SYSTEMATICS AND EVOLUTION OF THE GRUIFORMES (CLASS AVES)

3. PHYLOGENY OF THE SUBORDER GRUES

JOEL CRACRAFT

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CONTENTS

ABSTRACT

A COMPARATIVE ANALYSIS of both fossil and Recent species of the suborder Grues of the order Gruiformes is presented here. A phylogeny is proposed for the families studied and is constructed on the premise that monophyletic taxa can be defined only by the recognition of shared, derived character-states. The suborder Grues can be divided into two lineages, the infraorders Ralli and Grui. Two families comprise the Ralli: the Rallidae and Laornithidae. The Grui diverged into two major radiations at the beginning of the Tertiary: (1) the Geranoidea (Geranoididae, Bathornithidae, Idiornithidae), and (2) the Gruoidea (Eogruidae, Ergilornithidae, Gruidae, Aramidae, Psophiidae). The Geranoididae are the most morphologically primitive members of the Grui. The bathornithids and idiornithids share many derived features, presumably inherited from a geranoidid-like ancestor. The ergilornithids were apparently derived from an eogruid-like ancestor. The Gruidae, Aramidae, and Psophiidae form a separate lineage within the Gruoidea, with the last two families having the closest relationship.

A new family of the infraorder Ralli, the Laornithidae, is described for the late Cretaceous species *Laornis edvardsianus* Marsh.

The new fossil species described are: *Palaeorallus brodkorbi* (Rallidae), *Quercyrallus quercy* (Rallidae), *Palaeoaramides minutus* (Rallidae), and *Idiornis gaillardi* (Idiornithidae).

Revisions are presented for the pre-Pleistocene extinct genera of the following families: Rallidae, Idiornithidae, Eogruidae, Ergilornithidae, Gruidae, and Aramidae. A number of genera are transferred from one family to another.

Various schemes of classification for the Grues are briefly discussed. It is suggested that a classification which expresses monophyletic relationships in a strict manner (i.e., dichotomously) is to be preferred.

INTRODUCTION

THE ORDER GRUIFORMES is a large heterogeneous assemblage of morphologically distinct families. That the interfamilial relationships are poorly understood is evidenced by the recognition of no fewer than eight suborders (e.g., Wetmore, 1960). The largest, and in some respects, the most "generalized" of the suborders is the Grues. My purpose in this paper is to present a revision of the fossil taxa of this suborder and to use these data, along with data gathered from a comparative study of recent osteological material, to construct a phylogeny of the families. One of the principal goals of this work is to provide a phylogenetic background for future studies on the adaptive radiation within the order. Many evolutionary phenomena cannot be fully appreciated until the phylogenetic relationships of the group have been determined.

A revision of the fossil taxa is presented in the systematic section of this paper. I have somewhat arbitrarily limited the content to the extinct genera of each family and to those genera older than the Pleistocene. I made these decisions for several reasons. First, it has been possible for me to examine and make comparative studies of almost all the pre-Pleistocene fossils of this suborder, but I have been unable to see many of the Pleistocene forms. It therefore seems best to wait until the latter can be examined before expressing an opinion on them. Second, I am interested in the interrelationships of the families and the broader evolutionary patterns within and between these families. The Pleistocene fossils do not provide much information in that regard because most of this material represents extinct species of living genera.

I have chosen to include the Geranoididae and Bathornithidae in this paper for completeness. However, because of my earlier revisions of these families (1968a, 1969, 1971), most of the detailed information about them is omitted.

In a later section of this paper an analysis of morphological variability is presented for a number of fossil species for which we have adequate data. This section provides a basis on which to interpret species limits of various fossil taxa and also provides some data on the amount of variability in fossil assemblages. Because this type of information is scarce, even for living species, all the relevant data are given.

The central conclusions of this study are summarized in the proposed phylogeny (fig. 46). I have discussed elsewhere the theories and working methods currently in use among avian systematists for determining the phylogenetic relationships of the higher taxa of birds (Cra-

craft, 1972b). Following the ideas set forth in that paper, I here use the term "relationship" in the sense of recency of common ancestry (genealogy); the problem of the degree of morphological similarity is not included in the definition. I follow some of the current systematic theory that assumes that monophyletic taxa can be delimited only by the recognition of shared derived character-states (Hennig, 1966). Any characters considered to be primitive to the group under study (here the suborder Grues and subordinate taxa) cannot be used as evidence of relationships for taxa within that group. There are a number of criteria for distinguishing primitive and derived character-states (e.g., see Hennig, 1966, and Cracraft, 1972b), but by far the most important is the distribution patterns of the character-states. It is assumed that a character-state is primitive to a group if that character-state is also present in presumably closely related taxa. In several instances it was not possible to recognize primitive-derived sequences, and consequently relationships could not be determined. At the family level, where morphological divergence is magnified, primitive-derived sequences could be recognized much more easily, and hence one can have a reasonable degree of confidence in the proposed phylogeny.

The diagnoses in the systematic section are not formed of derived character-states by themselves. Rather, I have attempted to include unique combinations of characters, both primitive and derived, that will facilitate recognition of those taxa.

In order to ease the reader's understanding of my opinions regarding the phylogenetic arrangement and systematic status of the various taxa discussed in this paper, this information is summarized as follows:

Order Gruiformes
  Suborder Grues
    Infraorder Ralli
      Superfamily Ralloidea
        Family Rallidae Vigors
          Genus *Palaeorallus* Wetmore
            P. troxelli Wetmore
            P. brodkorbi, new species
          Genus *Eocrex* Wetmore
            E. primus Wetmore
          Genus *Aletornis* Marsh, transferred from
            the Gruidae
            A. nobilis Marsh
            A. marshi (Shufeldt)

            A. pernix Marsh, assigned provisionally
          Genus *Fulicaletornis* Lambrecht
            F. venustus (Marsh)
          Genus *Telecrex* Wetmore
            T. grangeri Wetmore
          Genus *Ibidopsis* Lydekker, transferred from
            the Threskiornithidae
            I. hordwelliensis Lydekker
          Genus *Ludiortyx* Brodkorb
            L. hoffmanni (Gervais)
          Genus *Quercyrallus* Lambrecht
            Q. arenarius (Milne-Edwards)
            Q. ludianus Brodkorb
            Q. quercy, new species
            Q. dasypus (Milne-Edwards)
          Genus *Palaeocrex* Wetmore
            P. fax Wetmore
          Genus *Rallicrex* Lambrecht
            R. kolozsvarensis Lambrecht
          Genus *Palaeoaramides* Lambrecht
            P. christyi (Milne-Edwards)
            P. beaumonti (Milne-Edwards)
            P. minutus, new species
          Genus *Pararallus* Lambrecht
            P. dispar (Milne-Edwards)
          Genus *Paraortygometra* Lambrecht
            P. porzanoides (Milne-Edwards)
          Genus *Miofulica* Lambrecht, familial position tentative
            M. dejardinii (Van Beneden)
          Genus *Miorallus* Lambrecht
            M. major (Milne-Edwards)

Species Not Considered Members of the Rallidae:
    Genus *Palaeorallus* Wetmore
      P. alienus Kurotchkin
    Genus *Pararallus* Lambrecht
      P. hassenkampi Martini
    Genus *Megagallinula* Kurotchkin
      M. harundinea Kurotchkin
    Genus *Limicorallus* Kurotchkin
      L. saiensis Kurotchkin
    Genus *Thiornis* Navás
      T. sociata Navás
      Superfamily Laornithoidea, new superfamily
        Family Laornithidae, new family
          Genus *Laornis* Marsh
            L. edvardsianus Marsh
  Infraorder Grui
    Superfamily Geranoidea
      Family Geranoididae Wetmore
        Genus *Geranoides* Wetmore
          G. jepseni Wetmore
         Genus *Paragrus* Lambrecht
          P. prentici (Loomis)
          P. shufeldti Cracraft
         Genus *Palaeophasianus* Shufeldt
          P. meleagroides Shufeldt

P. incompletus Cracraft
Genus *Eogeranoides* Cracraft
  E. campivagus Cracraft
Genus *Geranodornis* Cracraft
  G. aenigma Cracraft
Family Bathornithidae Wetmore
  Genus *Eutreptornis* Cracraft
    E. uintae Cracraft
  Genus *Bathornis* Wetmore
    B. veredus Wetmore
    B. cursor Wetmore
    B. celeripes Wetmore
    B. geographicus Wetmore
    B. fricki Cracraft
    B. minor Cracraft
  Genus *Paracrax* Brodkorb
    P. antiqua (Marsh)
    P. wetmorei Cracraft
    P. gigantea Cracraft
Family Idiornithidae Brodkorb
  Genus *Gypsornis* Milne-Edwards, transferred from the Rallidae
    G. cuvieri Milne-Edwards
  Genus *Idiornis* Oberholser
    I. gallicus (Milne-Edwards)
    I. cursor (Milne-Edwards)
    I. minor (Milne-Edwards)
    I. gaillardi, new species
  Genus *Elaphrocnemus* Milne-Edwards
    E. phasianus Milne-Edwards
    E. crex Milne-Edwards
    E. gracilis Milne-Edwards
Superfamily Gruoidea
  Family Eogruidae Wetmore
    Genus *Eogrus* Wetmore
      E. aeola Wetmore
      E. wetmorei Brodkorb
  Family Ergilornithidae Kozlova
    Genus *Proergilornis* Kozlova
      P. minor Kozlova
    Genus *Ergilornis* Kozlova
      E. rapidus Kozlova
    Genus *Urmiornis* Mecquenem
      U. maraghanus Mecquenem
  Family Gruidae Vigors
    Genus *Palaeogrus* Portis
      P. princeps Portis
      P. geiseltalensis (Lambrecht)
      P. hordwelliensis (Lydekker)
      P. excelsus (Milne-Edwards)
    Genus *Eobalearica* Gureev, familial position tentative
      E. tugarinovi Gureev
    Genus *Geranopsis* Lydekker
      G. hastingsiae Lydekker
    Genus *Probalearica* Lambrecht
      P. problematica (Milne-Edwards)
      P. crataegensis Brodkorb

Genus *Pliogrus* Lambrecht
  P. germanicus Lambrecht
  P. pentelici (Gaudry)
Family Aramidae Bonaparte
  Genus *Aminornis* Ameghino, familial position tentative
    A. excavatus Ameghino
  Genus *Loncornis* Ameghino, familial position tentative
    L. erectus Ameghino
  Genus *Badistornis* Wetmore
    B. aramus Wetmore
  Genus *Gnotornis* Wetmore
    G. aramiellus Wetmore
  Genus *Aramornis* Wetmore
    A. longurio Wetmore
  Genus *Anisolornis* Ameghino, transferred from the Cracidae
    A. excavatus Ameghino

ACKNOWLEDGMENTS

ABBREVIATIONS

The following abbreviations are used:

ACM, Amherst College Museum

AMNH, Department of Vertebrate Paleontology, the American Museum of Natural History

BaM, Naturhistorisches Museum, Basel (hereafter termed Basel Museum)

BM(NH), British Museum (Natural History)

CMNH, Colorado Museum of Natural History

FAM, Frick Collection, the American Museum of Natural History

LGL, Laboratoire de Géologie de la Faculté des Sciences, Lyon

MCZ, Museum of Comparative Zoology, Harvard University

MHNL, Muséum d'Histoire Naturelle, Lyon

MU, Bayerischen Staatssammlung für Paläontologie und historische Geologie, Munich (hereafter termed Munich Museum)

PB, Pierce Brodkorb Collection, University of Florida

PIN, Institute of Paleontology, Soviet Academy of Sciences, Moscow

PM, Muséum National d'Histoire Naturelle, Paris (hereafter termed Paris Museum)

PU, Department of Geological and Geophysical Sciences, Princeton University

SDSM, Museum of Geology, South Dakota School of Mines and Technology, Rapid City

USNM, Division of Vertebrate Paleontology, National Museum of Natural History, Smithsonian Institution

YPM, Peabody Museum of Natural History, Yale University

MORPHOLOGY AND SYSTEMATICS

ORDER GRUIFORMES

SUBORDER GRUES

INFRAORDER RALLI

SUPERFAMILY RALLOIDEA

FAMILY RALLIDAE VIGORS

GENUS *PALAEORALLUS* WETMORE

Palaeorallus WETMORE, 1931, p. 108.

TYPE SPECIES: *Palaeorallus troxelli* Wetmore.

INCLUDED SPECIES: Type species; and *P. brodkorbi*, new species. Kurotchkin (1968a) has described another species, *P. alienus*, but I am removing it from the Rallidae (see below).

DISTRIBUTION: Early Eocene (Wasatchian) of Wyoming.

DIAGNOSIS: Tibiotarsus with condyles not parallel, the anterior ends being much more separated than the posterior ends. Internal condyle projecting distally well beyond level of external condyle (in distal view). External con-dyle slightly flattened distally, with posterior portion somewhat raised distally into noticeable apex. Anterior end of internal condyle raised only slightly distally relative to external condyle (in anterior view). Anterior end of internal condyle short proximodistally, with very slight notch distally.[1]

REMARKS: Wetmore (1931, p. 108) placed *Palaeorallus* in the Rallinae as a matter of convenience. However, the shape of the area of the supratendinal bridge and the shapes and positions of the condyles do not suggest any modern genera of rails. *Palaeorallus* is very distinct morphologically within the Rallidae.[2]

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[1] Diagnosis based only on specimens of *P. troxelli* and *P. brodkorbi*. See discussion of *P. alienus* at the end of the species accounts.

[2] A considerable amount of anatomical comparison is necessary before subfamilies can be defined (if possible) within the Rallidae, therefore I have refrained from their use.
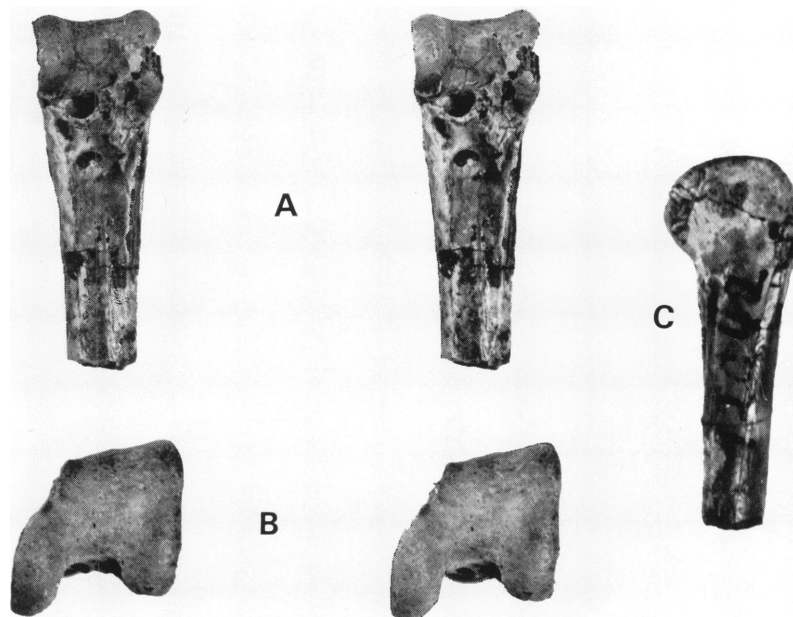
FIG. 1. *Palaeorallus troxelli*, holotype, USNM 12042, distal end of right tibiotarsus. A. Anterior view, stereo pair. About ×2. B. Distal view, stereo pair. About ×2.8. C. External condyle. About ×2.3.

Palaeorallus troxelli Wetmore

Figure 1

Palaeorallus troxelli WETMORE, 1931, p. 108.

HOLOTYPE: USNM 12042, distal part of right tibiotarsus.

HORIZON AND LOCALITY: Lower Eocene deposits, Willwood Formation; south of Preator's Ranch, south of Burlington, Bighorn County, Wyoming.

HYPODIGM: Holotype only.

DIAGNOSIS: Smallest species in genus (see table 1).

MEASUREMENTS: See table 1.

REMARKS: The type of *P. troxelli* is badly cracked posteriorly and across the outer surfaces of the external condyle, but the relative positions of the condyles and their general shape seem unaffected.

Palaeorallus brodkorbi, new species

Figure 2

HOLOTYPE: USNM 15161, distal end of left tibiotarsus.

HORIZON AND LOCALITY: Lower Eocene deposits, Wasatch Formation; 12 miles west of Worland, banks of 10 Mile Creek, Washakie County, Wyoming.

HYPODIGM: Holotype only.

DIAGNOSIS: Largest species in genus. Tibio-
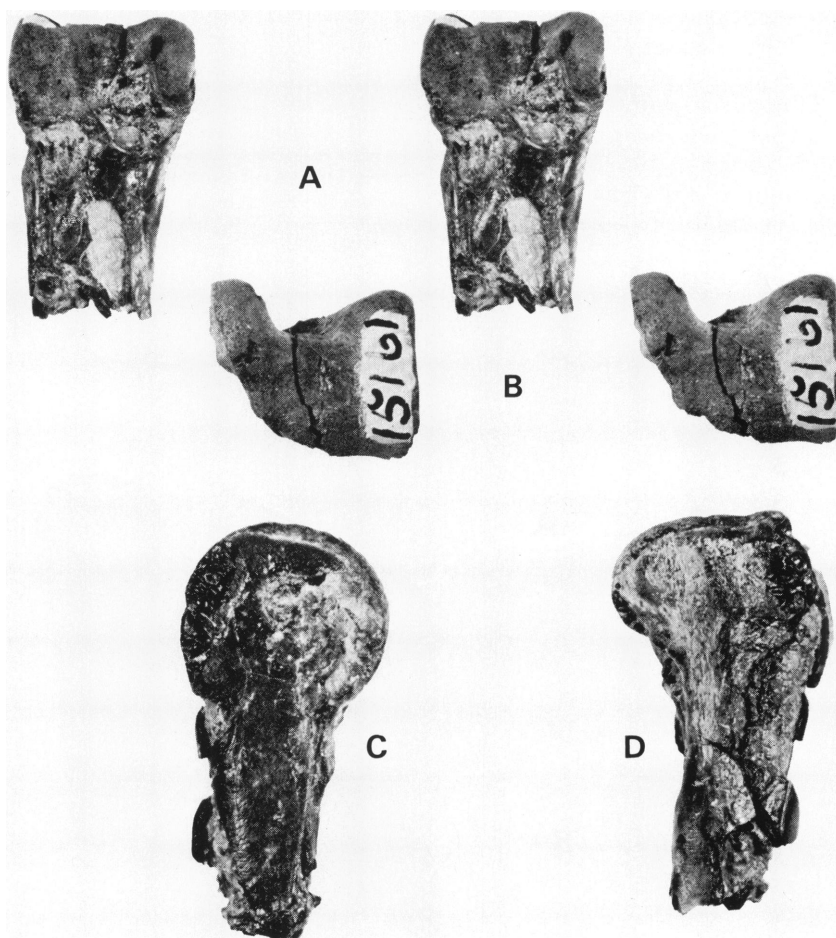
FIG. 2. *Palaeorallus brodkorbi,* holotype, USNM 15161, distal end of left tibiotarsus. A. Anterior view, stereo pair. About ×2. B. Distal view, stereo pair. About ×2.2. C. External condyle. About ×2.7. D. Internal condyle. About ×2.4.

TABLE 1

MEASUREMENTS (IN MILLIMETERS) OF TIBIOTARSI OF

Paleorallus troxelli AND *Palaeorallus brodkorbi*

	P. troxelli USNM 12042	P. brodkorbi USNM 15161
Depth (anteroposterior) of external condyle	7.8	10.3
Depth of internal condyle	8.3	11.5[a]
Breadth across posterior end of condyles	5.7	9.1[a]
Breadth across anterior end of condyles	8.1	12.2
Depth of anterior intercondylar fossa relative to external condyle	2.1	3.2

[a] Measurement approximate.

tarsus differing from that of *P. troxelli* as follows: (1) distal margin of external condyle somewhat more rounded, (2) condyles slightly more separated anteriorly.

MEASUREMENTS: See table 1.

REMARKS: This specimen is badly damaged especially posteriorly and internally along the shaft. However, the condyles appear in their natural positions. *Palaeorallus brodkorbi* is very close to *P. troxelli* in morphology, the larger size of the former being the major difference between the two species.

ETYMOLOGY: Named in honor of Dr. Pierce Brodkorb in recognition of his important contributions to the field of avian paleontology.

GENUS *EOCREX* WETMORE

Eocrex WETMORE, 1931, p. 107.

TYPE SPECIES: *Eocrex primus* Wetmore.
INCLUDED SPECIES: Type species only.

DISTRIBUTION: Early Eocene (Wasatchian) of Wyoming.

DIAGNOSIS: Tibiotarsus with condyles nearly parallel, being separated somewhat anteriorly. External condyle very gently rounded distally and raised posteriorly. Supratendinal bridge broad proximodistally and markedly depressed relative to walls of bridge (especially external wall). Anterior end of internal condyle rotated distally relative to external condyle. Internal condyle heavy, flattened distally, with slight notch on distal margin; condyle greatly rounded anteriorly, with margin meeting shaft at almost 80 degree angle. Deep pit between external condyle and external wall of supratendinal groove.[1]

REMARKS: *Eocrex* is compared with other genera at the end of this section.

Eocrex primus Wetmore

Figure 3

Eocrex primus WETMORE, 1931, p. 107.

HOLOTYPE: USNM 12043, distal end of right tibiotarsus.

HORIZON AND LOCALITY: Lower Eocene deposits, Wasatch Formation (Cathedral Bluffs Tongue); S13, T24N, R102W; Steamboat Springs, Sweetwater County, Wyoming.

HYPODIGM: Holotype only.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: See table 2.

[1] The term supratendinal groove refers to the channel or pathway situated immediately anterior to the supratendinal bridge. It is bounded internally and externally by "walls" or ridges situated more or less perpendicular to the bridge. In life ligamentous connective tissue spans the walls, and the groove provides a channel for the tendon of M. tibialis anterior.

TABLE 2

MEASUREMENTS (IN MILLIMETERS) OF TIBIOTARSI OF *Eocrex primus*, *Aletornis marshi*, AND *Aletornis pernix*

|	E. primus USNM 12043	A. marshi YPM 888	A. pernix YPM 64
Depth (anteroposterior) of external condyle	11.4	16.4	7.9
Depth of internal condyle	12.1	17.7	—
Breadth across posterior ends of condyles	8.1	11.8	—
Breadth across anterior ends of condyles	10.6	18.0	—
Depth of anterior intercondylar fossa relative to external condyle	3.7	5.7	—
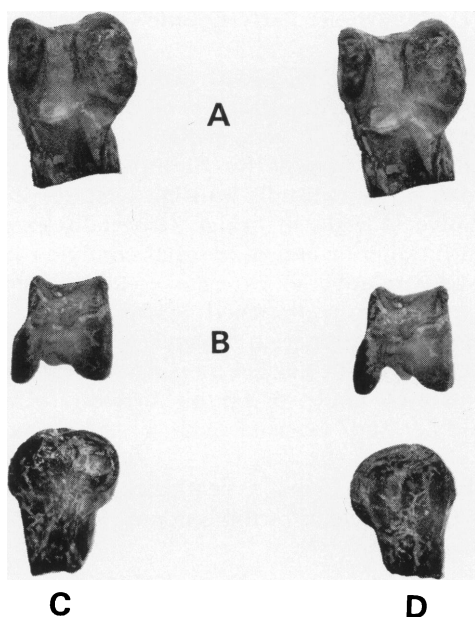
FIG. 3. *Eocrex primus*, holotype, USNM 12043, distal end of right tibiotarsus. A. Anterior view, stereo pair. About × 1.6. B. Distal view, stereo pair. About × 1.3. C. Internal condyle. About × 1.2. D. External condyle. About × 1.2.

REMARKS: See above and below under intrafamilial relationships.

GENUS *ALETORNIS* MARSH

Aletornis MARSH, 1872, p. 256.
Protogrus LAMBRECHT, 1933, p. 520.

TYPE SPECIES: *Aletornis nobilis* Marsh (by subsequent designation of Hay, 1902, p. 527).

INCLUDED SPECIES: Type species; *A. marshi* (Shufeldt); and *A. pernix* Marsh.

DISTRIBUTION: Middle Eocene (Bridgerian) of Wyoming.

DIAGNOSIS: Tibiotarsus with external condyle rounded, anterior end raised distally, posterior end not raised distally. Internal condyle strongly rounded anteriorly, margin meeting shaft at about 80 degree angle, anterior end raised distally. Moderately developed internal ligamental prominence present. Condyles widely separated anteriorly. Deep anterior intercondylar fossa. Supratendinal bridge broad proximodistally, external wall of bridge very steep. Tubercle on bridge moderately developed and separated from external condyle by marked groove.

REMARKS: The five species of *Aletornis* described by Marsh (1872) have been shown to constitute a heterogeneous assemblage of unrelated forms (Shufeldt, 1915a), a fact recognized by Marsh. Two of these species, *A. bellus* and *A. gracilis*, were considered limicoline by Shufeldt and have been placed in the scolopacid genus *Palaeotringa* Marsh by Brodkorb (1967, p. 184). The remaining three species, *A. nobilis*, *A. pernix*, and *A. venustus*, have been shifted back and forth among various gruiform taxa. Lambrecht (1933, p. 479) erected the genus *Fulicaletornis* (see below) for *A. venustus*, and this decision was followed by Brodkorb (1967, p. 128). In addition to *A. nobilis* and *A. pernix*, a third species, *A. marshi* Shufeldt, is currently included in *Aletornis* (Brodkorb, 1967, p. 147).

The type species, *A. nobilis*, is crushed, consequently a definite determination of familial relationships is not possible. The type tarsometatarsus of *A. nobilis* resembles rails in the following characters: (1) the inner trochlea is apparently turned posteriorly (2) the outer trochlea is about the same shape as those of rails, and (3) the relative proximodistal positions of the inner and outer trochleae are about the same as in rails. In reality *A. nobilis* is retained in the Rallidae as a matter of convenience and nomenclatural stability (see below).

Aletornis nobilis Marsh

Aletornis nobilis MARSH, 1872, p. 256.

HOLOTYPE: YPM 63, distal end of left tarsometatarsus.

HORIZON AND LOCALITY: Middle Eocene deposits, Bridger Formation (Black's Fork Member); Grizzly Buttes on Smith's Fork, one mile southwest of Mountainview, Uinta County, Wyoming.

HYPODIGM: Holotype only.

DIAGNOSIS: Larger than *A. pernix*; smaller than *A. marshi*.

MEASUREMENTS: Breadth (external-internal) of outer trochlea 5.6 mm.; other measurements not possible.

REMARKS: Both Marsh (1872, p. 256) and Shufeldt (1915a, pp. 30–31) thought that *A. nobilis* represented a cranelike bird; Shufeldt even placed this species in the genus *Grus*. Lambrecht (1933, p. 521) created the genus *Protogrus* for *A. nobilis* and *Grus marshi* Shufeldt, but as Wetmore pointed out (1956, p. 59),

Lambrecht was in error as Hay (1902, p. 527) had already designated *A. nobilis* as the type species of the genus *Aletornis*. Brodkorb (1952, p. 175) designated *A. nobilis* as the type species of *Protogrus*, which therefore becomes a synonym of *Aletornis*.

Brodkorb (1967, p. 147) placed *A. nobilis* in the subfamily Balearicinae of the Gruidae. It is possible that *A. nobilis* could have been a gruid, but because the specimen is crushed and fragmentary, a definitive statement cannot be made concerning its relationships. Because *A. nobilis* is the type species of the genus and because its characters do not rule out rallid affinities, I prefer to avoid erecting a new genus to accommodate *A. marshi*, and I therefore place *A. nobilis*, along with *A. marshi* and *A. pernix*, in the Rallidae. Although arbitrary (with respect to *A. nobilis*), this decision avoids having the genus *Aletornis* based only on a fragmentary specimen. There is, moreover, no evidence that *A. nobilis* and *A. marshi* are not congeneric.

Aletornis marshi (Shufeldt)

Figure 4A–D

Grus marshi SHUFELDT, 1915a, p. 41.
Aletornis marshi (Shufeldt): LAMBRECHT, 1933, p. 521.

HOLOTYPE: YPM 888, distal end of right tibiotarsus.

HORIZON AND LOCALITY: Middle Eocene deposits, Bridger Formation (Twin Buttes Member); Henry's Fork, Uinta County, Wyoming.

HYPODIGM: Holotype only.

DIAGNOSIS: Largest species in genus.

MEASUREMENTS: See table 2.

DESCRIPTION OF HOLOTYPE: External condyle (as seen from side) rounded distoanteriorly, posterodistal margin of condyle less round, located much less distad than anterodistal margin; anterior part of internal condyle greatly rounded, turning proximally to meet shaft at angle approaching 90 degrees; internal ligamental prominence moderately developed; deep pit located on internal face of internal condyle immediately anterior to ligamental prominence; posterior margin of internal condyle less rounded, thicker than anterior margin and slopes gently to shaft; broad, moderately deep depression between internal ligamental prominence and posterior margin; distal margin of internal condyle with slight indentation just posterior to

level of ligamental prominence; in distal view, internal and external condyles separated rather markedly at anterior ends, not parallel; depth of anterior intercondylar fossa approximately 40 percent of anteroposterior depth of external condyle; posterior intercondylar sulcus deep with deepest part near internal condyle; anteriorly, internal condyle situated slightly more distad relative to external condyle and proximal portion of internal condyle turned internally; supratendinal bridge broad and long, with rather large distal opening for tendon; moderately developed tubercle situated on distoexternal edge of supratendinal bridge and separated from base of external condyle by distinct groove; tubercle confluent with rather high ridge running in proximal direction to form external wall of supratendinal groove; in cross section, lower end of shaft rounded posteriorly and internally, somewhat more planar externally, with deep groove anteriorly; groove deepest on internal side.

REMARKS: *Aletornis marshi* was placed in the Gruidae by Lambrecht (1933, p. 521) and in the subfamily Balearicinae by Brodkorb (1967, p. 147). However, *A. marshi* possesses the following features not characteristic of cranes: (1) external condyle not deep anteroposteriorly, but rounded (without indentation on its distal margin), (2) tubercle on supratendinal bridge much less developed, and (3) internal condyle not as long proximodistally and not as flattened on distal margin but rounded. At the same time *A. marshi* resembles some genera of rails in these characters, e.g., in the shapes of the condyles and supratendinal bridge area.

The most distinctive feature of *A. marshi* is the shape of the external condyle (fig. 4D), which is decidedly not like that of a crane. Despite great amounts of abrasion along the edges, examination under a dissecting scope reveals that the shape of the condyle is almost certainly similar to that in life. In several places the smooth unworn surface overlaps the edge of the condyle.

Many features found in modern cranes were probably established by the late Eocene or early Oligocene. For example, cranelike features are found in *Palaeogrus hordwelliensis* (Lydekker) from the upper Eocene (Hordwell beds) of England. Also, a closely related family, the Eogruidae of the Mongolian Eocene, possessed a tibiotarsus very similar to that in gruids (Wetmore, 1934). As is suggested below, the evidence
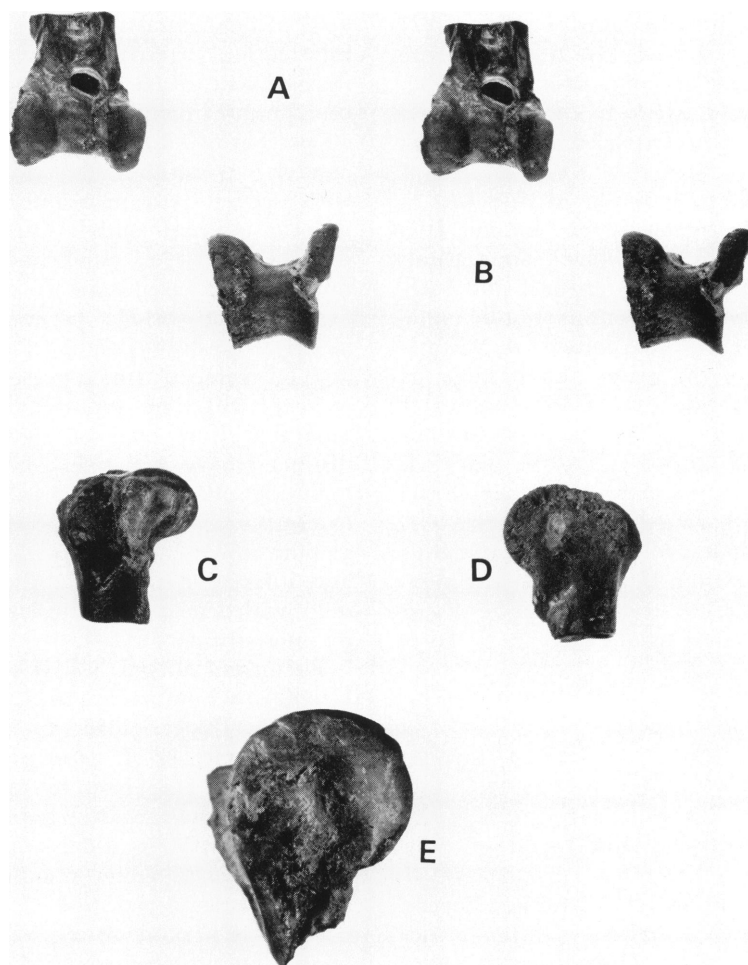
FIG. 4. A–D. *Aletornis marshi*, holotype, YPM 888, distal end of right tibiotarsus. A. Anterior view, stereo pair. B. Distal view, stereo pair. C. Internal condyle. D. External condyle. All about × 1. E. *Aletornis pernix*, holotype, YPM 64, distal end of left tibiotarsus. External condyle. About × 3.

indicates that the rounded external condyle of rails is derived with respect to the more flattened primitive condition of the cranes and their allies. Thus, morphological evidence favors placing *A. marshi* in the Rallidae at this time.

Aletornis pernix Marsh

Figure 4E

Aletornis pernix MARSH, 1872, p. 256.

HOLOTYPE: YPM 64, distal end of left tibiotarsus.

HORIZON AND LOCALITY: Middle Eocene deposits, Bridger Formation (Twin Buttes Member); Henry's Fork, Uinta County, Wyoming.

HYPODIGM: Holotype only.

DIAGNOSIS: Smallest species in genus. Differs from *A. marshi* in having the external condyle with posterior margin more strongly curved.

MEASUREMENTS: See table 2.

REMARKS: Shufeldt (1915a, p. 31) considered this specimen too fragmentary for identification. Brodkorb (1967, p. 147) retained *A. pernix* in *Aletornis* within the Balearicinae. There are several bone fragments catalogued under YPM 64, but the only one that can be identified is a broken end of a left tibiotarsus. Only the external condyle is present, but this is sufficient to

show that *A. pernix* is not gruid. The condyle (fig. 4E) is rounded anteriorly and distally, is not deep anteroposteriorly, and lacks any sign of an indentation on the distal margin. Because of the fragmentary nature of the fossil it is not possible to make a positive identification, but the roundness of the condyle suggests a tibiotarsus like that of a rail. The general outline of the condyle resembles that of *A. marshi* but differs as noted above. Unless better material becomes available and dictates otherwise, *A. pernix* should be kept in the genus *Aletornis*.

GENUS *FULICALETORNIS* LAMBRECHT

Fulicaletornis Lambrecht, 1933, p. 479.

TYPE SPECIES: *Fulicaletornis venustus* (Marsh).
INCLUDED SPECIES: Type species only.
DISTRIBUTION: Medial Eocene (Bridgerian) of Wyoming.
DIAGNOSIS: Tibiotarsus with rounded, nearly circular, external condyle, with anterior margin meeting shaft at about 50 degree angle. Internal condyle rounded anteriorly and anterodistally, with slight indentation on distal margin. Condyles nearly parallel, being separated anteriorly only slightly. Very shallow posterior intercondylar sulcus, internal notch very slight. Tubercle on supratendinal bridge poorly developed and located close to external condyle.
REMARKS: *Fulicaletornis* is compared with the other genera later in the paper.

Fulicaletornis venustus (Marsh)

Figure 5

Aletornis venustus MARSH, 1872, p. 257.
Fulicaletornis venustus (Marsh): LAMBRECHT, 1933, p. 479.

HOLOTYPE: YPM 206, distal end of left tibiotarsus.
HORIZON AND LOCALITY: Middle Eocene deposits, Bridger Formation (Twin Buttes Member); Henry's Fork, Uinta County, Wyoming.
HYPODIGM: Holotype; YPM 1027, distal end of left tibiotarsus; YPM 874, distal end of right tibiotarsus; all from same horizon and locality.
DIAGNOSIS: Same as for genus; only included species.
MEASUREMENTS: See table 3.
DESCRIPTION OF HOLOTYPE: External condyle very rounded anteriorly and distally but much less so posteriorly; anterior portion of condyle

TABLE 3

MEASUREMENTS (IN MILLIMETERS) OF TIBIOTARSI OF
Fulicaletornis venustus

	YPM 206 Holotype	YPM 1027	YPM 874
Depth (anteroposterior) of external condyle	6.8	7.0	7.0
Depth of internal condyle	6.8	7.4	—
Greatest breadth across condyles	7.3	6.8	—
Breadth of shaft 15 mm. from distal end	3.7	3.9	3.7
Depth of shaft 15 mm. from distal end	3.0	3.3	—

projecting only slightly more anteriorly than does external condyle; internal condyle greatly rounded anteriorly becoming slightly flattened proximodistally and meeting shaft at almost 90 degree angle; internal condyle slightly less rounded anterodistally; small notch on distal margin of condyle; internal ligamental prominence moderately well developed and separating two depressions, the more anterior one being much larger; posterior intercondylar sulcus very shallow with deepest portion situated close to internal condyle; anterior intercondylar fossa extending slightly over one-third the depth of external condyle; supratendinal bridge broad proximodistally; anterior face of bridge sloping noticeably in proximoposterior direction; large, rounded opening for tendon of M. extensor digitorum longus distal to bridge; tendinal groove well defined; external wall of bridge straight, directed toward external condyle, situated at external margin of shaft; moderately developed tubercle close to external condyle; groove for M. peroneus brevis deep; shaft flattened anteriorly, rounded internally, slightly less round posteriorly and externally.
REMARKS: One referred specimen (YPM 1027; fig. 5G, H) resembles the holotype (fig. 5A–D) in almost every detail. The major differences are that the referred specimen is more compressed lateromedially and has the external wall of the supratendinal bridge oriented more toward the internal condyle. I am inclined to regard these differences as individual variation.

