A NEW FAMILY OF PRIMITIVE LANDBIRDS FROM THE LOWER EOCENE GREEN RIVER FORMATION OF WYOMING

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ABSTRACT. A new family, Foratidae, is erected for *Foro panarium* new genus, new species, based on a nearly complete, associated skeleton from the Lower Eocene Green River Formation of Wyoming. The apparent lack of any of the locomotory or feeding specializations by which many modern families and orders of birds may be recognized makes assignment of this bird difficult. The skull and mandible are most similar to those in the Opisthocomidae, but the postcranial skeleton is very different, although some elements show similarity to the Musophagidae. The elongated hindlimb elements of *Foro*, especially the tarsometatarsus, suggest a more terrestrial mode of life than modern species of Musophagidae or Opisthocomidae, perhaps not unlike some of the terrestrial Cuculidae. Birds similar to the very generalized Foratidae could have given rise to the arboreal Opisthocomidae on one hand and to the terrestrial Cariamae on the other, and perhaps even to some of the diurnal raptors.

Key words: Eocene, Aves, Green River Formation, Foratidae, landbirds.

INTRODUCTION

Our knowledge of the Early Eocene avifauna of North America is increasing rapidly through study of excellent fossil material in freshwater limestone nodules from the Bighorn Basin of Wyoming (Houde, 1988; Houde and Olson, 1989) and from lacustrine shales and sandstones of the Green River Formation (e.g., Olson, 1977, 1987). The subject of the present paper (Fig. 1) is one of the best-preserved specimens recovered so far from the latter, a bird apparently otherwise unknown among the rather extensive Early Eocene collections now available and for which no other material has yet been recognized.

MATERIALS AND METHODS

The fossil was compared with a synoptic series of skeletons containing most of the modern families of non-passerine birds. After most of these were eliminated, the following specimens were used for more detailed comparisons and the descriptions. All catalogue numbers are in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Musophagidae: *Crinifer africanus zonurus* Rüppell 1835, 430522; *Corythaixoides concolor* (Smith 1833), 558534; *Musophaga violacea rossae* Gould 1852, 558255; *Corythaeola cristata* (Vieillot 1816), 291079. Cuculidae: *Coua ruficeps* Gray 1846, 432195; *Cuculus canorus* Linnaeus 1758, 603559; *Crotophaga major* Gmelin 1788, 500421; *Geococcyx californianus* (Lesson 1829), 499279; *Centropus goliath* Bonaparte 1850, 557169. Opisthocomidae: *Opisthocomus hoazin* (Müller 1776), 344065. Megapodiidae: *Megapodius freycinet* Gaimard 1823, 560650. Cracidae: *Ortalis vetula* (Wagler 1830), 288729. Falconidae: *Milvago chimachima* (Vieillot 1816), 343844, Accipitridae: *Accipiter gentilis* (Linnaeus 1758), 610350. Cariamidae: *Cariama cristata* (Linnaeus 1766), 19941; *Chunga burmeisteri* (Hartlaub 1860), 431487. Anatomical terminology is modified from Howard (1929).

SYSTEMATICS

Class Aves Linnaeus 1758

Subclass Ornithurae Haeckel 1866

CHARACTERS. The tail in the fossil consists of only 6 free caudal vertebrae and a well-developed pygostyle, unlike the reptilian tail of *Archaeopteryx* von Meyer 1861 (Saurirae).

Superorder Neognathae Pycraft 1900

CHARACTERS. The specimen is edentulous and cannot be included in any superorder containing *Hesperornis* Marsh 1872, *Ichthyornis* Marsh 1872, or their respective allies (the so-called Odontornithes, Odontognathae, or Odontoholcae of various authors). Although the palate itself cannot be discerned, the fossil clearly cannot be included in the superorder Palaeognathae either. The skull in paleognathous birds is adapted for what Zusi (1984:5) has termed "central rhynchokinesis," in which there is a "single bending zone of the dorsal bar . . . located approximately midway between the symphysis and the lateral bars and the nares extend back ro the cranial attachments of the lateral bars." Concomitant with this type of rhynchokinesis is the lack of fusion of the lateral bar of the nasal with the ventral bar of the premaxilla. The bill in the fossil, however, is short and stout, with rounded nostrils that do not extend far posteriad and a very heavy, complete, lateral nasal bar that is broadly fused to the ventral bar of the premaxilla (Fig. 2). This is, therefore, a holorhinal, prokinetic skull that by definition cannot have been paleognathous. The postcranial skeleton is not that of a flightless ratite, nor does it have any of the characteristic features of the Tinamidae or the Lithornithidae (Houde, 1988), the only known groups of volant paleognathous birds.

Figure 1. *Foro panarium* n. gen., n. sp., holotype (USNM 336261), nearly complete skeleton.

There is thus no reason to associate the fossil with any of the Palaeognathae, and it is typical of the modern radiation of neognathous birds.

