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A comprehensive multilocus phylogeny of the Neotropical cotingas (Cotingidae, Aves) with a comparative evolutionary analysis of breeding system and plumage dimorphism and a revised phylogenetic classification

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ABSTRACT

The Neotropical cotingas (Cotingidae: Aves) are a group of passerine birds that are characterized by extreme diversity in morphology, ecology, breeding system, and behavior. Here, we present a comprehensive phylogeny of the Neotropical cotingas based on six nuclear and mitochondrial loci (~7500 bp) for a sample of 61 cotinga species in all 25 genera, and 22 species of suboscine outgroups. Our taxon sample more than doubles the number of cotinga species studied in previous analyses, and allows us to test the monophyly of the cotingas as well as their intrageneric relationships with high resolution. We analyze our genetic data using a Bayesian species tree method, and concatenated Bayesian and maximum likelihood methods, and present a highly supported phylogenetic hypothesis. We confirm the monophyly of the cotingas, and present the first phylogenetic evidence for the relationships of *Phibalura flavirostris* as the sister group to *Ampelion* and *Doliornis*, and the paraphyly of *Lipaugus* with respect to *Tijuca.* In addition, we resolve the diverse radiations within the *Cotinga*, *Lipaugus*, *Pipreola*, and *Procnias* genera. We find no support for Darwin's (1871) hypothesis that the increase in sexual selection associated with polygynous breeding systems drives the evolution of color dimorphism in the cotingas, at least when analyzed at a broad categorical scale. Finally, we present a new comprehensive phylogenetic classification of all cotinga species.

1. Introduction

The cotingas (Cotingidae) are a diverse radiation of Neotropical, suboscine frugivores and omnivores that includes 66 species in 25 genera (Snow, 1982, 2004; Kirwan and Green, 2012). Cotingas are well known for their diversity in sexual dimorphism, plumage coloration and ornamentations, vocalizations, display behaviors, and breeding systems. The family includes species with concentrated leks (e.g. Guianan Cock-of-the-Rock, *Rupicola rupicola*), dispersed leks (e.g. *Phoenicircus* red cotingas), solitary leks (e.g. *Procnias* bellbirds), socially monogamous species (e.g. *Ampelion* cotingas, *Phytotoma* plantcutters, and *Pipreola* fruiteaters, etc.), and even group living territorial species with helpers at the nest (Purple throated Fruitcrow, *Querula purpurata*).

Cotingas also encompass a great diversity of avian plumage coloration mechanisms. Various cotingas produce plumage colors with (1) eumelanin and phaeomelanin pigments, (2) a tremendous diversity of dietary and physiologically modified carotenoid pigments, (3) spongy, medullary structural coloration in barb rami, (4) iridescent barbule structural coloration (in *Cephalopterus* umbrellabirds), and (5) combinations of barb structural coloration and carotenoid pigments (e.g. green plumages in *Pipreola* and female *Procnias*) (Prum et al., 1998, 1999; Prum et al., 2012; Saranathan et al., 2012).

Variation in cotinga plumage is not restricted to the coloration alone. Many male cotingas have unusual plumage ornaments like the vertical crests of Cocks-of-the-Rock, or the forward-bending crown feathers that give the *Cephalopterus* umbrellabirds their common name. Cotingas also exhibit a wide diversity of fleshy skin ornaments which includes the structurally colored bare blue crowns of *Perisocephalus tricolor*, the blue face and neck skin of *Gymnoderus foetidus*, the bare green throat skin of *Procnias nudicollis* (Prum and Torres, 2003), the bare black throat patch with dozens of thin, wormy wattles of *Procnias averano*, the single,

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feathered nasal wattle of *Procnias alba* (Burton, 1976), the three, bare black nasal and rictal wattles of *Procnias tricarunculata*, and the elongate bare or feathered breast wattle of the umbrellabirds.

Cotingas also vary strikingly in their vocal behavior and acoustic signaling. A few species vocalize very infrequently (*Carpodectes nitidus*, *C. antoniae*, and *Xipholena* sp.) (Kirwan and Green, 2012). However, the *Procnias* bellbirds and *Lipaugus* pihas produce some of the loudest bird vocalizations in the world (Nemeth, 2004). *Procnias* bellbirds are also the only members of the suboscine clade demonstrated to exhibit vocal learning (Saranathan et al., 2007; Kroodsma et al., 2013). In order to produce these diverse and variable vocal signals, the cotingas are tremendously diverse in syringeal morphology, and many genera are identifiable by unique syringeal morphology (Prum, 1990, Prum, unpubl. data). Several cotinga species also produce conspicuous mechanical wing-sounds as part of their courtship displays (e.g. *Rupicola*, *Phoenicircus*, and *Cotinga*) (Snow, 2004).

Further, cotingas vary in the relation between breeding system and sexual plumage dimorphism. Cotingas include polygynous, sexually monomorphic species that advertise with largely acoustic signals (eg. *Lipaugus*), monogamous, monomorphic species (eg. *Ampelion*, *Zaratornis*), monogamous, dimorphic species (eg. *Pipreola*, *Phytotoma*), and polygynous, dimorphic species (e.g. *Procnias*, *Cotinga*). Ohlson et al. (2007) first tested the hypothesis that the sexually dimorphic, polgynous state in the cotingas was derived from a sexually monomorphic, monogamous root state (Snow, 1973) but limited taxon sampling and poor resolution at the base of their tree resulted in equivocal reconstructions.

Comparative analysis of the evolution of the morphological, behavioral, and ecological diversity of cotingas requires a comprehensive species-level phylogeny of the family. Anatomical and molecular phylogenetic studies have largely resolved the previously confusing limits of the cotinga clade (Prum, 1990; Prum et al., 2000; Johansson et al., 2002; Ohlson et al., 2007, 2013; Tello et al., 2009), but previous phylogenetic analyses have not attempted to reconstruct the relationships among a comprehensive sample of cotinga species. Previous studies have also focused on analyzing single locus or concatenated data sets that assume gene-tree concordance.

Here, we present a comprehensive phylogeny of the cotingas based on molecular data for up to ~7500 base pairs of nuclear introns (MYO, G3PDH), exons (RAG-1, RAG-2), and mitochondrial genes (CYT-B, ND2) for a sample of 61 species in all 25 cotinga genera, and 22 species of suboscine outgroups. Our cotinga sample includes all but four currently recognized species in the family: Handsome Fruiteater *Pipreola formosa* and Golden-breasted fruiteater *Pipreola aureopectus*, Chestnut-capped Piha *Lipaugus weberi*, and Grey-winged Cotinga *Tijuca condita* (all are narrow endemics with few specimens available). We analyze these phylogenetic data using a Bayesian species tree method, and concatenated Bayesian and maximum likelihood methods. We then present a comparative phylogenetic analysis of the evolution of cotinga breeding systems and sexual plumage dimorphism. Specifically, we test the hypothesis that increased levels of sexual selection associated with polygyny have fostered the evolution of sexual dimorphism in plumage coloration.

1.1. Taxonomic history of cotingas

Traditionally, the cotinga family has included an even wider diversity of species than are currently placed in Cotingidae (Ridgway, 1907; Hellmayr, 1929; Snow, 1973, 1979). The historically broader limits to the family included becards (*Pachyrampus*), tityras (*Tityra*), purpletufts (*Iodopleura*), various genera of mourners (*Laniisoma*, *Laniocera*, *Rhytipterna*, and *Casiornis*), and often the Sharpbill (*Oxyruncus cristatus*). The traditional cotingas excluded the plantcutters (*Phytotoma*), which were often placed in the Phytotomidae (Snow, 1973, 1982; Lanyon and Lanyon, 1988), and *Rupicola* which was placed in Rupicolidae (Hellmayr, 1929).

On the basis of syringeal anatomy, Ames (1971) removed *Pachyrampus*, *Tityra*, *Rhytipterna*, and *Casiornis* from the cotingas, and transferred them to the tyrant flycatchers (Tyrannidae). Using cladistic analysis of syringeal characters and protein electrophoresis, Lanyon and Lanyon (1988) moved *Phytotoma* into the Cotingidae near the Andean *Ampelion* species, as first suggested by Küchler (1936). In the first phylogenetic test of the monophyly of cotingas, Prum (1990) identified a clade of cotingas based on a derived insertion of an extrinsic syringeal muscle – M. tracheolateralis – on the lateral syringeal membrane between the A1 and B1 supporting elements. However, unrecognized evolutionary derivation (*Lipaugus*) and loss (*Tityra*) of complex intrinsic syringeal muscles contributed ambiguity to diagnosis of cotinga monophyly. Prum et al. (2000) largely confirmed the monophyly of the cotinga clade with an analysis of sequences of the mitochondrial gene cytochrome-B (CYT-B). However, they erroneously placed *Oxyruncus* within the cotinga clade based on an untranscribed nuclear copy of CYT-B (Johansson et al., 2002). Prum et al. (2000) confirmed Ames' hypothesis that *Tityra* is closely related to *Pachyramphus* within the *Schiffornis* group– a novel clade made of former members of the cotinga, manakin, and flycatcher families (Prum and Lanyon, 1989).

Ohlson et al. (2007) provided a well-resolved phylogeny of 26 cotinga species in 22 genera based on ~2100 base pairs of nuclear and mitochondrial DNA (Fig. 1). They identified four main clades: (1) a montane fruiteater clade including *Pipreola* and *Ampelioides* as the sister group to the rest of the family, (2) the *Ampelion* clade including *Ampelion*, *Doliornis*, *Zaratornis*, and the *Phytotoma* plantcutters as the next sister group to the remainder of the family, (3) the *Rupicola–Phoenicircus* clade, and (4) a diverse clade of the 'core' cotingas including the fruitcrows, two clades of pihas, and a clade of 'canopy' cotingas. Tello et al. (2009) analyzed ~4000 bases of the nuclear RAG-1 and RAG-2 genes for a slightly different sample of 25 cotinga species in 23 cotinga genera. The Tello et al. (2009) phylogeny identified many of the same broad clades as Ohlson et al. (2007) but with a few slight differences: *Snowornis* was placed as the sister group to the *Rupicola–Phoenicircus* clade; this clade was sister group to the *Ampelion* clade; and the genus *Carpornis* was placed as the sister group to this larger clade. Within the fruiteaters, the *Ampelion* clade, and the fruitcrows, the phylogenetic relationships of Tello et al. (2009) and Ohlson et al. (2007) are highly congruent, but relationships between *Lipaugus*, *Cotinga*, and *Procnias* were inconsistent between the two studies (Fig. 1).

Most recently, Ohlson et al. (2013) analyzed three introns and two exons (~6300 bp) across 14 cotinga species (14 genera), and supported different phylogenetic relationships from both Tello et al. (2009) and Ohlson et al. (2007); the *Ampelioides–Pipreola* fruiteater clade was reconstructed as sister to all other cotingas in all three, but they inferred different relationships among the *Snowornis–Rupicola* clade, the 'core' cotinga clade, and the *Ampelion* clade. Further, Ohlson et al. (2013) placed *Lipaugus* within the 'core' cotingas, while Tello et al. (2009) placed it as the sister group to the rest of the clade. Regardless, inadequate taxon sampling in all prior analyses has limited overall resolution (Fig. 1).

