

American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N. Y. 10024

NUMBER 2449

FEBRUARY 11, 1971

Systematics and Evolution of the Gruiformes (Class Aves) 2. Additional Comments on the Bathornithidae, with Descriptions of New Species

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In an earlier paper I presented a review of the gruiform family Bathornithidae (Cracraft, 1968). Since the completion of that work a new genus and species from the Uintan (late Eocene) of Utah has been studied. This form, described below, is morphologically primitive within the family and possesses numerous features characteristic of the Geranoididae, the presumed ancestors of the bathornithids (Cracraft, 1969). In addition to describing the new Uintan genus, the present paper places on record new material of *Bathornis veredus*, *B. geographicus*, and *Paracrax antiqua*, describes a new species of *Bathornis* from the early Miocene of South Dakota, and makes further comments on *Paracrax wetmorei*.

MATERIALS EXAMINED

ABBREVIATIONS

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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., Department of Geological and Geophysical Sciences, Princeton University

S.D.S.M., Museum of Geology, South Dakota School of Mines and Technology, 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

In addition to the specimens described herein, I examined the following fossil material:

GERANOIDIDAE

Geranoides jepseni: P.U. No. 13257, type, tarsometatarsus, tibiotarsus

Paragrus prentici: A.C.M. No. 3626, type, tibiotarsus

Paragrus shufeldti: A.C.M. No. 6619, type, tibiotarsus; P.U. No. 18871, tarsometatarsus, tibiotarsus

Palaeophasianus meleagroides: A.M.N.H. No. 5128, type, tarsometatarsus, tibiotarsus; A.M.N.H. No. 5156, tarsometatarsus, tibiotarsus

Palaeophasianus incompletus: P.U. No. 19913, type, tarsometatarsus

Eogeranoides campivagus: P.U. No. 16179, type, tarsometatarsus, tibiotarsus

Geranodornis aenigma: A.M.N.H. No. 2628, type, tibiotarsus

BATHORNITHIDAE

Bathornis celeripes: M.C.Z. No. 2234, type, tarsometatarsus, tibiotarsus; M.C.Z. No. 2287, assorted tarsometatarsi; S.D.S.M. No. 422, tarsometatarsus, tibiotarsus, P.U. No. 16814, tarsometatarsus

Bathornis fricki: A.M.N.H. No. 2100, type, tibiotarsus

Bathornis veredus: P.U. No. 14400, tibiotarsus; P.U. No. 16813, tarsometatarsus

Bathornis cursor: M.C.Z. No. 2236, type, tarsometatarsus

Bathornis geographicus: S.D.S.M. No. 4030, type, tarsometatarsus, tibiotarsus

Paracrax wetmorei: F:A.M. No. 42998, type, postcranial skeleton (except hindlimb)

Paracrax gigantea: F:A.M. No. 42999, type, humerus; F:A.M. No. 42997, carpo-metacarpus

Paracrax antiqua: Y.P.M. No. 537, type, humerus

SYSTEMATICS AND MORPHOLOGY

ORDER GRUIFORMES

FAMILY BATHORNITHIDAE WETMORE, 1933

EUTREPTORNIS, NEW GENUS

TYPE SPECIES: *Eutreptornis uintae*, new species

DIAGNOSIS: Distal end of tibiotarsus differs from that of *Bathornis* in having the external condyles somewhat less robust, distal end of bone compressed more lateromedially and condyles elongated anteroposteriorly;

internal condyle with noticeable notch in distal border and posterior portion raised more distally (slight notch present in *B. veredus*, absent in other species of *Bathornis*); internal ligamental prominence better developed; supratendinal bridge broader proximodistally; anterior intercondylar fossa shallower relative to depth of external condyle; condyles not spread as much anteriorly.

Proximal end of tarsometatarsus differs from that of *Bathornis* in having the hypotarsus more elongated proximodistally; intercotylar prominence somewhat larger and more triangular in shape (when seen in anterior view); and bone decidedly more robust in appearance, the internal cotyla (when seen in side view) being much heavier.

