Molecular Phylogenetics and Evolution 55 (2010) 733–737

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Short Communication

A molecular phylogenetic hypothesis for the manakins (Aves: Pipridae)

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ARTICLE INFO

Article history:
Received 24 June 2009
Revised 21 January 2010
Accepted 19 February 2010
Available online 25 February 2010

Keywords:
Manakin
mtDNA
Nuclear
Phylogeny
Pipridae
Suboscine
Tyrannida

ABSTRACT

Phylogenetic relationships among the 14 manakin genera were inferred from DNA sequence data obtained from both mitochondrial and nuclear DNA loci. Phylogenetic analysis resulted in a well-supported hypothesis that corroborates a sister relationship between tyrant-manakins and the "core" manakins (*Antilophia, Chiroxiphia, Corapipo, Dixiphia, Heterocercus*, *Ilicura*, *Lepidothrix*, *Manacus*, *Masius*, *Machaeropterus*, *Pipra*, and *Xenopipo*). Our data strongly support these core manakin genera as a monophyletic group. Consistent with previous work, we find two major clades within the core manakins, although the placement of the genus *Xenopipo* with regards to these two clades is ambiguous. Generic relationships within these clades are generally well resolved. Although we find some concordance between our study and a previous manakin phylogeny based on syringeal characters, we note several fundamental differences between the phylogenies. Thus, we offer a new phylogenetic hypothesis for Pipridae.

1. Introduction

Manakins (Pipridae) are small, suboscine passerines distributed throughout the Neotropics (Snow, 2004). They are largely frugivorous and typically found in forested habitats at lower elevations (Snow, 2004). The family Pipridae is part of the parvorder Tyrannida (*sensu* Sibley and Ahlquist, 1990), which also includes the cotingas (Cotingidae) and tyrant flycatchers (Tyrannidae). Some notable characteristics of the manakins are their lek-based mating systems, extraordinary courtship displays, and elaborate plumage ornaments. Phylogenetically based comparative studies of these taxa could provide important insights into the evolution of sexual dimorphism and mating systems.

The most comprehensive manakin phylogenetic study to date (Prum, 1992) was based on syringeal morphology and was restricted to the "core manakins" (*sensu* Prum, 1990), which are diagnosed by a unique derived syringeal character that supports monophyly of the group. Monophyly of this group was further supported by an allozyme study of tyrannoids (Lanyon, 1985), which included nine manakin species (in nine genera). Manakins were also included in a tyrannoid phylogeny presented by Sibley and Ahlquist (1985, 1990) based on DNA hybridization, but the relationships between the piprid taxa were not well resolved. Several broad-level molecular phylogenetic studies of the basal relationships within the suboscines in general (Chesser, 2004) and the tyrannida in particular (Johansson et al., 2002; Ericson et al., 2006; Barber and Rice, 2007) included piprid taxa and provided at least two additional insights into manakin phylogeny: (1) corroboration of the monophyly of the core manakins and (2) placement of the tyrant-manakins (*Neopelma* and *Tyranneutes*) as a sister clade to the core manakins. Recently, Rego et al. (2007) used mtDNA sequence data to test and reject the idea that *Pipra*, *Lepidothrix*, and *Dixiphia* form a monophyletic assemblage. Here, we expand on previous work and present a phylogenetic hypothesis for all currently recognized piprid genera based on mitochondrial and nuclear sequence data.

2. Materials and methods

2.1. Samples

We obtained either tissue (muscle, liver, or heart) samples from the Louisiana State University Museum of Natural Science (LSUMZ) or blood samples from wild birds in Costa Rica. DNA from all blood samples is photo-vouchered at the Cincinnati Museum Center (CMC). All species for which blood samples were used involved

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doi:10.1016/j.ympev.2010.02.024

at least one unambiguously identified adult male specimen (with accompanying photo). In total, our analysis included 32 samples from 14 manakin species representing the 13 genera currently assigned to the Pipridae (Remsen et al., 2009) plus the monotypic genus *Dixiphia* (*Pipra pipra sensu* Remsen et al., 2009) because it is often placed in its own genus (Prum, 1992). When possible, we included two individuals of a species. We used the genera *Myiarchus, Laniisoma, Schiffornis, Piprites*, and *Cotinga* as outgroups. Sample information and GenBank Accession Numbers are provided in Table 1.

