A PHYLOGENY OF THE WOODCREEPERS (DENDROCOLAPTINAE)

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ABSTRACT.—A phylogeny of 42 species representing the 13 genera of woodcreepers (Furnariidae: Dendrocolaptinae) was constructed by means of a numerical-cladistic analysis of morphological characters from the hindlimb muscles, bill, nostrils, feet, and tail. A tree stable at the generic level was produced, but the characters used did not effectively delineate relationships between species in the large genera *Lepidocolaptes* and *Xiphorhynchus*. Monophyly of the Dendrocolaptinae was supported. *Drymornis bridgesii* was hypothesized to be the sister species of the other woodcreepers, followed by *Nasica longirostris*. Beyond these forms, the genera *Dendrocincla, Deconychura, Sittasomus,* and *Glyphorhynchus* lie basal to the remaining genera. This is consistent with their recognition as "intermediate forms," although the basal position of *Drymornis* and *Nasica* does not agree with that hypothesis. Among polytypic genera, the monophyly of *Dendrocincla, Campylorhamphus, Xiphocolaptes,* and *Dendrocolaptes* was supported, whereas *Deconychura* appears to be paraphyletic. Monophyly of *Hylexetastes, Xiphorhynchus,* and *Lepidocolaptes* remains uncertain. *Received 25 June 1993, accepted 13 November 1993.*

THE WOODCREEPERS (Furnariidae: Dendrocolaptinae), with 13 genera and 50 species, are part of a radiation of Neotropical passerine birds (Ridgway 1911, Peters 1951, Clench and Austin 1974, Sibley and Ahlquist 1990, Sibley and Monroe 1990). Although they vary in size, bill shape, and habits, woodcreepers share a common scansorial specialization, and climb vertical tree trunks suspended by their forward toes and braced by their stiffened tail. As an assemblage of significant size and diversity, whose members share a common specialization, the woodcreepers are excellent subjects for a study of phylogeny. Methods are now available to generate phylogenetic hypotheses specifying both the branching pattern of common descent and the distribution of character transformations. Such hypotheses describe phylogenetic relationships, furnish bases for classification, and provide frameworks for the analysis of adaptive evolution. This study was undertaken to: (1) ascertain whether the woodcreeper group is monophyletic; (2) clarify the phylogenetic relationships of the woodcreepers with the other passerine birds; and (3) delineate the phylogenetic relationships among the woodcreepers.

MATERIALS AND METHODS

Data.—Characters from the hindlimb muscles, bill, nostrils, feet, and tail were used in the phylogenetic analysis. Myology was studied by dissection of 42 species of Dendrocolaptinae (Table 1), representing all 13 genera. Two specimens were dissected for each of 13 species, 10 specimens were dissected for 1 species, and single specimens were dissected for the other 28 species. These numbers are sufficient to minimize the effects of intraspecific variation (Raikow et al. 1993). Seven or eight species, depending on classification, were not included because no specimens were available.

I also dissected, for use in the outgroup analysis, 11 species of the Neotropical ovenbirds of the subfamily Furnariinae (*Geositta cunicularia, Cinclodes fuscus, Leptasthenura andicola, Synallaxis gujanensis, Certhiaxis cinnamomea, Phacellodomus rufifrons, Lochmias nematura, Pseudocolaptes boissoneautii, Thripidectes holostictus, Automolus ochrolaemus, Xenops minutus*) and 3 of the typical antbirds of the family Thamnophilidae (*Thamnophilus doliatus, Formicivora mentalis, Cercomacra tyrannina*), giving a total of 78 specimens of 56 species. Comparisons were also made with five species of Furnariinae from Rudge and Raikow (1992), including *Margarornis squamiger, M. rubiginosus, Premnoplex brunnescens, Premnornis guttuligera,* and *Roraimia adusta.*

Specimen data, detailed muscle descriptions, character polarity determinations, and anatomical illustrations are given in Raikow (1993). The bill, nostril, and feet were studied in fluid-preserved specimens rather than study skins, where they are dry and distorted.

Phylogenetic analysis.—A phylogenetic analysis was performed with PAUP version 3.0s (Phylogenetic Analysis Using Parsimony; Swofford, 1991) on an Apple Macintosh IIfx computer. Character polarities were determined by outgroup comparison using successive

TABLE 1. Data matrix used in phylogenetic analysis.[a] Characters given in Table 2.

