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Systematics and Evolution of the Gruiformes (Class, Aves)

1. The Eocene Family Geranoididae and the Early History of the Gruiformes

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The Gruiformes have long been considered a heterogeneous order that possibly is polyphyletic in origin. The uncertainty of many workers with regard to gruiform relationships is displayed by some classifications of the Recent families. For example, Mayr and Amadon (1951) recognized 11 families in a single order. Stresemann (1959) emphasized his belief in the polyphyletic nature of these birds by acknowledging no fewer than 10 orders. Likewise, Verheyen (1960) thought many of the families sufficiently distantly related to warrant five orders. In a more conservative approach, Wetmore (1960) maintained his 12 families in a single order.

The present paper is the first in a series that will examine the systematics and evolution of the Gruiformes. The comparative functional morphology of Recent forms will provide most of the data used to discuss the relationships among the families. However, because the Gruiformes are well represented in the fossil record, emphasis will also be placed on their paleontological history in the expectation that it will provide us with considerable information about the adaptive radiation of these birds. Once adequate functional studies of Recent forms are available, it should be possible to interpret the morphological changes seen in the fossils

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in terms of functional differences. Indeed, a major goal of this and subsequent studies on the Gruiformes will be to provide data for a meaningful discussion of the factors influencing structural-functional changes in avian fossil populations.

The Gruiformes have the best fossil record of any avian order, there being slightly more than 80 known genera (Brodkorb, 1967). The oldest genus is *Telmatornis* Marsh, which includes three raillike species from the upper Cretaceous of New Jersey.[1] All other fossils placed in the order are Cenozoic in age. Gruiformes are fairly well represented in every epoch except the Paleocene and are especially numerous in Pleistocene deposits (see tables 1 and 2).

This paper is concerned with the Eocene family Geranoididae, which until now consisted of one species, *Geranoides jepseni* Wetmore, from the early Eocene of Wyoming. Additional material described herein indicates that the family had attained a remarkable diversity by the early Eocene and probably played a central role in the early radiation of certain gruiform families. Comparison of the geranoidids will be made with Recent families and with fossils from the Tertiary of North America. Some reference and comparison is also made with South American, European, and Asian fossils, particularly if specimens were available for study. A detailed examination of the abundant early Tertiary material from the Old World will have to be postponed until it can be studied on a comparative basis.

MATERIALS EXAMINED

Abbreviations

A.C.M., Amherst College Museum, Amherst

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

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

P.U., Princeton University Department of Geological and Geophysical Sciences

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

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[1] Re-examination of the type material of *Telmatornis* indicates that these species are probably not closely related to rails, even though they do resemble that family in some characters. The evidence is equivocal, but *Telmatornis* probably should still be referred to the Gruiformes (Cracraft, MS).

TABLE 1

STRATIGRAPHIC DISTRIBUTION AND ABUNDANCE OF TERTIARY FOSSIL GRUIFORMES (After Brodkorb, 1967)[a]

	Paleocene[b]	Eocene	Oligocene	Miocene	Pliocene	Pleistocene
Rallidae		6(8)[c]	2(2)	5(7)	4(6)	19(30)
Idiornithidae		2(8)				
Gastornithidae	3(5)					
Diatrymidae	1(1)	1(3)				
Gruidae[d]		7(12)	1(1)	3(4)	2(4)	2(3)
Ergilornithidae			2(2)		1(1)	
Aramidae			4(4)	1(1)		
Cunampaiidae			1(1)			
Phorusrhacidae[e]			2(2)	3(3)	2(4)	1(1)
Cariamidae[f]			4(6)	3(5)	2(3)	1(1)
Otididae		1(1)		1(1)		1(1)
Gryzajidae					1(1)	

[a] Excludes neospecies.
[b] If stratigraphy is in doubt, oldest possible age is used.
[c] Number of genera (number of species).
[d] Includes Geranoididae and Eogruidae.
[e] *Nomen oblitum;* should be Phororhacidae, see Cracraft, 1968a, p. 33.
[f] Includes some phororhacoids and Bathornithidae.

TABLE 2

GEOGRAPHIC DISTRIBUTION OF TERTIARY FOSSIL GRUIFORMES (After Brodkorb, 1967)[a]

	North America[b]	South America	Europe	Asia	Australia-New Zealand[b]	Africa[b]
Rallidae	11(18)[c]	1(2)	10(14)	1(1)	12(15)	2(2)
Idiornithidae	1(8)		2(7)			
Gastornithidae			3(5)			
Diatrymidae	1(2)		1(2)			
Gruidae[d]	6(8)		5(10)	3(4)		
Ergilornithidae				3(3)		
Aramidae	3(3)	2(2)				
Cunampaiidae		1(1)				
Phorusrhacidae[e]	1(1)	7(9)				
Cariamidae[f]	1(3)	7(12)				
Otididae			3(3)			
Gryzajidae				1(1)		

[a] Excludes neospecies.
[b] Includes records from nearby islands.
[c] Number of genera (number of species).
[d] Includes Geranoididae and Eogruidae.
[e] *Nomen oblitum;* should be Phororhacidae, see Cracraft, 1968a, p. 33.
[f] Includes some phororhacoids and Bathornithidae.

In addition to the specimens described as new, 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
Palaeophasianus meleagroides: A.M.N.H. No. 5128, type, tarsometatarsus, tibiotarsus; A.M.N.H. No. 5156, tarsometatarsus, tibiotarsus; Y.P.M. No. 896, tarsometatarsus

EOGRUIDAE

Eogrus aeola: A.M.N.H. No. 2936, type, tarsometatarsus; A.M.N.H. No. 2937, tarsometatarsus; A.M.N.H. No. 2939, tibiotarsus; A.M.N.H. No. 2940, tibiotarsus; A.M.N.H. No. 2944, tibiotarsus; A.M.N.H. No. 2947, tibiotarsus; A.M.N.H. No. 6600, tibiotarsi
Eogrus wetmorei: A.M.N.H. No. 2949, type, tibiotarsus

ARAMIDAE

Badistornis aramus: S.D.S.M. No. 3631, type, tarsometatarsus
Aramornis longurio: A.M.N.H. No. 6292, type, tarsometatarsus

BATHORNITHIDAE

Bathornis celeripes: M.C.Z. No. 2234, type, tarsometatarsus; M.C.Z. No. 2285, assorted tibiotarsi, tarsometatarsi; M.C.Z. No. 2503, assorted tibiotarsi, tarsometatarsi
Bathornis fricki: A.M.N.H. No. 2100, type, tibiotarsus
Bathornis veredus: U.S.N.M. No. 11717, cast of type, tarsometatarsus; M.C.Z. No. 2283, tibiotarsus; U.S.N.M. No. 12705, tarsometatarsus
Bathornis cursor: M.C.Z. No. 2236, type, tarsometatarsus
Bathornis geographicus: S.D.S.M. No. 4030, type, tarsometatarsus, tibiotarsus

PHORORHACIDAE

Phororhacos sp.: A.M.N.H. No. 9264, tarsometatarsus, tibiotarsus

PSILOPTERIDAE

Psilopterus australis: A.M.N.H. No. 9257, tarsometatarsus, tibiotarsus

The fossil material was compared with skeletons of Recent families in the collections of the Department of Ornithology, in the American Museum of Natural History.

SYSTEMATICS

CLASS AVES

ORDER GRUIFORMES

FAMILY GERANOIDIDAE WETMORE, 1933

GENUS *GERANOIDES* WETMORE, 1933

Geranoides jepseni Wetmore

Figure 1

MATERIAL: Type, distal ends of tarsometatarsus and tibiotarsus, P.U. No. 13257; from lower Eocene deposits, Willwood Formation; South

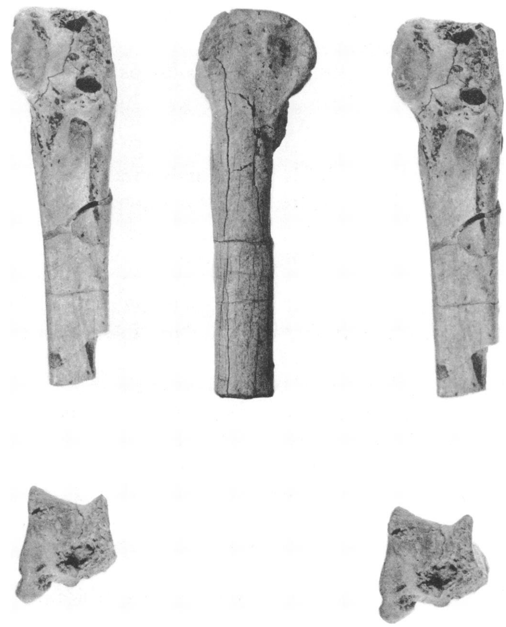

FIG. 1. *Geranoides jepseni,* P.U. No. 13257, distal end of left tibiotarsus, type specimen. *Upper left and right:* Stereophotographs of anterior view. *Upper center:* External condyle. *Lower:* Stereophotographs of distal end. All ×1.

Elk Creek, Bighorn County, Wyoming.

MEASUREMENTS: See Wetmore, 1933a.

DISCUSSION: Wetmore (1933a) proposed a new gruiform family, the Geranoididae, for a very peculiar distal end of a left tarsometatarsus. The relative positions of the trochleae, especially the development of a large intertrochlear notch, characterized a tarsometatarsus wholly unlike any other gruiform bird. A second element, the distal end of a left tibiotarsus, was not mentioned in detail, and for diagnostic purposes the emphasis was placed on the tarsometatarsus.

Re-examination of the type material leads me to the conclusion that the tarsometatarsus was probably distorted during preservation. If this conclusion is correct, statements about the relationships of this species must be made with great care. The specimen exhibits much abrasion, and several fracture lines are visible on the trochleae. Because of the unusual nature of the preservation, the second trochlea has probably "flowed" away from the third trochlea and thus did not shatter into many fragments as usually happens with avian fossils. This type of preservation is not too uncommon in fossil vertebrates, but it is often difficult to tell if it has taken place because the bones are still intact.

