Morphological Similarities between the Menurae and the Rhinocryptidae, Relict Passerine Birds of the Southern Hemisphere

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and
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ABSTRACT

Feduccia, Alan, and Storrs L. Olson. Morphological Similarities between the Menurae and Rhinocryptidae, Relict Passerine Birds of the Southern Hemisphere. *Smithsonian Contributions to Zoology*, number 366, 22 pages, 17 figures, 1 table, 1982.—The order Passeriformes is divided into two major groups: the oscines (Suborder Passeres), characterized by a derived condition of the syrinx, and the suboscines (Suborder Tyranni), characterized by a derived condition of the stapes. The only passerines yet identified that lack both the derived stapes and a fully oscine syrinx are the Australian lyrebirds (Menuridae) and scrub-birds (Atrichornithidae) of the suborder "Menurae," and the New Zealand "wrens" (Acanthisittidae). We document the first reported occurrence of a primitive stapes in an otherwise suboscine group—the genus *Melanopareia* of the South American family Rhinocryptidae. Our comparisons show that the osteology of the Menurae is utterly unlike that of the oscine families Ptilonorhynchidae or Paradisaeidae, to which the Menurae have recently been postulated to be related, whereas we show that many of their osteological peculiarities are shared only with the Rhinocryptidae. Although the Menurae may be the most primitive members of the suborder Passeres and the Rhinocryptidae are almost certainly the most primitive members of the superfamily Furnarioidea, they are nevertheless more similar to each other osteologically than either is to some other passerine group. We suggest that the Menurae and the Rhinocryptidae are among the most primitive of the Passeriformes and are representative of the ancestral stock that gave rise to the remainder of the passerines. The evidence suggests that the order Passeriformes is at least as old as most other modern orders of birds and probably arose in the Southern Hemisphere. In an appendix we show that the grallarine section of the Formicariidae exhibits some of the osteological traits of the Rhinocryptidae and it is suggested that the sequence of families in the superfamily Furnarioidea should be: Rhinocryptidae—Formicariidae—Furnariidae (including Dendrocolaptidae).

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Contents

Morphological Similarities between the Menurae and the Rhinocryptidae, Relict Passerine Birds of the Southern Hemisphere

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Introduction

For well over a century, the order Passeriformes has generally been recognized as being divisible into two major groups, the oscines and the suboscines, which are usually ranked as suborders under the names Passeres and Tyranni, respectively. The recognition of this fundamental division had its beginnings in the studies of Johannes Müller (1878) on the anatomy of the syrinx. Ames' (1971) monographic study of the passerine syrinx has now superceded Müller's and all subsequent investigations on the subject. Ames (1971:2) found the oscines to share a complex but remarkably uniform morphology of the syrinx "suggesting that the group is narrowly monophyletic." On the other hand, the great variability in syringeal morphology within the suboscines does not lend itself to a similar interpretation. Recently, however, a monophyletic origin of the suboscines was supported by new evidence from the morphology of the stapes (Feduccia, 1975b; 1977; 1979). Whereas all of the families of oscines exhibit the primitive condition of the stapes that is typical of the vast majority of living birds, as well as their reptilian ancestors, the suboscines possess a unique, derived morphology of the stapes characterized by a peculiar, inflated footplate region.

Thus, an attempt to find living relatives of the common ancestor of these two large suborders might focus on any passerine taxa that lack both the derived suboscine stapes and the derived oscine syrinx. To date, only two such groups have been identified: the Australian lyrebirds and scrub-birds (Menuridae and Atrichornithidae) and the New Zealand "wrens" (Acanthisittidae). The first two families have often been recognized as a separate suborder "Menurae," and all three families have at times been referred to as "suboscines," mainly because they do not possess the typical oscine syrinx. Feduccia (1975a; Ms), however, established that the stapes is primitive in the Menurae and the Acanthisittidae, so these families cannot be grouped with the remainder of the suboscines on the basis of this character.

The present paper came about as a result of our chance discovery of a primitive stapes in the South American birds of the genus *Melanopareia*. This revelation astonished us at the time because *Melanopareia* has always been regarded as a suboscine. Since 1926 (Wetmore, 1926), it has been placed in the Rhinocryptidae, which family Ames (1971) has shown to belong in the suboscine superfamily Furnarioidea, along with the Formi-

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cariidae, and Furnariidae (sensu lato). Further investigation led us to discover several previously overlooked osteological peculiarities in the Rhinocryptidae, which in turn led to our finding that many of these same distinctive characters were shared with the Menurae. Herein we document these observations and assess their importance in understanding the relationships of the Menurae and passerine evolution in general.

ACKNOWLEDGMENTS.—This study was conducted in part while Feduccia was on a Kenan Leave from the University of North Carolina. Specimens studied in the collections of the National Museum of Natural History, Smithsonian Institution, include the following taxa: *Pteroptochos tarnii* (skeleton and alcoholic), *P. megapodius* (skeleton), *Scelorchilus rubecula* (alcoholic), *Rhinocrypta lanceolata* (skeleton and alcoholic), *Teledromas fuscus* (alcoholic), *Liosceles thoracicus* (alcoholic), *Melanopareia maximiliani* (alcoholic), *M. elegans* (skeleton), *Scytalopus unicolor* (skeleton and alcoholic), *S. magellanicus* (skeleton and alcoholic), *S. argentifrons* (partial skeleton), *S. panamensis* (alcoholic), *S. latebricola* (alcoholic), *S. femoralis* (alcoholic), *Acropterynx orthonyx* (partial skeleton), and a variety of skeletons of Formicariidae, including *Grallaria* (three species), *Grallaricula nana*, *Pittasoma michleri*, *Formicarius analis*, *Chamaeza campanisoma*, and *Conopophaga lineata*; also, two skeletons of *Chlamydera nuchalis* and two partial skeletons of *Menura superba*.

The loan of skeletons from other institutions is greatly appreciated. These include: *Grallaria perspicillata* and *Scelorchilus rubecula* (R. W. Storer, University of Michigan Museum of Zoology), *Menura superba* (Charles G. Sibley, Peabody Museum, Yale University), *Myornis senilis*, *Liosceles thoracicus*, *Grallaria hypoleuca przewalskii*, and *G. erythroleuca* (John P. O'Neill, Louisiana State University Museum of Zoology), *Scelorchilus albicollis* (Ned K. Johnson, University of California Museum of Vertebrate Zoology), *Grallaria fulviventris* (Wesley E. Lanyon, American Museum of Natural History), and *Grallaria flavotincta*, *G. macularia*, and *Conopophaga aurita* (Jon C. Barlow, Royal Ontario Museum). We are grateful for having had access to parts of the skeleton of *Atrichornis clamosus* that was under study by various individuals under the supervision of Mary Heimerdinger Clench. We are also indebted to Robert J. Raikow for permitting us to examine his unpublished manuscript on the myology of the Menurae. The SEM Laboratory of the National Museum of Natural History was generously made available to us, and scanning electron micrographs of rhinocryptid stapes were taken by Walter R. Brown, Mary-Jacque Mann, and Susann G. Braden. Other photographs are by Victor E. Krantz. The osteological illustrations were rendered by Sigrid James Bruch, except for Figures 7A,B and 12 by Janine Higgins. For extensive critical comments on an earlier form of the manuscript we are indebted to Peter L. Ames and Robert J. Raikow. David W. Steadman read and commented on several drafts.

Review of the Classification of the Rhinocryptidae and Menurae

The Rhinocryptidae (tapaculos) consists of over 30 species of rather small, cryptic birds that are poorly known behaviorally or anatomically. The family is almost exclusively South American in distribution, with only one genus (*Scytalopus*) reaching Middle America. Many of the genera are confined to the southern parts of South America. In most current taxonomic treatments, the Rhinocryptidae lies obscurely buried between the Formicariidae and the Cotingidae, and the significance of the family has heretofore been overlooked.

The first few species of rhinocryptids known were originally described as warblers (Sylviidae) or wrens (Troglodytidae), but in 1847 Müller (1878) observed that *Scytalopus* had a "tracheophone" syrinx and shared a four-notched sternum with *Pteroptochos*. Therefore he created a family Scytalopidae for these two genera, which he removed from the oscines. This name, emended to Scytalopodidae, and the name Pteroptochidae Cabanis and Heine, 1859, both have priority over Rhinocryptidae Wetmore, 1930. The earliest

name for the family is based on the genus *Rhinomya*, which is a junior homonym of a non-avian taxon and which was replaced by *Rhinocrypta* (see synonymy in Brodkorb, 1978). Wetmore's action of creating a new family name based on *Rhinocrypta*, when two earlier familial names already existed, is of dubious validity. Brodkorb (1978) is probably correct in resurrecting Scytalopodidae for the family.

The family Rhinocryptidae was characterized by Sclater (1890:337) as a

> peculiar and limited group ... of well-marked Tracheophonine Passeres .... They are ground-birds, remarkable externally for the large and robust feet, with long claws, and their strangely formed bills, in which the nostrils are more or less covered by a membrane; and internally for the singular form of the syrinx and the double-notched sternum.

Very gradually, other genera were also admitted to the Rhinocryptidae and it was only relatively recently that the rhinocryptid affinities of *Melanopareia* and *Psiloramphus* were ascertained (Wetmore, 1926; Plótnick, 1958).

Syringeal morphology was responsible for the traditional inclusion of the Rhinocryptidae within the suboscine superfamily Furnarioidea, along with the Formicariidae, Furnariidae, and Dendrocolaptidae. In his more detailed studies of the syrinx, Ames (1971) confirmed that the Furnarioidea constitute a monophyletic group.

