

PHYLOGENETIC ANALYSIS OF THE NEST ARCHITECTURE OF NEOTROPICAL OVENBIRDS (FURNARIIDAE)

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ABSTRACT.—We reviewed the tremendous architectural diversity of ovenbird (Furnariidae) nests based on literature, museum collections, and new field observations. With few exceptions, furnariids exhibited low intraspecific variation for the nest characters hypothesized, with the majority of variation being hierarchically distributed among taxa. We hypothesized nest homologies for 168 species in 41 genera (ca. 70% of all species and genera) and coded them as 24 derived characters. Forty-eight most-parsimonious trees (41 steps, CI = 0.98, RC = 0.97) resulted from a parsimony analysis of the equally weighted characters using PAUP, with the Dendrocolaptidae and Formicarioidea as successive outgroups. The strict-consensus topology based on these trees contained 15 clades representing both traditional taxa and novel phylogenetic groupings. Comparisons with the outgroups demonstrate that cavity nesting is plesiomorphic to the furnariids. In the two lineages where the primitive cavity nest has been lost, novel nest structures have evolved to enclose the nest contents: the clay oven of *Furnarius* and the domed vegetative nest of the synallaxine clade. Although our phylogenetic hypothesis should be considered as a heuristic prediction to be tested subsequently by additional character evidence, this first cladistic analysis of the furnariids demonstrates the general utility of nest characters in reconstruction of avian relationships, and it provides a test of monophyly for several furnariid taxa. Received 29 July 1998, accepted 12 March 1999.

RECENT APPLICATIONS OF PHYLOGENETIC SYSTEMATICS to ethology have demonstrated that behavioral traits can be as historically informative as morphological and molecular characters (Prum 1990, de Queiroz and Wimberger 1993, Paterson et al. 1995, Irwin 1996, Kennedy et al. 1996). Nests are a detailed part of the extended phenotype of birds, and they provide a durable physical record of the behavior that resulted in their construction (Hansell 1984, Collias 1986). A wealth of quantifiable detail in nest structure, placement, and ontogeny makes nests amenable to comparative analysis. Nest architecture can provide evidence of phylogenetic relationships (Kiff 1977, Lanyon 1986, Prum 1993, Whitney et al. 1996). Furthermore, hypotheses of phylogeny can be used to discover historical patterns in the evolution of nest features and to test hypotheses about adaptation in nest design (Dekker and Brom 1992, Winkler and Sheldon 1993, Lee et al. 1996, Eberhard 1998, Sturmbauer et al. 1998). Here, we use nest architecture to generate a hypothesis of phylogenetic relationships for the Neotropical ovenbirds (Furnariidae), which exhibit

a broad diversity and complexity of nest structures.

The suboscine family Furnariidae, with 240 currently recognized biological species, is among the most morphologically, behaviorally, and ecologically diverse families of passerines (Ridgely and Tudor 1994, Skutch 1996). The furnariid radiation includes phenotypes convergent on numerous families of oscines, such as larks, jays, tits, creepers, nuthatches, wrens, thrushes, thrashers, dippers, and warblers (Leisler 1977). Representatives of the Furnariidae can be found in all Neotropical habitats, from coastal surf zone and sand dunes through dry and humid lowland and montane forests to the treeless puna of the Andes.

The diversity of nest placement and structure in the Furnariidae approaches that of the entire order Passeriformes (Narosky et al. 1983, Sick 1993, Collias 1997). Nests can be placed in excavated or adopted cavities under or above the ground. Non-cavity nests can be supported from below, attached by the side to a vertical support, or suspended from a branch or rock. Nest structural diversity ranges from shallow pads of loosely piled material to domed nests with constructed roofs of interlaced sticks, in-

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terwoven soft vegetation, or clay. Additional elaborations of domed nests include entrance tubes, tunnels with constrictions, awnings above the entrance, nonbreeding chambers, and adornment with conspicuous objects.

Over the last century, architectural features of furnariid nests have been recognized to be evolutionarily conservative, constituting potentially informative systematic characters (Ihering 1914, 1915; Vaurie 1971, 1980). However, previous authors have used nest architecture in an eclectic, noncladistic manner; no comprehensive phylogenetic analysis of the furnariids has been conducted, preventing rigorous study of the evolution of nest-construction behavior. Detailed hypotheses of homology among nest types have proven difficult to develop because of limited information about many species, paucity of behavioral information on the steps of nest building (i.e. ontogeny), and the historical lack of a phylogenetic methodology.

Our objective was to examine patterns of variation in nest structure and construction behavior within the Furnariidae and to perform a cladistic analysis of the family based on nest characters. We performed this analysis to yield hypotheses of phylogenetic relationships of major clades within the family and to evaluate the usefulness of nest characters for reconstructing avian phylogenies. We also propose and discuss new hypotheses regarding the evolution of furnariid nest-construction behavior.

Review of furnariid systematics.—The Furnariidae is a family of tracheophone suboscine passerines closely related to the woodcreepers (Dendrocolaptidae). The two families share a unique intrinsic syringeal muscle, *M. vocalis dorsalis* (Ames 1971). Monophyly of the Dendrocolaptidae has been supported by morphological synapomorphies (Raikow 1994, Clench 1995), but no morphological synapomorphy satisfactorily demonstrates the monophyly of the furnariids. Morphological characters traditionally used to diagnose the family (e.g. lack of horns on the processi vocales [Ames 1971] and pseudoschizorhinal nares [Feduccia 1973]) are primitive among tracheophones, and none is shared by all furnariid species (Feduccia 1973). We assumed that the Furnariidae and the Dendrocolaptidae are each monophyletic and are sister taxa, based on the Sibley and Ahlquist (1990) DNA-DNA hybridization hypothesis. The hypothesized sister group to the Fur-

nariidae + Dendrocolaptidae is a clade composed of the Formicariidae, Conopophagidae, and Rhinocryptidae (i.e. Formicarioidea sensu Sibley and Ahlquist 1990).

The generic limits within Furnariidae recognized in this study follow those of Peters (1951), with a few modifications following Ridgely and Tudor (1994) and Kratter and Parker (1997). Since the publication of Peters' (1951) volume, a surprising 14 new species and 1 new genus of furnariids have been described, 14 subspecies have been elevated to the rank of species, and 5 species have been synonymized (Ridgely and Tudor 1994, Pacheco and Gonzaga 1995, Silva 1995, Pacheco et al. 1996, Maijer and Fjeldså 1997, Zimmer 1997). As currently recognized, the Furnariidae consists of 240 species in 59 genera.

METHODS

Data.—Variation in nest architecture of furnariids and outgroup taxa was reviewed based on the scientific literature and on data associated with nest and egg specimens in major collections. The first author examined nest specimens in major New World collections (see Appendix 1) and collected new data describing 204 nests from 53 species during his field studies in Peru, Brazil, Paraguay, and Guyana (1994 to 1998). Results of the field work, including new ontogenetic information and nest descriptions for seven species with previously undescribed nests, will be published separately.

Nest information was gathered for 184 furnariid species from 50 genera; species for which nest descriptions were demonstrably erroneous or lacking critical details were subsequently excluded. Data for the remaining 168 species, representing 41 genera (ca. 70% of all species and genera), were used in the analysis (Appendix 2). A complete list of sources of nest descriptions for each species is presented in Appendix 1. Sample sizes varied considerably, with approximately 5% of the species represented by more than 50 nests each, the majority of species based on more than 10 nests, and about 20% of the species known from a single nest description.

We also assembled nest information for outgroup taxa: 37 species representing all 13 genera of Dendrocolaptidae; 19 species representing 8 of 12 genera of Rhinocryptidae; 19 species representing all 7 genera of Formicariidae; and 5 of the 8 species of Conopophagidae.

Phylogenetic analysis.—The number of ingroup taxa was reduced to 49 operational taxonomic units (OTU) by combining congeneric species having identical character states. Appendix 2 includes definitions of species groups composed of behaviorally

similar congeners used as OTUs. The outgroup species were condensed into two OTUs representing two successive outgroups, Dendrocolaptidae and Formicarioidea.

We based hypotheses of behavioral homologies on special detailed similarities in nest structure and ontogeny of nest construction. Variations in nest architecture were coded as 24 characters, of which 22 were binary and two trinary. Apparent autapomorphies were included in the data set because these characters are synapomorphies of polytypic terminal taxa (characters 4, 10, 20, 24). Genuine autapomorphies were also included because they may be shared by unidentified cryptic species within current species or shared with behaviorally unknown taxa and ultimately be phylogenetically informative (characters 3, 5, 8, 12, 19, 22). Character polarities were inferred by outgroup comparisons. In instances where the second outgroup was polymorphic, we used presumed phylogenetic relationships within the Formicarioidea to infer the primitive character state for the outgroups. Taxa exhibiting both ancestral and derived states of a given character were coded as polymorphic (0 and 1) for that character. All characters were weighted equally.

The most-parsimonious phylogenetic resolutions of the nest data were identified using PAUP 3.1.1 (Swofford 1993). We used a constraint tree assuming monophyly of the ingroup and the outgroup structure described above. We performed 100 replicate heuristic searches with random addition of taxa to minimize input order bias and ensure unbiased sampling of tree space. The tree bisection-reconnection algorithm was employed, and zero-length branches were collapsed to yield polytomies. We used a strict-consensus tree to summarize the set of maximally parsimonious topologies identified by PAUP. Character evolution was analyzed by examining parsimonious character optimizations on fundamental trees using MacClade 3.03 (Maddison and Maddison 1992).

CHARACTER ANALYSIS

Each nest character below includes a brief description of the derived state and its taxonomic distribution. Aspects of nest architecture analyzed include nest form and structure, materials, nest location and attachment to substrate, and details of construction behavior. The first nine characters describe nests placed in cavities (Fig. 1), whereas the remaining 15 characters focus on non-cavity nests (Fig. 2). The distribution of character states in both ingroup and outgroup taxa is given in Appendix 2. Each OTU is based upon at least one behaviorally well-known species. Species with partial nest

data that are consistent with those of their better known congeners are presumed to be members of the same OTU (see Appendix 2).

1. *Nest in cavity*.—The nest is placed in an adopted or self-excavated cavity, such as a subterranean burrow, rock crevice, termite mound, tree cavity, bamboo internode, cavity in a man-made structure, or enclosed construction of other birds or mammals. Nests placed in cavities are present in *Aphrastura*, *Anabazenops*, *Automolus*, *Chilia*, *Cinclodes*, *Furnarius*, *Geositta*, *Hylocryptus*, *Hyloctistes*, *Lochmias*, *Ochetorhynchus*, *Philydor*, *Pseudocolaptes*, *Pygarrhichas*, *Sclerurus*, *Thripadectes*, *Upucerthia*, and *Xenops*. In addition, we coded as polymorphic (0 and 1) the *Asthenes pyrrholeuca* group, *Leptasthenura*, and *Premnoplex brunnescens*, because these species place some nests in cavities and others in the open. Among the outgroup taxa, cavity nesting is present in all known dendrocolaptids and in several formicarioids.

