
Phylogeny of the ovenbird genus *Upucerthia*: a case of independent adaptations for terrestrial life

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Accepted: 27 November 2006
doi:10.1111/j.1463-6409.2006.00270.x

FjeldsÅ, J., Irestedt, M., Jønsson, K. A., Ohlson, J. I. & Ericson, P. G. P. (2007). Phylogeny of the ovenbird genus *Upucerthia*: a case of independent adaptations for terrestrial life. — *Zoologica Scripta*, 36, 133–141.

In view of the amount of adaptive radiation among ovenbirds, Furnariinae, the traditional taxonomy needs scrutiny. We used nuclear DNA data to study relationships of the genus *Upucerthia*. Five species belong in the Furnariini, as traditionally assumed. The other species represent two independent cases of specialisation for terrestrial life, in response to formation of arid habitats in the southern Andes, within the paraphyletic assemblage of arboreal species referred to as Philydorini.

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Introduction

The classification of the diverse Neotropical group of ovenbirds, Furnariinae, has been subject to continuous dispute (see Remsen 2003). An extraordinary amount of adaptive radiation in this group (Leisler 1977) would, per se, suggest high levels of parallelism. Nevertheless, the subdivision into ecologically distinctive sub-groups has been maintained with only small modifications up until today (e.g., Hellmayr 1925; Wetmore & Peters 1949; Vaurie 1980; Sibley & Monroe 1990; Dickinson 2003; Remsen 2003). These sub-groups are: the Philydorini, comprising stout arboreal birds foraging mainly in the vine-tangles of tropical lowland forests, the Synallaxini, which are tiny, acrobatic birds with long tails inhabiting scrubby vegetation, and the Furnariini, which are rather stout birds of terrestrial habits, often associated with edges of streams.

Molecular studies (Irestedt *et al.* 2002, 2006a; Chesser 2004a; FjeldsÅ *et al.* 2005; Olson *et al.* 2005) now suggest that the Philydorini represents a paraphyletic assemblage of deep lineages, but support the monophyly of the Synallaxini and Furnariini. However, certain species have been moved between these groups, and it is unknown to what extent some

of the large genera might indeed be ‘mixed bags’ of similar-looking but unrelated species.

Only two of the larger furnariine genera have yet been subject to a complete phylogenetic analysis, namely *Cinclodes* (with 11–14 species, depending on which classification is used; Chesser 2004b) and *Geositta* (with 10–11 species; Cheviron *et al.* 2005). However, in both cases the sampling for an out-group was rather narrow, assuming that the two genera had been correctly placed in the Furnariini. No clear-cut morphological differences have been defined separating *Cinclodes*, *Geositta* and *Upucerthia*, and *Cinclodes excelsior* and *aricomae* has variously been shifted to *Upucerthia* (Sclater 1890; Cory & Hellmayr 1924) and *Geositta* (Vaurie 1980). Yet the molecular evidence now suggests that *Geositta*, along with *Sclerurus*, represent an independent deep lineage outside the Furnariinae (Chesser 2004a; FjeldsÅ *et al.* 2005). There is also evidence suggesting that the Furnariini is more complex than assumed, as it includes *Lochmias nematura* (previously associated with *Sclerurus*) and two small marsh-dwelling birds, *Pbleocryptes melanops* and *Limnornis curvirostris* (previously in the Synallaxini) (Irestedt *et al.* 2002; Olson *et al.* 2005). Finally, the variation in morphology, habitats, nest-building

and vocalisations in the genus *Upucerthia* (see Fjeldså & Krabbe 1990; Remsen 2003 for review) could raise doubts about the monophyly of that genus. Thus, a thorough assessment is needed of the relationship of *Upucerthia* species. In order to relate adaptive shifts in the Furnariinae to events in earth history we also provide a divergence time estimate based on the substitution rate of the myoglobin intron 2, a gene that has not hitherto been used in this respect.

So far, the genus *Upucerthia* — or earthcreepers — has caused little controversy, as earlier researchers emphasised the fairly uniform earthy brown colours, longer tails than in other terrestrial furnariines, and long and slender bills, used for digging and probing. They resemble the North American thrashers (*Toxostoma*) in size and shape and also by their sneaky behaviour as they hop about on the ground and hide in or behind low scrubs at the slightest disturbance. It has been suggested to place forms with straight bills in a separate genus *Ochetorhynchus* (Wetmore & Peters 1949), but Vaurie (1980) emphasised that the bill is 'not a reliable index for generic relationship in the Furnariidae', and he had no doubts about the close relationship with *Upucerthia*. Ridgely & Tudor (1994) placed two of the straight-billed species, *certhioides* and *harterti*, in *Ochetorhynchus*, based on their different vocalisations and habits, but overlooked the fact that *Upucerthia ruficaudus* is the type species of *Ochetorhynchus*.

Materials and methods

Taxon sampling, amplification and sequencing

This study includes eight out of nine species of *Upucerthia* that are recognised in most classifications (e.g., Fjeldså & Krabbe 1990; Ridgely & Tudor 1994; Remsen 2003). The only species lacking is *Upucerthia albigula*, which is so similar to *U. jelskii* by morphology, general habits and vocalisations that we see no reason to doubt that they are closely related. We included *Chilia melanura* and *Eremobius phoenicurus*, which have been placed close to *Upucerthia* in various classifications. In order to place these taxa in a broader phylogenetic context, we included representatives from all main lineages of the Furnariinae recognised by earlier molecular studies (Irestedt *et al.* 2002, 2006a; Chesser 2004a; Fjeldså *et al.* 2005), altogether 46 taxa, selected on the basis of a broader on-going study of the family. *Sclerurus scansor* and *Geositta tenuirostris* were used as out-group, as these genera have been shown to form the sister group to woodcreepers and core-ovenbirds by several molecular markers (Irestedt *et al.* 2002, 2006a; Chesser 2004a).

