EVOLUTIONARY TRENDS IN THE NEOTROPICAL OVENBIRDS AND WOODHEWERS

BY
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ORNITHOLOGICAL MONOGRAPHS

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INTRODUCTION

The Neotropical ovenbirds (Furnariidae) and woodhewers (Dendrocolaptidae) have long been considered to be closely related on the basis of derived 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, usually 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 *Pseudocolaptes*, *Xenops*, *Pygarrhichas*, the *Margarornis* complex, 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 characters as the syrinx, cranial morphology, and feet. Common wing patterns are found in the Furnariidae and Dendrocolaptidae. In addition, syringeal and osteological characters ally the two groups. It is only within the Dendrocolaptidae and Furnariidae that two pairs of intrinsic syringeal (tracheo-bronchial) muscles are found (Ames, 1971).

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. Stresemann (1934) united the ovenbirds and woodhewers into one family. 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, 1873; 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, schizorhinal and holorhinal. In the former, the nasal opening extends posterior to the nasal-frontal hinge; in the latter, 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 Fürbringer (1888) proposed that the term pseudo-schizorhinal be applied 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 examined only 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 (1971) in his systematic conclusions of the Furnarii emphasized that the syringeal musculature of the ovenbirds and woodhewers was an indication of close affinity of the two groups. Both groups possess two pairs of intrinsic syringeal muscles, a character which separates the two families from the antbirds (Formicariidae) and tapaculos (Rhinocryptidae). However, the ovenbirds are apparently separable from the woodhewers on the basis of the absence in the ovenbirds of horns on the Processi vocales (except in the genus *Geositta*). It is also of interest to note that there is far more syringeal variation within the Formicariidae than within the woodhewer-ovenbird assemblage.

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
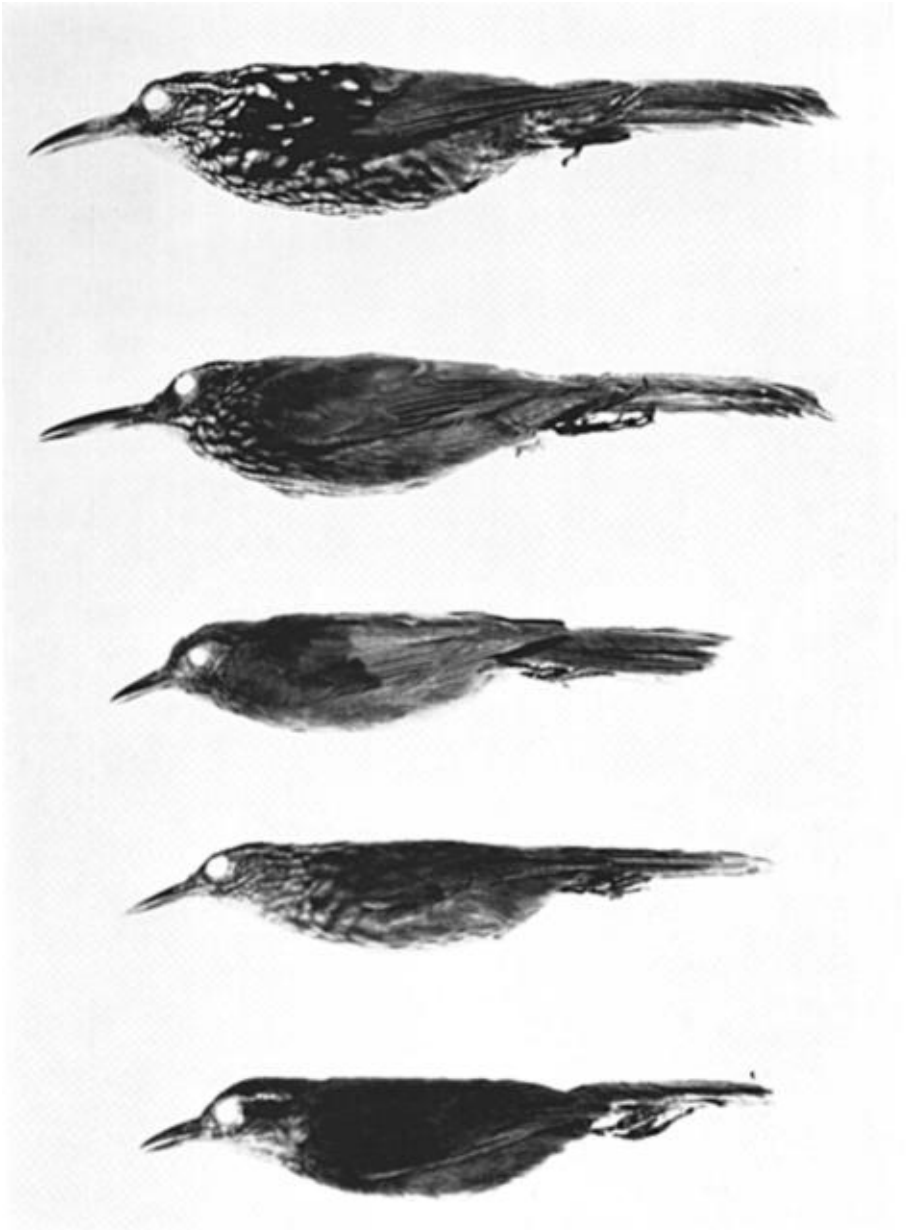
Figure 1. Two "strong-billed" woodhewers, an "intermediate," and two philydorine furnariids. From top to bottom: *Xiphorhynchus lachrymosus* (actual length, 229 mm), *Xiphorhynchus guttatus*, *Dendrocincla anabatina*, *Syndactyla subalaris*, *Automolus ochrolaemus*.

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 very closely allied, yet exhibit perhaps 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, *Dendrocincla, Sittasomus, Deconychura,* and *Glyphorhynchus,* 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 of this study (see Fig. 1).

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," *Dendrocincla, Sittasomus, Deconychura,* and *Glyphorhynchus,* are of particular interest. Except for *Dendrocincla* (which forages in a variety of postures) the "intermediates" are behaviorally 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,

Figure 2.   The wings of *Xiphorhynchus lachrymosus* (upper left), *Lepidocolaptes souleyetii* (upper right), *Dendrocolaptes certhia* (lower left), and *Campylorhamphus pusillus* (lower right).

however, some genera . . . *Sittasomus*, *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 are in some aspects also intermediate. One striking plumage character that seemed particularly significant was a rufous wing stripe (see Figs. 2 and 3) 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. My own field observations, as well as those of other authors, show *Dendrocincla* to be intermediate in behavior (see Feduccia, 1970). The species of *Dendrocincla* hitch up tree trunks like the other woodhewers, but also forage in a variety of other ways. Thus, the four genera, *Dendrocincla*, *Sittasomus*, *Deconychura*, and *Glyphorhynchus*, although not sharing identical characters, all possess some features that are intermediate between the Dendrocolaptidae and Philydorinae.

These "intermediates" may represent simply "old" forms that have retained many primitive characters. However, because the advanced (derived) character states within the "strong-billed" dendrocolaptids are indeed those that are concerned with tree-trunk foraging, and the "intermediates" (with the exception of *Dendrocincla*) are virtually identical to the "strong-billed" woodhewers in their climbing behavior, the situation is indeed curious. It would seem reasonable to expect the evolution of those characters that increase efficiency in climbing and tree-trunk foraging to occur, as has occurred in other unrelated tree-trunk foraging groups. One can test whether or not a given character state represents an actual climbing adaptation by looking at the same character state in unrelated groups of birds (see Richardson, 1942).

The possession by the "intermediates" of characters intermediate between perching and scansorial adaptations, plus the possession of plumage and
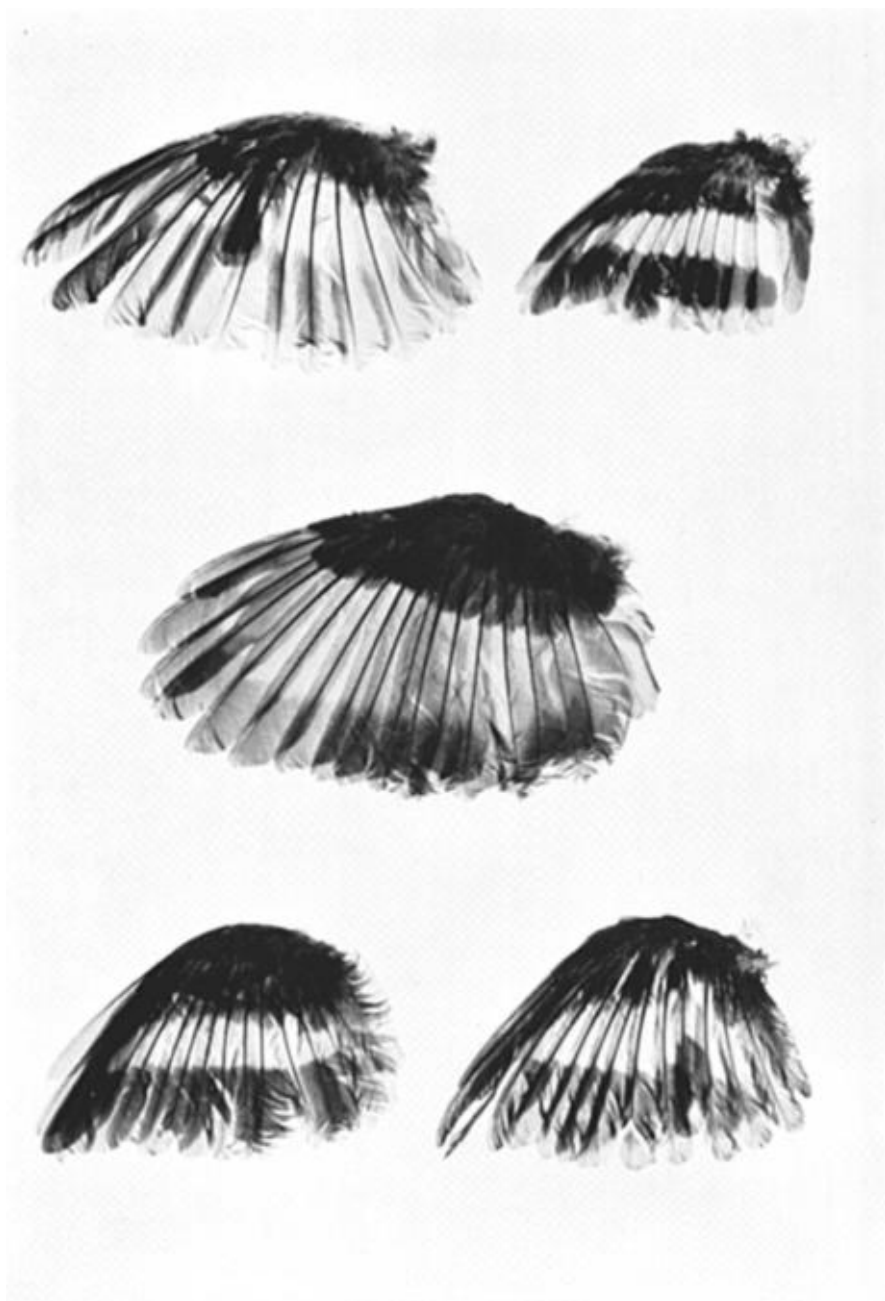
Figure 3. The wings of *Margarornis rubiginosus* (upper left), *Xenops minutus* (upper right), *Dendrocincla anabatina* (center), *Glyphorhynchus spirurus* (lower left), and *Sittasomus griseicapillus* (lower right).

other characters typical of the ovenbirds, makes the "intermediates" suspect of being separate evolutionary lines of woodhewers coming from ancestors that resembled the present-day philydorine furnariids. These forms may have reached dendrocolaptid grade with respect to the characters used to classify the family Dendrocolaptidae (= scansorial adaptations), but still possess many features which reveal a more recent ancestry from philydorine stock. In other words, the possibility of a di- or polyphyletic Dendrocolaptidae cannot be obviated. The alternative is that the "intermediates" are simply part of an original monophyletic radiation of woodhewers which have retained many "primitive" characters, and are forms occupying "intermediate" niches.

It was not surprising to find a statement by von Ihering (1915: 149) that ". . . we can presume that the Dendrocolaptinae sprang from two different groups of the Philydorinae." I therefore continued my investigations of this group in order to obtain evidence concerning the evolutionary lines involved in the ovenbird-woodhewer radiation, while emphasizing mainly the origin of the woodhewers. The main focus of this study has therefore been the dendro-colaptid-philydorine boundary, but data from the other groups of the Furnari-idae are used where necessary. I have made the general assumption that tree-trunk foragers represent the more derived condition. The assumption may be logically extended to include a philydorine-like ancestor as a logical choice for a pre-dendrocolaptid. This assumption is not only logical from anatomical studies, but also from zoogeography, as philydorines and dendro-colaptids share a near-common zoogeographical range, both reaching their highest density in Amazonia.

Anatomical studies often have failed to solve this type of problem because convergent adaptations may mask the actual phylogenies. It seemed to me that useful characters might be found in a comparison of proteins of the various groups. The use of electrophoretic patterns of proteins in systematics has been discussed by various authors and will not be reviewed here. The reader is referred to Kitto and Wilson (1966), and Sibley (1970) for examples of studies utilizing electrophoresis of proteins in birds. Although I examined various blood, muscle, and eye lens proteins, only with hemoglobins was I able to separate the two families.