The second specimen, YPM 874 (fig. 5E, F), differs from the holotype as follows: (1) external condyle less rounded and flatter anterodistally,
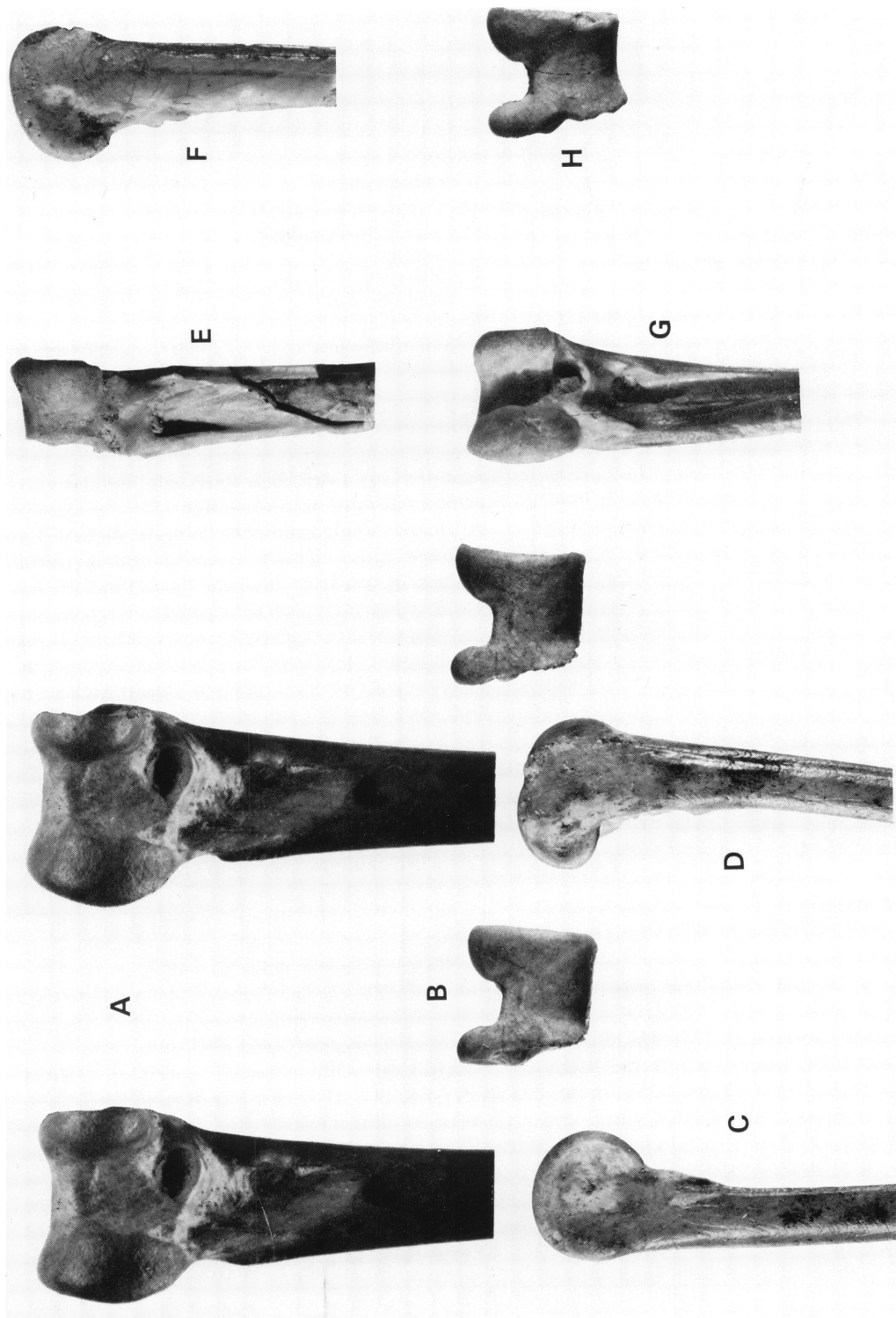
Fig. 5. *Fulicaletornis venustus*. A–D. Holotype, YPM 206, distal end of left tibiotarsus. A. Anterior view, stereo pair. About ×4. B. Distal view, stereo pair. About ×3. C. External condyle. About ×3. D. Internal condyle. About ×3. E–F. Referred specimen, YPM 874, distal end of right tibiotarsus. E. Anterior view. F. External condyle. Both about ×3. G–H. Referred specimen, YPM 1027, distal end of left tibiotarsus. G. Anterior view. H. Distal view. Both about ×3.

(2) posterior intercondylar sulcus slightly deeper, especially near the external condyle, and (3) external wall of supratendinal bridge oriented more toward internal rather than external condyle. These characters suggest a specific difference from the holotype. I refrain, however, from naming YPM 874 for several reasons. First, the bone is greatly damaged (the internal condyle is lacking) which could account for some of the differences. Second, there are general similarities in size and shape between the holotype and YPM 874. Finally, some of the characters of YPM 874 are also present in YPM 1027, such as the orientation of the external wall of the supratendinal bridge.

GENUS *TELECREX* WETMORE

Telecrex WETMORE, 1934, p. 13.

TYPE SPECIES: *Telecrex grangeri* Wetmore.
INCLUDED SPECIES: Type species only.
DISTRIBUTION: Late Eocene of Mongolia.
DIAGNOSIS: According to Wetmore (1934, p. 13): "Femur differing from that of all modern rails examined in having the head compressed and flattened; trochanter reduced, with the iliac facet elongated and narrowed; distal section of shaft considerably flattened."

REMARKS: Wetmore placed *Telecrex* in a separate subfamily, the Telecrecinae, within the Rallidae. *Telecrex* is decidedly raillike in the shape of the bone but distinct in the anteroposterior flattening of the head and shaft. Wetmore further commented (p. 14): "Apparently *Telecrex* had the habits of such modern rails as those of the genera *Rallus*, *Aramides*, and others associated with them." The shape of the femur and some differences in the extent and shape of several muscle scars argue against this conclusion. For these reasons, the conclusion that *Telecrex* "may be considered ancestral to the modern Rallinae, and connected more remotely with the swimming forms" must be re-evaluated.

Telecrex grangeri Wetmore

Telecrex grangeri WETMORE, 1934, p. 13.

HOLOTYPE: AMNH 2942, right femur with distal end missing.

HORIZON AND LOCALITY: Upper Eocene deposits, Irdin Manha Formation; Shara Murun region, Suiyuan Province, Chimney Butte, Inner Mongolia.

HYPODIGM: Holotype only.
DIAGNOSIS: Same as for genus; only included species.
MEASUREMENTS: See Wetmore, 1934, p. 14.
REMARKS: See generic remarks above.

GENUS *IBIDOPSIS* LYDEKKER

Ibidopsis LYDEKKER, 1891, p. 74.

TYPE SPECIES: *Ibidopsis hordwelliensis* Lydekker.
INCLUDED SPECIES: Type species only.
DISTRIBUTION: Late Eocene (inferior Ludian) of England.
DIAGNOSIS: Tibiotarsus with external condyle rounded and with noticeable apex, anterior margin meeting shaft at about 60 degree angle. Internal condyle shallow, with anterior portion short proximodistally, and not robust. Internal condyle projecting anteriorly only slightly more than external condyle. Condyles nearly parallel. Supratendinal bridge narrow proximodistally. Small tubercle situated close to external condyle. External wall of supratendinal groove moderately steep, oriented toward external condyle.

REMARKS: Lydekker (1891, pp. 74–75) placed *Ibidopsis* in the Threskiornithidae (=Plataleidae) and his decision has been followed by Lambrecht (1933, p. 332) and Brodkorb (1963a, p. 277). The tibiotarsus of *Ibidopsis* differs however from those of the threskiornithids in the following characters: (1) tubercle on supratendinal bridge not cup-shaped and near the middle of the bone but rounded and close to the external condyle, (2) anterior intercondylar fossa shallower, does not undercut posterior intercondylar sulcus distally but instead grades more smoothly into sulcus, (3) proximally, posterior intercondylar sulcus does not end abruptly to meet shaft in a sharp angle but grades in smoothly, (4) in distal view, anterior end of internal condyle much narrower, not broad at base (near the area of the anterior intercondylar fossa), (5) internal condyle projects less anteriorly relative to external condyle, (6) in lateral view, posterior portion of external condyle raised more distally, (7) anterior intercondylar fossa does not undercut proximal portion of base of internal condyle, and (8) in lateral view, anterior margin of external condyle grades in more smoothly with shaft rather than meeting it at 90 degree angle.

The above differences are distinct enough to
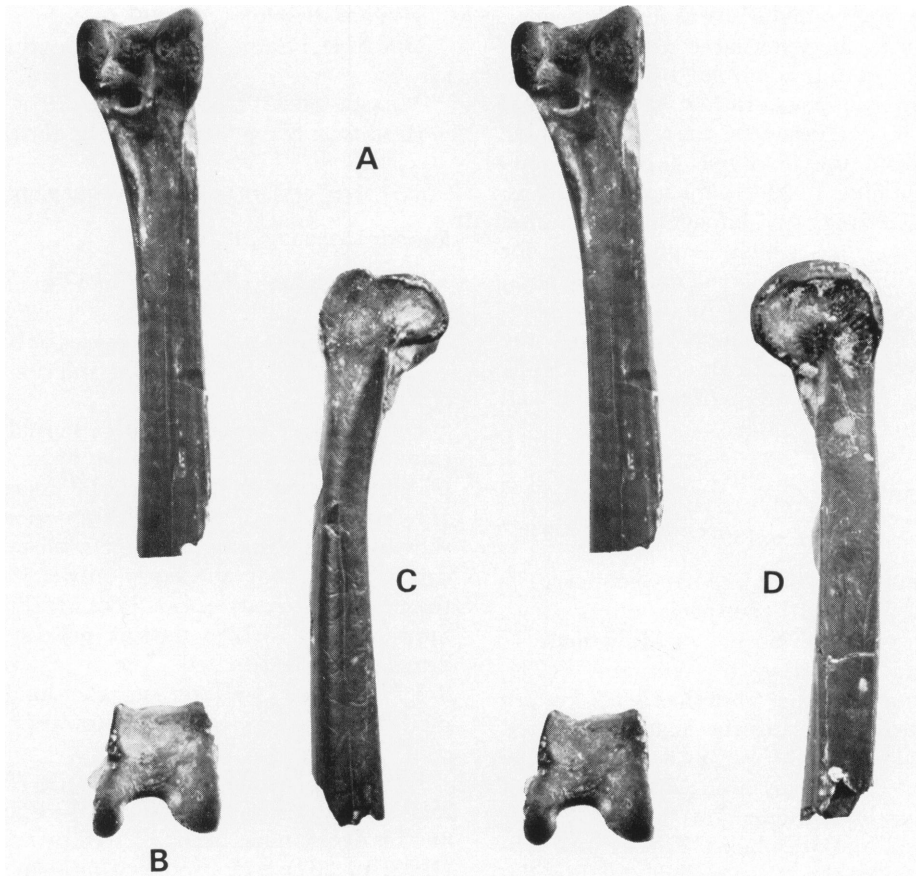
FIG. 6. *Ibidopsis hordwelliensis*, holotype, BM(NH) 36793, distal end of right tibiotarsus. A. Anterior view, stereo pair. B. Distal view, stereo pair. C. Internal condyle. D. External condyle. All about × 1.6.

warrant removing *Ibidopsis* from the Threskiornithidae, especially as these characters are very similar to those of rails, and a relationship to genera such as *Eocrex* is suggested. This is discussed in more detail below in the section on intrafamilial relationships.

Ibidopsis hordwelliensis Lydekker

Figure 6

Ibidopsis hordwelliensis LYDEKKER, 1891, p. 74.

HOLOTYPE: BM(NH) 36793, distal end of right tibiotarsus.

HORIZON AND LOCALITY: Upper Eocene deposits, Hordwell beds; Hampshire, Hordwell, England.

HYPODIGM: Holotype; BM(NH) 36794, damaged proximal left tibiotarsus; BM(NH) A146.

portion of cranial rostrum; BM(NH) 30332, damaged portion of right humerus; BM(NH) A2660, shaft of left tibiotarsus.

MEASUREMENTS: See table 4.

REMARKS: Because the referred material (Lydekker, 1891, pp. 75–76) is so fragmentary, it is impossible to assign them to *I. hordwelliensis* with complete confidence.

GENUS *LUDIORTYX* BRODKORB

Ludiortyx BRODKORB, 1964a, p. 298.
Eortyx BRODKORB, 1967, p. 111.

TYPE SPECIES: *Ludiortyx hoffmanni* (Gervais).
INCLUDED SPECIES: Type species only.
DISTRIBUTION: Late Eocene of France.
DIAGNOSIS: Compared to recent rallids, skull with cranium proportionately longer. Humerus

TABLE 4

MEASUREMENTS (IN MILLIMETERS) OF TIBIOTARSUS OF

Ibidopsis hordwelliensis

	BM(NH) 36793 Holotype[a]
Depth of external condyle	10.4
Depth of internal condyle	10.6
Breadth across posterior end of condyles	8.8
Breadth across anterior end of condyles	10.4
Breadth of shaft 20 mm. from distal end	5.8
Depth of shaft 20 mm. from distal end	4.9

[a] Measurements approximate; taken from cast of holotype.

much longer than ulna. Distal elements of wing somewhat reduced. (After Brunet, 1970, p. 42).

REMARKS: The holotype of the species on which this genus is based was originally described as *Tringa? hoffmanni* by Gervais (1848–1852). Milne-Edwards [1869 (1867–1871), vol. 2, p. 217] placed the species in his galliform genus *Palaeortyx*. Brodkorb (1964a, p. 298) maintained *P. hoffmanni* in the genus *Palaeortyx* on the apparent assumption that Milne-Edwards's notation [1869 (1867–1871), vol. 2, p. 217] "*Palaeortyx hoffmanni* nov. gen." designated this species as the type species of the genus. Brodkorb then placed (1964a, pp. 298–299) the other species of Milne-Edwards's genus *Palaeortyx* in a new genus *Ludiortyx*. Ballmann (1969, p. 30) noted that Milne-Edwards [1869 (1867–1871), vol. 2, p. 230] designated *P. gallica* as the type species of *Palaeortyx*. Therefore, Brodkorb (1967, p. 111) created a new genus, *Eortyx*, for *P. hoffmanni*.

Brunet (1970, pp. 33–44) restudied *Tringa? hoffmanni* and *Palaeortyx blanchardi*, the latter being the type species of Brodkorb's genus *Ludiortyx*, and concluded that they were conspecific. Moreover, Brunet thought that this combined species represents a rail rather than a galliform and placed it in the Rallidae as *Ludiortyx hoffmanni* (Gervais). Brodkorb (1964a, p. 299) included several other species besides *L. blanchardi* in his genus *Ludiortyx*, and when he transferred the genus to the Rallidae, Brunet mentioned (p. 43, footnote) that these species—

L. cayluxensis (Lydekker) and *L. gaillardi* (Lambrecht)—should perhaps be placed temporarily in the genus *Palaeortyx*. Because *Ludiortyx* predates *Eortyx* the latter becomes a synonym, and the type species of *Ludiortyx* is now *L. hoffmanni* (Gervais). The species *L. cayluxensis* and *L. gaillardi* are galliforms (unpublished observ.) and for convenience can be allocated to the Eocene genus *Paraortyx* Gaillard rather than the Miocene *Palaeortyx* (as recognized by Brodkorb, 1967, p. 112). I have restudied almost all the European galliform material and intend to discuss the systematics of these fossils in the near future.

The above generic diagnosis is modified from remarks by Brunet (1970) who has re-examined the type and discussed it in considerable detail. Brunet cited many characters such as the shape of the cranium, shape of cervical vertebrae, slender humerus, and absence of an intermetacarpal process that seemingly argue against a relationship with the Galliformes. In these characters *Ludiortyx* resembles the Rallidae. Unfortunately, the type specimen is preserved as a flattened skeleton, and thus it is difficult to recognize characters that can provide a diagnosis for *Ludiortyx*. Hence, the above diagnosis must be considered tentative until additional material is discovered.

Ludiortyx hoffmanni (Gervais)

Figures 7, 8

Tringa? hoffmanni GERVAIS, 1852, p. 229.
Palaeortyx hoffmanni (Gervais): MILNE-EDWARDS, 1869 (1867–1871), vol. 2, p. 217.
Eortyx hoffmanni BRODKORB, 1967, p. 111.
Palaeortyx blanchardi MILNE-EDWARDS, 1869 (1867–1871), vol. 2, p. 223.
Ludiortyx blanchardi (Milne-Edwards): BRODKORB, 1964a, p. 298.
Ludiortyx hoffmanni (Gervais): BRUNET, 1970, p. 33.

HOLOTYPE: PM 7996, flattened skeletal fragment.

HORIZON AND LOCALITY: Upper Eocene deposits, gypse de Montmartre; Montmartre, Dept. Seine, France.

HYPODIGM: Holotype (fig. 7); PM 7921, 7922, impression and counter impression of flattened skeleton; PM 7924, 7925, humeri (fragmentary?; not examined); PM 7994 (fig. 8), flattened skeleton (type of *P. blanchardi*). After Brunet 1970, p. 33.

FIG. 7. *Ludiortyx hoffmanni*, holotype, PM 7996. About × 0.80.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: See Brunet (1970).

REMARKS: I agree with Brunet (1970, pp. 39–40) that *L. hoffmanni* (Gervais) and *L. blanchardi* (Milne-Edwards) are probably conspecific and thus must take the older name *L. hoffmanni*. See Brunet (1970, pp. 33–44) for a complete description and comparison of this species.

GENUS *QUERCYRALLUS* LAMBRECHT

Quercyrallus LAMBRECHT, 1933, p. 461.

TYPE SPECIES: *Quercyrallus arenarius* (Milne-Edwards); designated by Brodkorb, 1952, p. 175.

INCLUDED SPECIES: Type species; *Q. ludianus* Brodkorb; *Q. quercy*, new species; and *Q. dasypus* (Milne-Edwards).

DISTRIBUTION: Late Eocene to possible medial Oligocene of France.

DIAGNOSIS: Skull with cranium and bill about equal length. Contour from top of cranium to nasal-frontal hinge forming sharp angle with long axis of bill. Culmen very straight; apparently little dorsal inflection of bill near nasal-frontal hinge.

Humerus with deltoid crest apparently low and lengthened distally. Internal tuberosity projecting noticeably internally. External tuberosity well developed. Entepicondyle low and not projecting much anconally or distally. Internal condyle only moderately raised distally relative to external condyle. Attachment of anterior articular ligament faces in external direction. Attachment of pronator brevis shallow. Shaft fairly heavy and robust. Ectepicondyle poorly developed. External tricipital groove shallow.

Distal end of femur with internal condyle rounded posteriorly. Portion of shaft proximal to distal end relatively straight, not curving much posteriorly. Fibular groove shallow. External condyle projecting noticeably distoanteriorly.

REMARKS: There are currently three species included in *Quercyrallus* (Lambrecht, 1933, p. 461; Brodkorb, 1967, p. 118): *Q. ludianus* Brodkorb (=*Rallus intermedius* Milne-Edwards),
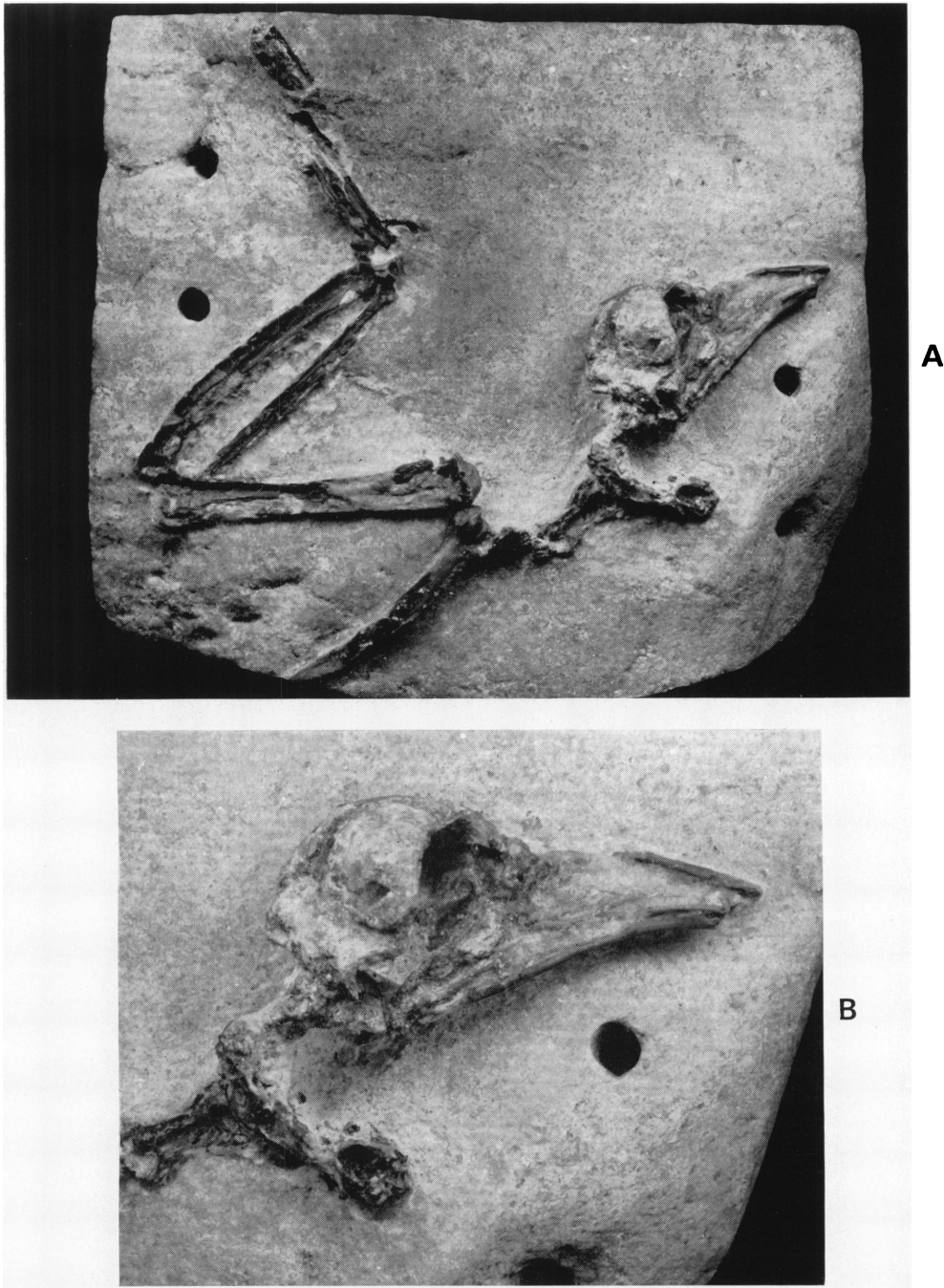
FIG. 8. *Ludiortyx hoffmanni*, referred specimen, PM 7994. A. Whole specimen. About × 1. B. Close-up of skull. About × 2. This specimen was type of *Palaeortyx blanchardi* Milne-Edwards.

Q. arenarius (Milne-Edwards), and *Q. dasypus* (Milne-Edwards). Lambrecht (1933, p. 461) diagnosed the genus as having a more strongly developed processus supracondyloideus externus (=ectepicondylar prominence) than in Recent rails. Unfortunately, this diagnosis was based on

FIG. 9. *Quercyrallus ludianus*, holotype, PM 7995. About × 1.4.

an incorrectly identified specimen figured by Gaillard (1908, p. 111, fig. 33) and which apparently was not examined by Lambrecht (see discussion of *Q. arenarius* below).

The species assigned to this genus are based on skeletal elements which are not always comparable. Thus, it is possible that they do not form a natural assemblage, but placing them in the same genus is preferable to creating a new genus on negative evidence.

Quercyrallus ludianus Brodkorb

Figure 9

Rallus intermedius MILNE-EDWARDS, 1869 (1867–1871), vol. 2, p. 144 (preoccupied by *Rallus intermedius* Hermann).
Quercyrallus ludianus BRODKORB, 1963c, p. 542.

HOLOTYPE: PM 7995, skeletal impression.
HORIZON AND LOCALITY: Upper Eocene deposits, gypse de Montmartre; Montmartre, Dept. Seine, France.
HYPODIGM: Holotype only.

DIAGNOSIS: Larger than *Q. arenarius*; smaller than *Q. quercy*; about same size as *Q. dasypus* (see remarks for *Q. dasypus* below).
MEASUREMENTS: Length of upper jaw along culmen 24.7 mm.; length of cranium from posterior part of supraoccipital area to nasal-frontal hinge 23.5 mm.
REMARKS: Although this specimen is badly crushed, the shapes of the skull and sternum are raillike (fig. 9). Unfortunately, not enough detail is preserved to discern relationships within the family, but the short bill is somewhat reminiscent of the genus *Porzana*. See Brunet (1970, pp. 28–32) for a detailed discussion of this species.

Quercyrallus arenarius (Milne-Edwards)

Figure 10A

Rallus arenarius MILNE-EDWARDS, 1891, p. 74.
Quercyrallus arenarius (Milne-Edwards): LAMBRECHT, 1933, p. 461.

HOLOTYPE: PM Qu3072, proximal end of left humerus.
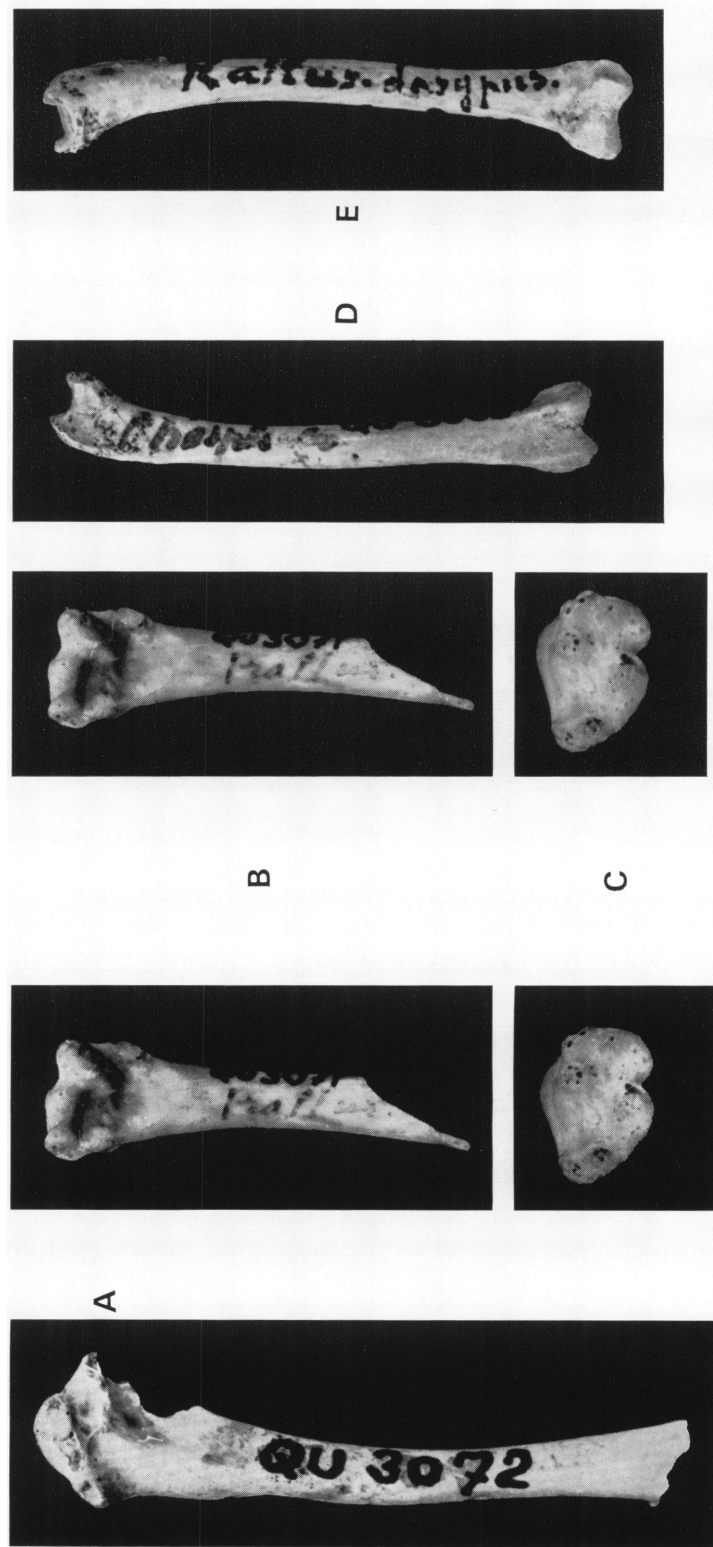
FIG. 10. A. *Quercyrallus arenarius*, holotype, PM Qu3072, left humerus. About ×3.4. B–C. *Quercyrallus quercy*, holotype, PM Qu3071, distal end of right humerus. B. Palmar view, stereo pair. About ×2. C. Distal view, stereo pair. About ×2.4. D–E. *Quercyrallus dasypus*, holotype, PM Qu3068, right femur. D. Anterior view. About ×1.7. E. Posterior view. About ×1.9.

	Q. arenarius PM Qu3072 Holotype	Q. quercy PM Qu3071 Holotype
Breadth across distal end	—	7.9
Depth of external condyle	—	4.8
Depth of internal condyle	—	3.5
Breadth of middle of shaft	2.2[a]	3.8[a]
Depth of middle of shaft	1.8[a]	3.5
Breadth of proximal end	6.1[a]	—

[a] Bone worn; measurement approximate.

HORIZON AND LOCALITY: Upper Eocene to middle Oligocene deposits, phosphorites du Quercy; Dept. Tarn-et-Garonne, France.

HYPODIGM: Holotype; distal humerus in Stuttgart Museum (according to Lambrecht, 1933, p. 461; systematic position questionable, see below).

DIAGNOSIS: Smallest species in genus.

MEASUREMENTS: See table 5.

REMARKS: The type specimen is too worn to make detailed comparisons with other rails. Indeed, it is questionable whether the type can be referred definitely to the Rallidae, although the general proportions and some details suggest that it is correctly placed in this family.

Gaillard (1908, p. 111, fig. 33) described another humerus which he assigned to this species. The humerus (MU 125) has since been lost but the figure and measurements correspond closely to a series of humeri in the Paris Museum. These humeri represent a charadriiform species rather than a rail. Because of this it is likely that the humerus mentioned by Lambrecht (1933, p. 461) is also misidentified.

Quercyrallus quercy, new species

Figure 10B, C

Rallus dasypus MILNE-EDWARDS, 1892, p. 74.
Quercyrallus dasypus (Milne-Edwards): LAMBRECHT, 1933, p. 461.

HOLOTYPE: PM Qu3071, distal end of right humerus.

HORIZON AND LOCALITY: Upper Eocene to possibly middle Oligocene deposits, phosphorites du Quercy; apparently near Saint Antonin, Dept. Tarn-et-Garonne, France.

HYPODIGM: Holotype only.

DIAGNOSIS: Largest species in genus.

MEASUREMENTS: See table 5.

REMARKS: This new species is erected for one of the specimens described as *Rallus dasypus* by Milne-Edwards (1892, pp. 73–74). The humerus described here is considerably larger than the femur which is considered the lectotype of *Q. dasypus*.

ETYMOLOGY: *Quercy*, in reference to the phosphorites du Quercy, France, where the type was collected.

Quercyrallus dasypus (Milne-Edwards)

Figure 10D, E

Rallus dasypus MILNE-EDWARDS, 1892, p. 73.
Quercyrallus dasypus (Milne-Edwards): LAMBRECHT, 1933, p. 461.

LECTOTYPE: PM Qu3068, complete right femur.

HORIZON AND LOCALITY: Upper Eocene to possibly middle Oligocene deposits, phosphorites du Quercy; apparently near Saint Antonin, Dept. Tarn-et-Garonne, France.

HYPODIGM: Lectotype only.

DIAGNOSIS: Larger than *Q. arenarius*; smaller than *Q. quercy*; apparently same size as *Q. ludianus* (see remarks below).

MEASUREMENTS: Total length 41.4 mm.; lateromedial breadth of distal end 6.9 mm.; depth of external condyle 5.4 mm.; depth of internal condyle 5.2 mm.

REMARKS: In his original description Milne-Edwards (1892, pp. 73–74) did not designate a type specimen for *Rallus dasypus*, and both the femur and humerus (PM Qu3071; type of *Q. quercy*) were considered the types of this species by Lambrecht (1933) and Brodkorb (1967). Because they represent two different species, I here designate the femur as lectotype of *Rallus dasypus*.

The femur (fig. 10D, E) is morphologically distinct from all recent rails I have examined. However, after comparison with other non-passeriform families, I am unable to find another family which resembles *Q. dasypus* more closely than do rails.

The femur of *Q. dasypus* is probably about the same size as that of *Q. ludianus*, although this

element is not preserved in the latter species. It is thus possible that these specimens are from the same species. Because they are not comparable and are from different stratigraphic levels, I am maintaining the two species names.

GENUS *PALAEOCREX* WETMORE

Palaeocrex WETMORE, 1927, p. 9.

TYPE SPECIES: *Palaeocrex fax* Wetmore.
INCLUDED SPECIES: Type species only.
DISTRIBUTION: Early Oligocene (Chadronian) of Colorado.
DIAGNOSIS: Tarsometatarsus with inner trochlea not turned far posteriorly relative to middle trochlea. Large internal intertrochlear notch present. External intertrochlear notch broad and deep proximodistally. Inner trochlea broad and heavy. Middle trochlea elongated proximodistally.
REMARKS: This genus stands apart from all other rails of the North American Tertiary both in size and morphology. Its characters suggest nonralline affinities but when compared with other families, *Palaeocrex* does seem closest to rails.

Palaeocrex fax Wetmore

Palaeocrex fax WETMORE, 1927, p. 9.

HOLOTYPE: CMNH 1078, distal end of left tarsometatarsus.
HORIZON AND LOCALITY: Lower Oligocene deposits, *Trigonias* quarry; Weld County, Colorado.
HYPODIGM: Holotype only.
DIAGNOSIS: Same as for genus; only included species.
MEASUREMENTS: See Wetmore (1927).
REMARKS: See above under genus and Wetmore (1927, pp. 9–11).

GENUS *RALLICREX* LAMBRECHT

Rallicrex LAMBRECHT, 1933, p. 463.

TYPE SPECIES: *Rallicrex kolozsvarensis* Lambrecht.
INCLUDED SPECIES: Type species only.
DISTRIBUTION: Late Oligocene of Romania.
DIAGNOSIS: Tarsometatarsus with external intertrochlear notch wide. Inner trochlea turned very far posteriorly. Distal foramen apparently rather large.

REMARKS: In his very brief diagnosis of *Rallicrex* Lambrecht (1933, p. 463) stated that the fossil is morphologically intermediate between the recent genera *Rallus* and *Crex*. Although the illustrations of *Rallicrex* are very poor, the genus does seem to differ from other fossil rails in having a broad external intertrochlear notch and an inner trochlea that is turned very far posteriorly. Lambrecht did not make any comparisons to other fossil rails.

Rallicrex kolozsvarensis Lambrecht

Rallicrex kolozsvarensis LAMBRECHT, 1933, p. 463.

HOLOTYPE: Museum Königlichen Ungarischen Geologischen Anstalt (Budapest), no number, distal end of left tarsometatarsus.
HORIZON AND LOCALITY: Probably middle or upper Oligocene deposits (between Stampian and Burdigalian in age), *Corbula* beds; south face of Zitadell zu Kolzsvár, Siebenburgen, Romania.
HYPODIGM: Holotype only.
DIAGNOSIS: Same as for genus; only included species.
MEASUREMENTS: According to Lambrecht (1933, p. 464), breadth across trochlea 6.0 mm.; breadth of middle trochlea 2.0 mm.
REMARKS: See above for genus and section on intrafamilial comparisons.

GENUS *PALAEOARAMIDES* LAMBRECHT

Palaeoaramides LAMBRECHT, 1933, p. 462.

TYPE SPECIES: *Palaeoaramides christyi* (Milne-Edwards).
INCLUDED SPECIES: Type species; *P. beaumonti* (Milne-Edwards); and *P. minutus*, new species.
DISTRIBUTION: Late Oligocene and/or early Miocene to late Miocene of France.
DIAGNOSIS: Tarsometatarsus with well-developed inner trochlea having broad base of attachment and turned far posteriorly. External intertrochlear notch moderate in width. Distal foramen slitlike. Hypotarsus with two well-defined tendinal grooves on internal surface. No canals formed. Intercotylar prominence tending to be low and blunt.
Tibiotarsus with rounded external condyle, raised posteriorly. Internal condyle projecting anteriorly slightly more than external condyle. Supratendinal bridge narrow proximodistally. Tubercle on supratendinal bridge slight or lacking.
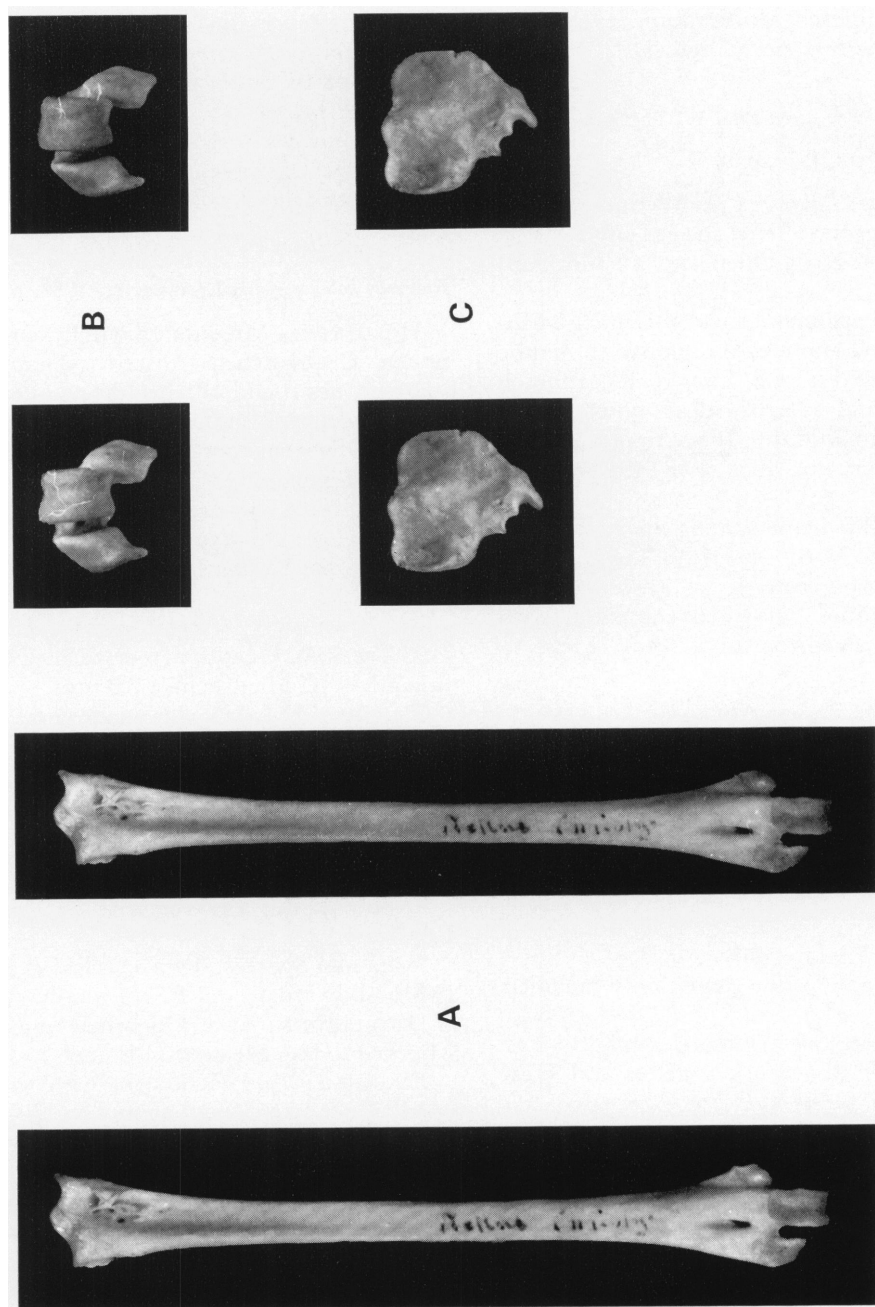
FIG. 11. *Palaeoaramides christyi*, lectotype, PM Av.2868, complete right tarsometatarsus. A. Anterior view, stereo pair. About ×1.6. B. Distal end, stereo pair. About ×2. C. Proximal end, stereo pair. About ×2.4.
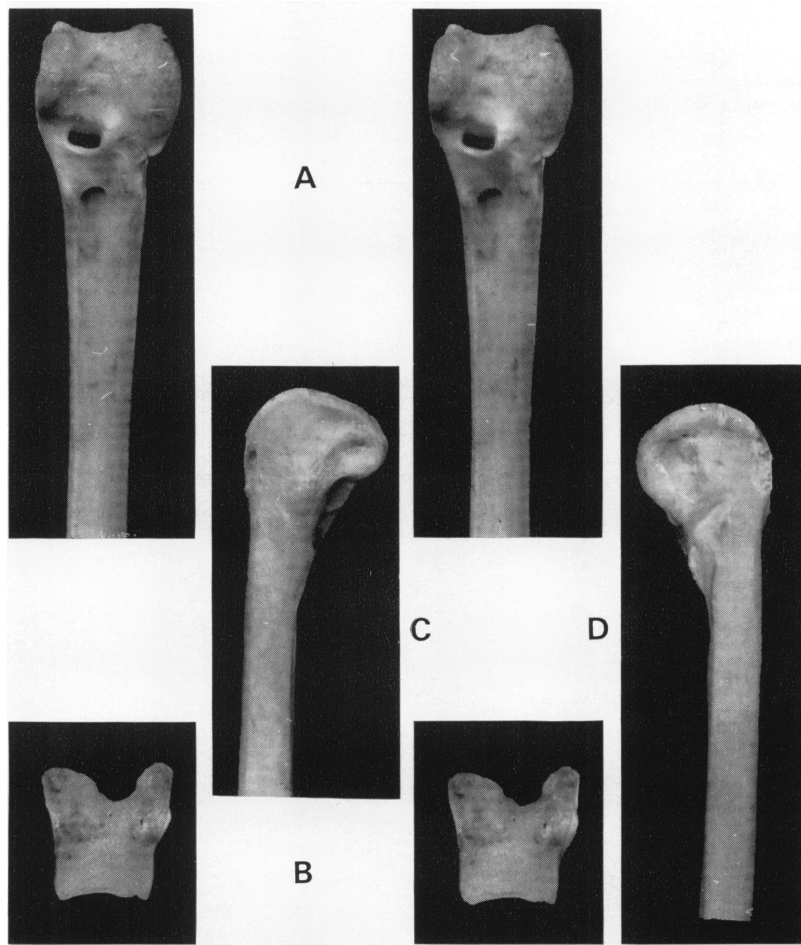
FIG. 12. *Palaeoaramides christyi*, referred specimen, PM Av.2867, distal end of right tibiotarsus. A. Anterior view, stereo pair. About ×2.5. B. Distal end, stereo pair. About ×2.2. C. Internal condyle. About ×2.2. D. External condyle. About ×2.2.