Four nuclear gene regions, myoglobin intron 2, ornithine decarboxylase (ODC) introns 6 to 7, glyceraldehyde-3-phosphate dehydrogenase (G3PDH) intron 11, and β -fibrinogen intron 5 (Fib 5) were sequenced and used for the phylogenetic interpretations. For each gene and taxon, multiple sequence fragments were obtained by sequencing with different

primers. These sequences were assembled to complete sequences with SEQMAN II™ (DNASTAR Inc.). Positions where the nucleotide could not be determined with certainty were coded with the appropriate IUPAC code. GenBank accession numbers are given in Table 1. Extractions, amplifications, and sequencing procedures for fresh tissue/blood samples follow Irestedt *et al.* (2002, 2004), Marini & Hackett (2002), Allen & Omland (2003) and Fjeldså *et al.* (2003). For amplification and sequencing from study skins we designed one new myoglobin primer, Myo345H (5'-TCC TCC AGG GTT TGC TCT AAA ATT GT-3') and two new Fib 5 primers, Fib5-furnL (5'-AAG GAG AGC CTG GCT CAT TCC TTA-3') and Fib5-furnH (5'-GAA GTT GAA GGA ATG CCC TGG TCT T-3') in order to amplify/sequence these two regions in two pieces each. For other primers, extraction and general lab procedures for the study skins see Irestedt *et al.* (2006b).

Phylogenetic inference and model selection

Due to a rather low number of insertions in the introns, the combined sequences could easily be aligned by eye. All gaps have been treated as missing data in the analyses. Bayesian inference (see, e.g., Huelsenbeck *et al.* 2001; Holder & Lewis 2003) was used to estimate the phylogenetic relationships. The models for nucleotide substitutions used in the analyses were selected for each gene individually by applying the Akaike Information Criterion (AIC, Akaike 1973) and the program MRMODELTEST 2.2 (Nylander 2005) in conjunction with PAUP* (Swofford 1998).

Posterior probabilities of trees and parameters in the substitution models were approximated with MCMC and Metropolis coupling using the program MRBAYES 3.1.1 (Ronquist & Huelsenbeck 2003). Analyses were performed for both the individual gene partitions and the combined data set. In the analysis of the combined data set, the models selected for the individual gene partition were used, but the topology was constrained to be the same. All chains were run for 10 million generations, with trees sampled every 100th generations. The trees sampled during the burn-in phase (i.e., before the chain had reached its apparent target distribution) were discarded, and final inference was made from the concatenated output.

Divergence time estimations

An estimate of the timing of the cladogenesis in furnariids was obtained by applying a molecular clock model to the myoglobin intron 2 data set. First an estimate of the average mutation rate in passerines was calculated by comparing myoglobin sequence divergences between 15 species of suboscines and 11 species of oscines (sequences available in GenBank). The average divergence observed in these 163 pairwise comparisons is 10.78% (SD: 0.99%). To correlate sequence divergences to time is problematic as no suitable

Table 1 Samples used in the study. Family and subfamily names follow the classification of Remsen (2003). Abbreviations: AMNH = American Museum of Natural History, New York; NRM = Swedish Museum of Natural History, Stockholm; USNM = US National Museum, Smithsonian Institution, Washington DC; ZMUC = Zoological Museum of the University of Copenhagen. References: (1) Irestedt *et al.* (2002), (2) Irestedt *et al.* (2004), (3) Ericson *et al.* (2002), (4) Fjeldså *et al.* (2005), (5) Olson *et al.* (2005), (6) Irestedt *et al.* (2006), and (7) Ericson *et al.* (2006). The three specimens for which no voucher exist are marked with an asterisk.

