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EVOLUTIONARY TRENDS IN THE AVIAN FAMILIES FURNARIIDAE AND DENDROCOLAPTIDAE

by

John Alan Feduccia

A dissertation submitted in partial fulfillment
of the requirements for the degree of
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Doctoral Committee:

Professor Robert W. Storer, Chairman
Professor Claude W. Hibbard
Professor Robert R. Miller
Professor Harrison B. Tordoff

ABSTRACT

EVOLUTIONARY TRENDS IN THE AVIAN FAMILIES
FURNARIIDAE AND DENDROCOLAPTIDAE

by

John Alan Feduccia

Chairman: Robert W. Storer

The relationships between the Neotropical avian families Furnariidae (ovenbirds) and Dendrocolaptidae (woodhewers) have remained an enigma for nearly a century. The controversy has generally taken the form of lumping or splitting the two families by various authors, with little thought given to the actual evolutionary pathways involved.

In this paper evidence is summarized to establish that the Furnariidae and Dendrocolaptidae are very closely related, more so to each other than to any other group of suboscine birds. Anatomical and other evidence further indicates that the Dendrocolaptidae are most closely allied to the members of the subfamily Philydorinae of the Furnariidae and that the Dendrocolaptidae very likely represent several separate offshoots from ancestors that closely resemble the present-day philydorine furnariids (Philydorinae).

The existence of "intermediate" woodhewer genera, Glyphorhynchus, Sittasomus, Deconychura, and Dendrocincla, suggests that the Dendrocolaptidae might represent several separate offshoots from philydorine-like ancestors. Although these genera possess all of the characters that are used to

characterize the family Dendrocolaptidae and are in their tree-trunk foraging behavior almost identical to other members of the Dendrocolaptidae, they possess osteological and plumage characters that closely ally them with the Furnariidae, particularly the Philydorinae. All of the dendrocolaptids except the "intermediates" appear to represent a monophyletic group within themselves. However, the possession in the "intermediates" of a large number of characters intermediate between typical perching and tree-trunk foraging adaptations strongly suggests that they may represent several separate offshoots from philydorine-like ancestors.

In an attempt to test the hypothesis with additional data, electrophoretic patterns of hemoglobin were established for both the Furnariidae and Dendrocolaptidae. Then the "intermediates" were examined. One, Glyphorhynchus, possesses the dendrocolaptid type of hemoglobin pattern. Sittasomus and Deconychura possess a hemoglobin electrophoretic pattern unlike either of the two families, but identical to each other, indicating a close relationship between the two, as was suggested by anatomical data. Dendrocincla, however, shows a hemoglobin electrophoretic pattern identical to that of the Furnariidae, thus lending support to the hypothesis for a separate origin for this form from philydorine-like ancestors.

It is recommended that a subfamily Dendrocolaptinae be placed near to the Philydorinae and that the "intermediate" genera be given subfamilial rank and placed between the Philydorinae and the Dendrocolaptinae.

ACKNOWLEDGMENTS

I am indebted to the following persons and institutions for assistance throughout this investigation. The members of my doctoral committee, Robert W. Storer, Claude W. Hibbard, Robert R. Miller, and Harrison B. Tordoff have provided criticism and encouragement during the entire study. John B. Burch of the Mollusk Division of The University of Michigan Museum of Zoology made his laboratory available to me for biochemical studies, and Gene Lindsay instructed me in various laboratory techniques. The Department of Zoology of The University of Michigan and John M. Allen provided various pieces of laboratory equipment. Various members of the Department of Biology of the University of Costa Rica and particularly Douglass Robinson provided laboratory space and other facilities. Charles F. Walker of The University of Michigan Museum of Zoology, Joe Tosi of the Tropical Science Center, and Jorge Campabadal of the Organization for Tropical Studies were of great help during the Central American phase of the study. Maxwell Cone kindly permitted me to use his finca for studies while I was in Costa Rica. Richard L. Zusi of the U. S. National Museum and James H. Hunt of the Louisiana State University Museum of Zoology

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INTRODUCTION

The Neotropical ovenbirds (Furnariidae) and woodhewers (Dendrocolaptidae) have long been recognized to be closely related on the basis of characters which are shared by the two groups but not found in other suboscine birds. General plumage patterns in the two groups are among the significantly striking similarities, as almost all species have light brown to reddish-brown body plumage with various degrees of spotting on the breast and back, often with light throat patches. A spiny tail, often of chestnut or ferruginous color, which is used in the woodhewers as a brace in climbing, is found in various degrees of development in many members of the Furnariidae and is well-developed in certain ovenbirds which forage like the woodhewers, by climbing up tree trunks. These scansorial furnariids, including Margarornis, Premnornis, Premnoplex, Pygarrhichas, and some species of Cranioleuca, are of interest in that although they are behaviorally similar to the woodhewers, being tree-trunk foragers and possessing stiff, spiny tails, they are clearly members of the Furnariidae on the basis of such important characters as the nature of the syrinx, nasal bones, and feet. Common wing patterns are also found in the two groups; these will

be discussed later. Aside from the above there are skeletal and other characters that ally the two groups.

This sharing of characters has led many ornithologists to question the distinctness of the two families. Thus the familial classification of the furnariids and dendrocolaptids has long been in a state of uncertainty, and at present there is little agreement among ornithologists concerning the recognition of families in the group. Recent classifiers have generally followed either von Ihering (1915), who presented evidence which he considered favored merging the two families, or Ridgway (1911), who recognized two families. In 1951 three classifications were proposed. Wetmore (1951) retained two families because he considered von Ihering's evidence inconclusive; Peters (1951) also recognized two families. However, Mayr and Amadon (1951) treated the entire group as a single family, as did Storer (1960).

Early classifiers (see Garrod, 1876, and Beddard, 1898) placed considerable importance on the condition of the nasal bones in the classification of the higher categories of birds. Two basic arrangements of the nasal openings were distinguished, holorhinal and schizorhinal. In the latter, the nasal opening extends posterior to the nasal-frontal hinge; in the former, the posterior extent of the opening is anterior to the hinge. The condition in Furnarius and other ovenbirds, which was originally

termed schizorhinal (see Garrod, 1877), was later recognized as not homologous to the condition in other schizorhinal birds (charadriiform birds, etc.), and Furbringer (1888) proposed that the term pseudo-schizorhinal be used to apply to the condition in those ovenbirds in which the posterior extent of the nasal opening is rounded, instead of ending in a slit as in "true" schizorhiny.

Garrod (1877) emphasized that the condition of schizorhiny (= pseudo-schizorhiny) in the ovenbirds was of sufficient taxonomic importance to separate the group from the holorhinal woodhewers. However, Garrod had only examined a small number of species. Von Ihering (1915) examined a much larger series of species and concluded that there was actually no clear cut division between the pseudo-schizorhinal ovenbirds and the woodhewers, and that the differences between pseudo-schizorhiny and holorhiny represented slight modifications from a basic pattern and were therefore of little taxonomic importance, except perhaps in characterizing genera. Ridgway (1911), however, had maintained that the difference in the arrangement of the nasal opening, plus the differences in the feet, were of sufficient importance to separate the Dendrocolaptidae from the Furnariidae. In the Furnariidae (sensu Ridgway) the outer toe is shorter than the middle toe and the hallux (without the claw) is not shorter than the inner toe (no. II) without the claw. The middle toe

is united to the outer toe by less than the whole of the second phalanx. In the Dendrocolaptidae (sensu Ridgway) the outer toe is about as long as the middle toe and much longer than the inner toe, and the hallux (without the claw) is shorter than the inner toe. The three anterior toes are united for the entire length of the basal phalanx, and the middle toe is fused to the outer by almost the full extent of the second phalanx.

Ames (1965) was able to separate the dendrocolaptids from most of the furnariids on the basis of syringeal anatomy but found that the syrinxes of furnariids and dendrocolaptids are similar and differ from those of other suboscine birds.

Heimerdinger (1964) found all of the families within the superfamily Furnarioidea to be pterylographically distinct, but the differences do not appear to be great to me.

Attempts by many classifiers to place animals into distinguishable groups without examining in detail the characters involved has led in many cases to classifications based on the most adaptive features of the birds, namely the bill and feet (the classical example being hawks and owls which were at one time classified together on the basis of having similar feet and bills) with little emphasis on deciphering the evolutionary pathways involved. The problem in the woodhewer-ovenbird

groups has been the same as that for other groups of passerine birds where there is a large amount of adaptive radiation for particular modes of life.

The woodhewer-ovenbird problem is of interest for several reasons. First, the two groups are closely allied, yet exhibit the greatest adaptive radiation in any group of New World passerine birds, with climbing forms apparently having evolved independently in many situations. Second, cranial morphology in the two groups differs; therefore, the possibility of resolving the polarity of this evolution exists. Most important, however, are four genera which are normally placed in the Dendrocolaptidae because they possess most of the characters of that family, but which show other characters that ally them with the Furnariidae. These forms, which I shall term the "intermediates" form the starting point for this study.

Initially, my main interest was in the evolution of the different types of cranial morphology in the ovenbirds and woodhewers. An examination of the skulls of woodhewers showed that most forms of the Dendrocolaptidae conformed to a basic pattern. These genera, which include all of the woodhewers except the four intermediates, are the forms that I shall term the "strong-billed" dendrocolaptids; they appear to represent a monophyletic group on the basis of the skull and other characters. The "intermediates," Sittasomus, Deconychura, Dendrocincla,

and Glyphorhynchus, are of particular interest. They are behaviorly like the woodhewers in that they forage by hitching up tree trunks. They also possess the woodhewer type of syrinx and foot arrangement. However, they are clearly intermediate between the holorhinal and pseudo-schizorhinal types of nasal bone arrangements. Further, it was of interest to find that, of the four subfamilies of the Furnariidae (which appear to be fairly well-defined), the members of the subfamily Philydorinae, the forest-dwelling furnariids, are the forms that possess an intermediate arrangement in the condition of the nasal bones, and some, such as Hyloctistes and Automolus, are similar to the "intermediate" woodhewers mentioned above. The other subfamilies of the Furnariidae, the Synallaxinae, Furnariinae, and Sclerurinae are composed almost entirely of members which are pseudo-schizorhinal, although in some species the nasal foramen is somewhat shortened.

This interesting situation led me to a literature survey in which I found the one important paper on the relationships of the woodhewers and ovenbirds, that of von Ihering (1915). In it he discusses the findings of his investigations of the cranial morphology of the two groups, and records much the same observations that I have discussed above. He stated (1915:147) that, "Pronounced holorhiny is found only among the Dendrocolaptinae of which, however, some genera ---- Sittasomus,

Figure 1. The wings of Xiphorhynchus lachrymosus (upper left), Lepidocolaptes souleyetii (upper right), Dendrocolaptes certhia (lower left), and Campylorhamphus pusillus (lower right).



Figure 2. The wings of Margarornis rubiginosus (upper left), Xenops minutus (upper right), Dendrocincla anabatina (center), Glyphorhynchus spirurus (lower left), and Sittasomus griseicapillus (lower right).



Dendrocincla and probably others ---- are typically schizorhinal." At that time he had not examined the genera Glyphorhynchus and Deconychura. He further stated that, "The Philydorinae (Philydor, Xenicopsis, Xenops, etc.) form a transition group leading up to the Dendrocolaptinae and the species are schizorhinal with the exception of Automolus and Anabazenops which have the nasal foramen shortened." Although von Ihering's divisions are not easy to discern it is clear that an intermediate condition of the nasal openings exists in members of the Dendrocolaptidae and the subfamily Philydorinae of the Furnariidae. An examination of the skins of these intermediate species of dendrocolaptids proved even more interesting, for in these forms the plumage patterns were in some aspects also intermediate. One striking plumage character that seemed particularly significant was a rufous wing stripe (see Figs. 1 and 2) which occurs in various members of the Furnariidae, but within the Dendrocolaptidae is found only in Glyphorhynchus and Sittasomus. In Dendrocincla anabatina there is a similar but more diffuse wing stripe. However, Dendrocincla is intermediate in other characters. The tail does not possess the striking, stiff, spine-like rectrices characteristic of all other members of the Dendrocolaptidae and is, in fact more like the type possessed by members of the Philydorinae. Also the bill and general body shape of Dendrocincla appear to be more

philydorine-like than dendrocolaptine. Personal field observations as well as those of other authors show Dendrocincla to be intermediate in behavior (see next section). Thus the four genera, Sittasomus, Deconychura, Glyphoryhnchus, and Dendrocincla, although not sharing identical characters, all possess some features that are intermediate between the Dendrocolaptidae and Philydorinae. Although the "strong-billed" dendrocolaptids appear to be uniform and monophyletic within themselves, the four intermediate genera may be more recent offshoots from philydorine stock, which, despite having reached dendrocolaptid grade with respect to the characters used to classify the group, still have features indicative of their immediate ancestry.

It was not surprising to find a statement by von Ihering (1915: 149) when he stated, "... we can presume that the Dendrocolaptinae sprang from two different groups of the Philydorinae." I therefore continued my investigations of this group of birds in order to obtain evidence either for or against the multiple origin hypothesis for the evolution of the Dendrocolaptidae. The main focus of this study has therefore been the dendrocolaptine-philydorine boundary, but data from the other groups of the Furnariidae are used where necessary.

Anatomical studies have failed to solve this problem, probably because of convergent adaptations for

creeping may mask the actual phylogenies. It seemed to me that useful conservative characters might be found in a comparison of proteins of the various groups. One would need to find a protein character that was consistent within each of the two major groups. Its conservatism could be tested by examining different morphological types within the Furnariidae. Then the crucial point would be examination of the intermediate genera, Sittasomus, Glyphorhynchus, Deconychura, and Dendrocincla.

Eye lens proteins, serum proteins, and hemoglobin were investigated, but only the hemoglobin proved to be consistent within each group.

The remainder of this paper is a presentation of the hemoglobin data and a documentation of the actual evolutionary trends supported by these findings combined with the anatomical data.

The use of electrophoretic patterns of proteins in systematics has been discussed by various authors and will not be covered here. The reader is referred to Sibley (1960), and Kitto and Wilson (1966) for examples of studies utilizing electrophoresis of proteins.

ELECTROPHORESIS OF HEMOGLOBIN

Methods and Materials

Because of the difficulty in obtaining live material, the birds were shot, and blood was extracted immediately either from the brachial region or from a slit in the throat. Most of the birds were still alive after being shot, but when the specimens died immediately, heart extraction was often necessary to obtain sufficient blood. The blood was extracted into a culture tube containing a tablet of potassium oxalate (Cambridge Chemical Products, Inc.) dissolved in 0.5 ml of physiological saline solution. The solution was then placed immediately on ice. Red blood cells were precipitated by centrifugation and hemoglobin was prepared by washing the red cells three times with saline and lysing the cells with distilled water. The final solution was about 5 percent hemoglobin.

Disc electrophoresis with acrylamide gel modified from the technique described by Ornstein (1964) and Davis (1964) was employed. This technique has been used previously for avian serum proteins by Desborough and Irwin (1966). In this technique one utilizes a 2.5 inch glass tube that is layered with three acrylamide gels, each of which is polymerized within the tube. The lower

or "running" gel, which is a 7.5 percent acrylamide solution is poured to a height of 2 inches. The next gel is a 1/4 inch layer of a 3 percent acrylamide solution known as the "spacer" gel. Having a larger pore size than the "running" gel, the "spacer" serves to stack the various protein components in decreasing order of mobility before reaching the "running" gel. The upper gel, which has the same gel composition as the "spacer" but is 50 percent more concentrated, is mixed with the sample. The tubes containing the gels are placed in the electrophoresis apparatus so as to bridge the gap between two buffer solutions of the same composition. The buffer used here was a Tris-glycine solution at pH 8.5. Brom-phenol blue was added to the buffer. Ten gel tubes were electrophoresed simultaneously, with each tube conducting 5 ma. The apparatus was kept in a cold room at a constant 50° F during the run time, which was approximately 30 minutes. The current was terminated when the Brom-phenol blue front had migrated 32 mm. Then the gel columns were removed from the glass tubes and stained for protein by 0.2 percent Amido Black in a 5:5:1 solution of water, methanol, and acetic acid. The gels were destained and stored in 8 percent acetic acid solution. To make sure that the resulting bands represented only hemoglobin, a dianisidine stain specific for hemoglobin was used occasionally as a check. As a control for gel consistency, human serum was

electrophoresed with each electrophoretic run. When the human serum runs were not consistent with previous samples, additional runs were made until consistency was achieved.

Because precise quantification of the hemoglobin samples that were electrophoresed was extremely difficult, several runs of different concentrations were made for each sample to insure that concentration did not effect the qualitative nature of the bands. The concentration in no way effected the nature of the bands, except their widths.

Densitometric tracings were made with a Canalco Model E microdensitometer.

Because all of the runs do not represent equal quantities of hemoglobin, the densitometric tracings are not always comparable. Therefore, only the average curves for each species are given.

Results and Discussion

In the system utilized here two anodally migrating hemoglobin bands were resolved. To check for cathodal bands, the tubes were reversed; no bands were noted. The hemoglobin pattern from the following species of the Dendrocolaptidae were nearly identical: *Xiphorhynchus triangularis*, *X. lachrymosus*, *X. guttatus*, *Campylorhamphus pusillus*, *Lepidocolaptes souleyetii*, and *Dendrocolaptes certhia* (Fig. 4). The "dendrocolaptid" pattern (Fig. 3) is characterized by one very strongly

staining band that migrates approximately 4-5 mm from the origin and a very lightly staining, faster migrating band that migrates approximately 12-13 mm from the origin. The hemoglobin patterns from the following species of the Furnariidae were nearly identical: Synallaxis albescens, Margarornis rubiginosus, Cranioleuca erythrops, Automolus ochrolaemus, Thripadectes rufobrunneus, Hyloctistes subulatus, Xenops minutus, and Pseudocolaptes lawrencii (Figs. 5 and 6). The "furnariid" pattern (Fig. 3) is characterized by two anodally migrating bands of more equal quantity than those of the dendrocolaptids. There is a stronger staining band that remains at the origin and a more lightly staining band that migrates approximately 10-11 mm from the origin. The patterns were so easily separable that I could distinguish within 15 minutes after the beginning of the run whether or not the tube in question contained furnariid or dendrocolaptid hemoglobin by observing the conspicuous red bands migrating within the gels. I am therefore confident, although in most cases the sample size is small, that the differences presented here are real, and are not due to any error in technique or procedure.

With patterns established for each group, it was of great interest to investigate the hemoglobin patterns from the "intermediate" genera of dendrocolaptids, Dendrocincla, Sittasomus, Deconychura, and Glyphorhynchus

(Figs. 6 and 7). Two samples were obtained from Glyphorhynchus spirurus; the hemoglobin pattern is indistinguishable from that of the other dendrocolaptids. One sample from each of Sittasomus and Deconychura was obtained. These two forms have hemoglobin patterns very much similar to each other and more like the dendrocolaptid than the furnariid pattern, but slightly different from the former. These two genera show one very strongly staining band approximately in the same position as the equivalent dendrocolaptid band, but the faster migrating band is stronger than its dendrocolaptid equivalent, and migrates 15 mm in both Sittasomus and Deconychura. Blood samples were obtained from three specimens of Dendrocincla anabatina; the pattern for this genus is indistinguishable from that of that of the furnariids.

Figure 3. Electrophoretic patterns of hemoglobin with diagrammatic illustrations of A, furnariids; B, dendrocolaptids; and C, Sittasomus and Deconychura.

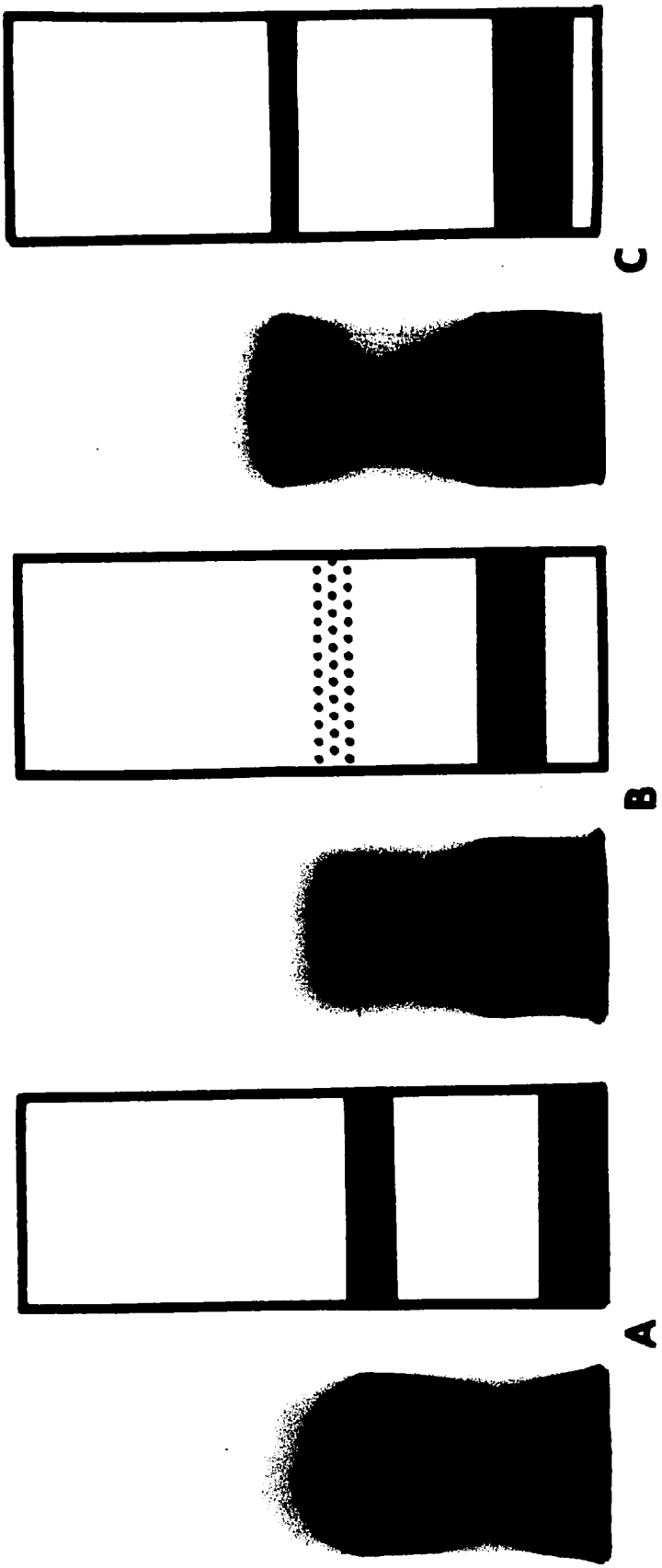
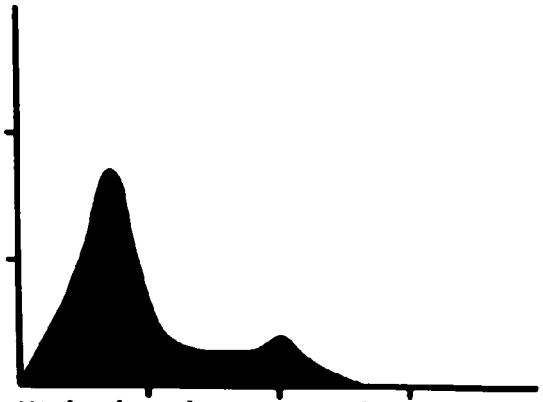
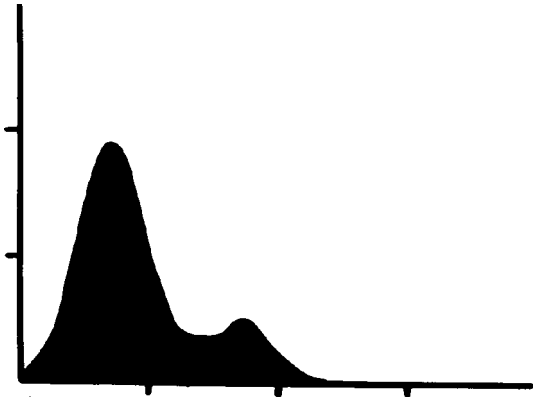

C
B
A

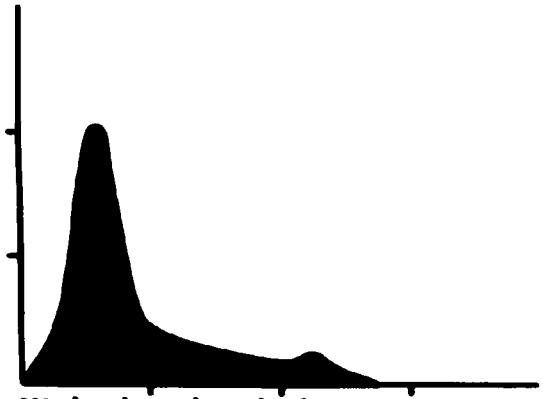
Figure 4. Average densitometric curves from hemoglobin electrophoretic patterns of dendrocolaptids. The marks on the abcissas and ordinates are equidistant from each other to serve as guidelines for comparison.