The two species of lyrebirds (Menuridae: *Menura superba*, *M. alberti*) and the two species of scrub-birds (Atrichornithidae: *Atrichornis clamosus*, *A. rufescens*) are endemic to Australia and have traditionally been set apart from other passerines. An isolated position for them was advocated by Garrod (1876) on the basis of syringeal morphology, and it was he who first placed *Menura* and *Atrichornis* in their own suborder, Menurae, between the oscines and the suboscines, a position they have generally occupied up to the present. Ames (1971), on the basis of the syrinx, and Raikow (1978), on the basis of appendicular myology, have confirmed that *Menura* and *Atrichornis* are closely related to one another.

Sibley (1974) reviewed the taxonomic history of the Menurae. Primarily on the basis of egg white proteins, he attempted to show that they were close allies of the oscine bowerbird/bird-of-paradise assemblage (Ptilonorhynchidae and Paradisaeidae). He concluded (Sibley, 1974:65) that

> the suborder Menurae should be dropped from the classification and that the families Menuridae and Atrichornithidae should be placed near the Ptilonorhynchidae and Paradisaeidae.

Subsequently, however, Brush (1979) has shown that the results obtained in Sibley's analyses of egg white proteins are equivocal because of problems of laboratory technique.

Apart from the data from egg white proteins, Sibley's arguments for the placement of the Menurae revolved around explaining away the singular morphology of their syrinx. As mentioned, the syrinx of *Menura* was first described by Garrod (1876:514–516), who concluded that it was "acromyodian," although not typically oscine. Garrod (1876:516) also described the syrinx of *Atrichornis* and stated that "it would require but little modification in either [*Atrichornis*] or *Menura* to convert their syringeal muscular masses into more numerous independent muscles." In other words, the logical sequence in syringeal evolution would lead from the anatomically simpler type found in the Menurae to the more complex syrinx typical of advanced oscines, in which there is very little variation in structure.

Ames (1971:163–164) likewise considered the syrinx of the Menurae to be morphologically close to that of the oscines, but distinct and primitive within that assemblage.

> The lyrebirds and scrub-birds are more alike in syringeal structure than was previously inferred from the work of Garrod (1876), who reported finding only two pairs of intrinsic muscles in *A. rufescens* .... Although the musculature is very close to the oscine pattern, there are major differences in the cartilages. In both muscles and cartilages, the Menurae lie well outside the range of variation shown by the vast array of recognized oscines. The syringeal evidence supports the osteological and pterylographic characters in separating the Menurae from the Passeres .... No single group of oscines can be considered syringeally primitive, in the sense that the Menurae can be considered so.

Because this view was incompatible with Sibley's (1974) hypothesis of a relationship between

the Menurae and the bowerbird/bird-of-paradise assemblage, Sibley asked Ames (in Sibley, 1974:74) to identify the hypothetical evolutionary steps that would be necessary to derive the menurine syrinx from the more complex syrinx of typical oscines. These were as follows:

1. Loss of the short ventral muscles, complete in *Menura*, partial in *Atrichornis*.
2. Loss of fusion of tracheal rings, complete in *Menura*, partial in *Atrichornis*.
3. Juxtaposition of M. sternotrachealis and M. bronchialis posticus.

Despite the complexity of this hypothetical evolutionary pathway, and despite the fact that Ames (in Sibley, 1974:74) continued to believe "that it is logical to assume that the 'most likely primitive condition'" is that found in Menurae, Sibley (1974:65) dismissed the syringeal structure of the Menurae as differing "in degree only." We reject this as special pleading that is inconsistent with the facts. It might also be noted that *Menura* is among the most accomplished songsters in the world, and therefore it is difficult to imagine what the adaptive advantage might be in the loss of syringeal muscles. We see no reason not to continue to regard the syringeal morphology of the Menurae as being primitive relative to that of typical oscines.

Raikow (1978:377) studied the appendicular myology of *Menura superba* and *Atrichornis clamosus* in detail and found that not only did they share unique traits indicating a close relationship between the two genera, they also differed greatly from the bird-of-paradise/bowerbird assemblage. He considered that "the Atrichornithidae and Menuridae are the most aberrant passerines yet studied in their limb myology."

In his discourse on *Menura*, Sibley (1974:68) stated that he had

> compared the skeleton of *Menura superba* with that of *Chlamydera lauterbachi* [Ptilonorhynchidae], element by element. The two are virtually identical except for the shape of the posterior margin of the sternum, the absence of an ossified hypocleidium in *Menura* and the difference in size of all elements.

After conducting our own extensive comparisons of these two genera, we were astounded that Sibley could have made such a statement. These two birds are probably as dissimilar osteologically as any two genera of passerines one might care to choose. In the following comparisons we show that the Menurae have no important points of

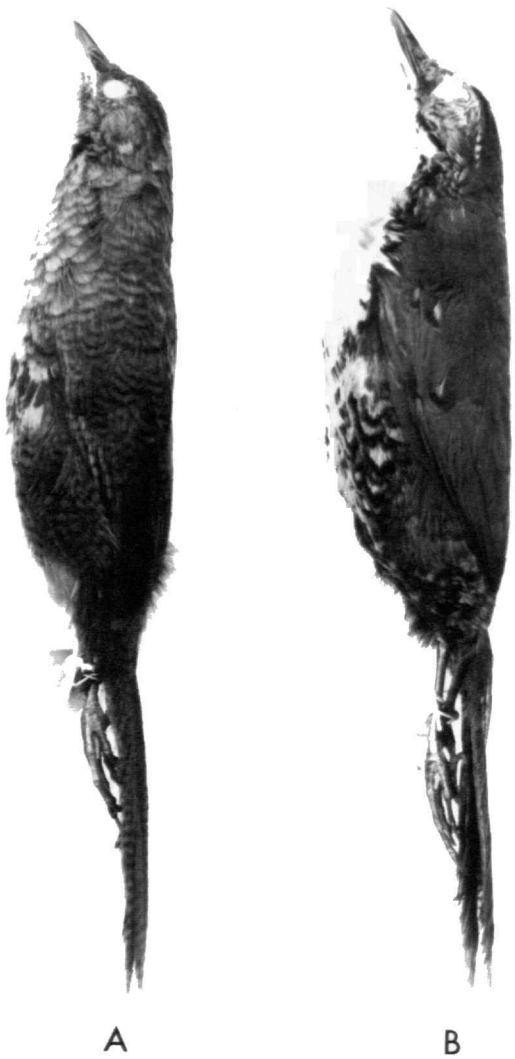


FIGURE 1.—Lateral view of study skins: A, *Atrichornis rufescens* (Atrichornithidae); B, *Liosceles thoracicus* (Rhinocryptidae). Note the overall similarity in proportions, plumage, and bill shape.

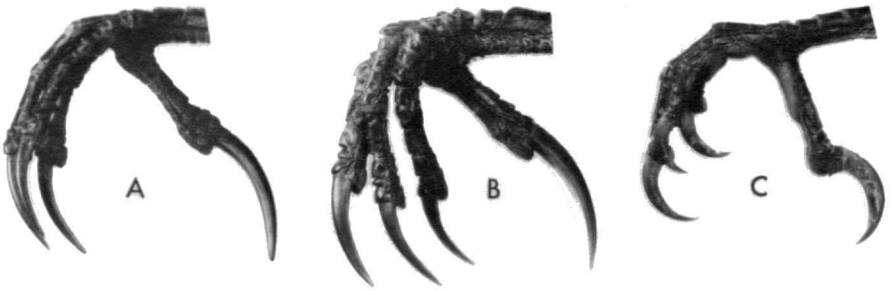


FIGURE 2.—External morphology of the foot to show the distinctive condition of the strong, straight claws shared between certain rhinocryptids (A, *Pteroptochos castaneus*) and lyrebirds (B, *Menura superba*, Menuridae). These differ altogether from the normal passerine condition seen in bowerbirds (C, *Chlamydera nuchalis*, Ptilonorhynchidae). Not to scale.

similarity in osteology with the birds-of-paradise and bowerbirds, and also that they share many characters with the Rhinocryptidae. At the end of the treatments of individual elements we have specifically contrasted *Menura* and *Chlamydera* to emphasize just how different the skeletons that Sibley found to be "virtually identical" really are. Although it would have been useful to have included the Acanthisittidae in our studies, we have not done so because of the scarcity of anatomical material.

Before proceeding with our osteological comparisons, it is worth noting that Cabanis and Heine (1859) once included *Menura* in their family Pteroptochidae (= Rhinocryptidae). Some years later Sclater (1874) voiced the opinion that *Atrichornis* doubtless belonged in the same assemblage. Although his assessment was based at least in part upon a possibly erroneous interpretation of sternal morphology, *Atrichornis* is nevertheless strikingly similar to the rhinocryptid genus *Liosceles* in size, general body proportions, plumage, and bill shape (Figure 1). External resemblances between rhinocryptids and the Menurae also include the long, strong front and hind claws that are dramatically similar between rhinocryptids, particularly *Pteroptochos*, and *Menura* (Figure 2), as was also noted previously by Eyton (1841:52). Finally, the character that gives the Rhinocryptidae its name, the external nasal operculum, is also present in both *Atrichornis* and *Menura*.

