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PHYLOGENETIC RELATIONSHIPS OF ANTPITTA GENERA (PASSERIFORMES: FORMICARIIDAE)

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ABSTRACT.—Phylogenetic relationships among the antpitta genera were studied using DNA sequence data from the mitochondrial genome. The clade representing the traditional “antpitta” genera (*Grallaria*, *Grallaricula*, *Hylopezus*, *Myrmothera*, and *Pittasoma*) were found to be paraphyletic, owing to the sister relationship of *Pittasoma* and *Conopophaga*. In a previously unreported relationship, *Pittasoma* was strongly supported as the sister genus to *Conopophaga* (Conopophagidae). The remaining antpitta genera form a fully resolved and well-supported monophyletic lineage with two major subclades. The first clade consists of the genus *Grallaria* and supports the subgenera identified by Lowery and O'Neill (1969). The second antpitta clade has *Hylopezus* as the sister genus to *Myrmothera*, with *Grallaricula* as their sister genus. The results here allow for a new interpretation of the morphological characters used in previous studies. *Received 14 July 2004, accepted 13 December 2004.*

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Phylogenetic relationships of antpitta genera (Passeriformes: Formicariidae)

RESUMEN.—Las relaciones filogenéticas entre los géneros de tororoíes (antpittas) se estudiaron con base en datos de secuencias del DNA del genoma mitocondrial. Se encontró quel clado que representa a los géneros tradicionalmente considerados en el grupo (*Grallaria*, *Grallaricula*, *Hylopezus*, *Myrmothera* y *Pittasoma*) es parafilético, debido a la relación de taxones hermanos entre *Pittasoma* y *Conopophaga*. En un estudio no reportado previamente, se apoya fuertemente la relación de *Pittasoma* como el género hermano de *Conopophaga* (Conopophagidae). El resto de los géneros de tororoíes forman un linaje monofilético totalmente resuelto y bien apoyado, que contiene dos subclados mayores. El primer clado consiste del género *Grallaria* y apoya los subgéneros identificados por Lowery y O'Neill (1969). El segundo clado tiene a *Hylopezus* como el género hermano de *Myrmothera*, con *Grallaricula* como el género hermano de ambos. Los resultados de este trabajo permiten una nueva interpretación de los caracteres morfológicos utilizados en estudios previos.

GROUND ANTBIRDS (FORMICARIIDAE) form a diverse clade (~60 species) of suboscine passerines found exclusively in the Neotropics. Formicariids are plainly colored but attractively patterned birds that hop or walk on or near the

ground. Because of their cryptic coloration and secretive habits, ground antbirds are more often heard than seen. The Formicariidae has not been the subject of any detailed phylogenetic study, with most published and ongoing research focused on alpha taxonomy and documentation of natural history (e.g. Graves 1987, Stiles 1992, Kratter 1995, Krabbe et al. 1999, Barber and Robbins 2002).

The most speciose group within the Formicariidae is the antpittas (*Grallaria*, *Grallaricula*,

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Hylopezus, *Myrmothera*, and *Pittasoma*). Antpittas come in an impressive range of body sizes and live in a variety of habitats in the Neotropics. Antpittas have disproportionately long legs, compared with their body size and short tails. The nests of only a few species have been described—generally sloppily constructed cups or saucers of sticks and leaves lined with rootlets or moss and placed 1–2 m above the ground (Weidenfield 1982). Antpittas reach maximum species diversity in the Andes, where they show marked altitudinal species replacements (Graves 1985). As access to remote areas in the Neotropics has increased and equipment for avian survey work has improved, numerous new antpitta species have been described (Lowery and O'Neill 1969, Schulenberg and Williams 1982, Graves 1987, Stiles 1992, Krabbe et al. 1999). However, no previous study has examined the phylogenetic history of the group. Here, we (1) reconstruct the evolutionary relationships of antpittas and (2) examine the evolution of selected morphological and vocal characters in a phylogenetic context.

History of antpitta taxonomy.—Ridgway (1911) followed Sclater (1890) in placing the antpittas as a subfamily of the Formicariidae (the Grallarinae), but expanded the subfamily to include eight genera: *Rhopoterpe*, *Pittasoma*, *Grallaricula*, *Grallaria*, *Hypsibemon*, *Oropezus*, *Myrmothera*, and *Hylopezus*. Ridgway (1911) added bill morphology, presence of rictal bristles, and tarsal scutellation to the characters used by Sclater (1890) to diagnose those genera. Cory and Hellmayr (1924) recognized six genera of antpittas in their subfamily Myrmotherinae (*Myrmornis*, *Pittasoma*, *Grallaricula*, *Thamnocharis*, *Myrmothera*, and *Grallaria*), but offered little explicit character support. Incongruously, *Myrmothera* was separated from *Grallaria* and *Thamnocharis* on the basis of the absence of rictal bristles; but *Hylopezus*, which also lacks rictal bristles, was included in *Grallaria* (Cory and Hellmayr 1924). That scheme was followed by Peters (1951), with the exception of the subfamilial divisions.