The remainder of this paper is a presentation of various characters of the ovenbirds and woodhewers and an evaluation of the position of the "inter-mediates" with respect to these characters. After the anatomical evolutionary trends are discussed, the hemoglobin data are presented, and phylogenetic considerations are made on the basis of all of the characters. In the various sections of this paper I have attempted to answer several primary questions. First, what are the major features of the anatomical evolutionary trends in-

volved in the evolution of the tree-trunk foraging (derived) woodhewers, and second, what anatomical and historical position do the "intermediates" occupy?

ACKNOWLEDGMENTS

COMPARATIVE OSTEOLOGY 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 inclusion of all the minute variations. Instead, I have attempted to condense the variations into meaningful character states in each group so as to
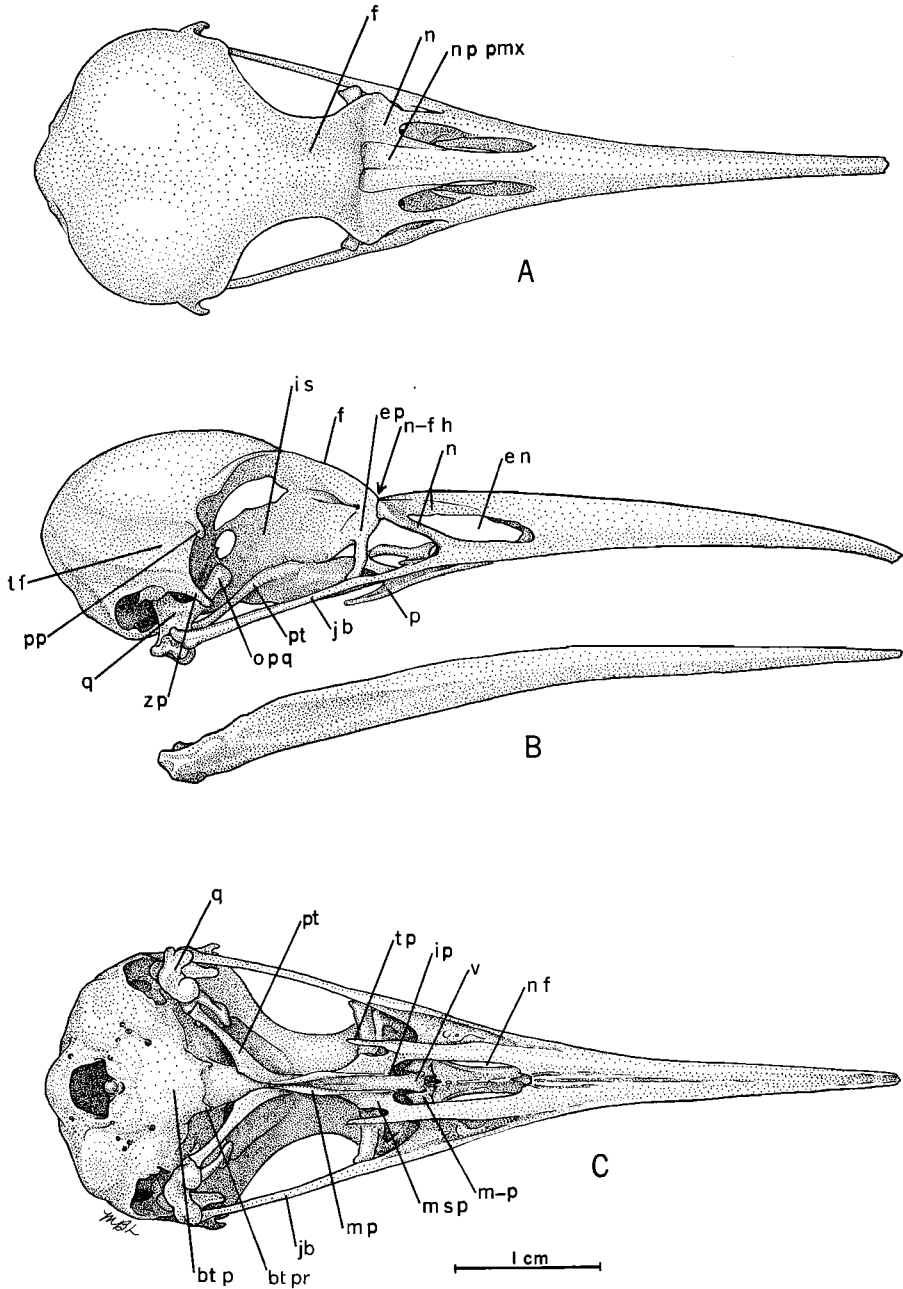
Figure 4.   Dorsal (A), lateral (B), and ventral (C) aspects of the skull of the wood-hewer, *Xiphorhynchus guttatus*.   Abbreviations are as follows: bt p, basitemporal plate; bt pr, basipterygoid process; e p, ectethmoid plate; e n, external naris; f, frontal;

attempt to uncover the general evolutionary trends, but not all of the intra-group variation. There is still controversy concerning osteological nomenclature; however, in this paper the terminology for skull characters generally follows that of Bock (1963).

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 melanops,* 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. erythrops,* 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; *Coryphistera 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, Glyphorhynchus spirurus, Dendrocolaptes certhia, Xiphorhynchus guttatus, X. lachrymosus, X. triangularis, Lepidocolaptes souleyetii, Campylorhamphus pusillus, Synallaxis albescens, Margarornis rubiginosus, Pseudocolaptes lawrencii,*

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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.

Hyloctistes subulatus, Automolus ochrolaemus and nestling, *Thripadectes rufobrunneus,* and *Xenops minutus* and nestling.

WOODHEWER SKULLS

The skull of *Xiphorhynchus* (Fig. 4) 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, and 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 laterally a bar 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 supraorbital 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 supraoccipital 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 premaxillae. 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 prominent dorso-medial processes 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 characteristic of passerines is obscured by ossification. The jugal bars are thin, but strong, and converge slightly anteriorly as they fuse imperceptibly with the maxillae in a broad area of fusion. The palatine process of the premaxilla is not visible and is probably fused. Bock (1960: 436) reported the palatine process of the premaxilla to be present in all genera of woodhewers, but the relative degree of fusion between the process and the palatine varies in the different genera. He generalized that the process is only slightly fused in species with a long curved bill, and heavily fused in species having a short, straighter and heavier bill. In *Xiphorhynchus* the process is slightly fused. The remaining characters of the base of the skull appear to be, in general, 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 struc-

ture 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* and proceeds to the greatly increased ossification in *Xiphocolaptes* (with the anterior part of the nasal region being imperforate) culminating in *Campylorhamphus* where ossification has occurred to the degree that the nasal opening is a small oval hole. The situation is somewhat different in *Dendrexetastes* (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 that the amphirhinal condition may be compensation for the lack of ossification in the nasal region.

OVENBIRD SKULLS

The description of typical ovenbird skulls is difficult. While the wood-hewers are very uniform with respect to skull structure, the ovenbird assemblage shows great diversity. However, for the purposes of this study only two types 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, such as those of certain members of the Philydorinae. Although one can otherwise generally 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 phily-dorine condition will be described. The skull of *Asthenes* (Fig. 5) 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 more 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 sep-

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Figure 5. Dorsal (A), lateral (B), and ventral (C) aspects of the skull of the oven-bird, *Asthenes modesta*. See Fig. 4 for abbreviations. New terms are: n s, nasal sep-tum; o p pt, orbital process of pterygoid; and p pm, palatine process of premaxilla.
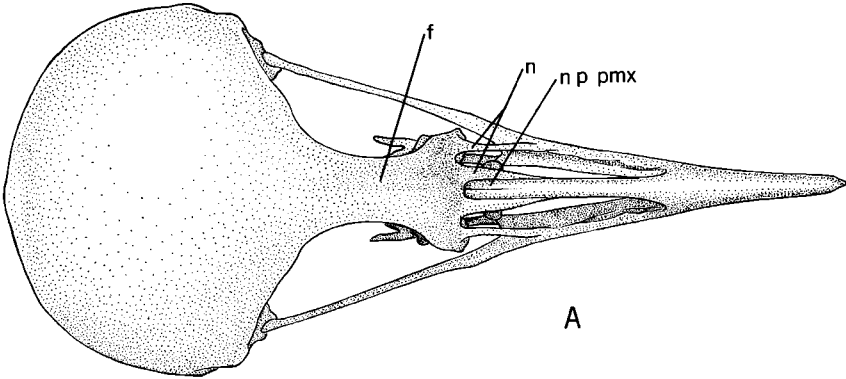
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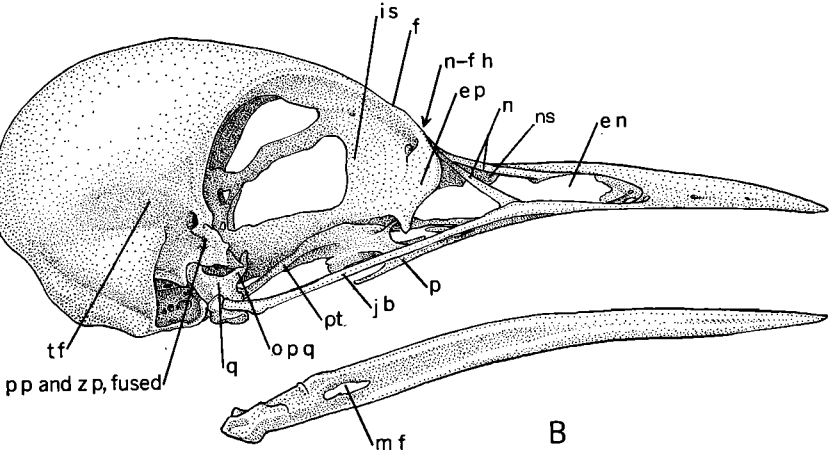
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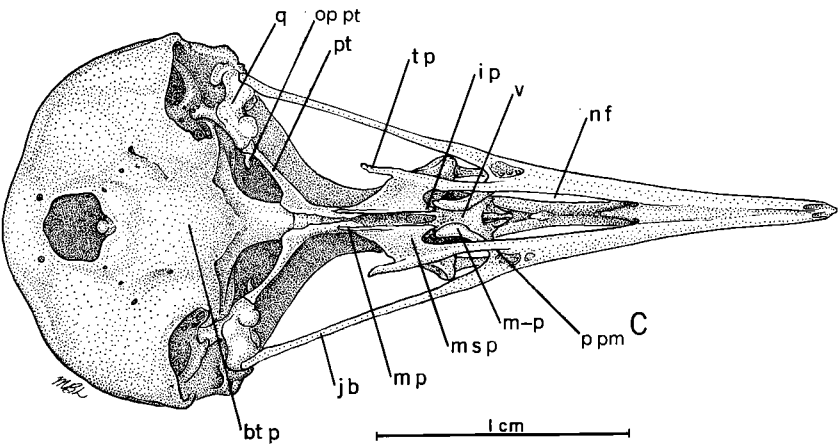
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tum. The long nasal opening extends posterior to the nasal-frontal hinge (inoperative in this case), but is rounded, unlike the "true" schizorhinal condition of the Charadriiformes, where the nasal opening ends posteriorly in a slit. The nasal-frontal 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, a bony 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. This broad plate has very little mesial constriction, and sends off 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 constitutes 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 *Xipho-*

rhynchus, is bifurcate, but continues relatively farther anteriorly than in wood-hewers. The median shelf of the palatine is relatively broader in *Asthenes* than in *Xiphorhynchus* and other woodhewers. Bock (1960: 436–438), re-ported 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 re-sembles an ossified tendon. Rarely is the process fused or absent as in the case of *Leptasthenura* or *Synallaxis*. The length of the process varies some-what between the genera." The process is unfused in *Asthenes*. As they con-tinue 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 wood-hewers and has a large mandibular foramen.

