SHORT COMMUNICATIONS

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FURTHER EVIDENCE FOR PARAPHYLY OF THE FORMICARIIDAE (PASSERIFORMES)

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Abstract. The historical relationships of ground antbirds and their relatives have long been unresolved. Here, I present a phylogenetic analysis of ground antbird (Formicariidae) relationships based on DNA sequence data from the cytochrome-*b* and ND2 genes. Results support novel hypotheses of historical relationships, including two revisions of suboscine taxonomy: (1) paraphyly of the Formicariidae with the tentative inclusion of at least some *rhinocryptids* (*Liosceles*, *Rhinocrypta*, and *Scytalopus*) in the ground antbird lineage, and (2) placement of *Pittasoma* with *Conopophaga* in the Conopophagidae.

Key words: antthrush, Conopophaga, *phylogeny*, Pittasoma, *tapaculo.*

Evidencia Adicional sobre el Carácter Parafilético de Formicariidae (Paseriformes)

Resumen. Las relaciones históricas entre los Formicariidae y sus parientes han permanecido sin resolver por mucho tiempo. Aquí presento un análisis filogenético de las relaciones de los Formicariidae basado en datos de secuencias de ADN de los genes citocromo-*b* y ND2. Los resultados apoyan nuevas hipótesis sobre las relaciones históricas, incluyendo dos revisiones acerca de la taxonomía de los suboscines: la inclusión tentativa de al menos algunos rinocríptidos (*Liosceles*, *Rhinocrypta* y *Scytalopus*) en Formicariidae, y el emplazamiento de *Pittasoma* en Conopophagidae.

The ground antbirds (Formicariidae) form a diverse clade of suboscine passerines that currently includes six genera: *Formicarius*, *Chamaeza*, *Grallaria*, *Grallaricula*, *Myrmothera*, and *Hylopezus* (Sibley and Ahlquist 1990, Ridgely and Tudor 1994, Rice 2000, 2005). Most species are plainly colored, and, as the name implies, are typically found on or near the ground. The Formicariidae has not been the subject of any detailed phylogenetic study, with most current research focused on alpha taxonomy and natural history (Graves 1987, Stiles 1992, Kratter 1995, Krabbe et al. 1997, Barber and Robbins 2002); however, Rice (2005) does provide an overview of generic-level phylogenetic relationships of the antpittas.

Ames (1971) examined a broad diversity of antbirds and separated them into two groups (ground antbirds and typical antbirds) on the basis of their syringeal morphology. He hypothesized that ground antbird syringes were intermediate between those of typical antbirds and tapaculos. Sibley and Ahlquist (1990) used DNA-DNA hybridization data to identify ground antbirds as a monophyletic lineage distinct from typical antbirds. The Conopophagidae (gnateaters) and Rhinocryptidae (tapaculos) were identified as their closest relatives. However, because Sibley and Ahlquist (1990) examined only six formicariid taxa, and radioactively labeled only one, a family-wide perspective was lacking.

Two recent studies of higher-level tracheophone systematics have suggested that the Formicariidae is paraphyletic (Irestedt et al. 2002, Chesser 2004). In both studies, the antthrushes (*Chamaeza* and *Formicarius*) and antpittas (*Grallaria*, *Grallaricula*, *Hylopezus*, and *Myrmothera*) each formed monophyletic lineages, but were not each other's sister lineage. Irestedt et al. (2002) and Chesser (2004) found that the antthrushes formed the sister group to the Dendrocolaptidae and Furnariidae, and in some analyses included tapaculos as their sister group. The antpittas were the sister group to the antthrushes + Dendrocolaptidae + Furnariidae lineage. As the focus of these recent studies was at the family- and subfamily-level, they thus included very few ground antbirds (one individual each of *Formi-*

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TABLE 1. Tissue numbers, collections, and Genbank numbers of the taxa examined in this study.