On the basis of plumage characteristics, skeletal characters, and morphometric measurements, Lowery and O'Neill (1969) revised the subfamily Grallarinae to near its current composition by including five antbird genera: *Grallaria*, *Grallaricula*, *Hylopezus*, *Myrmothera*, and *Pittasoma*. *Grallaria* was further divided into four subgenera (*Grallaria*, *Thamnocharis*, *Oropezus*, and *Hypsibemon*). The notion of

previous authors (Sclater 1890, Ridgway 1911, Cory and Hellmayr 1924, Peters 1951) that *Hylopezus*, *Myrmothera*, and *Grallaricula* were congeneric with *Grallaria* was disputed.

Lowery and O'Neill (1969) described *Hylopezus* and *Myrmothera* as having a type 5 or 6 sternum (following Heimerdinger and Ames 1967; four notches), lacking rictal bristles, and lacking scutellation and convolution on the inner edge of the tarsus. In contrast, *Grallaricula* was described as having conspicuous rictal bristles, as well as a type 5 sternum. Lowery and O'Neill (1969) made the greatest taxonomic changes within *Grallaria*, which they subdivided into the four subgenera on the basis of plumage, morphometrics, bill shape, and degree of tarsal scutellation. At the generic level, *Grallaria* was separated from other antpittas by having an indistinctly ridged culmen, rictal bristles, and a type 3 sternum (two notches).

Recent systematic work.—Sibley and Ahlquist (1990) offered the first molecular evidence for the separation of typical and ground antbirds. The ground antbirds showed a close relationship to the Conopophagidae and Rhinocryptidae. A single antpitta specimen was examined (*Grallaria ruficapilla*) and was found to be the sister lineage to the antthrushes (*Formicarius* and *Chamaeza*). Chesser (2004) examined the molecular systematics of the New World suboscines and included three antpitta genera (*Grallaricula*, *Myrmothera*, and *Grallaria*) and one antthrush (*Formicarius*) in the study. The three antpitta genera formed a monophyletic lineage sister to a large tracheophone clade that included the Rhinocryptidae, Furnariidae, Dendrocolaptidae, and *Formicarius* antthrushes; the antpittas and the *Formicarius* antthrush were paraphyletic. Irestedt et al. (2002) studied the biogeography of suboscine passerines and included four traditional genera from the Formicariidae (*Chamaeza*, *Formicarius*, *Grallaria*, and *Hylopezus*). As in Chesser (2004), the antpittas formed a monophyletic lineage, but the antthrushes grouped with the Rhinocryptidae. Irestedt et al. (2002) did not find support for a sister relationship between the antthrushes and antpittas.

MATERIALS AND METHODS

Taxa examined.—We analyzed DNA sequences for at least two species from each of the five

currently recognized antpitta genera. Given the diversity and morphological complexity of the genus, we included 8 representatives from *Grallaria*, for a total of 16 putative ingroup taxa. Representatives of other suboscine families were included: two conopophagids, two rhinocryptids, two thamnophilids, and one antthrush (*Chamaeza campanisona*) were also sequenced as outgroups, for a total of 23 species sampled (Table 1). We obtained freshly frozen or ethanol-preserved tissues (liver, heart, and muscle) 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). In each case, representatives of ingroup genera were chosen to be as phenotypically disparate as possible.

Molecular methods.—We extracted genomic DNA from each sample using QIAmp tissue extraction kits (Qiagen, Valencia, California). We amplified the 3' end of the

cytochrome-*b* gene (378 base pairs [bp]) and a segment of the ND2 gene (501 bp) using conventional thermal-cycling techniques (Kocher et al. 1989). Cytochrome-*b* primers (H-15915 5'-CCAGACCTCCTAGGAGACCCAGA-3' and L-15507 5'-AACTGCAGTCATCTCCGGT TTACAAGAC-3') were developed by S. Hackett (pers. comm.), and ND-2 primers (H-6313 5'-GGCTGAATRGGMCTNAAAYCARAC-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 s, annealing at 55°C for 30 s, and extension at 70°C for 90 s. Extension time was lengthened 4 s per cycle for 35 cycles. Target DNA amplified using the thermal cycler was then purified using low-melt (1%) NuSieve GTG agarose (FMC BioProducts, Rockland, Maine) gel electrophoresis for 45 min at 85–95 volts. We excised bands containing target products from the low-melt electrophoresis gel, and we recovered DNA using QIAquick spin columns. The purified product was amplified using