REMARKS. For the most part, the systematic position of the fossil may be further refined mainly by the absence of derived characters. The short, rather generalized holorhinal bill is not obviously adapted for probing, spearing, filter-feeding, grasping fish, tearing meat, gaping, or catching flying insects. The wings are rather short and lack any adaptations for gliding or soaring, rapid aerial locomotion or hovering, or propulsion under water. The hindlimb and pelvis exhibit no adaptations for swimming or diving, or for raptorial grasping, the legs being long and gracile. In addition, the coracoid has a broad, well-developed procoracoid process; there is no ectepicondylar spur on the humerus, the pectoral crest of which is broad and rounded, not pointed and triangular; the carpometacarpus is short, the intermetacarpal process is lacking, and the minor metacarpal is broad and bowed and does not extend distad beyond the major metacarpal; the foot is anisodactyl, with no hint of even incipient zygodactyly.

With regard to the major informal groupings of birds used by Olson (1985), this combination of characters eliminates from consideration all members of the waterbird assemblage except the Cariamidae, all of the higher landbirds, and the Cuculidae, Falconiformes, Turnicidae, Columbiformes, and Psittaciformes among the basal landbird assemblage.

Among the groups that remain, the Galliformes differ from the fossil in having a much larger, blade-like retroarticular process of the mandible; longer and narrower scapula; much longer and narrower coracoid with no procoracoid process; the sternum with large, fused spina externa and spina interna, the body much more elongated, especially on the midline, with the lateral notches situated much farther anteriorly; minor metacarpal not broad and flat; pectoral crest of the humerus much reduced and the head of the humerus more bulbous. The modern Cariamidae differ from the fossil in having a simple, block-like hypotarsus; a more elongate sternum, with only 2 notches; the acromion of the scapula much better developed; narrower procoracoid process; a smaller pectoral crest of the humerus; straighter shaft of the ulna; much weaker ectethmoid; and much more elongated bill.

This leaves only the Opisthocomidae and Musophagidae, with which the fossil indeed shares certain similarities. Both of these families have been included with the Cuculidae in or near an order Cuculiformes by some authors (e.g., Sibley and Ahlquist, 1973; de Queiroz and Good, 1988), although sometimes on indefensible evidence (Brush, 1979). The Opisthocomidae, Musophagidae, and Cuculidae probably do not constitute a monophyletic group in any sense of the word. If they are among the most primitive of the neognathous birds, as I have suggested (Olson, 1985), they may lack derived characters by which they can be united either as a group or with other orders or families of Neognathae. Nevertheless, if the fossil must be placed in any currently recognized ordinal taxon, it would by default have to be the Cuculiformes.

Order Cuculiformes Wagler 1830

CHARACTERS. By the retention of a very broad, prominent pectineal process of the pelvis, the fossil resembles most members of the Cuculiformes. In shape, this process in the fossil is most similar to that in the Musophagidae, whereas in the Cuculidae it is more slender and pointed, when present, as it has evidently been lost in some of the Cuculidae as well as in the Opisthocomidae. Elsewhere among the Neognathae, the pectineal process apparently occurs only in numerous genera of the galliform family Phasianidae, from which the fossil differs in the characters previously mentioned. The pectineal process is also present in all members of the Palaeognathae, and it is probably primitive within Aves.

Family Foratidae new family

TYPE GENUS. *Foro* new genus, the only included genus.

DIAGNOSIS. Holorhinal, anisodactyl Neognathae having open nostrils without secondary ossification; broad procoracoid process; accipitrid-like humerus with pectoral crest long, broad, curved, and proximally situated; short, broad, bowed minor metacarpal; and broad, prominent pectineal process of the pelvis. The overall shape of the cranium and bill; the strong, deep mandible; and the short, hook-like retroarticular process are similar to those of the Opisthocomidae. The vertebral number and overall shape of the coracoid, pelvis, carpometacarpus, and distal end of the tarsometatarsus are similar to the Musophagidae. The following characters distinguish the family from the Opisthocomidae: fewer presacral vertebrae; notarium absent; 5 rather than 6 caudal vertebrae; and sternum and furcula not bizarrely modified to accommodate the enlarged crop. From the Musophagidae, the Foratidae differ in not having the rostrum elevated and inflated; the spina externa of the sternum is not large and blade-like; the procoracoid process is not fused to the head of the coracoid to form a complete bony ring; the clavicles are united, rather than being unfused and articulating with each other by a synovial joint; and the scapular tuberosity and coracoidal facet are not nearly as well developed. In addition to lacking any hint of zygodactyly, the Foratidae differ from the Cuculidae in the much less elongated rostrum; the ectethmoid is not large and inflated; and the hypotarsus is longer with apparently only one, rather than two, enclosed bony canals. The Musophagidae and most Cuculidae have large, distinct papillae on the ulna for the attachment of secondary feathers, which is probably a condition that has been derived independently in several groups of birds, but which is lacking in the fossil and in the Opisthocomidae.

Foro new genus

TYPE SPECIES. *Foro panarium* new species.

DIAGNOSIS. As for family.