REMARKS: *Eutreptornis* is placed in the Bathornithidae on the basis of several characters shared with *Bathornis* (the third genus of the family *Paracrax* lacks hindlimb material): shape of the external and internal condyles; internal condyle deeper anteroposteriorly than external; internal condyle not robust but thin lateromedially; absence of tubercle on supratendinal bridge; short external wall of supratendinal bridge and tendinal groove; hypotarsus with single central canal. All these features differentiate the bathornithids from the geranoidids and appear to represent the derived condition within this lineage.

Eutreptornis also has several morphological features that are characteristic of the genera of the Geranoididae. Among these are the posterior portion of the internal condyle raised distally; supratendinal bridge broad proximodistally; anterior intercondylar fossa tends to be shallow relative to depth of external condyle; hypotarsus long proximodistally; intercotylar prominence pointed, not blunt and rounded.

***Eutreptornis uintae*, new species**

Figures 1-3

TYPE: Distal end of left tibiotarsus, proximal end of left tarsometatarsus, A.M.N.H. No. 2092; from upper Eocene deposits (Uinta Formation, base of Myton Member ["Uinta C"]); Uinta Basin, near Ouray Agency, White River, Uintah County, Utah.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: Tibiotarsus: anteroposterior depth of external condyle, 19.0 mm.; depth of internal condyle, 21.1 mm.; depth of anterior intercondylar fossa relative to external condyle, 6.7 mm.; breadth across posterior end of condyles, 12.5 mm.; breadth across anterior end of condyles, 16.9 mm.; breadth of shaft 50.0 mm. from distal end of external condyle, 9.8 mm.; depth of shaft 50.0 mm. from distal end of

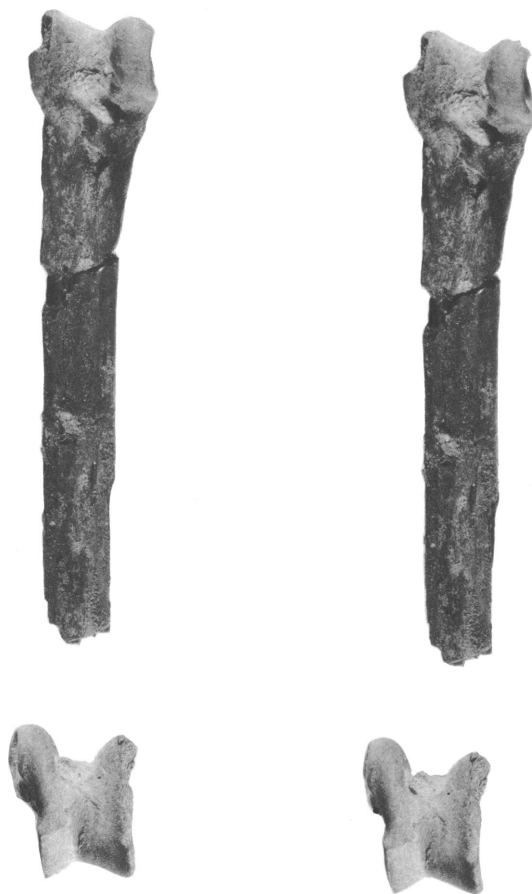


FIG. 1. *Eutryptornis uintae*, A.M.N.H. No. 2092, distal end of left tibiotarsus, type specimen. *Upper*: Stereophotographs of anterior view. *Lower*: Stereophotographs of distal end. All about $\times 1$.

external condyle, 9.6 mm. Tarsometatarsus: breadth across cotylae, 17.8+ mm.; depth from tip of intercotylar prominence to posterior part of hypotarsus, 21.6 mm. (approximate); anteroposterior depth of internal cotyla, 11.4 mm.; depth of shaft 40.0 mm. from tip of intercotylar prominence, 11.9 mm.; breadth of shaft 40.0 mm. from tip of intercotylar prominence, 9.3+ mm.; length of hypotarsus, 20.4 mm.