Although there is much variation in the skulls of ovenbirds, the basic pat-tern 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 open-ing, 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* will be described here as an example of the holo-rhinal ovenbird skull, intermediate in structure between the woodhewer and other pseudo-schizorhinal ovenbird skulls. The bill in *Automolus* (Fig. 6), like that in 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
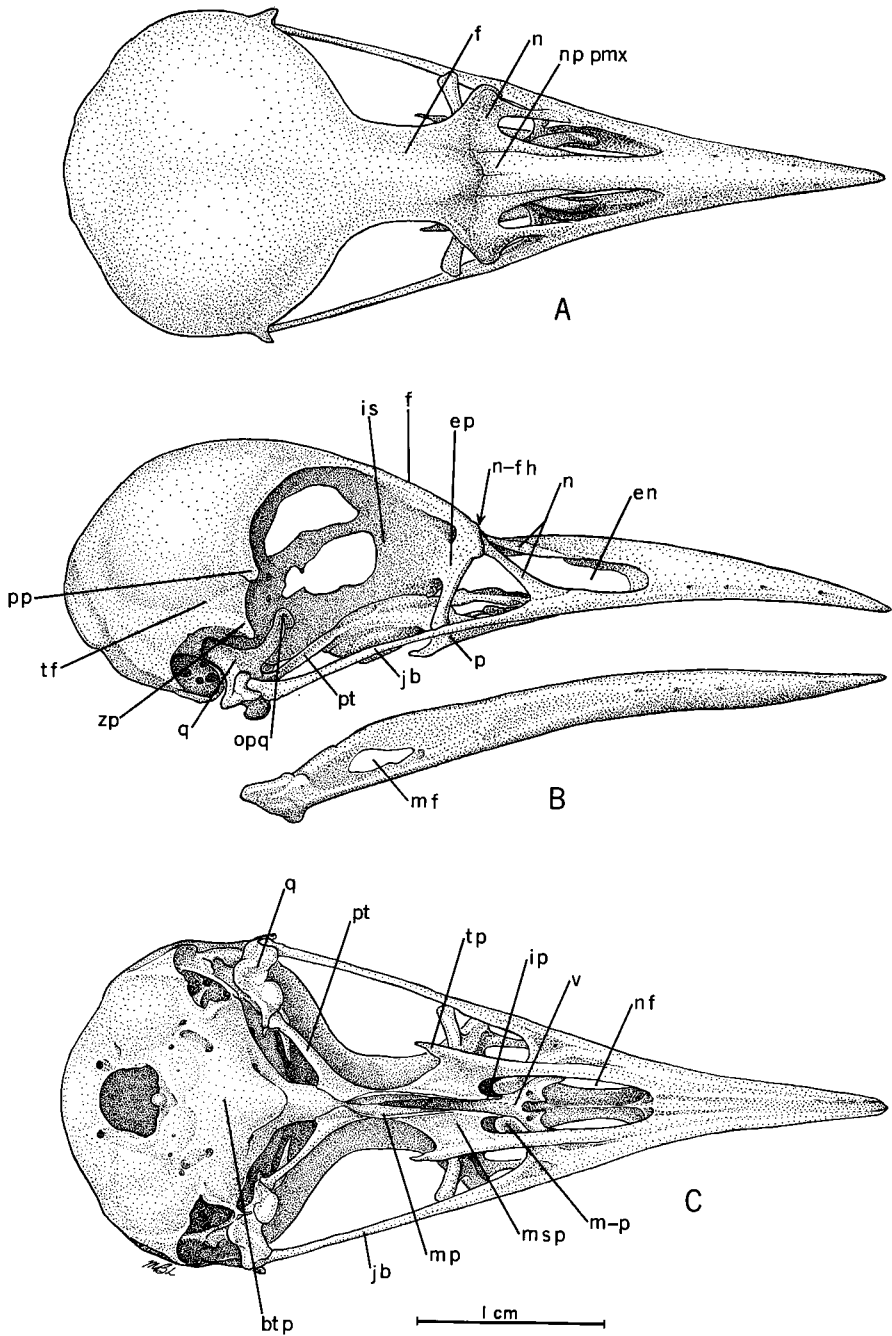
Figure 6. Dorsal (A), lateral (B), and ventral (C) aspects of the skull of *Automolus ochrolaemus*. See Fig. 4 for abbreviations.

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, though less so than in *Asthenes*, and in general they appear more like those of 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*. These characters indicate a strong adductor muscle.

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 the skulls, in general, 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

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Figure 7. Dorsal (A), lateral (B), and ventral (C) aspects of the skull of *Sittasomus griseicapillus*. See Fig. 4 for abbreviations.

A

B

C

1 cm
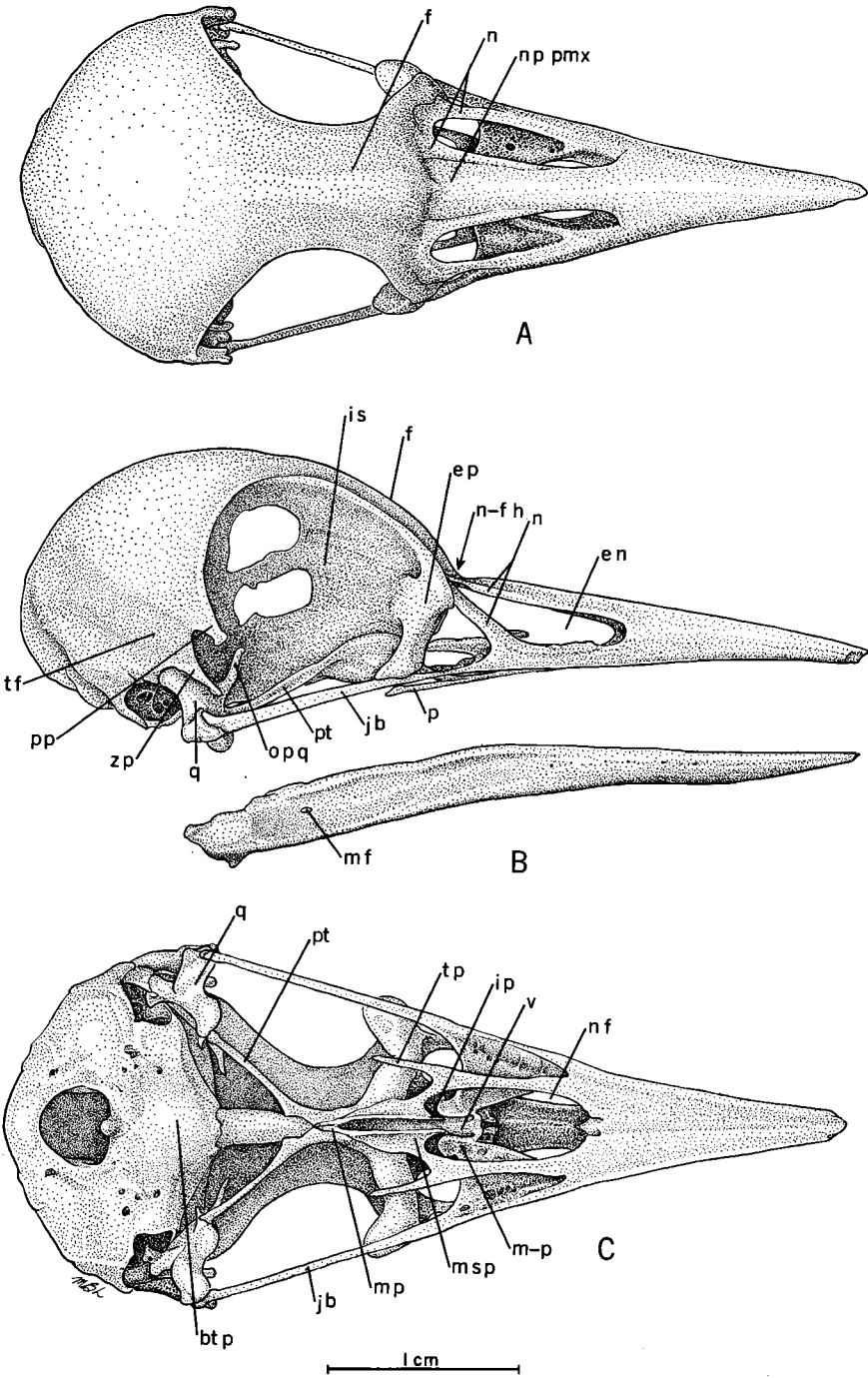
Dendrocolaptidae. The forms which most closely approach this condition are *Hyloctistes, Pseudocolaptes, Philydor, Automolus,* and *Anabacerthia.* Of the non-philydorines, *Sclerurus, Pygarrhichas, Margarornis,* and *Premnoplex* have somewhat dendrocolaptid-like ectethmoid complexes. Most of the palatal 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 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.

<center>SKULLS OF THE "INTERMEDIATES"</center>

The skulls of the genera *Sittasomus* (Fig. 7), *Deconychura, Dendrocincla* (Fig. 8), 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. 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 pos-

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Figure 8.   Dorsal (A), lateral (B), and ventral (C) aspects of the skull of *Dendrocincla anabatina.* See Fig. 4 for abbreviations.

A

B

C

1 cm
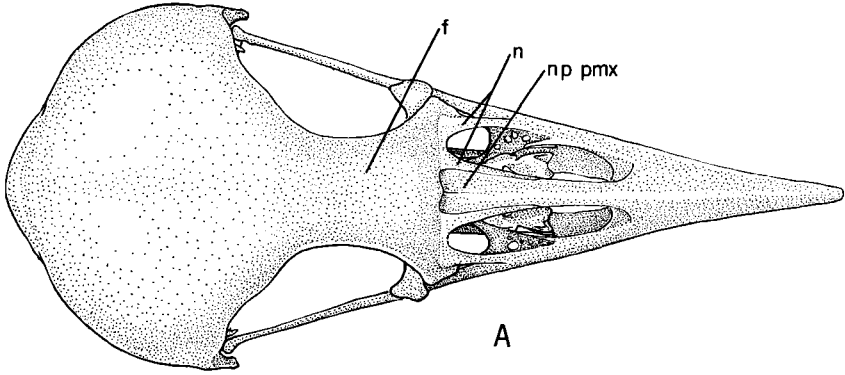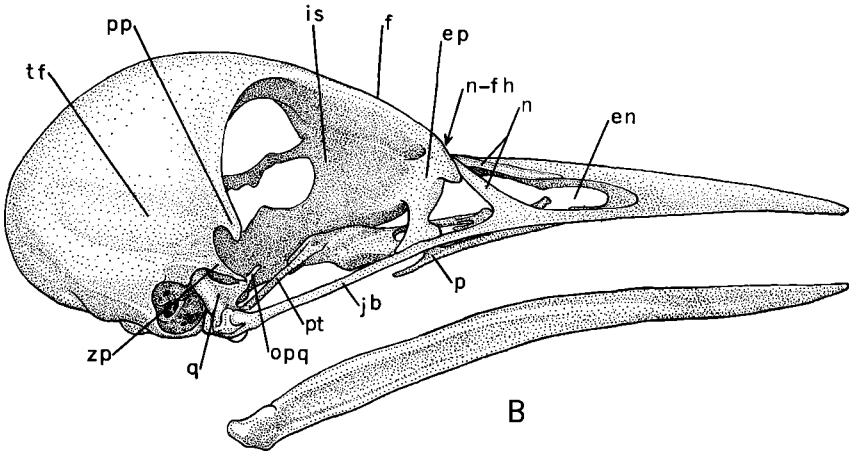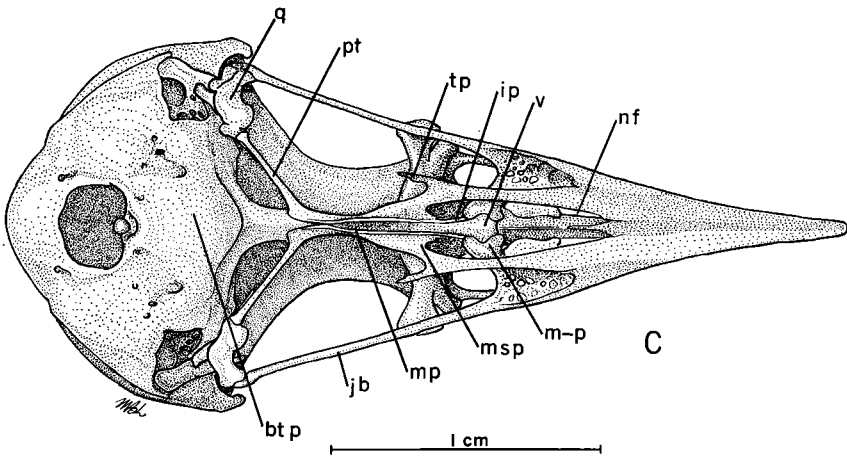
terior part of the vomer. Thus, the genera *Sittasomus* and *Deconychura* present a mosaic of dendrocolaptid and furnariid characters in their skulls.

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. An obvious pecking adaptation is found in the frontal bones being curved anteriorly over the nasals as in some woodpeckers. Otherwise, *Glyphorhynchus* 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, and an expanded supraorbital area of the frontal bones. In general appearance it is a strongly constructed skull.

The skull that is most like that of the ovenbirds 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. 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 maxillo-palatines 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 observed variation was confined to such variable areas of the skull as the palate and its associated parts, muscles will not be covered in this paper.

However, there are several jaw muscles that deserve special attention at this point. The tremendous development of M. adductor mandibulae is one of the most striking features of the exposed woodhewer head. Especially noteworthy are the externus rostralis portions of this muscle, 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 like that of ovenbirds. Since 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 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 phylydorines 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. 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 some of the character complexes is much the same in most birds. In this paper I am considering only those aspects of skull function that seem to bear directly on

TABLE 1
SUMMARY OF EXTREMES IN SKULL CHARACTERS

Character	Dendrocolaptidae	Furnariidae
bill	strongly built, approx. ⅔ skull length	weakly built, approx. ½ 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
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
temporal fossa	greatly expanded	medium development
mandibular foramen	absent	present

ovenbird and woodhewer skulls. Therefore, only those points of the jaw muscle anatomy that seem pertinent to the functional analysis will be discussed, and no detailed jaw muscle descriptions will be given, as I feel that they would add little to the over-all study.