2. *Form of cavity nest*.—We hypothesize two ordered derived states of nests built in cavities. (2.1) Non-pliable plant material is either piled or loosely interlaced to form a loose, usually unlined platform (Fig. 1A). Platforms are present in the *Automolus leucophthalmus* group, *Chilia*, *Hyloctistes*, *Pseudocolaptes*, *Pygarrhichas*, *Sclerurus*, and *Thripadectes melanorhynchus*. (2.2) Pliable plant material is woven and compacted into a shallow cup, often lined with nonvegetative material such as wool or feathers (Figs. 1B–D). Cups are present in *Anabazenops*, *Automolus rubiginosus*, *Cinclodes*, *Furnarius*, *Geositta*, *Hylocryptus*, *Ochetorhynchus certhioides*, *Philydor*, *Thripadectes rufobrunneus* group, *Upucerthia*, and *Xenops*. Cup-like nests of *Aphrastura*, *Leptasthenura*, *Spartonoica*, and some *Asthenes* are hypothesized to be nonhomologous because they represent reduced domed constructions (see character 11).

Although both platforms and cups are found in the two successive outgroups, the cup has a narrower taxonomic distribution and therefore is hypothesized to be independently derived. For example, when cup and platform are superimposed on the dendrocolaptid phylogeny of Raikow (1994), platforms are shared by most lineages including the most basal, whereas cups appear to have been derived independently in two lineages. Platforms of bark flakes or dry leaves shared by most dendrocolaptids, but not found in the ingroup, are assumed to

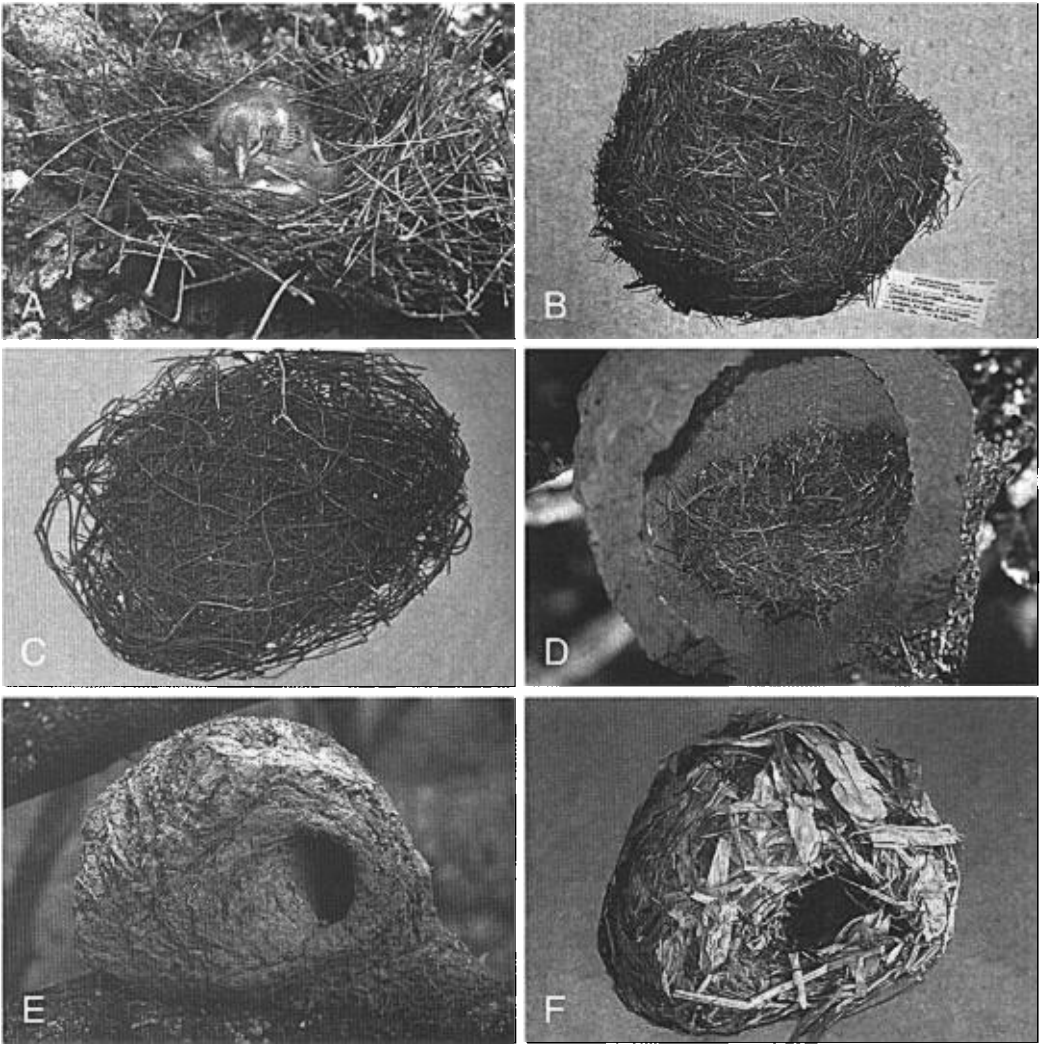


FIG. 1. Structure of furnariid nests placed in cavities. (A) *Hyloctistes subulatus*: platform of compound-leaf rachises (photo by N. Wheelwright). (B) *Cinclodes excelsior*: cup of dry grass (WFVZ 162881). (C) *Thripadectes virgaticeps*: cup of rootlets (WFVZ 159222). (D) *Furnarius rufus*: cross-section of clay oven revealing grass cup (KU 89623). (E) *Furnarius cristatus*: clay oven (KU 89619). (F) *Lochmias nematura*: domed nest of bamboo leaves (KU 89612). Nests A, B, C, and F were extracted from burrows.

be ancestral to the furnariid platforms coded below as characters 3 to 6.

3. *Platform of wood chips*.—Eggs rest directly on wood chips from cavity excavation, occasionally supplemented with sparse plant material or down. We hypothesize that this extremely reduced cavity lining is derived from a dendrocolaptid-like platform. Platforms of wood chips generated passively during cavity excavation are characteristic of *Pygarrhichas*.

4. *Platform of fern scales*.—A thick layer of

membraneous tree-fern scales (ramenta) is piled inside a cavity and is sometimes used to cover the eggs on departure of incubating birds. Ramenta are used exclusively by *Pseudocolaptes*.

5. *Platform of sticks and feathers*.—A fairly massive platform is constructed of dry sticks and feathers of larger birds (usually rectrices and remiges that have a distinctly stiff rachis). This character is present in *Chilia*.

6. *Platform of leaf rachises*.—A platform is con-

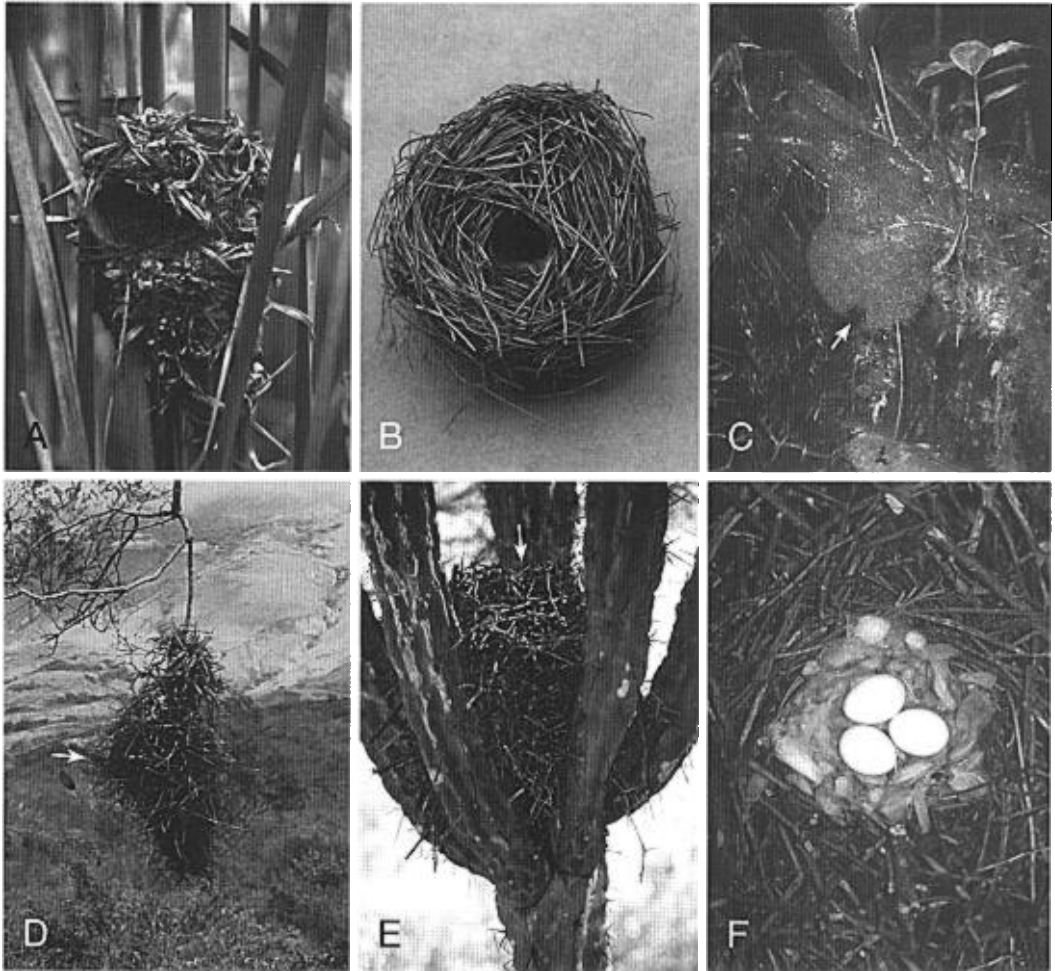


FIG. 2. Structure of non-cavity nests of furnariids. (A) *Phleocryptes melanops*: domed nest with awning above the entrance, attached to vertical stems. (B) *Leptasthenura andicola*: domed nest of dry grass (USNM 30597). (C) *Premnoplex brunnescens*: domed nest of moss, suspended from a log (photo by M. Marín). (D) *Phacelodomus dorsalis*: secondarily pensile nest of sticks (photo by J. O'Neill). (E) *Asthenes baeri*: nest of sticks saddled on a cactus. (F) *Schoeniophylax phryganophila*: restricted lining of conspicuous material, inside a domed stick nest (KU 89629). Arrows indicate nest entrances where necessary.

structured entirely of compound-leaf rachises, usually of a single plant species (Fig. 1A). This character is present in the *Automolus leucophthalmus* group, *Hylactistes*, *Sclerurus*, and *Thripadectes melanorhynchus*.

