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HIGH LEVELS OF MITOCHONDRIAL DNA DIFFERENTIATION IN TWO LINEAGES OF ANTBIRDS (*DRYMOPHILA* AND *HYPOCNEMIS*)

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ABSTRACT.—We assessed levels of genetic differentiation based on mitochondrial DNA sequences (portions of the cytochrome-*b* and ND2 genes) at several taxonomic levels in thamnophilid antbirds. Our focus was to investigate genetic differentiation among populations of two species in the genus *Drymophila* and to identify the sister genus to *Drymophila*. In addition, we present evidence of high levels of population subdivision in *Hypocnemis cantator* (Warbling Antbird). This widespread Amazonian taxon co-occurs, on a local scale, with *D. devillei* (Striated Antbird). Sequence divergences among populations of *D. devillei* and *D. caudata* (Long-tailed Antbird), two bamboo-specialists, often exceeded 2% between populations. Divergences within *H. cantator*, a species with more generalized habitat requirements and a more "continuous" distribution, were even higher, including 5.7% divergence between samples separated by 350 km of apparently continuous Amazonian forest. At higher taxonomic levels, genetic distances suggest that antbird genera and biological species are old. Genetic divergence between the two species that comprise the genus *Hypocnemis* was 9.3%, and divergence between *D. devillei* and *D. caudata* averaged 7.2%. Weighted parsimony and maximum-likelihood analyses supported *Hypocnemis* as the sister taxon to *Drymophila*; the genus *Myrmotherula* was not monophyletic, supporting previous allozyme analyses. In addition to the protein-coding sequences, we found that spacer regions between genes also provided phylogenetically informative characters from the level of suboscine families to within the biological species that we studied. *Received 31 March 1998, accepted 7 April 1999.*

WITH SOME 266 currently recognized biological species (Parker et al. 1996), the antbirds (formerly Formicariidae) recently have been divided into the Formicariidae (ground antbirds, 70 species) and Thamnophilidae (typical antbirds, 196 species) based on DNA-DNA hybridization data (Sibley and Ahlquist 1990). Members of these species-rich families are distributed throughout the Neotropics. Antbirds inhabit all levels of tropical forest and many different insectivorous niches such that as many as 40 species can occur at a single site. In this paper, we present data on genetic structure within and among three biological species (sensu Mayr 1963) of thamnophilid antbirds: *Drymophila devillei* (Striated Antbird), *D. caudata* (Long-tailed Antbird), and *Hypocnemis cantator* (Warbling Antbird).

The genus *Drymophila* has been considered to have eight species (Peters 1951), six of which are restricted to the Atlantic forests of eastern South America. The other two are the focus of this study and are thought to be restricted largely to areas of bamboo in the upper-tropical zone of the Andes (*D. caudata*) and in the western and southern parts of the Amazon basin (*D. devillei*; Fig. 1). The entire genus is currently under study by one of us (JMG) to understand its evolutionary history and how this history relates to current ecology and distribution.

Specialization on bamboo exhibited by *D. devillei* and *D. caudata* is known for a small guild of Neotropical birds (Parker 1982, Kratter 1997, Parker et al. 1997). Bamboo-specialist birds, like their preferred habitat, tend to have patchy distributions. In the Andean foothills, *D. caudata* occurs between 1,200 and 2,500 m from Venezuela to Bolivia. Three subspecies, with presumably disjunct distributions, have been described (Peters 1951), but even these subspecies probably are composed of disjunct populations subdivided by deep river valleys and high mountain ridges. Based on limited specimen data, *D. devillei* shows a similarly patchy distribution in the lowlands (Stotz 1990, Rid-

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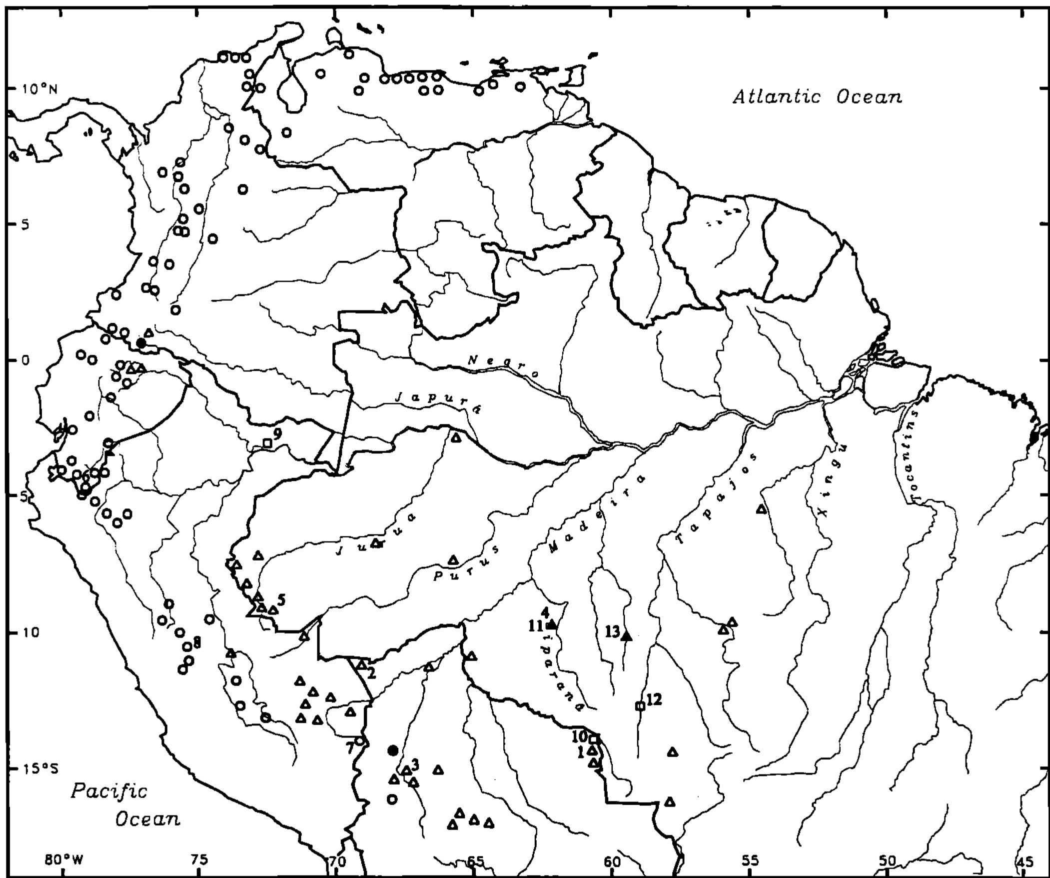

FIG. 1. Distribution of *Drymophila caudata* (circles) and *D. devillei* (triangles). In several places both species are known from the same sector (closed circles). Sites for samples of *Hypocnemis cantator* used in this study are also indicated (open squares); in several instances these sites correspond with localities where *D. devillei* occurs (dark triangles). Numbers depict localities in Appendix. The easternmost open triangle is where the type of *D. devillei subochracea* was collected. Locational data compiled and map prepared by M. and P. Isler.

gely and Tudor 1994, Stotz et al. 1997). Two subspecies have been described, both of which were considered to be probable biological species by Parker et al. (1996). The nominate form, *D. d. devillei,* is known from areas of bamboo in southeastern Peru and northern Bolivia, but several specimen records also exist from as far north as eastern Colombia (Stotz 1990). *Drymophila d. subochracea* is known from only a few localities that lie south of the Amazon, from the east bank of the Rio Madeira to a western tributary of the Rio Xingu in Brazil.

