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A Review of the Bathornithidae (Aves, Gruiformes), with Remarks on the Relationships of the Suborder Cariamae

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INTRODUCTION

Study of the magnificent paleontological collections amassed by the late Mr. Childs Frick and housed in the American Museum of Natural History is beginning to yield new information about the Tertiary history of certain groups of birds. Most of the avian fossils in the Frick Collection are from Pliocene and Miocene sediments of western North America, but a small portion is from still older, Oligocene times.

The birds described and discussed herein are all members of the extinct gruiform family Bathornithidae. The fossil record of these birds indicates that they were most abundant in the Oligocene and had their center of distribution in the northern Great Plains, especially in Colorado, Nebraska, South Dakota, and Wyoming. The bathornithids were flightless and apparently adapted to a cursorial way of life similar to that of the South American cariamas (Cariamidae). They exhibited a great diversity in size, ranging from birds no more than 2 or 3 feet tall to giant forms standing at least 6 and, more probably, 7 feet in height.

Although some of the bathornithids are represented by abundant material, elements from the forelimbs and axial portions of the skeleton are rare. Indeed, only a few fragments of the humerus, carpometa-

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carpus, and ulna are known, and these have never been described in detail. The elements discussed in the present paper include the humerus, carpometacarpus, ulna, sternum, coracoid, scapula, and pelvis. The additional bones enable us to understand better the relationships within the bathornithids and to assess those with other families.

The Bathornithidae, along with the living Cariamidae and the extinct family Prophororhacidae (=Hermosiorhacidae), have been included in the superfamily Caramoidea of the suborder Cariamae (Wetmore, 1960). The Prophororhacidae have recently been considered to be related to the phororhacoids rather than to the cariamids (Patterson and Kraglievich, 1960).

Presently, four congeneric species are recognized as comprising the Bathornithidae. The first species to be described (Wetmore, 1927) was *Bathornis veredus* from lower Oligocene sediments of Colorado. This species was placed by Wetmore in a monotypic subfamily, the Bathornithinae, in the Burhinidae. Later, in a paper describing two new species, *B. celeripes* and *B. cursor*, Wetmore (1933a) recognized the family Bathornithidae and came to the conclusion that their relationships were with the Cariamidae instead of the Burhinidae. This decision was based on the relative proportions of the phalanges, which are quite different in the two families, but it is also supported by other evidence. *Bathornis geographicus*, the fourth species, was described from late Oligocene sediments of South Dakota (Wetmore, 1942). In a series of short papers Wetmore (1933b, 1937, 1958) described additional material of *B. veredus* and *B. celeripes*.

MATERIALS AND METHODS

ABBREVIATIONS

A.M.N.H., Department of Vertebrate Paleontology, the American Museum of Natural History

F:A.M., Frick Collection, the American Museum of Natural History

M.C.Z., Museum of Comparative Zoology, Harvard University

P.U., Princeton University Department of Geology

S.D.S.M., South Dakota School of Mines, Rapid City

U.S.N.M., Division of Vertebrate Paleontology, United States National Museum, Smithsonian Institution

Y.P.M., Peabody Museum of Natural History, Yale University

During the course of this study I examined the following fossil material:

BATHORNITHIDAE

Bathornis celeripes: M.C.Z. No. 2234, type, tarsometatarsus; M.C.Z. No. 2234, plesiotype, tarsometatarsus, digits; M.C.Z. No. 2235, plesiotype, tarsometatarsus.

- tarsus; M.C.Z. No. 2285, assorted tibiotarsi, tarsometatarsi; M.C.Z. No. 2287, assorted tarsometatarsi; M.C.Z. No. 2288, carpometacarpi, ulna, humerus; M.C.Z. No. 2502, tibiotarsus, ulna, carpometacarpus, tarsometatarsus, phalanges; M.C.Z. No. 2503, assorted tibiotarsi, tarsometatarsi; P.U. No. 16814, tarsometatarsus; S.D.S.M. No. 422, tarsometatarsus; U.S.N.M. No. 12494, carpometacarpus, tarsometatarsus, tibiotarsus, phalanges; U.S.N.M. No. 12974, tibiotarsus
- Bathornis veredus*: U.S.N.M. No. 11717, cast of type, tarsometatarsus; M.C.Z. No. 2283, tibiotarsus, femora, phalanges; P.U. No. 16813, tarsometatarsus; S.D.S.M. No. 422, left and right humeri (originally identified as *B. celeripes*)
- Bathornis cursor*: M.C.Z. No. 2236, type, tarsometatarsus
- Bathornis geographicus*: S.D.S.M. No. 4030, type, tarsometatarsus, tibiotarsus
- Paracrax antiqua*: Y.P.M. No. 537, type, humerus

PHORORHACIDAE

- Phororhacos longissimus*: A.M.N.H. No. 7010, tarsometatarsus
- Phororhacos* sp.: A.M.N.H. No. 9146, tarsometatarsus; A.M.N.H. No. 9264, pelvis, tarsometatarsus, tibiotarsus; A.M.N.H. No. 9497, tibiotarsus, femur
- Palaeociconia cristata* (= *Phororhacos inflatus*): A.M.N.H. No. 7005, tarsometatarsus

BRONTORNITHIDAE

- Brontornis burmeisteri*: A.M.N.H. No. 6825, cast of tarsometatarsus, tibiotarsus, femur

PSILOPTERIDAE

- Psilopterus australis*: A.M.N.H. 7006, tibiotarsus; A.M.N.H. No. 2516, humerus; A.M.N.H. No. 9157, tibiotarsus, tarsometatarsus, coracoid, scapula; A.M.N.H. No. 9257, pelvis, humerus, tibiotarsus, tarsometatarsus; P.U. No. 15402, nearly complete skeleton

In comparing the bathornithids with extant gruiform groups, I have had access to the skeletal collections of the Department of Ornithology in the American Museum of Natural History, and the Division of Birds, United States National Museum. These collections contain adequate series of recent species of most gruiform families. Several minor families were not represented, but their absence does not affect the results of this study.

It would be appropriate in the present paper to bring to the attention of avian paleontologists the techniques of stereophotography and its uses in paleontological illustration. Stereophotography is perhaps the best method known for illustrating fossil material. Conventional illustrative techniques such as line drawings or non-stereoscopic photography are not so effective in the rendering of contours and areas of relief on fossils as is stereophotography. Other branches of vertebrate paleontology have utilized stereophotography since at least the time of Richard Owen in the last century. Workers in avian paleontology, however, have only

recently turned to this process (Cracraft, in press). The advantages of this type of illustration are obvious to those familiar with it. For example, with proper use of this technique the necessity of borrowing fossil material can be greatly lessened, because the fossils themselves will have been accurately reproduced.

The actual construction of the stereophotographic unit is simple and need not be described here. The reader, if interested, may turn to several good papers for further details: Gott (1945), Evitt (1949), and Lehmann (1956).

NOTES ON STRATIGRAPHY

Because two of the three new species described in this paper are from the Brule Formation of South Dakota, a few brief comments on the stratigraphic nomenclature of the area are necessary. Many different names have been associated with this formation. The terminology followed here is modified from that of Bump (1956). Bump recognized two members of the Brule Formation: the lower, or Scenic, member includes the *Oreodon* beds (except the upper *Oreodon* bed); the upper, or Poleslide, member consists of the upper *Oreodon* bed, the well-known *Protoceras* channel sandstones (Bump also included here the *Leptauchenia* beds), and an upper layer of gray silty ash. The reader is referred to Bump's paper for further details.

Wetmore (1933a), when he described *Bathornis celeripes* and *B. cursor*, quite naturally relied on the authority of E. M. Schlaikjer for the stratigraphic data. Schlaikjer was quoted (Wetmore, 1933a, p. 297) as stating that the "fossil deposit is of Oligocene age, its stratigraphic position being approximately eighty feet above the Chadron-Brule contact." Such a position would place these fossils in the upper Oligocene, which is the age that has been used by recent workers (see, for example, Brodkorb, 1967, pp. 167-168). The stratigraphy of the area near Torrington, Wyoming, is very complicated, and in many cases the ages of the various facies cannot be determined with any precision. However, the deposit in which *B. celeripes* and *B. cursor* were found has been visited by workers from the American Museum of Natural History, and the stratigraphy of the area is being studied in detail. Consequently, we can now say with some certainty that the deposit is not upper Oligocene but lower Oligocene, more specifically late Chadronian (M. F. Skinner, personal communication).

SYSTEMATICS

CLASS AVES

ORDER GRUIFORMES

FAMILY BATHORNITHIDAE WETMORE, 1933

GENUS *BATHORNIS* WETMORE, 1927*Bathornis cursor* Wetmore

With the placing of *Bathornis cursor* in the lower Oligocene (see above), the relationships of this species to *B. veredus* immediately become subject to question. Measurements for the two species show they are approximately the same size: the transverse breadth across the trochleae of the tarsometatarsus is 20.1 mm. in *B. cursor* and 19.7 mm. in *B. veredus*. However, after comparison of the type of *B. cursor* (M.C.Z. No. 2236) with a cast (U.S.N.M. No. 11717) of the type of *B. veredus*, there is little doubt that these birds are specifically distinct. *Bathornis cursor* differs from *B. veredus* in having: (1) the trochlea for digit 3 projecting less distally relative to the trochlea for digit 4, (2) the trochlea for digit 3 less heavy, being smaller in anteroposterior direction (but the same width lateromedially), (3) the trochlea for digit 4 smaller and less massive, with the anterior surface having a longitudinal groove down the middle of the trochlea (surface more planar in *B. veredus*), and (4) the anterior surface of the trochlea for digit 2 sloping much less posteriorly. A previously unpublished specimen (P.U. No. 16813) of *B. veredus* further supports the above conclusion. This bone, the distal end of a right tarsometatarsus from the Chadron of South Dakota ("Bottom? of middle *Titanotherium* beds. . . ."), was compared with the type of *B. cursor* and differed in the characters mentioned above.

Wetmore (1933a, p. 310) commented that *Bathornis cursor* is only a "large edition of *Bathornis celeripes* from the same deposits." Actually, however, *B. cursor* shows several additional differences from *B. celeripes*: (1) the trochlea for digit 2 is turned less posteriorly (seen in distal view), (2) the trochlea for digit 3 projects less distally relative to the trochlea for digit 4, and (3) the trochlea for digit 3 is more rounded distally, less pointed.

Bathornis celeripes Wetmore

Recently Wetmore (1958) identified the distal ends of left and right humeri (S.D.S.M. No. 422) as being those of *Bathornis celeripes*. Wetmore apparently made the identification on the basis of associated elements, including a complete tarsometatarsus and a complete tibiotarsus (both

S.D.S.M. No. 422). I have re-examined these bones and have compared them with the abundant material, including the type, of *B. celeripes* in the Museum of Comparative Zoology. The tibiotarsus and tarsometatarsus agree with the type material of *B. celeripes*, but some question exists as to the proper identification of the two humeri. Upon comparison with a fragmentary humerus of *B. celeripes* (M.C.Z. No. 2288), which Wetmore apparently overlooked in his 1958 account but did mention in his original description (1933a, p. 309), I find the two humeri are considerably larger—so large in fact that I seriously question whether they could represent the same species. The specimens agree in general features with the humerus of *B. celeripes*, but, because the latter is greatly damaged and has the condyles badly displaced, a detailed comparison is not possible. I think it is likely that the two humeri belong either to *B. veredus* or to *B. cursor* instead of to *B. celeripes*. The proportions of the measurements of the humerus of *B. celeripes* to those of the two larger humeri are about the same as the proportions of the tarsometatarsal measurements of *B. celeripes* and *B. veredus*.¹

The measurements for the *Bathornis celeripes* humerus (M.C.Z. No. 2288) are as follows: transverse breadth across trochleae, 19.0 mm.; diameter (anconal to palmar) of external condyle, 9.3 mm. (approximate); other measurements were not possible.