REMARKS: The type tibiotarsus and tarsometatarsus were articulated together within the matrix so there is no doubt they are from the same individual. Both bones were compressed lateromedially during preserva-

tion and show numerous fractures. The tibiotarsus has been least affected by the compression, and it is probable that the characters of the distal end are very close to their form during life. Several features of the tarso-metatarsus, on the other hand, exhibit the results of compression, and an entirely accurate interpretation of their form is not possible. Despite damage to the external cotyla and hypotarsus, it can be observed that



FIG. 2. *Eutreptornis uintae*, A.M.N.H. No. 2092, distal end of left tibiotarsus, type specimen. *Left*: External view. *Right*: Internal view. Both about $\times 1$.

the external cotyla is significantly smaller than the internal and that the hypotarsus has a single, centrally located canal.

ETYMOLOGY: *Eutreptornis* (Greek), alluding to a bird that is changing; *uintae*, in reference to the Uinta country of Utah where this specimen was found.

GENUS *BATHORNIS* WETMORE, 1927

Bathornis veredus Wetmore

Figure 4

Bathornis veredus WETMORE, 1927, p. 11

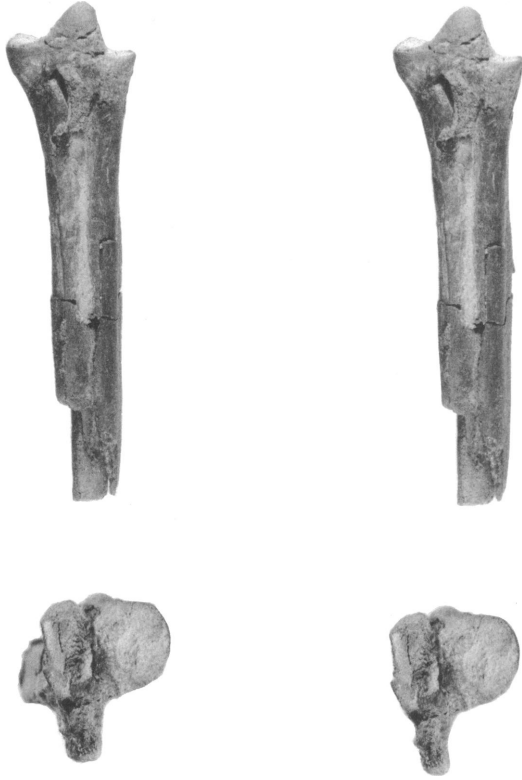


FIG. 3. *Eutreptornis uintae*, A.M.N.H. No. 2092, proximal end of left tarso-metatarsus, type specimen. *Upper*: Stereophotographs of anterior view. *Lower*: Stereophotographs of proximal end. All about $\times 1$.

MATERIAL: Distal end of left tibiotarsus, S.D.S.M. No. 5815, from lower Oligocene sediments (base of Crazy Johnson Member of Chadron Formation), NE $\frac{1}{4}$ of SW $\frac{1}{4}$, Section 6, T42N, R45W, Quinn Draw, Shannon County, South Dakota.

MEASUREMENTS: Breadth across anterior end of condyles, 17.2 mm.; breadth across posterior end of condyles, measurement not possible; anteroposterior depth of internal condyle, 16.2 mm.; depth of external condyle, 15.3 mm.; depth of anterior intercondylar fossa relative to external condyle, 6.2 mm.

REMARKS: This tibiotarsus is the fourth known specimen of *B. veredus*. The type is a distal end of a tarsometatarsus from the *Trigonias* quarry of Chadronian age (early Oligocene) of Colorado (Wetmore, 1927);

