group: *Ochthoeca, Tumbezia*
*''*Myiophobus''* *roraimae*
**Alectrurus* group: *Sublegatus*
Pyrocephalus
Fluvicola
Arundinicola
Gubernetes, *Alectrurus*
*UNNAMED HIGHER TAXON: Contopini + Xolmiini
TRIBE Contopini
Ochthornis group: *Ochthornis*
Cnemotriccus, *Lathrotriccus*
Sayornis group: *Mitrephanes*
Sayornis
Empidonax, *Contopus*
TRIBE **Xolmiini, new taxon** (type genus: *Xolmis* Boie 1826)
Knipolegus group: *Lessonia*
Knipolegus, *Hymenops*
Xolmis group: *Satrapa*, *Muscisaxicola*
Cnemarchus, *Polioxolmis*
Xolmis
Myiotheretes
Agriornis, *Neoxolmis*

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Phylogenetic analyses of the Tyrannides: Maximum likelihood tree of the combined RAG-1 and RAG-2 data ($-\ln L = 40\,223.2$, GTR + I + G model). Numbers above the branches represent bootstrap values. Nodes that received 100% bootstrap support are represented by an asterisk.

Figure S2. Phylogenetic analyses of the Tyrannides: strict consensus tree of 960 most parsimonious trees of the combined RAG-1 and RAG-2 data (CI = 0.37, branch length = 5373). Numbers above branches represent bootstrap values, number below branches represent Bremer decay indexes. Nodes that received 100% bootstrap support are represented by an asterisk.

Appendix 1

Collection data and voucher information for tissue samples used in this study

Family	Species	Voucher number*	Collector	Collection locality
Cotingidae	*Ampelioides tschudii*	LSUMNS B-6090	T.S. Schulenberg	Ecuador: Morona-Santiago
Cotingidae	*Ampelion rufaxilla*	AMNH. DOT 2508	M. Herrera	Bolivia: La Paz
Cotingidae	*Carpodectes hopkei*	LSUMNS B-11745	F.B. Gill	Ecuador: Esmeraldas
Cotingidae	*Carpornis melanocephalus*	LSUMNS B-35583	J.D. Weckstein	Brazil: Bahia
Cotingidae	*Cephalopterus ornatus*	FMNH 322452	J.W. Fitzpatrick	Peru: Cusco
Cotingidae	*Conioptilon mcilhennyi*	FMNH 395586	REAJ-174	Brazil: Acre
Cotingidae	*Cotinga cayana*	FMNH 390013	S.M. Lanyon	Brazil: Rondonia
Cotingidae	*Doliornis sclateri*	LSUMNS B-8399	T.J. Davis	Peru: Pasco
Cotingidae	*Gymnoderus foetidus*	FMNH 322446	S.M. Lanyon	Peru: Madre de Dios
Cotingidae	*Haematoderus militaris*	UKMNH 1349	D. Allicock	Guyana: Potaro-Siparuni
Cotingidae	*Iodopleura isabellae*	FMNH 334371	S.M. Lanyon	Brazil: Rondonia
Cotingidae	*Laniisoma elegans*	ANSP 1558	T.D. Peterson	Ecuador: Morona-Santiago
Cotingidae	*Lipaugus strepthophorus*	AMNH. DOT 11995	R.O. Prum	Venezuela: Bolivar
Cotingidae	*Lipaugus vosciferans*	AMNH. DOT 2973	C.J. Woodbury	Venezuela: Bolivar
Cotingidae	*Oxyruncus cristatus*	LSUMNS B-22890	D.L. Dittmann	Bolivia: La Paz
Cotingidae	*Perissocephalus tricolor*	AMNH. DOT 11946	R.O. Prum	Venezuela: Bolivar
Cotingidae	*Phoenicircus nigricollis*	AMNH. DOT 12751	S. Coates	Venezuela: Bolivar
