The Auk 127(2):430–439, 2010
© The American Ornithologists' Union, 2010.
Printed in USA.

POLYPHYLY OF *CAMPYLORHAMPHUS*, AND DESCRIPTION OF A NEW GENUS FOR *C. PUCHERANI* (DENDROCOLAPTINAE)

Santiago Claramunt,[1,4] Elizabeth P. Derryberry,[1] R. Terry Chesser,[2] Alexandre Aleixo,[3] and Robb T. Brumfield[1]

[1]*Museum of Natural Science and Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803, USA;*
[2]*U.S. Geological Survey, Patuxent Wildlife Research Center, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, D.C. 20013, USA; and*
[3]*Coordenação de Zoologia, Museu Paraense Emílio Goeldi, Caixa Postal 399, CEP 66040-170, Belém, Pará, Brazil*

Abstract.—We investigated the phylogenetic relationships of *Campylorhamphus pucherani* using DNA sequences from three mitochondrial genes and a nuclear intron, as well as 84 morphological characters from the skeleton, the integument, and the musculature. The molecular phylogeny indicated that *C. pucherani* is not part of *Campylorhamphus*; instead, it is the sister species to *Drymornis bridgesii*, in a clade that also contains *Lepidocolaptes*. The morphological phylogeny also placed *C. pucherani* in a clade that contains *Drymornis* and *Lepidocolaptes*. Using a morphometric analysis of size and shape diversity, we demonstrated that the inclusion of *C. pucherani* in *Drymornis* would create an excessively heterogeneous genus compared with other dendrocolaptine genera. Because no generic name is available for *C. pucherani*, we describe the new genus *Drymotoxeres* for this species. *Received 18 June 2009, accepted 12 October 2009.*

Key words: *Campylorhamphus*, Dendrocolaptinae, *Drymotoxeres*, morphometric heterogeneity, phylogeny, ranking criteria, taxonomy.

Polifilia de *Campylorhamphus* y la Descripción de un Nuevo Género para *C. pucherani* (Dendrocolaptinae)

Resumen.—Se investigaron las relaciones filogenéticas de *Campylorhamphus pucherani* usando secuencias de ADN de tres genes mitocondriales y un intrón nuclear, así como 84 caracteres morfológicos del esqueleto, del integumento y de la musculatura. La filogenia molecular indica que *C. pucherani* no es parte de *Campylorhamphus* sino que es la especie hermana de *Drymornis bridgesii*, en un clado que también incluye a *Lepidocolaptes*. La filogenia morfológica también ubica a *C. pucherani* en un clado con *Drymornis* y *Lepidocolaptes*. Un análisis morfométrico de diversidad de tamaño y forma demuestra que la inclusión de *C. pucherani* en *Drymornis* resultaría en un género excesivamente heterogéneo. Dado que no hay nombres genéricos disponibles para *C. pucherani*, describimos el género nuevo *Drymotoxeres* para esta especie.

The genus *Campylorhamphus* currently comprises five species of medium-sized woodcreepers (Furnariidae: Dendrocolaptinae) characterized most conspicuously by their long and decurved bills. Four species (*C. trochilirostris*, *C. pusillus*, *C. procurvoides*, and *C. falcularius*) form a morphologically homogeneous group that inhabits humid to seasonal tropical forests and lower montane forest mostly below 2,000 m, from northern Argentina to Costa Rica (Marantz et al. 2003). The distinctive fifth species, *C. pucherani*, is larger than the others, its bill is proportionally shorter and less decurved, and it is the only species restricted to upper montane forest, occurring from 1,500 to 3,000 m in the Andes of Colombia, Ecuador, and Peru (Fjeldså and Krabbe 1990, Marantz et al. 2003).

Campylorhamphus was described by Bertoni (1901) for *C. longirostris* (= *C. falcularius*). Ridgway (1911) included all taxa currently listed in the genus (Marantz et al. 2003) except *C. pucherani*, which does not occur in the region covered by Ridgway's work. Chapman (1917) added *C. pucherani* to the genus, probably because of its long, thin, decurved bill, although he did not provide a rationale for his placement. As part of a project to reconstruct the phylogeny of the Furnariidae, we sequenced all species of dendrocolaptines and found that *Campylorhamphus*, as currently recognized, is not monophyletic. To maintain a phylogenetic classification, we describe a new genus of woodcreeper here. In addition, we present a quantitative analysis of phenotypic heterogeneity that can be used to help guide taxonomic ranking decisions.

[4]E-mail: sclara1@tigers.lsu.edu

The Auk, Vol. 127, Number 2, pages 430–439. ISSN 0004-8038, electronic ISSN 1938-4254. © 2010 by The American Ornithologists' Union. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, http://www.ucpressjournals.com/reprintInfo.asp. DOI: 10.1525/auk.2009.09022

Methods

Taxon sampling.—Taxa sampled for this analysis included all species of *Campylorhamphus*, one species of each of the other strong-billed (*sensu* Feduccia 1973) woodcreeper genera (*Xiphorhynchus*, *Nasica*, *Dendrexetastes*, *Dendrocolaptes*, *Xiphocolaptes*, and *Hylexetastes*), and one representative (one species of *Dendrocincla*) of the small woodcreepers (Appendices 1 and 3). We also included representatives of the other two subfamilies (Moyle et al. 2009)—one species in the genus *Sclerurus* (Sclerurinae) and one *Furnarius* (Furnariinae)—as outgroups.

Molecular data.—We extracted DNA using DNeasy kits (Qiagen, Valencia California) and amplified the mitochondrial genes NADH dehydrogenase subunit 2 (ND2, polymerase chain reaction [PCR] primers H6313 [Johnson and Sorenson 1998] and L5215 [Hackett 1996], internal sequencing primers H5766 [Brumfield et al. 2007] and L5758 [Johnson and Sorenson 1998]), NADH dehydrogenase subunit 3 (ND3, primers L10755 and H11151 [Chesser 1999]), and cytochrome oxidase subunit II (COII, primers NF3-COII [Sanín et al. 2009], and SCTRCOII 5′-GGA TTT AAT TGT GGC ATD TCA TTA AGG-3′ designed by S.C.), as well as intron 7 of the nuclear gene β-fibrinogen (BF7, PCR primers FIB-BI7U and FIB-BI7L [Prychitko and Moore 1997], internal sequencing primers FIBI7-397U and FIBI7-439L [Chesser 2004]). Each 25-μL PCR reaction contained ~60 ng template DNA, 1.5 ηM $MgCl_2$, 0.2 mM dNTPs each, and 0.1 U *Taq* DNA polymerase (New England Biolabs, Ipswich, Massachusetts). Thermocycling conditions started with an initial denaturation of 94°C for 2 min, followed by 34 cycles of 30 s at 94°C denaturation, 30 s at 55°C annealing (45°C for ND3), and 30 s at 72°C extension, and ending with a final extension of 10 min (5 min for ND3) at 72°C. The PCR products were purified using PEG precipitation. BigDye Terminator kits (Applied Biosystems, Foster City, California) were used for the cycle sequence reaction, and products were cleaned in Sephadex columns before electrophoresis in an ABI 3100 Genetic Analyzer. New sequences generated in this study were deposited in GenBank (accession numbers GQ906710–GQ906753 and GQ922581–GQ922594). BF7 sequences were aligned in CLUSTAL W, version 2.0.9 (Thompson et al. 1994).