Taxa	Character states[b]							
	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36
Hypanc	00000	00000	00000	00000	00000	00000	00000	0
Dendrocincla tyrannina	00110	01110	00011	10000	021?1	01311	11100	0
D. anabatina	00110	01110	00011	10000	02101	01311	11100	0
Dendrocincla 3 spp.	00110	01110	00011	00000	02101	01311	11100	0
Deconychura longicauda	01120	01110	00011	02000	02111	02311	11011	0
D. stictolaema	00120	01110	00011	02000	02111	02011	11011	0
Sittasomus griseacapillus	01121	01110	00?01	02000	02111	02010	11011	0
Glyphorhynchus spirurus	01120	01110	00001	12100	0211?	02010	00011	0
Drymornis bridgesii	00020	00032	00020	01010	01010	02202	01000	0
Nasica longirostris	00120	01131	00000	20000	12111	021?2	01000	0
Dendrexetastes rufigula	11120	01110	00010	10011	12101	0?001	00011	0
Hylexetastes perrotii	01121	11122	11100	20111	12111	02001	00011	0
Xiphocolaptes promeropirhynchus	01121	11122	11100	21011	12111	02102	00011	0
X. major	11121	11122	11000	21111	12111	02102	00011	0
X. albicollis	11121	11122	11000	21111	12111	?2102	00011	0
Dendrocolaptes platyrostris	11121	11111	11001	00111	12111	12011	11011	0
D. certhia	1?121	11112	11001	20111	12111	12011	11011	0
D. hoffmannsi	11121	11112	11001	20111	12111	12011	11???	0
D. concolor	11121	11112	11001	23111	12111	12011	11011	0
D. picumnus	11121	11110	01001	00011	12111	12011	11011	0
Xiphorhynchus picus	?0120	01111	01001	02111	12111	02001	00011	0
X. obs.+lach.	10120	01111	01001	12111	12111	02001	00011	0
X. spixii	10120	01111	01001	12111	12111	020?1	00011	0
X. ocellatus	10120	01111	01001	12111	12111	02001	00011	0
X. elegans	?0120	01110	010?1	12111	12111	020?1	00011	0
X. eytoni	10120	01110	01011	12111	12111	02001	00011	0
X. flavigaster	11120	???10	010?1	12111	12111	02001	00011	0
X. erythropygius	11120	01110	01001	22111	12111	02001	00011	0
X. triangularis	10120	01110	01001	22111	12111	02001	00011	0
X. pardalotus	10120	01110	01001	12111	12111	020?1	00011	0
X. guttatus	10120	01110	01001	12111	12111	02001	00011	0
Lepidocolaptes leucogaster	11121	?1111	01000	02110	1211?	02101	00011	0
L. angustirostris	10121	01111	010?0	00110	12111	02101	00011	0
L. affinis	11120	01110	01001	10110	12111	02101	00011	0
L. squamatus	?1120	01111	01010	10110	12111	02101	00011	0
L. fuscus	10120	01110	01001	02111	12111	02101	00011	0
L. albolineatus	10120	01111	01000	00111	12111	02101	00011	0
Campylorhamphus trochilirostris	00120	01110	010?0	00111	12111	02202	00010	1
C. pusillus	10120	01110	01010	10111	12111	02202	00010	1
C. procurvoides	10120	01110	01000	10111	12111	02202	00010	1

[a] Dendrocincla 3 spp. = D. fuliginosa, D. merula, D. homochroa. Xiphorhynchus obs. + lach. = X. obsoletus, X. lachrymosus.

[b] Symbols: 0 = ancestral state; 1, 2, 3 = derived states; ? = missing data or polymorphism.

outgroups (Maddison et al. 1984) based on the relationships reviewed below. The precise sister-group relationships of the Dendrocolaptinae with the species of the Furnariinae are unknown because the phylogeny of the latter group is yet to be determined. Therefore, I used a selection of species from diverse genera of the Furnariinae as the first outgroup, and several more distant members of the Furnarii (the Thamnophilidae) as a second outgroup. For some characters I used the New World Tyranni and more distant taxa as further outgroups, employing data from McKitrick (1985, 1986) and Raikow (1987).

Several strategies were employed in a search for the optimal solution. A heuristic search method was used because for 40 taxa not all possible trees can be assessed in a reasonable amount of time. The tree-bisection-reconnection (TBR) branch swapping and MULPARS options were used. With MAXTREES set at 1,000, plus automatic increase, there was no limit to the number of trees that could be saved. Zero-length branches were collapsed to yield polytomies.

Character optimization was by the accelerated-transformation method (ACCTRAN), which favors reversals over parallelisms when the results are equally parsimonious. The characters were run in the unordered state (i.e. pathways of character transformation were not specified in advance). The consistency index, homoplasy index, retention index, and rescaled

TABLE 2. Characters used in phylogenetic analysis. For details of myological characters, see Raikow (1993).

1. M. iliotibialis lateralis acetabular gap: (0) absent or narrow and slitlike; (1) wide.

2. M. iliotibialis lateralis pars postacetabularis caudal margin arises: (0) even with caudal edge of M. iliofibularis; (1) cranial thereto.

3. M. iliotrochantericus caudalis: (0) fiber arrangement fan-shaped; (1) angled.

4. M. iliotrochantericus cranialis et medius: (0) separate; (1) single and narrow; (2) single and wide.

5. M. flexor cruris lateralis origin from caudal aponeurosis: (0) present; (1) absent.

6. M. flexor cruris lateralis insertion of pars accessoria: (0) fleshy; (1) semitendinous.

7. M. flexor cruris lateralis raphe in lateral view: (0) straight; (1) concave.

8. M. flexor cruris lateralis pars pelvica tibial lobe: (0) short; (1) long.

9. M. flexor cruris medialis insertion relative to M. flexor cruris lateralis: (0) coincident; (1) extended; (2) overlapping; (3) separate.