Cotingidae	*Phytotoma rutila*	FMNH 334522	A. Castillo	Bolivia: Cochabamba
Cotingidae	*Pipreola intermedia*	FMNH 433668	T. Pequeño S.	Peru: Cusco
Cotingidae	*Pipreola whitelyi*	FMNH 339665	S.M. Lanyon	Venezuela: Bolivar
Cotingidae	*Porphyrolaema porphyrolaema*	LSUMNS B-6989	P.E. Scott	Peru: Loreto
Cotingidae	*Procnias alba*	AMNH. DOT 12002	R.O. Prum	Venezuela: Bolivar
Cotingidae	*Pyroderus scutatus*	LSUMNS B-8137	T.J. Davis	Peru: Pasco
Cotingidae	*Querula purpurata*	FMNH 391194	O. Maillard Z.	Bolivia: La Paz
Cotingidae	*Rupicola rupicola*	AMNH. DOT 9713	P.R. Sweet	Venezuela: Bolivar
Cotingidae	*Snowornis cryptolophus*	LSUMNS B-6189	T.S. Schulenberg	Ecuador: Morona-Santiago
Cotingidae	*Xipholena atropurpurea*	FMNH 427187	J.G. Tello	Brazil: Alagoas
Cotingidae	*Zaratornis stresemanni*	FMNH 391915	G.P. Servat	Peru: Lima
Pipridae	*Antilophia galeata*	LSUMNS B-13809	G.H. Rosenberg	Bolivia: Santa Cruz
Pipridae	*Chiroxiphia boliviana*	AMNH. DOT 11821	R.I. Strimm	Bolivia: La Paz
Pipridae	*Chiroxiphia caudata*	AMNH. DOT 12073	R.T. Chesser	Argentina: Misiones
Pipridae	*Chloropipo uniformis*	AMNH. DOT 4750	G.F. Barrowclough	Venezuela: Bolivar
Pipridae	*Corapipo gutturalis*	LSUMNS B-48430	S. Claramunt	Guyana: Mazaruni-Potaro
Pipridae	*Dixiphia pipra*	AMNH. DOT 4250	G.F. Barrowclough	Venezuela: Amazonas
Pipridae	*Heterocercus flavivertex*	AMNH. DOT 12395	R.W. Dickerman	Venezuela: Amazonas
Pipridae	*Ilicura militaris*	FMNH 395456	D.F. Stotz	Brazil: Sao Paulo
Pipridae	*Lepidothrix coronata*	AMNH. DOT 8855	P. Escalante P.	Venezuela: Amazonas
Pipridae	*Lepidothrix serena*	AMNH. DOT 12333	R.W. Dickerman	Venezuela: Amazonas
Pipridae	*Machaeropterus pyrocephalus*	FMNH 391208	J.G. Tello	Bolivia: El Beni
Pipridae	*Manacus aurantiacus*	LSUMNS B-16105	J.M. Bates	Costa Rica: Puntarenas
Pipridae	*Manacus manacus*	FMNH 391544	J.M. Cardoso da Silva	Brazil: Amapa
Pipridae	*Masius chrysopterus*	LSUMNS B-11895	Unknown	Ecuador: Esmeraldas
Pipridae	*Neopelma aurifrons*	FMNH 395453	D.F. Stotz	Brazil: Sao Paulo
Pipridae	*Pipra erythrocephala*	AMNH. DOT 3872	G.F. Barrowclough	Venezuela: Amazonas
Pipridae	*Pipra filicauda*	AMNH. DOT 4246	G.F. Barrowclough	Venezuela: Amazonas
Pipridae	*Piprites chloris*	FMNH 322505	J.W. Fitzpatrick	Peru: Cusco
Pipridae	*Schiffornis turdinus*	AMNH. DOT 11874	R.O. Prum	Venezuela: Bolivar
Pipridae	*Tyranneutes stolzmanni*	AMNH. DOT 2997	C.J. Woodbury	Venezuela: Bolivar
Pipridae	*Xenopipo atronitens*	AMNH. DOT 4292	G.F. Barrowclough	Venezuela: Amazonas
Tyrannidae	*Agriornis micropterus*	AMNH. DOT 13600	P.R. Sweet	Argentina: Rio Negro
Tyrannidae	*Alectrurus risorus*	UKMNH 3432	K. Zyskowski	Paraguay: Concepcion