A few recent taxonomic changes have been recommended. Based on substantial genetic differentiation (Prum et al., 2000) and differences in syringeal morphology, Prum (2001) proposed the genus *Snowornis* for two Andean piha species-*cryptolophus* and *subalaris* – that were formerly in the genus *Lipaugus*. Ohlson et al. (2007) confirmed that *Snowornis* is monophyletic, and not closely related to *Lipaugus*. In sum, previous phylogenetic studies of cotingas have not included enough taxa to test the monophyly of cotinga genera. This is partly because cotinga genera are so

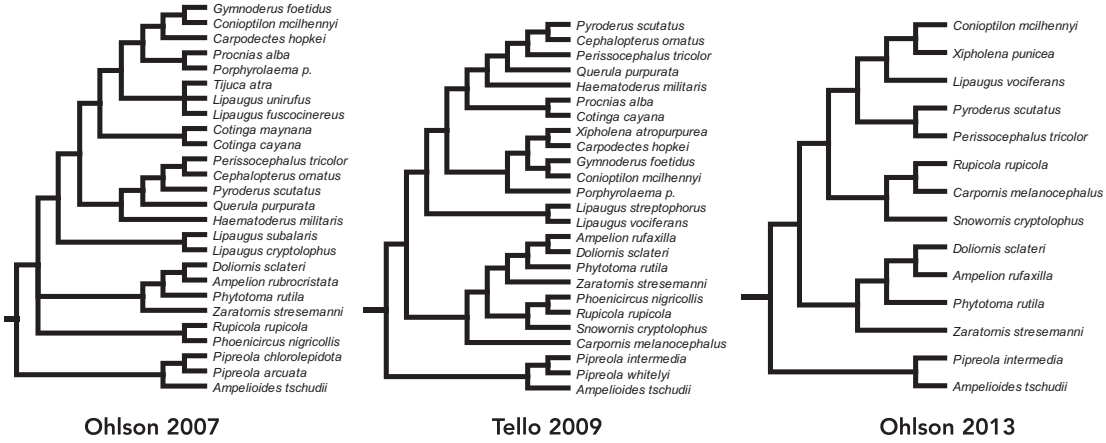

Fig. 1. Recent phylogenetic hypotheses of the cotingas. Ohlson et al. (2007) provided a well-resolved phylogeny of 26 cotinga species in 22 genera based on ~2100 base pairs of nuclear and mitochondrial DNA. Tello et al. (2009) analyzed ~4000 bases of the nuclear RAG-1 and RAG-2 genes for a slightly different sample of 25 cotinga species in 23 cotinga genera. Later, Ohlson et al. (2013) analyzed three introns and two exons (~6300 bp) across 14 cotinga species (14 genera).

highly split – an average of only 2.6 species per genus – as a consequence of taxonomic splits that reflect extreme diversity in secondary sexual traits.

2. Materials and methods

2.1. Taxon and character sampling

We sampled frozen or preserved tissue samples of 63 specimens of 49 different cotinga species (Table 1). Although we had no tissue for the species, sequences for two nuclear and one mitochondrial genes from this species were available for *Tijuca atra* through GenBank (Ohlson et al., 2007). An additional 12 species were represented by 21 toepad samples from museum study skins (collected 1926–1970). In order to assess geographic variation within some cotinga species, multiple populations were sampled and analyzed for 11 different species (Table 1).

Outgroups include multiple representatives from all major clades of the superfamily Tyranni, three members of the tracheophone Furnarii, and three Old World suboscines. We included four species each of manakins (Pipridae), tyrant flycatchers (Tyrannidae), tityrids (Tityridae), other Tyranni with unresolved relationships to tyrannids (*Oxyruncus cristatus*, *Piprites chloris*, *P. pileatus*, and *Calyptura cristata*), an antbird (Formicariidae), an ovenbird and a woodcreeper (Furnariidae) (Table 1).

We collected new DNA sequence data for four loci—two mitochondrial genes and two nuclear introns. The nuclear introns included myoglobin intron-2 (MYO) and glyceraldehyde-3-phosphate dehydrogenase intron-11 (G3PDH). The mitochondrial loci included cytochrome B (CYTB) and NADH dehydrogenase subunit 2 (ND2). Sequences of target loci that were already available from prior studies were downloaded from GenBank, as well as sequences of two protein coding nuclear loci, (the recombination activating genes (RAG) 1 and 2), for 25 ingroup species and 16 outgroup species which were produced by Tello et al. (2009). In most cases, these supplemental data were from the same individuals as in our study, or were from other individuals in the same population. See the Supplemental Appendix for details regarding PCR, DNA extraction and sequencing methods.

2.2. Tree inference strategies and genetic distance metrics

We explored our dataset with a three-pronged approach. For Bayesian species tree inference, we used the *BEAST multispecies coalescent method implemented in BEAST 1.7.5 (Heled and Drummond, 2010; Drummond et al., 2012). For phylogenetic analysis of the concatenated super-matrix, we used MrBayes 3.2.1 (Ronquist et al., 2012) and RAxML 7.4.4 (Stamatakis, 2006b; Stamatakis et al., 2008) to perform Bayesian and Maximum Likelihood tree inference. We also used MrBayes to infer gene trees for individual loci. For each analysis, we compared and ranked three partitioning schemes. For all phylogenetic reconstructions, we constrained the monophyly of New World suboscines and rooted trees with the Old World suboscines. With the exception of RAxML maximum likelihood analyses, all computations were carried out on the Omega Linux cluster at Yale West Campus.

To explore empirical variation between and among species and genera, we computed uncorrected *p*-distance matrices for each locus in MEGA 5.1 (Kumar et al., 2008). We also calculated net distances between genera using the formula dA = dXY – ((dX + dY)/2), where, dXY is the average distance between groups X and Y, and dX and dY are the mean within-group distances (Kumar et al., 2008). These data are discussed in the Supplementary Appendix.

2.3. Partitioning scheme and evolutionary model selection

Recent empirical and theoretical studies have demonstrated that the choice of molecular data partitions can have a pronounced effect on the inference of topology and relative divergence times (McGuire et al., 2007; Li et al., 2008; Poux et al., 2008; Papadopoulou et al., 2009; Ward et al., 2010; Leavitt et al., 2013; Powell et al., 2013; Wu et al., 2013). An inappropriate partitioning strategy can also lead to misleading support estimates (Brown and Lemmon, 2007).

To try to control for these issues, we used PartitionFinder v1.01 (Lanfear et al., 2012), which uses several statistical criteria to evaluate and rank alternative partitioning strategies while simultaneously performing nucleotide substitution model selection for each partition. Thus, subsequent usage of the phrase, "partitioning scheme" will refer to both the particular groupings of data partitions for a given dataset, and the best-fit nucleotide substitution models applied to those groupings.

Our general approach was to use PartitionFinder to choose an "optimal" partitioning scheme from a set of *a priori* schemes according to the Bayesian information criterion, or BIC (Schwarz, 1978). The BIC is defined as $-2\ell + K \log n$, where ℓ is the maximized log likelihood of the model, K is the number of estimable parameters, and n is the number of sites in the alignment. The

Table 1
Taxon sample list. Table of all individuals included in this study. Specimen types: T, tissue; S, skin; G, GenBank. GenBank accession numbers are reported in the Supplemental Appendix.

*BEAST species definition	Type	Institution	Institution #; Tissue #	Country	State
Ampelioides tschudii-Peru	T	LSUMZ	–; 5457	Peru	San Martin
Ampelioides tschudii-Ecuador	T	ANSP	–; 18542	Ecuador	Azuay
Ampelioides tschudii-Ecuador	T	ANSP	184088; 18564	Ecuador	Azuay
Pipreola chlorolepidota	T	LSUMZ	–; 5435	Peru	San Martin
Pipreola frontalis	T	LSUMZ	–; 5559	Peru	San Martin
Pipreola whitelyi	T	AMNH	12041; –	Venezuela	Bolivar
Pipreola lubomirskii-Peru	T	LSUMZ	170033; 32720	Peru	Cajamarca
Pipreola lubomirskii-Ecuador	T	ANSP	186238; 19778	Ecuador	Zamora Chinchipe
Pipreola jucunda	T	ANSP	–; 15820	Ecuador	Carchi
Pipreola pulchra	T	LSUMZ	–; 1625	Peru	Pasco
Pipreola arcuata	T	LSUMZ	–; 7654	Peru	Huanuco
Pipreola intermedia	T	LSUMZ	–; 574	Peru	Puno
Pipreola riefferii-Peru	T	LSUMZ	–; 297	Peru	Cajamarca
Pipreola riefferii-Venezuela	T	COP	77717; –	Venezuela	Aragua
Snowornis subalaris	T	ANSP	185671; 19464	Ecuador	Napo
Snowornis cryptolophus	T	ANSP	–; 19141	Ecuador	Zamora-Chinchipe
Carpornis cucullatus	S	LACM	28580, 27611, 28581; –	Brazil	Sao Paulo
Carpornis melanocephalus	T	LSUMZ	–; 35583	Brazil	Bahia
Rupicola peruviana	T	LSUMZ	–; 19004	Houston Zoo	–
Rupicola rupicola	T	AMNH	8790; –	Venezuela	Amazonas
Phoenicircus carnifex	T	LSUMZ	–; 20173	Brazil	Amazonas
Phoenicircus nigricollis	T	LSUMZ	–; 2898	Peru	Loreto
Zaratornis stresemanni	T	LSUMZ	–; 2074	Peru	Lima
Phytotoma rara	T	KUNHM	–; 11748	Argentina	Rio Negro
Phytotoma raimondii	T	LSUMZ	–; 451	Peru	Lambayeque
Phytotoma rutila	T	LSUMZ	–; 1211	Bolivia	La Paz
Phibalura flavirostris	T	CBF	–; 4246-7	Bolivia	Apolo
Phibalura flavirostris	S	LACM	45462; –	Brazil	Goias
Phibalura flavirostris	S	LACM	45432; –	Brazil	Goias
Doliornis sclateri	T	LSUMZ	–; 3562	Peru	Huanuco
Doliornis remseni	T	ANSP	185684; 19525	Ecuador	Zamora Chinchipe
Ampelion rubrocristatus	T	LSUMZ	–; 7664	Peru	Huanuco Department
Ampelion rufaxilla	T	LSUMZ	–; 1673	Peru	Pasco Department
Haematoderus militaris	T	KUNHM	–; 1348	Guyana	Kurupukari
Querula purpurata	T	LSUMZ	–; 2785	Peru	Loreto
Pyroderus scutatus-Paraguay	T	KU	88386; 77	Paraguay	Concepcion
Pyroderus scutatus-Peru	T	LSUMZ	–; 8137	Peru	Pasco
Cephalopterus glabricollis	T	USNM	–; B01560	Panama	Chiriqui
Cephalopterus penduliger	T	LSUMZ	–; 11737	Ecuador	Esmeraldas
Cephalopterus ornatus	T	LSUMZ	–; 12300	Bolivia	Santa Cruz Department
Perissocephalus tricolor	T	AMNH	11946; –	Venezuela	Bolivar
Lipaugus unirufus	T	ANSP	–; 17370	Ecuador	Esmeraldas
Lipaugus lanioides	S	YPM	80714; –	Brazil	Sao Paulo
Lipaugus vociferans-Bolivia	T	LSUMZ	–; 12598	Bolivia	Santa Cruz
Lipaugus vociferans-Venezuela	T	AMNH	11892; –	Venezuela	Bolivar
Lipaugus streptophorus	T	AMNH	11995; –	Venezuela	Bolivar
Lipaugus fuscocinereus	T	ANSP	185672; 19589	Ecuador	Zamora-Chinchipe
Lipaugus uropygialis-Peru	S	LSUMZ	98424; 25308	Peru	Puno
Lipaugus uropygialis-Peru	S	LSUMZ	98425; 25309	Peru	Puno
Lipaugus uropygialis-Bolivia	S	ANSP	–; 120115	Bolivia	La Paz
Tijuca atra	G	ZMUC	128821; –	Brazil	–
Procnias albus	T	KUNHM	–; 1244	Guyana	Kurupukari
Procnias albus	T	AMNH	–; 12002	Venezuela	Bolivar
Procnias albus	S	MPEG	–; 37214	Brazil	Para
Procnias tricarunculata	T	UWBM	–; 56120	Nicaragua	Matagalpa
Procnias tricarunculata	T	ANSP	187540, 187541; 20416, 20431	Panama	Veraguas
Procnias nudicollis	T	KUNHM	–; 1224	Paraguay	Concepcion
Procnias averano	S	ANSP	105021; –	Trinidad	–
Procnias averano	S	MPEG	–; 40911	Brazil	Maranhão
Procnias averano	S	MPEG	–; 40912	Brazil	Maranhão
Procnias averano	S	MPEG	–; 40913	Brazil	Maranhão
Procnias averano	S	ANSP	105021; –	Trinidad	Caura
Procnias averano	S	AMNH	–; 468475	Trinidad	Malajo forest
Cotinga maynana	T	ANSP	181680; 16580	Ecuador	Morona-Santiago
Cotinga maynana	T	LSUMZ	–; 4762	Peru	Loreto
Cotinga maynana	T	LSUMZ	–; 42921	Peru	Loreto
Cotinga cayana	T	FMNH	–; 390011	Brazil	Rondonia
Cotinga cayana	T	LSUMZ	–; 4977	Peru	Loreto
Cotinga amabilis	S	KUNHM	104761; –	Mexico	Veracruz
Cotinga amabilis	S	KUNHM	104762; –	Mexico	Veracruz
Cotinga nattererii	T	LSUMZ	–; 28771	Panama	Colon
Cotinga ridgwayi	S	AMNH	706142; –	Costa Rica	–
Cotinga maculata	S	LACM	66184; –	Brazil	–

