



Fourfold polyphyly of the genus formerly known as *Upucerthia*, with notes on the systematics and evolution of the avian subfamily Furnariinae

R. Terry Chesser^{a,b,*}, F. Keith Barker^c, Robb T. Brumfield^d

^a Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA

^b USGS Patuxent Wildlife Research Center, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, DC 20013, USA

^c Bell Museum of Natural History, University of Minnesota, 100 Ecology, 1987 Upper Buford Circle, St. Paul, MN 55108, USA

^d Museum of Natural Science, 119 Foster Hall, Louisiana State University, Baton Rouge, LA 70803, USA

Received 31 October 2006; revised 13 April 2007; accepted 16 April 2007

Available online 3 May 2007

Abstract

The traditional avian subfamily Furnariinae, a group of terrestrial ovenbirds typical of the Andean and Patagonian arid zones, consists of the genera *Furnarius*, *Cinclodes*, *Geositta*, *Upucerthia*, *Chilia*, and *Eremobius*. We investigated phylogenetic relationships within the Furnariinae, with particular attention to the nine species of the genus *Upucerthia*, using nuclear and mitochondrial DNA sequences from all genera in the subfamily. *Upucerthia* was found to be highly polyphyletic, its constituent species forming four non-sister clades: (1) a basal lineage consisting of two *Upucerthia* species, *U. ruficaudus* and *U. andaecola*, as well as the monotypic genera *Eremobius* and *Chilia*; (2) a lineage consisting of *U. harterti* and *U. certhioides*, two species behaviorally divergent from other *Upucerthia* species; (3) a lineage consisting of *U. serrana*, which is not closely related to any other *Upucerthia* species; and (4) a lineage, sister to *Cinclodes*, consisting of the four *Upucerthia* species *U. dumetaria*, *U. albogularis*, *U. validirostris*, and *U. jelskii*. The larger Furnariinae was also found to be highly polyphyletic; the terrestrial open country ecotype characteristic of this subfamily occurs in four unrelated clades in the family Furnariidae, including a basal lineage as well as derived lineages. Although the large degree of divergence among *Upucerthia* clades was not previously recognized, owing to ecological, behavioral, and morphological similarities, the groupings correspond closely to relationships suggested by plumage. This is in contrast to studies of other avian genera in which plumage patterns have been shown to be extensively convergent. The generic names *Upucerthia* and *Ochetorhynchus* are available for two of the former *Upucerthia* clades; new generic names may be warranted for the other two.

© 2007 Elsevier Inc. All rights reserved.

Keywords: *Upucerthia*; Furnariidae; *Ochetorhynchus*; *Chilia*; *Eremobius*; Systematics; Polyphyly; Ovenbirds; Andes

1. Introduction

The avian family Furnariidae (ovenbirds and woodcreepers) has long been recognized as an exemplar of continental adaptive radiation. Furnariid species vary tremendously in ecology, morphology, behavior, and nest structure, yet

many can be grouped into characteristic ecological, behavioral, and morphological types. Prominent among these are the terrestrial open country furnariids typical of the Andean and Patagonian arid zones and often grouped together under the subfamily Furnariinae, consisting of the genera *Chilia*, *Cinclodes*, *Eremobius*, *Geositta*, and *Upucerthia*, as well as the type genus *Furnarius*. Recent molecular studies have shown that *Geositta* lies outside the clade formed by most ovenbirds and woodcreepers (Chesser, 2004a; Fjeldså et al., 2005) and therefore appears to be distantly related to such similar genera as *Cinclodes* and

* Corresponding author. Address: USGS Patuxent Wildlife Research Center, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, DC 20013, USA. Fax: +1 202 357 1932.

E-mail address: Terry_Chesser@usgs.gov (R.T. Chesser).

Upucerthia. However, the full extent of potential convergence on the terrestrial, open country ecotype has yet to be explored.

Apart from clarification of phylogenetic relationships among furnariine genera, resolution of relationships within the genus *Upucerthia* would appear to be central to addressing the evolution of this ecotype. Both *Chilia* and *Eremobius* are monotypic genera, and the large genera *Cinclodes* and *Geositta* have been recently shown to be monophyletic as well (Chesser, 2004b; Cheviron et al., 2005). Five of the six *Furnarius* species share a strong behavioral synapomorphy (oven-shaped mud nest), and this genus is almost certainly monophyletic also (Zyskowski and Prum, 1999). Monophyly of *Upucerthia*, however, a group of nine species known as earthcreepers (Fjeldså and Krabbe, 1990; Sibley and Monroe, 1990; Remsen, 2003; Table 1), is less clear. Although *Upucerthia* species share behavioral and morphological features that distinguish them from most other furnariine genera (e.g., posture of tail, length of tail, skulking behavior), the genus has sometimes been split into two genera (see below), and it has recently been suggested that *Upucerthia* is paraphyletic with respect to the genus *Eremobius* (Remsen, 2003).

Within *Upucerthia*, relationships have traditionally been resolved using morphological characters. The species *U. albogularis*, *U. jelskii*, and *U. validirostris*, for example, have very similar plumage and have long been thought to be closely related, and *U. dumetaria* is generally considered a relative of this group (Cory and Hellmayr, 1925; Peters, 1951; Ridgely and Tudor, 1994; Remsen, 2003). Similarities in plumage have likewise suggested close relationships between *U. andaecola* and *U. ruficaudus* (Cory and Hellmayr, 1925; Vaurie, 1980; Ridgely and Tudor, 1994) and between *U. certhioides* and *U. harterti* (Cory and Hellmayr, 1925; Peters, 1951; Remsen, 2003). The ninth species, *U. serrana*, shows no obvious close relationship to any other *Upucerthia* species, although Cory and Hellmayr (1925) considered it closely related to *U. andaecola*, Vaurie (1980) paired it with *U. dumetaria*, and Ridgely and Tudor (1994) grouped it with *U. ruficaudus* and *U. andaecola*.

Bill morphology and behavior have also been used to describe relationships among *Upucerthia* species, and have sometimes occasioned splitting of the genus. For example, strongly decurved bills have been used to unite *U. albogularis*, *U. jelskii*, *U. validirostris*, and *U. dumetaria*. Wetmore and Peters (1949) separated *U. ruficaudus*, *U. certhioides*, and *U. harterti* into the genus *Ochetorhynchus* because their relatively straight bills differ markedly from those of the *U. albogularis* group and from those of *U. andaecola* and *U. serrana*, as well. However, *U. certhioides* and *U. harterti* differ substantially in voice and behavior from other *Upucerthia* species, including *U. ruficaudus*, and have recently been considered generically distinct from *U. ruficaudus* and the rest of *Upucerthia* (Ridgely and Tudor, 1994).

We used nuclear and mitochondrial sequence data from the nine species of *Upucerthia*, representatives of all other

genera of furnariines, and a sampling of twelve additional genera of Furnariidae to address the following questions:

- (1) Is *Upucerthia* monophyletic and, if not, what are the constituent groups currently contained within the genus?
- (2) Do phylogenetic relationships among *Upucerthia* species, as revealed by molecular data, correspond to ideas of relationship based on plumage, morphology, and behavior?
- (3) Is the subfamily Furnariinae, excluding the genus *Geositta* (Chesser, 2004a; Fjeldså et al., 2005), monophyletic?
- (4) What are the phylogenetic relationships among traditional furnariine genera?

2. Materials and methods

2.1. Taxon sampling

Tissues of *Upucerthia* species, other furnariid species, and outgroups were obtained during fieldwork in Argentina and Chile and from the genetic resources collections of the American Museum of Natural History, New York; the Field Museum of Natural History, Chicago; the Museum of Natural Science, Louisiana State University; the Marjorie Barrick Museum, University of Nevada Las Vegas; the Burke Museum, University of Washington; and the Zoological Museum, Copenhagen University. We sampled each of the nine currently recognized species of *Upucerthia*, the monotypic genera *Chilia* and *Eremobius*, and two representatives of each additional furnariine genus (Table 1), including *Furnarius figulus*, the nest of which differs from that of other *Furnarius* species. *Geobates*, sometimes recognized as a distinct genus, has been shown to be nested within *Geositta* (Cheviron et al., 2005) and consequently was not sampled. Twelve genera were sampled from the broader Furnariidae, providing a broad and representative sampling of the family (Chesser and Brumfield, unpublished data): three genera from the subfamily Dendrocolaptinae, three from the subfamily Synallaxinae, four from the subfamily Philydorinae, one genus (*Lochmias*) of uncertain affinities, and one species from the genus *Sclerurus* (Table 1). The species *Pteroptochos castaneus* (Rhinoctryptidae) and *Myrmothera simplex* (Formicariidae) were sampled as outgroups.