Morphological data.—We examined study skins of all species and skeletons of all genera of dendrocolaptines (see Acknowledgments). We coded as discrete characters morphological features of the skeleton and the external anatomy that varied among taxa (Appendix 2). Skeletons of adult *C. falcularius* and *C. procurvoides* were not available for examination, but skull characters for *C. procurvoides* were taken from Donatelli (1997). We also included hindlimb myological characters from Raikow (1994). Finally, we used morphometric variables derived from an analysis of size and shape as explained below.

We measured 11 external features on 87 study skins. We measured bill length from the anterior border of the nostril to the tip of the bill, and bill width and depth (vertically) at the level of the anterior border of the nostrils. Three wing measurements were taken from the carpal joint without flattening the natural curvature of the closed wing: (1) length to the longest primary; (2) length to the 10th primary, the most distal one in furnarioids; and (3) length to the first secondary. Maximum and minimum tail lengths were measured from the base of the central rectrices to the longest and to the shortest rectrix, respectively. The width of the central rectrix was measured at its midlength. Tarsus length and hallux length with claw were measured following Baldwin et al. (1931). All measurements were taken by S.C. with a Mitutoyo Digimatic Point Caliper.

Variables were log transformed, permitting measurements that differ in the same proportion to be analyzed on an arithmetic scale (Gingerich 2000). To separate morphometric variation into size and shape, we estimated the isometric size of each species as the mean of the 11 log-transformed variables, and we then calculated size-free (shape) variables by subtracting the log(size) of the species from each variable (Mosimann 1970, Mosimann and James 1979).

Phylogenetic inference.—We used maximum-likelihood methods to infer trees based on the molecular data. In addition, we used cladistic methods to analyze the morphological data and the molecular and morphological data combined. Maximum-likelihood inference was implemented in RAXML, version 7.0.4, on the Cipres Portal V 1.5 (Stamatakis et al. 2008) using the general time-reversible model of nucleotide substitution with rate heterogeneity among sites modeled by a gamma distribution (GTR+Γ). We ran analyses with four different data-partitioning schemes and used Akaike's information criterion (AIC) to choose the optimal partitioning strategy (Sullivan and Joyce 2005, McGuire et al. 2007). BF7 was always treated as a separate partition. Mitochondrial sequences were analyzed with four different partition schemes: (1) as a single unit, (2) partitioned by gene, (3) partitioned by codon position, and (4) only codon position 3 in a separate partition. Clade support was assessed using a fast bootstrap algorithm in RAXML (Stamatakis et al. 2008).

Parsimony analyses of morphological and combined data sets were conducted in PAUP* (Swofford 2003) using 84 parsimony-informative morphological characters (Appendices 2 and 3) and only parsimony-informative DNA sites. Multistate morphological characters were treated as ordered if their states showed a pattern of intermediacy (Slowinski 1993). Most-parsimonious trees were obtained using the branch-and-bound algorithm, and clade support was assessed using 1,000 bootstrap replicates and Bremer's decay indices (Bremer 1994). For bootstrap analyses, we used heuristic tree searches with 10 rounds of random taxon addition each followed by branch swapping using the tree bisection–reconnection algorithm. Congruence between data sets was assessed using the incongruence length difference (ILD) test (Farris et al. 1994) implemented in PAUP* with 1,000 replicates and heuristic tree searches as in the bootstrap analyses. Finally, using the Kishino-Hasegawa (KH) test as implemented in PAUP*, we tested for differences in fit between the most parsimonious trees and trees in which *Campylorhamphus* was constrained to be monophyletic.

Phenotypic heterogeneity.—To guide taxon-ranking decisions, we assessed the phenotypic heterogeneity of all non-monotypic genera in the Dendrocolaptinae. For each genus, we computed the total variance (Van Valen 1974) using the entire set of 11 morphometric variables, and we estimated the separate contribution of size and shape to the total variance using Darroch and Mosimann's (1985) method (i.e., we calculated the difference between the total variance of the original log matrix and the total variance of the log-shape matrix to obtain the residual log size, or the contribution of size to the total variation).

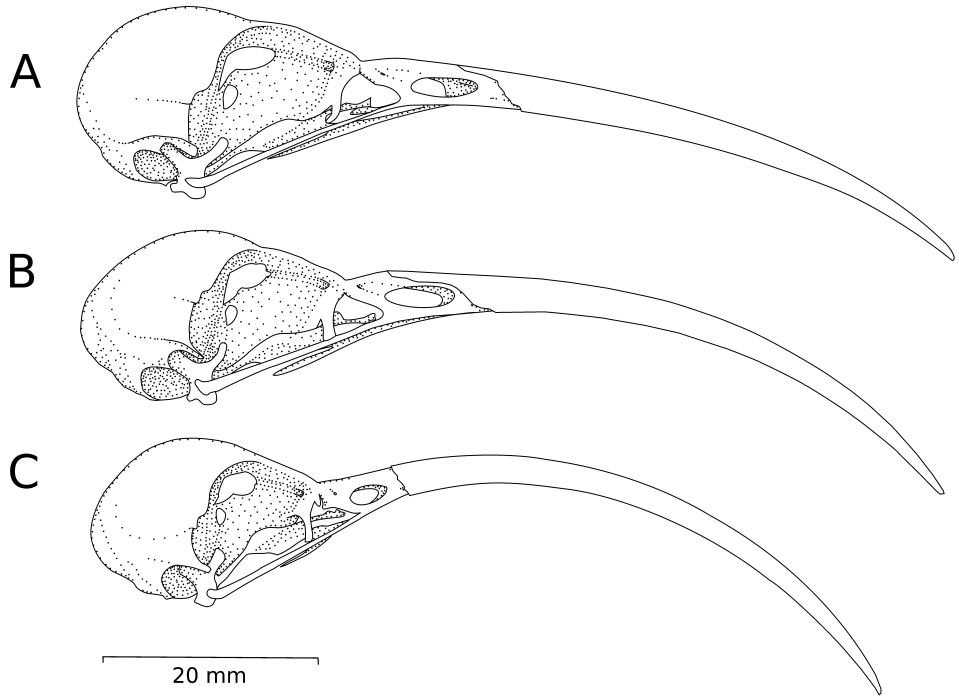

Fig. 1. Skulls with ramphothecae of (A) *Drymornis bridgesi* (MNHN 5221), (B) *Campylorhamphus pucherani* (LSUMZ 104407), and (C) *C. trochilirostris* (LSUMZ 65308).

Results

Morphological comparisons.—Campylorhamphus pucherani superficially resembles other *Campylorhamphus* spp. because of its extremely long and curved bill. However, the bill of *C. pucherani* is neither as long (in relation to body size) nor as decurved as the bills of other *Campylorhamphus* species (Fig. 1). In both bill and cranial morphology, *C. pucherani* resembles the genus *Drymornis* more closely than it resembles other species of *Campylorhamphus* (Fig. 1). The most distinctive aspect of the external anatomy of *C. pucherani* is its foot morphology. All four toes are remarkably long because of greater elongation of the distal phalanges (Fig. 2). As a result, *C. pucherani* has the longest hallux (27 mm) of all dendrocolaptines (range: 10–23 mm), in both absolute and relative terms. The hallux is as long as the tarsus in *C. pucherani*, whereas it is <85% of tarsus length in all other dendrocolaptines.