Measurements for the South Dakota humeri have never been published, and these can be recorded here (first measurement indicates the left humerus; second measurement, right humerus): transverse breadth across trochleae, 23.8, 23.2 mm.; diameter (palmar to anconal) of external condyle, 10.5, 10.1 mm.; smallest transverse breadth of shaft, 11.8 mm., —; other measurements were not possible. The discrepancy in the measurements between the left and right humeri suggests that these bones came from two individuals.

The transverse diameter across the trochleae of 16 specimens of tarsometatarsi of *Bathornis celeripes* shows a range of variation of 14.7 mm. to 16.7 mm., with an average of 15.6 mm. (Wetmore, 1933a, p. 305). Wetmore noted that some of this variation may be explained, in part, by sexual differences. Such seems to be the case, for, when this large series of bones is arranged according to size, two more or less distinct size classes are discernible.

An unpublished record of a tarsometatarsus (P.U. No. 16814) proves to be that of *Bathornis celeripes* and can be given here: Brule Forma-

¹ Although it is uncertain whether the humeri are of *Bathornis veredus* or *B. cursor*, for convenience they are assigned to *B. veredus* and are called such throughout this paper.

tion (lower *Oreodon* beds), 30 feet south of road at west end of Chamberlain Pass, 1½ miles east of Scenic, South Dakota; collected in 1932 by G. L. Jepsen.

Bathornis geographicus Wetmore

Brodkorb (1967, p. 168) synonymized *Bathornis geographicus* with *B. cursor*, largely, I suspect, on the basis of their being thought the same age. As is mentioned above, the age of the type locality of *B. cursor* is no longer believed to be upper Oligocene but is lower Oligocene. It is advisable, then, to examine the relationships of these species more closely.

The middle trochlea of *Bathornis geographicus* is slightly larger than that of *B. cursor*, and although the latter is worn, it certainly is not outside the range of variation we would expect for a single species. The tarsometatarsus of *B. geographicus* has been damaged, and the displacement of the trochleae makes it impossible for a truly proper comparison with *B. cursor*. *Bathornis geographicus* does seem to differ, however, in having the trochlea for digit 3 projecting more distally relative to the trochlea for digit 2, and in having the portion of the bone just posterior to the trochlea for digit 3 (when seen in an anterior view) more elevated relative to the portion of the bone behind the trochlea for digit 2. These two differences do not appear to be the result of displacement of the trochleae in *B. geographicus*.

I compared the type of *Bathornis geographicus* with the Princeton specimen (P.U. No. 16813) of *B. veredus*, and it seems to be correct, as Wetmore (1942) suggested, that *B. veredus* is ancestral to *B. geographicus*. Moreover, *B. veredus* is separated from *B. geographicus* by such a great expanse of time (at least, probably, as far as bird species are concerned) that I think it best to retain *B. geographicus* as a species distinct from *B. veredus*.

***Bathornis fricki*, new species**

Figures 1, 2

TYPE: Complete right tibiotarsus, A.M.N.H. No. 2100; from lower Miocene sediments (from an approximate Gering equivalent); on Willow Creek, near Lusk, Niobrara County (now Converse County), Wyoming; collected in 1938 by C. H. Falkenbach.

DIAGNOSIS: Complete right tibiotarsus similar to that of *Bathornis celeripes* Wetmore, but differing in having the internal condyle projecting more anteriorly; the inner cnemial crest projecting more anteriorly; the

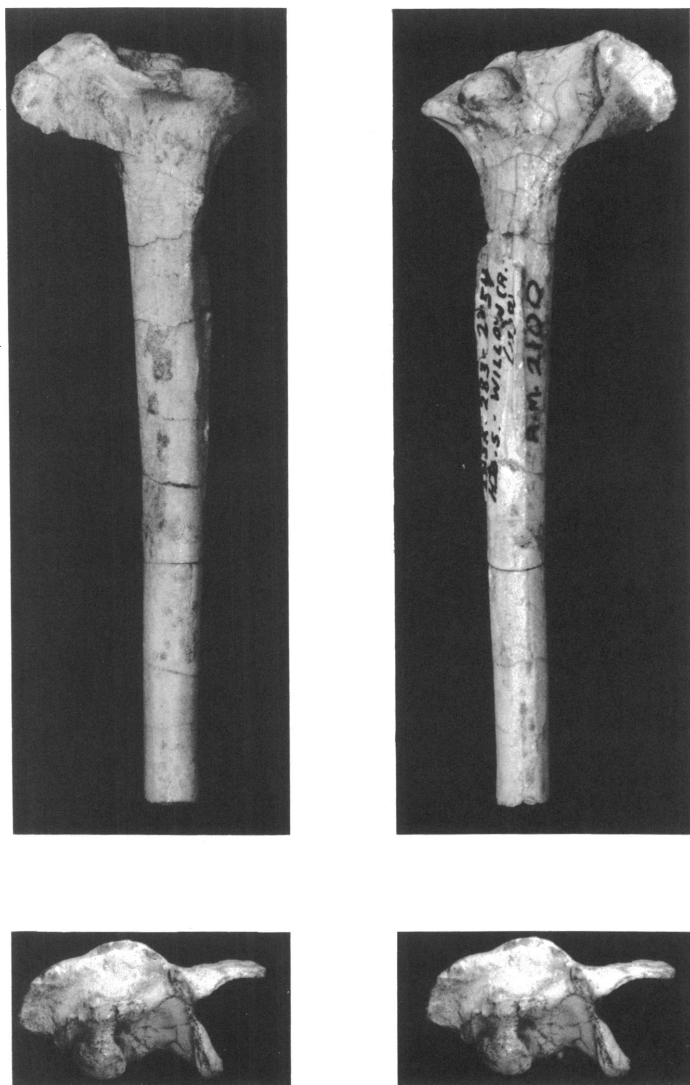


FIG. 1. *Bathornis fricki*, A.M.N.H. No. 2100, proximal portion of right tibio-tarsus, type specimen. *Upper left*: Internal view. *Upper right*: External view. *Lower*: Stereophotographs of proximal end. All $\times 1$.

internalmost edge of the head of the bone just posterior to the inner cnemial crest not so elevated; the bone decidedly larger.

MEASUREMENTS: Total length, 162.8 mm.; diameter (anterior to pos-

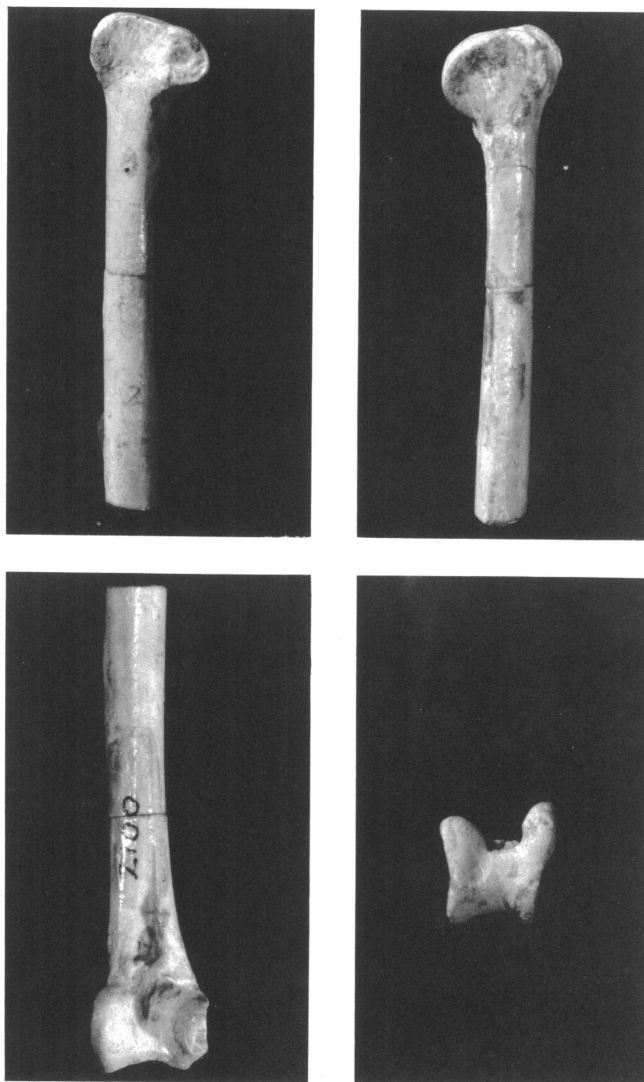


FIG. 2. *Bathornis fricki*, A.M.N.H. No. 2100, distal portion of right tibiotarsus, type specimen. *Upper left*: Internal condyle. *Upper right*: External condyle. *Lower left*: Anterior view. *Lower right*: Distal end. All $\times 1$.

terior) of external condyle, 13.7 mm.; diameter (anterior to posterior) of internal condyle, 15.9 mm.; breadth (external to internal) across condyles, 15.2 mm.; smallest breadth of shaft, 8.2 mm.; diameter of shaft

(anterior to posterior) at same point, 7.1 mm.; distance from tip of inner cnemial crest to posteriormost portion of head of tibiotarsus, 34.2 mm.; diameter (external to internal) across head, 18.0 mm.

REMARKS: The above-described tibiotarsus was referred to the Bathornithidae after an examination of material representing many allied families. Characters that indicate relationship to the bathornithids are the following: (1) the close resemblance of the external and internal condyles, (2) the meeting of the outer and inner cnemial crests at an angle of about 80 degrees and the not rounded or smooth but angular junction (but see, however, *Bathornis cursor* below), and (3) the shape of a well-developed ridge running from the base of the inner cnemial crest to the area between the internal and external articular surfaces.

There is considerable variation in the tibiotarsi of the genus *Bathornis*, but the characters of *B. fricki* are not such as to suggest relationship with any other family. For example, the tibiotarsus of *B. geographicus* (S.D.S.M. No. 4030) has the posterior portion of the external condyle much less elevated distally (when viewed from the external side) than is found in the other species of the genus. *Bathornis fricki* resembles *B. celeripes* very closely in the characters of the external condyle. The proximal end of the tibiotarsus of *B. cursor* (M.C.Z. No. 2283) shows a few differences from both *B. fricki* and *B. celeripes*: the outer and inner cnemial crests meet not at an angle but in a smooth, rounded contour, and the area between the outer cnemial crest and the external articular surface is slightly broader in expanse. In general, the tibiotarsus of *B. fricki* resembles the published figure of *B. veredus* (Wetmore, 1937), only differing perhaps in having the internal condyle slightly less thick (when viewed from distal end).