Tyrannidae	*Alectrurus tricolor*	UKMNH 165	M.B. Robbins	Paraguay: Misiones
Tyrannidae	*Anairetes flavirostris*	AMNH. DOT 10300	P.R. Sweet	Argentina: Neuquen
Tyrannidae	*Arundinicola (Fluvicola) leucocephala*	FMNH 339654	S.M. Lanyon	Venezuela: Sucre
Tyrannidae	*Atalotriccus pilaris*	USNM B12810	C.M. Milensky	Guyana: Wiwitau Mountain
Tyrannidae	*Attila citriniventris*	LSUMNS B-4836	T.J. Davis	Peru: Loreto
Tyrannidae	*Attila spadiceus*	FMNH 389961	J.W. Fitzpatrick	Brazil: Rondonia
Tyrannidae	*Camptostoma obsoletum*	AMNH. DOT 6081	J.J. Weicker	Bolivia: Santa Cruz
Tyrannidae	*Capsiempis flaveolus*	AMNH. DOT 12080	R.T. Chesser	Argentina: Misiones
Tyrannidae	*Casiornis rufus*	AMNH. DOT 2868	C.J. Vogel	Bolivia: Santa Cruz
Tyrannidae	*Cnemarchus erythropygius*	AMNH. DOT 2477	M. Hererra	Bolivia: La Paz

Appendix 1

(*Continued*)

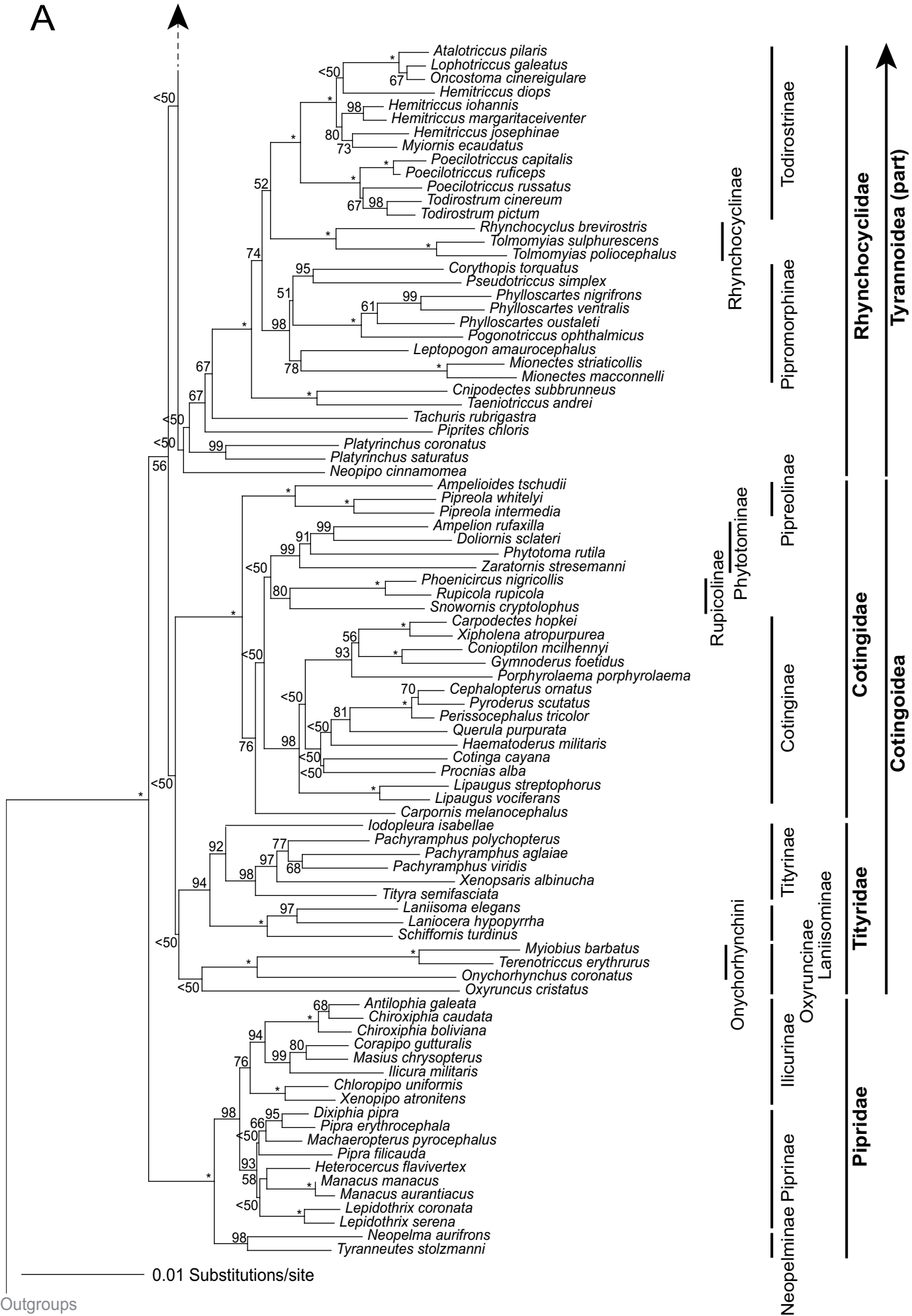
Family	Species	Voucher number*	Collector	Collection locality
Tyrannidae	*Cnemmotriccus fuscatus*	AMNH. DOT 2862	C.J. Vogel	Bolivia: Santa Cruz
Tyrannidae	*Cnipodectes subbrunneus*	FMNH 395582	REAJ-220	Brazil: Acre
Tyrannidae	*Colonia colonus*	FMNH 389962	A.T. Peterson	Brazil: Rondonia
Tyrannidae	*Colorhamphus parvirostris*	AMNH. DOT 12199	R.T. Chesser	Chile: Bio Bio
Tyrannidae	*Contopus fumigatus*	AMNH. DOT 12030	R.O. Prum	Venezuela: Bolivar
Tyrannidae	*Corythopis torquatus*	AMNH. DOT 12396	R.W. Dickerman	Venezuela: Amazonas
Tyrannidae	*Culicivora caudacuta*	LSUMNS B-13948	T.J. Davis	Bolivia: Santa Cruz
Tyrannidae	*Elaenia albiceps*	AMNH. DOT 2714	C.J. Vogel	Bolivia: La Paz
Tyrannidae	*Elaenia spectabilis*	AMNH. DOT 2253	A.L. Porzecanski	Bolivia: Santa Cruz
Tyrannidae	*Empidonax wrightii*	AMNH. DOT 4174	G.F. Barrowclough	United States: Arizona
Tyrannidae	*Empidonomus varius*	AMNH. DOT 6153	J.J. Weicker	Bolivia: Santa Cruz
Tyrannidae	*Euscarthmus meloryphus*	FMNH 334479	D.E. Willard	Bolivia: Santa Cruz
Tyrannidae	*Euscarthmus rufomarginatus*	LSUMNS B-14413	J.M. Bates	Bolivia: Santa Cruz
Tyrannidae	*Fluvicola pica*	AMNH. DOT 6044	J.J.Weicker	Bolivia: Santa Cruz
Tyrannidae	*Griseotyrannus aurantioatrocristatus*	AMNH. DOT 6116	J.J. Weicker	Bolivia: Santa Cruz
Tyrannidae	*Gubernetes yetapa*	LSUMNS B-6832	D.C. Schmitt	Bolivia: El Beni
Tyrannidae	*Hemitriccus diops*	AMNH. DOT 2442	A.P. Caparella	Argentina: Misiones
Tyrannidae	*Hemitriccus iohannis*	FMNH 395578	REAJ-064	Brazil: Acre
Tyrannidae	*Hemitriccus josephinae*	USNM B10527	M.J. Braun	Guyana: North side Acari Mountain
Tyrannidae	*Hemitriccus margaritaceiventer*	AMNH. DOT 2228	A.L. Porzecanski	Bolivia: Santa Cruz
Tyrannidae	*Hirundinea ferruginea*	AMNH. DOT 2936	C.J. Woodbury	Venezuela: Bolivar
Tyrannidae	*Hymenops perspicillatus*	AMNH. DOT 10328	P.R. Sweet	Argentina: Neuquen
