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Molecular data reveal some major adaptational shifts in the early evolution of the most diverse avian family, the Furnariidae

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Abstract A robust phylogeny estimate for the family Furnariidae (sensu lato) was obtained using sequences of two nuclear introns and one mitochondrial gene (cyt b). Contrary to the widely accepted sister-group relationship of ovenbirds (Furnariinae) and woodcreepers (Dendrocolaptinae), a basal clade is suggested for *Sclerurus* and *Geositta*, while *Xenops*, hitherto considered an aberrant ovenbird, was found to occupy a basal position on the woodcreeper lineage. The morphological variation is re-interpreted in view of this revised phylogenetic hypothesis. Presumably, the remarkable adaptive radiation in this family started as primitive, *Sclerurus*-likes forms, which used the tail as a prop during terrestrial feeding, lured up to seek food on tree-trunks. The two basal woodcreeper genera, *Xenops* and then *Glyphorynchus*, show strong cranial specializations for hammering in wood, thus presenting a remarkable parallelism with the family Picidae, *Xenops* resembling a piculet, *Glyphorynchus*, a diminutive woodpecker. However, this specialization was lost in other woodcreepers, which show a more normal passerine skull, adapted for probing and prying in tree-trunk crevices and sallying for escaping insects. The ovenbirds developed a more flexible (rhynchokinetic) bill, well suited for probing and retrieving hidden prey in dead-leaf

clusters and debris suspended in the vegetation, and in epiphyte masses. Adaptations to live in open terrain are secondary.

Keywords Adaptative shifts · Bayesian analysis · Dendrocolaptinae · Furnariinae · Nuclear introns

Introduction

The South American ovenbirds, Furnariinae, exhibit a morphological heterogeneity that is unparalleled among avian groups on that taxonomic level (Leisler 1977; Vaurie 1980; Renssen 2003). Inhabiting all habitats from tropical rainforest to deserts, and all strata, the currently recognized 236 species vary greatly in size and development of peculiar tail-shapes. This is in strong contrast to their presumed sister group (Sibley and Ahlquist 1990), the woodcreepers (Dendrocolaptinae), all 69 species of which nest in cavities and are scansorial with specialized tail-tips providing support as they climb on tree-trunks, like woodpeckers (Marantz et al. 2003).

The ovenbirds are traditionally divided into three broad groups (Hellmayr 1925; Vaurie 1971, 1980; Sibley and Ahlquist 1990, for historical review): the ground-living Furnarini, which resemble thrashers and slender-billed larks; the “spinetails” Synallaxini, which are small and acrobatic, with long and in many cases peculiarly shaped tails; and the Philydorini, which are more heavily built forest ovenbirds. *Sclerurus* leaf-tossers and the monotypic genus *Lochmias* have been regarded as a separate sub-family, Sclerurinae (Sclater 1890), but are placed near the end, or near the beginning, respectively, of the Philydorini sequence. However, characters have not been specified that clearly define the three groups, and aberrant forms have been embedded or placed at the ends of the taxonomic sequence of these groups, often with no other evidence than a superficial plumage similarity with some core members of that group. This is, for instance, the case with some ovenbirds with similar stiff tail-spines as the woodcreepers, namely *Aphrastura*, which are usually placed at

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the beginning of the synallaxine group, *Margarornis*, which is placed at beginning of the philydorine group, and *Pygarrhicas*, which is appended at the end of that group. The peculiar *Xenops* species, tiny canopy birds with recurved and laterally flattened bills, are also placed near the end of the philydorine sequence. *Geositta* is placed first in the entire ovenbird group, because of a primitive syringial character shared with the woodcreepers, and it is then followed by furnarines of similar body shape. These placements simply reflect the agony of choice when no clear character analysis was used to determine a sequence of phylogenetic branches. Without a clear phylogenetic hypothesis it is difficult to exclude the possibility that some of these aberrant genera could be ancestral forms, which would most logically be placed in the beginning of the classification.

Modern molecular systematics has provided numerous examples of taxonomic neglect caused by the past tendency to “bury” aberrant species and genera into larger and well-known groups based on overall similarity (e.g., “*Yuhina*” *zantholeuca*, see Cibois et al. 2002; *Sapayoa*, see Fjeldså et al. 2003; *Pseudopodoces*, see James et al. 2003). A preliminary molecular analysis of the tracheophone suboscine birds of South America (Irestedt et al. 2002) revealed some cases of neglected “ancestral” types, e.g., the “tapaculo” genus *Melanopareia* was found to represent an ancestral lineage from near the base of the entire tracheophone radiation, and *Sclerurus* was found to be a sister taxon to other ovenbirds and woodcreepers (see also Chesser 2004). We now follow this up with more thorough studies of individual tracheophone families (see Irestedt et al. 2004a, 2004b). Here, we aim to define the deep branching pattern of the ovenbird-woodcreeper radiation.

Since little is gained by just presenting new patterns of grouping that may be more high-tech and objective than traditional, morphology-based grouping (see Lipscomb et al. 2003), we will supplement the phylogenetic analysis by examining how some morphological characters vary among the deeper branches. By contrasting phylogenetic and morphological information we hope to provide evidence about the early adaptive shifts, and identify what adaptive changes may have spurred the spectacular adaptive radiation of the ovenbird-woodcreeper assemblage. By doing this we hope to provide a better basis for interpreting the many specializations that took place during the further diversification. However, the finer branching pattern of the ovenbird radiation, the allocation of genera to subgroups, and a suggested new classification, will be presented in another publication.

Materials and methods

Taxon sampling, amplification and sequencing

We include in this study 23 ovenbirds and 10 woodcreepers (see Table 1 for identifications and GenBank accession numbers; see also Supplementary Table 1 in

the Electronic Supplementary Material). These represent the major subgroups that previously have been suggested for ovenbirds (Hellmayr 1925; Vaurie 1971, 1980; Ridgely and Tudor, 1994) and woodcreepers (Feduccia 1973; Raikow 1994; Marantz et al. 2003; Irestedt et al. 2004a; the two latter papers based on molecular data). As the first phylogenetic analyses yielded unexpected placements of the genera *Geositta*, *Sclerurus* and *Xenops* (see below), one additional representative of each of these genera was added to verify the authenticity of the samples. Two representatives from the family Rhinocryptidae and one from the Formicariidae were used as outgroup taxa, as these families have been suggested as forming the sister clade to Furnariidae (Irestedt et al. 2002).

The following genetic markers were sequenced: the complete myoglobin intron 2 (along with 13 bp and 10 bp of the flanking exons 2 and 3, respectively), corresponding to position 303 (exon 2) through 400 (exon 3) in humans (GenBank accession number XM009949), the complete glyceraldehydes-3-phosphodehydrogenase (G3PDH) intron 11 (along with 36 bp and 18 bp of exons 11 and 12, respectively) corresponding to the region 3,915 to 4,327 in *Gallus gallus* (GenBank accession number M11213) and 999 bp of the cytochrome *b* gene, corresponding to positions 15,037 to 16,035 in the chicken mitochondrial genome sequence (Desjardins and Morais 1990) (for primer sequences see Table 2, and see also Supplementary Table 2 in the Electronic Supplementary Material; for laboratory procedures see Ericson et al. 2002; Irestedt et al. 2002; Fjeldså et al. 2003). Positions where the nucleotide could not be determined with certainty were coded with the appropriate IUPAC (ambiguity) code. Due to the low number of insertions in the introns, the combined sequences could easily be aligned by eye (Appendices 1 and 2 in the Electronic Supplementary Material). All gaps in the myoglobin and the G3PDH sequences were treated as missing data in the analyses. No insertions, deletions, stop or nonsense codons were observed in any of the cytochrome *b* sequences.