Maximum-likelihood analysis.—Partition of mitochondrial sequences by codon position was statistically more optimal (AIC = 25,761) than any other partition scheme analyzed (by gene AIC = 27,268, position 1 and 2 together AIC = 25,918, all mitochondrial sequences together AIC = 27,304); therefore, we used this partitioning scheme for all subsequent analyses. We note that the same well-supported clades appeared in all analyses, regardless of partitioning scheme (results not shown). The maximum-likelihood tree (Fig. 3) is fully dichotomous, with strong (>90%) bootstrap support for all relevant nodes. The strong-billed woodcreepers are divided into two major clades: a clade of mostly large, thick-billed genera (*Dendrocolaptes*, *Xiphocolaptes*, and allies)

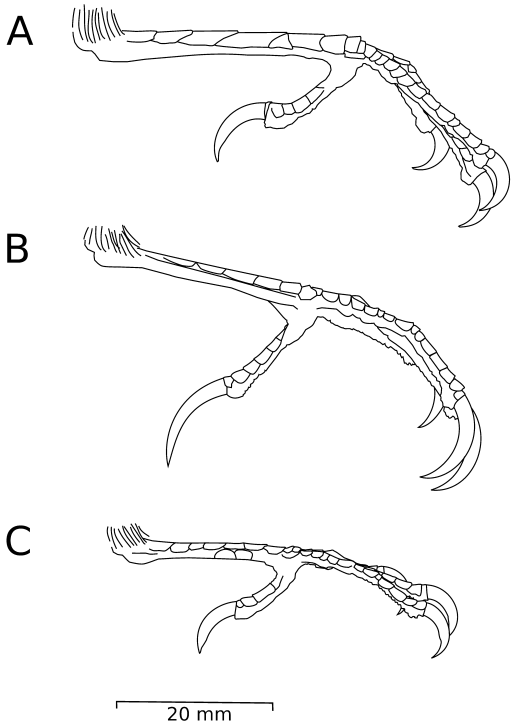

Fig. 2. Lateral view of the right foot of (A) *Drymornis bridgesi* (LSUMZ 153664), (B) *Campylorhamphus pucherani* (LSUMZ 92130), and (C) *C. trochilirostris* (LSUMZ 109736).

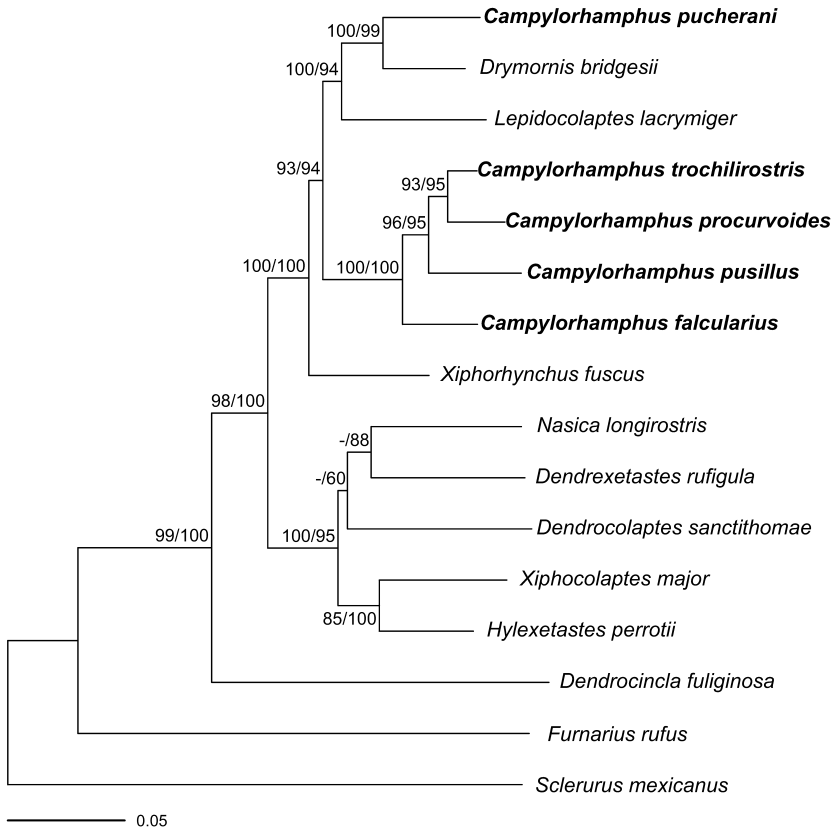

Fig. 3. Maximum-likelihood phylogram (–logL = 12,856) from a combined partitioned analysis of COII, ND3, and BF7 genes depicting evolutionary relationships among strong-billed woodcreepers (specimen data in Appendix 1). Numbers above branches are bootstrap support values of the maximum-likelihood (before slash) and maximum-parsimony (after slash) analyses.

and a clade formed by *Xiphorhynchus* and the curve-billed genera (*Lepidocolaptes*, *Campylorhamphus*, and *Drymornis*). With strong bootstrap support, *C. pucherani* appears as the sister species to the monotypic *Drymornis*; this grouping is strongly supported in the combined analysis (bootstrap: 100%) and in separate analyses of the mtDNA sequences (100%) and BF7 (99%). The *Drymornis*–*C. pucherani* clade is sister to *Lepidocolaptes* rather than to *Campylorhamphus*.

Parsimony analysis.—Parsimony analysis of morphological characters produced two most-parsimonious trees (length = 326, consistency index = 0.482, retention index = 0.593; Fig. 4). Well-supported morphological clades were congruent with those in the molecular tree, including basal relationships and monophyly of *Campylorhamphus* excluding *C. pucherani*. As in the molecular tree, *C. pucherani* was found in a clade with *Drymornis* and *Lepidocolaptes*. However, relationships within this clade were not clearly resolved. In one of the most-parsimonious trees, *C. pucherani* was sister to *Lepidocolaptes*, but in the other tree it was sister to a *Lepidocolaptes*–*Drymornis* clade. In addition, a tree with a monophyletic *Campylorhamphus* was not significantly worse (KH test: length difference = 7, $t = 0.81$, $P = 0.42$). Other conflicts between the molecular and the morphological trees were the positions of the genera *Nasica*, *Dendrexetastes*, and *Xiphorhynchus*. However, the incongruence between morphological and molecular trees involved poorly supported nodes in the morphological tree, and the two data sets were not significantly incongruent (ILD test, $P = 0.07$).

Parsimony analysis of the combined data set produced a single most parsimonious tree (length = 2,156, consistency index = 0.422, retention index = 0.440) with identical topology to the maximum-likelihood molecular tree. Interestingly, despite the apparent incongruence, inclusion of the morphological data resulted in slightly higher fit indices than an analysis of the molecular data alone (length = 1,818, consistency index = 0.414, retention index = 0.412). Enforcing the monophyly of *Campylorhamphus* resulted in a significantly worse topology (KH test: length difference = 30, $t = 3.5$, $P < 0.001$).