Tyrannidae	*Inezia inornata*	AMNH. DOT 6080	J.J. Weicker	Bolivia: Santa Cruz
Tyrannidae	*Inezia subflava*	FMNH 389222	D.F. Stotz	Brazil: Roraima
Tyrannidae	*Knipolegus poecilurus*	AMNH. DOT 12016	R.O. Prum	Venezuela: Bolivar
Tyrannidae	*Knipolegus signatus*	AMNH. DOT 2796	C.J. Vogel	Bolivia: Santa Cruz
Tyrannidae	*Laniocera hypopyrra*	AMNH. DOT 12791	S. Coates	Venezuela: Amazonas
Tyrannidae	*Lathrotriccus euleri*	AMNH. DOT 12054	R.T. Chesser	Argentina: Misiones
Tyrannidae	*Legatus leucophaius*	AMNH. DOT 6143	J.J. Weicker	Bolivia: Santa Cruz
Tyrannidae	*Leptopogon amaurocephalus*	AMNH. DOT 2443	A.P. Caparella	Argentina: Misiones
Tyrannidae	*Lessonia rufa*	AMNH. DOT 12208	R.T. Chesser	Chile: De La Araucana
Tyrannidae	*Lophotriccus galeatus*	AMNH. DOT 4304	G.F. Barrowclough	Venezuela: Amazonas
Tyrannidae	*Machetornis rixosus*	AMNH. DOT 6104	J.J. Weicker	Bolivia: Santa Cruz
Tyrannidae	*Mecocerculus leucophrys*	AMNH. DOT 2589	C.J. Vogel	Bolivia: La Paz
Tyrannidae	*Megarynchus pitangua*	FMNH 392550	MTE-012	Brazil: Para
Tyrannidae	*Mionectes (Pipromorpha) macconnelli*	AMNH. DOT 4812	G.F. Barrowclough	Venezuela: Bolivar
Tyrannidae	*Mionectes striaticollis*	AMNH. DOT 7061	O.M. Zallio	Bolivia: La Paz
Tyrannidae	*Mitrephanes phaeocercus*	AMNH. DOT 8417	P.Escalante P.	Mexico: Hidalgo
Tyrannidae	*Muscigralla brevicauda*	LSUMNS B-5172	S.W. Cardiff	Peru: Lambayeque
Tyrannidae	*Muscisaxicola albilora*	AMNH. DOT 12171	R.T. Chesser	Chile: Region Metropolitana
Tyrannidae	*Myiarchus swainsoni*	AMNH. DOT 2289	A.L. Porzecanski	Bolivia: Santa Cruz
Tyrannidae	*Myiarchus tyrannulus*	AMNH. DOT 6200	J.J. Weicker	Bolivia: Santa Cruz
Tyrannidae	*Myiobius barbatus*	FMNH 389975	A.T. Peterson	Brazil: Rondonia
Tyrannidae	*Myiodynastes luteiventris*	LSUMNS B28936	D.L. Dittmann	United States: Louisiana
Tyrannidae	*Myiodynastes maculatus*	AMNH. DOT 2190	A.L. Porzecanski	Bolivia: Santa Cruz
Tyrannidae	*Myiopagis flavivertex_1*	AMNH. DOT 8789	P. Escalante P.	Venezuela: Amazonas
Tyrannidae	*Myiopagis flavivertex_2*	AMNH. DOT 8788	P. Escalante P.	Venezuela: Amazonas
Tyrannidae	*Myiopagis gaimardii*	FMNH 391159	J.G. Tello	Bolivia: El Beni
Tyrannidae	*Myiopagis viridicata*	AMNH. DOT 6186	J.J. Weicker	Bolivia: Santa Cruz
Tyrannidae	*Myiophobus ochraceiventris*	FMNH 433612	B.J. O'Shea	Peru: Cusco
Tyrannidae	*Myiophobus roraimae*	AMNH. DOT 11861	R.O. Prum	Venezuela: Bolivar
Tyrannidae	*Myiornis ecaudatus*	FMNH 389981	T.S. Schulenberg	Brazil: Rondonia
Tyrannidae	*Myiotheretes fumigatus*	LSUMNS B-1921	D.F. Stotz	Peru: Pasco
Tyrannidae	*Myiotheretes striaticollis*	LSUMNS B-8384	M. Sanchez S.	Peru: Pasco
Tyrannidae	*Myiotriccus ornatus*	FMNH 433613	T. Pequeño S.	Peru: Cusco