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* (see Table 1). If we assume that the holorhinal skull is a derivative of the ovenbird pseudo-schizorhinal skull type, as seems logical 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

dendrocolaptids towards increased ossification in several character complexes. The 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. Concomitant 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 nasal septum to a point 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 postorbital 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 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
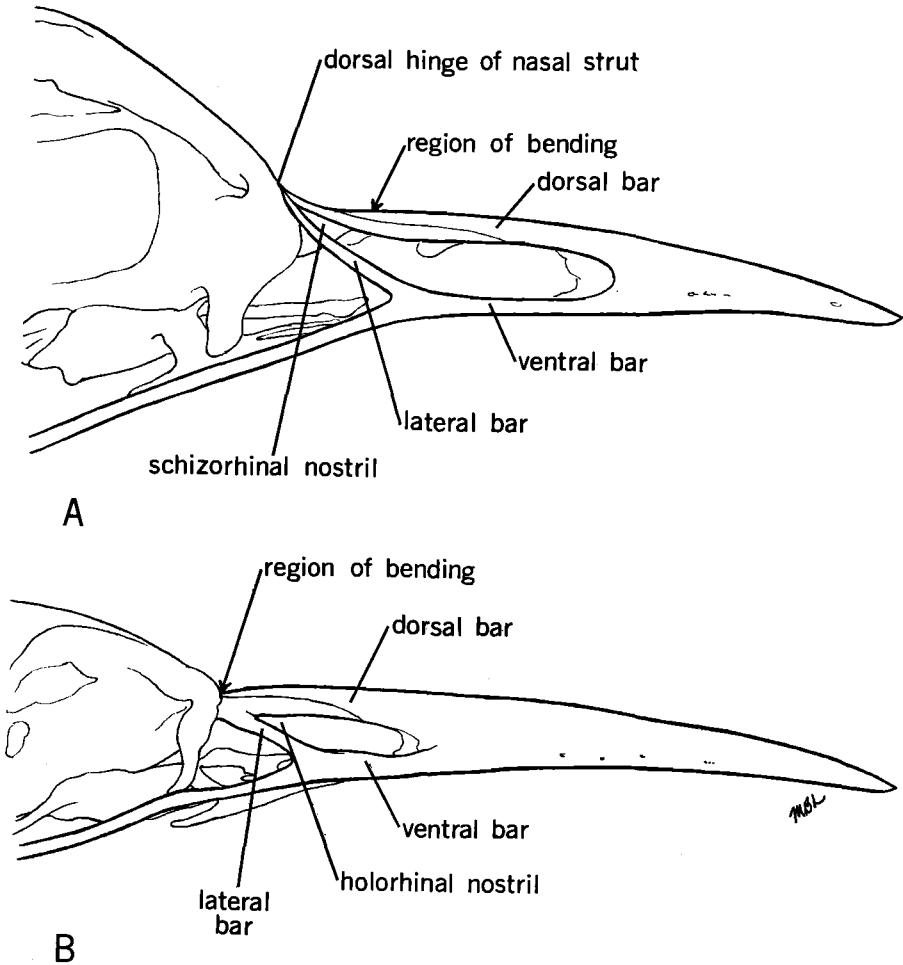
Figure 9.   The skulls of A, an ovenbird, and B, a woodhewer, to show the regions of bending in the skulls (diagrammatic).

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 that in the schizorhinal skull ". . . 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 rhynchokinetic 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 (Fig. 9). 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 ovenbirds 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 one extreme there appear to be typical rhynchokinetic skulls and at the other extreme, prokinetic skulls.

To summarize the foraging behavior of each group one might say that the woodhewers forage by using the bill in probing, prying, and some pecking.

TABLE 2

SUMMARY OF DISTRIBUTION AND NATURAL HISTORY OF FURNARIIDS AND DENDROCOLAPTIDS

	Dendrocolaptinae	Philydorinae	Synallaxinae
Center of distribution	Forest of Amazon Basin and periphery	Forest of Amazon Basin and 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, cling in vines and tangles, climb sideways, creep head downward, or hitch 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 2. (CONTINUED)

	Sclerurinae	Pygarrhichas	Furnariinae
Center of distribution	Humid tropical forests of Amazon Basin and 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. Nuthatch-like in behavior	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	Tunnel dug into banks as in the Philydorinae	Hole in trees, often excavated by the birds themselves	Tunnel dug in bank with nest mat placed at expanded termination, or domed mud structure (*Furnarius*)

The bill is also used in these forms in grasping rather large or strong-bodied prey. Though the woodhewer natural history literature typically contains accounts of these birds hitching up tree trunks and feeding most commonly by peering into bark crevices after insects and small vertebrates, woodhewers do probe and pry into bark, flake bark, and even pound on trunks upon occasions in typical woodpecker fashion (see Feduccia, 1970). Although there is great diversity among the ovenbirds, they may be characterized generally 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. Small cold-blooded vertebrates are also taken, and many species peck, pry, and probe in their foraging behavior (Table 2).

Although the precise functions of many parts of the skulls are still unknown, the characters in woodhewers seem to conform to functional anatomical predictions. In the woodhewers it results in a generally stronger, more completely ossified skull, and in the ovenbirds, 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, thereby strengthening the bill and forming a broad hinge. This hinge functions to protect the bill from the strong lateral forces to which it is subjected in prying, probing, and other such activities. 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 its extension phalange to contact the jugal bar. In general, the woodhewer skull shows great strength. As Bock (1963: 112) has pointed out in *Loria* (Paradisaeidae) 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 force 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 clearly seem to be 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 furnariines, the skulls are generally weaker than woodhewer skulls. The nares are pseudo-schizorhinal, the orbital septum is unossified, the post-orbital and zygomatic processes are small, and compared to woodhewers the temporal fossae are relatively smaller, the palate is weaker, and the jaw muscles are not so massive and powerful. These skull characters of synallaxines and most furnariines 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. True schizorhiny in shorebirds appears to be correlated with probing related to bill tip movement. It is of interest here that *Sclerurus*, which has well-developed pseudo-schizorhiny, does probe into soft mud on the forest floor. It might also be of interest to note that most ovenbirds lack a hooked bill tip, as is found in many passerines. Perhaps this is in some way associated with probing movements. One might think that the woodhewers 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 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 correlated with the type of foraging behavior and the food taken by these forms, as they approach the woodhewers in these characteristics.

We may now ask the question why does the pseudo-schizorhinal skull type occur in the furnariids and not in other generalized insect-eating passerine birds which appear to have similar feeding habits? Hofer (1954) 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 super-holorhinal (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 rhynchokinetic in the young to prokinetic 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 (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 is the type found in most other passerine birds. Such a skull has similar kinetic abilities to those of woodhewers but lacks ossification of the orbital septum and general strengthening of the woodhewer skull.

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.

THE STERNUM

The variation in the notches of the posterior border of the sternum is covered elsewhere (Feduccia, 1972) and will only be summarized here. The majority of both ovenbirds and woodhewers possess sterna with two posterior notches. These may show a tendency to open (more than two notches), or to close (less than two notches). Throughout the ovenbirds there is a two-notched sternum, but with a tendency to open. There is no ovenbird known which shows a tendency toward closure of the posterior border of the sternum. However, in the "strong-billed" woodhewers, although there is a tendency to open the posterior border in some, in many there is a strong tendency toward closure. I concluded (op. cit.) that this increase in ossification of

Figure 10. The sterna of *Cinclodes fuscus* (upper), and *Xiphorhynchus guttatus* (lower), left lateral aspect.

the posterior border of the sternum, which also occurs in the woodhoopoes, and by a different means in the woodpeckers, is probably associated with increasing the strength of the sternum for tree-trunk foraging.

It is of great interest at this point to consider the "intermediates," for all the genera are totally ovenbird-like with respect to the posterior border of the sternum. In all of the "intermediates" there is a typical two-notched sternum, a tendency to open the posterior border in two, *Sittasomus* and *Dendrocincla*, and no tendency toward closure in any species.

Another sternal character that differs between the ovenbirds and wood-hewers is the size and shape of the sternal keel (Fig. 10). 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 and type of flight performed by the woodhewers. There is much variation within the ovenbirds in the size and shape of the keel. As one might expect, the sternal keel in the wood-hewers is relatively more constant. The "intermediates" conform to the wood-hewer pattern of sternal keel.

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, seems to be well suited to perching, climbing or walking. For present purposes, I shall be concerned only with 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 at least some 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. In regard to many characters, the comparison of *Thryomanes* with *Dendrocolaptes* is much like a comparison of ovenbirds with woodhewers since in *Thryomanes* fewer actual climbing adaptations are found than in the other creeping forms. In general, characters of the pelvic region in most 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 points that I consider to be of greater importance here, 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, tarsometatarsus, 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) has discussed the use of such ratios. First, only elements which presumably vary somewhat independently of each other should be used for the ratios. Second, measurements that do not tend to vary adaptively from one species to another should be used rather than ones that vary, for example, according to the size of the organism. Although I cannot "prove" all of these qualifications in the use of sternal length, the obvious predictions emerge using ratios of the various limb elements to sternal length.

Measurements were taken from the following species of woodhewers and ovenbirds: *Dendrocincla anabatina* (3), *D. 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 antarcticus* (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 11 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 dendrocolaptid 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.

FEMUR

TIBIOTARSUS

TARSOMETATARSUS

TOTAL LEG LENGTH
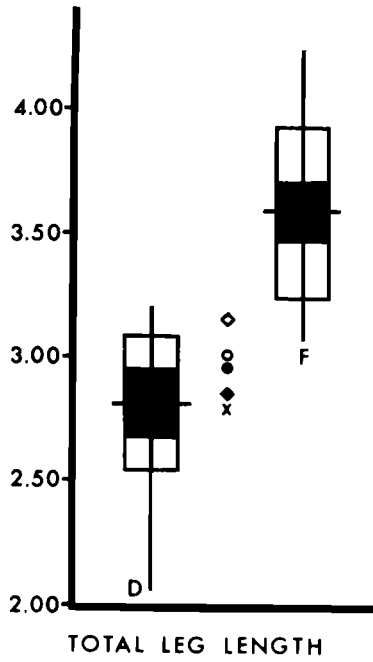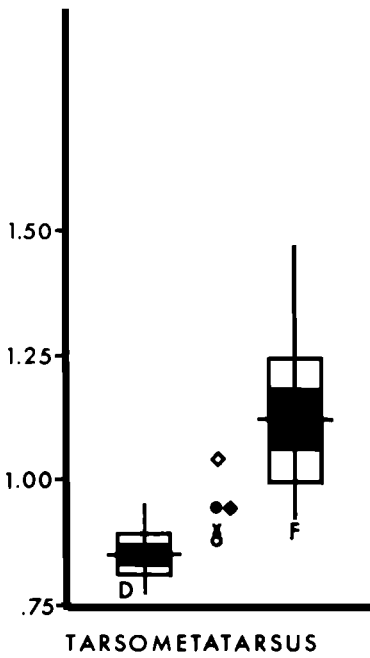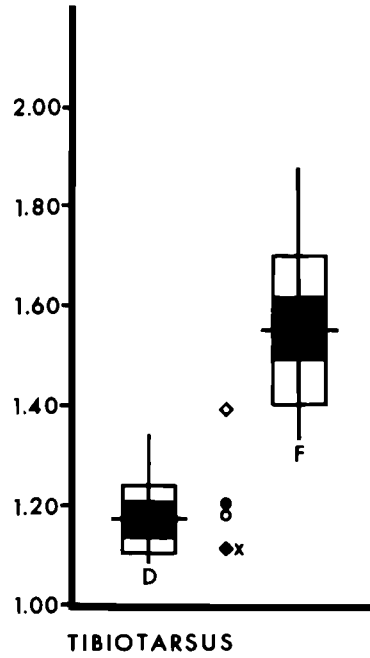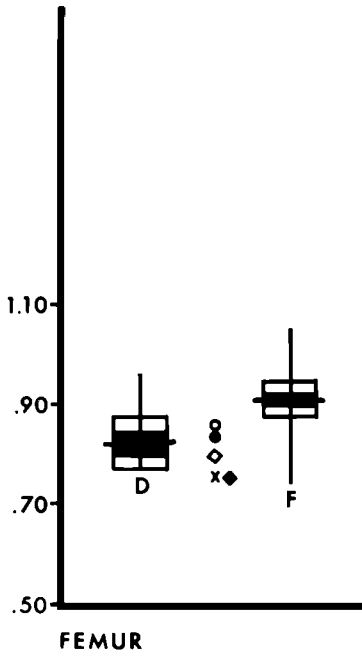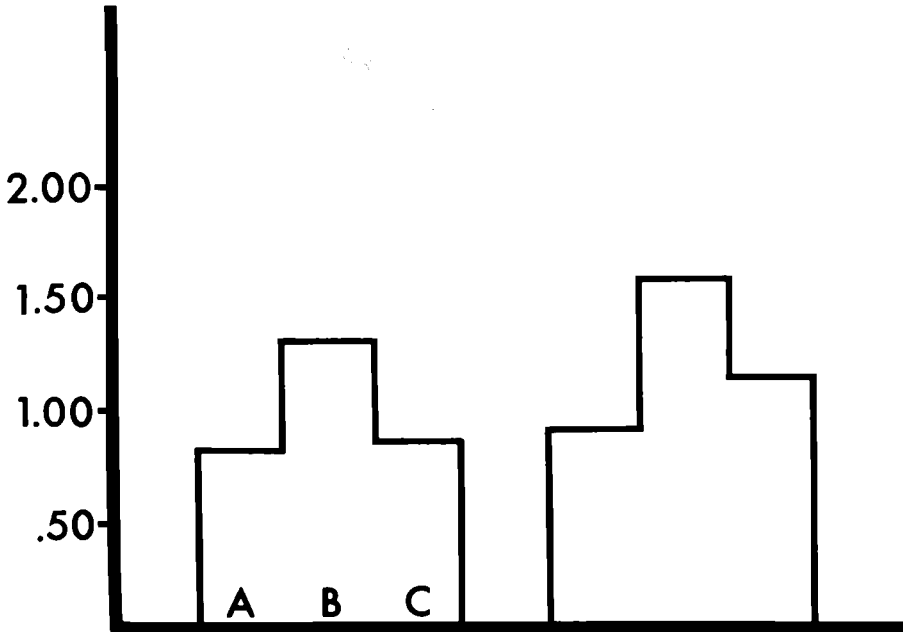
Figure 12. Ratios of the different leg elements to sternal length in the dendro-colaptids (left), and in the furnariids (right). The elements are A, femur; B, tibio-tarsus; and C, tarsometatarsus.