We present sequences from parts of the mitochondrial cytochrome-*b* (cyt *b*) and NADH dehydrogenase subunit 2 (ND2) genes for multiple populations of both subspecies of *D. devillei* and two populations of *D. caudata* from southern Peru. To establish the outgroup for the genus, we also obtained sequences from individuals representing a number of other small thamnophilids. To provide additional comparative data on genetic structure within biological species, we also included multiple samples of both biological species of *Hypocnemis.* Although these samples cover only a small portion of the geographic distribution of these two taxa (particularly for *H. cantator*), they provide more divergence data from another lineage from this part of Amazonia. Our results provide a clear picture of the high levels of genetic structure we believe are typical of many forest-dwelling Neotropical species.

Methods

DNA sequencing.—Samples of the 34 individuals used in this study were obtained from tissue collections of the Louisiana State University Museum of Natural Science (LSUMNS), the Academy of Natural Sciences in Philadelphia (ANSP), and the Bird Division of the Field Museum of Natural History (FMNH; Appendix). Voucher specimens are housed at these institutions, the Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG), and Museu de Zoologia da Universidade de São Paulo, Brazil (MZUSP). All DNA work was carried out in the Field Museum's Pritzker Laboratory for the Study of Molecular Systematics and Evolution. Samples were from the two species of *Drymophila* and eight other species of thamnophilids (*Terenura humeralis* [Chestnut-shouldered Antwren]; *Myrmotherula longipennis* [Long-winged Antwren]; *M. leucophthalma* [White-eyed Antwren]; *M. hauxwelli* [Plain-throated Antwren]; *Formicivora rufa* [Rusty-backed Antwren]; *F. grisea* [White-fringed Antwren]; *Hypocnemis hypoxantha* [Yellow-browed Antbird]; and *H. cantator*). We included multiple individuals of species in *Hypocnemis* because the genus has been hypothesized to be the closest relative of *Drymophila* (Ridgely and Tudor 1994:293). At the generic level, the goal of this sampling scheme was to confirm a suitable outgroup for genetic and ecological research on *Drymophila*, and not to reconstruct a phylogeny of thamnophilid genera. As a result, higher-level relationships among thamnophilids should be viewed as tentative. We also included a ground antbird (*Formicarius colma* [Rufous-capped Antthrush], Formicariidae), a woodcreeper (*Lepidocolaptes angustirostris* [Narrow-billed Woodcreeper], Dendrocolaptidae), an ovenbird (*Synallaxis albescens* [Pale-breasted Spinetail], Furnariidae), and a manakin (*Pipra pipra* [White-crowned Manakin], Pipridae). Using the phylogeny of Sibley and Ahlquist (1990), we designated the manakin as the outgroup.

DNA was extracted using either G NOME® or Puregene (Gentra Systems, Inc.) extraction kits. Pieces of two mitochondrial genes, cyt *b* and ND2, were amplified using the primers L15656 and H16065 for cyt *b* and L5215 and H5578 for ND2 (primer sequences are given in Hackett 1996). Fragments were PCR-amplified using standard conditions (available from the authors upon request; denaturation at 94°C, annealing between 45 and 54°C, and extension at 72°C in MJResearch PCR machines). A small aliquot of each amplicon was electrophoresed on an agarose gel to check for the correct fragment size and to verify the presence of a single clean PCR product. The remainder of the reaction was cleaned and concentrated using Microcon 100 tubes (Amicon) or Geneclean (BIO101). Cleaned double-stranded amplifications were cycle-sequenced using fluorescent dye terminator chemistry and the FS *Taq* enzyme (Applied Biosystems, Inc. [ABI]). Cycle-sequencing reactions were Nh_4OAc precipitated, rinsed in ethanol, dried, resuspended in a formamide-EDTA solution, and run on an ABI 377 Automated DNA Sequencer. Sequences were obtained from both strands of DNA, checked using the program Sequencher 3.0 (Gene Codes Corp.), aligned to the chicken (*Gallus gallus*) sequence (Desjardins and Morais 1990) to ensure there were no insertions or deletions of bases in the antbird sequences, and submitted to GenBank (AF118154 to AF118221; Appendix).

The following protocol was undertaken to ensure that the small fragments of DNA were mitochondrial in origin (not nuclear copies). (1) Sequences of selected individuals were verified by amplifying (with L14990 and H16065 for cyt *b* and L5215 and H6313 for ND2; sequences in Hackett [1996], except for H6313 [CCTTTATTTAAGGCTTTGAAGGC]) and sequencing a larger piece of mtDNA using the primers above. (2) Both DNA strands were sequenced to ensure accurate sequences. (3) Sequences were used only if they gave clean sequence (i.e. little background and no double peaks), and sequences were inspected for insertions, deletions, or stop codons that would indicate that the sequences would result in a nonfunctional protein. (4) Partition-homogeneity tests were performed to assess if the phylogenetic content of these two partial gene sequences was similar; nuclear copies would not necessarily be expected to have similar phylogenetic content to mitochondrial genes. (5) Genetic-distance matrices were generated separately for the two gene fragments and inspected for differences. (6) Sequences of individuals from the same collecting locality, population, or geographic region were expected to be genetically more similar than those of other populations or regions. If not, the sequences may not be mitochondrial and are in need of further analysis (e.g. cloning to assess the number of sequences represented in an individual).

Phylogenetic analyses.—All phylogenetic analyses were conducted with version 4.0d64 of PAUP*, written by David L. Swofford. We performed a partition-homogeneity test using 1,000 random partitions to determine if these partial gene sequences were incongruent with respect to their phylogenetic content (Farris et al. 1995, Cunningham 1997). In addition, we performed another partition-homogeneity test (1,000 random partitions) comparing third positions with first and second positions to determine if third positions gave a different phylogenetic signal (possibly because rate variation across codon positions may lead to saturation). After assessing the degree of saturation at all three codon positions (following Hackett 1996 and Griffiths 1997), we constructed maximum-parsimony trees on both unweighted and weighted sequence data. We present strict-consensus trees when more than one most-parsimonious tree was found. We explored the sensitivity of parsimony trees to the weighting scheme by down-weighting

transitions in saturated data partitions 2, 5, 10, 100, and 1,000 times. Weighted analyses based on results of saturation were accomplished using step matrices in PAUP*. For example, if transitions at third and first positions were down-weighted by a factor of 10, a weight of 10 was given to second positions to make their weight equivalent to a transversion at first or third positions. We assessed the amount of support for nodes using 100 bootstrap replicates (Felsenstein 1985). All searches were heuristic, with default options (keep best trees only, stepwise addition, swap on best tree only, quick swap enabled, hold 1 tree at each step, TBR branch-swapping, MULPARS, swap on best trees only) except for performing 100 random addition sequence replicates.