Taxa	Common name	Collection[a]	Tissue number	Genbank numbers[b]
Myrmornis torquata	Wing-banded Antbird	KUMNH	1311	AY370565, AY370602
Phlegopsis nigromaculata	Black-spotted Bare-eye	KUMNH	447	AY370561, AY370598
Thamnophilus doliatus	Barred Antshrike	FMNH	1286	AY370563, AY370600
Liosceles thoracicus	Rusty-belted Tapaculo	FMNH	4545	AY370558, AY370595
Rhinocrypta lanceolata	Crested Gallito	LSUMNS	18 813	AY370559, AY370596
Scytalopus magellanicus	Andean Tapaculo	LSUMNS	8343	AY370560, AY370597
Conopophaga lineata	Rufous Gnateater	FMNH	5288	AY370555, AY370592
C. peruviana	Ash-throated Gnateater	KUMNH	672	AY370554, AY370591
Chamaeza campanisona	Short-tailed Antthrush	LSUMNS	5385	AY370536, AY370573
C. mollissima	Barred Antthrush	FMNH	1490	AY370537, AY370574
Formicarius colma	Rufous-capped Antthrush	KUMNH	775	AY370550, AY370587
F. analis	Black-faced Antthrush	KUMNH	709	AY370551, AY370588
Grallaricula lineifrons	Cresent-faced Antpitta	ANSP	3869	AY370538, AY370575
G. flavirostris	Ochre-breasted Antpitta	LSUMNS	7973	AY370539, AY370576
Myrmothera campanisona	Thrush-like Antpitta	LSUMNS	9600	AY370548, AY370585
M. simplex	Tepui Antpitta	LSUMNS	7408	AY370549, AY370586
Hylopezus fulviventris	White-lored Antpitta	ANSP	4282	AY370552, AY370589
H. berlepschi	Amazonian Antpitta	FMNH	1421	AY370553, AY370590
Grallaria squamigera	Undulated Antpitta	LSUMNS	6254	AY370540, AY370577
G. varia	Variegated Antpitta	LSUMNS	7528	AY370541, AY370578
G. rufula	Rufous Antpitta	LSUMNS	1218	AY370542, AY370579
G. blakei	Chestnut Antpitta	LSUMNS	5620	AY370543, AY370580
G. ruficapilla	Chestnut-crowned Antpitta	ANSP	4810	AY370544, AY370581
G. watkinsi	Watkins' Antpitta	ANSP	2906	AY370545, AY370582
G. eludens	Elusive Antpitta	LSUMNS	11 263	AY370546, AY370583
G. dignissima	Ochre-striped Antpitta	ANSP	3229	AY370547, AY370584
Pittasoma rufopileatum	Rufous-crowned Antpitta	LSUMNS	11 860	AY370556, AY370593
P. michleri	Black-crowned Antpitta	LSUMNS	2285	AY370557, AY370594
Procnias nudicollis	Bare-throated Bellbird	KUMNH	110	AY370571, AY370608
Rupicola rupicola	Guianan Cock-of-the-rock	LSUMNS	7575	AY370572, AY370609

[a] Collection acronyms are as follows: KUMNH = University of Kansas Natural History Museum, LSUMNS = Louisiana State University Museum of Natural Science, FMNH = Field Museum of Natural History, ANSP = Academy of Natural Sciences of Philadelphia.

[b] Genbank numbers are cytochrome-*b* and ND-2, respectively.

carius, *Chamaeza*, *Grallaria*, and *Hylopezus* [Irestedt et al. 2002], and one individual each of *Formicarius*, *Grallaria*, *Myrmothera*, and *Grallaricula* [Chesser 2004]). Here, I present additional molecular evidence for the paraphyly of the ground antbirds using improved taxon sampling from the ground antbird (18 species) and tapaculo (three species) lineages.

METHODS

TAXA EXAMINED

DNA sequences were analyzed for at least two species from each currently recognized genus of ground antbird, and eight species from *Grallaria*, accounting for nearly one-third of all ground antbird species. Representatives of four other suboscine families, four conopophagids, three rhinocryptids, three thamnophilids, and two cotingids were also sequenced, for a total of 30 species sampled (Table 1). In each case, representatives of genera or families were chosen to be as phenotypically disparate as possible. Freshly frozen or ethanol-preserved tissues (liver, heart, and muscle) were obtained from the Louisiana State University Museum of Natural Science (LSUMNS), Field Museum of Natural History (FMNH), Academy of Natural Sciences (ANSP), and University of Kansas Natural History Museum (KUNHM).

