The Auk 119(3):621–640, 2002

MOLECULAR SYSTEMATICS AND THE ROLE OF THE ''VÁRZEA''–''TERRA-FIRME'' ECOTONE IN THE DIVERSIFICATION OF *XIPHORHYNCHUS* WOODCREEPERS (AVES: DENDROCOLAPTIDAE)

ALEXANDRE ALEIXO[1]

Department of Biological Sciences, and Museum of Natural Science, Louisiana State University, 119 Foster Hall, Baton Rouge, Louisiana 70803, USA

ABSTRACT.—The phylogeny of all known *Xiphorhynchus* (Dendrocolaptidae) species and many of its subspecies was reconstructed to evaluate species limits in this taxonomically challenging genus and investigate the possible role played by the Amazonian ''várzea'' (floodplain forest)–''terra-firme'' (upland forest) ecotone in its diversification. Phylogenies were inferred based on 2,430 bp of the mitochondrial DNA genes ND2, ND3, and cytochrome *b*. All phylogeny estimates supported the monophyly of all extant *Xiphorhynchus* species to the exclusion of the sibling species pair Straight-billed (*X. picus*) and Zimmer's (*X. kienerii*) woodcreeper. Confirming findings of previous molecular and anatomical studies, strong support was found to include the Lesser Woodcreeper (*Lepidocolaptes fuscus*) in *Xiphorhynchus*. Levels of sequence divergence among some subspecies of Buff-throated (*X. guttatus*), Ocellated (*X. ocellatus*), and Spix's (*X. spixii*) woodcreepers reached or exceeded those found between closely related, undisputed biological species of *Xiphorhynchus*. High levels of sequence differentiation and the paraphyly of some *Xiphorhynchus* species indicated that the following taxa should be recognized as species: Lafresnaye's (*X. guttatoides*), Tschudi's (*X. chunchotambo*), and Elegant (*X. elegans*) woodcreepers. All *Xiphorhynchus* species restricted to terra-firme forest in lowland Amazonia formed a well supported monophyletic group, whereas species restricted to várzea forest were either basal to a clade containing species found in a wide variety of habitats (Striped Woodcreeper [*X. obsoletus*]) or belonged to a distinct lineage likely to be regarded as a separate genus (*X. kienerii*). These findings falsified an anticipated sister relationship between várzea and terra-firme species, as expected if the várzea–terra-firme ecotone had played a decisive role in population differentiation and speciation within *Xiphorhynchus*. Instead, phylogeny estimates suggested that the várzea–terra-firme habitat specialization evolved early on in the evolutionary history of *Xiphorhynchus* and that subsequent differentiation occurred mostly within the terra-firme habitat. *Received 15 June 2001, accepted 16 April 2002.*

RESUMEN.—Se reconstruyó la filogenia de todas las especies conocidas y de muchas de las subespecies de *Xiphorhynchus* (Dendrocolaptidae) para evaluar los límites de las especies en este género taxonómicamente complejo y para investigar el rol del ecotono entre ''várzea'' (bosque de inundación) y ''terra-firme'' (bosque de tierras altas) del Amazonas en su diversificación. Las filogenias fueron inferidas a partir de 2,430 pares de bases de los genes de ADN mitocondrial ND2, ND3 y citocromo *b*. Todas las estimaciones filogenéticas avalaron la monofilia de todas las especies vivientes de *Xiphorhynchus*, con excepción del par de especies hermanas *X. picus* y *X. kienerii*. Se encontró fuerte respaldo para incluir a *Lepidocolaptes fuscus* en *Xiphorhynchus*, confirmando estudios moleculares y anatómicos previos. Los niveles de divergencia en las secuencias entre algunas subespecies de *X. guttatus*, *X. ocellatus* y *X. spixii* alcanzaron o excedieron aquellos encontrados entre especies biológicas cercanamente emparentadas de *Xiphorhynchus*. Los altos niveles de diferenciación en las secuencias y la parafilia de algunas especies de *Xiphorhynchus* indicaron que los siguientes taxones deberían ser reconocidos como especies: *X. guttatoides*, *X. chunchotambo* y *X. elegans*. Todas las especies de *Xiphorhynchus* restringidas a las áreas de bosque de terra-firme de las tierras bajas del Amazonas formaron un grupo monofilético fuertemente respaldado, mientras que las especies restringidas a bosques de várzea aparecieron en la base del clado que contenía a aquellas encontradas en una amplia variedad de hábitats (*X. obsoletus*) o pertenecieron a un linaje separado que probablemente pueda ser considerado como un género separado (*X. kie-*

[1] E-mail: aaleixo@lsu.edu

nerii). Estos resultados falsifican la relación de hermandad esperada entre las especies de várzea y terra-firme que se esperaría si el ecotono de várzea y terra-firme hubiera jugado un rol importante en la diferenciación entre poblaciones y en la especiación de *Xiphorhynchus*. En cambio, las estimaciones filogenéticas sugirieron que la especialización de hábitat de várzea y terra-firme evolucionó temprano en la historia evolutiva de *Xiphorhynchus* y que las diferenciaciones subsecuentes ocurrieron principalmente en el hábitat de terra-firme.

AVIAN SPECIES RICHNESS in the Neotropics has traditionally been explained by allopatric speciation models, such as the ''refuge'' (Haffer 1969), ''river'' (Snethlage 1913), and ''Andean uplift'' (Chapman 1917) hypotheses. Alternative hypotheses involving sympatric and parapatric speciation scenarios have been largely dismissed as secondary in importance (Haffer 1992), despite the scarcity of explicit tests evaluating their predictions under a phylogenetic framework (but see Bates and Zink 1994, Arctander and Fjeldså 1994). Endler (1982) argued that strong divergent selection across sharp ecological gradients can account for differentiation and speciation among tropical organisms. Evidence for such an important role played by ecotones as areas of population differentiation was found in studies on population genetics and morphometrics of two phylogenetically distinct central African bird species (Smith et al. 2001).

In the Amazon Basin, two distinct and adjacent forest types dominate the landscape: the ''várzea'' forest (which floods every year) and the ''terra-firme'' forest (which does not flood on a regular basis). About 15% of the terrestrial Amazonian avifauna is known to be restricted or nearly restricted to várzea forests (Remsen and Parker 1983). Little is known about the origin and evolution of this characteristic avifauna, in part because of the paucity of phylogenetic studies on Neotropical bird groups. One possible scenario, as suggested by the abrupt replacement of many congeneric avian species pairs across the várzea–terra-firme ecotone (Robinson and Terborgh 1997), is that this ecological gradient contributed directly to population differentiation and ultimately to speciation within those lineages. An important prediction of this hypothesis is that congeneric species pairs replacing each other across the várzea–terra-firme ecotone should be recently derived sister taxa (Moritz et al. 2000).

With species restricted to both várzea and terra-firme forests, the avian genus *Xiphorhynchus* provides an ideal model for studying the history of habitat specialization and its role as a possible speciation mechanism among Amazonian organisms (Table 1). In the only phylogenetic hypothesis proposed so far for Dendrocolaptidae (sensu American Ornithologists' Union [AOU] 1998), relationships within *Xiphorhynchus* are largely unresolved, with most species making part of a polytomy that includes taxa grouped in other genera as well, such as *Campyloramphus*, *Dendrexetastes*, and *Lepidocolaptes* (Raikow 1994). Raikow (1994) suggested that the anatomical characters he studied could not distinguish species level differences in the genera *Hylexetastes*, *Xiphorhynchus*, and *Lepidocolaptes*, stating that ''the solution . . . must await analysis of other types of data that show sufficient variation at the appropriate taxonomic level.'' More recently, García-Moreno and Silva (1997) found molecular evidence indicating that the Lesser Woodcreeper (*Lepidocolaptes fuscus*) is actually more closely related to *Xiphorhynchus* than to any of the six *Lepidocolaptes* species they sampled. Despite their findings, those authors suggested caution concerning the inclusion of *Lepidocolaptes fuscus* in *Xiphorhynchus* before a phylogeny of all *Xiphorhynchus* species is available. As yet, neither the monophyly nor the position of *Xiphorhynchus* within Dendrocolaptidae has been properly assessed. The situation at lower taxonomic levels is also poorly resolved: many polytypic *Xiphorhynchus* species have several well differentiated populations once considered separate species (Cory and Hellmayr 1925). In fact, even today there is no consensus regarding the taxonomic status of many subspecies of *X. guttatus* and *X. spixii* (contrast Ridgely and Tudor 1994 with Stotz et al. 1996 and Haffer 1997).

The current lack of resolution concerning the evolutionary history of *Xiphorhynchus* prevents its use as a model to study the role of habitat specialization as a possible diversification mechanism in the Neotropics. Here, a phylogenetic hypothesis for the genus *Xiphorhynchus* is presented based on mitochondrial DNA

TABLE 1. Common name, habitat preferences, and distribution of currently recognized species of *Xiphorhynchus*[a].

Species	Common name	Habitat[b]	Distribution
X. erythropygius	Spotted Woodcreeper	L, M	Central America and Chocó
X. flavigaster	Ivory-billed Woodcreeper	L, M, D, S, PO	Central America
X. guttatus	Buff-throated Woodcreeper	L, TF, V, S	Amazonia and eastern Brazil
X. kienerii[c]	Zimmer's Woodcreeper	V	Amazonia
X. lachrymosus	Black-striped Woodcreeper	L, MA	Central America and Chocó
X. obsoletus	Striped Woodcreeper	V	Amazonia
X. ocellatus	Ocellated Woodcreeper	TF, M[d]	Amazonia and eastern slope of the Andes
X. pardalotus	Chestnut-rumped Woodcreeper	TF, M[d]	Amazonia and Tepuis
X. picus	Straight-billed Woodcreeper	V, D, S, MA	Panama, northern South America, Amazonia, and eastern Brazil
X. spixii	Spix's Woodcreeper	TF, M[d]	Amazonia and eastern slope of the Andes
X. susurrans	Cocoa Woodcreeper	L, D, S, MA	Central America and trans-Andean South America
X. triangularis	Olived-backed Woodcreeper	M	Western slope of the Andes

[a] Following the taxonomy of Zimmer (1934a), Peters (1951), and AOU (1998). The taxon *X. striatigularis*, known only by its type specimen, is now regarded as an aberrant individual of *X. flavigaster* (Winker 1995).

[b] Based on Stotz et al. (1996) and complemented with personal observations. D—tropical deciduous forest; L—tropical lowland evergreen forest; M—montane evergreen forest; MA—mangrove forest; PO—pine-oak forest; S—secondary forest; TF—Amazonian terra-firme forest; V—Amazonian várzea forest.

[c] Formerly known as *X. necopinus*, name now considered a junior synonym of *X. kienerii* (Aleixo and Whitney 2002).

[d] Restricted to terra-firme forest in lowland Amazonia.

(mtDNA) sequences to (1) evaluate the monophyly of *Xiphorhynchus* and its relationship with other Dendrocolaptidae genera; (2) assess species limits within some polytypic *Xiphorhynchus* species; and (3) evaluate the prediction of sister relationships between várzea and terra-firme species, as expected if the várzea–terra-firme ecotone played a decisive role in population differentiation and subsequent speciation within *Xiphorhynchus*.