Bar graphs of the means of the ratios of the limb elements for both families are given in Figure 12. 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 *Dendro-colaptes* 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 (Fig. 12). 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

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Figure 11. Comparison between ratios of lengths of femur, tibiotarsus, tarso-metatarsus, and total leg to sternal length in the dendrocolaptids (D), and the furnariids (F). The "intermediates" are designated as follows: *Glyphorhynchus spirurus*, an X; *Sittasomus griseicapillus*, open diamond; *Deconychura longicauda*, 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.
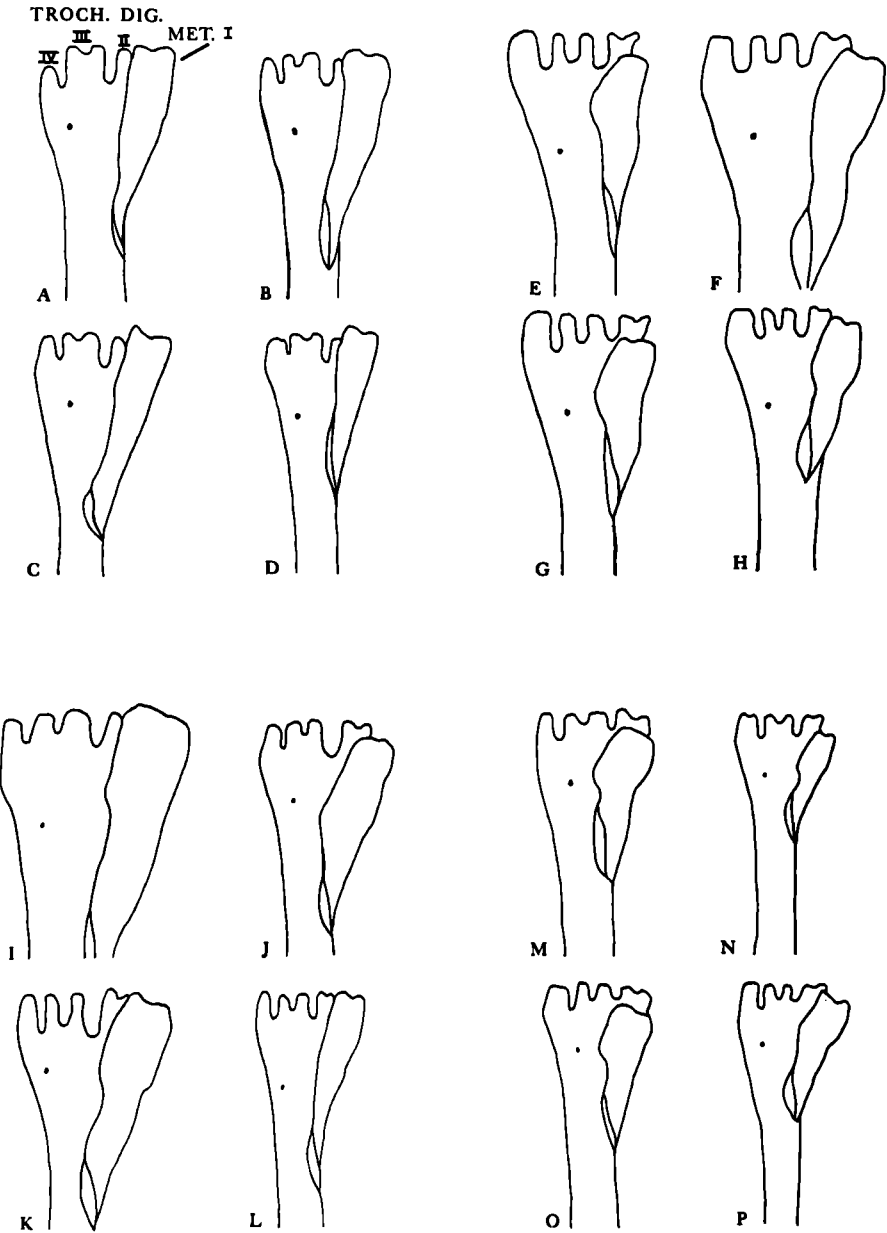
Figure 13. Camera lucida drawings of the posterior surface of the distal ends of tarsometatarsi of A, *Phacellodomus striaticollis;* B, *Syndactyla rufosuperciliata;* C, *Philydor lichtensteini;* D, *Synallaxis albescens;* E, *Dendrexetastes rufigula;* F, *Dendrocolaptes certhia;* G, *Xiphorhynchus guttatus;* H, *Lepidocolaptes souleyetii;* I, *Pseudocolaptes lawrencii;* J, *Margarornis rubiginosus;* K, *Pygarrhichas albogularis;* L, *Xenops*

to extend the intertarsal joint is decreased with the shortening of the tibio-tarsus." 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 anteriorly to a better position for climbing.

For each limb element the position of the "intermediates" 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 from climbing habits, they are often at the end of the range of the dendrocolaptids, nearing the furnariid range, and in only a few cases ex-tend towards the extreme range of the dendrocolaptids. However, the "inter-mediates" clearly possess woodhewer "climbing" adaptations with respect to the relative length of the leg elements. *Sittasomus*, however, 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. Fig-ure 13 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 meta-tarsal, 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 hallucis longus (see Richardson, 1942, for a more complete dis-cussion of this character). The size of metatarsal I is directly correlated with the length of the hallux. In the woodhewers, metatarsal I is short, correspond-ing to a short hallux, a character that is associated with climbing. In the oven-birds 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 inter-mediate, 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.

The degree 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 rela-tively greater separation of the trochlea for the digits than in the ovenbirds.

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minutus; M, *Dendrocincla anabatina*; N, *Glyphorhynchus spirurus*; O, *Deconychura longicauda*; and P, *Sittasomus griseicapillus*. A through D are typical ovenbirds, E–H, "strong-billed" woodhewers, I–L, aberrant ovenbirds, and M–P, the "intermediates."
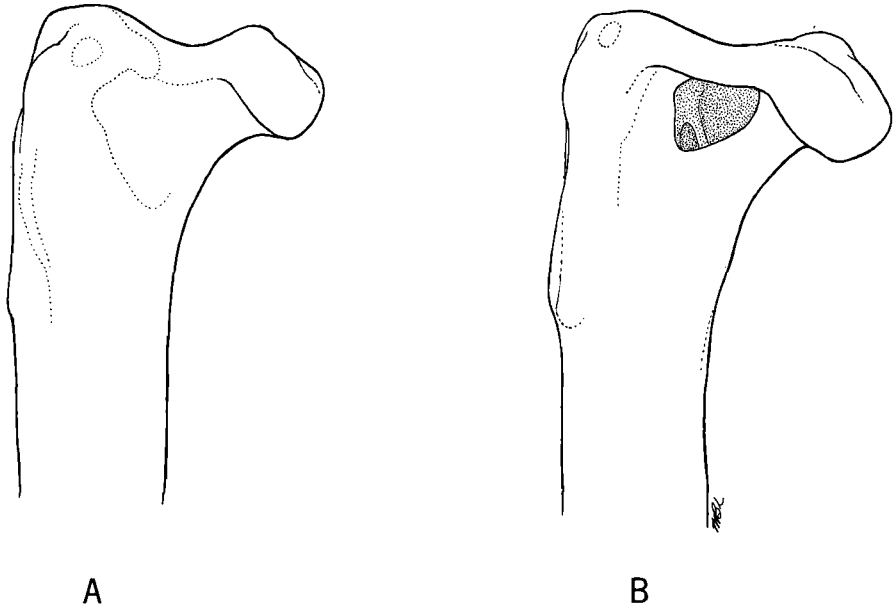
Figure 14.   Posterior surface aspects of the proximal ends of the left femora of A, *Furnarius rufus*, and B, *Xiphorhynchus guttatus*.

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 seems 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 Figure 13 shows, *Pseudocolaptes*, *Margarornis*, *Pygarrhichas*, and *Xenops*, all climbing types among the ovenbirds, show varying degrees of excavation of the trochlea. Excavation 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.

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 in-

volved 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. 14), present and well defined in all of the woodhewers and in the "intermediates" except in *Glyphorhynchus* (nearly absent in *Dendrocincla*). A foramen is 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 or not this represents a trend towards increased pneumatization and hence reduction of weight in the pelvic region is unknown.

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 to increase 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 15 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 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. 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 16.
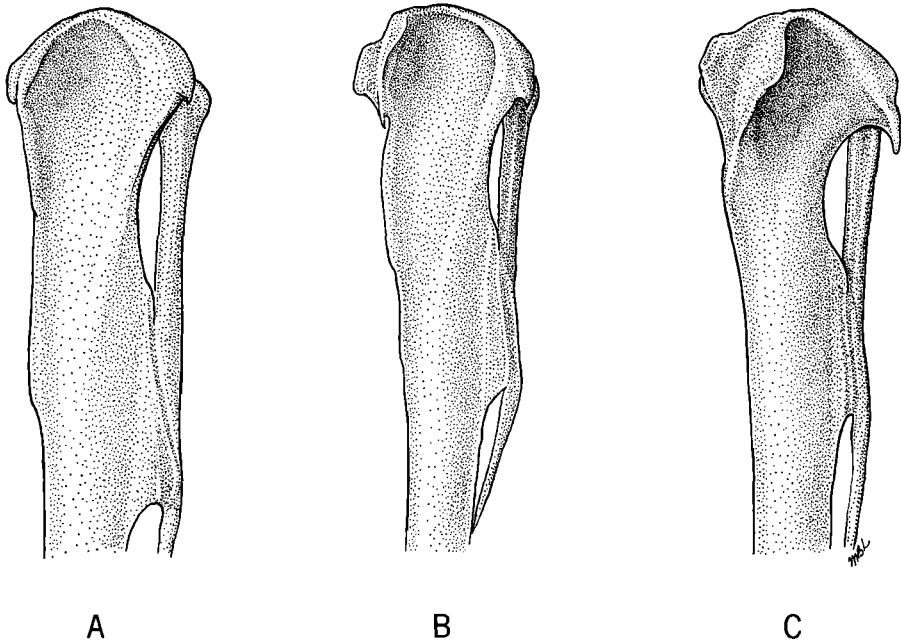
Figure 15. Anterior surface of proximal ends of tibiotarsi of A, a woodpecker, *Dendrocopus villosus*, B, *Xiphorhynchus guttatus*, and C, *Furnarius rufus*.

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 toward 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 tree in climbing by the long, often bare, inward-curving shafts. No attempt was made here to correlate with trunk-climbing the length of the tail and the strength of the shafts. 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 by the philydorines, would certainly be a good preadaptation for tree-trunk foraging. The tail of *Dendrocincla* shows a lesser amount of stiffening of the rectrices than does that of the other woodhewers.

As an index of 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. These measurements are expressed as ratios to the sternal length (Fig. 17). As expected, the woodhewers show a much greater development of the pygostyle than do the ovenbirds. The "intermediates" are plotted between the range diagrams. Note the position of *Dendrocincla* (closed circle). The points that compose the upper part of the furnariid range are the tree-trunk foragers.

SYRINGEAL ANATOMY

In his excellent study of the passeriform syrinx, Ames (1971: 146) 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 [*sic*] suggests 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
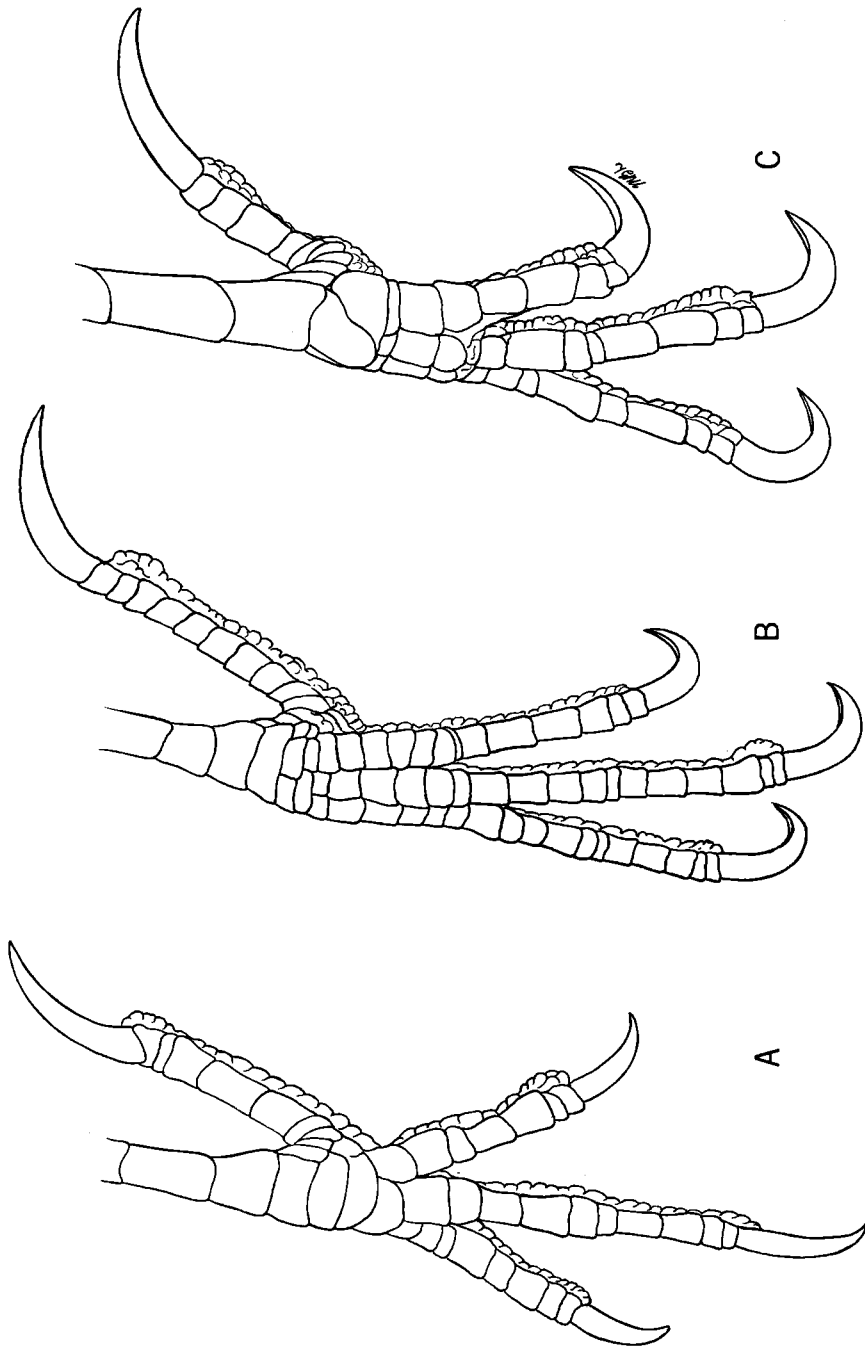
Figure 16. Right feet of A, *Synallaxis albescens*, B, *Pygarrhichas albogularis*, and C, *Xiphorhynchus guttatus*. Each line represents one cm.