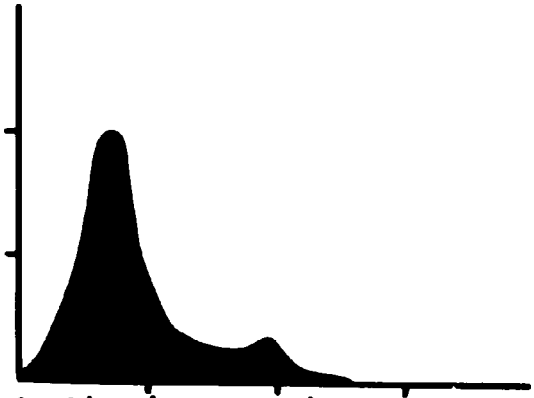
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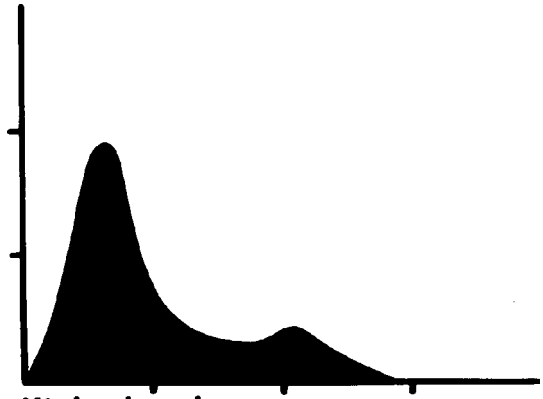
Campylorhamphus pusillus



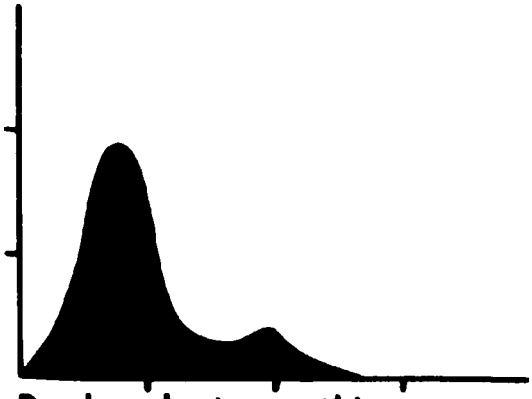
Xiphorhynchus lachrymosus



Lepidocolaptes souleyetii

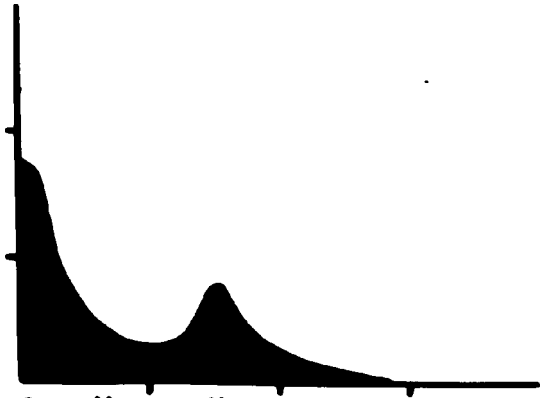


Xiphorhynchus guttatus

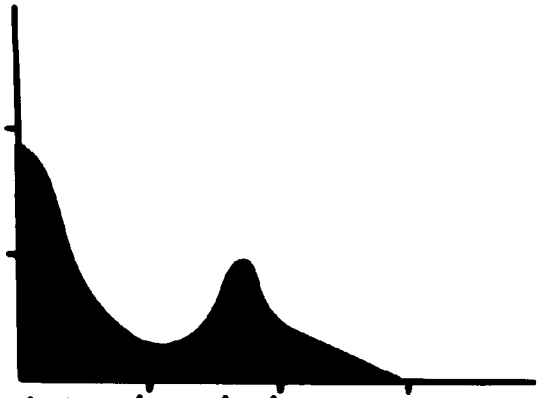


Dendrocolaptes certhia

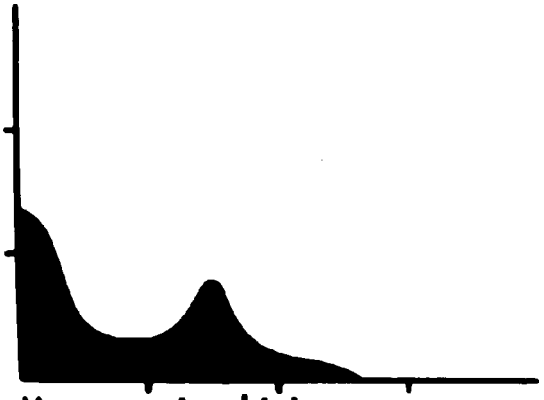
Figure 5. Average densitometric curves from hemoglobin electrophoretic patterns of furnariids.



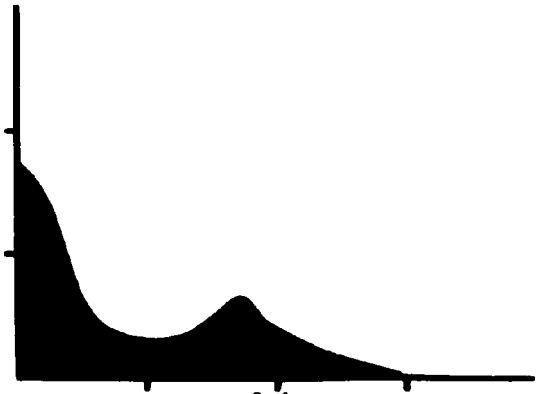
Synallaxis albescens



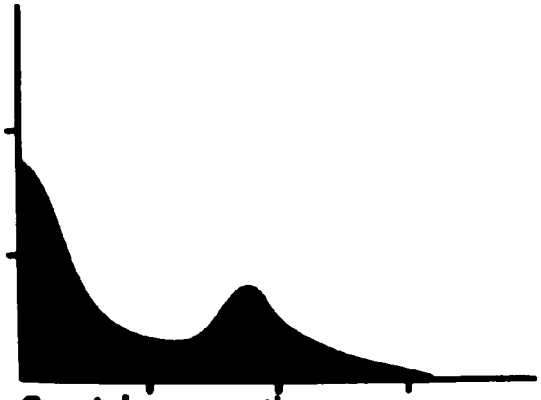
Automolus ochrolaemus



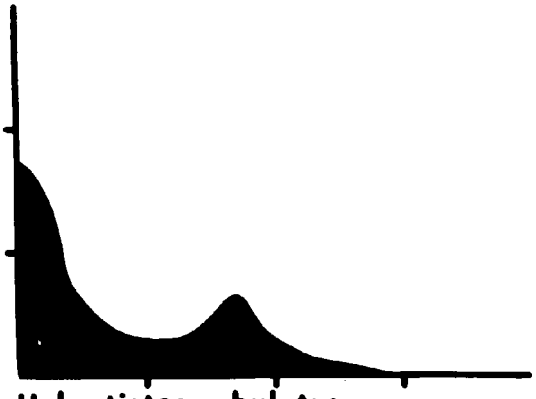
Margarornis rubiginosus



Thripadectes rufobrunneus

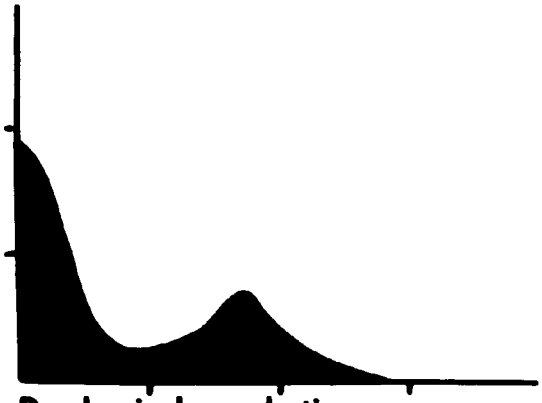


Cranioleuca erythrops

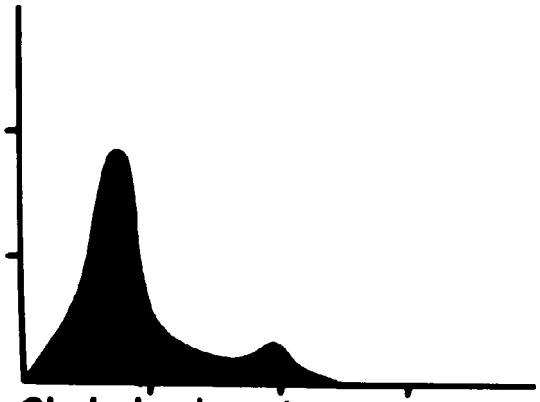


Hyloctistes subulatus

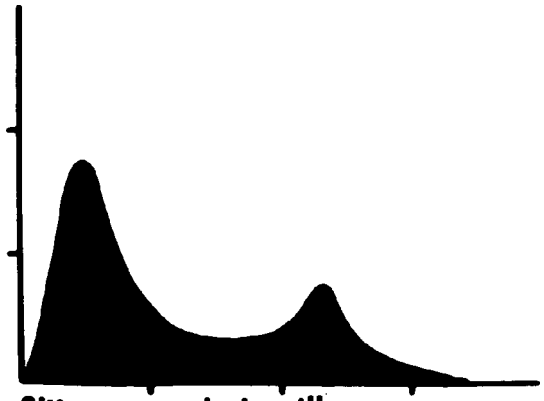
Figure 6. Average densitometric curves from hemoglobin electrophoretic patterns of the four intermediate genera, Dendrocincla, Glyphorhynchus, Sittasomus, and Deconychura, and from two species of furnariids (bottom).



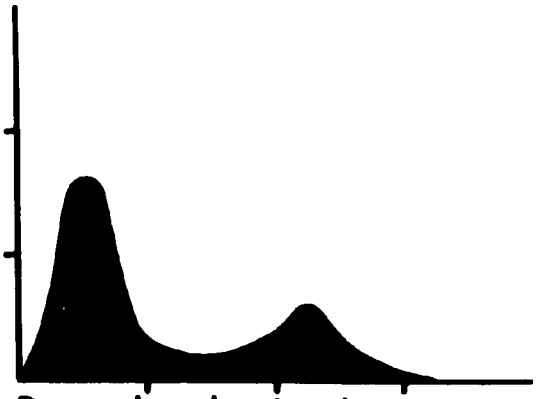
Dendrocincla anabatina



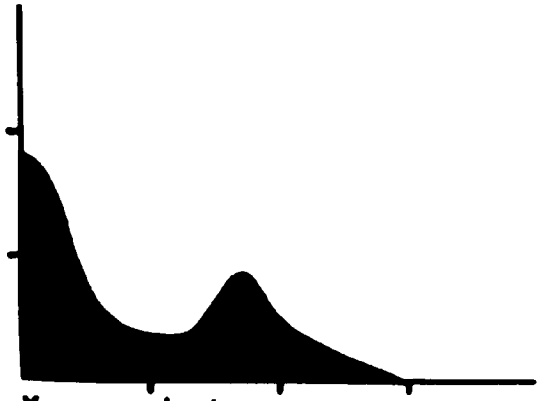
Glyphorhynchus spirurus



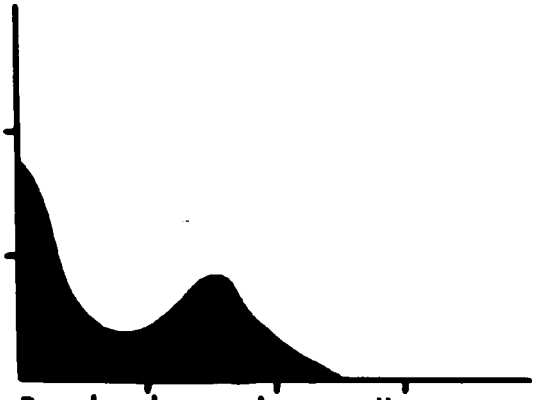
Sittasomus griseicapillus



Deconychura longicauda

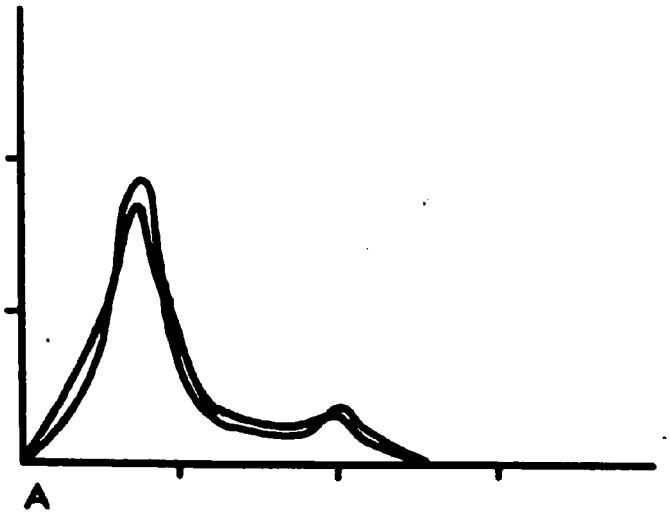


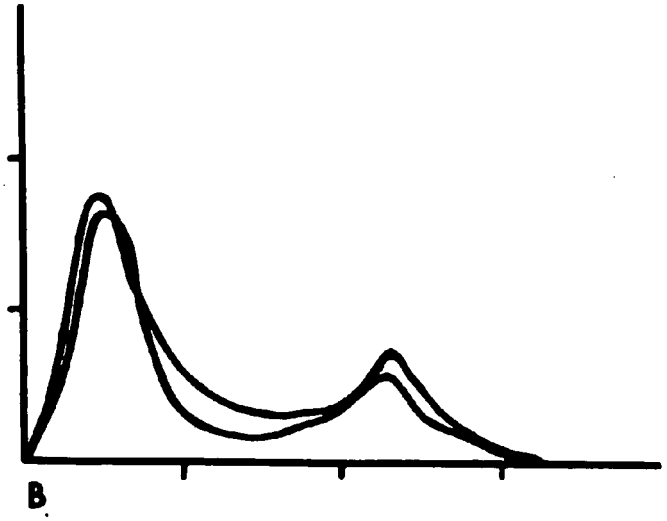
Xenops minutus

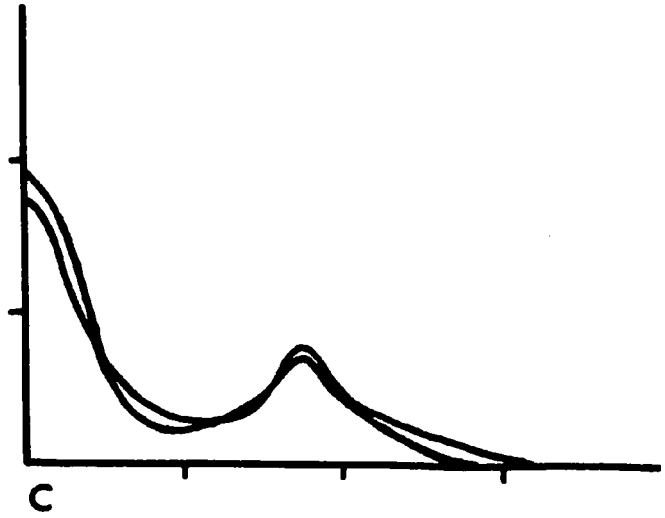


Pseudocolaptes lawrencii

Figure 7. Superimposed densitometric curves from hemoglobin electrophoretic patterns of A, Glyphorhynchus spirurus and Xiphorhynchus lachrymosus; B, Deconychura longicauda and Sittasomus griseicapillus; and C, Dendrocincla anabatina and Cranioleuca erythrops.


A


B


C

NATURAL HISTORY AND ZOOGEOGRAPHY

The information in this section is derived from many sources, including my own observations in Central and South America. Except for very specific information, individual citations are not made, since the information for a given species may be much the same in many sources and my own notes. Most of the useful information on the natural history of the groups was derived from Johnson (1967), Miller (1963), Sclater and Hudson (1888), Skutch (1945, 1952), Slud (1960, 1964), and Wetmore (1926). Other sources include the following: Belcher and Smooker (1936), Chubb (1916-1921), Davis (1940), Dickey and van Rossem (1938), Edwards and Lea (1955), Eisenmann (1952), Euler (1867), Goeldi (1894, 1896), Harper (1932), Hartman (1957), Haverschmidt (1967), Herklots (1961), Howell (1957), Hudson (1920), Koepcke (1954, 1964, and 1965), Mac Donagh (1933), Miller (1960), Naumburg (1930), Otvos (1967), Paynter (1955), Pereyra (1927), Renard (1918), Rodriguez (1918), San Martin (1927), Schafer and Phelps (1954), Skutch (1945, 1947, and 1967), Todd and Carriker (1922), Van Tyne (1926, 1935), Vuilleumier (1967), Wetmore (1939), Willis (1966, 1967), and Young (1925). Zoogeographical information was obtained from Eisenmann

(1955), Meyer de Schauensee (1966), and Peters (1951). Although the above sources are by no means a complete list of the literature on the Furnariidae and Dendrocolaptidae, I do feel that they represent most of our present knowledge of the groups.

Dendrocolaptidae

The Dendrocolaptidae are an extremely uniform group, and, with a few notable exceptions which will be discussed later, are similar to one another in both anatomy and behavior. Even the "intermediates," with the exception of Dendrocincla, conform to the general behavioral pattern of the group. The 48 species which comprise this family are distributed from tropical southern Mexico through Central America and South America except in the high Andean regions and in the southern portions of the continent. The Dendrocolaptidae may be considered South American with some representation in Central America, largely of forms widespread in South America. There are only five species of woodhewers confined to the Central American region. Three of these species, Dendrocincla anabatina, Xiphorhynchus flavigaster, and Lepidocolaptes affinis occur throughout much of Central America; Lepidocolaptes leucogaster is known only from western and central Mexico; and Xiphorhynchus striatigularis is known from one specimen taken in Tamaulipas,

Mexico. Also, there is no striking species diversity from north to south through Central America, again an indication of the widespread ranges of the Central American species. There are 13 species of woodhewers in Mexico, 12 in Guatemala, 8 in British Honduras, 13 in Honduras, 7 in El Salvador, 14 in Nicaragua, 16 in Costa Rica, and 17 in Panama. In South America the great diversity of woodhewers is centered in the Amazon Basin, the number of species diminishing in the periphery of the forested basin. There are none in the high Andes, most of the area west of the Andes, and in southern South America. The number of species diminishes with increasing altitude in the forested Andean foothills and in the more arid areas (this is also true of Central America). There are 38 species known to occur in Brazil (mainly within the Amazon Basin), 26 in Peru, 26 in Colombia, 23 in Ecuador, 26 in Venezuela, 22 in the Guianas, 20 in Bolivia, 12 in Argentina, 12 in Paraguay, 2 in Uruguay, and none in Chile. The distribution pattern of the Dendrocolaptidae shows restriction to lowland tropical forest, and strongly suggests an Amazon Basin origin for the family.

Woodhewers of the genus Xiphorhynchus are fairly typical of the family and will be used as the basis of comparison with other forms. Species of this genus, although primarily forest forms, also occur in semi-open situations and forest borders. Some occur in mangroves.

They forage, like most woodhewers, by hitching up the trunks of trees or along branches. They use the stiff, spiny tail as a brace in climbing, and with the feet positioned well out laterally from the sides of the body, the birds are well away from the surface of the tree. They hitch straight up the trees or in spirals, searching for insects, other invertebrates, or small cold-blooded vertebrates (small frogs, salamanders and lizards), frequently stopping to peer under loose bark, and into moss clusters, vegetation clusters, or ephiphytic plants, looking up into the cracks and crevices of these situations with one eye, then proceeding. Although peering is more typical foraging behavior, there are many instances of woodhewers probing, prying, and pecking at bark and small objects. After "completing" a tree they fly in a strong, undulating flight to or near the base of another tree to begin the cycle again. Some species are found high in the forest, while others forage primarily at the lower levels. Several species have been recorded feeding on the ground. They are usually seen singly or in two's, often accompanying mixed species foraging flocks, and some species often follow army ant swarms, taking insects that are scared up by the ants off the bark of trees, or fly-catching for them.

Dickey and van Rossem (1938: 323) recorded the following concerning Xiphorhynchus flavigaster: "In its

methods of procuring food it is almost as versatile as a flicker and frequently descends to the ground, working among the litter of dead leaves with quick side strokes of the bill. Fallen logs and dead trees are also favorite hunting places, the smaller slabs of bark being pried off and not picked or hammered. Dead branches are often hammered, not with the rhythm of a woodpecker, but in irregular raps like a nuthatch." They further add of X. flavigaster, "Backing down, a most unwoodpecker-like proceeding, is done almost as quickly as climbing the tree."

Species of the genus Lepidocolaptes resemble small forms of the genus Xiphorhynchus, and in their behavior are very similar.

Wetmore (1939: 215:216), recorded of Lepidocolaptes souleyetii that, "My attention was attracted to one by its steady pecking at the trunk of a tree, a noise that I attributed at first to some woodpecker." Wetmore (1926: 236), stated of L. angustirostris that, "Their long bills were frequently thrust into the recesses of small air plants, or under moss and loose bark, which was pried away with a quick twist of the head to expose any animal life concealed beneath."

Slud (1964: 201), says of L. souleyetii, "Sometimes it playfully juggles a hard-bodied insect from the tip of the bill to its mouth. Other woodhewers may do

so, too, but less frequently. It also flakes bark."

Dickey and van Rossem (1938: 325), stated concerning the habits of L. souleyetii, "Beginning at the bottom of a tree, they work slowly upward, usually spiraling the trunk and branches, then sail downward to the butt of the next. That they can back down a tree almost as well as they can climb was observed several times."

Miller (1963: 21), stated of L. lachrymiger, "We watched one digging at, or 'hewing,' the mossy covering of a trunk."

Skutch (1945: 86), stated of the bill of L. souleyetii that, "Chiefly, it is a probe for extracting insects from the fissures where they lurk; but sometimes the bird will pry off a loose flake of bark or will pull the moss from the trees." He also recorded this species once descending head downward, and in approaching its nest, hitching down tail first.

The genus Dendrocolaptes, and the largest of the woodhewers, the genus Xiphocolaptes, are also typical woodhewers in their foraging behavior. Of interest, however, is Xiphocolaptes major which Wetmore (1926: 241) has recorded feeding on the ground in fairly open groves. Sclater and Hudson (1888: 201) recorded a communication from White concerning the habits of X. major as follows: "Common here in the dense forest, where their continued

hard pecking at the lofty tree-trunks is very accentuated. Two or three at a time maintain a continued race up a magnificent clear stem as far as the branches, when they fly to the bottom of the next and do likewise." Drymornis bridgesii, the only species of the genus, is known only from Argentina, Paraguay, and Uruguay, where it is usually seen in small flocks in fairly open forest. Although it often forages like a typical woodhewer, hitching up tree trunks, it also uses its long, slightly decurved bill for probing in the ground, and small flocks may be seen foraging on the ground. When collected they are often noted to have mud caked on the base of the bill.

Sclater and Hudson (1888: 200), citing a communication from Barrows, wrote, "In the stomach of the first one killed I found the silken sac, three fourths of an inch in diameter, or the eggs of a large spider, which makes holes ten or twelve inches deep in the hard soil everywhere." Wetmore (1926: 241) records, "Though they climbed readily, they seemed to prefer to rest on a sloping limb of good size and in such situations frequently ran along the branches instead of hitching about with the aid of the tail. The species of Campylorhamphus, commonly known as the scythebills because of their long decurved bills, generally forage like typical woodhewers, hitching up tree trunks, commonly searching among vegetation clusters and bromeliads for food. Slud (1964: 202)

says of C. pusillus that, "Unlike the other woodhewers of Costa Rica, it sometimes investigates a fallen trunk." Walter Markl (pers. comm.) recorded a scythebill in northern Peru foraging by hanging upside down on small, moss-covered Bombax branches; he recovered scorpions from the stomach of the collected specimen. Deconychura and Sittasomus are small woodhewers that are generally encountered in forest at low to medium heights; they forage like typical woodhewers. Glyphorhynchus, the wedge-billed woodhewer, is another small member of the family. It forages like most woodhewers, climbing vertically up tree trunks, and also along branches, usually at medium heights in the forest, peering, and prying away small pieces of bark. Glyphorhynchus also often pecks like a small woodpecker, producing a loud tapping sound comparable to that produced by a Downy Woodpecker. I have collected two specimens which had woodpulp caked about the base of the bill. Species of the genus Dendrocincla are found in the lower levels in the forest and are usually encountered in small groups following army ant swarms, picking up insects off the ground or from low tree trunks, foraging in the typical woodhewer fashion, or fluttering out to catch insects in the air which are flushed by the army ants. The versatile woodhewers of the genus Dendrocincla are the most ovenbird-like of the group and are often seen perched in a "normal" fashion,

unlike typical woodhewers, and in many respects resemble the philydorine furnariids (see discussion for further information on the genus Dendrocincla).

Woodhewers typically nest in natural cavities or holes, stumps, or abandoned woodpecker holes from a few feet above the ground to medium heights in the forest. Two white eggs are generally laid. Few sources list food items for the woodhewers. Haverschmidt (1967) gives the orders and some families of insects and other food items taken by the species which occur in Surinam, but he does not give percentages of the diet that each food type composes. It is of use, however, to list the food items that he gives. For Dendrocincla fuliginosa are listed the Orthoptera, Coleoptera, and Arachnoidea; Glyphorhynchus spirurus, Coleoptera, Diptera, and Isoptera; Dendrexetastes, Coleoptera (Lamellicornia), and Orthoptera (Locustidae); Hylexetastes, Coleoptera (Lamellicornia, and Curculionidae), and Hymenoptera (Vespidae); Dendrocolaptes certhia and picumnus, Coleoptera (Elateridae, Curculionidae, and Cerambycidae), Orthoptera (ootheca of Mantidae, and Blattidae), Hymenoptera (Formicidae and Apidae), Diptera, Hemiptera (Heteroptera and Homoptera: Fulgoridae), Arachnoidae (Araneida and Scorpionidae), and Mollusca (Gastropoda); and for Xiphorhynchus picus, obsoletus, guttatus, and pardalotus, Orthoptera (Locustidae, Blattidae, Gryllidae, and ootheca of Blattidae), Coleoptera

(Elateridae and Xylopidae), Hymenoptera (Homoptera: Cicadidae and Fulgoridae, and Heteroptera), Arachnoidea (Araneida), Lepidoptera (larvae), and small lizards (Teidae).

Otvos (1967) recorded one stomach of Lepidocolaptes affinis which contained 37 percent Coleoptera and the remainder insects and other arthropods, and two stomachs of Dendrocolaptes certhia which contained 60 percent Orthoptera, plus other insects.

Dickey and van Rossem (1938) recorded for food items of Xiphorhynchus flavigaster, larvae of wood borers, small beetles, and other insect remains; and for Dendrocolaptes certhia, large insects and a centipede, and Slud (1942: 198) states that D. certhia preys on "invertebrates and cold-blooded small vertebrates."

I examined the stomachs of the woodhewers that I collected and recovered the following food items. Three stomachs of Dendrocolaptes certhia contained mainly medium-sized, hard-bodied beetles, but also one roach, one centipede, and one coleopteran. Three stomachs of Xiphorhynchus lachrymosus produced a small frog, a small lizard, many hard-bodied beetles of medium size, a roach, a cicada, two centipedes, and two silken spider egg sacs. Two stomachs of Xiphorhynchus guttatus contained many hard-bodied beetles, and a spider egg sac; and two stomachs of Xiphorhynchus triangularis contained many hard-bodied

beetles, one roach, and other insects. One stomach of Campylorhamphus pusillus contained mainly beetles, but also one spider and an orthopteran. Four stomachs of Lepidocolaptes souleyetii contained mainly medium-sized, hard-bodied beetles, but also ants, one roach, a large grasshopper, and two silken spider egg cases. Three stomachs of Dendrocincla anabatina contained many medium-sized beetles, small insects, and several ants and a scorpion. One stomach of Deconychura longicauda produced small insects, mainly beetles, some orthopterans, one scorpion, one cicada, and other small insects.

Philydorinae

The distribution of the subfamily Philydorinae, the subfamily of the Furnariidae which contains members most closely resembling the woodhewers morphologically, is almost identical to that of the Dendrocolaptidae. The 50 species of the Philydorinae occur from southern tropical Mexico, south throughout Central and South America except in the high Andean regions, the arid regions west of the Andes and in the extreme south of the continent. Again, like the Dendrocolaptidae, the Philydorinae are primarily South American, with extra-limital representation in Central America. There is only one philydorine species, Thripadectes rufobrunneus, which is confined to Central America, the remainder of

the Central American forms being widespread South American species. There is no striking increase in species in this subfamily from north to south through Central America until one reaches Costa Rica and Panama, where the number greatly increases due to the influx of South American species. Four species occur in Mexico, 4 in Guatemala, 4 in Honduras, 2 in British Honduras, 1 in El Salvador, 4 in Nicaragua, 10 in Costa Rica, and 11 in Panama. In South America this group closely parallels the Dendrocolaptidae in distribution, being primarily a lowland tropical forest group, with some representation in the forest of the eastern Andean slopes and with a few species in the drier areas. But, the great majority of species is confined to the Amazon Basin and its periphery. The philydorines are, however, better represented in the highland areas than are the woodhewers. There are 32 species which are known to occur in Brazil, primarily in the forested Amazon Basin, 26 in Peru, 27 in Colombia, 28 in Ecuador, 23 in Venezuela, 18 in the Guianas, 17 in Bolivia, 11 in Argentine, 11 in Paraguay, 2 in Uruguay, and none in Chile. Again, as in the Dendrocolaptidae, this group increases in diversity towards the Amazon Basin, suggesting this area as the place of origin for the group.