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

Taxa	Collection	Tissue number	GenBank numbers ^a
<i>Myrmornis torquata</i>	KUNHM	1311	AY370565, AY370602
<i>Phlegopsis nigromaculata</i>	KUNHM	447	AY370561, AY370598
<i>Liosceles thoracicus</i>	FMNH	4545	AY370558, AY370595
<i>Rhinocrypta lanceolata</i>	LSUMNS	18813	AY370559, AY370596
<i>Conopophaga lineata</i>	FMNH	5288	AY370555, AY370592
<i>C. peruviana</i>	KUNHM	672	AY370554, AY370591
<i>Chamaeza campanisona</i>	LSUMNS	5385	AY370536, AY370573
<i>Grallaricula lineifrons</i>	ANSP	3869	AY370538, AY370575
<i>G. flavirostris</i>	LSUMNS	7973	AY370539, AY370576
<i>Myrmothera campanisona</i>	LSUMNS	9600	AY370548, AY370585
<i>M. simplex</i>	LSUMNS	7408	AY370549, AY370586
<i>Hylopezus fulvoiventris</i>	ANSP	4282	AY370552, AY370589
<i>H. berlepschi</i>	FMNH	1421	AY370553, AY370590
<i>Grallaria squamigera</i>	LSUMNS	6254	AY370540, AY370577
<i>G. varia</i>	LSUMNS	7528	AY370541, AY370578
<i>G. rufula</i>	LSUMNS	1218	AY370542, AY370579
<i>G. blakei</i>	LSUMNS	5620	AY370543, AY370580
<i>G. ruficapilla</i>	ANSP	4810	AY370544, AY370581
<i>G. watkinsi</i>	ANSP	2906	AY370545, AY370582
<i>G. eludens</i>	LSUMNS	11263	AY370546, AY370583
<i>G. dignissima</i>	ANSP	3229	AY370547, AY370584
<i>Pittasoma rufopileatum</i>	LSUMNS	11860	AY370556, AY370593
<i>P. michleri</i>	LSUMNS	2285	AY370557, AY370594

^a GenBank numbers are cytochrome-*b* and ND-2 genes, respectively.

Abbreviations: KUNHM = University of Kansas Natural History Museum, FMNH = Field Museum of Natural History, LSUMNS = Louisiana State University Museum of Natural Science, and ANSP = Academy of Natural Sciences.

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 s, annealing at 50°C for 5 s, 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 analysis.—We assembled separate character-state matrices for cytochrome-*b* and ND2 gene sequences. We spliced and aligned heavy and light strands using the clustal algorithm of SEQUENCE NAVIGATOR (ABI Prism). Data were analyzed using maximum-parsimony (MP) and maximum-likelihood (ML) optimizations, with anthruses, tapaculos, typical antbirds, and gnateaters designated as outgroups. We selected outgroups on the basis of their reported close relationships to antpittas in previous higher-level phylogenetic studies (Sibley and Ahlquist 1990, Irestedt et al. 2002, Chesser 2004).

Parsimony analyses of the equally weighted, unordered data set were conducted, using heuristic searches with 1,000 random-taxon addition replications, and the tree bisection-reconnection and steepest descent options of PAUP*, version 4 (Swofford 2002). Although no saturation was detected for the ingroup antpitta taxa, saturation existed over the entire data set. To assess the potential affect of saturation on the phylogenetic results, we performed additional analyses 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 1,000 replications, each with 20 random-taxon-addition replications, and Bremer branch-support values (Bremer 1988, 1994; Sorenson 1996).

Maximum-likelihood analyses were performed on the data set, using heuristic searches with 10 random-addition replications in PAUP* (Swofford 2002). I used MODELTEST, version 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 model for optimizing sequence evolution for

that data set, with the following parameters: probability [A-C] = 0.5082, probability [A-G] = 20.0627, probability [A-T] = 0.6865, probability [C-G] = 1.0346, probability [C-T] = 7.5196, probability [G-T] = 1.0000; frequency [A] = 0.3603, frequency [C] = 0.3728, frequency [G] = 0.0474, frequency [T] = 0.2195; shape parameter = 0.8387; and proportion of invariant sites = 0.3650. Support for particular clades was assessed on the ML topology by bootstrapping, using 100 heuristic searches with random-addition replicates.