I agree with Wetmore that the tarsometatarsus and tibiotarsus are gruiform in their general morphology, but I would hesitate to make a decision as to familial affinities on the basis of the tarsometatarsus. Wetmore placed the Geranoididae in the superfamily Gruoidea, and more recently, Brodkorb (1967, p. 146) put *Geranoides* in its own subfamily within the Gruidae. The affinities of the Geranoididae are discussed in detail after a consideration of other related genera.

GENUS *PARAGRUS* LAMBRECHT, 1933

Paragrus prentici (Loomis)

Figure 2

Gallinuloids prentici Loomis, 1906, p. 481.

MATERIAL: Type, distal end of left tibiotarsus (also included: distal end of right femur, proximal end of fibula, phalanges, ungues), A.C.M. No. 3626 ("b4"); from lower Eocene deposits, Willwood Formation; from head of Elk Creek, 10 miles west of Otto, Bighorn County, Wyoming.

MEASUREMENTS : See table 3.

DESCRIPTION OF TYPE TIBIOTARSUS: The type tibiotarsus of *Paragrus prentici* has never been characterized adequately, and a description follows (see fig. 2): Distal end of left tibiotarsus with external condyle rounded anteriorly and posteriorly but flattened distally; posterior margin of external condyle grades smoothly into shaft, whereas anterior margin meets shaft more abruptly; in anterior view, external condyle relatively heavy and robust; anterior portion of internal condyle very rounded; distalmost edge of posterior portion of internal condyle situated more distally than edge of anterior portion; noticeable indentation situated at midline of distal border (as seen in internal view); posterior edge of internal condyle crescent-shaped; anterior intercondylar fossa

FIG. 2. *Paragrus prentici,* A.C.M. No. 3626, distal end of left tibiotarsus, type specimen. *Upper:* Stereophotographs of anterior view. *Center:* Stereophotographs of distal end. *Lower left:* External condyle. *Lower right:* Internal condyle. All ×1.

moderately deep, occupying nearly one-third the anteroposterior length of external condyle; posterior intercondylar sulcus only moderately deep, its deepest portion being very close to internal condyle, so that external side of sulcus (seen in distal view) is about three times the length of internal side of sulcus; external condyle projects posteriorly and anteriorly more than internal condyle; external condyle elevated slightly more distally relative to internal condyle.

Much of the anterior end of the *P. prentici* tibiotarsus is covered with a hard matrix, hence the characters of the supratendinal bridge and its tubercle cannot be known. However, this area is well preserved in the right tibiotarsus of *P. shufeldti* and is described below.

DISCUSSION: In his original description Loomis (1906) thought *Gallinuloides prentici* had galliform affinities. Shufeldt (1915, p. 42) expressed the opinion that *G. prentici* was gruiform and recommended placing it in the genus *Grus.* Lambrecht (1933, p. 520) erected a new genus, *Paragrus,* for this species.

TABLE 3

MEASUREMENTS (IN MILLIMETERS) OF *Paragrus Prentici* AND *P. Shufeldti*

	P. prentici Type (A.C.M. No. 3626)	*P. shufeldti* Type (A.C.M. No. 6619)	*P. shufeldti* Referred specimen (P.U. No. 18871)
Tibiotarsus			
Length of external condyle (anterior-posterior)	21.2	19.1	18.6
Length of internal condyle	20.5	20.1	—
Breadth (external-internal) across posterior portion of condyles	15.0	14.7	13.9
Breadth across anterior portion of condyles	19.7	19.9	—
Tarsometatarsus			
Breadth (external-internal) across trochleae	—	—	21.8
Breadth across middle trochlea	—	—	7.4
Depth of internal intertrochlear notch to tip of middle trochlea	—	—	10.7
Depth of external intertrochlear notch to tip of middle trochlea	—	—	9.5

The material catalogued under A.C.M. No. 3626 originally included the distal ends of a left and right tibiotarsus. Loomis chose what he thought was the right tibiotarsus as the type of *P. prentici;* this element was found associated with the femur, fibula, and other scraps of bone. The type, however, is actually a left tibiotarsus. According to Loomis the "left [sic] tibiotarsus was found in the same layer about 100 yards" from the type material. This referred element, the right tibiotarsus, was the specimen that Loomis chose to illustrate in his figure 1 and which was apparently mistaken as being the type of *P. prentici* by Brodkorb (1967, p. 146), who recognized the error of Loomis. As discussed below, this second tibiotarsus is referable to a new species. The type of *P. prentici,* then, is the left tibiotarsus and is faintly marked with the number "b4" as Loomis described.

Paragrus Shufeldti, new species

Figures 3,4,5

MATERIAL: Type, distal end of right tibiotarsus (fig. 3), A.C.M. No.

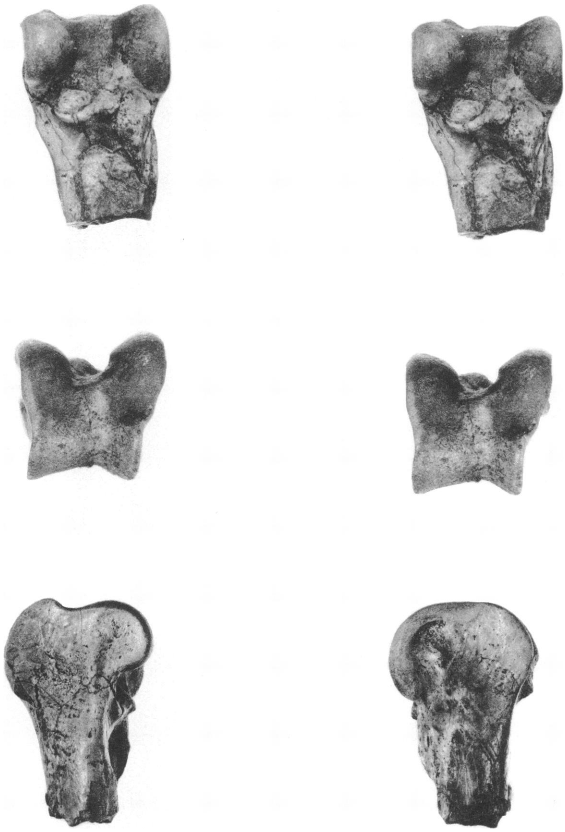

FIG. 3. *Paragrus shufeldti,* A.C.M. No. 6619, distal end of right tibiotarsus, type specimen. *Upper:* Stereophotographs of anterior view. *Center:* Stereophotographs of distal end. *Lower left:* Internal condyle. *Lower right:* External condyle. All ×1.

6619; from lower Eocene deposits, Willwood Formation; head of Elk Creek, 10 miles west of Otto, Bighorn County, Wyoming.

DIAGNOSIS: Distal end of tibiotarsus resembles that of *Paragrus prentici* (Loomis) but differs in being smaller; in having external condyle decidedly less elongated in anteroposterior direction, hence projecting much less anteriorly relative to internal condyle; the internal condyle less compressed lateromedially and meets shaft (anteroproximally) more abruptly; and the posterior intercondylar sulcus deeper.

MEASUREMENTS: see table 3.

DISCUSSION: *Paragrus shufeldti* has a well-pronounced tubercle on the anterior face of the externodistal edge of the supratendinal bridge. The tubercle is situated nearly in the middle of the bone, being offset slightly to the external side, and separated from the external condyle by a rather broad groove. The supratendinal bridge is broad proximodistally and wide lateromedially.

ETYMOLOGY: The species is named in honor of Robert W. Shufeldt, who made numerous contributions to avian paleontology and anatomy.

REFERRED MATERIAL OF *PARAGRUS SHUFELDTI*

Figures 4, 5

MATERIAL: Distal end of right tibiotarsus, distal end of right tarsometatarsus, various additional scraps of bone, P.U. No. 18871; from lower Eocene deposits, Willwood Formation; vicinity of Bone Hill, SE$\frac{1}{4}$ S16, T54N, R97W, Bighorn County, Wyoming.

DESCRIPTION: Tibiotarsus: the type (A.C.M. No. 6619) and referred tibiotarsus are nearly identical in size and morphology. There are some minor differences which I am inclined to treat as intraspecific variation. An examination of skeletons of Recent and fossil gruiform species suggests that the differences seen in the two tibiotarsi can be attributed to individual variation. Furthermore, the two fossils are very close stratigraphically and geographically. The referred tibiotarsus differs from the type in the following characters: (1) it is slightly smaller, (2) the anterior portion of the external condyle is slightly less robust, (3) the posterior edge of the external condyle is somewhat thicker, and (4) the posterior portion of the external face of the external condyle is slightly more excavated, and the excavation is more distinct.