Tyrannidae	*Myiozetetes cayanensis*	AMNH. DOT6192	J.J. Weicker	Bolivia: Santa Cruz
Tyrannidae	*Myiozetetes luteiventris*	LSUMNS B-9021	K.V. Rosenberg	Bolivia: Pando
Tyrannidae	*Neopipo cinnamomea*	AMNH. DOT 12400	R.W. Dickerman	Venezuela: Amazonas
Tyrannidae	*Neoxolmis rufiventris*	LSUMNS B-14024	A.P. Capparella	Chile: Magallanes y Antartica Chilena
Tyrannidae	*Ochthoeca cinnamomeiventris*	AMNH. DOT 7057	O.M. Zallio	Bolivia: La Paz
Tyrannidae	*Ochthoeca oenanthoides*	FMNH 391906	G.P. Servat	Peru: Lima

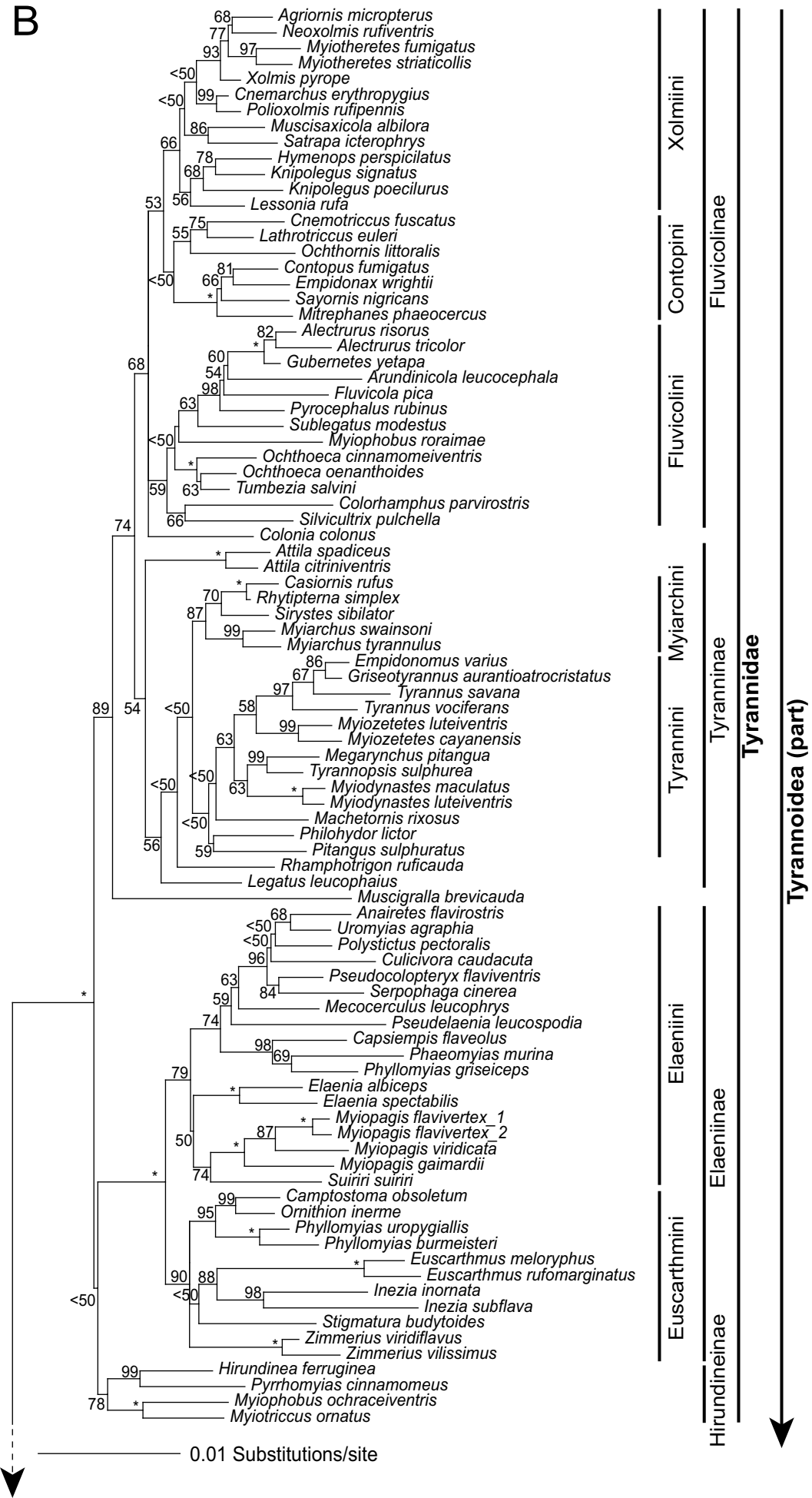
Appendix 1

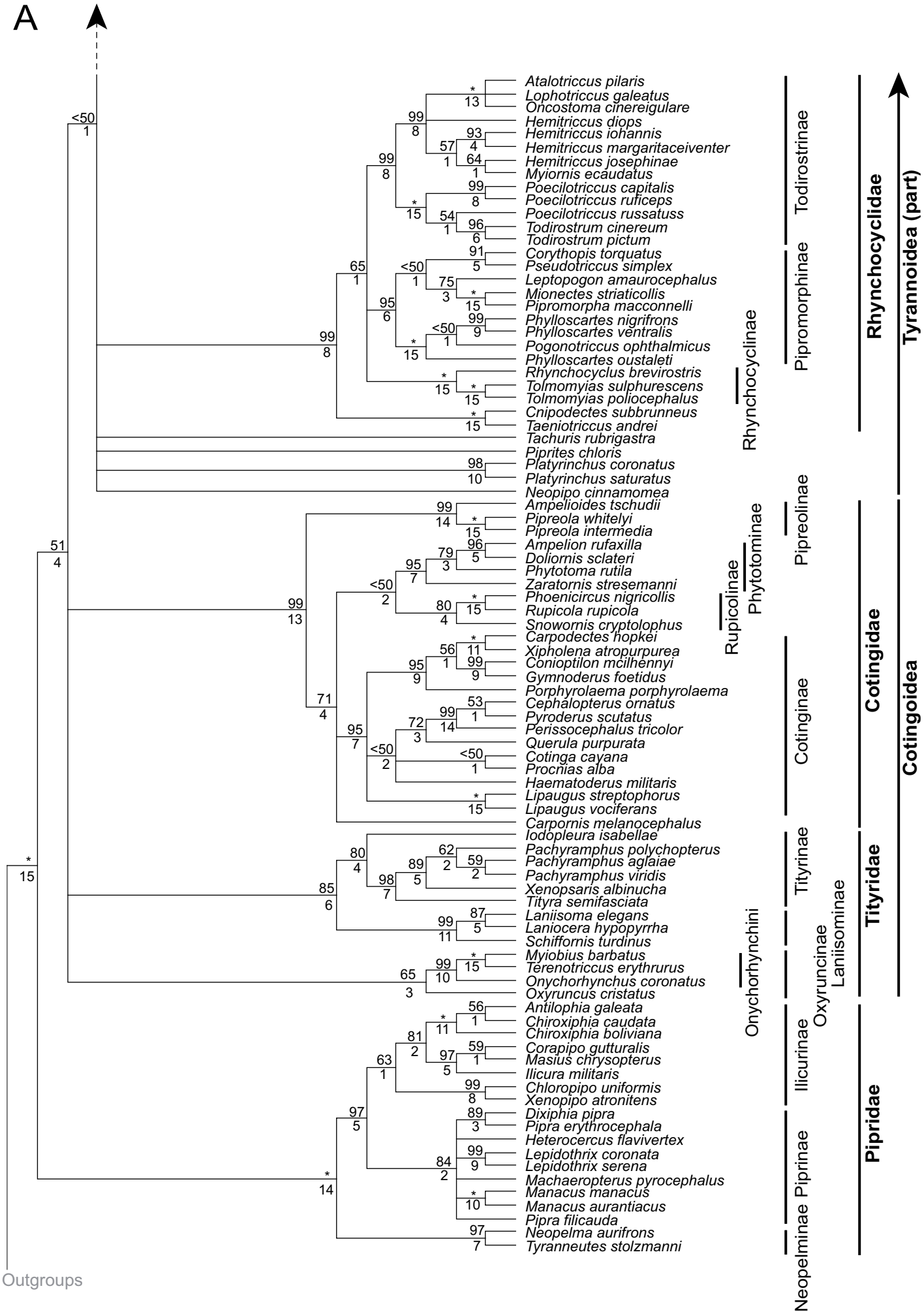
(*Continued*)

Family	Species	Voucher number*	Collector	Collection locality
Tyrannidae	*Ochthornis littoralis*	AMNH. DOT 8783	P. Escalante P.	Venezuela: Amazonas
Tyrannidae	*Oncostoma cinereigulare*	FMNH 434038	B.J. O'Shea	El Salvador: Ahuachapan
Tyrannidae	*Onychorhynchus coronatus*	AMNH. DOT 3864	G.F. Barrowclough	Venezuela: Amazonas
Tyrannidae	*Ornithion inerme*	USNM B04449	M.B. Robbins	Guyana: Berbice
Tyrannidae	*Pachyramphus (Platypsaris) aglaiae*	AMNH. DOT 3688	G.F. Barrowclough	Costa Rica: Puntarenas
Tyrannidae	*Pachyramphus polychopterus*	AMNH. DOT 2286	A.L. Porzecanski	Bolivia: Santa Cruz
Tyrannidae	*Pachyramphus viridis*	AMNH. DOT 2280	A.L. Porzecanski	Bolivia: Santa Cruz
Tyrannidae	*Phaeomyias murina*	FMNH 389215	D.F. Stotz	Brazil: Roraima
Tyrannidae	*Philohydor lictor*	AMNH. DOT 6189	J.J. Weicker	Bolivia: Santa Cruz
Tyrannidae	*Phyllomyias burmeisteri*	FMNH 389212	D.F. Stotz	Brazil: Sao Paulo
Tyrannidae	*Phyllomyias griseiceps*	FMNH 389213	D.F. Stotz	Brazil: Roraima
Tyrannidae	*Phyllomyias uropygialis*	AMNH. DOT 2761	C.J. Vogel	Bolivia: La Paz
Tyrannidae	*Phylloscartes nigrifrons*	AMNH. DOT 4819	G.F. Barrowclough	Venezuela: Bolivar
Tyrannidae	*Phylloscartes oustaleti*	FMNH 395443	D.F. Stotz	Brazil: Sao Paulo
Tyrannidae	*Phylloscartes ventralis*	USNM B5763	B.K. Schmidt	Argentina: Tucuman
Tyrannidae	*Pitangus sulphuratus*	AMNH. DOT 6131	J.J. Weicker	Bolivia: Santa Cruz
Tyrannidae	*Platyrinchus coronatus*	AMNH. DOT 4315	G.F. Barrowclough	Venezuela: Amazonas
Tyrannidae	*Platyrinchus saturatus*	AMNH. DOT 8861	P. Escalante P.	Venezuela: Amazonas
Tyrannidae	*Poecilotriccus capitalis*	FMNH 334372	T.S. Schulenberg	Brazil: Rondonia
Tyrannidae	*Poecilotriccus ruficeps*	LSUMNS B-5976	T.S. Schulenberg	Ecuador: Morona-Santiago
Tyrannidae	*Poecilotriccus russatus*	AMNH. DOT 4707	G.F. Barrowclough	Venezuela: Bolivar
Tyrannidae	*Pogonotriccus ophthalmicus*	FMNH 433658	T. Pequeño S.	Peru: Cusco
Tyrannidae	*Polioxolmis rufipennis*	FMNH 391982	G.P. Servat	Peru: Lima
Tyrannidae	*Polystictus pectoralis*	FMNH 389223	D.F. Stotz	Brazil: Roraima
Tyrannidae	*Pseudelaenia leucospodia*	LSUMNS B-5185	S.W. Cardiff	Peru: Lambayeque