Species	Family/subfamily	Sample no.	Myoglobin	G3PDH	ODC	FIB 5
<i>Chilia melanura</i>	Furnariidae: Furnariinae	NRM 569434	EF212135	EF212144	EF212094	EF212046
<i>Cinclodes fuscus</i>	Furnariidae: Furnariinae	ZMUC 5220	AY590054 (ref. 4)	AY590065 (ref. 4)	EF212134	EF212087
<i>Eremobius phoeicurus</i>	Furnariidae: Furnariinae	NRM 569436	EF212136	EF212145	EF212099	EF212051
<i>Furnarius cristatus</i>	Furnariidae: Furnariinae	NRM 966772	AY064255 (ref. 3)	AY590066 (ref. 4)	DQ435482 (ref. 7)	EF212052
<i>Furnarius leucopus</i>	Furnariidae: Furnariinae	ZMUC 125590	AY996345 (ref. 5)	AY996357 (ref. 5)	EF212100	EF212053
<i>Geositta tenuirostris</i>	Furnariidae: Furnariinae	ZMUC 5292	AY590053 (ref. 4)	AY590063 (ref. 4)	EF212101	EF212054
<i>Upucerthia andicola</i>	Furnariidae: Furnariinae	NRM 569430	EF212137	EF212146	EF212122	EF212075
<i>Upucerthia certhioides</i>	Furnariidae: Furnariinae	NRM 569433	EF212141	EF212150	EF212131	EF212084
<i>Upucerthia dumetaria</i>	Furnariidae: Furnariinae	ZMUC 1984-02-14	EF212142	EF212151	EF212132	EF212085
<i>Upucerthia harterti</i>	Furnariidae: Furnariinae	ZMUC 126223	EF212138	EF212147	EF212123	EF212076
<i>Upucerthia jelskii</i>	Furnariidae: Furnariinae	ZMUC 5439	AY065756 (ref. 1)	AY590064 (ref. 4)	EF212124	EF212077
<i>Upucerthia ruficaudus</i>	Furnariidae: Furnariinae	NRM 569431	EF212139	EF212148	EF212125	EF212078
<i>Upucerthia serrana</i>	Furnariidae: Furnariinae	ZMUC 124995	EF212143	EF212152	EF212133	EF212086
<i>Upucerthia vilidirostris</i>	Furnariidae: Furnariinae	NRM 569435	EF212140	EF212149	EF212126	EF212079
<i>Anumbius annumbi</i>	Furnariidae: Synallaxinae	NRM 966903	AY065765 (ref. 1)	AY590072 (ref. 4)	EF212088	EF212040
<i>Asthenes cactorum</i>	Furnariidae: Synallaxinae	ZMUC 5150	AY065761 (ref. 1)	AY590070 (ref. 4)	EF212089	EF212041
<i>Asthenes urubambensis</i>	Furnariidae: Synallaxinae	ZMUC 5172	AY998232 (ref. 6)	AY998214 (ref. 6)	EF212090	EF212042
<i>Coryphistera alaudina</i>	Furnariidae: Synallaxinae	NRM 966910	AY065766 (ref. 1)	AY590073 (ref. 4)	EF212095	EF212047
<i>Cranioleuca pyrrhophia</i>	Furnariidae: Synallaxinae	NRM 966821	AY065764 (ref. 1)	AY590069 (ref. 4)	EF212096	EF212048
<i>Leptasthenura pileata</i>	Furnariidae: Synallaxinae	ZMUC 5338	AY590055 (ref. 4)	AY590067 (ref. 4)	EF212104	EF212057
<i>Limnornis curvirostris</i>	Furnariidae: Synallaxinae	USNM 82735	AY996346 (ref. 5)	AY996359 (ref. 5)	EF212105	EF212058
<i>Phacelodorus ruber</i>	Furnariidae: Synallaxinae	NRM 947206	AY590056 (ref. 4)	AY590071 (ref. 4)	EF212109	EF212062
<i>Schizoeaca harterti</i>	Furnariidae: Synallaxinae	ZMUC 52398	AY998226 (ref. 6)	AY998207 (ref. 6)	EF212116	EF212069
<i>Schoeniophylax phryganophilus</i>	Furnariidae: Synallaxinae	NRM 947184	AY998228 (ref. 6)	AY998209 (ref. 6)	EF212117	EF212070
<i>Synallaxis ruficapilla</i>	Furnariidae: Synallaxinae	NRM 956643	AY065763 (ref. 1)	AY590068 (ref. 4)	EF212119	EF212072
<i>Synallaxis scutata</i>	Furnariidae: Synallaxinae	ZMUC 125635	AY998229 (ref. 6)	AY998210 (ref. 6)	EF212120	EF212073
<i>Automolus leucophthalmus</i>	Furnariidae: Philydorinae	NRM 937251	AY590058 (ref. 4)	AY590078 (ref. 4)	EF212091	EF212043
<i>Berlepschia rikeri</i>	Furnariidae: Philydorinae	ZMUC 51214	AY590057 (ref. 4)	AY590075 (ref. 4)	EF212092	EF212044
<i>Heliobletus contaminatus</i>	Furnariidae: Philydorinae	ZMUC 127191*	AY998240 (ref. 6)	AY998222 (ref. 6)	EF212102	EF212055
<i>Hylocryptus erythrocephalus</i>	Furnariidae: Philydorinae	ZMUC 124862	AY998239 (ref. 6)	AY998221 (ref. 6)	EF212103	EF212056
<i>Lochmias nematura</i>	Furnariidae: Philydorinae	ZMUC 52577	AY065755 (ref. 1)	AY590081 (ref. 4)	EF212106	EF212059
<i>Margarornis squamiger</i>	Furnariidae: Philydorinae	ZMUC 51112*	AY065759 (ref. 1)	AY590074 (ref. 4)	EF212107	EF212060
<i>Megaxenops parmaguae</i>	Furnariidae: Philydorinae	ZMUC 125605	AY998241 (ref. 6)	AY998223 (ref. 6)	EF212108	EF212061
<i>Philydor atricapillus</i>	Furnariidae: Philydorinae	NRM 937334	AY065758 (ref. 1)	AY590076 (ref. 4)	EF212110	EF212063
<i>Premnoplex brunnescens</i>	Furnariidae: Philydorinae	ZMUC 124927	AY998234 (ref. 6)	AY998216 (ref. 6)	EF212111	EF212064
<i>Premnornis guttuligera</i>	Furnariidae: Philydorinae	ZMUC 128014	AY998233 (ref. 6)	AY998215 (ref. 6)	EF212112	EF212065
<i>Pseudocolaptes boissonneautii</i>	Furnariidae: Philydorinae	ZMUC 124935	AY998235 (ref. 6)	AY998217 (ref. 6)	EF212113	EF212066
<i>Pseudoseisura lophotes</i>	Furnariidae: Philydorinae	NRM 976799	AY998236 (ref. 6)	AY998218 (ref. 6)	EF212114	EF212067
<i>Pygarrhichas albogularis</i>	Furnariidae: Philydorinae	AMNH PRS1128	AY065760 (ref. 1)	AY590084 (ref. 4)	EF212115	EF212068
<i>Sclerurus scansor</i>	Furnariidae: Philydorinae	NRM 937258	AY065772 (ref. 1)	AY590080 (ref. 4)	EF212118	EF212071
<i>Syndactyla rufosuperciliata</i>	Furnariidae: Philydorinae	ZMUC 124972	AY998238 (ref. 6)	AY998220 (ref. 6)	EF212121	EF212074
<i>Xenops minutus</i>	Furnariidae: Philydorinae	ZMUC 5451	AY590060 (ref. 4)	AY590082 (ref. 4)	EF212127	EF212080
<i>Xenops rutilans</i>	Furnariidae: Philydorinae	ZMUC 5452	AY590061 (ref. 4)	AY590083 (ref. 4)	EF212128	EF212081
<i>Campylorhamphus trochilirostris</i>	Dendrocolaptidae	NRM 947183	AY442961 (ref. 2)	AY590085 (ref. 4)	EF212093	EF212045
<i>Deconychura longicauda</i>	Dendrocolaptidae	ZMUC 51249	AY442963 (ref. 2)	AY590086 (ref. 4)	EF212097	EF212049
<i>Dendrocincla tyrannina</i>	Dendrocolaptidae	NRM 976662	AY065770 (ref. 2)	AY590087 (ref. 4)	EF212098	EF212050
<i>Xiphocolaptes major</i>	Dendrocolaptidae	NRM 966847	AY065769 (ref. 1)	AY590093 (ref. 4)	EF212129	EF212082
<i>Xiphorhynchus erythropygius</i>	Dendrocolaptidae	ZMUC 51616*	AY442971 (ref. 2)	AY590094 (ref. 4)	EF212130	EF212083