Tarsometatarsus: Distal end of right tarsometatarsus with inner trochlea rather massive and attached to shaft by broad base that is flattened on its anterior side; inner trochlea projects distally slightly more than half the length of middle trochlea; internal (medial) edge of inner trochlea curves markedly posteroexternally (as seen in distal view); not quite one-third of inner trochlea projects posteriorly beyond posterior edge of middle trochlea (as seen in distal view); outer trochlea rather large but slightly less so than inner trochlea; outer trochlea projects distally about three-fourths the length of middle trochlea; seen from distal end, slightly less than one-fourth of outer trochlea projects posteriorly beyond posterior edge of middle trochlea; in distal view, trochleae arranged in gentle curve with convexity slightly more toward internal side; internal side of outer trochlea and external side of middle trochlea not quite parallel, outer trochlea slanted slightly posterointernally; external intertrochlear notch wide, slightly more so than internal intertrochlear notch; middle

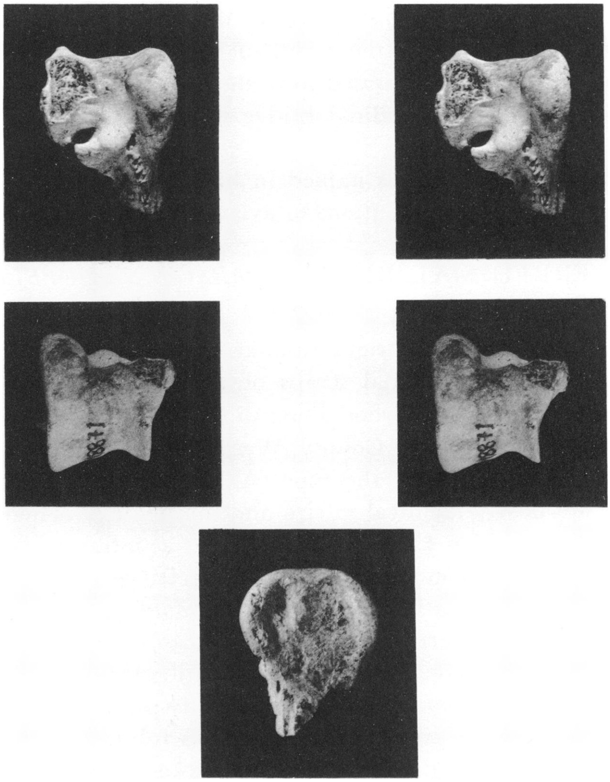

FIG. 4. *Paragrus shufeldti,* P.U. No. 18871, distal end of right tibiotarsus, referred specimen. *Upper:* Stereophotographs of anterior view. *Center:* Stereophotographs of distal end. *Lower:* External condyle. All $\times 1$.

trochlea large, rounded distally, each side possessing shallow, cupped excavation, sides nearly parallel, having a deep groove all around articulating surface; inner trochlea with extensive deep excavation on external side, and with small well-marked pit on internal side; very slight groove runs over articulating surface of inner trochlea; posteriorly directed bladelike projection on external side of inner trochlea missing; outer trochlea with extensive excavation on internal side, and external side apparently (slightly damaged) with small pit; posteriorly directed bladelike projection on external side of outer trochlea missing.

MEASUREMENTS: See table 3.

DISCUSSION: The elements of *Paragrus* call to mind features characteristic of the Bathornithidae. However, the tibiotarsi of *Paragrus* resemble that of *Geranoides* and differ from those of the bathornithids (using *Bathornis geographicus, B. celeripes,* and *B. fricki* for comparison) in having:

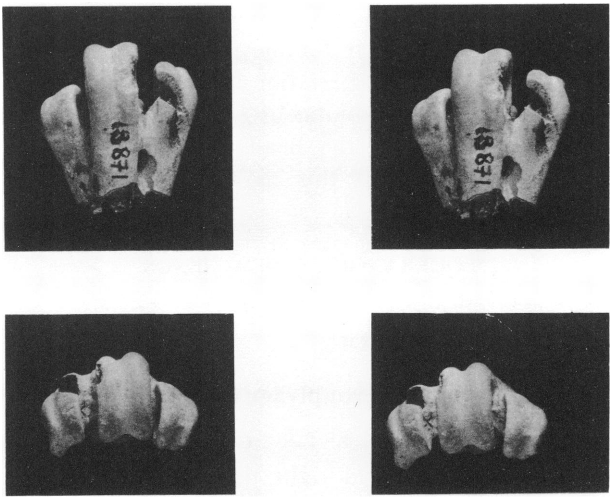

FIG. 5. *Paragrus shufeldti,* P.U. No. 18871, distal end of right tarsometatarsus, referred specimen. *Upper:* Stereophotographs of anterior view. *Lower:* Stereophotographs of distal end. All ×1.

(1) a well-pronounced tubercle on the external side of the supratendinal bridge and in having the tubercle separated from the external condyle by a broad groove, (2) very similar contours of the external condyle in being flatter distally (*B. geographicus* more closely approaches *Geranoides* and *Paragrus* in this character than do the other *Bathornis*), and (3) the anterior intercondylar fossa tending to be less deep relative to the anteroposterior length of the external condyle. Because the internal condyle is lacking in *Geranoides,* this portion cannot be compared with *Bathornis.* On the other hand, *Paragrus* shows some marked differences from *Bathornis* in the shape of the internal condyle. In *Paragrus* the posterior portion of the condyle is raised distally, and an indentation is present midway along its distal edge; hence, the internal condyle of *Bathornis* is much flatter in profile.

The tibiotarsi of *Paragrus* differ from that of *Geranoides,* as follows: (1) the posterior border of the external condyle meets the shaft in a more gradual curve, (2) the anterior border of the external condyle meets the shaft somewhat more abruptly, less smoothly, (3) the external condyle is relatively heavier and more massive, and (4) the tubercle on supratendinal bridge is slightly larger.

Until better material becomes available, I am of the opinion that *Geranoides* and *Paragrus* should be regarded as distinct genera; surely the morphological evidence indicates they were distinct in many features. In comparison with other families, the similarities of these two genera also suggest a fairly close relationship.

Included with the referred tibiotarsus and tarsometatarsus are many small fragments consisting of the head of a femur, phalanges, and parts of bone shafts. None of this material is complete enough to warrant detailed study.

EOGERANOIDES, NEW GENUS

TYPE: *Eogeranoides campivagus,* new species.

DIAGNOSIS: See below for species.

Eogeranoides campivagus, new species

Figure 6

TYPE: Distal ends of left and right tibiotarsi, proximal end of left tarsometatarsus, and distal ends of left and right tarsometatarsi, other scraps of bone, P.U. No. 16179; from lower Eocene deposits, Willwood Formation; Foster Gulch, south of Lovell, Bighorn Basin, Big Horn County, Wyoming.

DIAGNOSIS: Distal end of left tibiotarsus similar to that of *Paragrus shufeldti* but differs in that anterior end of external condyle projects slightly more anterior; posterior end of external condyle not as rounded but with a more noticeable apex (apex less diagnostic when comparison is made with type of *Paragrus shufeldti* rather than with P.U. No. 18871); tubercle on anterior face of supratendinal bridge situated more externally and much nearer to external condyle, with narrower groove between tubercle and condyle; and when viewed from distal end, posterior intercondylar sulcus apparently more curved in profile, not V-shaped, and external side of sulcus more irregular and not as planar.

MEASUREMENTS: See table 4.

ETYMOLOGY: *Eogeranoides,* referring to an early bird that was crane-like; *campivagus,* referring to wandering the plains.

DISCUSSION: The left tibiotarsus lacks the entire internal condyle, and the area of the supratendinal bridge is crushed; the right tibiotarsus has both condyles present, but they are greatly deformed, and the entire area of the supratendinal bridge and anterior intercondylar fossa is damaged beyond recognition. In spite of the need for caution when making comparisons, these elements provide us with considerable information about relationships.

Eogeranoides seems allied to the geranoidids on the basis of the presence of the tubercle on the supratendinal bridge, in having the anterior

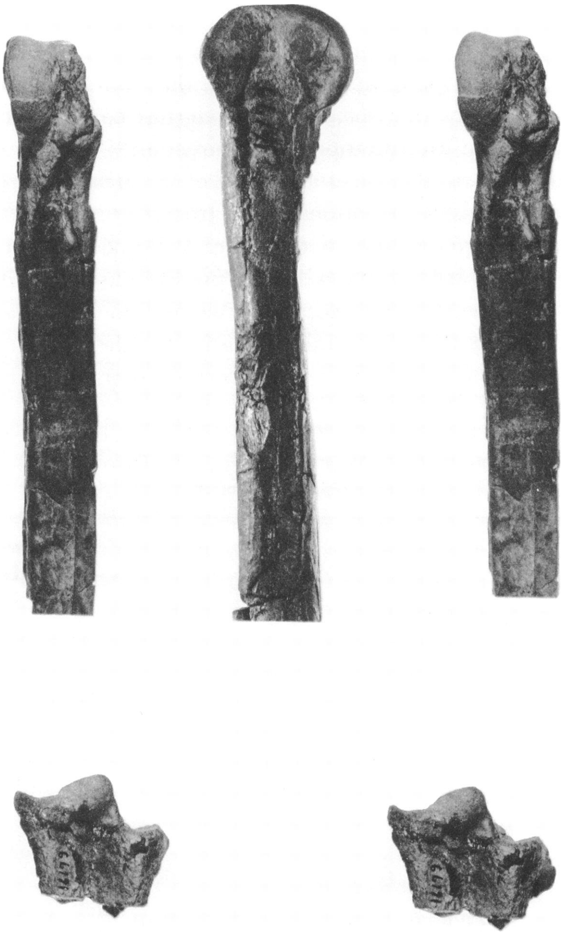

FIG. 6. *Eogeranoides campivagus,* P.U. No. 16179, type specimens. *Upper left and right:* Stereophotographs of distal end of left tibiotarsus, anterior view. *Upper center:* External condyle. *Lower:* Stereophotographs of proximal end of left tarsometatarsus, anterior view. All ×1.

intercondylar fossa much less deep relative to the anteroposterior length of the external condyle (the validity of this character in *Eogeranoides* is uncertain because of the state of preservation), and in having the external condyle flatter distally and of the same general shape. These characters, at the same time, set *Eogeranoides* apart from the bathornithids.

The tibiotarsus of *Eogeranoides* differs from that of *Geranoides* in the same characters as it does from *Paragrus*. The posterior borders of the external condyles are similar in *Geranoides* and *Eogeranoides* in that a slight apex is developed, in contrast to the rounded condyle as in *Paragrus*. Compared with *Geranoides* the external condyle of *Eogeranoides* is more elongated in an anteroposterior direction.