Tyrannidae	*Pseudocolopteryx flaviventris*	AMNH. DOT 12095	R.T. Chesser	Argentina: Buenos Aires
Tyrannidae	*Pseudotriccus simplex*	FMNH 430018	T. Pequeño S.	Peru: Paucartambo
Tyrannidae	*Pyrocephalus rubinus*	AMNH. DOT 10389	P.R. Sweet	Argentina: Neuquen
Tyrannidae	*Pyrrhomyias cinnamomeus*	AMNH. DOT 2832	C.J. Vogel	Bolivia: Santa Cruz
Tyrannidae	*Ramphotrigon ruficauda*	AMNH. DOT 12403	R.W. Dickerman	Venezuela: Amazonas
Tyrannidae	*Rhynchocyclus brevirostris*	FMNH 343247	J. Vega. M	Mexico: Veracruz
Tyrannidae	*Rhytipterna simplex*	AMNH. DOT 11896	R.O. Prum	Venezuela: Bolivar
Tyrannidae	*Satrapa icterophrys*	AMNH. DOT 9901	P.R. Sweet	Argentina: Buenos Aires
Tyrannidae	*Sayornis nigricans*	AMNH. DOT 5948	J.J. Weicker	United States: California
Tyrannidae	*Serpophaga cinerea*	FMNH 433651	T. Pequeño S.	Peru: Cusco
Tyrannidae	*Silvicultrix pulchella*	FMNH 433629	B.J. O'Shea	Peru: Cusco
Tyrannidae	*Sirystes sibilator*	FMNH 389238	D.F. Stotz	Brazil: Roraima
Tyrannidae	*Stigmatura budytoides*	AMNH. DOT 6014	J.J. Weicker	Bolivia: Santa Cruz
Tyrannidae	*Sublegatus modestus*	AMNH. DOT 6195	J.J. Weicker	Bolivia: Santa Cruz
Tyrannidae	*Suiriri suiriri*	AMNH. DOT 2245	A.L. Porzecanski	Bolivia: Santa Cruz
Tyrannidae	*Tachuris rubrigastra*	AMNH. DOT 12161	R.T. Chesser	Chile: Valparaiso
Tyrannidae	*Taeniotriccus andrei*	USNM B06904	G.R. Graves	Brazil: Para
Tyrannidae	*Terenotriccus erythrurus*	AMNH. DOT 4247	G.F. Barrowclough	Venezuela: Amazonas
Tyrannidae	*Tityra semifasciata*	AMNH. DOT 3682	G.F. Barrowclough	Costa Rica: Puntarenas
Tyrannidae	*Todirostrum cinereum*	AMNH. DOT 8873	P. Escalante P.	Venezuela: Falcon
Tyrannidae	*Todirostrum pictum*	USNM B09173	M.B. Robbins	Guyana: Northwest District
Tyrannidae	*Tolmomyias poliocephalus*	AMNH. DOT 11906	R.O. Prum	Venezuela: Bolivar
Tyrannidae	*Tolmomyias sulphurescens*	AMNH. DOT 6754	J. Vargas	Bolivia: La Paz
Tyrannidae	*Tumbezia salvini*	LSUMNS B-5170	D.L. Dittmann	Peru: Lambayeque
Tyrannidae	*Tyrannopsis sulphurea*	FMNH 391525	J.M. Cardoso da Silva	Brazil: Amapa
Tyrannidae	*Tyrannus savana*	AMNH. DOT 2203	A.L. Porzecanski	Bolivia: Santa Cruz
Tyrannidae	*Tyrannus vosciferans*	AMNH. DOT 4166	G.F. Barrowclough	United States: Arizona
Tyrannidae	*Uromyias agraphia*	LSUMNS B-8276	G.H. Rosenberg	Peru: Pasco
Tyrannidae	*Xenopsaris albinucha*	ANSP 8359	D. Agro	Guyana: Potaro-Siparuni
Tyrannidae	*Xolmis pyrope*	AMNH. DOT 12144	R.T. Chesser	Chile: Region Metropolitana
Tyrannidae	*Zimmerius vilissimus*	AMNH. DOT 5019	G.F. Barrowclough	Venezuela: Aragua
Tyrannidae	*Zimmerius viridiflavus*	LSUMNS B-8009	T.S. Schulenberg	Peru: Pasco

*Family designations follow Fitzpatrick (2004a) and Snow (2004a,b).