7. *Cup composition*.—We hypothesize two unordered derived states for cup composition. (7.1) A cup constructed of ribbon-like vegetative material, such as grass leaves and strips of inner bark (Figs. 1B,D), is present in *Anabazenops*, *Cinclodes*, *Furnarius*, *Geositta*, *Ochetorhynchus certhioides*, and *Upucerthia*. (7.2) A cup

built of wiry plant material such as rootlets, root fibers, or fungal rhizomorphs of *Marasmius* (Fig. 1C) is present in *Automolus rubiginosus*, *Hylocryptus*, *Philydor*, *Thripadectes rufobrunneus* group, and *Xenops*.

8. *Profuse lining of snake exuviae*.—A large quantity of snake exuvia or human-made material of similar appearance (e.g. cellophane) lines a vegetative cup. This character is present in *Ochetorhynchus certhioides*.

9. *Tree-cavity excavation*.—The birds themselves excavate a cavity in soft wood. *Pygarrhi-*

chas and *Xenops* are the only furnariids known to excavate such cavities, but even they occasionally adopt existing holes.

10. *Clay dome*.—An igloo-shaped structure, often described as an "oven," is constructed of clay mixed with plant fibers, hair, or dung (Fig. 1E). The wall at one side of the entrance is folded inward to divide the globe into two helically arranged chambers: an inner incubation chamber, and an outer antechamber; only the inner chamber is lined (Fig. 1D). Clay-oven construction has been reported from all species of *Furnarius*, but some populations of *F. figulus* may be obligate adopters of existing ovens and other cavities (Studer and Vielliard 1990, A. Whittaker pers. comm., K. Zyskowski pers. obs.).

11. *Domed vegetative structure*.—Vegetative material is used to construct a domed nest with an entrance reduced to a hole on the side, top, or bottom of the nest (Figs. 1F and 2A–E). Domed vegetative nests are present in *Acrobatornis*, *Anumbius*, *Asthenes*, *Certhiaxis*, *Coryphistera*, *Cranioleuca*, *Eremobius*, *Gyalophylax*, *Leptasthenura*, *Limnocietes*, *Limnornis*, *Lochmias*, *Margarornis*, *Oreophylax*, *Phacellodomus*, *Phleocryptes*, *Poecilurus*, *Premnoplex brunnescens*, *Pseudoseisura*, *Schizoeaca*, *Schoeniophylax*, *Siptornis*, *Sylviorthorhynchus*, *Synallaxis*, and *Thriphopha fusciceps*; apparently, they are independently derived in several rhinocryptids in the second outgroup.

Cup-shaped nests of *Aphrastura spinicauda*, a cavity-nester, are probably homologous with domed nests because their lining is not restricted to the bottom of the cavity but also partially covers its walls (Johnson 1967:175). In support of this hypothesis, some species of *Leptasthenura* and *Asthenes* construct fully domed nests in open situations but only much reduced cups (much like those of *Aphrastura*) when placed inside cavities. All three genera are coded as derived for this character.

Similarly, *Spartonoica* construct rather rudimentary ground nests sometimes interpreted as open cups. Because these nests usually are placed in a hollow in the base of a clump of rushes or grass, the surrounding dense vegetation functions as the roof and walls (Narosky 1973). We hypothesize that such constructions are homologous with domed vegetative nests, and hence code them as derived.

12. *Mud-coated vegetation*.—Strips of macerated plant material, coated with mud that hard-

ens upon drying, are woven into the nest wall. Mud-daubing is known only in *Phleocryptes*.

13. *Outer shell of stems*.—A vertically ovoid nest of fresh *Sphagnum* moss is loosely encapsulated by herbaceous stems. This character is present in *Schizoeaca* and *Oreophylax*.

14. *Sticks*.—Bulk of domed nest is composed of dry and often thorny, woody sticks that are tightly interlaced (Figs. 2D–F). In human-altered habitats, sticks can be replaced with wire, including barbed wire (Sick 1993:434). Present in *Acrobatornis*, *Anumbius*, *Asthenes humicola* group, *Asthenes anthoides*, some *Asthenes pyrrholeuca* group (coded as polymorphic), *Certhiaxis*, *Coryphistera*, *Eremobius*, *Gyalophylax*, *Phacellodomus*, *Poecilurus*, *Pseudoseisura*, *Schoeniophylax*, and *Synallaxis*. Although the *Cranioleuca pyrrhophia* group is known to incorporate sticks during nest construction, the bulk of the nest is made of interwoven pliable materials, so we coded this OTU as lacking the derived state.

15. *Extent of lining*.—We hypothesize two unordered derived states for the extent of stick nest lining. (15.1) The entire or large portion of a nest interior is lined with soft plant material, feathers, or hair. This extensive lining is present in *Acrobatornis*, *Anumbius*, *Asthenes anthoides*, *Asthenes humicola* and *A. pyrrholeuca* groups, *Coryphistera*, and *Phacellodomus*. (15.2) A thin circular pad of soft, often brightly colored material (usually green, pubescent dicotyledonous leaves, but sometimes orange or white arthropod cocoons and oothecas) is restricted to the bottom of the incubation chamber (Fig. 2F). The restricted lining is present in *Certhiaxis*, *Gyalophylax*, *Poecilurus*, *Pseudoseisura*, *Schoeniophylax*, and *Synallaxis*. Some nests of *Certhiaxis* and *Pseudoseisura* are found with eggs resting directly on an unlined floor of a brood chamber, perhaps indicating that the lining is added during incubation (e.g. *Certhiaxis cinnamomea*; K. Zyskowski pers. obs.). Species of *Pseudoseisura* are significantly larger than the remaining taxa listed above, and they line their nests with coarser material such as flakes of bark, small sticks, or dung.

16. *Thatch*.—A varying quantity of sticks and plant detritus is placed over the brood chamber forming a pile. Thatch is present in *Certhiaxis*, *Gyalophylax*, *Poecilurus*, *Schoeniophylax*, and *Synallaxis*.

17. *Roof adornment*.—Conspicuous objects of animal or human origin (e.g. whitened bones,

brightly colored or shiny pieces of plastic or glass, etc.) are placed on the roof and around the entrance of a domed nest after it is completed. Present in *Anumbius* and *Coryphistera*. We are uncertain whether adornment with large feathers reported for *Pseudoseisura lophotes* (Nores and Nores 1994) is homologous (coded "?").

18. *Entrance tube*.—Entrance to domed nest has a tubular extension that is either horizontal or curves upward. Entrance tubes are present in *Acrobatornis*, *Asthenes humicola* group, some *Asthenes pyrrholeuca* group (coded polymorphic), *Certhiaxis*, *Eremobius*, *Gyalophylax*, *Phacellodomus*, *Poecilurus*, *Pseudoseisura*, *Schoeniophylax*, and *Synallaxis*. We follow Narosky et al. (1983:8) in considering tubes not homologous with tunnels, which represent extensions of entrance passages that are entirely imbedded within a globular nest structure.

19. *Double entrance*.—Two ascending entrance tubes on opposite sides of a nest converge into a single superior brood chamber. Although the tubes are largely imbedded within the walls of a nest, they are tightly woven and well differentiated from the vegetative strands loosely draped over them (K. Zyskowski pers. obs.). This character is present in *Thripophaga fusciceps*.

20. *Entrance-tube constriction*.—Floor elevation inside the tubular entrance results in formation of a small antechamber (false nest) in front of the main chamber; both chambers are lined. Constricted entrance passages are present in *Phacellodomus*.

21. *Entrance awning*.—Semicircular awning of woven plant material projects over the lateral entrance of a domed nest (Fig. 2A). Such elaboration is present in *Phleocryptes*, *Limnortites*, and *Limnornis*. We hypothesize that the awning of loosely projecting sticks reported in some nests of *Cranioleuca pyrrhophia* (Narosky et al. 1983) is not homologous.

22. *Attachment to vertical stems*.—A nest is attached by the sides to vertical stems of reeds or rushes (Fig. 2A). Ribbon-like vegetative strands originating from nest walls are tightly wound around the supporting stems. Adhesive properties of mud brought along with macerated plant material assure firm attachment of the nest to the smooth surfaces of movable reeds. This mode of nest attachment is present only in *Phleocryptes*.

Nests of other marsh-nesting furnariids, especially those of *Cranioleuca sulphurifera*, sometimes appear to be attached to vertical stems. These species are not coded as derived, however, because in such instances the materials of the nest wall are not attached firmly to upright stems, and the actual nest support comes from the vegetation below the nest. In some cases, *Cranioleuca sulphurifera* even use old *Phleocryptes* constructions as a nest foundation (Narosky et al. 1983).

23. *Pensile nest*.—Voluminous nest, with a small brood chamber entered from below, is constructed from the top down (cf. character 24), presumably by draping long strands of green moss or strips of other plant material from a branch or other woody or rocky overhang. Present in the *Cranioleuca albiceps* group, *Margarornis*, *Premnoplex brunnescens*, *Siptornis*, and *Thripophaga fusciceps*.

Nests of *Premnoplex brunnescens* and *Margarornis* appear homologous with pensile moss constructions of the *C. albiceps* group because they are also built largely of moss, have a disproportionately small brood chamber entered from below, and usually are attached to an underside of a log or rocky overhang (Fig. 2C). Some nests of *P. brunnescens* (e.g. WFVZ 157319 and 157401; see also Vaurie 1980:231) are even suspended from hanging vines in a manner very similar to that of the *C. albiceps* group.

24. *Secondarily pensile nest*.—A boot-shaped nest of sticks, with a horizontal tubular entrance, is built from the bottom up. Nest begins as a platform resting on a distal part of a branch, and usually (but not always) becomes pensile by progressive accumulation of mass (Fig. 2D). Hanging stick nests have been reported in all *Phacellodomus*. Even *P. striaticollis*, with typically non-pensile nests (Narosky et al. 1983), tends to place its constructions on distal parts of branches, where they occasionally become pensile (e.g. Pereira 1938:fig. 29).