Comparative Osteology

STAPES.—We discovered that the stapes is primitive (Figure 3) in the rhinocryptid genus *Melanopareia* (two specimens of *M. elegans* and one

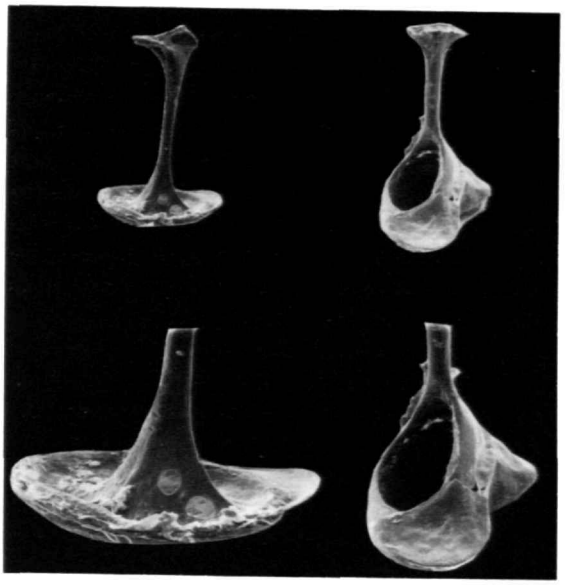


FIGURE 3.—Scanning electron micrographs of the bony stapes (top row) and enlarged view of footplate (bottom row) of *Melanopareia elegans* (left), and *Pteroptochos megapodius* (right). Both of these species belong to the Rhinocryptidae but *Melanopareia* is the only genus in the family, or among the suboscines, that possesses the primitive morphology of the stapes typical of the oscines.

of *M. maximiliani*). In addition to the two species of *Melanopareia*, we examined the stapes in the following species of Rhinocryptidae, all of which were found to possess the derived, bulbous condition typical of suboscines: *Pteroptochos tarnii*, *P. megapodius*, *Scelorchilus albicollis*, *S. rubecula*, *Rhinocrypta lanceolata*, *Liosceles thoracicus*, *Myornis senilis*, *Teledromas fuscus*, *Scytalopus unicolor*, *S. magellanicus*, *S. argentifrons*, and *S. femoralis*. On the basis of its syringeal morphology (Ames, 1971), *Melanopareia* belongs in the Furnarioidea, and our examinations showed its osteology to be in accordance with its placement in the Rhinocryptidae. In possessing the primitive stapes, *Melanopareia* differs not only from all other rhinocryptids examined, but from all other members of the suborder Tyranni for which the stapes is known (see Feduccia, 1975b).

SKULL AND MANDIBLE.—Huxley (1867:451) noted that in *Menura* "the vomer, though broad and deeply cleft posteriorly, is more rounded off than abruptly truncated at its anterior end," thus differing from the typical aegithognathous condition of passerines, in which the vomer is broadly truncated anteriorly (Figure 4). *Menura* also lacks transpalatine processes on the palatines. Inasmuch as *Atrichornis*, which is certainly the closest living relative of *Menura*, has a typically aegithognathous vomer and well-developed transpalatine processes, these conditions in *Menura* must be viewed as unique to it alone and therefore of no value in determining relationships.

A peculiar condition is found in the rostrum of half of the genera of Rhinocryptidae, in which the osseous ridge of the culmen is variously developed into a crest (Figures 5, 6). A distinct crest is present in *Liosceles* and *Myornis*, and is less developed in *Scytalopus*. From skins it would appear that *Merulaxis* also has a slight crest on the bony culmen. In skins of *Eugralla*, this crest is seen to be very well developed and quite flattened, a condition that reaches its extreme in *Acropternis*, in which the crest is very high and excessively broad and flattened (Figure 6). No such crest is present in skeletons of *Melanopareia*, *Scelorchilus*, or *Pteroptochos*, nor does it appear to be present in skins of *Psiloramphus*, *Rhinocrypta*, or *Teledromas*.

The most immediately outstanding feature of the rostrum of *Atrichornis* is the well-developed crest on the culmen, whereas no such structure is present in *Menura*. In the relative slenderness of the bill, size and shape of the nostril, and the development of the crest on the culmen, *Atrichornis* does not stand apart from the Rhinocryptidae in any way, and in these respects could be interpreted as being nearly perfectly intermediate between *Liosceles* and *Myornis* on one hand, and *Eugralla* and *Acropternis* on the other (Figures 5, 6). The crested culmen in *Atrichornis* appears to be shared only with some of the Rhinocryptidae and has not been noted elsewhere in the Passeriformes. *Atrichornis* contrasts with *Menura* and agrees with the Rhinocryptidae in that the interorbital septum is almost completely unossified and the fenestra in the anterior wall of the cranium is large, though not so much as in most rhinocryptids.

It is of interest that while half of the genera of rhinocryptids show similarity to *Atrichornis* in having a crest on the culmen, the morphology of the skull in the remaining genera is actually quite similar to that in *Menura*. The slender, weakly ossified bill and the overall architecture of the skull in *Melanopareia*, for example, is quite like that of *Menura*. Although *Melanopareia* differs from *Menura* in having distinct transpalatine processes, a typical passerine vomer, a broader interorbital bridge, and a fused lacrimal, each of these characters except the last is also found in *Atrichornis*.

In the suboscine superfamily Tyrannoidea, the lacrimal is present, lying along side the ectethmoid and resting upon the quadratojugal arches. In the Furnarioidea, however, the lacrimal appears to be lacking and only a large ectethmoid plate is present. In this case, however, it is difficult to ascertain whether the lacrimal is actually missing, or if it has been entirely incorporated into the ectethmoid plate, leaving no suture in the adult skull. The rhinocryptids show the latter possibility to be likely, as the lacrimal is present and is partly fused to the ectethmoid plate. The condition of the lacrimal in the Rhinocryptidae is thus intermediate between having the lacrimal entirely free and either losing it or incorporating it into the ectethmoid plate. In this respect, rhinocryptids are therefore probably primitive within

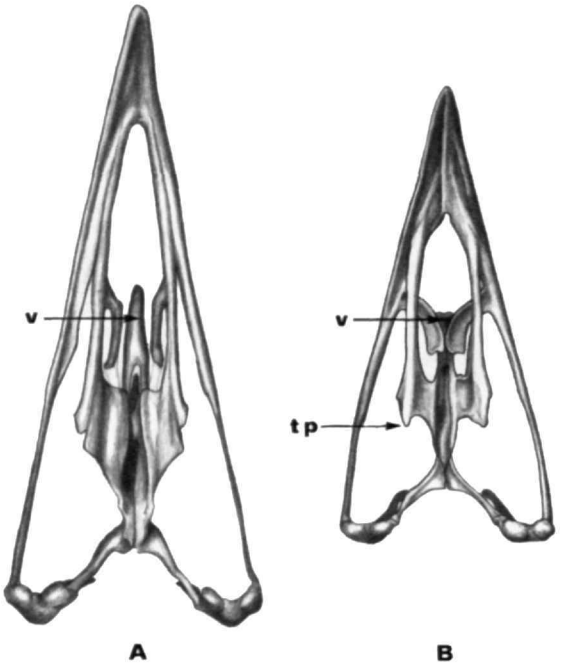


FIGURE 4.—Ventral view of palate: A, *Menura superba* (Menuridae); B, *Chlamydera nuchalis* (Ptilonorhynchidae). The slender rounded vomer (v) of *Menura* is unique among passerines. In this respect and in its lack of transpalatine processes (tp), *Menura* differs even from its closest relative, *Atrichornis*.

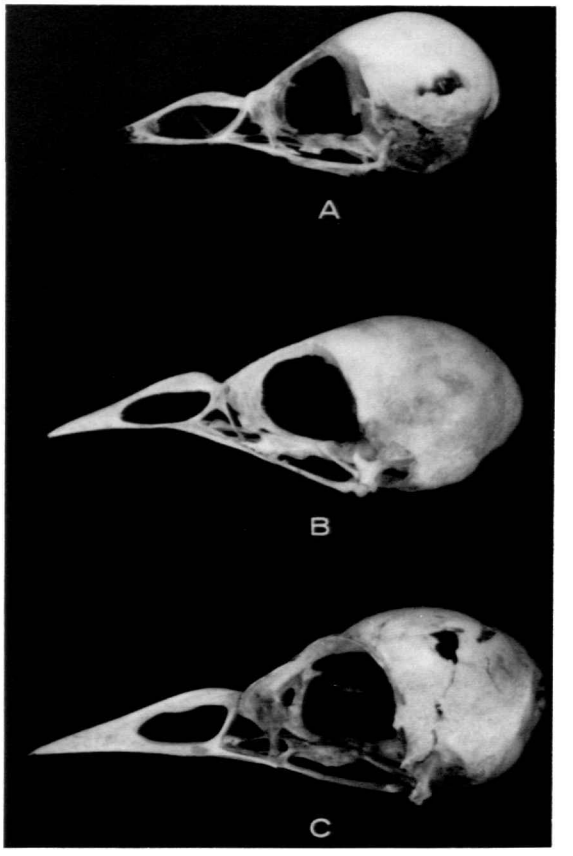


FIGURE 5 (right top).—Lateral view of the skull: A, *Myornis senilis* (Rhinocryptidae); B, *Atrichornis clamosus* (Atrichornithidae); C, *Liosceles thoracicus* (Rhinocryptidae). Note that the unusual condition of the ossified crest on the culmen of *Atrichornis* is intermediate between that of the rhinocryptid genus *Acropternis* (Figure 6) and the two rhinocryptids shown here.

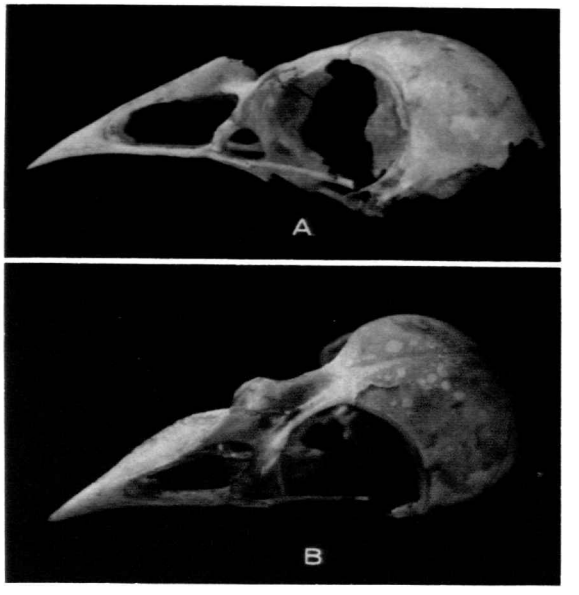


FIGURE 6 (right bottom).—Lateral (A) and dorsolateral (B) views of the skull of *Acropternis orthonyx* (Rhinocryptidae) to show the very high and flattened osseous ridge on the culmen.

the Furnarioidea, inasmuch as the entirely free lacrimal, such as seen in the Menurae, is almost certainly primitive.