Humerus with entepicondyle projecting noticeably anconally and distally. Attachment of pronator brevis absent or very poorly developed. Pits on side of entepicondyle not well defined. External tricipital groove deep. Olecranal fossa deep. Internal condyle rounded, not greatly elongated lateromedially. Ectepicondylar prominence poorly developed. External tuberosity well developed. Ligamental furrow deep and elongated lateromedially. Capital groove deep and broad anconal-palmarly.

REMARKS: See below under intrafamilial comparisons.

Palaeoaramides christyi (Milne-Edwards)

Figures 11, 12

Rallus christyi MILNE-EDWARDS, 1869 (1867–1871), vol. 2, p. 146.
Rallus eximus MILNE-EDWARDS, 1869 (1867–1871), vol. 2, p. 149.
Palaeoaramides christyi (Milne-Edwards): LAMBRECHT, 1933, p. 462.
Palaeoaramides eximus (Milne-Edwards): BRODKORB, 1967, p. 119.

LECTOTYPE: PM Av.2868, complete right tarsometatarsus.

TABLE 6

MEASUREMENTS (IN MILLIMETERS) OF TARSOMETATARSI OF *Palaeoaramides christyi* AND *Palaeoramides minimus*

	PM Av.2868 Lectotype	*P. christyi* PM Av.2865[a]	BM(NH) A732	*P. minimus* BM(NH) A332 Holotype
Total length	64.0	61.2	60.2	25.1[b]
Lateromedial breadth across trochleae	8.5	7.8	7.4	3.3
Breadth of inner trochlea	2.4	2.3	1.9	1.0
Breadth of middle trochlea	3.3	3.0	2.9	1.2
Breadth of outer trochlea	2.9	2.3	2.7	1.1
Depth of middle trochlea	4.6	4.5	4.3	1.5
Breadth of middle of shaft	3.4	3.5	—	1.5
Depth of middle of shaft	3.3	3.3	—	1.2
Breadth of proximal end	7.8	7.8	7.0	3.2
Depth of proximal end	8.8	7.6	—	—

[a] Type of *P. eximus* (Milne-Edwards).
[b] Measurement approximate; bone worn.

HORIZON AND LOCALITY: Upper Oligocene or lower Miocene deposits; Langy, Dept. Allier and Saint Gérand-le-Puy, Montaigu, Dept. Allier, France. Lambrecht (1933, p. 462) recorded a specimen in the Munich Museum from Montaigu, Dept. Allier, but this specimen was apparently destroyed during World War II.

HYPODIGM: Lectotype; PM Av.2865 and BM(NH) A732, complete right tarsometatarsi; PM Av.2867 and BM(NH) A732, complete right tibiotarsi; BaM uncatalogued, distal left tibiotarsus.

DIAGNOSIS: Largest species in genus.
MEASUREMENTS: See tables 6 and 7.
REMARKS: In his original description of *Rallus christyi* Milne-Edwards [1869 (1867–1871), vol. 2, pp. 146–148] treated both the tarsometatarsus (PM Av.2868; fig. 11) and tibiotarsus (PM Av.2867; fig. 12) as the type material, and subsequent authors (Lambrecht, 1933, p. 462; Brodkorb, 1967, p. 119) did likewise. To my knowledge there is no evidence that these two bones were associated and therefore I here designate the tarsometatarsus as the lectotype.

TABLE 7

MEASUREMENTS (IN MILLIMETERS) OF TIBIOTARSI OF THE SPECIES OF *Palaeoaramides*

	P. christyi PM Av.2867	BM(NH) A732	BaM uncatalogued	*P. beaumonti* PM Sa1205 Lectotype	PM Sa1217
Total length	95.0–100.0[a]	83.4	—	—	—
Depth (anteroposterior) of external condyle	8.0	6.9	6.1	5.0	5.3
Depth of internal condyle	8.3	7.0	6.4	5.1[b]	5.6
Breadth across posterior ends of condyles	5.8	5.1	4.5	3.7	3.9
Breadth across anterior ends of condyles	7.8	6.7	5.9	4.9	5.4
Breadth of middle of shaft	4.0	3.4	3.1	—	—
Depth of middle of shaft	3.5	3.1	3.0	—	—
Depth of proximal end	—	10.0	—	—	—

[a] Total length estimated.
[b] Condyle slightly worn.
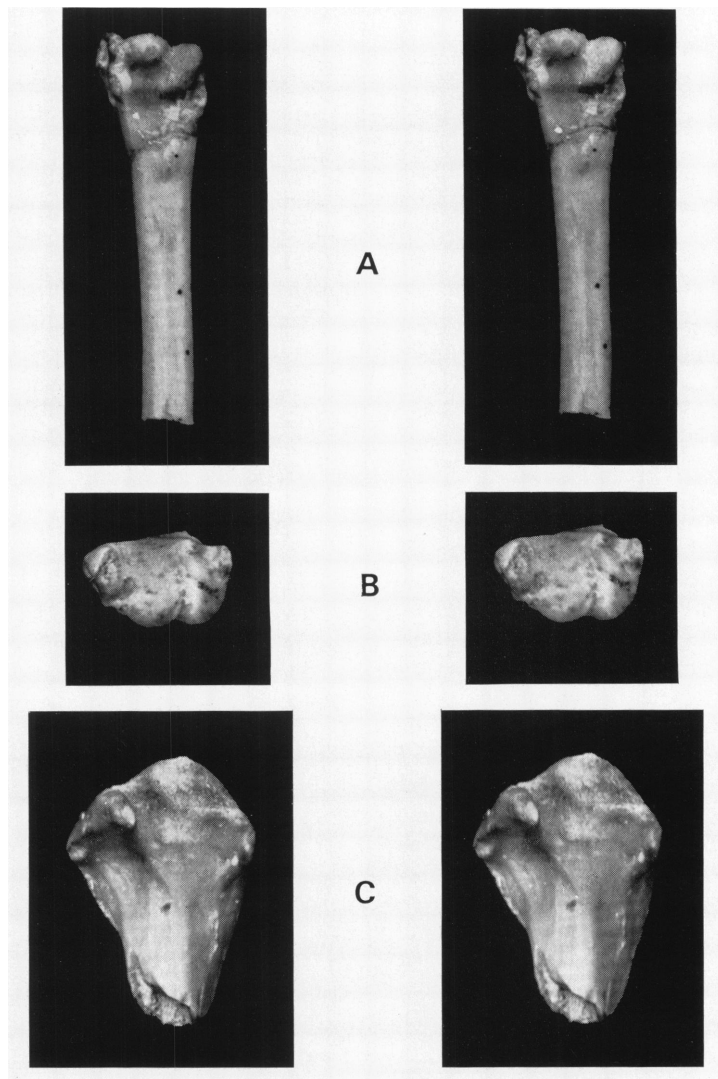
FIG. 13. *Palaeoaramides beaumonti*, referred specimens. A–B. PM Sa1203, distal end of right humerus. A. Palmar view, stereo pair. About ×2.4. B. Distal end, stereo pair. About ×3.2. C. PM Sa1204, proximal end of right humerus, stereo pair. About ×3.

Rallus eximus was described for a complete right tarsometatarsus, PM Av.2865 [Milne-Edwards, 1869 (1867–1871), vol. 2, p. 149]. Lambrecht (1933, p. 462) considered *P. eximus* to be conspecific with *P. christyi*, and he explained the differences in size as sexual dimorphism. Brodkorb (1967, p. 119) recognized two species but noted that *P. eximus* may be the female of *P. christyi*. I found no significant morphological differences among the tarsometatarsi

or tibiotarsi included in the hypodigm. The tarsometatarsi are very similar in size and are all easily within the range of variability of a single species. On the other hand the tibiotarsi exhibit a greater degree of size variation than do the tarsometatarsi. An unnumbered distal left tibiotarsus in the Basel Museum from the Saint Gérand-le-Puy of Montaigu is considerably smaller than the lectotype but is probably within the range of variability of a single species; other

TABLE 8

Measurements (in Millimeters) of Humeri of

Palaeoaramides beaumonti and *Pararallus dispar*

	P. beaumonti PM Sa1203	P. beaumonti PM Sa1204	P. dispar PM Sa1201 Lectotype
Lateromedial breadth across distal end	6.2	—	5.7
Depth of external condyle	3.6	—	3.5
Depth of internal condyle	1.9	—	1.8
Breadth middle of shaft	—	—	3.0
Depth middle of shaft	—	—	2.4
Breadth of proximal end	—	8.9	—

fossil rail populations show as great a difference in tibiotarsi size as do these specimens (see section on morphological variability). The tibiotarsus from Basel may not be strictly coetaneous with the other specimens of *P. christyi* and may represent a temporal size variation of the same species.

The referred material catalogued under BM(NH) A732 is similar to the type of *P. christyi* in morphology although they are slightly smaller than the latter. The referred tibiotarsus and tarsometatarsus are catalogued together, but it is unknown whether they were associated.

Palaeoaramides beaumonti (Milne-Edwards)

Figure 13

Rallus beaumonti Milne-Edwards, 1869 (1867–1871), vol. 2, p. 152.

Pararallus beaumonti (Milne-Edwards): Brodkorb, 1967, p. 120.

Lectotype: PM Sa1205, distal end of right tibiotarsus.

Horizon and Locality: Upper Miocene deposits; Sansan, Dept. Gers, France.

Hypodigm: Lectotype; PM Sa1203, distal end of right humerus; PM Sa1204, proximal end of right humerus; PM Sa1217, distal end of left tibiotarsus.

Diagnosis: Much smaller than *P. christyi* and much larger than *P. minutus*.

Measurements: See tables 7 and 8.

Remarks: This species is included in the genus *Palaeoaramides* on the basis of the tibiotarsus, which does not differ in any significant characters (except size) from those of *P. christyi*.

The four elements assigned to *P. beaumonti* are all within the general size range of a single species, although it is rather certain that they came from different individuals. Milne-Edwards [1869 (1867–1871), pl. 104, figs. 10–12] included a distal tarsometatarsus in the type material of *P. beaumonti*; this specimen (PM Sa1206) almost certainly is not a rail because the inner trochlea projects far distally relative to the middle trochlea and is not turned posteriorly.

Lambrecht (1933, p. 467) made no decision about the systematic status of "*Rallus*" *beaumonti*, but he noted that the above-mentioned tarsometatarsus was not rallid. Brodkorb (1967, p. 120) provisionally included *P. beaumonti* in the genus *Pararallus* along with *P. dispar*.

Palaeoaramides minutus, new species

Figure 14

Holotype: BM(NH) A332 an almost complete right tarsometatarsus.

Horizon and Locality: Upper Miocene deposits, La Grive Saint-Alban, Isère, France.

Hypodigm: Holotype only.

Diagnosis: Smallest species in genus (see also remarks).

Measurements: See table 6.

Remarks: This new species is provisionally included in *Palaeoaramides* until better material is found. The type tarsometatarsus agrees with that of *P. christyi* in a number of characters, and I therefore think present evidence suggests a relationship with this genus rather than to some other. Some of these shared characters include a slitlike distal foramen and an external intertrochlear notch that is moderate in width. In addition to size *P. minutus* differs from *P. christyi* in having the distal foramen relatively larger, the external intertrochlear notch somewhat wider, and the outer trochlea projecting somewhat less distally relative to the middle trochlea. Unfortunately, the hypotarsus of the holotype is damaged, and until this is known I believe it prudent to assign *P. minutus* to *Palaeoaramides*. Eventually hypotarsal evidence may provide support for relationships to some other genus.

Palaeoaramides minutus differs from *Paraortygometra porzanoides* of the same deposits in that the former is smaller (compare tables 6 and 11) and has the distal foramen slitlike instead of circular. The new species also differs from *Pararallus dispar* in having a much broader
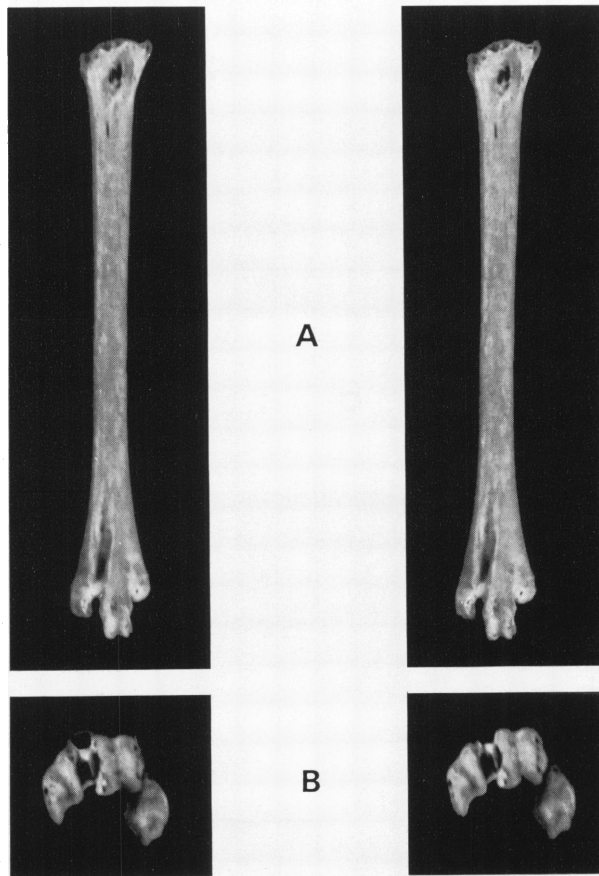
FIG. 14. *Palaeoaramides minutus*, holotype, BM(NH) A332, right tarsometatarsus. A. Anterior view, stereo pair. About × 3. B. Distal end, stereo pair. About × 5.

external intertrochlear notch, an inner trochlea turned less posteriorly, and an outer trochlea projecting less distally relative to the middle trochlea.

ETYMOLOGY: *Minutus*, Latin, in reference to the small size of the species.

GENUS *PARARALLUS* LAMBRECHT

Pararallus LAMBRECHT, 1933, p. 466.

TYPE SPECIES: *Pararallus dispar* (Milne-Edwards).

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Early Oligocene to late Miocene (Helvetian) of France and Germany.

DIAGNOSIS: Humerus with shallow brachial depression. Ectepicondylar prominence very poorly developed. Entepicondyle projecting strongly anconally but not distally. External tricipital groove deep. External condyle somewhat elongated anconal-palmarly. Olecranal fossa deep. Attachment of pronator brevis very poorly developed or absent.

Tibiotarsus with external condyle very round and anterior margin meeting shaft at nearly 90 degree angle. Internal condyle not projecting noticeably anterior to external condyle, but both condyles nearly even. Anterior intercondylar fossa deep. Internal ligamental prominence situated near middle of condyle.

Tarsometatarsus with two grooves on internal side of hypotarsus; no canals formed. Internal trochlea large with broad base. External intertrochlear notch very narrow.
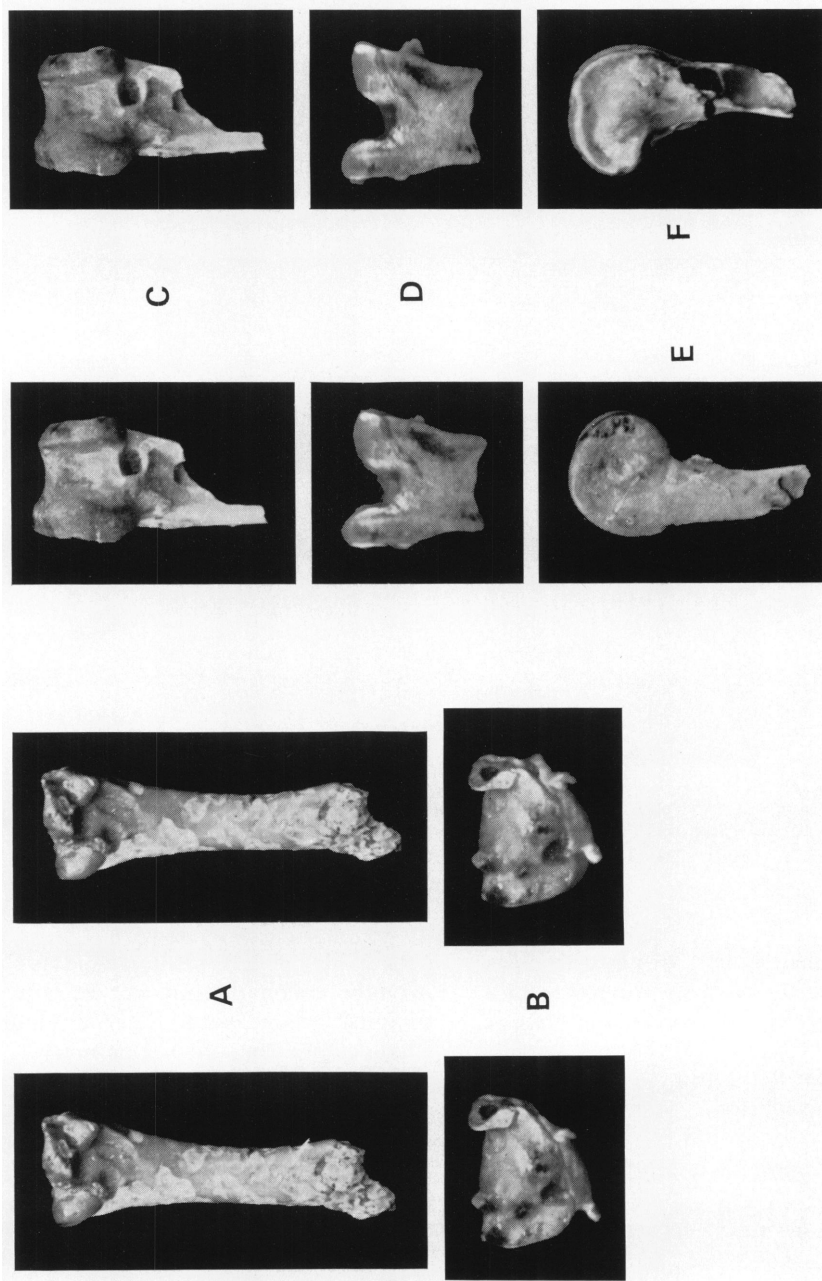
FIG. 15. *Pararallus dispar*, lectotype, PM Sal1201, distal end of left humerus. A. Palmar view, stereo pair. About ×2.6. B. Distal end, stereo pair. About ×3.7. C–D. Referred specimen, PM Sal1202, distal end of left tibiotarsus. C. Anterior view, stereo pair. D. Distal end, stereo pair. E. External condyle. F. Internal condyle. All about ×4.
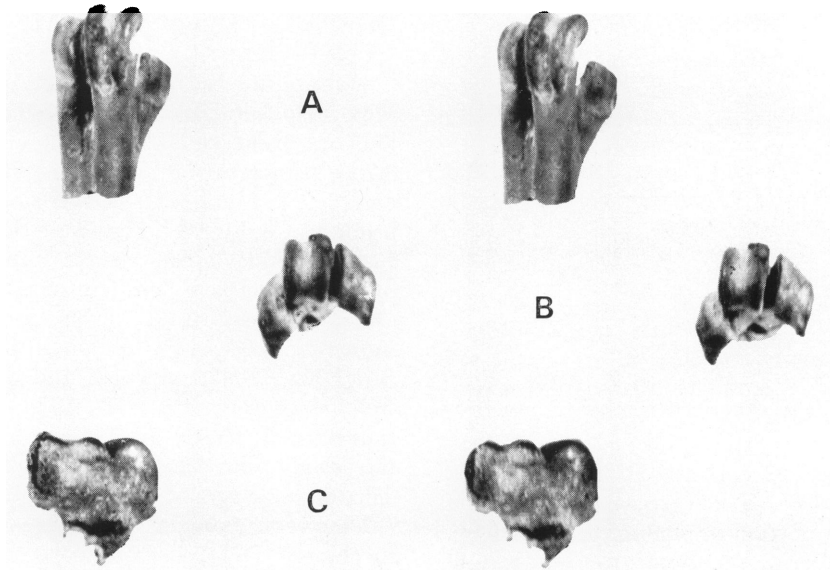
FIG. 16. *Pararallus dispar*, referred specimens. A–B. PM Sa1210, distal end of left tarsometatarsus. A. Anterior view, stereo pair. B. Distal end, stereo pair. Both about × 3.4. C. PM Sa1208, proximal end of right tarsometatarsus, stereo pair. About × 3.7.

REMARKS: As is explained below in the species accounts, this genus probably did not extend back into the Oligocene; at least the evidence is very circumstantial. The genus *Pararallus* of Brodkorb (1967, p. 120) included *P. dispar* and *P. beaumonti*, but the latter species is removed to the genus *Palaeoaramides* (see above).

Pararallus dispar (Milne-Edwards)

Figures 15, 16

Rallus dispar MILNE-EDWARDS, 1869 (1867–1871), vol. 2, p. 155.
Pararallus dispar (Milne-Edwards): LAMBRECHT, 1933, p. 466.

LECTOTYPE: PM Sa1201, distal end of a left humerus.

HORIZON AND LOCALITY: Middle to upper Miocene deposits; Sansan; Dept. Gers, France.

HYPODIGM: Lectotype; PM Sa1202, distal end of left tibiotarsus; PM Sa1214, distal end of right tibiotarsus; PM Sa1207, proximal end of right tarsometatarsus; PM Sa1208, proximal end of right tarsometatarsus; PM Sa1209, proximal end of left tarsometatarsus; PM Sa1210, distal end of left tarsometatarsus; PM Sa1211, distal end of left tarsometatarsus (greatly damaged).

DIAGNOSIS: Smallest species in genus.
MEASUREMENTS: See tables 8 to 10.

REMARKS: In the original description Milne-Edwards [1869 (1867–1871), vol. 2, pp. 155–157] did not choose a type specimen, therefore I designate the humerus (PM Sa1201) as the lectotype (fig. 15A, B). The specimens included in the hypodigm come from several individuals, and almost certainly none of the elements were associated. All are from a rail of about the same size, so it is reasonable to consider them conspecific until proved otherwise. *Pararallus dispar* is smaller than *Palaeoaramides beaumonti* and *Miorallus major* which are also known from the deposits of Sansan.

GENUS *PARAORTYGOMETRA* LAMBRECHT

Paraortygometra LAMBRECHT, 1933, p. 462.

TYPE SPECIES: *Paraortygometra porzanoides* (Milne-Edwards).

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Late Oligocene or early Miocene (Aquitanian) of France.

DIAGNOSIS: Tarsometatarsus with two canals on internal side of hypotarsus and two long, well-marked grooves on external side. Internal

TABLE 9

MEASUREMENTS (IN MILLIMETERS) OF TIBIOTARSI OF

Pararallus dispar

	PM Sa1202	PM Sa1214
Anteroposterior depth of external condyle	4.3	4.5
Depth of internal condyle	4.6	4.8
Breadth across posterior end of condyles	3.2	3.3
Breadth across anterior end of condyles	4.2	4.7

trochlea turned only moderately far posteriorly.

Humerus with capital groove undercutting head. Internal portion of pneumatic fossa deep. Ligamental furrow tending to be round. Entepicondyle moderately developed in anconal direction. Brachial depression deep. External tricipital groove shallow. Attachment of pronator brevis well developed.

REMARKS: See discussion of intrafamilial relationships.

Paraortygometra porzanoides (Milne-Edwards)

Figure 17

Rallus porzanoides MILNE-EDWARDS, 1869 (1867–1871) vol. 2, p. 150.
Paraortygometra porzanoides (Milne-Edwards): LAMBRECHT, 1933, p. 463.

LECTOTYPE: PM Av.2871, complete right tarsometatarsus.

HORIZON AND LOCALITY: Upper Oligocene or lower Miocene deposits; Saint Gérand-le-Puy,

Dept. Allier, France; upper Miocene deposits, La Grive Saint-Alban, Isère, France.

HYPODIGM: Lectotype; PM Av.2869, complete right humerus; PM catalogue number unknown, distal end of right femur; BM(NH) A733, complete right humerus; BaM SG7719, complete left humerus; BaM SG7718, distal left humerus; BaM SG7721, distal right humerus; BaM SG5710, distal right humerus; BaM SG7709, complete left femur, all from Saint Gérand-le-Puy; LGL 139, proximal right humerus; LGL 140, proximal left humerus; BM(NH) A1063, proximal and distal portions of left humerus; BM(NH) A328, proximal left humerus; BM(NH) 1064 distal left tarsometatarsus, all from Le Grive-Saint-Alban (Isère), Tortonian in age.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: See tables 11 to 13.

REMARKS: The type material of Milne-Edwards [1869 (1867–1871), vol. 2, pp. 150–152] included a tarsometatarsus (PM Av.2871), humerus (PM Av.2869), and a femur (PM no number). Because there is no evidence for association of these elements, I here designate the tarsometatarsus as lectotype (fig. 17A–C). All the type material is from a rail of about the same size.

The other Aquitanian material listed above is similar to the type material in size and morphology and is therefore referred to *P. porzanoides*.

The material from La Grive, although from deposits of a much younger age (probably at least 10 million years), is not separable from the Aquitanian forms, although there cannot be

TABLE 10

MEASUREMENTS (IN MILLIMETERS) OF TARSOMETATARSI OF *Pararallus dispar*

	PM Sa1208	PM Sa1207	PM Sa1209	PM Sa1210
Lateromedial breadth across trochleae	—	—	—	4.8
Breadth of inner trochlea	—	—	—	1.1[a]
Breadth of middle trochlea	—	—	—	1.9
Breadth of outer trochlea	—	—	—	1.5
Depth of middle trochlea	—	—	—	2.1
Breadth of proximal end	4.9	4.3	5.0	—
Depth of proximal end from tip of intercotylar prominence to end of hypotarsus	4.8	3.9	4.9	—

[a] Bone worn; measurement approximate.

FIG. 17. *Paraortygometra porzanoides*. A–C. Lectotype, PM Av.2871, right tarsometatarsus. A. Anterior view, stereo pair. About ×2.6. B. Proximal end, stereo pair. About ×4. C. Distal end, stereo pair. About ×3.9. D–E. Referred specimen, PM Av.2869, right humerus. D. Palmar view, stereo pair. E. Anconal view, stereo pair. Both about ×2.6.

TABLE 11

MEASUREMENTS (IN MILLIMETERS) OF TARSOMETATARSI
OF *Paraortygometra porzanoides*

	PM Av.2871	BM(NH) A1064
Total length	32.2	—
Breadth across trochleae	4.6	—
Breadth of inner trochlea	1.4	1.3
Breadth of middle trochlea	1.7	1.8
Breadth of outer trochlea	1.7	—
Depth of middle trochlea	2.4	2.3
Breadth middle of shaft	2.1	2.1
Depth middle of shaft	1.8	2.0
Breadth of proximal end	4.5	—
Depth of proximal end	4.9	—

TABLE 13

MEASUREMENTS (IN MILLIMETERS) OF FEMORA OF
Paraortygometra porzanoides

	PM unnumbered	BaM SG7709
Total length	—	32.1
Lateromedial breadth of distal end	5.0	4.8
Anteroposterior depth of external condyle	3.6	4.1
Depth of internal condyle	3.5	3.6
Breadth of middle of shaft	2.2	2.3
Depth of middle of shaft	2.3	2.3
Breadth of proximal end	—	5.6
Depth of head	—	2.3

much doubt that they represent a separate species. Hence I am tentatively referring this material to *P. porzanoides*. In addition to the Lyon specimens from La Grive listed above, Ballmann (1969, pp. 185–186) also referred several other humeri and carpometacarpi to *P. porzanoides*. However, after examination of this material I do not think these are rails and am omitting them here.

GENUS *MIOFULICA* LAMBRECHT

Miofulica LAMBRECHT, 1933, p. 48.

TYPE SPECIES: *Miofulica dejardinii* (Van Beneden).

INCLUDED SPECIES: Types species only.
DISTRIBUTION: Middle Miocene of Belgium.
DIAGNOSIS: Not possible.
REMARKS: See below.

Miofulica dejardinii (Van Beneden)

Fulica dejardinii VAN BENEDEN, 1871, p. 261.
Fulica desjardini VAN BENEDEN: SHARP, 1894, p. 209.
Miofulica dejardini (Van Beneden): LAMBRECHT, 1933, p. 480.
Miofulica dejardinii (Van Beneden): BRODKORB, 1967, p. 128.

HOLOTYPE: Distal end of femur; museum and catalogue number unknown.
HORIZON AND LOCALITY: Middle Miocene

TABLE 12

MEASUREMENTS (IN MILLIMETERS) OF HUMERI OF *Paraortygometra porzanoides*

	A[a]	B	C	D	E	F	G
PM Av.2869	30.9	4.5	2.0	1.8	2.2	1.9	6.4
BM(NH) A733	31.9	4.6	2.6	1.1	2.1	2.0	6.5
BM(NH) A1063 (proximal end)	—	—	—	—	—	—	6.6
BM(NH) A1063 (distal end)	—	4.8	2.1[b]	1.5	—	—	—
BM(NH) A328	—	—	—	—	2.0	1.9	6.5
LGL 139	—	—	—	—	—	—	6.8
LGL 140	—	—	—	—	—	—	7.2
BaM SG7719	31.5	4.9	2.2	1.5	2.1	2.1	—
BaM SG7718	—	4.6	—	—	2.1	2.0	—
BaM SG7721	—	4.6	2.6	1.5	2.0	1.9	—
BaM SG5710	—	4.7	2.5	1.4	2.2	1.9	—

[a]*Abbreviations*: A, total length; B, breadth of distal end; C, depth of external condyle; D, depth of internal condyle; E, breadth middle of shaft; F, depth middle of shaft; G, breadth of proximal end.

[b]Measurement approximate.
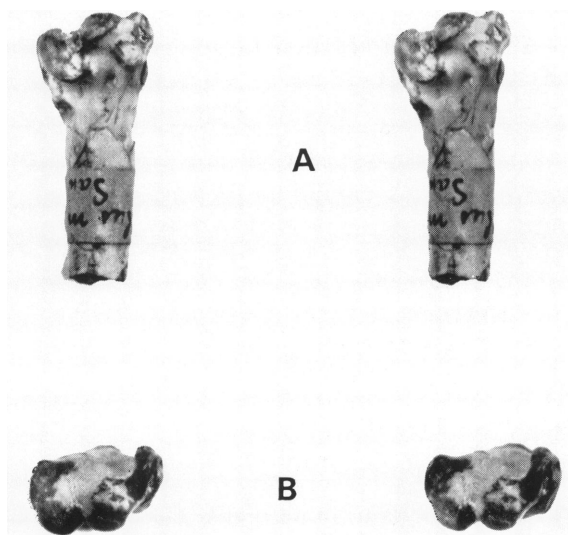
FIG. 18. *Miorallus major*, holotype, PM Sa1200, distal end of left humerus. A. Anterior view, stereo pair. B. Distal end, stereo pair. Both about × 1.9.

deposits (Anversian Black Sand); near Antwerp, Belgium.

HYPODIGM: Holotype only.

DIAGNOSIS: Not possible.

REMARKS: Lambrecht (1933, p. 480) diagnosed his new genus as having a broader intercondyloid fossa than in *Fulica*. This diagnosis is inadequate and will have to be expanded when the holotype is located and restudied. The illustration of Van Beneden (1871) is very poor, but the shaft appears to be too straight to be that of a rail.

GENUS *MIORALLUS* LAMBRECHT

Miorallus LAMBRECHT, 1933, p. 466.

TYPE SPECIES: *Miorallus major* (Milne-Edwards).

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Middle Miocene (Helvetian) of France.

DIAGNOSIS: Humerus with entepicondyle projecting distally and anconally. Attachment of anterior articular ligament broad and directed distopalmarly. Internal condyle round, bulbous, projecting distally well beyond external condyle. Attachment of pronator brevis well developed. Impression of M. brachialis anticus narrow. External tricipital groove shallow. Bone heavy and robust.

TABLE 14

MEASUREMENTS (IN MILLIMETERS) OF HUMERUS OF *Miorallus major*

	PM Sa1200
Breadth across distal end	9.0
Depth of external condyle	5.1
Depth of internal condyle	3.1

REMARKS: See intrafamilial comparisons below.

Miorallus major (Milne-Edwards)

Figure 18

Rallus major MILNE-EDWARDS, 1869 (1867–1871), vol. 2, p. 157.

Miorallus major (Milne-Edwards): LAMBRECHT, 1933, p. 466.

HOLOTYPE: PM Sa1200, distal end of left humerus.

HORIZON AND LOCALITY: Middle Miocene deposits; Sansan, Dept. Gers, France.

HYPODIGM: Holotype only.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: See table 14.

REMARKS: See intrafamilial comparisons below.

SPECIES NOT CONSIDERED MEMBERS OF THE RALLIDAE

I discuss here five species which I believe to be incorrectly placed in the Rallidae. I have examined types or casts of types of all but one of these taxa; *Pararallus hassenkampi* Martini was not seen.

GENUS *PALAEORALLUS* WETMORE

Palaeorallus alienus Kurotchkin

Palaeorallus alienus KUROTCHKIN, 1968a, p. 329.

HOLOTYPE: PIN 475–1786, distal end of left tibiotarsus.

HORIZON AND LOCALITY: Middle Oligocene deposits; Tatal-Gol, near Lake Tsagan-Nur, 50 km. north of Baga-Bogdo, western Gobi, Mongolia.

HYPODIGM: Holotype only.

DIAGNOSIS: See remarks.

MEASUREMENTS: Lateromedial width across condyles 5.1 mm.; anteroposterior depth of external condyle 5.5 mm.; depth of internal condyle 5.8 mm. (after Kurotchkin, 1968a). All measurements approximate (see below).

REMARKS: Dr. E. N. Kurotchkin has been kind enough to provide me with a cast of this specimen. On comparison with the type of *P. troxelli* and *P. brodkorbi* (see earlier discussion of genus) it is readily apparent that *P. alienus* does not belong in the genus *Palaeorallus* nor in the family Rallidae. Unfortunately the specimen is quite damaged (not apparent in Kurotchkin's figures) and has both the anterior end of the internal condyle and the posterior end of the external lacking. Enough of this specimen is present to indicate that it is most probably a galliform bird, perhaps a phasianid (*sensu lato*). However, neither a positive identification nor a diagnosis is possible.

GENUS *PARARALLUS* LAMBRECHT

Pararallus hassenkampi Martini

Pararallus hassenkampi MARTINI, 1967, p. 289.

HOLOTYPE: Geologisch-Paläontologisches Instituts Universität Würzburg F1238, portion of tarsometatarsus and phalanges.

HORIZON AND LOCALITY: Lower Oligocene deposits (Dysodil von Sieblos); Sieblos an der Wasserkuppe, Rhön, Germany.

HYPODIGM: Holotype only.

DIAGNOSIS: Largest species in genus (but see below).

MEASUREMENTS: See Martini, 1967, p. 290.

REMARKS: Martini (1967, p. 289) stated in his diagnosis that the posterior border of the outer trochlea lies in about the same plane as the inner trochlea. If true, then it would indicate that *P. hassenkampi* is probably not a rail, let alone a member of the genus *Pararallus*. The tarsometatarsus is badly crushed, and I strongly question whether any characters are discernible. In any case, Martini has presented no evidence that this fossil is a rail, and there certainly is no justification for including the species in *Pararallus*.

GENUS *MEGAGALLINULA* KUROTCHKIN

Megagallinula KUROTCHKIN, 1968c, p. 96.

TYPE SPECIES: *Megagallinula harundinea* Kurotchkin.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Medial Oligocene of central Kazakhstan.

DIAGNOSIS: Ulna with attachment of M. brachialis anticus deep and well marked. Proximal radial depression broad and deep. External cotyla without palmar projection. Olecranon short and heavy and separated from internal cotyla by well-developed ridge. Attachment of anterior articular ligament well developed. Humero-ulnar depression deep. In side view, shaft relatively straight. (Modified, in part, after Kurotchkin, 1968c, p. 86).

REMARKS: I have compared a cast of the type ulna (see below) with specimens of nearly all avian families. It is my belief that *Megagallinula* is almost certainly not a rallid, but I am unable to place this genus in any other family. At this time I can only list characteristics which suggest that *Megagallinula* is not a member of the Rallidae: (1) in side view the shaft is relatively straight, not noticeably curved, (2) the proximal radial depression is broad and deep, (3) the olecranon is separated from the internal cotyla by a well-developed ridge (olecranon is not more or less continuous with the cotyla), (4) the humero-ulnar depression is deep, (5) the attachment of the anterior articular ligament is pronounced, and (6) the external cotyla lacks a palmarly directed projection.

Megagallinula harundinea Kurotchkin

Megagallinula harundinea KUROTCHKIN, 1968b, p. 97.

HOLOTYPE: PIN 1399–122, proximal end of left ulna.

HORIZON AND LOCALITY: Middle Oligocene deposits, *Indricotherium* beds; Chelkar-Teniz area; Kur-Say gorge, central Kazakhstan.

HYPODIGM: Holotype only.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: Width across cotylae 8.9 mm.

REMARKS: See above for genus.

GENUS *LIMICORALLUS* KUROTCHKIN

Limicorallus KUROTCHKIN, 1968b, p. 98.

TYPE SPECIES: *Limicorallus saiensis* Kurotchkin.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Medial Oligocene of central Kazakhstan.

FIG. 19. *Thiornis sociata*, holotype, BM(NH) A1620. About ×0.70.

DIAGNOSIS: See remarks.

REMARKS: In describing this genus Kurotch-kin (1968c, p. 87) noted that it was not typically rallid and that it had many charadriiform features. After examining a cast of the type humerus (see below), I am of the firm opinion that *Limicorallus* is a member of the Anatidae. The distal end of the humerus of anatids has a number of characteristics peculiar to non-passeriforms, and *Limicorallus* has all of these features.

At this time I have not been able to compare *Limicorallus* with other anatids sufficiently to determine the validity of the genus or to provide a diagnosis.

Limicorallus saiensis Kurotchkin

Limicorallus saiensis KUROTCHKIN, 1968b, p. 99.

HOLOTYPE: PIN 1442–262, distal end of left humerus.

HORIZON AND LOCALITY: Middle Oligocene deposits, *Indricotherium* beds; Lake Chelkar-Teniz area, Myn-Say gorge, central Kazakhstan.

HYPODIGM: Holotype only.

DIAGNOSIS: See above generic remarks.

MEASUREMENTS: Lateromedial breadth across condyles 8.6 mm.; depth of shaft at level of brachial impression 3.3 mm.

REMARKS: See above for genus.

TABLE 15

COMPARISON OF ELEMENT RATIOS OF *Thiornis sociata* AND DIFFERENT RAILS

	$\dfrac{\text{Humerus}}{\text{Ulna}}$	$\dfrac{\text{Humerus}}{\text{Tarsometatarsus}}$	$\dfrac{\text{Humerus}}{\text{Tibiotarsus}}$	$\dfrac{\text{Humerus}}{\text{Total leg}^a}$	$\dfrac{\text{Femur}}{\text{Total leg}^a}$
Thiornis sociata[b]	1.04	1.62	0.99	0.48	0.22
Porzana albicollis	1.13	0.97	0.61	0.26	0.30
Rallus longirostris	1.22	1.10	0.69	0.30	0.29
Fulica leucoptera	1.16	1.16	0.69	0.32	0.27

[a] Total leg equals femur, tibiotarsus, and tarsometatarsus lengths.
[b] Calculated from measurements in Navás, 1922, p. 60.