2.2. PCR and sequencing

We extracted whole genomic DNA from each sample using a standard phenol–chloroform separation followed by ethanol precipitation. We amplified and sequenced two mitochondrial (mtDNA) genes and one nuclear gene region. We amplified the mtDNA cytochrome *c* oxidase subunit I (COI) gene using the BIRDF1 and BIRDR1 primers described by Hebert et al. (2004), the mtDNA NADH dehydrogenase subunit 2 (ND2) gene using the primers L5216 and H6313 (Sorenson et al., 1999), and the 3rd intron of the Z-linked muscle-specific kinase (MUSK) gene using the primers MUSK-I3F and MUSK-I3R (Kimball et al., 2009). PCR was performed on a MJ Research PTC-100 thermocycler with a thermal profile of 94 °C for 4 min followed by 30 cycles of 1 min at 94 °C, 1 min at 50 °C, and 2 min at 72 °C, and then 10 min at 72 °C. Primers and excess dNTPs were removed from the PCR products with ExoSAP-IT (USB Corporation) according to the manufacturer's instructions. Using amplification primers, the ExoSAP-IT treated PCR products were sequenced using BigDye kit v. 3.0 and separated on an ABI 3700 automated sequencer according to recommended protocols (Applied Biosystems). The ND2 gene was also sequenced using the internal sequencing primers L5758 and H5766 (Sorenson et al., 1999). All loci were sequenced entirely in both directions and deposited in GenBank (Table 1).

2.3. Phylogenetic analysis

We aligned sequences of the two mitochondrial and one nuclear locus by eye, and found no significant ambiguities among the taxa sampled. We took two approaches to model-fitting for these data. First, we estimated the best-fit model (as defined by AIC value) using ModelTest v3.7 (Posada and Crandall, 1998), for *a priori*-defined partitions corresponding to the three gene regions. Alternatively, we analyzed the data using a mixture model allowing four patterns, without defined partitions (Pagel and Meade, 2004). For *a priori*-partitioning, subsequent to model-fitting we analyzed the data using both likelihood (ML) and Bayesian methods. Likelihood searches were performed using RAxML v7.0.4 (Stamatakis 2006), using rapid hill climbing algorithm (-f d), and the discrete rate category model followed by fitting with Γ-distributed rates (-m GTRMIX -c 25). Separate model parameters were allowed for each partition (-q), but branch lengths were enforced to proportionality (i.e., -M not invoked) due to artifacts obtained when analyzing an incomplete (some genes missing for some taxa) matrix. The ML search was repeated 50 times from parsimony starting trees to assess convergence on a single optimum. Support for individual relationships was assessed by the non-parametric bootstrap ($N = 200$; Felsenstein 1985). Bayesian analyses with *a priori* partitioning were performed with MrBayes v3.1.2 (Ronquist and Huelsenbeck,

Table 1
Sample, museum catalog numbers, and GenBank Accession Numbers for all samples included in this study. Acronyms: LSUMZ = Louisiana State University Museum of Natural Science; CMC = Cincinnati Museum Center.