REMARKS. The hindlimb elements, especially the tarsometatarsus, are quite slender and elongated, being similar in absolute size to those of a roadrunner (*Geococcyx* Wagler 1831: Cuculidae). This suggests that the bird was to some extent terrestrial, unlike the Opisthocomidae and Musophagidae, which are exclusively arboreal. Lengthening of the tarsometatarsus as an apparent terrestrial adaptation may occur within an otherwise arboreal family (e.g., Cuculidae, Columbidae) or even within a genus [e.g., *Athene* (*Speotyto auct.*) *cunicularia* (Molina 1782): Strigidae].

ETYMOLOGY. See etymology of species.

Foro panarium new species

Figures 1–7

HOLOTYPE. Essentially complete associated skeleton, vertebrate paleontological collections of the National Museum of Natural History, Smithsonian Institution, USNM 336261; collected in 1982.

DIAGNOSIS. As for family.

Figure 2. Detail of skull of holotype of *Foro panarium* n. gen., n. sp. (USNM 336261). 1.5×.

TYPE LOCALITY. "Thompson Quarry," northwest of Kemmerer, Lincoln County, Wyoming: NW¼, SW¼, sec. 22, T22N, R117W (Kemmerer 15-minute quadrangle); 41°44′N, 110°31′W. This is the site indicated in Feldmann et al. (1981:789, fig. 1) and is among the F-2 localities of Grande (1984).

HORIZON. Fossil Butte Member of the Green River Formation, upper Lower Eocene (Wasatchian Land Mammal age).

ETYMOLOGY. Dedicated to Pierce Brodkorb, of whose name this is a direct latinization: L. *foro, foratus,* pierce, bore (cf. perforate, foramen); *panarium,* breadbasket (*ex* Brodkorb, from German *Brot* or *Brod,* bread, and *Korb,* basket). By analogy with *Vireo,* also a first-person singular verb, the generic name may be considered masculine in gender. The specific name is a noun in apposition. I would have preferred these names in reverse order but unfortunately *Panarium* is preoccupied by a genus of Protista (Haeckel, 1882).

MEASUREMENTS (mm) OF HOLOTYPE. Skull: total length, 60.1; length of rostrum from nasofrontal hinge, 22.9; length of premaxillary symphysis, 9.9; length of nostril, 12.1; length of mandible, 45.9. Sternum: approximate length, 43; width at posteriormost costal facet, 24.5. Coracoid: length to internal sternal angle, 25.3; width of sternal end, 14.1. Scapula: length, 43.9; width of articular end, 8.8; least width of neck, 3.3. Humerus: length, 52.5; distal width, 9.0. Ulna: length, 50.0. Radius: length, 44.5. Carpometacarpus: length, 26.7; proximal depth, 8.8. Alular digit: length of phalanx 1, 8.6; length of phalanx 2, 2.0. Major digit: length of phalanx 1, 10.8; length of phalanx 2, 7.7. Pelvis: length along midline, 43.1; length to posteriormost point of ischium, 58.9; width across antitrochanters, 29.2. Femur: length, 54.1. Tibiotarsus: length from inner cnemial crest, 88.4; depth through external condyle, 7.5. Tarsometatarsus: length, 61.3; distal width, ca. 9.3. Metatarsal I: length, 5.4. Lengths of phalanges of pes: I1, 9.2; I2, 4.8; II1, 12.4; II2, 10.9; II3, 7.3; III1, 13.9; III2, 12.1; III3, 11.6; III4, 8.3; IV1, 8.9; IV2, 7.0; IV3, 6.3; IV4, 7.3; IV5, 6.6. Tracheal rings: greatest diameter (average of 5), 5.5. Pygostyle: length, 15.4.

PRESERVATION OF THE SPECIMEN. The fossil (Fig. 1) is brown in color and it is preserved in a block of cream-colored shale containing scales and coprolites of fish. Most of the bones are present in their entirety (not split longitudinally) with the long bones being reasonably three dimensional, though with the shafts variously crushed. The slab had been broken into at least four pieces, all the cracks having been neatly repaired with little damage to the specimen except for a large crack running in front of the pectoral apparatus and the left wing. Damage in this area has destroyed the left alular metacarpal and phalanges, obliterated all details of the left carpometacarpus, and probably removed at least one vertebra and a number of tracheal rings. As preserved and prepared, the bird is seen essentially in dorsal view, with the head thrown back and the vertebral column variously disarticulated.

The skull, complete with sclerotic ring and mandible, is seen in right lateral view, with 7 cervical vertebrae in articulation. The vertebral column continues as a loop of 6 vertebrae (one represented by a zygapophysis only) in front of the pectoral apparatus, and, as mentioned, at least one vertebra has probably been completely destroyed in this area. Three thoracic vertebrae lie directly on top of the sternum, which is seen in dorsal view, and the last two lie in articulation to the right of the sternum. The pelvis is disassociated from the body and from the femora and lies in dorsal and right lateral view, partially obscuring the proximal end of the right tibiotarsus. The left ischium is bent completely under the pelvis and protrudes with its medial side uppermost in the space between the posterior processes of the ilia. The tail is removed a short distance from the pelvis and has 6 free caudals (probably all that were present) in articulation

Figure 3. Detail of pectoral apparatus, in dorsal view, of *Foro panarium* n. gen., n. sp., holotype (USNM 336261). Arrow indicates the medial sternal notch; the remains of the lateral sternal notch are mostly obscured by the displaced portion of the posterior lateral process. The two portions of the broken clavicle are indicated by F. 1.5×.