(*continued on next page*)

Table 1 (*continued*)

*BEAST species definition	Type	Institution	Institution #; Tissue #	Country	State
Cotinga cotinga	T	ANSP	187801; 21444	Guyana	Upper Takutu-Upper Essequibo
Cotinga cotinga	T	ANSP	187799; 21918	Guyana	Potaro-Siparuni
Porphyrolaema porphyrolaema	T	LSUMZ	–; 6989	Peru	Loreto
Porphyrolaema porphyrolaema	T	ANSP	183371; 18193	Ecuador	Sucumbios
Conioptilon mcilhennyi	T	KU	–; 1416	Peru	Madre de Dios
Gymnoderus foetidus	T	LSUMZ	–; 9586	Bolivia	Pando
Xipholena punicea	T	LSUMZ	–; 20833	Houston Zoo	-
Xipholena lamellipennis	S	KUNHM	52657; –	Brazil	Maranhão
Xipholena atropurpurea	T	FMNH	–; 427187	Brazil	Alagoas
Carpodectes hopkei	T	ANSP	–; 17352	Ecuador	Esmeraldas
Carpodectes antoniae	S	YPM	56777; –	Costa Rica	Puntarenas
Carpodectes nitidus	S	LSUMZ	75501; 25310	Panama	Bocas del Toro
Outgroups	Type	Institution	Institution#; Tissue #	Country	State
Chloropipo unicolor	T	AMNH	11988; –	Venezuela	Bolivar
Manacus manacus	T	LSUMZ	–; 8913	Bolivia	Pando
Lepidothrix suavissima	T	AMNH	12036; –	Venezuela	Bolivar
Pipra cornuta	T	AMNH	–; 11877	Venezuela	Bolivar
Schiffornis virescens	G	NRM	937315; –	Paraguay	–
Laniisoma elegans	T	ANSP	181681; 16543	Ecuador	Morona-Santiago
Iodopleura fusca	T	ANSP	187808; 21600	Guyana	Potaro-Siparuni
Pachyramphus polychopterus	T	YPM	–; 1015	Uruguay	Artigas
Tityra inquisitor	T	LSUMZ	–; 18568	Bolivia	Santa Cruz Department
Hirundinea ferruginea	T	YPM	–; 1183	Uruguay	Cerro Largo
Euscarthmus meloryphus	T	YPM	–; 1044	Uruguay	Artigas
Elaenia parvirostris	T	YPM	–; 978	Uruguay	Artigas
Tyrannus forficatus	T	KU	–; 87603	USA	Kansas
Oxyruncus cristatus	T	KUNHM	–; 220	Paraguay	Caazapa
Piprites chloris	T	KUNHM	–; 329	Paraguay	–
Piprites pileata	G	ZMUC	128817; –	Brazil	–
Calyptura cristata	G	ZMUC	379; –	Brazil	Rio de Janerio
Thamnophilus caerulescens	T	YPM	–; 1016	Uruguay	Artigas
Lochmias nematura	T	YPM	–; 1141	Uruguay	Cerro Largo
Lepidocolaptes angustirostris	T	YPM	–; 1011	Uruguay	Artigas
Pitta baudi	T	ANSP	–; 16224	East Malaysia	Sabah
Smithornis rufolateralis	T	YPM	–; 451	Equatorial Guinea	–
Philepitta castanea	G	ZMUC	S458; –	Madagascar	–

BIC penalizes model complexity for increasing the number of parameters and the sample size. In contrast, the popular Akaike information criterion, or AIC ($-2\ell + 2K$) (Akaike, 1974), accounts only for the number of model parameters, and tends to favor models that are more complex than those selected by the BIC (Posada and Buckley, 2004). Simulation studies also support the use of the BIC over the AIC for substitution model selection (Luo et al., 2010).

2.4. Species tree and gene tree inference

For species tree inference, we first used PartitionFinder to evaluate partitioning schemes for each locus separately. For protein coding loci, we compared three commonly tested schemes: (S1) codon positions 1, 2, and 3 together; (S2) positions 1 and 2 together and position 3 separately; (S3) all codon positions separate. We then estimated a species tree with *BEAST, using the partitioning scheme with the lowest BIC score (best model) for each locus. In order to test the sensitivity of the inferred topology, we also estimated a species tree with alternative schemes.

To allow each locus to evolve along independent topologies, the trees for nuclear loci were unlinked. We applied a lognormal relaxed clock to each locus, and selected the default Yule Process (pure birth) as the species tree prior to minimize the dimensionality of the analysis. Because no reliable biogeographic or fossil ingroup calibrations are available for all subocine passerines, we calibrated the evolutionary rates of five of the six loci with previously published rates from other studies of passerine birds (Supplementary Table 6). We assumed a normal prior distribution for each rate calibration, and applied the conditional reference prior to the remaining un-calibrated locus (RAG-2) for which no explicit priors were available (Ferreira and Suchard, 2008). We ran six independent analyses for 6.5×10^8 generations, sampling every 1.0×10^5 generations, which gave us 6.5×10^3 trees per simulation (run). After discarding the first 1.5×10^3 trees per run (~23%), we combined the output files for each set of six analyses and summarized the maximum clade credibility (MCC) tree with median node heights across the final posterior distribution of 3.0×10^4 trees.

We inferred individual gene trees in MrBayes using the partitioning schemes with the best BIC score as selected by PartitionFinder (Supplementary Table 5). We allowed each partition to evolve under its own model of evolution in MrBayes by unlinking all parameters across data partitions (using the commands: unlink shape = (all), pinvar = (all), statefreq = (all), revmat = (all)). We also allowed all partitions to evolve under different evolutionary rates by setting ratepr = variable. For each gene tree, we summarized four Metropolis-coupled Markov chain Monte Carlo analyses (MCMCMC), each with four incrementally heated chains. Instead of specifying an upper limit to the chain length, we used the automatic stopping criterion built into MrBayes (stopval = 0.01), and summarized 50% majority rule consensus trees after discarding the first 25% of the sampled trees as burn in. Individual gene trees as estimated by MrBayes are reported as Supplemental Figs. 3–8.

2.5. Analyses of concatenated loci

For analyses under the assumption of among gene-tree concordance, we considered two *a priori* partitioning schemes (C1, C2), and one scheme (C3), which was heuristically chosen by PartitionFinder's "greedy" algorithm to optimize the groupings of the 12 codon and 2 intron partitions. Scheme C1 analyzed each of the six loci under their own models (partitions by locus). In contrast,

scheme C2 represented the "maximally" partitioned dataset, with 14 partitions.

For analysis of the concatenated dataset in MrBayes, we applied the settings described in the previous section for individual loci to allow partitions to evolve under their own models and rates. After testing with default mixing settings, we decreased the temp parameter from 0.1 to 0.025 to increase the acceptance rates for swaps between different chains of the analysis. All other parameters and priors were left at their default settings. For each partitioning scheme, we ran two independent analyses of 1.0×10^8 generations with four incrementally heated chains, sampled every 1.0×10^4 generations. This gave us a final distribution of 1.0×10^4 trees for each analysis, from which we generated a 50% majority rule consensus tree after discarding the first 25% of the sampled trees as burn in.

For maximum likelihood analysis of the concatenated dataset, we used the RAxML-HPC2 on XSEDE (Stamatakis, 2006b; Stamatakis et al., 2008) application through the CIPRES Science Gateway (Miller et al., 2010) to compute 1000 rapid bootstrap replicates using partitioning schemes C1–C3. We selected the default option to use the GTRCAT model for the bootstrapping phase and the GTRGAMMA model for the final tree inference (Stamatakis, 2006a). Finally, we summarized bootstrap support values on the best scoring ML tree.

2.6. Assessing convergence of Bayesian analyses

For Bayesian inference, including concatenated, individual locus, and species tree approaches, we examined the output log files by plotting log-likelihood values against the number of generations in the MCMC Trace Analysis Tool v1.5, "Tracer," to assess whether of not the MCMC analysis had run long enough (Rambaut and Drummond, 2009). We also used the online tool AWTY ("Are We There Yet?")," to graphically assess clade stability (Nylander et al., 2008). Using Tracer, we also ensured that the trace statistics of replicate analyses had converged on the same posterior distributions and that the effective sample sizes for all statistics were greater than 200 (most were greater than 1000). Where appropriate, we used the 'sump' command in MrBayes to check that the potential scale reduction factors (Gelman and Rubin, 1992) were close to one, and that the average standard deviation of split frequencies (Ronquist et al., 2012) was close to zero.

2.7. Evolution of breeding system and sexual dimorphism in color

Breeding systems and plumage color dimorphism were coded as binary traits (Monogamous = 0, Polygynous = 1; Monomorphic = 0, Dimorphic = 1). We obtained data on cotinga breeding behavior and sexual dimorphism from a recent comprehensive literature review (Kirwan and Green, 2012) and other recent publications (del Hoyo et al., 2004; Avalos, 2011; Belmonte-Lopes et al., 2011). There are scientific studies of breeding biology for some cotinga species; for many species however, there are only scattered observations or no information at all. For poorly known species, observations of female only nest attendance (e.g. *Snowornis cryptolophus*), or male lek display behavior were treated as evidence of polygyny. For some species, breeding systems were inferred from closely related congeners: e.g. all *Carpodectes* were presumed to be polygynous based on their male display behavior and observation of female-only nest attendance in *C. nitidus*. Six of ten species of *Pipreola* have undescribed nests or breeding systems, but all four known species with data have monogamous, biparental care (Kirwan and Green, 2012).

The sister group to the cotingas is a very diverse clade of mostly monogamous tyrannids and tityrids (Ohlson et al., 2013), so by outgroup comparison monogamy was assumed to be primitive to the cotinga clade. Because polygynous species were over-represented in our original outgroup sample, we pruned all outgroups for ancestral state reconstructions. Additionally, we pruned biogeographic replicates when appropriate.

Sexual dimorphism was coded from visual inspection of study skins from the collections of the Yale Peabody Museum of Natural History and the American Museum of Natural History, which includes all the cotinga species of analyzed. Species were coded as sexually dimorphic if any plumage patches were diagnosably distinct in color or brightness between the sexes. Because cotingas have four color-cones, including a violet cone with broad sensitivity into the near ultraviolet, they perceive an additional ultraviolet dimension to color diversity (Ödeen and Håstad, 2003; Stoddard and Prum, 2008). Therefore, our analysis based on human visual sensitivity is conservative with respect to possible sexual dimorphism in cotinga coloration.