Taxa	Origin	DNA source	Tissue/Field ID no.	GenBank accession no.		
				COI	ND2	MUSK
Antilophia galeata	LSUMZ	Tissue	B-13806		GU985490	GU985473
	LSUMZ	Tissue	B-13809	EF111037	GU985491	GU985474
Chiroxiphia linearis	CMC	Blood	B41252	EF111027	GU985492	GU985475
	CMC	Blood	B41253	EF111030	GU985493	
Corapipo altera	CMC	Blood	B41248	EF11103	GU985494	GU985476
	CMC	Blood	B41249		GU985495	
Heterocercus linteatus	LSUMZ	Tissue	B-12692	EF111028	GU985499	GU985478
	LSUMZ	Tissue	B-12701	EF111039	GU985500	
Ilicura militaris	GenBank	N/A	N/A		AY136621	
Lepidothrix coronata	CMC	Blood	B41245	EF111043	GU985508	GU985482
Manacus manacus	LSUMZ	Tissue	B-2583	EF111033	GU985503	GU985480
	LSUMZ	Tissue	B-2678	EF111041	GU985504	
Machaeropterus deliciosus	LSUMZ	Tissue	B-11761	EF111029	GU985501	GU985479
	LSUMZ	Tissue	B-12180	EF111032	GU985502	
Neopelma sulphureiventer	LSUMZ	Tissue	B-46006	EF111036	GU985506	GU985481
	LSUMZ	Tissue	B-46021	EF111042	GU985507	
Masius chrysopterus	LSUMZ	Tissue	B-11881	EF111035	GU985505	
Pipra mentalis	CMC	Blood	B41246	GU985469	GU985509	GU985483
	CMC	Blood	B41247	GU985470	GU985510	
Pipra (Dixiphia) pipra	CMC	Blood	B41250		GU985497	GU985477
	CMC	Blood	B41251	EF111031	GU985498	
Tyranneutes stolzmanni	LSUMZ	Tissue	B-3027	EF111046	GU985515	
	LSUMZ	Tissue	B-9573	EF111049	GU985516	GU985487
Xenopipo unicolor	LSUMZ	Tissue	B-43607	EF111047	GU985517	GU985488
	LSUMZ	Tissue	B-43735	EF111048	GU985518	GU985489
Outgroups						
Cotinga cayana	LSUMZ	Tissue	B-40581	GU985468	GU985496	
Laniisoma elegans	GenBank	N/A	N/A	EF458614		
Myiarchus cinitus	GenBank	N/A	N/A	AY666501		
Piprites chloris	LSUMZ	Tissue	B-3229	EF111044	GU985512	GU985485
	LSUMZ	Tissue	B-103506	EF111045	GU985511	GU985484
Schiffornis major	LSUMZ	Tissue	B-3630	GU985471	GU985513	
	LSUMZ	Tissue	B-7346	GU985472	GU985514	GU985486

2003), with two simultaneous runs of 2×10^6 generations, Metropolis coupling with three heated chains, and partitions allowed to have separate model parameters and branch lengths. Burn-in of the Markov chains and convergence of parameters and likelihoods was assessed using Tracer v1.4.1 (Rambaut and Drummond 2003), and convergence of nodal posterior probabilities using AWTY (Nylander et al. 2004). In order to assess incongruence among the partitions, the Bayesian analyses were repeated for each partition separately, and nodal posterior probabilities were examined for conflict. Mixture model analysis was performed using BayesPhylogenies (Pagel and Meade, 2004), allowing four site patterns (each with a general time-reversible model with discretely-approximated Γ-distributed rates ($k = 4$ categories), running one unheated chain for 2×10^6 generations.

3. Results

For the two protein-coding mtDNA genes, we observed no insertions-deletions (indels) or stop codons, and most variation appeared at degenerate sites, so it is unlikely that nuclear copies of mtDNA (numts; Sorenson and Quinn, 1998) were sequenced. General congruence between mtDNA and nuclear gene topologies (see below) is further evidence against the presence of numt sequences in our dataset.

Our data yielded a generally well-supported hypothesis of relationships among manakin genera. Model-fitting indicated that the GTR+I+G model was the best fit to the two mitochondrial genes, whereas the TVM + G model was most appropriate for the MUSK intron. Since HKY + G was the next best ($\delta = 0.0447$) model actually implemented in MrBayes, the latter was used in analyses of the nuclear locus. Separate Bayesian analyses of the three gene regions yielded generally well-supported non-conflicting hypotheses of relationship, with one exception. The placement of *Xenopipo* showed strong conflict between ND2, which showed strong support ($P = 1.00$) for its placement with the clade (*Chiroxiphia*, *Antilophia*, *Ilicura*, *Masius* and *Corapipo*) and MUSK, which placed it ($P = 1.00$) with (*Lepidothrix*, *Heterocercus*, *Manacus*, *Machaeropterus*, *Pipra*, *Dixiphia*). The second mtDNA gene (COI) failed to resolve the relationships of *Xenopipo*, and thus was consistent with either hypothesis. Bearing this conflict in mind, we proceeded with combined analyses of the partitioned data. The likelihood and both *a priori* and mixture model Bayesian analyses agreed in essentially every detail regarding hypothesized relationships among manakin genera (Fig. 1).