MOLECULAR METHODS

DNA extraction, amplification, and sequencing protocols follow those outlined in Rice et al. (2003) and Rice (2005). Genomic DNA was extracted from each sample using Qiamp tissue extraction kits (Qiagen, Valencia, California). The 3′ end of the cytochrome-*b* gene (378 bp) and a segment of the ND2 gene (501 bp) were amplified using conventional thermal-cycling techniques (Kocher et al. 1989). Cytochrome-*b* primers (H-15915, 5′–CCAGACCTCCTAGGAGACCCAGA–3′ and L-15507, 5′–AACTGCAGTCATCTCCGGTTTACAAGAC–3′) were developed by S. Hackett (pers. comm.), and ND-2 primers (H-6313, 5′–GGCTGAATRGGMCTNAAYCARAC–3′ and L-5757, 5′–CTCTTATTTAAGGCTTTGAAGGC–3′) were developed by M. Sorenson (pers. comm.). The thermal profile used for both primer sets was denaturing at 95°C for 30 sec, annealing at 55°C for 30 sec, and extension at 70°C for 90 sec. Extension time was lengthened 4 sec

per cycle for 35 cycles. Target DNA amplified using the thermal cycler was then purified using low-melt (1%) NuSieve GTG agarose gel (FMC BioProducts, Rockland, Maine) electrophoresis for 45 min at 85–95 volts. Bands containing target products were excised from the low-melt electrophoresis gel and the DNA was recovered using Qiaquick spin columns (Qiagen, Valencia, California). Purified product was amplified using only one primer (heavy or light) and sequenced with an ABI Prism Genetic Analyzer (Model 310, Applied Biosystems, Foster City, California). The thermal profile used for both primer systems was denaturing at 96°C for 10 sec, annealing at 50°C for 5 sec, and extension at 60°C for 4 min, repeated for 25 cycles. Negative controls were used at each step of DNA preparation to test for reagent contamination. All DNA sequences are deposited in Genbank (Table 1).

DATA ANALYSES

Separate character-state matrices were assembled for cytochrome-*b* and ND2 gene sequences. Heavy and light strands were spliced and aligned using the clustal algorithm of Sequence Navigator (ABI Prism, Foster City, California). Phylogenetic analyses were conducted for both data sets individually and combined to assess congruence of data sets. Data were analyzed using maximum parsimony and maximum likelihood optimizations, with the cotingids *Rupicola rupicola* and *Procnias nudicollis* designated as outgroups.

Parsimony analyses of the equally weighted, unordered datasets were conducted using heuristic searches with 1000 random-taxon addition replications, and the tree bisection-reconnection and steepest descent options of PAUP 4.0b10 (Swofford 2002). Although no saturation was detected in the dataset, additional analyses were performed using various weighting schemes to test the sensitivity of the results to assumptions, including a 2:1 weighting of transversions-transitions and downweighting of third position bases by factors of 2, 5, and 10. Lineage support was assessed using bootstrap values based on 1000 replications, each with 20 random taxon addition replications, and Bremer branch-support values (Bremer 1994, Sorenson 1996).

Maximum likelihood analyses were performed on the datasets using heuristic searches with 10 random addition replications in PAUP 4.0b10 (Swofford 2002). I used MODELTEST 3.0 (Posada and Crandall 1998) to assess 56 models of DNA sequence evolution and determine the model that best explained the sequences analyzed. The GTR + G + I model was found to be the most efficient at optimizing sequence evolution for this dataset, with the following parameters: prob. [A–C] = 0.29, prob. [A–G] = 13.32, prob. [A–T] = 0.46, prob. [C–G] = 0.65, prob. [C–T] = 4.81, prob. [G–T] = 1.00; freq. [A] = 0.37, freq. [C] = 0.38, freq. [G] = 0.04, freq. [T] = 0.21; shape parameter = 0.75; and proportion of invariant sites = 0.36. Support for particular clades was assessed on the maximum likelihood topology by bootstrapping using 100 heuristic searches with random addition replicates.

RESULTS

MOLECULAR RESULTS

The aligned data matrix included 879 molecular characters (378 from cytochrome-*b* and 501 from ND2); 470 (54%) of which were phylogenetically informative. Inspection of sequences did not reveal any insertions, deletions, or sequencing artifacts and sequences translated successfully into amino acids, suggesting that the sequences are mitochondrial and not nuclear pseudogenes. Mean uncorrected pairwise divergence among taxa included in this study was 21% and ranged from 5% (between the two *Myrmothera* species) to 26% (between *Liosceles* and *Pittasoma rufopileatum*). The base frequencies calculated from the dataset were: [A] = 32%, [C] = 33%, [G] = 9%, and [T] = 27%, and the transition-transversion ratio calculated from the most parsimonious tree was 1.41.