Maximum-likelihood (ML) analyses have been suggested to perform better under long-branch attraction conditions (Huelsenbeck and Hillis 1993); therefore, we used PAUP* to estimate ML trees to compare with parsimony analyses. Because of time constraints associated with ML analyses, individuals differing only slightly from each other were excluded from the analysis (e.g. only one individual from the Rondônia sample of *D. devillei* [DEVI] was used). The ML data set contained 20 individuals. Using the suggested procedure of Huelsenbeck and Rannala (1997), likelihood-ratio tests (LRTs) were performed to select the model of evolution for the detailed ML tree search. A preliminary neighbor-joining (NJ) tree was generated using Kimura 2-parameter distances, and the likelihood score for that tree was noted under a simple HKY (Hasegawa et al. 1985) model (two substitution types, all sites assumed to evolve at the same rate, molecular clock not enforced). LRTs were performed by adding parameters to the model and testing for a significant improvement in likelihood scores on this neighbor-joining tree. In this analysis, the HKY model, which assumes only two substitution types, was compared with a general time-reversible model (Yang 1994) that has six substitution types. These models were compared both with and without rate heterogeneity (proportion of invariant sites and gamma distribution shape parameters estimated). Finally, the assumption of a molecular clock was assessed using ML analyses. A lack of significant difference in likelihood scores with the addition of parameters dictated that the less parameter-rich model would be used in further ML searches. ML searches were then performed with the model of evolution suggested by the LRTs and the starting parameters (empirical base frequencies, matrix of substitution types, proportion of invariant sites, and shape of gamma distribution) estimated from the original NJ tree. Ten addition sequence replicates were performed using heuristic searches. Only one addition sequence replicate was performed for each of the 100 bootstrap replicates because of time limitations.

RESULTS

Mitochondrial or nuclear copies.—Only one instance occurred where a sequence amplified from the small fragment differed from the larger one. The small fragment of cyt *b* from *Hypocnemis hypoxantha* REAJ232 resulted in a sequence that was missing a few bases compared with the sequences from the larger amplified fragment. The larger fragment sequence differed by only two nucleotides from the other *H. hypoxantha* individual that we had in our data set and therefore was hypothesized to be mitochondrial. Sequences of all other individuals were from both strands of DNA, had little background or double peaks, and translated without stop codons. Partition-homogeneity tests and genetic-distance matrices revealed no significant differences between the two partial gene sequences. Individuals from the same collecting locality or geographic region were genetically more similar to each other than to individuals from other geographic regions or species. Therefore, we believe that these sequences were mitochondrial in origin.

Informative variation.—The gene regions we studied are positions 5241 to 5577 in ND2 and 15664 to 16035 in cyt *b* (numbers correspond to the chicken sequence; Desjardins and Morais 1990). We also report sequences of the spacer region between cyt *b* and the threonine t-RNA (bases 16036 to 16038 of chicken; Table 1). Length variation occurs in this spacer (ranging from two to four bases in different suboscine families). Therefore, the data set contains 713 characters (337 ND2, 372 cyt *b*, 4 spacer). Parsimony-informative sites are evenly distributed in both genes (119 ND2 [35.3% of total bases], 133 cyt *b* [35.8%]). Both genes have a similar proportion of informative sites across codon positions except that ND2 has proportionally twice as many informative second-position sites compared with cyt *b* (10.7% vs. 4.0%).

Neither partition-homogeneity test was significant, suggesting that differences in phylogenies from these pieces of cyt *b* and ND2 (P = 0.16) can be attributed to sampling error, as can differences between first and second codon positions compared with third (P = 0.65). Thus, sequence data from all regions (cyt *b*, ND2, and spacer regions) were combined for phylogenetic analyses.

TABLE 1. Sequence variation of spacer between cyt-*b* and threonine t-RNA genes.

Taxon	Family	Spacer sequence
Pipra pipra	Pipridae	CT
Formicarius colma	Formicariidae	CT
Lepidocolaptes angustirostris	Dendrocolaptidae	AC
Dendrocolaptes certhia	Dendrocolaptidae	AC[a]
Synallaxis albescens	Furnariidae	AACC
Smithornis sharpei	Eurylaimidae	CGCA[a]
Herpsilochmus rufimarginatus	Thamnophilidae	CGT
Myrmotherula leucophthalma	Thamnophilidae	CGT
Hypocnemis cantator (Mato Grosso)	Thamnophilidae	CGT
Drymophila devillei devillei (La Paz, Pando, Acre)	Thamnophilidae	CGT
Drymophila caudata	Thamnophilidae	CGT
Hylophylax naevia	Thamnophilidae	CGT[b]
Hylophylax punctulata	Thamnophilidae	CGT[b]
Hylophylax naevioides	Thamnophilidae	CGT[b]
Formicivora grisea	Thamnophilidae	CGC
Formicivora rufa	Thamnophilidae	CAC
Teremura humeralis	Thamnophilidae	CAC
Myrmotherula longipennis	Thamnophilidae	CAC
Phlegopsis nigromaculata	Thamnophilidae	CAC
Hypocnemis hypoxantha	Thamnophilidae	CAC
Hylophylax poecilinota	Thamnophilidae	CAC[b]
Hypocnemoides maculicauda	Thamnophilidae	CAC[b]
Drymophila devillei "subochracea" (Rondônia, Santa Cruz)	Thamnophilidae	CAC
Hypocnemis cantator (Rondônia, Santa Cruz)	Thamnophilidae	CAT
Myrmotherula hauxwelli	Thamnophilidae	CAT
Thamnophilus doliatus	Thamnophilidae	CCC[a]

[a] Mindell et al. 1998.
[b] J. M. Bates unpubl. data.

Equally weighted parsimony analyses.—Equally weighted parsimony analyses resulted in a single most-parsimonious tree (length 997; CI = 0.41, excluding uninformative characters; RI = 0.67; Fig. 2). The formicariid antbird (*Formicarius colma*) is separated from the thamnophilid antbirds, and *Formicarius* is in a clade with the woodcreeper (*Lepidocolaptes*) and ovenbird (*Synallaxis*). This relationship is not supported by bootstrap analyses, nor is a sister relationship between the woodcreeper and ovenbird. Monophyly of thamnophilids receives only 56% bootstrap support. Among higher-level antbird relationships, bootstrap values (Fig. 2) indicate strong support for monophyly of *Formicivora* and for a clade including *Myrmotherula longipennis* and *Formicivora* (although these taxa are not very similar to each other genetically, differing by 11% uncorrected sequence divergence; Table 2). *Hypocnemis* is not monophyletic in equally weighted analyses, and *Hypocnemis cantator* is the sister taxon to *Drymophila* (although this relationship is not supported by bootstrap analyses). Strong support exists for nodes within *Drymophila* species, monophyly of each species of *Drymophila,* and a sister-group relationship between the two *Drymophila* species. Deep mitochondrial divergences also occur among populations of *Hypocnemis cantator* (up to 6% sequence divergence), and some relationships receive strong support. Saturation analyses suggest that substitutions within and among both *Drymophila* and *Hypocnemis* species are not saturated. Therefore, relationships within these genera as suggested by the equal-weight analyses are preferred.