GENUS *THIORNIS* NAVÁS

Thiornis NAVÁS, 1922, p. 59.

TYPE SPECIES: *Thiornis sociata* Navás.
INCLUDED SPECIES: Type species only.
DISTRIBUTION: Early Pliocene of Spain.
DIAGNOSIS: Not possible.
REMARKS: The type specimen is too crushed to make a certain identification even to order or family. However, ratios calculated from measurements given by Navás (see below), strongly suggest that *Thiornis* might not be a rallid (see table 15). As noted by Navás the humerus is very large, and it is probably too large to be from a rail. Moreover, the femur is relatively shorter than in rails.

Thiornis sociata Navás

Figure 19

Thiornis sociata NAVÁS, 1922, p. 59.

HOLOTYPE: BM(NH) A1620, skeletal impression.
HORIZON AND LOCALITY: Lower Pliocene deposits, bituminous shales; Libros, Prov. Teruel, Spain.
HYPODIGM: Holotype only.
DIAGNOSIS: See remarks above.
MEASUREMENTS: Humerus 76 mm.; ulna 73 mm.; femur 35 mm.; tibiotarsus 77 mm.; tarsometatarsus 47 mm.; all probably estimated lengths and probably inaccurate (Navás, 1922, p. 60).
REMARKS: A rather large number of flattened skeletons from the bituminous shales of Libros are present in various European museums; undoubtedly further specimens of *T. sociata* will be found among this material.

INTRAFAMILIAL RELATIONSHIPS OF THE RALLIDAE

It is clear from the foregoing systematic section that the Tertiary rails are very diverse morphologically. In general this diversity is greater in the Eocene and Oligocene and less in the post-Oligocene forms. The fossil record also shows that some rails existing in the Eocene and Oligocene were very similar to modern-day genera and therefore that the family itself undoubtedly had an origin sometime in the Cretaceous. The purpose of this section is to comment on the comparative morphology of the Tertiary rails with respect to possible relationships and evolutionary trends (most of the anatomical data are presented in tabular form). Sufficient comparative material is available for only three elements—humerus, tibiotarsus, and tarsometatarsus—so I restrict the discussion to them.

Because one can only surmise that the Rallidae had a common ancestor with cranes and their allies sometime in the late Cretaceous, any conclusions about primitive-derived sequences in the rails are dependent to a certain extent on comparisons with the Geranoididae, which are probably the most primitive members of the crane group. Unlike the Grui, which is a striking example of a diverse radiation of families, the Ralli consists only of two families, and thus the problems of determining character sequences are increased.[1]

[1] With further work there will undoubtedly be additions to the Ralli. Obvious possibilities are the Heliornithidae and Eurypygidae, which some authors have considered close to rails.

TABLE 16

MORPHOLOGICAL COMPARISON OF HUMERI OF SOME TERTIARY RALLIDAE

	Quercyrallus arenarius	*Quercyrallus quercy*	*Palaeoaramides beaumonti*	*Pararallus dispar*	*Paraortygometra porzanoides*	*Miorallus major*
Internal and external condyles	Unknown	Internal condyle rounded and bulbous; projects moderately distad to external. Groove between condyles deep, distinct distally. External condyle well developed and rounded distally	Internal condyle compressed slightly anconally-palmarly; projects moderately distad to external. Groove deep and distinct distally. External condyle only moderately developed and rounded distally	Internal condyle small, compressed anconal-palmarly; projects only slightly distad to external. Groove shallow distally. External condyle apparently poorly developed, flattened distally, compressed latero-medially	Internal condyle rounded; projects moderately distad to external. Groove deep and distinct distally. External condyle moderately well developed and rounded distally	Internal condyle rounded and bulbous; projects noticeably distad to external. Groove deep distally. External condyle well developed and flattened distally
Entepicondyle	Unknown	Broad, projects moderately anconally; projects only slightly distally	Moderately narrow, projects far anconally; projects far distally	Broad, projects far anconally; projects little distally	Pointed, not blunt; projects slightly distally beyond internal condyle	Broad; projects very far anconally; projects only slightly distally
Ectepicondylar prominence	Unknown	Moderately developed but low	Moderately developed but low	Very low; essentially absent	Low	Apparently very low; slightly developed
External tricipital groove	Unknown	Shallow	Moderately deep	Deep	Shallow to moderately developed	Shallow
Attachment of pronator brevis	Unknown	Shallow	Very poorly developed	Very poorly developed	Well developed	Deep
Attachment of anterior articular ligament	Unknown	Elevated; oriented externopalmarly	Elevated; oriented externopalmarly	Low, oriented palmarly	Elevated; oriented externopalmarly	Elevated; oriented distopalmarly
Brachial depression	Unknown	Broad, shallow; internal condyle not undercut or only slightly so	Broad, moderately deep; internal condyle moderately undercut	Broad, shallow; internal condyle not undercut or only slightly so	Broad, moderately deep; internal condyle moderately undercut	Broad, moderately deep; internal condyle noticeably undercut
External tuberosity	Moderately to well developed	Unknown	Moderately developed	Unknown	Poorly developed	Unknown
Capital groove	Moderately shallow; slightly undercuts head	Unknown	Moderately shallow; slightly undercuts head	Unknown	Deep; greatly undercuts head	Unknown
Ligamental furrow	Unknown	Unknown	Deep, elongated	Unknown	Shallow, rounded	Unknown
Bicipital crest	Unknown	Unknown	Poorly developed, not rounded	Unknown	Moderately developed, rounded	Unknown
Internal tuberosity	Well developed; apparently somewhat narrow	Unknown	Well developed, blunt	Unknown	Well developed, tends to be narrow	Unknown
Shaft	Moderately robust	Robust, with noticeable curve at distal end	Moderately light, with noticeable curve at distal end	Moderately light	Very light and thin; noticeable continuous curve	Apparently robust; with little curve at distal end

HUMERUS

Morphological data about Tertiary rail humeri are summarized in table 16. I have been unable to recognize primitive-derived sequences for any of the humeral characters and thus cannot make reliable statements about relationships using this element. Hypotheses about relationships must be based, in this case, on overall similarity. Each genus is quite distinct morphologically despite some shared characters with other genera. *Quercyrallus quercy* and *Palaeoaramides beaumonti* are very similar, differing in only a few characters: depth of brachial depression, entepicondyle, and proportions of the shaft (see table 16). It is possible that these two genera are fairly closely related.

Miorallus major is distinct with respect to three features: (1) the well-pronounced entepicondyle projecting far anconally, (2) the large, bulbous internal condyle, and (3) the distally oriented attachment of the anterior articular ligament. Only a few similarities are shared with other genera. The bulbous internal condyle resembles that of the recent genus *Fulica*, although the condyle projects much farther distally relative to the external condyle in the fossil genus.

Pararallus dispar is also distinct, but some of its features may be due to the effects of preservation. The poor development of the condyles, shallow brachial depression, and well-developed entepicondyle characterize this genus. *Pararallus* shows no particular resemblances to any other genus of fossil or Recent rail.

Palaeoaramides and *Quercyrallus* are both similar to Recent rails of the genus *Rallus* and provide evidence that modern rails, as represented by the humerus, have a history extending back to the late Eocene or early Oligocene. With detailed comparison of humeri from all the recent genera it probably would be difficult to recognize the distinctness of these latter two fossil genera.

TIBIOTARSUS

A morphological comparison of some Tertiary rail tibiotarsi is given in table 17. Unlike the situation with the humerus, it appears possible to make some tentative statements regarding primitive-derived sequences in tibiotarsal characters. Based on a comparison with the early Tertiary Grui, the following character-states of the rail tibiotarsus are probably primitive: (1)

distal end of external condyle flattened, not rounded (2) tubercle on supratendinal bridge well developed (3) supratendinal bridge broad proximodistally (4) condyles of about equal length anteroposteriorly (5) posterior intercondylar sulcus deep (6) anterior intercondylar fossa shallow and narrow (7) internal ligamental prominence moderately developed, and (8) the external wall of the supratendinal groove well developed. These decisions about primitiveness are tentative, because we still do not know whether the relationships of the Rallidae are close enough to the Grui to use the geranoidid condition as a basis of comparison. If the Rallidae have a considerable Cretaceous history, as seems fairly certain, then it is possible that many of the character-states are secondarily derived and not primitive.

Based on the above assumptions the two most primitive Tertiary genera would seem to be *Aletornis* and *Eocrex* from the North American Eocene. Both have a broad supratendinal bridge, a tubercle on the bridge (reduced in *Eocrex*), condyles of about equal length, deep posterior intercondylar sulci, and a deep external wall of the supratendinal groove. *Eocrex* also has a flattened external condyle and the condyles nearly parallel (this latter character may be a specialization within rails). The external condyle of *Aletornis* is rounded, but the shape is quite distinct from other rails (see systematic section). Both resemble each other in having the anterior end of the internal condyle elevated noticeably distad relative to the external condyle. The other two North American genera known from tibiotarsi, *Palaeorallus* and *Fulicaletornis*, have acquired a greater number of derived characters than *Eocrex* or *Aletornis*.

Wetmore (1931, p. 107) considered *Eocrex* to be intermediate between the Rallinae and Gallinulinae but closer to the latter. I do not believe *Eocrex* is a good morphological intermediate. Rather, on the basis of the anterior end of the internal condyle being raised distally, I think the genus may be far removed from these subfamilies. Little can be said about its relationships.

Shufeldt (1915a, pp. 31–32) believed *Fulicaletornis* (=*Aletornis*) *venustus* exhibited many similarities to the coots (Fulicinae) and he placed the species in the genus *Fulica*. Actually, there are a number of differences between *Fulicaletornis* and coots including the shapes and

TABLE 17

MORPHOLOGICAL COMPARISON OF TIBIOTARSI OF SOME TERTIARY RALLIDAE

	Palaeorallus troxelli	*Eocrex primus*	*Aletornis marshi*	*Fulicaletornis venustus*	*Ibidopsis hordwelliensis*	*Palaeoaramides christyi*	*Pararallus dispar*
Internal condyle	Proximoanterior end meets shaft at about 70° angle; projects noticeably anterior to external condyle; raised slightly distally relative to external; somewhat pointed anteriorly	Meets shaft at about 85° angle; projects only slightly anteriorly; anterior end raised sharply distad; rounded anteriorly; posterior margin well developed	Meets shaft at about 85° angle; projects only slightly anteriorly; anterior end raised sharply distally; rounded anteriorly; posterior margin well developed	Meets shaft at about 90° angle; projects only slightly anteriorly; anterior end raised only slightly distally; somewhat pointed anteriorly; posterior margin moderately developed	Meets shaft at about 85° angle; projects only slightly anteriorly; anterior end raised only slightly; somewhat pointed anteriorly; posterior margin well developed	Meets shaft at about 90° angle; projects only slightly anteriorly; anterior end not raised much distally; somewhat pointed anteriorly; posterior margin moderately developed	Meets shaft at about 70° angle; projects only slightly anteriorly; anterior end not raised much distally; rounded anteriorly; posterior margin well developed
External condyle	Rounded, but flattened distally; posterior end raised distally; anterior end meets shaft at about 60° angle	Rounded, but flattened distally; posterior end raised distally; meets shaft at about 45° angle	Very rounded anteriorly; anterior end raised noticeably distally; meets shaft at about 50° angle	Very rounded; posterior end raised slightly distally; meets shaft at about 60° angle	Rounded but slightly; flattened distally; meets shaft at about 60° angle	Very rounded; anterior end meets shaft at about 60° angle	Very rounded; posterior end raised somewhat distally; meets shaft at about 35° angle
Position of condyles	Internal noticeably deeper than external; posterior ends narrowed	Internal slightly deeper; nearly parallel	Internal slightly deeper; separated anteriorly	Both about same depth; nearly parallel	Both about same depth; nearly parallel	Internal slightly deeper; slightly separated anteriorly	Internal slightly deeper; separated anteriorly
Internal ligamental prominence	Very low	Very low	Moderately developed	Moderately developed	Moderately developed	Low	Very low
Anterior intercondylar fossa	Shallow, broad	Deep, narrow	Deep, broad	Moderately deep; narrow	Moderately shallow; moderately broad	Moderately shallow; narrow	Moderately deep; broad
Supratendinal bridge	Narrow proximo-distally; tubercle essentially absent	Broad; tubercle very slightly developed	Broad; tubercle moderately developed	Narrow; tubercle very low or absent	Narrow; tubercle very low	Narrow; tubercle low	Narrow; tubercle essentially absent
External wall of supratendinal groove	Very low	Moderately developed	Deep	Moderately developed	Moderately developed to deep	Moderately developed	Moderately developed
Posterior intercondylar sulcus	Shallow	Deep	Deep	Shallow	Deep	Deep	Deep

positions of the condyles, area of the supratend-
inal bridge, anterior intercondylar fossa, pos-
terior intercondylar sulcus, and the contours of
the shaft. Despite the many ralline characters in
Fulicaletornis, the genus still had not attained the
morphological level of modern rallids as seen in
such Tertiary genera as *Palaeoaramides*. But given
the amount of time available for subsequent
evolution, it is possible that *Fulicaletornis* was
near the origin of a number of modern rails
similar to gallinules and true rails (i.e., Ral-
linae).

Wetmore (1931, p. 108) placed *Palaeorallus* in
the subfamily Rallinae as a matter of conven-
ience. The genus *Palaeorallus* is so distinct
osteologically that it is difficult for me to see any
clear relationship to any modern group of rails.
The numerous unique features—shallow pos-
terior intercondylar sulcus, very deep internal
condyle projecting far anteriorly, shallow ex-
ternal wall of the supratendinal groove, and the
positions of the condyles—set *Palaeorallus* apart
from all other fossil and Recent rails.

In summary, none of the Eocene rails of
North America appears to have any obvious
relationships with one another, and only one
genus, *Fulicaletornis*, may have had something to
do with the origin of a modern group.

Three genera of European rails are known
from a tibiotarsus. *Ibidopsis* is very similar to
Eocrex and differs from that genus in only one
major character, namely in having a more
rounded external condyle. This appears to be a
derived condition. If these two genera have a
close relationship, it could serve as another
example of an interchange between North
American and European faunal elements during
the Eocene. Like *Eocrex*, *Ibidopsis* has no striking
resemblances to modern genera.

Palaeoaramides christyi and *P. beaumonti* are
both known from tibiotarsi that are exceedingly
similar to those of recent genera such as *Rallus*
and *Gallinula*. I find no strong characters that
could define *Palaeoaramides*. This indicates that,
based on the structure of the tibiotarsus, modern
rails go back as far as the late Oligocene or
early Miocene.

Pararallus dispar from the Miocene of France
is also close to modern genera and presumably
had a fairly close relationship to *Palaeoaramides*.

TARSOMETATARSUS

Only a few tarsometatarsi of European Terti-

ary rails are available (table 18), and these are
very similar to modern genera. I will restrict my
discussion to *Palaeoaramides*, *Pararallus*, and *Para-
ortygometra*, since these are the only genera I
have examined.

The tarsometatarsus of *Palaeoaramides christyi*
cannot be distinguished easily from those of
modern genera. The hypotarsus is very similar
to that of *Rallus* in having two well-developed
grooves on its internal side. The hypotarsus of
Pararallus dispar is like that of *P. christyi*.

The hypotarsus of *Paraortygometra porzanoides*
differs from that of *P. christyi* and *P. dispar* in
having the two internal grooves covered over
with a thin sheet of bone thus creating two
bony canals. Theoretically, it should be rela-
tively easy (evolutionarily and morphologically)
to derive the *Palaeoaramides* hypotarsus from
that of *Paraortygometra* or vice versa simply by
the addition or subtraction of the bony sheet.
This is the type of change that probably could
take place relatively rapidly in evolution. One
of these grooves is commonly closed over in the
modern genus *Gallinula*. There is no evidence to
suggest which of these conditions might be
primitive.

The distal end of the tarsometatarsus of *P.
dispar* is close to those of modern genera.

The tarsometatarsus also provides evidence
for a modern raillike morphology in the late
Oligocene or early Miocene.

LAORNITHOIDEA, NEW SUPERFAMILY

LAORNITHIDAE, NEW FAMILY

TYPE GENUS: *Laornis* Marsh.

DISTRIBUTION: Late Cretaceous of North
America.

DIAGNOSIS: Tibiotarsus with distal end of bone
almost square in shape (seen in distal view).
External condyle almost perfectly circular,
anterior margin meeting shaft at about 50 degree
angle. Internal condyle somewhat elongate with
moderately well-developed notch in distal
border. Internal condyle rounded anteriorly
with anterior margin meeting shaft at about 90
degree angle. Condyles slightly separated an-
teriorly. Internal condyle projecting anteriorly
slightly more than external. Tubercle on supra-
tendinal bridge lacking. Posterior intercondylar
sulcus broad and very shallow. Internal liga-
mental prominence very large.

REMARKS: This new monotypic family is

TABLE 18

MORPHOLOGICAL COMPARISON OF TARSOMETATARSI OF SOME TERTIARY RALLIDAE

	Palaeocrex fax	*Rallicrex kolozsvarensis*	*Palaeoaramides christyi*	*Pararallus dispar*	*Paraortygometra porzanoides*
Middle trochlea	Very well developed; elongated proximo-distally	Moderately developed	Moderately developed	Moderately developed	Moderately developed
Inner trochlea	Not turned far posteriorly	Turned very far posteriorly	Turned moderately far posteriorly	Turned moderately far posteriorly	Turned moderately far posteriorly
External intertrochlear notch	Broad and deep	Broad	Moderately broad	Very narrow	Moderately broad
Internal intertrochlear notch	Broad and moderately shallow	Very narrow	Very narrow	Very narrow	Very narrow
Distal foramen	Apparently of moderate size	Apparently rather large	Slitlike	Moderately large	Narrow, but somewhat rounded
Hypotarsus	Unknown	Unknown	With two well-defined grooves on internal surface; two very shallow grooves on external surface	With two well-defined grooves on internal surface; two shallow grooves on external surface	With two bony canals on internal surface; two shallow grooves on external surface

placed in the Gruiformes on the basis of its resemblance to several families of this order. Although it is difficult to form a final conclusion regarding affinities based only on the tibiotarsus, several features suggest a close relationship to the Rallidae. The rounded external condyle, the shape of the internal condyle, the general proportions of the shaft and its relationship to the distal end of the bone, and the shape of the area of the supratendinal bridge are features shared with some rails. When *Laornis* is linked morphologically to Recent rails through such Eocene genera as *Aletornis* and *Eocrex*, the resemblances to rallids are even more striking.

The Laornithidae differ from the Rallidae in the following characters of the tibiotarsus: (1) seen in distal view, the bone is compressed more anteroposteriorly rather than lateromedially (2) the anterior ends of the condyles are separated more (3) the anterior intercondylar fossa is shallower (4) the posterior intercondylar sulcus is much shallower (5) the posterior side of the shaft near the distal end is rounded rather than being more angular both laterally and medially (6) the internal ligamental prominence is better developed (7) the internal condyle is slightly more massive, and (8) a marked tendinal groove does not extend so far proximally.

The distinctness of *Laornis* from the Rallidae and other gruiform families warrants placing this genus in its own family. The evidence is insufficient to indicate that *Laornis* is close enough to rallids to be included in that family.

With the removal of the Cretaceous genus *Telmatornis* from the Rallidae and placement in the Charadriiformes (Cracraft, 1972a), *Laornis* becomes the earliest known gruiform genus.

GENUS *LAORNIS* MARSH

Laornis MARSH, 1870, p. 206.

TYPE SPECIES: *Laornis edvardsianus* Marsh.
INCLUDED SPECIES: Type species only.
DISTRIBUTION: Late Cretaceous of New Jersey.
DIAGNOSIS: Same as for family; only genus in family.
REMARKS: When he described *Laornis* in 1870, Marsh made few comparisons with living genera. Shufeldt (1915a, pp. 21–23) restudied the type and compared it with a greater variety of birds, but he only came to the conclusion that it was "one of the generalized types of *Waders*."

Shufeldt particularly noted its similarities to *Grus canadensis*. Lambrecht (1933, p. 526) placed *Laornis* as a genus *incertae sedis* near the Aramidae; Wetmore (1956, p. 104) also considered this genus *incertae sedis*. *Laornis* was not included in Brodkorb's catalogue (1967) of fossil gruiforms.

Laornis edvardsianus Marsh

Figure 20

Laornis edvardsianus MARSH, 1870, p. 206.

HOLOTYPE: YPM 820, distal end of right tibiotarsus.

HORIZON AND LOCALITY: Upper Cretaceous deposits (late Maestrichtian in age), lower part of Hornerstown Formation; pits of Pemberton Marl Company, Birmingham, Burlington County, New Jersey (see Baird, 1967, for data on stratigraphy and age of *Laornis*).

HYPODIGM: Holotype only.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: Depth (anteroposterior) of external condyle 19.3 mm.; depth of internal condyle 21.3 mm.; breadth across posterior end of condyles 19.7 mm.; breadth across anterior end of condyles 22.7 mm.; width of shaft 40 mm. from distal end of external condyle 12.2 mm.; depth of shaft 40 mm. from distal end of external condyle 10.4 mm.

DESCRIPTION OF HOLOTYPE: In distal view, end of bone compressed somewhat anteroposteriorly but almost square in shape; external condyle rounded throughout margin; posterior margin of condyle meeting shaft in smooth, almost straight contour; anterior margin of condyle meeting shaft at about 50 degree angle; anterior margin of condyle elevated slightly more distally than posterior margin; well-developed groove for M. peroneus brevis with large nutrient foramen in groove; internal condyle flattened distally with moderately well-developed notch in distal margin; rounded anterior end of condyle projecting noticeably anteriorly; posterior margin of condyle meeting shaft in smooth, almost straight contour; anterior margin of condyle meeting shaft at approximately 90 degree angle; internal ligamental prominence very large; posterior intercondylar sulcus broad and very shallow, being deepest near internal condyle; anterior intercondylar fossa relatively shallow, being about one-fourth
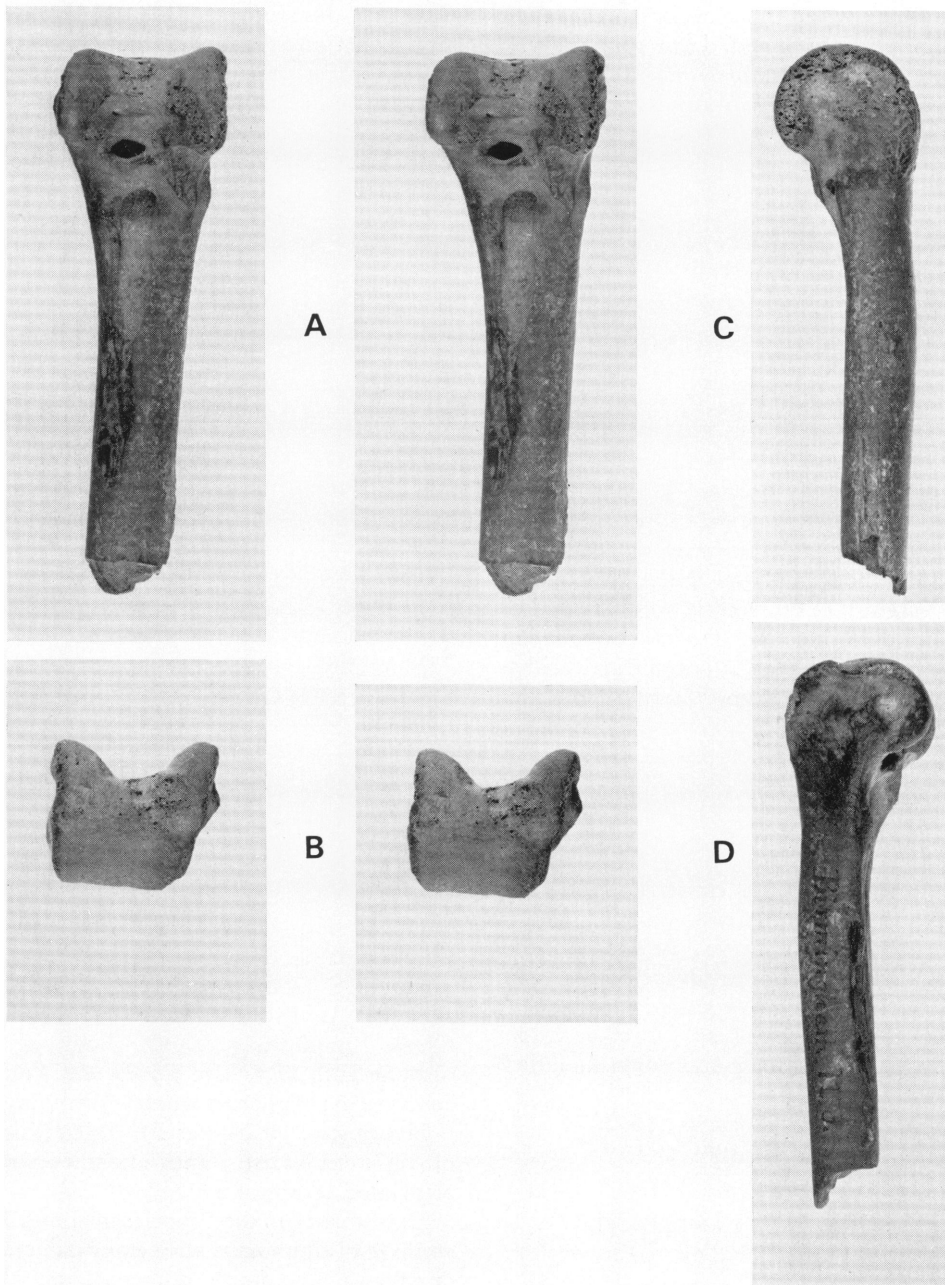
Fig. 20. *Laornis edvardsianus*, holotype, YPM 820, distal end of right tibiotarsus. A. Anterior view, stereo pair. B. Distal end, stereo pair. C. External condyle. D. Internal condyle. All about × 1.

the depth of the external condyle; supratendinal bridge broad, moderately long proximodistally, and moderately depressed; internal wall of supratendinal groove not developed; external wall of groove moderately developed, directed toward distal border of internal condyle; area between supratendinal bridge and external condyle broad and rather flattened; tubercle on

bridge absent or at most very small; shaft rounded and slightly flattened anterolaterally.

REMARKS: *Laornis edvardsianus* was a huge bird, being somewhat larger than any Recent species of rail (e.g., the species of *Megacrex*, *Gallirallus*, or *Notornis*).

INFRAORDER GRUI

SUPERFAMILY GERANOIDEA

FAMILY GERANOIDIDAE WETMORE

GENUS *GERANOIDES* WETMORE

Geranoides WETMORE, 1933a, p. 115.

TYPE SPECIES: *Geranoides jepseni* Wetmore.
INCLUDED SPECIES: Type species only.
DISTRIBUTION: Early Eocene (Wasatchian) of Wyoming.
REVISED DIAGNOSIS: Tibiotarsus with external condyle only moderately well developed, not especially broad lateromedially. Anterior end of external condyle meeting shaft at about 45 degree angle. Tubercle on supratendinal bridge small and separated from external condyle. Anterior intercondylar fossa very shallow.
REMARKS: See Cracraft, 1969, pp. 6–7.

Geranoides jepseni Wetmore

Geranoides jepseni WETMORE, 1933a, p. 115.

HOLOTYPE: PU 13257, distal ends of left tibiotarsus and tarsometatarsus.
HORIZON AND LOCALITY: Lower Eocene deposits, Willwood Formation; South Elk Creek, Bighorn County, Wyoming.
HYPODIGM: Holotype only.
DIAGNOSIS: Same as for genus; only included species.
MEASUREMENTS: See Wetmore, 1933a.
REMARKS: See Cracraft, 1969.

GENUS *PARAGRUS* LAMBRECHT

Paragrus LAMBRECHT, 1933, p. 520.

TYPE SPECIES: *Paragrus prentici* (Loomis).
INCLUDED SPECIES: Type species; *P. shufeldti* Cracraft.
DISTRIBUTION: Early Eocene (Wasatchian) of Wyoming.
REVISED DIAGNOSIS: Tibiotarsus with very well-developed external condyle. Anterior end of external condyle thick lateromedially, meeting shaft at angle approaching 90 degrees.

Tubercle on supratendinal bridge well pronounced. Condyles moderately spread anteriorly.

Tarsometatarsus with trochleae showing little curve when seen in distal view. Inner trochlea well developed and projecting distally slightly more than half the length of the middle trochlea and turned slightly posteriorly.
REMARKS: See Cracraft, 1969, pp. 7–14.

Paragrus prentici (Loomis)

Gallinuloides prentici LOOMIS, 1906, p. 481.
Gallinuloids prentici Loomis: CRACRAFT, 1969, p. 7 (typographical error).
Paragrus prentici (Loomis); LAMBRECHT, 1933, p. 520.

HOLOTYPE: ACM 3626 ("b4"), distal end of left tibiotarsus.
HORIZON AND LOCALITY: Lower Eocene deposits, Willwood Formation; head of Elk Creek, 10 miles west of Otto, Bighorn County, Wyoming.
HYPODIGM: Holotype only.
DIAGNOSIS: Largest species in genus. External condyle deeper anteroposteriorly relative to depth of internal condyle.
MEASUREMENTS: See Cracraft, 1969, p. 9.
REMARKS: See Cracraft, 1969, p. 7–11.

Paragrus shufeldti Cracraft

Paragrus shufeldti CRACRAFT, 1969, p. 9.

HOLOTYPE: ACM 6619, distal end of right tibiotarsus.
HORIZON AND LOCALITY: Lower Eocene deposits, Willwood Formation; head of Elk Creek, 10 miles west of Otto (holotype) vicinity of Bone Hill, SE¼, S16, T54N, R97W (referred specimens); Bighorn County, Wyoming.
HYPODIGM: Holotype; PU 18871, distal ends of right tibiotarsus and tarsometatarsus and associated scraps of bone.
DIAGNOSIS: Smallest species in genus. External condyle of tibiotarsus with external condyle less deep relative to depth of internal condyle.
MEASUREMENTS: Depth (anteroposterior) of external condyle 18.9 mm.; depth of internal condyle 20.7 mm.; breadth across posterior end of condyles 14.7 mm.; breadth across anterior end of condyles 20.7 mm. The first two measurements are corrections of previous measurements (Cracraft, 1969, p. 9), although the differences are slight.
REMARKS: See Cracraft, 1969, pp. 9–14.

GENUS *PALAEOPHASIANUS* SHUFELDT

Palaeophasianus SHUFELDT, 1913, p. 291.

TYPE SPECIES: *Palaeophasianus meleagroides* Shufeldt.

INCLUDED SPECIES: Type species; *P. incompletus* Cracraft.

DISTRIBUTION: Early Eocene (Wasatchian) of Wyoming.

REVISED DIAGNOSIS: Tibiotarsus with condyles nearly parallel, not spread much anteriorly. Condyles nearly same depth and internal condyle projecting anteriorly only slightly beyond external.

Tarsometatarsus with inner trochlea projecting distally, about 40 percent the length of the middle trochlea. Inner trochlea turned very little posteriorly.

REMARKS: See Cracraft, 1968b, pp. 281–285 and Cracraft, 1969, pp. 16–23.

Palaeophasianus meleagroides Shufeldt

Palaeophasianus meleagroides SHUFELDT, 1913, p. 291.

HOLOTYPE: AMNH 5128, distal end of left tibiotarsus, proximal and distal ends of left tarsometatarsus, scraps of bone.

HORIZON AND LOCALITY: Lower Eocene deposits, Willwood Formation (Gray Bull fauna); Elk Creek, east of Dry Camp 2 (holotype), and 12 miles up Five Mile Creek (referred specimens); Bighorn County, Wyoming.

HYPODIGM: Holotype; AMNH 5156, distal and proximal ends of right tarsometatarsus, distal end of right tibiotarsus, scraps of bone.

DIAGNOSIS: Smallest species in genus.

MEASUREMENTS: See Cracraft, 1969, p. 23.

REMARKS: I no longer consider the middle Eocene (Bridger Formation) distal tarsometatarsus (YPM 896) as belonging to the genus *Palaeophasianus*. This specimen differs from *Palaeophasianus* in having the external intertrochlear notch very narrow and the distal end of the bone relatively broader. The preservation of this specimen is so poor that a reliable determination of its relationships is probably impossible.

Palaeophasianus incompletus Cracraft

Palaeophasianus incompletus CRACRAFT, 1969, p. 21.

HOLOTYPE: PU 19913, distal end of right tarsometatarsus.

HORIZON AND LOCALITY: 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.

HYPODIGM: Type species only.

DIAGNOSIS: Largest species in genus.

MEASUREMENTS: See Cracraft, 1969, p. 23.

REMARKS: See Cracraft, 1969, pp. 21–23.

GENUS *EOGERANOIDES* CRACRAFT

Eogeranoides CRACRAFT, 1969, p. 14.

TYPE SPECIES: *Eogeranoides campivagus* Cracraft.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Early Eocene (Wasatchian) of Wyoming.

REVISED DIAGNOSIS: Tibiotarsus with tubercle on supratendinal bridge located very close to external condyle. External condyle not rounded posteriorly but contour has apex. External condyle only moderately heavy anteriorly, not especially broad lateromedially relative to size of bone. Posterior intercondylar sulcus curved in profile, not V-shaped.

REMARKS: See Cracraft, 1969, pp. 14–16.

Eogeranoides campivagus Cracraft

Eogeranoides campivagus CRACRAFT, 1969, p. 14.

HOLOTYPE: PU 16179, distal ends of left and right tibiotarsi, proximal end of left tarsometatarsus, distal ends of left and right tarsometatarsi, other scraps of bone.

HORIZON AND LOCALITY: Lower Eocene deposits, Willwood Formation; Foster Gulch, south of Lovell, Bighorn Basin, Bighorn County, Wyoming.

HYPODIGM: Holotype only.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: See Cracraft, 1969, p. 16.

REMARKS: See Cracraft, 1969, pp. 14–16.

GENUS *GERANODORNIS* CRACRAFT

Geranodornis CRACRAFT, 1969, p. 24.

TYPE SPECIES: *Geranodornis aenigma* Cracraft.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Medial Eocene (Bridgerian) of Wyoming.

REVISED DIAGNOSIS: Tibiotarsus with external

condyle slightly rounded distally, not flattened. Tendinal groove well marked. Tubercle on supratendinal bridge located fairly close to external condyle.

REMARKS: See Cracraft, 1969, pp. 24–25. Family position tentative.

Geranodornis aenigma Cracraft

Geranodornis aenigma CRACRAFT, 1969, p. 24.

HOLOTYPE: AMNH 2628, distal end of right tibiotarsus.

HORIZON AND LOCALITY: Middle Eocene deposits, Bridger Formation; Church Buttes, Church Buttes, Uinta County, Wyoming.

HYPODIGM: Holotype only.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: See Cracraft, 1969, p. 25.

REMARKS: See Cracraft, 1969, pp. 24–25.

FAMILY BATHORNITHIDAE WETMORE

GENUS EUTREPTORNIS CRACRAFT

Eutreptornis CRACRAFT, 1971, p. 2.

TYPE SPECIES: Eutreptornis uintae Cracraft.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Late Eocene (Uintan) of Utah.

REVISED DIAGNOSIS: Tibiotarsus with distal end compressed lateromedially. Internal condyle with noticeable notch in distal border and posterior portion raised distally. Internal ligamental prominence fairly well developed. Supratendinal bridge moderately broad proximodistally. Anterior intercondylar fossa shallow relative to depth of external condyle. Condyles not spread much anteriorly.

Tarsometatarsus with hypotarsus elongated proximodistally. Intercotylar prominence large and triangular in shape.

See Cracraft (1971) and discussion section later in this paper for further details.

REMARKS: See Cracraft (1971, pp. 2–5) and discussion section in present paper.

Eutreptornis uintae Cracraft

Eutreptornis uintae CRACRAFT, 1971, p. 3.

HOLOTYPE: AMNH 2092, distal end of left tibiotarsus, proximal end of left tarsometatarsus.

HORIZON AND LOCALITY: Upper Eocene deposits, Uinta Formation, base of Myton Member ("Uinta C"); Uinta Basin, near Ouray Agency, White River, Uintah County, Utah.

HYPODIGM: Holotype only.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: See Cracraft (1971, pp. 3–4).

REMARKS: See Cracraft (1971, pp. 2–5) and discussion section in present paper.

GENUS BATHORNIS WETMORE

Bathornis WETMORE, 1927, p. 11.

TYPE SPECIES: Bathornis veredus Wetmore.

INCLUDED SPECIES: Type species; B. cursor Wetmore; B. celeripes Wetmore; B. geographicus Wetmore; B. fricki Cracraft; and B. minor Cracraft.

DISTRIBUTION: Early Oligocene to early Miocene of North America.

REVISED DIAGNOSIS: Tibiotarsus with condyles not so compressed lateromedially compared to Eutreptornis. Internal condyle with notch in distal border very slight or absent. Internal ligamental prominence very poorly developed. Supratendinal bridge narrow proximodistally. Anterior intercondylar fossa deep. Condyles spread anteriorly.

Tarsometatarsus with hypotarsus short proximodistally. Intercotylar prominence smaller than in Eutreptornis.

Humerus with internal condyle raised somewhat distally relative to external condyle (more than in Paracrax). Intercondylar furrow fairly well marked. Distal end of shaft slightly curved in side view.

Carpometacarpus (compared to that of Paracrax) with process of metacarpal I directed more proximally. Area of internal ligamental fossa less depressed. External rim of carpal trochlea less sharply elevated proximally relative to internal rim.

REMARKS: See Cracraft (1968a, 1971).

Bathornis veredus Wetmore

Bathornis veredus WETMORE, 1927, p. 11.

HOLOTYPE: CMNH 805, distal end of right tarsometatarsus.

HORIZON AND LOCALITY: Lower Oligocene deposits, Trigonias quarry (Chadronian in age), Weld County, Colorado (holotype); Chadron Formation ("Titanotherium beds"). 11 miles northwest of Crawford, Nebraska (Wetmore,

1933b); Chadron Formation ("middle Titan-
othere beds") on Indian Creek, Pennington
County, South Dakota (Wetmore, 1937);
Chadron Formation (base of Crazy Johnson
Member), Quinn Draw, Shannon County,
South Dakota (Cracraft, 1971); and middle
Oligocene deposits, Hat Creek Basin, Sioux
County, Nebraska (Cracraft, 1971).

HYPODIGM: Holotype; USNM 12705, distal
end of left tarsometatarsus (Wetmore, 1933b);
PU 14400, distal end of left tibiotarsus (Wet-
more, 1937); SDSM 5815, distal end of left
tibiotarsus (Cracraft, 1971); and AMNH 8371,
distal end of right tibiotarsus (Cracraft, 1971).

DIAGNOSIS: Larger than *B. celeripes*, *B. minor*,
and *B. fricki*; smaller than *B. geographicus*. Tarso-
metatarsus differs from that of *B. geographicus* in
having smaller, less robust middle trochlea.

Tarsometatarsus differs from that of *B. cursor*
in having middle trochlea projecting more distad
relative to outer trochlea, middle trochlea
heavier and deeper anteroposteriorly, outer
trochlea larger and more massive, and anterior
surface of inner trochlea sloping more posteriorly
(Cracraft, 1968a, p. 5).

MEASUREMENTS: See Wetmore (1927, p. 13).

REMARKS: See papers cited above.

Bathornis cursor Wetmore

Bathornis cursor WETMORE, 1933c, p. 310.

HOLOTYPE: MCZ 2236, distal end of left
tarsometatarsus.

HORIZON AND LOCALITY: Lower Oligocene
deposits (Chadronian in age), 4 miless from
Torrington, S½ of NW¼, S32, T24N, R61W,
Goshen County, Wyoming.

HYPODIGM: Holotype only.

DIAGNOSIS: Larger than *B. celeripes*, *B. fricki*,
and *B. minor*; smaller than *B. geographicus*;
slightly smaller than *B. veredus* (for additional
differences from *B. veredus*, see above).