Morphometric heterogeneity.—Dendrocolaptine genera differed considerably in patterns of morphometric heterogeneity (Fig. 5). *Dendrocincla* was the most heterogeneous genus with respect to size and one of the most diverse with respect to shape (Fig. 5). The traditional genus *Campylorhamphus* was highly heterogeneous in both size and shape, but once *C. pucherani* was removed it showed levels of heterogeneity comparable to that found in other genera. Merging *C. pucherani* into the genus *Drymornis*, one of the taxonomic options we considered for *C. pucherani*, resulted in a relatively homogeneous genus with respect to size but an extremely heterogeneous genus with respect to shape. Shape

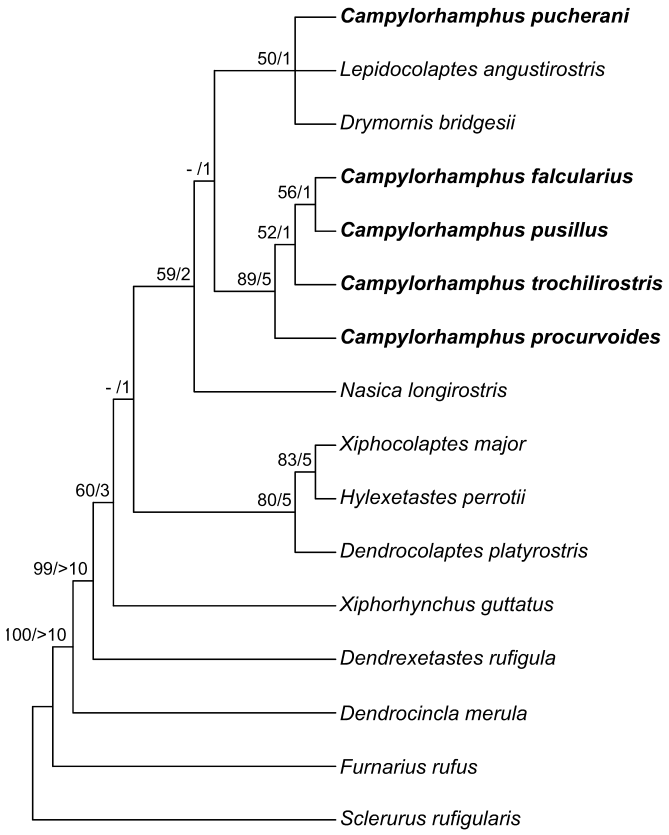

FIG. 4. Consensus tree of two most parsimonious trees from the analysis of 85 morphological characters (Appendices 2 and 3). Numbers above branches are bootstrap support values (before slash) and Bremer decay indices (after slash).

heterogeneity of an expanded *Drymornis* would be nearly twice that of the next most diverse dendrocolaptine genus.

To maintain a phylogenetic classification, it is necessary to remove *C. pucherani* from *Campylorhamphus*. Given that transferring *C. pucherani* to *Drymornis* would create an exceptionally heterogeneous genus and that there are no generic names available for *C. pucherani*, we here describe a new genus.

Drymotoxeres gen. nov.
Figures 1B and 2B

Type species.—*Xiphorhynchus pucherani* Des Murs 1849. Monotypic.

Diagnosis.—A large dendrocolaptine (63–78 g; Marantz et al. 2003) with a long decurved bill (Fig. 1B) and relatively long toes

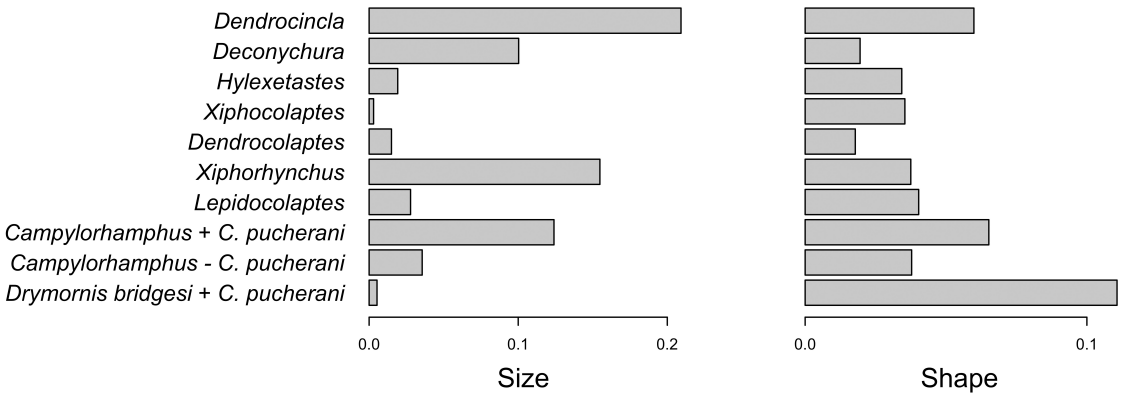

FIG. 5. Morphometric heterogeneity of polytypic dendrocolaptine genera and alternative taxonomic groupings as estimated using 11 log-transformed external measurements. Morphometric heterogeneity was estimated using the total variance, which was decomposed into size and shape components using Darroch and Mosimann's (1985) method. See text for details.

and claws, especially the hallux, which is longer than toe II and as long as the tarsus (Fig. 2B). Other characters that separate *Drymotoxeres* from *Campylorhamphus* are its shorter and less decurved bill (Fig. 1), its more elongated nostrils with a vestigial nasal operculum, and its clearly delineated light superciliary and mustachial bands. *Drymotoxeres* differs from *Drymornis* by its more decurved bill (Fig. 1) and its relatively undeveloped nasal operculum.

Etymology.—The name is masculine, from the Greek *drymos* (woods) and *toxeres* (furnished with a bow) treated as a noun, referring, respectively, to the habitat and the thin bow-shaped bill of *D. pucherani*.

Remarks.—*Drymotoxeres pucherani* can be maintained in its current position in the linear sequence, before *Campylorhamphus*, but we recommend transferring *Drymornis* to a position between *Lepidocolaptes* and *Drymotoxeres*, to make the linear sequence consistent with phylogenetic relationships.

Discussion

Although *Drymotoxeres* superficially resembles *Campylorhamphus*, a more detailed analysis of its morphology revealed several differences with its former congeners. The most distinctive features of *Drymotoxeres* are its elongated toes and claws. In passerines, long toes and claws are associated with tree-trunk climbing, especially in species that do not use their tail for support (Richardson 1942, Osterhaus 1962, Norberg 1986). Long toes and claws allow birds to grasp branches and provide stability during vertical tree-trunk climbing. Most dendrocolaptines do not have elongated toes, presumably because they use their tails for additional support and stability. The elongated toes and claws of *Drymotoxeres* may be related to greater use of the thin trunks and branches that are typical of many high-elevation trees. Alternatively, the elongated toes and claws may represent specializations for climbing the moss-covered trees of the cloud forest. The elongated claws can penetrate the thick layer of moss, allowing the bird either to cling to the mass of soft material or to reach a firmer substrate underneath. Detailed studies of the locomotor behavior of *Drymotoxeres* are needed to test these hypotheses.