To reconstruct the evolution of cotinga breeding biology across the MCC species tree, we followed Wiens et al. (2011) and used a maximum likelihood strategy in Mesquite 2.75 (Maddison and Maddison, 2011). For both characters, we compared the fit of a one-parameter (equal transition rates) Markov *k*-state model (Lewis, 2001), and a two-parameter (unequal transition rates) asymmetrical Markov *k*-state model (Pagel, 1997; Mooers and Schluter, 1999), and assumed equilibrium root state frequencies. For stand-alone reconstructions, we used likelihood ratio tests and information criteria to discriminate between these two models. In order to account for phylogenetic uncertainty in branch lengths and tree topology, we examined models of trait evolution across the distribution of 3.0×10^4 post-burn-in trees from our Bayesian species tree analyses, and report the mean and 95% confidence intervals of likelihood scores and *p*-values. Finally, we report preferred reconstructions of trait evolution mapped onto the species tree topology.

To examine the potential co-evolutionary relationship between breeding system and sexual dimorphism, we used Pagel's (1994) correlation test implemented in Mesquite 2.75 (Maddison and Maddison, 2011). This method tests the independent evolution of two binary characters by fitting two models of evolution to the data and the phylogeny with maximum likelihood; one in which transition rates in one character evolve independently of the state of the other (H_o – 4 parameter), and a second in which the transition rates of each character are allowed to depend on the state of the other (H_1 – 8 parameter). To calculate statistical significance, we compared the log-likelihoods derived from 1000 Monte Carlo simulations (with 100 likelihood search iterations each) of the independent and dependent models. As described above, we also examined how topological variation across the posterior distribution of trees affected this test's statistical significance by comparing the log-likelihoods derived from 100 Monte Carlo simulations (with 10 likelihood search iterations each) of the independent and dependent models, calculated across a random sample of 10,000 post-burn-in trees.

3. Results

3.1. Data partitioning

For our species tree analysis, partitioning schemes were evaluated for each locus separately; PartitionFinder indicated that the maximally partitioned scheme S3 (with each codon position on different partitions) was significantly preferred for all protein-coding loci with the exception of RAG2 (ND2, $\Delta BIC_{S2-S3} = 133$; CYTB, $\Delta BIC_{S2-S3} = 94$; RAG1, $\Delta BIC_{S2-S3} = 22$). For RAG2, the intermediately partitioned scheme S2 (with the first two codon positions grouped together and the third separately) was preferred (RAG2,

ΔBIC_{S1-S2} = 157). A ΔBIC of 10 units or more is considered to represent a large improvement in model fit (Robert Lanfear, *personal communication*). Here, ΔBIC refers to the difference in model fit between the preferred scheme and the next best scheme.

In comparing partition schemes for the concatenated analysis, scheme C1 (minimally partitioned) and C2 (maximally partitioned), PartitionFinder indicated scheme C2 was significantly preferred (ΔBIC_{C1-C2} = 3370). Using PartitionFinder's "greedy" search algorithm, we identified a novel partitioning scheme (C3; ΔBIC_{C2-C3} = 179) that was further preferred overall, and was composed of seven data partitions: (Partitions 1–3) The first, second, and third codon positions of ND2 and CYTB were each grouped together to form three data partitions, (Partition 4) the first codon positions of RAG-1 and RAG-2, (Partition 5) the second codon positions of RAG-1 and RAG-2, (Partition 6) the third codon positions of RAG-1 and RAG-2 and the MYO intron, (Partition 7) the G3PDH intron. Detailed results from our tests of alternative partitioning schemes are summarized in Supplemental Tables 3–5.

3.2. Sequence characteristics and distance matrices

Newly generated sequence data are deposited in GenBank (Accession Nos. KJ810194–KJ810513). Final alignment sizes were: MYO, 790 bp; G3PDH, 440 bp; CYTB, 1143 bp; ND2, 1041 bp; RAG-1, 2871 bp; and RAG-2, 1152 bp. The final concatenated alignment length was 7437 bp. Post-burn-in data characteristics and estimated substitution model parameters are listed in Supplemental Table 2. The ranges of pairwise uncorrected sequence divergences for all loci and ingroup (cotingas) taxa are: ND2 (0.1–27%), CYTB (0.3–21.1%), G3PDH (0.0–11.1%), MYO (0.1–6.4%), RAG1 (0.2–3%), RAG2 (0.5–4%). Average *p*-distances for all pairwise comparisons of cotingas are reported in Supplementary Table 9.

3.3. Species tree topology

The monophyly of the cotinga clade was supported with a posterior probability of one. As in some previous studies, the cotingas were found to be composed of five monophyletic clades that are the successive sister-groups to the rest of the family (Figs. 2 and 3).

Our analysis reconstructs the fruiteaters as the sister group to all other cotingas. Within the fruiteaters, the monotypic *Ampelioides* is resolved as the sister group to the diverse genus *Pipreola*. Although not currently recognized as separate subspecies, the two east Andean populations of *Ampelioides tschudii* sampled from Ecuador and Peru exhibited an average genetic distance of 1.2%, indicating underestimated diversity within this quite ancient lineage. Within *Pipreola*, a clade including the two smallest-bodied species—*P. chlorolepidota* and *P. frontalis*—is the sister group to all other *Pipreola*. Then, *P. whitelyi*, from the isolated tepuis of southern Venezuela and Guyana, is the sister group to a lineage consisting of two well-resolved Andean clades. The first of these clades contains three mid-sized species, with *lubomirskii* as the sister group to the well-differentiated *jacunda,* and *pulchra*. The last clade in *Pipreola* consists of the three large species, with *arcuata* as the sister-group to *intermedia* and *riefferii*. All clades within *Pipreola* were very highly supported, except for the monophyly of the sister group to *P. whitelyi*, (posterior probability, or PP, = 0.58). *P. formosa* and *P. aureopectus* were not available for this study; however, *formosa* is likely to be a member of the *chlorolepidota-frontalis* clade, and *aureopectus* is likely to be closely related to *lubomirskii*, *jacunda,* and *pulchra* (Snow, 1982).

The next cotinga clade consists of a novel group of four genera—*Rupicola*, *Phoenicircus*, *Snowornis*, and *Carpornis* (PP = 0.78). As in previous studies, *Rupicola* and *Phoenicircus* are sister groups, and we confirm the monophyly of each genus. Their sister group is a new clade consisting of the two Andean *Snowornis* species and the two southeast Brazilian *Carpornis* species (PP = 0.79). Our tree also confirms that *Snowornis* and *Carpornis* are each monophyletic.

The third cotinga clade is the *Ampelion* group, which consists of its now traditional members – *Zaratornis*, *Phytotoma*, *Doliornis*, and *Ampelion* – but with a new addition – the Swallow-tailed Cotinga, *Phibalura flavirostris*. *Zaratornis stresemanni* is the sister group to the other four genera. The three species of *Phytotoma* form the next lineage in the clade, with *rara* as the sister group to *rutila* and *raimondii*. Then, *Phibalura flavirostris* is placed as the sister group to the *Doliornis–Ampelion* clade, and each of these genera is monophyletic. All clades in this assemblage received maximal support, except for the monophyly of the *Phibalura–Doliornis–Ampelion* clade (PP = 0.56).

The fourth cotinga clade consists of the five genera of fruitcrows. The resolution of this clade matches previous studies (Ohlson et al., 2007; Tello et al., 2009), with *Haematoderus militaris*, *Querula purpurata*, and *Pyroderus scutatus* as the successive sister groups to a clade including *Cephalopterus* and *Perissocephalus*. Intriguingly, in this first test of the monophyly of the three species of *Cephalopterus* umbrellabirds, the Capuchinbird *Perissocephalus tricolor* was placed as the sister to the Amazonian Umbrellabird *C. ornatus* (PP = 0.84). This resolution seems to be driven by the increased weighting of mitochondrial genes CYT-B and ND2 in the species tree analysis; *P. tricolor* was grouped with *C. penduliger* in the MYO gene tree, and its relationships were unresolved in GP3DH. Tello et al. (2009) placed *Perissocephalus* as the sister group to a *Cephalopterus–Pyroderus* clade on the basis of RAG-1 and RAG-2.

The final major clade includes a diverse radiation traditionally recognized as the 'core' cotingas (Prum et al., 2000). We resolve the *Lipaugus* pihas, with *Tijuca atra* embedded within, as the sister group to the other core cotingas. Within *Lipaugus*, *Lipaugus unirufus*, from Central America and the Chocó, is placed as the sister group to all others. The next branching lineage consists of a southeast Brazillian clade containing *L. lanioides* and *T. atra*. Known from only a single specimen, *Tijuca condita* was not available for this study, but based on plumage and behavior, it is likely to be the sister species to *atra*. The rest of *Lipaugus* consists of two clades. One of these clades contains the broadly distributed, lowland *L. vociferans* and the Rose-collared Piha *L. streptophorus* of the tepuis of eastern Venezuela and Guyuna. Their sister group is an Andean clade including *L. fuscocinereus* and *L. uropygialis*. The recently described Chesnut-capped Piha *L. weberi*, from the north Colombian Andes, was unavailable for this analysis, but morphologically and acoustically it appears to be a member of the *fuscocinereus-uropygialis* clade (Cuervo et al., 2001, R. O. Prum, pers. obs.).

The monophyly of the sister group of the *Lipaugus–Tijuca* clade is supported with a posterior probability of 0.94. The first branch within this clade consists of the four species of the genus *Procnias*. Within *Procnias*, there are two well-supported clades, an *averano–nudicolllis* clade, and an *albus–tricarunculata* clade (All PP = 1.0).

The next successive clade consists of the monophyletic genus *Cotinga*, in which *maynana* and *cayana* are successive sister groups to the rest of the genus. Then, *amabilis* is placed as the sister group to two clades consisting of *nattererii* and *ridgwayi*, and *maculata* and *cotinga*. These relationships were all well supported (PP $\geqslant$ 0.95) except for the placement of *amabilis* (PP = 0.67). This proposed relationship may be a affected by the paucity of data for some these taxa (we were only able to sequence ND2 from toe pads of *amabilis*, *nattererii,* and *maculata*).

Throughout our analyses, the most problematic ("rogue") taxon to place phylogenetically was the Plum-throated Cotinga *Porphyrolaema porphyrolaema* (see Section 3.4 below). In the species tree, *Porphyrolaema* was placed as sister group to a clade of four genera with powder down – a special type of powder producing feathers – that has been identified in previous studies (Prum et al., 2000; Ohlson et al., 2007; Tello et al., 2009). This relationship for *Porphy-*