In *Menura* the lacrimal is a broad, inflated structure, which although unfused, articulates solidly with the ectethmoid. The lacrimal in *Atrichornis* on the other hand, is small, attenuated, and entirely free, having no osseous connection

with the ectethmoid. It moves with the rostrum during kinesis. In the Rhinocryptidae, the suture that remains between the lacrimal and the ectethmoid in such forms as *Scelorchilus* shows that the original shape of the lacrimal in rhinocryptids was attenuate, as in *Atrichornis*.

In most Rhinocryptidae, the orbital process of the quadrate is longer and more slender than in *Menura* or *Atrichornis*, and the posterior portion of the jugal bar bends dorsally and articulates by more of a socket-like arrangement than in rhinocryptids. *Melanopareia*, however, differs from the typical rhinocryptid condition and resembles the Menurae.

The mandible in *Atrichornis* is a rather weak bone and in lateral view the dorsal edge of the postdentary portion dips ventrally to make that part of the ramus more slender. The same condition is found in the Rhinocryptidae in *Liosceles* and *Myornis*. In most Rhinocryptidae, the internal process of the mandibular articulation is very long and attenuate and lacks a pneumatic foramen. *Melanopareia* differs, however, in having the articulation more robust and truncate and in having a pneumatic foramen in the internal process. *Atrichornis* also has a pneumatic foramen in the internal process, and its mandibular articulation is almost perfectly intermediate in structure between that of *Melanopareia* and the remainder of the Rhinocryptidae.

The skull of *Menura* differs completely from that of *Chlamydera* as follows: (1) anterior end of vomer slender, not broad and truncate; (2) transpalatine processes of palatines lacking; (3) maxillopalatines long and slender, as opposed to short and broad; (4) rostrum very small relative to cranium; (5) cranium very high and domed; (6) nostril elongate, tip of rostrum straight, whereas in *Chlamydera* the nostril is shorter and oval, and the tip of the rostrum is decurved; (7) lacrimal very wide and inflated, as opposed to slender and elongate in *Chlamydera*; (8) orbital process of quadrate shorter; (9) only the lacrimal contacts the jugal bar, whereas in *Chlamydera* both the lacrimal and the ectethmoid contact the jugal.

The mandible of *Menura* differs from that of *Chlamydera* as follows: (1) much weaker and more elongate; (2) symphysis much shorter; (3) mandibular foramen narrower; (4) articulation very different, expanded and much more cup-like.

STERNUM.—The family Rhinocryptidae was long ago characterized by having a four-notched sternum (Figure 7), i.e., "with a lateral and a medial notch on each side," the "type 6" condition of Heimerdinger and Ames (1967:6). The only other passerines that are certainly known to have a four-notched sternum are two genera of grallarine Formicariidae (see Appendix). Heimerdinger and Ames were equivocal as to which sternal type is primitive in passerine birds. However, the sternum is four-notched in almost all non-passerine land birds that might be closely related to the Passeriformes, e.g., Coliiformes, Piciformes, and most Coraciiformes (including the Galbulae, see Olson, in press), and the early Eocene family Primobucconidae. This condition is almost certainly primitive in passerines.

Atrichornis clamosus has a two-notched sternum (Figure 7). Sclater (1874) stated that the sternum in *A. rufescens* was four-notched. The specimen in the Cambridge University Museum of Zoology upon which he based this statement has apparently been lost, an unfortunate occurrence because Garrod (1876) illustrates a two-notched sternum for *A. rufescens* and A. R. McEvey (in litt. to Olson, 1981) indicates that more recently taken specimens also have a two-notched sternum. Both two-notched and four-notched sterna occur in different species of the formicariid genus *Grallaria* (see Appendix) and it is not impossible that this character could vary individually within species of *Atrichornis*.

If we disregard the number of notches, the sternum in *Atrichornis* is otherwise quite similar to that in the Rhinocryptidae in that the notches are very deep and the sternocoracoidal processes are very long, attenuate, and anteriorly directed (Figure 7). The sternum in *Menura* is highly modified and is different from that in any other passerines (Huxley, 1867:472; Heimerdinger and Ames, 1967). Thus it is not indicative of relationships. Notwithstanding the great differences be-

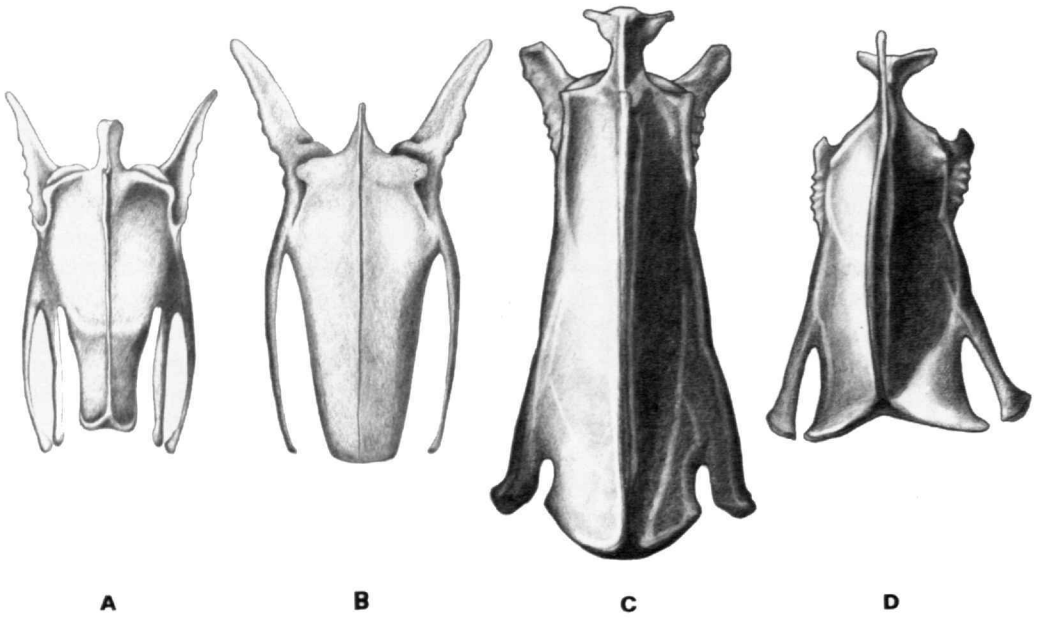
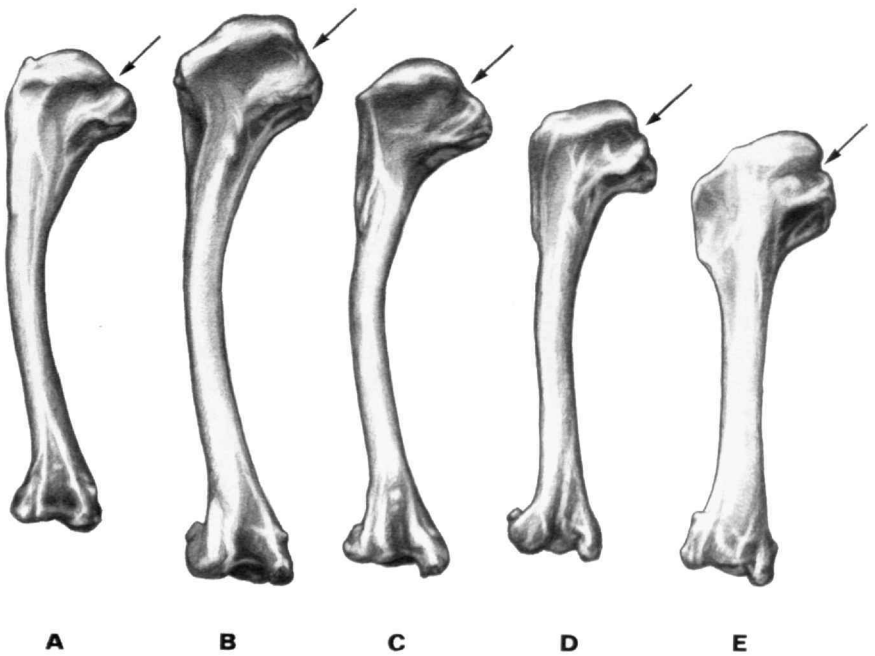


FIGURE 7.—Ventral view of sterna: A, *Pteroptochos megapodius* (Rhinocryptidae); B, *Atrichornis clamosus*, (Atrichornithidae); C, *Menura superba* (Menuridae); D, *Chlamydera nuchalis* (Ptilonorhynchidae). The four-notched sternum is known to occur in passerines only in the Rhinocryptidae and a few species of Formicariidae. Apart from the number of notches, the rhinocryptid sternum is very similar to that of *Atrichornis*, whereas the sternum of *Menura* is unique. None of these birds resembles the typical oscines, such as *Chlamydera*, in sternal morphology.

tween the sterna of *Menura* and *Atrichornis*, the sternal structure in the Menurae is still utterly different from that in *Chlamydera* (Ptilonorhynchidae), which is representative of the typical passerine condition (Figure 7).