Nonmolecular data.—Previous authors have suggested that plumage, skeletal characters, and syringeal morphology can be useful in diagnosing major antpitta lineages (e.g. Heimerdinger and Ames 1967, Lowery and O'Neill 1969, Ames 1971). Here, morphological characters were cladistically scored for phylogenetic information and mapped onto the molecular-derived topology. Mapping of those key morphological characters onto the molecular phylogeny allowed for added discussion of the evolution of morphological characters in antpittas and elucidation of significant morphological synapomorphies for the lineage.

RESULTS

Molecular results.—The aligned data matrix included 879 molecular characters (378 from cytochrome-*b* and 501 from ND2), 419 (47.7%) of which were phylogenetically informative. No insertions, deletions, or stop codons were observed. All sequences translated into amino acids, so it is unlikely that nuclear copies of the mitochondrial DNA were sequenced. Mean uncorrected pairwise divergence among the taxa included in the study was 20.2% and ranged from 4.8% (between the two species of *Myrmothera*) to 26.4% (between *Liosceles* and *Conopophaga lineata* and *Pittasoma rufopileatum*). Within antpittas, sequence divergence ranged from 4.8% to 20.1% (between *Grallaria ruficapilla* and *Grallaricula flavirostris*), with an average of 16.7%. The base frequencies calculated from the data set were [A] = 31.6%, [C] = 32.9%, [G] = 8.7%, and [T] = 26.8%. The transition:transversion ratio calculated from the most parsimonious tree was 1.53.

Phylogenetic results.—Maximum-parsimony analysis of the combined data set produced a single most parsimonious tree (tree length [TL] = 1,794, consistency index [CI] = 0.429, retention index [RI] = 0.481, rescaled consistency index

[RC] = 0.286; Fig. 1). Maximum-likelihood analysis of the combined sequence data produced a most likely tree (score $-\ln = 8362.1173$) that is identical in topology to the parsimony tree. Bootstrap support for the completely resolved tree was high, with most ingroup clades being detected by more than 80% of bootstrap replicates in both MP and ML analyses. The structure of the single most parsimonious tree was robust to the various weighting schemes employed, given that none of the unequal weightings changed the tree topology. Additional optimization models (TVM + G + I and TIM + G + I, the models selected by MODELTEST as next most likely to explain this molecular data set) were used to produce most-likely trees, and all produced topologies were identical to the original topology described below.

Nonmolecular results.—I selected 14 nonmolecular characters to map onto the molecular-based phylogeny. Of those, two were skeletal (Heimerdinger and Ames 1967), seven were based on plumage or soft-part colors (Lowery and O'Neill 1969), and five dealt with tarsal scutellations (Cory and Hellmayr 1924), rectal bristles (Lowery and O'Neill 1969), and egg color (Weidenfield 1982). A modified phylogenetic tree of the antpittas examined in the study show the polarity of the 14 nonmolecular characters (Fig. 2). Only two of those characters show reversals on the antpitta-only tree: bluish-gray tarsi are synapomorphic for *Grallaria* but are reversed in *G. watkinsi*, and pink tarsi are synapomorphic for all other antpittas (*Grallaricula*, *Hylopezus*, and *Myrmothera*), except *Grallaricula lineifrons*.

Tree topology.—Regardless of analysis technique or weighting scheme, the same tree topology was produced from the combined data set. With anthrushes, tapaculos, typical antbirds, and gnateaters as outgroups, the remaining taxa formed a completely resolved and well-supported monophyletic group of two major lineages. The first lineage includes the thamnophilid genera *Myrmornis* and *Phlegopsis* as sister taxa to a previously undescribed relationship of the gnateater genus *Conopophaga* and the antpitta genus *Pittasoma*. Although moderate support (79% MP, 52% ML) exists for the thamnophilids + conopophagids + *Pittasoma* relationship, the sister relationship of *Conopophaga* + *Pittasoma* is supported in 100% of bootstrap replicates in both MP and ML analyses.

The second major lineage of the ingroup includes the antpitta genera *Grallaricula*, *Hylopezus*, *Myrmothera*, and *Grallaria*, supported by 69% (MP) and 90% (ML) of bootstrap replicates. Within that lineage are two well-supported subclades. The first subclade includes *Myrmothera* + *Hylopezus*, with the diminutive *Grallaricula* as their sister clade. All those clades are supported by at least 92% bootstrap values (MP and ML). The second subclade is the speciose genus *Grallaria*. Within *Grallaria*, *G. eludens* and *G. dignissima* are sister taxa and form a sister lineage to *G. ruficapilla* + *G. watkinsi*; *Grallaria rufula* + *G. blakei* form the sister lineage to that first group of four species. The basal lineage within the genus *Grallaria* are the larger-sized antpittas, *G. squamigera* and *G. varia*. Most of the relationships within *Grallaria* are supported in >80% of the bootstrap replicates in both MP and ML. Aside from a very few minor deviations, tree topologies based on the individual data sets (not shown) were completely congruent with analyses of the combined molecular data sets.