2.2. Sequencing and alignment

DNA was extracted from tissue samples using a 5% Chelex solution (Walsh et al., 1991). Intron 7 of the nuclear gene β -fibrinogen (FGB-I7) and the complete mitochondrial genes *ND3* and *COII* were sequenced for all taxa. Amplifications were performed using the polymerase chain reaction; primers used for initial and second amplifications were those detailed previously for these genes (Chesser,

Table 1

List of tissue reference numbers, collecting localities, and traditional taxonomic placement for sequenced individuals of *Upucerthia*, other furnariiid genera, and outgroups

Species	Tissue number	Locality	Traditional placement
<i>Upucerthia dumetaria</i>	AMNH RTC 368	Argentina: Prov. Río Negro, Cerro Perito Moreno, ca. 20 km N El Bolson, 800 m	Furnariidae: Furnariinae
<i>U. albicula</i>	LSU B-103914	Peru: Depto. Ayacucho, 48 km on Nazca-Puquio road, 2675 m	Furnariidae: Furnariinae
<i>U. validirostris</i>	UWBM 54396	Argentina: Prov. Tucumán, El Infiernillo, ca. 50 km W San Miguel de Tucumán, 3100 m	Furnariidae: Furnariinae
<i>U. jelskii</i>	ZMCU S437	Peru: Depto. Arequipa, Cerro Quishuarniyoc	Furnariidae: Furnariinae
<i>U. serrana</i>	ZMCU S444	Peru: Depto. Pasco, upper Huallaga, Pariamarca	Furnariidae: Furnariinae
<i>U. andaecola</i>	LSU B-1199	Bolivia: Depto. La Paz, 2.5 km by road S Mecapaca, ca. 26 km by road S Calacoto, 3050 m	Furnariidae: Furnariinae
<i>U. ruficaudus</i>	MBM 5427	Argentina: Prov. Jujuy, 70 km W and 13 km N Tilcara, 3500 ft	Furnariidae: Furnariinae
<i>U. certhioides 1</i>	MBM 5444	Argentina: Prov. Salta, 37 km SE J.V. Gonzalez on Rt. 16, 3 km S. at Macapillo, 380 m	Furnariidae: Furnariinae
<i>U. certhioides 2</i>	MBM 5493	Argentina: Prov. Salta, 17.5 km NE J.V. Gonzalez, 1250 ft	Furnariidae: Furnariinae
<i>U. harterti</i>	LSU B-6574	Bolivia: Depto. Santa Cruz, Río San Isidro valley, 2.5 km N Tambo, 1500 m	Furnariidae: Furnariinae
<i>Geositta isabellina</i>	AMNH RTC 430	Chile: Region Metropolitana, ca. 15 km ENE Embalse El Yeso, 3400 m	Furnariidae: Furnariinae
<i>G. cunicularia</i>	AMNH APC 3280	Chile: Region XII (Magallanes), Tierra del Fuego, Estancia Los Tehuelches, 50 m	Furnariidae: Furnariinae
<i>Eremobius phoenicurus</i>	AMNH PRS 1144	Argentina: Prov. Río Negro, 20 km E Norquinco, 1000 m	Furnariidae: Furnariinae
<i>Chilia melanura</i>	AMNH RTC 398	Chile: Region Metropolitana, ca. 4 km SSW peak of Cerro de El Roble, 1600 m	Furnariidae: Furnariinae
<i>Cinclocetes fuscus 1</i>	AMNH RTC 360	Argentina: Prov. Río Negro, Cerro Perito Moreno, 1500 m	Furnariidae: Furnariinae
<i>C. fuscus 2</i>	AMNH RTC 418	Chile: Region Metropolitana, ca. 2 km ENE Embalse El Yeso, 2500 m	Furnariidae: Furnariinae
<i>C. nigrofumosus</i>	AMNH RTC 413	Chile: Region V (Valparaíso), Roca Brava, ca. 2 km N Zapallar, sea level	Furnariidae: Furnariinae
<i>Furnarius rufus</i>	AMNH RTC 389	Argentina: Prov. Buenos Aires, ca. 8 km SW Loma Verde, sea level	Furnariidae: Furnariinae
<i>F. figulus 1</i>	FMNH 392828	Brazil: Depto. Alagoas, Piranhas, Fazenda Bela Vista	Furnariidae: Furnariinae
<i>F. figulus 2</i>	FMNH 392829	Brazil: Depto. Alagoas, Piranhas, Fazenda Bela Vista	Furnariidae: Furnariinae
<i>Leptasthenura aegithaloides</i>	AMNH RTC 374	Argentina: Prov. Río Negro, ca. 41 km E Norquinco on Rta. Prov. 6, 900 m	Furnariidae: Synallaxinae
<i>Synallaxis spixi</i>	AMNH RTC 349	Argentina: Prov. Buenos Aires, ca. 15 km N Belén de Escobar, sea level	Furnariidae: Synallaxinae
<i>Certhiaxis cinnamomeus</i>	FMNH 4750	Bolivia: Depto. Santa Cruz, San Jose-San Ignacio road, 350 m	Furnariidae: Synallaxinae
<i>Sclerurus mexicanus</i>	AMNH ROP 108	Venezuela: Depto. Bolívar, Río Carapo, Guaiquinima	Furnariidae: Philydorinae
<i>Pseudocolaptes lawrencii</i>	AMNH GFB 1011	Costa Rica: Prov. Cartago, 3 km N Villa Mills, 3000 m	Furnariidae: Philydorinae
<i>Thripadectes rufobrunneus</i>	AMNH GFB 985	Costa Rica: Prov. San José, Cerro de la Muerte, 3350 m	Furnariidae: Philydorinae
<i>Philydor pyrrhodes</i>	AMNH PEP 2040	Venezuela: Depto. Amazonas, Mrakapiwie	Furnariidae: Philydorinae
<i>Automolus rufipileatus</i>	AMNH GFB 2079	Venezuela: Depto. Amazonas, Río Mavaca, 120 m	Furnariidae: Philydorinae
<i>Lochmias nematura</i>	AMNH RTC 323	Argentina: Prov. Misiones, Parque Prov. Urugua-i, 1 km N park headquarters, 400 m	Furnariidae: <i>incert. sedis</i>
<i>Xiphorhynchus fuscus</i>	AMNH APC 96-11	Argentina: Prov. Misiones, Parque Prov. Urugua-i, 1 km N park headquarters, 400 m	Furnariidae:
<i>Dendrocincla fuliginosa</i>	AMNH SC 771	Venezuela: Prov. Amazonas, Río Baria, Cerro de la Neblina base camp	Dendrocolaptinae
<i>Drymornis bridgesii</i>	LSU B-25799	Paraguay: Depto. Alto Paraguay, Madrejón	Furnariidae:
<i>Pteroptochos castaneus</i>	AMNH RTC 471	Chile: Region VIII (Bío-Bío), 6 km WSW Termas de Chillán, 1200 m	Dendrocolaptinae
<i>Myrmothera simplex</i>	AMNH GFB 2136	Venezuela: Depto. Amazonas, Cerro Tamacuari, 1270 m	Rhinocryptidae
			Formicariidae

1999, 2000, 2004a). Sequencing was conducted using dye-terminator chemistry on an ABI 377 automated sequencer (Applied Biotechnologies). Sequences were aligned using Sequencer 4.1 (GeneCodes Corp., 2000). Apparent heterozygosities were coded using the IUPAC ambiguity codes. All new sequences used in this study have been deposited in GenBank (Accession Nos. EF635308–EF635370).

2.3. Phylogenetic analyses

Five data sets were analyzed, including each gene region separately, the two mitochondrial genes in combination, and all gene regions in combination. All data sets were subjected to equally-weighted parsimony (MP), uniform model maximum likelihood (ML), and uniform model Bayesian

phylogenetic analyses. Parsimony and ML analyses were conducted using PAUP* v4.0b10 (Swofford, 2000), and Bayesian analyses using MrBayes v3.0b4 (Huelsenbeck and Ronquist, 2001). Models for ML and Bayesian analyses were chosen via hierarchical likelihood ratio evaluation as implemented in ModelTest v3.06 (Posada and Crandall, 1998), starting from an arbitrarily chosen tree derived from MP analysis. The standard hierarchy was supplemented by fitting the optimal model chosen with the additional constraint of a molecular clock. In addition to the standard parameterization, a site-specific rates (SSR) model was fit to the data under both ML and Bayesian inference, recognizing the three gene regions as separate rate categories, and otherwise imposing the most general parameterization favored for the three genes in combination. Partitioned Bayesian analyses were performed recognizing both two (mtDNA and nuclear) and three (*COII*, *ND3*, and FGB-I7) partitions, unlinking all parameters across partitions, constraining branch length equality, constraining branch length proportionality, or allowing branch lengths to vary freely (Altekar et al., 2004; Nylander et al., 2004). Stationarity of base composition for each gene region and each codon position of the two mitochondrial genes was evaluated by a χ^2 goodness-of-fit test for each taxon, using the across-taxon averages as expectations, and correcting for multiple comparisons.