CLAVICLES.—Virtually all passerines have a typical U-shaped furcula formed by the fused clavicles. We found, however, that the clavicles were unfused and reduced to nearly three-fourths of their expected length in *Myornis senilis* and in all of the species of *Scytalopus* we examined. The reduced clavicles articulate proximally with the coracoid and scapula to form a triosseal canal, but terminate distally as a weak spine. All other rhinocryptids examined have a typical furcula. Although reduced clavicles occur in various nonpasserine groups (e.g., Ramphastidae, Psittacidae, and Mesoenatidae), the only other passerine known to have unfused clavicles is *Atrichornis*. Raikow (Ms) found that in *A. clamosus* the clavicles were unfused and greatly reduced, only the head and a short portion of the shaft remaining. This confirms Garrod's (1876) similar observation for *A. rufescens*. Although the condition of the clavicles in *Atrichornis* and two genera of Rhinocryptidae is unquestionably a shared derived character, this could have arisen independently in the two groups, as the condition is a degenerative one. Nevertheless, such a condition has never been expressed elsewhere in the Passeriformes.

HUMERUS.—The humerus of rhinocryptids is practically unique among passerine birds, otherwise being similar only to *Atrichornis* and a few species of the grallarine formicariids. The most distinctive feature of the rhinocryptid humerus is the slender, curved shaft, as opposed to the stouter, straight shaft of typical passerines (Figure 8).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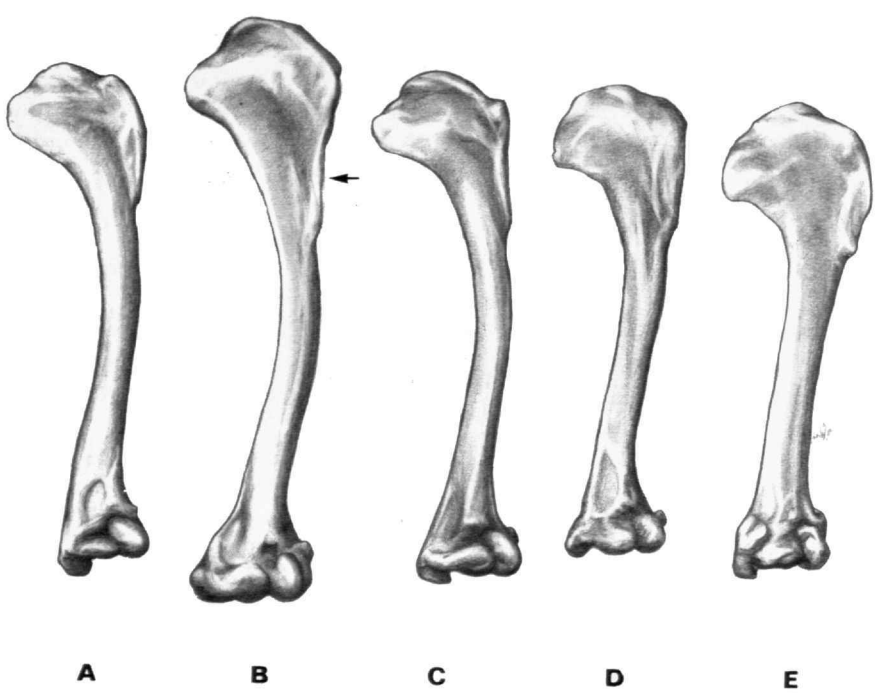
A
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The proximal end of the humerus in rhinocryptids is also distinctive in having a reduced, curved deltoid crest that is distinctly incised when viewed in palmar aspect (Figure 9). In typical passerines a broad, straight deltoid crest runs parallel to the shaft and shows no incision. In rhinocryptids, unlike typical passerines, the capital groove is very wide and deep and the head is correspondingly reduced and is slanted distally towards the curving deltoid crest. In typical passerines the head is a broad structure that forms almost a right angle with respect to the shaft. As in all suboscines, there is a single pneumatic tricipital fossa in rhinocryptids. The distal end of the humerus is more typically passerine, except the entepicondyle is somewhat less developed. The humerus of *Atrichornis*, though somewhat degenerate, has a curved shaft and is quite similar to that of rhinocryptids.

The typical passerine humerus is quite distinctive and is virtually diagnostic for the order, whereas the rhinocryptid humerus in some respects is more similar to that in such non-passerines as certain Coraciiformes (Figures 8, 9), including the Galbulae (Olson, in press) and the Eocene Primobucconidae (Feduccia and Martin, 1976).

The humerus of *Menura* differs from that of *Chlamydera* (Figure 10) as follows: (1) much smaller relative to overall body size; (2) ectepicondylar process reduced, less spur-like; (3) capital groove much wider; (4) internal tuberosity and capital groove oriented almost parallel to shaft, whereas these features are almost perpendicular to the shaft in *Chlamydera*; (5) internal tuberosity much deeper; (6) head not as bulbous, more elongate and angled relative to the shaft; (7) deltoid crest reduced.

RADIUS AND ULNA.—The radius and ulna of *Menura* differ radically from those of *Chlamydera*, particularly in being much shorter relative to body size, as these elements in *Menura* are only a few millimeters longer than in *Chlamydera*, which is a much smaller bird. Other differences were noted as follows: ulna in *Menura* (1) much stouter; (2) olecranon heavier, not as pointed; (3) papillae for attachment of secondaries fewer but very much more prominent, projecting as distinct, heavy knobs rather than barely visible as in *Chlamydera*; radius in *Menura* (4) excavated proximally, with a bladelike projection from the shaft.

CARPOMETACARPUS.—The rhinocryptid carpometacarpus (Figure 11) is relatively short and stout, with a broad intermetacarpal tubercle and an exceptionally large carpometacarpal process, a protuberance present at approximately the midpoint of the outer edge of the major metacarpal and that shows considerable variation in passerines (Pocock, 1966; Harrison, 1968). The carpometacarpus in *Menura* is quite similar to that in the Rhinocryptidae, as is that of *Atrichornis*, in which, however, the carpometacarpus is somewhat degenerate. The morphology of the carpometacarpus in the Menurae is very different from that in *Chlamydera* (Figure 11), which exhibits the more typical oscine condition.

The carpometacarpus of *Menura* differs from that of *Chlamydera* as follows: (1) much stouter and deeper; (2) carpometacarpal process on major metacarpal well developed, as opposed to almost lacking in *Chlamydera*; (3) intermetacarpal tubercle more robust; (4) external portion of carpal trochlea more rounded, not pointed as in *Chlamydera*; (5) internal side of distal symphysis not deeply excavated as in *Chlamydera*.

PELVIS.—The pelvis in *Menura*, *Atrichornis*, and the Rhinocryptidae (Figure 12) shows evidence of heavy muscularization and is characterized by a very deep ischium and relatively short, rounded

FIGURE 8 (facing page, top).—Left humeri in anconal view: A, *Brachypteracias leptosomus* (Brachypteraciidae, Coraciiformes); B, *Pteroptochos tarnii* (Rhinocryptidae); C, *Grallaria quitensis* (Formicariidae); D, *Grallaria perspicillata* (Formicariidae); E, *Tityra inquisitor* (Cotingidae). The slender curved shaft and broad capital groove (arrows) in the Rhinocryptidae are more like some non-passerines (e.g., *Brachypteracias*) than typical passerines (e.g., *Tityra*). The differences are nearly bridged within the genus *Grallaria* (see Appendix).

FIGURE 9 (facing page, bottom).—Left humeri in palmar view: A, *Brachypteracias leptosomus;* B, *Pteroptochos tarnii;* C, *Grallaria quitensis;* D, *G. perspicillata;* E, *Tityra inquisitor.* See legend for Figure 8. Also note the uniquely indented deltoid crest (arrow) in the Rhinocryptidae (*Pteroptochos*) and the lesser indication of this condition in *Grallaria.*

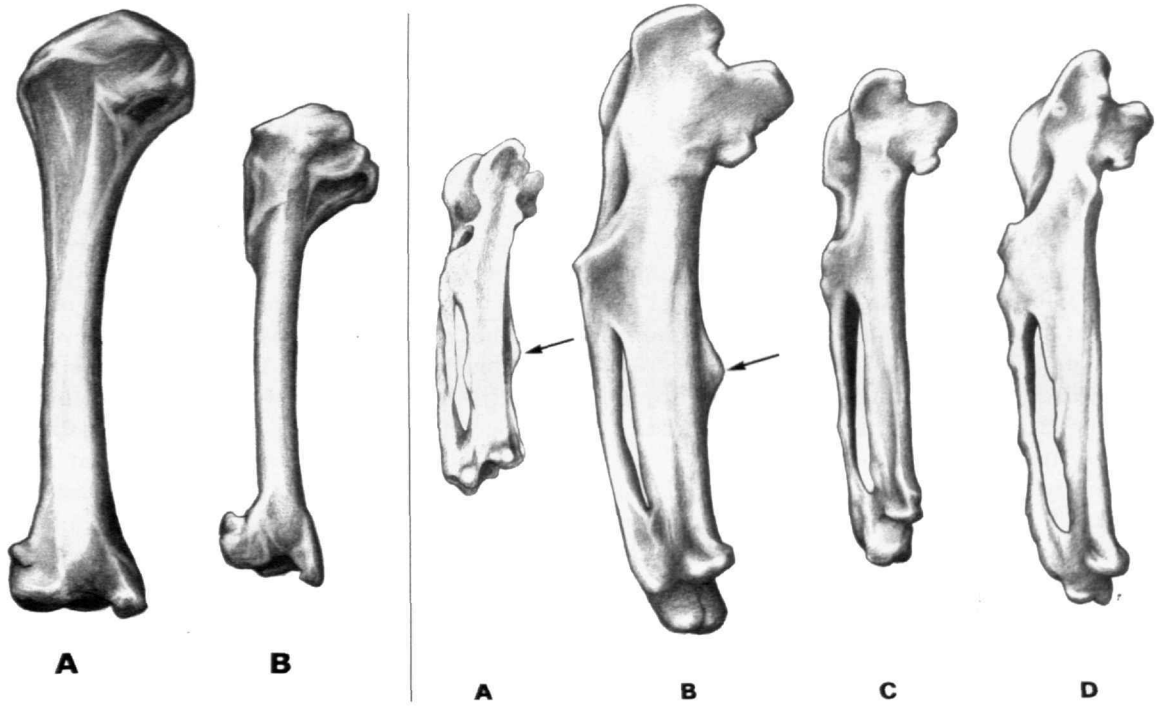

FIGURE 10 (above, left).—Left humeri in anconal view: A, *Menura superba* (Menuridae); B, *Chlamydera nuchalis* (Ptilonorhynchidae). This demonstrates but one of many ways in which *Menura* differs from bowerbirds and allies.

