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Mitochondrial DNA based phylogeny of the woodpecker genera *Colaptes* and *Piculus*, and implications for the history of woodpecker diversification in South America

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ABSTRACT

The woodpecker genus *Colaptes* (flickers) has its highest diversity in South America and the closely related genus *Piculus* is restricted to South and Central America. Two species of flickers occur in North America, and one species is endemic to Cuba. We conducted a Bayesian phylogenetic analysis of three mitochondrial encoded genes (*cyt b*, *COI*, *12S* rRNA) and confirmed that the two genera are paraphyletic. Three species historically classified as *Piculus* are actually flickers. We found that the Cuban endemic *C. fernandinae* is the most basal species within the flickers and that the Northern Flicker is the next most basal species within the *Colaptes* lineage. The South American clade is most derived. The age of the South American diversification is estimated to be 3.6 MY, which is synchronous with the emergence of the Isthmus of Panama. The pattern of diversification of South American flickers is common among South American woodpeckers. Although woodpeckers have their greatest diversity in South America, we hypothesize that woodpeckers (Family Picidae) originated in Eurasia, dispersed to North America via the Bering land bridge, and multiple lineages entered South America as the Isthmus approached its final closing.

1. Introduction

Colaptes and *Piculus* are woodpecker genera distributed in the New World, primarily in the tropics. These two genera are so closely related that inclusion of species in one genus or the other is often not certain, with assignment based on plumage coloration and pattern, and on ecological and behavioral traits. In general, species traditionally assigned to *Colaptes*, commonly called flickers, occur in relatively open woodlands, savannas and woodland edges where they forage on the ground for a diet comprising mostly ants. The plumage coloration of the back is brownish or tends towards that color in most species, and all species have transverse-barred color patterns on their backs, which appear to provide camouflage when the birds forage on the ground. In contrast, species traditionally assigned to *Piculus* occur in relatively dense woodlands, where they forage primarily in trees. The back plumage is solid and green in most species, washed in red in several species and predominantly red in *rivolii*, the Crimson-mantled woodpecker. The solid dorsal coloration also appears to provide camouflage as these species forage on branches and trunks in dark, verdant woodlands. Even the Crimson-mantled Woodpecker is remarkably inconspicuous as it forages quietly in the humid Yungas woodlands along the eastern slopes of the Andes, which support a rich epiphytic flora (Short, 1982). Consistent with their more arboreal foraging ecology, the skulls of *Piculus* species are more massive and apparently adapted for a more "woodpeckering" life style (Short, 1972, 1982).

We have summarized in Table 1 the varying assignment of species to genera in several historically significant classifications. It is apparent that there is considerable uncertainty regarding the generic assignments of these species. In addition to *Piculus* and *Colaptes*, Peters assigned the Cuban endemic *fernandinae* to a monotypic genus *Nesoceleus* and three species to the genus *Chrysoptilus*; various earlier classifications assigned species to yet other genera (see Peters, 1948): *Chloronerpes* (*rubiginosus*) and *Hypoxanthus* (*rivolii*).

Most recently, the SACC (South American Classification Committee) and the IOC (International Ornithological Congress) reassigned two species to *Colaptes* that were traditionally assigned to *Piculus*: *rivolii* and *rubiginosus*. The IOC went a step further and assigned *auricularis* to *Colaptes*. These reassignments were based on several DNA studies focused on higher level systematics of woodpeckers or on assessing the utility of various genes for resolving relationships among woodpeckers and included only small and

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Table 1
Historical classification of woodpecker genera *Colaptes* and *piculus*.

Species[1]	Common name	Genera assigned by classification						
		Peters (1948)	Short (1982)	Sibley and Monroe (1990)	Winkler and Christie (2002)	Dickinson (2003)	SACC, Remsen et al. (2009)	IOC, Gill and Donsker (2010)
chrysochloros	Golden-green Woodpecker	*Piculus*	*Piculus*	*Piculus*	*Piculus*	*Piculus*	*Piculus*	*Piculus*
aurulentus	White-browed Woodpecker	*Piculus*	*Piculus*	*Piculus*	*Piculus*	*Piculus*	*Piculus*	*Piculus*
leucolaemus	White-throated Woodpecker	*Piculus*	*Piculus*	*Piculus*	*Piculus*	*Piculus*	*Piculus*	*Piculus*
simplex	Rufous-winged Woodpecker	*Piculus*	NA[2]	*Piculus*	*Piculus*	*Piculus*	NA	*Piculus*
callopterus	Stripe-cheeked Woodpecker	NA	NA	*Piculus*	*Piculus*	*Piculus*	NA	*Piculus*
litae	Lita Woodpecker	NA	NA	*Piculus*	*Piculus*	*Piculus*	*Piculus*	*Piculus*
flavigula	Yellow-throated Woodpecker	*Piculus*	*Piculus*	*Piculus*	*Piculus*	*Piculus*	*Piculus*	*Piculus*
rubiginosus	Golden-olive Woodpecker	*Piculus*	*Piculus*	*Piculus*	*Piculus*	*Piculus*	*Colaptes*	*Colaptes*
auricularis	Gray-crowned Woodpecker	*Piculus*	*Piculus*	*Piculus*	*Piculus*	*Piculus*	NA	*Colaptes*
aeruginosus	Bronze-winged Woodpecker	*Piculus*	NA	NA	NA	NA	NA	NA
rivolii	Crimson-mantled Woodpecker	*Piculus*	*Piculus*	*Piculus*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*
fernandinae	Fernandina's Woodpecker	*Nesoceleus*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	NA	*Colaptes*
auratus	Northern Flicker	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	NA	*Colaptes*
chrysoides	Gilded Flicker	*Colaptes*	NA	*Colaptes*	*Colaptes*	*Colaptes*	NA	*Colaptes*
rupicola	Andean Flicker	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*
pitius	Chilean Flicker	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*
melanochloros	Green-barred Woodpecker	*Chrysoptilus*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*
punctigula	Spot-breasted Woodpecker	*Chrysoptilus*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*
campestris	Campo Flicker	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*
atricollis	Black-necked Woodpecker	*Chrysoptilus*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*	*Colaptes*