10. M. caudofemoralis tendon of origin: (0) short; (1) medium; (2) long.

11. M. caudofemoralis femoral segment of belly: (0) narrow; (1) wide.

12. M. caudofemoralis tendon of insertion: (0) long; (1) short.

13. M. caudofemoralis insertion relative to M. pubocaudalis internus: (0) deep; (1) medial.

14. M. pubo-ischio-femoralis pars cranialis relative to M. flexor cruris lateralis: (0) adjacent; (1) overlapping; (2) separated.

15. M. pubo-ischio-femoralis pars caudalis tendon of origin: (0) short; (1) long.

16. M. fibularis longus aponeurosis of origin: (0) slight; (1) moderate; (2) extreme.

17. M. plantaris: (0) typical; (1) ossified; (2) fused to M. gas. p. intermedia; (3) absent.

18. M. gastrocnemius pars medialis: (0) wide; (1) narrow.

19. M. gastrocnemius pars medialis: (0) rounded; (1) tapered.

20. Nostril shape: (0) elongate; (1) roundish.

21. Nasal operculum: (0) present; (1) absent.

22. Length of toe 4 relative to 3: (0) much shorter; (1) slightly shorter; (2) equal.

23. M. gastrocnemius pars intermedia: (0) elongate distal to tendon G; (1) truncate.

24. M. flexor hallucis longus tarsal tendon segment: (0) unossified; (1) ossified.

25. M. flexor cruris lateralis pars accessoria: (0) wide; (1) narrow.

26. Maxillary tomium: (0) smooth; (1) notched.

27. Extent of tendon ossification: (0) almost none; (1) extensive; (2) more extensive.

28. Bill shape: (0) straight; (1) slightly decurved full length; (2) strongly decurved full length; (3) straight with tip of maxilla decurved.

29. Bill at level of nares: (0) compressed; (1) depressed.

30. Length of bill: (0) short (much shorter than head); (1) intermediate (more or less length of head); (2) long (much longer than head).

31. Culmen: (0) more or less distinctly rounded; (1) more or less distinctly ridged.

32. Gonys: (0) more or less distinctly rounded; (1) more or less distinctly ridged.

33. Termination of rectrices: (0) acuminate; short barbs on projecting shafts; (1) broadly rounded with short, downward-projecting, barbless tips of shafts.

34. Rectrices in lateral view: (0) straight to slightly decurved; (1) distinctly decurved.

35. Distal end of rectricial shafts: (0) straight; (1) twisted.

36. Width of bill from fusion of rami to tip: (0) tapered; (1) uniform.

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consistency index were calculated. These measures of homoplasy depict the extent to which the number of character transformations exceed the potential minimum. Introductory discussions are provided by Wiley et al. (1991) and Swofford (1991). Trees were rooted to a hypothetical ancestor (Hypanc) having all ancestral states.

Separate searches were made using the simple-addition, as-is-addition, closest-addition and random-addition sequences, the latter with 10 replications. In the above analyses all characters were weighted equally. I also did a search using the successive-weighting method (Swofford 1991:66). This did not yield trees shorter than in the original analysis, and will not be discussed further.

The data matrix (Table 1) had 42 species plus the hypothetical ancestor. The species were condensed to 40 OTUs because a few species had identical states. Of 36 characters (Table 2), 23 dealt with the hindlimb musculature, 7 with the bill, 2 with the nostrils, 1 with the foot, and 3 with the tail. Because several

characters had multiple derived states, there were 49 possible character transformations.

Three types of consensus trees were computed; they provide different kinds of information and together allow a more comprehensive summary than any single method (Swofford 1991, Wiley et al. 1991). The strict-consensus tree shows only clades that occur in all of the fundamental trees; it provides the highest confidence, but often has poor resolution. The semi-strict-consensus tree shows the same groups as the strict tree, plus clades that occur in some fundamental trees without contradiction in the rest. The majority-rule-consensus tree shows clades that occur in more than half of the trees; it can provide excellent resolution, but with reduced confidence in certain parts.

RESULTS

Higher-level relationships of woodcreepers.—The position of the woodcreepers relative to other birds, and the question of woodcreeper mono-

phyly, were approached through an analysis of previous studies. The monophyly of the Passeriformes was demonstrated by a morphological cladistic analysis (Raikow 1982) and corroborated by DNA-DNA hybridization (Sibley and Ahlquist 1990). The major subgroups of the passerine tree were delimited by morphology (Raikow 1987) and corroborated by DNA-DNA hybridization (Sibley and Ahlquist 1990). These phylogenies were found to have a high level of congruence (Bledsoe and Raikow 1990:257 and fig. 3). In both studies it was found that the following groups formed clades: oscines, broadbills (Eurylaimidae), pittas (Pittidae), broadbills plus pittas, and Old World suboscines plus New World suboscines. There were differences in resolution but only one incompatibility, the position of the New Zealand wrens (Acanthisittidae).