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* represents an independent appearance from those in the woodhewers."

He further states in his systematic conclusions (p. 146) 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* could be taken to indicate that *Geositta* is more closely allied to the woodhewers than to the ovenbirds (Furnariidae) but it appears to be a fairly typical ovenbird in other respects. 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.*

ELECTROPHORESIS OF HEMOGLOBIN
METHODS AND MATERIALS

Because of the difficulty of 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 2.0 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 approximately 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 ¼-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 as a standard marker. 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% Amido Black in a 5:5:1 solution of water, methanol, and acetic acid. The gels were destained in 8% acetic acid and stored in a solution of the same composition. To assure that the resulting electrophoretic 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 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 affect the qualitative nature of the bands. The concentration in no way affected the nature of the bands, except their widths.

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 (Fig. 18) from the following species of woodhewers were nearly identical: *Xiphorhynchus triangularis*, *X. lachrymosus*, *X. guttatus*, *Campylorhamphus pusillus*, *Lepidocolaptes souleyetii*, and *Dendrocolaptes certhia*. The "dendrocolaptid" pattern 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 ovenbirds were nearly identical: *Synallaxis albescens*, *Margarornis rubiginosus*, *Cranioleuca erythrops*, *Automolus ochrolaemus*, *Thripadectes rufobrunneus*, *Hyloctistes subulatus*, *Xenops minutus*, and *Pseudocolaptes lawrencii*. The "furnariid" pattern 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 lighter 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*. Two
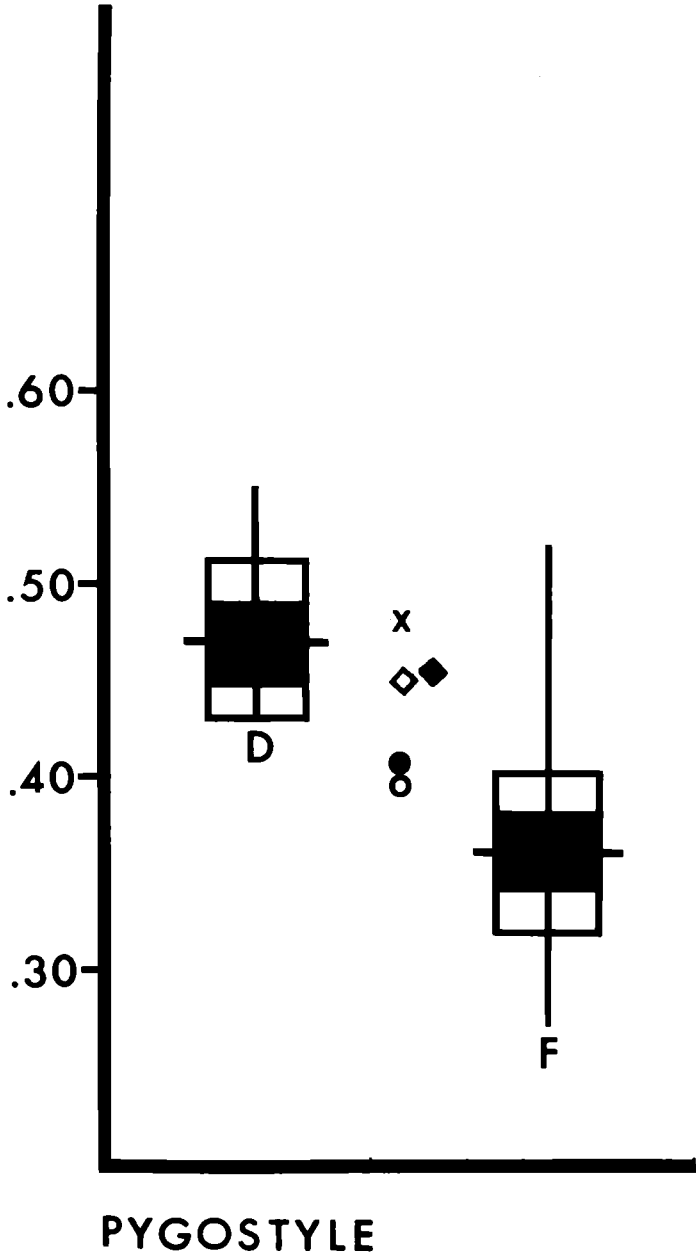
PYGOSTYLE

Figure 17. Comparison between ratios of height of pygostyle to sternal length in dendrocolaptids (D), and furnariids (F). The "intermediates" are designated as in Fig. 14, and the statistics are of the same type.

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*, but unfortunately from no other species of the genus *Dendrocincla*. The hemoglobin electrophoretic pattern is indistinguishable from that of the furnariids. Owing to the consistency of the hemoglobin electrophoretic patterns within other genera of birds I shall tentatively assume that *D. anabatina* is typical of the genus.

Hemoglobin from four specimens representing four genera of Tyrannidae and two of Cotingidae was examined; both groups were characterized by two strong bands each migrating from the origin. In addition, three genera of Formicariidae proved different also, being characterized by only one band. Thus, although these comparisons are meager, they do illustrate the difference of the woodhewer and ovenbird electrophoretic profiles from those of other closely allied suboscines; however, these data should serve only to prompt further study.

CLUSTER ANALYSIS

The purpose of this exercise is to attempt to categorize the characters that I have discussed throughout this paper in some more orderly fashion, and to cluster the ovenbird and woodhewer groups in a more objective fashion, without overemphasizing certain characters to which I am biased.

Since the publication of "Principles of numerical taxonomy" (Sokal and Sneath, 1963), much progress has been made in methodology and very refined computer clustering programs now exist. The gleaning of evolutionary information from such clusters is another more complex problem. I have utilized a clustering program now known as the "Prim Network" (see Prim, 1957; Edwards and Cavalli-Sforza, 1964; Kluge, 1969; and Zug, 1971, for more detailed information) which expresses phenetic difference (which is, ". . . linear sum of unit character differences." Farris, 1967) between any two species (OTUs: Operational Taxonomic Units) as a numerical value from which one may construct the type of diagram presented in Figure 19. The lines between OTUs in Figure 19 are the linear sums of character differences between the two OTUs.
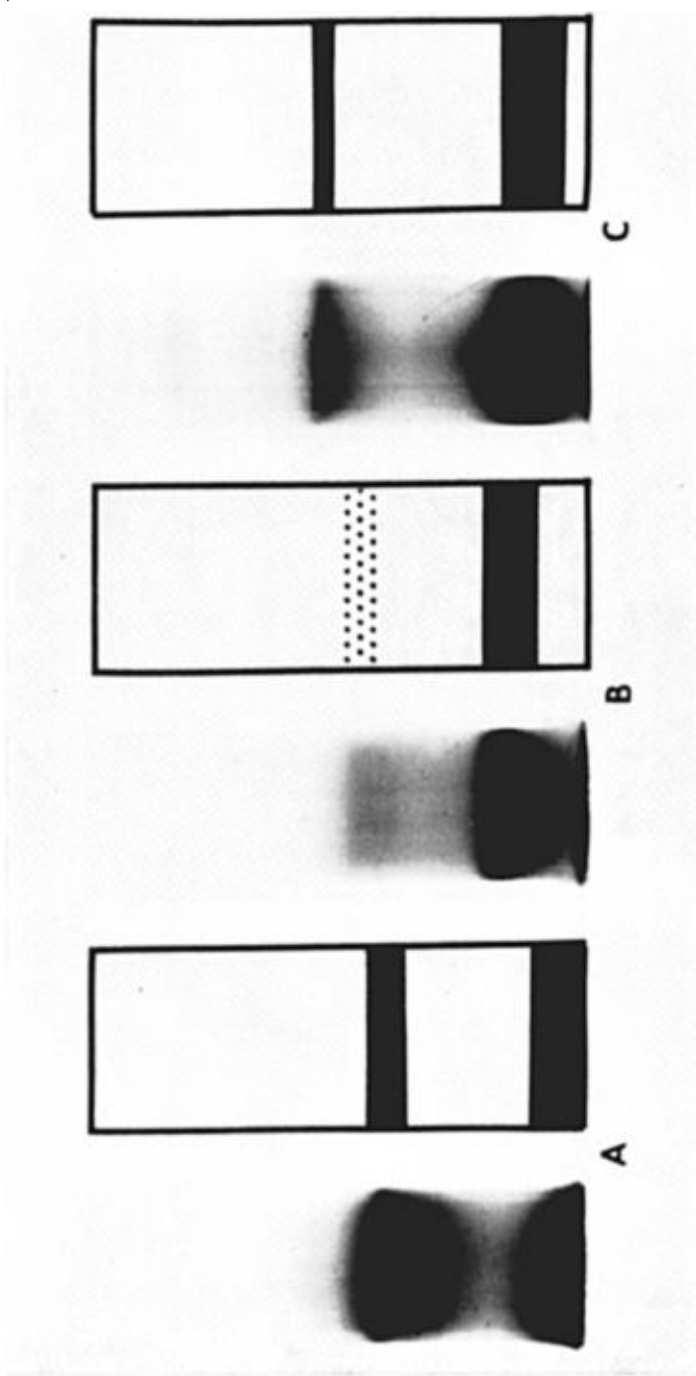
Figure 18. Photographic and diagrammatic illustrations of electrophoretic patterns of hemoglobin of A, furnariids; B, dendrocolaptids; and C, *Sittasomus griseicapillus* and *Deconychura longicauda*.

CHARACTER CODING

The process of coding characters presents many problems, especially in dealing with the transition of qualitative, non-morphometric data to a coded data set. An even greater problem in passerine birds is the limitation presented by the lack of characters from the birds themselves. In the data set (Table 3) I find that I have weighted certain features by the mere number of coded characters used from given complexes, but I have attempted to choose a "reasonable" number of characters from each complex. There are seven characters associated with the hind limb (nos. 1–7), six with hemoglobin (nos. 10–15), six with cranial morphology (nos. 20–25), two with tail structure (nos. 8 and 18), two with wing pattern (nos. 17 and 18), one with syrinx (no. 9), one with sternum (no. 19), one with nest (no. 26), and one with the habitat (no. 27). Therefore, the characters with the most weight in the analysis are the hind limb, cranial morphology, and hemoglobin, with the tail, wing pattern, syrinx, sternum, nest, and habitat playing a significant although minor role. One might criticize the use of hemoglobin as six separate characters. However, the only effect of deemphasizing hemoglobin is to reduce the distance between OTUs at points where hemoglobin differs; that is, there is no change in the diagram from *Dendrocincla* to the far left or from *Xiphorhynchus triangularis* to the far right (see results section).

The types of characters that I have coded are not the types that vary greatly between closely related genera. The purpose of this analysis is to cluster the major natural groups within the ovenbirds and woodhewers, and for this purpose the coding of minor derived character states that characterize some genera but primarily species seems superfluous. One should immediately note from the data set that the only characters that separate a number of closely related forms are those involving morphometric data.

CHARACTER CODING (TABLE 4)

1–4. Ratios of limb elements and pygostyle (Figs. 11 and 17). The mean lengths of the tarsometatarsus (character no. 1), tibiotarsus (no. 2), femur (no. 3), and pygostyle (no. 4), are expressed as ratios to sternal length. These are the only morphometric characters used.

5. Fossa in proximal end of femur (Fig. 14). The fossa is generally absent (0) in the ovenbirds and present (2) in the woodhewers. The intermediate condition (1) is the state of having a medium-sized fossa, or a number of very small foramina.