The distal ends of the tarsometatarsi of *Eogeranoides* are so greatly distorted that the relative positions of the trochleae in an anteroposterior direction cannot be determined with accuracy. Some comments, however, are possible in regard to the relative proximodistal positions of the trochleae. The outer trochlea seems to be in about the same position (perhaps being slightly less distally) relative to the middle trochlea as it is in *Paragrus*. In *Eogeranoides* the internal trochlea projects slightly less distally relative to the middle trochlea. The tarsometatarsi of *Eogeranoides* and *Paragrus* are apparently similar, but only additional material can confirm this.

TABLE 4

Measurements (In Millimeters) of Left Tibiotarsus of *Eogeranoides Campivagus*

	Eogeranoides campivagus (P.U. No. 16179)
Length of external condyle	20.3
Width (external-internal) of shaft 40 mm. from distal end	10.5
Depth (anterior-posterior) of shaft 40 mm. from distal end	9.7

GENUS *PALAEOPHASIANUS* SHUFELDTI, 1913

Palaeophasianus meleagroides Shufeldt

Figures 7, 8

Material: Type, distal end of left tibiotarsus, proximal and distal ends of left tarsometatarsus, assorted scraps of bone, A.M.N.H. No. 5128; from lower Eocene deposits, Willwood Formation (Gray Bull fauna); Elk Creek, east of Dry Camp 2, Bighorn Basin, Bighorn County, Wyoming.

Measurements: See table 5.

Discussion: When first described, *Palaeophasianus* was thought to be a gallinaceous bird (Shufeldt, 1913), so this poorly preserved and incompletely prepared fossil was later tentatively placed in the Cracidae by Brodkorb (1964, p. 303). After further preparation of the type I restudied *Palaeophasianus* and concluded that it was not galliform but gruiform, and I advocated placing this genus in the Aramidae (Cracraft, 1968b).

Additional sorting and identification of the avian fossils in the collection of the Department of Vertebrate Paleontology of the American Museum of Natural History, have uncovered more unstudied material of *Palaeophasianus.* Fortunately, these elements are better preserved than the type, and more accurate statements about the relationships of this species can now be made. Although I no longer consider *Palaeophasianus* to be an aramid (in the sense of having attained the morphological grade of the Recent genus *Aramus* or the fossil genera *Badistornis, Gnotornis,* and *Aramornis*), it is possible that the group (geranoidids) to which *Palaeophasianus* belonged may have been near the ancestry of the Aramidae. This possibility is discussed in more detail later.

REFERRED MATERIAL OF *PALAEOPHASIANUS MELEAGROIDES*

Figures 7, 8

MATERIAL: Distal and proximal ends of right tarsometatarsus, distal end of right tibiotarsus, other scraps of bone including distal and proximal ends of femora, A.M.N.H. No. 5156; from lower Eocene deposits, Willwood Formation (Upper Gray Bull fauna); 12 miles up Five Mile Creek, Bighorn County, Wyoming.

MEASUREMENTS: See table 5.

DISCUSSION: Some differences in size and morphology suggest that the referred specimen might represent a species distinct from *P. meleagroides.* Most of these differences may not be significant because of the fragmented and abraded condition of the type. I have decided, therefore, to consider these two fossils conspecific. It is likely that more material will be found in the near future, and the problem can be resolved then.

It is of interest to record here the differences between the type and referred specimen (compare figs. 7 and 8 with fig. 1 in Cracraft, 1968b), not only to note the diagnostic characters in case two species are involved, but also to show the intraspecific variation should they be conspecific.

The referred tarsometatarsus differs from the type in having: (1) a somewhat greater size, (2) intercotylar prominence slightly more massive and directed more proximally, (3) the area immediately distal to external rim of internal cotyla projecting more, and (4) in having the hypotarsus projecting slightly less posteriorly. The cotylae of the type are much smaller, but this is almost certainly a reflection of the somewhat smaller size of the entire bone and of the great abrasion of the

FIG. 7. *Palaeophasianus meleagroides,* A.M.N.H. No. 5156, referred specimens. *Upper:* Stereophotographs of distal end of right tarsometatarsus, anterior view. *Upper center:* Stereophotographs of distal end of right tarsometatarsus. *Lower center:* Stereophotographs of proximal end of right tarsometatarsus, anterior view. *Lower:* Stereophotographs of proximal end of right tarsometatarsus. All $\times 1$.

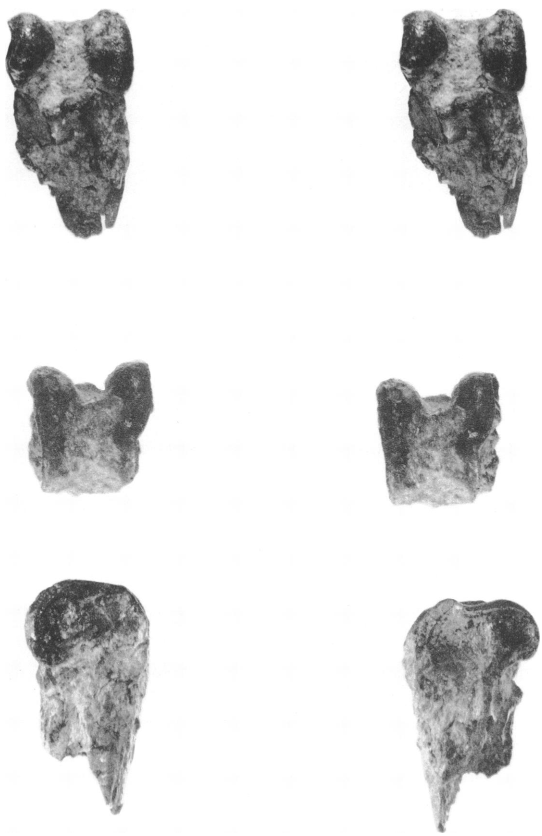

FIG. 8. *Palaeophasianus meleagroides,* A.M.N.H. No. 5156, distal end of right tibiotarsus, referred specimen. *Upper:* Stereophotographs of anterior view. *Center:* Stereophotographs of distal end. *Lower left:* External condyle. *Lower right:* Internal condyle. All $\times 1$.

rims of the cotylae (many of the measurements of the type are only approximate because of damage). Seemingly, the most important difference is the shape of the intercotylar prominence. The prominences are quite distinct, and I am uncertain if this can be attributed to intraspecific variation. The more slender hypotarsus of the type is probably a result of compression during preservation. The hypotarsus of the referred specimen apparently had three calcaneal ridges with a canal located on the internal side. The shapes of the anterior metatarsal grooves are similar in the two specimens, thus documenting the fact that this genus possessed a groove of considerable depth.

Concerning the distal end of the tibiotarsus, there is now some new information available. As I noted in the earlier paper, the positions of the condyles of the type are misleading because the bone is fragmented. The referred specimen shows clearly that the condyles are much more nearly parallel, the anterior end of the internal condyle having been displaced in the type. The shapes of the external condyles are similar in the two specimens, but the condyle of A.M.N.H. No. 5156 is much less abraded. Aside from the displacement of the internal condyle of the type, the condyles of both specimens conform closely in shape. The referred tibiotarsus shows that in *Palaeophasianus* the distoanterior part of the internal condyle curves proximally to form a distinct notch in the distal margin of the condyle (as seen from the side). Also, the posterior part of the condyle projects sharply in a distal direction.

The referred material is also important in that it reveals the characters of the supratendinal bridge; this portion of the tibiotarsus is obliterated in the type. In *Palaeophasianus* there is a well-pronounced tubercle separated from the external condyle by a moderately broad groove.

A comparison of the distal ends of the tibiotarsi shows that the posterior intercondylar sulcus in the referred specimen is much more U-shaped. There actually might be some difference between the specimens, but the surface of the sulcus is abraded in A.M.N.H. No. 5156, and this could account for its shape.

The distal end of the tarsometatarsus in the type is so fragmented that no comparisons with the referred tarsometatarsus are possible. It can be mentioned that the outer trochlea of the referred specimen is fractured and seems to be displaced slightly too much posteriorly.

An Additional Specimen of *Palaeophasianus meleagroides*

Material: Distal end of right tarsometatarsus, Y.P.M. No. 896; from middle Eocene deposits, Bridger Formation; Henry's Fork, Uinta County, Wyoming.

Discussion: This specimen was first recorded by Shufeldt (1915, p. 50, plate II, fig. 20). Recently, I compared Y.P.M. No. 896 with the type of *P. meleagroides* but was not certain of its identification because the tarsometatarsus of the type was damaged beyond recognition (Cracraft, 1968b). However, since referred specimen A.M.N.H. No. 5156 includes a fairly well-preserved tarsometatarsus, a comparison is now possible.

The size and shape of the shaft and the shapes of those remaining portions of the condyles indicate that Y.P.M. No. 896 is probably *P. meleagroides*. The specimen from Henry's Fork lacks the inner trochlea and the distal portion of the middle trochlea. The external intertrochlear notch is very narrow, but the outer trochlea was apparently compressed medially during preservation. Little can be said about this specimen, and it will be ignored in further discussions of *Palaeophasianus*.

Familial Relationships of *Palaeophasianus*

I consider *Palaeophasianus* to be a geranoidid on the basis of three lines of evidence: (1) similarity to the distal end of the tarsometatarsus of *Paragrus,* (2) similarity to the proximal end of the tarsometatarsus of *Eogeranoides,* and (3) similarity to the distal ends of the tibiotarsi of *Geranoides* and *Paragrus.*

Palaeophasianus resembles *Paragrus* in the general features of the tarsometatarsus. The trochleae are in similar relative positions, the main difference being that the inner trochlea of *Palaeophasianus* is turned less distally relative to the middle trochlea. The intertrochlear notches are wider in *Palaeophasianus,* but this difference may be partially a result of displacement of the inner and outer trochleae in *Palaeophasianus.*

Even though the proximal end of the tarsometatarsus of *Eogeranoides* is greatly damaged, the shape of the intercotylar prominence, the relative proximodistal positions of the cotylae, and the deep anterior metatarsal grooves all point to a close relationship with *Palaeophasianus* (compare figs. 6 and 8).