FIGURE 11 (above, right).—Right carpometacarpi in external view; A, *Scelorchilus albicollis* (Rhinocryptidae); B, *Menura superba* (Menuridae); C, *Chlamydera nuchalis* (Ptilonorhynchidae); D, *Rupicola peruviana* (Cotingidae). The overall configuration and enlarged metacarpal process (arrows) are similar in rhinocryptids and *Menura*, but neither bears any close resemblance to bowerbirds or even to most other suboscines.

anterior iliac shields. The pelvis of *Atrichornis* is virtually indistinguishable from that of *Rhinocrypta* except that the most posterior part of the ilium overhangs farther, although this condition is found in other rhinocryptids (e.g., *Scelorchilus*).

The pelvis of *Menura* differs markedly from that of *Chlamydera* in most aspects of its morphology (Figure 12): (1) relative width greater; (2) anterior iliac shield relatively shorter and much deeper and rounded; (3) anterior tip of ilium with a broad lateral flange that is absent in *Chlamydera*; (4) iliac crests much more pronounced, extending posteriorly as a marked projection; (5) ischium very much deeper; (6) obturator foramen much larger; (7) ischio-pubic fenestra shorter and wider; (8) antitrochanter much larger; (9) pectineal process small but present (absent in *Chlamydera*); (10) space between antitrochanter and iliac crest much greater.

FEMUR.—The rhinocryptid femur is distinctive in having a strongly developed lateral trochanteric ridge on the proximal end of the shaft that may extend down the shaft as much as a fourth or more of the total length of the bone. The same is true of the femur of *Menura* (Figure 13), in which there is an extremely pronounced lateral

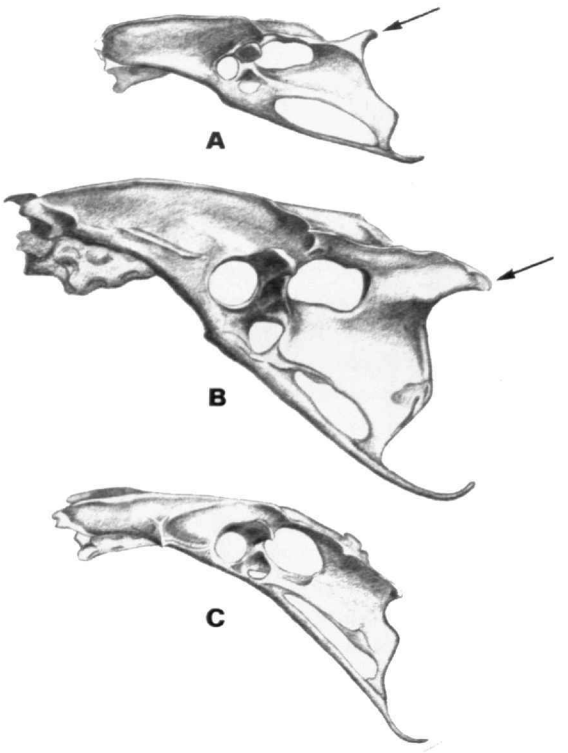

FIGURE 12.—Pelves in left lateral view: A, *Pteroptochos megapodius* (Rhinocryptidae); B, *Menura superba* (Menuridae); C, *Chlamydera nuchalis* (Ptilonorhynchidae). The configuration of the pelvis in *Menura*, particularly in the broad, deep ischium and great posterior projection of the iliac crests (arrows), is very similar to that in the Rhinocryptidae and bears no resemblance to that of bowerbirds.

trochanteric ridge extending over a quarter of the length of the shaft. The femur in *Atrichornis* is less robust and less compressed anteroposteriorly than in *Menura*.

The femur of *Menura* differs from that of *Chlamydera* as follows: (1) proportionately shorter and stouter; (2) lateral trochanteric ridge much better developed; (3) lateral surface broader and flattened posteriorly; (4) fibular groove much deeper; (5) internal condyle projecting much farther proximally; (6) neck shorter; (7) trochanter much deeper in proximal view.

TIBIOTARSUS.—The rhinocryptid tibiotarsus is characterized by having the proximal end offset medially from the midline of the shaft, thus causing the region of the shaft between the proximal end of the fibular crest and the outer cnemial crest to be deeply indented (Figure 14). On the medial side of the proximal end of the shaft, a very distinctive ridge runs from approximately the level of the middle of the fibular crest to a point just distal to the region of the cnemial crests. In some species, this ridge is less extensive, beginning at the level of the proximal end of the fibular crest, and exhibits a very well-defined ligamental attachment proximally. In typical passerines, no indentation occurs on the lateral portion of the shaft and no ridge exists on the medial face, where there is only a trace of a ligamental attachment proximally on the shaft of the tibiotarsus. The distal end of the tibiotarsus is also distinctive in rhinocryptids (Figure 15) in having a very deep excavation between the posterior borders of the external and internal condyles; in this intercondylar space is a particularly well defined ridge.

The tibiotarsus in *Menura* presents, in exaggerated fashion, the distinctive characters of that element in the Rhinocryptidae, with the proximal

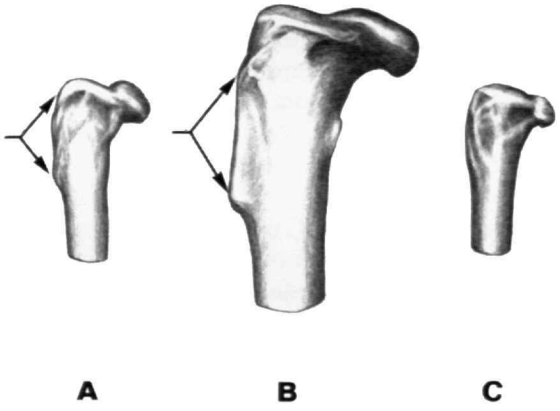

FIGURE 13.—Proximal end of left femur in posterior view: A, *Pteroptochos megapodius* (Rhinocryptidae); B, *Menura superba* (Menuridae); C, *Chlamydera nuchalis* (Ptilonorhynchidae). Note the similarity in the development of the large lateral trochanteric ridge (arrows) in rhinocryptids and *Menura*, whereas this is absent in bowerbirds and other passerines examined.

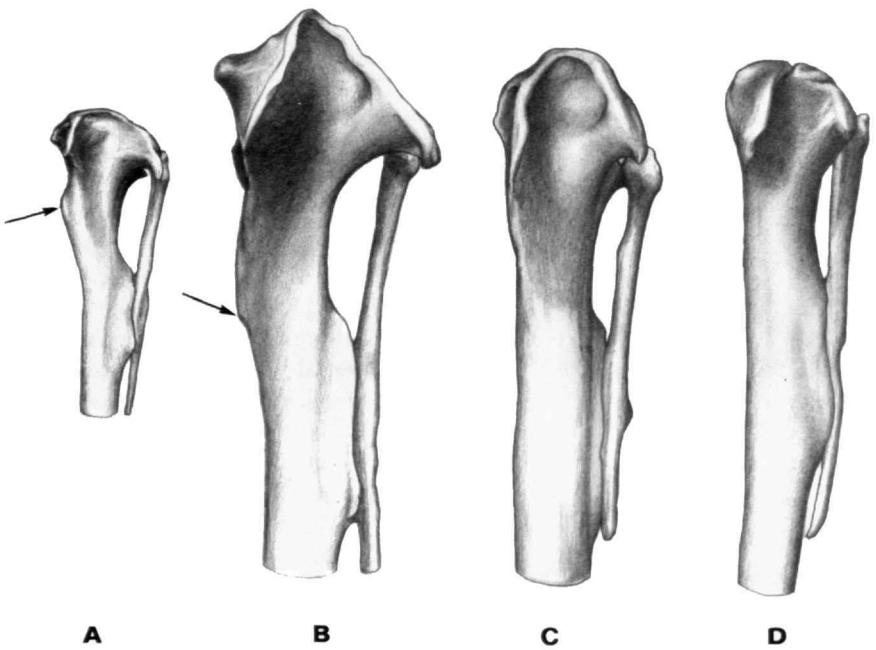

FIGURE 14.—Anterior view of proximal end of left tibiotarsi and fibulae: A, *Scelorchilus albicollis* (Rhinocryptidae); B, *Menura superba* (Menuridae); C, *Chlamydera nuchalis* (Ptilonorhynchidae); D, *Rupicola peruviana* (Cotingidae). Note the marked medial deflection of the proximal end, and the enlarged medial crest (arrows) of the Rhinocryptidae and *Menura*, whereas these taxa differ utterly from bowerbirds and most other passerines, in which the shaft is typically straight and lacks a medial crest.

end markedly offset and the medial ridge very well developed (Figure 14). The distal condyles are very pronounced posteriorly, as is the ridge between them (Figure 15). The proximal end of the tibiotarsus in *Atrichornis* is less offset than in *Menura* or most rhinocryptids, but is still much more offset than in most passerines. The medial proximal crest is less developed than in most rhinocryptids except *Melanopareia*.