There are two New World suboscine assemblages. One of these is the Furnarii, also known as the Furnarioidea or Tracheophonae. Its members share a complex feature, the tracheophone syrinx (Ames 1971). Because this occurs in some passerines but is lacking in nonpasserines, it is shown by outgroup comparison to be derived within the Passeriformes, and shows the Furnarii to be monophyletic. Within this clade the idea that the group of ovenbirds (Furnariinae) plus woodcreepers (Dendrocolaptinae) is monophyletic is supported by the vocalis dorsalis muscle of the syrinx, which is lacking in other members of the Furnarii and in other passerines (Ames 1971). This grouping is corroborated by DNA-DNA hybridization studies (Sibley and Ahlquist 1990).

Monophyly of the woodcreepers. —The monophyly of the Dendrocolaptinae was initially postulated from traditional characters that outgroup comparison showed to be derived. The "horns" (muscle attachments) of the syrinx (Ames 1971) are lacking both in the Furnariinae (except *Geositta*) and in the outgroups discussed below. The proportions and fusion of the toes (Ridgway 1911) also tend to unite the group. The tail feathers, heavily stiffened and with spiny tips, likewise appear to be derived for the woodcreepers.

I found additional evidence for woodcreeper monophyly in the hindlimb morphology. These derived characters show no significant variation among the woodcreepers, but distinguish them collectively from the ovenbirds. First, Mm. flexor digitorum longus (FDL) and flexor hal-

lucis longus (FHL) have an origin in which FHL shows reduction of its heads to tendons, whereas FDL has an expanded femoral head whose origin is intermingled in a distinctive way with that of FHL (Raikow 1993: figs. 18 and 19). This condition is found in all dendrocolaptines studied and in none of the outgroups and, therefore, is a synapomorphy of the Dendrocolaptinae. Second, the insertion of M. pubo-ischio-femoralis pars caudalis in woodcreepers is tendinous onto the femur, rather than fleshy onto M. gastrocnemius pars intermedia, another synapomorphy (Raikow 1993: fig. 6). Finally, the phylogenetic analysis (see below) revealed seven additional synapomorphies of the woodcreepers.

Sibley and Ahlquist (1990:598-601) analyzed 10 species from 8 of 13 woodcreeper genera using DNA-DNA hybridization, and found that they form a cluster. This is consistent with the hypothesis of woodcreeper monophyly.

The phylogenetic hypothesis. —The searches using the simple- and closest-addition sequences each found 5,655 equally parsimonious trees with a length of 110 steps, whereas that using the as-is-addition sequence found 5,654 such trees. The analysis with the random-addition sequence found 7,935 trees of the same length. The trees had a consistency index (*CI*) of 0.445, a homoplasy index (*HI*) of 0.555, a retention index (*RI*) of 0.781, and a rescaled consistency index (*RCI*) of 0.348. The outcome of the random-addition search will be used for analysis because it represents the widest sampling of fundamental trees.

The results of the consensus analysis are shown in Figure 1, where the groupings from the strict, semistrict, and majority-rule trees are combined for ease of comparison. Transformations were mapped onto the tree as a hypothesis of character evolution in the woodcreepers (Figs. 2–5). Several of them are ambiguous in the sense that they would occur in alternate, equally parsimonious positions if different character optimizations had been used (indicated by asterisks in Figs. 3–5). One clade (three species of *Dendrocolaptes*) occurred in 50% of the fundamental trees (Fig. 1), but is unsupported under the current optimization.