The distal end of the tibiotarsus in *Palaeophasianus* exhibits strong resemblances to those of *Paragrus* and, to a lesser extent, those of *Geranoides.* As seen from the side, the external condyles of *Palaeophasianus* and *Geranoides* are very similar in their contours. However, the condyle is heavier in *Palaeophasianus,* the posterior intercondylar sulcus is more U-shaped (but see previous discussion on this character), and the anterior intercondylar fossa is apparently deeper. Comparison of *Palaeophasianus* with *Paragrus* shows that the similarities of the tibiotarsi far outweigh any differences. The configurations of the internal condyles are almost identical, as is the area of the supratendinal bridge. The external condyle is slightly elongated in *Paragrus.* The condyles of *Palaeophasianus* also appear to be more nearly parallel, but this difference is not great.

Palaeophasianus incompletus, new species

Figure 9

Material: Type, distal end of right tarsometatarsus, P.U. No. 19913; from lower Eocene deposits, Willwood Formation; Dorsey Creek, 2.5 miles south of Wardell's Ranch, 6 miles south of Otto, 12 miles southwest of basin (S10, T50N, R95W), Bighorn County, Wyoming.

Diagnosis: Similar to *Palaeophasianus meleagroides* but differs in being decidedly larger.

MEASUREMENTS: See table 5.

DISCUSSION: The type of *P. incompletus* and the referred tarsometatarsus of *P. meleagroides* are slightly damaged, and a detailed comparison of the positions of the trochleae is not possible. If the unnatural posterior displacement of the outer trochlea in *P. meleagroides* is taken into account, then the positions of the trochleae in these two elements would be in close agreement.

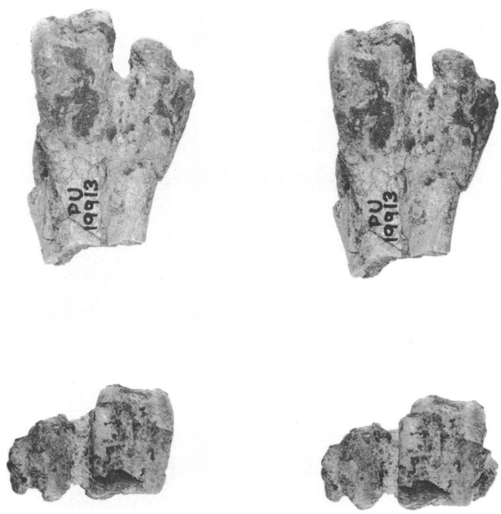

FIG. 9. *Palaeophasianus incompletus* P.U. No. 19913, distal end of right tarsometatarsus, type specimen. *Upper:* Stereophotographs of anterior view. *Lower:* Stereophotographs of distal end. All $\times 1$.

In the type of *P. incompletus* the inner trochlea is lacking, the shaft proximal to the outer trochlea is somewhat crushed, and the outer trochlea is broken and perhaps displaced slightly too much posteriorly and laterally.

Because the inner trochlea is absent, it is not possible to clearly distinguish *P. incompletus* from *Paragrus* as compared with *Palaeophasianus.* I am putting *P. incompletus* in the latter genus more or less arbitrarily; this decision is tentative and may have to be changed when new material is found.

Palaeophasianus incompletus is the largest known geranoidid.

TABLE 5

MEASUREMENTS (IN MILLIMETERS) OF *Palaeophasianus Meleagroides* AND *P. Incompletus*

	P. meleagroides Type (A.M.N.H. No. 5128)	*P. meleagroides* Referred specimen (A.M.N.H. No. 5156)	*P. incompletus* Type (P.U. No. 19913)
Tibiotarsus			
Length of external condyle	16.0	16.9	—
Length of internal condyle	—	16.6	—
Breadth across condyles at posterior end	—	12.8	—
Breadth across condyles at anterior end	16.5	16.2	—
Width of shaft 30 mm. from distal end	9.6	—	—
Depth of shaft 30 mm. from distal end	7.5	—	—
Tarsometatarsus			
Breadth (external-internal) across cotylae	18.5	20.7	—
Depth of proximal end (from inter-cotylar prominence to posterior edge of hypotarsus)	19.0	17.4	—
Width of shaft 30 mm. from tip of intercotylar prominence	11.7	11.1	—
Depth of shaft 30 mm. from tip of intercotylar prominence	9.9	9.8	—
Breadth across trochleae	—	23.0	—
Breadth of middle trochlea	—	6.8	10.4
Depth (anterior-posterior) of middle trochlea	—	11.1	15.5

GERANODORNIS, NEW GENUS

TYPE: *Geranodornis aenigma,* new species.

DIAGNOSIS: See below for species.

Geranodornis aenigma, new species

Figure 10

TYPE: Distal end of right tibiotarsus, A.M.N.H. No. 2628; from

FIG. 10. *Geranodornis aenigma,* A.M.N.H. No. 2628, distal end of right tibiotarsus, type specimen. *Upper left and right:* Stereophotographs of anterior view. *Upper center:* External condyle. *Lower:* Distal end. All ×1.

middle Eocene deposits, Bridger Formation; Church Buttes, Church Buttes, Uinta County, Wyoming.

DIAGNOSIS: Similar to *Geranoides jepseni* Wetmore but differs in that the external condyle is more rounded and not flattened distally and decidedly heavier; anterior intercondylar fossa slightly deeper relative to the anteroposterior length of external condyle; tubercle on supratendinal bridge located more distally (relative to main part of bridge) and closer to external condyle, the groove between tubercle and condyle not so broad; supratendinal bridge broader proximodistally and depressed more on internal side; and tendinal groove more marked.

MEASUREMENTS: See table 6.

ETYMOLOGY: *Geranodornis*, referring to a cranelike bird; *aenigma*, referring to the uncertain relationships of the species.

DISCUSSION: The inclusion of *Geranodornis* in the Geranoididae is based mainly on the features of the area of the supratendinal bridge and their similarity to those of the other genera discussed above. The closeness of the tubercle to the external condyle recalls that in *Eogeranoides*, although the contours of the external condyles are very different in these genera.

TABLE 6

MEASUREMENTS (IN MILLIMETERS) OF *Geranodornis Aenigma*

	Geranodornis aenigma (A.M.N.H. No. 2628)
Length of external condyle	15.8
Width of shaft 30 mm. from distal end	9.0
Depth of shaft 30 mm. from distal end	7.3

The external condyle of *Geranodornis* is unlike those of the other geranoidid genera in being more rounded distally and not flattened. The internal condyle is lacking in *Geranodornis*.

No other family of fossil or Recent gruiforms with which I am acquainted possess the characters of *Geranodornis*. Its age, geographic distribution, but especially its morphological resemblances to geranoidid genera (compared with other gruiforms) are all strong arguments for including *Geranodornis* in the Geranoididae at this time.

RELATIONSHIPS WITHIN THE GERANOIDIDAE

It is possible that the Geranoididae, as defined above, are polyphyletic. If true, the Geranoididae could be considered to represent two or more gruiform lineages that attained a similar morphological grade. However, I am unable to place any genus of this family clearly in another family, fossil or Recent, and various characters of the different elements seem to unite the genera. Hence, I will assume that they form a natural group.

It is extremely difficult to reach concrete conclusions about relationships within the family. Several characters of one genus might suggest affinities with another genus, but one or more unique features of either would appear to rule out this relationship. It will probably be impossible to reach a decision about the relative "goodness" of given taxonomic characters until we have more information regarding the functional morphology of the hind limb. All that can be done now is to point out probable affinities and to discuss the evidence pro and con.

I have already compared and noted the differences between the tibiotarsi and tarsometatarsi of *Palaeophasianus* and *Paragrus*. The similarities of the external and internal condyles and the area of the supratendinal bridge in the tibiotarsi strongly indicate a close relationship of these genera. Although the tarsometatarsi are somewhat more distinct, I do not believe they are so distinct as to be used as evidence against an immediate common origin. It may be necessary to unite *Paragrus* and *Palaeophasianus* into a single genus when additional *Paleophasianus* material is discovered, but present evidence suggests their distinctness.

The shape of the external condyle in *Eogeranoides* closely approaches that of *Paragrus prentici* (less so than that of *P. shufeldti*) and seems to indicate affinity. However, the different position of the tubercle on the supratendinal bridge questions this conclusion. Several hypotheses can be advanced to explain this difference. The position of the tubercle in *Eogeranoides* could be the result of damage in preservation or simply a consequence of variation. If so, *Eogeranoides* would probably best be included in *Paragrus*. Detailed examination has convinced me that the position of the tubercle in *Eogeranoides* is probably not the result of events during preservation; the tubercle and the ridge situated immediately proximal to it appear in their natural position. The difference in the position of the tubercle is greater than what I would expect as characteristic of individual or intrageneric variation, but still the factor of variation cannot be discounted. Second, *Paragrus prentici* may not actually be similar to *P. shufeldti* in the characters of the supratendinal bridge (the similarities of the external condyles in *P. prentici* and *Eogeranoides* suggest this possibility). This hypothesis cannot be determined because of the hard matrix on the type of *P. prentici*. If this second alternative were true, and if the tubercle were in the same position as in *Eogeranoides*, then *P. prentici* and *Eogeranoides* could be placed either separate from *P. shufeldti* (which would emphasize the differences of the tubercle) or united with that species. I believe the great similarities between the two species of *Paragrus* suggest that the tubercle of *P. prentici* will in fact be found to resemble that of *P. shufeldti* when the former is finally known. The distinctness of *Paragrus* and *Eogeranoides* is further indicated by the greatly distorted right tibiotarsus of the latter genus. The anterior end of the internal condyle is not damaged significantly, and it apparently differs from that of *Paragrus* in being longer anteroposteriorly and less robust lateromedially. Thus, I think *Eogeranoides* will prove to be generically distinct from *Paragrus.* A relatively close relationship of *Paragrus* and *Eogeranoides* is indicated by the resemblance between the proximal ends of the tarsometatarsi of *Eogeranoides* and *Palaeophasianus.*

Geranoides is related to *Eogeranoides, Paragrus,* and *Palaeophasianus* but probably more closely to the latter two genera. The shape of the external condyle and the configuration of the supratendinal bridge are similar in *Geranoides, Paragrus,* and *Palaeophasianus* (the differences were noted earlier). Furthermore, even if we admit the distortion of the tarsometatarsus of *Geranoides* it is still possible that the intertrochlear notches were wide originally. If so, then the tarsometatarsus of *Geranoides* is very similar to those of *Paragrus* and *Palaeophasianus* in the positions of the trochleae.