RESULTS

The 24 nest characters support 48 most-parsimonious trees, each with a length of 41 steps, consistency index of 0.98, and rescaled consistency index of 0.97. The strict-consensus topology based on these trees contains 15 clades (Fig. 3; multigeneric lineages labeled as clades A to J). The distribution of characters support-

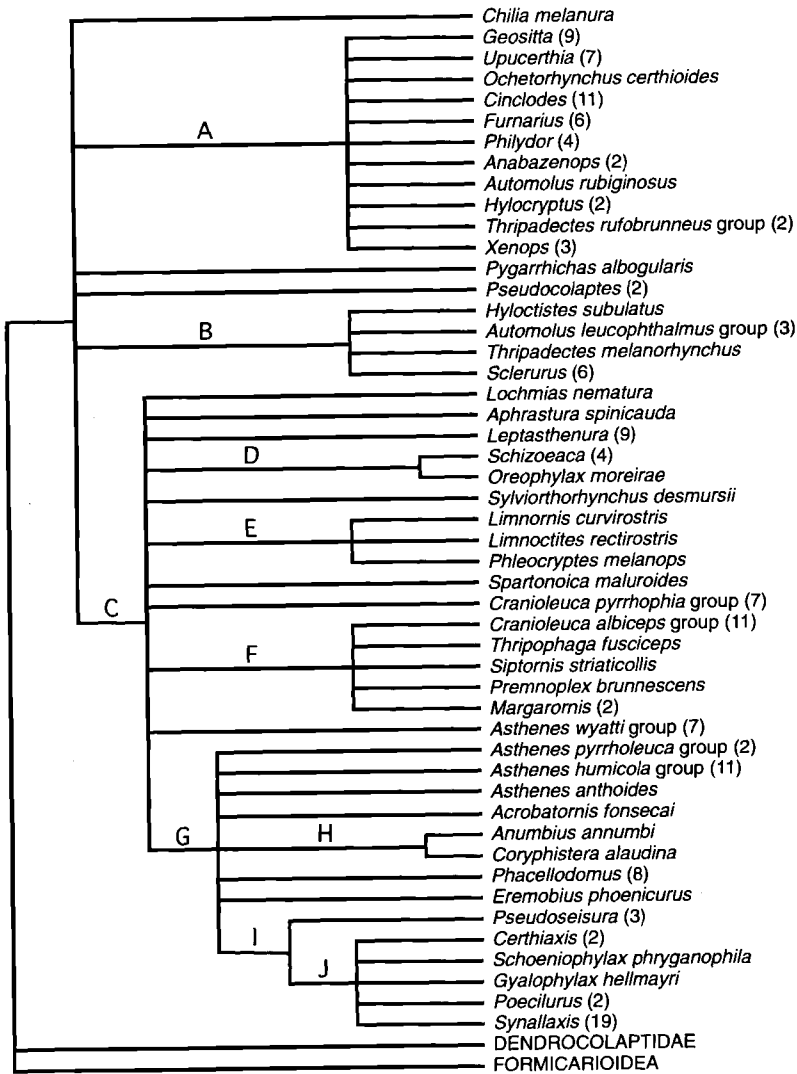


FIG. 3. Strict consensus of 48 most-parsimonious trees (length = 41, CI = 0.98, RC = 0.97) based on 24 nest-architecture characters. Dendrocolaptidae and Formicarioidea were used as the successive outgroups. Nodes A to J are multigeneric lineages diagnosed by nest characters. Number of species is indicated in parentheses. Species groups are defined in Appendix 2.

ing these clades is shown on one of the fundamental trees (Fig. 4). The basal polytomy of the consensus tree includes six diagnosable groups with unresolved interrelationships. The largest of them (clade C) is composed of the furnariids that build domed nests of plant material. The remaining five groups (clades A and B, plus *Chilia*, *Pygarrhichas*, and *Pseudocolaptes*) include species that nest in cavities, as do most of the outgroup taxa.

Each of the five cavity-nesting lineages is

supported by a single derived character. Clades A and B are diagnosable by the woven cup (character 2.2) and the platform of leaf rachises (character 6), respectively. *Chilia* is distinguished by the stick-and-feather platform (character 5). *Pygarrhichas* is unique among the cavity-nesting furnariids in that it lays eggs on the floor of a tree cavity that remains essentially unlined except for the passive accumulation of wood chips (character 3). *Pseudocolaptes* is supported by the behavior of piling up

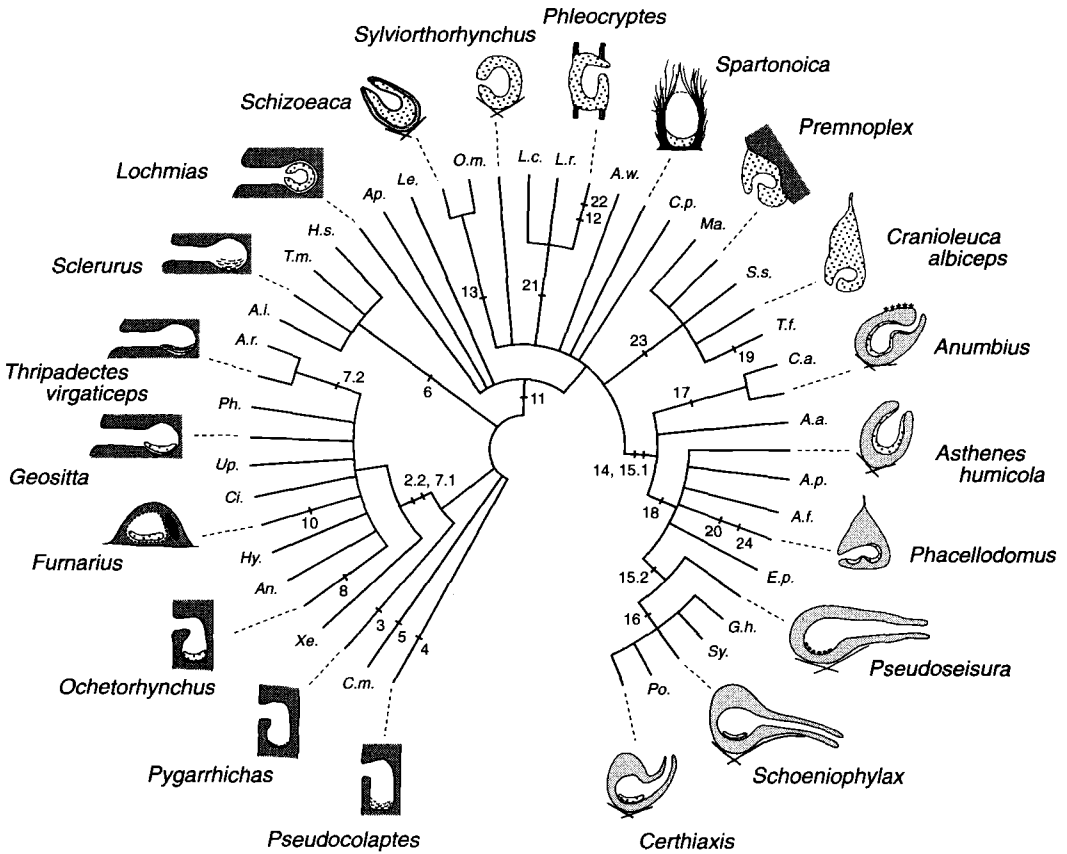


FIG. 4. One of 48 fundamental trees showing distribution of synapomorphies and autapomorphies and diagrams of selected nest designs. Characters with multiple optimizations (1, 2.1, and 9) are not shown. Numbers correspond to nest characters in text, and names of OTUs are abbreviations of those in the strict-consensus tree (Fig. 3).

fern scales on the bottom of a tree cavity (character 4).

The woven-cup clade (A) is composed of furnariids that construct nests of grass-like material (*Ochetorhynchus certhioides* and all behaviorally known species of *Geositta*, *Upucerthia*, *Cinclodes*, *Furnarius*, and *Anabazenops*) and those that build nests of rootlets (*Philydor*, *Hylocryptus*, *Automolus rubiginosus*, *Thripadectes rufobrunneus* group, and *Xenops*). Although relationships within clade A are unresolved in the strict-consensus tree, the rootlet-cup OTUs form a clade in some of the fundamental trees (either imbedded within or sister to the grass-cup clade). Among the grass-cup builders, the clade of *Furnarius* is supported by the clay-oven (character 10), and *Ochetorhynchus certhioides* is unique in lining its nest with large amounts of snake exuvia (character 8). The genera *Auto-*

molus and *Thripadectes* are represented by different members in clades A and B; *Hylocistetes* and all *Sclerurus* are included in clade B.

The diverse clade C, diagnosable by domed nests constructed of plant material, includes 11 basal lineages with unresolved relationships. Three of these lineages, *Lochmias*, *Aphrastura*, and *Leptasthenura*, are in an unresolved basal position because they build domed or semi-domed vegetative nests inside of cavities (see characters 1 and 11). The *Schizoeaca-Oreophylax* clade (D) is supported by a unique nest of *Sphagnum* moss encapsulated by herbaceous stems (character 13). The three marsh-nesting furnariids, *Phleocryptes*, *Limnornis*, and *Limnortites* (clade E), are united by construction of a small awning over the nest entrance (character 21). *Phleocryptes* is the only furnariid known to attach its nest to vertical reed stems (character

22) and build it using plant material coated with mud (character 12). Clade F, composed of *Thripophaga fusciceps*, *Siptornis*, *Premnoplex brunnescens*, *Margarornis*, and 11 species of the *Cranioleuca albiceps* group, is diagnosed by pensile nests of pliable material (character 23). In contrast, the nests of the seven species of the *C. pyrrhophia* group are supported from below (i.e. not pensile). Nests of *Thripophaga fusciceps* are unique in having two entrances (character 19). We failed to find any derived nest characters to diagnose or resolve relationships among *Syloiorhynchus*, *Spartonoica*, *Cranioleuca pyrrhophia* group, and *Asthenes wyatti* group.

Within the stick-nest clade (G), members of *Asthenes* (except the *A. wyatti* group), *Acrobatornis*, *Anumbius*, *Coryphistera*, *Phacellodomus*, and *Eremobius* line not only the bottom area that cushions the eggs, but also the walls and ceiling of the incubation chamber (character 15.1). *Anumbius* and *Coryphistera* form a clade (H) diagnosed by the nest-roof adornment (character 17), and *Phacellodomus* is supported by the entrance constriction (character 20) and the secondarily pensile nest (character 24). A nest lining restricted to the floor of a brood chamber (character 15.2) distinguishes clade I (clade J plus *Pseudoseisura*). Clade J, composed of *Certhiaxis*, *Schoeniophylax*, *Gyalophylax*, *Poecilurus*, and *Synallaxis*, is supported by the presence of thatch (character 16).

Relationships among members of clade G are unresolved in the strict-consensus tree. However, a diverse clade of entrance-tube builders (character 18), including members of clade I, *Eremobius*, *Acrobatornis*, *Phacellodomus*, *Asthenes humicola* group, and sometimes the *Asthenes pyrrholeuca* group, appears in many fundamental trees with the builders of non-tube stick nests as basal to this clade. The entrance-tube clade does not appear in the strict-consensus tree because the *A. pyrrholeuca* group is polymorphic for characters 18 (presence of entrance tube), 13 (presence of sticks), and 1 (nest placement inside cavity).

DISCUSSION

A phylogenetic analysis of the explosive diversity in nest architecture in the Furnariidae demonstrates that the majority of variation in nest construction is hierarchically distributed among higher taxa, rather than within species.

Our analysis supports a partially resolved phylogenetic hypothesis for the family. Among the resulting 15 clades, nest characters provide support for traditional as well as novel phylogenetic groupings. Although we do not advocate the exclusive use of nest characters for phylogenetic reconstruction, we present this hypothesis as a heuristic test of utility of nest characters in avian systematics. We also use these results to propose new hypotheses for the evolution of the diversity of nest architecture in furnariids, which has long been subject to comparative analyses.