Numbers of phylogenetically informative and variable sites varied by the gene region analyzed as well as by coding position. For the cytochrome-*b* gene region, there were 193 variable sites, and 175 of these were phylogenetically informative. Partitioning by codon position revealed that first positions had 49 variable sites (42 phylogenetically informative), second positions had 21 variable sites (15 phylogenetically informative), and there were 124 variable sites for third positions (118 phylogenetically informative). For the ND2 gene region, 337 variable sites were detected, of which 295 were phylogenetically informative. Partitioning by codon position revealed that first positions displayed 105 variable sites (90 phylogenetically informative), second positions had 68 variable sites (48 phylogenetically informative), and there were 164 variable sites for third positions (157 phylogenetically informative).

PHYLOGENETIC RESULTS

Parsimony analysis of the combined molecular dataset resulted in three most parsimonious trees (Fig. 1, tree length = 2436, consistency index = 0.34, homoplasy index = 0.66, retention index = 0.44, rescaled consistency index = 0.15). The only difference among these trees was that in one tree the sister relationship between the antthrushes and tapaculos was not recognized. In another, the sister relationship between the typical antbirds and *Pittasoma* + *Conopophaga* was not recognized. In all the most parsimonious trees, the tracheophones formed a monophyletic lineage, with the tapaculos and ground antbirds (excluding *Pittasoma*) forming a monophyletic lineage. Maximum likelihood analyses of the same dataset produced a single most likely tree (Fig. 1, score = −Ln 10 767) that was topologically identical to the majority rule consensus tree.

Using two cotingid taxa as outgroups, the 28 tracheophones included in this analysis formed a well-supported monophyletic lineage of two major clades. The first clade was the sister relationship between the typical antbirds and *Pittasoma* + *Conopophaga*. The second major tracheophone lineage included the ground antbirds and tapaculos sequenced for this study, and is well supported by bootstrap replicates in both character optimization analyses.

Within this second tracheophone lineage are two subclades, the antpittas (*Grallaria*, *Grallaricula*, *Hylopezus*, and *Myrmothera*) and the antthrushes (*Chamaeza* and *Formicarius*) + tapaculos (*Liosceles*, *Rhinocrypta*, and *Scytalopus*). The antpittas form a well-supported clade of two sublineages. In one lineage,

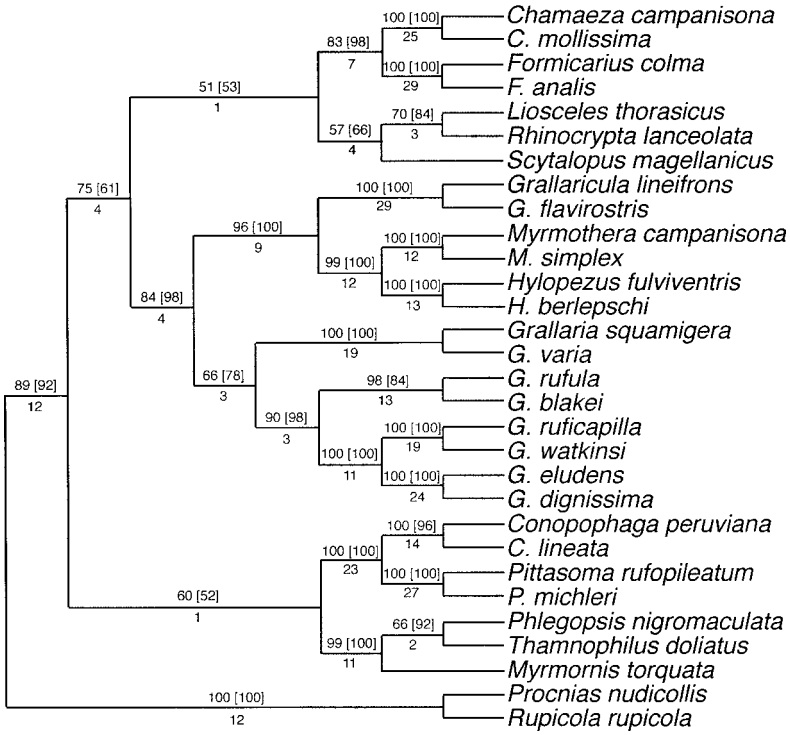

FIGURE 1. Most parsimonious (majority rule consensus) and most likely tree topology of the combined molecular dataset for the ground antbirds. Numbers above each internode refer to bootstrap values (maximum likelihood bootstrap values in brackets). Numbers below each internode refer to Bremer Decay Indices.