fossil exists. However, the split between suboscines and oscines has been estimated to occur either at 71 Ma (Ericson *et al.* 2002) or at 76–77 Ma (Barker *et al.* 2004). These values yield two estimate of the average mutation rate in myoglobin

intron 2 in passerines: 0.15% Ma⁻¹ and 0.14% Ma⁻¹, and we decided to use the mean of these estimates: 0.145% Ma⁻¹.

We used PATHd8 (Britton *et al.* 2006) to obtain a linearised tree from which the dates of the phylogenetic splits

could be calculated. PATHd8 is a non-parametric method, which smoothes substitution rates sequentially by taking averages over paths lengths from an internode to all its descending terminals. The smoothing is thereby done between sister groups, as opposed to most other methods, where rate smoothing is done between mother and daughter lineages. This has the effect of preserving more of the pattern of heterogeneous branch lengths that we find in the phylogram. Another property of the method is that zero or near-zero branch-lengths collapse, which seems reasonable, considering that these branch-lengths probably represents short time or uncertainties in the phylogeny (or both).

Results

Sequence lengths and alignments

We were able to sequence all four gene regions almost completely for all taxa, but in the ODC region, all sequences obtained from study skins lack a short fragment of 22 bp in the exon 7, as we use overlapping primers to amplify the two ODC fragments. The sequences obtained varied in length between 667 and 701 bp for the myoglobin intron 2, 349–401 bp for the G3PDH intron 11, 524–553 for the intron 5 in β -fibrinogen, and between 531 and 580 bp in the ODC region (taking into account the missing region in exon 7 in the study skin sequences).

Most indels observed in the introns were autapomorphic and mainly found in particularly variable and repetitive regions. In these variable regions, some indels vary in length between taxa, which makes it difficult to know if these indels are homologous or represent independent evolutionary events. However, several apparently synapomorphic indels were observed when mapping the data onto the tree topology obtained from the Bayesian analyses of the combined data set. A few indels were also found to be incongruent with the phylogenetic tree obtained from the analysis of the combined data set. These were generally found in the most variable regions and some of the single base pair insertions actually consist of different bases. For more details of indel lengths and positions see the alignments of the individual gene regions in GenBank.

Models for nucleotide substitutions and phylogenetic relationships

The *a priori* selection of nucleotide substitution models suggested that the GTR+ Γ model had the best fit for myoglobin, ODC and Fib 5, while HKY+I+ Γ had the best fit for G3PDH. We applied a partitioned analysis of the combined data set, but since the same substitution model was selected for myoglobin and ODC gene regions, and since they were found to have similar nucleotide state frequencies and gamma distribution, these two gene regions were linked together in the combined analysis. After discarding the burn-in phase the inference for the individual gene partitions and

the combined data set were based on a total of 80 000 samples, respectively. The posterior distribution of topologies is presented as a majority-rule consensus tree from the combined analysis in Fig. 1.