METHODS

Taxa sequenced.—In addition to all known *Xiphorhynchus* species, at least one species belonging to all extant woodcreeper genera was sampled, except *Dendrocincla*, *Deconychura*, and *Drymornis* (Appendix). Studies based on anatomical characters indicate that the latter genera are not closely related to *Xiphorhynchus* (Feduccia 1973, Raikow 1994); instead, the genera *Lepidocolaptes* (Lineated Woodcreeper [*L. albolineatus*], Narrow-billed Woodcreeper [*L. angustirostris*], and *L. fuscus*) and *Campyloramphus* (Black-billed Scythebill [*C. falcularius*], Curve-billed Scythebill [*C. procurvoides*], and Red-billed Scythebill [*C. trochilirostris*]) were sampled more thoroughly because of their supposed closer relationship with *Xiphorhynchus* (Feduccia 1973, Raikow 1994, García-Moreno and Silva 1997). At the generic level, the goal was to assess the monophyly of *Xiphorhynchus* and its relationships with other woodcreeper genera rather than to propose a phylogenetic hypothesis for the whole family Dendrocolaptidae. No genera from other families were included in the analysis because the monophyly of Dendrocolaptidae has been supported by studies based on DNA–DNA hybridization (Sibley and Ahlquist 1990) and morphological characters (Raikow 1994, Clench 1995). At lower taxonomic levels, subspecies of species whose limits have been controversial according to taxonomists working on Neotropical birds were sampled (Cory and Hellmayr 1925, Zimmer 1934a, Peters 1951, Pinto 1978, Ridgely and Tudor 1994, Haffer 1997). Thus, taxa belonging to the following species were sampled: *brevirostris*, *chunchotambo*, *ocellatus*, and *weddellii* (*X. ocellatus*); *aequatorialis* and *insolitus* (*X. erythropygius*); *eytoni*, *dorbignyanus*, *guttatoides*, *guttatus*, *polystictus*, and *susurrans* (*X. guttatus*); *elegans*, *juruanus*, *ornatus*, and *spixii* (*X. spixii*); and finally *bangsi* and *intermedius* (*X. triangularis*). These taxa do not represent an exhaustive list of subspecies belonging to those polytypic species, but they cover major divisions within those species based primarily on plumage patterns (Cory and Hellmayr 1925, Zimmer 1934a). Subspecies belonging to species whose limits are not con-

troversial were also sampled to contrast their intraspecific level of genetic variation with those of the controversial polytypic species listed above. Thus, the following taxa were sampled: *eburneirostris* and *flavigaster* (*X. flavigaster*); and *altirostris*, *bahiae*, *phalara*, and *picus* (*X. picus*).

DNA sequencing.—Total genomic DNA was extracted from tissue samples using a Qiagen tissue extraction kit or a standard phenol–chloroform method (Hillis et al. 1990). Samples from STRI were obtained as lyophilized DNA. Fragments of the mitochondrial genome were amplified using 11 primers spanning most of ctytochrome-*b* (1,035 bp) and the entire NADH dehydrogenase subunits 2 (ND2; 1,041 bp) and 3 (ND3; 354 bp) genes. Primers used for cytochrome *b* were L14990 (Kocher et al. 1989), L15389 (Hackett 1996), H15710 (Helm-Bychowski and Cracraft 1993), HXIPH (CATTCTGGTTTGATGTGGGG; designed specifically for this project), L15505 (CTAACCTTCCTACACGAAACC; designed specifically for this project), L15656 (Helm-Bychowski and Cracraft 1993), and H16065 (Hackett 1996). Primers used for ND2 were L5215 (Hackett 1996), H5578 (Hackett 1996), L5758X (modified from primer published by Johnson and Sorenson [1998; GGATGAGCRGGYCTAAAYCARAC]), and H6313 (Johnson and Sorenson 1998). For ND3, primers L10755 and H11151were used (Chesser 1999). All primer numbers refer to the 3′ base of the published chicken (*Gallus gallus domesticus*) mtDNA sequence (Desjardins and Morais 1990). Fragments were PCR amplified using standard conditions available upon request: denaturation at 94°C, annealing between 50 and 57°C, and extension at 72°C in a Hybaid OMN-E thermal cycler. A small aliquot of each amplification was electrophoresed on an agarose gel to check for the correct fragment size and to ensure that only a single amplification product was obtained. Amplification products were cleaned with a Qiagen PCR purification kit and cycle-sequenced using a Big Dye Terminator kit (Perkin Elmer, Norwalk, Connecticut), and all amplification primers listed above. Cycle sequencing reactions were NH_4OAC precipitated, dried, resuspended in a formamide EDTA, and run on an ABI 377 automated DNA sequencer. Sequences from both strands within and between species were aligned and reconciled using SEQUENCHER 3.1.1 (Genecodes, Madison, Wisconsin). The following measures outlined by Sorenson and Quinn (1998) and Bates et al. (1999) were taken to ensure that the DNA fragments amplified were accurate and of mitochondrial origin (not pseudogenes): (1) most sequences were amplified in large fragments (>1,000 bp); (2) both DNA strands were sequenced; (3) sequences were aligned with the chicken complete mtDNA sequence, and inspected for insertions, deletions, and stop codons that would result in a nonfunctional protein; (4) sequences were expected to exhibit high transition to transversion substitution ratios characteristic of mitochondrial, not nuclear substitution patterns; and (5) a partition homogeneity test was performed to evaluate if the phylogenetic signal of the three different gene sequences were similar. Pseudogenes do not necessarily yield the same phylogenetic signal as mitochondrial genes. Evidence of pseudogenes in the sequences used for this study could not be detected. After those procedures, sequences were submitted to GenBank (AY089790–AY089918; Appendix).

Phylogenetic analyses.—A partition homogeneity test was performed as implemented in PAUP* 4.0b7 (Swofford 1998) with 100 replicates to determine if the different mitochondrial genes sequenced could be combined for phylogenetic analysis (Farris et al. 1995). Another partition homogeneity test compared third with first and second codon positions to evaluate if third positions gave a different phylogenetic signal due to saturation at deeper divergence levels. Maximum-parsimony and maximum-likelihood heuristic searches were conducted with PAUP* 4.0b7. Maximum-parsimony analyses were based on unweighted sequence data. The likelihood-ratio test was used as implemented in MODELTEST (Posada and Crandall 1998) to select the best and simplest model of molecular evolution fitting the dataset, which was then used in all maximum-likelihood analyses. One-hundred nonparametric bootstrap replications were used to evaluate confidence levels of nodes for all phylogenies obtained with maximum parsimony and maximum likelihood (Felsenstein 1985). Because of computer limitations, only one addition-sequence replicate was performed for each bootstrap replicate in the likelihood analyses. To further explore the sensitivity of the data to methods of analysis, a Bayesian inference of phylogeny was also performed using the MRBAYES software, version 1.11 (Huelsenbeck 2000). Bayesian analysis provides posterior probability values for different phylogenetic parameters, such as topology, branch lengths, and substitution patterns, producing essentially the same result as maximum likelihood given the same model of nucleotide substitution (Huelsenbeck 2000). However, instead of estimating these parameters by maximizing their likelihoods on a single tree (like maximum likelihood), the Bayesian approach samples multiple trees and parameter values from their near optimal position (i.e. near their global maximum). That produces a posterior probability distribution from which a consensus tree is generated. The interpretation of the result of a Bayesian estimate of phylogeny is straightforward: the posterior probability of any single clade in a given phylogeny is the percentage of time that the clade appeared in the sample of trees representing the posterior distribution. Because the posterior probabilities of all possible trees add up to 1, a given clade with a support of 1 or 100% occurred in all possible trees generated by MRBAYES under a wide variety

of substitution parameters, assuming a specific model of sequence evolution. In general, Bayesian analyses generate consensus trees with higher posterior probabilities than bootstrap proportions under a maximum-likelihood approach (Rannala and Yang 1996). MRBAYES 1.11 was run with the following specifications: (1) assuming a general time reversible model of nucleotide substitution with estimated base frequencies, proportion of invariable sites, and rates for variable sites following a gamma distribution (model GTR + G + I), as selected by MODELTEST; and (2) running the Markov chain for 500,000 generations, sampling 1 tree every 100 generations. Following recommendations outlined by Huelsenbeck and Hall (2001), I discarded trees obtained before the Markov chain reached convergent and stable likelihood values. PAUP* 4.0b7 was used to compute a majority-rule consensus tree of the sampled trees. The proportion of times a given clade was sampled equal to its posterior probability of occurrence. Because the increase in computational time required for the completion of maximum-likelihood and Bayesian analyses grow with the number of taxa, these analyses were divided into two parts: (1) one containing only one individual each of the 25 sampled species (all the 12 *Xiphorhynchus* species plus 13 outgroups) and (2) another containing 29 taxa belonging to 10 *Xiphorhynchus* species defined as monophyletic by the first analysis plus three outgroups. The purpose of the first analysis was to assess the monophyly of *Xiphorhynchus*, whereas the second analysis dealt with polytypic *Xiphorhynchus* species limits.

Results

Informative variation.—For most taxa, the dataset upon which phylogenetic analyses were inferred contained 2,430 characters, corresponding to positions 5241 to 6278 (ND2), 10776 to 11127 (ND3), and 15001 to 16035 (cyt *b*) of the mtDNA chicken sequence (Desjardins and Morais 1990). Parsimony informative sites were evenly distributed among the three genes: 330 ND2 (31.7% of total bases), 112 ND3 (31.6%), and 291 cty *b* (28.1%). A partition homogeneity test performed among the three genes did not detect significant differences in their phylogenetic content ($P = 0.3$). Another partition homogeneity test contrasting first and second with third codon positions also did not uncover significantly different phylogenetic signals among these data partitions ($P = 0.39$). Therefore, sequence data from all genes and codon positions were combined for phylogenetic analyses.

Sequence divergence.—Uncorrected (''*P*'') sequence divergence levels among all *Xiphorhynchus* taxa ranged from 0.08% (between two subspecies of *X. picus*) to 11.2 % (between *X. ocellatus* and *X. picus*; Table 2). When *X. picus* and *X. kienerii* are excluded, sequence divergence levels among the remaining monophyletic *Xiphorhynchus* taxa ranged from 0.37% (between two subspecies of *X. guttatus*) to almost 10% (between *X. obsoletus* and *X. ocellatus*; Table 2). Levels of sequence divergence between *Xiphorhynchus* (excluding *X. picus* and *X. kienerii*) and outgroups (excluding *L. fuscus*) ranged from 9.2% (between *L. angustirostris* and *X. spixii ornatus*) to almost 15% (between *X. guttatus dorbignyanus* and *Sittasomus griseicapillus* [Olivaceous Woodcreeper]; Table 2). When *X. picus* and *X. kienerii* were excluded, even third codon position substitutions accumulated linearly with overall genetic distance within and among *Xiphorhynchus* species (plot available upon request), indicating that saturation does not seem to be a problem among those taxa. Levels of genetic differentiation among some subspecies of *X. guttatus*, *X. ocellatus*, and *X. spixii* reached or exceeded those found between undisputed sister biological species of *Xiphorhynchus*, such as *X. flavigaster* and *X. lachrymosus* ($P = 4.2$–4.4%; Table 2) or between *X. ocellatus* and *X. pardalotus* ($P = 3.4$–3.9%; Table 2). In contrast, subspecific genetic differentiation between subspecies of *X. erythropygius*, *X. flavigaster*, and *X. triangularis* averaged ~1% (Table 2).