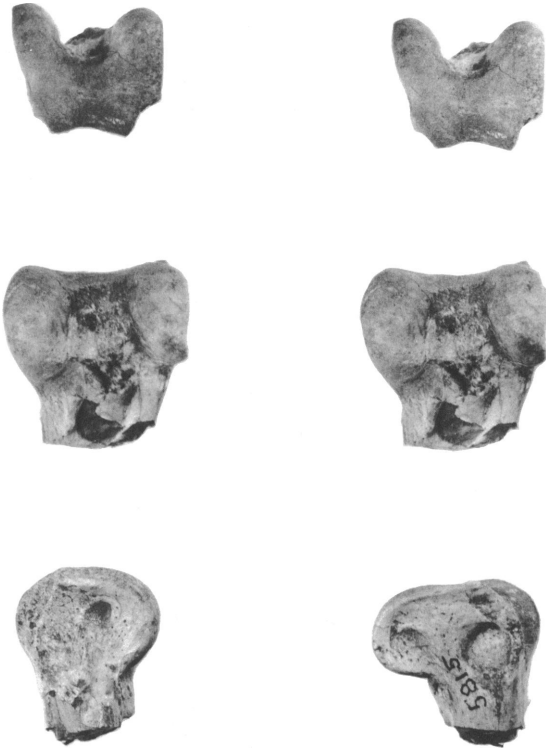


FIG. 4. *Bathornis veredus*, S.D.S.M. No. 5815, distal end of left tibiotarsus, referred specimen. *Upper*: Stereophotographs of distal end, about $\times 1$. *Center*: Stereophotographs of anterior view, about $\times 1.4$. *Lower left*: External condyle, about $\times 1.2$. *Lower right*: Internal condyle, about $\times 1.2$.

there is another distal tarsometatarsus from the Chadron Formation ("Titanotherium beds"; lower Oligocene) of Nebraska (Wetmore, 1933) and a distal tibiotarsus from the Chadron Formation ("middle Titanotherium beds") of South Dakota (Wetmore, 1937). The specimen reported on here is slightly smaller than the tibiotarsus (P.U. No. 14400) described by Wetmore (1937). It also differs from that specimen in having the area of the internal ligamental prominence slightly less developed and the internal condyle somewhat more robust.

I have also examined a distal right tibiotarsus (A.M.N.H. No. 8371) which may be referable to *B. veredus*. The specimen is badly damaged, and the internal condyle is missing. Precise geological data are lacking, but it probably comes from middle Oligocene deposits of Hat Creek Basin, Sioux County, Nebraska (M. F. Skinner, personal commun.). This

tibiotarsus differs from S.D.S.M. No. 5815 in being smaller (depth of external condyle, 14.6 mm.; depth of anterior intercondylar fossa relative to external condyle, 4.7 mm.) and with a shallower anterior intercondylar fossa. This specimen is mentioned here because it may represent an extension of *B. veredus* into the middle Oligocene.

Bathornis geographicus Wetmore

Bathornis geographicus WETMORE, 1942, p. 3

MATERIAL: Proximal end of left tarsometatarsus, S.D.S.M. No. 40155, from upper Oligocene sediments (from the *Protoceras* Channel Sandstone, Poleslide Member of Brule Formation); 7 miles east of Rockyford, Shannon County, South Dakota.

MEASUREMENTS: Breadth across cotylae, 19.4 mm.; anteroposterior depth of internal cotyla, 10.7 mm.; depth of external cotyla, 7.8 mm.

REMARKS: This is the second known specimen of *Bathornis geographicus* (see Wetmore, 1942, for a description of the type, a complete tarsometatarsus and tibiotarsus). The portions of the bone posterior to the cotylae are lacking. This tarsometatarsus agrees with the type (S.D.S.M. No. 4030) in nearly every detail except that the latter is slightly larger. The type specimen of *B. geographicus* also comes from the *Protoceras* Channel Sandstone (Brule Formation) of Shannon County, South Dakota.

***Bathornis minor*, new species**

Figure 5

TYPE: Proximal end of right tarsometatarsus, S.D.S.M. No. 6239, from lower Miocene deposits (middle of Sharps Formation), South Dakota School of Mines and Technology locality V624¹ Shannon County, South Dakota.

REFERRED SPECIMEN: Proximal end of right tibiotarsus, S.D.S.M. No. 6240; same geological and locality data as type.

DIAGNOSIS: Proximal end of tarsometatarsus differs from that of *Bathornis celeripes* Wetmore in having: the intercotylar prominence relatively less developed; internal cotyla located less distally relative to external cotyla (cotylae more nearly on same level); bone about 20 per cent smaller.

Proximal end of tibiotarsus differs from that of *Bathornis fricki* Cracraft

¹ Policy of the institution owning the holotype prohibits publication of precise locality data because of the danger that amateur collectors may cause by undue disturbance of the site. Qualified persons can obtain data from the South Dakota School of Mines and Technology.