Museum abbreviations: AMNH = American Museum of Natural History; FMNH = Field Museum of Natural History; LSUMNS = Louisiana State University Museum of Natural Science; USNM = National Museum of Natural History; UKMNH = University of Kansas Museum of Natural History; ANSP = Academy of Natural Sciences of Philadelphia.


A
Atalotriccus pilaris
Lophotriccus galeatus
Oncostoma cinereigulare
Hemitriccus diops
Hemitriccus iohannis
Hemitriccus margaritaceiventer
Hemitriccus josephinae
Myiornis ecaudatus
Poecilotriccus capitalis
Poecilotriccus ruficeps
Poecilotriccus russatus
Todirostrum cinereum
Todirostrum pictum
Rhynchocyclus brevirostris
Tolmomyias sulphurescens
Tolmomyias poliocephalus
Corythopis torquatus
Pseudotriccus simplex
Phylloscartes nigrifrons
Phylloscartes ventralis
Phylloscartes oustaleti
Pogonotriccus ophthalmicus
Leptopogon amaurocephalus
Mionectes striaticollis
Mionectes macconnelli
Cnipodectes subbrunneus
Taeniotriccus andrei
Tachuris rubrigastra
Piprites chloris
Platyrinchus coronatus
Platyrinchus saturatus
Neopipo cinnamomea
Ampelioides tschudii
Pipreola whitelyi
Pipreola intermedia
Ampelion rufaxilla
Doliornis sclateri
Phytotoma rutila
Zaratornis stresemanni
Phoenicircus nigricollis
Rupicola rupicola
Snowornis cryptolophus
Carpodectes hopkei
Xipholena atropurpurea
Conioptilon mcilhennyi
Gymnoderus foetidus
Porphyrolaema porphyrolaema
Cephalopterus ornatus
Pyroderus scutatus
Perissocephalus tricolor
Querula purpurata
Haematoderus militaris
Cotinga cayana
Procnias alba
Lipaugus streptophorus
Lipaugus vociferans
Carpornis melanocephalus
Iodopleura isabellae
Pachyramphus polychopterus
Pachyramphus aglaiae
Pachyramphus viridis
Xenopsaris albinucha
Tityra semifasciata
Laniisoma elegans
Laniocera hypopyrrha
Schiffornis turdinus
Myiobius barbatus
Terenotriccus erythrurus
Onychorhynchus coronatus
Oxyruncus cristatus
Antilophia galeata
Chiroxiphia caudata
Chiroxiphia boliviana
Corapipo gutturalis
Masius chrysopterus
Ilicura militaris
Chloropipo uniformis
Xenopipo atronitens
Dixiphia pipra
Pipra erythrocephala
Machaeropterus pyrocephalus
Pipra filicauda
Heterocercus flavivertex
Manacus manacus
Manacus aurantiacus
Lepidothrix coronata
Lepidothrix serena
Neopelma aurifrons
Tyranneutes stolzmanni
0.01 Substitutions/site
Outgroups
Rhynchocyclinae
Todirostrinae
Pipromorphinae
Rupicolinae
Phytotominae
Pipreolinae
Cotinginae
Onychorhynchini
Tityrinae
Oxyruncinae
Laniisominae
Ilicurinae
Piprinae
Neopelminae
Rhynchocyclidae
Cotingidae