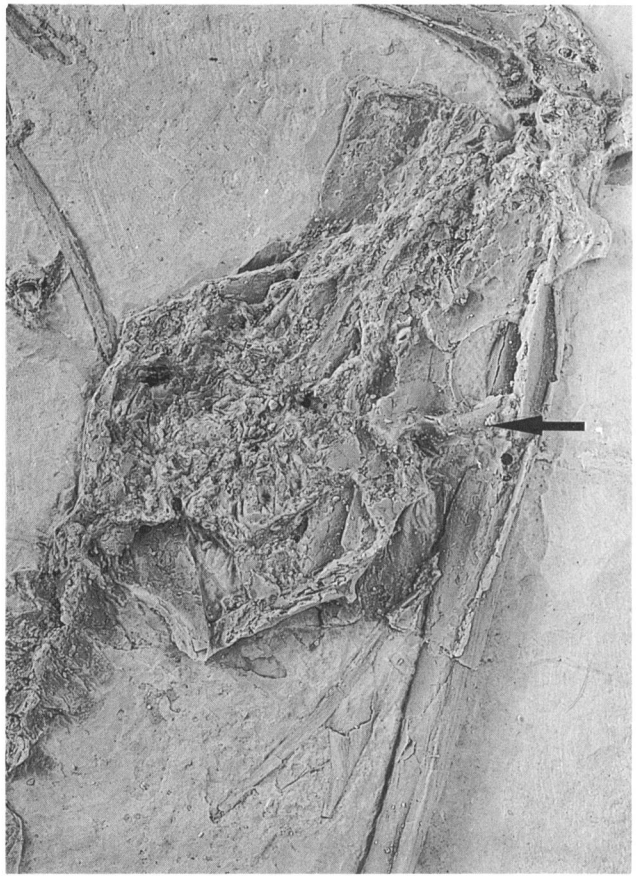

Figure 4. Detail of pelvis of holotype of *Foro panarium* n. gen., n. sp. (USNM 336261). Arrow indicates the large pectineal process. 1.5×.

with the pygostyle, which is turned so as to be seen in left lateral view.

The furcula is almost completely exposed, with the left ramus broken and lying at right angles to the remainder. Both ends of the left coracoid are obscured by the sternum and left clavicle, but the shaft and procoracoid process are visible. The right coracoid is overlain by the right scapula, but most of its outline except the procoracoid process may be discerned. Both scapulae are nearly fully exposed in dorsal view. The entire left margin of the sternum, except the sternocoracoidal process, is obscured by the left scapula and ribs.

The left wing is seen in dorsal view, with the carpometacarpus and alular digit missing or obliterated, but major and minor digits remain in close articulation. The right wing is seen in ventral view, with the phalanges being completely disarticulated, and that of the minor digit apparently missing. The distal phalanx closest to the alular metacarpal is identical in size and shape to phalanx 2 of the major digit of the left wing. Therefore, the phalanx abutting the right carpometacarpus at right angles, which is longer than the other, is taken to be the alular phalanx, or rather I should say the proximal alular phalanx, because at its distal end is a small bone that I interpret as a second phalanx, or wing claw.

Both femora and tibiotarsi are seen in lateral view, with much of the shaft of the left tibiotarsus missing. The right tarsometatarsus is seen in posterior view, with the toes in ventral view; the left tarsometatarsus and toes are essentially in left lateral view.

DESCRIPTION AND COMPARISONS. The overall similarity of the skull and mandible (Fig. 2) is decidedly closer to that in the Opisthocomidae than to either the Musophagidae or Cuculidae. The cranium in lateral view is rather elongate and ovoid, and the bill fairly deep and quite short, much less than half the total length of the skull. The rostrum is not elevated and inflated, as in all the Musophagidae, nor elongated as in the Cuculidae.

The nostril is open and unossified, the ventral nasal bar being quite distinct and broad. This is in contrast to the Musophagidae, Opisthocomidae, and most Cuculidae, in which the nostril is heavily ossified and the opening greatly reduced in size. Even in those members of the Cuculidae in which the nostril is relatively open, and the ventral nasal bar distinct, the nasal septum is still heavily ossified and the nares are not obviously perforate, as they are in the fossil.