Phylogenetic inference and model selection

We used Bayesian inference for estimating phylogenetic hypothesis from our DNA data (see recent reviews by Huelsenbeck et al. 2002; Holder and Lewis 2003). Prior to the analyses, the models for nucleotide substitutions were selected for each gene individually by using Akaike Information Criterion (AIC; Akaike 1973) and the program MrModeltest (Nylander 2002) in conjunction with PAUP* (Swofford 1998). The gene partitions were first analyzed separately. The selected models for each gene partition (with the topology constrained to be the same) were used in the analysis of the combined dataset.

The posterior probabilities of trees and parameters in the substitution models were approximated with

Table 1 Samples used in the study. Family and subfamily names follow the classification of Remsen (2003). Abbreviations: AHMN American Museum of Natural History, New York; NRM Swedish Museum of Natural History; ZMUC Zoological Museum of the University of Copenhagen. References: (1) Irestedt et al. (2002); (2) Irestedt et al. (2004b); (3) Ericson et al. (2002)

Species	Family: subfamily	Voucher no.	Cytochrome <i>b</i>	Myoglobin	G3PDH
<i>Geositta rufipennis</i>	Furnariidae: Furnariinae	ZMUC S290	AY590042	AY590052	AY590062
<i>Geositta tenuirostris</i>	Furnariidae: Furnariinae	ZMUC S292	AY590043	AY590053	AY590063
<i>Upucerthia jelskii</i>	Furnariidae: Furnariinae	ZMUC S439	AY065700 (ref. 1)	AY065756 (ref. 1)	AY590064
<i>Cinclodes fuscus</i>	Furnariidae: Furnariinae	ZMUC S220	AY590044	AY590054	AY590065
<i>Furnarius cristatus</i>	Furnariidae: Furnariinae	NRM 966772	AY064279 (ref. 3)	AY064255 (ref. 3)	AY590066
<i>Leptasthenura pileata</i>	Furnariidae: Synallaxinae	ZMUC S338	AY590045	AY590055	AY590067
<i>Synallaxis ruficapilla</i>	Furnariidae: Synallaxinae	NRM 956643	AY065707 (ref. 1)	AY065763 (ref. 1)	AY590068
<i>Cranioleuca pyrrhophia</i>	Furnariidae: Synallaxinae	NRM 966821	AY065708 (ref. 1)	AY065764 (ref. 1)	AY590069
<i>Asthenes cactorum</i>	Furnariidae: Synallaxinae	ZMUC S150	AY065705 (ref. 1)	AY065761 (ref. 1)	AY590070
<i>Phacellodomus ruber</i>	Furnariidae: Synallaxinae	NRM 947206	AY590046	AY590056	AY590071
<i>Anumbius annumbi</i>	Furnariidae: Synallaxinae	NRM 966903	AY065709 (ref. 1)	AY065765 (ref. 1)	AY590072
<i>Coryphistera alaudina</i>	Furnariidae: Synallaxinae	NRM 966910	AY065710 (ref. 1)	AY065766 (ref. 1)	AY590073
<i>Margarornis squamiger</i>	Furnariidae: Philydorinae	ZMUC S1112	AY065703 (ref. 1)	AY065759 (ref. 1)	AY590074
<i>Berlepschia rikeri</i>	Furnariidae: Philydorinae	ZMUC S1214	AY590047	AY590057	AY590075
<i>Philydor atricapillus</i>	Furnariidae: Philydorinae	NRM 937334	AY065702 (ref. 1)	AY065758 (ref. 1)	AY590076
<i>Thripadectes flammulatus</i>	Furnariidae: Philydorinae	ZMUC S428	AY065701 (ref. 1)	AY065757 (ref. 1)	AY590077
<i>Automolus leucophthalmus</i>	Furnariidae: Philydorinae	NRM 937251	AY590048	AY590058	AY590078
<i>Sclerurus mexicanus</i>	Furnariidae: Philydorinae	ZMUC S1443	AY590049	AY590059	AY590079
<i>Sclerurus scansor</i>	Furnariidae: Philydorinae	NRM 937258	AY065715 (ref. 1)	AY065772 (ref. 1)	AY590080
<i>Lochmias nematura</i>	Furnariidae: Philydorinae	ZMUC S2577	AY065699 (ref. 1)	AY065755 (ref. 1)	AY590081
<i>Xenops minutus</i>	Furnariidae: Philydorinae	ZMUC S451	AY590050	AY590060	AY590082
<i>Xenops rutilans</i>	Furnariidae: Philydorinae	ZMUC S452	AY590051	AY590061	AY590083
<i>Pygarrhichas albogularis</i>	Furnariidae: Philydorinae	AMNH PRS1128	AY065704 (ref. 1)	AY065760 (ref. 1)	AY590084
<i>Campylorhynchus trochilirostris</i>	Furnariidae: Dendrocolaptinae	NRM 947183	AY442987 (ref. 2)	AY442961 (ref. 2)	AY590085
<i>Deconychura longicauda</i>	Furnariidae: Dendrocolaptinae	ZMUC S1249	AY442989 (ref. 2)	AY442963 (ref. 2)	AY590086
<i>Dendrocicla tyrannina</i>	Furnariidae: Dendrocolaptinae	ZMUC S1110	AY442985 (ref. 2)	AY442959 (ref. 2)	AY590087
<i>Drymornis bridgesii</i>	Furnariidae: Dendrocolaptinae	NRM 966930	AY065711 (ref. 1)	AY065768 (ref. 1)	AY590088
<i>Glyphorhynchus spirurus</i>	Furnariidae: Dendrocolaptinae	ZMUC S1521	AY442992 (ref. 2)	AY442966 (ref. 2)	AY590089
<i>Lepidocolaptes fuscus</i> ^a	Furnariidae: Dendrocolaptinae	NRM 937283	AY442993 (ref. 2)	AY442967 (ref. 2)	AY590090
<i>Nasica longirostris</i>	Furnariidae: Dendrocolaptinae	ZMUC S1831	AY442995 (ref. 2)	AY442969 (ref. 2)	AY590091
<i>Sittasomus griseicapillus</i>	Furnariidae: Dendrocolaptinae	NRM 967031	AY065714 (ref. 1)	AY065771 (ref. 1)	AY590092
<i>Xiphocolaptes major</i>	Furnariidae: Dendrocolaptinae	NRM 966847	AY065712 (ref. 1)	AY065769 (ref. 1)	AY590093
<i>Xiphorhynchus erythropterygius</i>	Furnariidae: Dendrocolaptinae	ZMUC S1616	AY442997 (ref. 2)	AY442971 (ref. 2)	AY590094
<i>Chamaeza meruloides</i>	Formicariidae	ZMUC S2053	AY065718 (ref. 1)	AY065776 (ref. 1)	AY590095
<i>Pteroptochos tarnii</i>	Rhinocryptidae	AMNH RTC467	AY065717 (ref. 1)	AY065774 (ref. 1)	AY590096
<i>Scytalopus spillmanni</i>	Rhinocryptidae	ZMUC S540	AY065716 (ref. 1)	AY065773 (ref. 1)	AY590097

^a Alexio (2002) has suggested that this species should be placed in the genus *Xiphorhynchus*

Markov chain Monte Carlo and Metropolis coupling using the program MrBayes (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). Trees were sampled every 100th generations, and the trees sampled during the burn-in phase (i.e., before the chain had reached its apparent target distribution) were discarded.