Bathornis fricki is stratigraphically closest to *B. geographicus*, but it differs from the latter in enough characters to establish the fact that they are not conspecific. Not only is *B. geographicus* larger, but, as noted above, the posterior portion of the external condyle is less elevated distally. Also, the internal condyle of *B. geographicus* does not project anteriorly as much as it does in *B. fricki*.

The species is named in honor of the late Mr. Childs Frick, who made possible the outstanding paleontological collections from which some of the specimens described in this paper were taken.

GENUS *PARACRAX* BRODKORB, 1964

TYPE: *Paracrax antiqua* (Marsh).

DIAGNOSIS: As given for the new species, *Paracrax wetmorei*, described below.

Paracrax wetmorei, new species

Figures 3-10

TYPE: Complete right humerus (fig. 3), F:A.M. No. 42998, from upper Oligocene sediments (from one of the lowest *Protoceras* channels, about 100 feet above the base of the Poleslide member of the Brule Formation); northeast of Indian Stronghold on divide between west Big Corral Draw and Cottonwood Creek, Washington County, South Dakota; collected in 1938 by M. F. Skinner, R. L. Mefferd, and associates.

DIAGNOSIS: Complete right humerus resembling that of *Bathornis veredus* but differing in that internal condyle less distinctly raised relative to external condyle, intercondylar furrow being less well marked; entepicondyle slightly less raised distally relative to internal condyle (when seen from palmar side); brachial depression slightly less deep; distal end of shaft straighter, not curved (when viewed from side); area of attachment of anterior articular ligament slightly less pronounced; external condyle turned more internally (seen from palmar side).

MEASUREMENTS: Transverse breadth across condyles, 31.7 mm.; diameter of external condyle from palmar surface to anconal surface, 14.9 mm.; smallest transverse breadth of shaft, 15.1 mm.; depth of shaft (anconal to palmar) at same point, 11.8 mm.; total length of bone, 149.1 mm.

DESCRIPTION: Head of humerus apparently broad and rounded, greatly damaged and with external portion missing; capital groove well developed and V-shaped, and directed at about a 45-degree angle to longitudinal axis of shaft; internal tuberosity large and rounded, not constricting disto-externally into well-marked median crest, but instead crest broad and not well marked; pneumatic foramen apparently small, greatly distorted by crushing; ligamental furrow apparently only moderately developed; external side of shaft moderately straight throughout length, curving only gently at proximal and distal ends (seen from palmar side), internal side of shaft with gentle curve throughout length; shaft somewhat compressed in anconal-palmar direction; proximal end of anconal surface of shaft rounded and becoming more planar toward distal end; proximal end of palmar surface of shaft rounded but less so than anconal side and becoming more planar at distal end; when viewed from side, shaft becoming narrower distally; brachial depression only moderately well marked, internal ridge (edge of depression) poorly pronounced; area of attachment of anterior articular ligament and of entepicondylar prominence poorly developed; attachment for pronator brevis elliptical, deep, and situated on side of shaft; attachment for



FIG. 3. *Paracrax wetmorei*, F:A.M. No. 42998, complete right humerus, type specimen. *Left*: Palmar view. *Right*: Anconal view. Both $\times 1$.

flexor carpi ulnaris round and deep, and situated on palmar side of entepicondyle; entepicondyle well developed, rounded distally and pro-

jecting slightly more distad than internal condyle; entepicondyle well pronounced anconally and sloping abruptly mediad and distad to meet well-marked olecranal fossa; internal condyle rounded distally but flattening out at internal edge to form a ridge joining entepicondyle; distinct lip formed on proximal part of palmar surface of internal condyle, proximal to lip surface curving abruptly and merging with brachial depression; external surface of internal condyle sloping at about 45-degree angle to join external condyle; surface of external condyle (when viewed from side) very round; well-marked groove found where shaft meets proximal border of external condyle; ectepicondyle poorly developed; ectepicondylar prominence projecting externally beyond ectepicondyle; area between ectepicondyle and ectepicondylar prominence pronounced, elliptical, and with small irregular ridges; anconally no tricipital grooves developed so that surface slopes gently from external condyle toward entepicondyle and olecranal fossa.

REMARKS: The only humeri of *Bathornis* available for comparison are those of *B. celeripes* and *B. veredus*. Both left and right humeri (S.D.S.M. No. 422) of *B. veredus* have been somewhat crushed in a palmar-anconal direction. The distal ends curve so radically away from the longitudinal axis of the shaft that one suspects the acute curvature is not natural but is, rather, the result of fossilization. However, both bones show this curvature (the left humerus being slightly more curved), and thus possibly they are close to their original shape. The shaft of *Paracrax wetmorei* is very straight at its distal end (when viewed from the side). This can be explained partially as an artifact of preparation, since the distal end is cemented to the shaft, but the humerus of *wetmorei* almost certainly did not curve so much as did that of *B. veredus*.

Regardless of the variation possibly present in the curvature (in a palmar-anconal direction) of the humeri, other characters of the bones support the idea that *Bathornis veredus* and *Paracrax wetmorei* should be included in the same family. The general relationship of the condyles to each other, the external-internal straightness of the shafts (seen from the palmar side), the absence of tricipital grooves (and thus the accompanying smooth contours of the disto-anconal surface), and the positions of the attachments for the pronator brevis and flexor carpi ulnaris all point to a close relationship.

The humerus of *Paracrax wetmorei* is slightly less than one and a half times the size of the humeri of *Bathornis veredus*.

A more detailed comparison of the resemblances of the humerus and associated elements of *Paracrax wetmorei* to those of other families is made in the section on relationships (below).

The species is named in honor of Dr. Alexander Wetmore for his many contributions to our knowledge of the Bathornithidae and for his valuable assistance in my paleontological work.

ASSOCIATED ELEMENTS OF *PARACRAX WETMOREI*

Preserved in juxtaposition to the humerus described above were the remains of numerous other elements. Because of this close association during preservation, and because of the obvious size and morphological relationships of all the bones, there can be little doubt that they represent a single individual. All are catalogued under the same number, F:A.M. No. 42998.

ULNA

Figure 4

MATERIAL: Complete left and right ulnae. The right ulna is greatly crushed, thus requiring that the description and measurements be based almost entirely on the left ulna.

DESCRIPTION: Olecranon not elevated, but low and blunt; internal cotyla only moderately depressed, surface oriented to long axis of shaft at about 45-degree angle, palmar edge pronounced; intercotylar area slightly raised to form small ridge between cotylae; external cotyla well developed, about as large as internal cotyla, externodistal edge of internal cotyla produced to form hooklike process, surface of external cotyla slightly depressed, especially toward olecranon; impression of brachialis anticus well developed; prominence for anterior articular ligament well marked, oblong; shaft robust, nearly round in cross section, but slightly flattened in anconal-palmar direction; trochlea for external condyle (when viewed from external side) somewhat elliptical, reaching an apex distally; proximalmost portion of trochlea increasing in curvature, slight notch present where trochlea meets shaft; tendinal pit well marked, round; internal condyle pronounced, especially distally; carpal tuberosity very well developed, apex of which is somewhat wedge-shaped and oriented almost parallel to long axis of shaft; distal radial depression moderately developed, running in externo-internal direction; apparently eight papillae present for secondaries.

MEASUREMENTS: Width from tip of carpal tuberosity to external surface of bone, 13.8 mm.; width across cotylae, 20.5 mm.; width of shaft (external to internal) 80.0 mm. from proximal end of bone, 10.0 mm.; depth of shaft (anconal to palmar) 80.0 mm. from proximal end of bone, 9.1 mm.; total length of bone, 149.0 mm.

REMARKS: Included in a series of bone fragments (M.C.Z. No. 2502),

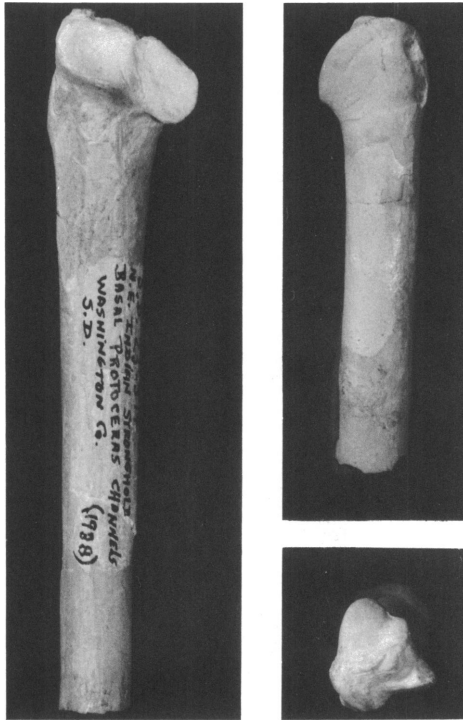


FIG. 4. *Paracrax wetmorei*, F:A.M. No. 42998, complete left ulna, type specimen. *Upper left*: Palmar view of proximal end. *Upper right*: Anconal view of distal end. *Lower right*: distal end. All $\times 1$.

which are identified simply as *Bathornis* (probably *B. celeripes*, possibly *B. veredus* or *B. cursor*), is a highly fragmented portion of the proximal end of an ulna. This bone shows many similarities to the ulna of *Paracrax wetmorei*, namely, in the shape of the much-reduced olecranon, the shape of the internal cotyla, and the proportions of the shaft. A crushed distal end of an ulna of *B. celeripes* (M.C.Z. No. 2288) is also in general agreement with the characters of *P. wetmorei*. Thus, the ulna offers additional evidence supporting the inclusion of *P. wetmorei* in the Bathornithidae.

The ulna of *Paracrax wetmorei*, like the humerus, is about one and one-half times the size of the ulna of *Bathornis celeripes*.

CARPOMETACARPUS

MATERIAL: Distal end of right carpometacarpus (somewhat crushed).

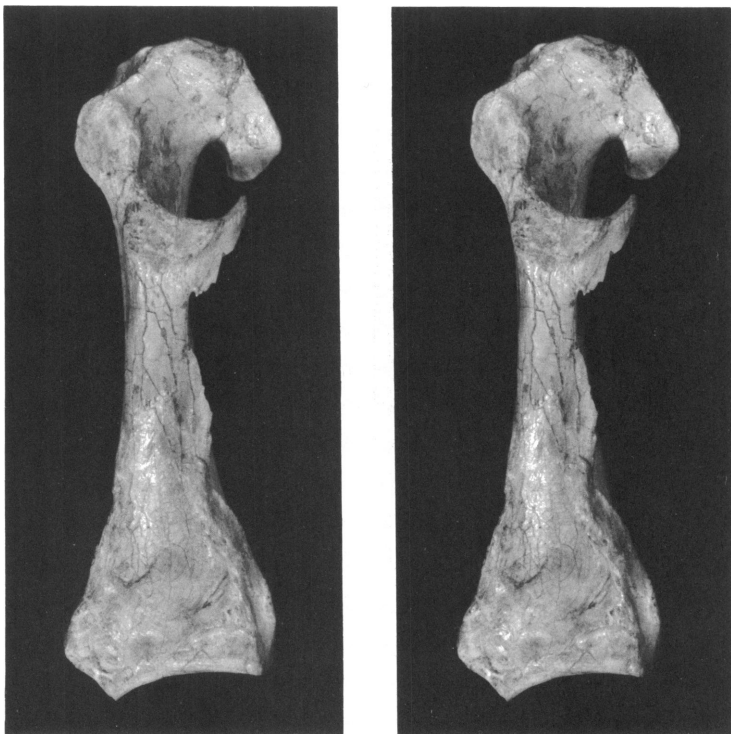


FIG. 5. *Paracrax wetmorei*, F.A.M. No. 42998, complete left coracoid, type specimen. Stereophotographs showing dorsal view. $\times 1$.