The only genus that seems truly to stand apart is *Geranodornis.* The position of the tubercle relatively near the external condyle is reminiscent of *Eogeranoides* rather than of the other genera. The shape of the external condyle is unlike any of the geranoidid genera. I have already listed reasons for including *Geranodornis* in the Geranoididae, but this decision is tentative pending new material.

In summary, then, I would argue in favor of a more recent common ancestry for *Geranoides, Paragrus,* and *Palaeophasianus,* with *Eogeranoides* possibly diverging earlier from the line leading to these three genera. *Geranodornis* separated still earlier or perhaps had a unique origin altogether.

RELATIONSHIPS OF THE GERANOIDIDAE

Geranoides jepseni was first allocated to its own family within the superfamily Gruoidea (Wetmore, 1933a). This arrangement has been accepted by most workers until recently when Brodkorb (1967) considered *Geranoides,* Balearicinae (including *Paragrus*), Eogruinae, and Gruinae to be separate subfamilies of the Gruidae.

In an effort to understand the significance of the geranoidids with regard to the early history of the Gruiformes, a comparison was made with certain gruiform families.

COMPARISON WITH THE GRUIDAE

The geranoidids exhibit clear morphological differences from the gruids (= the Gruinae *sensu stricto* and Balearicinae *sensu* Brodkorb, 1967). Compared with *Grus* and *Balearica* the following differences of the tibiotarsus are shown by all genera of the Geranoididae: (1) distal margin of external condyle without an indentation (indentation absent from *Balearica* but shape of condyle very different from geranoidids), (2) condyles not nearly as separated anteriorly, (3) in anterior view, internal side (i.e., internal condyle, internal ligamental prominence) projects much less, (4) tubercle on supratendinal bridge less developed, and (5) internal condyle less elongated anteroposteriorly. Many other differences can be tabulated when the comparison is made with the individual genera of the Geranoididae. The external condyle of *Grus* would be similar to that of the geranoidids (especially that of *Paragrus* and *Eogeranoides*) if it were not for the indentation. The internal condyle of the gruids tends to be flatter distally, more elongated, and with a larger internal ligamental prominence.

Marked differences are also seen in a comparison of the tarsometatarsi. The geranoidids (based upon *Paragrus, Geranoides,* and *Palaeophasianus*) differ in having: (1) the inner trochlea turned much less posteriorly and more in a plane with other trochleae, (2) the middle trochlea more elongated anteroposteriorly (as seen in distal view), and (3) the outer trochlea turned slightly less posteriorly relative to the middle trochlea.

The proximal end of the tarsometatarsus in *Palaeophasianus* shows some important differences from those of the gruids. In *Palaeophasianus* the hypotarsus is much nearer the external side, whereas in the cranes it is situated more in the middle or even somewhat toward the internal side. Moreover, the gruid hypotarsus becomes much narrower posteriorly and hence is more triangular in shape. The external cotyla of *Palaeophasianus* is about the same size as the internal cotyla and not decidedly smaller as in the cranes. The intercotylar prominence of *Palaeophasianus* is not as broad lateromedially nor as blunt as its tip.

Comparison with the Eogruidae

There can be little doubt that the Eogruidae are fairly closely related to the Gruidae (Wetmore, 1934; Brodkorb, 1967). The Eogruidae are particularly interesting because they are Eocene in age and can thus provide, when compared with the contemporary geranoidids, a better measure of divergence among early gruiform groups.

In a comparison of the tibiotarsus the geranoidids appear more similar to *Eogrus* than to the gruids. The external condyle is similar in the first two families, but in *Eogrus* the posterior portion of the condyle is elevated more distally so that its profile is diagonal instead of horizontal. The external condyle of *Eogrus* has only a slight indentation in its distal margin. The resemblances of *Eogrus* are stronger to the geranoidid genera *Paragrus* and *Eogeranoides* because of their having a more elongated external condyle.

The condyles of *Eogrus* are more nearly parallel than in the gruids and resemble the geranoidids more closely. The tubercle on the supratendinal bridge is also less well developed in *Eogrus* than in the gruids.

The internal condyle of *Eogrus* shows no significant differences from those of *Paragrus*. *Eogrus* differs from *Palaeophasianus* in perhaps having the condyles slightly more elongated.

The differences *Eogrus* shows in the characters of the tibiotarsus can be summarized, as follows: (1) the shape of external condyle is as noted above, but also the condyle projects more posteriorly, and (2) the supratendinal bridge is much narrower proximodistally.

In the characters of the tarsometatarsus *Paragrus* and *Palaeophasianus* differ from that of *Eogrus*, as follows: (1) the outer and inner trochleae are situated more distally relative to the middle trochlea, (2) the middle trochlea is less elongated proximodistally, (3) the outer and inner trochleae are relatively heavier, more massive, especially at their bases, and (4) the outer trochlea is turned slightly less posteriorly with the outer intertrochlear notch less wide at its base (this assumes unnatural displacement of the outer trochlea in *Palaeophasianus*). As seen from the distal ends, the relative positions of the trochleae are very similar in the genera.

The proximal end of the tarsometatarsus of *Palaeophasianus* also resembles that of *Eogrus* more than it does the gruids. In *Eogrus* and *Palaeophasianus* the hypotarsus is in the same relative position and the cotylae are of the same relative size. The intercotylar prominence of *Eogrus* is intermediate in shape between *Palaeophasianus* and the gruids. There are several minor differences between *Eogrus* and *Palaeophasianus*, but they are not significant.

Comparison with the Aramidae

Because of my earlier belief that *Palaeophasianus* was aramid in some of its characters (Cracraft, 1968b) and because *Geranodornis* also appears aramid-like, it is necessary to make a comparison with the limpkins.

Of the geranoidid genera, *Geranodornis* most closely resembles the Recent genus *Aramus*, mainly because of the round shape of the external condyle; the condyles of these two genera are exceedingly similar in shape and position. *Geranodornis* does differ from *Aramus* in some important characters: (1) the tubercle is less well developed and separated from the external condyle by a shallow groove (in *Aramus* the tubercle is larger, directed more internally, and is without a well-marked groove); (2) supratendinal bridge is not as depressed but is situated more anteriorly relative to position of tubercle, and (3) the anterior intercondylar fossa is less deep relative to length of external condyle. Because the internal condyle of *Geranodornis* is missing, additional characters are not available for comparison.

Despite the differences stated above, *Geranodornis* and *Aramus* share some similarities that suggest relationship: the shape of the external condyles and posterior intercondylar sulcus, the presence of a tubercle (also present in other families), and the shape of the tendinal groove and shaft.

Two fossil aramids, *Badistornis aramus* from the middle Oligocene of South Dakota and *Aramornis longurio* from the middle Miocene of Nebraska, were available for comparison with the geranoidids (see Wetmore, 1926, 1940). Both fossil aramids are represented by a tarsometatarsus.

Badistornis is quite distinct from both *Paragrus* and *Palaeophasianus* in having the inner trochlea turned very far posteriorly. The inner trochleae of *Aramornis* and *Aramus,* on the other hand, are situated only slightly more posteriorly than they are in *Paragrus* and *Paleophasianus.* The aramids differ from the geranoidids in having the inner trochlea also situated less distally relative to the middle trochlea. The tarsometatarsi of the geranoidids differ from those of the aramids in that the intertrochlear notches are wider (especially in *Palaeophasianus*) and the bones are more robust. The middle and outer trochleae of *Paragrus, Aramornis,* and *Aramus* are very similar in shape and position.

The proximal end of the tarsometatarsus of *Badistornis* is damaged but some similarities to *Palaeophasianus* can be noted: (1) the cotylae of *Badistornis* are of the same size, (2) the intercotylar prominence is of the same general shape (somewhat rounder in *Badistornis*) and projects in the same direction (as seen in side view), and (3) the relative proximodistal positions of the cotylae are similar (the relationships of *Badistornis* are uncertain and will be discussed in detail at a future date). The hypotarsus of *Aramus* differs from that of *Palaeophasianus* only in being somewhat broader at its base and in projecting posteriorly slightly less.

Comparison with the Bathornithidae

Except for one species from the early Miocene, the Bathornithidae are an Oligocene group that previously has been considered most closely related to the South American phororhacoids and cariamids (Wetmore, 1933b, 1933c, 1937, 1942, 1958; Cracraft, 1968a). However, the bathornithids also show significant similarities to the Geranoididae.

The tibiotarsus of *Paragrus* differs from that of *Bathornis* in the following characters: (1) the external condyle is flatter distally, with posterior portion not raised in distal direction, (2) a tubercle is present on the supratendinal bridge (absent from *Bathornis*), and (3) the internal condyle is not flattened distally but the posterior portion is raised distally to form a slight notch in the middle of the condyle. There are some remarkable similarities, however, especially in the general shape and relative positions of the condyles, the posterior intercondylar sulcus, and the anterior intercondylar fossa.