The trees obtained from the Bayesian analyses of the individual gene partitions are not topologically congruent, and especially the tree derived from the Fib 5 data set deviates. The woodcreepers are, for example, not recognised as sister group to core-ovenbirds, but placed at a more terminal position. However, this data set has few variable positions and an odd placement of the root in this tree could most likely be explained by lack of phylogenetic information, as the other gene regions used in this study are congruent in this respect with the results of Irestedt *et al.* (2002, 2006a) and Chesser (2004a). Nevertheless, most other discrepancies between the gene trees mainly occur at weakly supported nodes (less than 0.95 posterior probability), and most terminal radiations are actually supported by all four gene trees. The tree obtained from the combined analyses is also generally congruent with the tree presented by Irestedt *et al.* (2006a), and like this tree, terminal nodes are generally well supported while several deeper nodes are poorly supported or unresolved. Most importantly, we find strong support for polyphyly of *Upucerthia* and for associating its separate components with specific lineages (Fig. 1). Thus, we will not comment on the poorly resolved early evolution of the Furnariinae as a whole, but only on the relationships of species that are traditionally placed in the genus *Upucerthia*.

Within the paraphyletic complex traditionally referred to as Philydorinae, *Upucerthia andicola* and *ruficaudus* clusters, with strong support, with *E. phoenicurus* and *C. melanura* and, as the deepest branch, *Pygarrhichas albogularis*. *Upucerthia barterti* and *certhioides* are together, with strong support, and usually with *Premmornis* and *Pseudocolaptes* as their sister clade, although this receives variable support (from 1.00 based on G3PDH to 0.80 with myoglobin, but unresolved with ODC).

Upucerthia dumetaria, *jelskii*, *validirostris* (and undoubtedly also *U. albigula*, see above) and *U. serrana* and *Cinclodes fuscus* form a well-supported clade, but it is remarkable that *U. serrana* is robustly placed in the combined tree as sister to all the others. Unfortunately, Chesser's (2004b) study of *Cinclodes* phylogeny used other genetic markers than us (COII and ND3, vs. our myoglobin, G3PDH, ODC and Fib5), and we are therefore unable to fully evaluate the relationship between *Cinclodes* and these forms of *Upucerthia*. This complex is robustly nested in the Furnariini, along with *Furnarius*, *Lochmias*, *Limmornis* and *Phleocryptes* (see Olson *et al.* 2005).

The estimations of divergence times should be taken as a rough first attempt with myoglobin intron 2. They suggest that the diversifications between in-group taxa generally occurred in the Miocene. All lineages with terrestrial furnariids