Maximum-parsimony analyses.—Equally weighted maximum-parsimony analyses resulted in two most parsimonious trees (length 3,433; CI = 0.35; RI = 0.6). Figure 1 shows a strict consensus of those two most parsimonious trees and bootstrap confidence values for its nodes. All *Xiphorhynchus*, *Lepidocolaptes*, and *Campyloramphus* species were monophyletic at 97% bootstrap support. The only difference between the topologies of the two most parsimonious trees pertained to the position of the sibling species pair *X. picus* and *X. kienerii*: one tree placed those species as basal to the entire *Lepidocolaptes–Campyloramphus–Xiphorhynchus* clade, whereas the other tree placed them as the sister group only to the *Campyloramphus–Lepidocolaptes* clade. Monophyly of *Lepidocolaptes fuscus* and all *Xiphorhynchus* species, except *X. picus* and *X. kienerii*, received 98% bootstrap sup-

TABLE 2. Uncorrected (*p*) sequence divergence among taxa.

Taxon	1	2	3	4	5	6	7	8
Glyphorynchus spirurus								
Sittasomus griseicapillus	0.156							
Nasica longirostris	0.148	0.148						
Dendrocolaptes certhia	0.144	0.141	0.112					
Lepidocolaptes albolineatus	0.138	0.138	0.125	0.121				
L. angustirostris	0.138	0.141	0.119	0.119	0.044			
L. fuscus	0.137	0.136	0.124	0.115	0.099	0.093		
Campyloramphus trochilirostris	0.141	0.139	0.123	0.125	0.103	0.100	0.106	
C. procurvoides	0.140	0.133	0.123	0.123	0.104	0.102	0.102	0.041
C. falcularius	0.142	0.136	0.125	0.123	0.099	0.099	0.100	0.073
Hylexetastes perrotii	0.146	0.144	0.116	0.107	0.119	0.110	0.118	0.120
Xiphocolaptes promeropirhynchus	0.139	0.142	0.109	0.106	0.117	0.115	0.112	0.124
Dendrexetastes rufigula	0.139	0.141	0.105	0.102	0.120	0.115	0.114	0.117
Xiphorhynchus erythropygius Panama	0.148	0.141	0.127	0.123	0.099	0.104	0.093	0.106
X. erythropygius Ecuador	0.147	0.142	0.130	0.122	0.101	0.106	0.094	0.109
X. flavigaster Mexico	0.132	0.141	0.128	0.117	0.105	0.104	0.088	0.104
X. flavigaster Belize	0.131	0.139	0.126	0.117	0.102	0.104	0.083	0.103
X. guttatus guttatus	0.140	0.146	0.127	0.115	0.102	0.104	0.090	0.106
X. g. dorbignyanus	0.141	0.148	0.126	0.119	0.097	0.099	0.087	0.104
X. g. eytoni	0.137	0.145	0.128	0.121	0.102	0.100	0.087	0.105
X. g. guttatoides south Amazon	0.141	0.149	0.127	0.120	0.099	0.101	0.087	0.107
X. g. guttatoides north Amazon	0.140	0.149	0.128	0.122	0.097	0.100	0.088	0.106
X. g. polystictus	0.141	0.147	0.127	0.117	0.102	0.105	0.092	0.108
X. g. vicinalis	0.140	0.148	0.127	0.121	0.099	0.101	0.087	0.105
X. kienerii	0.149	0.137	0.124	0.123	0.105	0.099	0.104	0.105
X. lachrymosus	0.136	0.145	0.129	0.122	0.101	0.102	0.089	0.106
X. obsoletus	0.139	0.146	0.127	0.122	0.107	0.100	0.092	0.106
X. ocellatus ocellatus	0.137	0.134	0.115	0.115	0.101	0.098	0.079	0.103
X. o. brevirostris	0.140	0.137	0.116	0.114	0.105	0.102	0.077	0.111
X. o. chunchotambo	0.139	0.134	0.113	0.114	0.104	0.099	0.076	0.108
X. o. weddellii	0.137	0.137	0.117	0.121	0.105	0.097	0.082	0.111
X. pardalotus	0.134	0.128	0.112	0.111	0.101	0.096	0.076	0.103
X. picus Venezuela	0.141	0.153	0.130	0.125	0.103	0.097	0.096	0.103
X. picus Trinidad	0.140	0.147	0.128	0.122	0.097	0.092	0.100	0.104
X. picus Amazon	0.141	0.152	0.130	0.126	0.103	0.097	0.096	0.104
X. picus southeast Brazil	0.142	0.153	0.129	0.126	0.103	0.097	0.096	0.103
X. spixii spixii	0.137	0.138	0.120	0.113	0.098	0.100	0.067	0.108
X. s. ornatus	0.139	0.129	0.114	0.109	0.090	0.092	0.067	0.100
X. s. elegans	0.140	0.137	0.116	0.114	0.095	0.097	0.069	0.104
X. s. juruanus	0.141	0.133	0.117	0.111	0.092	0.093	0.067	0.104
X. susurrans	0.143	0.146	0.126	0.115	0.104	0.104	0.093	0.105
X. triangularis Peru	0.140	0.140	0.126	0.117	0.093	0.097	0.091	0.102
X. triangularis Bolivia	0.141	0.140	0.127	0.117	0.094	0.097	0.093	0.105

port. When the two maximum-parsimony trees recovered are constrained (using software MACCLADE 4.0; Maddison and Maddison 2000), so that *X. picus* plus *X. kienerii* becomes the sister clade to all remaining *Xiphorhynchus* plus *Lepidocolaptes fuscus*, a cladogram with six additional steps is obtained. Within the *Xiphorhynchus–L. fuscus* clade, two other major well-supported clades existed: (1) one containing all Amazonian *Xiphorhynchus* species specialized in terra-firme forest with the Atlantic forest endemic *L. fuscus* as their sister taxon; and (2) another clade containing the remaining *Xiphorhynchus* species, found throughout the Neotropics. The strict maximum-parsimony consensus tree (Fig. 1) also had nodes with high bootstrap values indicating the paraphyly of two *Xiphorhynchus* biological species: *X. guttatus* and *X. ocellatus*. The lowland Amazonian *X. o. ocellatus* and *X. o. weddellii* were sisters to the Guyanan endemic *X. pardalotus*, whereas the two Andean foothill subspecies of *X. ocellatus* (*chunchotambo* and *brevirostris*) were basal to this clade. Lowland Amazonian subspecies of *X. guttatus* were also paraphyletic: *X. g. guttatus* from eastern Brazil and *X. g. polystictus* from

TABLE 2. Extended.

9	10	11	12	13	14	15	16	17	18	19	20	21
0.073												
0.120	0.126											
0.123	0.121	0.090										
0.115	0.116	0.112	0.106									
0.109	0.108	0.119	0.117	0.119								
0.110	0.112	0.119	0.115	0.118	0.014							
0.104	0.106	0.121	0.122	0.117	0.077	0.077						
0.106	0.106	0.119	0.120	0.120	0.073	0.074	0.017					
0.109	0.110	0.121	0.124	0.120	0.080	0.083	0.062	0.063				
0.108	0.104	0.121	0.126	0.117	0.073	0.077	0.058	0.057	0.046			
0.110	0.105	0.123	0.127	0.117	0.073	0.077	0.057	0.057	0.048	0.022		
0.112	0.107	0.122	0.124	0.118	0.074	0.078	0.061	0.059	0.046	0.006	0.023	
0.110	0.106	0.120	0.125	0.118	0.075	0.078	0.060	0.059	0.046	0.005	0.022	0.004
0.111	0.110	0.122	0.125	0.121	0.080	0.082	0.063	0.063	0.004	0.047	0.050	0.048
0.110	0.105	0.120	0.125	0.119	0.075	0.079	0.058	0.059	0.047	0.007	0.024	0.011
0.108	0.107	0.116	0.129	0.115	0.106	0.106	0.111	0.109	0.107	0.107	0.107	0.107
0.106	0.112	0.125	0.121	0.122	0.080	0.082	0.042	0.044	0.063	0.061	0.061	0.063
0.102	0.111	0.126	0.120	0.124	0.083	0.086	0.082	0.079	0.079	0.077	0.077	0.077
0.098	0.100	0.119	0.118	0.110	0.094	0.094	0.091	0.089	0.095	0.094	0.092	0.096
0.107	0.100	0.119	0.117	0.115	0.095	0.095	0.089	0.085	0.091	0.092	0.090	0.093
0.105	0.101	0.119	0.116	0.115	0.092	0.092	0.088	0.082	0.089	0.089	0.088	0.091
0.104	0.106	0.119	0.117	0.116	0.094	0.096	0.096	0.093	0.098	0.097	0.096	0.097
0.096	0.096	0.111	0.109	0.111	0.092	0.091	0.084	0.083	0.089	0.086	0.084	0.089
0.096	0.105	0.114	0.121	0.121	0.106	0.107	0.106	0.105	0.104	0.106	0.105	0.105
0.103	0.107	0.115	0.118	0.122	0.107	0.109	0.106	0.106	0.107	0.105	0.104	0.104
0.098	0.106	0.115	0.121	0.121	0.107	0.108	0.105	0.105	0.104	0.106	0.105	0.105
0.095	0.105	0.113	0.120	0.121	0.107	0.108	0.106	0.106	0.105	0.107	0.106	0.106
0.104	0.101	0.117	0.108	0.115	0.090	0.088	0.080	0.075	0.085	0.083	0.082	0.084
0.099	0.098	0.110	0.108	0.112	0.083	0.085	0.084	0.077	0.080	0.084	0.083	0.084
0.104	0.103	0.114	0.112	0.114	0.082	0.083	0.086	0.081	0.086	0.083	0.083	0.083
0.101	0.100	0.113	0.110	0.113	0.081	0.083	0.083	0.078	0.080	0.082	0.083	0.082
0.108	0.108	0.120	0.125	0.121	0.080	0.081	0.062	0.064	0.035	0.054	0.053	0.053
0.105	0.107	0.109	0.107	0.113	0.049	0.046	0.077	0.076	0.081	0.074	0.074	0.074
0.106	0.107	0.108	0.107	0.115	0.051	0.049	0.079	0.078	0.080	0.075	0.075	0.076

coastal northeastern Amazonia were sisters to the Central American *X. susurrans*, to the exclusion of southern and western Amazonian subspecies of *X. guttatus*.

Maximum-likelihood analyses.—For both maximum-likelihood analyses performed, independent likelihood-ratio tests as implemented in MODELTEST (Posada and Crandall 1998) selected a general time reversible model of nucleotide substitution with estimated base frequencies, proportion of invariable sites, and rates for variable sites following a gamma distribution (Figs. 2 and 3). The first maximum-likelihood analysis produced a tree with all *Xiphorhynchus* species forming a well-supported monophyletic group (bootstrap = 95%) to the exclusion of *X. picus* and *X. kienerii* (Fig. 2). These latter species were placed as the sister clade to the genera *Campyloramphus* and *Lepidocolaptes*, as depicted in one of the two maximum-parsimony trees. However, in the maximum-likelihood analysis, the node linking *X. picus* and *X. kienerii* to *Campyloramphus* and *Lepidocolaptes* had a low bootstrap (28%). As in maximum-parsimony analyses, within the clade containing all *Xiphorhynchus* species (excluding *X. picus* and *X. kienerii*), two clades supported by high bootstrap values were found: (1) a ''first'' clade contain-

TABLE 2. Continued.