Components of variation in nest architecture.—Some of the intraspecific variation in nest placement and architecture is adaptively correlated with proximate biotic and abiotic factors (Collias and Collias 1984, Kern and van Riper 1984, Franklin 1995). As a part of the extended phenotype, however, bird nests are an expression of various genotypes in different environments. Variation in nest phenotype within and among populations can be partitioned into genetic and environmental components. The genetic component can evolve and yield fixed differences within lineages that may become informative systematic characters. The environmental component of nest phenotype also can evolve by selection for increased or decreased plasticity in the face of environmental variation. Comparative studies of nest diversity need to evaluate the various components of variation in nest phenotype to determine the relative contribution of historical and proximate factors to the observed variation. Like other systematic characters, a behavior may be phylogenetically informative in one lineage but variable in another.

Sample sizes of nests of several furnariids were large enough to permit us to assess many aspects of intraspecific variation in nest architecture. With but few exceptions, furnariids exhibited low variation within species and populations for the nest characters hypothesized. Even for some poorly sampled taxa, limited variation among species within genera indicated that phenotypic plasticity within species was low. For example, the nests of each of the six species of *Sclerurus* are known from only a handful of reports, but each species constructs a nest of compound-leaf rachises. Other examples of consistent material preferences in poorly sampled lineages include use of bam-

boo leaves by *Lochmias*, tree-fern scales by *Pseudocolaptes*, and *Sphagnum* moss by *Schizoeaca*. Such consistencies support the conclusion that variation in furnariid nest-construction behavior has been determined primarily by natural selection and less by proximate phenotypic plasticity.

Some nest features, however, are quite variable within and among furnariids, such as the use of wool and feathers in the nest lining and the dimensions of nests and cavities. Some intraspecific variation is correlated with environmental variation in material availability. For example, many species in clade G (Fig. 3) seem to prefer thorny sticks for nest construction but use non-thorny sticks if the preferred material is unavailable (e.g. Nores and Nores 1994). Exceptional examples of extensive geographic polymorphism exist in *Asthenes pyrrholeuca* and *A. modesta*. Various populations construct domed nests of thorny sticks with tubular entrances in the branches of shrubs, whereas other populations construct reduced, cup-shaped nests without sticks in burrows or other cavities. No known geographic or ecological gradients are correlated with this variation (Contreras 1980). Further study is required to elucidate the causes of this polymorphism, but multiple species may actually be involved, especially in the polytypic *A. modesta*.

Phylogenetic utility of nest characters.—The coherent patterns of nest homology shared by furnariid lineages indicate that nest placement, structure, and construction behavior can provide informative phylogenetic characters. The ultimate test of the phylogenetic utility of nest characters in furnariids will be provided by congruence with independently derived data sets.

A few studies have successfully used nest characters in phylogenetic reconstruction (e.g. Lanyon 1986, 1988). Recent analyses of avian nest features have reached diverse conclusions about the phylogenetic content of nest variation. For example, Prum (1993), Winkler and Sheldon (1993), Nunn et al. (1996), Eberhard (1998), and Sturmbauer et al. (1998) documented substantial congruence between nest architecture and phylogeny, indicating that nests can provide valuable systematic characters. In contrast, Lee et al. (1996) concluded that nest characters were not phylogenetically informative within swiftlets (Collocaliini). This conclu-

sion, however, was based on only four very general features of swiftlet nests. One character, the incorporation of feathers, was as phylogenetically consistent as the average molecular character used to produce the phylogenetic hypothesis. Another character, nest proximity, actually is an aspect of social behavior, not nest architecture. Detailed analyses of nest structure and construction behavior in the Collocaliini and other swifts could yield other more-specific and informative nest homologies. For example, the use of saliva as an adhesive in nest construction occurs in all apodimorphs (Apodidae + Hemiprocnidae) except *Hirundapus* and Cypseloidinae (Chantler and Driessens 1995) and is a clear synapomorphy of the larger clade with a reversal in the latter two taxa.

In general, the strength of a proposed behavioral character is related to the amount of detail supporting the primary hypothesis of homology (sensu Pinna 1991). Unlike many behaviors, nest construction is amenable to detailed analysis because nests can be collected, dissected, and examined thoroughly (Hansell 1984, Collias 1986). Furthermore, nest-construction behaviors can be quite elaborate. For example, Thaler (1976) distinguished 15 behavioral acts performed during nest construction by kinglets (*Regulus* spp.). Although such behaviors are poorly known in furnariids, some species employ several distinct stereotyped movements during nest construction (Vaz-Ferreira et al. 1993). Detailed analyses of the modal action patterns involved in nest construction could provide a rich source of phylogenetic information. In addition, the ontogeny of nests can bring special detail to hypotheses of homology and provide robust phylogenetic characters (see below). Architectural characters are phylogenetically informative in several groups of non-avian species as well (Hansell 1984, Wenzel 1992). This result further supports the utility of nest characters in phylogenetic reconstruction.

Evolution of nest architecture in furnariids.—Whether maintained by natural selection or by phylogenetic constraint, enclosed nests occur throughout the Furnariidae and are achieved by a variety of architectural solutions in multiple lineages (Fig. 4). As Skutch (1996:161) stated, "the only feature that all [furnariid nests] have in common is their provision of a domed, roofed space for eggs, nestlings, and

attendant parents. . . ." Comparisons with the outgroups demonstrate that cavity nesting is plesiomorphic to the family. In the two lineages where the primitive cavity nest has been lost, novel structures have evolved to enclose the nest contents: the clay oven of *Furnarius*, and the domed vegetative nest of the synallaxine clade. Even the simple nests of *Spartonoica*, which some authors interpret as the loss of a dome (Collias 1997), essentially are enclosed in thick vegetation that provides a complete covering for the nest.

Our phylogeny suggests several specific hypotheses about the history of nest evolution in the Furnariidae. For example, the domed clay nest of *Furnarius* is unique in birds. Doello-Jurado (1919) proposed that the clay oven of *Furnarius* is homologous to the domed nest of mud-daubed plant material in *Phleocryptes*. However, our phylogenetic hypothesis indicates that the discrete grassy cup in the adobe dome made by *Furnarius* is not homologous with the vegetative nest of *Phleocryptes*. Rather, our results indicate that the clay dome of *Furnarius* is homologous to the burrow or cavities of other furnariids, and that the grass cup is a homology shared with other cavity-nesting furnariids. This hypothesis is further supported by the observation that some *Furnarius* are facultative or obligate cavity nesters (Sclater and Salvin 1873, Studer and Vielliard 1990, Sick 1993, K. Zyskowski pers. obs.).

Nest ontogeny.—In addition to the nest and the behavioral acts used to construct it, a great deal of information exists in the ontogeny of the nest. The sequence of events in the construction of nests may reveal additional information about the homology of cryptically homologous or superficially similar but analogous nests. For example, the nest of most *Phacellodomus* begins as a mat of sticks near the tip of a horizontal branch and eventually becomes pensile as the supporting branch droops under the mass of the nest. In contrast, pensile nests of *Thripophaga fusciceps* (placed in *Phacellodomus* by Vaurie [1980]) are built by draping strands of vegetation from the supporting branch downward. In this instance, a superficial similarity that could be a proposed homology, "pendant nest," is falsified by ontogenetic information.

Ontogeny has also been proposed as a criterion for polarizing character variation among taxa (e.g. Meier 1997). According to this crite-

ron, features appearing earlier in ontogeny are more broadly distributed among taxa, whereas features acquired in subsequent developmental stages have narrower distributions and are hypothesized as derived. The ontogenetic criterion performs well when novelties result from terminal additions to developmental sequences (Meier 1997).

The ontogenetic criterion can often be used to determine polarity of nest characters because of the physical or engineering constraints that are imposed on the development of three-dimensional constructions. For example, because no avian nests are constructed and subsequently attached to a substrate, the necessity of attachment or placement constrains the ontogeny and evolution of nests. The primitive form of the domed stick nest found in clade G is a platform supported from below. The secondarily pensile stick nest of *Phacellodomus*, in which the nest is initially supported from below but becomes pensile as its increasing mass causes the supporting branch to collapse, is unique among birds. The primitive ontogeny within this group (i.e. platform supported from below) precluded the evolution of a typical pensile nest, which is built from the top down, but this constraint also fostered the evolution of a truly novel method of constructing a hanging domed nest.

Winkler and Sheldon (1993) used nest ontogeny to polarize variation in nest architecture within mud-nesting swallows (Hirundinidae). They argued that closed and retort nests evolved from an open mud cup because the nest begins as a cup that is subsequently enclosed, and to which the retort entrance tunnel is finally added. It is likely that the ontogenetic criterion will have other successful applications to polarization of avian nest characters.

Phylogeny of the Furnariidae.—Our analysis supports a partially resolved phylogenetic hypothesis for the Furnariidae. The phylogeny includes three novel basal clades (clades A to C) and three genera (*Chilia*, *Pygarrhichas*, and *Pseudocolaptes*) with unresolved relationships. The largest resolved group (clade C) includes 27 genera that build domed vegetative nests. This nest type unites not only all traditional Synallaxinae analyzed but also *Eremobius* (traditionally placed in Furnariinae) and *Margarornis*, *Premnoplex*, *Pseudoseisura*, and *Lochmias* (usually placed in Philydorinae). Within this

expanded "synallaxine" clade, additional nest synapomorphies provide support for several more-resolved subclades (D to J), including several novel phylogenetic relationships. For example, we found behavioral support for a clade (E) that includes the three monotypic marsh-nesting genera (*Limnornis*, *Limnoctites*, and *Phleocryptes*) and for a clade (J) that unites *Certhiaxis* with the *Synallaxis* assemblage (sensu Vaurie 1980).

We also identified a nest synapomorphy to support a clade (F) that includes the *Cranioleuca albiceps* group, *Margarornis*, *Premnoplex brunneus*, *Siptornis*, and *Thripophaga fusciceps*. Although a relationship of *Siptornis* to *Cranioleuca* has been proposed previously (Vaurie 1980), this entire assemblage is novel. Until now, these genera have been placed in two subfamilies (*Cranioleuca* and *Thripophaga* in Synallaxinae; *Margarornis* and *Premnoplex* in Philydorinae), despite the apparent behavioral and vocal similarities among them (Ridgely and Tudor 1994).

The monophyly of two diverse genera (*Asthenes* and *Cranioleuca*) is not supported by our results. In the case of *Asthenes*, the *A. wyatti* group is a basal member of the domed vegetative nest clade (C), whereas the *A. pyrrholeuca* and *A. humicola* groups, and *A. anthoides*, are members of clade G, which is diagnosed by highly derived stick nests. These "grass-nesting" and "stick-nesting" assemblages of *Asthenes* have been recognized previously, and they can also be diagnosed using plumage characters and vocalizations (Narosky et al. 1983, Pacheco et al. 1996). In contrast, the two groups of *Cranioleuca* recognized here based on nest architecture do not parallel those identified using molecular, morphological, or distributional evidence (Maijer and Fjeldså 1997, J. García-Moreno pers. comm.).