Table 2 Primers used for amplification (Amp) and sequencing (Seq) of the three gene fragments

Primer name	Used for	Primer sequence (5' to 3')	Reference
Cytochrome <i>b</i>			
L14841	Amp; Seq	AAC TGC AGT CAT CTC CGG TTT ACA AGA C	Kocher et al. (1989)
H15915	Amp; Seq	CCA TCC AAC ATC TCA GCA TGA TGA AA	Edwards and Wilson (1990)
Thr 1	Amp; Seq	TCT TTG GCT TAC AAG ACC AA	Johansson et al. (2002)
P5L	Seq	CCT TCC TCC ACG AAA CAG GCT CAA ACA ACC C	Johansson et al. (2002)
H658	Seq	TCT TTG ATG GAG TAG TAG GGG TGG AAT GG	Johansson et al. (2002)
Myoglobin, intron 2			
Myo 2	Amp; Seq	GCC ACC AAG CAC AAG ATC CC	Slade et al. (1993)
Myo 3F	Amp; Seq	TTC AGC AAG GAC CTT GAT AAT GAC TT	Heslewood et al. (1998)
Myoint.c	Seq	AGC CCT GAG GGA TCC ATT GG	Irestedt et al. (2002)
Myoint.nc	Seq	CCA ATG GAT CCT CCA GGG CT	Irestedt et al. (2002)
Myoint. H1	Seq	TGA CAG GTC TTA TGT AAT ATA G	Irestedt et al. (2002)
Myoint. H2	Seq	TCT AAA CTT GGA TAT TCA CAT	Irestedt et al. (2002)
Myoint. L1	Seq	CTA TAT TAC ATA AGA CCT GTC A	Irestedt et al. (2002)
Glyceraldehydes-3-phosphodehydrogenase (G3PDH), intron 11			
G3P13b	Amp	TCC ACC TTT GAT GCG GGT GCT GGC AT	Fjelds� et al. (2003)
G3P14b	Amp; Seq	AAG TCC ACA ACA CGG TTG CTG TA	Fjelds� et al. (2003)
G3PintL1	Seq	GAA CGA CCA TTT TGT CAA GCT GGT T	Fjelds� et al. (2003)

Two runs, starting from different, randomly chosen trees, were made to ensure that the individual runs had converged on the same target distribution (Huelsenbeck et al. 2002). The final inference was made from concatenated output from the two runs.

Morphology

Skeletons of *Geositta cunicularia*, *Glyphorhynchus spirurus*, *Sclerurus scansor* and *Xenops rutilans*, which have not previously been properly described, were prepared and examined, and observations made were compared with the comprehensive description and character matrices provided by Feduccia (1973). We will not present comprehensive descriptions here, but will emphasize novel observations of importance for interpreting some of the early adaptive shifts in the ovenbird-woodcreeper radiation.

Results

Variation in the molecular data set

The concatenated alignment of DNA sequences was 2,176 bp long, of which 677 (*Philydor*) to 716 bp (*Chamaeza*) were myoglobin intron 2, whereas 287 (*Chamaeza*) to 401 bp (*Pygarrhichas*) were G3PDH intron 11. The uncorrected pairwise distances ranged between 0.7% (*Sclerurus mexicanus* and *scansor*) and 9.8% (*Upucerthia* and *Pterotochos*) in myoglobin, 0.0% (*Xenops minutus* and *rutilans*) and 13.2% (*Berlepschia* and *Scytalopus*) in G3PDH, and between 11.0% (*Lochmias* and *Upucerthia*) and 24.0% (*Chamaeza* and *Synallaxis*) in cytochrome *b*. In both the myoglobin intron 2 and G3PDH intron 11 some autapomorphic indels were found in particularly variable and repeatable regions (Appendices 1 and 2 in the Electronic Supplementary Material). However, given the tree topologies obtained from the Bayesian analyses of the combined data set, some synapomorphic indels were also observed. In the myoglobin intron 2, all ovenbirds and woodcreepers lack 28 bp present in the outgroup (*Scytalopus* is also lacking 12 of these bp, but shares the remaining 16 bp with the other outgroup taxa). All woodcreeper representatives share a deletion of 12 bp. In the relatively more indel-rich G3PDH intron 11, *Geositta rufipennis* and *tenuirostris* share a deletion of 23 bp, *Deconychura*, *Dendrocincla* and *Sittasomus* share two deletions of 34 and 1 bp; *Geositta rufipennis* and *tenuirostris* and *Xenops minutus* and *rutilans* share a deletion of 1 bp; *Chamaeza*, *Pterotochos* and *Scytalopus* share a deletion of 1 bp; and the latter two taxa share a deletion of 2 bp.

Four indels (all in G3PDH intron 11) were found to be incongruent with the phylogenetic tree obtained from the analysis of the combined data set. These are a 1 bp insertion in *Cinclodes* and *Deconychura*; a 1 bp insertion

in *Automolus* and *Philydor*; a 10 bp deletion in *Drymornis* and *Xiphorhynchus* and a 3 bp insertion in *Glyphorhynchus*, *Campylorhamphus*, *Drymornis*, *Lepidocolaptes*, *Nasica*, *Xiphocolaptes* and *Xiphorhynchus*.

Model selection and phylogenetic inference

The priori selection of substitution models showed that the GTR+I+ Γ model had the best fit for the cytochrome *b* partition, while GTR+ Γ and HKY+ Γ were selected for myoglobin intron 2 and the G3PDH intron 11, respectively. These models were used in Bayesian analyses of the individual genes as well in the combined analyses. Inference for the individual genes were based on a total of 39,600 saved trees, while the combined analysis was based on 39,000 trees. For the phylogenetic inference, the mode of the posterior distribution of topologies was presented as a majority-rule consensus tree from each analysis.

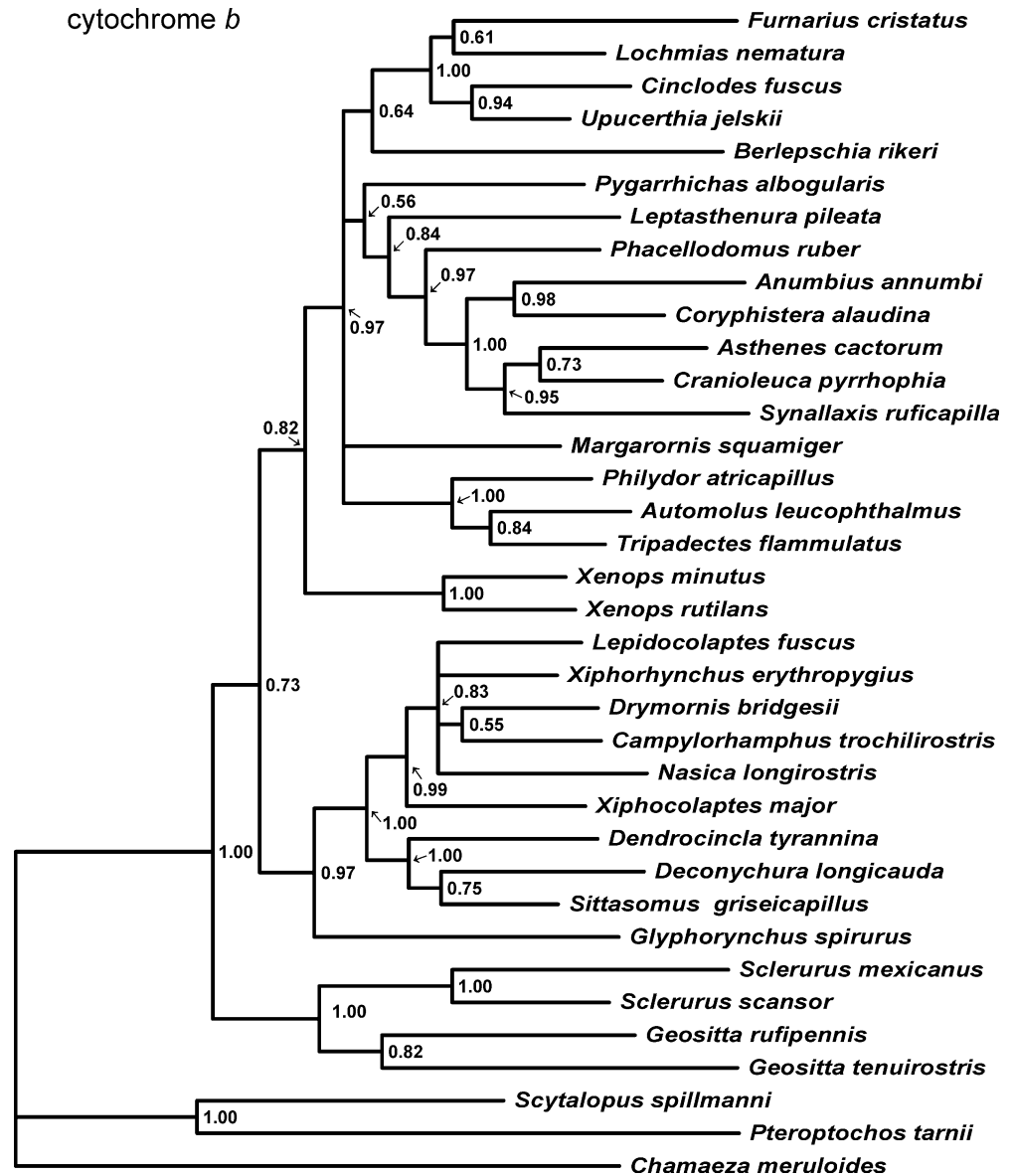
The trees obtained from the Bayesian analyses of the cytochrome *b* (Fig. 1), myoglobin (Fig. 2) and G3PDH genes (Fig. 3), show a similar degree of resolution and also agree well topologically. For example, all genes support a sister relationship between the genera *Geositta* and *Sclerurus* (1.00, 0.90 and 0.99 posterior probability for the cytochrome *b*, myoglobin and G3PDH genes, respectively). Also a sistergroup relationship between *Geositta* and *Sclerurus* on the one hand, and all other ovenbirds and woodcreepers on the other, is congruently supported (1.00 for all genes). However, there are also some topological disagreements between individual genes, but most of these occur at short internodes with posterior probability values below 0.90. The only obvious strong conflict between the individual genes concerns the relative position of *Glyphorhynchus spirurus* within the woodcreeper clade, where cytochrome *b* places it basal to all woodcreepers (0.97), while myoglobin places it as sister to *Nasica longirostris* and *Xiphocolaptes major* (0.98).