The philydorine furnariids, commonly known as the foliage-gleaners, are heavy-bodied forest forms. Pseudocolaptes, a highland member of the group is usually

encountered singly or in pairs. Continually on the move, it climbs like a woodhewer up tree trunks, vines, and the under sides of limbs, and also forages around bromeliads, vine clusters, and other such growths. Thripadectes, another highland and subtropical genus, is found in dense undergrowth and thickets. It forages in a variety of ways, hopping along limbs, and examines vegetation clusters and epiphytes. It may also climb lianas, or cling upside down in the manner of a titmouse. Species of the genus Automolus show a decided preference for the dark, thick undergrowth of the forest where they forage busily, creeping along branches and vines, clinging to vegetation clusters, and gleaning bromeliads and other such growths. Automolus ochrolaemus has been noted creeping head downward, climbing sideways, and clinging in inverted posture in vine tangles. Although there is little information in the literature on the genus Philydor, the species of this genus appear to be typical of the philydorine furnariids. These forms are arboreal and forage among vines and dense vegetation in heavy forest. The species of Anabacerthia, like the forms mentioned previously, show great diversity in foraging behavior. Although their stance in foraging is usually horizontal, they may hang upside down and forage much like a titmouse, or dart about among the branches in search of food. They have been noted frequently hammering objects and pecking

twigs. Hyloctistes, also a typical philydorine, forages by creeping and clinging about in the thick foliage, investigating vegetation tangles, bromeliads, and similar growth, usually at greater heights in the forest than other philydorines. The species of Syndactyla are found in dense growths in the forest in the lower levels, where they rummage about like the forms of Automolus or other philydorines. The species of Xenops are small-bodied and have a peculiar wedge-shaped bill, upturned below. They are found at all levels of the forest, but primarily at medium heights, and often occur in the company of mixed species foraging flocks. They are best known for their foraging behavior which is very similar to that of the North American titmice and chickadees. They are commonly seen in leaf and vine tangles in search of food, often clinging to small branches, or hanging upside down. They also work up or down lianas, right side up or in inverted posture, and may assume a woodhewer posture and hitch up branches. Xenops minutus is frequently recorded pecking on tree trunks, branches, or leaf clusters like a small woodpecker or piculet. The three species of Pseudoseisura, an aberrant genus of the Philydorinae, occur in the dry, fairly open country in parts of southern South America. In their size, crests, and chattering notes, they resemble jays. They are found in small groups in dense growths of thorny scrub where they forage near the

ground, often feeding on the ground in company with the woodhewer, Drymornis bridgesi (Wetmore, 1926: 241). The typical philydorine furnariids, such as Automolus, Anabacerthia, Thripadectes, etc., have the same nesting habits. The nest is a hole tunneled in the side of a bank, expanded at the end where two white eggs are placed on a nest mat of rootlets or similar material. Xenops nests in natural cavities, perhaps partially excavated by the birds themselves, which are located at medium heights in trees. Two white eggs are laid in the nest, which is made of fine plant fibers. The nest of Pseudoseisura is a huge stick structure up to three feet in diameter, which is placed in a bush near the ground. There is a tube in the side leading to the brood chamber in the center. Naumburg (1930: 242-243), records that the nest cavity of P. cristata "... was lined with bits of bark and several pieces of cast snake skin, also throughout the entire nest-mass were interspersed many long quill feathers (from black vultures, ibises, and hawks), some snail shells, land-crab shells, and pieces of bone." Three to four white eggs are laid.

Haverschmidt (1967) recorded food items for some of the philydorines. For Philydor erythrocercus and pyrrhodes are listed Orthoptera (Locustidae and ootheca of Blattidae), Coleoptera, Hymenoptera (Formicidae), and Arachnoidea (Araneida); Automolus ochrolaemus, Arachnoidea,

Orthoptera (Blattidae), and Hymenoptera (Formicidae); and Xenops minutus and tenuirostris, Orthoptera (Gryllidae), Hymenoptera (Formicidae), Coleoptera (Xylopidae).

Van Tyne (1926) reported collecting a female of Automolus ochrolaemus as it was carrying Anolis limifrons to its nest. I examined the stomach contents of the two nestlings which are now in the UMMZ alcoholic collection and recovered various insect remains, two large spider egg sacs, and remains of Anolis.

Stomachs from two specimens of Pseudocolaptes lawrencii contained mainly beetles, but one scorpion, and many other medium-sized insects. Two stomachs of Xenops minutus contained only small insects, mainly coleopterans. One stomach of Automolus ochrolaemus produced one large grasshopper. One stomach of Thripadectes rufobrunneus contained small beetles and two caterpillars, and one stomach of Hyloctistes subulatus contained one medium-sized beetle, and many small insects.

Furnariinae

This subfamily of the Furnariidae, which contains the ovenbirds, Furnarius, has no Central American representatives. The 39 species that comprise this group are confined to areas in South America generally outside of the Amazon Basin region, mainly in the open country of the Andes up to very high altitudes, the drier areas west

of the Andes, and southern South America, going to the extreme southern tip and Tierra del Fuego. There are 11 species in Brazil, 20 in Peru, 13 in Bolivia, 3 in Ecuador, 3 in Colombia, 1 in Venezuela, 1 in the Guianas, 4 in Paraguay, 5 in Uruguay, 22 in Argentina, and 17 in Chile.

The Furnariinae is composed almost entirely of terrestrial and semi-terrestrial furnariids that inhabit open and semi-open areas of the Andean region and southern South America, but there are several forest forms. Species of the genus Cinclodes occur in a number of habitats, but primarily in the high Andean areas in the northern part of their range and descend to lower elevations and coastal regions in the southern part of their range. They are normally found in the Andes near swift-running streams where they walk on the ground in quick bobbing movements, with a constant wagging of the tail. Although usually seen foraging in rocky situations on the ground, they occasionally fly in low undulating flight to alight in a small bush. Some species forage along the coast in the littoral zone. The thrasher-like genus Upucerthia occurs in fairly open country, scattered with bushes. They walk and run along the ground, but are also seen perched low in shrubs, and when alarmed, they fly with a strong undulating flight just above the bushes. Ochetorhynchus is very similar in appearance and in habits to Upucerthia but has a straight

instead of a curved bill as in the latter. Members of the lark-like genus Geositta are terrestrial inhabitants of grassy pampas, sandy slopes, and other similar open country from sea level well into the high Andes, where they are seen walking or running along the ground, pausing, and with jerking mannerisms, repeating the process, often flying for a short distance. The monotypic genus Geobates is somewhat similar to Geositta, and Naumburg (1930: 222) stated that, "In habits this bird acts much like one of the small larks. It frequents the more open parts of the savanna country and was never seen to perch in trees." Eremobius occurs in the steppe country of Argentina where it is found in patches of low thorny brush. Usually concealed among the brush, it runs along the ground with the tail held at an angle over the back; it occasionally flies for short distances low over the ground. The aberrant monotypic genus Chilia occurs in scanty vegetation in semi-arid situations in Chile where it frequents rocky outcrops or clumps of vegetation. The species of Furnarius, the ovenbirds, forage almost exclusively on the ground, nodding their heads in a nervous manner. They normally occur in areas with some woodland cover, and a lowland Amazon species occurs near streams. The name ovenbird is derived from the nest of Furnarius which is a domed mud structure resembling an oven. The nest is generally placed off the ground in a tree or post; two to five white

eggs are normal. Species of the genus Cinclodes prefer to use a hole or burrow for a nesting site, but nests of some species have been recorded on the girders of shearing sheds, interiors of abandoned houses, etc. Three to four white eggs are typical. The nest of Chilia is placed among rocks, in a hole in a cactus or dug in an earth bank; three to four white eggs are placed in the bulky nest which is made of dry sticks lined with feathers. The nests of Upucerthia, Ochetorhynchus, and Geositta are tunnels dug in a sand dune or bank, three to ten feet in length, at the end of which is a chamber lined with grass or other soft material on which two to five white eggs are laid.

Johnson and Goodall (1967) indicate that the food of the Furnariinae includes some seeds but is mainly small insects. Cinclodes feeds on insects, grubs, fresh-water crabs, small crustaceans, and other forms of aquatic life, and the littoral forms feed on the marine equivalents. However, for the most part the members of the Furnariinae are insectivorous.

Sclerurinae

The genus Sclerurus is an extremely uniform group of six species which range from southern Mexico south throughout much of the Amazon Basin where they occur in the rather dense humid subtropical and tropical forests, and are found either on the ground, or rarely on

low perches. No species is confined to Central America.

These terrestrial forms obtain almost all of their food from the soft ground and humus of the forest floor by the peculiar habit of seizing leaves with the bill and throwing them aside, and then probing into the soft ground in search of larvae and small insects. Often when specimens are collected, their beaks are covered with mud. The species of Sclerurus also probe the decaying parts of rotting logs on the forest floor. They progress along the forest floor in short leaps, occasioanlly fluttering along close to the ground. When disturbed they may fly away a short distance in a low flight and alight again on the ground. They exhibit the erratic movements typical of the forest ovenbirds, alighting on buttresses or large roots and making quick jerky movements with a downward bobbing of the tail. Their nests are tunnels dug either in the steep banks of a forest path or along some small creek. The entrance of the tunnel is usually several inches in diameter, and the tunnel may extend several feet deep, often deviating slightly to the right or left, and ending in a larger cavity where a nest of loose plant material is placed. Two white eggs are typical.

The other member of the subfamily Sclerurinae, Lochmias nematura, is a wren-like furnariid which occurs in the Darien region of Panama and in South America. This species lives low near the ground among bushes and low-

lying vegetation. The nest is similar to that of Sclerurus.

Pygarrhichas

The systematic position of this monotypic genus remains uncertain. This species, which occurs in forested areas of Argentina, hitches up and down trunks and branches, using its stiff, spiny, woodhewer-like tail as a brace in climbing. Pygarrhichas bores its own hole for a nesting site in decayed trunks or branches, but more particularly stumps left in areas gutted by fire. It is interesting that although woodpecker holes are available, they are not used as nesting sites. The nest is generally at a height of from 12-20 feet, and two to three white eggs are laid on the debris produced by the drilling (Johnson, 1967).

Synallaxinae

The subfamily Synallaxinae is composed of small to medium-sized furnariids which generally occur in non-forested areas, or forest periphery. Like the previous groups, the Synallaxinae are South American. There are only three out of the 115 species of the subfamily confined to the Central American region. These are Synallaxis erythrothorax, which occurs throughout much of Central America, and two species of Margarornis, which are confined to the mountains of Costa Rica resulting from the occurrence there of primarily South American species. There is one species known to occur in Mexico, one in Guatemala, one in British Honduras,

two in Honduras, one in El Salvador, one in Nicaragua, five in Costa Rica, and seven in Panama. In South America this subfamily reaches its greatest diversity in areas outside of the Amazon Basin, in the open, drier areas, the high Andes and areas west of the Andes, and in the southern areas, from mid-Brazil south. There are 41 species known to occur in Brazil, 55 in Peru, 39 in Bolivia, 29 in Ecuador, 32 in Colombia, 25 in Venezuela, 10 in the Guianas, 38 in Argentina, 18 in Paraguay, 16 in Uruguay, and 10 in Chile.

The Synallaxinae comprises insect-eating birds that have radiated into a large number of habitats. The long-tailed Sylviorthorhynchus inhabits the rain-forest belt in Chile where it occurs primarily in bamboo thickets and thick undergrowth. The two species of Aphrastura, spine-tailed forms, are inhabitants of thick forest where they forage in a similar manner to titmice, working rapidly over the branches. Phleocryptes is a close counterpart to the long-billed marsh wren and occurs exclusively in reed beds in marshes and lakes. The small, long-tailed species of Leptasthenura closely resemble titmice in their foraging mannerisms, often hanging head downwards in search of insects. Usually in small groups, they frequent fairly dense wooded areas, or thickets. Spartanoica is another wren-like form which occurs in tidal marshes, fresh-water marshes, and moist situations on the pampas.

It forages on the ground or in clumps of grass or rushes. Schoeniophylax is an open savanna inhabitant, occurring mainly in clumps of grass and low bushes. The 24 species of the genus Synallaxis generally occur in dense growths of thorny scrub, weeds, and dense thickets in the open or in areas adjacent to forest, and in heavy growth along roadsides where they forage for insects. They usually remain hidden among the thick cover. Species of the genus Asthenes closely resemble Synallaxis morphologically. They are inhabitants of dense situations, often occurring in heavy grassland, marshy situations, thick bushy country, or in cactus where, although found occasionally on the ground, they are encountered most frequently in low bushes or in clumps of grass. Species of the genus Phacellodomus are usually found in thickets or in marshes grown up with saw grass, where they forage on the ground or low in bushes. One species occurs in open woodland. Members of the genus Poecilurus occur in the fringes of mangroves and in tidal flats, and also in thorny scrub and more arid areas where they forage by hopping along and scratching on the ground in pursuit of insects. The species of the genus Cranioleuca exhibit several behavioral types. C. sulphurifera is found in marshes of saw grass, where it is seen perched on the tops of clumps of grass. However, most of the members of Cranioleuca are suggestive of titmice in foraging behavior, hopping about on small limbs of trees,

but frequently (at least in C. antisiensis) hitching up the trunks and limbs of trees in typical woodhewer fashion, closely resembling the species of Margarornis. They may also forage somewhat like a nuthatch, going down branches head first. Slud (1964: 203) says of C. erythrops that: "Actively creeping, climbing, clinging, and rummaging, the bird investigates thickets, vines, trunks, and epiphytes." The genera Margarornis, Premnornis, and Premnoplex have often been placed in the same genus because of morphological and behavioral similarities. These forms are generally found in wet, mossy, forested areas in fairly dense situations, where they climb up tree trunks and branches in woodhewer fashion, using the tail as a brace, or forage in a manner more typical of the furnariids, clinging upside down like a Xenops, hanging below limbs, or foraging through the foliage in company with mixed species flocks. Premnornis frequently forages in wren-like fashion near the bases of trees, and Margarornis may occasionally drop to the ground in its foraging. Coryphastera inhabits dry, open scrub country where it is normally encountered in small groups feeding on the open ground among low bushes, but also is seen frequently perched near the ground. The gait is much like that of Furnarius. Anumbius, another terrestrial form, is much like Coryphastera in habits. It feeds largely on the ground in low thorn scrub country, often resting on a fence or other similar perches.

Sylviorthorhynchus makes a round grass nest which is placed just above the ground; four white eggs are laid. Aphrastura places its nest in a crack or crevice between the bark and the trunk of a tree; three white eggs are laid. Phleocryptes builds a round structure made of marsh plant downs from cat-tails and other marsh material. It lays two to three blue eggs. The nests of Leptasthenura are located in holes in trees or cactus plants, in crevices in man-made structures, or in the domed nests of other birds such as the ovenbird. Two to four white eggs are normal. Spartanoica builds a somewhat open structure of grass which is placed in marshy situations; the eggs are white. Species of the genera Synallaxis, Schoeniophylax, Phacellodomus, Coryphastera, and Anumbius all build large stick structures, often several feet in length, with an entrance tunnel leading to the actual nesting cavity. The nests are placed at medium heights in trees. They may lay three or four white or bluish-white immaculate eggs. The nest of Certhiaxis is a domed stick structure with an entrance tunnel. It is placed in low bushes, and four white eggs with a greenish tint are laid. In the genus Asthenes the nest may be placed on the ground, as in the grassland forms, or low in a bush or cactus plant. Its composition depends on the habitat of the species, being either of thorny twigs like nests of Synallaxis, or of grass composition, but usually with a runway leading to

the actual nest cavity. Two to three white eggs are laid. A nest of Cranioleuca erythrops recorded by Miller (1963: 22), "... was a bulky, hanging, covered mass of vegetation on a hanging limb." The eggs were white. I have seen a nest of Margarornis rubiginosus which was apparently in a clump of moss on the underside of a limb about twelve feet from the ground. Premnoplex also builds a dome-shaped mossy nest, in which two white eggs are laid (Skutch, 1967).

For the synallaxines, Haverschmidt (1967) recorded the following food items. For Synallaxis albescens, gujanensis, and rutilans, he listed Coleoptera, Lepidoptera (larvae), Orthoptera (Locustidae and Blattidae), Hymenoptera (Formicidae), Hemiptera (Homoptera), and Arachnoidea (Araneida); and for Certhiaxis cinnamomea, Lepidoptera (larvae), and Hemiptera (Homoptera).

I examined one stomach of Synallaxis albescens which contained only very small insects, including some coleopterans and orthopterans. One stomach of Cranioleuca erythrops contained very small insects, as did a single stomach of Premnoplex. Five stomachs of Margarornis rubiginosus held only small insects, mainly coleopterans.

Most of the available sources indicate that the synallaxines eat almost entirely small insects, and in their feeding habits are like many of the oscine passerines.

	Dendrocolaptidae	Philydorinae	Synallaxinae
Center of distribution	Forest of Amazon Basin and its periphery	Forest of Amazon Basin and its periphery	Non-forested areas or forest periphery, generally outside of Amazon Basin proper
Type of locomotion in foraging	Hitch up tree trunks and branches	Rummage about in dense growths in forest, clinging in vines and tangles, climbing sideways, creeping head downward, or hitching up trunks and branches	Great variety, but generally forage about branches in a "normal" manner. Some forms hitch up tree trunks, and some are semi-terrestrial
Food	Medium to large-sized insects, and small cold-blooded vertebrates	Small and medium-sized insects, but often large, hard-bodied forms, and small cold-blooded vertebrates	Small insects
Nest	Natural holes in trees stumps, etc., or abandoned woodpecker holes	Holes tunneled in the side of a bank, expanded at end where nest mat is placed	Large stick structures with tunnel entrances, usually at medium heights

TABLE 1. Summary of distribution and natural history of furnariids and dendrocolaptids.

	Sclerurinae	Pygarrhichas	Furnariinae
Center of distribution	Humid tropical forests of Amazon Basin and its periphery	Forested areas of Chile and Argentina	Primarily Andes and drier areas west of Andes, but peripheral to Amazon Basin
Type of locomotion in foraging	Terrestrial. Obtain food by probing into soft ground of forest floor (Sclerurus). Lochmias is more wren-like in habits and occurs in semi-open country.	Hitches up tree trunks and branches, often sideways	Terrestrial and semi-terrestrial in open and semi-open country
Food	Larvae and small insects	Small insects	Mainly small insects, but some seeds, and crustaceans and other small aquatic life
Nest	Tunnels dug into banks as in the Philydorinae	Holes in trees, often excavated by the birds themselves	Tunnels dug in bank with nest mat placed at expanded termination, or domed mud structures (Furnarius)

TABLE 1. (continued)

COMPARATIVE ANATOMY OF THE SKULL

Although this section covers most of the skull types found in the Furnariidae and Dendrocolaptidae, it is not intended as an extensive treatise on the skulls with the inclusion of all the minute variations. Instead, I have attempted to condense the variations into meaningful character states in each group so as to uncover the general evolutionary trends, not all of the intra-group variation. This variation will be covered in detail in a generic review of the two groups which I plan to have completed within the near future.

Anatomical Material

The following is a list of the skeletal material examined during the course of this study: The species Dendrocincla fuliginosa, 2 specimens; D. anabatina, 2; Deconychura longicauda, 2; Sittasomus griseicapillus, 11; Glyphorhynchus spirurus, 10; Dendrexetastes rufigula, 1; Xiphocolaptes promeropirhynchus, 1; Dendrocolaptes certhia, 2; D. picumnus, 2; D. platyrostris, 3; Xiphorhynchus picus, 3; X. obsoletus, 2; X. pardalotus, 2; X. guttatus, 7; X. flavigaster, 4; X. lachrymosus, 1; X. triangularis, 7; Lepidocolaptes leucogaster, 4; L. angustirostris, 4;

L. affinis, 3; L. albolineatus, 3; Campylorhamphus pusillus, 1; Geositta paytensis, 1; G. cunicularia, 4; Upucerthia dumetaria, 3; U. validirostris, 1; Ochetorhynchus ruficaudus, 2; O. certhioides, 2; Cinclodes antarcticus, 2; C. fuscus, 5; C. atacamensis, 2; C. taczanowskii, 1; Furnarius rufus, 8; Sylviorthorhynchus desmursi, 1; Aphrastura spinicauda, 4; Phleocryptes malanops, 5; Leptasthenura andicola, 1; L. aegithaloides, 1; L. platensis, 3; Spartanoica maluroides, 4; Schoeniophylax phryganophila, 11; Synallaxis ruficapilla, 1; S. frontalis, 6; S. albescens, 4; S. brachyura, 6; S. gujanensis, 2; S. rutilans, 2; Certhiaxis cinnamomea, 6; Cranioleuca sulphurifera, 2; C. obsoleta, 2; C. pyrrhophia, 1; C. erhythrops, 1; Asthenes dorbignyi, 1; A. baeri, 2; A. humicola, 1; A. modesta, 2; A. humilis, 1; A. hudsoni, 2; Phacellodomus rufifrons, 1; P. striaticollis, 8; Coryphastera alaudina, 5; Anumbius annumbi, 4; Margarornis rubiginosus, 4; Premnoplex brunnescens, 3; Pseudocolaptes lawrencii, 2; Pseudoseisura lophotes, 3; Hyloctistes subulatus, 2; Syndactyla rufosuperciliata, 16; Anabacerthia striaticollis, 3; Philydor lichtensteini, 6; P. rufus, 1; Automolus ochrolaemus, 6; Heliobletus contaminatus, 1; Thripadectes rufobrunneus, 1; Xenops minutus, 3; Pygarrhichas albogularis, 1; Sclerurus guatemalensis, 1. Alcoholic specimens of the following species were examined: Dendrocincla anabatina, Deconychura longicauda, Glyphorhyn-

chus spirurus, Dendrocolaptes certhia, Xiphorhynchus guttatus, X. lachrymosus, X. triangularis, Lepidocolaptes souleyetii, Campylorhamphus pusillus, Synallaxis albescens, Margarornis rubiginosus, Pseudocolaptes lawrencii, Hyloctistes subulatus, Automolus ochrolaemus and nestling, Thripadectes rufobrunneus, and Xenops minutus and nestling.

Woodhewer Skulls

The skull of Xiphorhynchus (Fig. 8) is typical of the woodhewers and will be used as the basis of the description of the skulls of the group.

The upper jaw differs little in basic structure from that of other passerine birds, except for the rather long, slightly decurved, heavily ossified bill. The bill accounts for approximately three-fifths of the length of the entire skull, but its characteristics are typically passerine, there being a long, oval external naris, and an unossified nasal septum (perforate naris). The posterior extent of the nasal opening ends well anterior to the nasal-frontal hinge; it is therefore holorhinal. The nasal-frontal hinge is well developed as in most passerines as an area of thinning of the nasal bones posteriorly; the sutures of the nasal bones are visible. There is a slight depression of the frontal bones at the junction of the nasal bones, but they do not curve anteriorly over the nasals, as in many woodpeckers. The actual nasal-frontal hinge area appears very broad in relation to the rest of

the skull. This is owing not only to the broad hinge, but also to the dorsal articulations of the lateral bars of the nasal bones which are thick and meet the frontal bones at an area of broadening, but are at approximately the same level as the nasal-frontal hinge. The lachrymal is apparently absent. The ectethmoid is a fairly thick bone which is constricted mesially and sends a thin but stout bar laterally which approaches the jugal bar. There is a single foramen where the ectethmoid bone fuses imperceptibly with the nasal and frontal bones and the orbital septum dorsally and mesially. The orbital septum is very well ossified, but there are two major openings posteriorly, a fontanelle postero-dorsally, and a large foramen for the passage of the optic nerve. There are several small foramina for the passage of other nerves and vessels. The orbital septum ends at the area where the ectethmoid plates meet mesially, just below the nasal-frontal hinge; there is no extension of the septum into the nasal cavity. The postorbital and zygomatic processes are present; both are strongly built, but of medium length for passerines. The two processes are well separated from each other by the large temporal fossa. The remainder of the brain case is typically passerine with several exceptions. The supra-orbital area of the frontal bones is extraordinarily broad, the temporal fossa is extremely large, and the two fossae almost meet each other posteriorly at the supra-

occipital region. The quadrate is a strong, well-developed bone. There are three articular condyles, but the lateral condyle merges smoothly into the posterior condyle. There is a large sesamoid bone present at the posterior condyle in some specimens. The quadrate sends out a massive orbital process that is expanded at its tip.

The ventral aspect of the skull is characterized by being heavily ossified anteriorly except for the internasal septum which is essentially absent and the floor of the nasal cavity. The maxillo-palatines are medium-sized, but the distal ends are not exceptionally broadened, as in many passerines, and only come into slight contact with the vomer mesially. The palatines are situated far apart anteriorly at their fusion with the premaxillary. The transpalatine process is fairly broad at its base, but tapers rapidly making an extremely long, thin structure pointed at its tip. The interpalatine process is present, but short. The mediopalatine plate is constricted and ends quickly to give rise to the large mediopalatine processes, which are somewhat folded and fuse posteriorly with the pterygoids. The pterygoids are heavy and have a prominent dorso-medial process near the quadrate articulations, which are the orbital processes of the pterygoids. The vomer is a short, broad plate of bone that is divided anteriorly in typical passerine fashion, but the posterior diastema typical of passerines is obscured by ossification.

The jugal bars are thin, but strong, and converge slightly anteriorly as they fuse imperceptibly with the maxillaries in a broad area of fushion. The palatine process of the premaxillary is not visible and its probably fused. Bock (1960: 436) reported of the palatine process of the premaxilla that it is, "... present in all genera of woodhewers, but the amount of fushion between the process and the palatine varies greatly in the different genera. As a broad generalization, the process is only slightly fused in the long, curved-billed species and heavily fused in those species having a short, straighter and heavier bill. Some of the observed variation may be age, but some is almost certainly correlated with the strength of the bill." In Xiphorhynchus the process is slightly fused. The remaining characters of the base of the skull appear to be typically passerine.