All heuristic searches were performed using stepwise taxon addition, with 20 (ML) or 50 (MP) random addition sequence replicates, followed by tree-bisection-and-reconnection branch swapping. ML model parameters other than branch lengths were held constant during searches, but parameters were re-optimized on the final trees, and additional searches were made under the new estimates in order to evaluate the effect of this constraint. For Bayesian analyses, Metropolis-coupled Markov chain Monte Carlo methods with four incrementally heated chains (using the default heating parameter) were used to estimate the posterior probability distribution (Huelsenbeck and Ronquist, 2001). Analyses were performed using the default priors (with one exception, see Results) and proposal parameters, and allowed to proceed for 2×10^6 generations, sampling every 100 generations. All analyses were repeated at least once, and posterior parameter estimates from the stationary portion of each chain were compared for consistency. Robustness of individual nodes in all MP and ML analyses was evaluated via the non-parametric bootstrap (Felsenstein, 1985), with 1000 replicates for each analysis; robustness of nodes in MP analyses was also assessed using branch support (Bremer, 1988, 1994), which was computed using the computer program TreeRot, version 2 (Sorenson, 1999). Under ML, bootstrapping was simplified by using starting trees generated via neighbour-joining (Saitou and Nei, 1987), with ML distances estimated using the optimal model parameters from the original data set, and by fixing those parameters across all searches. PAUP* does not support bootstrapping under the site-specific rates model, so we generated 100 bootstrap replicates and an accompany-

ing batch file that applied the site-specific rates model in a site-appropriate fashion to each replicate, using a program in R (R Development Core Team, 2004). As in the uniform model analyses, relative rates and other non-branch length parameters in the SSR model were fixed across bootstrap replicates.

Four methods were used to evaluate incongruence among phylogenetic estimates from the three gene regions. First, we calculated the significance of two- and three-partition versions of the ILD test. Although interpretation of this test's significance is problematic (Dolphin et al., 2000; Darlu and Lecointre, 2002; Barker and Lutzeni, 2002), it has been suggested that the test might serve as an initial screen for incongruence, given its propensity toward Type I rather than Type II error (Hipp et al., 2004). Second, we compared optimal trees from these gene regions under the ML criterion. Trees from the five uniform model ML analyses and from the site-specific rates analysis were compared to one another simultaneously using the method of Shimodaira and Hasegawa (1999) and Shimodaira's approximately unbiased (AU) test (Shimodaira, 2002). Site likelihoods were calculated in PAUP* for each tree using each of the five data sets under their optimal models, plus the overall combined data set under the SSR model. These site likelihoods were analyzed using the re-estimated log-likelihood method (100,000 replicates) as implemented in the program *consel* (Shimodaira and Hasegawa, 2001). Although the log-likelihood deviations for individual trees are constant, the two methods offer slightly different perspectives on the significance of these deviations, with the SH test being more conservative in generally failing to reject a larger population of alternative trees. Third, we examined individual analyses for evidence of robustly supported conflicting hypotheses of relationship, as evaluated by the bootstrap (Felsenstein, 1985). Finally, using Bayesian methods, we performed two- and three-partition analyses that allowed either parameter values or parameter values and estimated trees (either topologies or topologies and branch lengths) to vary among partitions, and compared the fit of these models to uniform model analyses using Bayes factors (Nylander et al., 2004).

3. Results

3.1. Phylogenetics

We obtained complete *COII*, *ND3*, and FGB-I7 sequences for all target taxa, except for the 5' half of FGB-I7 from *Upucerthia andaecola*. Data set characteristics are summarized in Table 2. The alignments of the mitochondrial genes *COII* and *ND3* contained no length variation, and were of 684 and 351 bases in length, respectively. The two genes differed substantially in levels of variation, with 38% of sites variable in *COII* and 47% in *ND3* (31% and 39% of sites potentially informative). The alignment of FGB-I7 from these taxa was 892 bases in length, with the introns of individual taxa varying from 844 to

Table 2

Results of parsimony and uniform model maximum likelihood analyses for individual and combined mitochondrial and nuclear data sets

	COII	ND3	mtDNA combined	FGB-I7	All combined
Length of alignment	684	351	1035	892	1927
No. of variable characters	260	165	425	370	795
No. of informative characters	213	138	351	195	546
No. of MP trees (# nodes)	2 (29)	14 (23)	1 (32)	8 (29)	1 (32)
Tree length (MP)	1193	710	1927	549	2503
CI, RI	0.31, 0.49	0.35, 0.51	0.32, 0.49	0.78, 0.81	0.42, 0.54
Model selected	TrN + I + Γ	GTR + I + Γ	GTR + I + Γ	HKY + Γ	GTR + I + Γ
−ln(L)	5595.5	3287.1	8924.1	4449.2	13892.3
No. of ML trees (# nodes)	3 (31)	9 (30)	1 (32)	3 (31)	1 (32)
Tree length (ML)	2.854	3.652	3.092	0.669	1.892
π_A	0.361	0.306	0.322	0.309	0.322
π_C	0.310	0.366	0.331	0.180	0.256
π_G	0.080	0.093	0.121	0.197	0.152
π_T	0.249	0.235	0.226	0.315	0.269
r_{AC}	1.000	3.357	7.652	1.000	1.267
r_{AG}	13.160	24.223	56.665	4.300	5.227
r_{AT}	1.000	5.209	15.856	1.000	1.238
r_{CG}	1.000	0.799	0.673	1.000	0.696
r_{CT}	17.915	48.559	157.770	4.300	14.063
p_{iv}	0.586	0.494	0.549	—	0.310
α	1.380	1.607	1.553	1.541	0.496

Likelihood parameter estimates for each data set are those for the optimal model chosen by hierarchical likelihood ratio tests (ModelTest; Posada and Crandall, 1998) fit to an arbitrarily-chosen unweighted parsimony tree derived from that data set.

MP, maximum parsimony; ML, maximum likelihood; CI, ensemble consistency index; RI, ensemble retention index; L, likelihood; π_i , ML nucleotide proportion estimate; r_{ij} , ML nucleotide substitution rate estimate; p_{iv} , ML proportion of invariant sites estimate; α , ML estimate of among site rate heterogeneity.

881 bases. Alignment was straightforward, and we did not identify any regions of particular ambiguity. The intron alignment showed a similar percentage of variable sites to the two mitochondrial protein coding genes (41%), but substantially fewer potentially informative sites (22%), consistent with differences in rate and selective constraint between the two regions.

All combined (Figs. 1 and 2) and nuclear (Fig. 3) analyses (MP, ML, and Bayesian) yielded single best trees with virtually identical topologies (see Table 2 for sequence characteristics and tree statistics). The basic higher level topology included a core clade of ovenbirds and woodcreepers, excluding *Geositta* and *Sclerurus*, and sister clades of ovenbirds and woodcreepers within this core clade. Within the core ovenbird clade, four distinct lineages contained *Upucerthia* species: (1) a basal lineage, sister to the remaining taxa, consisting of *Ereniobius*, *Chilia*, and two *Upucerthia* species, *U. ruficaudus* and *U. andaecola*; (2) a lineage consisting of *U. harterti* and *U. certhioides*; (3) a lineage consisting of *U. serrana*, which was sister to *Lochmias* and not closely related to any other *Upucerthia* species; and (4) a lineage, sister to *Cinclodes*, consisting of the four species *U. dumetaria*, *U. albigena*, *U. validirostris*, and *U. jelskii*. Within the core ovenbird clade, the three synallaxes *Synallaxias*, *Leptasthenura*, and *Certhiaxis* formed a monophyletic group, as did three of the four non-*Sclerurus* philydorines (*Philydor*, *Automolus*, and *Thripadectes*). The two *Cinclodes* species formed a monophyletic group that was sister to the four species *Upucerthia* clade, and the

two *Furnarius* species also formed a monophyletic group, sister to the *Cinclodes/Upucerthia* clade in most analyses.

Bootstrap support and posterior probabilities were generally high for the combined and nuclear analyses, although a few nodes were more difficult to resolve and received lower support (Figs. 1–3 and Table 3). Analyses of the mitochondrial genes, whether singly or combined, resulted in topologies similar in many respects to the nuclear and combined analyses, but which received poor support in all but the most shallow nodes of the resulting phylogenies (Fig. 3). Individual data partitions and tree details are discussed more fully below.