The tree obtained from the analysis of the combined data set (Fig. 4) is similar to the trees obtained from the individual genes. The only topological conflict supported by posterior probability above 0.90 between this tree and any of the individual gene trees again concerns the position of the *Glyphorhynchus spirurus*: the combined tree is congruent with the cytochrome *b* tree (and in strong conflict with the myoglobin tree) in giving strong support (1.00) for a basal position of *Glyphorhynchus* among all traditional woodcreeper genera.

Morphological observations

We focus here on some cranial characters that received some attention in earlier discussions of ovenbird and woodcreeper relationships, and examine how these characters differ between the deep branches defined in the molecular phylogeny.

Fig. 1 Majority rule consensus tree obtained from the Bayesian analysis of the cytochrome *b* data set of the Furnariidae. Numbers right of the nodes indicate posterior clade probabilities

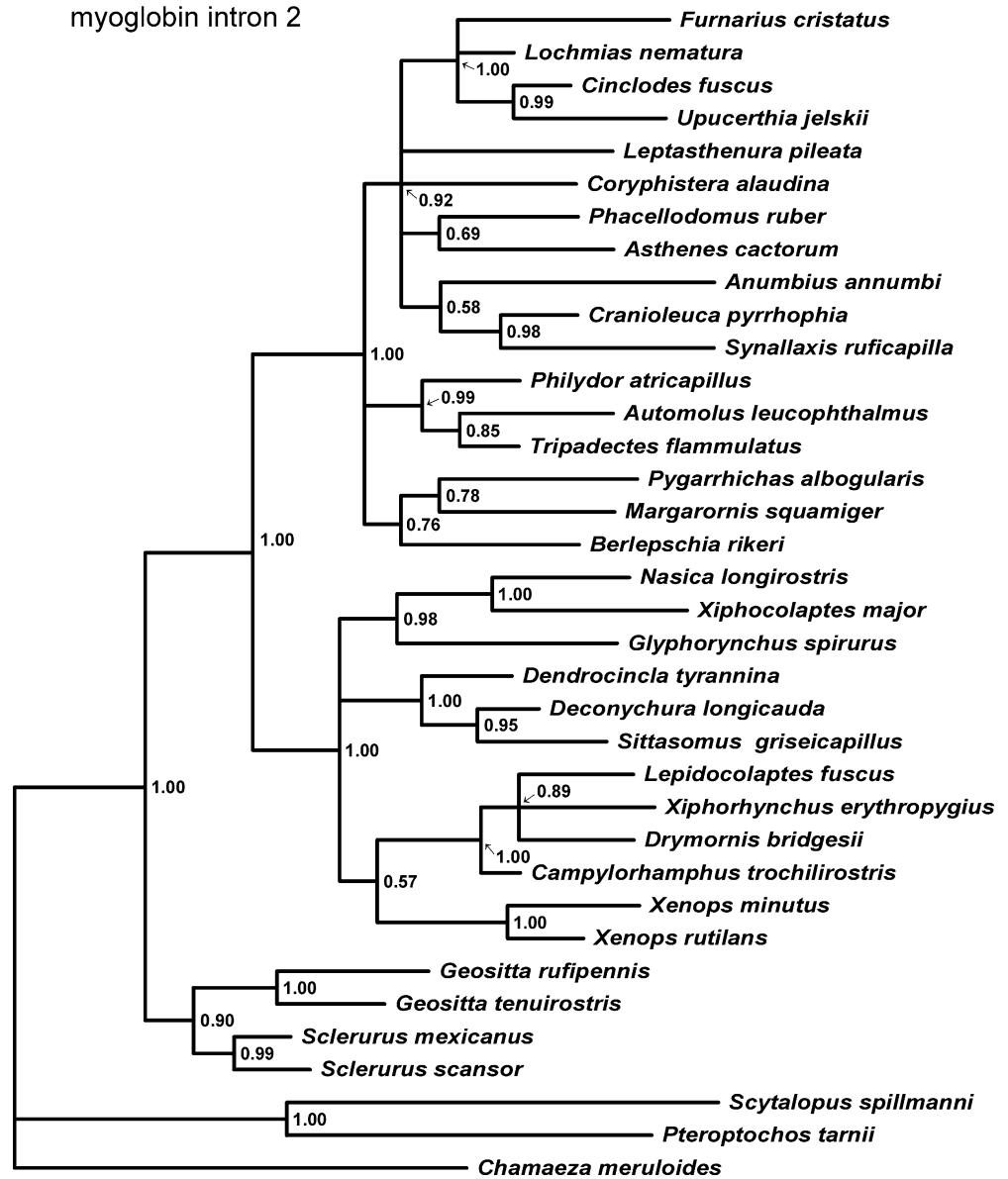


Ovenbirds have been described as having an unusual “pseudoschizorhinal” skull (Fig. 5d) in which the nasal openings extend posteriorly to the base of the bill, but without the slit-like separation of the nasal struts characterizing truly schizorhinal bird groups (Fürbringer 1888). An extension of the inter-orbital septum in front of the mesethmoids prevents prokinetic movements at the base of the upper mandible (Bock 1964; Zusi 1967), which instead has a more distally placed flexible zone allowing precision movements near the tip of the bill (rynchokinesis). In contrast, woodcreepers possess a typical holorhinal avian condition with relatively small and rounded nasal openings on a solid and unflexible bill, well in front of the fronto-nasal hinge (Fig. 5h). Feduccia (1973), assuming that woodcreepers evolved from ovenbirds, interpreted this as a reversal to the primitive passerine prokinetic condition where the upper mandible can only be raised or lowered by rotation

around the basal hinge. He also pointed out that the philydorine ovenbirds and the woodcreeper genera *Dendrocincla*, *Sittasomus*, *Deconychura* and *Glyphorhynchus* form a transition towards the advanced (“strong-billed”) woodcreepers.