MEASUREMENTS: See Wetmore (1933c, p. 310).

REMARKS: See Wetmore (1933c, pp. 310–311)
and Cracraft (1968a, p. 5).

Bathornis celeripes Wetmore

Bathornis celeripes WETMORE, 1933c, p. 302.

HOLOTYPE: MCZ 2234, complete left tarso-
metatarsus.

HORIZON AND LOCALITY: Lower Oligocene
deposits (Chadronian in age), 4 miles from
Torrington, S½ of NW¼, S32, T24N, R61W,

Goshen County, Wyoming (holotype); middle
Oligocene deposits, Brule Formation (lower
Oreodon beds), 30 feet south of road at west end
of Chamberlain Pass, 1½ miles east of Scenic,
South Dakota (Cracraft, 1968a, pp. 6–7);
middle Oligocene deposits (*Oreodon* beds), Ever-
son Ranch, 12 miles northwest of Crawford,
Nebraska (Wetmore, 1933c, p. 308).

HYPODIGM: Numerous elements are known
for this species and it is unnecessary to list all of
them here; the reader can consult Wetmore
(1933c) and Cracraft (1968a) for a complete
list.

DIAGNOSIS: Larger than *B. minor*; smaller than
all remaining species in genus.

MEASUREMENTS: See Wetmore (1933c) and
tables 45 to 48.

REMARKS: See Wetmore (1933c) and Cracraft
(1968a).

Bathornis geographicus Wetmore

Bathornis geographicus WETMORE, 1942, p. 3.

HOLOTYPE: SDSM 4030, almost complete left
tarsometatarsus.

HORIZON AND LOCALITY: Upper Oligocene
deposits, Brule Formation (Poleslide Member,
Protoceras Channel Sandstone, *Leptauchenia* clays),
25 miles southeast of Scenic, 6 miles east of
Rockyford (holotype); 7 miles east of Rockyford
(Cracraft, 1971); Shannon County, South
Dakota.

HYPODIGM: Holotype; same catalogue num-
ber as holotype, distal end of left tibiotarsus;
SDSM 40155, proximal end of left tarsometa-
tarsus (Cracraft, 1971).

DIAGNOSIS: Largest species in genus. See
diagnoses above.

MEASUREMENTS: See Wetmore (1942, pp. 5–6)
and Cracraft (1971, p. 8).

REMARKS: See Wetmore (1942) and Cracraft
(1968a, 1971).

Bathornis fricki Cracraft

Bathornis fricki CRACRAFT, 1968a, p. 7.

HOLOTYPE: AMNH 2100, complete right
tibiotarsus.

HORIZON AND LOCALITY: Lower Miocene
deposits (from an approximate Gering equiv-
alent); on Wilson Creek, near Lusk, Niobrara
County, Wyoming.

HYPODIGM: Holotype only.

DIAGNOSIS: Larger than *B. minor* and *B.*

celeripes; smaller than *B. veredus*, *B. cursor*, and *B. geographicus*. Tibiotarsus differs from that of *B. celeripes* in having "internal condyle projecting more anteriorly; the inner cnemial crest projecting more anteriorly; the internalmost edge of the head of the bone just posterior to the inner cnemial crest not so elevated" (Cracraft, 1968a, pp. 7–8). See also below.

MEASUREMENTS: See Cracraft (1968a, pp. 8–10).

REMARKS: See Cracraft (1968a, pp. 7–10).

Bathornis minor Cracraft

Bathornis minor CRACRAFT, 1971, p. 8.

HOLOTYPE: SDSM 6239, proximal end of right tarsometatarsus.

HORIZON AND LOCALITY: Lower Miocene deposits, middle of Sharps Formation; South Dakota School of Mines and Technology locality V624, Shannon County, South Dakota.

HYPODIGM: Holotype; SDSM 6240, proximal end of right tibiotarsus.

DIAGNOSIS: Smallest species in genus. Tarsometatarsus differs from that of *B. celeripes* in having intercotylar prominence relatively less developed, and internal cotyla located less distally relative to external cotyla so that cotylae more nearly on same level.

Tibiotarsus differs from that of *B. fricki* in having the ridge running from the base of the inner cnemial crest to internal edge of external articular surface not raised as much, and the bone somewhat less elongated anteroposteriorly.

MEASUREMENTS: See Cracraft (1971).

REMARKS: See Cracraft (1971).

GENUS *PARACRAX* BRODKORB

Paracrax BRODKORB, 1964a, p. 303.

TYPE SPECIES: *Paracrax antiqua* (Marsh).

INCLUDED SPECIES: Type species; *P. wetmorei* Cracraft; and *P. gigantea* Cracraft.

DISTRIBUTION: Early or medial Oligocene to late Oligocene of North America.

REVISED DIAGNOSIS: Humerus with internal condyle raised only slightly distad to external condyle. Intercondylar furrow shallow, not well marked. Distal end of shaft fairly straight in side view (see also Cracraft, 1968a, p. 11).

Carpometacarpus (compared with that of *Bathornis*) with process of metacarpal I directed less proximally. Area of internal ligamental fossa more depressed. External rim of carpal trochlea

more sharply elevated proximally relative to internal rim.

See Cracraft (1968a) for further information.

REMARKS: See Cracraft (1968a, 1971) and Brodkorb (1964b).

Paracrax antiqua (Marsh)

Meleagris antiquus MARSH, 1871, p. 126.
Phalacrocorax mediterraneus SHUFELDT, 1915a, p. 58.
Paracrax antiqua (Marsh): BRODKORB, 1964a, p. 303.

HOLOTYPE: YPM 537, distal end of right humerus.

HORIZON AND LOCALITY: Lower or middle Oligocene deposits; Gerry's Ranch, Weld County, Colorado (see Galbreath, 1953, p. 40, for comments on the geology of Gerry's Ranch).

HYPODIGM: Holotype; YPM 943, proximal end of right carpometacarpus (formerly type of *Phalacrocorax mediterraneus* Shufeldt; see Cracraft, 1971).

DIAGNOSIS: Smallest species in genus.

MEASUREMENTS: See Cracraft (1968a, p. 29; 1971, p. 10).

REMARKS: See Cracraft (1968a, 1971).

Paracrax wetmorei Cracraft

Paracrax wetmorei CRACRAFT, 1968a, p. 11.

HOLOTYPE: FAM 42998, partial skeleton including humerus, ulna, sternum, coracoid, scapula, pelvis.

HORIZON AND LOCALITY: Upper Oligocene deposits, Brule Formation (one of lowest *Protoceras* Channel Sandstones, about 100 feet above base of Poleslide Member); northeast of Indian Stronghold on divide between west Big Corral Draw and Cottonwood Creek, Shannon County, South Dakota.

HYPODIGM: Holotype only.

DIAGNOSIS: Much larger than *P. antiqua*; much smaller than *P. gigantea*.

MEASUREMENTS: See Cracraft (1968a, pp. 11–22).

REMARKS: See Cracraft (1968a, 1971).

Paracrax gigantea Cracraft

Paracrax gigantea CRACRAFT, 1968a, p. 24.

HOLOTYPE: FAM 42999, distal end of right humerus.

HORIZON AND LOCALITY: Upper Oligocene deposits, Brule Formation (*Leptauchenia* beds, Poleslide Member); 2 miles northeast of Cedar

Pass, Jackson County, South Dakota (holotype); Brule Formation (middle *Protoceras* channels, about 175 feet above base of Poleslide Member); between West Fork of Big Corral Draw and Cottonwood Creek, Shannon County, South Dakota (referred specimen).

HYPODIGM: Holotype; FAM 42997, proximal end of right carpometacarpus (Cracraft, 1968a, pp. 26–28).

DIAGNOSIS: Largest species in genus.

MEASUREMENTS: See Cracraft (1968a, pp. 24–26).

REMARKS: See Cracraft (1968a, pp. 24–28).

FAMILY IDIORNITHIDAE BRODKORB

GENUS *GYPSORNIS* MILNE-EDWARDS

Gypsornis MILNE-EDWARDS, 1869 (1867–1871), vol. 2, p. 140.

TYPE SPECIES: *Gypsornis cuvieri* Milne-Edwards.
INCLUDED SPECIES: Type species only.
DISTRIBUTION: Late Eocene of France.
DIAGNOSIS: Tarsometatarsus with two hypotarsal ridges enclosing bony canal. External edge of hypotarsus confluent with border of external cotyla. External ridge of hypotarsus moderately long proximodistally.

REMARKS: From the time of Milne-Edwards (1869 [1867–1871]) to the present all authorities (e.g., Lambrecht, 1933; Brodkorb, 1967; Brunet, 1970) have considered *Gypsornis* to be a member of the Rallidae. Gaillard (1908, pp. 118–119) noted Milne-Edwards's observation that *Gypsornis* and *Idiornis* showed some similarities but apparently accepted Milne-Edwards's conclusion (1869 [1867–1871], vol. 2, p. 140): "Les proportions générales sont à peu près les mêmes, mais la disposition du talon, où l'on remarque une gouttière tubulaire, rapproche les Gypsornis des Rallides et les éloigne des Orthocnémides." Thus, it appears that the presence of a bony canal in the hypotarsus has been the principle character aligning *Gypsornis* with the rails and separating them from the idiornithids.

Gypsornis differs from rails in several characters which at the same time indicate a relationship to the idiornithids: (1) the bony canal of the hypotarsus is formed by two ridges directed posteriorly and is situated centrally rather than being formed by a sheet of bone that closes off tendinal grooves which are situated on the internal surface of the hypotarsus (2) the internal surface of the hypotarsus is a depressed area for muscular attachment and lacks tendinal grooves (3) the intercotylar prominence is very well developed and more distinctly delimited from the cotylae, especially the internal, and (4) the bone, especially the most proximal portion, is not slender and delicate in appearance, but is broad and robust.

The above differences from rails and similarities with idiornithids argue strongly for a close relationship between *Gypsornis* and the idiornithids. Moreover, the structure of the hypotarsus in *Gypsornis* fits nicely into the morphological trends postulated for the idiornithids (see fig. 50), whereas it would be difficult to construct a tenable morphological series between *Gypsornis* and post-Eocene rails.

A more detailed morphological comparison with *Idiornis* and *Elaphrocnemus* is presented at the end of this section and in the discussion.

Gypsornis cuvieri Milne-Edwards

Figure 21

Gypsornis cuvieri MILNE-EDWARDS, 1869 (1867–1871), vol. 2, p. 140.

HOLOTYPE: PM 7983, proximal end of left tarsometatarsus.

HORIZON AND LOCALITY: Upper Eocene deposits, gypse de Montmartre; Dept. Seine, Montmartre, France.

HYPODIGM: Holotype; a middle trochlea of a tarsometatarsus, two phalanges, and two claws were apparently assigned to this species by Milne-Edwards. All of these elements are with the holotype and apparently share the same catalogue number.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: Breadth across proximal end of tarsometatarsus 11.7 mm.; depth of proximal end 11.9 mm.

REMARKS: None of the other elements with the holotype provide any useful systematic information.

GENUS *IDIORNIS* OBERHOLSER

Orthocnemus MILNE-EDWARDS, 1892, p. 74.
Idiornis OBERHOLSER, 1899, p. 202.

TYPE SPECIES: *Idiornis gallicus* (Milne-Edwards).
INCLUDED SPECIES: Type species; *I. cursor*
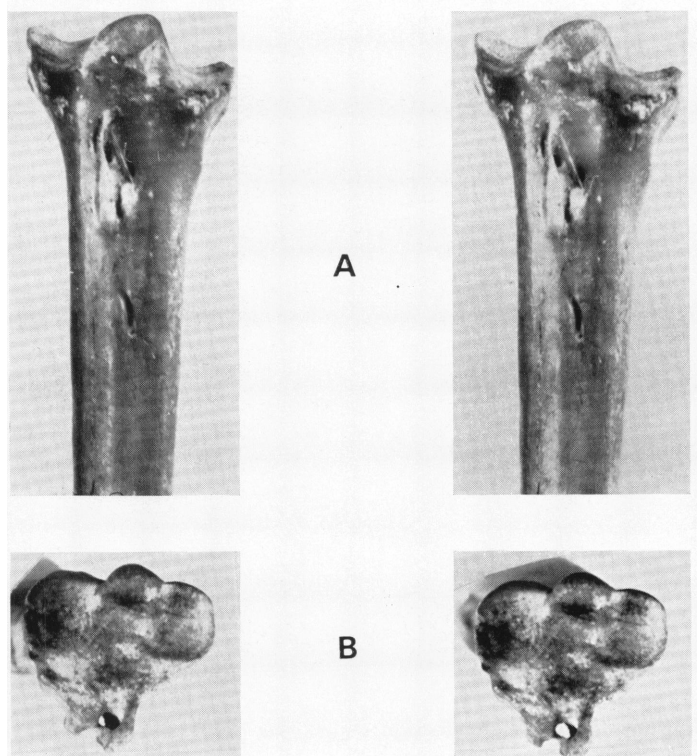
FIG. 21. *Gypsornis cuvieri*, holotype, PM 7983, proximal end of left tarsometatarsus. A. Anterior view, stereo pair. B. Proximal end, stereo pair. Both about ×2.3.

(Milne-Edwards); *I. minor* (Milne-Edwards); and *I. gaillardi*, new species.

DISTRIBUTION: Late Eocene to possibly medial Oligocene of France.

DIAGNOSIS: Tarsometatarsus without bony canals in hypotarsus. Broad and shallow groove on posterior surface of hypotarsus with external ridge only slightly developed and internal ridge moderately developed and directed postero-internally. Edges of hypotarsus sharply delimited from adjacent cotylae. Deep anterior metatarsal groove. Anterior face of middle trochlea strongly curved, meeting surface of shaft at noticeably sharp angle. In posterior view, inner trochlea projects distally well beyond base of middle trochlea.

REMARKS: In almost all cases the type material of the species in this genus consisted of small collections of bones. No type specimens were designated by previous workers, and in several instances the type material of a species included more than one taxon. Thus, in the species accounts that follow it was necessary to designate lectotypes. Moreover, in order to study this material at the Paris Museum it was also necessary to catalogue almost their entire collection of fossils from the phosphorites du Quercy.

The original name for the genus, *Orthocnemus* Milne-Edwards, was shown to be preoccupied by *Orthocnemus* Jekel and has been replaced by *Idiornis* (Oberholser, 1899, p. 202), which becomes the type genus of the family (Brodkorb, 1965).

Idiornis gallicus (Milne-Edwards)

Figures 22, 23

Orthocnemus gallicus MILNE-EDWARDS, 1892, p. 74.
Idiornis gallicus (Milne-Edwards): OBERHOLSER, 1899, p. 202.

LECTOTYPE: PM Qu3002, complete right tarsometatarsus.
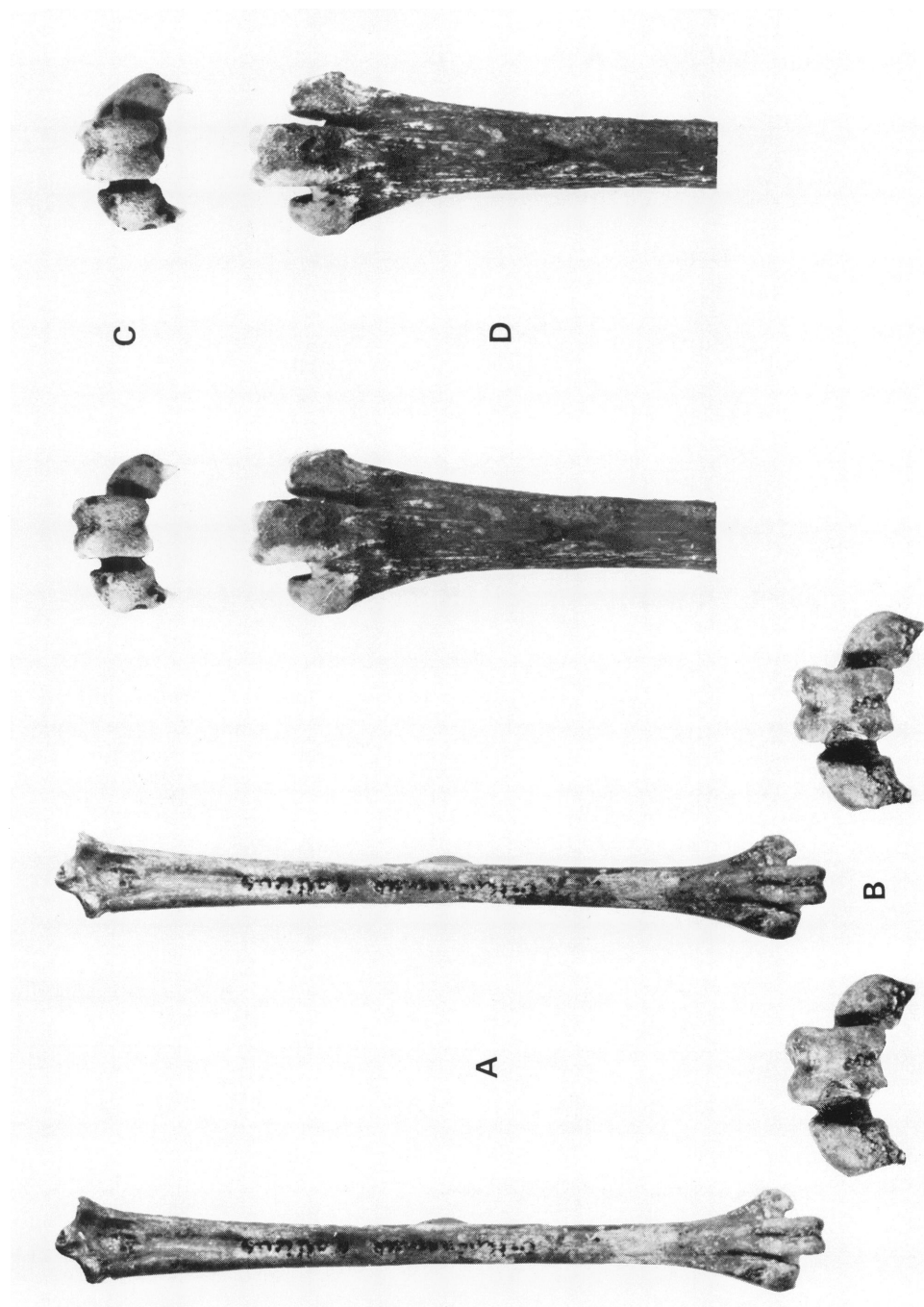
FIG. 22. *Idiornis gallicus*. A–B. Lectotype, PM Qu3002, right tarsometatarsus. A. Anterior view, stereo pair. About ×1. B. Distal end, stereo pair. About ×1.9. C–D. Referred specimen, PM Qu3001, distal end of right tarsometatarsus. C. Distal end, stereo pair. D. Anterior view, stereo pair. Both about ×1.6.
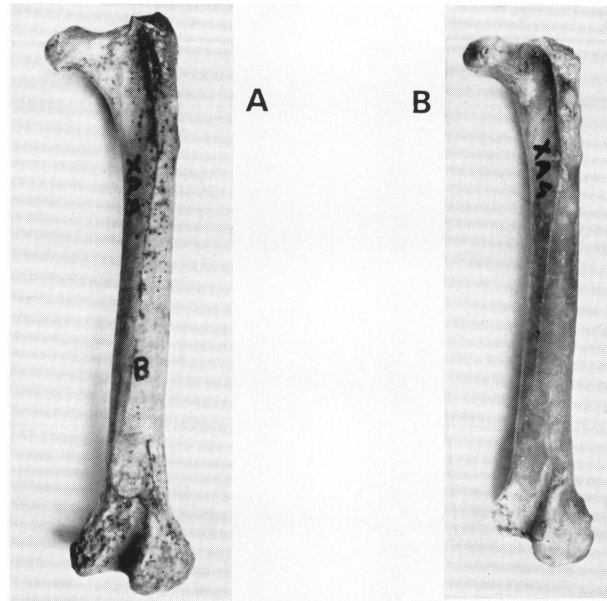
FIG. 23. *Idiornis gallicus*, referred specimens. A. PM Qu3007, left femur. About × 1.1. B. PM Qu3003, left femur. About × 1.

HORIZON AND LOCALITY: Upper Eocene to possibly middle Oligocene deposits, phosphorites du Quercy; plateau du Quercy, France.

HYPODIGM: Lectotype; PM Qu3001, distal end of right tarsometatarsus; BaM QH184, distal end of right tarsometatarsus; MHNL PQ1042, cast of proximal end of right tarsometa-

tarsus; PM Qu3003 and Qu3007, complete left femora; PM Qu3057, complete right femur.

DIAGNOSIS: Largest species in genus. Tarsometatarsus with shaft and trochleae heavier and more robust, anterior metatarsal groove shallower than in other species.

MEASUREMENTS: See tables 19 and 20.

TABLE 19

MEASUREMENTS (IN MILLIMETERS) OF TARSOMETATARSI OF *Idiornis gallicus* AND *Idiornis cursor*

	A[a]	B	C	D	E	F	G	H	I	J
Idiornis gallicus										
PM Qu3002 Lectotype	107.5	14.9	4.4	5.7	4.2	7.5	6.0	5.1	12.8	11.0[b]
PM Qu3001	—	13.8	4.8	5.3	3.4	7.0	—	—	—	—
BaM QH184	—	13.0	3.5	5.1	3.7	7.0	—	—	—	—
MHNL PQ1042[c]	—	—	—	—	—	—	5.7	5.1	13.7	12.1
Idiornis cursor										
PM Qu3008 Lectotype	97.0	12.2	3.4	4.7	3.2	6.2	5.0	4.4	13.0	10.2
PM Qu3005	—	—	—	—	—	—	—	—	13.3	11.3
PM Qu3010	—	—	—	—	—	—	—	—	11.7	10.1
PM Qu3067	—	—	—	5.0	3.6	6.4	—	—	—	—

[a]*Abbreviations*: A, total length; B, breadth across trochleae; C, breadth of outer trochleae; D, breadth of middle trochlea; E, breadth of inner trochlea; F, depth of middle trochlea; G, breadth of middle of shaft; H, depth of middle of shaft; I, breadth of proximal end; J, depth of proximal end.

[b]Bone worn; measurements approximate.

[c]Cast; measurements approximate.

TABLE 20

Measurements (in Millimeters) of Femora of

Idiornis gallicus

	PM Qu 3003	PM Qu 3007	PM Qu 3057
Total length	65.0	—	70.4
Lateromedial breadth of distal end	13.6	13.8	15.0
Anteroposterior depth of external condyle	11.8	12.4	13.0
Depth of internal condyle	9.8[a]	9.3	11.0[a]
Breadth of proximal end	15.8	15.9	16.3
Depth of head	5.8	5.8	5.7
Breadth middle of shaft	—	—	6.6
Depth middle of shaft	—	—	5.7

[a] Bone worn; measurement approximate.

REMARKS: The type material of "*Orthocnemus*" *gallicus* consists of PM Qu3000 to Qu3003. One, PM Qu3000 (a proximal left tarsometatarsus), is more properly placed in the genus *Elaphrocnemus* (see below). I here designate PM Qu3002 as the lectotype of *I. gallicus* (fig. 22A, B).

The three tarsometatarsi referred to *I. gallicus* are similar in size and exhibit no important differences in form. The proximal end of the lectotype is badly damaged, making it impossible to discern the features of the hypotarsus; the distal end of the lectotype has the characteristics of the genus as given in the diagnosis.

The three femora included in the hypodigm are allocated to *I. gallicus* for convenience. One of these bones (PM Qu3003; fig. 23B) was part of the type material of *I. gallicus*, another (PM Qu3007, fig. 23A) was in the type series of "*Orthocnemus*" *cursor*, and the third (PM Qu3057) was labeled "*Orthocnemus gallicus.*" All three bones are so close in size that they could easily represent a single species. Because none of these femora were associated with other limb elements, I am currently unable to assign them unequivocally to either *Idiornis* or *Elaphrocnemus*. Their size suggests a bird about the size of *I. gallicus*, and I have tentatively allocated them to this species. The rationale for considering them to be idiornithid in the first place is that they appear to be from a gruiform bird and have a close resemblance to some of the fragmentary femora assigned to the Geranoididae. It seems reasonable to assume these femora

belong to the idiornithids of the phosphorites du Quercy.

A cast of a proximal right tarsometatarsus (MHNL PQ1042) is somewhat intermediate in size between *I. cursor* and *I. gallicus*. The specimen is identified as *I. major* (=*I. cursor*) but probably is too large for this species. The original specimen was housed in the Munich Museum but was destroyed during World War II.

Idiornis cursor (Milne-Edwards)

Figure 24

Orthocnemus cursor MILNE-EDWARDS, 1892, p. 76.
Orthocnemus major MILNE-EDWARDS, 1892, p. 76.
Idiornis cursor (Milne-Edwards): OBERHOLSER, 1899, p. 202.
Idiornis major (Milne-Edwards): OBERHOLSER, 1899, p. 202.

LECTOTYPE: PM Qu3008, complete left tarsometatarsus.

HORIZON AND LOCALITY: Upper Eocene to possibly middle Oligocene deposits, phosphorites du Quercy; plateau du Quercy, France.

HYPODIGM: Lectotype; PM Qu3005, Qu3010, proximal ends of right tarsometatarsi; PM Qu3067, distal end of left tarsometatarsus.

DIAGNOSIS: Tarsometatarsus differs from that of *I. gallicus* in being smaller, less robust, with anterior metatarsal groove deeper; shaft narrower; and inner trochlea less robust. Larger than *I. minor* and *I. gaillardi*.

MEASUREMENTS: See table 19.

REMARKS: *Idiornis cursor*, as recognized here, includes *I. major* (Milne-Edwards). The original type material of "*Orthocnemus*" *cursor* included PM Qu3007 and Qu3008. The former specimen, a femur, has been transferred to *I. gallicus*. I designate the tarsometatarsus, PM Qu3008, as lectotype of *I. cursor* (fig. 24A). The type material of "*Orthocnemus*" *major* consisted of PM Qu3005 and Qu3006. The latter specimen, a distal left tarsometatarsus, belongs in the genus *Elaphrocnemus*.

Idiornis major has been considered a separate species from *I. cursor* mainly on the basis of size, but the differences are so slight that I believe this separation is not warranted. The type tarsometatarsus of *I. major* (PM Qu3005; fig. 24B, C) is slightly more robust than the lectotype of *I. cursor*, but when comparisons are made with specimens in other museums, this char-
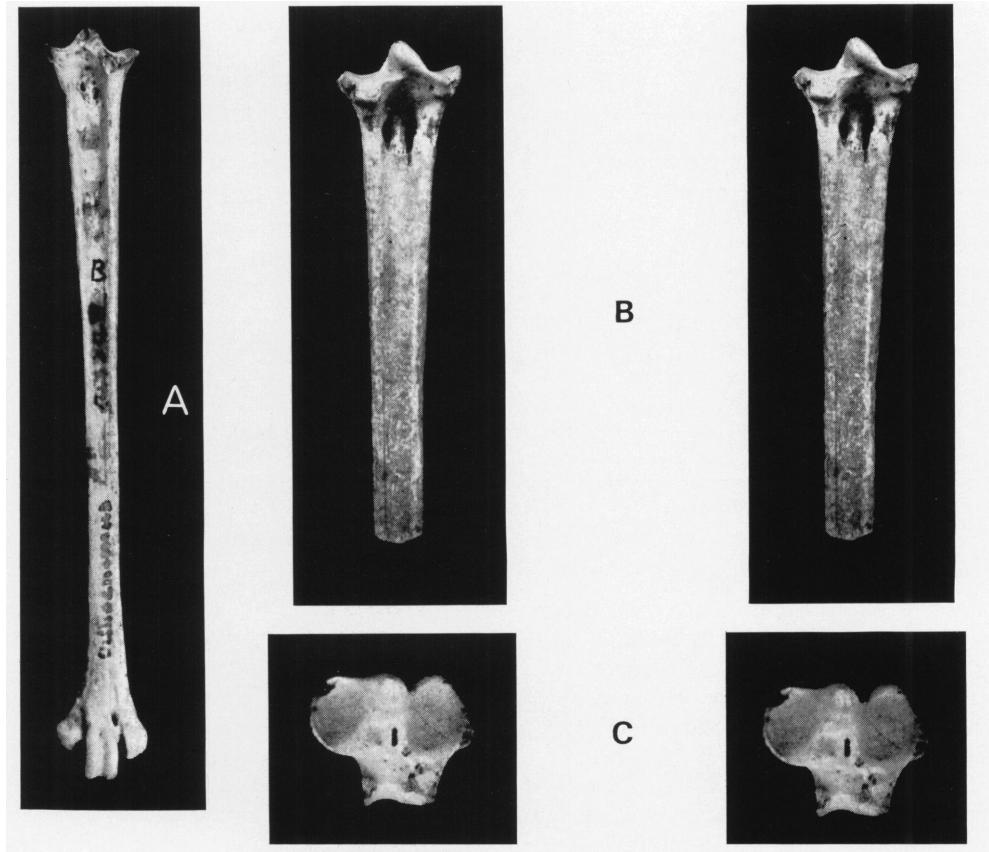
FIG. 24. *Idiornis cursor.* A. Lectotype, PM Qu3008, left tarsometatarsus. About × 1. B–C. Referred specimen, PM Qu3005, proximal end of right tarsometatarsus. B. Anterior view, stereo pair. About × 1.3. C. Proximal end, stereo pair. About × 1.7.

acter appears to be individual variation. Hence, it seems best to recognize one species until additional material proves otherwise.

If one accepts that a large amount of intra-specific size variation is possible within *Idiornis*, then the hypothesis that *I. gallicus* and *I. cursor* could be conspecific must be examined. It is possible that the very deep anterior metatarsal grooves in *I. cursor* could be the result of unusual preservation, but to my knowledge this is not found in other fossils from the phosphorites du Quercy. Size alone cannot be used to separate *I. gallicus* and *I. cursor.* The differences in size among the specimens in table 19 do not show patterns suggestive of sexual dimorphism, but the sample is admittedly small. *Idiornis gallicus* can be separated from *I. cursor* principally on the basis of morphological form, although some specimens of *I. cursor* (PM Qu3010 and BaM

QD219) tend toward *I. gallicus* in certain features.

Idiornis minor (Milne-Edwards)

Figure 25

Orthocnemus minor MILNE-EDWARDS, 1892, p. 77.
Idiornis minor (Milne-Edwards): OBERHOLSER, 1899, p. 202.

HOLOTYPE: PM Qu3004, distal end of right tarsometatarsus.

HORIZON AND LOCALITY: Upper Eocene to possibly middle Oligocene deposits, phosphorites du Quercy; plateau du Quercy, France.

HYPODIGM: Holotype; PM Qu3047, complete left tarsometatarsus; BaM QD228, almost complete right tarsometatarsus.

DIAGNOSIS: Smaller than *I. gallicus* and *I. cursor*; larger than *I. gaillardi.* Tarsometatarsus
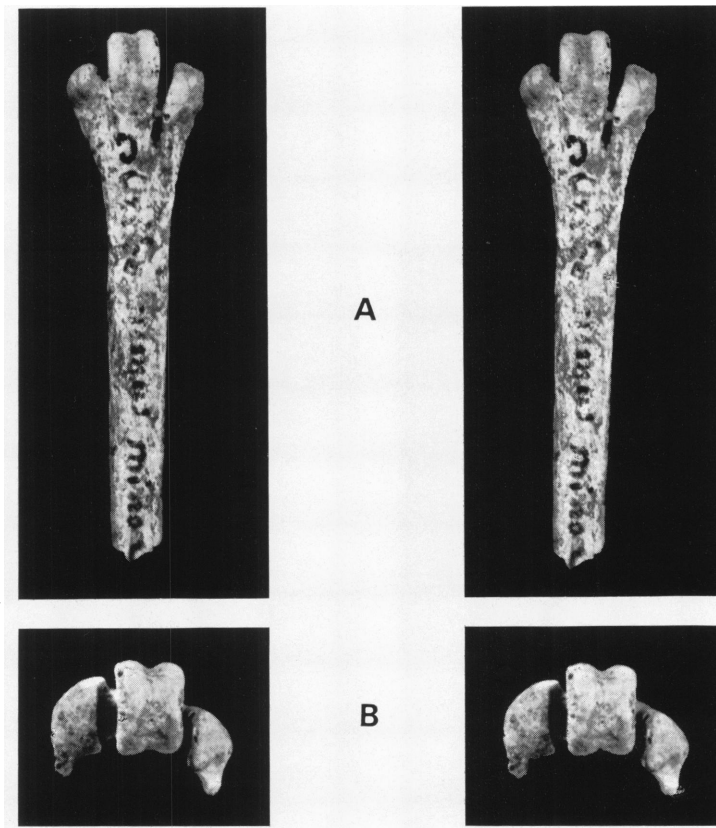
Fig. 25. *Idiornis minor*, holotype, PM Qu3004, distal end of right tarsometatarsus. A. Anterior view, stereo pair. About × 1.7. B. Distal end, stereo pair. About × 2.4.

more slender than those of *I. gallicus* and *I. cursor*.

MEASUREMENTS: See table 21.

REMARKS: The holotype (fig. 25) is similar to the other species of *Idiornis* in the shapes and positions of the trochleae. One referred tarsometatarsus (PM Qu3047) shows some differences from the holotype. The former is slightly smaller, the shaft somewhat narrower, the inner trochlea smaller, and the distal end of the bone more compressed lateromedially. In this case I think the morphological differences are due primarily to factors of preservation. The second referred specimen (BaM Q D228) lacks the middle and inner trochleae. The hypotarsus is slightly damaged, but the ridges are separated and the contour of the hypotarsus does not grade smoothly into the external cotyla. The

measurements of this bone conform with those of the other specimens of *I. minor*.

Idiornis gaillardi, new species

Figure 26

HOLOTYPE: PM Qu3034, complete left tarsometatarsus.

HORIZON AND LOCALITY: Upper Eocene to possibly middle Oligocene deposits, phosphorites du Quercy; plateau du Quercy, France.

HYPODIGM: Holotype only.

DIAGNOSIS: Smallest species in genus. Tarsometatarsus differing from those of other species in that middle trochlea is rounder (not so elongated proximodistally), intercotylar prominence shorter and blunter, and shaft decidedly narrower.
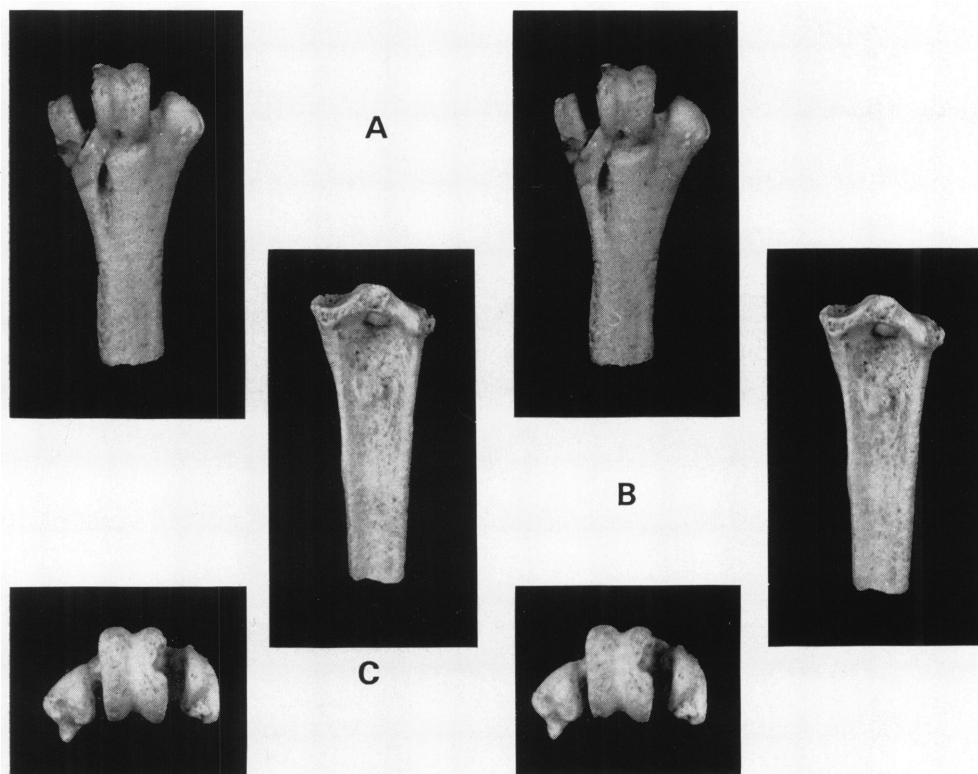
FIG. 26. *Idiornis gaillardi*, cast of holotype, PM Qu3034, distal end of left tarsometatarsus.
A. Anterior view of distal end. About ×2.5. B. Anterior view of proximal end. About ×2.2.
C. Distal end. About ×2.8. All stereo pairs.

TABLE 21

MEASUREMENTS (IN MILLIMETERS) OF TARSOMETATARSI OF *Idiornis minor* AND *Idiornis gaillardi*

		I. minor		*I. gaillardi*
	PM Qu3004 (Holotype)	PM Qu3047	BaM QD228	PM Qu3034 (Holotype)
Total length	—	78.8	78.8[a]	50.9
Breadth across trochleae	10.3	9.0	—	8.5
Breadth of outer trochlea	3.2	2.8	3.2	1.9
Breadth of middle trochlea	3.9	3.6	—	3.4
Breadth of inner trochlea	2.8	2.5	—	2.6
Depth of middle trochlea	5.3	5.0	—	4.8
Breadth of middle of shaft	—	4.1	4.4	3.6
Depth of middle of shaft	—	3.9	4.1	3.0
Breadth across proximal end of bone	—	9.3	10.6	7.8
Depth of proximal end of bone	—	8.2	9.1	6.5

[a] Length to tip of outer trochlea; middle trochlea lacking, thus true measurement slightly greater.

MEASUREMENTS: See table 21.

REMARKS: *Idiornis gaillardi* is the smallest of all the species of *Idiornis*. Its affinities appear to lie with *I. cursor* and *I. minor* rather than with *I. gallicus*, based on the deep excavation of the anterior metatarsal groove.

ETYMOLOGY: The species is proposed in honor of Dr. C. Gaillard who made significant contributions to our knowledge of the birds of the phosphorites du Quercy.

GENUS *ELAPHROCNEMUS* MILNE-EDWARDS

Elaphrocnemus MILNE-EDWARDS, 1892, p. 77.

TYPE SPECIES: *Elaphrocnemus phasianus* Milne-Edwards; designated by Richmond, 1902, p. 680.

INCLUDED SPECIES: Type species; *E. crex* Milne-Edwards; and *E. gracilis* Milne-Edwards.

DISTRIBUTION: Late Eocene to possibly medial Oligocene of France.

DIAGNOSIS: Tarsometatarsus without bony canals in hypotarsus. Narrow and deep groove on posterior side of hypotarsus. Two ridges forming groove directed posteriorly and well developed. External edge of hypotarsus running smoothly into contour of external cotyla, not sharply delimited from the latter. Anterior metatarsal groove moderately deep. Anterior face of middle trochlea moderately rounded, meeting surface of shaft in smooth contour. In posterior view, inner trochlea situated proximal to base of middle trochlea or projecting only slightly distad to base of middle trochlea.

Tibiotarsus with posterior portion of external condyle tending to be raised sharply distad. Anterior ends of condyles separated, not more or less parallel, thus anterior intercondylar fossa is wide.

REMARKS: The original description of the genus (Milne-Edwards, 1892) was made for three species, *E. phasianus*, *E. crex*, and *E. gracilis*. Most authorities (e.g., Gaillard, 1908, 1938; Lambrecht, 1933) have followed Milne-Edwards, but Brodkorb (1967, p. 138) tentatively included *Phasianus alfhildae* Shufeldt in the genus as well (discussed in more detail below).

The material of *Elaphrocnemus*, especially of *E. phasianus*, is much more abundant than has been previously realized, and almost all of it has remained unstudied until now. Specimens assigned to *Elaphrocnemus* exhibit considerable variability in size, which creates numerous

problems in determining species limits within the genus. In the species arrangement accepted here a primary assumption is that all the species show great sexual size dimorphism. If this assumption were not followed, it would have been necessary to recognize several new species. Present evidence does not justify the latter approach.