DISCUSSION

Using anthrushes, tapaculos, typical antbirds, and gnateaters as outgroup taxa resulted in a phylogenetic tree that consisted of three major lineages. The tree topology was well supported and conserved, regardless of character optimization criteria or search methodology. Of the three major lineages in the phylogeny, one represents a completely new and previously undocumented sister relationship of the antpitta genus *Pittasoma* and the gnateater genus *Conopophaga*. The remaining two lineages include traditional antpitta genera: the first is the large and complex genus *Grallaria*, and the second includes *Hylopezus* as sister to *Myrmothera*, and *Grallaricula* as their sister taxon.

The gnateaters.—One of the best-resolved and best-supported results of the present study is the previously unreported clade composed of *Pittasoma* + *Conopophaga*. Although the two genera differ appreciably in size, they share several interesting morphologically derived similarities. Both genera have broad, flat, "flycatcher-like" bills that can be used for flycatching during brief sorties from the ground or low perches (Sick 1993, Ridgely and Tudor 1994, Whitney 2003, N. H. Rice pers. obs. in *Conopophaga*). Species of *Pittasoma* and most *Conopophaga* have

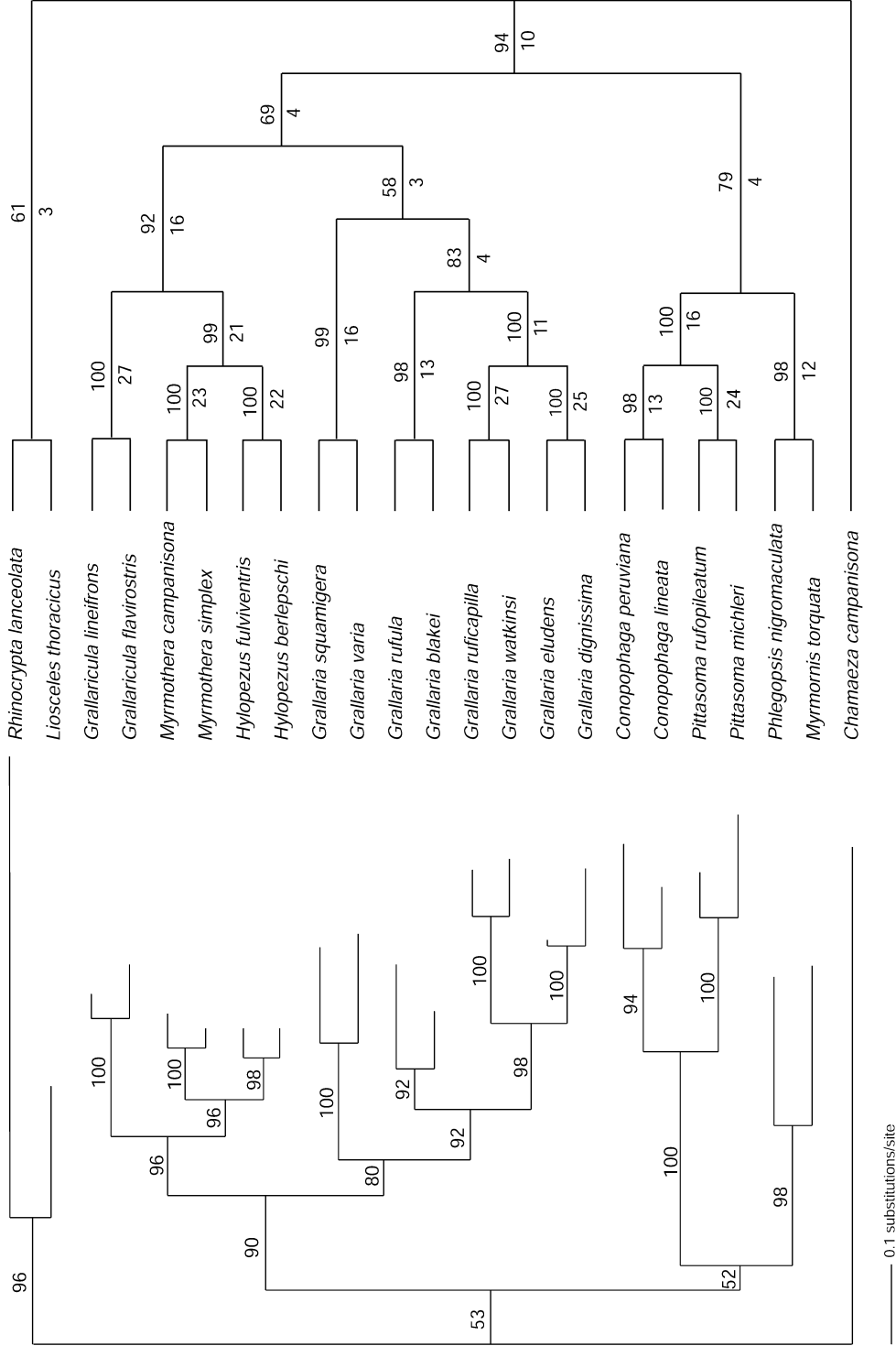


FIG. 1. Most likely (left) and most parsimonious (right) tree topology of the combined molecular data set. Numbers above each internode refer to bootstrap values. Numbers below each internode refer to Bremer Decay Indices (in parsimony tree) or substitutions per site (likelihood tree).

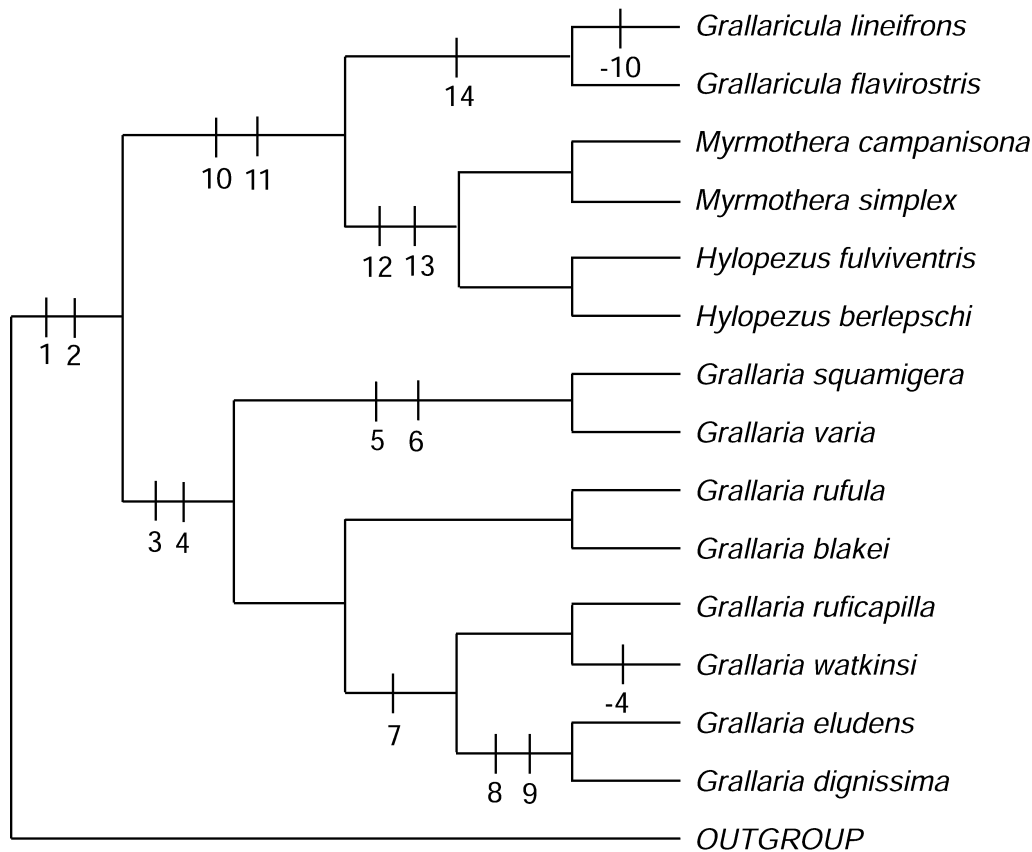


FIG. 2. Major morphological features coinciding with the molecular phylogeny. Numbers refer to the following characters: (1) holospidean tarsal scutellation, (2) bluish-greenish eggs, (3) two-notched sternum, (4) bluish-gray tarsi, (5) black or white malar stripe, (6) barring or scaling on upper breast, (7) dark feather shafts on flank feathers, (8) elongated brown flank feathers, (9) streaked breast and flanks, (10) pink tarsi, (11) four-notched sternum, (12) no rictal bristles, (13) scutes fused, and (14) rictal bristles.

bold eyestripes: black in *Pittasoma* and white for males or gray for females in *Conopophaga*. Several *Conopophaga* (e.g. *C. melanops* and *C. peruviana*) and *Pittasoma* also have a unique spotting pattern on their wing coverts.