3.2. Comparison of datasets

The three sampled regions differed substantially in their evolutionary dynamics, as evaluated by model parameterization of each alone (Table 2). In particular, the mitochondrial genes supported fine-scaled substitution rate differentiation (TrN and GTR versus HKY) and more complex patterns of among site rate heterogeneity (I + Γ versus Γ alone). In base composition (low frequency of G versus relatively high AT), among nucleotide substitution rates (high versus low transition:transversion ratios), and overall evolutionary rate (~3 versus 0.7 substitutions/site, an approximately fourfold rate difference), the mitochondrial genes were more similar to one another than either was to the intron. In addition, the data sets differed in the degree of among lineage rate heterogeneity exhibited,

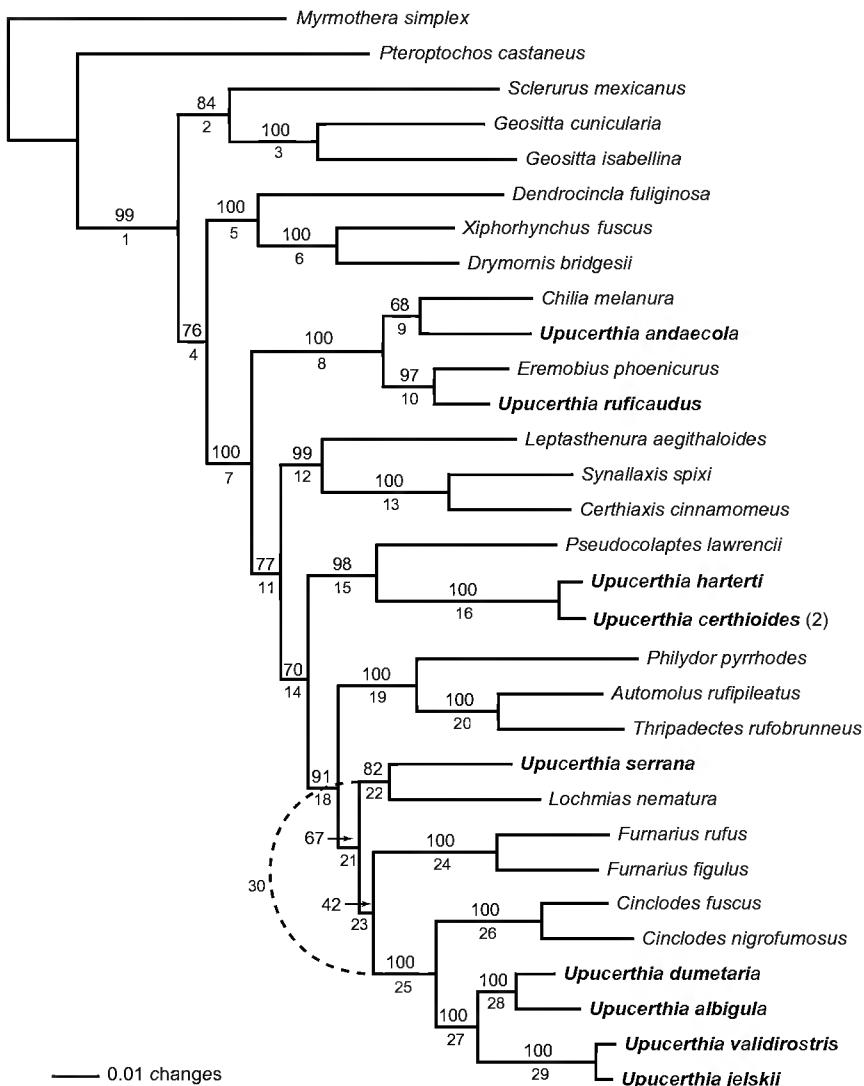


Fig. 1. Maximum likelihood estimate of relationships among *Upucerthia* species (in bold) and selected species of Furnariidae based on combined analysis of *COII*, *ND3*, and β -fibrinogen intron 7. This topology was recovered under both the uniform GTR + I + Γ and GTR + SSR models: see Tables 4 and 5 for model parameters and likelihoods. Values above branches indicate ML bootstrap support for each node; numbers below correspond to support indices reported in Table 3. The single dashed arc indicates an alternative relationship supported by the mtDNA data and bootstrap analysis of the combined data under the GTR + I + Γ model.

with the *COII* data allowing rejection of a molecular clock ($-2 \ln \Lambda = 53.2$, $p = 0.01$, $df = 32$), the *ND3* data nearing significance ($-2 \ln \Lambda = 50.5$, $p = 0.02$), and the FGB-I7 data evolving slightly more uniformly ($-2 \ln \Lambda = 46.6$, $p = 0.05$). In combination, the mtDNA data strongly rejected the molecular clock ($-2 \ln \Lambda = 77.4$, $p < 0.0001$). These qualitative differences were highlighted by partitioned analyses of the data (see below). Evaluation of base composition variability among taxa failed to identify any outliers, excepting the third position base frequency of the *Synallaxis COII* sequence, which had a near-significant ($p = 0.005$, not significant with Bonferroni correction) excess of thymine residues, suggesting that the assumption of stationarity was generally valid for these taxa and genes.

Separate analyses of *COII* and *ND3* using MP, ML, and Bayesian inference were congruent, in that no robustly supported nodes (receiving $\geq 75\%$ bootstrap or

≥ 0.95 estimated Bayesian posterior probability) conflicted between the two (not shown). Furthermore, combined analyses of the mtDNA data yielded only one node in potentially substantial conflict with relationships estimated from FGB-I7 (Fig. 3). This involved the placement of *Furnarius*, which the mtDNA placed in a grouping with *Philydor*, *Automolus*, *Thripadectes*, and *Leptasthenura*, to the exclusion of a grouping containing *Lochmias*, *Cinclodes*, and some *Upucerthia*. This latter grouping received poor to mediocre support from MP and ML, but had a high estimated Bayesian posterior probability (0.99; Fig. 3). The FGB-I7 data differed from the mtDNA in placing *Furnarius* within this latter group, with substantial bootstrap support (72% and 76% from MP and ML), as well as high estimated posterior probability (1.00; Fig. 3). This conflict is of particular interest because the combined uniform model analyses varied in

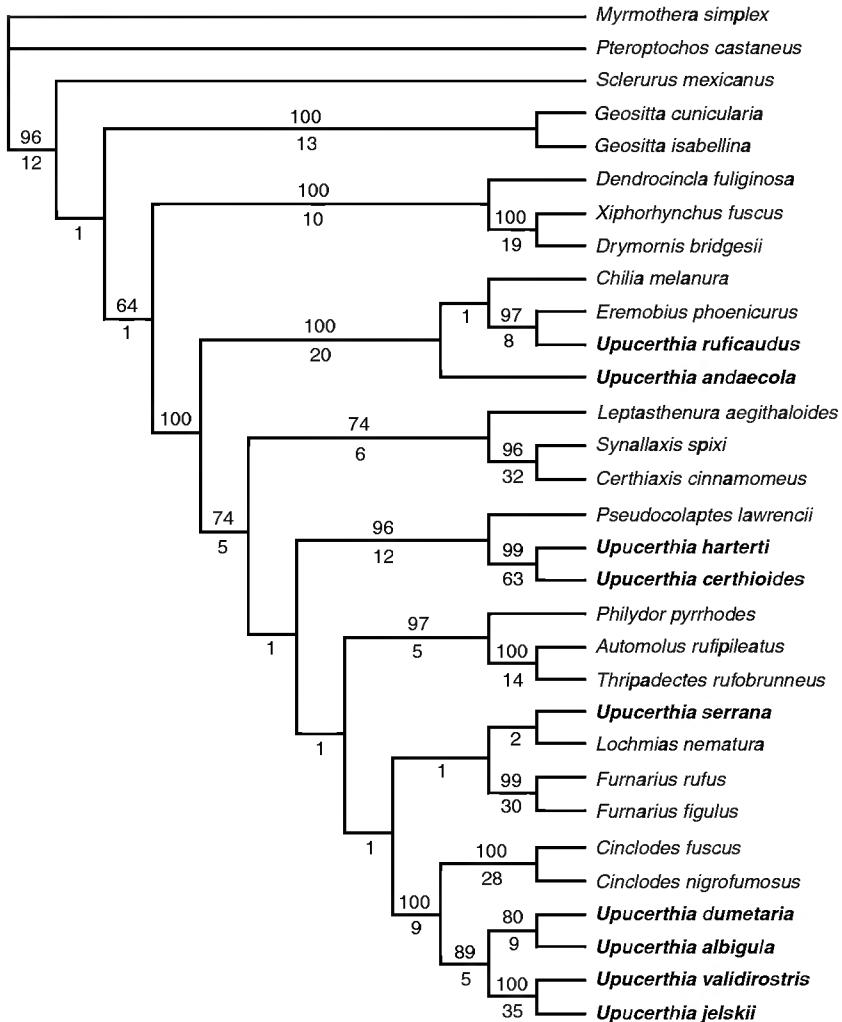


Fig. 2. Maximum parsimony estimate of relationships among *Upucerthia* species (in bold) and selected species of Furnariidae based on combined analysis of *COII*, *ND3*, and β -fibrinogen intron 7. Numbers above branches are bootstrap support values and numbers below are decay indices; branches lacking bootstrap support values are <50.

the relative placement of *Furnarius*. The optimal tree derived from analysis of the combined data using the GTR + SSR model (Fig. 1) agreed with the FGB-I7 data in placing *Furnarius* as sister to a *Cinclodes/Upucerthia* clade, and in placing *Upucerthia serrana* as sister to *Lochmias* (the latter not in substantial conflict with the mtDNA tree). ML analysis under a GTR + I + Γ model yielded the same tree, although bootstrap analysis under the same model recovered an alternative arrangement (Node 30, Fig. 1) in 57% of replicates (Table 3). In another variation, MP analysis placed *Furnarius* as sister to the *U. serrana/Lochmias* clade (Fig. 2). None of these arrangements had strong support (the 57% quoted above was the highest bootstrap observed) and none of the estimated Bayesian posterior for these nodes exceeded 0.95 (Table 3).