Taxon	22	23	24	25	26	27	28	29
Glyphorynchus spirurus								
Sittasomus griseicapillus								
Nasica longirostris								
Dendrocolaptes certhia								
Lepidocolaptes albolineatus								
L. angustirostris								
L. fuscus								
Campyloramphus trochilirostris								
C. procurvoides								
C. falcularius								
Hylexetastes perrotii								
Xiphocolaptes promeropirhynchus								
Dendrexetastes rufigula								
Xiphorhynchus erythropygius Panama								
X. erythropygius Ecuador								
X. flavigaster Mexico								
X. flavigaster Belize								
X. guttatus guttatus								
X. g. dorbignyanus								
X. g. eytoni								
X. g. guttatoides south Amazon								
X. g. guttatoides north Amazon								
X. g. polystictus	0.047							
X. g. vicinalis	0.010	0.049						
X. kienerii	0.107	0.107	0.109					
X. lachrymosus	0.061	0.063	0.063	0.102				
X. obsoletus	0.077	0.081	0.077	0.108	0.083			
X. ocellatus ocellatus	0.095	0.095	0.094	0.105	0.098	0.098		
X. o. brevirostris	0.093	0.092	0.092	0.104	0.092	0.099	0.050	
X. o. chunchotambo	0.091	0.090	0.089	0.105	0.091	0.099	0.051	0.010
X. o. weddellii	0.096	0.098	0.095	0.110	0.099	0.100	0.039	0.058
X. pardalotus	0.088	0.089	0.085	0.106	0.087	0.095	0.034	0.047
X. picus Venezuela	0.105	0.106	0.106	0.078	0.097	0.108	0.111	0.107
X. picus Trinidad	0.103	0.108	0.106	0.078	0.098	0.108	0.109	0.109
X. picus Amazon	0.104	0.106	0.105	0.078	0.097	0.108	0.112	0.108
X. picus southeast Brazil	0.105	0.105	0.106	0.079	0.099	0.109	0.110	0.107
X. spixii spixii	0.083	0.086	0.083	0.104	0.085	0.090	0.067	0.061
X. s. ornatus	0.084	0.080	0.084	0.093	0.088	0.092	0.062	0.061
X. s. elegans	0.083	0.087	0.085	0.097	0.089	0.092	0.065	0.066
X. s. juruanus	0.082	0.081	0.082	0.093	0.083	0.089	0.063	0.063
X. susurrans	0.052	0.035	0.054	0.107	0.065	0.082	0.093	0.095
X. triangularis Peru	0.074	0.081	0.077	0.100	0.076	0.081	0.093	0.096
X. triangularis Bolivia	0.076	0.080	0.079	0.101	0.079	0.083	0.094	0.098

ing all *Xiphorhynchus* species restricted to terra-firme forest plus *L. fuscus* as their sister taxon (bootstrap = 95%), and (2) a ''second'' clade with the remaining *Xiphorhynchus* species (bootstrap = 100%). The second maximum-likelihood analysis produced a tree depicting the same relationships among subspecies of polytypic *Xiphorhynchus* species as the maximum-parsimony trees but with higher bootstrap support for many nodes (Fig. 3). Both maximum-likelihood trees differed from the maximum-parsimony trees in their placement of *Xiphorhynchus obsoletus*: maximum-parsimony trees placed that species as the sister taxon to all the remaining species grouped in the ''second'' *Xiphorhynchus* clade defined above, whereas maximum-likelihood trees placed that species as sister only to the clade containing *X. flavigaster*, *X. guttatus*,*X. lachrymosus*, and *X. susurrans*. However, in both maximum-likelihood analyses, the node linking *X. obsoletus* with the latter species to the exclusion of *X. erythropygius* and *X. triangularis* was short and not well supported by bootstrap analyses (Figs. 2 and 3).

TABLE 2. Extended.

30	31	32	33	34	35	36	37	38	39	40	41	42
0.056												
0.047	0.040											
0.105	0.109	0.108										
0.106	0.109	0.108	0.028									
0.106	0.109	0.109	0.002	0.029								
0.106	0.109	0.108	0.001	0.029	0.003							
0.063	0.066	0.061	0.106	0.106	0.105	0.106						
0.059	0.067	0.062	0.099	0.100	0.100	0.100	0.043					
0.063	0.066	0.063	0.101	0.103	0.101	0.102	0.043	0.019				
0.061	0.063	0.060	0.098	0.099	0.098	0.099	0.041	0.018	0.016			
0.091	0.100	0.094	0.102	0.104	0.102	0.102	0.089	0.081	0.084	0.078		
0.092	0.090	0.087	0.106	0.108	0.107	0.107	0.090	0.087	0.086	0.085	0.079	
0.094	0.090	0.087	0.108	0.110	0.109	0.109	0.091	0.088	0.087	0.086	0.080	0.004

Bayesian inference of phylogeny.—Mirroring maximum-parsimony and maximum-likelihood trees, the first Bayesian inference of phylogeny depicting higher level relationships between *Xiphorhynchus* and other Dendrocolaptidae genera contained a clade with high probability of occurrence (99%) grouping all *Campyloramphus*, *Lepidocolaptes*, and *Xiphorhynchus* species (Fig. 4). Within that clade, two subclades existed: (1) one with a posterior probability of 100%, containing *Lepidocolaptes fuscus* and all *Xiphorhynchus* species except *X. picus* and *X. kienerii*, and (2) a second clade with a posterior probability of 64% containing *X. picus*, *X. kienerii*, two *Lepidocolaptes* species, and *Campyloramphus* (Fig. 4). As in maximum-parsimony and maximum-likelihood analyses, *Xiphorhynchus* species specialized in terra-firme forest formed a monophyletic group sister to *L. fuscus* with a posterior probability of 100% (Fig. 4). The second Bayesian inference of phylogeny yielded a majority-rule consensus tree depicting the same relationships among subspecies of polytypic *Xiphorhynchus* species as the maximum-parsimony and maximum-likelihood trees. However, the posterior probabilities of occur-

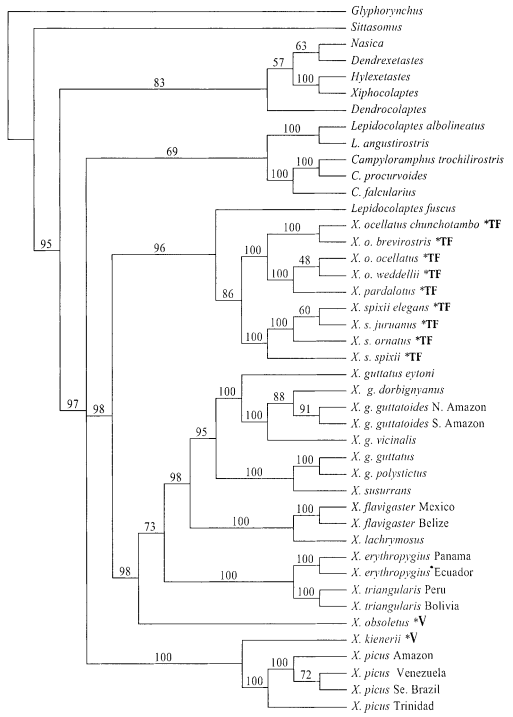

FIG. 1. Strict consensus of two most parsimonious trees (length = 3,433, CI = 0.35, RI = 0.6) obtained with unweighted sequence data. Numbers above branches refer to bootstrap support based on 100 replicates. Note the monophyly of species restricted to terra-firme forest in lowland Amazonia (taxa indicated by an asterisk followed by TF) and the polyphyly of várzea specialist species (taxa indicated by an asterisk followed by V).

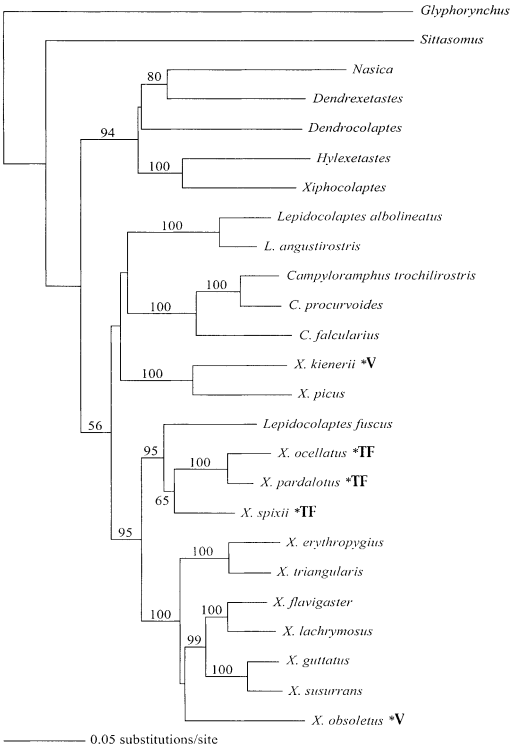

FIG. 2. Single most likely tree obtained with maximum-likelihood under the GTR+G+I model of molecular evolution (−ln likelihood = 15421.05). Estimated base frequencies were A = 0.33, C = 0.35, G = 0.09, T = 0.23; proportion of sites estimated to be invariant = 0.56; estimated value of gamma shape parameter = 1.68. Numbers above or under branches refer to bootstrap support of 50% or higher based on 100 replicates. Note the monophyly of species restricted to terra-firme forest in lowland Amazonia (taxa indicated by an asterisk followed by TF) and the polyphyly of várzea specialist species (taxa indicated by an asterisk followed by V).

rence of clades tended to be higher than bootstrap values supporting those same clades in maximum-parsimony and maximum-likelihood trees (Fig. 5). Reflecting the conflicting position of *X. obsoletus* between maximum-parsimony and maximum-likelihood trees, the two Bayesian inferences of phylogeny obtained also differed in their placement of this species. The first Bayesian inference favors the arrangement found by maximum-parsimony analyses, whereas the second Bayesian inference agrees with maximum-likelihood analyses (Figs. 2–5). Consistently, in both Bayesian inferences of phylogeny, the lowest posterior probabilities of occurrence involved clades containing *X. obsoletus* or *X. erythropygius* plus *X. triangularis* as the sister group to the well-supported *X. flavigaster–X. guttatus–X. lachrymosus–X. susurrans* clade (Figs. 4 and 5).

DISCUSSION

Monophyly of Xiphorhynchus *and its relationship with other Dendrocolaptidae genera.*—Two previous studies on dendrocolaptid systematics agreed in placing *Xiphorhynchus* in a group (Feduccia 1973) or a clade (Raikow 1994) together with the following genera: *Campyloramphus*, *Dendrexetastes*, *Dendrocolaptes*, *Hylexetastes*, *Lepidocolaptes*, and *Xiphocolaptes*. Those two studies differed only in their placement of the genera *Nasica* and *Drymornis*. On the basis primarily of osteological characters, Feduccia (1973) considered them as members of the ''strong billed'' woodcreeper assemblage,

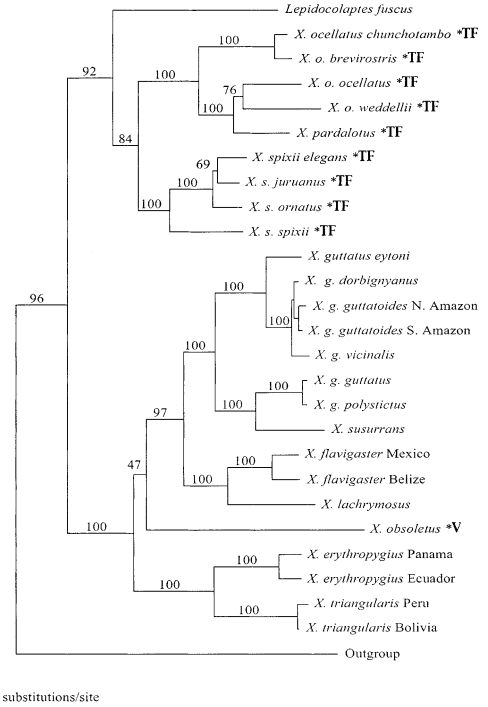

FIG. 3. Results of maximum-likelihood analyses under the GTR+G+I model of molecular evolution (−ln likelihood = 11603.4). Estimated base frequencies were A = 0.31, C = 0.34, G = 0.10, T = 0.25; proportion of sites estimated to be invariant = 0.59; estimated value of gamma shape parameter = 1.86. Numbers above or next to branches refer to bootstrap support based on 100 replicates. Short branches without numbers received at least 82% support and are not shown here for sake of clarity. Taxa restricted to terra-firme and várzea forests in lowland Amazonia are indicated by asterisks followed by the codes TF and V, respectively.