Vocal characters can also provide evidence of a shared history between genera. Several species of *Conopophaga* (*C. aurita*, *C. roberti*, and *C. melanops*), along with *P. rufopileatum*, produce primary songs composed of a series of clear “tu” notes, often rising in pitch and decreasing in frequency at the end of each vocalization (Hilty 1975, Ridgely and Tudor 1994, Isler and Whitney 2002). Other species in the group produce songs reminiscent of harsh and raspy *Sciurus*-squirrel vocalizations (*P. michleri*, *C.*

castaneiceps, *C. melanogaster*; Karr 1971, Robbins et al. 1985). The remaining species in the group produce vocalizations of an intermediate quality, ranging from the *Myiarchus* flycatcher-like voice of *C. peruviana* (“wheep” notes given in succession) to the rolling scratchy vocalizations of *C. ardesciaca* and *C. castaneiceps*. Although the syrinx of *Conopophaga* has been described as being “ground antbird-like,” the syrinx of *Pittasoma* is as yet undescribed (Ames 1971). Additional research is needed in the areas of tracheophone song evolution and polarization of vocal characters to completely understand the level of phylogenetic information in voice.

Both *Conopophaga* and *Pittasoma* have exaspidian tarsal scutellation (Ridgway 1911, Ames et

al. 1968), which is unique to the tracheophone suboscines. Indeed, only the tyrannoids share that scutellation pattern in the suboscine lineage. All antpitta genera, except *Pittasoma*, have holaspidean scutellation; anthruses, tapaculos, and typical antbirds all have taxaspidean scutellation patterns (Ames et al. 1968).

Natural history evidence of the nests and eggs of *Pittasoma* and *Conopophaga* also support a shared history. Species of both genera make relatively thin-walled cup nests constructed of dark rootlets (Zimmer and Isler 2003). As with typical antbirds, nests of *Conopophaga* and *Pittasoma* are typically placed in the fork of a branch or in the crown of a palm (Oniki and Willis 1982, Zimmer and Isler 2003). Eggs of *Conopophaga* and *Pittasoma* have the shared derived character of rusty or purplish coloration, in contrast to antpittas, which tend to have a bluish or greenish coloration (Zimmer and Isler 2003). Biogeographically, a *Pittasoma* + *Conopophaga* sister relationship would suggest an ancient radiation, with *Pittasoma* west of the Andes and *Conopophaga* to the east. That scenario is supported by the rather profound level of sequence divergences (16.2–19.1%) between the *Pittasoma* and *Conopophaga* species sampled here.

Using more characters, Chesser (2004) and Irestedt et al. (2002) uncovered weak support for a sister relationship between typical antbirds and gnateaters. Using fewer characters but examining more taxa, I found moderate support for a thamnophilid + conopophagid relationship, also including *Pittasoma*. It is interesting to note that species from this clade all show fairly strong sexual dichromatism and the unique plumage character of white interscapular feathers, both likely synapomorphies for the lineage. The syrinxes of those two clades, however, are quite different. Gnateaters (and presumably *Pittasoma*) have a simple insertion of the extrinsic sternotracheal muscle and completely lack intrinsic sternotracheal muscles, whereas typical antbirds have a bifurcation at the insertion of the extrinsic sternotracheal muscles and have well-developed intrinsic sternotracheal muscles (Ames 1971).

The antpittas.—With the deletion of *Pittasoma*, the group is identical to the Grallarinae of Lowery and O'Neill (1969). Within that clade are two well-supported sublineages: (1) the large and complex genus *Grallaria* and (2) the generally smaller antpittas *Grallaricula*, *Myrmothera*, and

Hylopezus (Fig. 2). Members of both subclades hop on the ground in an upright position; have short tails, deep and robust bills, and holospidean tarsal scutellation; and generally lay round bluish or greenish eggs (Lowery and O'Neill 1969, Fjeldså and Krabbe 1990, Sick 1993).

Grallaria clade.—Heimerdinger and Ames (1967) found that all of the *Grallaria* specimens they examined had two-notched sterna (Fig. 2). Additionally, all *Grallaria* antpittas (except *G. watkinsi*) have bluish-gray tarsi (Ridgely and Tudor 1994; Fig. 2). Results of parsimony and likelihood analyses support the monophyly of *Grallaria* and suggest two major clades within the genus. The first clade is composed of large-bodied antpittas of the subgenus *Grallaria* (*G. squamigera* and *G. varia*). Species of that lineage have ochraceous breasts with contrasting scaled gray heads and backs (Fig. 2). The presence of either black or white (or both) malar stripes is probably synapomorphic for that clade, as is the prominent barring pattern of the upper breast of most species (Fig. 2). Members of that lineage also have unique vocalizations that likely represent synapomorphies: they give loud vocalizations that carry far and consist of a long series of repeated "hoots," often ending in a crescendo.