As with the species of *Idiornis* I have designated lectotypes within *Elaphrocnemus*. In light of the abundant material and confusion with regard to recognizing species limits, the designation of lectotypes should provide some measure of stability.

An intergeneric comparison of *Elaphrocnemus* will be presented below.

Elaphrocnemus phasianus Milne-Edwards

Figures 27, 28

Elaphrocnemus phasianus MILNE-EDWARDS, 1892, p. 77.

LECTOTYPE: PM Qu3014, complete left tarsometatarsus.

HORIZON AND LOCALITY: Upper Eocene to possibly middle Oligocene deposits, phosphorites du Quercy; plateau du Quercy, France.

HYPODIGM: Lectotype; PM Qu3015, Qu3061, Qu3063, Qu3204, Qu3206, Qu3207, MHNL PQ1, BaM QH158, all complete right tarsometatarsi; PM Qu3062, Qu3064, Qu3065, Qu3200, Qu3205, Qu3208, Qu3212, BaM QH155, all complete left tarsometatarsi; PM Qu3213, Qu3210, Qu3217, Qu3218, BaM QH193, QW1575, QH159, QH151, QH153, QD531, all distal ends of right tarsometatarsi; PM Qu3209, Qu3215, Qu3211, Qu3214, Qu3203, Qu3202, BaM QW510, QL707, all distal ends of left tarsometatarsi; PM Qu3201, BaM QD309, QD366, QD379, QD385, QD224, QD325, QD383, QD219, all proximal ends of right tarsometatarsi; BAM QD308, proximal end of left tarsometatarsus; BaM QD330, complete right tibiotarsus; PM Qu3046, BaM QD274, QD302, QD396, QD324, QD240, all distal ends of right tibiotarsi; PM Qu3050, Qu3053, Qu3048, Qu3049, Qu3104, BaM QD 225, QD373, QD232, QD245, QN828, QU97, all distal ends of left tibiotarsi; PM Qu3052, BaM QD326, QD342, all proximal ends of right tibiotarsi; PM Qu3051, Qu3054, Qu3045, BaM QD210, QD215, all proximal ends of left tibiotarsi.

DIAGNOSIS: Tarsometatarsus shorter than that
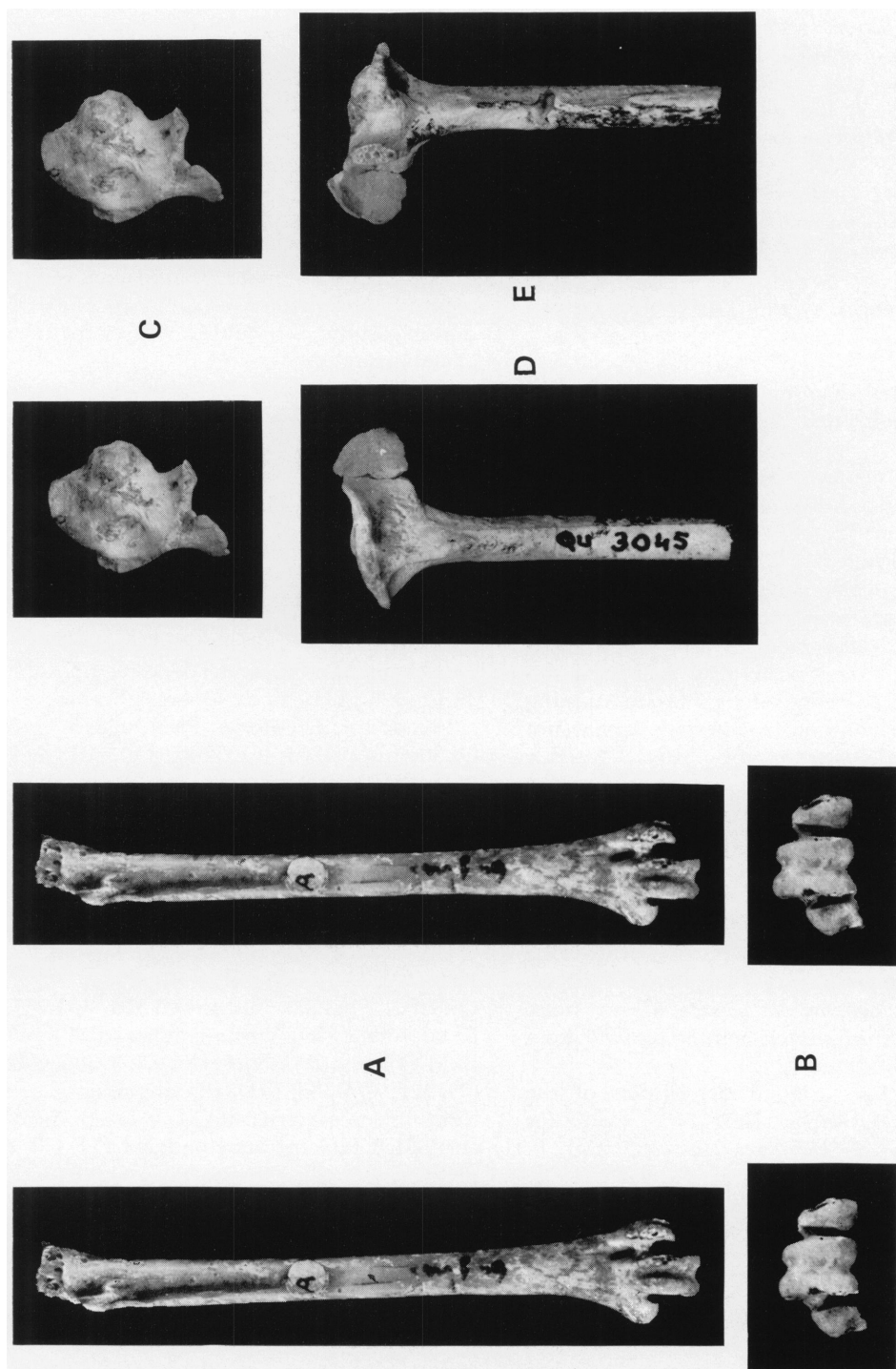
FIG. 27. *Elaphrocnemus phasianus*. A–B. Lectotype, PM Qu3014, left tarsometatarsus. A. Anterior view, stereo pair. About ×1.4. B. Distal end, stereo pair. About ×1.9. C–E. Referred specimen, PM Qu3045, proximal end of left tibiotarsus. C. Proximal end, stereo pair. D. Internal view. E. External view. All about ×1.3.

TABLE 22

MEASUREMENTS (IN MILLIMETERS) OF TARSOMETATARSI OF *Elaphrocnemus phasianus*

	A[a]	B	C	D	E	F	G	H	I	J
PM Qu3014 Lectotype	65.2	10.3	2.2	4.6	2.2	5.9	4.3	3.7	—	—
PM Qu3015	63.3	—	—	4.3	—	5.6	4.3	3.6	—	—
PM Qu3061	75.8	11.8	2.7	5.0	3.0	6.4	4.7	4.2	11.4	9.8
PM Qu3062	70.9	11.3	2.7	4.8	3.0	6.5	4.6	4.6	10.5	9.3
PM Qu3063	75.6	11.7	3.1	5.0	3.1	6.3	4.7	4.3	11.4	10.2
PM Qu3064	74.0	11.8	2.4	4.4[b]	3.0	6.4[b]	4.9	4.4	10.9	9.9
PM Qu3065	74.6	11.3	2.7	4.7	3.1	6.6	4.8	4.6	10.6	10.9
PM Qu3200	63.4	10.5	2.3	4.5	2.5	6.1	4.4	3.8	10.1	9.4
PM Qu3204	63.1	10.9	2.6	4.1	3.1	5.6	4.3	3.6	10.1	8.9
PM Qu3205	70.2	11.7	2.8	4.9	3.3	—	4.9	4.5	—	9.9
PM Qu3206	71.0	11.1	2.8	4.4	2.7	6.1	4.8	4.4	10.1	9.1
PM Qu3207	74.7	11.6	2.9	4.8	3.2	6.2	4.4	4.0	10.7	9.8
PM Qu3208	72.1	11.8	—	4.7	3.4	6.3	4.9	4.4	10.5	9.5
PM Qu3212	67.9	11.1	2.8	4.5	3.4	5.5	4.3	4.9	10.3	9.2
PM Qu3201	—	—	—	—	—	—	4.4	3.6	10.6	9.0
PM Qu3209	—	11.6	2.8	4.4	3.5	6.0	4.5	3.8	—	—
PM Qu3213	—	11.5	3.1	4.2	3.4	6.1	4.2	3.7	—	—
PM Qu3215	—	11.4	2.6	4.3	3.5	6.1	4.3	3.6	—	—
PM Qu3211	—	—	3.1	4.5	—	5.9	4.5	3.5	—	—
PM Qu3214	—	11.9	3.1	4.6	3.3	6.2	—	—	—	—
PM Qu3210	—	11.8	2.9	4.5	3.4	6.1	—	—	—	—
PM Qu3203	—	11.4	2.9	4.7	—	6.4	—	—	—	—
PM Qu3217	—	11.6	2.5	4.6	3.0	6.5	—	—	—	—
PM Qu3218	—	10.6	2.8	4.3	3.2	5.9	—	—	—	—
PM Qu3202	—	10.6	2.1	4.4	3.2	5.7	—	—	—	—
MHNL PQ1	69.4	10.8	2.4	4.4	2.6	6.1	4.6	4.2	10.4	9.1
BaM QH193	—	10.4	2.3	4.0	2.9	5.7	—	—	—	—
BaM QW1575	—	10.0	2.4	4.1	2.5	5.3	—	—	—	—
BaM QH159	—	11.2	2.6	4.3	3.2	5.8	—	—	—	—
BaM QH151	—	11.1	3.0	4.4	2.9	5.9	—	—	—	—
BaM QH153	—	—	2.9	4.0	—	5.8	—	—	—	—
BaM QW510	—	11.0	2.5	4.9	2.9	6.4	—	—	—	—
BaM QL707	—	12.0	2.5	4.7	3.2	6.3	—	—	—	—
BaM QD309	—	—	—	—	—	—	—	—	10.4	9.1
BaM QD366	—	—	—	—	—	—	—	—	9.8	8.5
BaM QD379	—	—	—	—	—	—	—	—	10.5	8.8[b]
BaM QD385	—	—	—	—	—	—	4.2	4.0	10.5	9.4
BaM QD224	—	—	—	—	—	—	4.7	3.9	10.7	9.7
BaM QD308	—	—	—	—	—	—	—	—	10.1	—
BaM QD325	—	—	—	—	—	—	—	—	10.3	8.9
BaM QD383	—	—	—	—	—	—	—	—	10.0	8.8
BaM QD531	—	11.3[b]	3.2	4.9	—	6.6	—	—	—	—
BaM QD219	—	—	—	—	—	—	4.6	3.5	10.6	10.5
BaM QH158	63.6	10.4	2.5	4.0	2.8	5.6	4.1	3.8	10.4	9.2
BaM QH155	68.1	11.8	2.7	4.7	3.4	6.2	4.5	3.7	11.4	10.2

[a]*Abbreviations*: A, total length; B, breadth across trochleae; C, breadth of inner trochlea; D, breadth of middle trochlea; E, breadth of outer trochlea; F, depth of middle trochlea; G, breadth of middle of shaft; H, depth of middle of shaft; I, breadth of proximal end of bone; J, depth of proximal end of bone.

[b]Bone worn; measurement approximate.

TABLE 23

MEASUREMENTS (IN MILLIMETERS) OF TIBIOTARSI OF *Elaphrocnemus phasianus*

	A[a]	B	C	D	E	F	G	H	I	J
PM Qu3050	—	8.5	9.2	7.3	9.2	3.3	—	—	—	—
PM Qu3053	—	8.5	9.6	6.9	8.8	3.4	—	—	—	—
PM Qu3048	—	9.2	10.1	8.0	9.7	3.4	5.6	4.5	—	—
PM Qu3049	—	8.9	9.7	7.5	9.9	3.8	5.4	4.1	—	—
PM Qu3051	—	—	—	—	—	—	5.2	4.1	17.2	—
PM Qu3052	—	—	—	—	—	—	—	—	15.8	11.8
PM Qu3054	—	—	—	—	—	—	5.2	4.3	—	10.5
PM Qu3046	—	8.9	10.0	7.6	9.9	3.3	—	—	—	—
PM Qu3045	—	—	—	—	—	—	—	—	19.2	11.9
BaM QD225	—	9.4	10.0	8.7	10.5	3.3	—	—	—	—
BaM QN828	—	9.3	10.0	7.7	9.5	3.3	6.3	4.6	—	—
BaM QU97	—	9.6	10.3	7.9	9.9	3.4	6.1	5.0	—	—
BaM QD373	—	8.7	9.5	7.3	9.3	3.7	5.0	4.2	—	—
BaM QD274	—	8.3	9.6	7.4	9.6	3.0	—	—	—	—
BaM QD302	—	8.5	9.4	7.8	9.9	2.7	—	—	—	—
BaM QD232	—	9.2	10.1	7.8	10.1	3.2	—	—	—	—
BaM QD396	—	8.6	9.4	7.1	9.3	2.3	4.6	4.0	—	—
BaM QD324	—	8.1	9.0	7.2	9.3	2.6	4.9	4.2	—	— .
BaM QD245	—	8.6	9.4	8.0	9.2	3.1	—	—	—	—
BaM QD240	—	8.4	9.2	7.7	9.4	2.0	4.9	3.9	—	—
BaM QD326	—	—	—	—	—	—	—	—	19.4	13.7
BaM QD210	—	—	—	—	—	—	—	—	18.0	12.9
BaM QD342	—	—	—	—	—	—	—	—	17.0	13.2
BaM QD215	—	—	—	—	—	—	—	—	20.0	14.2
BaM QD330	101.8	9.3	9.6	7.9	9.8	—	5.7	4.5	17.0[b]	11.2
PM Qu3104	—	8.8	9.9	6.8	9.5	—	—	—	—	—

[a]*Abbreviations*: A, total length; B, anteroposterior depth of external condyle; C, depth of internal condyle; D, breadth across posterior end of condyles; E, breadth across anterior end of condyles; F, depth of anterior intercondylar fossa relative to external condyle; G. breadth of middle of shaft; H, depth of middle of shaft, I, anteroposterior length of proximal end; J, width of proximal end.

[b]Bone worn; measurement approximate.

of *E. crex*, with narrower and less robust shaft. Bone longer than that of *E. gracilis*.

MEASUREMENTS: See tables 22 and 23.

REMARKS: The type material of *E. phasianus* included PM Qu3014 and Qu3015, and I designate the former as the lectotype (fig. 27A, B). Unfortunately, neither specimen is well preserved. The proximal end of the lectotype is very worn, and PM Qu3015 has the inner and outer trochleae missing and the proximal end damaged.

Gaillard (1908, p. 115) illustrated a complete left tarsometatarsus (BaM QH155) which he assigned to *Orthocnemus* (=*Idiornis*) *minor*. This specimen appears to belong to *E. phasianus*. Contrary to Gaillard the bone is too short and robust to conform to the type of *I. minor*. The hypotarsus is like that of *Elaphrocnemus* in that

there are two hypotarsal ridges close together and the hypotarsus merges with the outer margin of the external cotyla. The distal end of the bone is also like that in *Elaphrocnemus*. The inner trochlea projects only slightly beyond the base of the middle trochlea, and the middle trochlea grades smoothly into the anterior surface of the shaft.

There is a complete right tibiotarsus (BaM QD330) with QH155 that is also labeled *I. minor*, but the specimen resembles closely the series of *E. phasianus* tibiotarsi in the Paris Museum. This specimen thus allows positive identification of isolated proximal and distal ends of tibiotarsi.

Gaillard (1908, p. 123) figured a complete right tarsometatarsus (BaM QH158) which he assigned to *E. phasianus*. This specimen agrees
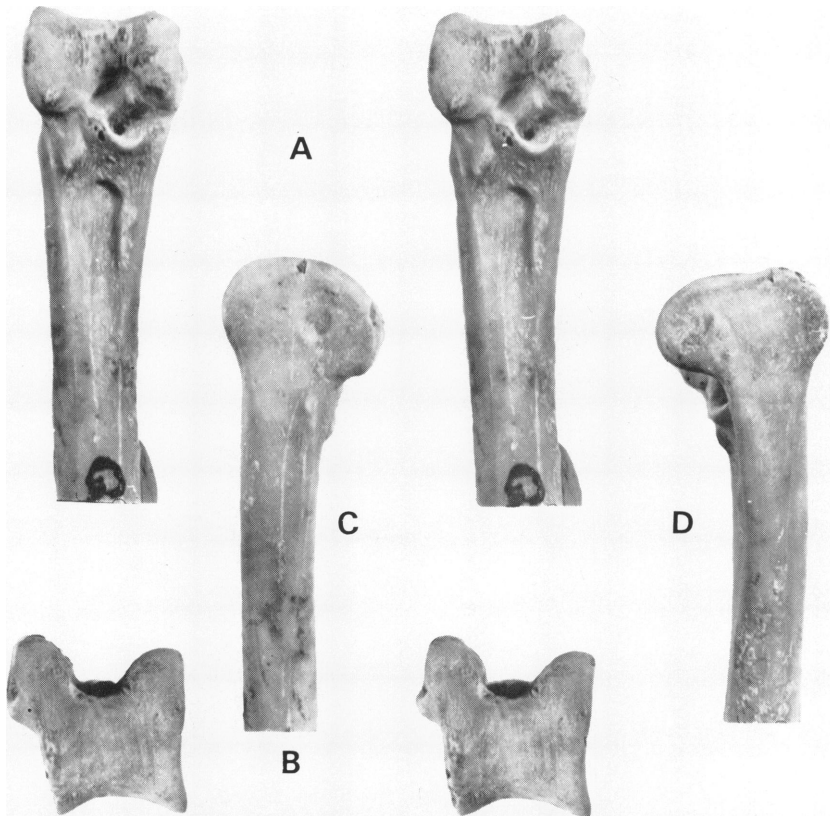
FIG. 28. *Elaphrocnemus phasianus*, referred specimen, PM Qu3048, distal end of left tibiotarsus. A. Anterior view, stereo pair. About ×2.2. B. Distal end, stereo pair. About ×2.4. C. External condyle. About ×2.4. D. Internal condyle. About ×2.3.

in size and morphology with the lectotype.

The tarsometatarsi of *E. phasianus* exhibit considerable variability in length (tables 22 and 46). Although there is more or less a continuum in measurements, the extremes probably represent sexual differences. The rationale behind this statement will become clearer when the variability within *E. crex* and *E. gracilis* are discussed. Only one complete tibiotarsus of *E. phasianus* is known, and measurements other than length show a continuum in size without distinct size classes. A more detailed analysis of variability of *E. phasianus* is presented in a separate section of this paper.

The tibiotarsi listed in the hypodigm are assigned to this genus and species for the following reasons: (1) tarsometatarsi of *Elaphrocnemus* greatly outnumber those of *Idiornis* in phosphor-

ites du Quercy deposits, therefore it is logical to associate the large number of tibiotarsi with *Elaphrocnemus*, and (2) the tibiotarsi are within the size range of *E. phasianus*. Unfortunately, no example of *in siti* association of a tarsometatarsus and tibiotarsus is known. All the tibiotarsi of *E. phasianus* agree with each other in general morphology and size (figs. 27C, D, E; 28).

Elaphrocnemus crex Milne-Edwards

Figures 29, 30

Elaphrocnemus crex MILNE-EDWARDS, 1892, p. 78.

LECTOTYPE: PM Qu3012, complete right tarsometatarsus.

HORIZON AND LOCALITY: Upper Eocene to possibly middle Oligocene deposits, phosphorites du Quercy; plateau du Quercy, France.
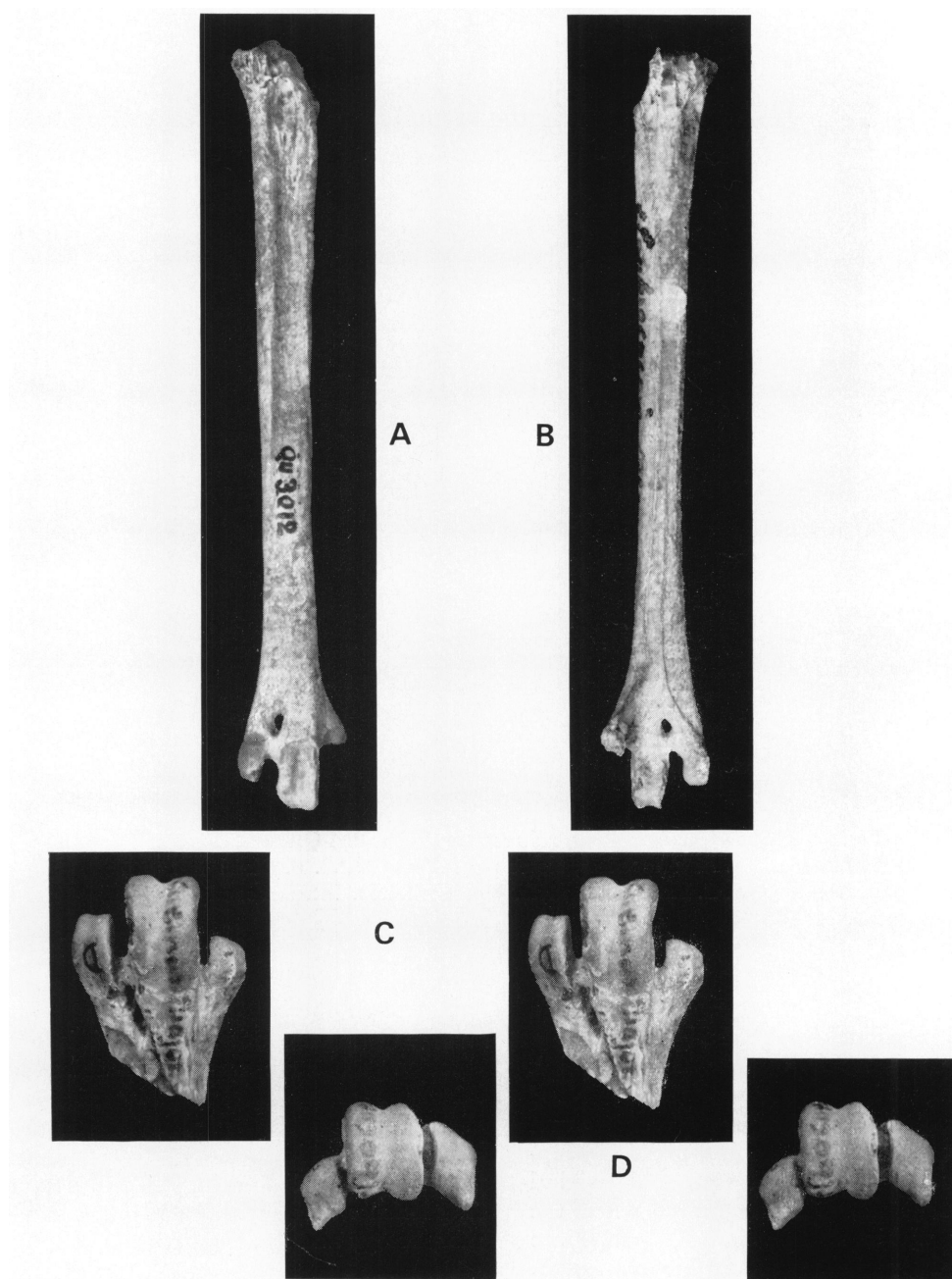
FIG. 29. *Elaphrocnemus crex.* A–B. Lectotype, PM Qu3012, right tarsometatarsus. A. Anterior view. B. Posterior view. Both about × 1.2. C–D. Referred specimen, PM Qu3006, distal end of left tarsometatarsus. C. Anterior view, stereo pair. D. Distal end, stereo pair. Both about × 1.7.

HYPODIGM: Lectotype; PM Qu3018, complete right tarsometatarsus; PM Qu3066, complete left tarsometatarsus; PM Qu3013, BaM QH149, both distal ends of right tarsometatarsi; PM Qu3006, BaM QH92, both distal ends of left tarsometatarsi; BM(NH) A1217, distal ends
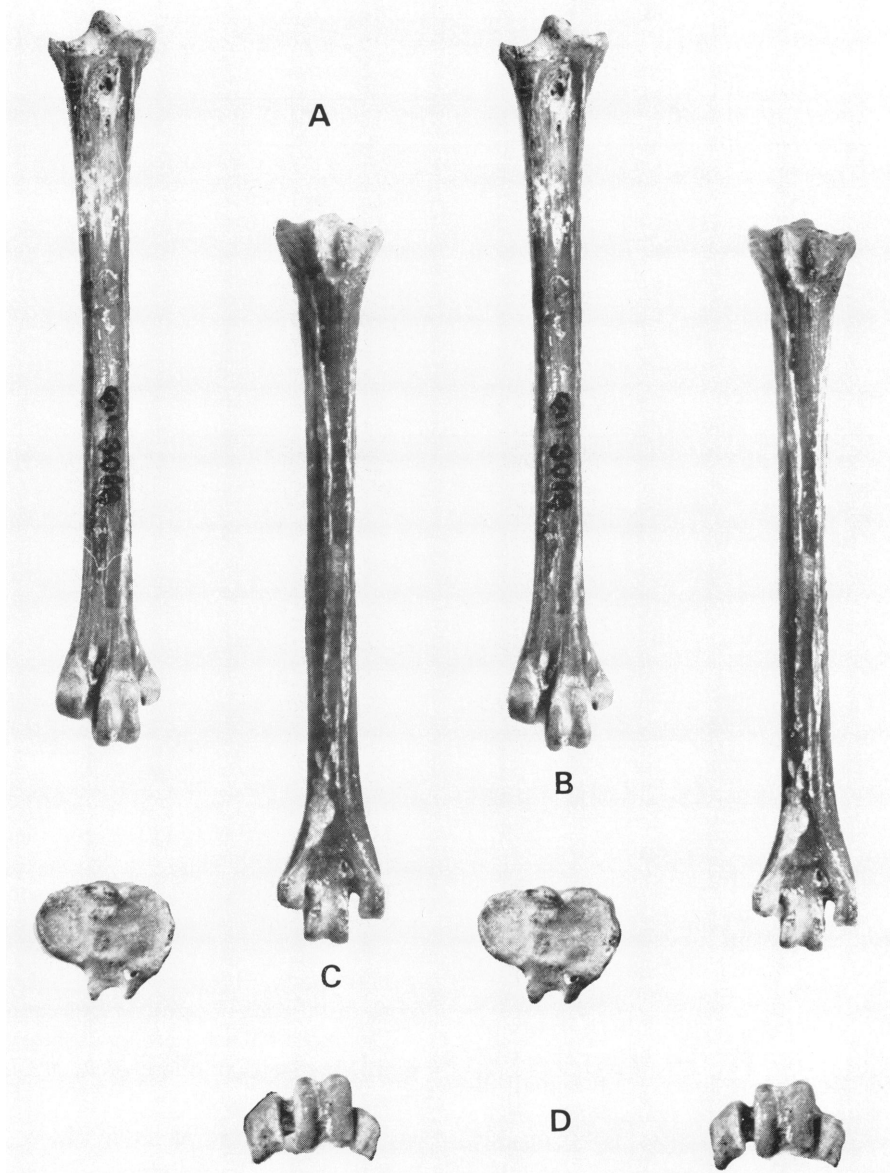
FIG. 30. *Elaphrocnemus crex*, referred specimen, PM Qu3018, right tarsometatarsus. A. Anterior view, stereo pair. About × 1.2. B. Posterior view, stereo pair. About × 1.2. C. Proximal end, stereo pair. About × 1.6. D. Distal end, stereo pair. About × 1.5.

of right and left tarsometatarsi; PM Qu3000, proximal end of left tarsometatarsus.

DIAGNOSIS: Tarsometatarsus longer and more robust than those of *E. phasianus* and *E. gracilis*.

MEASUREMENTS: See table 24.

REMARKS: The original type material of *E.* *crex* included PM Qu3012 and Qu3013, and I designate the former as the lectotype (fig. 29A, B). These two specimens show minor differences in size, which can be accounted for in part by abrasion (the trochleae of the lectotype are badly worn). Two specimens of the hypodigm,

TABLE 24

MEASUREMENTS (IN MILLIMETERS) OF TARSOMETATARSI OF *Elaphrocnemus crex*

	A[a]	B	C	D	E	F	G	H	I	J
PM Qu3012[b] Lectotype	86.2	12.4	2.2	4.9	3.2	7.0	6.3	5.1	—	—
PM Qu3013	—	12.7	3.1	4.6	2.8	6.5	—	—	—	—
PM Qu3018	79.3	11.9	2.6	5.1	3.1	6.5	5.3	4.9	12.2	10.2
PM Qu3066	79.4	11.9	2.5	5.6	2.9	6.6	5.1	4.5	11.5	9.8
BaM QH149	—	—	—	5.1	—	7.3	5.7	5.0	—	—
BM(NH) A1217 (right)	—	12.8	3.0	4.8	3.3	7.3	—	—	—	—
BM(NH) A1217 (left)	—	12.2	3.0	4.9	3.5	6.5	—	—	—	—
BaM QH92[b]	—	12.5	2.8	5.2	—	6.7	—	—	—	—
PM Qu3000	—	—	—	—	—	—	—	—	14.0	12.3
PM Qu3006	—	14.4	3.5	6.1	4.1	7.9	—	—	—	—

[a]*Abbreviations*: A, total length; B, breadth across trochleae; C, breadth of inner trochlea; D, breadth of middle trochlea; E, breadth of outer trochlea; F, depth of middle trochlea; G, breadth of middle of shaft; H, depth of middle of shaft; I, breadth of proximal end; J, depth of proximal end.

[b]Bone worn; measurements approximate.

PM Qu3000 and Qu3006, were included in the type material of species of *Idiornis*. The former was one of four specimens in the type series of *I. gallicus*, and the latter (fig. 29C, D) was one of two specimens in the type series of *I. major*. Both elements, however, are distinctly *Elaphrocnemus* in morphology and are here assigned to *E. crex*.

Although there is continuous variation in size within the tarsometatarsi of *E. crex*, two specimens (PM Qu3000 and Qu3006) are noticeably larger than the others. I think it is probable that this difference represents sexual size variation. Other possible examples of sexual dimorphism within this small sample are more difficult to prove. The difference in length between PM Qu3012 as compared with PM Qu3018 (fig. 30) and Qu3066 may also be sexual but other measurements of these bones overlap. Indeed, the measurements of all tarsometatarsal characters except length overlap between *E. crex* and *E. phasianus*. Bones of these two species can be separated on their length and general robustness, but these characters are probably not valid in all cases. In the section on morphological variability it will be shown that in many of these fossil gruiforms bone length is much less variable than other skeletal measurements. This suggests that length may be a fairly good criterion for species limits.

Elaphrocnemus gracilis Milne-Edwards

Figure 31

Elaphrocnemus gracilis MILNE-EDWARDS, 1892, p. 78.

HOLOTYPE: PM Qu3011, complete left tarsometatarsus.

HORIZON AND LOCALITY: Upper Eocene to possibly middle Oligocene deposits, phosphorites du Quercy; plateau du Quercy, France.

HYPODIGM: Holotype; PM Qu3056, Qu3078, both distal ends of right tarsometatarsi.

DIAGNOSIS: Tarsometatarsus shorter and much more slender than those of *E. phasianus* and *E. crex*.

MEASUREMENTS: See table 25.

REMARKS: The holotype is badly worn and damaged at both ends. Most of the middle trochlea and all of the inner are lacking; the hypotarsus is also damaged. On the basis of the referred specimens *E. gracilis* is certainly congeneric with *E. phasianus* and *E. crex*, but because of wear the holotype does not exhibit most of the diagnostic characters of the genus (e.g., hypotarsal structure and relative position of the inner trochlea). The shapes and relative positions of the cotylae, intercotylar prominence, and the anterior metatarsal groove of the holotype are similar to those of *E. phasianus* and *E. crex*.
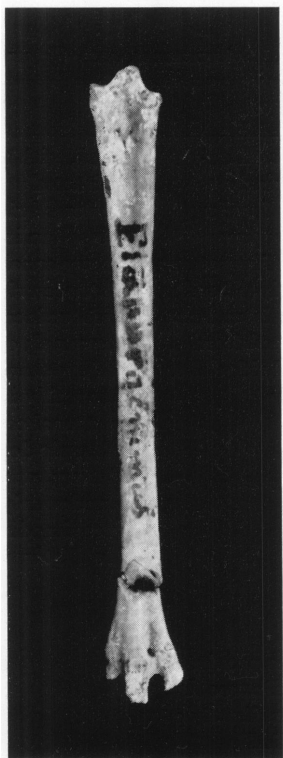
FIG. 31. *Elaphrocnemus gracilis*, holotype, PM Qu3011,
left tarsometatarsus. About × 1.7.

Referred specimen PM Qu3056 is very well
preserved and is typically *Elaphrocnemus* in
morphology. This specimen is much larger than
the holotype, but considering the amount of

variation recognized within the other species of
the genus, it seems advisable to consider PM
Qu3011 and Qu3056 as conspecific. It can be
noted that the length of PM Qu3056 is well
below the smallest measurement of *E. phasianus*.

The other referred specimen, PM Qu3078,
differs from Qu3056 in being smaller, with the
inner trochlea turned somewhat less posteriorly.
This referred specimen is intermediate in size
between Qu3056 and the holotype.

SYSTEMATIC POSITION OF
Phasianus alfhildae Shufeldt

Shufeldt (1915a, p. 71) described a series of
bones from the upper Eocene (Washakie B) of
Haystack Butte, Wyoming, under the name
Phasianus alfhildae. Included in the type material
(YPM 947) are the distal ends of a left and right
tarsometatarsus, a fragmentary distal right
humerus, and a fragmentary left coracoid.
Shufeldt was definite in his opinion that they
were galliform.

Brodkorb (1967, p. 138) placed *P. alfhildae* in
the genus *Elaphrocnemus* with the comment
"position tentative; apparently not galliform."

I have restudied this material, although not in
detail, and can state unequivocally that it does
not belong to an idiornithid. Moreover, it does
not have noticeably close affinities with any of
the families discussed in the present paper.
Although some of these elements may be grui-
form, others are more probably ciconiiform or
phoenicopteriform. I cannot express a definite
opinion at this time. This material, along with

TABLE 25

MEASUREMENTS (IN MILLIMETERS) OF TARSOMETATARSI OF *Elaphrocnemus gracilis*

	PM Qu3011 Holotype[a]	PM Qu3078	PM Qu3056
Total length	49.8	—	—
Breadth across trochleae	—	7.3	8.4
Breadth of inner trochlea	—	1.8	2.2
Breadth of middle trochlea	1.8	2.7	3.1
Breadth of outer trochlea	1.6	2.4	2.5
Depth of middle trochlea	—	3.8	4.4
Breadth of middle of shaft	3.1	—	3.2
Depth of middle of shaft	2.6	—	3.0
Breadth of proximal end	6.1	—	—
Depth of proximal end	5.4	—	—

[a]Holotype badly worn; measurements approximate.

TABLE 26

Morphological Comparison of Tarsometatrsi of *Idiornis, Elaphrocnemus,* AND *Gypsornis*

	Idiornis	*Elaphrocnemus*	*Gypsornis*
Hypotarsus	Rather broad, rectangular in shape with broad shallow groove posteriorly; external ridge only slightly developed; internal ridge moderately developed and directed posterointernally; edges of hypotarsus sharply delimited from borders of cotylae	Broad, with two well developed, posteriorly directed ridges forming deep central groove; external edge of hypotarsus runs smoothly into border of external cotyla and not sharply delimited from latter; external ridge short proximodistally	Broad, with two ridges directed posteriorly; external ridge projects less than internal; bony canal formed between ridges with groove located posterior to canal; external edge of hypotarsus runs smoothly into border of external cotyla and not sharply delimited from latter; external ridge moderately long proximodistally
Anterior metatarsal groove	Tendency to be deeper than in *Elaphrocnemus* but this may be artifact of preservation	Shallower	Like *Elaphrocnemus*
Inner trochlea	In posterior view, inner trochlea projects distally well beyond base of middle	Inner trochlea lies proximal to base of middle trochlea or only projects distally even with base of middle	—
Middle trochlea	Anterior face of trochlea tends to be more rounded and meets surface of shaft at a noticeably sharp angle	Anterior face tends to be less rounded and meets surface of shaft in smooth contour	—
Outer trochlea	Projects about one-half the length of middle trochlea	Projects about one-half the length of middle trochlea	—

additional specimens that seem to show resemblances to *P. alfhildae*, is being studied in detail and will be reported on at a later date.

The genus *Elaphrocnemus*, then, contains only three recognized species.

RELATIONSHIPS AND EVOLUTIONARY TRENDS WITHIN THE IDIORNITHIDAE

Conclusions about relationships and evolutionary trends among the genera of the idiornithids must necessarily involve a comparison of the morphological characters of closely related families. As I discuss below, the Idiornithidae apparently have their closest affinities with the Bathornithidae of the North American Tertiary rather than with the Rallidae as

previously thought (Wetmore, 1960; Brodkorb, 1967). Here I discuss the probable evolutionary trends based on a comparison with the Geranoididae, Bathornithidae, and other gruiform families. The reasons for considering certain character-states to be primitive or derived are given but should become more apparent after the section on interfamilial relationships.

A morphological comparison of the tarsometatarsi of *Gypsornis, Idiornis,* and *Elaphrocnemus* is summarized in table 26. Only the proximal end of the tarsometatarsus is known for *Gypsornis*. but the evidence is clear in suggesting that *Gypsornis* is the most primitive of the idiornithids. *Gypsornis* still possesses a bony canal in the central portion of the hypotarsus, a character shared with many early Tertiary gruiforms (in-

cluding the Geranoididae, Bathornithidae, and Eogruidae), whereas *Idiornis* and *Elaphrocnemus* have lost this canal (fig. 50). *Gypsornis* differs from the above-mentioned families and tends toward *Idiornis* and *Elaphrocnemus* in having the canal formed laterally and medially by two ridges which project posteriorly to form a tendinal groove posterior to the canal (fig. 21B). In the other families, for example in the genus *Palaeophasianus* of the Geranoididae (Cracraft, 1968b, p. 282, fig. 1; 1969, p. 18, fig. 7), a groove is not formed posterior to the canal.

The loss of the hypotarsal canal is clearly a derived character in *Idiornis* and *Elaphrocnemus* and indicates that they have a closer relationship to each other than either does to *Gypsornis*. In characters of the proximal end of the tarsometatarsus *Elaphrocnemus* is decidedly more primitive than *Idiornis*. In *Elaphrocnemus* the posterior ridges of the hypotarsus are close together to form a narrow groove and the external edge of the hypotarsus runs smoothly into the outer edge of the external cotyla (fig. 30B, C). Both of these characters are found in *Gypsornis*, and the relationship of the hypotarsus to the external cotyla is also present in other Tertiary gruiforms; therefore, the assumption that these characters represent the primitive condition is justified. In *Idiornis* the ridges have separated to form a broad posterior groove, and the hypotarsus is sharply delimited from the edge of the external cotyla (fig. 23C).

The anterior metatarsal grooves of *Elaphrocnemus* and *Gypsornis* are shallow compared with *Idiornis* and resemble those of other gruiform families. Hence, the relatively deep groove of *Idiornis* probably is the derived condition.

The morphological trends of the distal end of the tarsometatarsus are somewhat more difficult to interpret than those of the proximal end. On the one hand, the rounded middle trochlea of *Idiornis* (figs. 22D, 25A) is probably derived from the more gently curving trochlea of *Elaphrocnemus* and the other gruiforms. However, the reduced inner trochlea (relative to the middle) of *Elaphrocnemus* (figs. 27A, 29A) is no doubt derived from the condition found in the Eocene Geranoididae and thus links the idiornithids with the bathornithids (figs. 48, 49). In contrast to the proximal end, the distal tarsometatarsus of *Idiornis* and *Elaphrocnemus* appears to be a mosaic of primitive and derived characters.

SUPERFAMILY GRUOIDEA

FAMILY EOGRUIDAE WETMORE

GENUS *EOGRUS* WETMORE

Eogrus WETMORE, 1934, p. 3.

TYPE SPECIES: *Eogrus aeola* Wetmore.

INCLUDED SPECIES: Type species; *E. wetmorei* Brodkorb.