We found that the skulls of *Sclerurus* and *Geositta* closely resemble those of the “transitory woodcreepers”. Especially the *Sclerurus* skull (Fig. 5a) is very similar to that of *Dendrocincla* and *Sittasomus*, except for a more slender base of the bill and a less complete inter-orbital septum. The nasal openings are pushed well back, but do not reach the level of the fronto-nasal hinge, and there is no indication of a protrusion of the inter-orbital wall. Mandibular fontanellae are well developed, as in ovenbirds. In woodcreepers, this is only indicated in *Sittasomus* and *Glyphorhynchus* (Fig. 5f). The examined *Geositta* skull is similar in most respects, but a small ossified structure (arrow in Fig. 5b) protrudes 1.3 mm in

Fig. 2 Majority rule consensus tree obtained from the Bayesian analysis of the myoglobin intron 2 data set. *Numbers* right of the nodes indicate posterior clade probabilities



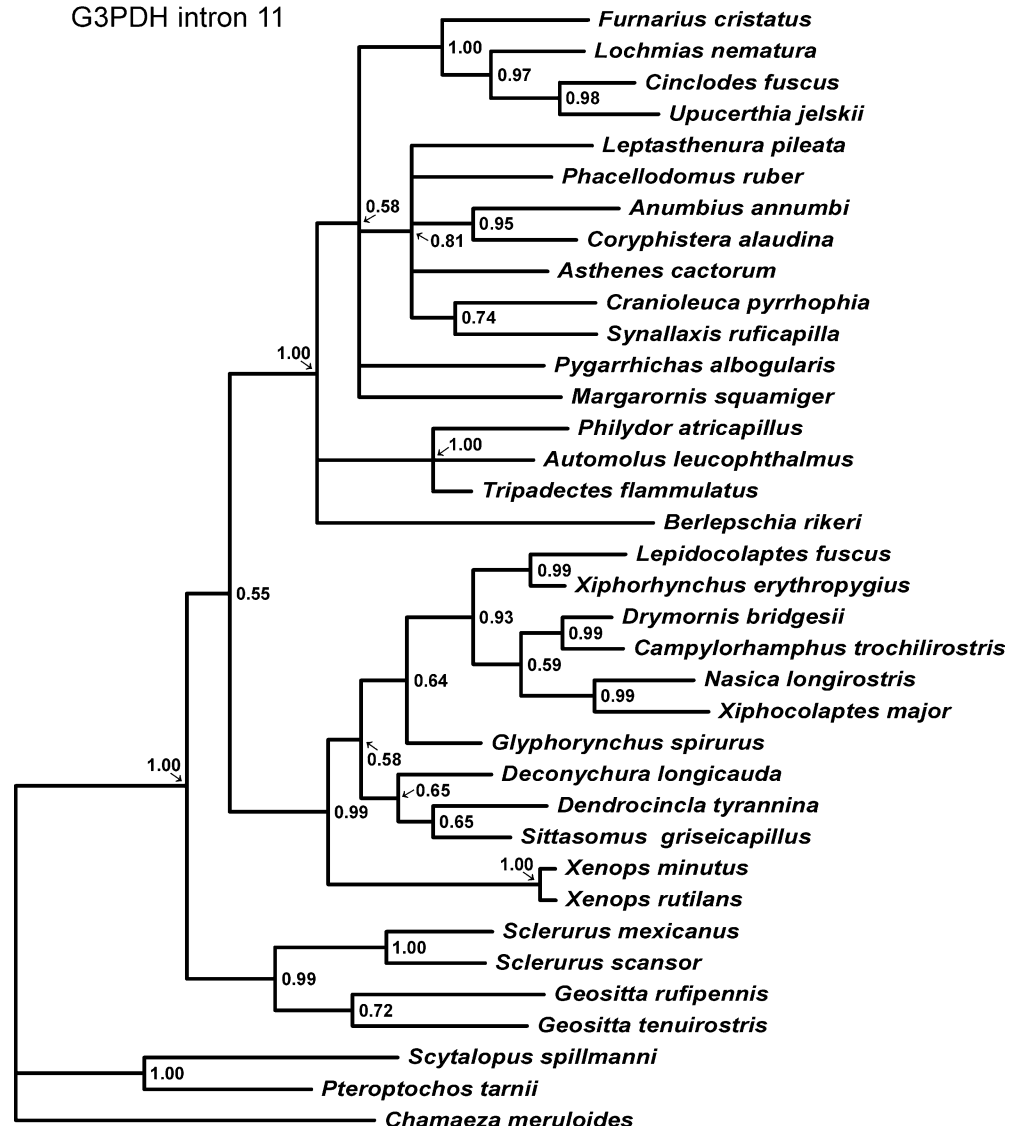
front of the inter-orbital septum, apparently fused with that septum but not with the caudo-dorsal part of the upper mandible, and therefore not preventing prokinetic movement. Another small median ossification is found further rostrad, below the dorsal bar of the upper mandible.

Most other skeletal characters in *Sclerurus* and *Geositta* fall within the range of variation among other ovenbirds, but *Sclerurus* has a low-keeled sternum of antpitta/gnateater type (Type 5 of Heimerdinger and Ames 1967, with a pair of large medial fenestra). Large medial fenestra are also reported in *Pygarrhichas* and one *Xenops* individual, but other ovenbirds and woodcreepers lack medial fenestra. The examined *Geositta* skeleton had a strong sternum with deep keel, but a small (3.5×2 mm) fenestrum in one side, as also reported by Heimerdinger and Ames (1967). These authors also reported the occasional occurrence of such variants in

some other ovenbirds and woodcreepers. All traditional woodcreepers have a unique shape of the sternum with a low keel (Feduccia 1973).

In *Xenops*, the anterior part of the skull is strongly ossified, with a “swollen” forehead and thick interorbital wall with spongy bone structure, as in the most advanced woodpeckers (Figures 8 and 9 in Bock 1999). This, combined with strong ossifications in the area of the internasal septum (one, marked x in Fig. 5c, extending 2.3 mm rostrad from the interorbital septum, and another, y in Fig. 5c, further rostrad) and lateral compression of the distal part of the bill seem to prevent any kinetic movement at the base of the upper mandible when these birds hammer in wood. *Glyphorhynchus* shows a similar and even more advanced condition, with strongly “swollen” forehead (Fig. 5e), vertical lateral extensions of the dorsal nasal bars (as in woodpeckers) and a large, keel-shaped ossification in the proximal part

Fig. 3 Majority rule consensus tree obtained from the Bayesian analysis of the G3PDH intron 11 data set. Numbers right of the nodes indicate posterior clade probability



of the inter-nasal septum (x in Fig. 5f) clearly demarcated towards the inter-orbital septum and broadly fused with the caudo-dorsal part of upper mandible, and with the ossified middle portion of the inter-nasal septum (y in Fig. 5f) ending at the dorsoventrally flattened distal part of the bill. Laterally, to either side of this septum, are two large, projecting struts. *Xenops* and *Glyphorhynchus* also have strongly modified pterygoids and quadrate bones for attachment of large palatal protractor muscles, as in woodpeckers (see Fig. 6 in Bock 1999).

The described median septa in the bill apparently correspond to what other authors have referred to as extensions of the interorbital septum, but these seem to be non-homologous structures, as the elements found in the internasal region have a different microstructure, appearing more like calcified cartilage (P. Christiansen, personal communication).

Xenops resembles woodcreepers in some modifications of the tibiotarsus (Feduccia 1973) and in having

basally fused outer toes and similarly curved claws, as do woodcreepers, in spite of the fact that *Xenops* climbs on thin branches and not on tree-trunks. However, the outer and middle toes of *Xenops* are as long as those of woodcreepers. *Xenops* has only 112 feathers in the dorsal tract (Clench 1995), which is outside the range of 128–164 feathers in ovenbirds (including *Sclerurus* and *Geositta*), but just inside the reduced number of 92–112 feathers found among woodcreepers. All of this is in good agreement with the basal placement of *Xenops* on the woodcreeper lineage in Fig. 4.