4. Discussion

Consistent with previous work, we recovered three main clades within the Pipridae. Our data strongly support monophyly of the core manakins (*sensu* Prum, 1990), corroborating a previous hypothesis of monophyly based on the unique derived syringeal character shared by species in this group (Prum, 1990). We also recovered a sister-group relationship between the tyrant-manakins (*Tyranneutes* and *Neopelma*) and the core manakins, a result consistent with other molecular studies that included members of these two groups (e.g. Prum et al., 2000; Barber and Rice, 2007). Furthermore, we found that the core manakins are broadly divided into two main clades: one containing the genera *Xenopipo, Chiroxiphia, Antilophia, Ilicura, Masius,* and *Corapipo*; and another containing the genera *Lepidothrix, Heterocercus, Manacus, Machaeropterus, Pipra*, and *Dixiphia*. This split is consistent with the conclusions of Lanyon (1985), an allozyme study that included seven genera of "core" manakins and supported two main clades: *Manacus*/*Machaeropterus*/*Pipra* and *Chiroxiphia*/*Masius*/*Corapipo*/*Chloro-*

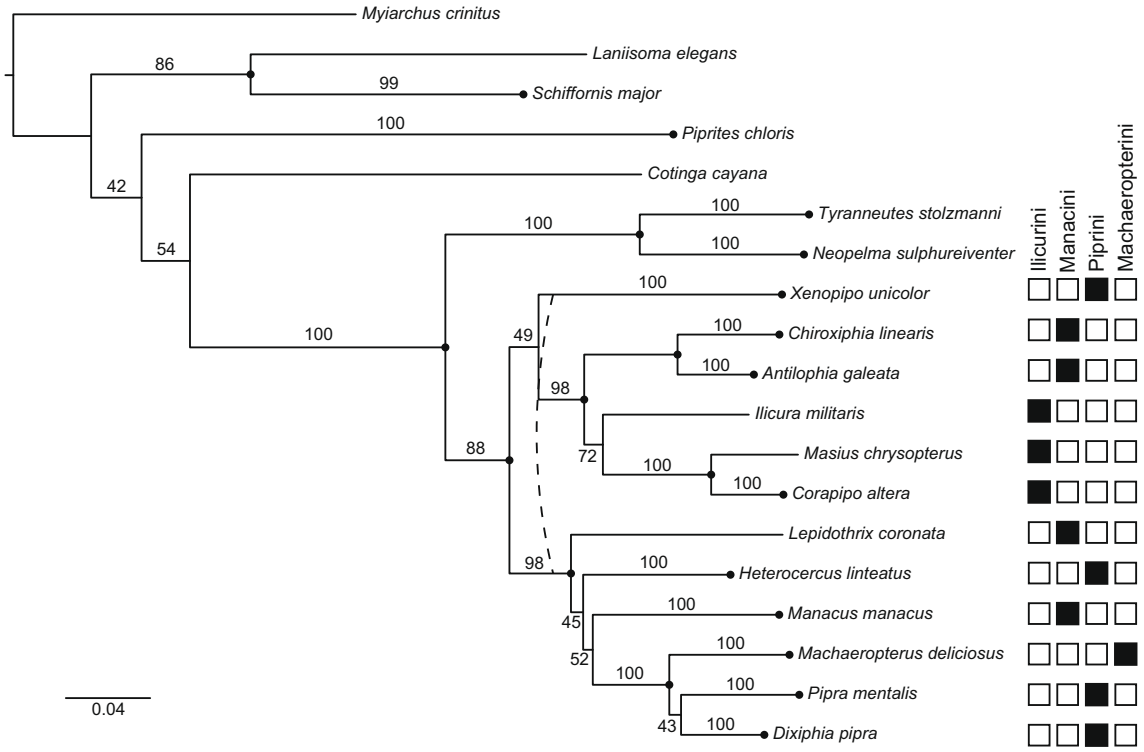

Fig. 1. Relationships among manakin genera based on combined analysis of mitochondrial (ND2 and COI) and nuclear (MUSK intron 3) loci. Shown is the maximum likelihood tree inferred by a three-partition likelihood analysis, which is identical to the majority-rule consensus of trees sampled by partitioned Bayesian MCMC. Nodes highlighted by circles received an estimated posterior probability of 1 (circles at tips indicate monophyly of multiple samples from a given taxon), and bootstrap percentages from the partitioned likelihood analysis are shown near the corresponding branches. The dashed line connecting *Xenopipo* and the *Lepidothrix-Dixiphia* clade indicates the conflict between mtDNA (which places the genus as shown here) and the nuclear locus (which places it in the latter clade). Generic membership in the four tribes recognized by Prum (1992) is shown by closed squares to the right of the tree.

pipo. The studies of Rego et al. (2007) based on mtDNA sequence data and Brumfield and Braun (2001) based on isozymes presented trees consistent with a division between these two clades. These two main clades are generally well supported, with the exception of the placement of *Xenopipo*. The ND2 dataset placed this genus in one group, whereas the MUSK dataset placed it in the other (see Fig. 1). The COI dataset left the placement of *Xenopipo* as unresolved. The piprid phylogeny presented by Rego et al. (2007) based on the cytochrome *b* and 16S mtDNA genes also failed to resolve the exact placement of this genus. In future analyses, adding other members of *Xenopipo* as well as including data from additional loci might clarify the phylogenetic position of *Xenopipo*.