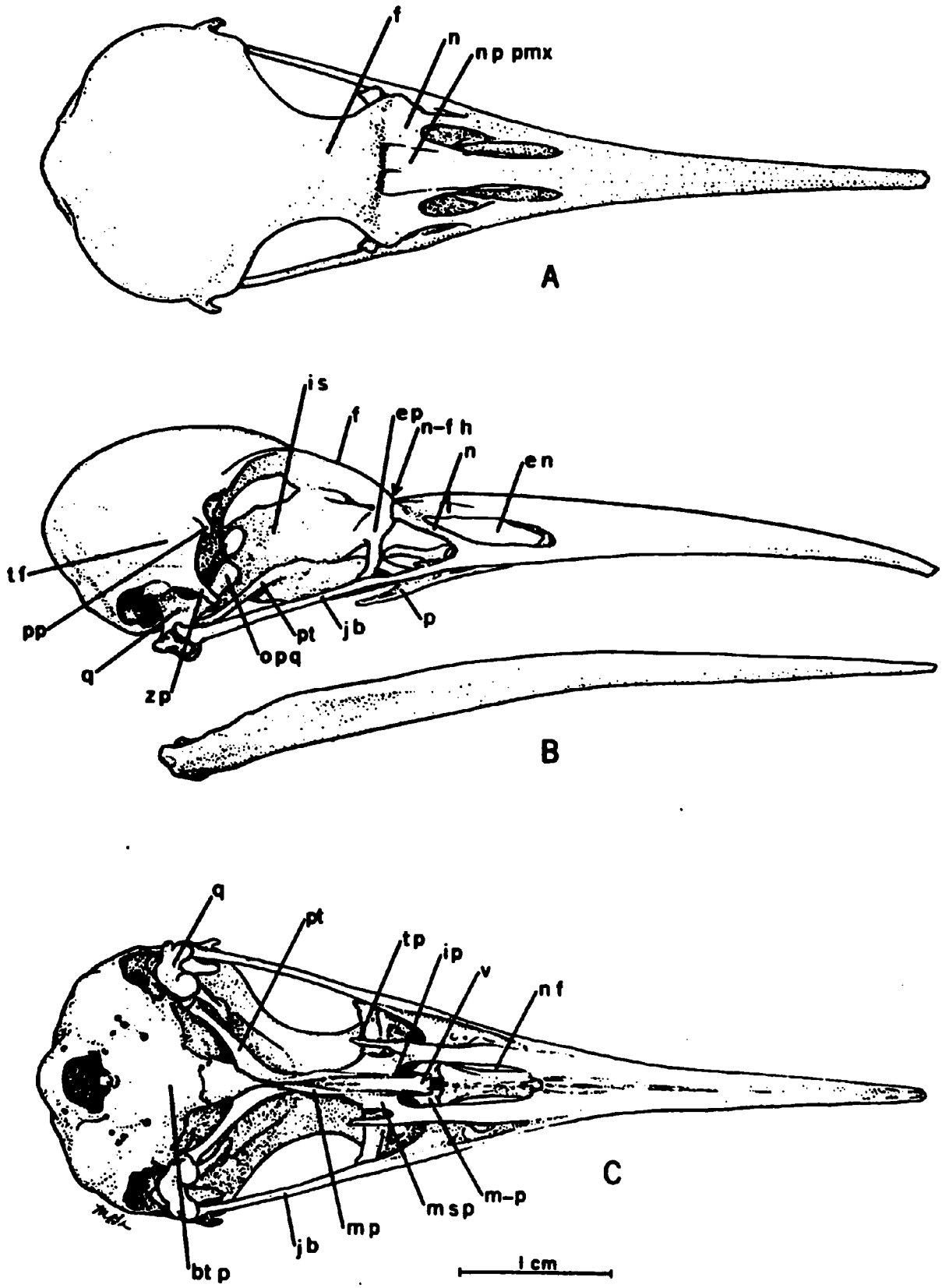
Anteriorly, the strong lower jaw is fused together for approximately two-fifths of its entire length. There are no outstanding features of the woodhewer lower jaw except for its sturdy structure and the near absence of a mandibular foramen typical of passerines. The foramen is reduced to an almost invisible vestige of pinhole size, or is completely absent.

The forms that I shall term the "strong-billed" woodhewers, Dendrocolaptes, Xiphorhynchus, Xiphocolaptes, Dendrexetastes, Lepidocolaptes, and Campylorhamphus

generally conform in skull characters to the foregoing description. Although I have not examined the skulls of the genera Hylexetastes, Nasica, and Drymornis, they appear to be typical of the group from external morphology and skull X-rays of study skins. The variation in the skulls of the "strong-billed" woodhewers involves such characters as length and shape of the bill, which varies somewhat going from the Xiphorhynchus-Lepidocolaptes type of moderate length, somewhat curved at the tip, to the broad-based type found in Dendrocolaptes, to the very long, curved bill of Campylorhamphus. However, it is of interest that the basic type of bill structure does not seem to alter greatly the other skull characters. There are minor differences which will be treated in a generic review of the group which I am presently preparing but none that leave any doubt as to a given bird being within this group.

In the wide-billed Dendrocolaptes, and in Dendrexetastes and Xiphocolaptes, the medial palatine plate is somewhat more expanded than in Xiphorhynchus. There is also other palate variation that seems to be correlated with the type of bill, but the basic structure is the same. There is some variation in the amount of ossification of the nasal region. This anatomical series begins with less ossified nasal regions in Lepidocolaptes, Xiphorhynchus, and Dendrocolaptes to the greatly increased ossification in Xiphocolatpes (with the anterior part of

Figure 8. Dorsal (A), side (B), and ventral (C) views of the skull of the woodhewer, Xiphorhynchus guttatus. Abbreviations are as follows: bt p, basitemporal plate; e p, ectethmoid plate; e n, external naris; f, frontal; i p, interpalatine process; i s, interorbital septum; j b, jugal bar; m f, mandibular foramen (not present in Xiphorhynchus); m p, mediopalatine process; m-p, maxillo-palatine; m s p, median shelf of the palatine; n nasal; n f, nasal floor; n-f h, nasal-frontal hinge; n p pmx, nasal process of the premaxilla; o p q, orbital process of the quadrate; p, palatine, p p, postorbital process; pt, pterygoid; q, quadrate; t f, temporal fossa; t p, transpalatine process; v, vomer; z p, zygomatic process.


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the nasal region being imperforate) to Campylorhamphus where ossification has occurred to the point that the nasal opening is a small oval hole. The situation is somewhat different in Dendrexetastes, which is one of the very strong-skulled dendrocolaptids, where the actual nasal opening ends close to the nasal-frontal hinge, but the skull is amphirhinal (see Feduccia, 1967). It would appear in this case as though the amphirhinal condition were compensation for the lack of other ossification in the nasal region.

Ovenbird Skulls

To describe a typical ovenbird skull presents many more problems than for the woodhewers, for whereas the woodhewers are very uniform with respect to skull structure, the ovenbird assemblage shows great diversity. However, for the purposes of this study only two types of ovenbird skulls need be distinguished, those that are typically pseudo-schizorhinal which are found in the subfamilies Synallaxinae, Furnariinae, and Sclerurinae (Pygarrhichas is also pseudo-schizorhinal), and those that tend towards holorhiny, as in certain members of the Philydorinae. Although one can characterize the various subfamilies of the Furnariidae, they are only partially separable by the structure of the skull, so for this study only the typical pseudo-schizorhinal skull and the intermediate philydorine condition will be described. The skull of Asthenes (Fig. 9)

is clearly pseudo-schizorhinal and forms the basis for the description of that skull type.

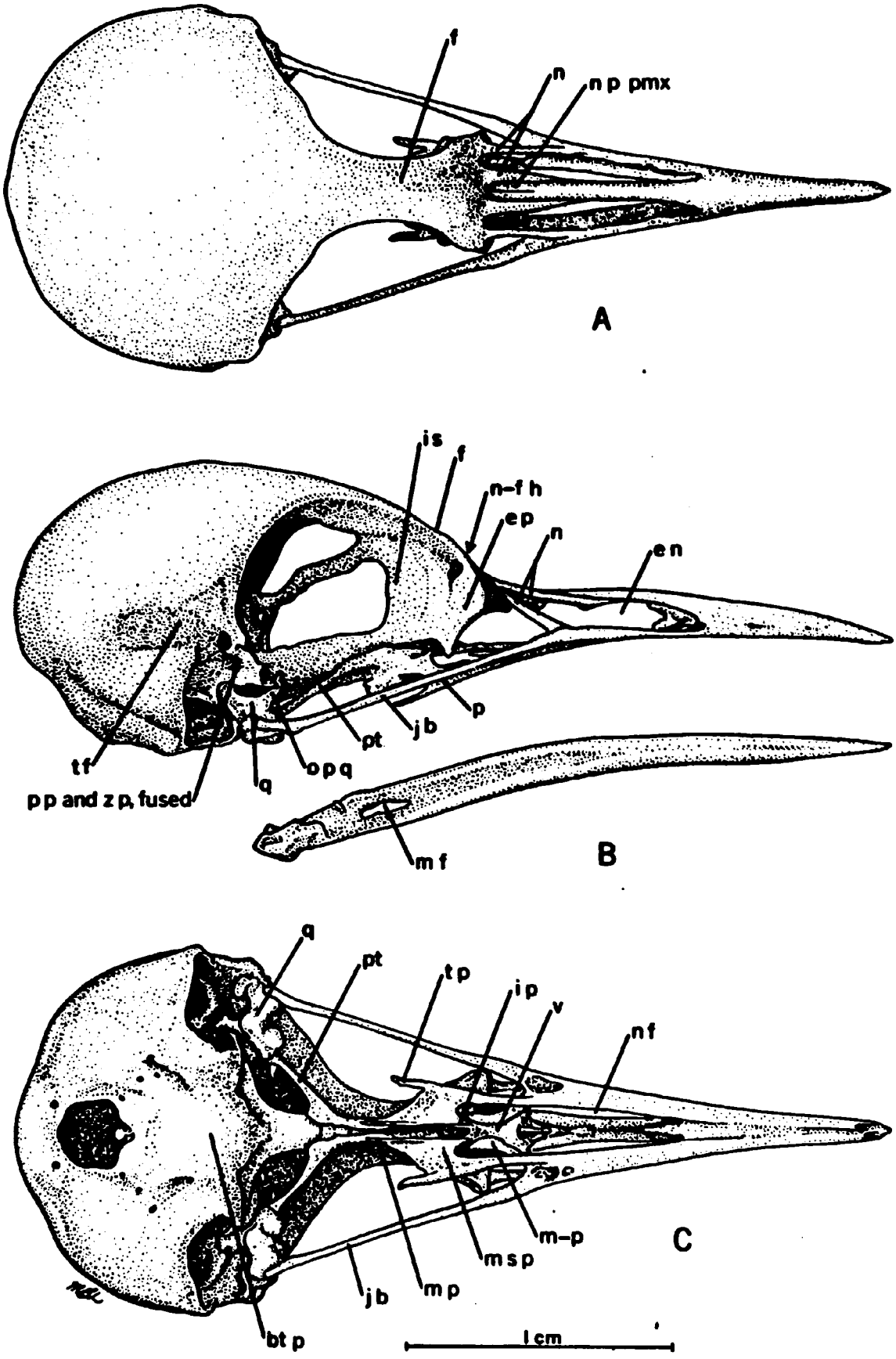
In general form the skull appears fragile compared to the massive bones that compose the woodhewer skull. The slightly decurved bill is small and thin and constitutes less than half the length of the entire skull. The nasal septum is very long and is perforate. There is no ossification within the septum. The long nasal opening extends posterior to the nasal-frontal hinge, but is rounded, unlike the "true" schizorhinal condition of the Charadriiformes, where the nasal opening ends posteriorly in a slit. The nasal-frontal hinge is visible as an area of thinning of the nasal bones posteriorly. The dorsal bar of the upper mandible is very thin as are the ventral bars. The frontal bones meet the nasals smoothly, there being no anterior curving of the former. The nasal struts, unlike those of the woodhewers, are very thin. The dorsal hinges of the nasal struts are displaced dorso-caudally, unlike the condition in Xiphorhynchus where the dorsal hinges form the lateral areas of the nasal-frontal hinge. Therefore, the actual area of the nasal-frontal hinge is very constricted compared to that of the woodhewers. There is very little ossification of the orbital septum, but there is a small, thin plate of bone anterior in the septum, which meets the mesial extent of the ectethmoid plates. Unlike the condition in the woodhewers, the interorbital

septum extends anteriorly just beneath the dorsal bar of the upper mandible, slightly anterior to the nasal-frontal hinge area. No lachrymal is present, as is also true of the woodhewers, but the ectethmoid plate is, unlike the woodhewer condition, a broad bony plate with very little mesial constriction, and with a very slight lateral strut that does not reach the jugal bar. The dorsal foramen of the ectethmoid plate is relatively much smaller than that of the woodhewers, but is single. The lateral borders of the entire ectethmoid plate are tilted anteriorly, unlike the woodhewer condition in which the plates are almost at right angles to the orbital septum. The postorbital and zygomatic processes are fused to form a foramen for the passage of the adductor muscle. The temporal fossa is small and much more poorly developed than that of the woodhewers. The supraorbital area of the frontal bones is constricted, unlike the woodhewer condition and more like the condition found in most other passerines, but the remainder of the brain case shows no exceptional features. The quadrate is very weak compared to that of the woodhewers. The quadrate has three articular processes and as in the woodhewers, the lateral condyle merges smoothly with the posterior condyle. However, the lateral condyle is a broader area than in the woodhewers. A sesamoid, which is retained in some preparations, is present at the posterior condyle. The orbital process of the quadrate is

thin and the tip is not expanded.

In ventral view, the skull is generally less heavily built and shows less ossification than in Xiphorhynchus. The maxillo-palatines are very thin, small, and form a long posteriorly projecting plate as in most passerines, but fail to fuse with the vomer. The vomer is a bony plate, which like that of most passerines, has a median diastema that extends anterior to the level of the maxillo-palatines. Anteriorly, the vomer appears much like that of Xiphorhynchus, is bifurcate, but is relatively closer together at their junction with the premaxilla than in the woodhewers and continue relatively farther anteriorly. There is generally less ossification in the premaxilla and hence less fusion with other bones. The median shelf of the palatines is relatively broader in Asthenes than in Xiphorhynchus and other woodhewers. Bock (1960: 436-438), reported on the palatine process of the premaxilla in furnariids as follows: "In most genera, the process is present, lying along the palatine and not fused with that bone. In Furnarius . . . the process lies free in the space between the palate and the dentary process of the premaxilla and in some ways resembles an ossified tendon. Rarely is the process fused or absent as in the case of Leptasthenura or Synallaxis. The length of the process varies somewhat between the genera." The process is unfused in Asthenes.

Figure 9. Dorsal (A), side (B), and ventral (C) views of the skull of the ovenbird, Asthenes modesta. See Fig. 8 for abbreviations.


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tp
ip
v
nf
m-p
msp
mp
jb
bt p
1 cm
C

As they continue posteriorly, the palatines diverge laterally, but do not become wider until they merge with the main bony plate of the palatine posteriorly. The interpalatine process is present, but does not extend far anteriorly. The mediopalatine process is small and extends slightly posterior. The palatines are fused to the pterygoids posteriorly. The pterygoids show no special features except for their orbital processes which are relatively much smaller than in the woodhewers. The jugals are thin and their anterior fusion with the maxillae is marked with a slight change in angle with the ventral bar of the upper jaw. There is no contact of the lateral wing of the ectethmoid with the jugal bar. The lower jaw is relatively much weaker than that of the woodhewers and has a large mandibular foramen.

Although there is much variation in the skulls of ovenbirds, the basic pattern seems to remain fairly constant until the philydorines are included (see next section). The main variation is seen in the amount of ossification of the interorbital septum, the position of the posterior extent of the nasal opening, and size of nasal opening, the shape of the bill, and the general strength of the entire skull. There is also variation in the postorbital and zygomatic processes. In some species the two processes are fused, forming a canal for the passage of the adductor muscle; in other species they

are separate and the temporal fossa is larger in these cases. Also, the ectethmoid plate varies somewhat, with some species approaching the woodhewer condition of the character. Aside from these points, there is uniformity in ovenbird skull anatomy.

Philydorine Skulls

The genus Automolus shall be described here as an example of the holorhinal ovenbird skull, intermediate in structure between the woodhewer and ovenbird skulls. The bill in Automolus (Fig. 10), like that of most of the ovenbirds, accounts for about half the length of the entire skull, but in this genus the bill is much more heavily built than in Asthenes and the synallaxines in general. There is a fairly long, oval-shaped external naris, comparatively less extensive than in Asthenes, but more so than in Xiphorhynchus. The dorsal and ventral bars of the upper mandible are stronger than in Asthenes, but weaker than in Xiphorhynchus. As in other ovenbirds the naris is perforate. The nasal-frontal hinge is visible as an area of thinning of the nasal bones. The frontal bones meet the nasals smoothly. The dorsal hinges of the nasal struts are somewhat displaced dorsocaudally but less so than in Asthenes, and in general appear more like the condition found in the woodhewers, where they form the lateral borders of the nasal-frontal hinge. The skull of Automolus is typically holorhinal, and the

external naris ends anterior to the nasal-frontal hinge. The nasal struts are thicker than those of Asthenes but thinner than those of Xiphorhynchus. The orbital septum is like that of Asthenes, there being a large postero-dorsal fontanelle and an anterior perforation of the septum, but the bony part of the septum is of much stronger material than that of Asthenes. The anterior part of the orbital septum meets the mesial extent of the ectethmoid plates. The bony interorbital septum extends only slightly anterior into the nasal cavity. The actual ectethmoid plates are more like those of the woodhewers; they are composed of strong material and are greatly constricted mesially. They send out laterally a long thin bar which meets the jugal bar. The lateral extension of the ectethmoids is tilted slightly anteriorly, but less so than in Asthenes; more so than in the woodhewers. There is a single dorsal foramen as in the other ovenbirds and in the woodhewers, but it is relatively larger than in Xiphorhynchus. The postorbital and zygomatic processes are well-developed (but less so than in Xiphorhynchus), and are separated by a broad and deep temporal fossa, similar to that of Xiphorhynchus but relatively less extensive. The supraorbital area of the frontal bones is broader than in Asthenes, but more constricted than in Xiphorhynchus. The supraoccipital region is somewhat bulged, but less so than in Xiphorhynchus. The quadrate is a strong bone with three

articular condyles, and like those of Asthenes and Xiphorhynchus, the lateral articular condyles merge smoothly into the posterior condyle, but the jugal articulation is broadened laterally, as in Asthenes. The quadrate sends off a strong orbital process with an expanded tip as in Xiphorhynchus. The vomer of Automolus is somewhat like that of Asthenes, being bifurcate anteriorly with a large median diastema that extends to the level of the maxillo-palatines anteriorly. The maxillo-palatines are thin as in other ovenbirds and form a plate that extends posteriorly, and they almost meet the anterior extent of the interpalatine processes. The median shelf of the palatines is broad as in Asthenes and other ovenbirds. The interpalatine processes are small and extend slightly forward, and the mediopalatine processes are relatively larger than in Asthenes and are slightly flared laterally at their posterior extent. The palatines are fused to the pterygoids posteriorly. The pterygoids are relatively stronger than in Asthenes and each sends off an orbital process of relatively greater size. The jugal bars are relatively thicker than those of Asthenes.

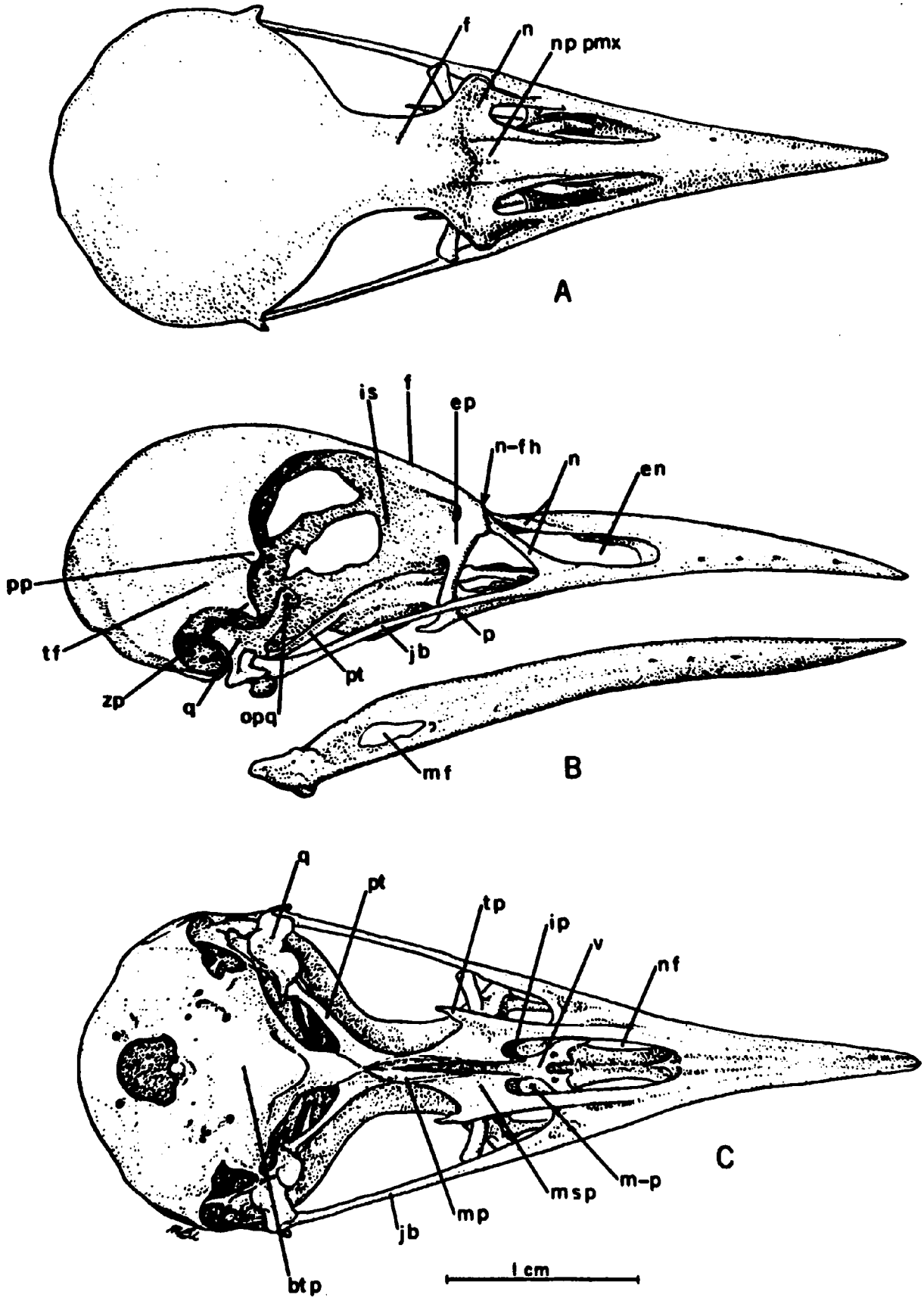
The skull of Automolus, which is fairly representative of the philydorine furnariids, is somewhat intermediate between that of the majority of the ovenbirds which have a weakly built pseudo-schizorhinal skull, and that of the woodhewers, typified by the strong, holorhinal

skull of Xiphorhynchus. The upper jaw of Automolus is stronger than that of the typical ovenbirds, the external naris is of intermediate expansion, and the nostril is holorhinal, but the dorsal articulations of the nasal struts are somewhat dorso-caudally displaced as in the ovenbirds. The ectethmoid plate is more like that of the woodhewers, but in some respects is intermediate. The orbital septum is stronger than that found in most ovenbirds, but is typical of the furnariids, having large fontanelles. The supraorbital region is constricted like that of other ovenbirds, but less so than that of the typically pseudo-schizorhinal types. The postorbital and zygomatic processes and the temporal fossae are more like the condition of Xiphorhynchus than that of Asthenes, an indicator of a strong adductor muscle, but other ovenbirds show this condition. In general the palate is more like that of most ovenbirds. The vomer is clearly bifurcated anteriorly, and there is a large median diastema in the vomer. The medial palatine plate is broad like that of most ovenbirds, and the transpalatine processes are ovenbird-like. The maxillo-palatines are thin and have a posteriorly extending plate like that of most ovenbirds. The quadrate has the lateral bulge of the jugal articulation as in the other ovenbirds, but has a strong orbital process with an expanded tip as is typically found in the woodhewers. There is a mandibular foramen in the lower

jaw as in the other ovenbirds.

Most of the philydorine furnariids are not quite so intermediate in skull characters as is Automolus, and there is a complete anatomical series going from the fragile ovenbird pseudo-schizorhinal skull type to the strong holorhinal type found in Automolus. Most of the philydorines tend to be less holorhinal than Automolus, with the dorsal articulations of the nasal struts being more dorso-caudally displaced. Also, in most species the bill and, in general, the skulls are of weaker construction. The orbital process of the quadrate is not expanded at its tip in most species, and there is an anatomical series going from Philydor and Anabacerthia with no expansion of the tip, through Hyloctistes and Thripadectes with slight expansion, to Automolus which has the tip expanded to the extent found in the woodhewers. In most of the philydorines the ectethmoid plate tends to be more like that found in the Dendrocolaptidae. The forms which most closely approach this condition are Hyloctistes, Pseudocolaptes, Philydor, Automolus, and Anabacerthia. Of the non-philydorines, Sclerurus, Pygarrhichas, Margarornis, and Premnoplex have somewhat dendrocolaptid-like ectethmoid complexes. Most of the palatal characters of the philydorines are clearly ovenbird like, and even the strong-billed forms such as Automolus show much the same palatal structure. There is a

Figure 10. Dorsal (A), side (B), and ventral (C) views of the skull of Automolus ochrolaemus. See Fig. 8 for abbreviations.


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msp
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mp
jb
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C
1 cm

complete series in the relative extent of the supraorbital area of the frontal bones, from the very constricted condition in the synallaxine furnariids such as Asthenes to the philydorines, where such forms as Xenops are more like the woodhewers in this character.

Skulls of the "Intermediates"

The skulls of the genera Sittasomus (Fig. 12), Deconychura, Dendrocincla (Fig. 11), and Glyphorhynchus deserve special attention. The skulls of Sittasomus and Deconychura are very similar in structure and are described together.

Both Sittasomus and Deconychura are weak-billed woodhewers that share characters of the skull with both the ovenbirds and the "strong-billed" woodhewers. The bills of both genera are weakly constructed, and the nasal opening is very long, the posterior extent ending at the level of, or slightly posterior to, the nasal-frontal hinge. The dorsal articulations of the nasal struts are somewhat dorso-caudally displaced. The supraorbital region of the frontals is somewhat broader than that of most of the ovenbirds, but less so than the "strong-billed" dendrocolaptids. The remainder of the brain case shows no exceptional features. There is a supraoccipital bulge, the postorbital and zygomatic processes are fairly well-developed, and the temporal fossa is well-developed as in the philydorines and

woodhewers. The articular surface of the quadrate is like that of the woodhewers, but the orbital process of the quadrate is like that of the ovenbirds, being slender with a non-expanded tip. The orbital septum is less ossified than that typical of the woodhewers, and there is a large postero-dorsal fontanelle, and also, as in the ovenbirds, an anterior opening through the septum is present. The ectethmoid plate is the philydorine-dendrocolaptine type, but its lateral border is tilted anteriorly as in the ovenbirds, although less so than in most. The palatines and pterygoids show no outstanding features that would be of any help in this analysis. The medial palatine plate is small in Sittasomus, but larger in Deconychura. The vomer is bifurcated anteriorly, and in Deconychura there is no median diastema. However, in Sittasomus there is a slight diastema in the most posterior part of the vomer. Thus, the genera Sittasomus and Deconychura present a mosaic of dendrocolaptid and furnariid characters in their skulls.