We obtained a well-supported phylogeny for all genera of strong-billed woodcreepers, including all *Campylorhamphus* species. Most intergeneric relationships are congruent with previous molecular analyses (Aleixo 2002, Irestedt et al. 2004, Moyle et al. 2009). In particular, all molecular analyses as well as our morphological phylogeny recovered a clade of curve-billed woodcreepers composed of *Lepidocolaptes*, *Drymornis*, *Drymotoxeres*, and *Campylorhamphus*. The position of *Xiphorhynchus* needs to be further investigated. An analysis of myoglobin intron II placed *Xiphorhynchus* and *Lepidocolaptes* in a single clade, well within the curve-billed clade (Irestedt et al. 2004). By contrast, mitochondrial genes and nuclear RAG genes placed *Xiphorhynchus* outside the curve-billed clade (Aleixo 2002, Irestedt et al. 2004, Moyle et al. 2009). BF7 did not resolve this relationship. Our study is the first to include sequences of *Drymotoxeres pucherani*. We found that *D. pucherani* does not form a monophyletic group with *Campylorhamphus* but instead forms a clade with *Lepidocolaptes* and *Drymornis* in both the molecular and morphological analyses. Furthermore, we found strong molecular support for a sister relationship between *Drymotoxeres* and *Drymornis*.

An alternative approach to erecting a monotypic genus for *D. pucherani* would be to transfer it to *Drymornis*. Such an alternative may be favored from a strictly phylogenetic point of view because a classification with two monotypic sister genera does not contain information on their status as a monophyletic group (de Queiroz and Gauthier 1992). However, in the Linnean classification system, formal names are not assigned to every monophyletic group, and ancillary ranking criteria are needed to circumscribe named taxa. Our analyses demonstrated that transferring *D. pucherani* to *Drymornis* would produce a genus that is uncharacteristically morphologically heterogeneous compared with other dendrocolaptine genera. Therefore, the description of a new genus, in this case, is a conservative approach in the sense that it results in a more coherent generic classification in Dendrocolaptinae, in which other morphologically distinct and likely sister taxa such as *Nasica* and *Dendrexetastes* are grouped as monotypic genera (Fig. 3).

Finally, the proposed classification is also consistent with ecological and behavioral differences between *Drymotoxeres* and *Drymornis*. *Drymotoxeres pucherani* inhabits the Andean cloud forest, one of the most humid terrestrial habitats on the continent, whereas *Drymornis bridgesi* inhabits dry forests in the Chaco-Espinal lowlands. In addition, whereas *D. pucherani* forages on trees, *D. bridgesii* is the only woodcreeper that is specialized in ground foraging (Marantz et al. 2003). Therefore, *Drymotoxeres* and *Drymornis* represent different adaptive morphotypes within the dendrocolaptine radiation.

Acknowledgments

We are grateful to the following people and institutions for providing tissue samples: G. Barrowclough and P. Sweet, Department of Ornithology, American Museum of Natural History; J. Bates and D. Willard, Bird Division, Field Museum of Natural History; F. Sheldon and D. Dittmann, Genetic Resources Collection, Louisiana State University Museum of Natural Science; and Laboratório de Genética e Evolução Molecular de Aves, Universidade de São Paulo. For access to anatomical specimens, we thank J. Cracraft and P. Sweet, Department of Ornithology, American Museum of Natural History; J. V. Remsen and S. Cardiff, Louisiana State University Museum of Natural Science; and J. Cuello, Museo Nacional de Historia Natural (MNHN), Uruguay. We are grateful to G. Bravo, P. Chakrabarty, A. Cuervo, L. Naka, J. V. Remsen, and three anonymous reviewers for comments and discussion concerning the manuscript. This research was supported in part by National Science Foundation grants DBI-0400797 and DEB-0543562 to R.T.B. Use of trade, product, or firm names does not imply endorsement by the U.S. Government.

Literature Cited

Aleixo, A. 2002. Molecular systematics and the role of the "várzea"–"terra-firme" ecotone in the diversification of *Xiphorhynchus* woodcreepers (Aves: Dendrocolaptidae). Auk 119:621–640.

Baldwin, S. P., H. C. Oberholser, and L. G. Worley. 1931. Measurements of birds. Scientific Publications of the Cleveland Museum of Natural History, no. 2.

Baumel, J. J., A. S. King, J. E. Breazile, H. E. Evans, and J. C. Vanden Berge, Eds. 1993. Handbook of Avian Anatomy: Nomina Anatomica Avium, 2nd ed. Publications of the Nuttall Ornithological Club, no. 23.

Bertoni, A. de W. 1901. Aves Nuevas del Paraguay. H. Kraus, Asunción.

Bremer, K. 1994. Branch support and tree stability. Cladistics 10: 295–304.

Brumfield, R. T., J. G. Tello, Z. A. Cheviron, M. D. Carling, N. Crochet, and K. V. Rosenberg. 2007. Phylogenetic conservatism and antiquity of a tropical specialization: Army-ant-following in the typical antbirds (Thamnophilidae). Molecular Phylogenetics and Evolution 45:1–13.

Chapman, F. M. 1917. The distribution of bird-life in Colombia: A contribution to a biological survey of South America. 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.

Chesser, R. T. 2004. Molecular systematics of New World suboscine birds. Molecular Phylogenetics and Evolution 32:11–24.

Claramunt, S., and A. Rinderknecht. 2005. A new fossil furnariid from the Pleistocene of Uruguay, with remarks on nasal type, cranial kinetics, and relationships of the extinct genus *Pseudoseisuropsis*. Condor 107:114–127.

Darroch, J. N., and J. E. Mosimann. 1985. Canonical and principal components of shape. Biometrika 72:241–252.

de Queiroz, K., and J. Gauthier. 1992. Phylogenetic taxonomy. Annual Review of Ecology and Systematics 23:44–480.

des Murs, M. A. 1849. Iconographic Ornithologique. Paris.

Donatelli, R. J. 1997. Osteologia e miologia cranianas de Dendrocolaptidae (Passeriformes, Tyranni) 1. Gêneros *Glyphorhynchus*, *Campylorhamphus*, *Dendrocincla*, *Xiphorhynchus* e *Dendrocolaptes*. Ararajuba 5:19–37.

Emerson, S. B., and P. A. Hastings. 1998. Morphological correlations in evolution: Consequences for phylogenetic analysis. Quarterly Review of Biology 73:141–162.

Farris, J. S., M. Källersjö, A. G. Kluge, and C. Bult. 1994. Testing significance of incongruence. Cladistics 10:315–319.

Feduccia, J. A. 1967. The amphirhinal condition in the Passeriformes. Wilson Bulletin 79:453–455.

Feduccia, [J.] A. 1972. Variation in the posterior border of the sternum in some tree-trunk foraging birds. Wilson Bulletin 84:315–328.

Feduccia, [J.] A. 1973. Evolutionary trends in Neotropical ovenbirds and woodhewers. Ornithological Monographs, no. 13.