Bathornis geographicus, more so than *B. celeripes* or *B. fricki,* resembles *Paragrus* in the shape of the external condyle, but, on the other hand, *B. geographicus* differs more than *B. celeripes* in having the anterior intercondylar fossa much deeper.

Of the other genera of the Geranoididae, *Geranodornis* shows no similarities to the bathornithids except perhaps in having the external condyle slightly raised posteriorly. *Palaeophasianus* resembles and differs from *Bathornis* in the same characters as does *Paragrus.* The external condyle of *Eogeranoides* superficially resembles that of *B. geographicus,* but this probably has little significance compared with the differences. *Geranoides* resembles *B. geographicus* (but not *B. fricki* or *B. celeripes*) closely in the shape of the external condyle but differs from that species in the same characters as does *Paragrus.*

Bathornis approaches *Paragrus* and *Palaeophasianus* in having the posteromedial side of the shaft and internal condyle depressed. This region appears less depressed in *Geranodornis* and in *Geranoides.*

With regard to the positions and shapes of the trochleae, the tarsometatarsi of *Paragrus* and *Bathornis celeripes* are extremely similar. *Paragrus* differs in having: (1) the external intertrochlear notch wider, (2) the inner trochlea projecting slightly more distally relative to the middle trochlea, and (3) the entire bone more stubby and massive. The tarsometatarsus of *B. celeripes* is more slender distally rather than being broad as in *Paragrus.*

The tarsometatarsi of *B. veredus, B. cursor,* and *B. geographicus* are stubbier and more massive than that of *B. celeripes* and thus are closer in form to that of *Paragrus.* Compared with *B. cursor* the tarsometatarsus of *Paragrus* differs in having: (1) the inner trochlea turned slightly more posteriorly, (2) the external intertrochlear notch wider, and (3) the middle trochlea larger, not quite so blunt, with distal tip less rounded and with a slight apex.

Paragrus differs from a fragmentary specimen (U.S.N.M. No. 12705) of *B. veredus* and from *B. geographicus* in that (1) the inner trochlea is more massive and turned somewhat more posteriorly, (2) the inner trochlea projects more distally relative to the middle trochlea, and (3) the middle trochlea is more elongated anteroposteriorly (as seen in distal view).

The tarsometatarsus of *Palaeophasianus* is somewhat compressed anteroposteriorly and thus resembles *Bathornis celeripes* to a certain degree. The trochleae of the two genera are very similar in shape and position (except for the wider notches in *Palaeophasianus*).

The proximal end of the tarsometatarsus in *Palaeophasianus* and *Eogeranoides* exhibits some general resemblances to that of *Bathornis* in the shape and position of the hypotarsus (more similar to *B. geographicus,* less so to *B. celeripes*), the relative sizes of the cotylae, the shape of the anterior metatarsal groove, and the shape of the intercotylar prominence. *Bathornis* differs in having well-developed lips present on the anterior rims of the cotylae, the slope of the side of the shaft just distal to the internal cotyla (as seen in anterior view) straight and not bulging, and the side of the shaft just distal to the external cotyla (in anterior view) directed more laterally and not more in line with the longitudinal axis of the shaft. In *Bathornis celeripes* the external cotyla is situated slightly more distad relative to the internal cotyla than it is in *Palaeophasianus;* the latter genus and *B. geographicus* are similar in the relative positions of the cotylae.

Comparison with the Phororhacoids

Because the bathornithids show possible affinities to the phororhacoids, the geranoidids were compared with the latter group in the hope of clarifying their early history.

The tibiotarsi of *Psilopterus* and *Phororhacos* (Psilopteridae and Phororhacidae, respectively) resemble those of the bathornithids more than they do those of the geranoidids. The external condyles of the phororhacoids are rounder distally, slightly more elevated posteriorly, and do not project anteriorly so much. The internal condyle, although not similar to those of the bathornithids, is also quite different from those of the geranoidids. In phororhacoids the condyle is flat distally, without an indentation, and is proportionally much larger anteriorly. The phororhacoids resemble the bathornithids, but not the geranoidids, in the absence of a tubercle on the supratendinal bridge. The posterior intercondylar sulcus is more U-shaped and not so angular as in the geranoidids. The anterior intercondylar fossa of the phororhacoids is deeper relative to the length of the external condyle and is also longer proximodistally.

The tarsometatarsi of the phororhacoids resemble those of the geranoidids more than do the tibiotarsi. The geranoidids differ in having: (1) intertrochlear notches wider, (2) the shaft not as flattened anteroposteriorly near distal end, and (3) the outer and inner trochleae broader lateromedially and slightly more elongated proximodistally. There is, however, a general similarity in the distal ends of the tarsometatarsi.

The proximal ends of the tarsometatarsi are similar in the phororhacoids and geranoidids except for the shape of the hypotarsus. The hypotarsus of the phororhacoids is rectangular in shape with no canals and hence is extremely different from that of the geranoidids (as represented by *Palaeophasianus*). The two groups are similar in the shape of the anterior metatarsal groove, the relative sizes and proportions of the cotylae, and the shape and position of the intercotylar prominence (the prominence does appear proportionally larger in the phororhacoids).

Comparison with the Cariamidae

The cariamids appear related to the bathornithids and phororhacoids, so they are here compared with the geranoidids.

The tibiotarsus of *Cariama* is more similar to those of the phororhacoids and bathornithids than to those of the geranoidids. The external condyle of *Cariama* closely resembles those of *Geranoides, Paragrus,* and *Palaeophasianus* but is raised more posteriorly. The internal condyle of *Cariama* is flatter distally, without the deep indentation found in the geranoidids. In *Cariama* the tubercle on the supratendinal bridge is poorly developed, a groove between the tubercle and external condyle is lacking, and the supratendinal bridge is narrower proximodistally and somewhat more depressed. *Cariama* and the geranoidids do show a basic similarity in the positions of the condyles, the posterior intercondylar sulcus, and other features.

The tarsometatarsi of *Cariama* and the geranoidids are similar in the general positions of the trochleae, but the latter genera differ in having the intertrochlear notches wider, the inner trochlea turned more posteriorly, and the shaft more robust and less flat.

Many features of the proximal ends of the tarsometatarsi in the cariamids and geranoidids resemble each other; for example, the relative positions and sizes of the cotylae, the direction of the intercotylar prominence, and the anterior metatarsal groove. The hypotarsus of *Cariama* is, however, different in being rectangular as in the phororhacoids.

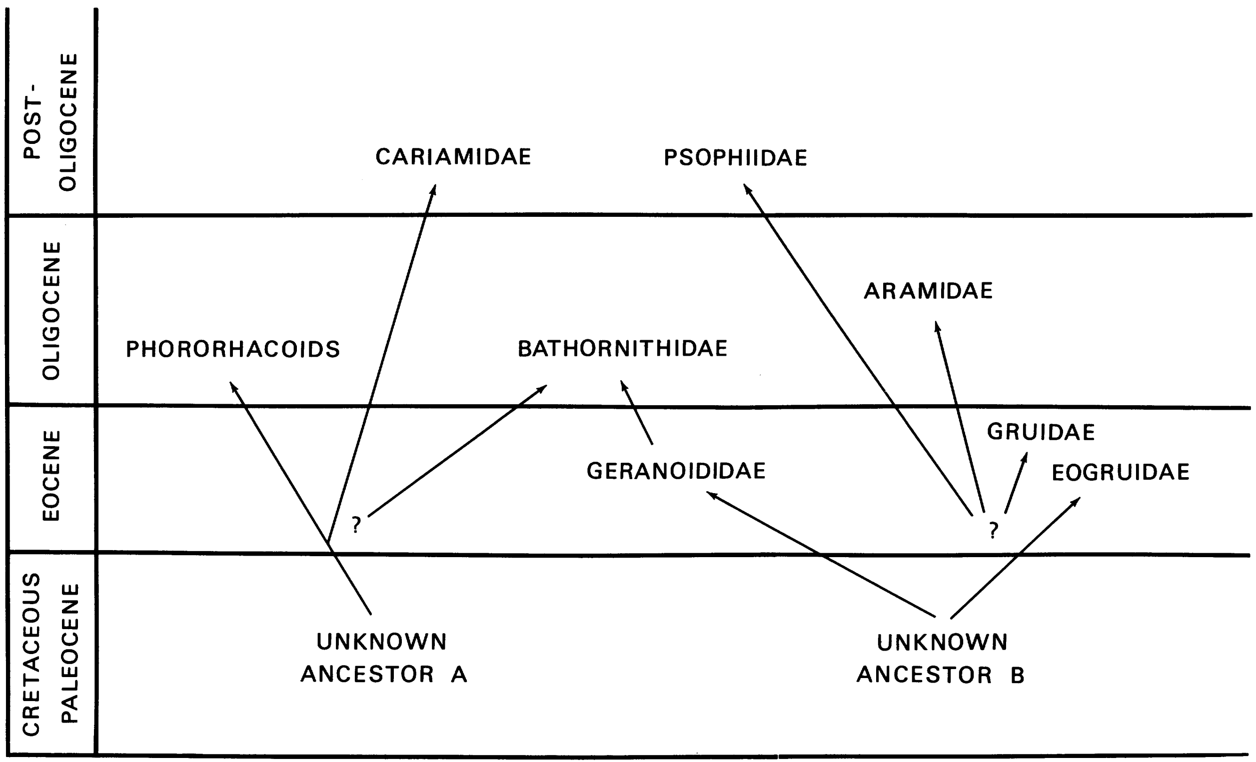

FIG. 11. Possible phylogeny of some gruiform families. Unknown ancestors A and B would be of family or subfamily rank but, in any case, related. See text.

Comparison with the Psophiidae

The Psophiidae are seemingly as close morphologically to the geranoidids as is any other family of Recent birds.