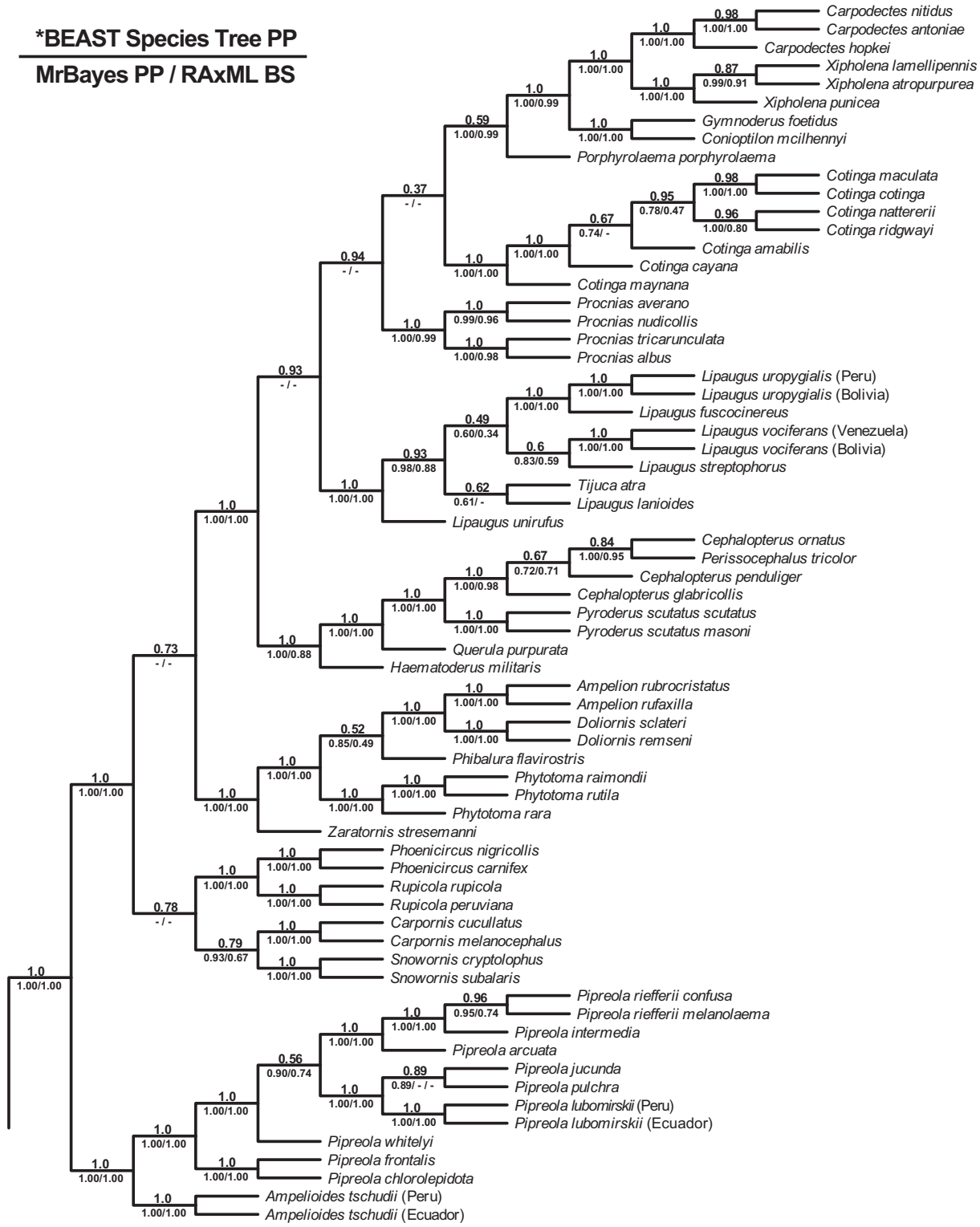

Fig. 2. *BEAST species tree topology. Numbers above branches are Bayesian posterior probabilities derived from the species tree analysis. Numbers below branches are (right) posterior probabilities derived from MrBayes, and (left) RaxML bootstrap support values. A hyphen at a particular position indicates a given node was not recovered by that method.

rolaema was supported with a posterior probability of 0.59. Within the powder down clade, as in previous studies (all PP = 1.0), *Conioptilon mcilhennyi* and *Gymnoderus foetidus* form a clade that is sister group to a clade including the monophyletic *Xipholena* and *Carpodectes*. Within *Xipholena*, *X. punicea* is the sister group to *lamellipennis* and *atropurpurea*. Within *Carpodectes*, *hopkei* is the sister group to the barely differentiated *nitidus* and *antoniae*.

3.4. Congruence with concatenated analyses

The result of the concatenated Bayesian analysis was highly congruent with the species tree analysis (91.5% topological similarity, see Supplemental Appendix), and differed only in regard to the resolution of four clades (Supplementary Fig. 2). The concatenated Bayesian analysis did not recognize the *Rupicola–Phoeni-*

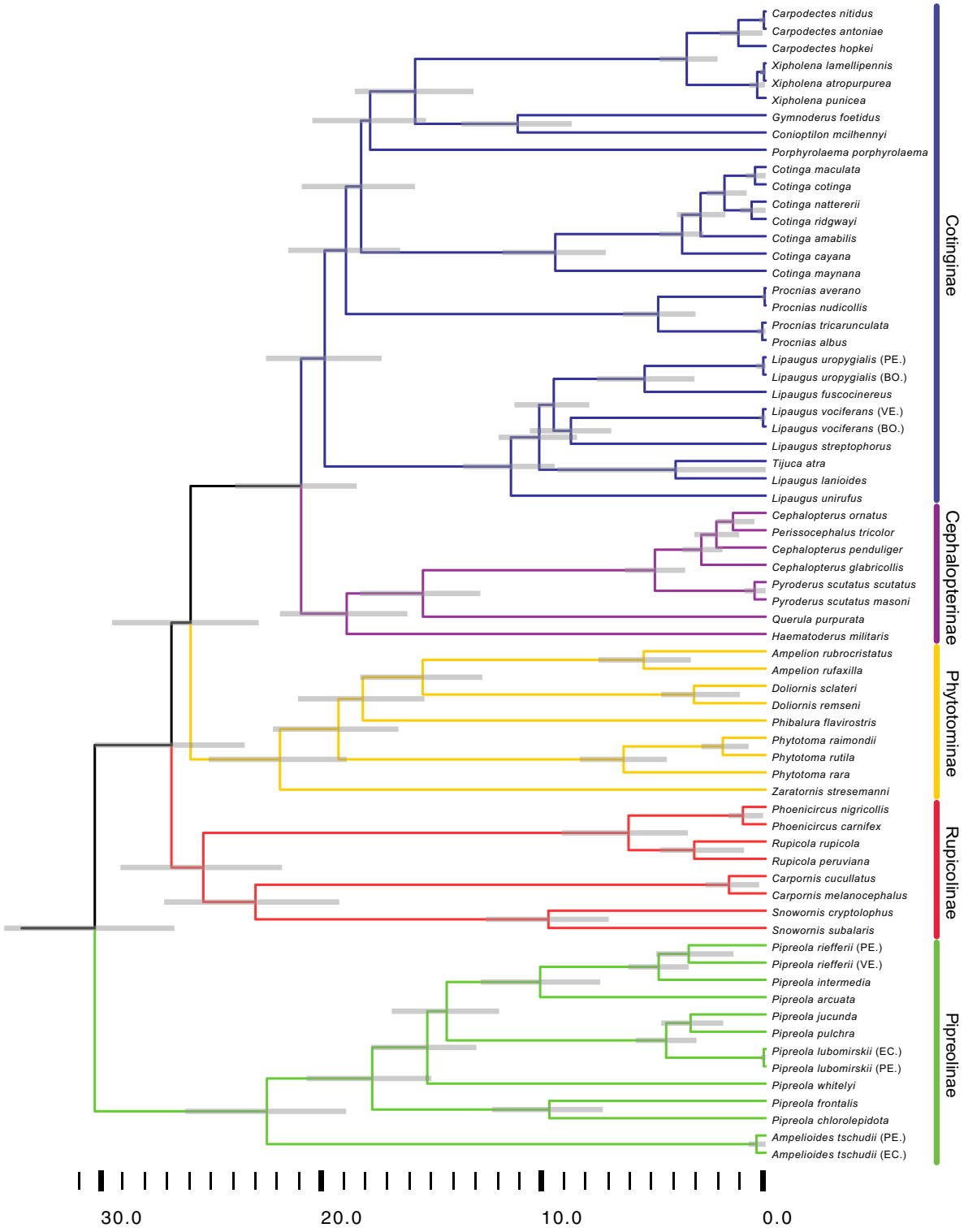

Fig. 3. Ultrametric species tree chronogram. The time scale (below) is in millions of years, and was estimated from five molecular rate calibrations from previous studies of passerine birds using lognormal relaxed clocks. Colors and vertical bars indicate our proposed subfamily classification. Horizontal node bars represent the 95% HPD (highest posterior density) estimate of node height.

circus clade and the *Snowornis–Carpornis* clade as sister groups. Rather, these clades were placed as separate, successive sister groups to the large core cotinga clade. Unlike the species tree, the concatenated Bayesian tree placed the *Ampelion* clade as more closely related to the core cotingas than the *Rupicola–Phoenicircus* and *Snowornis–Carpornis* clades. Within the core cotingas, the concatenated Bayesian tree placed the genus *Cotinga* outside the *Lipaugus–Tijuca* clade, which was then the sister group to *Procnias*, *Porphyrolaema*, and the power down clade. Lastly, within the genus *Pipreola*, the concatenated Bayesian trees placed *P. jucunda* as sister to *P. lubomirskii* instead of *P. pulchra*.

The results of the concatenated maximum likelihood analysis identified the same trees as the concatenated Bayesian analyses with a single difference. In the maximum likelihood tree, *Tijuca atra* was placed as the sister group to *Lipaugus* excluding *L. unirufus*, while *L. lanioides* was placed as the sister group to the Andean *fuscocinereus–uropygialis* clade.

3.5. Outgroup relationships

Our extensive sample of outgroup taxa provided substantial resolution to the phylogenetic relationships among the suboscines, which were identical among all analyses (Supplemental Figs. 1 and 2). Within the New World subsocines, the tracheophone Furnarii were recognized as monophyletic with a *Thamnophilus* antbird as the sister to two ovenbirds– *Lochmias* and *Lepidocolaptes*. The monophyly of the Tyranni was recognized, with manakins as the sister group to the rest of the Tyranni. The sister group to the cotingas is a diverse clade consisting of the tityrids (Tityridae), *Oxyruncus, Piprites*, *Calyptura*, and the tyrant flycatchers (*Tyrannidae*). The proposed relationships were mostly congruent with the recent broad and better sampled studies of Tello et al. (2009) and Ohlson et al. (2013).

3.6. Divergence time estimations and evolutionary rates

Applying calibrations from previous literature, our species tree analysis estimated the age of the split between New World and Old World suboscines at 62.7 MY (95% highest posterior density (HPD): 54.4–71.6 MY), and the age of Cotingidae at 31.2 MY (95% HPD: 26.6–34.3 MY). The updated estimates of substitution rates for the lognormal relaxed clocks per locus are listed in Supplementary Table 7. When viewed in the Tracer software, the ucld.stdev frequency histograms for ND2, RAG1, and RAG2 were abutting against zero, which indicates that we cannot reject the hypothesis of a strict clock for these loci (Drummond et al., 2007). MYO, G3PDH, and CYTB, however, do exhibit a small amount of significant branch rate heterogeneity. ND2 exhibited the least ($\sigma = 0.11$), while G3PDH exhibited the most ($\sigma = 0.54$). As expected, the average estimated mtDNA substitution rate (2.283%/MY) was significantly higher (~16×) than the average estimated nuclear rate (0.15%/MY).

3.7. Evolution of cotinga breeding system and plumage dimorphism

All analyses supported a symmetrical rate of breeding system and sexual plumage dimorphism evolution (i.e., equal rates of evolutionary gains or losses). For reconstructions of breeding system evolution, a likelihood ratio test and AIC selection criterion failed to discriminate between symmetrical one-rate ($-\log l = 17.1, \mathrm{AIC} = 36.23$) and asymmetrical two-rate ($-\log l = 16.6, \mathrm{AIC} = 37.17$) models of character evolution ($\chi^2_1 = 1.064, p = 0.23, \Delta\mathrm{AIC} = 0.94$). Likewise, reconstructions of sexual dimorphism evolution recovered similar results for symmetrical one-rate ($-\log l = 26.94, \mathrm{AIC} = 55.88$) and asymmetrical two-rate ($-\log l = 25.17, \mathrm{AIC} = 54.33$) evolutionary models ($\chi^2_1 = 3.55, p = 0.06, \Delta\mathrm{AIC} = -1.55$), all at a critical value of $\alpha = 0.05$. When examined across the posterior distribution of 3.0×10^4 trees, the, model comparisons from the MCC topology were robust to phylogenetic uncertainty (indicative of a high level of consistency across the posterior distribution of trees). Because two-rate models were never statistically preferred, we used the simpler single rate models for ancestral state reconstructions of sexual dimorphism and breeding system.