Feduccia, [J.] A., and S. L. Olson. 1982. Morphological similarities between the Menurae and the Rhinocryptidae, relict passerine birds of the Southern Hemisphere. Smithsonian Contributions to Zoology 366:1–22.

Felsenstein, J. 1988. Phylogenies and quantitative characters. Annual Review of Ecology and Systematics 19:445–471.

Fjeldså, J., and N. Krabbe. 1990. Birds of the High Andes. Zoological Museum, University of Copenhagen, and Apollo Books, Svendborg.

Gingerich, P. D. 2000. Arithmetic or geometric normality of biological variation: An empirical test of theory. Journal of Theoretical Biology 204:201–221.

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

Heimerdinger, M. A., and P. L. Ames. 1967. Variation in the sternal notches of suboscine passeriform birds. Postilla 105:1–44.

Irestedt, M., J. Fjeldså, and P. G. P. Ericson. 2004. Phylogenetic relationships of woodcreepers (Aves: Dendrocolaptinae)—Incongruence between molecular and morphological data. Journal of Avian Biology 35:280–288.

Johnson, K. P., and M. D. Sorenson. 1998. Comparing molecular evolution in two mitochondrial protein coding genes (cytochrome b and ND2) in the dabbling ducks (Tribe: Anatini). Molecular Phylogenetics and Evolution 10:82–94.

Marantz, C. A., A. Aleixo, L. R. Bevier, and M. A. Patten. 2003. Family Dendrocolaptidae (Woodcreepers). Pages 358–447 *in* Handbook of the Birds of the World, vol. 8: Broadbills to Tapaculos (J. del Hoyo, A., Elliott, and D. A. Christie, Eds.). Lynx Edicions, Barcelona, Spain.

McGuire, J. A., C. C. Witt, D. L. Altshuler, and J. V. Remsen. 2007. Phylogenetic systematics and biogeography of hummingbirds: Bayesian and maximum likelihood analyses of partitioned data and selection of an appropriate partitioning strategy. Systematic Biology 56:837–856.

Mosimann, J. E. 1970. Size allometry: Size and shape variables with characterization of the lognormal and generalized gamma distributions. Journal of the American Statistical Association 65:930–945.

Mosimann, J. E., and F. C. James. 1979. New statistical methods for allometry with application to Florida Red-winged Blackbirds. Evolution 33:444–459.

Moyle, R. G., R. T. Chesser, R. T. Brumfield, J. G. Tello, D. J. Marchese, and J. Cracraft. 2009. Phylogeny and phylogenetic classification of the antbirds, ovenbirds, woodcreepers, and allies (Aves: Passeriformes: infraorder Furnariides). Cladistics 25:386–405.

Norberg, R. A. 1986. Treecreeper climbing; mechanics, energetics, and structural adaptations. Ornis Scandinavica 17:191–209.

Osterhaus, M. B. 1962. Adaptive modifications in the leg structure of some North American warblers. American Midland Naturalist 68:474–486.

Parker, W. K. 1877. On aegithognathous birds (Part 1). Transactions of the Zoological Society of London 9:289–352.

Prychitko, T. M., and W. S. Moore. 1997. The utility of DNA sequences of an intron from the b-fibrinogen gene in phylogenetic analysis of woodpeckers (Aves: Picidae). Molecular Phylogenetics and Evolution 8:193–204.

Raikow, R. J. 1993. Structure and variation in the hindlimb musculature of woodcreepers (Aves: Passeriformes: Dendrocolaptinae). Zoological Journal of the Linnean Society 107:353–399.

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

Richardson, F. 1942. Adaptive modifications for tree-trunk foraging in birds. University of California Publications in Zoology 46:317–368.

Ridgway, R. R. 1911. The birds of North and Middle America: A descriptive catalogue. Part V. Bulletin of the U.S. National Museum, no. 50.

Sanín, C., C. D. Cadena, J. M. Maley, D. A. Lijtmaer, P. L. Tubaro, and R. T. Chesser. 2009. Paraphyly of *Cinclodes fuscus* (Aves: Passeriformes: Furnariidae): Implications for taxonomy and biogeography. Molecular Phylogenetics and Evolution 53: 547–555.

Simpson, S. F., and J. Cracraft. 1981. The phylogenetic relationships of the Piciformes (class Aves). Auk 98:481–494.

Slowinski, J. B. 1993. "Unordered" versus "ordered" characters. Systematic Biology 42:155–165.

Stamatakis, A., P. Hoover, and J. Rougemont. 2008. A rapid bootstrap algorithm for the RAxML web-servers. Systematic Biology 75:758–771.

Sullivan, J., and P. Joyce. 2005. Model selection in phylogenetics. Annual Review of Ecology, Evolution, and Systematics 36: 445–66.

Swiderski, D. L., M. L. Zelditch, and W. L. Fink. 1998. Why morphometrics is not special: Coding quantitative data for phylogenetic analysis. Systematic Biology 47:508–519.

Swofford, D. L. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), version 4. Sinauer Associates, Sunderland, Massachusetts.

Thompson, J. D., D. G. Higgins, and T. J. Gibson. 1994. CLUSTAL W: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic Acids Research 22: 4673–4680.

Thorpe, R. S. 1984. Coding morphometric characters for constructing distance Wagner networks. Evolution 38:244–255.

Van Valen, L. 1974. Multivariate structural statistics in natural history. Journal of Theoretical Biology 45:235–347.

von Ihering, H. 1915. The classification of the family Dendrocolaptidae. Auk 32:145–153.

Zusi, R. L., and B. C. Livezey. 2006. Variation in the os palatinum and its structural relation to the palatum osseum of birds (Aves). Annals of Carnegie Museum 75:137–180.

Associate Editor: J. Klicka

Appendix 1. Tissue samples used in the molecular analysis.

Species	Collection[a]	Number	Locality
Sclerurus mexicanus	AMNH	DOT 11828	VENEZUELA: Estado Bolívar; Río Carapo, Guaiquinima.
Furnarius rufus	AMNH	DOT 10431	ARGENTINA: Prov. Neuquén; Depto. Confluencia, Centenario.
Dendrocincla fuliginosa	AMNH	DOT 12706	VENEZUELA: Estado Amazonas; Río Baria, Cerro de la Neblina.
Drymornis bridgesii	LSUMZ	B25799	PARAGUAY: Depto. Alto Paraguay; Madrejón.
Nasica longirostris	LSUMZ	B4491	PERU: Depto. Loreto; Lower Río Napo region, E bank Río Yanayacu, 90 km N Iquitos.
Dendrexetastes rufigula	FMNH	389815	BRAZIL: Estado Rondônia; Cachoeira Nazaré, W bank Rio Ji-paraná.
Hylexetastes perrotii	FMNH	392022	BRAZIL: Estado Mato Grosso; Município Alta Floresta, upper Rio Teles Pires-Rio Cristalino.
Xiphocolaptes major	AMNH	DOT 2194	BOLIVIA: Depto. Santa Cruz; Prov. Cordillera, Izozog, Comunidad Karapari, Estancia San Julián, 1 km W Parapetí.
Dendrocolaptes sanctithomae	AMNH	DOT 3689	COSTA RICA: Prov. Puntarenas; 0.8 km NW Cuatro Cruces on Route 1.
Xiphorhynchus fuscus	LSUMZ	B35576	BRAZIL: Estado Bahia; ca 16 km W Porto Seguro, RPPN Vera Cruz.
Lepidocolaptes lacrymiger	AMNH	DOT 7051	BOLIVIA: Depto. La Paz; Parque Nacional Apolobamba.
Campylorhamphus pucherani	LSUMZ	B34815	PERU: Depto. Cajamarca; Cordillera del Cóndor, Picorana.
C. trochilirostris	AMNH	DOT 2234	BOLIVIA: Depto. Santa Cruz; prov. Cordillera, Izozog, Comunidad Karapari, Estancia San Julian, 1000 m W of Parapetí.
C. falcularius	LGEMA	1529	BRAZIL: Estado de São Paulo; Estação Ecológica Itaberá.
C. procurvoides	LSUMZ	B7501	VENEZUELA: Estado Amazonas; Cerro de la Neblina.
C. pusillus	LSUMZ	B33216	PERU: Depto. Cajamarca; ca 3 km NNE San José de Lourdes.