Weighted parsimony analyses.—Although saturation does not appear to be a problem within and among antbird species, when other antbird genera are included, transitions at first and third positions are saturated (plots not shown). We applied step matrices to these data partitions that counted 2 to 1,000 steps for a transversion and only one step for a transition, thereby down-weighting the transitions. Because second positions were not saturated in this analysis, they were given a weight of 2 to 1,000 to make them equal to the transversions at first and third positions.

The 2× weighted analysis resulted in four most-parsimonious trees (length 1,294; strict-consensus tree shown in Fig. 3A). A sister-

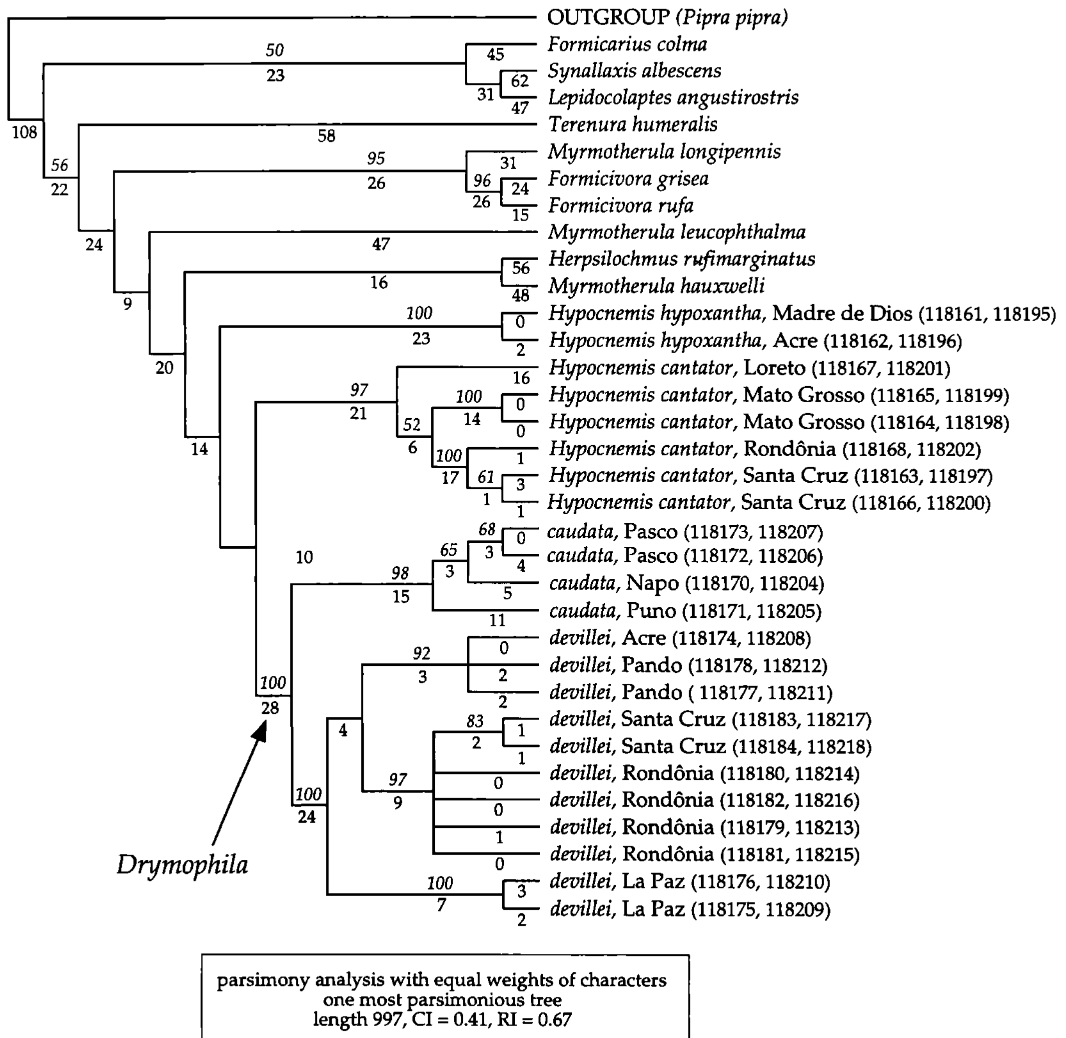

FIG. 2. Parsimony analysis with equal weights of mitochondrial cytochrome-*b* and ND2 characters. Numbers above the branches are bootstrap values for nodes with 50% support or better. Numbers below the branches are branch lengths.

group relationship between the ovenbird (*Synallaxis*) and the woodcreeper (*Lepidocolaptes*) was supported in 77% of the bootstrap replicates. Monophyly of the thamnophilids was supported by a 90% bootstrap value. Relationships within *Drymophila* and *Hypocnemis* were unchanged from equal weighting with this weighting scheme (not shown). However, a sister-taxon relationship between the two *Hypocnemis* species was recovered in three of the four most-parsimonious trees (bootstrap support of 55%), and these species are placed as sister to *Drymophila* with high bootstrap support (82%).

The relationship between *Myrmotherula longipennis* and *Formicivora* was found with this weighting scheme as well (98% bootstrap).

The 5× weighting resulted in one most-parsimonious tree (length 2,178; Fig. 3B) and differed from 2× weighting in supporting a basal position for the woodcreeper/ovenbird clade with the formicariid (*Formicarius colma*) as sister to the thamnophilids. *Hypocnemis* is monophyletic (88% bootstrap) and sister to *Drymophila* (89% bootstrap), as in the 2× weighted analysis. Relationships among other antbird genera vary depending on weighting scheme.

Relationships within *Drymophila* and *Hypocnemis* remained unchanged from unweighted analyses.

Analyses down-weighting first- and third-position transitions by 10, 100, and 1,000× resulted in the same topology (Fig. 3C) with relatively similar bootstrap values. These trees differ in the placement of *Terenura humeralis*; all other relationships are unchanged from the 5× weighted analysis.