Three types of character transformations are defined. An *establishment* is the first appearance of a given derived state in a lineage arising from the root of the tree. A *reversal* is the transformation of a derived state to an ancestral state.
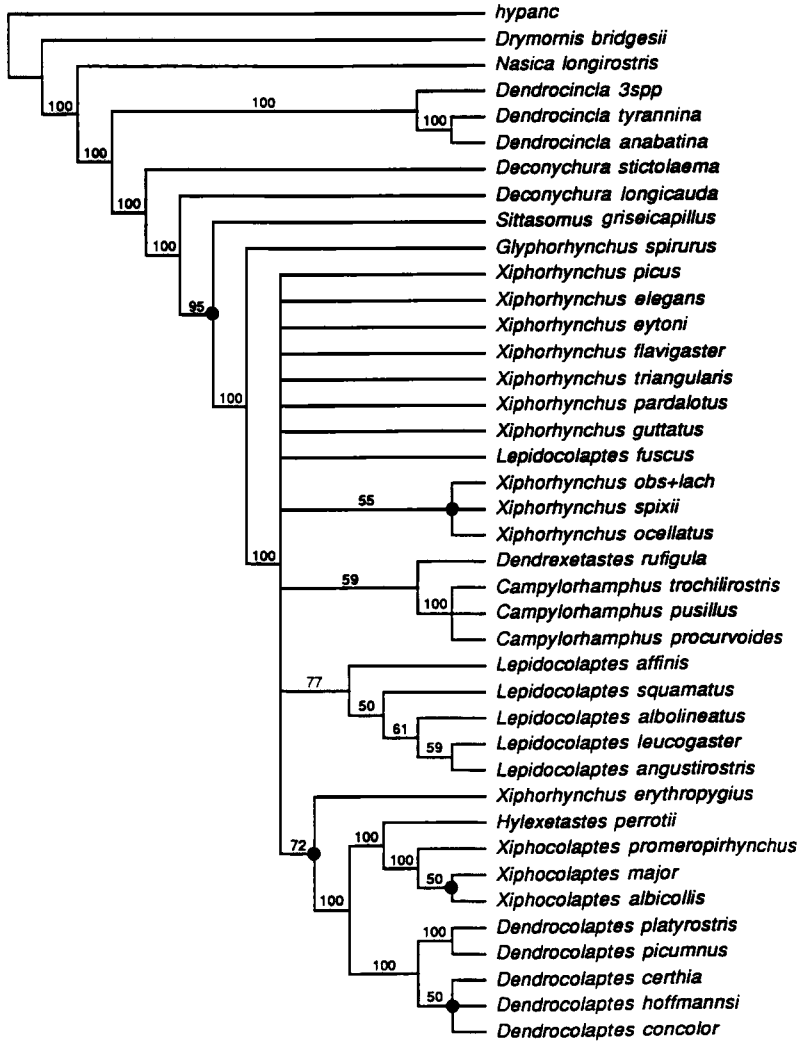
Fig. 1. Combined consensus tree. Number on each clade indicates percentage of fundamental trees in which that clade occurred. Groups occurring at 100% frequency collectively constitute strict-consensus tree. Groups with frequency of less than 100% are of two types. Those marked with dot occurred in both semistrict- and majority-rule-consensus trees. Groups with less than 100% frequency and without a dot occurred in majority-rule tree only.

A *reestablishment* is the second or subsequent appearance of a given derived state in a lineage. For a given character transformation, each of these types may be designated as *unique* or *non-unique* depending on its occurrence once or more than once in the tree (Fig. 2).

Woodcreeper monophyly is supported by seven derived states at the base of the clade (Fig. 3): all are unique establishments. The first bifurcation of the tree separates *Drymornis bridgesii* as the sister group of the remaining woodcreepers (Fig. 3). The clade from which *Drymornis* is

excluded is supported by seven uniquely established derived states. *Drymornis* is anatomically the least-derived species in its hindlimb myology, retaining the ancestral condition for several muscles that are derived in all other dendrocolaptines (Table 1). M. iliotrochantericus caudalis has a distinctive "angled" fiber architecture (Fig. 3, character 3.1) in all woodcreepers other than *Drymornis*, which retains the ancestral "fan-shaped" arrangement (3.0) found not only in the outgroups, but in all passerines as far as is known (Raikow 1993: fig. 3). The

tibial lobe of M. flexor cruris lateralis remains short in *Drymornis*, whereas it is elongated in other woodcreepers (Fig. 3, character 8.1; illustrated in Raikow 1993: fig. 7). In all other woodcreepers M. gastrocnemius pars intermedia is truncated distally (Fig. 3, character 23.1), while *Drymornis* retains the ancestral, elongated form (see Raikow 1993: fig. 15). M. flexor cruris lateralis pars accessoria becomes narrow in most species (Fig. 3, character 25.1) while remaining wide in *Drymornis* (Raikow 1993: fig. 7). Several other characters also support this division (Fig. 3).

At the next node, *Nasica longirostris* is the sister taxon of the remaining woodcreepers. The relationship between *Nasica* and *Drymornis* is intriguing. Ridgway (1911) did not consider them closely related, yet they are similar in general appearance, plumage, and size, and have long, decurved bills. However, they differ in several myological traits (Fig. 3). They also differ in the form of the nasal operculum, which is large and feathered in *Drymornis*, but lacking in *Nasica*. It is independently lacking in most woodcreepers (Fig. 4, character 21.1).

The genus *Dendrocincla* is hypothesized to be monophyletic (Fig. 3), a provisional characterization because one of the six species was not available for dissection. Synapomorphies supporting this clade include a narrow form of M. iliotrochantericus cranialis et medius (Fig. 3, character 4.1; illustrated in Raikow 1993: fig. 4). A distinctive feature of *Dendrocincla* is a reduction in the extent to which the tendons of the crural muscles are ossified (characters 24.0, 27.1). For a discussion of tendon ossification in woodcreepers see Bledsoe et al. (1993). *Dendrocincla* species also have a unique rectricial structure (character 33.1) and a distinct bill shape (28.3).