We evaluated the significance of these observed conflicts using the parsimony-based ILD test and the maximum likelihood-based SH and AU tests. Both two- and three-partition versions of the former test indicated significant

conflict between the mtDNA and nuclear data ($p < 0.001$), though comparison of the two mitochondrial genes was not significant ($p > 0.05$). However, the significant result likely reflects the significant rate heterogeneity between the mtDNA and nuclear partitions (Barker and Lutzoni, 2002). Both ML-based tests (Table 4) indicated that neither the *COII* nor the *ND3* data could reject the combined mtDNA tree, though each rejected the optimal tree derived from the other. Importantly, data from the individual *COII* and *ND3* genes, as well as the combined mtDNA dataset, allowed rejection of trees derived from FGB-I7 (and the converse was true), supporting the significance of conflict between the two. However, under the null hypothesis of shared history, the most appropriate comparison may be to combine estimates of phylogenetic relationship. In this regard, it is significant to note that neither the combined mtDNA data nor the FGB-I7 data allow rejection of the combined data tree using the SH test. The AU test, which is known to be less conservative than the SH test (Shimodaira, 2002), yields significance for these

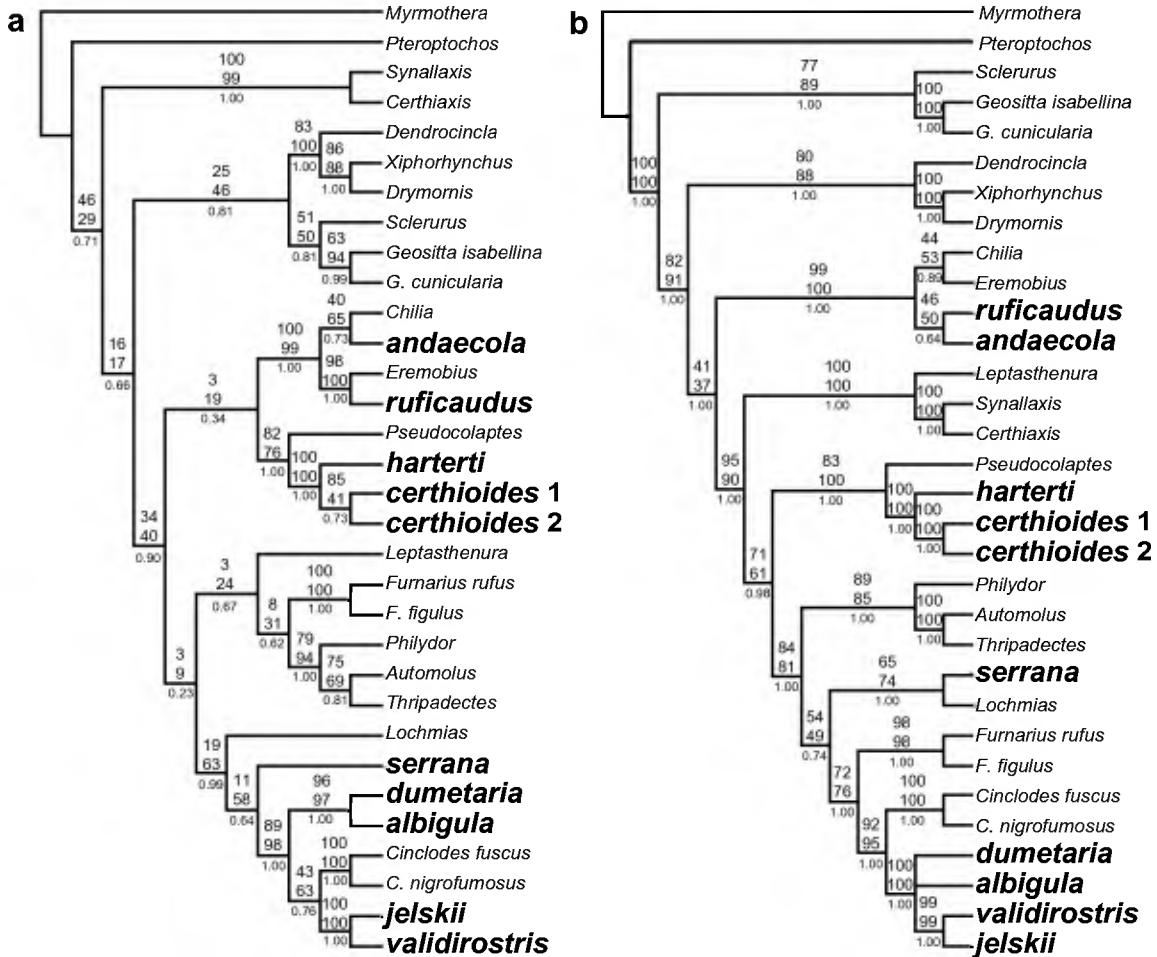


Fig. 3. Maximum likelihood estimates of relationships among *Upucerthia* species, Furnariinae, and Dendrocolaptinae based on (a) combined mtDNA data (*COII* and *ND3*), and (b) β -fibrinogen intron 7: see Table 2 for analysis parameters and likelihoods. Species of *Upucerthia* are highlighted in bold. Numbers at each node represent the percentage of maximum likelihood and unweighted parsimony bootstrap replicates recovering that node (above), and its estimated posterior probability (below).

comparisons in the $0.01 < p \leq 0.05$ range. Overall, these results suggest that there is some substantial conflict between the mtDNA and nuclear data, but this conflict appears to be topologically isolated and of minimal effect (Fig. 3, Table 4).

3.3. Bayesian analyses

Partitioned Bayesian analyses of the data yielded important insights into among dataset heterogeneity and the robustness of phylogenetic inference to it. Table 5 reports estimated marginal likelihoods for the eleven models applied to the data, and Table 6 summarizes estimated substitution parameter marginal distributions from uniform, two-partition, and three-partition analyses of the data. Two-partition analyses indicated that the 95% credibility intervals of all but two parameters (π_A and α) estimated from the mtDNA and intron data are exclusive (Table 6). This is consistent with a previous hierarchical ML analysis of combined mtDNA and intron data from birds (Barker, 2004). The three-partition analysis recovered no parameter that varied substantially

between *COII* and *ND3*, though the intervals for p_{iv} barely overlapped. These patterns are evident in comparison of the harmonic means of the marginal likelihoods from these analyses using estimated Bayes factors (Nylander et al., 2004). With uniform branch lengths, the Bayes factor B_{10} for comparison of the uniform and two-partition analyses was 457, suggesting highly credible increase in model validity, whereas the two and three-partition comparison yielded $B_{10} \approx 0$ (11 for the proportional branch length comparison), suggesting little merit in additional partitioning of the data with regard to nucleotide substitution parameters (Table 5). However, the partitions clearly differed in evolutionary rates, as proportional branch length models greatly improved the model fit over equality ($B_{10} = 358$ for the two-partition comparison, and 368 for the three-partition), and independent branch lengths were an improvement over proportional branch lengths ($B_{10} = 116$, $B_{10} = 139$). Majority rule consensus trees derived from partitioned Bayesian analyses of the data were identical to the ML results (Fig. 3), excepting the relationships of *Chilia*, which was placed as sister to *Eremobius* and *U. ruficaudus* in these

Table 3
Support measures for nodes represented in Fig. 1

Node	mtDNA		FGB-17		Combined data				
	MP	ML	MP	ML	MP	ML GTR + I + Γ	ML GTR + SS	B12	B13
1	46	29	100	100*	96	95*	99*	1.00	1.00
2	52	49	81	89*	58	87*	84*	1.00	1.00
3	62	95*	100	100*	100	100*	100*	1.00	1.00
4	29	10	90	90*	64	65*	76*	1.00	1.00
5	84	100	87	87*	100	99*	100*	1.00	1.00
6	87	89*	100	100*	100	100*	100*	1.00	1.00
7	24	38	53	37	100	95*	100*	1.00	1.00
8	100	99*	100	100*	100	100*	100*	1.00	1.00
9	40	65	2	1	42	48	68*	0.18	0.16
10	98	100*	—	—	97	92*	97*	1.00	1.00
11	4	—	94	90*	74	79*	77*	1.00	1.00
12	—	11	100	100*	74	100*	99*	1.00	1.00
13	99	100*	100	100*	96	100*	100*	1.00	1.00
14	1	—	74	62*	44	55*	70*	1.00	1.00
15	82	79*	84	83*	96	95*	98*	1.00	1.00
16	100	100*	100	100*	99	100*	100*	1.00	1.00
17	92	43	100	100*	98	100*	100*	1.00	1.00
18	2	10	90	81*	45	95*	91*	1.00	1.00
19	80	94*	90	86*	97	99*	100*	1.00	1.00
20	76	69	100	100*	100	100*	100*	1.00	1.00
21	5	10	66	49	37	49	67*	0.88	0.92
22	7	—	68	75*	45	59	82*	0.99	1.00
23	1	1	79	75*	12	33	42	0.90	0.95
24	100	100*	97	97*	99	100*	100*	1.00	1.00
25	89	98*	93	95*	100	100*	100*	1.00	1.00
26	100	100	100	100*	100	100*	100*	1.00	1.00
27	26	31	100	100*	89	97*	98*	1.00	1.00
28	97	98*	—	—	80	97*	100*	1.00	1.00
29	100	100*	99	99*	99	100*	100*	1.00	1.00
30	19	64*	—	—	22	57	42	0.10	0.05