The short-billed Glyphorhynchus, the wedgebill, is different from all other genera of woodhewers. Because this woodhewer, unlike the others, pecks tree trunks and branches like a small woodpecker or piculet, its cranial features are different and shall be covered in detail in a separate paper. For the purposes of this paper it is sufficient to note that Glyphorhynchus is intermediate

between the ovenbirds and woodhewers in some cranial characters. The posterior extent of the nasal opening is almost to the nasal-frontal hinge, and the nasal struts are very thin. The ectethmoid has a slight anterior tilt. The orbital process of the quadrate is thin and does not have an expanded tip, and the jugal articulation of the quadrate is pronounced laterally. The foregoing are ovenbird skull characters. The obvious pecking adaptation is found in the frontal bones being curved anteriorly over the nasals as in some woodpeckers. Otherwise it is like the woodhewers in having a large temporal fossa with well-developed postorbital and zygomatic processes, dendrocolaptine-philydorine type of ectethmoid complex, ossified interorbital septum, an expanded supraorbital area of the frontal bones, and in general appearance is a strongly constructed skull.

The most ovenbird-like skull is that of Dendrocincla which resembles many of the philydorine furnariids. Its basic skull characters are like those of Sittasomus and Deconychura, but the skull is more heavily built, and in general form very closely resembles the philydorine genera Hyloctistes and Thripadectes. The posterior extent of the long nasal opening ends slightly anterior to, or at the level of, the nasal-frontal hinge, but the nasal struts are sturdier than in Sittasomus and Deconychura and are less displaced dorso-caudally at their dorsal articulations.

Figure 11. Dorsal (A), side (B), and ventral (C) views of the skull of Dendrocincla anabatina. See Fig. 8 for abbreviations.

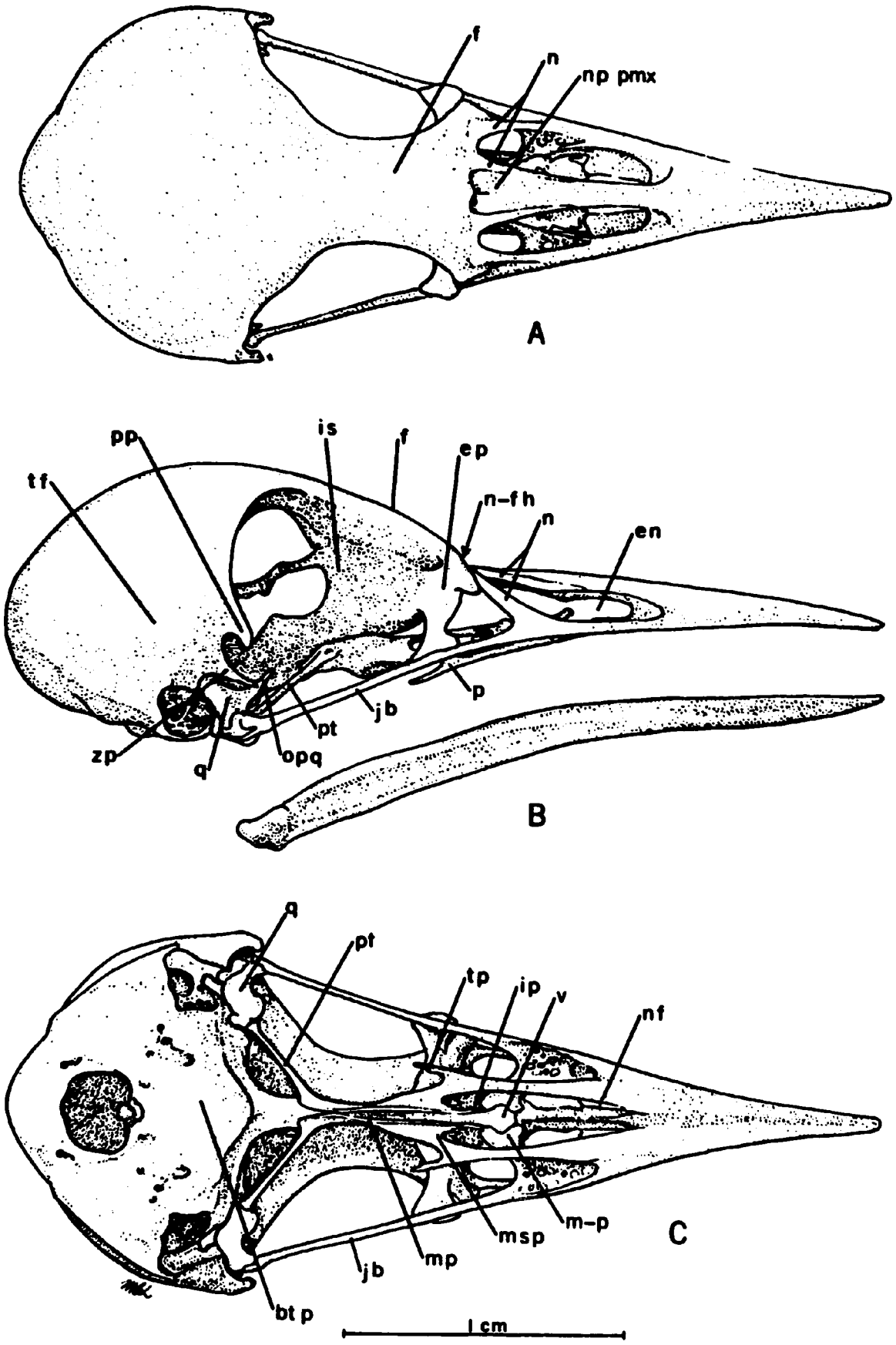
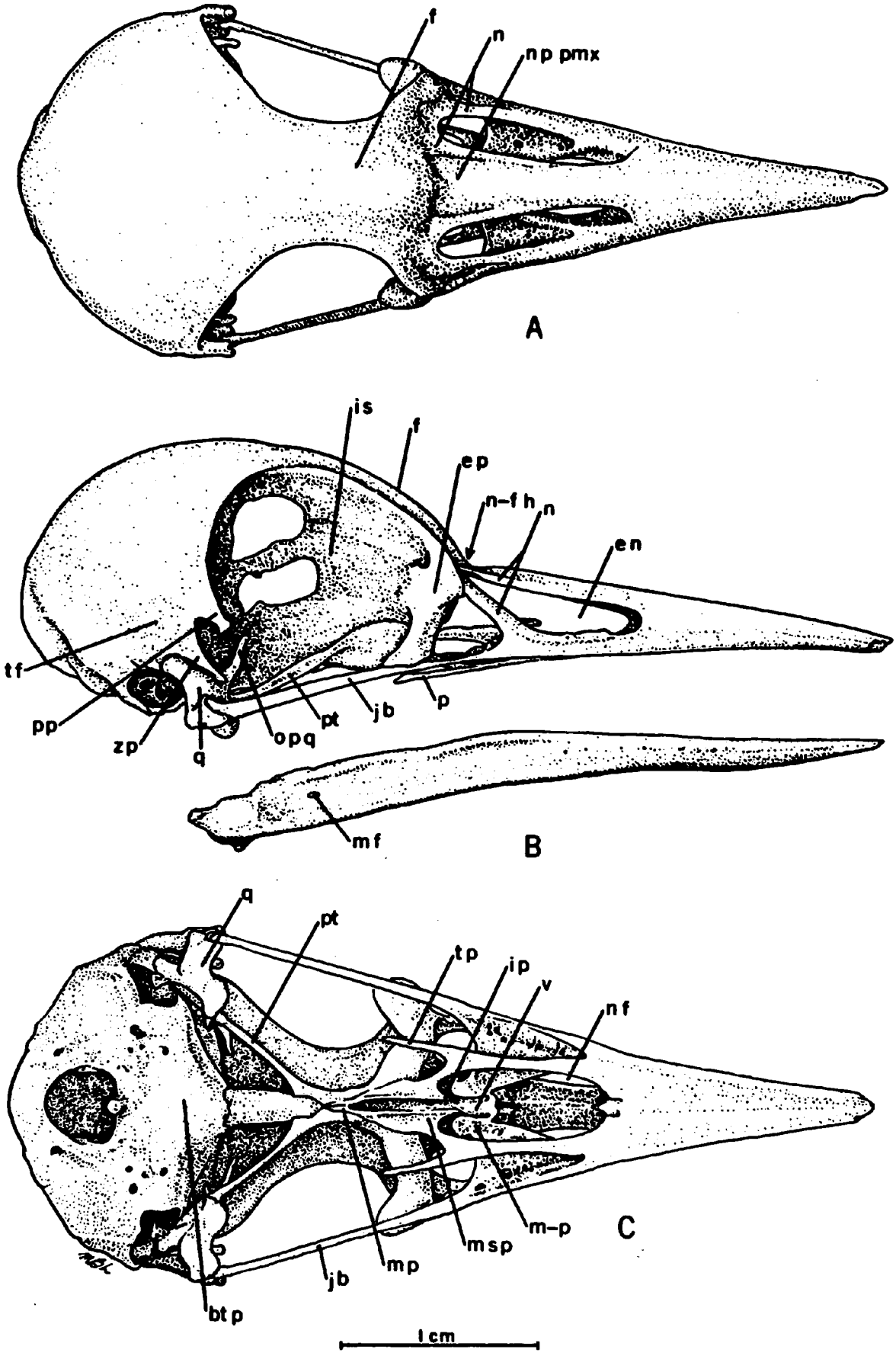

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Figure 12. Dorsal (A), side (B), and ventral (C) views of the skull of Sittasomus griseicapillus. See Fig. 8 for abbreviations.


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zp
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mf
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pt
tp
ip
v
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m-p
msp
mp
jb
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C
1 cm

The ectethmoid plates are more bulbous than in the other forms but are displaced very slightly anteriorly. The supraorbital area of the frontals is expanded relatively more than in the philydorines but less so than in the "strong-billed" woodhewers. This character varies somewhat in the three species of Dendrocincla that I examined. The orbital septum is more ossified than in Sittasomus or Deconychura but still has an opening through the septum. The postorbital and zygomatic processes are well-developed, and there is a well-developed temporal fossa. The quadrate, like that of Sittasomus and Deconychura, sends out an orbital process with a non-expanded tip. The palate shows no diagnostic features. The maxillopalatines are unusually broad, and the vomer has a slight diastema posteriorly.

Jaw Muscles

Alcoholic specimens of ovenbirds and woodhewers were examined to determine if there were any significant differences in jaw musculature between the two groups that were not deciphered from the skull anatomy. As most of the variation that was observed was confined to such variable areas of the skull as the palate and its associated parts, it shall not be covered in this paper. However, there are several jaw muscles that deserve special attention at this point.

One of the most striking features of the exposed

woodhewer head is the tremendous development of M. adductor mandibulae, especially the externus rostralis portion, the posterior extents of which nearly meet at the posterior median plane of the skull above the occipital condyle. This strongly bipennate muscle has fibers converging on a central aponeurosis which is ossified in the "strong-billed" woodhewers and is often preserved in the dried skeletons. The muscle is much less developed in the ovenbirds. Of great interest here are the "intermediates," all of which appear to be more like the woodhewers. In Dendrocincla, however, M. adductor mandibulae is more poorly developed and is more ovenbird-like. Although no alcoholic specimen of Sittasomus was available, the outline of the origin of this muscle on the skull forms the basis of my observation. The areas of origin of both M. adductor mandibulae and M. depressor mandibulae are clearly visible in the dried skull, and the extent of these origins is easily ascertainable. In Sittasomus M. adductor mandibulae is more like that of the woodhewers, but is apparently less developed than in the "strong-billed" forms. M. depressor mandibulae is another muscle which is much more strongly developed in the woodhewers. Dendrocincla is again intermediate in this character. The only other jaw muscle of great interest for the purposes of this paper is the M. pseudotemporalis profundus, which is, again, very strongly developed in the

woodhewers. This muscle, which originates on the orbital process of the quadrate, is clearly correlated in its size with the relative degree of expansion of the tip of this process. Since none of the intermediates exhibits an expanded tip of the orbital process of the quadrate, M. pseudotemporalis profundus is likewise not enlarged. In the philydorines which have an expanded tip of the orbital process of the quadrate, for example, Automolus, M. pseudotemporalis profundus is correspondingly large and resembles that of the woodhewers. The major jaw ligaments are well-developed in both the ovenbirds and woodhewers but, as expected from other characters, are heavier in the woodhewers than in the ovenbirds.

Functional Aspects of the Skull Types

Several recent papers deal with the function of the avian skull. The reader is referred to the works of Bock (1964) and Zusi (1962, 1967) for the clearest statements and summaries of the subject. The function of the various character complexes is much the same in all birds. So, in this paper I am only considering those aspects of skull function that will bear directly on ovenbird and woodhewer skulls. Therefore, only those points of the jaw muscle anatomy pertinent to the functional analysis will be discussed, and no detailed jaw muscle descriptions shall be given, as I feel that they would add little to the over-all study.

Table 2. Summary of extremes in skull characters.

Character	Dendrocolaptidae	Furnariidae
bill	strongly built, approx. 2/3 skull length	weakly built, approx. 1/2 skull length
nasal condition	holorhinal	pseudo-schizorhinal
external naris	short, oval	long, oval
nasal septum	perforate	perforate
orbital septum	ossified, does not extend anterior to nasal-frontal hinge	largely perforate, and extends slightly anterior to nasal-frontal hinge
ectethmoid	greatly constricted mesially, lateral process abuts against jugal bar	expanded, lateral process does not meet jugal bar
lachrymal	absent	absent
supraorbital area of frontal bones	broad	narrow
maxillo-palatines	short, slightly expanded	long, expanded
vomer	median diastema absent	median diastema present
median shelf of palatine	somewhat constricted	broad
orbital process of quadrate	tip expanded	tip not expanded
postorbital and zygomatic processes	large, well-developed	medium development, sometimes fused

Table 2. (continued)

Character	Dendrocolaptidae	Furnariidae
temporal fossa	greatly expanded	medium development
mandibular foramen	absent	present

In beginning this section it seems advisable to state the differences between the pseudo-schizorhinal type of skull described earlier for Asthenes and the holorhinal skull found in the "strong-billed" dendrocolaptids, typified by Xiphorhynchus. If we assume that the holorhinal skull is a derivative of the ovenbird pseudo-schizorhinal skull type, as we must from previous arguments, then it would follow that the character states leading to the woodhewer holorhinal condition have been molded by selection forces operating on dendrocolaptid evolution. These character states should be correlated with the behavioral information for the group. This type of correlation shall therefore be attempted, after a summary description.

As has been stated previously, there appears to be a general trend in the drndrocolaptids towards increased ossification in several systems. This anatomical series goes from the philydorines that show tendencies in this direction toward the "strong-billed" woodhewers in which it culminates. This increase in ossification appears to be the first step in the transition from pseudo-schizorhiny to holorhiny in these birds. Those trends which have taken place in the evolution of the woodhewer skull include ossification of the nasal region to the point that the dorsal articulations of the nasal struts form the lateral borders of the nasal-frontal hinge. Concommitant

with these changes in the ventral displacement of the dorsal articulations of the nasal struts are a parallel movement of the ectethmoid plate and retraction of the anterior part of the orbital septum posterior to the nasal-frontal hinge. Other changes include a general thickening of the nasal struts, along with a strengthening of the bill. In the brain case there is a broadening of the supraorbital area of the frontal bones, a deepening of the temporal fossa, and a strengthening of the post-orbital and zygomatic processes. There is also a great increase in the ossification of the orbital septum, enlargement of the orbital process of the quadrate, expansion of the tip of the orbital process, a general increase in the strength of the bones that comprise the palate, and obliteration of the median diastema of the vomer. The type of variations that exist in the characters of the palate and in the ectethmoid complexes makes difficult deciphering the trends in these systems. In the lower jaw the mandibular foramen is obliterated by ossification. Let us now consider the functional consequences of these changes, and their behavioral correlations.

In order to understand better the evolution of the skull types, one must first consider the functioning skull. Birds possess a kinetic skull, that is, there is movement within the skull and the upper jaw moves relative to the brain case. As it is beyond the purposes of this

paper to discuss in detail the kinetics of the avian skull, the reader is referred to Bock (1964) for a detailed discussion of the topic. Here I shall only be concerned with the differences in function between the woodhewer and ovenbird skulls.

Bock (1964) distinguishes two basic functional types of skulls, prokinetic and rhynchokinetic. Bock (1964: 4 and 14) stated that, "The prokinetic skull is characterized by a hinge or region of bending at the junction of the nasal and frontal bones; hence the upper jaw moves as a unit.... The rhynchokinetic skull is characterized by a region of bending located somewhere along the dorsal bar of the upper jaw." The prokinetic skull is the common avian skull, and is the characteristic passerine skull; rhynchokinetic skulls are commonly found in the Charadriiformes and in some other groups. One striking feature of these skull types is that prokinetic skulls are generally associated with the holorhinal nasal condition, and rhynchokinetic skulls with a schizorhinal nasal condition. In the rhynchokinetic skull the orbital septum is present anterior to the base of the upper jaw, thus making any bending at the area of the old nasal-frontal hinge impossible. Therefore, the area of bending in the rhynchokinetic skull is somewhere along the dorsal bar of the upper jaw between the anterior extent of the orbital septum and the posterior extent of

the nasal septum. As Bock (1964: 14) pointed out, "Rotation of the upper jaw in rhynchokinetic skulls occurs when the ventral bars are pushed forward exactly as in the prokinetic skull. But only the anterior section of the upper jaw moves upward while the base of the dorsal bar remains stationary." He further stated that "... the ventral bar, which moves forwards and backwards, must be isolated from the stationary base of the dorsal bar, a problem unique to the rhynchokinetic skull..." This separation of the dorsal and ventral bars is accomplished by the schizorhinal nostril in the Charadriiformes. "The lateral bar is thus free to move with the ventral bar, bending at its junction with the brain case, i.e., at the region of the old nasal-frontal hinge (Bock, op. cit.) Zusi (1962: 37) pointed out of the schizorhinal skull that, "...the dorsal hinges of the nasal struts, which in holorhinal birds form the lateral extremes of the fronto-nasal hinge, are displaced dorsocaudally. This means that the nasal struts are no longer integral parts of the upper jaw, but that they swing about their own pivots, and tend to change the shape of the upper jaw during protraction or retraction." Since the nasal struts are no longer associated with the upper jaw proper, they form a new set of hinges, thus making a double set of hinges for the schizorhinal jaw. So, the functional consequences of this system are that the upper jaw, instead of moving

about one hinge and as a single unit as in the prokinetic birds (woodhewers), has a long area of bending along the dorsal bar which effects bill shape change during protraction and retraction and bill tip movement. The only anatomical differences appear to be in the bony hinge system, and as Bock (1964: 15) pointed out, "All other parts of the skull, ligaments and jaw muscles of the rhynochokinetic skull are similar to those in the prokinetic skull. Thus it is reasonable to assume that the operating mechanism is the same in the two types of kinesis."

In the case of the typical ovenbirds, the nostril is schizorhinal, but the orbital septum extends only a very short distance beyond the old nasal-frontal hinge. The result is that although the type of kinesis falls within the rhynchokinetic range, since the area of bending is along the dorsal bar of the upper jaw instead of at an easily definable nasal-frontal hinge, the area of bending is generally very close to the base of the upper jaw so that for the most part the upper jaw moves as a unit. The main difference seems to be that some bending does occur, and as a consequence the tip of the bill does move to some degree independently of the movement of the entire upper jaw. As Bock (loc. cit.) pointed out, "Some birds have a form of kinesis that cannot be easily assigned to either prokinesis or rhynchokinesis. In the gull (Larus),

for example, the region of bending is of the rhynchokinetic type, but it is so close to the base of the skull that the entire upper jaw moves as a unit." Within the ovenbird series there is such a continuous series going from the typical schizorhinal types through the philydorines to the holorhinal types that many cannot be assigned to a specific type of kinesis. One can only say that at the extremes there appear to be typical rhynchokinetic skulls and at the other extreme, prokinetic skulls.

To summarize the foraging behavior of each group we might say that the woodhewers forage by using the bill in probing, prying, and some pecking. The bill is also used in these forms in grasping rather large or strong-bodied prey. Although there is great diversity among the ovenbirds, they may be generally characterized as insect-eaters, and most of the food taken is small insects. Among the philydorines, which show a general strengthening of the skull and a reduction of schizorhiny, the food taken is often heavier and harder-bodied insects than in the synallaxines and furnariines and small cold-blooded vertebrates, and many species peck, pry, and probe in their foraging behavior.

Although the precise functions of many parts of the skulls are still unknown, the characters in these two groups seem to conform to functional anatomical predictions, in the woodhewers for a generally stronger, more completely

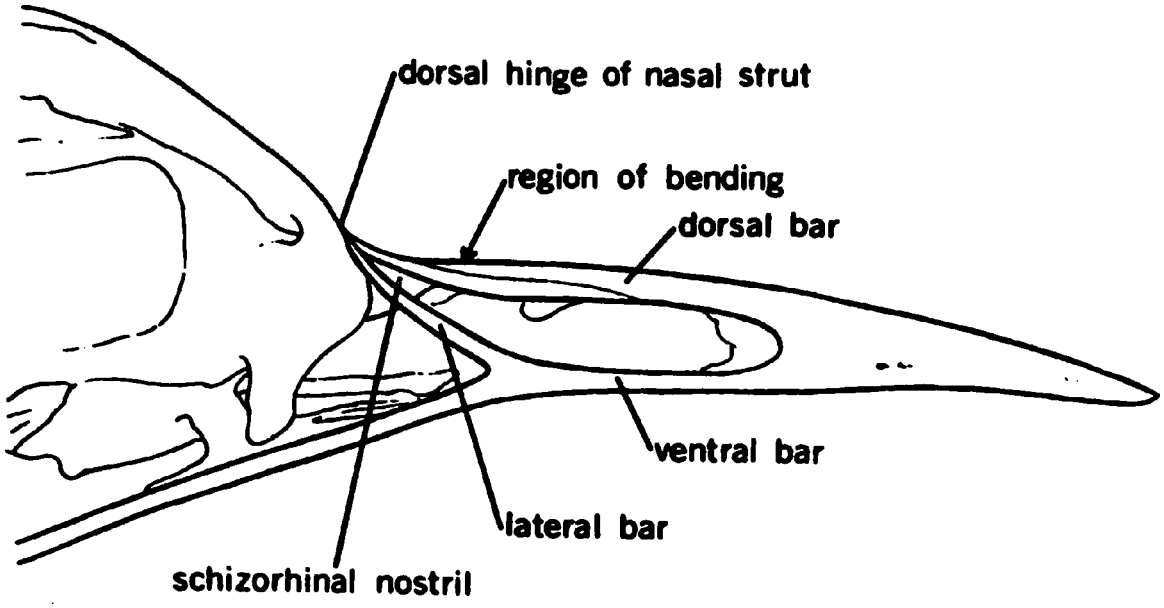
ossified skull, and in the ovenbirds, for a weak, less ossified skull.

In the woodhewers, the bill is generally strong, and the dorsal articulations of the nasal struts form the lateral borders of the nasal-frontal hinge, therefore strengthening the bill and forming a broad hinge which functions to protect the bill from the strong lateral forces to which it is subjected in prying, probing, and other such activity. In addition, woodhewers are powerful graspers. These functions require a general strengthening of the skull, which is shown in the bill, the ossification of the orbital septum, the strengthening of the nasal struts, enlargement of the postorbital and zygomatic processes, deepening of the temporal fossa (hence enlargement of the adductor muscle), general strengthening and broadening of the palatal bones, strengthening of the orbital process of the quadrate and expansion of its tip, strengthening of the jugal bar, strengthening of the ectethmoid plate, and extension of its wing to contact the jugal bar. In general, the woodhewer skull shows great strength. As Bock (1963: 112) has pointed out in Loria concerning the expanded tip of the orbital process of the quadrate and the large M. pseudotemporalis profundus muscle, two characters that the woodhewers possess, "These features are clearly correlated with one another functionally; they act to close the mouth more

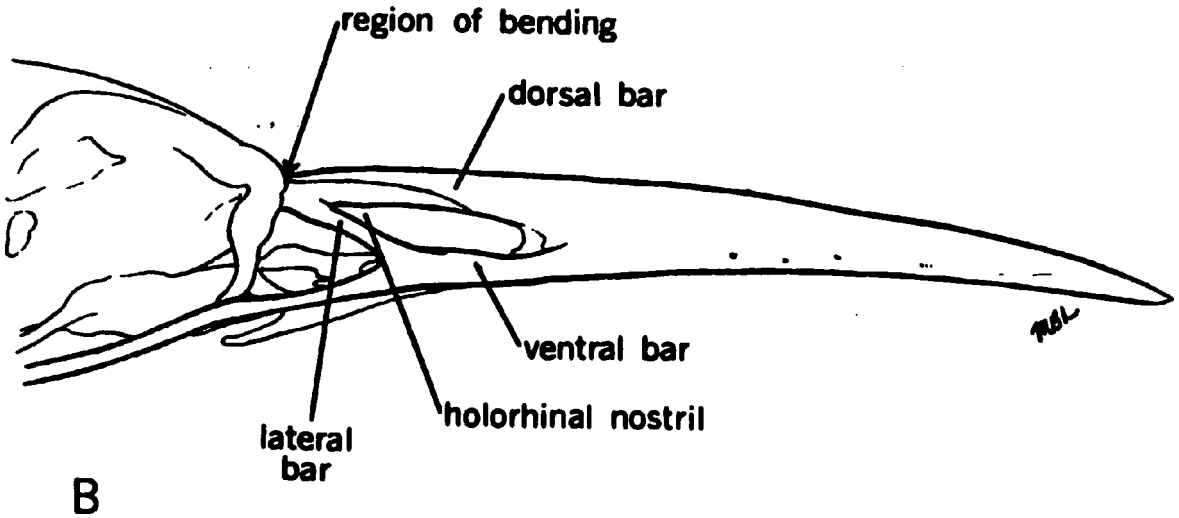
forcibly either by depressing the upper jaw or raising the mandible." One functional aspect of the strong power for adduction would be holding and crushing strong-bodied insects and small cold-blooded vertebrates, food commonly taken by woodhewers. Thus, the strong skulls and powerful jaw muscles of the woodhewers seem to be clearly correlated with the foraging behavior and type of food taken.

