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

ALAN FEDUCCIA
and
STORRS L. OLSON

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

Alan Feduccia
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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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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 subosine 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 subosine. Since 1926 (Wetmore, 1926), it has been placed in the Rhinocryptidae, which family Ames (1971) has shown to belong in the subosine superfamily Furnarioidea, along with the Formi-
cariiidae, 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. argentifer (partial skeleton), S. magellanicus (skeleton and alcoholic), S. argentinensis (partial skeleton), S. panamensis (alcoholic), S. latibranci (alcoholic), S. femoralis (alcoholic), Acrpyteryx orthonyx (partial skeleton), and a variety of skeletons of Formicariidae, including Grallaria (three species), Grallariella nana, Pittasoma messleri, 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. erythroloenca (John P. O’Neill, Louisiana State University Museum of Zoology), Scelorchilus albicolli (Ned K. Johnson, University of California Museum of Vertebrate Zoology), Grallaria fulviventris (Wesley E. Lanyon, American Museum of Natural History), and Grallaria flavoveincta, 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 *Rhino-
mya*, 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 *Rhinocyr-
pta*, 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 Tracheo-
phonine 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 *Melan-
opareia* and *Psiloramphus* were ascertained (Wet-
more, 1926; Plotnick, 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 Fur-
Narioidea constitute a monophyletic group.

The two species of lyrebirds (Menuridae: *Men-
ura superba*, *M. alberti*) and the two species of scrub-
birds (Atrichornithidae: *Atrichornis clamosus*, *A. ru-
fescens*) are endemic to Australia and have tradition-
ally been set apart from other passerines. An
isolated position for them was advocated by Gar-
rod (1876) on the basis of syringal morphology,
and it was he who first placed *Menura* and *Atri-
chornis* 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 bowerybird/bird-of-
paradise assemblage (Ptilonorhynchidae and Para-
disaeidae). He concluded (Sibley, 1974:65) that
the suborder Menurae should be dropped from the clas-
sification and that the families Menuridae and Atrichornithi-
daes should be placed near the Ptilonorhynchidae and Para-
disaeidae.

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

Apart from the data from egg white proteins,
Sibley’s arguments for the placement of the Men-
urae revolved around explaining away the sin-
gular morphology of their syrinx. As mentioned,
the syrinx of *Menura* was first described by Gar-
rod (1876:514–516), who concluded that it was “ac-
romyodian,” although not typically oscine. Gar-
rod (1876:516) also described the syrinx of *Atri-
chornis* 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 muscu-
larure 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 charac-
ters in separating the Menurae from the Passeres .... No
single group of oscines can be considered syringeally primi-
tive, in the sense that the Menurae can be considered so.

Because this view was incompatible with Sib-
ley’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 *Atrichomis*.
2. Loss of fusion of tracheal rings, complete in *Menura*, partial in *Atrichomis*.

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 *Atrichomis 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 lauterbachii* (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, Atrichomis rufescens (Atrichornithidae); B, Liosceles thoracicus (Rhinocryptidae). Note the overall similarity in proportions, plumage, and bill shape.](image-url)
similarly 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
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*, *Scolorchilus albicollis*, *S. rubecula*, *Rhinocrypta lanceolata*, *Lioseles thoracicus*, *Myornis senilis*, *Teledromas fuscus*, *Scytalopus unicolor*, *S. magellanicus*, *S. argentifrons*, and *S. femoralis*. On the basis of its syringal morphology (Ames, 1971), *Melanopareia* appears to be shared only with some of the Rhinocryptidae and has not been noted elsewhere in the Passeriformes. *Atrichornis* contrasts with *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 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 slimanus* (Atrichornithidae); C, *Liascelis 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 arbomys* (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 Menuridae, 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 ect-
ethmoid 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 rhino-
cryptids. 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 con-
dition is found in the Rhinocryptidae in Lioscelis
and Myornis. In most Rhinocryptidae, the internal
process of the mandibular articulation is very
long and attenuate and lacks a pneumatic fora-
men. Melanopareia differs, however, in having the
typical rhinocryptid condition and resembles the
Menurae.

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) man-
dibular 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” condi-
tion 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). Heimer-
dinger and Ames were equivocal as to which
sternal type is primitive in passerine birds. How-
ever, the sternum is four-notched in almost all
non-passerine land birds that might be closely
related to the Passeriformes, e.g., Coliiformes,
Piciiformes, and most Coraciiformes (including
the Galbulae, see Olson, in press), and the early
Eocene family Primobuccconidae. 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 appar-
ently been lost, an unfortunate occurrence be-
cause 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 mod-
ified and is different from that in any other
passerines (Huxley, 1867:472; Heimerdinger and
Ames, 1967). It is not indicative of relation-
ships. 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.