Shown are the percentages of bootstrap pseudoreplicates recovering a given node under the parsimony (MP) and maximum likelihood (ML) criteria, as well as the estimated Bayesian posterior probabilities for those nodes using both two- and three-partition analyses (B12 and B13). Nodes receiving estimated posterior probabilities greater than 0.95 in unpartitioned analyses (using the model estimated under ML) are indicated by an asterisk next to corresponding ML bootstrap values.

Table 4
Results of tree selection using optimal trees from separate and combined analyses to form the candidate pool

Data	Model	Trees					Combined
		COI1	ND3	mtDNA	FGB-17		
COI1	Trn + I + Γ	5595.5	63.0 **/**	9.6 ns/ns	39.7 */**	17.2 ns/ns	
ND3	GTR + I + Γ	40.1 **/**/ /	3287.1 ns/ns	10.1 ns/ns	41.1 **/**/ /	28.2 */**	
mtDNA	GTR + I + Γ	16.7 ns/ns	35.9 ns/*	8924.1 ns/*	64.6 **/**/ ns/*	26.5 ns/*	
FGB-17	HKY + Γ	226.5 **/**/ /	256.9 **/**/ /	151.2 **/**/ /	4449.2 ns/**	8.0 ns/*	
Combined	GTR + I + Γ	170.8 **/**/ /	206.3 **/**/ /	92.2 **/**/ /	33.6 ns/**	13892.3	
Combined	GTR + SS	274.5 **/**/ /	360.8 **/**/ /	158.1 **/**/ /	62.4 ns/**	14935.6	

Shown are the negative log-likelihoods of individual trees (columns) for the data sets (rows) from which they were inferred, along with deviations of suboptimal competing trees in log-likelihood units. Note that the combined data tree was identical for two models (GTR + I + Γ and GTR + SS), but comparisons with other trees were made under both. Significance is shown under each deviation, using both the method of Shimodaira and Hasegawa (1999, before the slash) and the approximately unbiased test of Shimodaira (2002, after the slash).

ns $p > 0.05$.

* $p \leq 0.05$.

** $p < 0.01$.

Table 5

Estimated model marginal likelihoods for partitioned and unpartitioned Bayesian analyses of the combined COI1, ND3, and β -fibrinogen intron 7 data

Partitions	1 Tree			2 Trees		
	=	Prop	≠	mt =	mt Prop	mt ≠
All combined	13945.2	—	—	—	—	—
mtDNA + FGB-17	13716.6	13537.8	13480.0	13446.6	—	—
COI1 + ND3 + FGB-17	13716.5	13532.3	13462.6	13439.6	13440.1	13426.3

Likelihoods shown are the harmonic mean estimates (Nylander et al., 2004). Analyses assuming a single tree were either constrained to have equal branch lengths (=) or proportional branch lengths (Prop) for each recognized partition, or branch lengths were allowed to vary independently (≠). Analyses allowing two trees (one for the mtDNA data and another for the intron) and recognizing the two mitochondrial genes as partitions similarly forced equality (mt =) or proportionality (mt Prop), or allowed the two to vary independently (mt ≠).

Table 6

Nucleotide substitution model parameters estimated from uniform and partitioned Bayesian analyses of furnariid data

Parameter	One-partition	Two-partition		3 Partition		
	mtDNA + FGB-17	mtDNA	FGB-17	COI1	ND3	FGB-17
π_A	0.32 (0.30–0.34)	0.33 (0.30–0.35)	0.32 (0.29–0.35)	0.34 (0.30–0.37)	0.31 (0.27–0.36)	0.32 (0.29–0.35)
π_C	0.26 (0.25–0.28)	0.34 (0.32–0.36)	0.17 (0.15–0.19)	0.33 (0.30–0.35)	0.37 (0.33–0.41)	0.17 (0.15–0.19)
π_G	0.15 (0.14–0.17)	0.11 (0.09–0.13)	0.18 (0.16–0.21)	0.11 (0.09–0.15)	0.09 (0.06–0.12)	0.19 (0.17–0.21)
π_T	0.27 (0.25–0.29)	0.22 (0.21–0.24)	0.33 (0.30–0.36)	0.22 (0.20–0.24)	0.23 (0.20–0.26)	0.33 (0.30–0.36)
r_{AC}	1.26 (0.85–1.81)	2.66 (1.22–4.41)	1.07 (0.68–1.60)	1.69 (0.54–3.21)	2.54 (0.60–6.30)	1.10 (0.69–1.67)
r_{AG}	5.41 (3.94–7.48)	25.77 (12.79–41.43)	3.99 (2.83–5.54)	24.52 (11.6–41.50)	20.75 (5.75–47.75)	4.10 (2.82–5.70)
r_{AT}	1.25 (0.85–1.79)	7.12 (3.39–10.76)	0.49 (0.31–0.74)	7.42 (3.50–11.36)	4.26 (1.00–10.26)	0.50 (0.31–0.77)
r_{CG}	0.71 (0.03–1.08)	0.24 (0.01–0.88)	1.90 (1.21–2.86)	0.14 (0.01–0.68)	0.39 (0.01–1.90)	1.95 (1.23–3.00)
r_{CT}	14.47 (10.39–20.01)	73.00 (35.26–98.56)	3.89 (2.71–5.41)	74.59 (37.55–98.86)	43.07 (11.55–91.30)	3.99 (2.78–5.75)
p_{iv}	0.30 (0.21–0.37)	0.53 (0.49–0.57)	0.11 (0.01–0.27)	0.57 (0.52–0.61)	0.47 (0.41–0.53)	0.11 (0.01–0.26)
α	0.49 (0.38–0.62)	1.36 (1.05–1.75)	4.90 (1.34–26.82)	1.41 (1.00–1.90)	1.33 (0.85–1.98)	4.99 (1.35–29.84)
c	—	1.62 (1.57–1.65)	0.28 (0.24–0.33)	1.47 (1.26–1.66)	1.91 (1.54–2.35)	0.28 (0.24–0.33)
$-\ln(L)$	13945.2	13537.8	↔ joint estimate	13532.3	↔ joint estimate	↔ joint estimate

Shown are the mean values of the estimated posteriors for the nucleotide proportions (π_i), among nucleotide substitution rates (r_{ij}), proportion of invariant sites (p_{iv}), parameter of the Γ -distribution for among site rate heterogeneity (α), and the partition-specific rate parameters (for partitioned analyses only). For each of the three analyses, the harmonic mean estimate of the marginal log-likelihood ($-\ln[L]$) is shown.

analyses, rather than sister to *U. andaecola*, although this relationship was recovered with low posterior probability (~0.8). Partitioned analyses also failed to resolve the conflict over placement of *Furnarius* (nodes 21 and 23; Fig. 3, Table 3), although the three-partition analysis favored the ML position ($\hat{P} = 0.94$). In agreement with the likelihood-based evaluation given above, Bayesian analyses that allowed trees to vary between mtDNA and the intron substantially improved the estimated marginal likelihood ($B_{10} = 67$ for the two-partition case, and $B_{10} = 73$ for the three-partition). The estimated nodal posterior probabilities for these partitioned analyses agreed with the separate analyses in indicating that this conflict is attributable in large part to the placement of *Furnarius* (not shown).

4. Discussion

4.1. Systematics and evolution

Our results indicate that species traditionally placed in the genus *Upucerthia* actually constitute four separate clades, each of which represents a variation on the upucerthine behavioral, ecological, and morphological type. The first clade, sister to the rest of the “core clade” of ovenbirds (the traditional Furnariidae, but excluding *Geositta*, *Sclerurus*, and the woodcreepers), contains two *Upucerthia* spe-

cies and two species typically included in other genera. This well supported clade consists of the Andean species *U. ruficaudus* and *U. andaecola*, the Chilean endemic *Chilia melanura*, and the Patagonian species *Eremobius phoenicurus*. Within the group, *U. ruficaudus* and *E. phoenicurus* receive strong support as sister taxa (Figs. 1 and 2); although the nuclear data (Fig. 3) suggest that *U. ruficaudus* and *U. andaecola* may be sisters, support for this relationship is weak and the result is likely influenced by the missing data for *U. andaecola*. In the combined analyses, *Chilia* and *U. andaecola* appear either to form a sister clade to *U. ruficaudus–E. phoenicurus* (Fig. 1) or to be successive sisters to *U. ruficaudus–E. phoenicurus* (Fig. 2).