In the ovenbirds the situation is somewhat more difficult because there is such diversity in skull structure. In the synallaxines and most of the furnarines, the skulls are generally weak as compared to the woodhewer skulls. The nares are pseudo-schizorhinal, the orbital septum is unossified, the post-orbital and zygomatic processes are small, the temporal fossa is relatively smaller than that of the woodhewers, the palate is weaker than that of woodhewers, and the jaw muscles are not so massive and powerful as those of the woodhewers. These skull characters seem to correlate with the feeding habits of these forms as they are generally small-insect eaters. But perhaps the main question that has not been answered and the one that will probably not receive a completely satisfactory answer at this stage is why the nasal condition is pseudo-schizorhinal in the ovenbirds, and not holorhinal as in, for example, the wood warblers and most passerines, which feed on much the same type of food and in much the same manner. One might think that the wood-

Figure 13. Diagrammatic illustrations of the skull of A, an ovenbird, and B, a woodhewer, to show the regions of bending in the skulls.


dorsal hinge of nasal strut
region of bending
dorsal bar
ventral bar
lateral bar
schizorhinal nostril

A


region of bending
dorsal bar
ventral bar
holorhinal nostril
lateral bar

B

hewers need slow, powerful jaw action for the large, hard-bodied prey that they take, and this is certainly achieved by the woodhewer skull. Perhaps for the ovenbirds, a quicker action of the tip of the bill is advantageous for insect eating. This quicker tip action is achieved by pseudo-schizorhiny in which the tip may move somewhat independently of the movement of the entire upper jaw.

Whatever were the exact selection forces for the evolution of the pseudo-schizorhinal skull in the ovenbirds, now it is certainly a functionally diverse skull and is used in many diverse ways, including the building of large stick nests and hole excavation. But, in general, the skull type seems to be adapted for a generalized insect-eating mode of life.

As has been pointed out previously, the strengthening of the skull in the philydorines seems to be clearly correlated with the type of foraging behavior and the food taken by these forms, as they approach the woodhewers in these characteristics.

Evolution of Schizorhiny

We may now ask the question as to why the pseudo-schizorhinal skull type occurs in the furnariids and not in other generalized insect-eating passerine birds, which appear to have similar feeding habits. Hofer (1955) presents a good discussion of the holorhinal skulls as

compared to schizorhinal, and further asks the question as to which is the more primitive; Jollie (1958) follows with this general theme. The holorhinal nostril is considered the typical and primitive condition in the Passeriformes owing to its widespread occurrence, and as Jollie (op. cit.) points out, the schizorhinal and superholorhinal (with a more rounded nasal margin as in many passerines with short, thick, bills) skull types are probably the most specialized. However, how many different types of holorhiny occur in passerines is a question that remains uninvestigated, and one would have to look at the entire jaw apparatus to discover this. The point is that the type of holorhiny in one group of passerines may be more primitive than another type of holorhiny in another group. The terms holorhinal and schizorhinal are general terms that refer to a large spectrum of possible nasal conditions. It is of interest here that certain birds undergo ontogenetic changes in the condition of the nostril and consequently in the type of cranial kinesis. Bock (1964: 15) points out that in Rynchops, Balaeniceps, and Rhinoplax, the kinetic hinge shifts from a rhynchokinetic hinge in the young to a prokinetic condition in the adult. This change in the position of the kinetic hinge corresponds to changes in the nasal condition from schizorhiny in the young to holorhiny in the adults. It should be apparent by now that the holorhinal skull type in the

woodhewers represents the specialized, derived type in the furnariid-dendrocolaptid assemblage, and has possibly, and I think very likely, evolved under selection pressures for stronger bite, grasp, and probing abilities that cause exceptional forces to be exerted on the woodhewer bill. But, a weak holorhinal skull, that is, a skull with similar kinetic abilities but without ossification of the orbital septum and general strengthening of the woodhewer skull is the type of skull that is found in most other passerine birds. In other words, although the feeding behavior of most passerines is most similar to the ovenbirds, the skull type and kinetic properties of these birds are more like that of the woodhewers. Although at first this would appear to be enigmatic, several hypotheses exist. I shall build on the one that I feel has the most credence.

In the early evolution of passerine birds, it seems likely that the typical holorhinal, prokinetic skull was then not as efficient for the generalized insect eater as is the modern version of the skull that is found in the passerines today. As Bock (1967: 65) has put it, "... the degree of adaptation may be expressed in a variety of ways. One possible way is in some terms of relative efficiency, such as the amount of energy required by the animal to carry out the particular biological role associated with the selection force acting upon it." It is in this sense that I use the term efficient. It may

have been that during the early evolution of passerine birds, which was, I think, primarily of suboscine types, the pseudo-schizorhinal skull type evolved as a more efficient skull for generalized insect eating. This relatively greater efficiency for the pseudo-schizorhinal skull may be the reason for the great success of the furnariids in South America even today. From this original pseudo-schizorhinal type of skull could have evolved the philydorine furnariids in the forest habitat, and the synallaxines in the non-forest habitat and in the Andean regions. From the philydorines' pseudo-schizorhinal type arose the forms that tend towards holorhiny in skull structure such as Automolus, and further to forms such as the "intermediate" woodhewer genera. From this type of beginning arose the "strong-billed" woodhewers under increased selection forces for even stronger skulls, with even more complete ossification. However, it may have been that in the evolution of other groups of passerine birds, the old ancestral holorhinal, prokinetic skull type had undergone radical modifications to become a "better" skull for the generalized insect-eater. This new passerine skull would then have been "better adapted" for the generalized insect eater than its ancestral type, but perhaps on an equal level with the pseudo-schizorhinal type that has evolved from similar beginnings. In other words, there were, in the evolution of passerine birds, two

solutions to the problem of providing an efficient skull for a generalized insect-eater.

However, the pseudo-schizorhinal skull of furnariids, like the holorhinal skull of other passerines, is now not confined only to generalized insect eating, for it serves in its same anatomical form as a skull capable of building the large stick nests found in the ovenbirds and the earth excavations that some species make. It even serves for excavating nesting holes in trees in Pygarrhichas. This same functional diversity is also found, but perhaps to a lesser degree, in the "true" schizorhinal birds such as the shorebirds, etc., where the same general anatomical skull type is certainly not confined to one functional end.

An alternative hypothesis might be that the type of pseudo-schizorhinal skull found in the ovenbirds represents the primitive passerine skull. However, this would seem less likely since all of the passerines except the ovenbirds possess the holorhinal type of skull.

The Sternum

The variation in the notches of the posterior border of the sternum has been reported recently by Heimerdinger and Ames (1967). They examined almost a thousand specimens and divided the sternal types into six categories, grading from those with no notches, (type 1) to those with four complete notches (type 6). In a more recent paper (Ames, Heimerdinger, and Warter,

1968: 8-9), the anatomical variation of the sternum of the furnariids and dendrocolaptids is condensed in the following summary: "Of the five furnarioid families, the Dendrocolaptidae exhibit the greatest amount of variability within the family, genus and species. Of 173 specimens in nine genera, the large majority was two-notched (type 3), but types 2, 3, and 4 were sometimes found in the same species. No specimens were seen with either type 5 or type 6. In general, the woodcreepers tend to have rather solid sterna, one specimen even being devoid of performations (type 1).

"The ovenbirds also have predominately two-notches (type 3) sterna, with a few specimens of the more perforate types. Type 5 sterna were found in five of the 199 specimens examined; they were specimens of: Xenops rutilans (one out of two specimens); Pygarrhichas albogularis (one out of three); Sclerurus rufigularis (one out of one); and S. guatemalensis (two out of two)." A type 5 sternum is one with a lateral notch and a large medial fenestra on each side (Heimerdinger and Ames, 1967: 6).

Before I had examined the sternal variation in detail, I thought that since most of the variation was found in the Dendrocolaptidae a functional solution to the problem would be readily available, especially since the sternal type within the Furnariidae seemed to be fairly constant. The fact that the typical dendrocolaptid

is in almost all respects a "stronger" bird, with generally more increased ossification in most skeletal parts than in the furnariids, pointed to the possibility of this being a hint to the selection forces operative on the sternal border, and also the form in which no sternal notches were found, Xiphocolaptes promeropirhynchus, is one of the strongest, most highly ossified forms in many skeletal characters. However, the situation is probably much more complex than it at first appears. For example, if we expect the closure of sternal notches to occur with the evolution of tree-trunk foraging behavior, then we should be able to find a similar condition in other climbing birds. In the woodpeckers there are clearly four sternal notches, and the woodpeckers would seem to represent a group with enough evolutionary history behind them to produce the condition of closure of the posterior border if selection forces were operative in this direction on trunk-foragers. However, there is definitely more closure of the posterior border of the sternum in the Picidae (woodpeckers) than in the other picine birds, indicating that selection is operating for closure of the sternal border in these trunk foragers. The possibility also exists that there are more potent selection forces operative in the woodpecker line for maintainance of flexibility in the posterior border of the sternum, and that this, combined with selection to close the sternum has produced the

present sternum of the Picidae. Perhaps otherwise the sum total of the selection forces would favor closure of the posterior border of the sternum.

Another sternal character that differs between the ovenbirds and woodhewers is the size and shape of the sternal keel. In the ovenbirds the keel is generally large, and in profile has a somewhat rounded appearance in many species. In the woodhewers the keel is relatively smaller, and does not appear rounded in profile, but tapers in a straight line posteriorly. This character might be correlated with the position of woodhewers on tree trunks, but is probably also associated with the amount of variation within the ovenbirds in the size and shape of the keel. As one might expect, the sternal keel in the woodhewers is relatively more constant.

EVOLUTION OF THE SCANSORIAL FOOT

The type of foot found within the furnariids and dendrocolaptids is the typical anisodactyl foot found in all other passerine birds. This type of foot structure is characterized by having the hallux (generally long) posterior to the tarsometatarsus, and the second, third, and fourth toes pointing anteriorly. Within the Passeriformes the anisodactyl foot, with minor modifications, seem to be well-suited as a perching, climbing or walking foot. For present purposes, I shall be concerned only with the modifications that have occurred in the transition to the creeping or scansorial type of foot found in the Dendrocolaptidae. The foot type within the ovenbirds is, with a small amount of variation, the same. As many of these observations have already been covered by Richardson (1942) and Bock and Miller (1959), only the main points will be treated in this section.

If we assume that the dendrocolaptids arose from the philydorine furnariids, then the differences between the two groups should indicate the climbing adaptations of the anisodactyl type of foot and the selection forces operative in this case.

Richardson (1942), in his paper on tree-trunk

foraging in birds, compared Certhia, Sitta, Thryomanes, Dryobates, and Dendrocolaptes. He felt that features in common between the different tree-trunk foragers would be hints to the actual adaptations for tree-trunk foraging. With respect to many characters, the comparison of Thryomanes to Dendrocolaptes is much like a comparison of ovenbirds to the woodhewers since in Thryomanes fewer actual climbing adaptations are found than in the other creeping forms, and since, in general, the pelvic region characters of the ovenbirds are closer to Thryomanes than to the dendrocolaptids, owing to the perching types of feet found in both. It would be redundant to cover all the points made by Richardson (1942), so I have chosen the main points that I consider to be of great importance, and also points that were not covered by Richardson. For the general myological features, the reader is referred to Richardson (1942), as most of the gross comparisons are covered. Here I stress the osteological differences between the ovenbirds and the woodhewers, with special reference to the climbing adaptations in the woodhewers, and the position of the "intermediates" with respect to these characters.

Many of the points covered by Bock and Miller (1959) are only briefly treated here. The reader is referred to their excellent paper on the evolution of perching and climbing feet in birds.

Limb Proportions

One of the most significant changes in the evolution of climbing birds occurs in the proportions of the pelvic limb elements. Here I have considered the relative lengths (in millimeters) of the femur, tibiotarsus, tarsometatatsus, and the total leg, and have compared the ovenbirds to the woodhewers by using ratios of these bone lengths to the length of the sternum (greatest length from the metasternum to the posterior border of the sternum). The ratio of each limb element to the sternum was calculated, and the mean of the ratios from each species was used as part of the sample from each family. The sternum was the only body measurement that was possible for most skeletons, as many specimens were disarticulated. Engels (1940) discusses the use of such ratios. The basic idea is to use for the ratios measurements of elements that vary independently of each other and to use on measurement that does not tend to vary adaptively from one species to another, rather one that varies according, say, to the size of the animal. Although I cannot prove this qualification for sternal length, it does seem to "work" and follows the obvious predictions.

Measurements were taken from the following species of woodhewers and ovenbirds: Dendrocincla anabatina (3), Dendrocincla fuliginosa (3), Deconychura longicauda (3), Sittasomus griseicapillus (9), Glyphorhynchus spirurus (7),

Dendrexetastes rufigula (1), Dendrocolaptes certhia (1), D. picumnus (1), Xiphorhynchus picus (3), X. obsoletus (2), X. pardalotus (2), X. guttatus (6), X. flavigaster (4), X. lachrymosus (1), X. triangularis (7), Lepidocolaptes leucogaster (4), L. souleyetii (4), L. angustirostris (4), L. affinis (3), L. albolineatus (3), Campyloramphus pusillus (1), Geositta paytensis (1), G. cunicularia (2), Upucerthia dumetaria (3), U. validirostris (1), Ochetorhynchus certhioides (2), Cinclodes antarticus (2), C. fuscus (4), C. atacamensis (1), C. taczanowskii (1), Furnarius rufus (8), Aphrastura spinicauda (2), Phleocryptes melanops (5), Leptasthenura andicola (1), L. aegithaloides (1), L. platensis (1), Spartanoica maluroides (2), Schoeniphylax phryganophila (10), Synallaxis frontalis (6), S. albescens (4), S. brachyura (5), Cranioleuca sulphurifera (1), C. erythrops (1), Asthenes modesta (2), A. baeri (2), A. hudsoni (2), Phacellodomus striaticollis (4), Coryphastera alaudina (5), Anumbius annumbi (3), Premnoplex brunnescens (3), Hyloctistes subulatus (2), Anabacerthia striaticollis (3), Philydor lichtensteini (6), Automolus ochrolaemus (4), Heliobletus contaminatus (1), Thripadectes rufubrunneus (1), Xenops minutus (3), Pygarrhichas albogularis (1).

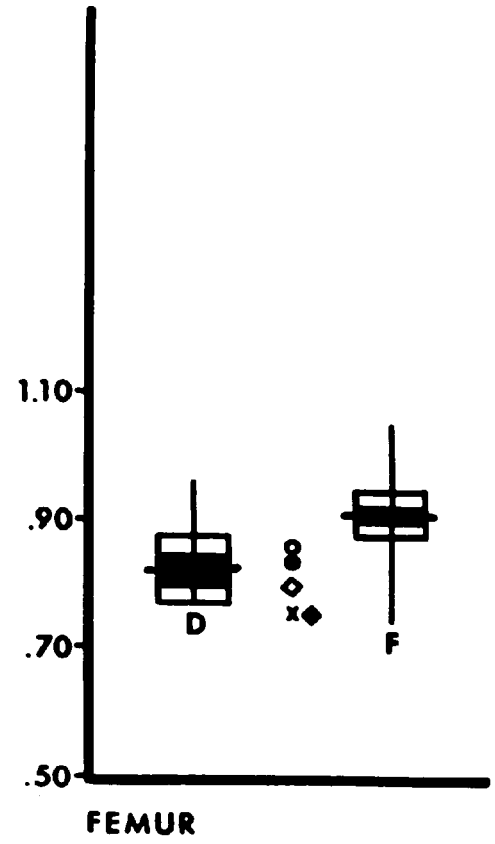
In figure 14 the ratios of the limb elements to the sternal length are given. It seems apparent from the figures that the main modifications in the evolution of the

dendrocolaptic pelvic limb elements are the reduction in the length of the tibiotarsus and the tarsometatarsus. The femur data are less obvious. Total leg length seems to be clearly reduced in the dendrocolaptids. Histograms of the means of the ratios of the limb elements for both families are given in figure 15. The intermediates are not included in these data.

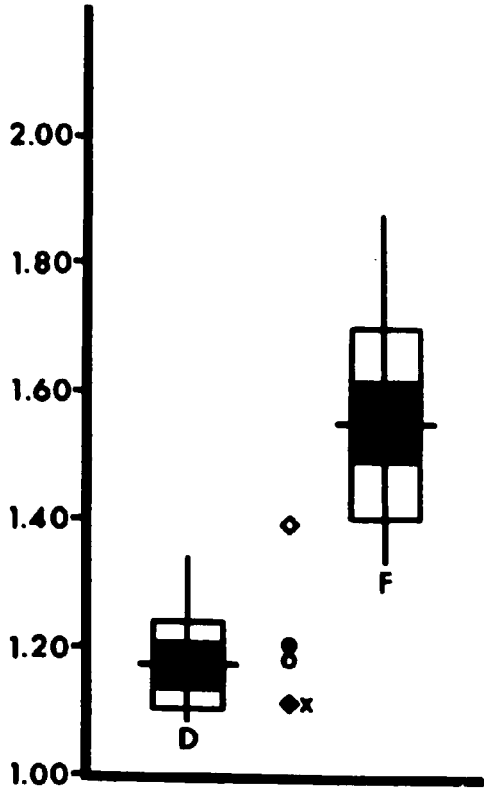
Richardson (1942) found much the same thing from his comparisons that I have presented here. His data indicated that, "Dryobates and Dendrocolaptes have relatively very short legs when compared to either Thryomanes or Corvus." Richardson's statement that probably the most significant factor in the shortening of the leg in trunk-foraging is the shortening of the tibiotarsus seems to hold true from my data. He pointed out, also referring to the work of Stolpe (1932), that, "The weight of the body of the climbing bird continually acts through the leg to pull the bird outward and downward, and to extend the joints of the leg. . . The leverage of this force of gravity acting to extend the intertarsal joint is decreased with the shortening of the tibiotarsus." This does seem to be one factor involved in the shortening of the legs, but, as Richardson also pointed out, this shortening also brings the feet farther anteriorly to a better position for climbing.

For each limb element the position of the "inter-

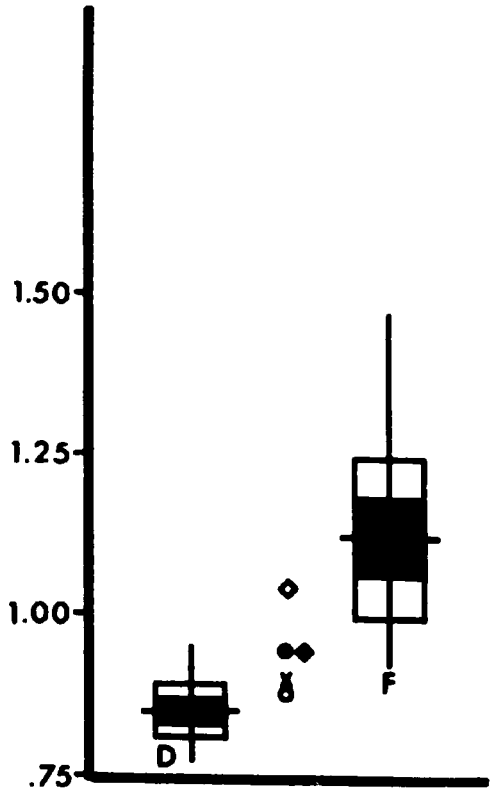
Figure 14. Comparison of ratios of lengths of femur, tibiotarsus, tarsometatarsus, and total leg to sternal length for the dendrocolaptids (D), and the furnariids (F). The "intermediates" are designated as follows: Glyphorhynchus, an X; Sittasomus, open diamond; Deconychura, closed diamond; Dendrocincla anabatina, open circle; and Dendrocincla fuliginosa, closed circle. The observed range and mean ± 1 standard deviation (enclosed area) and ± 2 standard errors of the mean (black area) are shown for each group.



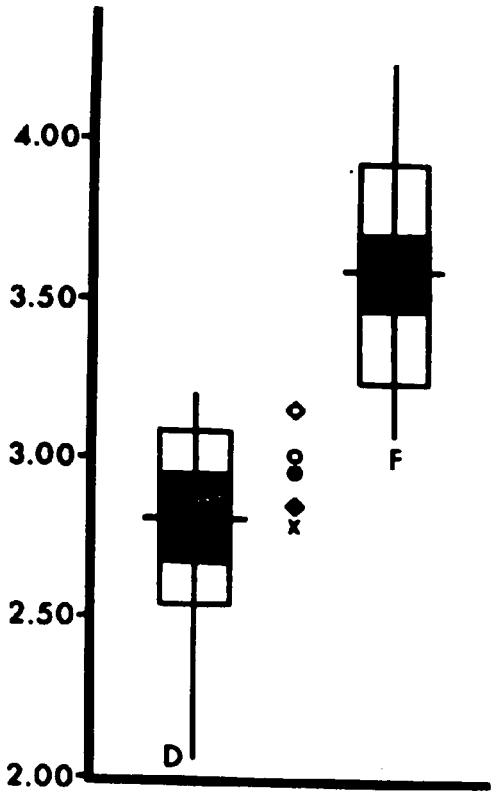
FEMUR



TIBIOTARSUS

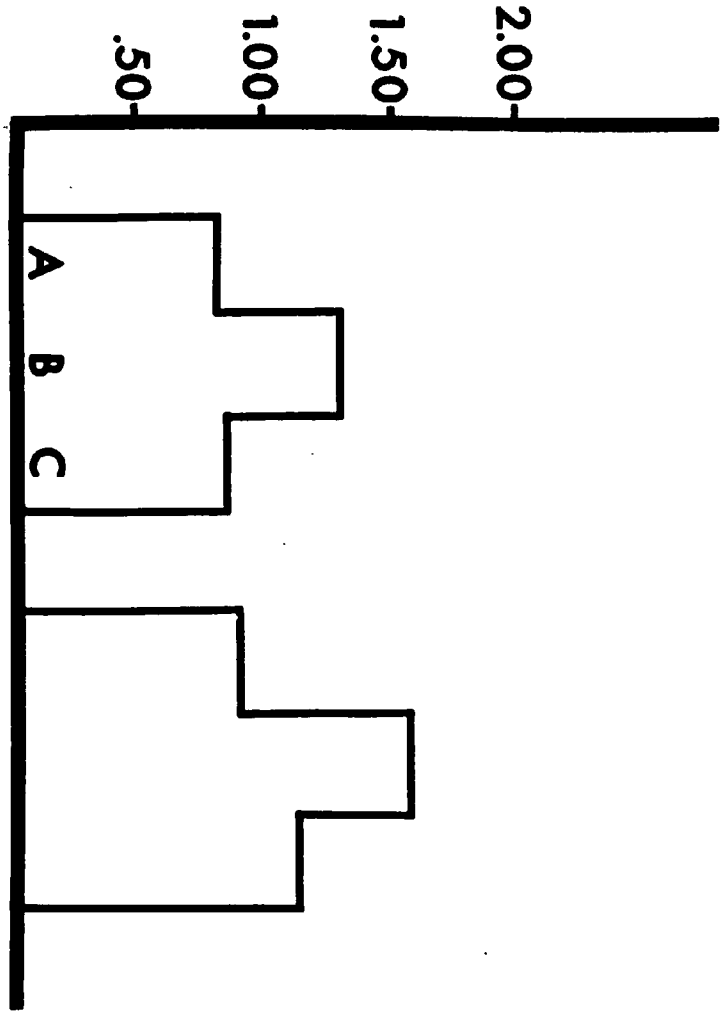


TARSOMETATARSUS



TOTAL LEG LENGTH

Figure 15. Histogram illustrating ratios of the different leg elements to sternal length in the dendrocolaptids (left), and in the furnariids (right). The elements are A, femur; B, tibiotarsus; and C, tarsometatarsus.


.50
1.00
1.50
2.00
A
B
C

mediates" with respect to the range of the two families is shown between the two family range diagrams. Although these forms generally conform to the dendrocolaptid range, as one might expect owing to their climbing habits, they are often at the end of the range of the dendrocolaptids, nearing the furnariid range, and in only a few cases extend towards the extreme range of the dendrocolaptids. However, the "intermediates" clearly possess woodhewer "climbing" adaptations with respect to the relative length of the leg elements. Although Sittasomus is closer to the ovenbirds in a number of these limb characters.

Distal End of the Tarsometatarsus

The distal end of the tarsometatarsus shows striking differences between the woodhewers and ovenbirds and therefore deserves special attention. Figure 16 shows the distal ends of the tarsometatarsi in a variety of ovenbirds and woodhewers. Several main points are immediately apparent. First, the size of the metatarsal I varies greatly between the two groups. This metatarsal, the only one to remain unfused in passerine birds, functions as an articular surface for the base of the hallux and also as a pulley for the tendon of M. flexor hallicis longus (see Richardson, 1942, for a more complete discussion of this character). The size of metatarsal I is directly correlated with the length of the hallux. In the woodhewers, metatarsal I is short, corresponding to a short

hallux, a character that is associated with climbing. In the ovenbirds the metatarsal is long, indicating a long hallux, a common feature of perching birds. Of special interest here are the "intermediates," which are in the woodhewer range with respect to this character but are somewhat intermediate, especially Dendrocincla and Sittasomus. Of the climbing types of furnariids, Pygarrhichas and Xenops show some reduction of metatarsal I, and the condition in Margarornis approaches that of the woodhewers.

Second, the amount of separation of the articular condyles is an expression of the amount of basal spread of the toes. In climbing birds, where selection forces are operative for a strong set of opposable toes, spread of the condyles could help facilitate this end. In the woodhewers this is the case, and there is relatively greater separation of the trochlea for the digits than in the ovenbirds. The "intermediates" are somewhat intermediate in this character, although I found no quantitative means of showing the difference.