DISTRIBUTION: Medial or late Eocene to late Miocene or early Pliocene of eastern Asia.

REVISED DIAGNOSIS: Tibiotarsus with external condyle flattened distally, with indentation in distal margin. Condyles of equal depth anteroposteriorly, parallel, not spread anteriorly. Supratendinal bridge narrow proximodistally.

Tarsometatarsus with inner and outer trochleae reduced in size. Trochleae almost on same level, not very curved in distal view. Intercotylar prominence short, broad-based. Cotylae almost on same level. Anterior metatarsal groove deep.

REMARKS: See discussion section below and Wetmore (1934).

Eogrus aeola Wetmore

Figures 47–50

Eogrus aeola WETMORE, 1934, p. 3.

HOLOTYPE: AMNH 2936, almost complete right tarsometatarsus.

HORIZON AND LOCALITY: Middle or upper Eocene deposits, Irdin Manha Formation, Ulan Shireh beds; Shara Murun region, Chimney Butte, Suiynan Province, Inner Mongolia; Camp Margetts, 25 miles southwest of Iren Dabasu (Wetmore, 1934, p. 9); lower Oligocene deposits, Ardyn Obo beds; near Ardyn Obo, Inner Mongolia (Wetmore, 1934, p. 12).

HYPODIGM: Holotype; numerous other elements are known (see Wetmore, 1934).

DIAGNOSIS: Largest species in genus.

MEASUREMENTS: See Wetmore (1934).

REMARKS: See discussion section of this paper and Wetmore (1934).

Eogrus wetmorei Brodkorb

Eogrus sp. WETMORE, 1934, p. 12.
Eogrus wetmorei BRODKORB, 1967, p. 150.

HOLOTYPE: AMNH 2949, distal end of tibiotarsus.

HORIZON AND LOCALITY: Upper Miocene or lower Pliocene deposits, Tung Gur Formation;
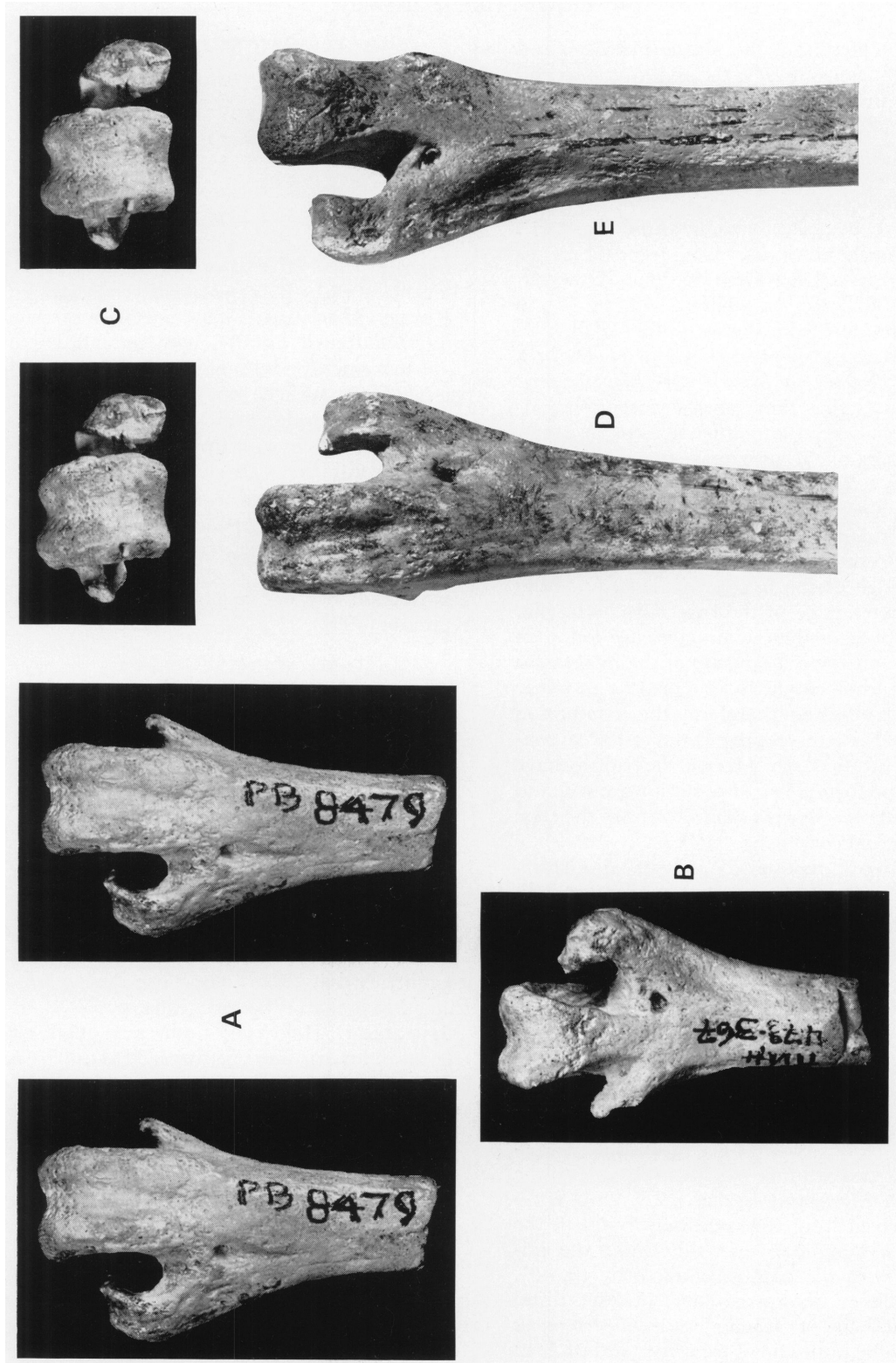
Fig. 32. A–C. *Proergilornis minor*, cast of holotype, PIN 473–367, distal end of left tarsometatarsus. A. Anterior view, stereo pair. B. Posterior view. C. Distal end, stereo pair. All about × 1.5. D–E. *Ergilornis rapidus*, cast of holotype, PIN 473–357, distal end of right tarsometatarsus. D. Anterior view. E. Posterior view. Both about × 1.4.

TABLE 27

MEASUREMENTS (IN MILLIMETERS) OF TARSOMETATARSI OF SPECIES OF THE ERGILORNITHIDAE

| | Ergilornis rapidus BM(NH) A3642[a] | Proergilornis minor BM(NH) A3641[a] | Urmiornis maraghanus | | |
			PM no number Lectotype	BM(NH) A3643[a]	BM(NH) A3644[a]
Total length	—	—	280.0[b]	—	—
Breadth of distal end	—	—	21.2	—	—
Breadth of outer trochlea	7.8[b]	6.7	7.3	8.3[b]	7.6
Depth of outer trochlea	9.7[b]	9.4	—	14.3	10.8
Breadth of middle trochlea	12.5	12.0	12.3	11.5	12.3
Depth of middle trochlea	16.0	14.0	16.1	16.9	14.8
Breadth of shaft 40 mm. from distal end of middle trochlea	13.3	10.9	—	10.8	11.2
Depth of shaft 40 mm. from distal end of middle trochlea	10.0	8.4	—	10.3	11.2
Breadth middle of shaft	—	—	10.9	—	—
Depth middle of shaft	—	—	14.4	—	—
Breadth of proximal end	—	—	29.7	31.5	—
Depth of proximal end	—	—	—	27.0	—
Depth of external cotyla	—	—	12.5	—	—
Depth of internal cotyla	—	—	14.5	—	—

[a] Measurements made on cast.
[b] Measurement approximate.

40 miles southeast of Iren Dabasu, Inner Mongolia.

HYPODIGM: Holotype only.

DIAGNOSIS: Smallest species in genus.

MEASUREMENTS: See Wetmore (1934, p. 12).

REMARKS: There is no doubt that the tibiotarsus of *E. wetmorei* is referable to *Eogrus*, and it differs from *E. aeola* only in being slightly smaller. If the stratigraphic data are correct, this would suggest that the tibiotarsus of *Eogrus* exhibited essentially no change from the medial Eocene to the early Pliocene.

FAMILY ERGILORNITHIDAE KOZLOVA

GENUS *PROERGILORNIS* KOZLOVA

Proergilornis KOZLOVA, 1960, p. 327.

TYPE SPECIES: *Proergilornis minor* Kozlova.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Early or medial Oligocene of Inner Mongolia.

DIAGNOSIS: Tarsometatarsus with inner trochlea greatly reduced and present as a small stub.

REMARKS: See discussion of intergeneric relationships.

Proergilornis minor Kozlova

Figure 32A–C

Proergilornis minor KOZLOVA, 1960, p. 327.

HOLOTYPE: PIN 473–367, distal end of left tarsometatarsus.

HORIZON AND LOCALITY: Lower or middle Oligocene deposits; Ergil-Obo, southeast Gobi, Inner Mongolia.

HYPODIGM: Holotype only [cast, BM(NH) A3641].

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: See table 27.

REMARKS: See discussion of intergeneric relationships.

GENUS *ERGILORNIS* KOZLOVA

Ergilornis KOZLOVA, 1960, p. 323.

TYPE SPECIES: *Ergilornis rapidus* Kozlova.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Early or medial Oligocene of Inner Mongolia.

DIAGNOSIS: Tarsometatarsus with inner troch-

lea essentially absent (present as a very slight stub).

REMARKS: See discussion of intergeneric relationships.

Ergilornis rapidus Kozlova

Figure 32D, E

Ergilornis rapidus KOZLOVA, 1960, p. 323.

HOLOTYPE: PIN 473–357, distal end of right tarsometatarsus.

HORIZON AND LOCALITY: Lower or middle Oligocene deposits; Ergil-Obo, southeast Gobi, Inner Mongolia.

HYPODIGM: Holotype only [cast, BM(NH) A3642].

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: See table 27.

REMARKS: See discussion of intergeneric relationships.

GENUS *URMIORNIS* MECQUENEM

Urmiornis MECQUENEM, 1908, p. 54.

TYPE SPECIES: *Urmiornis maraghanus* Mecquenem.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Late Miocene (?) to early Pliocene of western Asia.

DIAGNOSIS: Tibiotarsus with condyles unequal in anteroposterior depth. Internal condyle with deep notch distally. Both condyles massive anteriorly. Tubercle on supratendinal bridge very large, and situated in middle of shaft, thus large groove between tubercle and external condyle.

Tarsometatarsus with inner trochlea lacking. External intertrochlear notch narrow. Anterior metatarsal groove shallow. Intercotylar prominence low and broad-based. Cotylae almost on same level.

REMARKS: See discussion of intergeneric relationships.

Urmiornis maraghanus Mecquenem

Figures 33, 34

Urmiornis sp. MECQUENEM, 1908, p. 54.
Urmiornis maraghanus MECQUENEM, 1925, p. 27.

LECTOTYPE: PM no catalogue number, complete left tarsometatarsus.

HORIZON AND LOCALITY: Upper Miocene or lower Pliocene deposits, Tiraspol, Moldavia, Ukraine (PIN 298–1); lower Pliocene deposits, Maragha, Lake Urmia, Iran (lectotype); Kalmakpai, Kazakhstan (PIN 2433–1).

HYPODIGM: Lectotype; PM no catalogue number, distal end of right tibiotarsus (with lectotype); PIN 298–1 [cast, BM(NH) A3643], complete right tarsometatarsus; PIN 2433–1 [cast, BM(NH) A3644], distal end of right tarsometatarsus; PIN 2433–2, 2433–3, 2433–4, phalanges.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: See table 27; PM tibiotarsus —depth of external condyle 22.7 mm.; depth of internal condyle 24.8 mm.; breadth across posterior ends of condyles 21.5 mm.; breadth across anterior ends of condyles 26.7 mm.; depth of anterior intercondylar fossa relative to external condyle 8.9 mm.

REMARKS: The type material of *U. maraghanus* consists of a distal right tibiotarsus and a complete left tarsometatarsus, both housed in the Paris Museum. The tibiotarsus is said by Mecquenem (1908; 1925, p. 27) to be from the left side, but examination of the specimen and of his figures reveals that the bone is a right tibiotarsus (fig. 34) and is incorrectly articulated with the left tarsometatarsus in his figure (Mecquenem, 1908, fig. 16; 1925, fig. 16). Mecquenem wrote that the tibiotarsus showed many characters of both gruiforms and storks (Ciconiidae), but the error just noted may have caused him to think of some features as being storklike. Because one cannot be certain that the tibiotarsus and tarsometatarsus came from the same individual (although it seems likely they did), I here designate the tarsometatarsus as the lectotype of *U. maraghanus*.

There are some morphological differences between the lectotype and the tarsometatarsus from Tiraspol, and the former differs in having the shaft more slender relative to the proximal end of the bone, the intercotylar prominence somewhat less massive, the middle and outer trochleae less compressed lateromedially and therefore less deep anteroposteriorly, and the intertrochlear notch narrower. There is thus some question whether the different specimens represent a single species. For the purposes of this paper all the above specimens are referred to *U. maraghanus*. The systematics of these specimens and of some newly discovered material
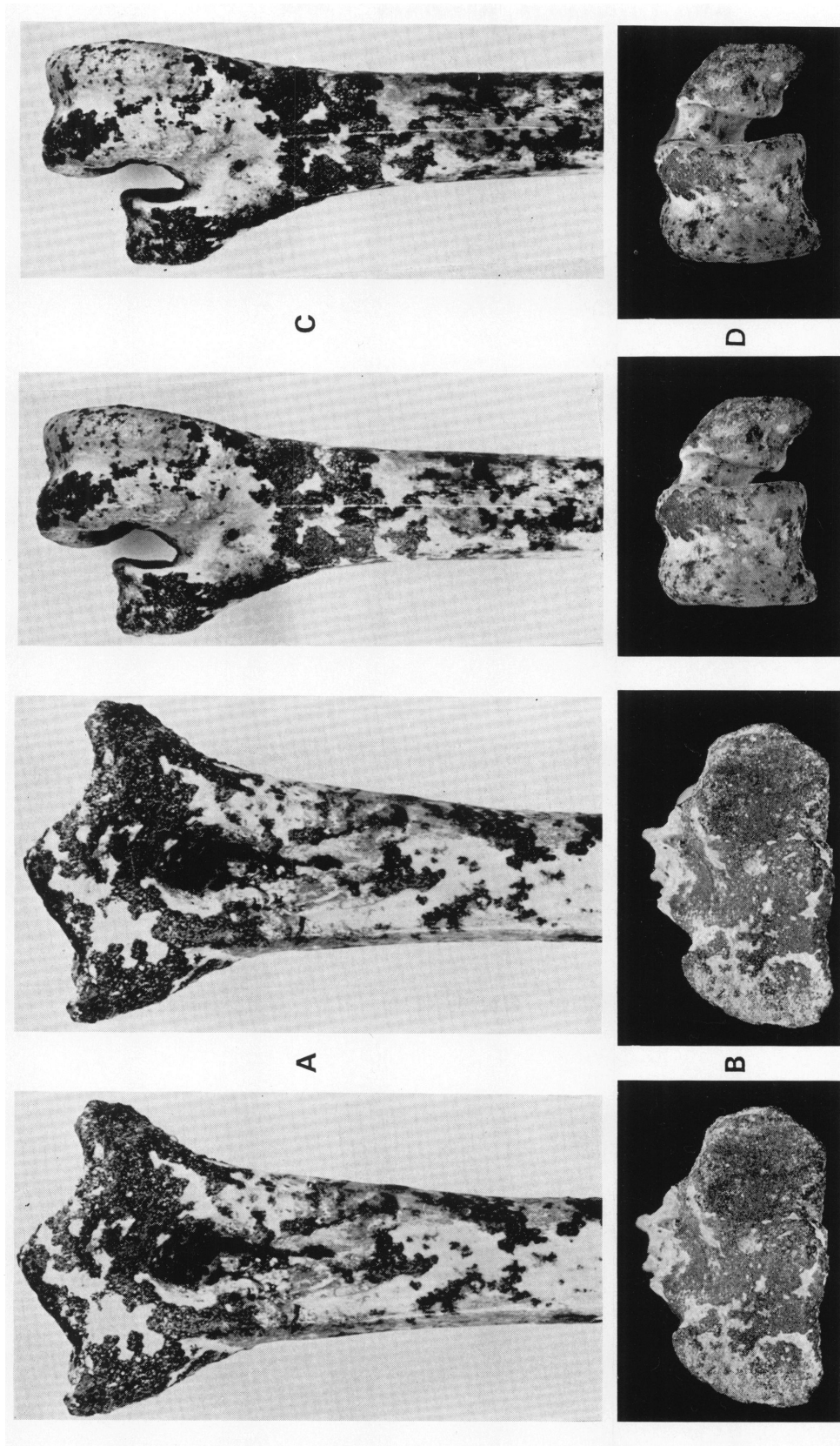
Fig. 33. *Urmiornis maraghanus*, lectotype, PM no catalogue number, left tarsometatarsus. A. Anterior view of proximal end. B. Proximal end. C. Anterior view of distal end. D. Distal end. All stereo pairs. All about × 1.6.

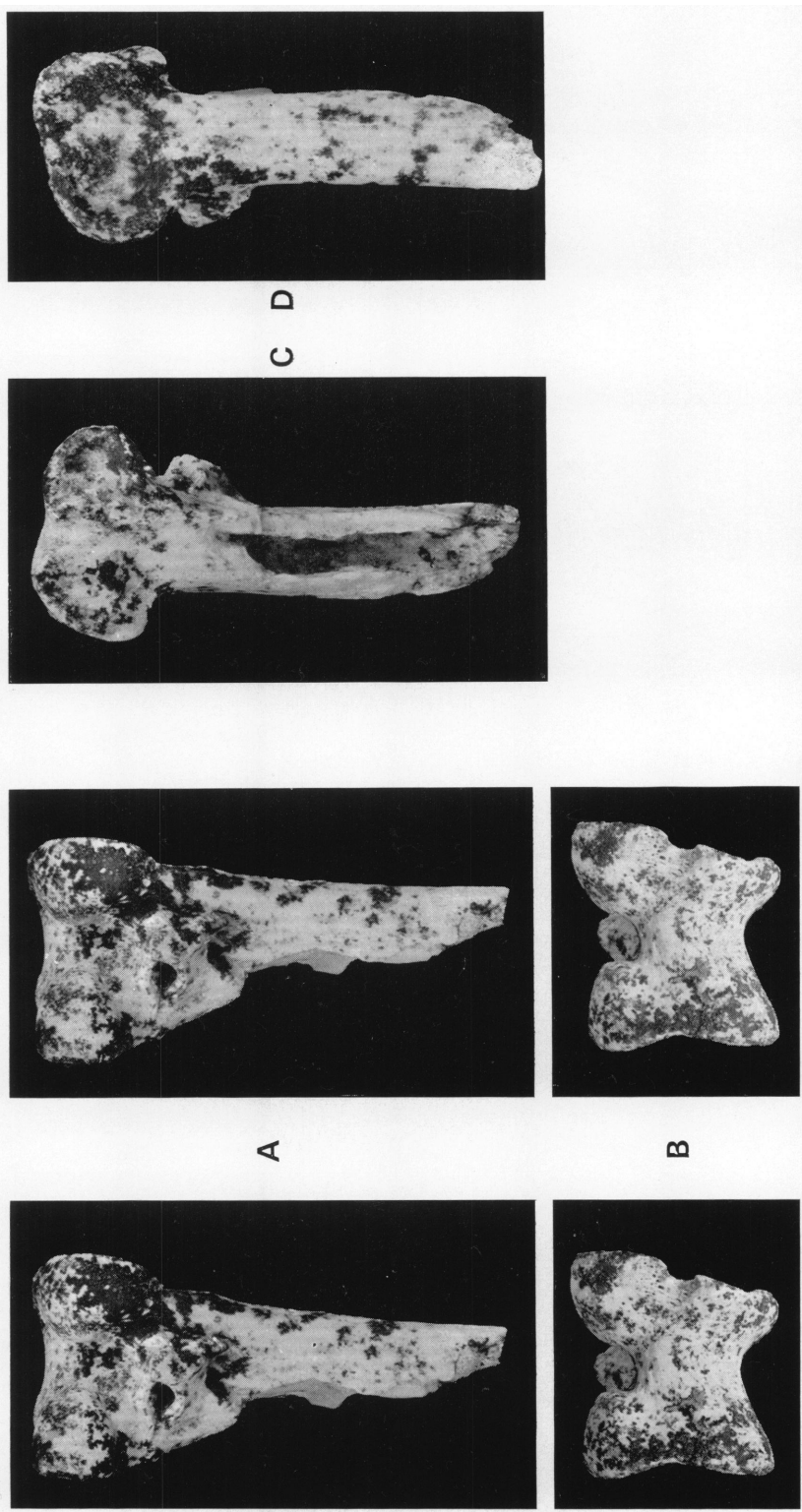Fig. 34. *Urmiornis maraghanus*, referred specimen, PM no catalogue number, distal end of right tibiotarsus. A. Anterior view, stereo pair. B. Distal end, stereo pair. C. Internal condyle. D. External condyle. All about ×1.2.

which bears on this problem will be discussed elsewhere (Kurotchkin, in preparation).

Considerable confusion exists as to the correct bibliographic citation of this genus and species. In 1908 Mecquenem apparently provisionally described the Paris Museum material and called it "*Urmiornis*(?)" (1908, p. 54). This becomes the original date of description for the generic name. Later Mecquenem (1925, p. 27) fully described this material as "*Urmiornis Maraghanus* nov. gen., nov. sp." Under the rules of the International Commission of Zoological Nomenclature it appears that 1925 is not the date of description for the genus name but would be correct for the species name. It should be noted that the 1925 paper was the second part of a longer paper (begun in 1924) and that there are two series of paginations, one for the paper as a whole (carried over from 1924) and one for volume 14 (1925). Thus, the page number (p. 55) cited in Brodkorb (1967, p. 154) is that of the whole paper and not volume 14, which should be page 27.

INTERGENERIC RELATIONSHIPS

Ergilornis and *Proergilornis* differ from each other in three main features: (1) *Proergilornis* is smaller and relatively less heavy and robust, (2) the inner trochlea of *Proergilornis* is a noticeable projection whereas in *Ergilornis* it is a stub and is almost absent, and (3) the outer trochlea of *Proergilornis* projects slightly less distally relative to the length of the middle trochlea. A problem exists in explaining these differences, and it is questionable whether they are correctly attributable simply to intergeneric differences as Kozlova (1960) assumed. Table 27 gives the measurements of the ergilornithids. The size differences between *Proergilornis* and *Ergilornis* are not great and are easily within the size range of a single species (e.g., compare the measurements of *Eogrus aeola* in Wetmore, 1934). Although the tarsometatarsus of *Proergilornis* is significantly less robust than that of *Ergilornis*, even this difference could be related to individual variation or to sexual dimorphism in size. The differences in development of the inner trochleae in the two genera seem to be important, but rudimentary or "vestigial" structures can sometimes be highly variable. It is therefore possible that the different sizes of the inner trochlea may not be diagnostic taxonomic characters in these birds.

Until we have more material it will be impossible to reach a final decision about the status of these two genera. Because there are a number of potentially significant differences, it probably is best to maintain both generic names, if nothing more than for convenience and descriptive purposes.

The tarsometatarsus of *Urmiornis* differs from that of *Ergilornis* in a number of characters: (1) the shaft is decidedly more slender, (2) the middle trochlea is flattened more lateromedially rather than more anteroposteriorly (less of a difference in the lectotype of *U. maraghanus*), (3) the middle trochlea projects distally beyond the outer trochlea relatively more, and (4) the base of the outer trochlea is somewhat less flattened anteroposteriorly. In the characters of the tarsometatarsus, *Proergilornis* and *Ergilornis* resemble each other more than either resembles *Urmiornis*, but the resemblance of the former two genera involve a number of primitive characters and thus are of no phylogenetic significance.

FAMILY GRUIDAE VIGORS

GENUS *PALAEOGRUS* PORTIS

Palaeogrus PORTIS, 1885, p. 362.
Ornitocnemus Zigno, 1875: LAMBRECHT, 1933, p. 518.

TYPE SPECIES: *Palaeogrus princeps* Portis.

INCLUDED SPECIES: Type species; *P. geiseltalensis* Lambrecht; *P. hordwelliensis* (Lydekker); and *P. excelsus* (Milne-Edwards).

DISTRIBUTION: Medial Eocene to early Miocene of Europe.

DIAGNOSIS: Tibiotarsus with external condyle slightly flattened distally, but distal margin smooth and without evidence of indentation. Anterior end of internal condyle moderately thick, especially proximally. Tubercle on supratendinal bridge moderately developed.

Tarsometatarsus with intercotylar prominence well developed and more or less pointed (but rounded) at apex. Anterior metatarsal groove fairly well developed. Side of bone immediately proximal to internal cotyla low, not projecting. Hypotarsus moderately long proximodistally. Posterior side of shaft (distal to hypotarsus) developed into narrow ridge, not flattened and rounded.

Humerus with well-developed internal condyle projecting noticeably distad beyond external condyle. Anterior articular surface high

and protruding. Axis of external condyle at about 45 degree angle to long axis of shaft.

REMARKS: Considerable confusion has existed over the correct generic name to be applied to the four species of this genus. Portis (1885, p. 362) created the name *Palaeogrus princeps* for a fragmentary tibiotarsus given to him by Baron A. De Zigno. Apparently De Zigno had provisionally given this tibiotarsus the name *Ornitocnemus robustus* (see Portis, 1885, p. 362), but to my knowledge this name was never published by De Zigno. Lambrecht (1933, p. 518) listed "*Ornitocnemus robustus* Zigno 1875" in the synonymy of *Palaeogrus princeps*. Brodkorb (1967, p. 147) used the name *Ornitocnemus robustus* Zigno, apparently because of presumed priority, and listed the original citation as "Zigno, 1876, Mem. Ist. veneto Sci., vol. 20, p. 445." Previously, both Portis (1885) and Lambrecht (1933) cited De Zigno (1875) as the source for the name. *Ornitocnemus robustus*. I have been unable to find any paper by De Zigno published in 1876 bearing on this problem. Furthermore, De Zigno (1875) pertains to fossil mammals and contains no mention of the name *Ornitocnemus robustus*, and presumably this name was only mentioned verbally to Portis. Portis, in turn, was followed by Lambrecht and Brodkorb neither of whom saw the original paper of De Zigno. Therefore, *Palaeogrus* Portis should be the correct generic name and *P. princeps* the type species of the genus.

When he described *P. hordwelliensis* Lydekker (1891, p. 165) was of the opinion that that species and *P. princeps* were not generically distinct from the Recent genus *Grus*. Lambrecht (1933, p. 518) disagreed and stated that *Palaeogrus* differs from *Grus* in the absence of the tubercle on the external condyle, onto which he claimed the M. peroneus profundus inserts. This is clearly an error, also noted by Brodkorb (1963b, p. 164), as M. peroneus profundus (=M. peroneus brevis) does not insert onto the tibiotarsus, and the tubercle which Lambrecht figures for *Grus* (1933, p. 518, fig. 155C, D) is on the internal condyle, whereas the muscle runs along the external surface of the leg. The tubercle figured by Lambrecht is more properly called the internal ligamental prominence. On the basis of the tibiotarsus *Palaeogrus* is definitely not congeneric with *Grus* and differs from that genus in several characters. For example, in *Paleogrus* the internal ligamental prominence is

reduced, the external condyle is straight in profile (in distal view), is not elongated anteroposteriorly, and lacks a deep indentation in its distal margin, the anterior end of the internal condyle is somewhat thicker lateromedially, and the tubercle on the supratendinal bridge is not so well developed. *Palaeogrus* also differs from *Grus* in the proximal end of the tarsometatarsus as follows: the intercotylar prominence is higher and more pointed, the anterior metatarsal groove is deeper and broader, and the hypotarsus is shorter proximodistally.

In the characters of the tibiotarsus it would be difficult to separate *Palaeogrus* from the Recent genus *Balearica*, and this is no doubt the reason why Brodkorb (1967, pp. 147–148) included the genus in the subfamily Balearicinae. *Palaeogrus* differs from *Balearica* in a few characters, namely in having the tubercle on the supratendinal bridge somewhat lower, and the external condyle flatter distally and with a straighter contour (seen in distal view). *Palaeogrus* shows greater differences from *Balearica* than from *Grus* in the features of the tarsometatarsus; the intercotylar prominence is higher and more pointed, the anterior metatarsal groove deeper, the ligamental tubercles on the sides of the cotylae much lower, and the hypotarsus is longer proximodistally. On the basis of the above comparisons *Palaeogrus* can be regarded as a valid genus.

Palaeogrus princeps Portis

Palaeogrus princeps PORTIS, 1885, p. 362.
Ornitocnemus robustus Zigno, 1875: LAMBRECHT, 1933, p. 518.

HOLOTYPE: Whereabouts of holotype unknown, distal end of left tibiotarsus.

HORIZON AND LOCALITY: Middle Eocene deposits (Lutetian in age); Monte Zuello, Italy.

HYPODIGM: Holotype only.

DIAGNOSIS: Largest species in genus; depth of distal end of tibiotarsus apparently about same as width.

MEASUREMENTS: Anteroposterior depth of distal end 20 mm.; breadth of distal end 21.0 mm.; breadth of shaft 12.0 mm.; depth of shaft 10.5 mm. (all measurements probably approximate; after Portis, 1885, p. 362).

REMARKS: See generic remarks above for comments on this species. I was unable to locate the type in Torino where Portis worked, but it
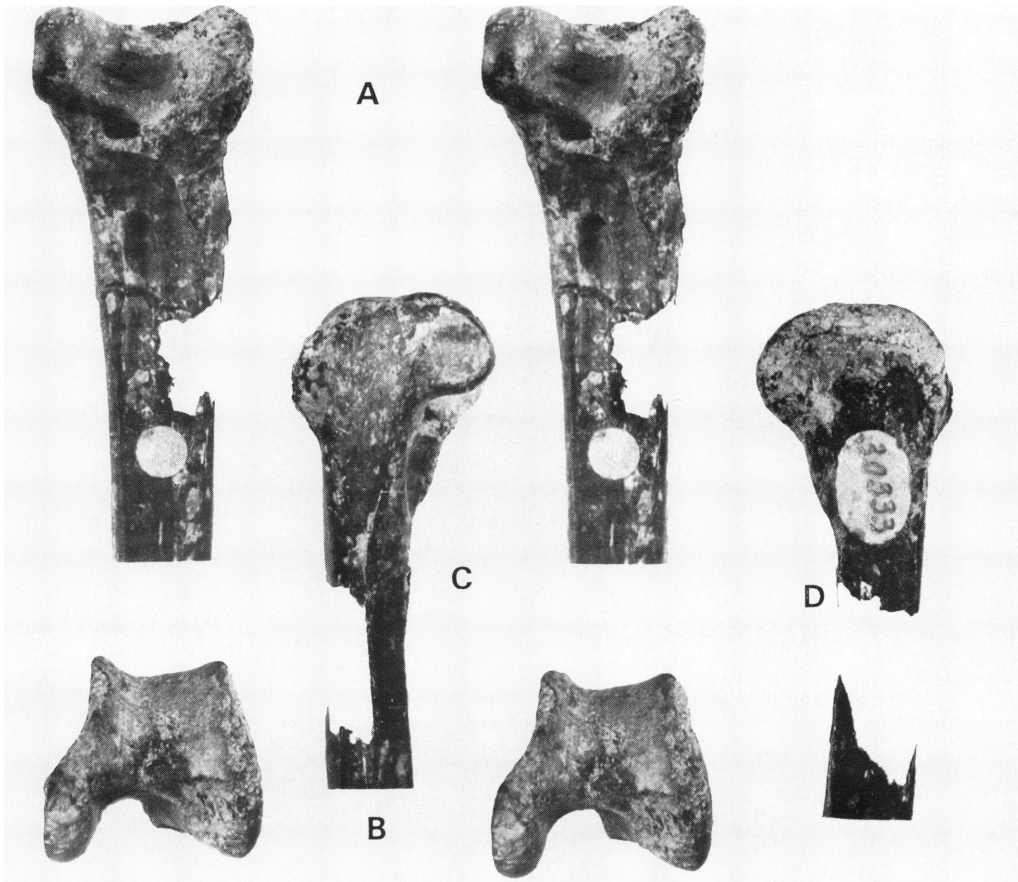
FIG. 35. *Palaeogrus hordwelliensis*, holotype, BM(NH) 30333, distal end of right tibio-tarsus. A. Anterior view, stereo pair. B. Distal end, stereo pair. C. Internal condyle. D. External condyle. All about ×1.8.

TABLE 28

MEASUREMENTS (IN MILLIMETERS) OF TIBIOTARSI OF THE SPECIES OF *Palaeogrus* AND *Probalearica*

	Palaeogrus hordwelliensis BM(NH) 30333 Holotype	*Palaeogrus excelsus* PM Av.8556 Lectotype	PM Av.8555	BaM MA2629	*Probalearica crataegensis*[a] PB 8503 Holotype
Depth of external condyle	15.5	18.6	—	20.8	13.9
Depth of internal condyle	16.5	20.2	21.5	22.6	14.4
Breadth across anterior end of condyles	16.3	21.0	20.8	21.5	13.9[b]
Breadth across posterior end of condyles	11.1	14.7	—	15.8	—
Breadth of shaft 40 mm. from distal end	8.3	11.7[c]	—	12.1[c]	—
Depth of shaft 40 mm. from distal end	7.4	9.5[c]	—	10.0[c]	—

[a] Measurements after Brodkorb (1963).
[b] Width of distal end.
[c] Measurement taken in middle of shaft.
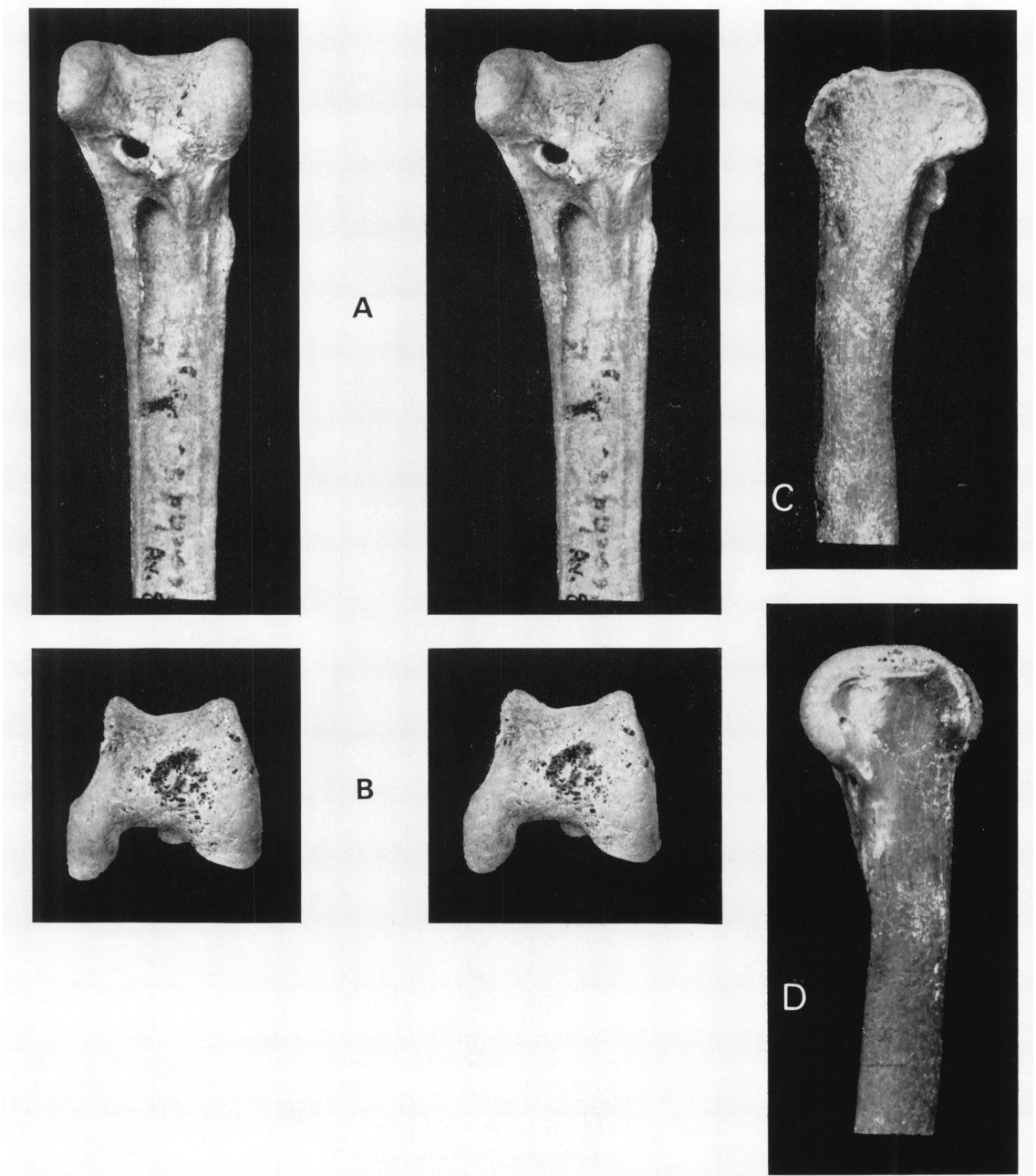
FIG. 36. *Palaeogrus excelsus*, lectotype, PM Av.8556, distal end of right tibiotarsus. A. Anterior view, stereo pair. B. Distal end, stereo pair. C. Internal condyle. D. External condyle. All about × 1.4.

may eventually be found in some other Italian museum.

Palaeogrus geiseltalensis Lambrecht

Palaeogrus geiseltalensis LAMBRECHT, 1935, p. 361.

Ornitocnemus geisteltalensis (Lambrecht): BRODKORB, 1967, p. 148.

HOLOTYPE: Geiseltalmuseum no number, fragmentary complete right tibiotarsus and tarsometatarsus.
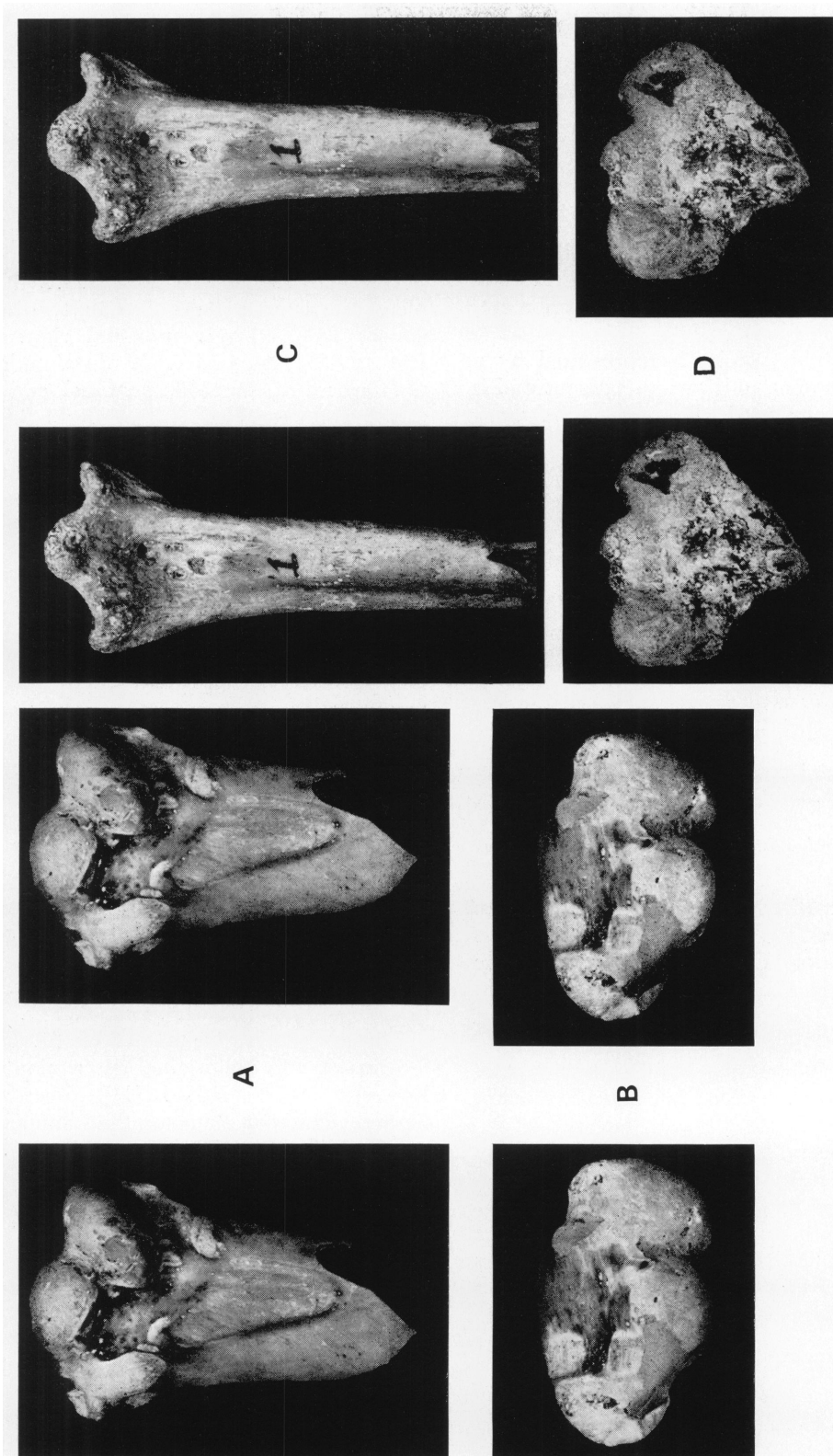
FIG. 37. *Palaeogrus excelsus*, referred specimens. A–B. PM Av.8548, distal end of right humerus. A. Palmar view. About ×1. B. Distal end. About ×1.2. C–D. PM Av.8557, proximal end of right tarsometatarsus. C. Anterior view. About ×1.1. D. Proximal end. About ×1.4. All stereo pairs.