[1] Species printed in bold are included in this study; indented species considered subspecies or members of superspecies by some authors.
[2] NA, Not applicable: outside of range of study, not recognized as a species, etc.

varying subsets of species belonging to *Colaptes* or *Piculus* (Moore and DeFilippis, 1997; Prychitko and Moore, 1997; Prychitko and Moore, 2000; DeFilippis and Moore, 2000; Weibel and Moore, 2002a,b, 2005; Benz et al., 2006; Fuchs et al., 2006; Moore et al., 2006; Fuchs et al., 2007, 2008). In fact, no molecular data have as yet been reported in the literature for one of the reassigned species, *auricularis*. Its reassignment was based on its overall similarity to *rubiginosus* (Benz et al., 2006).

The primary purpose of this study is to resolve the relationships among species usually assigned to the genus *Colaptes* (Short, 1982; Sibley and Monroe, 1990; Winkler and Christie, 2002) and their relationships to species of *Piculus* based on the nucleotide sequences of three mitochondrial encoded genes, *cyt b*, *COI* and *12S rRNA*. We will also explore the biogeography of species comprising these two genera in context of the phylogeny. With the exception of the Northern Flicker, which ranges across most of North America and Fernandina's Flicker, which is a Cuban endemic, the species of both genera are restricted to Central and South America. The high diversity of *Colaptes* and *Piculus* in the Neotropics suggests that they originated there, but our phylogeny suggests they originated in North America, underwent some diversification there and early lineages invaded South America at about the time the Isthmus of Panama was formed. Once in South America, these primal lineages rapidly diversified. We review and synthesize data and literature that indicate this is a common evolutionary history among New World woodpeckers.

Our taxon sample includes all eight species of *Colaptes* recognized by Short (1982) including *C. fernandinae*, which is endemic to Cuba and listed as endangered by Birdlife International (Winkler et al., 1995), and the Chilean Flicker, *C. pitius*, which is restricted to Chile and adjacent regions of Argentina. Tissues of *Piculus* species available to us were limited but include representatives of species sufficient to substantiate the reciprocal paraphyly of *Colaptes* and *Piculus* suggested in previous DNA-based studies and to infer the deeper structure of the tree.

Previous studies indicate that the woodpeckers (subfamily Picinae) form a relatively young clade, probably arising less than 15 MYBP and that the clade comprising the species presently assigned to *Colaptes* and *Piculus* less than 4 MYBP (Moore et al., 1999; Fuchs et al., 2007). Over this window of evolutionary time, mitochondrial genes provide a stronger source of phylogenetic signal than do nuclear gene introns (Moore et al., 1999; Prychitko and Moore, 2000; Weibel and Moore, 2002b). Although it would be ideal to include one or more nuclear gene intron sequences in the study, the mitochondrial-genome tree has a higher probability of tracking the species tree than do nuclear gene trees, with regard to ambiguity resulting from incomplete lineage sorting (Moore, 1995). Thus, we limited our study to sequencing mitochondrial encoded genes because they appear to provide the highest probability of resolving the species tree within the limited financial resources available to us.

2. Materials and methods

2.1. Specimens

Specimens representing all species of *Colaptes* and *Piculus* recognized by Short (1982) were included in this study except *Piculus aurulentus*, which forms a superspecies with *P. chrysochloros* (Short, 1982; Sibley and Monroe, 1990; Winkler and Christie, 2002). We also lacked specimens of three additional taxa sometimes considered distinct species, but sometimes considered subspecies or part of a superspecies complex represented by a species in our sample (*P. simplex* and *P. litae*, *P. leucolaemus*; *P. aeruginosus*, *P. auricularis*). *Colaptes auratus chrysoides* (Gilded Flicker) was also returned to species status subsequent to Short's classification (American Ornithologists' Union., 1998); it is not included in our study, but it is very closely related to *C. auratus cafer*, with which it hybridizes (Moore et al., 1991). Thus, our taxon sample should suffice to resolve relationships at levels deeper than those within species and superspecies.

Specimens included are listed in Table 2 along with voucher numbers, locales and NCBI Accession Numbers. With two exceptions, we determined either *de novo* or from sequences previously accessioned to NCBI the nucleotide sequence for a minimum of two individuals for each ingroup species and compared the intraspecific sequences with each other as part of the vetting process. Verification of one sequence against the other greatly reduces the chance of including a contaminant or chimeric sequence in the study. The first exception was *C. fernandinae* for which only one individual was available. The second exception was the *cyt b* gene