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).
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 Menuridae 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 musculation and is characterized by a very deep ischium and relatively short, rounded
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.

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 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.
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-
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.

Toes.—In the Rhinocryptidae, the proximomedial corner of the basal phalanx of digit IV is distinctly notched to accommodate 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 pilonorhynchid 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 *Melanopararia*, 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 Philipittiidae 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, Chamaea, 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, Chamaea, 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 rugicapilla, 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 parietales 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 Myormis 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)

<table>
<thead>
<tr>
<th>Species</th>
<th>4-notched sternum</th>
<th>Curved humerus</th>
<th>Broad, grooved tarsal trochleae</th>
<th>Notched basal phalanges</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grallaria fulviventris</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>G. perspicillata</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>G. quitensis</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>G. erythroleuca</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>G. flavosinca</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>G. hypoleuca</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
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<td>+</td>
<td>+</td>
<td>-</td>
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<td>G. macularia</td>
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<td>-</td>
<td>+</td>
<td>-</td>
</tr>
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<td>G. guatimalensis</td>
<td>-</td>
<td>?</td>
<td>?</td>
<td>?</td>
</tr>
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<td>G. hoplonota</td>
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<td>?</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Pittasoma michleri</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Chamaea campanisoma</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
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<tr>
<td>Formicarius analis</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Conopophaga aurita</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>C. lineata</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Grallaricula nana</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
</tbody>
</table>

* 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, Chamaea, Grallaricula, Formicarius, and Conopophaga, and then the remainder of the family.
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Synonymy in the zoology and paleobiology series must use the short form (taxon, author, year:page), with a full reference at the end of the text, in “Literature Cited.” For the botany series, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in the “Literature Cited”) is optional.

Footnotes, when few in number, whether annotative or bibliographic, should be typed at the bottom of the text page on which the reference occurs. Extensive notes must appear at the end of the text in a notes section. If bibliographic footnotes are required, use the short form (author/brief title/page) with a full reference at the end of the paper under “Literature Cited.”

Text-reference system (author/year/page within the text, with the full reference in a “Literature Cited” at the end of the text) must be used in place of bibliographic footnotes in all scientific series and is strongly recommended in the history and technology series: “(Jones, 1910:122)” or “... Jones (1910:122).”

Bibliography, depending upon use, is termed “References,” “Selected References,” or “Literature Cited.” Spell out book, journal, and article titles, using initial caps in all major words. For capitalization of titles in foreign languages, follow the national practice of each language. Underline (or italics) book and journal titles. Use the colon-parentheses system for volume/number/page citations: “10(2):5–9.” For alignment and arrangement of elements, follow the format of the series for which the manuscript is intended.

Legends for illustrations must not be attached to the art nor included within the text but must be submitted at the end of the manuscript—with as many legends typed, double-spaced, to a page as convenient. Illustrations must not be included within the manuscript but must be submitted separately as original art (not copies). All illustrations (photographs, line drawings, maps, etc.) can be intermixed throughout the printed text. They should be termed Figures and should be numbered consecutively. If several “figures” are treated as components of a single larger figure, they should be designated by lowercase italic letters (underlined in copy) on the illustration, in the legend, and in text references: “Figure 9b.” If illustrations are intended to be printed separately on coated stock following the text, they should be termed Plates and any components should be lettered as in figures: “Plate 9b.” Keys to any symbols within an illustration should appear on the art and not in the legend.

A few points of style: (1) Do not use periods after such abbreviations as “mm, ft, yds, USNM, NNE, AM, BC.” (2) Use hyphens in spelled-out fractions: “two-thirds.” (3) Spell out numbers “one” through “nine” in expository text, but use numerals in all other cases if possible. (4) Use the metric system of measurement, where possible, instead of the English system. (5) Use the decimal system, where possible, in place of fractions. (6) Use day/month/year sequence for dates: “9 April 1976.” (7) For months in tabular listings or data sections, use three-letter abbreviations with no periods: “Jan, Mar, Jun,” etc.

Arrange and paginate sequentially EVERY sheet of manuscript—including ALL front matter and ALL legends, etc., at the back of the text—in the following order: (1) title page, (2) abstract, (3) table of contents, (4) foreword and/or preface, (5) text, (6) appendixes, (7) notes, (8) glossary, (9) bibliography, (10) index, (11) legends.