The unspecialized (short and soft) tail of *Xenops* is markedly different from that of woodcreepers but, as indicated in Fig. 4, tail-feather shapes vary tremendously in the ovenbird-woodcreeper radiation. Tail-tips with projecting, thick shafts are found in all traditional woodcreepers (most strongly developed, as decurved “claws”, in *Deconychura*, *Glyphorhynchus* and *Sittasomus* (Fig. 4), and in another version in *Xiphorhynchus* and *Lepidocolaptes*), and in the ovenbirds *Pygarrhichas* and

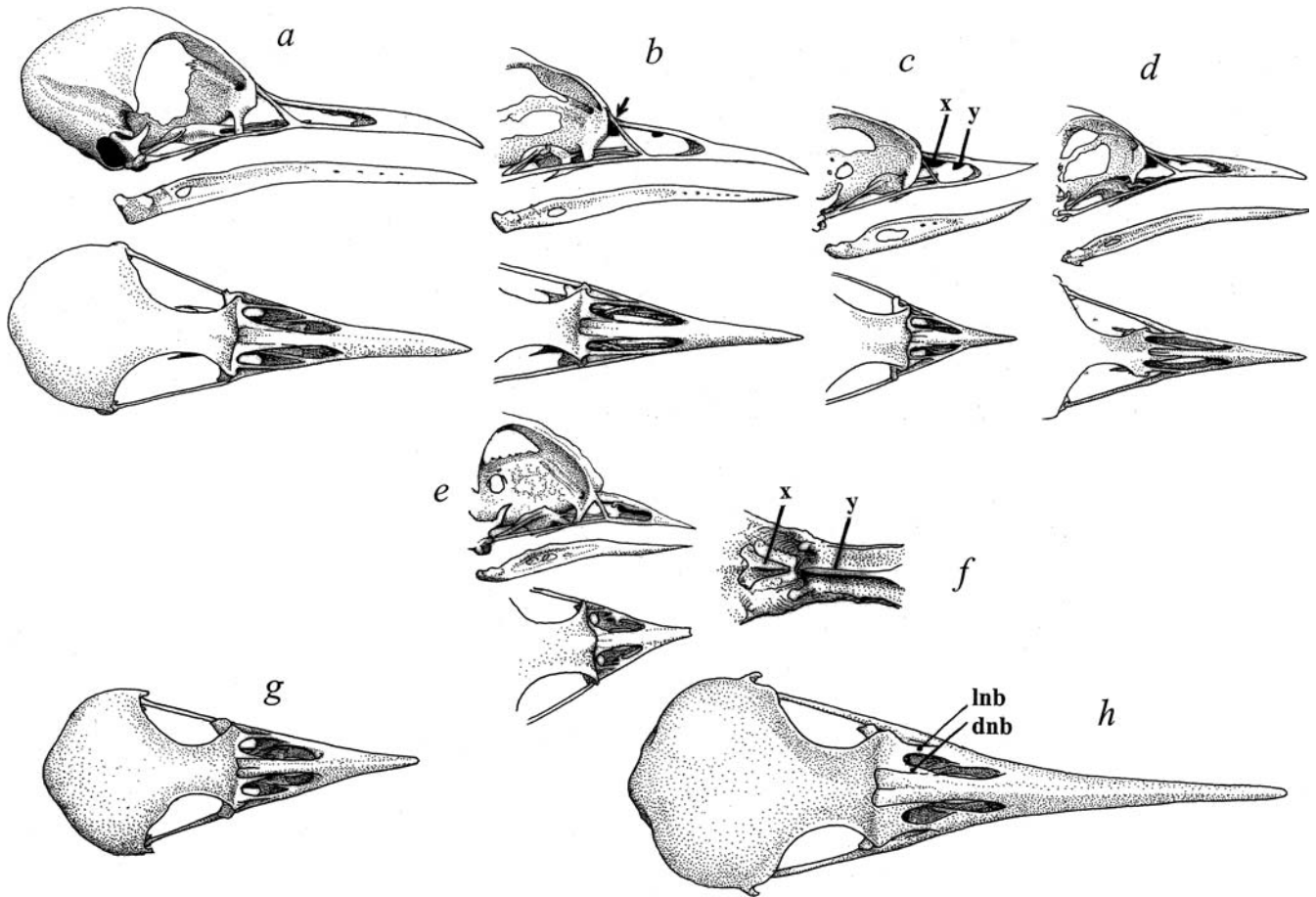


Fig. 4 Skulls (dorsal and lateral views) of *Sclerurus* (a), *Geositta* (b), *Xenops* (c), a “typical ovenbird, *Asthenes* (d), *Dendrocincla* (e), *Glyphorhynchus* (f, g showing details of the caudo-dorsal part of the upper mandible) and *Xiphorhynchus* (h) (d, e and h redrawn from Feduccia 1973); *l* lateral, and *d* dorsal nasal bars; *x* and *y* mark two unique ossifications in the region of the inter-nasal septum

Aphrastura (the latter not included in this study). Many ovenbirds, including *Sclerurus*, have sharply pointed tail-tips, some with thickened and slightly projecting shafts, or at least it is often observed that the slightly thickened shafts are projecting when the feathers are worn.

Discussion

Phylogeny

It is evident from this phylogenetic analysis that the traditional classification of the Furnariidae does not reflect the phylogeny of the group, and that many aspects of the early evolution need to be re-interpreted in the light of the molecular phylogeny. While a new classification should await the completion of a phylogenetic analysis based on a broader taxon sampling (in progress), we will here discuss the deep branching and

what we can infer from this about the adaptive shifts preceding the remarkable diversification of ovenbirds.

The combined phylogeny is well resolved overall (see support values in Fig. 4). The branching pattern is fully congruent with those described by Irestedt et al. (2002) and Chesser (2004) based on a less comprehensive taxon sampling, and by Irestedt et al. (2004a) based on a denser taxon sampling for the woodcreeper group. With respect to the ovenbird group, the tribes Furnariini and Synallaxini can be recognized as sister groups, but having a different composition from Vaurie’s (1980) classification: *Lochmias* (previously after *Margarornis*, in the beginning of the philydorine sequence) is included in the Furnariini and *Pseudoseisura* (previously near the beginning of the philydorine sequence) is included in the Synallaxini (Irestedt et al. 2002). The Philydirini, on the other hand, may be a paraphyletic assemblage, with *Margarornis* (probably with *Premnoplex*) and *Pygarrhicas* separated from the core group of typical foliage-gleaners, and the aberrant *Berlepschia* apparently representing a long and deep branch by itself.

The most striking discoveries, compared with the traditional grouping (Sibley and Ahlquist 1990 for historical review), are the well-supported basal clade consisting of *Sclerurus* (traditionally in the Philydorinae) and *Geositta* (traditionally in the Furnarinae), a finding confirmed by Chesser (2004) with different genetic

markers, and the placement of *Xenops* (traditionally in the Philydorinae) as a basal woodcreeper. Here, the phylogenetic incongruence between the nuclear introns and the mitochondrial cytochrome *b* gene requires a comment. It has been suggested that the mitochondrial gene trees are less likely to be affected by lineage sorting (as the mitochondrial genome is haploid and transmitted only matrilineally), and thus may be more likely to reflect species phylogeny than a single nuclear gene (Moore 1995; Moore and DeFilippis 1997). On the other hand, organelle genomes have been suggested to be more susceptible to “horizontal transfer” between taxa via hybridization (although much less commonly in animals than in plants). There are also examples where species trees calculated from nuclear data yield more reasonable estimates of the true evolutionary relationships (when judged from the available biogeographical and morphological information) than the trees obtained from mitochondrial data (Degnan 1993; Alström & Ödeen 2002). The phylogenetic congruence between the two independent nuclear introns supports the view that *Xenops* is more likely a basal woodcreeper than a basal ovenbird. Consequently, we suggest that the position of *Xenops* in the mitochondrial gene tree is incorrect and may possibly be due to stochastic lineage sorting, earlier hybridizations events, and/or inadequacies in substitution model selected for the analysis of this data set.