Relationships among the cavity-nesting lineages of furnariids are not so well resolved. However, these lineages include several clades diagnosed by distinctive nest synapomorphies. The largest of these groups is the cup-nest clade (A) that includes *Furnarius*. Although *Furnarius* traditionally has been associated with many of the genera in clade A, our study has identified the first behavioral synapomorphy that supports this relationship. Our phylogenetic hypothesis also suggests that *Automolus* and *Thripadectes* are polyphyletic, but ad-

ditional evidence is required to confirm this notion.

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APPENDIX 1. Sources of information on nest architecture of furnariids. Species are arranged in alphabetical order with generic names in bold. References are listed separately for subspecific taxa that have been hypothesized to deserve species rank (Ridgely and Tudor 1994). All suspected cases of uncertain species identification are coded "id." Rather than providing an exhaustive list of references from the scientific literature, we selected a minimal set of publications for each species, giving priority to compilations and more recent papers. Published information is followed by unpublished photographic or specimen-based sources. Specimen data and VIREO images are listed as collector's or photographer's name followed by institution code and catalog number(s). Information obtained through personal communications is presented by listing a contributor's name alone. Abbreviations used for frequently cited sources are: B84 (Belton 1984), FK90 (Fjelds  and Krabbe 1990), HB86 (Hilty and Brown 1986), J67 (Johnson 1967), N83 (Narosky et al. 1983), P87 (de la Pe a 1987), S93 (Sick 1993), V80 (Vaurie 1980), AW (A. Whittaker), BW (B. Whitney), and KZ (K. Zyskowski). Institutional codes are: AMNH (American Museum of Natural History, New York), BMNH (Natural History Museum, Tring), DMNH (Delaware Museum of Natural History, Greenville), FMNH (Field Museum of Natural History, Chicago), HMNH (Finnish Museum of Natural History, Helsinki), KU (University of Kansas Natural History Museum), MNRJ (Museu Nacional, Universidade Federal de Rio de Janeiro), MPEG (Museu Paraense Emilio Goeldi, Bel m, Brazil), PMHN (Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima), SBCM (San Bernardino County Museum, Redlands, California), USNM (National Museum of Natural History, Smithsonian Institution), WFFVZ (Western Foundation of Vertebrate Zoology, Camarillo, California), and VIREO (Visual Resources for Ornithology, Academy of Natural Sciences of Philadelphia).

Acrobatornis fonsecai: Whitney et al. 1996; *Anabacerthia striaticollis*: V80 (Schaefer, HMNH 13249), T. McNish (VIREO M42/1/092-094, pers. comm.); *A. variegaticeps*: Wagner 1980; *Anabazenops dorsalis*: Kratter 1994; *A. fuscus*: S93, BW; *Anumbius annumbi*: V80, N83, B84, Mason 1985, P87, S93, Vaz-Ferreira et al. 1993, Belcher (HMNH 13079), Crossin (WFFVZ 160674-7), Holt (USNM 41089), MacIntyre (DMNH 23685), Ridgely (VIREO R10/13/064-8), Young (DMNH 23684), R. Parrini, AW, KZ; *Aphrastura spinicauda*: J67 (Johnson and Goodall, WFFVZ 55514-9), V80, N83, P87, Crossin (WFFVZ 160700), P. Rasmussen (VIREO R17/1/017, pers. comm.); *Asthenes anthoides*: N83, Colias 1997, Belts (DMNH uncat., id); *A. arequipae*: J67 (Johnson and Goodall, WFFVZ 55551), V80, FK90, Dorst (WFFVZ 151796); *A. baeri*: N83, B84, P87, Girard (WFFVZ 53772), KZ; *A. berlepschi*: Collar et al. 1992, BW; *A. cactorum*: Koepcke 1959, V80, T. Schulenberg; *A. dorbignyi*: V80, N83, Fraga and Narosky 1985, P87; *A. huancavelicae*: Morrison 1939, FK90, Collar et al. 1992, Hocking (PMHN uncat.); *A. hudsoni*: V80, N83, Goodall (DMNH 23671), Wetmore (USNM 34128), Young (DMNH 23672); *A. humicola*: J67 (Goodall and Johnson: DMNH 23664-70; USNM 39973; WFFVZ 23408, 53168, 55540-50), N83, P87, Mar n (WFFVZ 120289); *A. humilis*: V80; *A. luizae*: BW; *A. maculicauda*: KZ; *A. modesta*: J67 (Goodall and Johnson: WFFVZ 53169-70, 55552-65), V80, N83, P87, FK90, Venero 1990, Pemberton (WFFVZ 15148-58), BW; *A. patagonica*: V80, N83, Fraga and Narosky 1985, FK90, Vuilleumier 1993, Whitney et al. 1996, Wetmore (USNM 36250); *A. pudibunda*: Koepcke 1958; *A. pyrrholeuca*: J67 (Goodall and Johnson: WFFVZ 55636-7), V80, N83, P87, Pemberton (WFFVZ 15144-7), Smyth (DMNH uncat., HMNH 13060), Wetmore (USNM 36249); *A. sclateri*: N83, Fraga and Narosky 1985, P87; *A. steinbachi*: N83, Salvador 1992; *A. urubambensis*: KZ; *A. virgata*: BW; *A. wyatti aequatorialis* group: HB86, Phelps 1977; *A. w. graminicola*: Dorst 1963 (WFFVZ 151795), BW; *Automolus infuscatus*: Pinto 1953, Koepcke 1972, V80, Tostain et al. 1992; *A. leucophthalmus*: V80, N83, M. Raposo, AW, KZ; *A. melanopezus*: E. Barnes; *A. ochrolaemus*: Skutch 1969, V80, Kiff (WFFVZ 58600-1), Stiles (WFFVZ 58620), Williams (WFFVZ 59367); *A. rubiginosus*: Rowley 1966 (WFFVZ 21315), V80, Mar n and Carrion 1991 (WFFVZ 158304); *Berlepschia rikeri*: V80, S93; *Certhiaxis cinnamomea*: Cherrie 1916 (WFFVZ 120131), Belcher and Smooker 1936 (DMNH 23662); HMNH 11976-8, 11980, 13056-7), V80, N83, B84, HB86, P87, S93, Haverschmidt and Mees 1994, Carriker (WFFVZ 154606, 154984; SBCM 20184-92, 20383, 20433), Contino (WFFVZ 156061, 158445), Crandall (DMNH 23661, WFFVZ 117042), MPEG uncat., KZ; *C. mustelina*: V80, BW; *Chilia melanura*: J67 [Behn (WFFVZ 55493), Goodall and Johnson (USNM 39975; WFFVZ 53175-6, 55489-92)], V80, M. Mar n; *Cinclodes antarcticus*: Pettingill 1973, V80, N83, Belts (DMNH, 3 uncat.); *C. atacamensis*: Morrison 1939, J67 (WFFVZ 55508), N83, Salvador and Narosky 1984, P87, Ralde (WFFVZ 55509); *C. comechingonus*: N83, P87; *C. excelsior*: Graves and Arango 1988, Mar n et al. (WFFVZ 162880-1); *C. fuscus*: J67 (Johnson and Goodall: WFFVZ 53114-5, 55504-7), V80, N83, P87, Venero 1990, Salvador 1992, Carrion (WFFVZ 161930), Kiff et al. (WFFVZ 162874), Pemberton (WFFVZ 15132-4), KZ; *C. nigrofumosus*: J67 (Goodall, WFFVZ 55503; Millie, WFFVZ 55502), V80; *C. olrogii*: N83, P87; *C. oustaleti*: J67 (Goodall, WFFVZ 55510), N83; *C. pabsti*: B84, S93; *C. patagonicus*: J67 (Goodall: WFFVZ 53110-3, 55494-501), N83, Pemberton (WFFVZ 15135); *C. taczanowskii*: V80, BW; *Coryphistera alaudina*: V80, N83, P87, Dinelli (WFFVZ 150668), Girard (WFFVZ 53759), R. Parrini, KZ; *Cranioleuca albicapilla*: Peters and Griswold 1943, Parker and O'Neill 1980 (id), E. Barnes, J. Fjelds ; *C. albiceps*: Remsen 1984; *C. antisimensis*: Koepcke 1958, D. Lane; *C. baroni*: FK90; *C. curta*: M. Cohn-Haft, C. Stiles; *C. demissa*: BW (id); *C. erythrops*: Skutch 1969, V80, Willis 1988, Skutch 1996, Mar n (WFFVZ 157422), G. Stiles (WFFVZ 68520, pers. comm.); *C. gutturata*: HB86, E. Barnes, M. Reid, M. Robbins, AW, KZ; *C. hellmayri*: HB86; *C. marcapatae*: Parker and O'Neill 1980 (id), KZ; *C. muelleri*: BW, AW; *C. obsoleta*: B84; *C. pallida*: V80, S93, AW, BW, KZ; *C. pyrrhophia*: V80, N83, B84, P87, Girard (WFFVZ 53771), R. Parrini; *C. semicinerea*: Teixeira and Luigi 1989; *C. subcristata*: V80; *C. sulphurifera*: V80, N83, P87, Runnacles (SBCM 22271); *C. vulpina*: Cherrie 1916 (WFFVZ 120131), Teixeira and Luigi

APPENDIX 1. Continued.