These four species are characterized among upucerthines by their straight to slightly decurved bills and by a preference in most species (excepting *E. phoenicurus*) for rocky habitat. Resemblance among these four species in general behavior and morphology was presciently observed by Vuilleumier (in Vaurie, 1980, p. 341), and *C. melanura* was originally described as congeneric with *E. phoenicurus* (Gray, 1846, using the genus name *Enicornis*). However, nest type is quite variable within the group. As with most species traditionally placed in *Upucerthia*, the nests of *U. ruficaudus* and *U. andaecola* are shallow grassy or fibrous cups placed at the end of tunnels or in rocky crevices or earth banks (Hoy, 1980; Narosky et al., 1983; de la Peña,

1987). The nest of *C. melanura* differs somewhat from this general form, consisting instead of a bulky globular mass of dry sticks placed in a cavity under a rock, or occasionally in a hole in a cactus or earth bank (Johnson, 1967). *Eremobius phoenicurus*, in contrast, builds a large domed stick nest in a small bush or cactus, a structure that differs markedly from nests of all other furnariines but bears an extreme resemblance to those of synallaxine ovenbirds (Narosky et al., 1983).

Such heterogeneity among closely related species is notable given the utility of nest type as an informative phylogenetic character in furnariids and other birds (e.g., Winkler and Sheldon, 1993; Zyskowski and Prum, 1999). Indeed, the remarkable convergence of *E. phoenicurus* and the synallaxines on the complex domed stick nest has caused some investigators (e.g., Vaurie, 1971, 1980) to place *E. phoenicurus* in the subfamily Synallaxinae. Perhaps even more remarkable is the fact that this nest type is associated with a large radiation of more than 100 species in the synallaxines (Chesser and Brumfield, unpublished data), but occurs in only a single species in the basal *Eremobius/Chilia/Upucerthia* clade.

The second group of *Upucerthia* species consists of two taxa, *U. harterti* and *U. certhioides*, which also constitute a well supported clade. These species occur at lower elevation than most of their putative congeners, inhabiting eastern Andean slopes or lowlands from 1430 to 3000 m in Bolivia (*U. harterti*) or up to 1800 m in Bolivia, Argentina, and western Paraguay (*U. certhioides*; Remsen, 2003). They occur in more wooded habitats than other upucerthines, often inhabiting denser scrub or woodland, especially where terrestrial bromeliads are common understory plants (Ridgely and Tudor, 1994; Remsen, 2003). These species also differ vocally from other *Upucerthia* species (Ridgely and Tudor, 1994; Remsen, 2003); songs of both species consist of series of notes that increase in intensity while descending in pitch (Remsen, 2003). The nest of *U. harterti* is unknown (Remsen, 2003), but detailed descriptions of the nest of *U. certhioides* (Narosky et al., 1983; de la Peña, 1987), indicate that it generally builds a typical *Upucerthia* cup, placed not at the end of a tunnel or burrow as in most other species, but instead in a rock crevice, a hole in a tree, an abandoned enclosed nest (e.g., that of the hornero, *Furnarius rufus*), or a cavity in a human dwelling. The cup occasionally may be constructed of sticks (Pereyra, 1942) in addition to the usual softer material (Narosky et al., 1983; de la Peña, 1987), but we know of no descriptions that support suggestions that this species builds stick nests in trees (e.g., Fjeldså and Krabbe, 1990).

The third *Upucerthia* clade consists of the Peruvian Andean species *U. serrana*. This species is evidently not closely related to any other furnariine species, nor to any other furnariid species, either in the limited sampling presented here or in much more extensive sampling of the family (Chesser and Brumfield, unpublished data). This species resembles the typical *Upucerthia* species in general habits and appearance, and builds the characteristic shallow nest

placed at the end of a tunnel; however, it is the darkest of the *Upucerthia* species and its bill is rather stout for an upucerthine. Its closest extant relative may be *Lochmias nematura* (Figs. 1 and 2; Chesser and Brumfield, unpublished data), a terrestrial species of forest understory sometimes considered furnariine (e.g., Gray, 1846; Sclater, 1890; Fjeldså et al., 2005; this study).

The final *Upucerthia* clade is comprised of one Andean-Patagonian species (*U. dumetaria*) and three Andean species (*U. albogula*, *U. validirostris*, and *U. jelskii*); these taxa form a well supported group, sister to *Cinclodes*. These species are distinguished from others traditionally placed in *Upucerthia* by their long, slender, strongly decurved bills (Wetmore and Peters, 1949; Ridgely and Tudor, 1994). They are typical *Upucerthia* species in ecology and behavior: terrestrial species of open habitats that build cup nests at the ends of tunnels, or occasionally in holes or crevices. Phylogenetically, they occupy the traditional placement of *Upucerthia*, near the ecologically and behaviorally similar genera *Cinclodes* and *Furnarius*, although the clade is far from its traditional close relative *Geositta*.

Remarkably, these four divisions correspond closely to the relationships among *Upucerthia* species suggested by plumage (as above). This finding is in contrast to other studies in which plumage patterns have been shown to be extensively convergent (e.g., Chesser, 2000). Nevertheless, it was not previously recognized that these four morphologically, ecologically, and behaviorally similar groups are only distantly related, forming four separate evolutionary lineages, nor that *Chilia* and *Eremobius* are contained within one of the groups. Likewise, the terrestrial, open country ecotype characteristic of the traditional subfamily Furnariinae is found in four separate evolutionary lineages. One of these lineages contains a large number of traditional furnariines, including the genera *Cinclodes* (13 species) and *Furnarius* (6 species) and five *Upucerthia* species (*serrana*, *dumetaria*, *albigula*, *validirostris*, and *jelskii*), as well as the monotypic genus *Lochmias*. The other lineages contain smaller numbers of traditional furnariines and are constituted as follows: (1) the genus *Geositta* (11 species); (2) the clade consisting of *Chilia*, *Eremobius*, *U. andaecola*, and *U. ruficaudus*; and (3) the clade consisting of *U. harterti* and *U. certhioides*.

4.2. Taxonomy

The extreme polyphyly of *Upucerthia*, as currently constituted, indicates that several taxonomic changes are warranted. The type species of *Upucerthia* is *U. dumetaria* (Saint-Hilaire, 1832); thus the genus name *Upucerthia* would stay with the clade consisting of *U. dumetaria*, *U. albogula*, *U. validirostris*, and *U. jelskii*. No generic name is available for the second group, consisting of *U. certhioides* and *U. harterti*, nor for the distinctive species *U. serrana*, sole taxon in the third group. Both of these groups are distantly related to all other furnariids and new generic names would appear to be warranted for both.

The remaining species group provides a less straightforward case, turning on whether the four species in this group are to be placed in a single genus. *Upucerthia ruficaudus* was described as *Ochetorhynchus ruficaudus* and is the type species of that genus (Meyen, 1834). *Eremobius phoenicurus* (Gould, 1839) is the type species of *Eremobius*, and *Chilia melanura*, originally described as *Enicornis melanura* (Gray, 1846), is the type of *Chilia* (Salvadori, 1908). If the four species are considered congeneric, the generic name *Ochetorhynchus* has priority. An alternative to this, given the uncertainty of the positions of *Chilia* and *U. andaecola* within the group, would be to place all species into separate genera: *Eremobius*, *Chilia*, *Ochetorhynchus*, and a new genus for *U. andaecola*. This seems to us excessive splitting of a reasonably homogeneous group—ecologically, morphologically, behaviorally (nesting aside), and genetically—and we recommend that these four species be merged into *Ochetorhynchus*.