Maximum-likelihood analyses.—Likelihood-ratio tests suggested a model of evolution with the following properties: (1) general time-reversible (six substitution types; substitution matrix estimated from original NJ tree); (2) proportion of invariant sites estimated using maximum likelihood (on NJ tree); (3) rates for variable sites follow a gamma distribution with shape parameter estimated by maximum likelihood (on NJ tree); (4) empirical nucleotide frequencies; and (5) no assumption of a molecular clock. The following parameters were derived from the initial NJ tree and were input into the maximum-likelihood algorithm of PAUP* prior to searches: empirical base frequencies, A = 0.31086, C = 0.32217, G = 0.10711, T = 0.25987; proportion of invariant sites, 0.539972; rates for variable sites following a gamma-shape distribution, 1.39454 (four rate categories, average represented by mean); and a substitution-rate matrix (which can be reconstructed from the original data or obtained from the authors upon request). Using these input parameters and 10 addition sequence replicates, one tree resulted (−ln likelihood score = 4779.89182; Fig. 4). This tree has relationships among genera exactly as 10 to 1,000× weighted analyses, including monophyly of *Hypocnemis* and its sister relationship to *Drymophila.*

DISCUSSION

Genetic structure in Drymophila devillei, Drymophila caudata, *and* Hypocnemis cantator.—Our data demonstrate high levels of genetic differentiation between the two *Drymophila* species (7.2%) and substantial genetic differentiation among different populations of all three biological species that we examined. For *D. devillei,* multiple individuals were available for most localities, and individuals from the same localities exhibited little, if any, differentiation. Two clades are supported, one containing birds from sites in northern Bolivia (DEVI La Paz, DEVI Pando and DEVI Acre; Fig. 3) and another of birds from sites in eastern Bolivia and western Brazil (DEVI Santa Cruz and DEVI Rondônia). Both populations from northern Bolivia have white breasts and are referable to nominate *D. d. devillei.* However, substantial differentiation exists between samples from these two localities (2.5% sequence divergence; Table 2), which are separated by about 370 km.

The taxonomic identity of birds from eastern Bolivia (DEVI Santa Cruz) and the Rio Jiparaná (western Brazil, DEVI Rondônia) is more problematic. Parker et al. (1997) described the Jiparaná birds as also being the nominate form. However, a recent reexamination of these specimens by JMB (in MPEG), in which males of nominate *devillei* were compared with a male from the Rio Jiparaná and a male identified as *D. d. subochracea* from the Rio Aripuanã (ca. 350 km east-southeast of the Rio Jiparaná site [Novaes 1976]), revealed that the Jiparaná male was buffy below and thus more like the Aripuanã bird than nominate *devillei.* Although no comparative material was available, three females from the Rio Jiparaná site also were buffy below (matching the original description of *D. d. subochracea;* Chapman 1921). The specimens from the Jiparaná have not been directly compared with Santa Cruz specimens; however, JMB has seen both series and considers them to be identical. An additional problem arises because D. F. Stotz (pers. comm.) notes that the Rio Jiparaná and Santa Cruz birds could represent a distinct population of *D. devillei.* The type locality of *D. d. subochracea* is the Rio Curuá, a tributary of the Rio Iriri and subsequently the Rio Xingu (Fig. 1; Chapman 1921, specimens in the Museu Nacional, Rio de Janeiro, Brazil; no tissues available for genetic analyses). Thus, this site lies in a different area of endemism from the Jiparaná and Santa Cruz sites (the Pará area of endemism rather than the Rondônian area, following Cracraft [1985]). As a result, it is conceivable that populations from the Rondônian area of endemism (DEVI Rondônia and DEVI Santa Cruz) may represent an undescribed taxon. They are clearly genetically and morphologically distinct from populations west of the Madeira (DEVI La Paz and DEVI Pando).

Although additional sampling and specimen

TABLE 2. Uncorrected sequence divergence between taxa. Numbers in parentheses are the last three digits of GenBank accession numbers.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13
1 *Pipra*	—												
2 *Lepidocolaptes*	0.223	—											
3 *Synallaxis*	0.217	0.153	—										
4 *Formicarius*	0.219	0.180	0.165	—									
5 *Herpsilochmus*	0.218	0.176	0.178	0.180	—								
6 *Formicivora grisea*	0.214	0.190	0.180	0.179	0.142	—							
7 *Formicivora rufa*	0.224	0.187	0.183	0.173	0.152	0.055	—						
8 *Terenura*	0.215	0.193	0.190	0.181	0.169	0.154	0.166	—					
9 *Myrmotherula longipennis*	0.215	0.197	0.185	0.200	0.147	0.111	0.101	0.167	—				
10 *Myrmotherula leucophthalma*	0.219	0.198	0.170	0.181	0.150	0.149	0.147	0.159	0.145	—			
11 *Myrmotherula hauxwelli*	0.245	0.205	0.174	0.196	0.146	0.153	0.153	0.162	0.152	0.153	—		
12 *H. hypoxantha* (161, 195)	0.224	0.184	0.160	0.159	0.140	0.138	0.138	0.160	0.132	0.136	0.129	—	
13 *H. hypoxantha* (162, 196)	0.224	0.183	0.159	0.162	0.143	0.135	0.135	0.162	0.132	0.135	0.129	0.003	—
14 *H. cantator* Loreto (167, 201)	0.232	0.186	0.166	0.172	0.129	0.132	0.125	0.163	0.126	0.136	0.135	0.093	0.093
15 *H. cantator* Rond (168, 202)	0.229	0.186	0.175	0.165	0.128	0.125	0.121	0.162	0.135	0.140	0.139	0.089	0.089
16 *H. cantator* S. Cruz (166, 200)	0.227	0.185	0.173	0.168	0.131	0.123	0.121	0.162	0.135	0.142	0.141	0.090	0.090
17 *H. cantator* S. Cruz (163, 197)	0.231	0.186	0.174	0.165	0.132	0.126	0.122	0.159	0.136	0.143	0.139	0.093	0.093
18 *H. cantator* M. Gros (164, 198)	0.220	0.197	0.166	0.162	0.132	0.125	0.124	0.162	0.139	0.138	0.136	0.089	0.087
19 *H. cantator* M. Gros (165, 199)	0.219	0.197	0.166	0.162	0.132	0.125	0.124	0.162	0.139	0.138	0.136	0.088	0.087
20 *D. devillei* La Paz (175, 209)	0.245	0.203	0.180	0.166	0.142	0.139	0.148	0.176	0.163	0.148	0.136	0.125	0.128
21 *D. devillei* La Paz (176, 210)	0.245	0.201	0.176	0.169	0.139	0.136	0.149	0.176	0.160	0.146	0.136	0.125	0.125
22 *D. devillei* Pando (177, 211)	0.253	0.211	0.187	0.170	0.143	0.140	0.145	0.178	0.167	0.156	0.145	0.125	0.128
23 *D. devillei* Pando (178, 212)	0.249	0.208	0.184	0.167	0.140	0.140	0.145	0.176	0.164	0.153	0.142	0.122	0.125
24 *D. devillei* Acre (174, 208)	0.250	0.208	0.184	0.167	0.140	0.138	0.142	0.176	0.164	0.153	0.142	0.122	0.125
25 *D. devillei* Rond (179, 213)	0.245	0.207	0.181	0.169	0.145	0.136	0.140	0.166	0.154	0.154	0.138	0.121	0.124
26 *D. devillei* Rond (180, 214)	0.243	0.205	0.180	0.167	0.143	0.138	0.142	0.164	0.156	0.153	0.136	0.119	0.122
27 *D. devillei* Rond (181, 215)	0.243	0.205	0.180	0.167	0.143	0.138	0.142	0.164	0.156	0.153	0.136	0.119	0.122
28 *D. devillei* Rond (182, 216)	0.243	0.205	0.180	0.167	0.143	0.138	0.142	0.164	0.156	0.153	0.136	0.119	0.122
29 *D. devillei* S. Cruz (183, 217)	0.242	0.204	0.178	0.166	0.143	0.136	0.140	0.163	0.152	0.152	0.136	0.118	0.121
30 *D. devillei* S. Cruz (184, 218)	0.245	0.207	0.181	0.169	0.146	0.139	0.143	0.166	0.154	0.154	0.139	0.121	0.124
31 *D. caudata* Puno (171, 205)	0.238	0.203	0.169	0.167	0.150	0.140	0.152	0.170	0.160	0.154	0.131	0.112	0.115
32 *D. caudata* Pasco (172, 206)	0.242	0.204	0.169	0.163	0.150	0.143	0.152	0.164	0.164	0.153	0.129	0.101	0.104
33 *D. caudata* Pasco (173, 207)	0.239	0.200	0.169	0.160	0.146	0.138	0.146	0.159	0.162	0.150	0.125	0.098	0.101
34 *D. caudata* Napo (170, 204)	0.243	0.204	0.174	0.167	0.149	0.140	0.153	0.159	0.166	0.154	0.131	0.107	0.110