The second major lineage of *Grallaria* antpittas contains all other taxa included in the study, forming three well-supported lineages. The first is the *Grallaria rufula* complex of relatively small-sized antpittas of restricted range in the Andes. Vocalizations of the two described species are quite different from one another. *Grallaria rufula* has a song that is a series of slurred whistles, whereas songs of *G. blakei* consist of a long series of relatively staccato notes.

Another sublineage within *Grallaria* includes the lowland Amazonian antpitta taxa *G. dignissima* and *G. eludens*. Several morphological characters are likely synapomorphies: elongated brownish flank feathers with cream-colored median vanes and rachis (also present on the lower back) and a boldly streaked pattern on the breast and flanks (Fig. 2). Lowery and O'Neill (1969) reported that specimens of those species consistently have only eight tail feathers. Vocalizations of those taxa are virtually identical, consisting of a two-note song, the second being longer than the first and rising slightly at the end.

The final sublineage within the clade is *G. watkinsi* + *G. ruficapilla*. On the basis of plumage

morphology, distribution, and vocalizations, *G. bangsi* and *G. kaestneri* can also be placed with the clade. Species in this clade have moderately streaked upper breast patterns and some rufous patterning on the head or throat. Vocalizations generally consist of two- or three-noted whistles, with the final note rising or wavering slightly. An interesting exception to that pattern is *G. watkinsi*, which has four or five introductory notes, leading to a final note that ascends in frequency. That antpitta is unique in that it lacks the bluish-gray tarsi common to all other *Grallaria* antpittas (Fig. 2) and has more introductory notes than its closest relatives.

For the species included here, molecular characters supported the subgenera delineated by Lowery and O'Neill (1969). Within *Grallaria*, the streak-breasted subgenus *Hypsibemon* (*G. watkinsi* + *G. ruficapilla*) is the sister group to the enigmatic subgenus *Thamnocharis* (*G. eludens* + *G. dignissima*). All members of that group (*Hypsibemon* + *Thamnocharis*) have distinctive dark feather shafts and elongated flank feathers (Fig. 2). The small, plain-breasted subgenus *Oropezus* (*G. rufula* + *G. blakei*) forms the sister lineage to *Hypsibemon* + *Thamnocharis*. The large-bodied subgenus *Grallaria* (*G. varia* + *G. squamigera*) is sister to the *Oropezus* + *Hypsibemon* + *Thamnocharis*.

Hylopezus, *Myrmothera*, and *Grallaricula* antpittas generally have smaller bills (shorter and shallower) than in *Grallaria*. With the exception of *G. lineifrons*, members of this lineage have pinkish tarsi (Fig. 2). According to Heimerdinger and Ames (1967), all taxa in the group have four-notched sterna (Fig. 2). All my analyses supported *Hylopezus* as sister to *Myrmothera*. Members of the clade are all found in lowland Amazonian habitats, with just two being somewhat "highland" taxa (*M. simplex* of the Venezuelan tepuis and *H. nattereri* of the southern Brazilian highlands; Ridgely and Tudor 1994). *Hylopezus* and *Myrmothera* are the only antpitta genera that lack rectal bristles and have weakly defined tarsal scutellation (Ridgely 1911, Cory and Hellmayr 1924, Lowery and O'Neill 1969; Fig. 2). *Grallaricula* is strongly supported as sister to *Hylopezus* + *Myrmothera*. Unlike its sister group, *Grallaricula* have well-developed rectal bristles (Fig. 2).

Interpretation of morphological characters.—Variation in sternal notching has long been used to "separate" groups of suboscine passerines (e.g. Ames et al. 1968). The results here

delineated two broad categories of sternal morphology: two-notched and four-notched forms. Within each category outlined by Ames and colleagues are numerous intermediate levels ("types"). When placed in a phylogenetic context, sternal morphology appears to be useful only at the coarsest levels. For example, for taxa examined here, *Grallaria* antpittas all have two-notched sterna; whereas *Hylopezus*, *Myrmothera*, and *Grallaricula* all have four-notched sterna (Fig. 2). It seems impossible to further atomize the character into the "types" outlined by Ames et al. (1967). Extreme variation at the "type" level is likely attributable to ontogenetic changes, age of the specimen, and preparation type, rather than an indication of phylogenetic signal.

Like sternal notch variation, tarsal scutellation has long been used to diagnose major bird groups (Ridgely 1911, Sclater 1890). At the family level within the suboscine lineage, however, tarsal scutellation appears not to be historically informative (e.g. tyrannids and gnateaters both have exaspidean scutellation). Within tracheophones, scutellation mirrors the history of the lineage, with antpittas having holaspidean scutellation and *Conopophaga* and *Pittasoma* exaspidean scutellation.

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