The sclerotic ring is in place and the number and pattern of

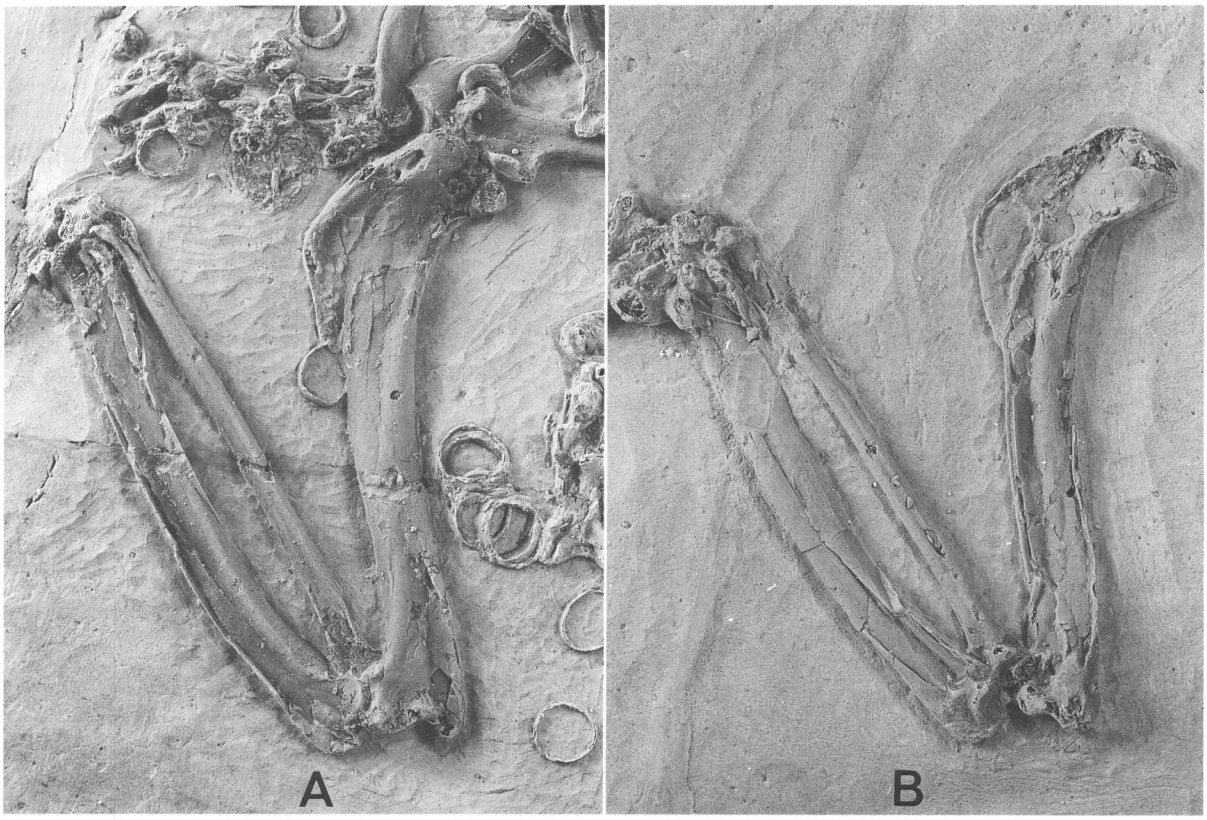

Figure 5. Humeri, radii, and ulnae of the holotype of *Foro panarium* n. gen., n. sp. (USNM 336261). **A.** Left wing in anconal view. **B.** Right wing in palmar view. 1.5×.

overlap of the ossicles can be discerned reasonably well. Variation in the sclerotic ring of the Galliformes and Cuculiformes has been analyzed and discussed by de Queiroz and Good (1988). The number of ossicles in the fossil appears to be 13. The anterior portion of the ring has suffered some damage and it is the more difficult to interpret, so that it is possible that the number may be 14. The pattern of overlap, following the numbering convention adopted by de Queiroz and Good (1988), is 1+, 4−, 7+, 10−. This number and pattern is essentially identical to that illustrated by de Queiroz and Good (1988:fig. 1f) for the Musophagidae except that the 10th rather than the 9th ossicle is overlapped on both sides by adjacent ossicles. The typical number of ossicles in the Musophagidae is 13 (varying from 11 to 14), whereas in the Cuculidae and Opisthocomidae it is usually 12 (varying from 11 to 14 and 11 to 13, respectively) and in the Galliformes 14 or 15 (sometimes 13). Although the modal number of ossicles may be characteristic for a given higher-level taxon, variation within species and families would appear to render this character largely inconclusive for taxonomic purposes when dealing with a single specimen.

Very little detail can be made out concerning the rest of the skull, except that there is a small, thin ectethmoid plate present, similar to that in the Musophagidae and Opisthocomidae and unlike the larger and much more inflated ectethmoid in the Cuculidae. Because of damage, the presence of a prefrontal (lacrimal) bone cannot be ascertained, though if present it would have to be quite small.

The mandible is deep and straight, with a robust, pointed symphysis, in which respects it bears strong resemblance to that in the Opisthocomidae. There is no marked ventral depression of the dentary portion as in the Musophagidae. The extent of what appears to be an open mandibular foramen is difficult to determine because of underlying bone that has been crushed into it, perhaps from the opposite ramus. There is a well-marked, short, upturned retroarticular process, very similar to that in the Opisthocomidae. This process is absent in the Musophagidae and Cuculidae.