6. Proximal end of tibiotarsus (Fig. 15). The typical passerine conformation for the proximal end of the tibiotarsus (0) is present in most of the ovenbirds. Great expansion of the proximal end of the tibiotarsus for the origin

TABLE 3

DISTRIBUTION OF CHARACTER STATES IN OVENBIRD AND WOODHEWER GENERA

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Furnarius	1.18	1.55	0.80	.27	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Cinclodes	1.03	1.45	0.80	.32	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Upucerthia	0.96	1.35	0.83	.31	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Geositta	0.98	1.36	0.77	.27	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Coryphistera	1.04	1.45	0.80	.34	1	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Anumbius	0.93	1.34	0.79	.31	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Synallaxis	1.20	1.70	1.02	.36	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Certhiaxis	1.09	1.48	0.93	.36	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Asthenes	1.13	1.54	0.97	.34	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Cranioleuca	1.21	1.70	1.00	.39	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Phacellodomus	0.99	1.54	1.01	.38	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Margarornis	1.22	1.63	0.93	.42	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1
Phleocryptes	1.30	1.88	1.05	.32	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Pseudocolaptes	1.07	1.52	0.91	.44	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	0	1	0	0	1	1	1
Hyloctistes	0.93	1.37	0.90	.37	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1	1	2	0	0	1	1	1
Syndactyla	1.14	1.60	0.95	.36	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	1	0	0	1	1	1
Anabacerthia	0.98	1.39	0.85	.37	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	2	0	0	1	1	1

TABLE 3 (CONTINUED)

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Philydor	0.95	1.39	0.85	.37	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	2	0	0	1	1	1
Automolus	0.92	1.36	0.88	.33	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2	2	2	0	0	1	1	1
Thripadectes	1.14	1.58	1.02	.35	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	2	2	2	0	0	1	1	1
Xenops	0.94	1.33	0.85	.35	1	1	1	1	0	1	0	0	1	0	0	1	0	0	1	1	0	1	1	1	1	2	1
Dendrocincla	0.89	1.19	0.85	.40	1	1	1	1	1	1	0	0	1	0	0	0	0	2	1	1	0	2	2	1	1	2	1
Sittasomus	1.04	1.29	0.79	.46	2	2	1	2	1	0	0	1	0	0	1	1	0	3	0	1	0	2	1	1	1	2	1
Deconychura	0.94	1.11	0.75	.45	2	2	1	2	1	0	0	1	0	0	1	0	1	3	1	1	0	2	1	1	1	2	1
Glyphorhynchus	0.90	1.11	0.75	.48	1	2	1	2	1	0	1	0	0	1	0	1	0	3	1	1	1	1	2	2	1	2	1
Lepidocolaptes	0.81	1.13	0.77	.49	2	2	2	2	1	0	1	0	0	1	0	0	1	3	2	2	2	2	2	2	2	2	1
X. erythropygius	0.79	1.09	0.78	.45	2	2	2	2	1	0	1	0	0	1	0	0	1	3	1	2	2	2	2	2	2	2	1
X. guttatus	0.81	1.08	0.77	.44	2	2	2	2	1	0	1	0	0	1	0	0	1	3	2	2	2	2	2	2	2	2	1
Dendrocolaptes	0.95	1.20	0.88	.53	2	2	2	2	1	0	1	0	0	1	0	0	1	3	2	2	2	2	2	2	2	2	1
Campylorhamphus	0.89	1.25	0.91	.51	2	2	2	2	1	0	1	0	0	1	0	0	1	3	1	2	2	2	2	2	2	2	1
Dendrexetastes	0.88	1.34	0.96	.55	2	2	2	2	1	0	1	0	0	1	0	0	1	3	1	2	2	2	2	2	2	2	1

of the extensor muscle of the toes (2) is found in most woodhewers. A number of intermediates (1) are present.

7. Distal end of tarsometatarsus (Fig. 13). The typical passerine condition (0) with a large metatarsal I, only slight excavation of the trochlea for digit III, and a not greatly expanded base of the distal end is found in most of the ovenbirds. The woodhewer tarsometatarsus (2) exhibits a small metatarsal I (an indication of a small hallux), great excavation of the trochlea for digit III, and expansion of the base of the distal end. A number of intermediate character states are known (1).

8. General foot structure (Fig. 16). The typical anisodactyl foot (0) is found in most ovenbirds. There are intermediates (1) which lead to the woodhewer condition (2) in which the third and fourth toes are of equal length, a reduced hallux is present, and there is external fusion of the basal phalanges, and strongly curved anterior claws.

9. Syrinx. There are two character states of the syringes of ovenbirds and woodhewers. The woodhewer condition (1) with elaborate *Processi* having projecting horns for the attachment of muscles is derived from the ovenbird condition (0) in which horns are lacking on the *Processi*. Although Ames (1971) did not examine certain genera included here, I am assuming tentatively that *Coryphistera, Cranioleuca, Margarornis, Hyloctistes, Syndactyla, Anabacerthia,* and *Thripadectes* among the furnariids possess the syrinx without horns on the *Processi,* and that *Deconychura* and *Dendrexetastes* among the unexamined dendrocolaptids possess the syrinx with horns on the *Processi.*

10–15. Hemoglobin electrophoretic pattern (Fig. 18). Each OTU is coded for the absence (0) or presence (1) of each of the six different hemoglobin bands that occur in the ovenbirds and woodhewers. Those ovenbirds and woodhewers for which no hemoglobin data are available are assumed to possess that of their respective group.

16. Wing stripe (Fig. 3). A rufous wing stripe (1) is present in many furnariids and in the "intermediates," but absent (0) in the "strong-billed" dendrocolaptids. The diffuse wing stripe in *Dendrocincla anabatina* is coded as 1.

17. Solid reddish wing (Fig. 2). The "strong-billed" woodhewers possess a solid reddish wing (1). All other forms are coded 0.

18. Tail (see skin photographs, Fig. 1). The degree of stiffening of the tail is coded from the lack of stiffness (0) to the most advanced condition of stiffening found in the woodhewers (3).

19. Sternal notches (see Feduccia, 1972). The posterior border of the sternum

TABLE 4
COMPARISON OF THE CLASSIFICATIONS OF SCLATER (1890), AND
HELLMAYR (1925)

SCLATER	HELLMAYR
Family Dendrocolaptidae	Family Furnariidae
Subfamily Furnariinae	Subfamily Furnariinae
Subfamily Synallaxinae	Subfamily Synallaxinae
Subfamily Philydorinae	Subfamily Margarornithinae
Subfamily Sclerurinae	Subfamily Philydorinae
Subfamily Dendrocolaptinae[1]	Subfamily Sclerurinae
	Family Dendrocolaptidae[2]

[1] Sclater included *Margarornis*, *Premnornis*, *Premnoplex*, and *Pygarrhichas* within the Dendrocolaptinae. Excluding those genera, Sclater's order for the subfamily was: *Sittasomus*, *Glyphorhynchus*, "strong-billed" woodhewers, *Dendrocincla* (which included *Deconychura*), and the "strong-billed" dendrocolaptids.
[2] The order in Hellmayr's Dendrocolaptidae is: "strong-billed" woodhewers, *Glyphorhynchus*, *Sittasomus*, *Deconychura*, and *Dendrocincla*.

of most ovenbirds is generally type 3. Many species possess type 3 sterna but show a tendency to open further (0), some possess only type 3 sterna (1), and some possess type 3 sterna but with some tendency to close further (2).

20. Nasal condition (Figs. 4–8). The pseudo-schizorhinal condition is found in a large number of ovenbirds (0). An intermediate condition (1) leads to the solid holorhinal skull (2) found in most of the woodhewers.

21. Orbital process of the quadrate (Figs. 4–8). The tip of the orbital process of the quadrate goes from the condition in the ovenbirds with no expansion (0) through intermediate stages of expansion (1) to the great expansion found in the "strong-billed" woodhewers (2).

22. Ectethmoid complex (Figs. 4–8). The ovenbird condition (0) of having a broad plate tilted anteriorly, with a slight wing that does not meet the jugal bar, goes through intermediate stages (1) to the woodhewer condition (2) of having a relatively smaller but stronger plate which is not tilted anteriorly, but which is constricted mesially and sends out a large wing that meets and abuts against the jugal bar.

23. Supraorbital area of frontal bones (Figs. 4–8). The narrow condition of the supraorbital area of the frontal bones (0) in the ovenbirds goes through intermediate stages (1) to the broad condition (2) found in the woodhewers.

24. Interorbital septum (Figs. 4–8). An unossified interorbital septum (0) in the ovenbirds goes through intermediate stages of ossification in the

philydorines (1) to the extremely ossified condition (2) found in the wood-
hewers.

25. Zygomatic and postorbital processes and temporal fossa (Figs. 4–8).
Small processes and a small fossa (0) are present in most of the ovenbirds.
Intermediates in the philydorines (1) lead to the strong processes and deep
fossa (2) that characterize the "strong-billed" woodhewers.

26. Nest. Most of the ovenbirds build large stick structures (0). The mud
structure of *Furnarius* is arbitrarily coded (0). Some ovenbirds excavate
tunnels (1) or nest in holes or cavities in trees or stumps (2) as do the wood-
hewers.

27. Habitat. The habitat is coded as non-forest (0), or forest (1).

RESULTS AND CONCLUSIONS

The results of the Prim Network are shown in Figure 19. The Prim Net-
work supports the following.

The "strong-billed" woodhewers represent a cohesive taxonomic unit, fairly
well separated from the furnariids, but bridged by four intermediate genera.
There is no attempt here to decipher any cladistic information from the Prim
Network. However, I should point out that the Network in no way con-
tradicts either a monophyletic or multiple origin hypothesis for the Dendro-
colaptidae (*sensu* Ridgway), but in fact, the Prim Network does show *Den-
drocincla* closer to the philydorine furnariids than to the "strong-billed"
dendrocolaptids. Additionally, it shows *Sittasomus* and *Deconychura* as be-
ing very closely allied, and *Glyphorhynchus* approximately halfway between
the philydorines and the "strong-billed" dendrocolaptids. As suspected the
philydorines as a group are closer to the woodhewers than are any of the
other ovenbirds. Also, the philydorines seem to form a cohesive taxonomic
unit, thus lending support to their subfamilial status. The placement of
Xenops closest to the "intermediates" and other woodhewers is not surprising,
and has been suggested at different places throughout this paper on the basis
of single characters. The area of the synallaxines and furnariines on the Prim
Network is more confused, for these two groups are probably more closely
allied to each other than is either to any other group within the ovenbird-
woodhewer assemblage. The lack of a large number of derived specific char-
acters in this analysis prohibits drawing any major conclusions from the far
left-hand side of the Prim Network, except that the synallaxines and fur-
nariines are very closely related. The only point of interest is that most of the
presently classified synallaxines cluster with each other, as do the furnariines.

Again, one might question the use of hemoglobin as six separate characters
instead of one. I must emphasize that it has little effect on the major con-

clusions of the Prim Network, for when the same computer program is run without using any hemoglobin characters the only effects are as follows: 1) the phenetic differences between *Dendrocincla* and *Sittasomus*, and between *Dendrocincla* and *Glyphorhynchus* are reduced by a linear distance of approximately one-half the length shown in Figure 19; and 2) *Xiphorhynchus triangularis* comes off from *Deconychura* rather than from *Glyphorhynchus*. In other words, *Glyphorhynchus* is less woodhewer-like if hemoglobin is excluded from consideration.

A PHYLOGENY

A hypothetical phylogeny of the furnariids and dendrocolaptids is shown in Figure 20.

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 possibly one or several different lines, and on the other hand the synallaxines have probably 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, whereas 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.

The anatomical evidence 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 may 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 ovenbirds, but has the electrophoretic hemoglobin pattern of the woodhewer group.
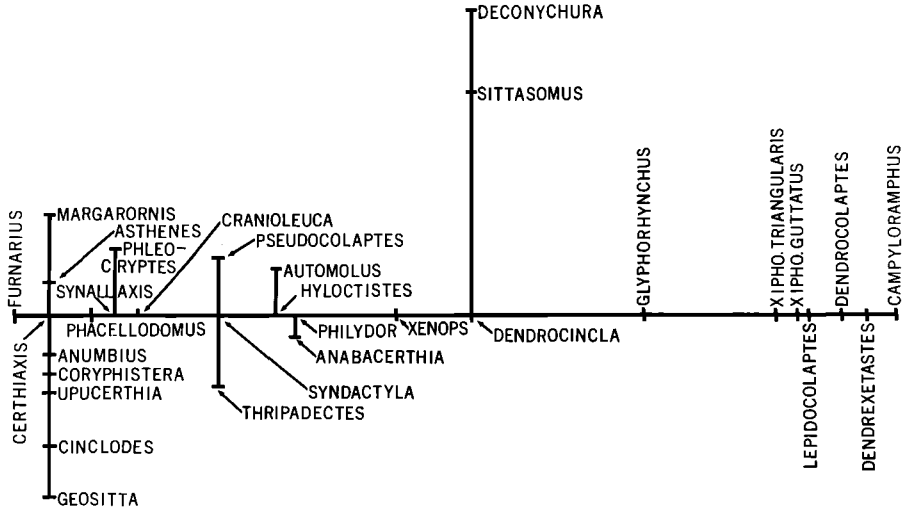
Figure 19. The Prim Network. The length of the lines between the various OTUs is a direct indication of the phenetic distance as deciphered by the computer. The actual names of the OTUs are as follows: *Furnarius rufus, Certhiaxis cinnamomea, Synallaxis brachyura, Margarornis rubiginosus, Anumbius annumbi, Coryphistera alaudina, Upucerthia dumetaria, Cinclodes fuscus, Geositta cunicularia, Phacellodomus striaticollis, Cranioleuca erythrops, Phleocryptes melanops, Syndactyla rufosuperciliata, Pseudocolaptes lawrencii, Thripadectes rufobrunneus, Hyloctistes subulatus, Automolus ochrolaemus, Philydor lichtensteini, Anabacerthia striaticollis, Xenops minutus, Dendrocincla anabatina, Sittasomus griseicapillus, Deconychura longicauda, Glyphorhynchus spirurus, Xiphorhynchus triangularis, Xiphorhynchus guttatus, Lepidocolaptes souleyetii, Dendrocolaptes certhia, Dendrexetastes rufigula,* and *Campylorhamphus pusillus.*

Deconychura and *Sittasomus* also appear to be closer to philydorine-like ovenbirds. 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 ovenbirds. 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 very philydorine-like in its characters. 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; *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 ovenbirds 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 woodhewer type of syrinx; *Geositta*, however, a typical furnariid in most other characters, 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. Whether or not subsequent offshoots from the philydorine-like ancestors resulted in the "intermediate" genera (see Fig. 20) is difficult to determine. The alternative to a more recent origin of the "intermediates" from philydorine stock is that they simply represent woodhewers of an initial monophyletic radiation that have retained many primitive characters, but as we are dealing with tree-trunk foragers one wonders why a woodhewer would retain primitive (=less efficient) tree-trunk foraging adaptations through time. The total phenetic distance within the ovenbirds and woodhewers is expressed by a computer clustering program (Fig. 19). These data are compatible with either a mono- or polyphyletic origin of the woodhewers.