1989, Holt (USNM 41091-2); *Eremobius phoenicurus*: V80, N83, Vuilleumier 1993, Crossin (WFVZ 160701), Pemberton (WFVZ 15136-40); *Furnarius cristatus*: N83, P87, KZ; *F. figulus*: V80, Studer and Vielliard 1990, S93, AW, KZ; *F. l. cinnamomeus*: Taczanowski 1884, Marín in Skutch 1996, Kiff et al. (WFVZ 162164), D. Lane, KZ; *F. l. leucopus* group: Ihering 1914, Naumburg 1930, Koepcke 1972, Dyrz 1987, S93, Smooker (HMNH 13070-1), KZ; *F. l. longirostris*: Allen 1905, Carriker (SBCM 20356, 20358); *F. minor*: Sclater and Salvin 1873, Chagas (WFVZ 24442); *F. rufus*: V80, N83, B84, Mason 1985, P87, S93, Vaz-Ferreira et al. 1993, Blake (FMNH 2269, 14756), Chagas (WFVZ 24443, 53777), Crossin (WFVZ 160680-3), Dunlap (USNM 40707), Garrett (DMNH 23633), Holt (USNM 41090), Mason (WFVZ 146877), Meyer (USNM 47248), Sobrinho (HMNH 13067), Wetmore (USNM 36251, 36333), Young (DMNH 23632), MNRJ uncat., KZ; *F. torridus*: Sclater and Salvin 1873; *Geobates poecilopterus*: S93; *Geositta antarctica*: J67 (Johnson and Goodall, WFVZ 55478), N83, Hermiston (DMNH uncat.); *G. cunicularia cunicularia* group: J67 (Johnson and Goodall, WFVZ 53103-4, 55470-4), N83, B84, P87, S93, Belcher (HMNH 13064), Marín (WFVZ 129185), Pemberton (WFVZ 15128-9); *G. c. deserticolor*: J67 (Millie, WFVZ 55475-6); *G. c. frobeni* group: J67 (Johnson and Goodall, WFVZ 55477), Venero 1990, R. McNeal; *G. isabellina*: V80, N83; *G. maritima*: J67; *G. peruviana*: Williams 1981, D. Lane, KZ; *G. punensis*: J67, V80, N83, Ralde (WFVZ 55481); *G. rufipennis*: J67 (Johnson and Goodall, WFVZ 55479-80), V80, N83, P87, Pemberton (WFVZ 15130); *G. saxicolina*: Taczanowski 1884; *G. tenuirostris*: Taczanowski 1884, Salvador et al. 1984, R. McNeal; *Gyalophylax hellmayri*: Ihering 1914, Teixeira 1992, S93, AW; *Hylocryptus erythrocephalus*: Collar et al. 1992, M. Robbins, KZ; *H. rectirostris*: S93, T. Abreu, R. Parrini; *Hyloctistes s. subulatus*: Sclater and Salvin 1873 (id); *H. s. virgatus*: N. Wheelwright; *Leptasthenura a. aegithaloides*: J67 (Goodall and Johnson: WFVZ 53031-7, 55532-6); *L. a. berlepschi*: J67 (Johnson and Goodall, WFVZ 55539), N83, P87; *L. a. griseescens*: J67 (Millie, WFVZ 55538); *L. a. pallida*: N83, Fraga and Narosky 1985, P87, Vuilleumier 1993, Pemberton (WFVZ 15141-3); *L. andicola*: V80, HB86, Briceno (USNM 30597), Fjeldså and Krabbe (WFVZ 162898), Kiff and Garrett (WFVZ 162947), Marín (WFVZ 162891), M. Robbins (VIREO R08/9/024, pers. comm.), C. Sharpe; *L. fuliginiceps*: V80, N83, Contino (WFVZ 156116); *L. pileata*: I. Franke (PMHN uncat., pers. comm.); *L. platensis*: V80, N83, B84, Mason 1985, P87, S93, MacIntyre (DMNH uncat.), Malcolm (DMNH 23634), Short (WFVZ 160691); *L. setaria*: B84, Andrade 1996, AW; *L. striolata*: B84, BW; *L. xenothorax*: C. Byers and KZ; *L. yanacensis*: Vuilleumier 1969; *Limnornis rectirostris*: N83, Ricci and Ricci 1985, S93; *Limnornis curvirostris*: V80, N83, B84; *Lochmias nematura*: V80, N83, B84, S93, AMNH 13846-7, T. Abreu, T. Davis, BW, KZ; *Margarornis rubiginosus*: J. Sánchez, D. Watson; *M. squamiger*: HB86, FK90; *Metopothrix aurantiacus*: Fraga 1992, Ridgely and Tudor 1994, A. Begazo, P. Greenfield, R. McNeal, M. Robbins, B. Walker, BW; *Ochetorhynchus certhioides*: N83, P87, KZ; *Oreophylax moreirae*: Sick 1970, S93; *Phacellodomus dorsalis*: Ridgely and Tudor 1994, J. O'Neill (VIREO O03/2/178, pers. comm.), B. Walker; *P. e. erythrophthalmus*: Euler 1900, S93, E. Mendonça, KZ; *P. e. ferrugineigula*: Ihering 1900, V80, R. Parrini; *P. maculipectus*: N83, Salvador 1992, Mazar Barnett et al. 1998; *P. ruber*: V80, N83, S93, P87, Crossin (WFVZ 160690), Pettingill (VIREO P03/7/075), AW, KZ; *P. rufifrons inornatus* group: Skutch 1969, Thomas 1983, HB86, Phelps and Avelado 1987, Collias 1997, C. Brady; *P. r. peruvianus*: Taczanowski 1884, J. O'Neill (VIREO O03/2/177), D. Lane, KZ; *P. r. rufifrons* group: Naumburg 1930, N83, P87, S93, Whitney et al. 1996, Girard (WFVZ 53774), AW, KZ; *P. sibilatrix*: V80, N83, Mason 1985, P87, KZ; *P. striaticeps*: V80, N83, P87, KZ; *P. striaticollis*: V80, N83, B84, Mason 1985, P87, S93; *Philydor atricapillus*: Ruschi 1981 (id), S93, BW, KZ; *P. erythrocerus*: Tostain et al. 1992; *P. lichtensteini*: Saibene 1995, AW, BW; *P. rufus columbianus* group: V80 (Schaefer, HMNH 13254; Schwartz in "A Portfolio of Venezuelan Birds," undated publ. of Cornell Lab. Orn.); *P. r. riveti*: HB86; *P. r. rufus*: V80, Ruschi 1981 (id), N83, BW, J. Minns, KZ; *Phleocryptes melanops*: Taczanowski 1884, J67 (Goodall and Johnson: DMNH 23677; USNM 39977; WFVZ 53021-30, 55520-31), V80, N83, B84, Mason 1985, P87, S93, Felippone (USNM 37417-8), Garrett (DMNH 23679), MacIntyre (DMNH 23678), Marín (WFVZ 120291, 129189-92), Peña (USNM 2730), Wetmore (USNM 34127) Williams (WFVZ, 3 uncat.), KZ; *Poecilurus candei*: V80, Bosque and Lentino 1987; *P. scutatus*: Teixeira and Luigi 1993, SBCM 20362; *Premnoplex brunnescens*: Skutch 1967 (WFVZ 158848), V80, FK90, Marín and Carrion 1994 (WFVZ 157401, 159225, 162250, 162895-6), Sibley (WFVZ 157319, labeled as *Lochmias nematura*); *Pseudocolaptes boissonneaultii*: Sclater and Salvin 1879; *P. lawrencii*: Skutch 1969, G. Stiles (WFVZ 151475, pers. comm.); *Pseudoseiura cristata*: Ihering 1914, Naumburg 1930, V80, S93, AW; *P. gutturalis*: V80, N83, P87, Collias 1997, Pemberton (WFVZ 15159-60); *P. lophotes*: V80, N83, P87, S93, Nores and Nores 1994, Goodall (DMNH 23690), MacIntyre (DMNH 23686), Malcolm (DMNH 23689), Smyth (HMNH 13074), KZ; *Pygarrhynchus albogularis*: J67 (Goodall and Johnson (WFVZ 55567-9), V80, N83, FK90; *Schizoeaca fuliginosa*: HB86, M. Robbins; *S. griseomurina*: D. Christian; *S. harterti*: Vuilleumier 1969; *S. helleri*: T. Schulenberg (WFVZ, 2 uncat.; pers. comm.); *Schoeniophylax phryganophila*: V80, N83, B84, P87, S93, Crossin (WFVZ 160678-9), MacIntyre (DMNH uncat.), AW, KZ; *Sclerurus albigularis*: Belcher and Smooker 1936 (HMNH 13061-3), V80, HB86, Carriker (WFVZ 154607-8; SBCM 20113-22, 20193-8), T. Davis; *S. caudacutus*: Pinto 1953, KZ; *S. guatemalensis*: Skutch 1969, V80, Walters 1995, D. Robinson, Stiles (WFVZ 64490), Williams (WFVZ 58180); *S. mexicanus*: Tostain et al. 1992, Stiles (WFVZ 143838, 158873); *S. ruficularis*: Haverschmidt and Mees 1994, M. Cohn-Haft; *S. scansor*: V80, N83, S93, Sobrinho (DMNH 23691), AW, M. Raposo, KZ; *Siptornis striaticollis*: Ridgely and Tudor 1994, P. Greenfield; *Siptornopsis hypochondriacus*: Braun and Parker 1985, T. Schulenberg, M. Robbins; *Spartonoica maluoides*: V80, N83; *Sylviorhynchus desmursii*: J67

APPENDIX 1. Continued.

(Goodall, WFVZ 55513), V80, N83; *Synallaxis albescens*: Sclater and Salvin 1879, Cherrie 1916 (WFVZ 119328, 120127–8), Belcher and Smooker 1936 (DMNH 23655; HMNH 11662–6, 13080), Skutch 1969, V80, N83, P87, Tostain et al. 1992, Haverschmidt and Mees 1994, Fiala (WFVZ 68051), Smyth (DMNH 23640), Stiles (WFVZ 141906), Young (DMNH 23639), KZ; *S. albigularis*: V80, HB86; *S. albilora*: Naumburg 1930 (photos, id); *S. a. azarae* group: Taczanowski 1884, KZ; *S. a. elegantior* group: Taczanowski 1884, HB86, KZ; *S. a. superciliosa*: N83, P. Martin; *S. brachyura*: Skutch 1969, V80, HB86, Kiff (WFVZ 58437, 58466, 58583–5, 78161, 158324, 158336, 158340), Smith (USNM 39797, WFVZ 69290–2), Stiles (WFVZ 58626–7), Williams (WFVZ 58441); *S. chinchipensis*: KZ; *S. cinerascens*: V80, HB86; *S. cinamomea* group: Belcher and Smooker 1936 (HMNH 11671–2, 11979), V80; *S. c. cinamomea* group: V80, HB86; *S. c. terrestris*: Belcher and Smooker 1936; *S. erythrothorax*: Lea 1951, Skutch 1969 and 1996, V80, Skinner (USNM 32475–9); *S. frontalis*: V80, N83, P87, Girard (WFVZ 53760), KZ; *S. gujanensis*: Sneath 1935, Pinto 1953, HB86, Haverschmidt and Mees 1994, Myers (HMNH 13081), G. Stiles, KZ; *S. macconnelli*: AW; *S. propinqua*: BW; *S. ruficapilla*: V80, N83, S93, Chagas (WFVZ 24485; SBCM 20880–1), KZ; *S. rutilans omissa*: Pinto 1953, Chagas (WFVZ 24487); *S. r. rutilans*: Haverschmidt and Mees 1994; *S. spixi*: V80, N83, B84, Fraga and Narosky 1985, P87, Isoldi 1992, S93, Chagas (WFVZ 24486), Smyth (DMNH 23656, 23660), Sobrinho (DMNH 23657–9), E. Mendonça, KZ; *S. stictothorax*: Taczanowski 1884, Marchant 1960, Corado and Kiff (WFVZ 158327–8, 158330, 158373), M. Marín, KZ; *S. subpudica*: HB86; *S. tithys*: Balchin 1996, KZ; *S. zimneri*: I. Franke (PMHN uncat., pers. comm.); *Syndactyla guttulata*: V80 (id); *S. rufosuperciliata*: N83, B84, KZ; *Thripadectes flammulatus*: V80, HB86, G. Stiles; *T. holostictus*: P. Alden (VIREO A01/1/371, pers. comm.; id), BW; *T. melanorhynchus*: Kiff et al. 1989 (WFVZ 156103); *T. rufobrunneus*: Skutch 1969, Marín and Schmitt (WFVZ 154831), G. Stiles, Worth (WFVZ 154898); *T. scrutator*: M. Robbins, BW; *T. virgaticeps*: HB86, Marín and Carrion 1994 (WFVZ 159222); *Thripophaga fusceps*: Whitney et al. 1996, E. Barnes, S. Hilty, M. Cohn-Haft, AW, KZ; *T. macroura*: Collar et al. 1992, Whitney et al. 1996, R. Parrini, AW; *Upucerthia albigula*: J67 (Johnson and Goodall, WFVZ 55487), Schulenberg 1987, FK90; *U. andaeicola*: N83, Fraga and Narosky 1985, P87; *U. dumetaria*: J67 [Goodall and Johnson (DMNH, 2 uncat.; WFVZ 53171–3, 55482–4), Millie (WFVZ 55485–6)], V80, N83, P87, Pemberton (WFVZ 15131); *U. jelskii*: Taczanowski 1884, N83, Venero 1990, Mazar Barnett et al. 1998; *U. ruficauda*: J67, N83, P87; *U. serrana*: FK90, V80; *U. validirostris*: N83, P87, Salvador 1992; *Xenerpestes minlosi*: Ridgely and Gwynne 1989 (id), Whitney et al. 1996 (id), M. Reid; *X. singularis*: T. Davis (id), P. Greenfield; *Xenops milleri*: AW; *X. minutus genibarbis* group: Skutch 1969, V80, D. Robinson; *X. m. minutus*: Euler 1900; *X. rutilans*: Belcher and Smooker 1936 (HMNH 11677–8), Willis 1988, KZ.