The tibiotarsus of *Menura* differs from that of *Chlamydera* as follows: (1) proximal end offset from line of shaft; (2) well developed bladelike crest on internal side of proximal end of shaft present (absent in *Chlamydera*); (3) internal and external cnemial crests much larger and of a different shape; (4) tendinal bridge deeper; (5) intercondylar groove much wider; (6) posterior margins of condyles much more expanded posteriorly; (7) distinct raised ridge between posterior margins of condyles.

TARSOMETATARSUS.—The typical passerine tarsometatarsus (e.g., *Chlamydera*) is peculiar in having the inner and outer trochleae extremely nar-

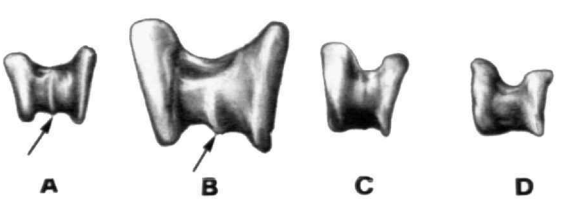

FIGURE 15.—Left tibiotarsi in distal view: A, *Pteroptochos megapodius* (Rhinocryptidae); B, *Menura superba* (Menuridae); C, *Chlamydera nuchalis* (Ptilonorhynchidae); D, *Rupicola peruviana* (Cotingidae). In the broad anterior intercondylar fossa, the greater posterior projection of the condyles, and the posterior ridge between the condyles (arrows), the rhinocryptids are similar to *Menura* and both differ completely from bowerbirds and most other passerines.

row and ungrooved, whereas the middle trochlea is somewhat broader and is slightly grooved. The Rhinocryptidae and Menurae differ completely from this configuration in having the inner and outer trochleae very broad and distinctly grooved (Figure 16).

In *Atrichornis* the two most posterior hypotarsal canals are not ossified and there is hardly a sign of tendinal grooves. This is unlike *Menura* and virtually all other passerines examined, in which most of the flexor tendons are completely enclosed by bony canals. Interestingly, however, the rhinocryptid genera *Pteroptochos, Scelorchilus,* and *Myornis* present a nearly perfectly intermediate condition between that in *Atrichornis* and that in other passerines.

The tarsometatarsus of *Menura* differs from that of *Chlamydera* as follows: (1) attachment for tibialis anticus longer and situated more towards the midline of the shaft; (2) scar for hallux deeper; (3) distal foramen situated more proximally; (4) inner and outer trochleae much wider and grooved, not relatively simple flanges as in *Chlamydera.*

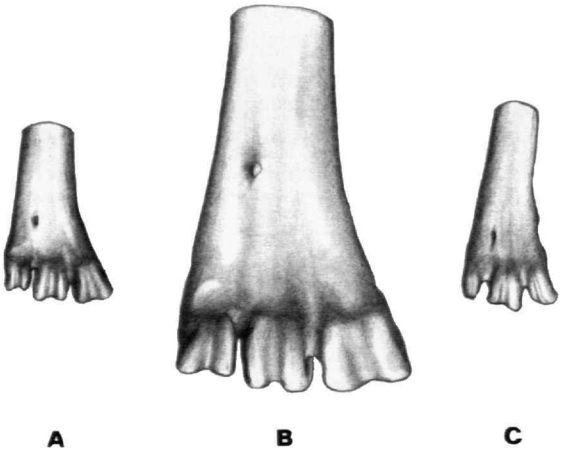

FIGURE 16.—Distal end of right tarsometatarsi in anterior view: A, *Pteroptochos megapodius* (Rhinocryptidae); B, *Menura superba* (Menuridae); C, *Chlamydera nuchalis* (Ptilonorhynchidae). In the broad, grooved inner and outer trochleae, rhinocryptids and *Menura* differ from the derived condition in bowerbirds and all other passerines examined (except *Atrichornis* and certain formicariids) in which the inner and outer trochleae are narrow, ungrooved flanges.

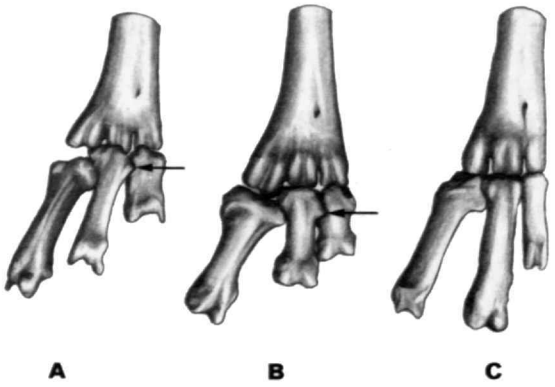

FIGURE 17.—Distal end of left tarsometatarsi and basal phalanges in anterior view: A, *Pteroptochos megapodius* (Rhinocryptidae); B, *Menura superba* (Menuridae); C, *Chlamydera nuchalis* (Ptilonorhynchidae). The distinctive interlocking notch and protuberance (arrows) of the basal phalanges of the outer and middle toes sets the Rhinocryptidae and Menurae apart from bowerbirds and most other passerines. Note also that the proportions of the toes in *Menura* are very different from those of *Chlamydera* but are more similar to those of *Pteroptochos.*

TOES.—In the Rhinocryptidae, the proximomedial corner of the basal phalanx of digit IV is distinctly notched to accomodate a knob protruding from the proximo-lateral corner of the basal phalanx of digit III. This condition is also present in *Menura* (Figure 17) and *Atrichornis.* In typical passerines, the basal phalanges of digits III and IV are narrower and devoid of this interlocking arrangement.

The toes of *Menura* differ from those of *Chlamydera* as follows: (1) interlocking notch and protuberance of basal phalanges of digits III and IV present (absent in *Chlamydera*); (2) most phalanges shorter and much wider and more robust; (3) phalanx 4 of digit IV proportionately much longer; (4) ungual phalanges long and straight, not short and curved as in *Chlamydera*; (5) proximal articulation of phalanx 1 of hallux completely different, being deeper and of a totally different shape; (6) shaft of phalanx 1 of hallux not greatly flattened and curved as in *Chlamydera.*

Discussion

Our study and that of Raikow (1978; Ms.) shows that the osteology and appendicular myology of the Menurae are utterly different from that of the oscine bird-of-paradise/bowerbird assemblage. Sibley's (1974:68) statement that the skeletons of *Menura* and the ptilonorhynchid genus *Chlamydera* are "virtually identical" is completely controverted by our observations. The osteology of these two birds is actually extraordinarily divergent, especially in light of the relative osteological homogeneity of the vast majority of Passeriformes.

In the configuration of the basal pedal phalanges, tarsometatarsal trochleae, proximal and distal ends of the tibiotarsus, proximal end of the femur, humerus, carpometacarpus, and pelvis, the Menurae are much more similar to the Rhinocryptidae than to any other passerine group. Most of the characters shared by these two groups are not found elsewhere in the Passeriformes. Whereas the sternum of *Menura* is unique, that of *Atrichornis*, apart from the number of notches, is more similar to that of the Rhinocryptidae than to typical passerines. Both the Menurae and Rhinocryptidae have an enlarged nasal operculum, a feature not found in the bowerbird assemblage, although we have not attempted to determine its distribution elsewhere in the order. Other characters found only in one or the other of the two genera of Menurae are shared only with certain sections of the Rhinocryptidae. Thus, the peculiar crest on the culmen of *Atrichornis* is found only in six of the 12 genera of Rhinocryptidae. The lack of ossification of the hypotarsal canals in *Atrichornis* is approached only in three genera of rhinocryptids, and the lack of fusion of the clavicles in *Atrichornis* occurs elsewhere in passerines only in two genera of rhinocryptids. The long, straight claws characteristic of *Menura* are found in several of the rhinocryptids but are most similar to those in *Pteroptochos*, whereas the overall similarity of the skull of *Menura* is most like that of *Melanopareia*. The genus *Melanopareia* differs from other rhinocryptids and more closely resembles the Menurae in features of the quadrate and mandible and, of course, in possessing the primitive stapes.

In our present state of knowledge, we feel that it is very difficult in most instances to place these characters in a primitive-derived sequence. If one were to invoke the often-used criterion of limited taxonomic distribution, most of the characters shared by the Menurae and Rhinocryptidae would have to be regarded as derived. Yet in some cases, this would almost certainly seem to be erroneous. For example, the overall configuration of the tarsometatarsus in the Menurae and Rhinocryptidae is not found in any other group of birds, yet the broad, relatively unmodified condition of the tarsal trochleae appears likely to be primitive within passerines. The four-notched sternum of rhinocryptids is clearly primitive, arguing for a "basal" position for the group, at least within the Furnarioidea, if not within Passeriformes as a whole.

Mayr (1976:466) reminds us that similarity "is an important index of the amount of shared genotype" and that "the retention of a large number of ancestral characters is just as important an indicator of 'relationship' (traditionally defined) as the joint acquisition of a few 'derived' characters." In overall osteological similarity, the Menurae more closely resemble the Rhinocryptidae than any other family of passerines examined. In the complex mosaic of similarities shared between various members of these two groups are characters that are very likely to be uniquely derived. However, on the basis of syringeal morphology, the species of Rhinocryptidae belong in the superfamily Furnarioidea, within which they are clearly the most primitive members. The syrinx in the Menurae on the other hand, is like that of the oscines, but more primitive. Thus the Menurae and the Rhinocryptidae appear to be close to the base of two of the major radiations of passerines. The overall similarity of these birds to each other can be interpreted as their having diverged less from the original ancestral passerine stock than have any other Passeriformes, with the possible exception of the Acanthisittidae. In this

sense, they may be considered "related," at least genotypically, if not in the strict redefinition of monophyly advocated by cladists.