The sister group of *Dendrocincla* is a large clade supported by three characters. The fusion of M. plantaris with M. gastrocnemius pars intermedia (character 17.2) is unique to this node as an establishment, but subsequently reverses. Later it is reestablished in *Lepidocolaptes leucogaster* (Fig. 5). The other characters relate to a derived form of the tail feathers in which the ends of the shafts become distinctly decurved (character 34.1) and twisted (character 35.1). At the base of this clade, the genus *Deconychura* is hypothesized to be paraphyletic (Fig. 3). *Deconychura longicauda* is grouped apart from *D. stictolaema* by one character (2.1), but perhaps as significant is the absence of any characters that would cluster the two species of *Deconychura* with each
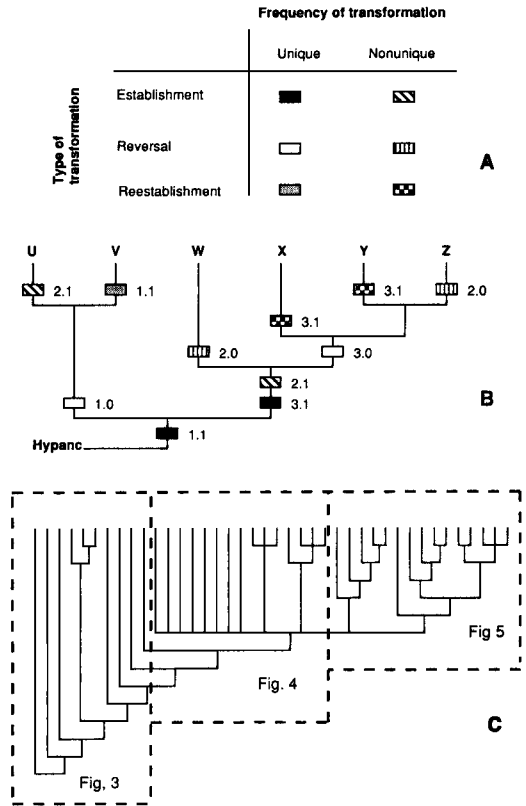

Fig. 2. Key to analysis of character evolution. (A) Six forms of character transformation are defined on basis of type and frequency of occurrence. *Unique establishment*, sole example in tree of first appearance of given derived state in lineage arising from root of tree; *nonunique establishment*, one of two or more first appearances of given derived state in different lineages; *unique reversal*, sole example of transformation of given derived state to ancestral state; *nonunique reversal*, one of two or more transformations of given derived state to ancestral state; *unique reestablishment*, sole example of second or subsequent appearance of given derived state; *nonunique reestablishment*, one of two or more examples of second or subsequent appearance of given derived state. (B) Explanatory diagram illustrating examples of six forms of character transformation. (C) Topology of majority-rule tree is divided into three sections corresponding to Figures 3, 4, and 5.

other. If this is supported by future studies, *Deconychura* would require reclassification under the principle that paraphyletic groups should not be recognized as formal taxa (Raikow 1985).

The sister clade to *Deconychura longicauda* is weakly supported by two reversals, one of which
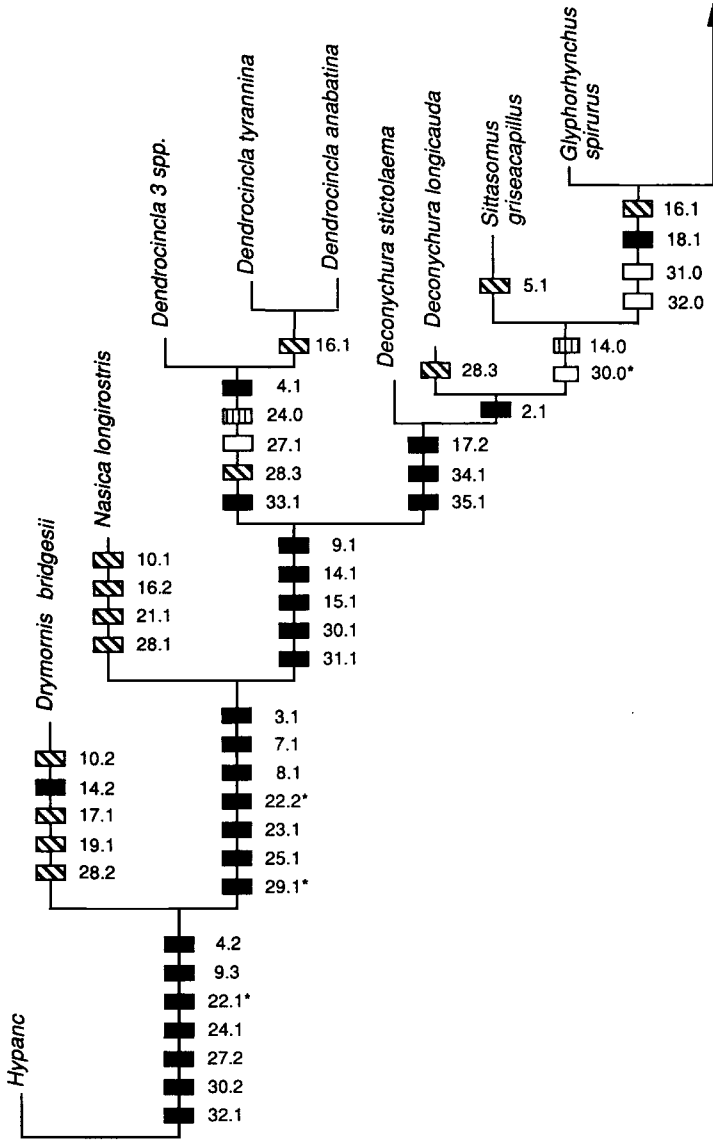
Fig. 3. Branching pattern and character-state distributions optimized on basal portion of consensus tree. See Figure 2 for explanation of symbols, and text for discussion. Asterisk indicates a state whose location varies with different methods of character optimization.