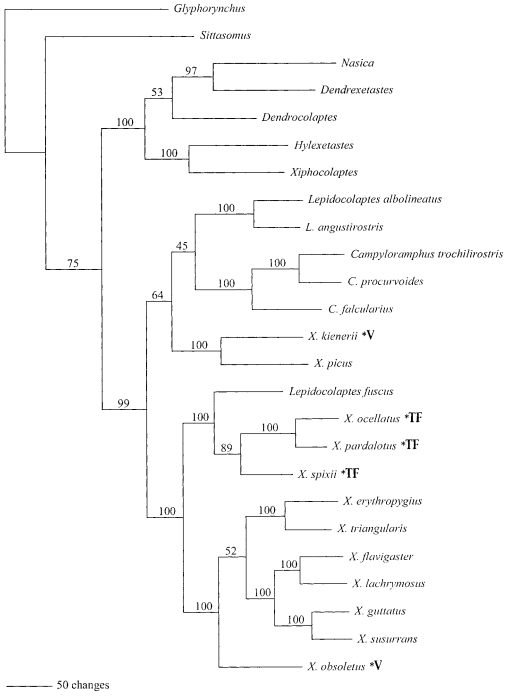

FIG. 4. Majority-rule consensus of 4,000 trees obtained by a Bayesian inference of phylogeny under a variety of substitution parameters assuming the GTR+G+I model of molecular evolution. Numbers above branches refer to the posterior probability of occurrence of clades. Note the monophyly of species restricted to terra-firme forest in lowland Amazonia (taxa indicated by an asterisk followed by TF) and the polyphyly of várzea specialist species (taxa indicated by an asterisk followed by V).

which included all the aforementioned genera and excluded the remaining so-called ''intermediate'' dendrocolaptid genera *Dendrocincla*, *Deconychura*, *Glyphorynchus*, and *Sittasomus*. Raikow's (1994) phylogeny was based primarily on myological characters and placed *Nasica* and *Drymornis* as sisters to all remaining strong billed and intermediate woodcreeper genera alike. In the present study, all strong billed genera except *Drymornis* and two of the four existing intermediate genera as defined by Feduccia (1973) were sampled. Phylogeny estimates obtained by the present study support Feduccia's (1973) placement of *Nasica* in the strong billed assemblage (Figs. 1, 2, and 4). In addition, the phylogenetic results presented here provide much better resolution of the noncontroversial part of the strong billed clade consisting of *Campyloramphus*, *Dendrexetastes*, *Dendrocolaptes*, *Hylexetastes*, *Lepidocolaptes*, *Xiphocolaptes*, and *Xiphorhynchus* than the most complete phylogenetic hypothesis previously available for the Dendrocolaptidae (Raikow 1994). Within the strong billed clade, phylogenies reconstructed with three alternative criteria (maximum parsimony, maximum likelihood, and Bayesian inference of phylogeny) pointed to a clade grouping species of *Campyloramphus*, *Lepidocolaptes*, and *Xiphorhynchus*. Statistical support for that relationship was high in maximum-parsimony and Bayesian analyses but only modest in the maximum-likelihood tree (bootstrap = 56%; Fig. 2). Unlike maximum-likelihood bootstrap analyses, Bayesian inference of phylogeny uses full models of DNA

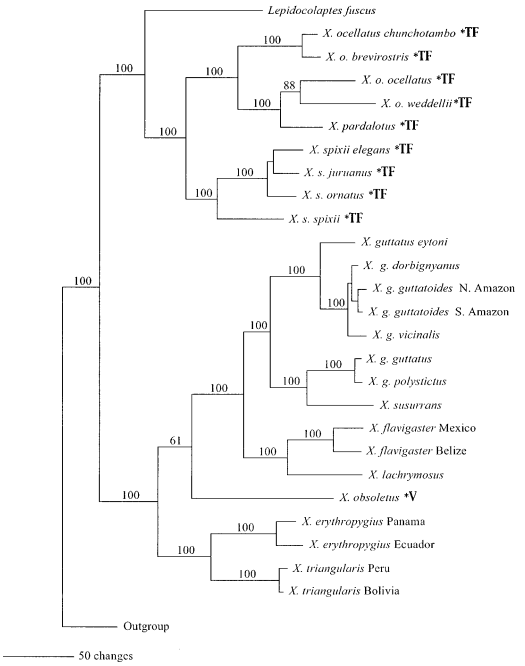

FIG. 5. Majority-rule consensus of 4,000 trees obtained by a Bayesian inference of phylogeny under a variety of substitution parameters assuming the GTR+G+I model of molecular evolution. Numbers above branches refer to the posterior probability of occurrence of clades. Short branches without numbers had a posterior probability of occurrence of at least 87% and are not shown here for sake of clarity. Taxa restricted to terra-firme and várzea forests in lowland Amazonia are indicated by asterisks followed by the codes TF and V, respectively.

substitution and samples the entire available data set to generate alternative tree topologies, thus providing a more robust evaluation of the statistical support for the different nodes of a tree. When compared to posterior probabilities derived from a Bayesian inference of phylogeny, maximum-likelihood bootstrap proportions are likely to underestimate the probability of clades with inherent high probabilities of occurrence (Rannala and Yang 1996). Supporting this view, when the maximum-likelihood and the Bayesian majority-rule consensus trees obtained in this study were compared, despite their nearly identical topologies, bootstrap proportions for nodes of the maximum-likelihood tree were never higher than posterior probabilities of clades in the Bayesian tree (Figs. 2 and 4).

Higher level relationships within the *Campyloramphus–Lepidocolaptes–Xiphorhynchus* clade were conflicting and to some extent poorly supported. All phylogeny estimates obtained suggest a sister relationship between all *Campyloramphus* and two *Lepidocolaptes* species. This relationship received moderate support only in maximum-parsimony analyses and little support in maximum-likelihood and Bayesian analyses (Figs. 1, 2, and 4). All phylogeny estimates strongly supported the monophyly of the genus *Campyloramphus* and the paraphyly of the genus *Lepidocolaptes*. According to all trees, *L. fuscus* was nested, with high support, within a clade containing only *Xiphorhynchus* species (Figs. 1, 2, and 4). These findings agree with two independent morphological and molecular data sets (Raikow 1994, García-Moreno and Silva 1997). On the basis of 36 anatomical characters, mostly myological, Raikow (1994) also found *Campyloramphus* to be monophyletic (he sampled two of the three species sampled in the present study plus the Brown-billed Scythebill [*C. pusillus*]). When Raikow's (1994) and the present study are viewed together, the only *Campyloramphus* species not sampled is the Greater Scythebill (*C. pucherani*), supporting the notion that at least four of the five extant species of *Campyloramphus* are monophyletic. Also in agreement with the present study, Raikow (1994) found *Lepidocolaptes* to be paraphyletic, with *L. fuscus* lying outside a clade containing five *Lepidocolaptes* species (two of them sampled by the present study). García-Moreno and Silva (1997) sequenced fragments of the ND2 and cyt-*b* mtDNA genes for all existing *Lepidocolaptes* species (following the taxonomy of Stotz et al. 1996), except the White-striped Woodcreeper (*L. leucogaster*); they also found that *Lepidocolaptes* is monophyletic to the exclusion of *L. fuscus*, which was found to be the sister taxon to one of their outgroups, namely *X. spixii*. Raikow's (1994) and García-Moreno and Silva's (1997) studies can be regarded as complementary because together they sampled all species of *Lepidocolaptes*. Their findings and those of the present study strongly indicated that the genus *Lepidocolaptes* is not monophyletic because *L. fuscus* is, in fact, a *Xiphorhynchus*.

All phylogeny estimates produced by the present study also show the genus *Xiphorhynchus* (sensu Peters 1951, Stotz et al. 1996) as pa-

raphyletic. The sibling species pair *X. picus* and *X. kienerii* is never found as the sister group or within the highly supported clade containing all remaining *Xiphorhynchus* species plus *L. fuscus*, regardless of the tree building method considered (Figs. 1, 2, and 4). However, the phylogenetic position of *X. picus* plus *X. kienerii* within the *Campyloramphus–Lepidocolaptes–Xiphorhynchus* clade was either conflicting (according to maximum-parsimony analyses; Fig. 1) or poorly supported (according to a maximum-likelihood analysis; Fig. 2). Topologies of one of the two most parsimonious trees found by maximum-parsimony and those of maximum-likelihood and Bayesian consensus trees place *X. picus* plus *X. kienerii* as sister to a clade containing *Campyloramphus* plus *Lepidocolaptes*. Only the Bayesian estimate of phylogeny supported this relationship modestly (Fig. 4). The second maximum-parsimony tree (not shown) placed *X. picus* plus *X. kienerii* as the sister group to all members of the *Campyloramphus–Lepidocolaptes–Xiphorhynchus* clade. Although no phylogeny recovered supported the monophyly of all *Xiphorhynchus* species, this relationship cannot be totally ruled out, given the low statistical support for the placement of *X. picus* and *X. kienerii* within the *Campyloramphus–Lepidocolaptes–Xiphorhynchus* clade. In any event, all phylogenetic hypotheses obtained strongly indicated that *X. picus* plus *X. kienerii* belong to a separate clade not nested within the genera *Campyloramphus*, *Lepidocolaptes*, or *Xiphorhynchus*. The distinctiveness of *X. picus* and *X. kienerii* was recognized by early taxonomists who grouped these species in a separate genus: *Dendroplex* (Cory and Hellmayr 1925, Zimmer 1934b). Without formal analysis, Todd (1948) transferred *kienerii* to *Xiphorhynchus* but kept *picus* in *Dendroplex*. Later, Peters (1951) lumped *Dendroplex* and *Xiphorhynchus* because the type of *Dendroplex* (consisting only of a published painting) is apparently a *Xiphorhynchus*, the name that has priority. In accordance with older taxonomy, phylogeny estimates of the present study supported the grouping of *X. picus* and *X. kienerii* in a separate genus.