MEASUREMENTS: Width of distal end, 12.2 mm. (approximate); width of metacarpal II at distal metacarpal symphysis, 8.8 mm. (approximate).

REMARKS: Little can be said about this fragment. The facet for digit II is distinct from the area of the tuberosity of metacarpal II (when seen from distal end). In addition, the facet for digit III is separated from the facet for digit II by a moderately well-developed groove. This element is in very close agreement with the fragmented distal end of a carpometacarpus of *Bathornis celeripes* (M.C.Z. No. 2288). Another specimen of *B. celeripes* (U.S.N.M. No. 12494) is damaged and cannot be accurately compared.

CORACOID

Figures 5, 6

MATERIAL: Complete left coracoid.

DESCRIPTION: Sternal facet narrow in width, broader internally (where

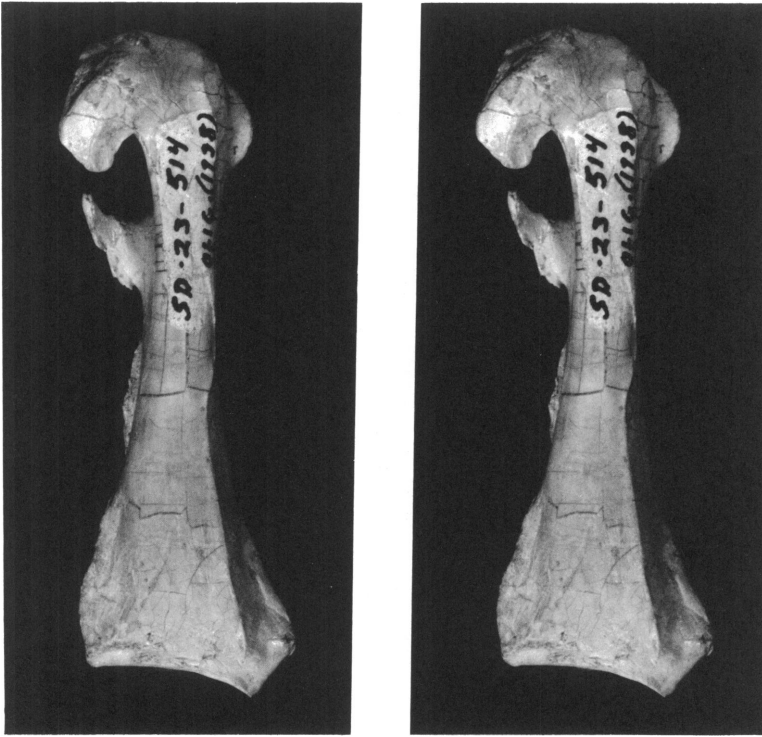


FIG. 6. *Paracrax wetmorei*, F:A.M. No. 42998, complete left coracoid, type specimen. Stereophotographs showing ventral view. $\times 1$.

it extends onto dorsal surface of bone), surface of facet smooth, not depressed; sternocoracoidal impression deep, extending distally (toward glenoid facet) almost to level of coracoidal fenestra, but not including (or at least much less deep here) externalmost portion of sternocoracoidal process; sternocoracoidal impression becoming very deep toward main axis of shaft, progressively shallower distally; sternocoracoidal process not pronounced, square; internal edge of bone proximal (i.e., toward sternum) to coracoidal fenestra lipped externally over sternocoracoidal impression to form short, stout process (attachment of coracobrachialis?), internal edge of bone proximal to this process passing almost perpendicular to surface of sternal facet, area of internal distal angle not projecting internally; coracoidal fenestra enclosed internally to form foramen (slightly damaged); procoracoid tapering to fine point that curves distally toward brachial tuberosity; surface of scapular facet planar, not depressed, roughly crescent-shaped, broader (in proxi-

modistal direction) externally; surface of scapular facet oriented nearly parallel to long axis of bone and directed slightly internally; surface of glenoid facet planar, not depressed, round, surface parallel to long axis of bone and directed slightly externally; coracohumeral surface well developed, distinctly depressed, roughly in shape of parallelogram; area of brachial tuberosity greatly pronounced, curving internally and then proximally to form hooklike process opposite procoracoid, dorsal surface of process flat, but ventral surface raised in form of well-developed ridge that diminishes externally toward head of coracoid; ventrally, surface of coracoidal shaft narrow distally (just proximal to level of brachial tuberosity), internal edge angular as surface passes dorsally, external edge rounded as surface passes dorsally; proximally, ventral



FIG. 7. *Paracrax wetmorei*, F:A.M. No. 42998, nearly complete left scapula, type specimen. Dorsal view. $\times 1$.

surface becoming broader, edges rounded both internally and externally; on ventral surface slight ridge beginning in area of sternocoracoidal process and running distally for about one-half of length of bone.

MEASUREMENTS: Total length of bone, 85.9 mm.; width from externalmost edge of glenoid facet to internalmost edge of brachial tuberosity (as seen from ventral side), 27.8 mm.; width from tip of sternocoracoidal process to tip of internal distal angle, 28.7 mm.

REMARKS: This is the only known coracoid in the Bathornithidae.

SCAPULA

Figure 7

MATERIAL: Nearly complete left scapula.

DESCRIPTION: Blade slightly flattened owing to crushing, posterior apex lacking; blade narrowed anteriorly, with edges straight and parallel, broadening posteriorly (at about midpoint of bone), then gently curving and decreasing in width to apex; surface of glenoid facet planar, not depressed, roughly round; furcular articulation lacking (broken off);

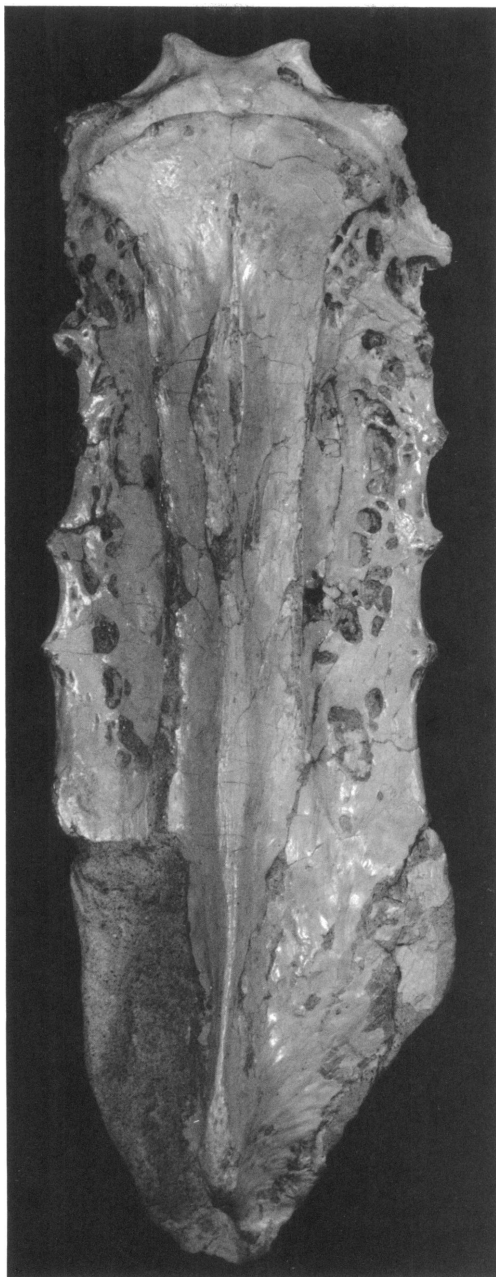


FIG. 8. *Paracrax wetmorei*, F:A.M. No. 42998, complete sternum, type specimen. Ventral view. $\times 1$.

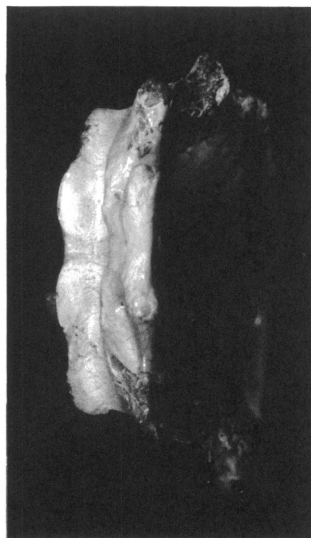


FIG. 9. *Paracrax wetmorei*, F.A.M. No. 42998, complete sternum, type specimen. *Upper*: Left side, showing anterior and posterior elevations of the keel. *Lower*: Anterior end, showing continuous coracoidal sulcus. Both $\times 1$.

very large pneumatic foramen present anteriorly between glenoid facet and area of furcular articulation; smaller pneumatic foramen present on ventral surface of scapula opposite glenoid facet; coracoidal articulation poorly developed, not raised.

MEASUREMENTS: Width of neck, 11.3 mm.; width of blade, 11.5 mm.; length of bone, 101.5 mm. (estimated 25 mm. lacking posteriorly); width of bone on line through glenoid facet, 19.5 mm.

REMARKS: This is the first record of a scapula for the family.

STERNUM

Figures 8, 9

MATERIAL: Complete, slightly damaged posteriorly.

DESCRIPTION: Coracoidal sulcus deep, quite uniform in depth except at lateralmost edges; ventral lip of coracoidal sulcus smooth and crescent-shaped, edge passing only slightly posteriorly at median line, there being no ventral manubrial spine; dorsal lip of coracoidal sulcus well developed, with two short, anteroventrally directed processes (possibly dorsal manubrial spines) on each side of midline, there being no single dorsal manubrial spine at midline; ventral labial prominence not developed, but rather its edge merging imperceptibly into ventral lip of coracoidal sulcus; sternocoracoidal process not prominent; behind sternocoracoidal process five articulations for ribs indicated, spaced evenly apart; sternal plate about same width to level of fourth rib, from there plate narrowing posteriorly; intermuscular line well marked, thickness of sternum becoming much thinner dorsal to intermuscular line; keel unusual in shape, poorly developed, slightly elevated at level of second and third ribs (apex bluntly pointed; slightly damaged and broken), curving gently dorsally (i.e., resulting in absence of keel), becoming once again elevated (i.e., produced ventrally) at posterior end of sternum (posterior apex distinctly more rounded, its posterior edge passing abruptly dorsad to sternal plate), both elevations quite low; posterolateral portions of sternum absent; in dorsal view, large pneumatic foramen situated a marked distance from dorsal lip of coracoidal sulcus, found just slightly anterior to level of first rib; apparently two additional foramina situated slightly anterolaterally on each side of large pneumatic foramen.

MEASUREMENTS: Total length (from anterior end of dorsal manubrial spine to most posterior part of bone), 161.2 mm. (approximate); height of anterior elevation of keel above intermuscular line, 10.5 mm. (approximate); height of posterior elevation of keel above surface of sternal plate (intermuscular line absent), 17.1 mm. (approximate); width of

sternum at fourth rib articulation, 53.7 mm.; length of keel at base, 129.0 mm. (approximate); width of coracoidal sulcus, 39.5 mm.