The relationships within the ovenbirds are even less clear. The exact position of the synallaxines, furnariines, and sclerurines would be very difficult to ascertain. It seems reasonable, however, that some "holorhinal" pre-passerine or passerine probably 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, general ossification of the skull increased in the philydorines due to selection forces for stronger skulls associated with foraging habits. This led to a series of holorhinal philydorines, which, concomitant with scansorial tendencies, gave rise to woodhewer-like forms, and eventually to a radiation of woodhewers into their new adaptive zone.

A Behavioral Model

If we assume that the woodhewers are derived from ancestors resembling the living philydorine 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 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
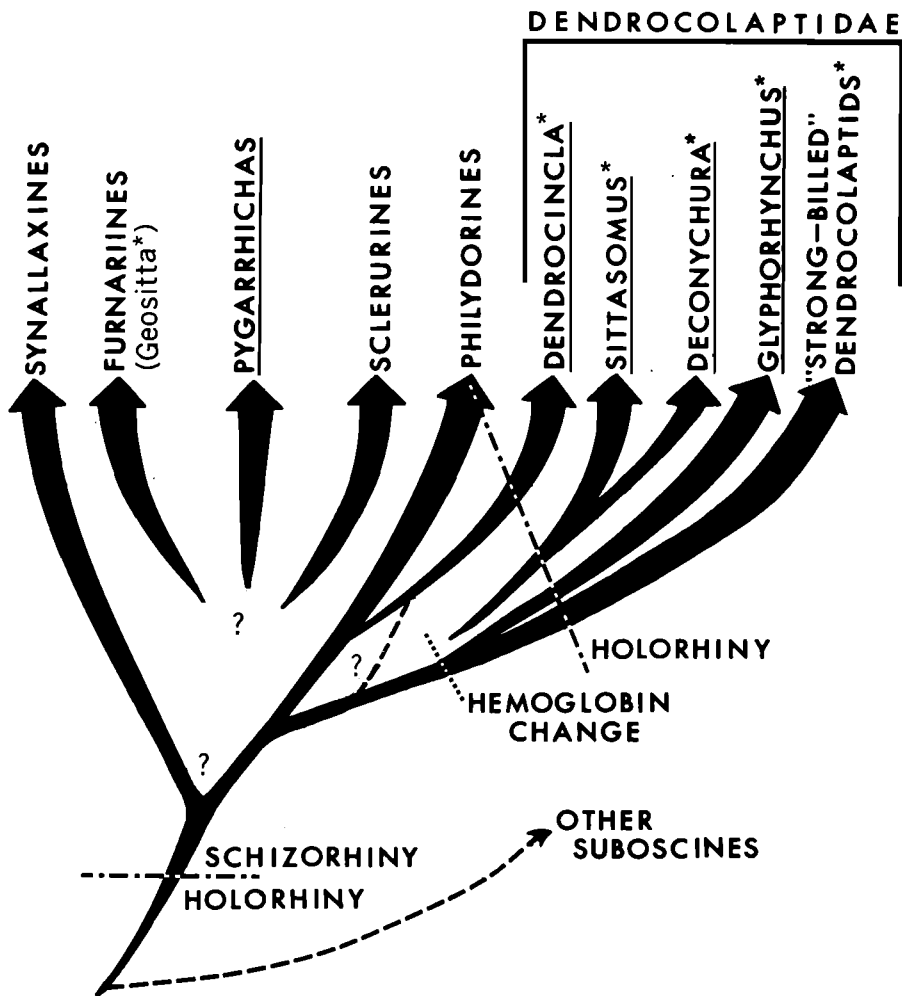
Figure 20. Hypothetical phylogeny of furnariids and dendrocolaptids. Bracketed groups shown to the right above were included in the Dendrocolaptidae *sensu* Ridgway.

also, and there are climbing forms in many of the passerine families. In the furnariids, the preadaptations for trunk climbing seem 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 diverse foraging behavior, to include new strategies in foraging behavior and thereby increase their 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. 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, and one can imagine how a scansorial foraging strategy might be advantageous. The majority of philydorines 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 margarornithine furnariids (*Margarornis* and related genera), and *Pseudocolaptes* frequently forage like woodhewers, hitching up tree trunks. In the high Andes, *Cranioleuca antisiensis* forages by hitching up tree trunks; it exists in areas where no woodhewers are present, as does *Pygarrhichas* of southern South America.

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, as in lowland rain forest situations. 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, 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 the ratites, or 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 less specialized forms first in the sequence. The evidence now seems 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 indicating a close affinity of woodhewers to philydorine furnariids. These lines of evidence do not seem incompatible with the classification used by Sclater (see Table 4), with a few changes. I would recommend that the more generalized Synallaxinae precede the more specialized Furnariinae. The terrestrial or semi-

terrestrial Furnariinae are perhaps likely derivatives of the more "generalized" synallaxines. Sclater had included *Margarornis*, *Premnornis*, and *Premnoplex* (the margarornithines) within the Dendrocolaptinae probably owing to their scansorial habits, and general resemblance to the woodhewers. These forms, however, are clearly "ovenbirds" and are probably closely allied to the synallaxines, at least in cranial osteology. I would recommend their placement at the end of the Synallaxinae. Sclater had also included the enigmatic genus *Pygarrhichas* within the Dendrocolaptinae. Because its systematic position remains elusive it should be placed in or near the Sclerurinae and Philydorinae, perhaps as "*incertae sedis*." The placement of the "intermediates" within the Dendrocolaptinae should be as follows: *Dendrocincla* (most ovenbird-like), followed by *Sittasomus*, *Deconychura*, *Glyphorhynchus*, and the "strong-billed" woodhewers. It is my opinion that the foregoing classification would best reflect any of the alternate phylogenies of the group. In addition, I would propose that the family name Furnariidae be used because the preponderance of species are found within the Furnariinae.

SUMMARY

1. The furnariids (ovenbirds) and dendrocolaptids (woodhewers) are two very closely related groups of suboscine birds. The group of ovenbirds most closely related to the woodhewers is the subfamily Philydorinae, which shares an almost identical range with the dendrocolaptids. The philydorines are the heavy-bodied forest furnariids, and they form the link in an almost perfect anatomical series going from the synallaxines and furnariines to the woodhewers. There are four genera of woodhewers, *Dendrocincla*, *Sittasomus*, *Deconychura*, and *Glyphorhynchus*, which appear to be the most primitive of the woodhewers (less diverged from the ovenbird pattern), and in fact, share many characters with the ovenbirds including a wing stripe peculiar to the furnariids. These four genera are termed the "intermediates." The remainder of the woodhewers, which are called the "strong-billed" woodhewers are very homogeneous. The problem of paramount interest involves deciphering the evolutionary relationships. Are the "intermediates" separate offshoots from philydorine ancestral stock, or are they simply woodhewers which have retained many primitive character states? The great chance for convergence in tree-trunk foraging birds makes deciphering the phylogenies very difficult. Anatomical and other characters are evaluated by establishing anatomical series from non-creeping to creeping forms, and then the character states of the "intermediates" are examined. The primary assumption is that the woodhewers represent an advanced state of derived characters and that the ovenbirds' suite of characters more closely resembles the primitive state.

2. The skulls of furnariids differ from those of the "strong-billed" dendrocolaptids in many characters. Most of the furnariids are pseudo-schizorhinal; all of the "strong-billed" dendrocolaptids are holorhinal. A summary of the character differences is available in Table 2. The ovenbird skull is, in general, a much weaker and flexible skull, compared to the heavily ossified woodhewer skull. Most of the skull characters correlate with the foraging behavior and type of food taken. Most of the furnariids feed on small insects. Most of the "strong-billed" dendrocolaptids feed on medium-to-large sized hard-backed beetles, and on small vertebrates such as frogs or lizards, which occur on tree trunks. These birds may frequently forage by probing and prying into bark and leaf and vine clusters, etc., and some may occasionally peck like a woodpecker. Some of the philydorine furnariids and all of the "intermediate" woodhewer genera possess a mosaic of woodhewer-ovenbird characters. Those philydorines which approach the woodhewer skull condition are those heavy-bodied forest forms which (for those where information is available) feed more in a woodhewer manner and on large prey, and may peck, pry, and probe in their feeding behavior. There is an anatomical sequence from a weak, pseudo-schizorhinal skull through the philydorines and "intermediates" to the strong woodhewer skulls.

3. Both the furnariids and dendrocolaptids have basically a two-notched sternum, but with great variation. Some forms show a tendency toward opening of the posterior border of the sternum, while others show a tendency toward the closing of it. The furnariids show a tendency toward an open posterior border of the sternum; none shows a tendency toward its closure. The "strong-billed" dendrocolaptids show a tendency toward closure. The "intermediates" are clearly furnariid-like in this character. All possess two-notched sterna, but none with a tendency toward closure, and two forms with a slight tendency toward opening.

4. The hind limb bones (as expected from other creeping forms) are shorter in the woodhewers than in the ovenbirds. The "intermediates" are somewhat intermediate between the ovenbirds and woodhewers in these characters. The distal end of the tarsometatarsus in ovenbirds differs from that in woodhewers. In the woodhewers, metatarsal I is short, corresponding to a short hallux; the amount of separation between the condyles is great; and the trochlea for digit III is deeply excavated. The "intermediates" are between the ovenbirds and woodhewers in all of these characters. It is of interest here that some of the tree-trunk foraging furnariids are close to the woodhewer condition, indicating convergence. The femur of woodhewers has a foramen or many small foramina in the proximal end; ovenbirds generally lack the foramen. It is present in *Glyphorhynchus* (nearly absent in *Dendrocincla*), but absent in the other "intermediates." The proximal end of the tibiotarsus

in the woodhewers shows expansion of the area for the origin of the main extensor muscle of the toes. Most of the "intermediates" are woodhewer-like in these characters, but *Dendrocincla* is somewhat intermediate, and *Xenops*, a philydorine furnariid, is very woodhewer-like in its tibiotarsus. The feet (digits) of woodhewers differ from those of ovenbirds in having digits III and IV nearly equal in length, and this length is greater than that of digit II. Also, the three anterior toes are fused exteriorly for the entire length of their basal phalanges. The woodhewer hallux is short. The ovenbird foot is, for the most part, the typical passerine anisodactyl foot. Although woodhewers and ovenbirds are generally separable by the characters of the feet, there are some intermediates, and many tree-trunk foraging birds (including ovenbirds) approach the woodhewer condition.

5. Ames (1971) reported that the syringes of the ovenbirds and woodhewers are very similar, but differ between the two groups. The "intermediates" (*Deconychura* was not examined) possess the woodhewer type of syrinx, but *Geositta* (a typical furnariid in other characters) possesses the woodhewer type of syrinx.

6. The disc (acrylamide) electrophoretic patterns of hemoglobin in ovenbirds are different from those in woodhewers. Of the "intermediates," *Glyphorhynchus* shows a hemoglobin pattern identical to that of the woodhewers; *Sittasomus* and *Deconychura* show patterns like each other, but different from both the woodhewer and ovenbird patterns; and *Dendrocincla* (*anabatina*) shows a pattern identical to that of the ovenbirds.

7. A computer cluster analysis was performed to determine quantitatively the overall similarity of selected OTUs. The Prim Network (Fig. 19) confirms the position of the "intermediates."

8. There are two possible phylogenies for the woodhewers. The woodhewers may be of multiple origin from philydorine-like ancestors, or monophyletic, if the "intermediates" are simply forms which have retained many primitive characters.

9. A behavioral model involving competition for feeding space in mixed species foraging flocks may be a possible explanation for the origin of tree-trunk foraging behavior.

10. Classifications should best reflect phylogenies, and in linear should preferably begin with the more primitive forms (where known) and end with the more specialized. None of the existing classifications accomplishes this end, though Sclater's classification certainly approximates a primitive to specialized scheme (see Table 4). I would recommend following the classification of Sclater at the familial and subfamilial levels. However, I would strongly rec-

ommend that the more generalized Synallaxinae precede the more specialized (primarily terrestrial or semi-terrestrial) Furnariinae, and I would additionally recommend generic transfers (now commonly done) as follows. *Margarornis*, *Premnornis*, and *Premnoplex* are ovenbirds and should be transferred probably to the Synallaxinae. Sclater had included the margarornithines within the Dendrocolaptinae. *Pygarrhichas* (which Sclater had also included within the Dendrocolaptinae) should be placed in or near the Sclerurinae and Philydorinae as "*incertae sedis*"; its systematic position remains elusive. And finally, the sequence within the Dendrocolaptinae should be: *Dendrocincla*, *Sittasomus*, *Deconychura*, and *Glyphorhynchus*, followed by the "strong-billed" woodhewers. Finally, the family name Furnariidae is most appropriate for the ovenbird-woodhewer assemblage.

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