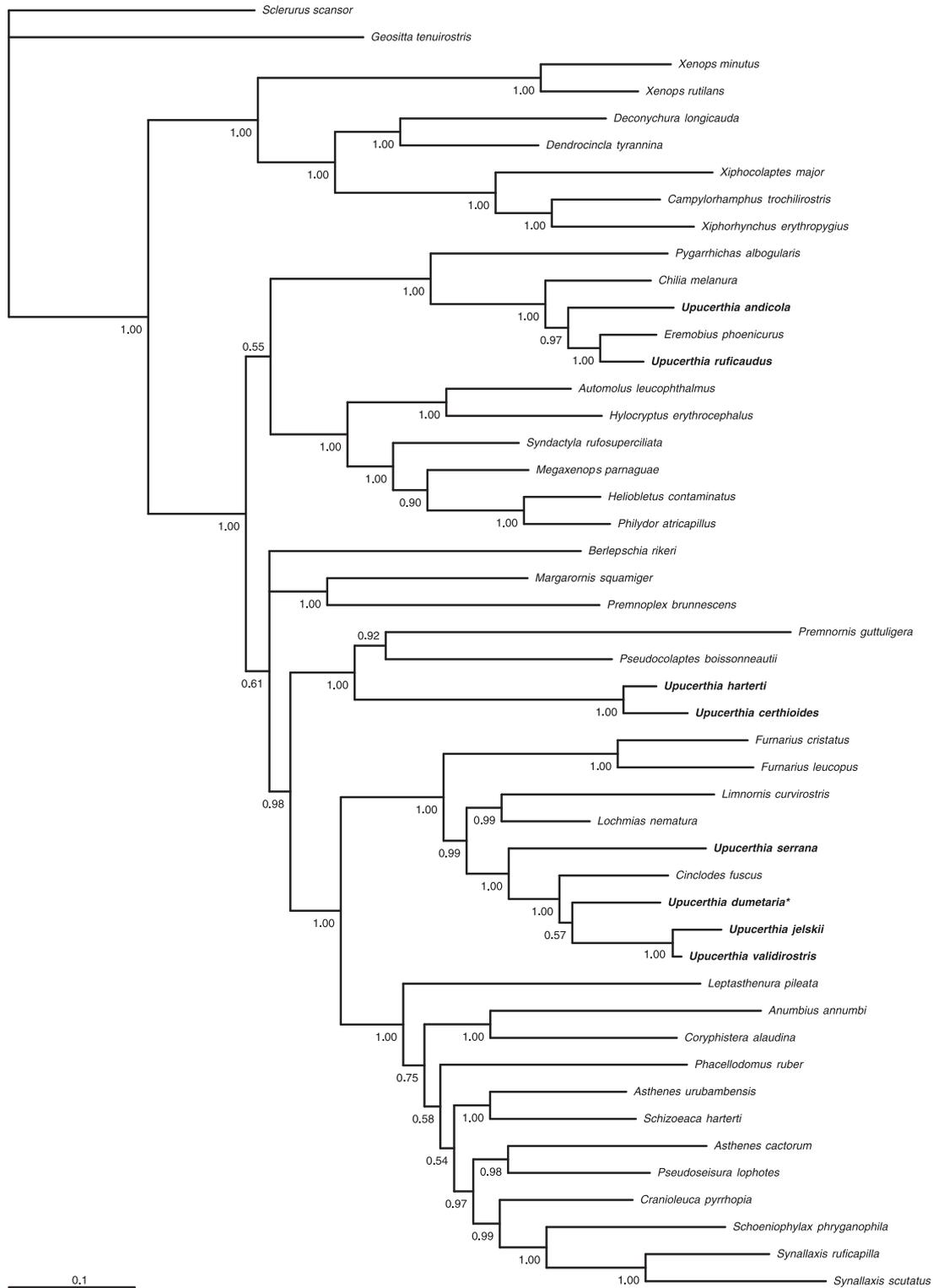


Fig. 1 The 50% majority rule consensus tree obtained from the analyses of the combined data set (myoglobin intron 2, ornithine decarboxylase introns 6 and 7, glyceraldehyde-3-phosphate dehydrogenase intron 11, and β -fibrinogen intron 5). Posterior probability values are indicated below the nodes. The species traditionally included in the genus *Upucerthia* (in bold) do not form a monophyletic group. The type species of *Upucerthia* is marked with an asterisk.

of rather dry habitats, including the three lineages with species hitherto included in *Upucerthia*, date 10–14 My back in time. The splits between *C. melanura*, *E. phoenicurus* and *U. ruficaudus* took place in the very late Miocene and Pliocene. The divergences between *U. harterti* and *U. certhioides*, and between *U. jelskii* and *U. validirostris*, are more recent, from late Pliocene and early Pleistocene. Based on these myoglobin datings, it seems that the most recent speciation events are similar to those in *Cinclodes* and *Geositta*, thus predating the major glaciations in the high Andes (Chesser 2004b; Cheviron et al. 2005) and the radiation of *Muscisaxicola*, which inhabit barren habitats close to the Andean snow-line (Chesser 2000).

Discussion

Morphological variation among clades

Several aspects of the phylogeny and evolution of ovenbirds has already been discussed by Irestedt et al. (2002, 2006a), Fjeldså et al. (2005) and Olson et al. (2005), or will be discussed elsewhere, and we will here limit ourselves to discussing taxa that have so far been placed in the genus *Upucerthia*, and their nearest relatives.

In the eyes of Vaurie (1980), *Upucerthia* belonged to a closely-knit group of terrestrial species along with *Geositta*, *Cinclodes*, *Chilia* and *Furnarius*, defined by their adaptations for terrestrial life: earth-like colours, fairly strong legs, and slender bills of variable length and curvature. No unique character-states are described that would unequivocally separate these genera, and there is a good deal of variation within each genus, notably in colours and patterns of the underparts (see descriptions in Vaurie 1980; Fjeldså & Krabbe 1990; Remsen 2003). All *Upucerthia* share rather rufous wing-linings and a rather weakly defined rufous wingbar (but only *U. dumetaria*, *jelskii* and *validirostris* are known to expose these in wing-flapping displays, as do *Cinclodes* spp.). They also share more or less rufous tails (least so in *U. jelskii* and *validirostris*, and *U. dumetaria*, which resembles *Cinclodes* [notably *C. pabsti*] in having buffy outer tail corners and a restricted but rather clearly demarcated wing-pattern). The tail may have a signal function, and is often raised or cocked right up, except in *U. certhioides* and *harterti*. It is noteworthy that *U. andaecola* and *ruficaudus* have a clear-cut blackish pattern on most tail-feathers (at least inner vanes), thereby approaching *Eremobius* and *Chilia*, which have more extensively blackish tails with rufous base (Fig. 2). The latter four taxa, and *Pygarrhichas*, share a striking white throat and upper breast and exceptionally long and fluffy, rufous feathers on the rump (personal observation).

In general, the long and more or less curved bills of *Upucerthia* seems well suited for probing in crevices and for digging in earth and dung, like most other birds feeding in this way in hard and stony soils. It is therefore interesting to

note that the lineage of *Eremobius* and *Upucerthia andaecola* and *ruficaudus* is characterised by almost straight bills (especially *ruficaudus*, but also *andaecola* specimens from the La Paz canyon; unpublished data). The bills of *Pygarrhichas* and *Chilia* of this lineage are absolutely straight (Fig. 2). *Pygarrhichas* feeds by chiselling and probing in bark and epiphytic moss, which has been suggested to be an ancestral adaptive state of the furnariid radiation (Fjeldså et al. 2005). However, straight tomia of the bills, and habits of pecking in decaying wood, is seen quite widely in Philydorini, and skulls of members of the *Pygarrhichas* clade (X-rays of study skins) resemble those of Philydorini and do not show woodpecker-like adaptations as described for *Xenops* and *Glyphorynchus* (Fjeldså et al. op. cit.). The long, straight bills of all members in this clade is remarkable considering the divergence between these species in other respects, *Pygarrhichas* being a small, compact scansorial bird with a short tail specialised for support on tree-trunks, the others terrestrial (Fig. 2).

Over all, the genus *Upucerthia* exhibits considerable morphological variation, and is homogeneous only to the extent that all species are adapted to similar dry scrubby and rocky habitats, while other Furnariini are more associated with water, either edges of streams (*Lochmias*, *Cinclodes*, certain *Furnarius*), seashores (certain *Cinclodes*) and reed-marsh (*Phelocryptes*, *Limnornis*; see Olson et al. 2005).