In the characters of the tibiotarsus, the two families resemble each other in that both: (1) have similarly shaped external condyles (slightly more raised posteriorly in *Psophia*), (2) possess a tubercle on the supratendinal bridge, separated from the external condyle by a groove, (3) possess similarly shaped internal condyles (indentation not well developed in *Psophia*), and (4) have condyles in same general positions, with posterior intercondylar sulci similar.

The tarsometatarsi of these two families are also close morphologically, but the geranoidids differ in having: (1) the intertrochlear notches slightly wider, (2) the inner trochlea turned slightly more posteriorly, and (3) the bone more robust and less flattened. The positions of the trochleae in the two families are about the same.

The proximal ends of the tarsometatarsi are similar in the anterior metatarsal groove, positions and sizes of the cotylae, intercotylar prominence, and in the general shape of the hypotarsus.

Summary of the Interfamilial Relationships

Table 7 summarizes the morphological comparisons of the families examined in this study. The possible phylogenetic relationships using this comparison are represented in figure 11. No family is considered to be polyphyletic, but the possible evolutionary pathways are indicated. The times of the cladistic events are, if anything, conservative and probably will have to be extended farther back in time. A phylogeny such as this is always subject to error because it is based mainly on comparisons with one family (in this case, the Geranoididae) rather than with all the families.

It is difficult to assign a probability factor to the various lineages. After studies of the functional morphology of the hind limb have been completed, structural convergences should be more easily recognized. Certainly new fossil material will clarify relationships. Of special importance is a detailed study of the lesser-known fossil gruiforms such as the Idiornithidae and Ergilornithidae and of the numerous Old World fossils currently referred to the Gruidae.

I consider it likely that the Geranoididae and Eogruidae shared a common ancestry. The Eogruidae are morphologically intermediate between the geranoidids and the gruids. I agree with Wetmore (1934) that the Eogruidae and Gruidae are related, and I believe that they

TABLE 7

MORPHOLOGICAL COMPARISON OF MAJOR DIFFERENCES AND SIMILARITIES TO GERANOIDIDAE EXHIBITED BY GRUIFORM FAMILIES EXAMINED

	Tibiotarsus (distal end)	Tarsometatarsus (distal end)	Tarsometatarsus (proximal end)[a]
Geranoididae	1. external condyle without indentation; flattened distally (except in *Geranodornis*)	1. inner and outer trochleae turned little posteriorly relative to middle trochlea (inner turned more than outer)	1. hypotarsus only slightly narrowed posteriorly
	2. condyles moderately separated (*Paragrus*) to more nearly parallel (*Palaeophasianus*)	2. intertrochlear notches relatively broad (external more so than internal)	2. hypotarsus located near external side
	3. projection of internal side moderate		3. cotylae about same size
	4. tubercle on bridge moderately developed		4. intercotylar prominence relatively pointed and not broad
	5. internal condyle not especially elongated (about same length as external condyle); well developed notch on internal condyle		
Gruidae	1. external condyle with indentation (except in *Balearica*)	1. inner trochlea turned more posteriorly	1. hypotarsus narrower posteriorly
	2. condyles separated more anteriorly	2. middle trochlea less elongated anteroposteriorly	2. hypotarsus located near middle or slightly to internal side
	3. internal side projects more		3. external cotyla decidedly smaller than internal cotyla
	4. tubercle on bridge larger		4. intercotylar prominence blunter and broader
	5. internal condyle elongated more; with less developed notch		
Eogruidae	1. condyle with only slight indentation; projects more posterodistally	1. relative positions of trochleae similar (in distal view)	1. hypotarsus nearer in shape to geranoidids than to gruids
	2. condyles more nearly parallel, similar to geranoidids	2. outer and inner trochleae less massive and less distally located relative to middle trochlea	2. hypotarsus in same relative position
	3. projection of internal side similar		3. cotylae same size
	4. tubercle similar in development to geranoidids; supratendinal bridge narrower		4. prominence blunter and broader
	5. internal condyle elongated slightly more; with moderately developed notch		

TABLE 7—(*Continued*)

	Tibiotarsus (distal end)	Tarsometatarsus (distal end)	Tarsometatarsus (proximal end)[a]
Aramidae[b]	1. external condyle similar only to *Geranodornis;* very different from other genera in being much rounder 2. condyles similar in position 3. projection of internal side similar 4. tubercle more distinct; bridge depressed more 5. internal condyle similar	1. inner trochlea located more posteriorly and less distally relative to middle trochlea 2. intertrochlear notches narrower	1. hypotarsus somewhat similar in shape, not projecting posteriorly as much 2. hypotarsus same position 3. cotylae same size 4. prominence slightly more distinct
Bathornithidae	1. external condyle less flat distally; more raised posterodistally (*Bathornis geographicus* more similar to geranoidids) 2. condyles similar in position 3. projection of internal side similar 4. tubercle absent; bridge similar 5. internal condyle flatter distally; without noticeable notch	1. positions of trochleae generally similar but inner trochlea turned slightly more posteriorly 2. external intertrochlear notch narrower	1. hypotarsus similar in shape 2. hypotarsus similar in position 3. internal cotyla slightly larger than external 4. prominence somewhat larger and broader
Phororhacoids (Psilopteridae, Phororhacidae)	1. external condyle rounder distally; elevated more posteriorly 2. condyles somewhat less separated anteriorly; anterior intercondylar fossa deeper; posterior intercondylar sulcus U-shaped 3. projection of internal side similar 4. tubercle absent 5. internal condyle flatter distally; without notch; much larger anteriorly	1. positions of trochleae similar (distal view) 2. intertrochlear notches narrower 3. shaft flatter anteroposteriorly 4. outer and inner trochleae more compressed lateromedially 5. sides of middle trochlea not parallel	1. hypotarsus very different in being rectangular and with no canals 2. cotylae same size 3. prominence similar (perhaps slightly larger)

TABLE 7—(*Continued*)

	Tibiotarsus (distal end)	Tarsometatarsus (distal end)	Tarsometatarsus (proximal end)[a]
Cariamidae	1. external condyle raised more posteriorly 2. positions of condyles similar 3. projection of internal side similar 4. tubercle very poorly developed; groove lacking between tubercle and condyle; bridge slightly narrower and more depressed 5. internal condyle flatter distally; without notch	1. positions of trochleae generally similar 2. intertrochlear notches narrower 3. inner trochlea turned less posteriorly and located more distally relative to middle trochlea	1. hypotarsus like that of phororhacoids 2. cotylae same size; external perhaps slightly larger than internal 3. prominence similar
Psophiidae	1. external condyle similar (slightly more raised posteriorly) 2. positions of condyles similar 3. projection of internal side similar 4. possess tubercle with groove as in geranoidids; bridge narrower and more depressed 5. internal condyle similar but with little or no notch	1. relative positions of trochleae generally similar 2. intertrochlear notches slightly narrower 3. inner trochlea turned slightly less posteriorly; outer trochlea located less distally relative to middle trochlea	1. hypotarsus similar in shape 2. hypotarsus similar in position 3. cotylae same size 4. prominence similar

[a] Based on a comparison only with *Palaeophasianus meleagroides*.
[b] *Badistornis* is excluded; based only on *Aramornis* and *Aramus*.

probably had a more recent common ancestor than the one that gave rise to the geranoidids and to the eogruid-gruid line. Hence, I think it less likely that the Eogruidae and Gruidae were independently derived from an ancestor that also gave rise to numerous other gruiform groups, as suggested by Howard (1950, p. 14, fig. 5). *Eogrus* apparently retained features found in its common ancestor with the geranoidids.

The Aramidae probably shared a common ancestry with the Gruidae, but present evidence does not permit us to say at what level in the phylogeny this occurred.

The position of the Psophiidae is uncertain and no meaningful statement is offered at this time. The problem is confounded by the lack of fossil psophiids. I noted above numerous similarities to the geranoidids, and it is possible the psophiids are closer to them than to the cranes or limpkins, although anatomical characters indicate a relationship to the latter groups (unpublished data).

The structure of the geranoidid tarsometatarsus, especially that of *Paragrus,* strongly suggests that they were the direct ancestors of the Bathornithidae. The relationship seems closest to the *Bathornis cursor-B. veredus-B. geographicus* line within the family (Cracraft, 1968a), but the other Oligocene genus of the bathornithids, *Paracrax,* is not represented by hind limb material. Thus, conclusions must be tentative. The Bathornithidae share numerous characters with the cariamids and phororhacoids, and it is possible that the bathornithid-geranoidid resemblances are the result of convergence (more likely the possibility is that the bathornithids are convergent to the phororhacoids and cariamids).

SUMMARY

The present paper reviews the relationships of some fossil gruiform birds from the Eocene of North America. *Geranoides jepseni* Wetmore is gruiform, but the type tarsometatarsus was distorted during preservation and cannot be used as a basis for phylogenetic inferences. *Paragrus prentici* (Loomis) is transferred from the Gruidae to the Geranoididae, and a new species *P. shufeldti* is described. New material of the fossil *Palaeophasianus meleagroides* Shufeldt establishes a rather close relationship to the geranoidids; the largest member of the family, *P. incompletus,* is described and tentatively placed in *Palaeophasianus.* Two new genera are described and allocated to the Geranoididae. The first is *Eogeranoides campivagus,* which has definite affinities to the Geranoididae. The second, *Geranodornis aenigma,* has doubtful relationships with the other genera

and may represent an independent line of Eocene gruiforms.

The Geranoididae are probably derived from a common ancestor with the Eogruidae of the Eocene of eastern Asia. Furthermore, the geranoidids are likely candidates for the ancestors of the Bathornithidae, thus suggesting that the latter family is not actually closely related to the cariamid-phororhacoid line of gruiforms. Another line of gruiforms, which is separable from the geranoidids and bathornithids, apparently includes the Eogruidae, Gruidae, Aramidae, and Psophiidae.

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