Validity of Xiphorhynchus kienerii.—Described in 1934 as a cryptic species of the widespread *X. picus* (Zimmer 1934b), *X. kienerii* remained unknown in life until 1993, when it was discovered by Bret M. Whitney in central Amazonia (Aleixo and Whitney 2002). Pinto (1947, 1978) questioned the validity of *X. kienerii*, attributing its diagnostic characters to individual variation within *X. picus*. That view has persisted in the literature since then, at least as a hypothesis that could not be totally refuted (Ridgely and Tudor 1994). The level of genetic differentiation between *X. kienerii* and *X. picus* ($P = 7.8–7.9\%$; Table 2) is nearly 3× higher than the highest divergence observed between any of the four taxa of *X. picus* sampled in this study, covering most of the latter species' range ($P = 2.9\%$; Table 2). The maximum-parsimony consensus tree obtained strongly supported the monophyly of *X. picus* relative to *X. kienerii*, suggesting a separate species status for *X. kienerii* (Fig. 1). This view is confirmed by great differences in song and ecology between *X. picus* and *X. kienerii*, which are maintained even when those taxa are found in syntopy (Aleixo and Whitney 2002).

Species limits within the Xiphorhynchus triangularis–erythropygius *superspecies*.—Because they share a similar overall greenish plumage color, unique among dendrocolaptids, these two largely allopatric, montane taxa were previously regarded as conspecific (Cory and Hellmayr 1925). Eventually, *X. triangularis* and *X. erythropygius* were recognized as separate species primarily on the basis of differences in the extent of crown spotting and back streaking (Wetmore 1972). A recent anatomical phylogeny placed these two species in separate, distantly related clades (Raikow 1994). However, the present study strongly supported the monophyly of the *X. triangularis–erythropygius* superspecies (Figs. 1, 3, and 5). Uncorrected sequence divergence between these two taxa averaged 4.8% ($n = 4$; Table 2), exceeding those observed between undisputed, biological sister species of *Xiphorhynchus*: $P = 3.4–4.4\%$ (Table 2). Consistently, sequence divergence between subspecies of *X. triangularis* and *X. erythropygius* was much lower, ranging from 0.3% in *X. triangularis* to 1.4% in *X. erythropygius* (Table 2). The level of uncorrected mtDNA sequence divergence observed between *X. triangularis* and *X. erythropygius* was consistent with long-term lineage sorting and reproductive isolation, a notion also supported by the lack of known hybrids between these species (AOU 1998).

Species limits within the Xiphorhynchus guttatus *superspecies*.—Trans-Andean populations of *X. guttatus* were split from their cis-Andean

counterparts under the name *susurrans* on the basis of song and size differences (Willis 1983), an arrangement followed by the AOU (1998). The present study supported the distinctiveness of *X. susurrans* as a basal taxon sister to two cis-Andean taxa of *X. guttatus*: *X. g. guttatus* from eastern Brazil and *X. g. polystictus* from coastal northeastern Amazonia (Figs. 1, 3, 5, and Appendix). Uncorrected sequence divergence between *X. susurrans* and those taxa was 3.5%, thus within the range of values observed between some undisputed, biological sister species of *Xiphorhynchus* (3.4–4.4%; Table 2). However, in contrast with the traditional view, the major division within the *X. guttatus* superspecies was not between cis- and trans-Andean populations (*susurrans* vs. remaining taxa), but between the southern and western Amazonian taxa (*dorbignyanus*, *eytoni*, *guttatoides*, and *vicinalis*) and the trans-Andean, coastal Guyanan, and eastern Brazilian taxa (*susurrans*, *polystictus*, and *guttatus*; Figs. 1, 3, and 5). Support for that relationship was high and uncorrected sequence divergence between these two clades ranged from 4.5 to 5.4%. That divergence was consistent with species-level differences in *Xiphorhynchus* (Table 2). Within those two clades, uncorrected sequence divergence levels were lower than between clade comparisons (0.37–2.4% within the southern-western Amazonian clade, and 0.37–3.5% within the trans-Andean–Guyanan–eastern Brazilian clade). Comparatively lower levels of uncorrected sequence divergence found within the southern–western Amazonian clade were consistent with subspecific differentiation and intergradation, as inferred from plumage characters of specimens collected in contact zones between the neighboring parapatric taxa *dorbignyanus*, *eytoni*, and *guttatoides* (Zimmer 1934a). Thus, molecular data supported the traditional treatment of these taxa and *vicinalis* (Todd 1948) as conspecifics. The current analysis sampled all cis-Andean subspecies of *X. guttatus* except *X. g. connectens* (Todd 1948), found on the Guyanan shield immediately north of the Amazon river. So far, *polystictus* appears to be restricted to coastal northeastern Brazilian Amazonia and the Guyanas, and the southern limit of its distribution and contact zone with *connectens*, if any, remain unknown (Peters 1951).

If trans-Andean *X. susurrans* is recognized as a valid species, then *X. guttatus* becomes a paraphyletic species (Figs. 1, 3, and 5). As mentioned before, some phenotypic characters in addition to the molecular evidence warranted the recognition of *X. susurrans* (Willis 1983) as a separate species. Unfortunately, no study so far has compared the variation in phenotypic characters among all taxa of the *X. guttatus* superspecies. In a study that provided an identification key for all cis-Andean taxa of *X. guttatus*, Pinto (1947) pointed to a close phenotypic similarity between nominate *guttatus* and *polystictus*, thus agreeing with the molecular data. The present study supported the recognition of at least three major evolutionary lineages in the *X. guttatus* superspecies: one including *dorbignyanus*, *eytoni*, *guttatoides*, and *vicinalis*, a second including *guttatus* and *polystictus*, and a third including trans-Andean populations. Relatively high levels of sequence divergence and reciprocal monophyly among those three mostly allopatric clades suggest long-term reproductive isolation and lack of recent widespread gene flow among them. Nevertheless, more samples from contact areas, coupled with analyses of morphological, vocal, and nuclear molecular characters are needed to better assess the existence or degree of gene flow between the three main lineages of *X. guttatus* detected in this study.

Species limits within the Xiphorhynchus pardalotus–ocellatus *superspecies.*—This study strongly supported the inclusion of *X. pardalotus* in a clade containing four subspecies of *X. ocellatus* (Figs. 1, 3, and 5), thus contradicting earlier views that included *X. pardalotus* in the *X. spixii* superspecies (Cory and Hellmayr 1925, but see Zimmer 1934a). This study also indicated that the major division within the *X. pardalotus–ocellatus* superspecies is not between the Guyanan (i.e. *X. pardalotus*) and non-Guyanan Shield taxa, as implied by current taxonomy, but instead between Andean foothill (*X. o. chunchotambo* and *X. o brevirostris*) and lowland Amazonian taxa (*X. pardalotus*, *X. o. ocellatus*, and *X. o. weddellii*), hence rendering *X. ocellatus* paraphyletic. Uncorrected levels of sequence divergence between those two clades ranged from 4.6 to 5.7% and were consistent with species-level differences in *Xiphorhynchus* (Table 2). Sequence divergence between the two Andean foothill taxa (P = 1%) was within the

range of those found between other subspecies of *Xiphorhynchus*, whereas that found between *X. o. ocellatus* and *X. o. weddellii* (3.8%) was slightly higher than that between *X. o. ocellatus* and *X. pardalotus* (3.4%), two taxa considered distinct biological species (Cory and Hellmayr 1925, Zimmer 1934a, Peters 1951).

The four divergent sequence types recovered for the *X. pardalotus–ocellatus* superspecies corresponded to taxa also diagnosable by discrete phenotypic characters. *Xiphorhynchus o. chunchotambo* is such a distinctive taxon that it was treated as a separate species by Cory and Hellmayr (1925), but was subsequently merged with *X. ocellatus* on the basis of putative intergradation with *X. o. napensis* (Zimmer 1934a). That intergradation was inferred from only two intermediate specimens (which I did not examine personally) collected in northeastern Peru, where the latter taxon and *X. o. chunchotambo* approach their ranges (Zimmer 1934a). Large series of specimens housed at the Louisiana State University Museum of Natural Science indicated that *X. o. chunchotambo* and *X. o. napensis* replace each other altitudinaly in northeastern Peru, with the latter taxon restricted to the lowlands (A. Aleixo pers. obs.); therefore, opportunities for interbreeding between *X. o. chunchotambo* and *X. o. napensis* might probably be rare. *Xiphorhynchus o. weddellii* is morphologically distinct as well, but closer to nominate *ocellatus* (Zimmer 1934a), which also agreed with the molecular data. Finally, *X. pardalotus* has always been treated as a distinct species (Cory and Hellmayr 1925, Zimmer 1934a, Peters 1951). In further agreement with the molecular data, the low level of genetic differentiation found between *X. o. brevirostris* and *X. o. chunchotambo* was matched by their great phenotypic similarity (Zimmer 1934a). Missing from the sample were only two of the six *X. ocellatus* subspecies, *X. o. napensis* and *X. o. perplexus*, both found in lowland western Amazonia, and the second described taxon of *X. pardalotus* (*caurensis*). *Xiphorhynchus o. perplexus* and *X. pardalotus caurensis* are not much differentiated from their respective nominate forms (Cory and Hellmayr 1925, Zimmer 1934a, Todd 1948). However, *X. o. napensis* is quite distinct and was considered either conspecific with *chunchotambo* (Cory and Hellmayr 1925) or with *ocellatus* (Zimmer 1934a). In addition to the paraphyly of *X. ocellatus* with respect to a traditionally undisputed biological species (*X. pardalotus*), the relatively high levels of sequence divergence found among three of its taxa (*chunchotambo*, *ocellatus*, and *weddellii*) suggest long-term reproductive isolation. Nevertheless, further studies with better sampling and nuclear molecular markers are needed to assess the extent of gene flow between lineages of the *X. pardalotus–ocellatus* superspecies, especially in areas where parapatric taxa approach their ranges.

Species limits within the Xiphorhynchus spixii–elegans *superspecies.*—In contrast with the traditional classification that considered *X. spixii* and *X. elegans* conspecifics (Zimmer 1934a, Ridgely and Tudor 1994), Haffer (1997) concluded, on the basis of an analysis of plumage characters of large series of specimens, that *X. spixii* is a monotypic species. Except for nominate *spixii*, all remaining taxa of that superspecies (*buenavistae*, *elegans*, *insignis*, *juruanus*, and *ornatus*) were grouped under *X. elegans* because they intergraded with parapatric neighbors along localized contact zones (Haffer 1997). This study corroborated Haffer's (1997) classification by revealing two well-supported clades: one containing only *X. spixii* and another with *X. s. elegans*, *X. s. juruanus*, and *X. s. ornatus* (Figs. 1, 3, and 5). Uncorrected sequence divergence between members of these two clades ranged from 4 to 4.3% and were consistent with species-level divergences between other sister species pairs of *Xiphorhynchus* (Table 2), and reproductive isolation as inferred from the lack of phenotypically intermediate specimens in areas where *X. spixii* and *X. s. elegans* come near each other in central Brazil (Haffer 1997). The range of uncorrected sequence divergence within the *X. elegans* clade (P = 1.6 to 1.8%) was within those observed among other subspecies of *Xiphorhynchus* (Table 2). The two subspecies of *X. spixii* missing from the molecular analyses (*buenavistae* and *insiginis*) are phenotypically weakly differentiated from *X. s. ornatus* (Zimmer 1934b, Haffer 1997), and their inclusion in the molecular data set would likely not change the topologies of the phylogenies obtained.