Biogeography and adaptation to local environments

Upucerthia andaecola and *ruficaudus*, *Eremobius*, *Chilia* and *Pygarrhichas* are distributed in the southern Andean region, with only rather marginal interspecific range overlap (Fig. 2) and with hardly any overlap with other philydorine taxa. *Pygarrhichas* inhabits the ancient southern beech forests, *Chilia* rocky slopes in central Chile, *Eremobius* the arid shrub-steppe of upland Patagonia, *U. ruficaudus* bushy places in ravines and rocky slopes in the arid puna of the southern Andes up to southern Peru, and *U. andaecola* bushy canyons in a restricted area in the highlands of Bolivia and northwestern Argentina.

Vuilleumier (1985) considered *Pygarrhichas* a relict of an autochthonous mid-Cenozoic Patagonian forest fauna. The facts that *Pygarrhichas* are in a basal position within this clade (Fig. 1) and share scansorial habits with the Dendrocolaptidae and several philydorine lineages, suggest that its forest dependence is ancestral (plesiomorphic). The news, then, is that *Pygarrhichas* is not a biogeographic relict but is part of a much more widespread clade whose other members adapted to, and speciated in, new habitats that developed as a consequence of the Andean uplift in the upper Miocene (Raven & Axelrod 1975; Delsuc et al. 2004).

The genus *Chilia* has been associated with *Geositta*, *Upucerthia* and *Cinclodes* in the Furnariini (Vaurie 1980; Vuilleumier 1980) or even with *Eremobius* (Remsen 2003). Our result suggests that it is indeed very close to *Eremobius* and

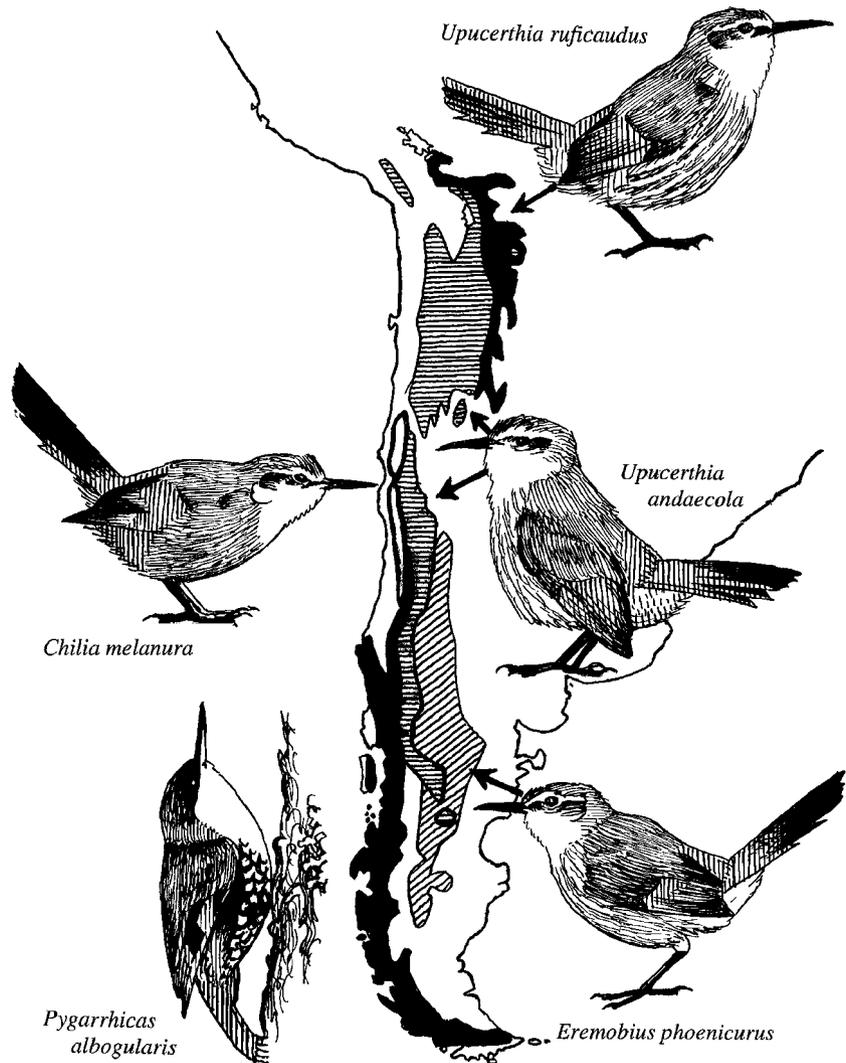


Fig. 2 Distribution and appearance of the members of a hitherto unrecognized deep clade in the furnariid phylogeny. Vertical hatching of wings and tail indicates rufous colours.