Assuming that one vertebra was lost through damage, there are 19 presacral vertebrae, as in the Musophagidae. In the Cuculidae there are 18 and in the Opisthocomidae 21, of which 4 thoracics are fused into a notarium, a feature definitely lacking in the fossil.

The sternum (Fig. 3) is short and rather square in outline, with a short, peg-like spina externa; short, blunt sternocoracoidal processes; and four shallow, rounded notches on the posterior border, the lateral notches being deeper than the medial. This is quite unlike the Musophagidae, in which the spina externa is large and blade-like and the four notches are much deeper and more V-shaped. The sternum in the Cuculidae may vary from four rather deep notches to two very shallow ones. In the Opisthocomidae, some individuals may have four notches that are somewhat similar to those in *Foro,* whereas in others these are reduced to two broad, shallow notches. Deep notches, such as those in the Musophagidae are probably primitive. Re-

duction in size and number of sternal notches is a prevalent phenomenon that has occurred in disparate lineages of birds (e.g., Fregatidae and Steatornithidae; see Olson, 1977, 1987).

The overall similarity of the coracoid (Fig. 3) is closer to the Musophagidae, but the procoracoid process does not fuse with the head to produce a coalesced ring that excludes the clavicle from the triosseal canal, a derived character of the Musophagidae. Also, the scapular facet is deeper. The coracoid is unlike that in the Cuculidae, in which the shaft is longer and more slender, the sternal end narrower, and the head more pointed. It is also unlike that in the Opisthocomidae, in which the shaft is also slender, with a pneumatic sternal end that abuts the adjacent coracoid on the midline of the sternum.

The blade of the scapula (Fig. 3) is more expanded than in the Musophagidae or especially the Cuculidae and is thus more similar to that in the Opisthocomidae. The acromion is not as well developed as that in the Opisthocomidae or Musophagidae, being shorter and blunter, more as in the Cuculidae.

The furcula (Fig. 3) is broadly U-shaped with rather wide, flat shafts, no apparent hypocleideum or scapular tuberosity, and poorly developed coracoidal facets. This is totally unlike the Musophagidae, in which the clavicles are unfused and there is a large scapular tuberosity and prominent coracoidal facet. It is also unlike the unusual Y-shaped furcula of *Opisthocomus* Illiger 1811, which is fused to the pectoral girdle both anteriorly and posteriorly. The furcula in the Cuculidae is variable, but it usually has a hypocleideum and narrower shafts that are not spaced as far apart. The furcula of *Foro* seems to be very generalized, especially compared with either the Musophagidae or Opisthocomidae.

The pelvis (Fig. 4) of *Foro* lacks the laterally flared points of the anterior part of the ilium seen in the Cuculidae, and its overall resemblance is close to the Opisthocomidae and Musophagidae, except that the ischium is more pointed and posteriorly directed, and the pectineal process is lacking in the Opisthocomidae.

The pectoral crest of the humerus (Fig. 5) is long and broad, with a curved apex, unlike the short, ventrally rotated crest in the Cuculidae or the pointed and much more distally situated crest in the Musophagidae or Opisthocomidae. The shaft is short and relatively straight, being much less curved than in most of the Cuculidae. The entepicondylar area is not as strongly produced ventrally as in most Cuculidae, and the bicipital crest is more pronounced than in any of the Cuculiformes. The overall similarity of the humerus is actually closest to that in the Accipitridae, a group of uncertain ancestry but postulated to have had a possible origin in the "cuculiform" basal landbirds (Olson, 1985). The diurnal raptors have a much longer forearm and manus than in *Foro*, however, and there are no other striking similarities between the fossil and the diurnal raptors.

The ulna (and radius) is proportionately short (Fig. 5). The olecranon is squared and scarcely projects beyond the cotylae. The shaft is relatively straight, with no evidence of the exaggerated papillae for the secondaries that are characteristic of the Musophagidae and most Cuculidae, but not the Opisthocomidae. Contrary to what has frequently been written about *Archaeopteryx* to the effect that its secondaries must have been weakly attached because there are no papillae for them on the ulna, many modern birds lack prominent papillae for the secondaries, the attachment of which may even be indicated by depressions in the ulna rather than protrusions. The exaggerated secondary papillae in the Musophagidae and most Cuculidae, as well as in the Pici, are exceptional and probably represent a derived state.

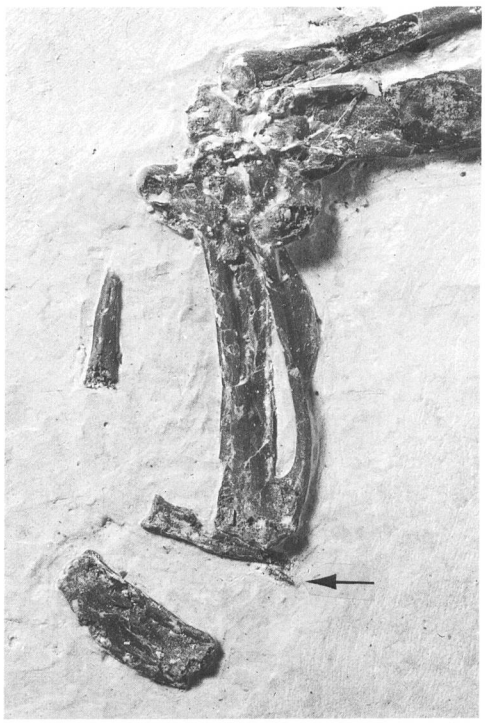

Figure 6. Detail of right manus of holotype of *Foro panarium* n. gen., n. sp. (USNM 336261). Arrow indicates the presumed second phalanx of the alular digit. 1.5×.