Acknowledgments

We thank the following for providing tissue for this study: George Barrowclough and Paul Sweet, Department of Ornithology, American Museum of Natural History; Fred Sheldon and Donna Dittmann, Genetic Resources Collection, Louisiana State University Museum of Natural Science; Gary Voelker, Marjorie Barrick Museum, University of Nevada Las Vegas; John Bates and David Willard, Bird Division, Field Museum of Natural History; Jon Fjeldså and Jaime García-Moreno, Zoological Museum, University of Copenhagen; and Scott Edwards and Chris Wood, University of Washington Burke Museum. R.T.C. is grateful to Paul Sweet, Angelo Capparella, and Juan Mazar Barnett for field assistance in Argentina and to Alfredo Ugarte P. and “Checho” Escobar S. for field assistance in Chile. Edgardo Anania, Ministerio de Ecología y Recursos Naturales Renovables, Prov. Misiones, Posadas, Argentina; Roberto Lini, Dirección de Bosques y Fauna, Prov. Río Negro, Viedma, Argentina; Adrienne Ricci, Ministerio de la Producción, Prov. Buenos Aires, La Plata, Argentina; Gustavo Porini, Secretaría de Recursos Naturales y Ambiente Humano, Buenos Aires, Argentina; and Juan Carlos Cuchacovich, Servicio Agrícola y Ganadero, Santiago, Chile, kindly granted collecting and export permits for their respective jurisdictions. This study was funded in part by the Frank M. Chapman Memorial Fund of the American Museum of Natural History, by Michael Nachman of the University of Arizona, and by NSF Grants DEB-0543562 and DBI-0400797 to RTB. We thank Adriana Kulczak for translating references from French and Latin, Richard Banks for advice on taxonomy, and Leslie Overstreet and David Steere for bibliographic assistance. Neal Woodman and Robert Reynolds provided helpful comments on a draft version of this manuscript. The research reported in this paper is a contribution from the Lewis B. and Dorothy Cullman Research Facility at The American Museum of Natural History and has received generous

support from the Lewis B. and Dorothy Cullman Program for Molecular Systematic Studies, a joint initiative of The New York Botanical Garden and The American Museum of Natural History.

References

- Altekar, G., Dwarkadas, S., Huelsenbeck, J.P., Ronquist, F., 2004. Parallel metropolis coupled Markov chain Monte Carlo for Bayesian phylogenetic inference. *Bioinformatics* 20, 407–415.
- Barker, F.K., 2004. Monophyly and relationships of wrens (Aves: Troglodytidae): a congruence analysis of heterogeneous mitochondrial and nuclear DNA sequence data. *Mol. Phylogenet. Evol.* 31, 486–504.
- Barker, F.K., Lutzoni, F.M., 2002. The utility of the incongruence length difference test. *Syst. Biol.* 51, 625–637.
- Bremer, K., 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* 42, 795–803.
- Bremer, K., 1994. Branch support and tree stability. *Cladistics* 10, 295–304.
- Chesser, R.T., 1999. Molecular systematics of the rhinocryptid genus *Pteroptochos*. *Condor* 101, 439–446.
- Chesser, R.T., 2000. Evolution in the high Andes: the phylogenetics of *Muscisaxicola* ground-tyrants. *Mol. Phylogenet. Evol.* 15, 369–380.
- Chesser, R.T., 2004a. Molecular systematics of New World suboscine birds. *Mol. Phylogenet. Evol.* 32, 11–24.
- Chesser, R.T., 2004b. Systematics, evolution, and biogeography of the South American ovenbird genus *Cinclodes*. *Auk* 121, 752–766.
- Cheviron, Z.A., Capparella, A.P., Vuilleumier, F., 2005. Molecular phylogenetic relationships among the *Geositta* miners (Furnariidae) and biogeographic implications for avian speciation in Fuego-Patagonia. *Auk* 122, 158–174.
- Cory, C.B., Hellmayr, C.E., 1925. Catalogue of birds of the Americas and the adjacent islands. *Field Mus. Nat. Hist. Zool. Ser.* 13, Part 4.
- Darlu, P., Lecointre, G., 2002. When does the incongruence length difference test fail? *Mol. Biol. Evol.* 19, 432–437.
- de la Peña, M., 1987. *Nidos y Huevos de Aves Argentinas*. Published by the author, Santa Fe, Argentina.
- Dolphin, K., Belshaw, R., Orme, C.D., Quicke, D.L.J., 2000. Noise and incongruence: interpreting results of the incongruence length difference test. *Mol. Phylogenet. Evol.* 17, 401–406.
- Felsenstein, J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39, 783–791.
- Fjeldså, J., Krabbe, N., 1990. Birds of the High Andes. Zoological Museum, University of Copenhagen.
- Fjeldså, J., Irestedt, M., Ericson, P.G.P., 2005. Molecular data reveal some major adaptational shifts in the early evolution of the most diverse avian family, the Furnariidae. *J. Ornithol.* 146, 1–13.
- GeneCodes Corp., 2000. Sequencer, version 4.1. GeneCodes Corp., Inc., Ann Arbor, MI.
- Gould, J., 1839. *The Zoology of the Voyage of the H.M.S. BeaglePart III: Birds*, vol. II. Smith, Elder and Co., London.
- Gray, G.R., 1846. *The Genera of Birds*, vol. I. Longman, Brown, Green, and Longmans, London.
- Hipp, A.L., Hall, J.C., Sytsma, K.J., 2004. Congruence versus phylogenetic accuracy: revisiting the incongruence length difference test. *Syst. Biol.* 53, 81–89.
- Hoy, G., 1980. Notas nidobiológicas del noroeste argentino, II. *Physis* (Secc. C) 39, 63–66.
- Huelsenbeck, J.P., Ronquist, F., 2001. MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* 17, 754–755.
- Johnson, A.W., 1967. *The Birds of Chile and Adjacent Regions of Argentina, Bolivia, and Peru*, vol. 2. Platt Establ. Gráficos Buenos Aires.
- Meyen, F.J.F., 1834. *Ochetorhynchus* and *Ochetorhynchus ruficaudus*, in *Beiträge zur Zoologie, gesammelt auf einer Reise um die Erde. Nova Acta Acad. Caes. Leop.-Carol. 16* (Suppl.), 80–81.

- Narosky, S., Fraga, R., de la Peña, M.L., 1983. Nidificación de la Aves Argentinas (Dendrocolaptidae y Furnariidae). Asociación Ornitológica del Plata, Buenos Aires.
- Nylander, J.A., Ronquist, F., Huelsenbeck, J.P., Nieves-Aldrey, J.L., 2004. Bayesian phylogenetic analysis of combined data. *Syst. Biol.* 53, 47–67.
- Pereyra, J.A., 1942. Avifauna argentina. *Mem. Jard. Zool. La Plata* 10, 171–274.
- Peters, J.L., 1951. Check-list of Birds of the World, vol. 7. Museum of Comparative Zoology, Cambridge, MA.
- Posada, D., Crandall, K.A., 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14, 817–818.
- R Development Core Team, 2004. R: A Language and Environment for Statistical Computing, version 1.9.0. R Foundation for Statistical Computing.
- Remsen, J.V., 2003. Family Furnariidae (Ovenbirds). In: del Hoyo, J., Elliott, A., Christie, D.A. (Eds.), *Handbook of Birds of the World. Broadbills to Tapaculos*, vol. 8. Lynx Edicions, Barcelona, pp. 162–357.
- Ridgely, R.S., Tudor, G., 1994. *The Birds of South America*, vol. 2. University of Texas Press, Austin.
- Saint-Hilaire, G., 1832. Genre Upucerthie, *Upucerthia*. *Nouv. Ann. Mus. Hist. Nat. Paris* 1, 393–395.
- Saitou, N., Nei, M., 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol. Biol. Evol.* 4, 406–425.
- Salvadori, T., 1908. On the genera *Henicornis* and *Chilia*. *Ibis* 1908, 451–454.
- Sclater, P.L., 1890. Catalogue of the Birds of the British Museum Tra- cheophonae, vol. XV. British Museum, London.
- Shimodaira, H., 2002. An approximately unbiased test of phylogenetic tree selection. *Syst. Biol.* 51, 492–508.
- Shimodaira, H., Hasegawa, M., 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Mol. Biol. Evol.* 16, 1114–1116.
- Shimodaira, H., Hasegawa, M., 2001. CONSEL: for assessing the confidence of phylogenetic tree selection. *Bioinformatics* 17, 1246–1247.
- Sibley, C.G., Monroe, B.L., 1990. *Distribution and Taxonomy of Birds of the World*. Yale University Press, New Haven, CT.
- Sorenson, M.D., 1999. TreeRot, version 2. Boston University, Boston, MA.
- Swofford, D.L., 2000. PAUP*. *Phylogenetic Analysis Using Parsimony (* and Other Methods)*, version 4.0b10. Sinauer Associates, Sunderland, MA.
- Vaurie, C., 1971. Classification of the ovenbirds (Furnariidae). H.F. & G. Witherby Ltd., London.
- Vaurie, C., 1980. Taxonomy and geographical distribution of the Furnariidae (Aves, Passeriformes). *Bull. Am. Mus. Nat. Hist.* 186, 1–357.
- Walsh, S.P., Metzger, D.A., Higuchi, R., 1991. Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. *BioTechniques* 10, 506–513.
- Wetmore, A., Peters, J.L., 1949. Remarks on the genus *Ochetorhynchus* Meyen. *Proc. Biol. Soc. Wash.* 62, 97–100.
- Winkler, D.W., Sheldon, F.H., 1993. Evolution of nest construction in swallows (Hirundinidae)—a molecular phylogenetic perspective. *Proc. Natl. Acad. Sci. USA* 90, 5705–5707.
- Zyskowski, K., Prum, R.O., 1999. Phylogenetic analysis of the nest architecture of Neotropical ovenbirds (Furnariidae). *Auk* 116, 891–911.