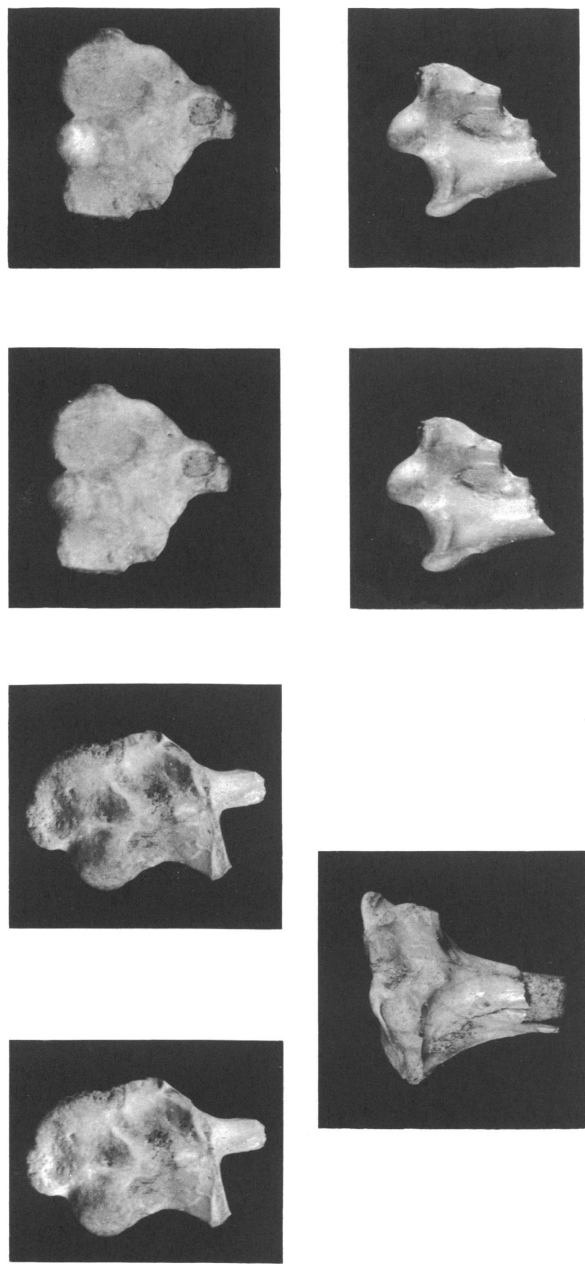


FIG. 5. *Bathornis minor*. Left, S.D.S.M. No. 6240, right tibiotarsus, referred specimen; right, S.D.S.M. No. 6239, right tarsometatarsus, type specimen. Upper left: Stereophotographs of proximal end, about $\times 1.2$. Upper right: External view, about $\times 1.2$. Lower left: Stereophotographs of proximal end, about $\times 2.1$. Lower right: Stereophotographs of anterior view, about $\times 1.7$.

A.M.N.H. No. 2100) in having the ridge running from base of inner cnemial crest to internal edge of external articular surface not raised so much, and the depressions on either side of ridge shallower; when seen in proximal view, bone somewhat less elongated anteroposteriorly; bone about 30 per cent smaller.

MEASUREMENTS: Type tarsometatarsus: breadth across trochleae, 12.2 mm.; depth of bone from tip of intercotylar prominence to posterior edge of hypotarsus, 11.9 mm.; Referred tibiotarsus: depth from tip of outer cnemial crest to posterior edge of bone, 18.3 mm.; diameter (external-internal) across head, 14.2 mm.

REMARKS: Unless additional material is found to prove the contrary, we can consider the tarsometatarsus and tibiotarsus as representing the same species. The fact that both elements were found in the same beds and were from a bathornithid of about the same size provides some measure of support, but not absolute evidence, for the conclusion of conspecificity.

There can be little doubt of a close relationship between *B. minor* and *B. fricki*, the latter species from the early Miocene of Wyoming (Cracraft, 1968, pp. 7-10). The configurations of the tibiotarsi are exceedingly similar. It seems likely *B. minor* and *B. fricki* shared a common ancestry that was on the line originating with *B. celeripes* of the early Oligocene.