The carpometacarpus (Fig. 6) is short, with a bowed minor metacarpal that is broad and flat proximally, as in most basal landbirds (Olson, 1985). The bowed condition is not as exaggerated as in most Cuculidae, in which there is a wider intermetacarpal space. The similarity is greater to the Musophagidae and Opisthocomidae. There appears to have been a second (ungual) phalanx on the alular digit (Fig. 6), as is the case in at least some adults of *Opisthocomus*, the young of which are renowned for their clawed fingers.

The shaft of the femur is relatively stouter and straighter than in the Musophagidae, Opisthocomidae, or Cuculidae, being somewhat more similar to the Accipitridae or Falconidae in this regard.

The tibiotarsus can be seen only in lateral view in the fossil. It is long and slender, with the outer cnemial crest much better developed than in the Musophagidae, Cuculidae, Opisthocomidae, or the diurnal raptors.

The tarsometatarsus (Fig. 7) is very long and slender, quite unlike that in the Opisthocomidae or Musophagidae. The hypotarsus is damaged on both sides of the specimen. It is relatively elongated, with a shallow medial groove and a very deep, more lateral groove that was probably enclosed or nearly so. Its similarity is thus closest to the Musophagidae and Opisthocomidae. It is decidedly unlike the short, block-like hypotarsus, with two enclosed canals, seen in the Cuculidae. The distal end of the tarsometatarsus shows no modification toward zygodactyly, and the overall configuration is very similar to that in the more primitive genera of Musophagidae such as *Crinifer* Jarocki 1821 or *Corythaixoides* Smith 1833.