It would be premature at this point to propose a phylogeny or any suggestions for classification, other than disallowing any association between the Menurae and the bowerbird assemblage. Our discoveries have otherwise raised more questions than they have answered. We have seen that the derived suboscine stapes may have arisen within the Rhinocryptidae, as presently defined, yet the rhinocryptids are part of the furnarioid assemblage defined by a derived condition of the syrinx. Where then, did the suboscine superfamily Tyrannoidea come from? Although the Tyrannoidea also have a derived stapes, some of the taxa have what appears to be a primitive syrinx. What are the patterns of interrelationships within the Rhinocryptidae? It is possible that *Atrichornis* and the rhinocryptids with ridged culmens form a monophyletic group within which the derived stapes originated? If so, where does this leave *Melanopareia*, which has a primitive stapes, and what might its relationships be with *Menura*? Are there other passerines in Australasia that are masquerading as oscines but that do not have an oscine grade of syrinx and that might transcend the differences between the Menurae and the typical oscines? And finally, what is the origin of the entire order Passeriformes? To which non-passerine group are the passerines most closely related? We believe that a full understanding of these and other questions will have to involve much more detailed knowledge of at least the Rhinocryptidae, the Menurae, and probably the Acanthisittidae. If the present study should channel the investigations of other researchers into this potentially fruitful area, we would consider it a success.

A relationship (in Mayr's sense) between the Menurae and Rhinocryptidae has interesting zoogeographical implications. Both of these groups have poor dispersal ability and if they are indeed the most primitive members of the oscine and furnarioid radiations, respectively, their origins are probably of considerable antiquity. Thus these birds could well be interpreted as remnants of a group that originally dispersed through the Southern Hemisphere, in accordance with what is now known of plate tectonics and continental drift. In most instances it is not possible to determine whether two such groups originated in the Southern Hemisphere or are remnants of a group whose distribution formerly extended through the Northern Hemisphere as well. In this case, however, there is considerable evidence against the latter hypothesis. There is no verifiable fossil record of the Passeriformes anywhere in the world before the Miocene (Olson and Feduccia, 1979), and in the Northern Hemisphere, where the most paleontological work has been done and the fossil record is much more complete, this fact assumes some significance. At least in North America and Europe there was a radiation of various groups of non-passerine land birds (mostly Coraciiformes, including the Galbulae) in the early Tertiary that presumably occupied some of the niches that passerines were later to assume (Feduccia and Martin, 1976; Olson, 1976; Feduccia, 1977; Olson and Feduccia, 1979). Furthermore, it is obvious from the great radiation of suboscines in South America, that passerines had to have been present there through much or all of the period of isolation of that continent during the Tertiary.

We would argue not only that the suboscines arose in the Southern Hemisphere, but that the entire order Passeriformes is of southern origin. It would appear that there is no reason to regard the order Passeriformes as being younger than most other extant orders of birds. In fact, if the Acanthisittidae should prove to be as primitive among the passerines as the Menurae and Rhinocryptidae, then it is conceivable that these weak-flying birds may have been isolated in New Zealand for a period as long as the rhychocephalian *Sphaenodon* or the primitive frogs of the genus *Leiopelma*.

It is interesting to observe that the groups we have identified as probably being the most primitive passerines are largely terrestrial birds. The Menurae are almost exclusively so. The majority of Rhinocryptidae are highly adapted for a ter-

restrial existence, as are the most primitive members of the Formicariidae (see Appendix). All but one of the species of Acanthisittidae are (or were) terrestrial. Within the Tyrannoidea, the Pittidae are exclusively terrestrial, with a body form much like that of the grallarine formicariids. One of the two genera of the Madagascan family Philepittidae is similarly adapted. The relationships of these last two families to other members of the Tyrannoidea are uncertain, but both have primitive syringes (Ames, 1971). This raises the interesting possibility that the original passerine adaptations were for life on the ground, and that this order as a whole, the epitome of "perching" birds, is only secondarily adapted for an arboreal existence.

Appendix

The Rhinocryptid-Formicariid Transition and Sequence of Families in the Furnarioidea

Ames (1971), on the basis of syringeal structure, identified certain members of the Formicariidae as being intermediate between the remaining genera of that family and the Rhinocryptidae. He was able to make a clear division of the Formicariidae into two groups: the "typical antbirds," distinguished as having one pair of intrinsic syringeal muscles, a very small processus, and M. sternotrachealis bifurcated near its insertion; and the "ground antbirds," characterized by the absence of intrinsic syringeal muscles, a large processus, and a simple sternotrachealis. To the latter group (page 154)

> belong *Grallaria*, *Chamaeza*, *Formicarius* and *Conopophaga*. Long-legged terrestrial birds, they appear to be intermediate between the Formicariidae and Rhinocryptidae. Such intermediacy is suggested by the presence of a four-notch [sic] metasternum, classically a rhinocryptid character, in some species of *Grallaria* and in *Pittasoma*.

As further evidence of their aberrant nature within the Formicariidae, *Grallaria*, *Formicarius*, *Chamaeza*, and *Conopophaga* were also found to differ in their pterylosis from other members of the family, as well as from each other, except that *Conopophaga* resembles *Grallaria* (Ames et al., 1968).

We found additional osteological characters within the "ground antbirds," or grallarine formicariids, that confirm them as bridging some of the differences with the rhinocryptids. We can confirm and somewhat expand the observation of Heimerdinger and Ames (1967) that the four-notched sternum occurs in the Formicariidae only in *Pittasoma michleri* and in three species of *Grallaria* (*G. fulviventris*, *G. perspicillata*, and *G. ochroleuca*) but not in the other species of *Grallaria* thus far examined (Table 1).

Within the Formicariidae, a rhinocryptid-like humerus is found only in *Grallaria quitensis*, *G. fulviventris*, *G. flavotincta*, and *G. erythroleuca*, among the species we examined (Table 1). In the other formicariids, the humerus was typically passerine, except in *Grallaria ruficapilla*, *Conopophaga aurita*, and *C. lineata*, which are intermediate. The rhinocryptid-like condition of the trochleae and basal phalanges, or some modification thereof, occurs variably within several genera in the grallarine sections of the Formicariidae (Table 1).

A distinctive, though variable, feature of the rhinocryptids is the lack of ossification of the orbital septum and the anterior wall of the braincase, which reaches its extreme in *Pteroptochos*. Possibly correlated with this condition is the weakly ossified lateral parietal region in certain genera. Of available species, poorly ossified parietals are found in *Pteroptochos megapodius*, *P. tarnii*, *Scytalopus magellanicus*, *S. unicolor*, *S. argentifrons*, *Scelorchilus rubecula*, *S. albicollis*, and *Liosceles thoracicus*. The condition is somewhat intermediate in *Myornis senilis* and absent in *Rhinocrypta lanceolata* and *Melanopareia elegans*. In certain species of *Grallaria* (e.g., *G. quitensis*), the ossification in the orbital region is intermediate between the rhinocryptid and the typical passerine condition.

Ames (1971) has shown on the basis of the syrinx that the Furnarioidea constitutes a monophyletic group. Within this group, the four-notched sternum, retention of the primitive stapes in *Melanopareia*, and possibly the broad tarsal trochleae identify the Rhinocryptidae as the most primitive family. The sequence of families within the superfamily Furnarioidea in general use today is that of Wetmore (beginning with Wetmore, 1930), who gave no reasons for listing the families

TABLE 1.—Summary of rhinocryptid-like characters found in grallarine members of the Formicariidae (+ = present; − = absent; ? = element not present in specimens available to us)

Species	4-notched sternum	Curved humerus	Broad, grooved tarsal trochleae	Notched basal phalanges
Grallaria fulviventris	+	+	+	−
G. perspicillata	+	−	+	+
G. quitensis	−	+	+	+
G. erythroleuca	−[a]	+	+	+
G. flavotincta	−	+	+	+
G. hypoleuca	−	?	?	?
G. ruficapilla	−	+[b]	+	+
G. macularia	−	−	+	+[d]
G. guatimalensis	−	?	?	?
G. haplonota	−	?	?	?
Pittasoma michleri	+	−	+	+[d]
Chamaeza campanisoma	−	−	+	+
Formicarius analis	−	−	+	+
Conopophaga aurita	−	+[b]	−[c]	−
C. lineata	−	+[b]	+[c]	−
Grallaricula nana	−	−	−	+[c]

[a] Small fenestra. [b] Intermediate. [c] Slight. [d] Less.

as Dendrocolaptidae—Furnariidae—Formicariidae—Conopophagidae—Rhinocryptidae. This sequence actually begins with the most highly specialized and proceeds to the most primitive members of the superfamily. It is the reverse of that employed by such authors as Ridgway (1911), Cory and Hellmayr (1924), and Mayr and Amadon (1951), viz. Rhinocryptidae—Conopophagidae—Formicariidae—Furnariidae—Dendrocolaptidae. Any sequence that reflects the phylogeny of the Furnarioidea should begin with the Rhinocryptidae. Because certain genera of formicariids share characters with the rhinocryptids, the Formicariidae should come next in the sequence, to be followed by the remaining family, the Furnariidae, in which we include the Dendrocolaptidae, which are clearly of specialized furnariid derivation (Feduccia, 1973). We follow Ames et al. (1968) in dismembering and dispersing the two genera of Conopophagidae and confirm the placement of *Conopophaga* with the grallarine formicariids. We further suggest that any sequential listing of the Formicariidae should begin with the genus *Grallaria*, which exhibits the most characters in common with the Rhinocryptidae, followed by some sequence of the following genera: *Pittasoma*, *Chamaeza*, *Grallaricula*, *Formicarius*, and *Conopophaga*, and then the remainder of the family.

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