Bathornis minor is the smallest species in the Bathornithidae and is, along with *B. fricki*, the last known survivor of the family.

GENUS *PARACRAX* BRODKORB

Paracrax antiqua (Marsh)

Figure 6

Meleagris antiquus MARSH, 1871, p. 126

Phalacrocorax mediterraneus SHUFELDT, 1915, p. 58

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

MATERIAL: Proximal end of right carpometacarpus, Y.P.M. No. 943; from lower or middle Oligocene deposits; Gerry's Ranch, Weld County, Colorado; collected August 6, 1870 by G. B. Grinnell (see Galbreath, 1953, p. 40, for comments on the geology and location of Gerry's Ranch).

MEASUREMENTS: Length from tip of pisiform process to posterior margin of internal rim of carpal trochlea, 10.0 mm.; width of carpal trochlea, 6.9 mm.; height (proximodistally) of base of metacarpal I, 8.9 mm.; other measurements not possible.

REMARKS: This specimen was first described as *Phalacrocorax mediterraneus* by Shufeldt (1915, p. 58, plate 15, fig. 138). Shufeldt was definite in his opinion that the carpometacarpus was from a cormorant, but in fact

Y.P.M. No. 943 differs in the following important features: the proximal end of the bone is much less compressed anteroposteriorly; the area between the pisiform process and metacarpal III is raised into a noticeable ridge; the internal margin of the carpal tuberosity possesses a "notch" just proximal to the beginning of metacarpal III, and metacarpal I is relatively much narrower (proximodistally) at its base.

There are several characters of the bathornithid carpometacarpus which, when taken in combination, seem to separate the family from all other nonpasserine families (see also Cracraft, 1968, p. 26) as follows: The pisiform process is well developed and blunt, not pointed; the ante-

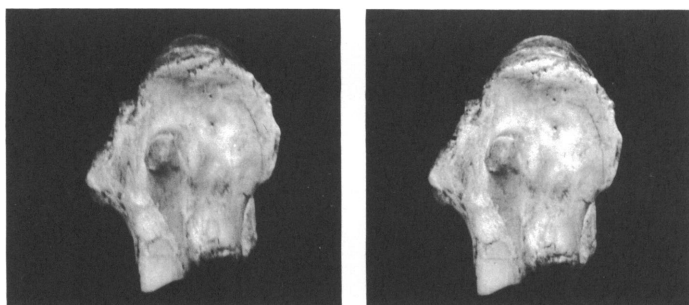


FIG. 6. *Paracrax antiqua*, Y.P.M. No. 943, proximal end of right carpometacarpus, referred specimen. Stereophotographs of internal view. About $\times 1.8$.

rior part of the carpal trochlea turns abruptly distad to meet the anterior carpal fossa at an angle approaching 90 degrees; the portion of the bone between the pisiform process and metacarpal III is distinctly raised into a broad ridge rather than being depressed; and the posterior margin of the internal rim of the carpal trochlea is "notched" just proximal to metacarpal III and the internal rim grades into the main portion of the shaft of metacarpal III. The Yale carpometacarpus described here conforms to the bathornithid pattern in all of these characters.

I refer Y.P.M. No. 943 to *Paracrax antiqua* because the specimen was collected from the same beds as the type of the species and because it is a bathornithid of about the same size. The carpometacarpus of *P. antiqua* differs from that of *P. gigantea* of the late Oligocene (Cracraft, 1968, pp. 24–28) in that the bone is about 40 per cent smaller, the external rim of the carpal trochlea is less sharply elevated proximally relative to the internal rim (but this area appears to be damaged in *P. antiqua*), and the ridge passing between the pisiform process and metacarpal III appears to be directed slightly less posteriorly.

Paracrax wetmorei Cracraft

Paracrax wetmorei CRACRAFT, 1968, p. 11

The extensive material of *Paracrax wetmorei* includes a morphologically unique sternum in which the keel is very poorly developed and with only two raised portions, one situated anteriorly and one posteriorly (Cracraft, 1968, pp. 19–24, figs. 8–9). In the earlier paper I emphasized too strongly that *P. wetmorei* probably was flightless, basing my decision on the peculiar nature of the sternum. After helpful conversations with Robert W. Storer and further consideration of the problem, I now believe that *P. wetmorei* probably had limited powers of flight. As the hindlimb elements of the species of *Paracrax* are unknown, we can only infer, using the morphology of *Bathornis* as an analogy, that *Paracrax* was predominately cursorial.