[a] Collections: AMNH = American Museum of Natural History, FMNH = Field Museum of Natural History, LSUMZ = Louisiana State University Museum of Natural Science, and LGEMA = Laboratório de Genética e Evolução Molecular de Aves, Universidade de São Paulo.

Appendix 2. Morphological Characters Used in the Cladistic Analysis

References are cited below that illustrate some of the characters examined in the study or describe them in more detail. For general descriptions and illustrations of furnariid skulls, see Feduccia (1973) and Donatelli (1997). Latin anatomical terms follow Baumel et al. (1993). Multistate characters treated as ordered in the cladistic analysis are indicated.

Skeleton

Skull

1. Palatal surface of the premaxillary rostrum, medial groove: (0) absent; (1) shallow; (2) deep (Claramunt and Rinderknecht 2005: fig. 2). Ordered.
2. Hump at the base of the culmen: (0) absent, smooth culmen (Fig. 2C); (1) a slight angle; (2) small hump (Fig. 1A, B). Called "crest" by Feduccia and Olson (1982: figs. 5 and 6). Ordered.
3. Ventral bar near the premaxillary rostrum: (0) thick; (1) flattened (*zona flexoria rostroventralis*; Baumel et al. 1993: fig. 5.2.A, Claramunt and Rinderknecht 2005: fig. 3).
4. Nasal septum (*septum nasi osseum*), ossification: (0) unossified, only the "recurrent lamina" present (Parker 1877); (1) a small crest bellow the dorsal bar (Claramunt and Rinderknecht 2005: fig. 3A, B).
5. Alinasal wall: (0) unossified; (1) partially ossified; (2) fully ossified. The ossification of the alinasal laminae produces the sheet of bone that covers the upper and caudal portion of the bony nares of some birds (Parker 1877: plate LVII.10), contributing to the formation of the amphirhinal condition (Von Ihering 1915, Feduccia 1967). Ordered.

6. Nasal wall: (0) unossified; (1) partially ossified; (2) fully ossified. The ossification of the nasal wall produces the sheet of bone that covers the median and lower portion of the bony nares of some birds (Parker 1877), contributing to the formation of the the amphirhinal condition (Von Ihering 1915, Feduccia 1967). Ordered.
7. Nares (*apertura nasi ossea*), caudal extension : (0) short; (1) slightly rostral to the craniofacial hinge; (2) surpasses the craniofacial hinge. Ordered.
8. Maxilopalatine process (*os maxillae: processus maxillopalatinus*), shaft: (0) thin; (1) broad.
9. Maxilopalatine process, plate: (0) small; (1) wide; (2) elongated. Ordered.
10. Transpalatine elements (*processsus accessorius palatinus*): (0) short; (3) long (Zusi and Livezey 2006).
11. Vomer and alinasal elements: (0) unfused or unossified alinasal turbinals; (1) the vomer fussed to the ossified alinasal turbinals form a compound bone (Feduccia 1973: fig. 4A, C). Parker (1877) describes the configuration of the vomer and the alinasal cartilages.
12. Orbital process of the quadrate (*os quadratum*: *processus orbitalis*), distal end: (0) acute; (1) slightly expanded; (2) spatulated. Ordered.
13. Ectethmoid (*os ectethmoidale*): (0) small; (1) intermediate; (2) large. Ordered.
14. Ectethmoid, jugal projection: (0) thin; (1) thick.
15. Interorbital fontanelle (*fonticuli interorbitale*): (0) wide, squared; (1) small, circular; (2) absent (Fig. 1). Ordered.
16. Frontal (*os frontale*) (Interorbital portion of the frontals): (0) narrow ; (1) intermediate; (2) broad. Ordered.
17. Fontal, frontal ridges: (0) absent; (1) poorly developed; (2) well developed. Ordered.
18. Orbital margin of the frontal bone (*os frontale: margo supraorbitalis*): (0) arched; (1) slightly sinusoidal near the postorbital process; (2) prominently sinusoidal (Fig. 1). Ordered.
19. Dome of the skull (*calvaria*): (0) tall (Fig. 2C); (1) intermediate (Fig. 1A, B); (2) low. Ordered.
20. Postorbital process (*processus postorbitalis*), size : (0) short (Fig. 1); (1) medium; (2) long. Ordered.
21. Parasphenoidal sheet (*lamina parasphenoidalis*), small processes in the rostral margin at both sides of the parasphenoidal rostrum (*rostrum parasphenoidale*): (0) small; (2) long rostral projections. The "spurs" of the basitemporal (Parker 1877: plate LIX.1).
22. Mandibular fenestra (*fenestra caudalis mandibulae*): (1) small; (2) pinhole; (3) absent. Ordered.

Sternum

23. Manubrium (*rostro sternalis*), pneumatic foramen: (0) absent; (1) present.
24. Keel (*carina sterni*): (0) small with a straight margin; (1) intermediate, margin slightly curved caudally; (2) large with an arched margin (Feduccia 1973).
25. Caudal margin of the sternum (*sternum*: *margo caudalis*): (0) continuous, with two windows (*fenestra lateralis*) (type 2 of Heimerdinger and Ames 1967); (1) with two notches (*incisura lateralis*) (type 3); (2) with two notches and small fonticuli (type 4). See Feduccia (1972) for a study of the sternum in the Dendrocolaptinae. Ordered.