Myrmothera is the sister genus to *Hylopezus*, and *Grallaricula* is their sister genus. The second antpitta clade is the large and complex genus *Grallaria*. Within *Grallaria*, *G. eludens* + *G. dignissima* is the sister lineage to *G. ruficapilla* + *G. watkinsi*, and *G. rufula* + *G. blakei* forms their sister lineage. The large bodied antpittas, *G. squamigera* + *G. varia*, formed the basal lineage of the *Grallaria* clade.

Within the larger ground antbird lineage, the antthrushes and tapaculos were weakly supported as sister taxa. In this clade, the antthrush genera *Formicarius* and *Chamaeza* were found to be monophyletic and each other's sister taxa. The three tapaculos sequenced for this study formed a monophyletic lineage with *Liosceles*, the sister to *Rhinocrypta*, and *Scytalopus* as their sister taxa.

DISCUSSION

One of the best-resolved and well-supported clades in this study was the antpitta lineage. It is interesting to note that the ''antpitta'' genus *Pittasoma* is strongly supported as the sister genus to *Conopophaga*, a relationship that is reinforced by several important morphological and vocal synapomorphies (Rice 2005). Following the results of Irestedt et al. (2002) and Chesser (2004), this study does not support a close relationship between antpittas and antthrushes, contra Sibley and Ahlquist (1990). In fact, average pairwise sequence divergence between antpittas and antthrushes was 22.5%, on the same order as that between typical antbirds and antthrushes (22.7%). In this study, the antthrushes were monophyletic and sister to the tapaculos.

The antpittas constitute one of the two major ground antbird clades. This group is identical to the Grallarinae of Lowery and O'Neill (1969), with the exclusion of *Pittasoma*. Within the antpitta clade are two well-supported sublineages: (1) the large and complex genus *Grallaria*, and (2) the generally smaller antpittas *Grallaricula*, *Myrmothera*, and *Hylopezus*. Members of both subclades hop on the ground in an upright position, have short tails, deep and robust bills, holospidean tarsal scutellation, and generally lay round bluish or greenish eggs (Lowery and O'Neill 1969, Fjeldså and Krabbe 1990, Sick 1993). The evolutionary history and morphological character evolution within the antpitta clade has been discussed elsewhere (Rice 2000, 2005).

Not surprisingly, the antthrush genera *Formicarius* and *Chamaeza* were placed as sister taxa. According to Ames et al. (1968), the antthrushes have unique spinal pterylae, heavily feathered in the posterior region, compared with other tracheophones. Natural history information is lacking for many antthrush taxa, although for the species that have been examined, all have spherically shaped white eggs. In addition, *Formicarius* and *Chamaeza* antthrushes also both nest in tree cavities (Fig. 2, Krabbe and Schulenberg 2003).

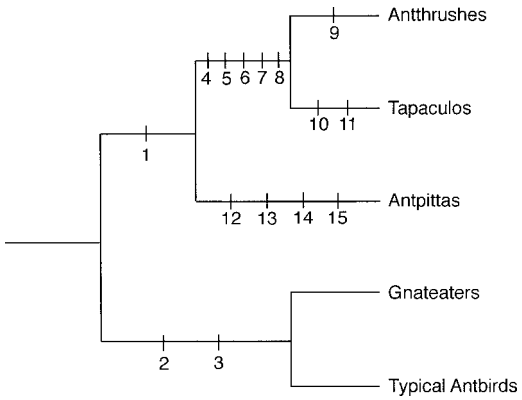

FIGURE 2. Simplified tree derived from the molecular phylogeny in Figure 1. Major lineages have been pruned to a single branch and common name moniker. Major morphological features discussed in the text and coinciding with the molecular phylogeny are mapped onto the tree. Numbers refer to the following characters: (1) simple insertion of the musculus sternotrachealis; (2) sexual dichromatism; (3) exaspidean tarsal scutellation; (4) whitish colored eggs; (5) walking is primary locomotion; (6) long tail held cocked; (7) taxaspidean tarsal scutellation; (8) nest placed in cavity; (9) heavily feathered dorsal pterylae; (10) dorsal origination of musculus vocalis; (11) unseparated lateral pterylae; (12) bluish/greenish colored eggs; (13) short tail held straight; (14) hopping is primary locomotion; (15) holospidean tarsal scutellation. Note that the clade labelled ''tapaculo'' does not include *Melanopareia* (following Irestedt et al. 2002) and the ''gnateater'' clade includes *Pittasoma* (following Rice 2005).