APPENDIX 2. Distribution of states of 24 nest-architecture characters in 168 species of furnariids and two composite outgroups. Furnariid taxa are condensed into 49 OTUs and listed in alphabetical order. Numbers in parentheses refer to the number of species within a given OTU. 0 = ancestral state; 1, 2 = derived states; P = polymorphism (i.e. 0 or 1); ? = unknown. See text for character descriptions and polarity assessments and Appendix 1 for sources of nest information.

Taxa ^{a,b}	Characters				
	1–5	6–10	11–15	16–20	21–24
<i>Acrobatornis fonsecai</i>	00000	00000	10011	00100	0000
<i>Anabazenops</i> (2)	12000	01000	00000	00000	0000
<i>Anumbius annumbi</i>	00000	00000	10011	01000	0000
<i>Aphrastura spinicauda</i>	10000	00000	10000	00000	0000
<i>Asthenes anthoides</i>	00000	00000	10011	00000	0000
<i>Asthenes humicola</i> group (11)	00000	00000	10011	00100	0000
<i>Asthenes pyrrholeuca</i> group (2)	P0000	00000	100P1	00P00	0000
<i>Asthenes wyatti</i> group (7)	00000	00000	10000	00000	0000
<i>Automolus leucophthalmus</i> group (3)	11000	10000	00000	00000	0000
<i>Automolus rubiginosus</i>	12000	02000	00000	00000	0000
<i>Chilia melanura</i>	11001	00000	00000	00000	0000
<i>Certhiaxis</i> (2)	00000	00000	10012	10100	0000
<i>Cinclodes</i> (11)	12000	01000	00000	00000	0000
<i>Coryphistera alaudina</i>	00000	00000	10011	01000	0000
<i>Cranioleuca albiceps</i> group (11)	00000	00000	10000	00000	0010
<i>Cranioleuca pyrrhophia</i> group (7)	00000	00000	10000	00000	0000
<i>Eremobius phoenicurus</i>	00000	00000	10011	00100	0000
<i>Furnarius</i> (6)	P2000	01001	00000	00000	0000

APPENDIX 2. Continued.

Taxa ^{a,b}	Characters				
	1-5	6-10	11-15	16-20	21-24
<i>Geositta</i> (9)	12000	01000	00000	00000	0000
<i>Gyalophylax hellmayri</i>	00000	00000	10012	10100	0000
<i>Hylocryptus</i> (2)	12000	02000	00000	00000	0000
<i>Hyloctistes subulatus</i>	11000	10000	00000	00000	0000
<i>Leptasthenura</i> (9)	P0000	00000	10000	00000	0000
<i>Limnoctites rectirostris</i>	00000	00000	10000	00000	1000
<i>Limnormis curvirostris</i>	00000	00000	10000	00000	1000
<i>Lochmias nematura</i>	10000	00000	10000	00000	0000
<i>Margarornis</i> (2)	00000	00000	10000	00000	0010
<i>Ochetorhynchus certhioides</i>	12000	01100	00000	00000	0000
<i>Oreophylax moreirae</i>	00000	00000	10100	00000	0000
<i>Phacellodomus</i> (8)	00000	00000	10011	00101	0001
<i>Philydor</i> (4)	12000	02000	00000	00000	0000
<i>Phleocryptes melanops</i>	00000	00000	11000	00000	1100
<i>Poecilurus</i> (2)	00000	00000	10012	10100	0000
<i>Premnoplex brunnescens</i>	P0000	00000	10000	00000	0010
<i>Pseudocolaptes</i> (2)	11010	00000	00000	00000	0000
<i>Pseudoseisura</i> (3)	00000	00000	10012	0?100	0000
<i>Pygarrhichas albogularis</i>	11100	00010	00000	00000	0000
<i>Schizoeca</i> (4)	00000	00000	10100	00000	0000
<i>Schoeniophylax phryganophila</i>	00000	00000	10012	10100	0000
<i>Sclerurus</i> (6)	11000	10000	00000	00000	0000
<i>Siptornis striaticollis</i>	00000	00000	10000	00000	0010
<i>Spartonoica maluroides</i>	00000	00000	10000	00000	0000
<i>Sylviorthorhynchus desmursii</i>	00000	00000	10000	00000	0000
<i>Synallaxis</i> (19)	00000	00000	10012	10100	0000
<i>Thripadectes melanorhynchus</i>	11000	10000	00000	00000	0000
<i>Thripadectes rufobrunneus</i> group (2)	12000	02000	00000	00000	0000
<i>Thripophaga fusciceps</i>	00000	00000	10000	00010	0010
<i>Upucerthia</i> (7)	12000	01000	00000	00000	0000
<i>Xenops</i> (3)	12000	02010	00000	00000	0000
Dendrocolaptidae	11000	00000	00000	00000	0000
Formicarioidea	PP000	PP000	P0000	00000	0000

^a Species representing composite OTUs (asterisks mark species with partial information): *Anabazenops* = *A. dorsalis* and *A. fuscus**; *Asthenes humicola* group = *A. arequipae*, *A. baeri*, *A. berlepschi**, *A. cactorum*, *A. dorbignyi*, *A. huancavelicae*, *A. humicola*, *A. luizae**, *A. patagonica*, *A. pudibunda*, and *A. steinbachi*; *Asthenes pyrrholeuca* group = *A. modesta* and *A. pyrrholeuca*; *Asthenes wyatti* group = *A. hudsoni*, *A. humilis*, *A. maculicauda*, *A. sclateri*, *A. virgata*, *A. urubambensis**, and *A. wyatti*; *Automolus leucophthalmus* group = *A. infuscatus*, *A. leucophthalmus*, and *A. ochrolaemus*; *Certhiaxis* = *C. cinnamomea* and *C. mustelina*; *Cinclodes* = *C. antarcticus*, *C. atacamensis*, *C. comechingonus*, *C. excelsior*, *C. fuscus*, *C. nigrofumosus*, *C. olrogi*, *C. oustaleti*, *C. pabsti*, *C. patagonicus*, and *C. taczanowskii**; *Cranioleuca albiceps* group = *C. albicapilla*, *C. albiceps*, *C. antisimensis*, *C. baroni*, *C. curtata*, *C. demissa*, *C. erythropis*, *C. hellmayri*, *C. marcapatae*, *C. subcristata*, and *C. vulpina*; *Cranioleuca pyrrhophia* group = *C. gutturata*, *C. muelleri*, *C. obsoleta*, *C. pallida*, *C. pyrrhophia*, *C. semicinerea*, and *C. sulphurifera*; *Furnarius* = *F. cristatus*, *F. figulus*, *F. leucopus*, *F. minor*, *F. rufus*, and *F. torridus*; *Geositta* = *G. antarctica*, *G. cucularia*, *G. isabellina**, *G. maritima**, *G. peruviana*, *G. punensis**, *G. rufipennis*, *G. saxicolina**, and *G. tenuirostris*; *Hylocryptus* = *H. erythrocephalus* and *H. rectirostris*; *Leptasthenura* = *L. aegithaloides*, *L. andicola*, *L. fuliginiceps*, *L. pileata*, *L. platensis*, *L. sertaria*, *L. striolata*, *L. xenothorax*, and *L. yanacensis*; *Margarornis* = *M. rubiginosus* and *M. squamiger*; *Phacellodomus* = *P. dorsalis**, *P. erythrophthalmus*, *P. maculipectus*, *P. ruber*, *P. rufifrons*, *P. sibilatrix*, *P. striaticeps*, and *P. striaticollis*; *Philydor* = *P. atricapillus*, *P. erythrocercus**, *P. lichtensteini**, and *P. rufus*; *Poecilurus* = *P. candei* and *P. scutatus*; *Pseudoseisura* = *P. cristata*, *P. gutturalis*, and *P. lophotes*; *Pseudocolaptes* = *P. boissonneauitii** and *P. lawrencii*; *Schizoeca* = *S. fuliginosa*, *S. griseomurina**, *S. harterti*, and *S. helleri*; *Sclerurus* = *S. albigularis*, *S. caudacutus*, *S. guatemalensis*, *S. mexicanus*, *S. rufigularis*, and *S. scansor*; *Synallaxis* = *S. albescens*, *S. albigularis*, *S. azarae*, *S. brachyura*, *S. chinchipensis*, *S. cinerascens*, *S. cinnamomea*, *S. erythrothorax*, *S. frontalis*, *S. gujanensis*, *S. macconnelli**, *S. propinqua**, *S. ruficapilla*, *S. rutilans*, *S. spixi*, *S. stictothorax*, *S. subpudica**, *S. tithys*, and *S. zimmeri*; *Thripadectes rufobrunneus* group = *T. rufobrunneus* and *T. virgaticeps*; *Upucerthia* = *U. albigula*, *U. andaecola*, *U. dumetaria*, *U. jelskii**, *U. ruficauda**, *U. serrana**, and *U. validirostris*; *Xenops* = *X. milleri**, *X. minutus*, and *X. rutilans*.

^b The genera *Anabacerthia*, *Berlepschia*, *Geobates*, *Metopothrix*, *Siptornopsis*, *Syndactyla*, and *Xenerpestes* were not included in the analysis because nest data were insufficient for character states to be coded accurately.