When averaged across the posterior distribution of trees, the symmetrical rate model inferred at least two origins of polygyny, and three re-gains of monogamy within the cotingas (5 steps) (Fig. 4, left). 71% of the trees in the analyzed posterior distribution predicted monogamy to be the most likely state at the root of the cotinga clade. The ancestor of the fruitcrows, pihas, and core cotinga genera was reconstructed as polygynous in 98% of trees. Within this major cotinga clade, subsequent reversals to monogamy were reconstructed in the lineages leading to *Querula purpurata* (100%) and the *Conioptilon–Gymnoderus* clade (80%). In contrast, the history of breeding system evolution in the *Rupicola–Snowornis* clade was more equivocal. There was an equivalent likelihood of a single common origin of polygyny in the most recent common ancestor of *Rupicola* and *Snowornis* with a subsequent reversal to monogamy in *Carpornis*, or two independent origins of polygyny in the *Rupicola–Phoenicircus* clade and the genus *Snowornis*.

The pattern of sexual plumage dimorphism evolution is more dynamic but less ambiguous than the pattern of breeding system evolution. The preferred hypothesis of dimorphism evolution supports a sexually dimorphic cotinga ancestor (100%), six independent derivations of sexual monomorphism, and two secondary transitions to sexual dimorphism (8 steps) (Fig 4, right). Gains of monomorphism are predicted along lineages leading to *Zaratornis* (100%), *Ampelion* (95%), *Pyroderus* (100%), *Perissocephalus*, *Lipaugus* (85%), and *Conioptilon* (100%). Within *Lipaugus*, two reversals of sexual dimorphism are predicted in *Tijuca atra* and in *L. streptophorus*.

Pagel's 1994 test of correlated character evolution between breeding system and sexual dimorphism indicated that the transition-dependent eight-parameter model was not a significantly better fit to the data than the transition-independent four-parameter model on the MCC tree ($\chi^2_4 = 1.65, p = 0.30, \Delta l = 0.83$, $\Delta\mathrm{AIC} = 6.36$), or when averaged across 10,000 post-burn in trees—average $p = 0.35$ [0.1—0.6]. Thus, breeding system and overall plumage dimorphism do not appear to be co-evolving in the cotingas, and this result appears robust to phylogenetic uncertainty.

4. Discussion

This comprehensive study of the relationships among the Neotropical cotingas establishes a strongly supported phylogenetic hypothesis for this highly diverse radiation. Our findings establish the first phylogenetic hypotheses for intrageneric relationships within the *Cotinga*, *Lipaugus*, *Pipreola*, and *Procnias* clades, and the first phylogenetic placement of the highly distinctive Swallow-tailed Cotinga *Phibalura flavirostris*.

4.1. Phylogenetic approach

This is the first estimate of the phylogeny of the cotingas or their tyrannoid outgroups using species tree approaches, which have the potential to account for the effects of both mutational and coalescent processes which affect DNA evolution (Barker et al., 2013). Because variance in coalescent processes can give rise to discordance among gene trees, analyzing discordant loci together may produce misleading phylogenetic results (Edwards et al., 2007; Kubatko and Degnan, 2007; Degnan and Rosenberg, 2009; Song et al., 2012). By estimating a species tree from a collection of gene trees that are allowed to have different topologies, species tree inference can potentially overcome some of the problems of concatenation, and may support emergent relationships that do not appear in any individually estimated gene tree (Barker et al., 2013). A recent simulation study also suggested that the *BEAST species tree algorithm is strikingly robust to missing data and terminals which only represent a single individual (Hovmöller et al., 2013).

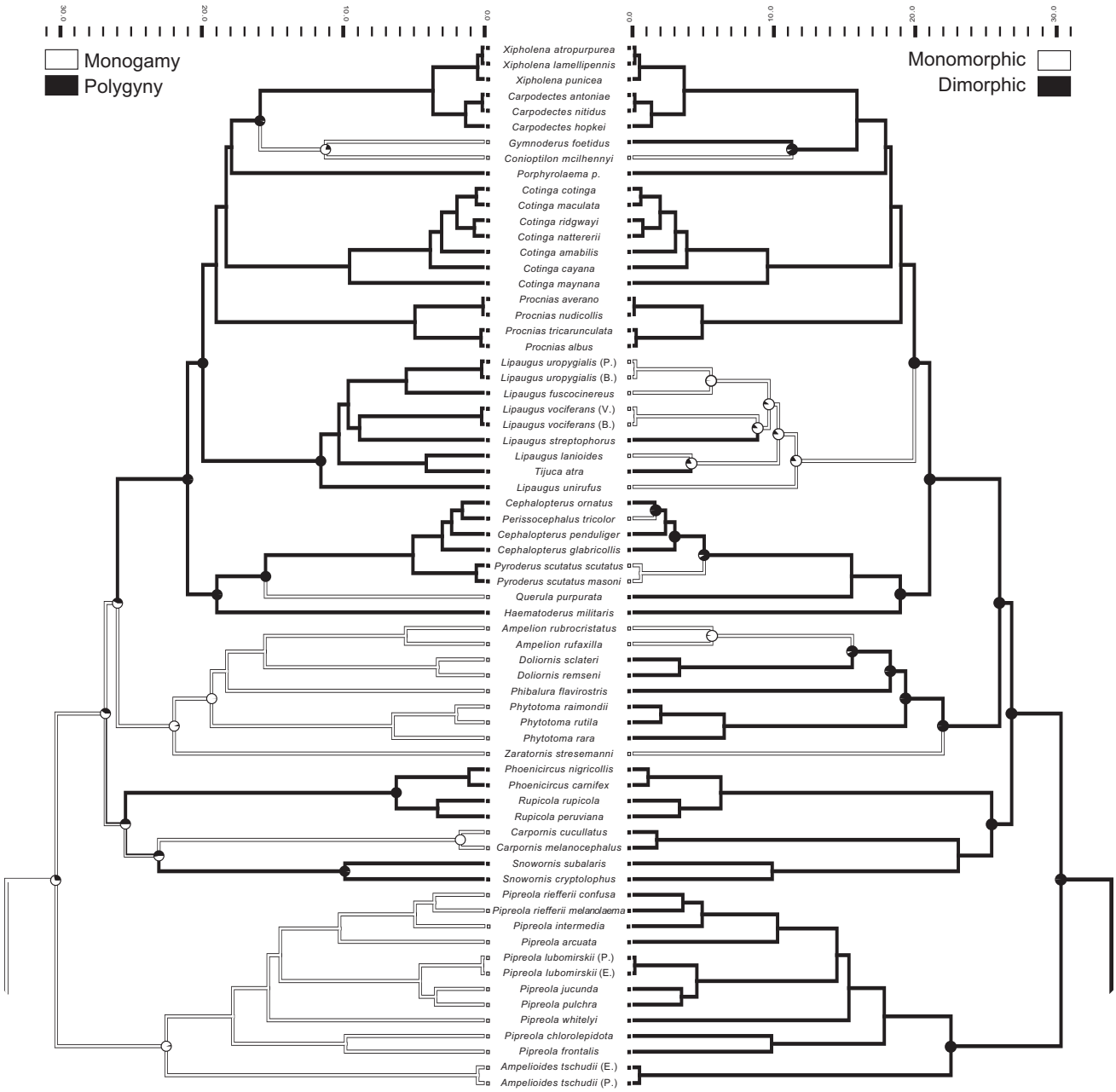

Fig. 4. Ancestral state reconstructions of cotinga breeding biology using the species tree. Left, the evolutionary history of cotinga breeding systems; right, the evolutionary history of sexual plumage dimorphism. Branch lengths are proportional to absolute time, indicated by the scale in millions of years. Branch mappings are derived from reconstructing character evolution on the single MCC topology, using symmetrical transition rate models. Pie charts indicate the character likelihood of a state for a given node, averaged across 10,000 randomly sampled post-burn in trees from the posterior distribution of the species tree analysis.

Because (1) a fair number of our samples are derived from museum specimens and contribute limited data, (2) most taxa in our study are represented by single individuals, and (3) of apparent gene-tree discordance (see Supplemental Appendix), we believe our species tree analysis (Figs. 2 and 3) should be preferred over our concatenated analyses (Supplemental Fig. 2). Thus, the application of species tree methods to the phylogeny of cotingas and their tyrannoid outgroups provides robust new support for their historical interrelationships. Our species tree was very similar to that derived from mtDNA alone (Supplemental Table 8; 97.8% similarity), which is consistent with the increased weighting given to haploid DNA in a *BEAST analysis (a smaller effective population size means mtDNA is more likely to track speciation, assuming no hybridization or interspecific gene flow).

Tree topologies varied remarkably little across tested partition schemes (not shown), but computation time varied widely. For instance, during our concatenated analyses, we noted that in comparison to typically applied schemes (C1, C2), we achieved a dramatic reduction ($\sim 10\times$) in the number of generations required to reach convergence on the same topology by utilizing the heuristically chosen scheme C3.

On the other hand, computation time was substantially increased in the species tree analyses after selecting the maximally partitioned scheme for most loci (as optimized by PartitionFinder). While topologies in our case were generally robust to the applied scheme, there is no way to evaluate whether or not the signal underlying a given phylogeny *is* robust to such methodological assumptions without testing them. Because easily implemented

approaches to evaluate alternative partitioning strategies are now available (Li et al., 2008; Lanfear et al., 2012; Wu et al., 2013), they should be included in phylogenetic pipelines, if only to offer an additional level of support for a given result.

4.2. Congruence with morphology

The monophyly of the cotinga clade can be diagnosed anatomically by the insertion of the extrinsic syringeal muscle M. tracheolateralis on the lateral A1/B1 syringeal membrane (Prum, 1990). Within the cotinga clade, there are two instances of the evolution of intrinsic syringeal musculature – in *Lipaugus* and in *Procnias*; these derived intrinsic muscles retain the plesiomorphic insertion of the M. tracheolateralis on the lateral membranes. Syringeal morphology confirms the proposed phylogenetic placement of *Phibalura*. Lanyon and Lanyon (1988) identified the derived lateral expansion of the syrinx at the membranous insertion of the M. tracheolateralis as a synapomorphy of an *Ampelion*, *Doliornis Phytotoma*, and *Zaratornis* clade. This same derived morphological character is present in the syringes of three *Phibalura flavirostris* specimens (R. O. Prum, unpubl. observ.). In contrast, no syringeal specimens are yet available to assess whether either species of *Tijuca* share the syringeal synapomorphies of the genus *Lipaugus*.

In most birds, including the tyrannids and tracheophone suboscines, the arterial supply to the hindlimb is provided by the ischiadic artery; however, in the manakins, tityrids, and most cotingas, the primary arterial supply to the hind limb is provided by the femoral artery (Garrod, 1876; Midtgård, 1982; Prum, 1990). Prum (1990) found that an eclectic group of cotinga genera – *Ampelioides*, *Pipreola*, *Rupicola*, *Phoenicircus*, *Carpornis*, and *Snowornis* – lack the derived femoral artery state found in other cotingas, and share the primitive ischiadic hindlimb arterial character state. Indeed, this unusual anatomical condition provided the first evidence that the two *Snowornis* species were unrelated to the *Lipaugus* pihas (Prum, 2001). In the context of this newly resolved molecular phylogeny, it is clear that the six cotinga genera with the primitive ischiadic artery character state consist of the members of the two basal clades of the family, indicating that there was likely a unique derivation of the derived hindlimb femoral artery condition in the most recent common ancestor of *Ampelion* and *Cotinga*. This morphological synapomorphy provides further support for this major cotinga clade, which only received moderate support in the species tree (PP = 0.73).