Given the morphological diversity within the Rhinocryptidae and among those included herein, it was interesting to find that the three genera included in this study formed a monophyletic lineage. All known tapaculo nests are enclosed structures, placed in burrows, holes, or crevices (Fjeldså and Krabbe 1990, Ridgely and Tudor 1994). Rhinocryptid syringes (at least those described) are similar to those found in ground antbirds, but have the derived feature of a dorsally originating musculus vocalis (Ames 1971). In addition, tapaculo pterylae are unique among tracheophones, in that they are unseparated in the flank margin (Fig. 2, Ames et al. 1968).

Although only weak molecular support exists for placing *Liosceles* + *Rhinocrypta* + *Scytalopus* as sister to the antthrushes, several interesting morphological synapomorphies support this relationship (Fig. 2). Members of both groups walk on the ground in a horizontal posture and have relatively long tails that are often held cocked, an apparently derived condition in the tracheophones (antpittas have very short tails and typical antbirds generally have tails of intermediate length that are held parallel to the main axis of the body). Tapaculos and antthrushes lay white eggs, in contrast to the bluish or greenish antpitta eggs. Most antthrushes and tapaculos also place their nests in some sort of cavity, either actively excavated or natural (e.g., rotten stump, tree root masses). Species of antthrushes and tapaculos also have taxaspidean tarsal scutellation, in contrast to the antpittas, which are holospidean. Although only three of 12 rhinocryptid genera were represented in this study, much of the diversity of the group was included, except for the aberrant *Psiloramphus* and *Melanopareia*. Inclusion of some or all rhinocryptids upon detailed study within the larger ground antbird clade may in the end prove reasonable, making Formicariidae paraphyletic.

Analyzing more molecular characters, but including fewer taxa, Irestedt et al. (2002) also found weak support for a sister relationship between tapaculos (excluding *Melanopareia*) and antthrushes. Chesser (2004) found that the ground antbird lineage was paraphyletic, but did not support a sister relationship between the tapaculos and antthrushes. Given that much of the phenotypic diversity of the Rhinocryptidae has been sequenced and found to be closely associated with antthrushes, it seems entirely feasible that the two groups are indeed sister taxa (regardless of the relatively weak statistical support in this study and in Irestedt et al. [2002]). In this case, the antthrushes and tapaculos would form a monophyletic family of suboscine passerines (Formicariidae) that is the sister lineage to a monophyletic antpitta family (Grallaridae, including *Grallaria*, *Grallaricula*, *Hylopezus*, and *Myrmothera*). It is also now well established that the family Conopophagidae should be redefined to include the former antpitta genus *Pittasoma*.

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AGE-BASED PLUMAGE CHANGES IN THE LANCE-TAILED MANAKIN: A TWO-YEAR DELAY IN PLUMAGE MATURATION

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Abstract. I investigated the relationship of plumage to age and sex in the Lance-tailed Manakin (Pipridae, *Chiroxiphia lanceolata*) in the lowlands of western Panama from 1999–2004. I captured birds in mist nets, categorized their plumages, examined them for molt, and followed them for several years to document plumage changes. Male Lance-tailed Manakins exhibited three distinct postjuvenal plumages. Males achieved definitive adult plumage through sequential changes that occurred in the same order as in other *Chiroxiphia* manakins. Definitive male plumage developed over the same time span as reported for *C. caudata* but one year faster than *C. linearis*. Juvenal male plumage was similar to that of females, and 5% of 226 females had plumage similar to formative male plumage. Genetic sexing verified that changes observed late in the formative male plumage unambiguously identified sex and age of individual birds. This information can be used in behavioral studies to identify the age of male Lance-tailed Manakins captured in any of the predefinitive plumage stages.

Key words: Chiroxiphia, *delayed plumage maturation, Lance-tailed Manakin, Panama, plumage development.*

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