is unique but of ambiguous location (character 30.0). Included within this clade is a cluster more strongly supported by four characters, one of which (the narrowing of M. gastrocnemius pars medialis; character 18.1) is a unique establishment. The next clade, the sister group of *Glyphorhynchus spirurus* (Figs. 4 and 5), is supported by eight synapomorphies of various types.

The middle part of the strict tree is poorly resolved, and the other consensus trees have

their least-resolved areas here. The cause of this problem, which also accounts for the large number of fundamental trees, is that the genera *Xiphorhynchus* and *Lepidocolaptes* have many species with few differences in the characters studied (Figs. 4 and 5). These two genera are completely unresolved in the strict tree (Fig. 1). In the majority-rule tree five of the six species of *Lepidocolaptes* form a clade in 77% of the fundamental trees, and this clade is supported by
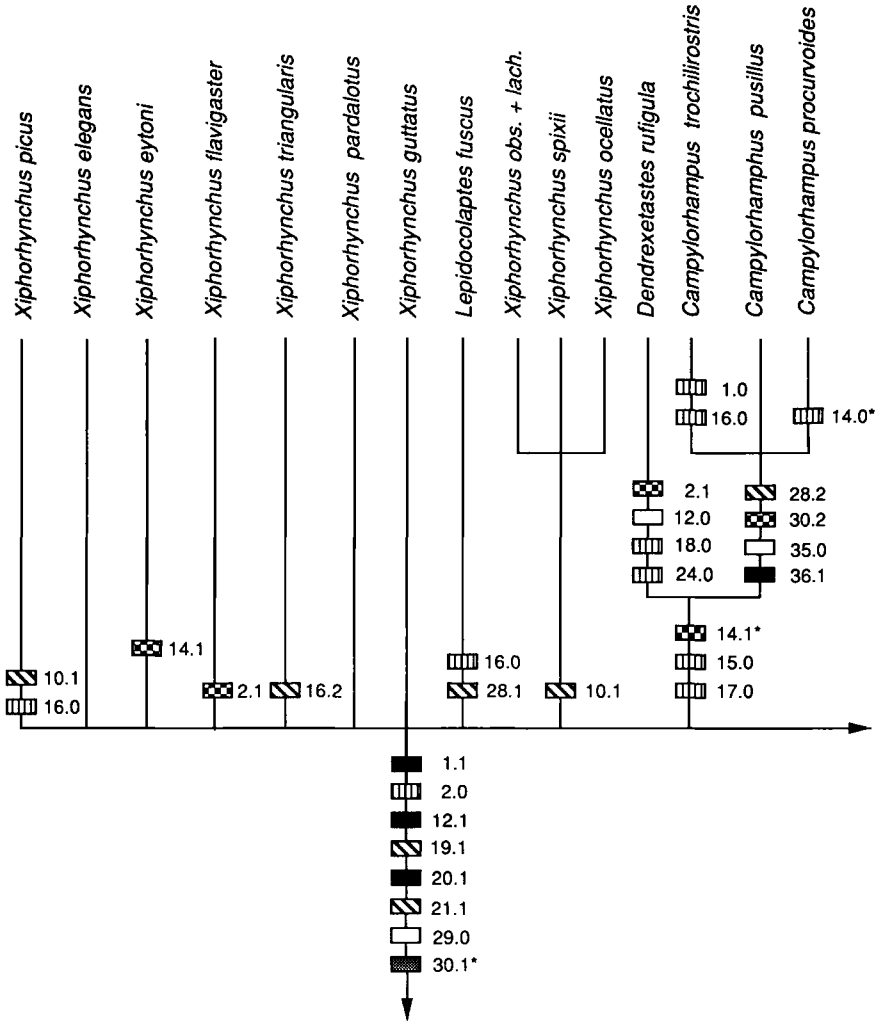
Fig. 4. Branching pattern and character-state distributions optimized on middle portion of consensus tree. See Figure 2 for explanation of symbols, and text for discussion.

four characters (Fig. 5). In *Xiphorhynchus*, three termini form a clade (Fig. 1) supported by a single, nonunique establishment (Fig. 4). *Xiphorhynchus erythropygius* is set apart from the rest (Figs. 1 and 5), and the other seven species remain unresolved. This region is the most weakly documented part of the phylogeny.