Despite a derived syringeal muscle character reported by Prum (1992) that is shared by *Manacus*, *Chiroxiphia*, and *Antilophia*, our data do not support the monophyly of these genera. Instead our sequence data indicate that *Manacus* is most closely related to a clade containing *Machaeropterus*, *Pipra*, and *Dixiphia*. This new hypothesis for the placement of *Manacus* also disagrees with the hypothesis of Hellmayr (1910), who placed *Manacus* near *Corapipo* based on male plumage color. Plumage color is known to be a misleading phylogenetic character in this group (Brumfield and Braun, 2001). The apparent convergence of syringeal morphology and plumage coloration among taxa suggests that sexual selection may lead to the loss and gain of these complex characters across genera, reminiscent of loss and gain of complex plumage patterns in New World Orioles (Omland and Lanyon, 2000).

We find strong support for a clade containing *Machaeropterus*, *Pipra*, and *Dixiphia*, though it is still somewhat ambiguous whether *Dixiphia* is sister to *Pipra* or to *Machaeropterus*. Rego et al. (2007) suggested that *Pipra* as currently defined (*sensu* Remsen et al., 2009) is paraphyletic, so more work on this clade, including the addition of more species, is needed. The relationships among *Lepidothrix*, *Heterocercus*, *Manacus*, and the *Machaeropterus*/*Pipra*/*Dixiphia* clade are also uncertain, and Rego et al. (2007) support an alternate arrangement, including strong support for *Manacus* as sister to the remaining genera.

With the exception of *Xenopipo*, relationships within the *Chiroxiphia*/*Antilophia*/*Ilicura*/*Masius*/*Corapipo* clade are well supported and do not conflict with any other published molecular phylogeny. In particular, we find strong support for a *Masius*/*Corapipo* clade, sister to the genus *Ilicura*, which agrees both with a cladistic analysis of male courtship display elements (Prum and Johnson, 1987) and with syringeal morphology (Prum, 1992). The remaining two genera, *Chiroxiphia* and *Antilophia*, form a well-supported monophyletic group that is corroborated with evidence from syringeal morphology (Prum, 1992; Fig. 1). This group is strongly supported as sister to the *Ilicura*/*Masius*/*Corapipo*). Overall, we find strong support for one of the tribes erected by Prum (1992) but refute the monophyly of two other tribes (Fig. 1).

Our study represents the most comprehensive molecular phylogeny of the Pipridae published to date. We recognize that some piprid genera are probably not monophyletic, and our limited sampling within genera means that some of the major clades supported in this study may be paraphyletic with regard to current taxonomy. Future studies should focus on elucidating the phylogenetic relationships we could not fully resolve, increasing sampling within genera, and adding data from additional genetic loci in order to more adequately address the causes and resolution of among-gene conflict.

Note added in proof

Subsequent to submitting our manuscript for publication, a phylogenetic study (Tello et al. 2009) appeared that includes many of the manakin genera we analyzed. Despite the use of different nuclear loci and in some cases different exemplar species, the well-supported relationships in this new study are consistent with the results presented here.

Acknowledgments

We thank D. J. Mennill for assistance in the field. We are grateful to R. Blanco and the Ministerio del Ambiente y Energía of Costa Rica for granting our research permits and to the curators and collection managers of the Louisiana State University Museum of Natural Science Collection of Genetic Resources for their generous provision of tissue samples. The Hill lab made helpful comments on the manuscript. Our research was funded by the Natural Sciences and Engineering Research Council of Canada, Sigma-Xi, the American Ornithologists' Union, the Wilson Ornithological Society, the Explorer's Club, the American Museum of Natural History, and Auburn University Graduate Research Grants (to SMD), as well as NSF grant IBN 0235778 (to GEH and HLM).

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