comparisons are needed, our findings demonstrate that *D. devillei* populations from east and west of the Rio Madeira (Fig. 1) are substantially differentiated from one another genetically, whereas populations from the same sides of the river are more similar. The genetic differentiation across the river is matched by plumage differences. Many other avian taxa are separated by the Rio Madeira (Hellmayr 1910), a pattern that is in contrast to recent genetic studies of rodents and marsupials along the smaller and more meandering Rio Juruá (Silva and Patton 1994). *Drymophila devillei* is the only bamboo specialist with described forms on opposite banks of the Rio Madeira. Because bamboo is considered a successional habitat occurring primarily along rivers, these patches would be predicted to be temporary. As a result, one might expect that birds associated with bamboo would require good dispersal capabilities in order to move to new patches as old ones disappeared through succession. Also, bamboo patches can be quite small, which might necessitate dispersal to new patches once a patch became saturated with territories. This leads to the prediction that bamboo-associated species would be more likely candidates than other forest birds to cross large rivers. With respect to *D. devillei* and the Rio Madeira, this does not seem to be the case.

As with many species having narrow distributions along the eastern slopes of the Andes, it is unknown whether *D. caudata* is truly discontinuously distributed (as shown in Ridgely and Tudor 1994), or incompletely sampled in many areas. Our data suggest that considerable differentiation exists between sites in central and southern Peru (2.4% divergence between Pasco and Puno). The foothills of the Andes are among the most bisected regions in the world, and a number of deep river valleys separate the populations we studied (most notably the Río Urubamba). As a result, we suspect that genetic differentiation among these populations results from population subdivision (lack of gene flow) and not from variation within a single population.

Genetic differentiation in our limited geographic sampling of *Hypocnemis cantator* was higher than that found within each species of *Drymophila*. The highest divergence was for samples separated by the Amazon River (5 to

TABLE 2. Extended.

14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
—																			
0.057	—																		
0.058	0.003	—																	
0.060	0.006	0.006	—																
0.051	0.044	0.046	0.049	—															
0.051	0.045	0.046	0.049	0.000	—														
0.124	0.128	0.128	0.131	0.122	0.122	—													
0.119	0.126	0.127	0.129	0.121	0.121	0.007	—												
0.119	0.115	0.116	0.115	0.113	0.112	0.025	0.025	—											
0.117	0.112	0.113	0.112	0.110	0.110	0.025	0.025	0.006	—										
0.117	0.112	0.113	0.112	0.110	0.110	0.022	0.022	0.003	0.003	—									
0.117	0.114	0.114	0.114	0.114	0.114	0.031	0.032	0.021	0.021	0.018	—								
0.115	0.112	0.113	0.112	0.113	0.112	0.030	0.031	0.020	0.020	0.017	0.001	—							
0.115	0.112	0.113	0.112	0.113	0.112	0.030	0.031	0.020	0.020	0.017	0.001	0.000	—						
0.115	0.112	0.113	0.112	0.113	0.112	0.030	0.031	0.020	0.020	0.017	0.001	0.000	0.000	—					
0.114	0.111	0.111	0.111	0.108	0.108	0.034	0.035	0.024	0.024	0.021	0.006	0.004	0.004	0.004	—				
0.117	0.114	0.114	0.114	0.111	0.111	0.034	0.035	0.024	0.024	0.021	0.006	0.004	0.004	0.004	0.003	—			
0.114	0.115	0.118	0.118	0.108	0.108	0.076	0.079	0.080	0.079	0.077	0.079	0.077	0.077	0.077	0.079	0.081	—		
0.111	0.105	0.107	0.107	0.103	0.103	0.075	0.079	0.073	0.073	0.070	0.072	0.070	0.070	0.070	0.072	0.074	0.024	—	
0.108	0.104	0.104	0.104	0.100	0.100	0.072	0.074	0.069	0.069	0.066	0.067	0.066	0.066	0.066	0.067	0.070	0.024	0.006	—
0.117	0.112	0.113	0.112	0.111	0.111	0.072	0.074	0.069	0.069	0.066	0.067	0.066	0.066	0.066	0.067	0.070	0.027	0.017	0.011

6%); however, the most striking finding was an apparently substantial genetic break (4.5% divergence) between populations occurring in the interfluvium between the Rio Madeira and the Rio Tapajós. This divergence possibly is predicted by the described subspecies (following Peters 1951), *Hypocnemis c. implicata* (for the Mato Grosso birds) and *H. c. ochrogyna* (for the Jiparaná and eastern Bolivian birds). Haffer (1997) has noted other avian taxa with similar contact zones in this region. This level of genetic divergence, over 350 km of essentially continuous forest with no large rivers or shifts in habitat, warrants additional study.

Relationships of Drymophila *to other antbird genera.*—All of our analyses support a sister relationship between *Hypocnemis* and *Drymophila.* Because of high levels of divergence among antbird genera (Table 2), incomplete taxon sampling, and low numbers of characters, we caution against over-interpretation of other higher-level antbird relationships suggested by our data. However, some aspects of these relationships are worth noting. First, all analyses suggest a separation of *Formicarius colma* from the other antbird genera, consistent with the formicariid and thamnophilid split. Second, three members of the large genus *Myrmotherula* are not monophyletic, which is consistent with results of earlier allozyme studies (Hackett and Rosenberg 1990). Also consistent with the allozyme results is the clustering of *Myrmotherula longipennis* with *Formicivora* relative to the other taxa surveyed. Using Kishino and Hasegawa (1989) maximum-likelihood tests to compare the unweighted or weighted tree topologies with topologies that include *Myrmotherula* as a monophyletic group, the sequence data reject monophyly of *Myrmotherula* ($P < 0.01$). Third, the high level of sequence divergence (9.3%) between the congeners *Hypocnemis cantator* and *H. hypoxantha* suggests that speciation events between these two took place several million years ago. This level of divergence is slightly higher than the average for avian congeners (Johns and Avise 1998), although it does not reach levels of divergence observed in some other Neotropical birds such as potoos (*Nyctibius* spp.; Mariaux and Braun 1996).