The species of *Campylorhamphus* are grouped by four characters (Fig. 4), three of which relate to the bill, which is strongly decurved throughout its length (character 28.2), and much longer than the head (character 30.2). The first of these traits is shared with *Drymornis*, and the second with *Drymornis* and *Nasica*. This similarity is outweighed by other characters, so that *Dry-*

mornis and *Nasica* are not phylogenetically close to *Campylorhamphus*. Character 36.1 is unique. In other forms the bill, viewed from above or below, tapers toward the tip, but in *Campylorhamphus* it is uniformly slender. Character 35.0 is a reversal of the twisted shape of the rectricial shafts. I studied only three of the five species of *Campylorhamphus*, so monophyly is tentative. However, as this clade occurred in all fundamental trees (Fig. 1), and because the other species have the same type of bill, it is probable that *Campylorhamphus* is monophyletic.

Hylexetastes, *Xiphocolaptes* and *Dendrocolaptes* form a clade in all of the fundamental trees (Fig. 1). It is supported by five characters (Fig. 5), two

Fig. 5. Branching pattern and character-state distributions optimized on distal portion of consensus tree. See Figure 2 for explanation of symbols, and text for discussion.

of which (characters 6.1 and 11.1) are unique establishments. Two other characters (5.1 and 10.2) are nonunique establishments, while one (17.0) is a nonunique reversal.

Hylexetastes perrotii is grouped with *Xiphocolaptes* in all fundamental trees (Fig. 1) with support by four characters (Fig. 5). Two of these are unique establishments (9.2 and 13.1), while two others (1.0 and 15.0) are nonunique reversals.

Xiphocolaptes is monophyletic in all trees (Fig. 1) on the basis of three characters (Fig. 5). Because I studied only three of the five species in this genus (Sibley and Monroe 1990), the conclusion of monophyly is tentative. Also, be-

cause I studied only one of two species of *Hylexetastes*, its monophyly is likewise undetermined. *Dendrocolaptes* is postulated to be monophyletic in all trees (Fig. 1) by four bill characters (Fig. 5). One of these (character 26.1) is a unique establishment, whereas the others are unique reestablishments.

Discussion

Comparison with earlier studies.—Feduccia (1973) studied anatomical and biochemical features of the woodcreepers and the related ovenbirds (Furnariinae). He recognized a group of "intermediate forms" (the genera *Dendrocincla, Sit-*

tasomus, Glyphorhynchus and *Deconychura*), and he proposed two hypotheses. One is that the Dendrocolaptinae is monophyletic, and that the "intermediates" are transitional to the remaining "strong-billed" woodcreepers. Feduccia's (1973) other hypothesis is that the two woodcreeper groups are separate radiations, so that the Dendrocolaptinae is diphyletic.

The results of my study contradict Feduccia's (1973) hypothesis of a diphyletic origin of the Dendrocolaptinae. His alternative idea, that the intermediates are transitional between the ovenbirds and the strong-billed woodcreepers, is supported in large part, but with a shift of *Drymornis* and *Nasica* to the base of the tree. *Drymornis bridgesii* is by far the most primitive woodcreeper as measured by the retention of ancestral character states, especially of the limb muscles, although its bill shape and groundforaging, open-country habits may represent specializations.

Sibley and Ahlquist (1990) showed *Sittasomus, Glyphorhynchus,* and *Dendrocincla* as offshoots of their basal node, with four strong-billed genera as a separate clade. This is consistent with Feduccia's views but, unfortunately, Sibley and Ahlquist (1990) were unable to study either *Drymornis* or *Nasica,* which in my study arose from the base of the tree apart from the other strong-billed woodcreepers (Figs. 1 and 3).

Evolutionary status of genera.—Eight of the traditionally recognized genera are polytypic. My study provides evidence that four of these (*Dendrocincla, Campylorhamphus, Xiphocolaptes,* and *Dendrocolaptes*) are monophyletic and one (*Deconychura*) is evidently paraphyletic; for three (*Hylexetastes, Xiphorhynchus,* and *Lepidocolaptes*) no decision about monophyly could be reached.

Evaluation of the hypothesis.—The discovery of nearly 8,000 equally parsimonius, minimumlength trees might suggest that the result of the phylogenetic analysis is not very definitive. However, inspection of the consensus trees shows that they are highly resolved in most areas, with lack of resolution being concentrated mainly in the numerous species of the genera *Lepidocolaptes* and, especially, *Xiphorhynchus.* In order to evaluate this problem, I performed an analysis of the data matrix with the species of *Xiphorhynchus* and *Lepidocolaptes* excluded. The result was dramatic. The structure of the tree was maintained, while eliminating almost all of the multiple trees generated from the full data set, as the number of trees declined from

7,935 to 10. The only change was the minor shift of the origin of *Dendrexetastes rufigula* one node toward the base of the tree. This suggests that the overall phylogeny is well supported. The problem is simply that the characters used in this study will not distinguish species-level differences in these genera, so the solution for that part of the tree must await analysis of other types of data that show sufficient variation at the appropriate taxonomic level.

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