Ovenbirds and woodcreepers were traditionally placed together because of overall similarity, especially in plumage colours, and a shared unique syringial structure with two pairs of intrinsic (tracheo-bronchial) muscles (Müller 1878; Ames 1971). They differ as the woodcreepers (and *Xenops*) have a unique pterylographic pattern (Clench 1995) and “primitive” horns on the *Processi Vocales*. This latter character state was also found in *Geositta* (Ames 1971), in agreement with its basal position in our phylogenetic analysis. Ames (1971), who examined two *Sclerurus* specimens, did not mention deviating syringial characters. However, the distinctive quality of its vocalizations may suggest a different syrinx structure from other ovenbirds.

Evolution of foraging habits and habitat use

Contrasting the consensus phylogeny with information about morphology and ecology (see Fig. 4 for three kinds of information) may give us some idea about the ecological adaptations of the immediate ovenbird-woodcreeper ancestor. Under the first doublet rule (Maddison et al. 1984), we can assume that the ancestral form was a ground-feeding inhabitant of humid tropical forest, like *Sclerurus*, ant-thrushes and tapaculos. *Sclerurus* and *Geositta* are obligate cavity-nesters, placing their woven cup-nests in burrows in the ground (Zyskowski and Prum 1999). This is also the case in most tapaculos, and may thus represent the original way of nesting in the ovenbird-woodcreeper lineage (Chesser 2004). This means that the adaptation of *Geositta* to open landscapes is a secondary

acquisition that evolved independently of the specialization for feeding on the ground and of the colonization of open landscapes that took place in the furnarines (especially *Cinclodes*, *Chilia* and *Upucerthia*). Indeed, the degree of convergence in proportions and plumage colours between *Geositta* and furnarines is so strong that Vaurie (1980) suggested the transfer of *Cinclodes excelsior* to *Geositta*! We suggest that the environmental shift in *Geositta* was a response to the aridification—and forest loss—in large portions of southern South America in the Tertiary (e.g., Raven and Axelrod 1975), as it adapted to the conditions of barren plains ranging from patches of recently burnt ground in the Brazilian “Cerrado” to shrub-steppes, short-grass plains and deserts in Patagonia and on the high Andean plateaus. Long and broad wings and short, notched tails with distinctive rufous/black color patterns may represent adaptations to enhance dispersal in these ecologically unstable environments, and for visual advertisement by flight display. This also explains the more deeply-keeled and strongly ossified sternum in *Geositta* compared with *Sclerurus*. Looking beyond what can be attributed to different habitats, *Geositta* and *Sclerurus* are quite similar (Fig. 5a, b). *Geositta* does not need particular feeding specializations to glean arthropods and seeds from the soil surface.

Judging from the habitat codes in Fig. 4, the most parsimonious interpretation of the next adaptive steps would be that ancestral ground-living forms started to feed in the trees, and that it was only later that some groups, mainly of furnarines and some synallaxines, invaded non-forest habitats. *Sclerurus* has needle-sharp, projecting tail-spines and apparently uses its tail for support when perching on tree-trunks, and also when probing and flicking away leaf litter on the forest floor (Remsen 2003, pp.198). Willis (1974), noting a close similarity between *Sclerurus* and *Dendrocincla* woodcreepers, proposed that tree-climbing woodcreepers evolved from terrestrial leaf-tossers that broadened their foraging niche upwards to exploit food on the bare trunks in forests (see also Sclater 1890).

Morphological evolution

Feduccia (1973) pointed out that the primitive syringial condition of *Geositta* was in conflict with its traditional systematic placement, but he abstained from changing its placement in the phylogeny. His main focus was on the apparent link between philydorine ovenbirds and “transitory woodcreepers”, according to which the development of a holorhinous and prokinetic skull in the woodcreeper lineage would represent a reversal from the unique, rhynchokinetic ovenbird condition to a plesiomorphic passerine state. Our discovery of a prokinetic skull in *Sclerurus* and *Geositta* (Fig. 5) would seem to resolve this conflict, but then Fig. 4 reveals an even more serious character conflict as a unique functional system in *Xenops* and *Glyphorhynchus*, for chiseling in wood, must have been lost in the “higher” woodcreepers.

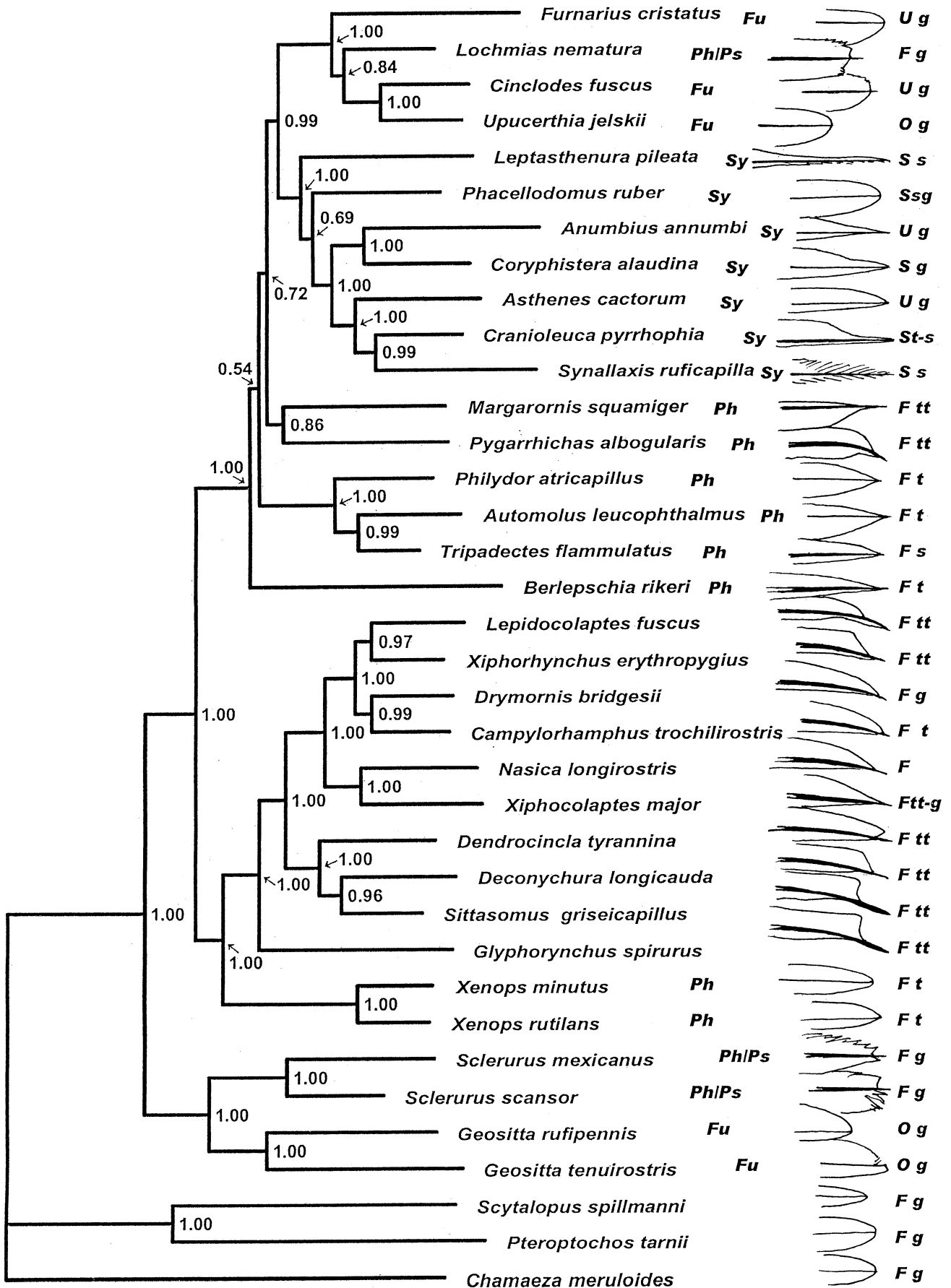




Fig. 5 Majority rule consensus tree obtained from the Bayesian analysis of the combined data set (the cytochrome *b*, myoglobin intron 2, and G3PDH intron 11 data sets). Numbers right of the nodes indicate posterior clade probabilities. Following the names of ovenbird species are their traditional allocation to tribes: *F* Furnariini, *S* Synallaxini, *P* Philydorini, *Ps* philydorines previously placed in a separate group Sclerurinae. To the right of the species names is information on morphology (simple drawing of tail-feather tips, illustrating the development of projecting spines) and habitat. Habitat codes: *F* forest birds, *S* those inhabiting edges and bushy terrain, *U* ubiquitous species which may use open terrain, and *O* obligate open-land species; *g* feeding on the ground, *t* feeding in trees, *tt* feeding on tree trunks, and *s* feeding in dense shrubbery and vine-tangles