The morphological diversity of the cotingas provides a great opportunity for future comparative studies of anatomical evolution. Even within the dominant diet of frugivory, cotingas exhibit extensive diversity in bill size and shape, gape width, and body size. For example, a phylogeny of the four species of *Procnias* provides an opportunity to reconstruct the evolution of their particularly diverse facial skin ornaments. A sparsely feathered, "bare" throat patch first evolved in the ancestor of the *averano–nudicollis* clade. This novelty subsequently gave rise to the evolution of a green structurally colored throat in *nudicollis* (Prum and Torres, 2003), and to the proliferation of numerous, fleshy, wiggling black throat wattles in *averano*. Given the critical function of dermal melanization in the production of collagen fiber structural color in avian skin (Prum and Torres, 2003), the evolution of dermal melanization likely evolved in the ancestor of *averano* and *nudicollis* before their subsequent differentiation into their unique species morphologies. In constrast, long, muscular facial wattles characterize males of the *albus–tricarunculata* clade. The central nasal wattle located at the base of the clumen at the nasofrontal junction is found in both species. In addition, *P. tricarunculata* sports two additional rictal wattles located at the junctions of the upper and lower mandibles. The nasal wattle apparently evolved first in the common ancestor of *albus* and *tricarunculata*. Then, the novel nasal wattle was duplicated into the rictal wattles of *tricarunculata* in an unusual form of ectopic anatomical expression, or homeotic evolution.

4.3. Evolution of cotinga breeding biology

This resolved phylogeny allows us to reconstruct the evolution of sexual dimorphism and breeding system in the cotingas for the first time. The evolutionary history of breeding system diversity in cotingas is highly concordant with their phylogeny. Only five evolutionary transitions between monogamy and polygyny are required to explain the distribution of breeding systems within the 65 species in the family – either two origins of polygyny with three reversals, or three origins of polygyny with two reversals (Fig. 4, left).

The evolutionary loss of extreme display polygyny, or lekking, is rather rare in birds (Prum, 1994). Examples include the Helmeted Manakin *Antilophia galeata* (Pipridae) (Prum, 1994) and the ptarmigans (*Lagopus*, Tetraoninae) (Drovetski, 2002). The complete evolutionary loss of paternal care behavior and the associated evolutionary investment in elaborate forms of secondary sexual display may create substantial barriers to the reevolution of monogamy and biparental care (Prum, 1994). Thus, the newly documented reversals from display polygyny to monogamy in the Purple-throated Fruitcrow *Querula purpurata*, and in the last common ancestor of the Bare-necked Fruitcrow *Gymnoderus foetidus* and the Black-faced Cotinga *Conioptilon mcilhennyi* provide two examples of this rare and interesting class of evolutionary reversals. The Purple-throated Fruitcrow is notable for the further evolution of a cooperative breeding system that appears to be unique among all suboscines (Snow, 1971). In contrast, the evolution of sexual dimorphism in plumage coloration in the cotingas has been much more dynamic, but still reveals strong phylogenetic signal. Color dimorphism appears to be primitive to the clade, and has been lost five times and re-evolved twice, both instances within the lekking *Lipaugus* piha clade.

Since Darwin (1871), the increase in sexual selection through mate choice associated with polygynous breeding systems has been hypothesized to foster the evolution of sexual dimorphism in plumage coloration. However, our analysis of the coevolution of breeding system and sexual plumage dimorphism indicates that these traits are evolutionarily uncorrelated in cotingas, at least at a broad categorical scale. Further, transitions between color dimorphism and monomorphism have occurred at approximately twice (Mk1 estimated rates: 0.016/0.009) the rate at which transitions between monogamy and polygyny have occurred, which further suggests these characteristics may be evolutionarily decoupled.

The two most diverse, monogamous lineages – the fruiteaters and the *Ampelion–Zaratornis* clade–consist exclusively or predominantly of sexually dimorphic species. Furthermore, several polygynous lineages have evolutionarily lost sexual plumage dimorphism – i.e. *Pyroderus*, *Perissocephalus*, and *Lipaugus*. Interestingly, as pointed out for other lineages of birds (Irwin, 1994) the loss or acquisition of sexual dimorphism can be achieved by different kinds of evolutionary change. For example, the loss of sexual dimorphism in *Lipaugus* and *Perissocephalus* appear to be a consequence of the loss of male plumage brightness, whereas the loss of sexual dimorphism in *Pyroderus* is a consequence of the derived evolution of female plumage brightness. The few evolutionary transitions that conform to the sexual selection prediction – the gains of sexual plumage dimorphism in polygynous *Tijuca* and *Lipaugus streptophorus*, and the losses of sexual dimorphism in the monogamous *Zaratornis*, *Ampelion*, and *Conioptilon* – are not enough to establish a significant evolutionary correlation across the entire family.

Although the cotingas include some of the most extravagant examples of sexual plumage dimorphism in birds – e.g. *Cotinga* and *Rupicola* species (Fig. 5) – polygyny itself does not explain our inferred evolutionary origins of plumage dimorphism. Furthermore, the breadth of ornamental advertisements available to birds– including elaborate vocal signals – means that sexual selection may switch to elaborating different classes of ornaments within different lineages. These types of evolutionary transitions among ornament classes are expected to be more frequent if mate choice evolution proceeds by a Fisherian, Lande–Kirkpatrick mechanism rather than by an honest advertisement mechanism (Prum, 1997, 2010).

The comparative analysis of breeding biology presented here is rather conservative because it relies on human vision, and because it does not take into account the heterogeneous evolutionary changes that can produce sexual dimorphism. Future analyses

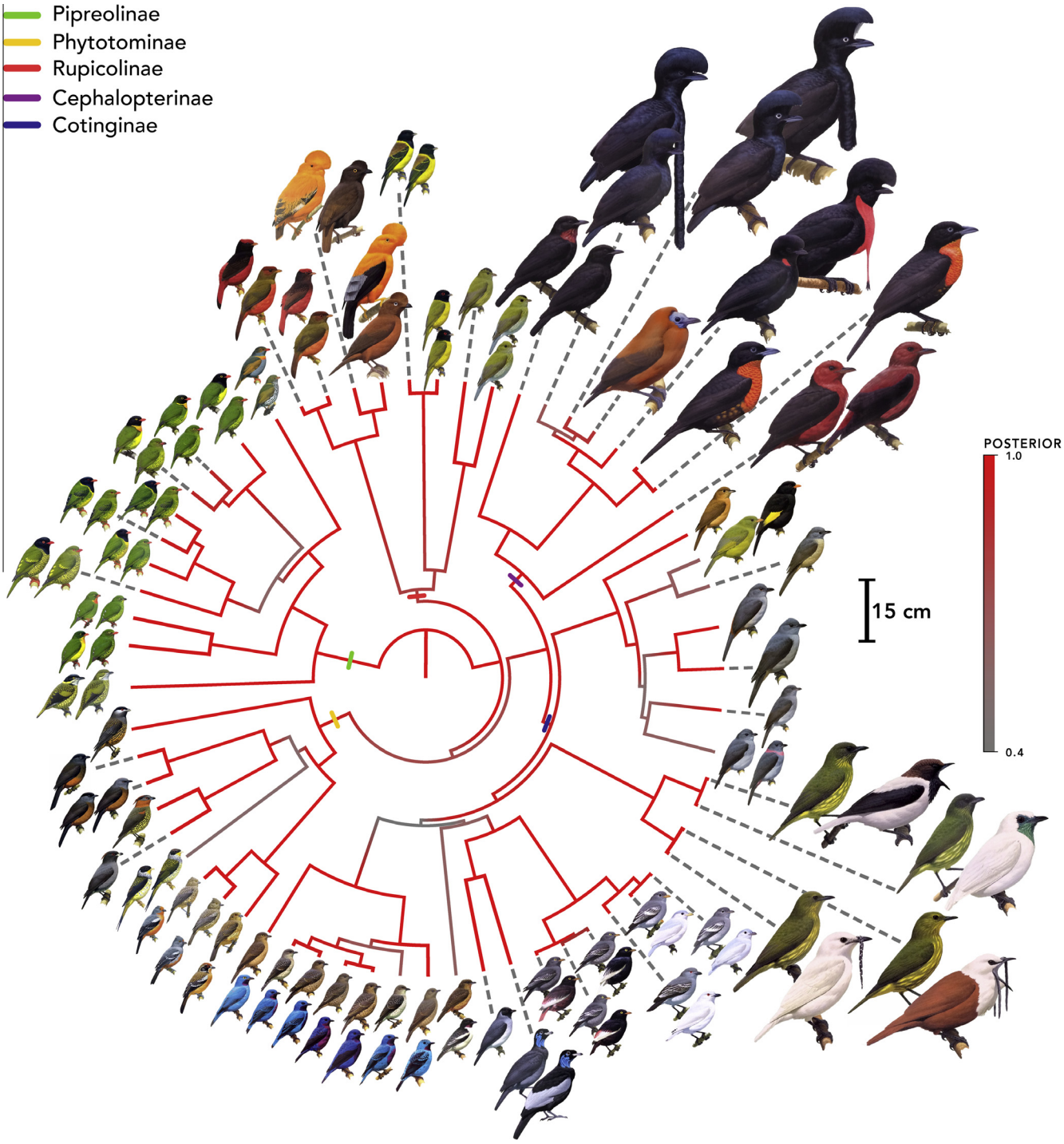

Fig. 5. Distribution of phenotypes, plumages, and size variation across the Cotingas. Illustrations are reproduced with permission from the *Handbook of the Birds of the World. Vol. 9. Cotingas to Pipits and Wagtails*, Lynx Editions 2004. Males are depicted towards the outer perimeter, while females are placed more interior. Color monomorphism is indicated by the presence of only a single illustration at a given terminal. Branches are colored according to their posterior probability, and the centimeter scale indicates relative sizes.

should employ more discriminating measures of sexual dimorphism in plumage coloration – including spectrophotometric measures of cotinga plumage reflectance and color space modeling of avian color vision (Stoddard and Prum, 2008; Prum et al., 2012) – to explore the effects of sexual selection on cotinga coloration evolution at a finer scale.

4.4. Historical biogeography

Although a full biogeographic analysis is outside the scope of this paper, this resolved species phylogeny for cotingas provides a new opportunity for observations about biogeographic history of various cotinga lineages.

Most cotinga clades show a strong pattern of lowland or montane distribution. Thus, the *Ampelioides–Pipreola*, *Snowornis–Carpornis*, and *Ampelion–Zaratornis* clades are all strongly montane or lower montane in distribution. The placement of the montane genus *Phibalura* within a largely montane clade further confirms the historical nature of this eco-biogeographic distribution. Most other cotinga clades are strongly tropical in distribution with a few notably lower montane lineages evolving from within them: i.e. *Pyroderus*, *Perissocephalus*, *Procnias*, and various *Lipaugus* and *Tijuca* species. Interestingly, the sister group to the southeast Brazilian genus *Tijuca* appears to be another southeast Brazilian endemic *Lipaugus lanioides*, indicating the existence of a radiation of pihas in the Serra do Mar area of endemism.

The evolutionary origin of the avifauna of the tepuis of southern Venezuela and the Guianas has been of particular interest in Neotropical ornithogeography (Mayr and Phelps, 1967). There are two cotinga species endemic to the tepuis. The Red-banded Fruiteater *Pipreola whitelyi* is phylogenetically embedded within a radiation of montane, Andean fruiteaters. Thus, *P. whitelyi* was likely derived from a lineage that dispersed from the Andes to the tepuis in the midst of an active evolutionary radiation within the Andes themselves. In contrast, the Rose-collared Piha, *Lipaugus streptophorus*, is the sister group to a broadly distributed Amazonian species, the Screaming Piha *L. vociferans.* It appears to be altitudinally derived from adjacent lowland populations. Thus, the phylogenetic relationships of tepui-endemic cotingas indicate that this isolated montane avifauna had complex evolutionary origins, and cannot be explained by a single generalized biogeographic mechanism.