In absolute size, the hallux is about equal to that in *Tauraco*

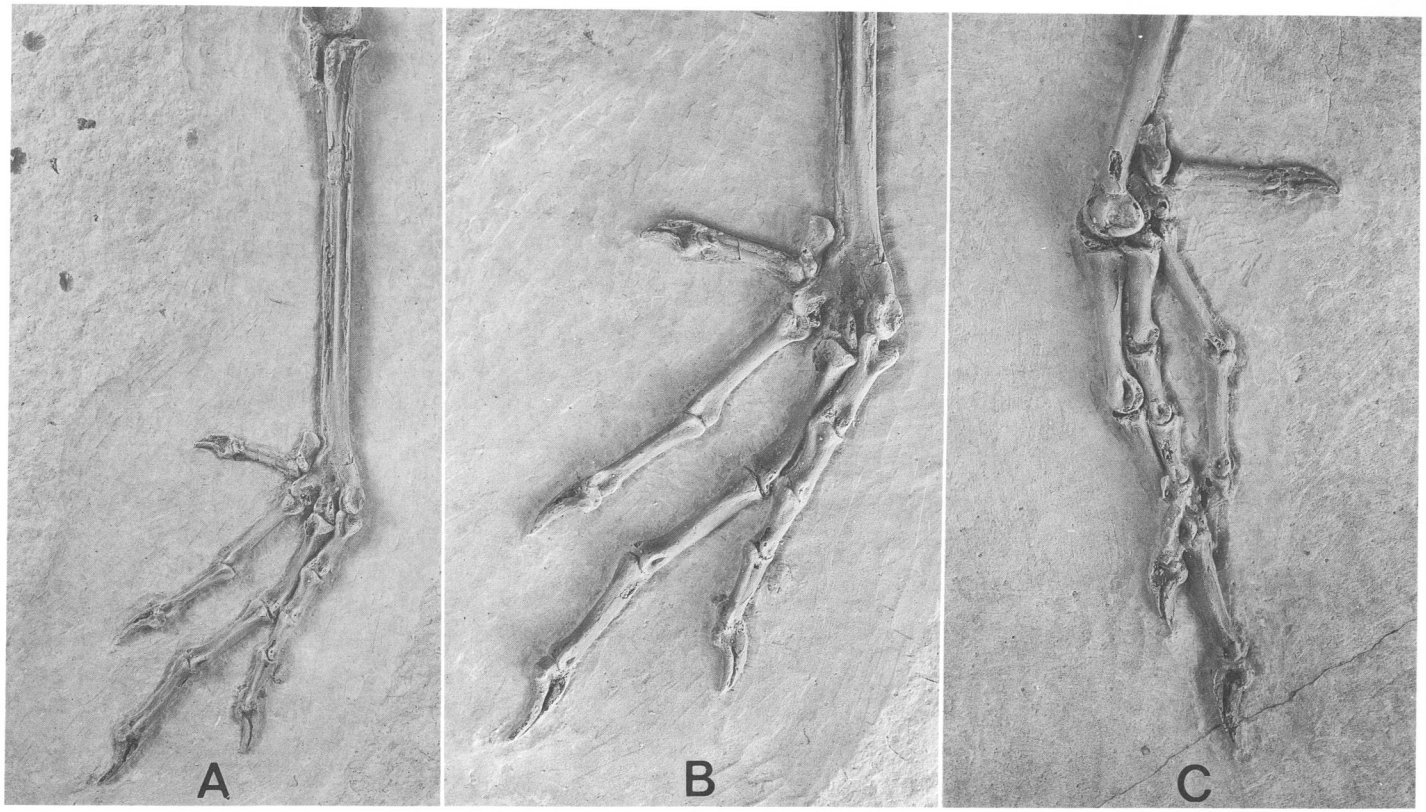

Figure 7. Feet of holotype of *Foro panarium* n. gen., n. sp. (USNM 336261). **A.** Right tarsometatarsus and toes (1×). **B.** Detail of right foot (1.5×). **C.** Detail of left foot (1.5×).

Kluk 1779, but shorter than in *Geococcyx*, whereas all the anterior toes are longer than in either of those genera. The claws are rather short and deep, unlike the longer more slender ones of *Geococcyx* but similar to *Tauraco*, except not as curved.

DISCUSSION

The overall similarity of the skull and mandible of *Foro* to those of *Opisthocomus* are actually quite striking, even to size and proportions. The chief observable difference is the posterior ossification of the nostril of *Opisthocomus*, which has reduced the size of the narial opening. This is, however, a pattern that is apparently repeated in completely different lineages, in which Early Eocene members have more open nostrils than their modern descendents [e.g., Steatornithidae (*Prefica* Olson 1987 vs. *Steatornis* Humboldt 1817; see Olson, 1987) and Fregatidae (*Limnofregata* Olson 1977 vs. *Fregata* Lacépède 1799; see Olson, 1977)].

The short, upcurved retroarticular process may be a derived character uniting *Foro* and *Opisthocomus*, one that perhaps foreshadows the longer, blade-like hook of the Galliformes. For this to be primitive it would have to have been lost in the Musophagidae and the Cuculidae, either once or independently.

The Opisthocomidae may be among the most primitive of living birds (Olson, 1985), and they are well known for the presence of well-developed reptilian-like claws on the wings of the young (Beddard, 1889). The adults of at least some individuals of *Opisthocomus* retain a second phalanx on the alular digit (its consistent presence is difficult to assess because this small bone is easily lost in skeletal preparations), as does the holotype of *Foro panarium*. This phalanx may be variously present in different groups of modern birds (Fisher, 1940).

Opisthocomus is highly arboreal, with a peculiar diet (for a bird) that includes a preponderance of leaves (Beebe, 1911). Consequently, it has a greatly enlarged crop for which the pectoral girdle, especially the sternum and furcula, is extremely modified (Perrin, 1875; Gadow, 1891; Böker, 1929). For these reasons, and also because of modifications of the vertebral column, most notably the presence of a notarium, there is little similarity in the postcranial skeletons of *Foro* and *Opisthocomus*, other than in the general resemblance of the pelves (except for the pectineal process, which is absent in *Opisthocomus*) and carpometacarpi and in the absence of secondary papillae on the ulna.

Miller (1953) described an avian cranium from the Miocene of Colombia as an opisthocomid, *Hoazinoides magdalenae*. I cautioned that this might have come from a bird with postcranial adaptations very different from those of *Opisthocomus* (Olson, 1985). As shown by *Foro panarium*, with its hoatzin-like head, such caution was well justified.

It has been suggested that there may be a much closer relationship berween the Opisthocomidae and the Cariamidae than had previously been suspected (Mourer-Chauviré, 1983; Olson, 1985). This conclusion arose in the similarity of some of the elements, particularly the humerus, of the fossil group Idiornithinae, to those in *Opisthocomus*. The Idiornithinae were included as a subfamily of the Cariamidae by Mourer-Chauviré (1983:139), although she remarked that they were "equally close to the genus *Opisthocomus*." The overall appearance of the tarsometatarsus of *Foro panarium* bears a strong resemblance to that of *Idiornis* Oberholser 1936 itself. In those elements that are known, the idiornithines differ from *Foro* and agree with the Cariamidae in the shape of the humerus and the size and position of the pectoral crest and also in the much straighter shaft of the ulna.

Nevertheless, because *Foro panarium* is such a generalized bird, it is not difficult to envision something similar as giving rise both to the Opisthocomidae and to the suborder Cariamae, which is now included in the Gruiformes. Furthermore, the humerus in *Foro* is sufficiently similar to that in the Accipitridae to suggest that their ancestry may also be traceable to a bird not unlike *Foro*. The mosaic of characters seen in *Foro* is not unexpected in so ancient a bird and, in the final analysis, may substantiate an origin of the modern neognath radiation among the basal landbirds.

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