Development of special structures (vertical septa in the bill, bulging forehead and spongy tissue in the skull, modifications of the palatines and quadrate bones, with associated muscular development) represent a complex functional system stabilizing the base of the bill and absorbing physical shocks, strikingly similar to that of woodpeckers (Bock 1999). *Xenops*, foraging on the thinner branches of trees, uses its re-curved and laterally flattened bill to split decayed twigs to extract insects and sometimes hammers vigorously and carves holes into decaying wood. *Glyphorynchus*, with a dorsoventrally flattened bill-tip, feeds on rough tree-trunks, flaking bark, hammering wood and gleaning (Marantz et al. 2003). Thus the two use quite similar foraging methods, but work in different parts of the trees. Apparently, the rest of the woodcreepers lineage changed feeding method, to prying and probing in tree-trunk crevices, and often sallying after flushed prey, some species even following army-ants to snatch escaping insects. Such fly-catching behaviour typically requires a broad base of the bill (see Fig. 5g, h), and effective cranial kinesis. Some species tear apart decaying wood and bark, but overall they feed very differently from the many sympatric woodpeckers.

We suspect that the shift in feeding adaptations in the woodcreeper lineage was a response to the strong diversification of medium-sized and fairly large woodpeckers in the Neotropical forests. Unfortunately, the evolutionary history of woodpeckers is still poorly understood, but the relative homogeneity of the Neotropical arthropod-eating groups (Colaptini and Campehilini) suggests that these represent fairly recent radiations. Thus, due to competition, a well-developed functional system, as described here for *Xenops* and *Glyphorynchus*, may have been replaced by another system with a functional fronto-nasal hinge. Here, the stronger ossification of the bill meant smaller nasal openings displaced away from the hinge (Fig. 5h). In other words, a holorhinous condition, similar to that of most other bird groups, was restored.

In this context it is worth noting that *Glyphorynchus* is smaller (10.5–21 g) than any woodpecker in its range, except for the piculets, *Picumnus*, which work on the thinner branches, like *Xenops*. Thus, *Glyphorynchus* may have managed to maintain its woodpecker-like foraging

behavior because it was smaller than the tree-trunk-feeding woodpeckers, which exploit other food resources. *Xenops tenuirostris*, *minutus* and *rutilans* may compete with piculets, and it is interesting to see that these forms share a peculiar pattern of dark and light longitudinal stripes in the tail, and also have similar vocalizations (Remsen 2003), which might suggest behavioral interaction between them.

According to this interpretation, the ossified internasal septum immobilizing the base of the upper mandible (as seen in *Xenops*, *Glyphorynchus* and ovenbirds, other than *Sclerurus* and *Geositta*), may initially have been an adaptation for rather forceful pecking. Among the ovenbirds, only *Pygarrhicas* pecks in wood, but all the others have the bony internasal septum as part of their rynchokinetic bill, suggesting that an initial adaptation for pecking was modified as the middle portion of the bill became more flexible and better suited for probing in internodes of bamboo, splitting vines, and probing and prying among masses of dead leaves and debris suspended among vines and branches, and in bromeliads (in philydorines; see Kratter and Parker 1997; Rosenberg 1997). Thus, the reason for the remarkable diversification in the ovenbird group may first of all be related to a modification of the cranial kinesis that allowed these birds to exploit hidden prey in the very complex tropical rainforest. Later, they also diversified in the Andean cloud-forest, exploiting food resources that are hidden in the epiphytic masses of mosses and lichens (in the *Margarornis* group and most synallaxines), and finally some subgroups ventured to feed on the ground.

Judging from Fig. 4, reinforced tail-spines as an adaptation for support were probably present already prior to the dichotomy between woodcreepers and ovenbirds. They were maintained, and developed to perfection, in woodcreepers and, perhaps independently, in *Pygarrhicas* and *Aphrastura*. *Berlepschia* uses the tail as a brace, often hanging upside-down when feeding from curled dead palm-fronds. Its tail-spines are not decurved, but otherwise well developed. The spines were lost in many other ovenbird lineages as their tails became modified and often strongly elongated to serve as a balance when the birds move acrobatically through dense vegetation. In some terrestrial groups, they became modified instead for visual signaling, as tails with distinctive rufous-and-black colors are often cocked up. In view of its lark-like behavior, it is unsurprising that *Geositta* lacks tail-spines, but it is more noteworthy that the scansorial *Xenops* does so. Tiny as it is (9–15 g), when maneuvering across the thinner branches *Xenops* may not need the tail for support, and apparently the tail was therefore “released” to serve other functions, precisely as has happened in the tiniest of woodpeckers, including *Picumnus*.

Overall, then, the early evolution of ovenbirds and woodcreepers can be interpreted in view of a few major ecological shifts, starting as tropical forest birds went from the ground up into the trees, primarily feeding by

pecking on tree-trunks, internodes, or masses of dead leaves captured above ground. The clade is clearly in need of taxonomic revision. Although a thorough revision has to await a study based on denser taxon sampling, all three genes used in this study, and the intron used by Chesser (2004), support the transfer *Geositta* to the Sclerurinae ovenbirds (sensu Irestedt et al. 2002).

Zusammenfassung

Molekulare Daten offenbaren einige bedeutende Anpassungsveränderungen in der frühen Evolution der artenreichsten Vogelfamilie, der Furnariidae

Ein robuste Phylogenie für die Familie Furnariidae (*sensu lato*) wurde mit Hilfe von DNA-Sequenzen zweier nuklearer Introns und eines mitochondrialen Gens (cyt b) erstellt. Das weithin akzeptierte Schwestergruppenverhältnis von Furnariinae und Dendrocolaptinae wurde nicht bestätigt. Vielmehr zeigte sich eine basale Gruppierung von *Sclerurus* und *Geositta*, während *Xenops*, der bisher als ein anormaler Töpfelvogel betrachtet wurde, eine basale Position in der Baumsteiger-Gruppe einnimmt. Die morphologische Variation wird angesichts dieser korrigierten phylogenetischen Hypothese neu interpretiert. Vermutlich begann die bemerkenswerte adaptive Radiation in dieser Familie mit primitiven *Sclerurus*-ähnlichen Formen, die die Schwanzfedern als Stütze während der Nahrungssuche am Boden nutzten und dann begannen, ihr Nahrungssuchsubstrat auf Baumstämme auszudehnen. Die zwei basalen Baumsteigergattungen *Xenops* und *Glyphorhynchus* zeigen starke Schädelpezialisierungen für das Hämmern im Holz und stellen so eine bemerkenswerte Konvergenz zu den Spechten Picidae dar, wobei *Xenops* einem Zwergspecht (*Picumnus*) und *Glyphorhynchus* einem kleinen Specht ähnelt. Jedoch ging diese Spezialisierung bei anderen Baumsteigern verloren, die einen normaleren passerinen Schädel aufweisen, angepaßt an eine Nahrungssuche in Rindenspalten und das Fangen fliehender Insekten. Die Furnariinae entwickelten einen flexibleren (rhynchokinetischen) Schnabel, angepasst zum Herauspickern versteckter Beute aus Ansammlungen toter, in der Vegetation hängender Blätter oder in Blattinternodien und Epiphyten. Morphologische Anpassungen zum Leben in offenem Gelände sind bei Furnariiden sekundär entstanden.

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