Evolution of várzea and terra-firme habitat specialization in Xiphorhynchus.—This study strongly supported the monophyly of *Xiphorhynchus* species restricted to terra-firme forest in lowland Amazonia (taxa belonging to the *X. pardalotus–ocellatus* and *X. spixii–elegans* super-

species; Figs. 1–5). In contrast, the two *Xiphorhynchus* species restricted to várzea forest, *X. obsoletus* and *X. kienerii*, were found in two distantly related clades, more appropriately regarded as separate genera (Figs. 1–5). *Xiphorhynchus obsoletus* was nested in a clade containing *Xiphorhynchus* species found in a wide variety of habitats, from tropical lowland to pine-oak forests (Table 1). *Xiphorhynchus kienerii* was found in a clade with *X. picus*, a species also found in a variety of habitats (Table 1). Topologies of the molecular trees supported the hypothesis that várzea forest specialization in *Xiphorhynchus* evolved independently in two separate and highly ecologically diverse lineages.

That várzea and terra-firme specialist species of *Xiphorhynhcus* appeared in separate clades falsifies the hypothetical sister relationship between várzea and terra-firme species, as expected if the várzea–terra-firme ecotone played a prominent role in the recent diversification of the genus *Xiphorhynchus*. The monophyly of all terra-firme specialist species and the basal position of *X. obsoletus* in a separate, ecologically diverse clade, suggest that the várzea–terra-firme habitat specialization evolved early on in the evolutionary history of *Xiphorhynchus*. Since then, the terra-firme clade has experienced a much higher rate of speciation leading to two superspecies composed of largely allopatric and genetically differentiated lineages. In contrast, as indicated by long branches separating *X. obsoletus* and *X. kienerii* from their closest relatives (Figs. 2 and 4), lineages containing várzea species have not diversified nearly as much as terra-firme species. These findings support the notion that a significant part of the recent diversification within *Xiphorhynchus* originated by allopatric speciation within the terra-firme forest habitat in lowland Amazonia.

Taxonomic recommendations.—In spite of its sampling limitations, the current data set provides new insights into the evolution and diversification of species in the genus *Xiphorhynchus*, which can be used to generate new hypotheses of classification. When proposing these hypotheses, I use the General Lineage Concept of Species (de Queiroz 1998) to draw species limits in the *X. guttatus*, *X. pardalotus–ocellatus*, and *X. spixii–elegans* superspecies. De Queiroz (1998) argued that most of the alternative species ''concepts'' in modern biology (including the Phylogenetic and Biological species concepts) are in fact different criteria of the same species concept, the General Lineage Concept of Species. Because the process of speciation is continuous, several sequential events must take place for speciation to be completed; different species criteria determine species limits by arbitrarily emphasizing different events occurring during the speciation process (de Queiroz 1998). Critical to the completion of speciation is the achievement of reciprocal monophyly between sister lineages; the ''monophyly criterion'' is well suited to establish species limits in a phylogeny (de Queiroz 1998), which is now finally available for the entire genus *Xiphorhynchus* and many of its taxa. By using the monophyly criterion, paraphyletic genera (*Lepidocolaptes* and *Xiphorhynchus*) and species (*X. guttatus* and *X. ocellatus*) were split as depicted in the phylogenies obtained. On the basis of this rational, the following recommendations are made regarding the taxonomy of *Xiphorhynchus*.

(1) Exclusion of *X. picus* and *X. kienerii* from *Xiphorhynchus* and their temporary return to *Dendroplex* Swainson 1827. The diagnosis of *Dendroplex* unmistakably refers to *X. picus* (Cory and Hellmayr 1925), but its designated type specimen turned out to be the painting of a bird presently classified as *X. ocellatus* (Peters 1951). A separate publication evaluating the nomenclatural validity of *Dendroplex* is under way (A. Aleixo unpubl. data).

(2) Removal of the Lesser Woodcreeper (*L. fuscus*) from the genus *Lepidocolaptes* and its inclusion in the genus *Xiphorhynchus*. In linear classifications, *X. fuscus* should be placed right before the *X. pardalotus–ocellatus* and *X. spixii–elegans* superspecies.

(3) Recognition of three species in the *X. guttatus* superspecies: (1) Buff-throated Woodcreeper (*X. guttatus*), containing nominate *guttatus* and *polystictus* as subspecies; (2) Cocoa Woodcreeper (*X. susurrans*), containing all trans-Andean subspecies of former *X. guttatus* (AOU 1998); and (3) Lafresnaye's Woodcreeper Lafresnaye, 1850 (*X. guttatoides*), available name with priority, which would include the following Amazonian taxa: *dorbignyanus*, *eytoni*, *guttatoides*, and *vicinalis*. The taxon *connectens* should be kept in *X. guttatus* until mtDNA sequences allowing its precise placement in the *X. guttatus* superspecies become available.

(4) Recognition of three species in the *X. pardalotus–ocellatus* superspecies: (1) Chestnut-rumped Woodcreeper (*X. pardalotus*), including nominate *pardalotus* and *caurensis*; (2) Ocellated Woodcreeper (*X. ocellatus*), including nominate *ocellatus*, *perplexus*, and *weddellii*; and (3) Tschudi's Woodcreeper Tschudi, 1844 (*X. chunchotambo*), including nominate *chunchotambo* and *brevirostris*. The taxon *napensis* should be kept in *X. ocellatus* until mtDNA data allowing its precise placement in the *X. pardalotus–ocellatus* superspecies become available.

(5) Recognition of two species in the *X. spixii–elegans* superspecies: (1) monotypic Spix's Woodcreeper (*X. spixii*); and (2) Elegant Woodcreeper Pelzeln, 1868 (*X. elegans*), including nominate *elegans*, *buenavistae*, *insignis*, *juruanus*, and *ornatus*.

Acknowledgements

I thank the following individuals and institutions for assisting me with tissue loans: J. M. Babin, D. Dittmann, and J. D. Weckstein (Louisiana State University Museum of Natural Science); J. Bates and D. Willard (Field Museum of Natural History); Leo Joseph and Nathan Rice (Academy of Natural Sciences, Philadelphia); Eldredge Bermingham (Smithsonian Tropical Research Institute); and Luís Fábio Silveira (Museu de Zoologia da Universidade de São Paulo). I thank the many collectors responsible for collecting, preparing, and taking tissues from specimens used in this study. The following organizations financed field and laboratory work: National Geographic Society; Museum of Natural Science, Louisiana State University (through the Lowery and Tropical Bird Research funds); the American Museum of Natural History (through the Frank Chapman Memorial Fund); the American Ornithologists' Union, and Sigma Xi. D. C. Oren (Museu Paraense Emílio Goeldi) provided invaluable institutional support in Brazil and was also instrumental in handling loan requests critical to the completion of the present project. J. D. Weckstein, D. P. Neto (Museu Paraense Emílio Goeldi), B. M. Whitney, M. Cohn-Haft, C. Strong, F. Olmos, V. da Riva, C. Azevedo-Ramos (Universidade Federal do Pará and Instituto de Pesquisas da Amazônia), O. de Carvalho, Jr. (Instituto de Pesquisas da Amazônia), T. B. Dantas (Vera Cruz Celulose), and many local people helped with field work in Brazil. Throughout this project, I was supported by an overseas doctoral fellowship from CNPq (The National Research Council of Brazil, grant # 200099/97-3). I also thank F. Dal'Ava and F. de Assis Néo of the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais for issuing collecting and export permits used throughout this study. I am grateful to C. Marantz, J. McGuire, J.V. Remsen, Jr., F. H. Sheldon, J. D. Weckstein, and C. C. Witt for reviewing drafts of this manuscript. J. M. Bates, R. O. Prum, and an anonymous reviewer provided valuable suggestions to an early version of this paper.

Literature Cited

Aleixo, A., and B. M. Whitney. 2002. *Dendroplex* (=*Xiphorhynchus*) *necopinus* Zimmer 1934 (Dendrocolaptidae) is a junior synonym of *Dendrornis kienerii* (=*Xiphorhynchus picus kienerii*) Des Murs 1855. Auk 119:520–523.

American Ornithologists' Union. 1998. Checklist of North American Birds, 7th ed. American Ornithologists' Union, Washington, D.C.

Arctander, P., and J. Fjeldså. 1994. Andean tapaculos of the genus *Scytalopus* (Aves: Rhinocryptidae): A study of modes of speciation using DNA sequence data. Pages 205–225 *in* Conservation Genetics (V. Loeschcke, J. Tomiuk, and S. K. Jain, Eds.). Birkhäuser Verlag, Basel, Switzerland.

Bates, J. M., and R. M. Zink. 1994. Evolution into the Andes: Molecular evidence for species relationships in the genus *Leptopogon*. Auk 111:507–515.

Bates, J. M., S. J. Hackett, and J. M. Goerck. 1999. High levels of mitochondrial DNA differentiation in two lineages of antbirds (*Drymophila* and *Hypocnemis*). Auk 116:1093–1106.

Chapman, F. M. 1917. The distribution of bird life in Colombia. Bulletin of the American Museum of Natural History, no. 36.

Chesser, R. T. 1999. Molecular systematics of the rhinocryptid genus *Pteroptochos*. Condor 101:439–446.

Clench, M. H. 1995. Body pterylosis of woodcreepers and ovenbirds (Dendrocolaptidae and Furnariidae). Auk 112:800–804.

Cory, C. B., and C. E. Hellmayr. 1925. Catalogue of birds of the Americas. Part 4. Field Museum of Natural History Zoological Series 13.

de Queiroz, K. 1998. The general lineage concept of species, species criteria, and the process of speciation: A conceptual unification and terminological recommendations. Pages 57–75 *in* Endless Forms: Species and Speciation (D. J. Howard and S. H. Berlocher, Eds.). Oxford University Press, Oxford.

Desjardins, P., and R. Morais. 1990. Sequence and gene organization of the chicken mitochondrial genome. Journal of Molecular Biology 212:599–634.

Endler, J. A. 1982. Pleistocene forest refuges: Fact or fancy? Pages 641–657 *in* Biological Diversification in the Tropics (G. T. Prance, Ed.). Columbia University Press, New York.

FARRIS, J. S., M. KÄLLERSJÖ, A. G. KLUGE, AND C. BULT. 1995. Testing significance of incongruence. Cladistics 10:315–319.

FEDUCCIA, A. 1973. Evolutionary trends in the Neotropical ovenbirds and woodhewers. Ornithological Monographs, no. 13.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 79:783–791.

GARCÍA-MORENO, J., AND J. M. C. SILVA. 1997. An interplay between forest and non-forest South American avifaunas suggested by a phylogeny of *Lepidocolaptes* woodcreepers (Dendrocolaptinae). Studies in Neotropical Fauna and Environment 32:164–173.

HACKETT, S. J. 1996. Molecular phylogenetics and biogeography of tanagers in the genus *Ramphocelus* (Aves). Molecular Phylogenetics and Evolution 5:368–382.

HAFFER, J. 1969. Speciation in Amazonian forest birds. Science 165:131–137.

HAFFER, J. 1992. Parapatric species of birds. Bulletin of the British Ornithological Club 112:250–264.

HAFFER, J. 1997. Contact zones between birds of southern Amazonia. Ornithological Monographs, no. 48.

HELM-BYCHOWSKI, K., AND J. CRACRAFT. 1993. Recovering phylogenetic signal from DNA sequences: Relationships within the corvine assemblage (Class Aves) as inferred from complete sequences of the mitochondrial cytochrome-*b* gene. Molecular Biology and Evolution 10:1196–1214.

HILLIS, D. M., A. LARSON, S. K. DAVIS, AND E. A. ZIMMER. 1990. Nucleic Acids III: Sequencing. Pages 318–372 *in* Molecular Systematics (D. M. Hillis and C. Moritz, Eds.). Sinauer Associates, Sunderland, Massachusetts.