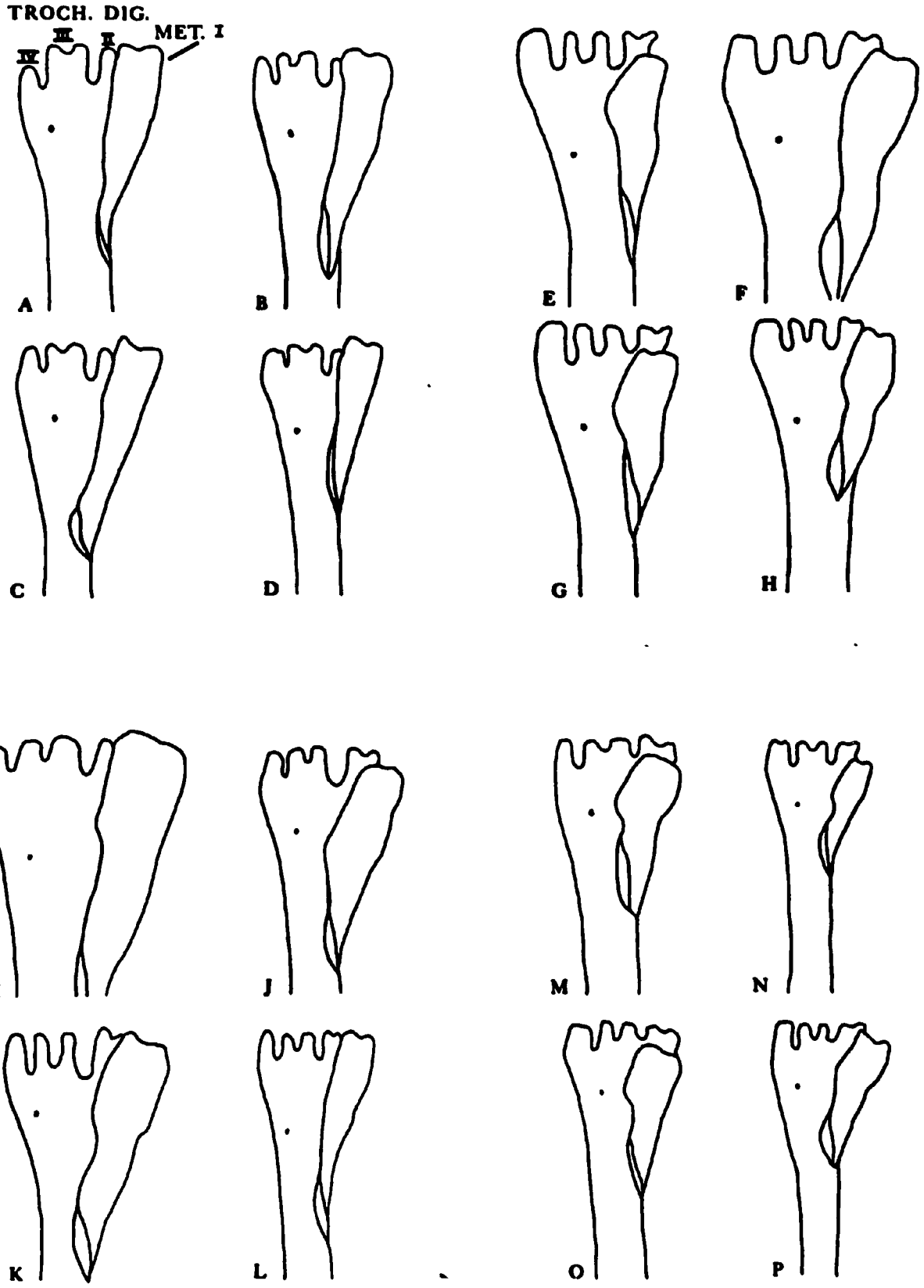
The third character of the distal end of the tarsometatarsus that is of interest is the trochlea for digit III. In the woodhewers this trochlea is deeply excavated; in the ovenbirds, much less so. Although this character state is not clearly understood, it would seem to serve to help hold the third toe in firm position, even when the

toes are fully extended. Whatever the exact function of this character, it is an obvious climbing adaptation since the same type of excavation of the trochlea for digit III is also found well-developed in Certhia and Sitta (see Richardson, 1942: 339), and as Fig. 16 shows, Pseudocolaptes, Margarornis, Pygarrhichas, and Xenops, all climbing types among the ovenbirds, show varying degrees of excavation of the trochlea. It is greatest in Pygarrhichas. The "intermediates" are of great interest with respect to this character as Dendrocincla and Glyphorhynchus are particularly intermediate between the woodhewers and typical ovenbirds in this character.

Femur and Tibiotarsus

Although there are very few characters that differ qualitatively between the woodhewers and ovenbirds in the pelvic region and the limb elements involved in that system, there are a few noteworthy exceptions. One is the presence of a foramen or several foramina in the proximal end of the femur (Fig. 17), which is present and well-defined in all of the woodhewers and in the "intermediates" except in Glyphorhynchus (nearly absent in Dendrocincla), but absent in most of the ovenbirds, except in the philydorines where it is present in about half of the forms examined. However, in the philydorines it is reduced where present and is usually represented by several small foramina. It is also present in a few other species of ovenbirds. Whether

Figure 16. Camera lucida drawings of the distal ends of tarsometatarsi of A, Phacelladomus; B, Syndactyla; C, Philydor; D, Synallaxis, E, Dendrexetastes; F, Dendrocolaptes; G, Xiphorhynchus; H, Lepidocolaptes; I, Pseudocolaptes; J, Margarornis; K, Pygarrhichas; L, Xenops; M, Dendrocincla; N, Glyphorhynchus; O, Deconychura; and P, Sittasomus. A through D are typical ovenbirds, E - H, "strong-billed" woodhewers, I - L, aberrant ovenbirds, and M - P, the "intermediates."


TROCH. DIG.
IV
III
II
MET. I
A
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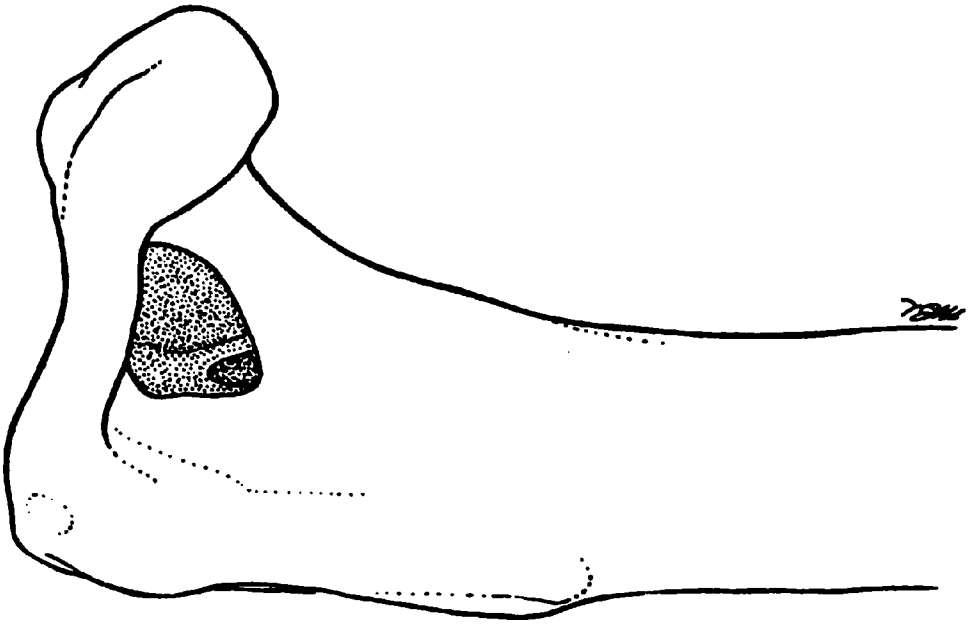
or not this represents a trend towards increased pneumatization, and hence reduction of weight in the pelvic region is impossible to determine.

The most striking qualitative difference in the limbs lies in the characters of the tibiotarsus. Whereas the proximal end of the ovenbird tibiotarsus is typical of passerine birds in general, the proximal end of the woodhewer tibiotarsus differs greatly from the passerine pattern and is almost identical to that of the woodpeckers. This remarkable example of convergence lies mainly in the expansion of the anterior region of the proximal end of the tibiotarsus for increasing the areas of origin of the flexor of the tarsometatarsus, M. tibialis anterior (see Richardson, 1942), and the extensor of the three anterior toes, M. extensor digitorum longus. Figure 18 shows the great similarity of the tibiotarsus of woodpeckers and woodhewers, as compared to the different "passerine" and ovenbird pattern. Some philydorines appear to approach the woodhewer condition of the proximal end of the tibiotarsus, but only in Xenops is this clearly the case. The "intermediates" show the woodhewer condition with respect to this character, but Dendrocincla is somewhat intermediate.

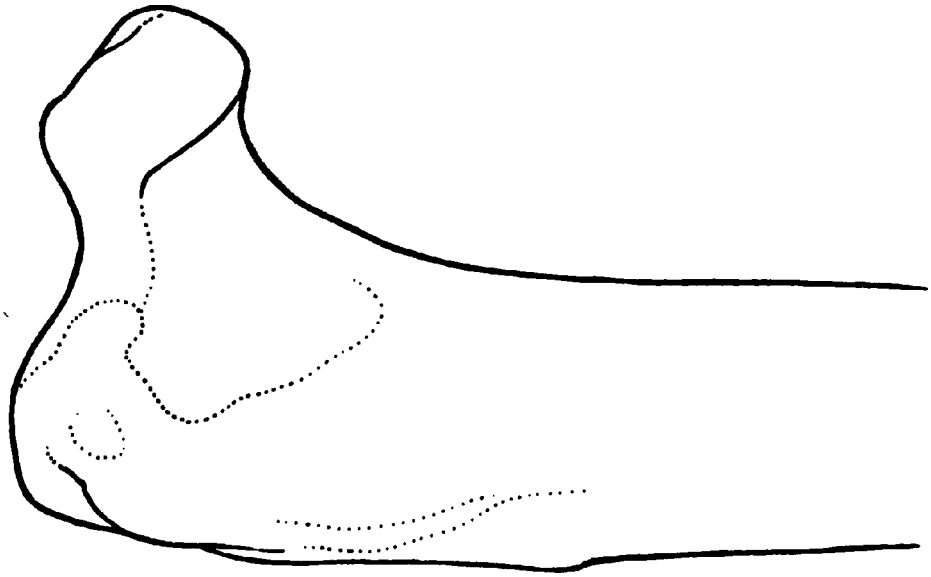
The Digits

The next foot character to deserve attention is the relative length of the various digits. This

Figure 17. Posterior views of the proximal ends of the left femora of A, Furnarius, and B, Xiphorhynchus.

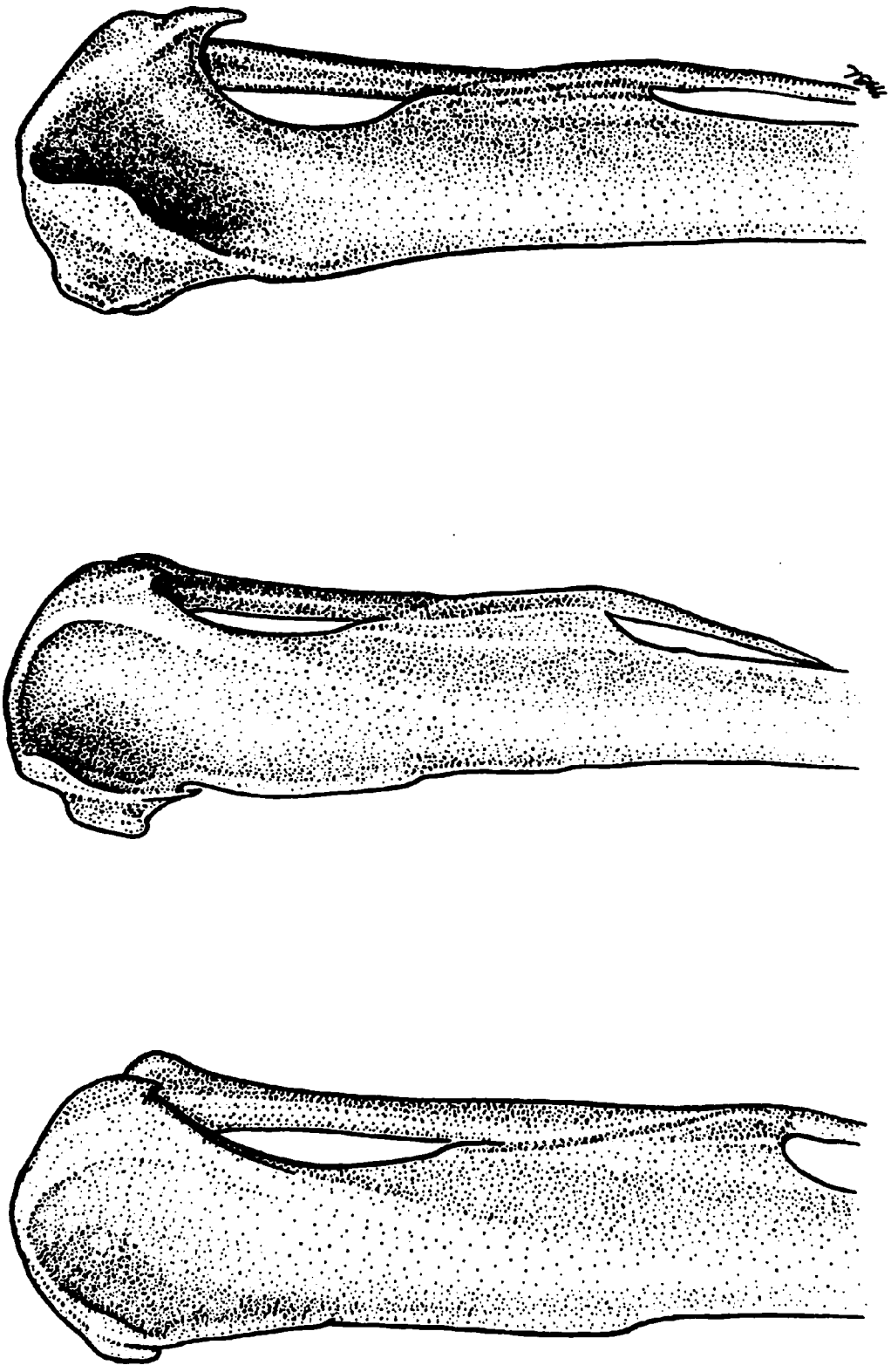


B



A

Figure 18. Proximal ends of tibiotarsi of A, a woodpecker, Dendrocopus, B, Xiphorhynchus, and C, Furnarius.


C
B
A

character complex is of particular interest since it was originally one of the main characters by which the family Dendrocolaptidae was separated from the Furnariidae. The woodhewers are separable from the ovenbirds by having the third and fourth toes approximately equal in length, and this length is greater than that of the digit II. The hallux is shorter than the inner toe, and the three anterior toes are united for the entire length of their basal phalanges. The middle toe is fused to the outer by almost the full extent of the second phalanx. In the ovenbirds, the toes are more like the typical passerine condition. Digits II and IV are about equal in length, and digit III is longer than either II or IV. The hallux without the claw is not shorter than the inner toe (No. II) without the claw. The basal phalanges of digits III and IV are fused together for most of their length. These two basic patterns are illustrated in figure 19.

Although the two basic patterns are generally reliable to separate the two groups as presently defined, there is much variation, especially among the various ovenbirds which engage in some types of climbing behavior.

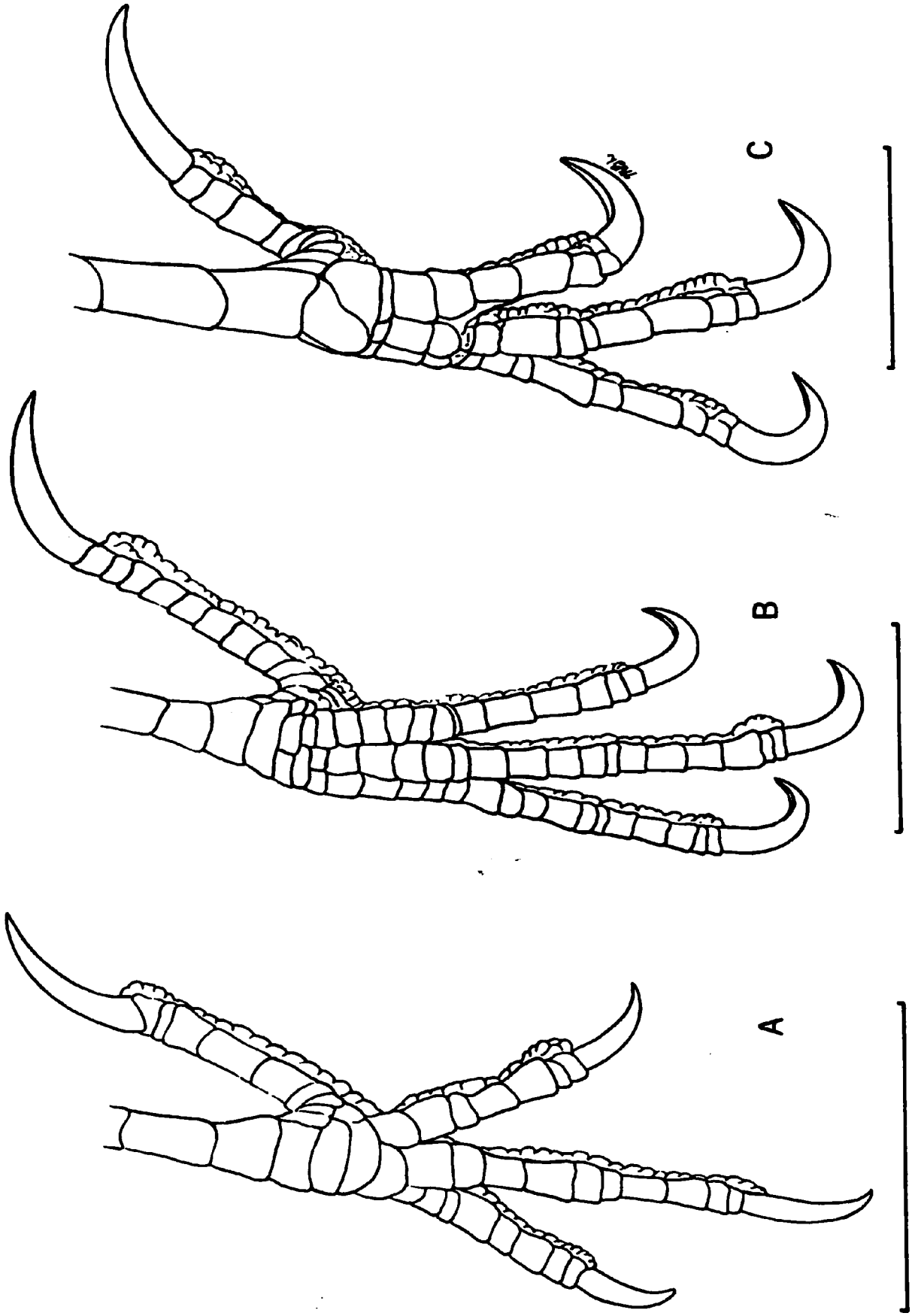
As Richardson (1942: 323) pointed out, the basal segments of the digits of Certhia, Sitta, and Thryomanes are hardly separable from each other, being fused. This

is also true of some of the climbing and clinging forms within the ovenbird assemblage. In Margarornis, Premnornis, Premnoplex and in some of the species of Cranioleuca there is a tendency toward this condition; The three basal phalanges are fused exteriorly for their entire length. In these species there is a slight amount of fusion between the second phalanges of digits III and IV. Many of the philydorines show the same tendency towards fusion of the basal phalanges, and Pygarrhichas and Xenops show essentially the woodhewer condition with respect to the fusion of the basal phalanges leading from the typical ovenbirds (the typical passerine condition) through the climbing ovenbirds and the philydorines and Pygarrhichas to the typical woodhewers. That this is a trend towards an efficient climbing type of foot seems to gain credence from the occurrence of the same condition in other climbing passerines such as Certhia and Sitta.

The Tail

Stiffening of the tail feathers is a characteristic feature of trunk-climbing birds, and the woodhewers show a high degree of modification of the tail with respect to this character. Woodhewers generally have long, stiff tails, the distal tips of which come into contact with the three in climbing by the long, often bare, inward-curving rami. No attempt was made here to correlate length of the tail and the strength of the rami with trunk-climbing.

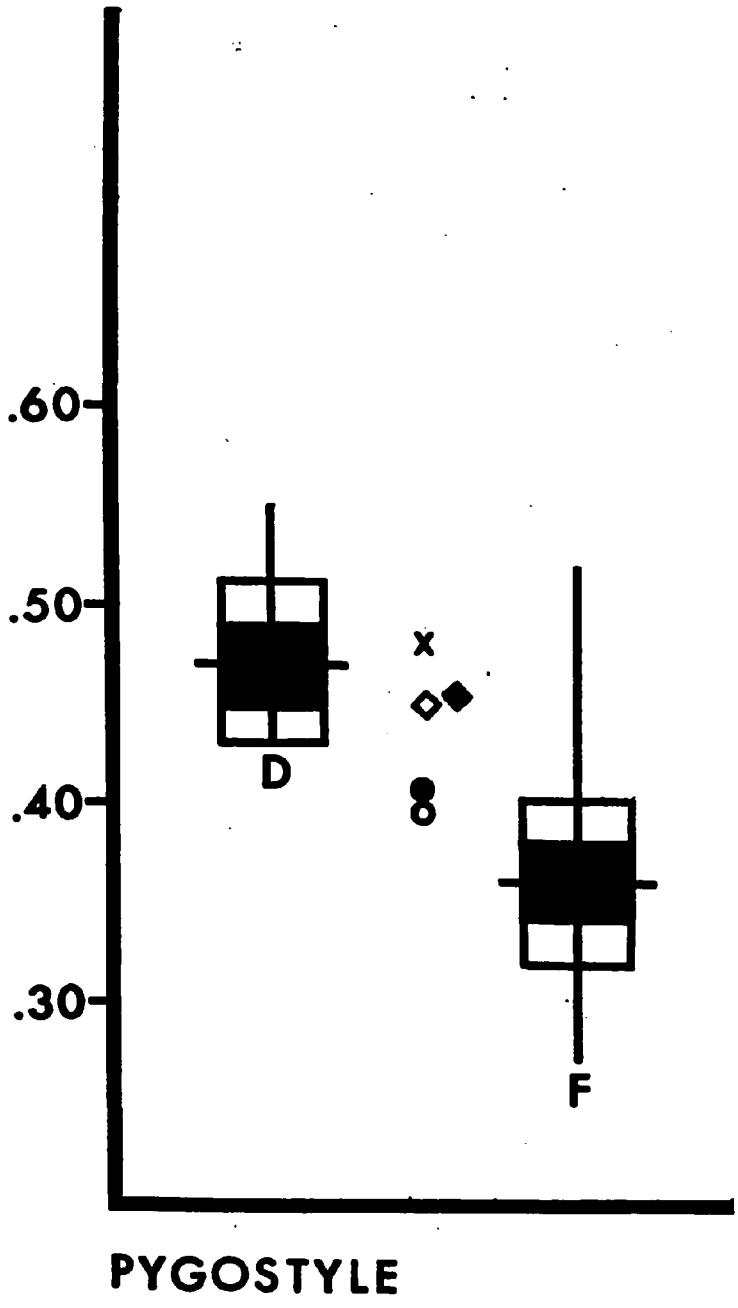
Figure 19. Drawings of the feet of A, Synallaxis, B, Pygarrhichas, and C, Xiphorhynchus. Each line represents one cm.


C
B
A

The main point of interest for the purpose of this paper is that most of the trunk-climbing ovenbirds show this tail adaptation and actually possess the stiff, woodhewer-like rectrices. The forms include Margarornis, Premnornis, Premnoplex, Pygarrhichas, some species of Cranioleuca, and others to a lesser degree. It is of interest here that many of the non-climbing ovenbirds possess some degree of stiffening of the tail feathers and may have the barbless rami protruding distally. Even the long-tailed, titmouse-like species of the genus Leptasthenura apparently use their stiff rectrices for support and balance in their foraging behavior. The possession of these types of tails, particularly in the philydorines, would certainly be a good pre-adaptation for tree-trunk foraging. The tail of Dendrocincla shows a lesser amount of stiffening of the rectrices than the other woodhewers.

As an index to the degree of general tail-muscle development, the pygostyles of woodhewers and ovenbirds (same species as for the limb data) were compared. The measurement taken was the height of the pygostyle from the dorsal extreme of its crest to the ventral margin of the disc, and they are expressed as ratios to the sternal length (Fig. 20). As expected, the woodhewers show a much greater development of the pygostyle than the ovenbirds. The "intermediates" are shown between the range diagrams. Note the position of Dendrocincla

Figure 20. Comparison of ratios of height of psygostyle to sternal length for dendrocolaptids (D), and furnariids (F). The intermediates are designated the same as in Fig. 14, and the statistics are of the same type.


.60
.50
.40
.30
D
F
PYGOSTYLE

(closed circle). The points that compose the upper part of the furnariid range are the tree-trunk foraging furnariids.

Syringeal anatomy

In his excellent study of the passeriform syrinx, Ames (1965: 234) stated of the Furnarioidea that, "This superfamily of the suborder has the most clear-cut phylogeny, from the syringeal point of view, of any passerine group, but their syrinx suggest nothing about their relation to other groups. The Membranae tracheales were probably nearly or wholly evolved before the group diversified into the wide variety of forms present today. The Membranae are the most uniform feature of the furnarioid syrinx, except for the absence of the pessulus. Apparently the pessulus was lost early in the evolution of this group, for no trace of it has been found in any modern furnarioid. The diversification of syringeal types led to two major stocks. The ovenbird-woodhewer line (Furnariidae and Dendrocolaptidae) evolved a dorsoventrally symmetrical syrinx with two pairs of muscles. The woodhewers evolved more elaborate Processi with projecting horns for the attachment of muscles. It is not clear whether the presence of horns on the Processi in Geositta represent an independent appearance from those in the woodhewers."

He further states in his systematic conclusions

(pp. 248-249) that, "The syrinx of the woodhewers is distinguished from those of other members of this suborder in possessing prominent dorsal and ventral horns on the processi vocales. Only this family and the Furnariidae possess two pairs of intrinsic syringeal muscles. The presence of horns on the processi of Geositta may indicate that this genus is more closely allied to the woodhewers than to the ovenbirds (Furnariidae) but further studies are needed to clarify its position. It is possible that the need for greater mechanical advantage for the syringeal muscles has caused the evolution of horns in the syrinx of Geositta, independently of the Dendrocolaptidae, but in this case one would expect to find horns on the processi of other ovenbirds, which must have been subjected to similar selective pressures." Ames states of the Furnariidae that, "The close relationship of this group to the woodhewers is indicated by the similarity of syringeal musculature, which sets the two families apart from the antbirds (Formicariidae) and tapaculos (Rhinocryptidae)."

So, although the differences in syringeal anatomy between the Furnariidae and Dendrocolaptidae are not great, the two groups are separable, and Geositta possesses the dendrocolaptid type of syrinx. Why Geositta should possess the woodhewer type of syrinx is difficult to understand. It strongly suggests that the syrinx may, at

times, be a homoplastic character. Geositta is clearly not a close ally of the woodhewers, and on the basis of anatomy and plumage characters occupies an unequivocal position in the subfamily Furnariinae of the Furnariidae. The origin of the woodhewer type of syrinx is further difficult to understand from a functional standpoint. Although we know little of syringeal function, it would seem reasonable to assume that selection would operate in the same directions for the same functional ends. In the case of Geositta, however, it is difficult to understand what similar function would be demanded of this lark-like open country bird, that would be similar to the deep-forest inhabiting woodhewers. The origin of the woodhewer-like syrinx in Geositta does suggest, however, that the origin of that type of syrinx may be a fairly simple change. Whether the woodhewer-type syrinx arose several times in the evolution of the dendrocolaptids, or if all of the dendrocolaptids arose from the philydorines with the woodhewer-type of syrinx is impossible to determine. One might expect that similar selection forces might operate on the syringes of trunk-foraging birds, but the problem must await further investigation.

The woodhewer type of syrinx was discovered by Ames in the following genera: Dendrocincla, Sittasomus, Glyphorhynchus, Drymornis, Xiphocolaptes, Dendrocolaptes, Xiphorhynchus, Lepidocolaptes, Campylorhamphus, and

Geositta, and the furnariid type was found in Furnarius, Cinclodes, Upucerthia, Limnornis, Aphrastura, Phleocryptes, Synallaxis, Certhiaxis, Asthenes, Phacellodomus, Anumbius, Pseudocolaptes, Pseudoseisura, Anabazenops, Philydor, Automolus, Heliobletus, Xenops, Megazenops, Pygarrhichas, and Sclerurus.