4.5. Divergence times and diversification

Our inferred divergence estimates (Figs. 3 and 4, Supplemental Fig. 1) are generally consistent with previous studies of passerine diversification that are based on molecular rate or biogeographic calibrations (e.g. Barker et al., 2004; Ohlson et al., 2013). Nonetheless, because there are no suboscine fossils of any kind, and very few significant fossils of any endemic radiation of Neotropical birds, the estimation of divergence times of suboscine passerines and many other Neotropical clades remains challenging and highly problematic. In the absence of any ingroup fossil calibrations, we have followed the molecular rate calibrations used in previous works of passerine molecular systematics, but recalibrations of passerine diversification dates that are consistent with fossil data are clearly needed.

Recent analyses of the temporal distribution of avian crown clade fossils place the divergence dates of the major basal lineages of Neognathous birds at immediately before the Cretaceous-Tertiary boundary (Longrich et al., 2011). Further, the well documented avifaunas of Green River Formation, Wyoming (~50 mya) and the Eocene Messel Formation, Germany (~47 mya) are diverse avifaunas dominated by basal neognathes, and basal lineages of other extant orders (Clarke et al., 2005; Longrich et al., 2011; Mayr, 2013). Thus, it seems improbable our inferred age of the diversification of the the basal sub-oscine passerines at ~50MY is correct when there are few if any fossils of this age that can be confidently placed within any extant bird family of anywhere in the world. Likewise, our estimates of 25–30MY (Figs. 3 and 4, Supplemental Fig. 1) for the ages of the earliest cotinga clades seem equally improbable to us.

However, estimates of relative divergence dates can be useful in analyzing patterns of net diversification across time. In our case, the lineage accumulation curve (not shown) is mostly linear over time, with a slightly more rapid rate of lineage accumulation for the first two-thirds of the radiation. The trajectory shows neither rapid bursts of diversification or a leveling off of diversity, and is close to the prediction of a consistent species 'birth–death' process with some limited historical noise.

4.6. Species limits

Sequence data from multiple individuals of eleven species of cotingas allows us to conduct a preliminary review of their monophyly and species limits. All multiply sampled species were monophyletic with respect to the other taxa analyzed. Comparisons of toe pad data from multiple populations of three species detected no DNA sequence differences: *Lipaugus uropygialis* from Peru and Bolivia, *Phibalura flavirostris flavirostris* from Brazil and *P. f. boliviana* from Bolivia and *Procnias albus* from Venezuela, Guyana, and Brazil. Three other pairs of intraspecific comparisons showed differentiation of less than 0.50%, including *Porphyrolaema porphyrolaema* from eastern Ecuador and Peru, *Cotinga cayana* from Rondonia, Brazil and Loreto, Peru, *Cotinga maynana* from Morona-Santiago, Ecuador and Loreto, Peru, and *Lipaugus vociferans* from Venezuela and Bolivia. These low levels of differentiation indicate that these populations are unlikely to be distinct evolutionary lineages that should be recognized as species. Notably, our preliminary data do not provide molecular support for the previously recommended split of the Brazilian and Bolivian subspecies of *Phibalura* into two species (Hennessey, 2011).

However, *Procnias averano averano* from Brazil differed in 0.53% of 932 bp of ND2 from *Procnias averano carnobarba* from Trinidad. These two subspecies are very different in body size, and these initial sequence data indicate that they may be more highly differentiated than currently recognized. Furthermore, the highly polytypic Red-ruffed Fruitcrow, *Pyroderus scutatus*, is broadly distributed in South America, and consists of 5 allopatrically distributed subspecies (Snow, 1979). We measured 0.9% average sequence differentiation between *Pyroderus scutatus scutatus* from Paraguay and *Pyroderus scutatus masoni* from Peru, including both significant mitochondrial and nuclear variation (ND2-1.5%, MYO-0.0%, G3PDH-0.9%). This level of differentiation indicates that some of the currently recognized forms *Pyroderus scutatus* may be distinct species, and that further research on the polytypic clade is highly recommended.

Although the Scaled Fruiteater, *Ampelioides tschudii* is currently monotypic, individuals of *tschudii* from San Martin, Peru and from Azuay, Ecuador exhibited 1.2% differentiation in mtDNA (CYTB-1.5%, ND2-1.1%). These two populations span a relatively short geographic distance within the total distribution of *Ampelioides* in the Andes from Venezuela to Bolivia. This variation may be expected given that *Ampelioides tschudii* is the basal lineage of the basal most clade within the cotingas, and potentially the most ancient species-lineage in the family (Supplementary Fig. 1).

Lastly, we found substantial, previously unappreciated genetic differentiation between two populations of the Green-and-Black Fruiteater *Pipreola riefferii.* Individuals of *Pipreola riefferii confusa* from Cajamarca, Peru and *Pipreola riefferii melanolaema* from Venezuela revealed 4.6% average sequence divergence, including substantial genetic differentiation in one nuclear intron (ND2-6.0%, CYTB-7.0%, G3PDH-5.6%, MYO-0.0%). This level of genetic differen-

tiation strongly indicates the existence of distinct evolutionary lineages indicative of separate species. *Pipreola riefferii melanolaema* is a morphologically distinctive form endemic to the coastal range of Venezuela. *Pipreola riefferii confusa* is one of five subspecies that are distributed in the Andes of western Venezuela and northern Colombia to central Peru, including the type population of *riefferii* (Snow, 1979; Kirwan and Green, 2012). Consequently, we recognize the well marked, allopatric, and genetic differentiated taxon *Pipreola melanolaema* as a distinct, monotypic species, to be called (the) Venezuelan Fruiteater. We recommend that all other recognized subspecies should currently remain in *Pipreola riefferii*, but the taxonomic status of these populations should be further investigated. The distinctive, smaller, red eyed, and allopatric *Pipreola riefferii tallmanorum* found in Dpto. Huánuco, Peru also seems very likely to be a distinct species.

Our results confirm that *Doliornis remseni* (Robbins et al., 1994) is strongly differentiated from *Doliornis sclateri* (4.5% average genetic distance). The allopatrically distributed and morphologically diagnosable Central American species of *Carpodectes nitidus* and *C. antoniae* are only slightly differentiated genetically (0.15%). However, their allopatric distribution, and well marked morphological and habitat differences support their continued recognition as distinct species.

4.7. Proposed phylogenetic taxonomy

We propose a hierarchical Linnaean classification of the cotingas based on our Bayesian species tree results. The four unanalyzed species– *Pipreola formosa*, *P. aureopectus*, *Lipaugus weberi*, and *Tijuca condita*– are placed in this classification based on their morphological similarities to other analyzed taxa. These portions of the classification are phylogenetic predictions to be tested by future analyses.

We recognize the same monophyletic subfamiles as Tello et al. (2009), but with one additional subfamily and some different limits. We recognize the new subfamily Cephalopterinae including the members of the fruitcrow clade. We place *Carpornis* in the Rupicolinae, and *Phibalura* in the Phytotominae. Further, given the strong evidence that *Lipaugus* is paraphyletic with respect to the genus *Tijuca*, we place *Tijuca atra* and *T. condita* within the genus *Lipaugus.* The only phylogenetically acceptable alternative would be to split *Lipaugus* into at least three genera for: (1) *unirufus* alone, (2) *lanioides* alone, and (3) all other *Lipaugus* species. This would create unnecessary taxonomic clutter. Indeed, placing *atra* and *condita* within *Lipaugus* communicates effectively that these highly distinctive species have actually evolved from sexually monomorphic piha ancestors.

Our species tree placed *Perissocephalus tricolor* within the genus *Cephalopterus* as the sister group to the Amazonian species *C. ornatus.* The five species of *Cephalopterus*, *Perrisocephalus*, and *Pyroderus* are all extremely closely related; they differ genetically by only 3%-6% (Supplementary Table 9). These three genera could very justifiably be placed within a single genus; *Cephalopterus* has priority. However, we prefer to wait for confirmation from additional data before placing *tricolor* in *Cephalopterus.*

Wherever possible, we follow a phylogenetic sequencing convention in which the first taxon (i.e. subfamily, genus, or species) in a list of taxa is the sister group to the remaining taxa in that list. Thus, the sequence of the five cotinga subfamilies recapitulates the phylogenetic relationships of these clades in the phylogeny. However, we refrain from creating new taxa within subfamilies or genera to precisely recognize each clade within the taxonomy. Authors who wish to refer to these clades can do so by coining names for these clades within specific works: e.g. the *Ampelion* group for members of *Phibalura*, *Doliornis*, and *Ampelion*.

Family Cotingidae Bonaparte, 1849
- Subfamily **Pipreolinae** Tello, Moyle, Marchese & Cracraft, 2009
  - *Ampelioides* Verreaux 1867
    - *Ampelioides tschudii*
  - *Pipreola* Swainson 1838
    - *Pipreola chlorolepidota*
    - *Pipreola frontalis*
    - *Pipreola formosa*
    - *Pipreola whitelyi*
    - *Pipreola lubomirskii*
    - *Pipreola jucunda*
    - *Pipreola pulchra*
    - *Pipreola aureopectus*
    - *Pipreola arcuata*
    - *Pipreola intermedia*
    - *Pipreola riefferii*
    - *Pipreola melanolaema*
- Subfamily **Rupicolinae** Bonaparte, 1853
  - *Snowornis* Prum 2001
    - *Snowornis subalaris*
    - *Snowornis cryptolophus*
  - *Carpornis* G.R. Gray 1846
    - *Carpornis cucullatus*
    - *Carpornis melanocephalus*
  - *Rupicola* Brisson 1760
    - *Rupicola peruviana*
    - *Rupicola rupicola*
  - *Phoenicircus* Swainson 1832
    - *Phoenicircus carnifex*
    - *Phoenicircus nigricollis*
- Subfamily **Phytotominae** Swainson, 1837
  - *Zaratornis* Koepcke 1954
    - *Zaratornis stresemanni*
  - *Phytotoma* Molina 1782
    - *Phytotoma rara*
    - *Phytotoma raimondii*
    - *Phytotoma rutila*
  - *Phibalura* Vieillot 1816
    - Phibalura flavirostris
  - *Doliornis* Taczanowski 1874
    - *Doliornis sclateri*
    - *Doliornis remseni*
  - *Ampelion* Tschudi 1845
    - *Ampelion rubrocristatus*
    - *Ampelion rufaxilla*
- Subfamily **Cephalopterinae** Reichenow, 1914
  - *Haematoderus* Bonaparte 1854
    - *Haematoderus militaris*
  - *Querula* Vieillot 1816
    - *Querula purpurata*
  - *Pyroderus* G.R. Gray 1840
    - Pyroderus scutatus
  - *Cephalopterus* E. Geoffroy Saint-Hilaire 1809
    - *Cephalopterus glabricollis*
    - *Cephalopterus penduliger*
    - *Cephalopterus ornatus*
  - *Perissocephalus* Oberholser 1899
    - *Perissocephalus tricolor*
- Subfamily **Cotinginae** Bonaparte, 1849
  - *Lipaugus* Boie 1828
    - *Lipaugus unirufus*
    - *Lipaugus ater*
    - *Lipaugus conditus*

Lipaugus lanioides
Lipaugus streptophorus
Lipaugus vociferans
Lipaugus fuscocinereus
Lipaugus uropygialis
Lipaugus weberi
Procnias Illiger 1811
Procnias albus
Procnias tricarunculata
Procnias nudicollis
Procnias averano
Cotinga Brisson 1760
Cotinga maynana
Cotinga cayana
Cotinga amabilis
Cotinga nattererii
Cotinga ridgwayi
Cotinga maculata
Cotinga cotinga
Porphyrolaema Bonaparte 1854
Porphyrolaema porphyrolaema
Conioptilon Lowery & O'Neill 1966
Conioptilon mcilhennyi
Gymnoderus Geoffroy Saint-Hillaire 1809
Gymnoderus foetidus
Xipholena Gloger 1841
Xipholena punicea
Xipholena lamellipennis
Xipholena atropurpurea
Carpodectes Salvin 1865
Carpodectes hopkei
Carpodectes antoniae
Carpodectes nitidus

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2014.09.001.

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