Utility of gene spacer regions for systematic questions.—Gene spacer regions in mitochondrial DNA are often sequenced because of primer

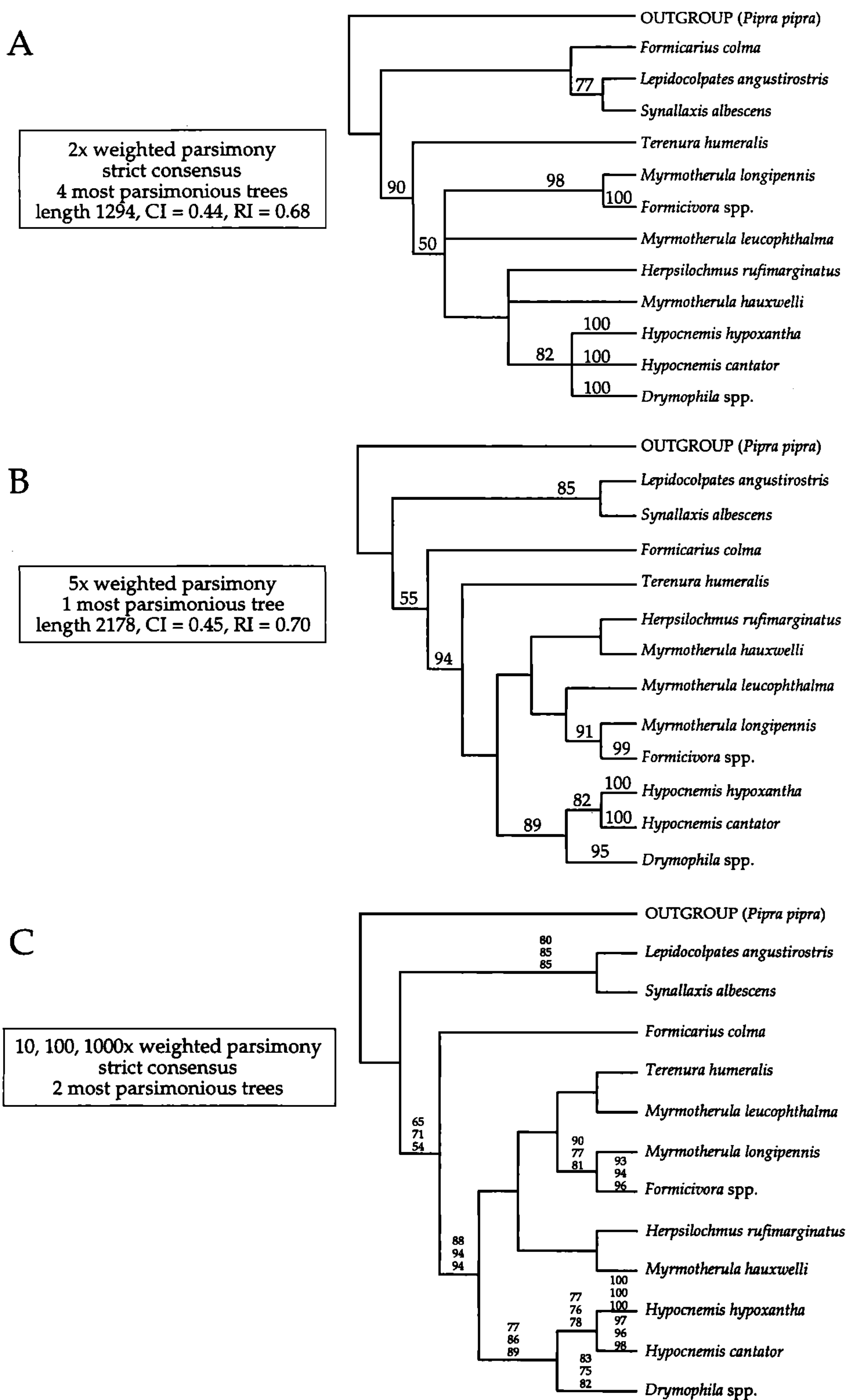

FIG. 3. Weighted parsimony analyses. (A) 2×; (B) 5×; (C) 10, 100, and 1,000×. Boostrap values shown above branches. In 3C, bootstrap values for 10, 100, and 1,000× are listed from top to bottom, respectively.

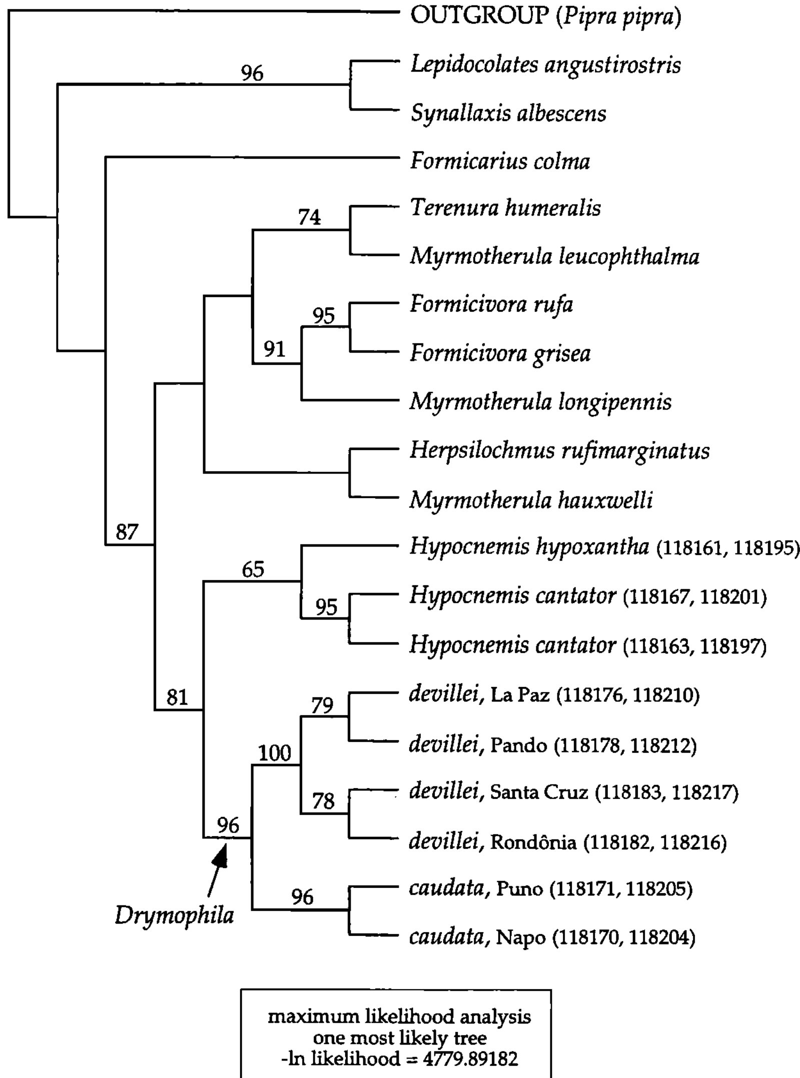

FIG. 4. Maximum-likelihood tree shown with bootstrap values indicated above branches.