REMARKS: The discovery of the sternum establishes beyond a reasonable doubt that *Paracrax wetmorei* was flightless, and because this is the only sternum known for the family, we can assume that all the species of the family were probably flightless. Such an assumption awaits further verification. The previous opinion, based on the fragments of the carpometacarpi of *Bathornis celeripes*, the humeri of *B. celeripes*, and the well-developed hind limb bones of the various species of *Bathornis*, was that the bathornithids were cursorial in habit, but capable of moderately strong flight (Wetmore, 1933a, 1958).¹ It is reasonable to assume, as was done by Wetmore, that well-developed wing bones are an indication of flight, but care must be taken with such a generalization. A good example is the flightless cormorant of the Galapagos, *Nannopterum harrisi*, which has wing bones only slightly smaller than those of the flying members of the family. Several biological roles other than flight can be postulated for fully developed wings, and among these might be use in display behavior (as seen in the virtually flightless Kagu, *Rhinochetus jubatus*) or for defense (again, in the Kagu, or in the strong-flying screamers of the family Anhimidae).

The sternum of *Paracrax* is unique morphologically in the class Aves. No other family possesses a sternum in which the keel consists of a slight anterior and a slight posterior elevation, with the intervening portion lacking. The possibility arises that this condition may be an anomaly in development, but I consider this unlikely. The remainder of the sternum shows no evidence of an abnormal condition, and the elevations themselves appear to be normally ossified. The unique features of the sternum cannot be overemphasized, and additional material is necessary before this peculiar condition is firmly substantiated.

An examination of the sternum leads me to suspect that a moderately developed pectoralis musculature was probably present. In addition to the two elevations of the keel, there exists some area for muscle attachment on each side of the intermuscular line. The total surface possibly would have been sufficient to provide attachment for muscles that could be used in display, but it is difficult to visualize enough musculature to operate the wings for defense. Display would have to involve only a slow raising and lowering of the wings against little

¹ Storer (1960, p. 703) mentioned the flightless nature of the Bathornithidae in his discussion of *Hesperornis*. This reference to the family was a typographical error and was intended, instead, to be to *Baptornis* (Storer, personal communication).



FIG. 10. *Paracrax wetmorei*, F.A.M. No. 42998, fragmentary pelvis, type specimen. Left side. $\times 1$.

resistance, but an effective defense behavior would undoubtedly necessitate a rapid, and forceful, beating motion.

PELVIS

Figure 10

Portions of the left side of the pelvis have been preserved, but the bone is greatly broken and crushed, especially anteriorly and posteriorly. Even though the pelvis is damaged, the following features are discernible: (1) the posterior iliac crest is poorly pronounced, (2) the pubis fuses with the portion of the ischium ventral to the ilio-ischiatic fenestra to form a closed obturator foramen, (3) a small process is present on the posterior iliac crest above the antitrochanter (where the anterior and posterior iliac crests meet), (4) the ilium is rather broad and distinctly depressed, and (5) the shield is well ossified and without noticeable fenestrae.

MISCELLANEOUS MATERIAL

Included with the well-preserved material described above are numerous fragmentary elements. These include a cervical vertebra, fused lumbosacral vertebrae, the head of a femur, the distal end of a right radius, and several other broken vertebral remains. All this material is so crushed and damaged that it is impossible to describe it in any meaningful way.

***Paracrax gigantea*, new species**

Figures 11, 12

TYPE: Distal end of right humerus (fig. 11), F:A.M. No. 42999, from upper Oligocene sediments (from *Leptuachenia* beds, Poleslide member of Brule formation), 2 miles north of east of Cedar Pass, Jackson County, South Dakota; collected in 1940 by M. F. Skinner, R. L. Mefferd, and associates.

DIAGNOSIS: Distal end of right humerus resembling that of *Paracrax wetmorei* but differing in being much larger, with all features proportionally more massive; external condyle curving slightly more internally (seen in palmar view).

MEASUREMENTS: Transverse breadth across condyles, 45.5 mm.; diameter of external condyle from palmar surface to anconal surface, 21.5 mm.; smallest transverse breadth of shaft, 22.2 mm.; depth of shaft (anconal to palmar) at same point, 18.4 mm.

REMARKS: Few characters seem to exist that distinguish *Paracrax gigantea* from *P. wetmorei* except those that are probably only a mani-

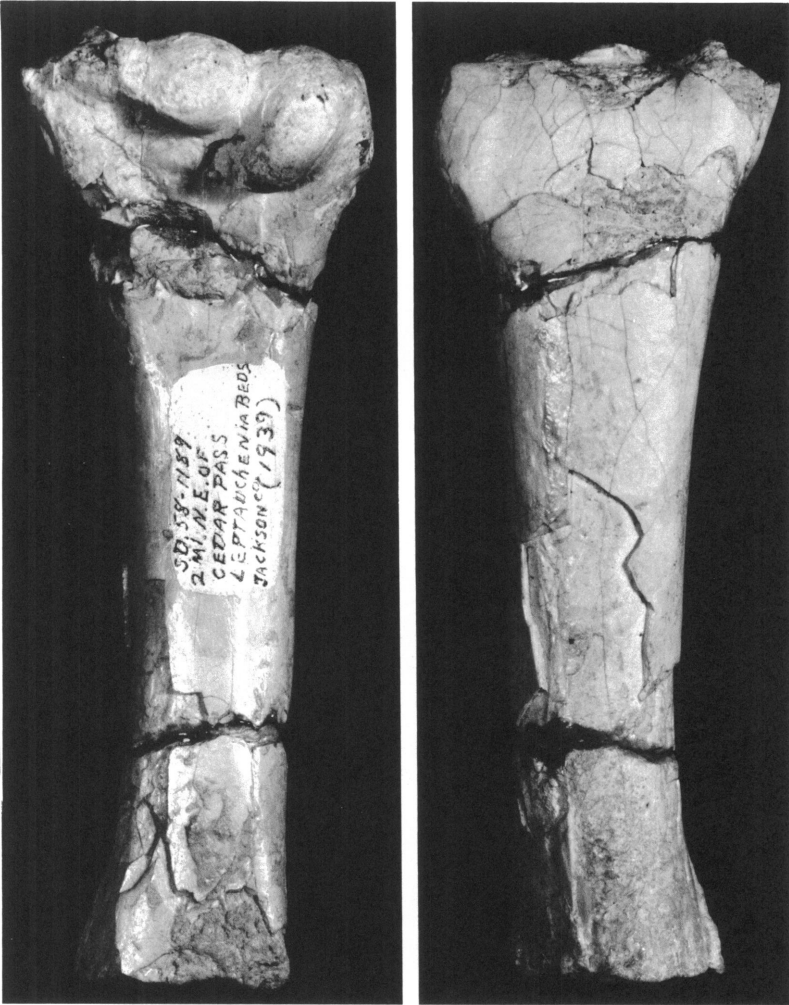


FIG. 11. *Paracrax gigantea*, F.A.M. No. 42999, distal end of right humerus, type specimen. *Left*: Palmar view. *Right*: Anconal view. Both $\times 1$.

festation of increased size. Moreover, the humerus of *P. gigantea* is so damaged in many places as to make impossible a meaningful comparison of certain features. But the shapes and topographical relationships of the condyles, the straightness of the shafts, and the absence of tri-cipital grooves, to name only a few characters, unequivocally support the notion of a close relationship between *P. wetmorei* and *P. gigantea*.

The noticeable curvature of the distal end of the humerus in *Paracrax gigantea* is definitely the result of preparation, but there apparently was more curvature than in the humerus of *P. wetmorei*. This further suggests that a great deal of variation existed in the curvature of the bathornithid humeri.

Paracrax gigantea was truly a huge bird, being about twice the size of *Bathornis veredus* and one and one-half times the size of *P. wetmorei*. If *P. gigantea* were of the same proportions as *Cariama cristata*, we could expect the former to stand between 7 and 8 feet in height. A more conservative estimate, which allows for the effect of allometry, would be about 6 feet.

REFERRED MATERIAL CARPOMETACARPUS

MATERIAL: Proximal end of right carpometacarpus (fig. 12), F:A.M. No. 42997, from upper Oligocene sediments (from middle *Protoceras* channels, about 175 feet above the base of the Poleslide member of the Brule Formation), between West Fork of Big Corral Draw and Cottonwood Creek, Washington County, South Dakota; collected in 1940 by M. F. Skinner, R. L. Mefferd, and associates.

MEASUREMENTS: Width of proximal end of bone on line from tip of process of metacarpal I through pisiform process, 29.9 mm.; width of carpal trochlea as seen from proximal end of bone, 12.3 mm.; distance from tip of process of metacarpal I to pisiform process, 13.7 mm.; height of base of metacarpal I, 13.6 mm.; measurements of metacarpal II not possible owing to distortion.

REMARKS: This carpometacarpus is referable, upon comparison with elements of *Bathornis celeripes*, to the family Bathornithidae. A comparison of the relative sizes of the carpometacarpus and humerus of *B. celeripes* indicates that a carpometacarpus the size of F:A.M. No. 42997 would have a corresponding humerus about the size of the one described above for *Paracrax gigantea*. Moreover, this carpometacarpus and the type humerus of *P. gigantea* are very close stratigraphically. Hence, it seems advisable to assign this bone to *P. gigantea*.

Based on the carpometacarpus of *Paracrax gigantea*, which is fairly well preserved, and on the six fragmentary proximal ends of *Bathornis celeripes* (M.C.Z. Nos. 2502, 2288), the characters of the bathornithid carpometacarpus are as follows: (1) pisiform process stubby and situated quite far anteriorly (close to anterior carpal fossa), (2) anterior part of carpal trochlea turned abruptly distad to meet anterior carpal fossa at an angle closely approaching 90 degrees, (3) portion of bone between



FIG. 12. *Paracrax gigantea*, F:A.M. No. 42997, proximal end of right carpo-metacarpus, referred specimen from upper Oligocene, Brule Formation. *Upper*: Stereophotographs of internal side. *Lower*: Stereophotographs of proximal end. All $\times 1$.

pisiform process and metacarpal III distinctly raised rather than depressed, (4) external (dorsal) rim of carpal trochlea rounded and not forming a noticeable apex, and (5) contour of internal (ventral) rim of carpal trochlea smooth and rounded in outline and not forming an apex posteriorly.

The carpometacarpus of *Paracrax gigantea* differs from the carpometa-



FIG. 13. *Paracrax antiqua* (Marsh), P.U. No. 537, distal portion of right humerus, type specimen. *Upper*: Palmar view. *Lower*: Stereophotographs, showing distal end. All $\times 1$.

carpi of *Bathornis celeripes* in having: (1) the process of metacarpal I directed less proximally, (2) the area of the internal ligamental fossa much more depressed, (3) the external rim of the carpal trochlea slightly more sharply elevated proximally relative to the internal rim, and (4) when viewed from posterior side, the surface of the carpal trochlea between the external and internal rims distinctly more angular and not smooth in profile (possibly an artifact of preservation).