HUELSENBECK, J. P. 2000. MRBAYES: Bayesian Inference of Phylogeny. [Distributed by the author.] University of Rochester, Rochester, New York.

HUELSENBECK, J. P., AND B. HALL. 2001. MRBAYES: A program for the Bayesian inference of phylogeny. [Online.] Available at http://brahms.biology.rochester.edu/software.html.

JOHNSON, K. P., AND M. D. SORENSON. 1998. Comparing molecular evolution in two mitochondrial coding genes (cytochrome *b* and ND2) in the dabbling ducks (tribe: Anatini). Molecular Phylogenetics and Evolution 10:82–94.

KOCHER, T. D., W. K. THOMAS, A. MEYER, S. V. EDWARDS, S. PAABO, F. X. VILLABLANCA, AND A. C. WILSON. 1989. Dynamics of mitochondrial DNA evolution in mammals: Amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences USA 86: 6196–6200.

MADDISON, D. R., AND W. P. MADDISON. 2000. MACCLADE: Analysis of Phylogeny and Character Evolution, version 4.0. Sinauer Associates, Sunderland, Massachusetts.

MORITZ, C., J. L. PATTON, C. J. SCHNEIDER, AND T. B. SMITH. 2000. Diversification of rainforest faunas: An integrated molecular approach. Annual Review of Ecology and Systematics 31:533–563.

PETERS, J. L. 1951. Check-List of Birds of the World, vol. 7. Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

PINTO, O. 1947. Contribuição à ornitologia do baixo Amazonas. Arquivos de Zoologia 5:311–482.

PINTO, O. 1978. Novo Catálogo das Aves do Brasil. Vol. 1, Empresa Gráfica da Revista dos Tribunais, São Paulo.

POSADA, D., AND K. A. CRANDALL. 1998. MODELTEST: Testing the model of DNA substitution. Bioinformatics 14:817–818.

RAIKOW, R. J. 1994. A phylogeny of the woodcreepers (Dendrocolaptinae). Auk 111:104–114.

RANNALA, B., AND Z. YANG. 1996. Probability distribution of molecular evolutionary trees: A new method of phylogenetic inference. Journal of Molecular Evolution 43:304–311.

REMSEN, J. V., JR., AND T. A. PARKER III 1983. Contribution of river-created habitats to bird species richness in Amazonia. Biotropica 15:223–231.

RIDGELY, R. S., AND G. TUDOR. 1994. The Birds of South America, vol. II. The Suboscine Passerines. University of Texas Press, Austin.

ROBINSON, S. K., AND J. TERBORGH. 1997. Bird community dynamics along primary successional gradients of an Amazonian whitewater river. Ornithological Monographs, no. 48.

SIBLEY, C. G., AND J. E. AHLQUIST. 1990. Phylogeny and Classification of Birds. Yale University Press, New Haven, Connecticut.

SMITH, T. B., C. J. SCHNEIDER, AND K. HOLDER. 2001. Refugial isolation versus ecological gradients. Testing alternative mechanisms of evolutionary divergence in four rainforest vertebrates. Genetica 112:383–398.

SNETHLAGE, E. 1913. Über die Verbreitung der Vogelarten in Unteramazonien. Journal für Ornithologie 61:469–539.

SORENSON, M. D., AND T. W. QUINN. 1998. Numts: A challenge for avian systematics and population biology. Auk 115:214–221.

STOTZ, D. F., J. W. FITZPATRICK, T. A. PARKER III, AND D. B. MOSKOVITS. 1996. Neotropical Birds: Ecology and Conservation. University of Chicago Press, Chicago.

SWOFFORD, D. L. 1998. PAUP*. Phylogenetic Analysis Using with Parsimony (* and Other Methods), version 4.0b7. Sinauer Associates, Sunderland, Massachusetts.

TODD, W. E. C. 1948. Critical remarks on the woodhewers. Annals of the Carnegie Museum 31:5–18.

WETMORE, A. 1972. The birds of the Republic of Panamá. Part 3. Smithsonian Miscellaneous Collections, vol. 150.

WILLIS, E. O. 1983. Trans-Andean *Xiphorhynchus* (Aves: Dendrocolaptidae) as army ant followers. Revista Brasileira de biologia 43:125–131.

WINKER, K. 1995. *Xiphorhynchus striatigularis* (Dendrocolaptidae): *Nomen monstrositatum*. Auk 112: 1066–1070.

ZIMMER, J. T. 1934a. Studies on Peruvian birds, no. 15. Notes on the genus *Xiphorhynchus*. American Museum Novitates, no. 756.

ZIMMER, J. T. 1934b. Studies on Peruvian birds, no. 14. Notes on the genera *Dendrocolaptes*, *Hylexetastes*, *Xiphocolaptes*, *Dendroplex*, and *Lepidocolaptes*. American Museum Novitates, no. 753.

Associate Editor: R. O. Prum

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

Taxon	Voucher institution[a]	Voucher number[b]	Tissue institution[a]	Collection locality	GenBank assession numbers
Glyphorynchus spirurus	MPEG	JDW 445	LSUMNS	Bahia, Brazil	AY089806, AY089833, AY089890
Sittasomus griseicapillus	CBF	SWC 6769	LSUMNS	La Paz, Bolivia	AY089796, AY089834, AY089894
Nasica longirostris	LSUMNS	115014	LSUMNS	Loreto, Peru	AY089797, AY089835, AY089880
Dendrocolaptes certhia	MHNJP	DLD 133	LSUMNS	Loreto, Peru	AY089817, AY089856, AY089917
Lepidocolaptes albolineatus	LSUMNS	153311	LSUMNS	Santa Cruz, Bolivia	AY089825, AY089865, AY089876
Lepidocolaptes angustirostris	MHNNKM	MDC 363	LSUMNS	Santa Cruz, Bolivia	AY089811, AY089838, AY089881
Lepidocolaptes fuscus	MPEG	AA 568	LSUMNS	Bahia, Brzil	AY089819, AY089851, AY089904
Campyloramphus trochilirostris	LSUMNS	153671	LSUMNS	Santa Cruz, Bolivia	AY089822, AY089857, AY089906
Campyloramphus procurvoides	FMNH	DEW 2685	LSUMNS	Amazonas, Venezuela	AY089795, AY089836, AY089903
Campyloramphus falcularius	MZUSP	LFS 99/378	MZUSP	Bahia, Brazil	AY089810, AY089837, AY089905
Hylexetastes perrotii	LSUMNS	150674	LSUMNS	Santa Cruz, Bolivia	AY089809, AY089873, AY089916
Xiphocolaptes promeropirhynchus	LSUMNS	CCW 718	LSUMNS	Cajamarca, Peru	AY089798, AY089872, AY089907
Dendrexetastes rufigula	MHNJP	SWC 2358	LSUMNS	Loreto, Peru	AY089829, AY089839, AY089902
X. erythropygius aequatorialis	ANSP	FHS 85	LSUMNS	Pichincha, Ecuador	AY089832, AY089847, AY089879
X. e. insolitus[c]	LSUMNS	163547	LSUMNS	Chiriqui, Panama	AY089830, AY089858, AY089898
X. flavigaster eburneirostris	FMNH	DSW 2986	LSUMNS	Toledo district, Belize	AY089799, AY089871, AY089912
X. flavigaster flavigaster[c]	FMNH	394017	FMNH	Oaxaca, Mexico	AY089828, AY089849, AY089896
X. guttatus guttatus	MPEG	AA 570	LSUMNS	Bahia, Brazil	AY089808, AY089869, AY089908
X. g. eytoni	MPEG	MR-003	LSUMNS	Para, Brazil	AY089794, AY089845, AY089884
X. g. dorbigignyanus	LSUMNS	153308	LSUMNS	Santa Cruz, Bolivia	AY089816, AY089840, AY089891
X. g. guttatoides	MPEG	AA 611	LSUMNS	Amazonas, Brazil	AY089792, AY089855, AY089892
X. g. guttatoides	MPEG	AA 695	LSUMNS	Amazonas, Brazil	AY089791, AY089866, AY089882
X. g. polystictus	MPEG	Ch202	FMNH	Amapá, Brazil	AY089814, AY089843, AY089887
X. g. vicinalis	MPEG	SML86-140	FMNH	Rondônia, Brazil	AY089803, AY089850, AY089888
X. kienerii	LSUMNS	165752	LSUMNS	Amazonas, Brazil	AY089818, AY089862, AY089911
X. lachrymosus	ANSP	185351	ANSP	Esmeraldas, Ecuador	AY089807, AY089870, AY089900
X. obsoletus obsoletus	ANSP	188595	ANSP	Iwokrama, Guyana	AY089823, AY089868, AY089913
X. ocellatus chunchotambo	LSUMNS	161705	LSUMNS	Loreto, Peru	AY089815, AY089844, AY089915
X. o. brevirostris	LSUMNS	101904	LSUMNS	La Paz, Bolivia	AY089793, AY089846, AY089885
X. o. ocellatus	MPEG	AA 581	LSUMNS	Pará, Brazil	AY089804, AY089861, AY089909
X. o. weddellii	LSUMNS	119520	LSUMNS	Loreto, Peru	AY089820, AY089859, AY089878
X. pardalotus	MPEG	AA 602	LSUMNS	Pará, Brazil	AY089831, AY089848, AY089910
X. picus picus	MPEG	MCH 362	LSUMNS	Amazonas, Brazil	AY089813, AY089867, AY089901
X. p. altirostris	—[d]	—[d]	STRI	Island of Trinidad	AY089790, AY089853, AY089877
X. p. bahiae	MPEG	AA 560	LSUMNS	Bahia, Brazil	AY089821, AY089860, AY089886
X. p. phalara[c]	—[d]	—[d]	STRI	Venezuela	AY089802, AY089854, AY089893
X. spixii elegans	MPEG	AA 290	LSUMNS	Rondônia, Brazil	AY089805, AY089852, AY089899
X. s. juruanus	MPEG	AA 236	LSUMNS	Rondônia, Brazil	AY089824, AY089874, AY089883
X. s. ornatus	LSUMNS	109706	LSUMNS	Loreto, Peru	AY089812, AY089841, AY089889
X. s. spixii	MPEG	MR-002	LSUMNS	Pará, Brazil	AY089801, AY089875, AY089897
X. susurrans	LSUMNS	163545	LSUMNS	Panamá, Panamá	AY089800, AY089863, AY089914
X. triangularis bangsi	LSUMNS	162637	LSUMNS	La Paz, Boliva	AY089826, AY089864, AY089918
X. t. intermedius	LSUMNS	105872	LSUMNS	Pasco, Peru	AY089827, AY089842, AY089895

[a] ANSP = Academy of Natural Sciences, Philadelphia; CBF = Colección Boliviana de Fauna, Museo Nacional, La Paz, Bolivia; FMNH = Field Museum of Natural History, Chicago; LSUMNS = Louisiana State University Museum of Natural Science, Baton Rouge; MHNJP = Museo de Historia Natural Javier Prado, Lima, Peru; 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, São Paulo, Brazil; STRI = Smithsonian Tropical Research Institue, Balboa, Panamá.
[b] When specimens have not been catalogued, collector or field numbers are provided.
[c] Tentative subspecific identification because of incomplete locality data or questionable taxon diagnosis.
[d] No voucher specimen collected.