Tityridae
Pipridae
Cotingoidea
Tyrannoidea (part)


B
Agriornis micropterus
Neoxolmis rufiventris
Myiotheretes fumigatus
Myiotheretes striaticollis
Xolmis pyrope
Cnemarchus erythropygius
Polioxolmis rufipennis
Muscisaxicola albilora
Satrapa icterophrys
Hymenops perspicilatus
Knipolegus signatus
Knipolegus poecilurus
Lessonia rufa
Cnemotriccus fuscatus
Lathrotriccus euleri
Ochthornis littoralis
Contopus fumigatus
Empidonax wrightii
Sayornis nigricans
Mitrephanes phaeocercus
Alectrurus risorus
Alectrurus tricolor
Gubernetes yetapa
Arundinicola leucocephala
Fluvicola pica
Pyrocephalus rubinus
Sublegatus modestus
Myiophobus roraimae
Ochthoeca cinnamomeiventris
Ochthoeca oenanthoides
Tumbezia salvini
Colorhamphus parvirostris
Silvicultrix pulchella
Colonia colonus
Attila spadiceus
Attila citriniventris
Casiornis rufus
Rhytipterna simplex
Sirystes sibilator
Myiarchus swainsoni
Myiarchus tyrannulus
Empidonomus varius
Griseotyrannus aurantioatrocristatus
Tyrannus savana
Tyrannus vociferans
Myiozetetes luteiventris
Myiozetetes cayanensis
Megarynchus pitangua
Tyrannopsis sulphurea
Myiodynastes maculatus
Myiodynastes luteiventris
Machetornis rixosus
Philohydor lictor
Pitangus sulphuratus
Rhamphotrigon ruficauda
Legatus leucophaius
Muscigralla brevicauda
Anairetes flavirostris
Uromyias agraphia
Polystictus pectoralis
Culicivora caudacuta
Pseudocolopteryx flaviventris
Serpophaga cinerea
Mecocerculus leucophrys
Pseudelaenia leucospodia
Capsiempis flaveolus
Phaeomyias murina
Phyllomyias griseiceps
Elaenia albiceps
Elaenia spectabilis
Myiopagis flavivertex_1
Myiopagis flavivertex_2
Myiopagis viridicata
Myiopagis gaimardii
Suiriri suiriri
Camptostoma obsoletum
Ornithion inerme
Phyllomyias uropygiallis
Phyllomyias burmeisteri
Euscarthmus meloryphus
Euscarthmus rufomarginatus
Inezia inornata
Inezia subflava
Stigmatura budytoides
Zimmerius viridiflavus
Zimmerius vilissimus
Hirundinea ferruginea
Pyrrhomyias cinnamomeus
Myiophobus ochraceiventris
Myiotriccus ornatus
0.01 Substitutions/site
Xolmiini
Contopini
Fluvicolini
Fluvicolinae
Myiarchini
Tyrannini
Tyranninae
Elaeniini
Euscarthmini
Elaeniinae
Hirundineinae
Tyrannidae
Tyrannoidea (part)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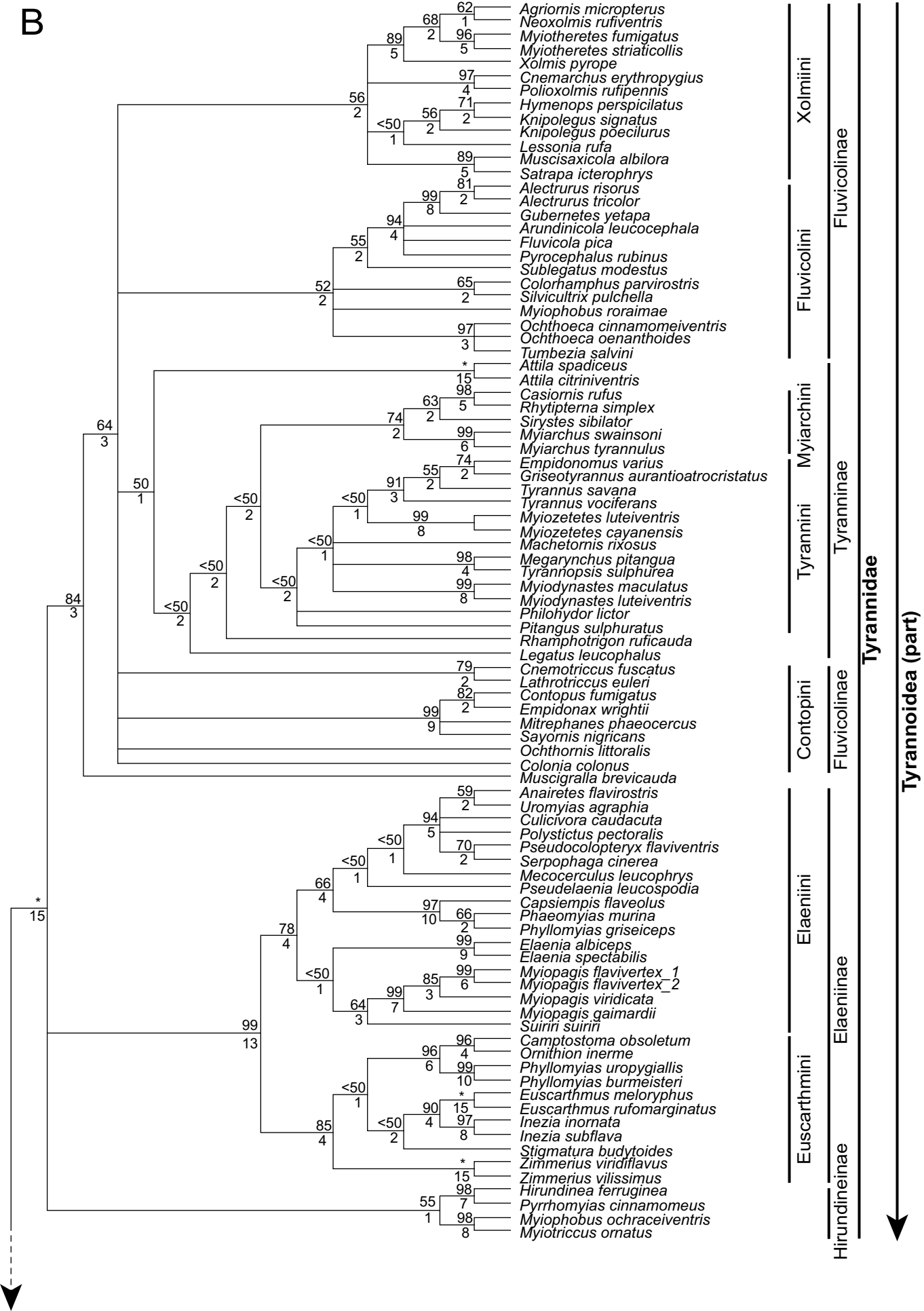
Pipridae
Cotingoidea
Tyrannoidea (part)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Myiarchini
Tyrannini
Contopini
Elaeniini
Euscarthmini
Hirundineinae
Fluvicolinae
Tyranninae
Elaeniinae
Tyrannidae
Tyrannoidea (part)