DISCUSSION

Suboscine evolution

In considering the question of whether or not the suboscines are more primitive than the oscines, it seems wise to consider first the reasoning behind the commonly held view that the passerine birds are more highly evolved than non-passerine birds. What is generally implied by the term "advanced" or "highly evolved" of most authors is not entirely clear, since, in fact, it can be said with certainty that all modern birds are "highly evolved." The question seems to boil down to distinguishing between the older, more slowly evolving groups and the groups of more recent origin that are in a period of rapid evolution. That our present classifications are based on this type of thinking is obvious, but the attempt to distinguish between "advanced" birds and "primitive" birds is probably almost never met with success. As Storer (1959: 152) pointed out, "The basic principle behind most systems of classification is that the older, more slowly-evolving groups are placed first and the newer, more rapidly-evolving groups last." He further points out that, "... it is difficult to find more highly specialized birds than the penguins, yet these birds are almost universally placed near the beginning of

classifications ...." So, we are basically concerned with either the time at which a group began to diverge or the amount of adaptive radiation exhibited by a group or both in considering the relative degree of advancement in a group of birds, but the two may not equally apply to any given group. For example, there is no reason why a group of birds could not have originated fifty million years ago, but have undergone most of its adaptive radiation, say, ten million years ago when some new habitat type became abundant.

Moreau (1966: 408) has an excellent summary of the possible reasons why the passerines are a more rapidly evolving group than many others. The reasons are that most passerines breed in their first year, therefore giving them the ability to respond more rapidly to selection pressures, implying a rapid turnover of species. Also, the higher categories of passerines are not so well-defined as those of most non-passerine groups, indicating a shorter age for passerines. It may also be that smaller animals are, in general, easier to isolate than larger ones, simply because of the size factor, and therefore divergence is more easily achieved. It is also true that small birds can undergo more radiation than can larger birds because of the physical factor of size; more small birds will fit into a given area than large forms. Also, there is the problem of habitat-niche availability.

It seems reasonable that there are, for example, more ways to be an arboreal bird than a wading type.

The whole problem of what is primitive and what is advanced in the class Aves is still a completely open question which first requires a statement of what is meant by the terms and second an attempt to find groups that fit the criteria. For the present we must be content with the fact that most if not all Recent birds are highly specialized, and that our present classifications do not show any kind of avian phylogeny for the major groups, say, at the ordinal level.

For the purposes of this paper it seems instructive to consider whether or not the oscines are more advanced than the suboscines in terms of actual age and degree of specializations, because an answer to this question may aid in answering certain questions of their evolutionary trends.

In his excellent paper on the passeriform syrinx, Ames (1965) concludes, as concerns the suboscine groups, that the Old World families that he examined, Eurylaimidae, Philepittidae, Pittidae, and Menuridae, (in addition to literature information on others) are, in their syringeal musculature, not definitely alignable with the New World groups of suboscines, but that all of the groups under consideration show primitive (less complex musculature) syringeal anatomy, therefore confirming earlier works.

Ames recommends division of the Passeriformes into five suborders on the basis of the syrinx as follows: Eurylaimi (including the Eurylaimidae and the Philepittidae), Furnarii, Tyranni, Menurae, (the Pittidae remaining "incertae sedis"), and the Passeres (Oscines). The point for the purposes of this discussion is that all of the suboscines, Old and New World, possess simple syringeal musculature and have rather simple songs. Whether or not the suboscines are as a group monophyletic or polyphyletic cannot be determined with the present state of our knowledge. The Passeres (Oscines) possess much more complex syringeal musculature and are, of course, capable of very complex vocalizations.

There are two schools of thought concerning the relative degree of primitiveness of the suboscines. What Slud (1960) has termed the case against the suboscines has been stated by Mayr and Amadon (1951: 12-13): "The various suboscine perching birds give every appearance of being in the process of replacement by the Oscines. Many of the families of the former group have a relict distribution in Madagascar, New Zealand, Australia, or South America. The last continent was of course isolated for a long time. It has few well-differentiated families of indigenous song birds, although the subfamilies of the tanager-pyrrhuloxine finch assemblage are richly developed. An adaptive radiation of the wrens, mimids, and other song birds of South America might reduce the suboscines of that continent to

the subordinate position they occupy in the Old World." Slud (1960: 137) cites similar reasoning from several other sources, and then comes to the defense of the suboscines, stating that, "Because of zoogeographical considerations, by imputation an Old World effeteness is ascribed to 1100 species of suboscines in the New World." He further points out that most of these authors he cites consider South America as "...a zoogeographical outpost providing a temporary refuge for remnants and a haven for relicts." Slud obviously does not accept the view expressed by Mayr and Amadon that with the evolution of the more advanced oscines, the suboscines decline in various parts of the world, and that South America has, due to its Tertiary isolation, served as a refugium for the various groups of New World suboscines. In tabular form Slud produces the necessary data to indicate that in numbers the suboscines show no sign of decrease as compared with the oscines in South America. Slud marshalls further evidence indicating that the suboscines of the New World are basically restricted to the Amazon Basin with extra-limital occurrence in Central America and some representation in North America. As Slud states, "The suboscines seem to have evolved primarily in the tropical belt in intimate association with the continuing development of preexisting "rain forest." From this equatorial wellspring the tyrannids and furnariids have streamed into austral

South America, where they have radiated as ecological counterparts of Old World types; they may or may not be better adapted to a temperate-region environment than their Old World homologues." What all this means for the purpose of this discussion is that the only place in the world where the suboscines have maintained themselves in great abundance is in equatorial South America (with some austral radiations of the tyrannids and furnariids), where they are present in equal abundance with oscine representatives, and these are for the most part the New World nine-primaried oscines. What this means in terms of ecological types is that a comparison of Old and New World avifaunas would probably produce ecologically equivalent oscines in the Old World to match oscines and suboscines in the New World. What Slud is apparently saying is that the suboscines indeed are not being pushed out or out-competed by the oscines in South America, but that there is little overlap in their basic ecological occupations. In other words, since the close of the Cretaceous in South America when the Amazonian seaway was closed out and the forested Amazon Basin began to form, the suboscines and oscines have evolved in harmony, whatever was the time of origin of each group. This makes a nice story at first glance, and could be true, but let us consider some other aspects of these arguments. For one thing, it is impossible to determine when the suboscines

or oscines arose or entered South America. We have a good idea that with the receding of the Cretaceous sea, the forested Amazon Basin probably began to form and its great age seems apparent from the richness of the forest with its great floral and faunal diversity. However, whether or not the suboscines and the South American oscines began their radiations with the beginning of the Amazon Basin forest is still another question. There is no pre-Pleistocene fossil record of any consequence for these groups in South America, so we must look elsewhere for an answer. But, whatever hypothesis emerges, it will be untestable owing to the fact that we are dealing with historical events. Slud (1960) would favor the argument that the suboscines are not like the marsupials of South America, which were for the most part apparently eliminated by placentals when the land bridge connected South and North America and are not being replaced by oscines but are holding their own in the face of oscine radiations in the same areas. There seems to be some confusion in these arguments as to the degree of primitiveness and whether or not a group should be replaced by another. For example, there is no evidence that cuckoos, which are generally thought of as being more primitive than passerines, are being replaced by passerine birds. Likewise, there is no evidence that the New World suboscines are presently being replaced by oscines. The New World suboscines are obviously

well-adapted to tropical forest. It is of interest here that most of the oscines in tropical forest (not including wintering forms) occur in the upper stories of the trees. Whether or not this is a sign of a more recent origin of oscines in tropical forests is impossible to determine, but it is an interesting situation.

I favor the following argument, which is that of most other authors on this subject. As Mayr and Amadon stated, the groups of Old World suboscines show a relict distribution. These groups are the Eurylaimidae (14 sp.), which occur in Central and southern Africa, the Himalayas, Indo-China, parts of the Malay Penninsula and the Philippines; the Pittidae (23 sp.), which occur over much of Africa, Australia and the Oriental Region; the Acanthisittidae (4 sp.), which are confined to New Zealand; the Philepittidae (4 sp.), which are confined to Madagascar; the Menuridae (2 sp.), which are confined to Australia; and the Atrichornithidae (2 sp.), which are confined to New South Wales and southwest Australia. These suboscines probably had much broader distributions during much of the early Tertiary and now show a decline, which is correlated with, although not necessarily a result of, tremendous oscine radiations in the Old World. Now let us look at the New World situation. The suboscines evolved in South America, probably during most of the Tertiary, a time when for the most part South America was separated

from North America by water gaps filled with varying series of island land masses which were Central America. These groups of suboscines are the Dendrocolaptidae (48 sp.), which clearly originated within the Amazon Basin; the Furnariidae (215 sp.), which show two different distribution patterns, on the one hand an Amazon Basin radiation, and on the other, a large peripheral radiation in the Andes and in southern South America; the Formicariidae (222 sp.), which are primarily a humid forest group; the Conophagidae (11 sp.), again a humid forest group (see Ames, Heimerdinger, and Warter, 1968, for taxonomic discussion of this group); the Rhinocryptidae (26 sp.), a group peripheral to the Amazon Basin; and the suborder Tyranni, which includes the Cotingidae (90 sp.), which is primarily a humid forest group; the Pipridae (59 sp.), which is again a forest group; the Tyrannidae (365 sp.), which although a forest group, has radiated into a very large variety of habitats and has extended in some numbers into North America, and two somewhat aberrant and small groups, the Oxyruncidae (1 sp.), and the Phytotomidae (3 sp.).

If condensed these suboscines form two large groups (which are cohesive taxonomically from the standpoint of syringeal anatomy). These are the superfamily Furnarioidea, which consists largely of humid forest types. The exceptions are the large radiations of the ovenbirds that have

occurred peripheral to the Amazon Basin, and the rhinocryptids, the 26 species of which are for the most part peripheral to the Amazon Basin. The other suborder, the Tyranni, consist of the Cotingidae-Pipridae-Tyrannidae group, which, with the exception of the Tyrannidae, which has radiated also in the periphery of the Amazon Basin region and extended northward, are a humid forest group, and the little known Oxyruncus and three species of Phytotoma. What this seems to indicate is that there were two large non-Amazonian radiations from the New World suboscines, the ovenbirds and the tyrannids. The tyrannids appear to have no oscine ecological counterparts in the New World as are the Muscicapidae (328 sp.) in the Old World. The furnariids, which have, aside from their Amazon Basin radiations, radiated mainly in the Andes and in southern "temperate" South America, exhibit a very large variety of ecological types (see natural history section). There are marsh wren, thrasher, nuthatch, lark, and tit types, and many more, most of which are ecological counterparts to oscine species in various parts of the world. So, in summary the furnariids are the only group of New World suboscines that have radiated out of the Amazon Basin into ecological types resembling already existing New World oscines. Also, this radiation would appear to be more recent, judging from the antiquity of the forested Amazon Basin region compared to the relative recency of the high

Andean regions.

If we summarize the distributional picture of the suboscines, and if we can assume that the suboscines represent the primitive types of passerines due to their relatively less complex syringeal musculature and were indeed early experiments in passerine evolution, then it would make sense that the suboscines, as evidenced by their relict distribution pattern in the Old World, were probably replaced there by oscine counterparts. In the New World the situation is greatly different. South America, the area in which the suboscines have undergone their radiations, was separated from other land areas during most of the Tertiary, and therefore large immigrations of oscines were at least partially inhibited. And, even if the oscines of the New World could have invaded, there do not appear to be groups in the New World equivalent to groups in the Old World that have undergone tremendous adaptive radiations into so many ecological types, such as the Timaliidae and the Muscicapidae. Why, in the New World, with all of its habitat diversity have there not been radiations of oscines equivalent to those of these Old World groups? It is possible that the New World oscines simply do not have the evolutionary potential for such radiations, although this is not, and probably never will be demonstrable. It may be that the oscines present in South America during the radiation of the suboscines

there were incapable of the adaptive radiations that the suboscines have undergone there. This might better explain why the suboscines have undergone no apparent diminutions in the New World, and why such groups as the tyrannids have been able to invade North America. However, all of this is speculation and remains and will remain, untestable.

A Phylogeny

The evolution of trunk-foraging types in the groups under consideration has involved two major ancestral types. On the one hand the philydorines have apparently given rise to the woodhewer groups from several different lines, and on the other hand the synallaxines have given rise to a number of creeping types, including the Margarornis-Premnornis-Premnoplex complex, and Cranioleuca, some species of which hitch up tree trunks in their foraging behavior. There is also Pygarrhichas, which, although closest to the members of the Furnariinae and Sclerurinae in cranial morphology, must remain in the category "incertae sedis." The zoogeographic data are perfectly compatible with the above statements. The Philydorinae and the woodhewers are both primarily Amazon Basin forest groups and occur in almost equal numbers in every country in which they are found. The synallaxines occur primarily outside of the Amazon Basin forested regions, as do also the trunk-foraging forms, Margarornis, Premnornis, Premnoplex, and Cranioleuca. Most of these forms occur in

highland situations where the numbers of woodhewer species are greatly reduced. Pygarrhichas occurs in a region which has no woodhewers.

Anatomically, the woodhewers are most closely allied to the philydorines that share many cranial characters with the woodhewers. The trunk-foraging synallaxines are clearly within the boundaries of the subfamily Synallaxinae in cranial morphology.

The anatomical evidence clearly advocates a derivation of the woodhewers from philydorine-like ancestors. There appears to have been one great radiation of woodhewers that resulted in what I term the "strong-billed" woodhewers, which includes the genera Drymornis, Nasica, Dendrexetastes, Hylexetastes, Xiphocolaptes, Dendrocolaptes, Xiphorhynchus, Lepidocolaptes, and Campylorhamphus. Other genera appear to be later derivatives from philydorine-like ancestors. Some possess a furnariid wing pattern and many anatomical features that ally them with the ovenbirds, although in creeping behavior they are identical to other woodhewers. These genera include Glyphorhynchus, which possesses some cranial characters and other anatomical features which ally it with the philydorines, and the wing stripe commonly found in the Furnariidae, but has the electrophoretic hemoglobin pattern of the woodhewer group. Deconychura and Sittasomus also appear to be more recent offshoots from philydorine-like ancestors. These

forms possess some cranial and other anatomical characters that ally them with the philydorines, but in skull structure are very similar to each other. Although Deconychura possesses the dendrocolaptid wing pattern, Sittasomus has the same wing stripe that is found in Glyphorhynchus and commonly in the Furnariidae. The hemoglobin patterns in both Sittasomus and Deconychura are different from either the woodhewer or the furnariid patterns, but are like each other. The last "intermediate," Dendrocincla, also appears to be a more recent offshoot of philydorine-like ancestral stock. Of the "intermediates" Dendrocincla is closest to the philydorines in skull structure and in other anatomical characters, and in behavior is a perfect intermediate between the philydorines and the woodhewers. The wing pattern of most of the species of Dendrocincla is like that of the woodhewers, but D. anabatina possesses a wing stripe similar to that of many furnariids but somewhat more diffuse. The hemoglobin of Dendrocincla is identical to that of the Furnariidae in its electrophoretic pattern.

Of all the characters analyzed in this paper, the "intermediates" appear furnariid-like in some and dendrocolaptid-like in others. One seemingly important woodhewer character which all of the "intermediates" possess is the syrinx. This is somewhat unexpected; however, Geositta, a typical furnariid, also has a dendrocolaptid-like syrinx.

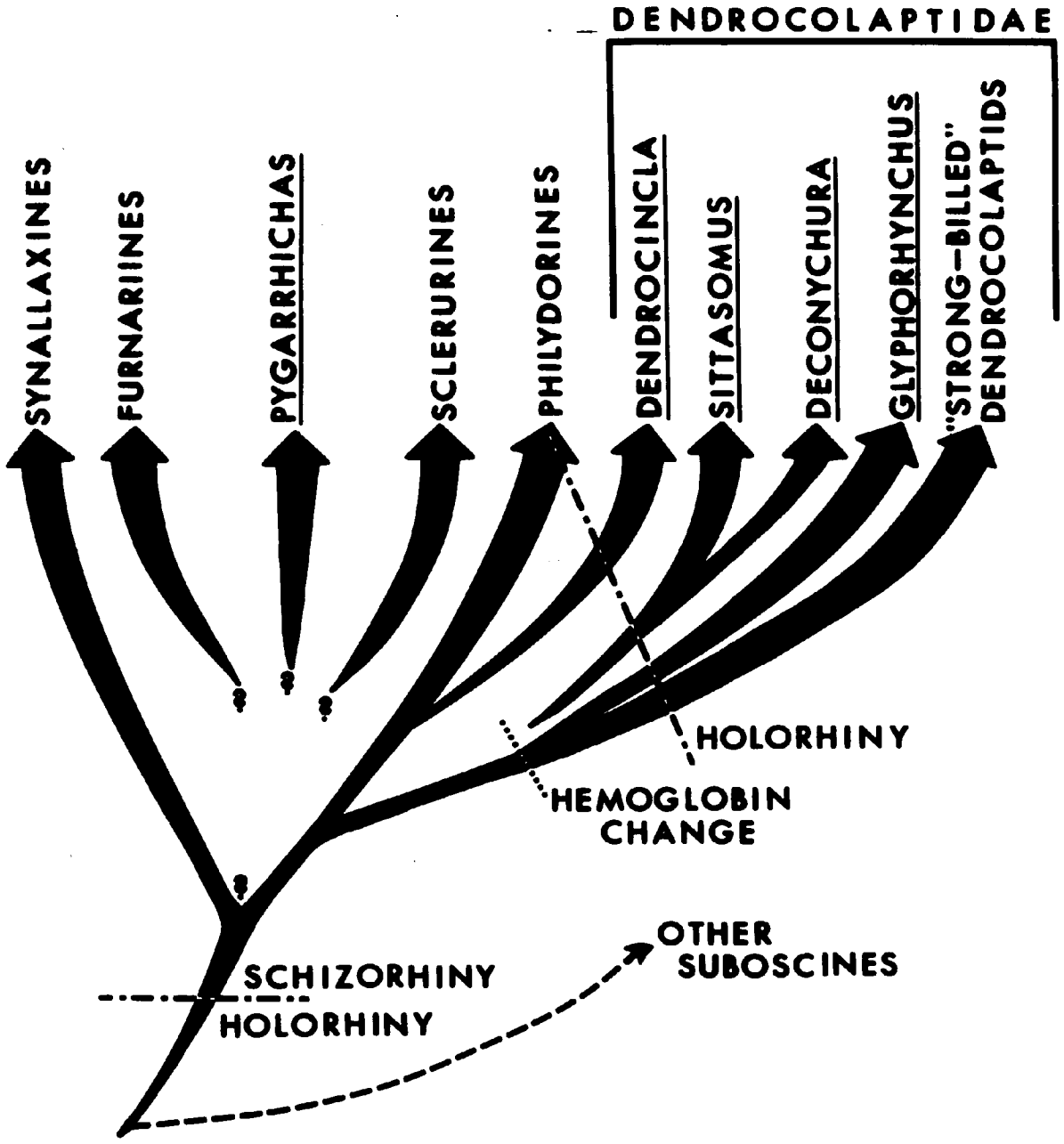
Heimerdinger (pers. comm.) has found that Dendrocincla, Sittasomus, and Glyphorhynchus conform to the woodhewer pterylographic pattern.

The total analysis seems to indicate that there was one large radiation of woodhewers from philydorine-like ancestors that resulted in the evolution of the "strong-billed" woodhewers, and subsequent offshoots that resulted in the "intermediate" genera (see Fig. 21). Relationships within the ovenbird groups are less clear. The exact position of the synallaxines, furnariines, and sclerurines would be difficult to ascertain. It seems reasonable, however, that some "holorhinal" pre-passerine gave rise to a "schizorhinal" group which resulted on the one hand in the evolution of the philydorines, the forest ovenbirds, and on the other hand, the synallaxine-furnariine groups. Later, the philydorines increased the ossification of the skull due to selection forces for stronger skulls. This led to series of holorhinal philydorines, which, concomitant with creeping tendencies, gave rise to woodhewer-like forms, and eventually to a radiation of woodhewers in their new adaptive zone.

A behavioral model

If we assume that the woodhewers are derived from the subfamily Philydorinae of the ovenbirds, and this seems to be a safe assumption on the basis of anatomy, behavior, and zoogeography, then we should be able to summarize more

Figure 21. Hypothetical phylogeny of furnariids and dendrocolaptids.


DENDROCOLAPTIDAE
SYNALLAXINES
FURNARIINES
PYGARRHICHAS
SCLERURINES
PHILYDORINES
DENDROCINCLA
SITTASOMUS
DECONYCHURA
GLYPHORHYNCHUS
"STRONG-BILLED" DENDROCOLAPTIDS
HOLORHINY
HEMOGLOBIN CHANGE
OTHER SUBOSCINES
SCHIZORHINY
HOLORHINY

properly the types of evolutionary trends involved in a transition to the woodhewer grade by looking at anatomical and behavioral series in the Recent forms. One thing that seems to be fairly well established is that all that is really needed to produce a climbing bird from any group of the Passeriformes is the necessary behavioral adaptations. The passerine body form, although typically for a perching bird, is suited for trunk climbing also, and there are climbing forms in many of the passerine families. In the furnariids, the preadaptations for tunk climbing seem to be very apparent. One of the more obvious of these is the stiff, spiny tail found in many non-climbing forms. Also, many of the philydorines that cling and forage in a variety of ways possess various degrees of development of curved claws, and other foot characters associated with climbing.

Of great interest is the genus Dendrocincla, members of which forage with diversity, both from a typical perching bird stance, and from the trunk climbing stance. As Willis (1966: 667) has summarized, "This woodcreeper . . . ordinarily clings to the trunks of trees and saplings in or near tropical lowland forests and sallies out like a flycatcher to snap prey off the ground or vegetation. It occasionally pecks prey off the surface vegetation, but it rarely moves about peering and probing into the bark or tangled vegetation in the fashion of many species in the

family Dendrocolaptidae." Willis (op. cit.) studied these birds in tropical forest situations where Dendrocincla is a normal constituent of mixed flocks that follow army ant swarms, where the arthropods and small vertebrates that flee the advance of the ant swarm are easy prey for the ant-following birds. In these situations Willis recorded the changes in the foraging behavior of Dendrocincla fuliginosa by recording ". . . changes of height of waiting birds or changes in heights at which prey items are taken." He (loc. cit.) found that, "When Plain-brown woodcreepers (Dendrocincla fuliginosa follow swarms of army ants on Barro Colorado Island, Panama Canal Zone, they forage in the zone near the ground more frequently when Ocellated Antthrushes (Phaenosticus mcleannani) are absent. The ground-foraging antthrushes regularly supplant the smaller woodcreepers, which then move to higher or to peripheral and less productive zones. This seems a clear example of competitive exclusion by dominance. On Trinidad, where competing low-foraging antbirds are nearly always absent, fuliginosa forages near the ground at swarms. In British Guiana, where several small antbirds saturate the lower levels over the ants, fuliginosa again forages high in the undergrowth." Thus, Dendrocincla fuliginosa appears to forage more diversely when competitors are present, and as Willis (op. cit., p. 670) says, "By widening its foraging zone in the presence

of competitors, fuliginosa probably obtains more food than it would if it continued to forage in the narrow zone near the ground." In other words, in this case it may be that competition in these mixed species foraging flocks causes some species, like Dendrocincla fuliginosa, which are capable of diversity in foraging behavior, to include new strategies in foraging behavior and thereby increase its food intake with a minimum of aggressive distractions.

Let us now examine what might be involved in the evolution of a woodhewer type from a philydorine furnariid. Of interest is the fact that the woodhewers and philydorines are distributed throughout their range in almost equal numbers, with their great center of abundance in the Amazon Basin rain forests. Further, both woodhewers and philydorines are frequent army ant followers, although forms of Dendrocincla are more nearly obligate followers than other woodhewers. In these situations where frequent aggressive encounters occur, it may be of great selective advantage to be very flexible in foraging behavior. In this respect we have already seen that the majority of philydorines (see natural history section) forage in a great variety of ways and many species hitch up tree trunks at times. In some highland situations where woodhewers are absent except for one or at most two species, the furnariids Margarornis and Pseudocolaptes both frequently forage like woodhewers, hitching up tree trunks. Since the necessary preadaptations

are present in the furnariids for tree-trunk foraging, all that is really necessary is selection for behavioral flexibility that will allow tree-trunk foraging to begin, whether because of the lack of woodhewers, or because of advantages gained where competition is great. In these cases, the first step may have been taken in becoming a woodhewer. Selection forces can then operate on perfection of these adaptations for tree-trunk foraging, and once this transition zone between creeping and perching is abandoned, then selection for adaptations for more effective trunk foraging may occur. These selection forces may then be operating on the perfection of climbing adaptations, including changes in cranial morphology, limb proportions, and other morphological features that lead to the woodhewer level of organization.

Classification

One of the practical problems that arises from this study is that of the classification of the group. In traditional linear classifications it has been customary to place those forms showing the greatest number of primitive characters first in the linear sequence. For most of the Class Aves this has been impossible, owing to the fact that we simply do not know which forms are the more primitive. For example, looking at the class as a whole, there is no compelling reason why such birds as loons and grebes should be placed near the beginning of the linear

sequence, thus implying that they are among the most primitive of birds. Both loons and grebes are very specialized. So, in most avian classifications the linear sequence represents a convenient classification that has no basis in terms of placement of primitive and advanced forms, but which is, in itself, useful. In the case of the furnariids and dendrocolaptids I would propose that we now have sufficient information at least to place those forms with the greatest number of advanced characters last and the Recent forms that probably represent the ancestral types first in the sequence. The evidence now seems to be compelling that the furnariids and dendrocolaptids are a monophyletic group within themselves and different from other suboscine birds. It also seems reasonable to follow the evidence presented in this paper that the woodhewers have been derived several different times from philydorine-like ancestors. These lines of evidence strongly advocate the following as the most acceptable means of classifying the group.

1) The forms that are thought to have reached dendrocolaptid grade may be retained as a family, and classified typologically, if phylogeny is not considered in the classification.

2) The Dendrocolaptidae may be further restricted to include only those "strong-billed" woodhewers, Drymornis, Nasica, Dendrexetastes, Hylexetastes, Xiphocolaptes,

Dendrocolaptes, Xiphorhynchus, Lepidocolaptes, and Campylorhamphus, which probably represent a monophyletic group.

3) The woodhewers may be given subfamilial rank and merged with the ovenbirds into a single family, which would then represent a monophyletic group. Then the "intermediates" could be assigned to new subfamilies.

I personally prefer the third choice. I would further suggest that three subfamilies be erected for Glyphorhynchus, Sittasomus and Deconychura, and Dendrocincla. The sequence of the subfamilies should be to place the subfamilies of the ovenbirds first, perhaps in the following order: Synallaxinae, Furnariinae, Sclerurinae, and Philydorinae. The main point here is that the Philydorinae be adjacent to the woodhewer groups. The placement of the "intermediates" should be in the following order: Dendrocincla, Sittasomus and Deconychura, and Glyphorhynchus. The "strong-billed" woodhewers would then be placed last in the sequence in the subfamily Dendrocolaptinae. It is my opinion that the foregoing classification would best reflect the phylogeny of the group. This classification shall be formalized and perhaps somewhat revised in a generic revision which is now in progress.

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