Paracrax antiqua (Marsh)

Meleagris antiquus MARSH, 1871, p. 126.

Paracrax antiqua (Marsh): BRODKORB, 1964a, p. 303.

MATERIAL: Distal end of right humerus (fig. 13), Y.P.M. No. 537, from middle Oligocene sediments (*Oreodon* beds of Brule Formation), Gerry's Ranch, Weld County, Colorado; collected in August, 1870, by G. B. Grinnell.

DIAGNOSIS: Distal end of right humerus similar to that of *Paracrax wetmorei* but differing in having intercondylar groove slightly better developed; entepicondyle raised more anconally; internal condyle more well defined, especially on internal edge; bone decidedly smaller.

MEASUREMENTS: Transverse breadth across condyles, 24.6 mm.; other measurements were not possible.

REMARKS: This fossil was first thought to be a turkey and was named *Meleagris antiquus* by Marsh (1871). However, it was later realized, first by Shufeldt (1913) and more recently by Howard (1963, p. 21), that the relationships were not with the turkeys. Howard (*loc. cit.*) examined Shufeldt's illustration of the bone and remarked that the features of the entepicondyle were "suggestive of the Cracidae rather than the Meleagrididae." Brodkorb (1964a, 1964b) created the genus *Paracrax* for the fossil humerus, and he too agreed, after an examination of the type, that the affinities of the fossil were with the Cracidae.

The distal ends of the humeri of *Paracrax wetmorei* and *P. gigantea* are indeed similar to the humeri of cracids in many characters, and, because of this convergence, I first suspected that these birds were allied with the galliforms. But associated skeletal elements were distinctly non-galliform. Accordingly, I borrowed the type of *Paracrax antiqua* and found that it was very similar to the humeri of *P. wetmorei* and *P. gigantea*. The characters of the humerus of *P. antiqua* which place it in the Bathornithidae are: (1) the absence of tricipital grooves, (2) the position and development of the attachments for the pronator brevis and flexor carpi ulnaris, and (3) the relations of the condyles to each other, in addition to other minor characters.

The bathornithids differ from the cracids in many features of the humerus, for example: (1) the internal condyle is less elevated distally relative to the external condyle, (2) the shaft is much straighter (seen in palmar view), (3) the external condyle is more rounded distally, (4) the entepicondyle is less raised in an anconal direction and thus the olecranal fossa is less deep, and (5) the area of the external tricipital groove is not so abruptly raised in an anconal direction.

The humerus of *Paracrax antiqua* is slightly larger than the two humeri assigned to *Bathornis veredus*, and therefore it is close to the size of a humerus we would expect in *B. geographicus*. However, the characters of *P. antiqua* are definitely those of *Paracrax* rather than of *Bathornis*.

RELATIONSHIPS WITHIN THE BATHORNITHIDAE

The temporal and geographical relationships of the eight species of the Bathornithidae are summarized in table 1. The fossil history of the family is significant in that it represents what probably is one of the best-documented records for an avian family within such a short time span. Furthermore, the record will almost certainly be improved as additional Eocene and Miocene deposits are studied in detail.

In an assessment of the morphological evidence bearing on the phylogenetic lines within the family, three broad groupings ("species groups") appear: (1) the *Paracrax antiqua*, *P. wetmorei*, and *P. gigantea* group, (2) the *Bathornis celeripes* and *B. fricki* group, and (3) the *Bathornis veredus*, *B. cursor*, and *B. geographicus* group.

1. THE *Paracrax antiqua*, *Paracrax wetmorei*, AND *Paracrax gigantea* GROUP

The evidence for a close relationship of these three species is particularly strong. Their humeri resemble one another in having the con-

TABLE 1
STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION OF THE BATHORNITHIDAE^a

Provincial Age	South Dakota	Wyoming	Nebraska	Colorado
Arikareean	<i>B. geographicus</i>	<i>B. fricki</i>		
Whitneyan	<i>P. gigantea</i> <i>P. wetmorei</i>			
Orellan	<i>B. veredus</i> <i>B. celeripes</i>		<i>B. celeripes</i>	<i>P. antiqua</i>
Chadronian	<i>B. veredus</i>	<i>B. celeripes</i> <i>B. cursor</i>	<i>B. veredus</i>	<i>B. veredus</i>

^a Genera: *Bathornis*, *Paracrax*.

dyles massive and robust, the internal condyle raised slightly less distad relative to the external condyle, and in having the anconal surface of the shaft at the distal end raised and less flat. *Bathornis celeripes* and *B. veredus* differ from this first species group in the above-mentioned characters, but, as is noted above, other features of the humeri support the inclusion of all species in the same family. Because fossil material of *Paracrax antiqua* and *P. gigantea* is scarce and because the bones that we have are so fragmentary, it is not possible to draw conclusions about the relationships within this species group. However, *P. antiqua* does appear to stand somewhat apart within the genus.

2. THE *Bathornis celeripes* AND *Bathornis fricki* GROUP

Bathornis celeripes has enough characters in common with *B. fricki* to support strongly the belief that it is the ancestor of the latter species. In *B. fricki* changes have taken place in some features of the tibiotarsus, namely, in the internal condyle, the inner cnemial crest (although there

is much intraspecific variation in this character), and the shape of the head. *Bathornis veredus* and *B. cursor* possess several features that indicate a slightly more distant relationship from the *B. celeripes* and *B. fricki* line.

3. THE *Bathornis veredus*, *Bathornis cursor*, AND *Bathornis gigantea* GROUP

We do not have much new information about the relationships of *Bathornis geographicus* since Wetmore's (1942) description. At that time he expressed the opinion (p. 5) that *B. geographicus* was "representative of *Bathornis veredus* of the Chadron beds, differing from that species in the material at hand so little as to make it appear certain that it is in the line of direct descent from the older form." I note above that in *B. geographicus* the posterior portion of the external condyle of the tibiotarsus is not elevated distally as it is in the other species of *Bathornis*, and it is this character that makes me believe that *B. geographicus* is more removed from the *B. celeripes* and *B. fricki* evolutionary line. Wetmore (*loc. cit.*) pointed out that the proximal end of the tarsometatarsus of *B. geographicus* is quite similar to that of *B. celeripes* except that the former is larger and more robust. To this I agree, and it is this similarity that indicates the distant relationship of the *B. celeripes* and *B. fricki* group to the *B. veredus*, *B. cursor*, and *B. geographicus* line. The robust form of the *B. veredus* tarsometatarsus does, however, seemingly offer better grounds for relationship to *B. geographicus* than to the more delicate elements of *B. celeripes* and *B. fricki*. I have compared the tibiotarsus (P.U. No. 14400), which Wetmore (1937) identified as *B. veredus*, with the type of *B. geographicus*. These elements are extremely similar, and I certainly agree with Wetmore's statement that *B. veredus* is probably the direct ancestor of *B. geographicus*.

It is very difficult to arrive at any concrete conclusions about the relationships of *Bathornis cursor*, since the similarities it shows to *B. celeripes* and to *B. veredus* do not place it unequivocally in one species group or the other. Hence, my decision to place *B. cursor* close to *B. veredus* and *B. geographicus* is based mainly on a trend toward a more robust tarsometatarsus seen in these latter two species in contrast to a tendency toward a less robust bone as found in *B. celeripes* and *B. fricki*. The *B. veredus*, *B. cursor*, and *B. geographicus* line is represented by very little material, but, as more becomes available, the evolutionary situation should become clearer.

The relationships of the eight species of the Bathornithidae, as I presently understand them, are diagrammatically represented in figure

but such absence of material probably reflects the immature stage of avian paleontology rather than an abrupt extinction of these birds.

RELATIONSHIPS WITHIN THE CARIAMAE

Soon after their discovery the Bathornithidae were acknowledged to be related to the extant family Cariamidae (Wetmore, 1933a). Current opinion places the Bathornithidae and the Cariamidae in the superfamily Cariamoidea of the suborder Cariamae, whereas the other superfamily of the Cariamae, the Phororhacoidea, has been erected to include the families Phororhacidae, Psilopteridae, and Brontornithidae (see Wetmore, 1960; Patterson, 1941; Patterson and Kraglievich, 1960).¹ Recently, Brodkorb (1967) has reduced most of the families of the Cariamae to subfamilies and the superfamilies to families; at the same time he has shifted several taxa between his subfamilies. The result is that the Cariamidae now comprise four subfamilies: the Bathornithinae, the Psilopterinae, the Prophororhacinae (=Hermosiornithinae of Psilopteridae of Patterson and Kraglievich, 1960), and the Cariaminae.

A review of the taxa included in the Gruiformes is far outside the scope of this paper. Indeed, the generic, subfamilial, and familial relationships of the birds generally united under the common name "phororhacoids" are badly in need of revision. However, in attempting to assess the relationships of the Bathornithidae, I found it necessary to examine material of nearly all the families of the Gruiformes. This investigation has revealed that some workers (e.g., Stresemann, 1959) have excluded many groups from the Gruiformes, most of which, as I believe can be demonstrated, should be united in a single monophyletic assemblage. Much of my work will be presented at a later date. Here I restrict my

¹ The original spelling of the type genus of the Phororhacidae is *Phorusrhacos* Ameghino, 1887. This spelling has been emended on numerous occasions by several different authors, including Ameghino himself, who used the name *Phororhacos* in 1889 and Phororhacidae in 1895. Since 1889 *Phororhacos* has been accepted by virtually all workers as the type genus for this family. Brodkorb (1963, p. 111) has revived the original spelling, *Phorusrhacos*, and has used this in forming the family-group name Phorusrhacidae (see also Brodkorb, 1967).

After remaining an unused senior synonym for approximately 74 years, *Phorusrhacos* is a *nomen oblitum* under Article 23b of the International Code of Zoological Nomenclature, and as such is an invalid name. Because the name *Phorusrhacos* is invalid and because the provisions of Article 40 state that the family-group name, Phororhacidae, cannot be changed to conform with a rejection of the type genus as a junior synonym, I use *Phororhacos* and Phororhacidae for, respectively, the type-genus and family-group names. There is not the slightest doubt that much greater nomenclatural stability will result if the rules of the Code are followed in this case.

remarks to the Cariamae, the group to which the bathornithids are clearly related. It also is not my purpose to consider the validity of the various taxa of the phororhacoids; rather, I wish to place in general perspective the relationships of the bathornithids to the cariamids and to the phororhacoids. The Psophiidae (trumpeters of South America) show some features of the Cariamae, but they maintain characters of the suborder Grues; a psophiid relationship to the cariamids has previously been suggested (Fürbringer, 1902; Beddard, 1898). The similarities and differences of *Psophia* and the bathornithids are noted for certain characters in the discussion that follows.

I have chosen to follow (with certain modifications) the arrangement of the families of the Cariamae by Wetmore (1960) rather than that of Brodkorb (1967) for several reasons. First, the shifts between the superfamilies advocated by Brodkorb have not been fully substantiated, and I am somewhat apprehensive about splitting the phororhacoids into two distinct phyletic lines. Although Brodkorb's arrangement may eventually be proved correct, the available evidence suggests a possible alternative. In any case a review of the phororhacoids will be necessary before we can arrive at a satisfactory solution. Second, the reduction of all taxa to the next lowest rank in the hierarchy results in an uneven classification with respect to the other gruiform families. For example, the family Cariamidae (*sensu* Brodkorb) contains at least three different taxa that are as morphologically distinct at the family level as are other gruiform families of different suborders (e.g., the Aramidae, the Gruidae, and other families).