The sternum of *P. wetmorei* most closely resembles that of the living *Opisthocomus hoazin* in the shape of the keel. In the Hoatzin the posterior projection of the keel is very large and square-shaped (not low and rounded as in *Paracrax*) and the anterior projection is a continuation of the furcula (not a continuation in *Paracrax* and not situated so far anteriorly as the coracoidal sulcus). Thus, if an analogy with the Hoatzin can be used, we can assume that *P. wetmorei* could fly, and the well-developed wing bones bear out this conclusion. I mentioned earlier (Cracraft, 1968, p. 22) that a moderately developed pectoralis musculature probably existed.

If *P. wetmorei* could fly, then it is probable (although not certain) that *P. gigantea* also had powers of flight. *Paracrax gigantea* is known only from a well-developed humerus and carpometacarpus (Cracraft, 1968, pp. 24–28).

DISCUSSION

The fossils described herein do not alter previous conclusions about the intrafamilial relationships (Cracraft, 1968, pp. 29–33). It still seems likely that *B. veredus* was near the ancestry of *B. geographicus*. Moreover, *B. celeripes* is almost certainly close to the line leading to *B. fricki* and *B. minor*.

Of interest is the fact that the fossil bathornithids suggest there were species of different sizes living contemporaneously (or very nearly so) over a long period of time. In Chadronian times *B. veredus* and *B. cursor* were found with the smaller *B. celeripes*. *Bathornis veredus* and *B. celeripes* are found together in the medial Oligocene (Orellan). In the late Oligo-

cene (Whitneyan) *Paracrax wetmorei* possibly coexisted with the larger *P. gigantea*. Finally, *B. fricki* and the smaller *B. minor* are found in the early Miocene. We cannot be certain that the above pairs of species were sympatric during their respective time periods, but the record does indicate that there may have been an evolution at a given time of bathornithids differing in size, which would be one method of subdividing available food resources.

SUMMARY

A new genus and species of bathornithid, *Eutreptornis uintae*, is described for a tibiotarsus and tarsometatarsus from the late Eocene of Utah. *Eutreptornis* exhibits many morphological features found in both the bathornithids and their presumed ancestors, the Geranoididae of the Eocene of North America.

An additional tibiotarsus of *Bathornis veredus* and a tarsometatarsus of *B. geographicus* are placed on record. A new species, *B. minor*, is described from the early Miocene of South Dakota. This species was the smallest member of the family and was closely related to *B. fricki*. Contrary to my earlier assumptions, *Paracrax wetmorei* probably could fly. *Phalacrocorax mediterraneus* Shufeldt is a bathornithid, and the type carpometacarpus is referred to *Paracrax antiqua*.

ACKNOWLEDGMENTS

I am grateful to the following persons for their comments on the manuscript: Drs. Walter J. Bock, Bobb Schaeffer, Lester L. Short, and Richard Tedford. I thank Messrs. G. Stuart Keith, Morris F. Skinner, and Dr. Robert W. Storer for their helpful advice. The following persons and institutions kindly lent or permitted examination of material: Dr. Malcolm C. McKenna, Department of Vertebrate Paleontology, the American Museum of Natural History; Dr. Albert E. Wood, Amherst College Museum, Dr. Raymond A. Paynter, Jr., Museum of Comparative Zoology, Harvard University; Drs. Glenn Jepsen and Donald Baird, Department of Geological and Geophysical Sciences, Princeton University; Dr. Robert W. Wilson, South Dakota School of Mines; Dr. Clayton Ray, Division of Vertebrate Paleontology, United States National Museum, Smithsonian Institution; and Drs. John Ostrom and Peter Galton, Peabody Museum of Natural History, Yale University. This study was supported by a Frank M. Chapman Fellowship, 1969–1970, from the American Museum of Natural History.

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