two members of the traditional *Upucerthia*, but that they are unrelated to the earthcreepers of the Furnariini group. By external appearance and behaviour, *E. phoenicurus* resembles a diminutive *U. ruficaudus*. Vaurie (1980) found it difficult to place *E. phoenicurus*, but, emphasizing its voluminous nest of thorny twigs placed in low scrubs, he placed it with *Annumbius* and *Coryphistera* in the Synallaxini, something that is clearly rejected by our result. *U. andaecola* and *ruficaudus* build a small grass-cup in their restricted nest-chambers excavated in earth banks, as in *Upucerthia* spp. of the Furnariini clade, and something that may represent a plesiomorphic nesting habit of all Furnariidae (Zyskowski & Prum 1999; Irestedt *et al.* 2006a). This is usually also the case in *Chilia*, but by lack of suitable substrates for digging in its rocky habitat, this species is known to sometimes build a large globular stick-nest in a rock crevice (Remsen 2003). Such a plasticity is also mentioned for *U. certhioides*, which some-

times build considerable nests in cavities or crevices, or stick nests in bushes or low trees (Remsen 2003). These examples suggest that substantial amounts of twigs and other debris may be assembled when nesting in larger cavities among rocks, and it seems that birds with such habits might switch over to building huge stick-nest inside dense shrubs (as in *Eremobius*).

Upucerthia certhioides and *barterti* may represent another case of early philydorines responding to the development of scrubby habitats south of the humid tropics, in the Chaco region (Short 1975). They are described as partly arboreal (Ridgely & Tudor 1994; Remsen 2003), but often forage among terrestrial bromeliads or on the ground, in the shade of dense shrubs. Considering that the nearest relatives (Fig. 1) are forest birds (with *Pseudocolaptes* specialised to forage among arboreal bromeliads), this looks like a parallel shift towards terrestrial life as is seen in the woodcreeper

Drymornis bridgesii in the same ecoregion (Irestedt *et al.* 2004). Vaurie (1980) remarks that *U. certhioides* ‘occupies a position somewhat apart’, which is his only hint of doubt about the unity of *Upucerthia*; although he did not support the suggested separation of the genus *Ochetorhynchus* (Wetmore & Peters 1949).

The main *Upucerthia* group, in the Furnariini, is a fairly homogeneous high-Andean group. The distinctive *U. serrana* inhabits stony places in oligothermic woodland (especially *Polylepis*) in central Peru, an area characterised by holding several other taxa with no close relatives (relicts): *Oreonympha nobilis*, *Polyonimus caroli*, *Zaratornis stresemanni* and *Xenodacnis parina*. *Cinclodes pabsti*, which represents the deepest branch in the *Cinclodes* phylogeny (Chesser 2004b), with rather long tail, like of *U. dumetaria*, inhabits another area with high relictual endemism in southern Brazil. Although *Cinclodes* seems, over all, to represent a close-knit group (Chesser 2004b), its monophyly cannot be ascertained without DNA sequence data that fully resolve the deeper branches in this complex.

Taxonomic implications

The type species for *Upucerthia* Geoffroy Saint-Hilaire, 1832, is *U. dumetaria*. If *U. serrana* were sister to the whole complex of *Cinclodes* and *U. dumetaria*, *jelskii*, *validirostris* and *albigula*, then it should have a new generic name. However, such a decision should await a more complete analysis where the same genetic markers are used for *Cinclodes* and *Upucerthia*. The generic name *Ochetorhynchus* Meyen, 1834, applied by Wetmore & Peters (1949) to *U. certhioides*, *harterti* and *ruficaudus* was initially given to the latter of these species. However, the name *Anabates* d’Orbigny and Lafresnaye, 1838, is available for *certhioides* and *harterti*. Judging from the relatively recent divergence and uniformity in morphology and vocalisations of *Chilia*, *Eremobius* and *Upucerthia andaecola* and *ruficaudus*, we suggest placing all these in the genus *Ochetorhynchus*. *Chilia* was separated (from *Cinclodes*) because of its straight bill and rather long and distinctly coloured tail, and for its specialisation for a dry and stony habitat (Vaurie 1980), but in fact all these features agree well with the relationship suggested by the molecular data. We therefore see no reason for maintaining the monotypic genera *Eremobius* Gould, 1839, for *phoenicurus*, and *Chilia* Salvadori, 1908, for *melanura*.

Concluding remarks

In the broader furnariine context, adaptations to open habitats and terrestrial life has happened several times, and lead to convergence to a degree that deceived former systematists to regard *Geositta*, *Cinclodes*, *Upucerthia* and *Chilia* as a natural unit. Clearly, the Furnariidae family is primarily forest-adapted (Fjeldså *et al.* 2005), and adaptive shifts to more open

habitats happened several times, independently, but mainly in connection with the development of a broad ‘dry diagonal’ from Patagonia over the Andean altiplano to the deserts of the Pacific slope.

This study should warn against basing classifications on external appearance in groups characterised by high adaptive plasticity. A thorough morphological analysis could possibly have revealed cases of convergence, but such work will still be hampered by insufficient anatomic collection, such as skeletons. Molecular studies will play an important role in revealing false relationships and will thus facilitate re-interpretation of the morphological variation.

Acknowledgements

Tissue and blood samples were mainly from the Zoological Museum of Copenhagen (with data collecting supported by the Danish Research Councils) and the Swedish Museum of Natural History (collected in collaboration with the Museo Nacional de Historia Natural del Paraguay, San Lorenzo). Important samples have also been obtained from the American Museum of Natural History and the U.S. National Museum, Smithsonian Institution. The Swedish Research Council (grant no. 621-2004-2913 to P.E.) funded the laboratory work. Tammes Menne made X-ray photos of selected furnariid specimens for determining skeletal characters. We want to thank Tom Britton and Cajsa L. Andersson for providing access to and help with an advance version of PATHd8.

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