In the discussion that follows the Bathornithidae are compared with the other families element by element.

HUMERUS

The bathornithid humerus is very similar to that of the Cariamidae but differs as follows: (1) shaft straighter (from an anconal view), (2) tricipital grooves absent, (3) olecranal fossa less deep and with entepicondyle elevated less anconally and distally, (4) attachment for flexor carpi ulnaris situated less on side of bone and more on palmar surface, (5) ectepicondylar process not so pronounced, (6) distal end of bone curving slightly more in palmar direction (viewed from internal side), and (7) capital groove situated more horizontal with respect to longitudinal axis of bone. Compared with other elements, the humerus indicates less clearly the relationships of the bathornithids to the cariamids.

The only phororhacoid humeri that I have examined are two speci-

mens of *Psilopterus australis*. One of these (A.M.N.H. No. 9257) is damaged at the distal end; this portion has been replaced by an artificial matrix. In spite of the damage, other characters can be compared. The humerus of *Paracrax* differs from that of *Psilopterus* in having: (1) a much straighter shaft (seen in palmar view), (2) the capital groove oriented much more horizontally (more nearly perpendicular) with respect to the long axis of the bone, (3) the internal tuberosity situated much more distad relative to the proximal end of the head, (4) in general, the distal end apparently widening more gradually (the deltoid crest is thus probably much better developed), and (5) the shaft distinctly more flattened (anconal to palmar). The Princeton humerus is damaged on its anconal side at the distal end, and a detailed comparison with that of *Paracrax* is impossible. External tricipital grooves do not appear to be present in *Psilopterus*, although the surface is distinctly raised. When examined in a palmar view, the relationships of the condyles of *Psilopterus* are very similar to those of *Paracrax*.

Ameghino (1895, p. 23) illustrated the distal end of the humerus of *Palaeociconia cristata* (= Ameghino's *Phororhacos inflatus*). If the bone has been correctly depicted in the drawing (which probably is doubtful), then some notable differences from that of *Paracrax* can be seen. The area of the entepicondyle is much more pronounced in *Palaeociconia*, and the internal condyle is much less well marked. Although the illustration is not clear, tricipital grooves are not apparent, and in this respect the bone resembles that of *Paracrax*.

Ameghino (1895, p. 50) described *Phororhacos modicus* on the basis of the distal end of the humerus. Brodkorb (1967, p. 162) has synonymized *P. modicus* with *Palaeociconia cristata*. The humeri resemble each other, but in *P. modicus* the internal condyle is much more well marked (again, providing the illustrations are accurate). A proper evaluation of these species must await an examination of the types. The humerus of *P. modicus* does not add any information to our understanding of the relationships of the bathornithids.

A consideration of the humeri suggests that the Bathornithidae are more closely related to the Psilopteridae than to other phororhacoids or to the Cariamidae. Other gruiforms show still more divergent humeri.

ULNA

The ulna of *Paracrax wetmorei* shows some similarities to that of the cariamids, most notably in the poorly developed olecranon and the over-all shape and proportions of the bone. There are many minor dif-

ferences. For example, *Cariama* differs in having (1) the intercotylar area slightly more pronounced (elevated), (2) the area immediately anconal to the prominence for the anterior articular ligament developed into a short blunt process, (3) the trochlea of the external condyle much more flattened distally (seen in anconal view) and not elevated in a rounded apex, (4) the carpal tuberosity less pronounced, and (5) the trochlea for the internal condyle less pronounced distally.

In general, the ulnae of the bathornithids differ from the ulnae of the other gruiform families in that (1) the olecranon is not developed (agrees with *Cariamidae*), (2) the shape of the trochlea of the external condyle is quite different, with an apex distally, and (3) the carpal tuberosity is essentially better developed, not so blunt in the other families.

A phororhacoid ulna was not available for examination, but the ulna of *Palaeociconia cristata* was pictured by Ameghino (1895, p. 23). Little can be ascertained from the drawing, but the ulna of *Palaeociconia* definitely has a better-developed olecranon and is shorter and stubbier in proportions.

It is difficult to assess the differences of the ulna of *Paracrax* when compared with that of other groups. Even within the gruiforms the ulna is highly variable in form, and, although the ulna of the bathornithids resembles that of the *Cariamidae* in some characters, it resembles to a lesser extent that of other families in other characters. The resemblances of the bathornithids to the phororhacoids are obscure at best and no closer than to the *cariamids*.

CARPOMETACARPUS

The carpometacarpus of *Paracrax* resembles that of the *Cariamidae* in having: (1) a stubby pisiform process situated far anteriorly (more so in the *Cariamidae*), (2) the anterior portion of the carpal trochlea turning distad to meet the anterior carpal fossa at an angle approaching 90 degrees, and (3) the portion of the bone between the pisiform process and metacarpal III distinctly raised. The bathornithids differ, however, from the *cariamids* in that: (1) the external rim of the carpal trochlea is rounded and lacks a pointed apex, (2) the process of metacarpal I is directed more proximally and not directly anteriorly, (3) the posterior portion of the internal rim of the carpal trochlea does not curve so much anteriorly, and (4) the pisiform process is not situated so far anteriorly (toward the anterior carpal fossa).

The distal end of the carpometacarpus of *Paracrax wetmorei* differs from that of the *Cariamidae* in having the facet for digit II distinct

from the area of the tuberosity of metacarpal II (when seen from the distal end). The distal end of the bone resembles that of *Cariama* in being robust and strong in appearance.

The carpometacarpus of *Paracrax* shows perhaps greater resemblance to that of the Psophiidae than to that of any other extant family. In *Psophia* the process of metacarpal I is directed slightly more proximally, the shape of the internal rim of the carpal trochlea is similar, and the external rim is rounded.

No carpometacarpus of the phororhacoids was examined, but comparisons can be made with the published figures of *Palaeociconia cristata* (Ameghino, 1895, p. 23) and *Psilopterus australis* (Ameghino, 1895, p. 60; Sinclair and Farr, 1932, pl. 27). Ameghino's figure of *Palaeociconia* shows many important differences from *Paracrax*: (1) a curved, not straight, metacarpal II, (2) a well-pronounced process of metacarpal I, (3) a longer (in proximodistal direction) metacarpal I relative to the width (in an anteroposterior direction), and (4) a meeting of the carpal trochlea with the anterior carpal fossa at an angle of approximately 40–50 degrees, not nearly 90 degrees. Ameghino did not illustrate the internal view of *Palaeociconia*, so a comparison of features such as the pisiform process or ligamental fossa cannot be made. The Ameghino figure of *Psilopterus* is an internal view, but it is so poorly drawn that any reliance on it for details would be spurious. From the illustration of Sinclair and Farr, the carpal trochlea meets the anterior carpal fossa at an angle approaching 90 degrees, thus agreeing with that of the bathornithids. The process of metacarpal I points directly anteriorly, and there are some other minor differences. The carpometacarpus of the Psilopteridae resembles that of the Cariamidae more than it does that of the Bathornithidae or that of the Phororhacidae.

CORACOID

Paracrax wetmorei shows great similarity to the cariamids in the shape of the coracoid, but there are, nevertheless, distinctive differences. In *Cariama* the procoracoid and brachial tuberosity fuse, whereas in *Paracrax* they do not quite meet. Also, the sternocoracoidal impression is deeper proximally (toward the tip of the process) in *Cariama* but does not extend distally up the shaft as far as it does in *P. wetmorei*. The internal edge of the bone proximal to the coracoidal fenestra is not lipped externally over the sternocoracoidal impression in *Cariama* as it is in *Paracrax*.

The coracoid of *Psophia* is highly modified, being greatly broadened in an external-internal direction.

The coracoid of the phororhacoids is very poorly developed and thus offers no similarity at all to the coracoid of *Paracrax*. In the phororhacoids the area of the brachial tuberosity is much reduced, the scapular facet is very small, and the procoracoid is lacking, to name only a few differences.

Quite clearly, the coracoid of *Paracrax* indicates a much closer relationship between *Paracrax* and the cariamids.

SCAPULA

Little if anything can be said about the relationships of the bathornithids based on the scapula. It should be sufficient to note that the scapula of *Paracrax wetmorei* is in general agreement with that of *Cariama*. The latter differs in having the coracoidal articulation less well developed and in lacking the large anterior pneumatic foramen.

STERNUM

As is mentioned above, the shape of the keel is unique among all birds. Furthermore, other features of the sternum are peculiar and make it difficult to determine the relationships of the family based on this element. A comparison with other groups of birds does give the impression that the sternum shows the most similarities with sterna of the Gruiformes, even though the order does exhibit a great deal of variability among the included families. No other order of birds is suggestive of relationships.

In *Paracrax wetmorei* the coracoidal sulcus is continuous in the midline and is not separated bilaterally by manubrial spines. A similar condition is found in several gruiform families such as the Otididae and the Heliornithidae, but in most families the sulcus is divided. The two anteroventrally directed processes (possibly dorsal manubrial spines) on the dorsal lip are peculiar, but they seem to resemble those of some of the Gruidae (e.g., *Balearica*), the Rhynochetidae, and the Eurypygidae. The sternum of *Paracrax* is square, in contrast to being rounded at the anterior end and then tapering posteriorly. Posterior lateral processes were apparently absent, but the state of preservation does not allow us to be certain. Gruiform families such as the Rhynochetidae and the Heliornithidae, and some species of the Gruidae, have a square sternum that resembles the sternum of *Paracrax*.

The above characters point to the gruiform nature of the sternum of *Paracrax*. However, it is not possible to place *Paracrax* closer to one family than to another on the basis of this element. Whereas other parts

of the skeleton point to a close affinity with the Cariamidae, the sternum offers no clear support for such a notion. In *Cariama* the keel is well developed, there are well-developed posterior lateral processes, and the coracoidal sulcus is not continuous, all characters that differ from those of *Paracrax*.

To my knowledge the only phororhacoid sternum is that of *Psilopterus australis* pictured by Sinclair and Farr (1932) and housed at Princeton University (P.U. No. 15402). The sternum of *Psilopterus* differs in important details from that of *Paracrax*. For example, *Psilopterus* has a large keel and apparently (the specimen is damaged) a discontinuous coracoidal sulcus. The posterior end tapers to a rounded point, and posterior lateral processes are absent. These sternal characters are, of course, those for only one group of phororhacoids, and it would not be wise to infer them beyond the Psilopteridae, especially for the Bronornithidae, which were so huge as to make it almost certain that they were flightless.

The sternum, then, does not offer much help for our determining the relationships of the Bathornithidae other than at the ordinal level. Instead, the sternal features of *Paracrax* definitely establish the unique character of the family among the gruiforms.