Pelvic limb

26. Pubis (*scapus pubis*) at the level of the ischial angle (*processus terminalis ischii*): (0) thin; (1) broad.
27. Distal end of the pubis (*apex pubis*): (0) acute; (1) spatulated.
28. Femur (*os femoris*), pneumatic foramen or foramina in the proximal posterior end: (0) absent; (1) present (Feduccia 1973: fig. 14).
29. Intercnemial groove (*tibiotarsus: sulcus intercnemialis*): (0) narrow; (1) broad (Feduccia 1973: fig. 15).
30. Distal end of tibiotarsus (*extremitas distalis tibiotarsi*): (0) narrow; (1) broad (Feduccia and Olson 1982: fig. 15A, B).
31. Hypotarsus, ossification of the posterolateral tendinal canal: (0) unossified, tendinal groove; (1) partially ossified, opened canal; (2) ossified, closed canal (Simpson and Cracraft 1981: fig. 6). Ordered.
32. Plantar ridge (*crista plantaris lateralis*): (2) with an oblicuous notch; (3) with a round fenestra; (4) with a small foramen for the passage of a cranial branch of the tendon of the *M. fibularis longus* (Raikow 1993). Ordered.
33. Distal end of the tarsometatarsus (*extremitas distalis tarsometatarsi*): (0) narrow; (1) broad (Feduccia 1973: fig. 13).
34. Trochlea II, size: (1) intermediate; (2) thick, as long as trochlea III, protrudes laterally from the shaft (Feduccia and Olson 1982: fig. 16A, B).
35. Trochlea II, inclination: (0) parallel to trochlea III; (1) divergent (Feduccia and Olson 1982: fig. 16A, B).
36. Trochlea III, size: (0) small; (1) large.
37. Trochlea III, groove: (0) slightly grooved; (1) moderately grooved (less than half the length of the trochlea); (2) deeply grooved (as deep as half the length of the trochlea or more) (Feduccia 1973: fig. 13). Ordered.
38. Trochlea IV, length: (0) short; (1) as long as trochlea III.
39. Trochlea IV, thickness and grooving: (0) thin, not grooved; (1) thick, slightly grooved (Feduccia and Olson 1982: fig. 16A, B).

External Morphology

Rostrum

40. Bill curvature: (1) straight (culmen straight or decurved, gonys straight or recurved); (2) semi-decurved (culmen decurved, gonys straight); (3) decurved (both culmen and gonys decurved). Ordered.
41. Culmen cross section: (0) tapered; (1) rounded; (2) ridged. Ordered.
42. Maxilla, apical hook (angle of the tomium's tip): (0) absent (<45 degrees); (1) poorly developed (~45 degrees); (2) well developed (>45 degrees). Ordered.
43. Maxillary tomium, subterminal notch: (0) absent; (1) minute; (2) conspicuous. Ordered.
44. Naris shape: (0) circular; (1) oblong; (2) slit-like.
45. Nasal operculum: (0) absent; (1) vestigial; (2) large.

Plumage color pattern

46. Supercilium: (0) absent; (1) discontinuous stripe in which each individual feather is distinguishable; (2) continuous stripe. Ordered.
47. Dorsal pattern: (0) uniform; (1) only hindneck patterned; (2) hindneck and back patterned. Ordered.

48. Breast: (0) uniform; (1) patterned.
49. Flanks: (0) uniform; (1) patterned.
50. Abdomen: (0) uniform; (1) patterned.

Rectrices

51. Rachis curvature: (0) straight; (1) uniformly slightly decurved; (2) decurved distally; (3) decurved distally but with the tip slightly recurved forming an slightly S-shaped tip (Feduccia 1973: fig. 1).
52. Rectrix I, symmetry of vanes: (0) internal < external; (1) roughly symmetrical; (2) internal > external.
53. Rectrix I, shape of apex vane: (0) rounded; (1) acute (a pointed end with margins that form an angle >90 degrees); (2) cuspidate (pointed with margins that form an angle of <90 but >45 degrees); (3) asymmetrical cuspidate (straight or convex margins form an angle of <45 degrees); (4) long attenuate; (5) bilobulated (concave margins). Character state names are based on botanical leaf-tip terminology.
54. Rectrix I, apex barbs type: (0) unspecialized; (1) long semirigid barbs; (2) stiff short barbs.
55. Rectrix I, apex barbs density: (0) dense; (1) sparse.
56. Rectrix I, rachis apex stiffness: (0) soft; (1) slightly stiffened; (2) stiff.

Foot

57. Relative length of toe IV: (0) roughly equal to II; (1) intermediate; (2) roughly equal to III (Fig. 2; Feduccia 1973: fig. 16).

Morphometrics

For the parsimony analysis, we used isometric size and only a subset of the 11 shape variables to minimize problems of character non-independence (Felsenstein 1988, Emerson and Hastings 1998). We used a variation of the segment-coding method (Thorpe 1984, Swiderski et al. 1998) to transform continuous variation into discrete characters. The range of variation of each character was divided into 10 equal segments, which were coded as 10 discrete states. States were excluded from the matrix if not assigned to any of the included species; therefore, the final states do not all range from 0 to 9 (see Appendix 3).

58. Isometric size, calculated as the arithmetic mean of the 11 log-transformed morphometric variables. Ordered.
59. Relative bill length = log(bill length) – Isometric size. Ordered.
60. Relative bill width = log(bill width) – Isometric size. Ordered.
61. Relative tarsus = log(tarsus length) – Isometric size. Ordered.
62. Relative hallux = log(hallux length) – Isometric size. Ordered.

Muscles

We used 22 hindlimb myological characters from Raikow (1994), who presented data for all species included in the present parsimony analysis (Appendix 3) except for *Campylorhamphus pucherani* and *C. falcularius*. We only excluded the relative insertion of the M. caudofemoralis (character 13 in Raikow 1994) because it was not parsimony-informative for the taxa included in this study.

Appendix 3. State matrix of osteological (1–39), external (40–57), and morphometric (58–62) characters used in the cladistic analysis (additional 22 myological characters from Raikow [1994] not shown). Polymorphic states: A = 0 and 1, B = 1 and 2, and C = 1 and 3.

	Characters						
Species	1–10	11–20	21–30	31–40	41–50	51–60	61–62
Sclerurus rufigularis	2110002000	0010001111	0102201000	2301110001	2121100000	0100021214	57
Furnarius rufus	1010002010	1010010112	0112100000	2201110001	1002200000	0100000513	66
Dendrocincla merula	1202001110	0111122012	0201101010	1311101101	1102200000	2052122426	41
Drymornis bridgesii	2202200011	0201220210	1102101111	2312102103	0002221111	1141012960	40
Nasica longirostris	2202220111	0201222220	1301101111	2411102102	1110020101	2131122965	00
Dendrexetastes rufigula	1200120110	0201220110	1300111111	2312002101	1B10000100	2131122728	10
Hylexetastes perrotii	1000000111	0201212111	1200001111	0411002111	0000000000	1132122828	22
Xiphocolaptes major	1202000101	0201210211	1100101111	0411002112	1000000101	1132122956	32
Dendrocolaptes platyrostris	0002010100	0201210111	1211101111	0411002101	2210012111	3132122837	11
Xiphorhynchus guttatus	1100000101	0201221220	1200000111	1411002111	1100012100	3032022734	12
Lepidocolaptes angustirostris	2202200021	0201220220	1202101111	2312002103	100A12AAAA	313B022452	12
Campylorhamphus pucherani	2202200021	0201221210	1200101111	2312002103	1001121A01	C131122863	15
C. trochilirostris	0002200101	1201221100	1201101111	2412102103	10000121A1	3031112681	00
C. falcularius	??????????	??????????	??????????	?????????3	1000012100	3?31112680	02
C. procurvoides	?00?200???	1201222110	??????????	?????????3	1000011100	3?31112572	00
C. pusillus	??02200101	1?01222200	A200111111	2412102103	1000002101	3131112670	03