placement in gene regions adjacent to the genes being studied. However, the phylogenetic utility of spacer DNA sequences between sequences of known function has not been explored often (but see McKnight and Shaffer 1997), and these sequences are not usually reported in data bases such as GenBank. Inclusion or exclusion of the small spacer region between cyt *b* and the threonine t-RNA did not change any of the results of our study, but the spacer region did contain phylogenetic information at all levels of the taxonomic hierarchy that we surveyed (Table 1). By combining our data with those from other suboscines (Mindell et al. 1998), we can show that both the length and base composition of the spacer vary across the group. Based on limited sampling, suboscine outgroups have either two bases (CT, Pipridae and Formicariidae; AC, Dendrocolaptidae) or four bases (AACC, Furnariidae; CGCA, Eurylaimidae), whereas all thamnophilids sampled have three bases. We found five different spacer types within thamnophilids (Table 1). Within *Drymophila devillei*, populations from eastern Bolivia and western Brazil (DEVI Santa Cruz and DEVI Rondônia, respectively) have a distinct spacer from La Paz and Pando populations. Different spacers also occurred in *Hypoc-*

nemis cantator samples. In both cases, these characters are consistent with phylogenetic patterns in the protein-coding sequences (see above). This also suggests that there is homoplasy in these sequences. For example, the spacer CAC occurs in some populations of *Drymophila devillei* (DEVI Santa Cruz and DEVI Rondônia) and in six other genera of thamnophilids. Although these spacer regions contain homoplasy and present character-coding problems typical of all non-coding DNA, they clearly contain phylogenetically informative information as well, and we advocate reporting the sequences of these regions and incorporating these data into phylogenetic reconstructions. In our study, including these characters did not affect the phylogenies, but they could in other situations.

The high levels of genetic divergence that we found within these biological species of Amazonian birds suggest that multiple distinct evolutionary lineages occur within many other Amazonian species. It remains to be seen whether this genetic diversity is consistent with other character sets such as vocalizations (e.g. Isler et al. 1998), but these data suggest that our current species-level classification greatly underestimates the diversity of Amazonian birds.

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APPENDIX. Voucher information for tissue samples used in this study.

Taxon	Voucher institution[a]	Voucher number[b]	Tissue institution[a]	Collection locality	GenBank accession number
Pipra pipra	LSUMNS	119977	LSUMNS	Loreto, Peru	AF118154, AF118188
Lepidocolaptes angustirostris	MPEG	Ch206[b]	FMNH	Amapá, Brazil	AF118185, AF118219
Synallaxis albescens	MPEG	Ch062[b]	FMNH	Amapá, Brazil	AF118186, AF118220
Formicarius colma	MPEG	51628	FMNH	Mato Grosso, Brazil	AF118155, AF118189
Herpsilochmus rufimarginatus	FMNH	339650	FMNH	Bolivar, Venezuela	AF118157, AF118191
Formicivora grisea	MZUSP	73357	FMNH	Roraima, Brazil	AF118169, AF118203
Formicivora rufa	MPEG	Ch001[b]	FMNH	Amapá, Brazil	AF118187, AF118221
Terenura humeralis	MPEG	DFS 86-130[b]	FMNH	Rondônia, Brazil	AF118156, AF118190
Myrmotherula longipennis	MPEG	51516	FMNH	Mato Grosso, Brazil	AF118159, AF118193
Myrmotherula leucophthalma	MPEG	51500	FMNH	Mato Grosso, Brazil	AF118158, AF118192
Myrmotherula hauxwelli	MPEG	51490	FMNH	Mato Grosso, Brazil	AF118160, AF118194
Hypocnemis hypoxantha	LSUMNS	156543	LSUMNS	Madre de Dios, Peru	AF118161, AF118195
Hypocnemis hypoxantha	MPEG	REAJ232[b]	FMNH	Acre, Brazil	AF118162, AF118196
Hypocnemis cantator	LSUMNS	110033	LSUMNS	Loreto, Peru	AF118167, AF118201
Hypocnemis cantator	MPEG	DW 3755[b]	FMNH	Rondônia, Brazil	AF118168, AF118202
Hypocnemis cantator	MHNNKM	EGA154	LSUMNS	Santa Cruz, Bolivia	AF118163, AF118197
Hypocnemis cantator	LSUMNS	137191	LSUMNS	Santa Cruz, Bolivia	AF118166, AF118200
Hypocnemis cantator	MZUSP	0300[b]	FMNH	Mato Grosso, Brazil	AF118164, AF118198
Hypocnemis cantator	MZUSP	0316[b]	FMNH	Mato Grosso, Brazil	AF118165, AF118199
Drymophila devillei devillei	LSUMNS	102125	LSUMNS	La Paz, Bolivia	AF118175, AF118209
Drymophila devillei devillei	LSUMNS	102129	LSUMNS	La Paz, Bolivia	AF118176, AF118210
Drymophila devillei devillei	LSUMNS	132782	LSUMNS	Pando, Bolivia	AF118177, AF118211
Drymophila devillei devillei	LSUMNS	132785	LSUMNS	Pando, Bolivia	AF118178, AF118212
Drymophila devillei devillei	MPEG	REAJ001[b]	FMNH	Acre, Brazil	AF118174, AF118208
Drymophila devillei subochracea	MPEG	39978	FMNH	Rondônia, Brazil	AF118179, AF118213
Drymophila devillei subochracea	MPEG	39979	FMNH	Rondônia, Brazil	AF118180, AF118214
Drymophila devillei subochracea	MPEG	39980	FMNH	Rondônia, Brazil	AF118181, AF118215
Drymophila devillei subochracea	MPEG	39981	FMNH	Rondônia, Brazil	AF118182, AF118216
Drymophila devillei subochracea	LSUMNS	150775	LSUMNS	Santa Cruz, Bolivia	AF118183, AF118217
Drymophila devillei subochracea	LSUMNS	153374	LSUMNS	Santa Cruz, Bolivia	AF118184, AF118218
Drymophila caudata	LSUMNS	98339	LSUMNS	Puno, Peru	AF118171, AF118205
Drymophila caudata	LSUMNS	106008	LSUMNS	Pasco, Peru	AF118172, AF118206
Drymophila caudata	LSUMNS	107208	LSUMNS	Pasco, Peru	AF118173, AF118207
Drymophila caudata	ANSP	185468	ANSP	Napo, Ecuador	AF118170, AF118204

[a] AMNH = American Museum of Natural History, New York; ANSP = Academy of Natural Sciences, Philadelphia; FMNH = Field Museum of Natural History, Chicago; LSUMNS = Louisiana State University Museum of Natural Science, Baton Rouge; MHNNKM = Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia; MPEG = Museu Paraense Emílio Goeldi, Belém, Brazil; MZUSP = Museu de Zoologia da Universidade de São Paulo, Brazil.

[b] Some FMNH tissues are not catalogued; personal collector or field collection voucher information is provided.