PELVIS

The pelvis of *Paracrax wetmorei* has been broken and crushed, especially anteriorly and posteriorly. Because of this damage, statements concerning resemblances to other families are definitely restricted. Within the Gruiformes the pelvis of *Paracrax* certainly resembles that of the Cariamidae more than it does, for example, that of the Gruidae, the Aramididae, or the Psophiidae, in at least one notable character: the latter three families have a very well-developed posterior iliac crest, whereas the crest is poorly pronounced in *Paracrax* and the Cariamidae. In *Paracrax* the pubis fuses with the portion of the ischium ventral to the ilioischiatric fenestra to form an entirely closed obturator foramen. This fusion does not take place in the above-mentioned families, and it is not present in the cariamids. The condition in *Paracrax* could, of course, be individual variation in the amount of ossification, but this is unlikely. The pubis comes close to joining with the ischium in the Cariamidae, but no fusion takes place.

The pelvis of the Burhinidae shows many differences from the pelvis of the Cariamidae. Unfortunately, many of these differences are not discernible on the fossil pelvis. The posterior iliac crest is slightly better developed in the Burhinidae compared with that of the *Paracrax*. The

Cariamidae and the Bathornithidae (and, to a lesser extent, the Gruidae) possess a small process on the posterior iliac crest above the antitrochanter (at the junction of the anterior and posterior iliac crests); this process is lacking in the Burhinidae. The ilium of the Burhinidae is rather narrow and much depressed to form a troughlike structure, whereas in the Cariamidae the ilium is broader and not depressed. The ilium of *Paracrax* is apparently somewhat intermediate. It does not appear to be narrow but tends to resemble that of the Cariamidae in being broad; the bone is, however, distinctly depressed as in the Burhinidae. Whether this depression reflects the situation found in life or, as seems possible, is a result of preservation is difficult to say. The pelvis of *Paracrax wetmorei* resembles that of the Cariamidae in one additional character. The shield is moderately well ossified and without noticeable fenestrae. The pelvic shield of the Burhinidae is relatively thin and possesses many fenestrae.

When the pelvis of *Paracrax* is compared with the pelvis of *Psilopterus*, several points of similarity are at once apparent: (1) the pubis is joined to the ischium to form a closed obturator foramen, (2) there is a well-developed antitrochanter, (3) both lack a posterior iliac crest, and (4) both have a rather broad ilium (but not depressed in *Psilopterus*). There are differences between these two groups, but they are minor and could be related to size.

No definite conclusions about bathornithid affinities can be made from the pelvis, but the bone suggests a closer relationship to that of the Cariamidae and of phororhacoids rather than to that of other gruiform groups.

TIBIOTARSUS

The distal ends of the tibiotarsi of *Bathornis* are extremely similar to those of the Cariamidae, and no important differences can be discerned. The proximal ends of the tibiotarsi are different but are similar enough to suggest a close relationship. The Bathornithidae agree with the Cariamidae in having a well-developed ridge between the articular surfaces and the inner cnemial crest, a situation not found in other gruiform families (except the Psophiidae) such as the Gruidae or the Aramidae, which have a much less distinct ridge. In the cariamids the cnemial crests do not meet at a sharp angle, and the internal articular surface is more depressed. The inner cnemial crest of the cariamids resembles that of *B. celeripes* but is unlike that of *B. fricki*.

The distal end of the tibiotarsus of *Bathornis* shows very great resemblance to that of *Psilopterus* but differs in having: (1) the tendinal groove

not quite so deep, (2) the external and internal condyles slightly more separated (when viewed from distal end), and (3) the external condyle not so round distally but flattened. With regard to the proximal end of the bone, *Bathornis fricki* differs from *Psilopterus* in that the cnemial crests are less separated and the ridge between the inner cnemial crest and the articular surfaces is better developed. Another psilopterid, *Lophiornis obliquus*, shows the condyles very much closer together when compared with those of *Bathornis* (Lambrecht, 1933, p. 505, fig. 151A).

The tibiotarsus of *Bathornis*, compared with that of *Phororhacos*, has the distal end of the internal condyle flatter and the anterior portion of the condyle more slender and less robust. The external condyle of *Bathornis* is flatter anterodistally, but the posterior edge is raised more distad. The posterior end of the tibiotarsus of *Bathornis* differs from that of *Phororhacos* in the same characters mentioned above for *Psilopterus*. In addition, *Bathornis* has the external articular surface less well developed in that it is less expanded internally and proximally.

The giant size of the *Brontornis* tibiotarsus requires that great care be exercised when comparing it with other forms. Increased size and the problem of supporting more weight have undoubtedly played a major role in determining the shape of the condyles and other articular surfaces. In some respects *Brontornis* resembles *Bathornis* more than do the other phororhacoids. The condyles are flatter distally, and the internal condyle is well pronounced anteriorly. The proximal end of the tibiotarsus of *Brontornis* is damaged and cannot be compared.

The relationships of the Bathornithidae as indicated by the tibiotarsus are definitely more with the Cariamidae and the phororhacoids than with any other gruiform family. Of these two groups *Bathornis* tends to resemble the Cariamidae more closely.

TARSOMETATARSUS

Bathornis differs from the Cariamidae in the following characters of the tarsometatarsus: (1) the trochlea for digit 3 is not so pronounced distally relative to the trochlea for digit 4 (slightly less pronounced in the type of *celeripes*), (2) the trochlea for digit 2 projects far less distad relative to the trochlea for digit 3, with the trochlea for digit 2 turning posteriorly slightly more (especially so in *B. celeripes* and *B. geographicus*, less so in *B. cursor*), (3) the internal cotyla is larger relative to the external cotyla (more nearly equal in size), (4) the hypotarsus is not rectangular but more like a triangle and projects more posteriorly, and (5) the posterior metatarsal groove is less developed.

Although *Psophia* differs from *Bathornis* in some of the above char-

acters, the former more closely approaches *Bathornis* in some important features. For example, the hypotarsus of *Psophia* is more triangular but still does not project posteriorly as much as in *Bathornis*. The features associated with the trochlea for digit 2 resemble those of *Bathornis* more closely than do those of *Cariama*. In general, the proximal end is quite similar to that of *Bathornis*.

The resemblances between the bathornithids and *Psilopterus* are many: (1) the external and internal cotylae are about equal in size, (2) when viewed from the side the intercotylar prominence is the same relative size and directed in the same direction, (3) the positional relationships of the cotylae are similar (from anterior view), (4) the anterior and posterior metatarsal grooves are similar in form, and (5) the whole configuration of trochleae is very similar. Despite these resemblances *Bathornis* exhibits some important differences from *Psilopterus*: (1) the hypotarsus is much narrower (external-internal) and not rectangular (when viewed from proximal end), (2) the trochlea for digit 3 is elevated slightly less distally relative to the trochlea for digit 4 (not really true for *B. cursor*), (3) the area of the internal side of the hypotarsus and the shaft (near inner proximal foramen) are much more depressed, and (4) the proximo-internal part of the shaft posterior to the external cotyla (near external proximal foramen) is less depressed. Few characters can be ascertained from the published figures (Rovereto, 1914, pl. 9) of another psilopterid, *Procariama cristata*, but those that are present show differences from *Bathornis* in the same manner as *Psilopterus*.

Bathornis is similar to *Phororhacos* but differs in having: (1) the internal cotyla less elevated proximally and less pronounced anteriorly relative to the external cotyla and (2) a non-rectangular hypotarsus. *Phororhacos* resembles *B. celeripes* and *B. cursor* in the form of the distal end, but in the latter two species the trochleae for digits 2 and 4 are turned slightly more proximally.

The Bathornithidae do not appear to be closer to the Cariamidae than to the phororhacoids on the basis of the tarsometatarsus. Indeed, both the cariamids and phororhacoids differ in having a rectangular hypotarsus. This point is interesting, because the Psophiidae do approach the bathornithids in this character. Again, we have an element that relates the bathornithids to a group of families rather than one specific family.

SUMMARY OF THE INTERFAMILIAL RELATIONSHIPS

This study supports the inclusion of the Bathornithidae within the suborder Cariamae, a position the family has had for a number of

years. Within the Cariamae, however, the position of the bathornithids is uncertain at this time. In an effort to show relationships within the suborder, most workers have used superfamilies (or families with subfamilies) to unite what were believed to be closely related groups. Almost invariably little supporting evidence was given for these subgroupings of the Cariamae. My opinion is that it is probably unwise to recognize subgroups within the Cariamae. After a thorough revision of the phororhacoid families, it may then be possible to delimit natural subdivisions. The Psilopteridae and the Phororhacidae have been considered to be closely related and have been included in the same superfamily (Patterson and Kraglievich, 1960; Wetmore, 1960). My comparison tends to confirm this viewpoint, and I do not think there is sufficient ground for considering these phororhacoids as members of two phyletic lines as was implied by Brodkorb's (1967) classification. The psilopterids and phororhacids are probably distinct at the family level (Patterson and Kraglievich, 1960; Brodkorb, 1963), but they are much less distinct from each other than they are from the Cariamidae and the Bathornithidae. Perhaps the major conclusion of this study is that the Bathornithidae are a distinct evolutionary line within the Cariamae showing affinities to a group of families rather than to a particular family. Because it is difficult to define natural subdivisions within the suborder, I propose the following sequence of families:

Order Gruiformes

Suborder Cariamae

- Family Cunampaiidae
- Family Brontornithidae
- Family Palaeoconiidae
- Family Prophororhacidae
- Family Phororhacidae
- Family Psilopteridae
- Family Bathornithidae
- Family Cariamidae

SUMMARY

The fossil history of the Bathornithidae (Gruiformes, suborder Cariamae) is reviewed. All previously described species of *Bathornis* (*celeripes*, *veredus*, *geographicus*, *cursor*) are considered to be valid. The fossil deposits near Torrington, Wyoming, in which *B. celeripes* and *B. cursor* were first discovered, are not upper Oligocene but are, instead, lower Oligocene (late Chadronian). A new species, *Bathornis fricki*, is described from lower Miocene deposits of Wyoming. *Paracrax antiqua* (Marsh) is transferred from the Cracidae (Galliformes) to the Bathornithidae, and two new

species are described for that genus. The first, *P. wetmorei* from upper Oligocene sediments, is represented by abundant material, including the ulna, humerus, coracoid, scapula, sternum, and pelvis. The sternum is unique morphologically within the class Aves, because the keel is very much reduced and has small anterior and posterior elevations. The condition of the sternum indicates that *P. wetmorei* was flightless. The second species described, *P. gigantea*, is based on a humerus and carpo-metacarpus, both of which were collected in upper Oligocene deposits (Brule Formation) in South Dakota. This bird was quite large, perhaps standing 6 or 7 feet in height.

Three evolutionary lines are recognizable within the family. The first includes *Bathornis celeripes*, which was probably ancestral to *B. fricki*. The second line consists of *B. veredus*, *B. geographicus*, and *B. cursor*. *Bathornis veredus* was probably ancestral to *B. geographicus*; *B. cursor* shows doubtful relationships to this second line. The last group encompasses the three species of *Paracrax*. Although no species was ancestral to any other, *P. wetmorei* and *P. gigantea* were apparently more closely related, whereas *antiqua* stands somewhat apart.

This study reaffirms the view that the family is closely related to the Cariamidae and phororhacoids. However, a major conclusion is that the Bathornithidae are morphologically distinct and should not be placed in the same family as the cariamids and phororhacoids. Furthermore, little supporting evidence is seen for recognizing natural subdivisions within the Cariamae and for splitting the phororhacoids into several phyletic lines, as some authors have done. A linear sequence of families within the Cariamae is suggested at this time.

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