HORIZON AND LOCALITY: Middle Eocene deposits, Braunkohle des Geiseltales; Grube Halle near Halle/Saxony, Germany.

HYPODIGM: Holotype only.

DIAGNOSIS: Smaller than *P. princeps* and *P. excelsus*; apparently heavier than *P. hordwelliensis*.

MEASUREMENTS: Total length of tibiotarsus 250.0 mm.; total length of tarsometatarsus about 193.0 mm. (according to Lambrecht, 1935).

REMARKS: This species is represented by a flattened tibiotarsus and tarsometatarsus and is very poorly preserved. *Palaeogrus geiseltalensis* was approximately the same size as the living *Balearica pavonina*. Probably *P. geiseltalensis* was about the same size as *P. hordwelliensis*, but Lambrecht's figures (1935, pl. 1, fig. 1) suggest that the species had more massive bones. This may be an artifact of preservation however. Further study of the holotype, which I have not seen, will be necessary before the systematic position of *P. geiseltalensis* can be clarified.

Palaeogrus hordwelliensis (Lydekker)

Figure 35

Grus hordwelliensis LYDEKKER, 1891, p. 165.
Palaeogrus hordwelliensis (Lydekker): LAMBRECHT, 1933, p. 519.
Ornitocnemus hordwelliensis (Lydekker): BRODKORB, 1967, p. 148.

HOLOTYPE: BM(NH) 30333, distal end of right tibiotarsus.

HORIZON AND LOCALITY: Upper Eocene deposits, Hordwell beds; Hampshire, Hordwell, England.

HYPODIGM: Holotype only.

DIAGNOSIS: Tibiotarsus smaller than that of *P. princeps* and *P. excelsus*; less massive than *P. geiseltalensis*.

MEASUREMENTS: See table 28.

REMARKS: *Palaeogrus hordwelliensis* is excellently preserved and provides definite confirmation of the presence of a *Balearica*-like crane in the late Eocene. The tibiotarsus of *P. hordwelliensis* is very similar to that of *P. excelsus* in form but is smaller (compare figs. 35 and 36).

Palaeogrus excelsus (Milne-Edwards)

Figures 36, 37

Grus excelus MILNE-EDWARDS, 1871, vol. 2, p. 24.
Palaeogrus excelsa (Milne-Edwards): LAMBRECHT, 1933, p. 519.

Ornitocnemus excelsus (Milne-Edwards): BRODKORB, 1967, p. 148.

LECTOTYPE: PM Av.8556, distal end of right tibiotarsus.

HORIZON AND LOCALITY: Lower Miocene deposits (Aquitanian in age); Chavroches and Langy, Dept. of Allier; Saint Gérand-de-Puy; France.

HYPODIGM: Lectotype; BaM S.G.15493, complete left femur; BaM S.G.5651, distal left femur; LGL 91.611, proximal right femur; PM Av.8555, BaM MA2629, distal ends of left tibiotarsi; PM Av.8558, proximal end of left tarsometatarsus; PM Av.8557, BaM S.G.1253, proximal ends of right tarsometatarsi; MHNL St.G.64, almost complete right tarsometatarsus; PM Av.8559, shaft of tarsometatarsus; PM Av.8560, Av.8561, phalanges; PM Av.8548, Av.8550, Av.8549, LGL 91.606, BaM S.G.141, S.G.5920, all distal ends of right humeri; LGL 91.609, distal end of left humerus; PM Av.8549a, shaft of humerus; PM Av.8552, complete right ulna; PM Av.8551, proximal end of right ulna; PM Av.8553, proximal end of left ulna; LGL 91.610, distal end of right ulna; LGL 91.608, distal end of left ulna; PM Av.8547, MHNL St.G.62, complete right coracoids; MHNL St.G.63, complete left coracoid; BaM S.G.3971, fragmentary left coracoid; BaM S.G.5912, Ph.1810, fragmentary right coracoids; PM Av.8554, fragmentary carpometacarpus; LGL 91.612, fragment of sternum, LGL 91.613, fragment of furcula; BaM S.G.2783, posterior part of cranium.

DIAGNOSIS: Smaller than *P. princeps*, larger than *P. geiseltalensis* and *P. hordwelliensis*.

MEASUREMENTS: See tables 28 to 33.

REMARKS: In his original description Milne-Edwards [1871 (1867–1871)] discussed and figured numerous elements that composed the type series (all Paris Museum specimens). I here designate the distal right tibiotarsus, PM Av.8556, as the lectotype (fig. 36). This element was chosen because it can be compared throughout the genus, whereas this is not possible with the other elements. To my knowledge there is no evidence concerning which part of the type series was associated *in situ*, and because several individuals are represented, designation of a lectotype is advisable.

The tibiotarsus of *P. excelsus* is very similar to that of *P. hordwelliensis* but the latter differs in having the distal end slightly more compressed

TABLE 29

MEASUREMENTS (IN MILLIMETERS) OF TARSOMETATARSI OF *Palaeogrus excelsus*

	MHNL St.G.64	PM Av.8558	PM Av.8557	BaM S.G.1253
Total length	210.0[a]	—	—	—
Breadth across trochleae	22.0	—	—	—
Breadth of inner trochlea	6.1	—	—	—
Breadth of middle trochlea	9.2	—	—	—
Breadth of outer trochlea	7.2	—	—	—
Depth of middle trochlea	12.1	—	—	—
Breadth of middle of shaft	8.9	—	—	—
Depth of middle of shaft	7.7	—	—	—
Breadth of proximal end	—	22.1	24.3	20.0
Depth of proximal end	—	21.0	23.3	20.0

[a] Bone worn and damaged; estimated length.

TABLE 30

MEASUREMENTS (IN MILLIMETERS) OF HUMERI OF *Palaeogrus excelsus*

	PM Av.8548	PM Av.8550	PM Av.8549	LGL 91.609	BaM S.G.141	BaM S.G.5920
Breadth of distal end	33.4	32.5+	—	31.1	27.4	31.8[a]
Depth of external condyle	17.6	17.6	—	18.9	15.7	—
Depth of internal condyle	11.2	11.1	12.5	10.8.	9.0	10.7[a]
Breadth middle of shaft	—	—	—	—	14.4	—
Depth of middle of shaft	—	—	—	—	12.2	—

[a] Bone worn; measurement approximate.

TABLE 31

MEASUREMENTS (IN MILLIMETERS) OF ULNAE OF *Palaeogrus excelsus*

	PM Av.8552	PM Av.8551	PM Av.8553	LGL 91.610	LGL 91.608
Total length	219.0	—	—	—	—
Depth of external condyle	13.0	—	—	17.3	16.9
Depth distal end	13.9	—	—	—	—
Breadth of cotylae	19.8	19.5	19.3	15.4	14.9
Breadth middle of shaft	9.2	9.7	—	—	—
Depth middle of shaft	8.6	8.6	—	—	—

TABLE 32

MEASUREMENTS (IN MILLIMETERS) OF CORACOIDS OF *Palaeogrus excelsus*

	PM Av.8547	MHNL St.G.63	MHNL St.G.62	BaM S.G.3971	BaM S.G.5912
Total length	83.4	82.0	79.9	—	—
Breadth at sternal end	—	40.3	—	—	—
Breadth middle of shaft	14.3	12.3	12.2	12.2	11.7
Depth of middle of shaft	—	8.9	9.1	10.1	9.6
Breadth from procoracoid to posterior portion of scapular facet	—	23.8	22.7	—	—

TABLE 33

Measurements (in Millimeters) of Femora of *Palaeogrus excelsus*

	LGL 91.611	BaM S.G.15493	BaM S.G.5651
Total length	—	117.6	—
Breadth across distal end	—	23.4	—
Depth of external condyle	—	21.5	—
Depth of internal condyle	—	18.6	—
Breadth of middle of shaft	—	9.6	10.4
Depth of middle of shaft	—	10.2	11.6
Breadth of proximal end	24.5	22.5	—
Depth of head	10.4	9.7	—

lateromedially, the tubercle on the supratendinal bridge slightly less pronounced, and the anterior end of the internal condyle somewhat less thick lateromedially.

All the specimens of each element listed in the hypodigm show relatively little variation. Undoubtedly there is additional material of *P. excelsus* in museums that I did not visit, and when the large Aquitanian collections at the Paris Museum are studied in detail, more material will possibly be found. It can be noted that numerous bones in several museums were incorrectly identified as *P. excelsus*, when in fact many of them were of a ciconiid.

GENUS *EOBALEARICA* GUREEV

Eobalearica Gureev, 1949, p. 249.

Type Species: *Eobalearica tugarinovi* Gureev.
Included Species: Type species only.
Distribution: Apparently late Eocene of Uzbek, SSR.
Revised Diagnosis: Tibiotarsus with external condyle rounded distally, not flattened and without indentation in distal margin. Anterior end of condyle apparently relatively long proximodistally and in general massive. Posterior intercondylar sulcus apparently shallow. Anterior intercondylar fossa apparently very shallow.
Remarks: The specimen on which this genus is founded is so poorly preserved that it is doubtful whether reliable comparisons can be made with other genera. The characters listed in the diagnosis (based on the figure of Gureev) strongly suggest that this genus does not belong in the Gruidae. Although the fossil looks

vaguely gruiform, I am not convinced that the genus belongs in this order.

Eobalearica tugarinovi Gureev

Figure 38

Eobalearica tugarinovi Gureev, 1949, p. 249.

Holotype: PIN no number, distal end of left tibiotarsus.
Horizon and Locality: Upper (?) Eocene deposits, Ferghana beds; Ferghana sink, Uzbek, SSR.
Hypodigm: Holotype only.
Diagnosis: Same as for genus; only included species.
Measurements: See Gureev (1949, p. 249).
Remarks: See generic discussion above.

GENUS *GERANOPSIS* LYDEKKER

Geranopsis Lydekker, 1891, p. 166.

Type Species: *Geranopsis hastingsiae* Lydekker.
Included Species: Type species only.
Distribution: Late Eocene of England.
Revised Diagnosis: Coracoid with bone noticeably depressed dorsoventrally. Procoracoid directed medially. Sternal facet forms well-developed groove. Sternocoracoidal process blunt. Internal distal angle short, not projecting.
Remarks: Lydekker (1891, p. 166) provisionally included this genus in the Gruidae, basing his decision on the presence of a large pneumatic foramen on the dorsal surface of the bone. On the basis of the coracoid *Geranopsis* seems to be a gruid and is clearly closer to *Balearica* than to *Grus*. The coracoid of *Geranopsis* is not so
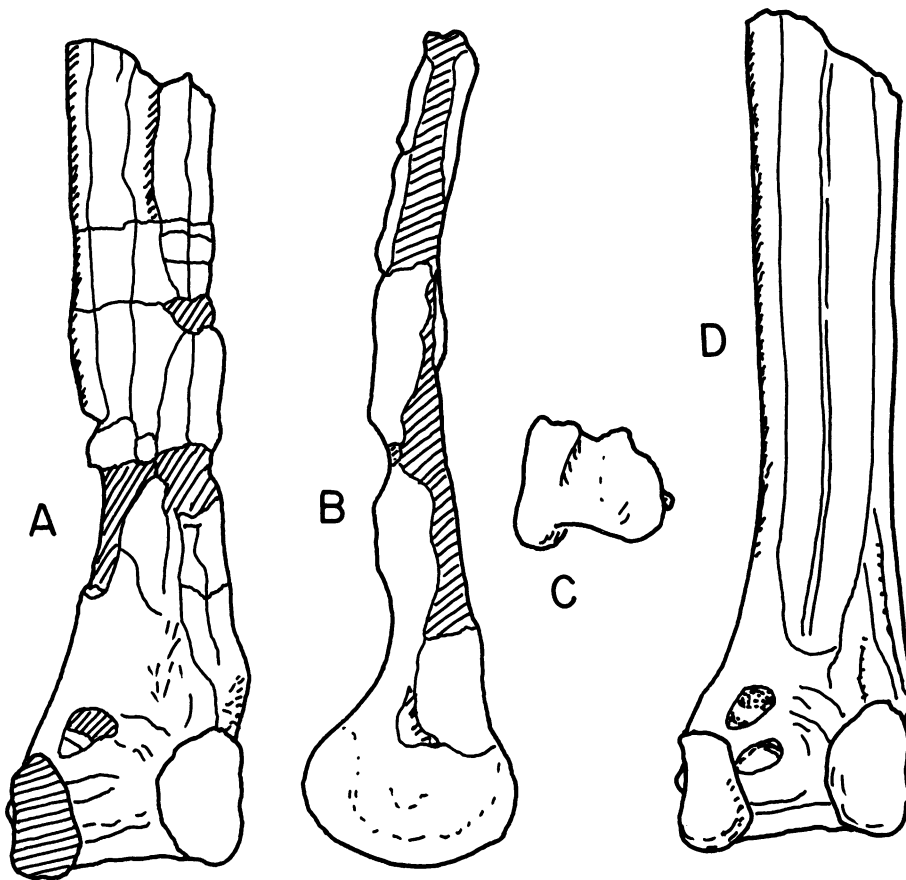
FIG. 38. *Eobalearica tugarinovi*, holotype, PIN no catalogue number, distal end of left tibio-tarsus. A. Anterior view. B. External condyle. C. Distal end. D. Reconstruction of anterior view. All about × 1. (After Gureev, 1949.)

heavy as that of *Grus*, the shaft is not rounded and thickened, and the proximal end is flattened more dorsoventrally and not so strongly curved. *Geranopsis* differs from *Balearica* in the following characters: (1) internal distal angle projects much less (2) sternal facet seems to be a more well-developed groove (3) bone compressed more dorsoventrally (some of this may be due to crushing during preservation, but much of it seems real) (4) sternocoracoidal process is somewhat blunter (5) procoracoid does not turn distally so much but instead is directed more medially (6) furcular facet less elongated and more rounded (7) seen in ventral view, area proximolateral to furcular facet less excavated and forms less distinct groove, and (8) area of neck less pronounced (seen in dorsal view).

Milne-Edwards (1892, p. 72) described a second species for the genus, *Geranopsis elatus*, based on a distal right tibiotarsus. Lambrecht (1933) considered G. *elatus* to be a synonym of G. *hastingsiae* but he obviously had not examined the specimens. Brodkorb (1967, pp. 148–149) recognized two species in the genus. The type of G. *elatus* (PM Qu3101) was apparently lost before Gaillard's studies on the phosphorites du Quercy and then returned to the Paris Museum in 1909, one year after Gaillard's paper (1908). Because G. *elatus* is not referable to the Gruidae and probably does not belong in the Gruiformes, I will not discuss it further. At the present time the affinities of G. *elatus* are uncertain and will be treated in detail at a later date.
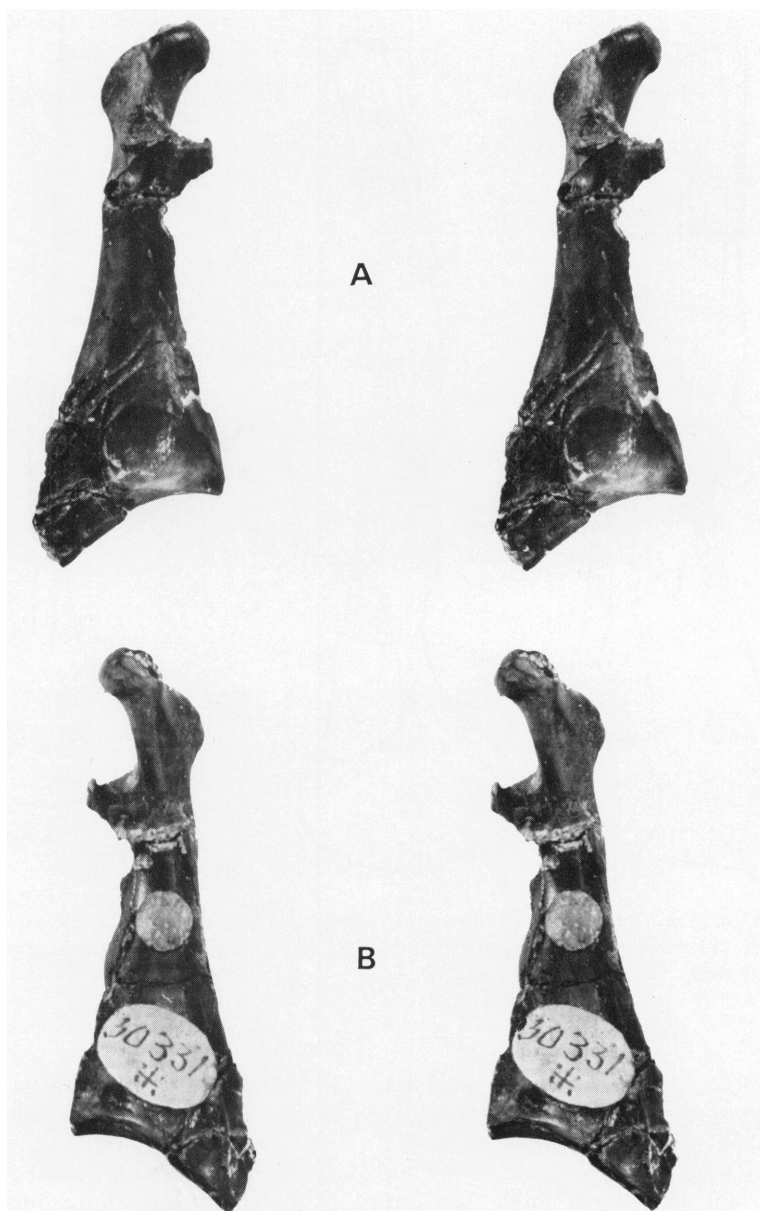
FIG. 39. *Geranopsis hastingsiae*, holotype, BM(NH) 30331, left coracoid. A. Dorsal view. B. Ventral view. Both stereo pairs. Both about × 1.8.

Geranopsis hastingsiae Lydekker

Figure 39

Geranopsis hastingsiae LYDEKKER, 1891, p. 166.

HOLOTYPE: BM(NH) 30331, complete left coracoid.

HORIZON AND LOCALITY: Upper Eocene deposits, Hordwell beds; Hordwell, Hampshire, England.

HYPODIGM: Holotype only.

DIAGNOSIS: Same as for genus; only included species.
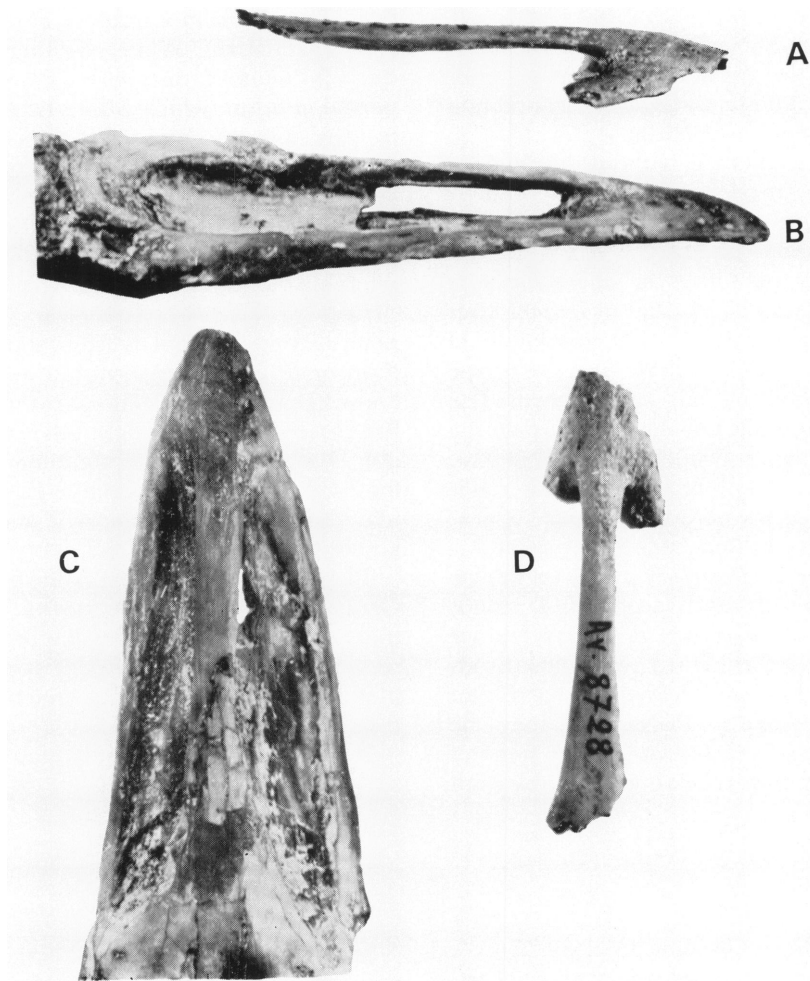
FIG. 40. *Probalearica problematica.* A, D. Holotype, PM Av.8728, distal end of upper jaw. B, C. Referred specimen, PM no catalogue number, upper jaw assigned to *Paloelodus ambiguus* (see text). A, B. Lateral view. C, D. Dorsal view. All about × 1.7.

MEASUREMENTS: Total length 39.4 mm.; length from internal distal angle to tip of sternocoracoidal process 13.0 mm.; narrowest width (lateromedial) of shaft 5.3 mm.; length from tip of procoracoid to tip of furcular head 9.6 mm. (approximate).

REMARKS: The holotype is damaged in places, thus it is difficult to be certain about all its characters. See also comments above for genus.

GENUS *PROBALEARICA* LAMBRECHT

Probalearica LAMBRECHT, 1933, p. 519.

TYPE SPECIES: *Probalearica problematica* (Milne-Edwards).

INCLUDED SPECIES: Type species; *P. crataegensis* Brodkorb.

DISTRIBUTION: Late Oligocene to early Miocene of France and North America.

DIAGNOSIS: Upper jaw with distal end broad, sides (seen from above) forming about a 45 degree angle at tip; portion of culmen posterior to anterior end of nostrils almost horizontal and inclined dorsally only very little.

Distal end of tibiotarsus without pronounced inward swing anteriorly (in distal view); internal ligamental prominence almost vertical. See Brodkorb (1963b, p. 164).

REMARKS: The mandible on which the type species is based is similar to that of *Balearica* but does differ in proportions. The mandible of *Probalearica* is much more robust, and this is true of both the tip of the bill and culmen. The culmen apparently did not slope upward to the nasal-frontal hinge so much as in *Balearica*. Although it appears that some cranial material is available (see species accounts below), it was not possible for me to study this in any detail.

The tibiotarsus of *Probalearica* is very similar to those of *Palaeogrus*, and at present I cannot justify placing *P. crataegensis* in *Probalearica* rather than *Palaeogrus*. Accordingly I will follow Brodkorb (1963b; 1967) and leave this species in *Probalearica*. Eventually *Probalearica* may be lumped with *Palaeogrus*, but at present none of the material of *P. problematica* is comparable with other genera.

Probalearica problematica (Milne-Edwards)

Figure 40

Grus problematica MILNE-EDWARDS, 1871, vol. 2, p. 30.
Probalearica problematica (Milne-Edwards): LAMBRECHT, 1933, p. 519.

HOLOTYPE: PM Av.8728, distal end of upper jaw.

HORIZON AND LOCALITY: Upper Oligocene or lower Miocene deposits (Aquitanian in age); Saint Gérand-le-Puy and Gannat, Dept. Allier, France.

HYPODIGM: Holotype; location unknown, crushed and fragmentary sternum (Milne-Edwards, 1871, pl. 76, figs. 3, 4); number unknown, bill of *Paloelodus ambiguus* on exhibit in Paris Museum Gallerie de Paléontologie (see remarks); MHNL St.G.60, cranium.

DIAGNOSIS: Largest species in genus.

MEASUREMENTS: Width of bill at anterior end of nasal opening 9.6 mm. (holotype), 9.5 mm. (*P. ambiguus* specimen, Paris Museum).

REMARKS: The holotype (fig. 40A, D) appears to be from a *Balearica*-like crane, and it differs

from *B. pavonina* in a number of characters (see generic remarks). While studying fossils at the Paris Museum I discovered that the bill and partial cranium which Milne-Edwards assigned to the phoenicopteriform species *Paloelodus ambiguus* (1871, pl. 82) is essentially identical with that of *P. problematica* (compare fig. 40A and B and 40 C and D). In addition, I found another cranium (MHNL St.G.60) that is also referable to this species and which was labeled "*Hidopodia palustris.*"[1] It is clear, however, that none of this material is from a phoenicopteriform or from a threskiornithid as we presently know them. The evidence that the flamingo-like *Paloelodus* had a straight bill is very questionable. Because there are vast quantities of avian fossils from Saint Gérand-le-Puy, additional material of *P. problematica* will undoubtedly be found.

The only other crane known from Saint Gérand-le-Puy is *Paleogrus excelsus*. If we assume that these birds had the general proportions of a species like *B. pavonina*, then it appears that the mandible of *P. problematica* is much too small for that of *P. excelsus*.

It was not possible for me to study the sternum assigned to *P. problematica* by Milne-Edwards (see Lambrecht, 1933, p. 520).

Probalearica crataegensis Brodkorb

Probalearica crataegensis BRODKORB, 1963b, p. 163.

HOLOTYPE: PB 8503, distal end of right tibiotarsus.

HORIZON AND LOCALITY: Lower Miocene deposits, Hawthorne Formation; Tallahassee, north of "Runaway Track," Switchyard B, Seaboard Airline RR, SE¼ of NE¼ sect. 3, T1S, R1W, Leon County, Florida.

HYPODIGM: Holotype only.

DIAGNOSIS: Smallest species in genus; see generic diagnosis.

MEASUREMENTS: See table 28.

REMARKS: Brodkorb (1963b, p. 163) placed this species in *Probalearica* principally because of its general similarity to *Balearica* and probably also because it is approximately the same age as *P. problematica*. For convenience I leave *P.*

[1] This name apparently refers to the threskiornithid *Ibidopodia palustris* Milne-Edwards, but I am unaware of its having been published and Brodkorb (1963a, p. 278) does not mention the name. More than likely this is a spelling error on the label.
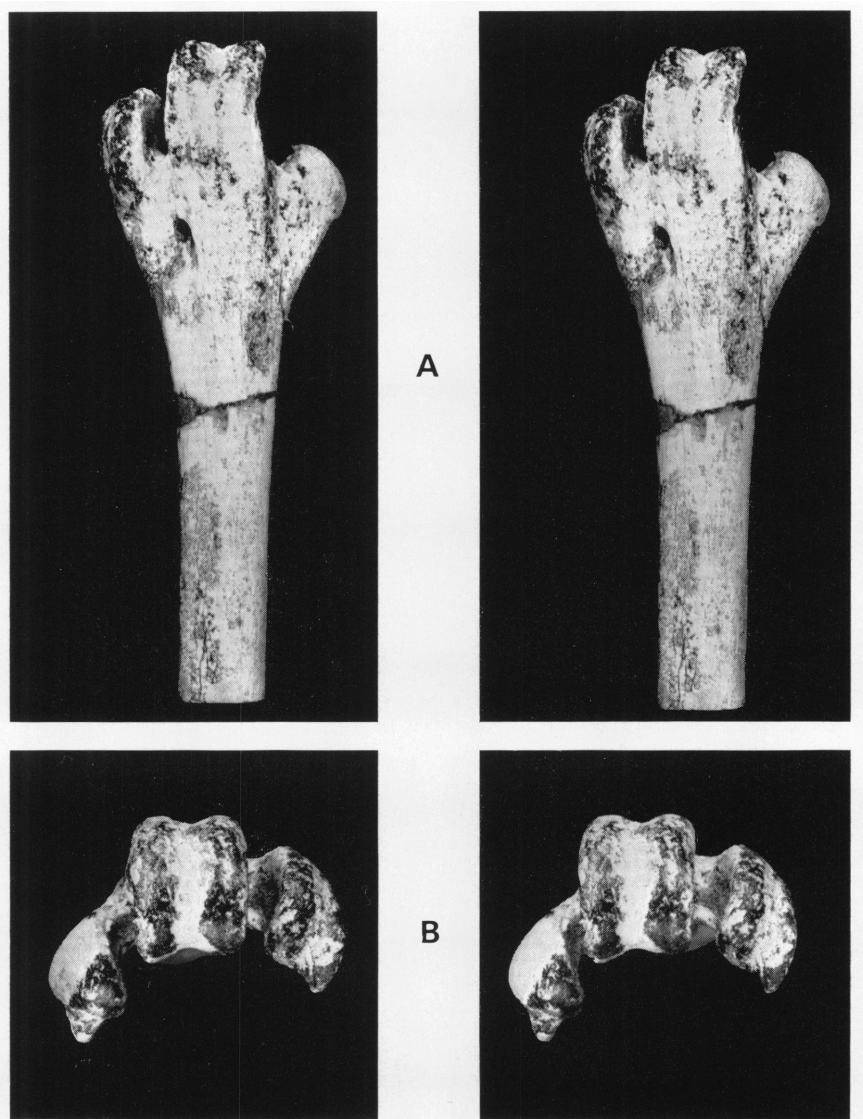
FIG. 41. *Pliogrus pentelici*, lectotype, PM no catalogue number, distal end of left tarsometatarsus. A. Anterior view, stereo pair. About × 1.3. B. Distal end, stereo pair. About × 1.5.

crataegensis in this genus although there are no significant differences from the species of *Palaeogrus* in the structure of the tibiotarsus (see above).

GENUS *PLIOGRUS* LAMBRECHT

Pliogrus LAMBRECHT, 1933, p. 522.

TYPE SPECIES: *Pliogrus germanicus* Lambrecht; designated by Brodkorb (1952, p. 175).

INCLUDED SPECIES: Type species; *P. pentelici* (Gaudry).

DISTRIBUTION: Early Pliocene of Europe.

REVISED DIAGNOSIS: Tibiotarsus with external condyle without prominence at point of attachment of M. peroneus profundus. Distal end apparently compressed considerably anteroposteriorly.

Tarsometatarsus with scar for attachment of
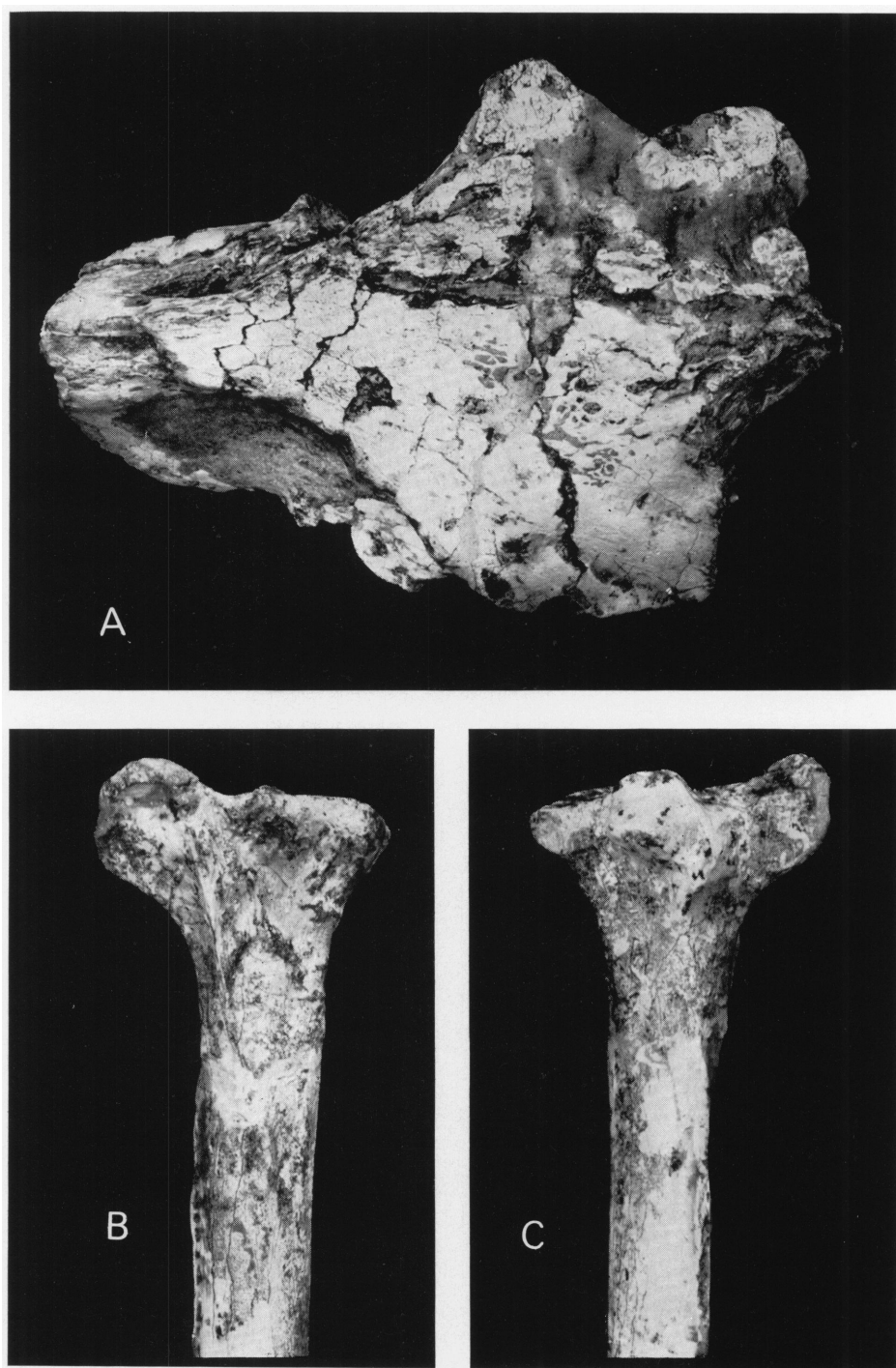
Fig. 42. *Pliogrus pentelici*, referred specimens, PM no catalogue numbers. A. Pelvis. About × 1. B–C. Proximal end of right tibiotarsus. B. Internal view. C. External view. Both about × 1.3.

metatarsal I very shallow. Distal foramen opens very close to outer intertrochlear notch (in posterior view).

REMARKS: Lambrecht's figures (1933, p. 522) of *P. germanicus* are so poor that few characters of the tibiotarsus can be evaluated; thus this portion of the diagnosis will have to be considered tentative. The elements of *P. pentelici* are very similar to those of *Grus*. At best, this genus appears weakly defined.

Pliogrus germanicus Lambrecht

Pliogrus germanicus LAMBRECHT, 1933, p. 522.

HOLOTYPE: Museum Preussichen Geologischen Landesanstalt, Berlin, apparently uncatalogued, distal end of left tibiotarsus.

HORIZON AND LOCALITY: Lower Pliocene deposits, Dinotheriensande; Mainz basin, Eppelsheim, Germany.

HYPODIGM: Holotype; fragment of scapula (same museum as holotype).

DIAGNOSIS: Smallest species in genus.

MEASUREMENTS: Breadth of distal end of tibiotarsus 11.5 mm.; length of glenoid facet of scapula, 7.0 mm. (after Lambrecht, 1933, p. 523).

REMARKS: Lambrecht's (1933, p. 522) illustrations are so poor that little can be said about this species. I was unable to examine the holotype.

Pliogrus pentelici (Gaudry)

Figures 41, 42

Grus pentelici GAUDRY, 1862, p. 504.
Pliogrus pentelici (Gaudry): LAMBRECHT, 1933, p. 523.

LECTOTYPE: PM uncatalogued, distal end of left tarsometatarsus.

HORIZON AND LOCALITY: Lower Pliocene deposits; Pikermi, Attica, Greece (Gaudry, 1862); marnes de la Croix-Rousse, near Lyon, France (Depéret, 1887); Esterházy Cave near Csákvár, County Fejer, Hungary (Kretzoi, 1957).

HYPODIGM: Lectotype; PM uncatalogued, proximal end of right tibiotarsus; PM uncatalogued, pelvic fragment; PM uncatalogued, complete crushed right humerus; MHNL (?), proximal end of radius; Museum unknown, fragment of coracoid (Kretzoi, 1957); other Paris Museum elements mentioned by Brodkorb (1967, p. 150) not seen.

DIAGNOSIS: Largest species in genus.

MEASUREMENTS: Lectotype—breadth across trochleae 26.0 mm.; breadth of inner trochlea 6.4 mm.; breadth of middle trochlea 9.8 mm.; breadth of outer trochlea 7.0 mm.; depth of middle trochlea 11.8 mm.; PM tibiotarsus—anteroposterior depth of proximal end 32.4 mm. (approximate); breadth of proximal end through external articular surface 20.6 mm.; PM pelvic fragment—width at level of acetabulum 37.0 mm. (approximate); greatest width 73.5 mm. (approximate); PM humerus—total length 256.0 mm. (approximate); breadth of distal end 36.9 mm.; depth of external condyle 16.0 mm.; depth of internal condyle 10.3 mm.; breadth of proximal end 48.0 mm.

REMARKS: There is no way of knowing if the Paris Museum material was associated, therefore I designate the distal left tarsometatarsus as lectotype (fig. 41).

Depéret (1887, p. 287) tentatively assigned a radius to this species. I have not examined this specimen.

Kretzoi (1957, p. 248) also assigned a fragmentary coracoid to *P. pentelici*. Kretzoi noted the "small fossa scapularis with its indistinct edge, the wholly identical shape of the fossa glenoidalis, as well as the above mentioned uniformity of the size" when he compared it with the type material (I did not see the coracoid in the type series).

FAMILY ARAMIDAE BONAPARTE

GENUS *AMINORNIS* AMEGHINO

Aminornis AMEGHINO, 1899, p. 9.

TYPE SPECIES: *Aminornis excavatus* Ameghino.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Early Oligocene of Argentina.

DIAGNOSIS: Coracoid similar to *Grus* but anterior extremity strongly uncinate, subclavicular process curved, tip narrow, without pneumatic foramen on its internal border, medial part of bone cylindrical (translated from Ameghino, 1899, p. 9).

REMARKS: Ameghino (1899) considered this genus to belong to the Gruidae. Lambrecht (1933) did not include a discussion of this genus in his book on fossil birds, and Brodkorb (1967, p. 155) placed *Aminornis* in the Aramidae without explanation.

Ameghino's collection is apparently distributed in the British Museum (Natural History),

Museo de Ciencias Naturales de La Plata, and Museo Argentino de Ciencias Naturales (Buenos Aires). I have examined the collections of all three museums and have been unable to locate the holotype, but it probably is still in one of the Argentinian institutions.

I am retaining *Aminornis* in the Aramidae simply for convenience, although there is no evidence the genus belongs in this family.

Aminornis excavatus Ameghino

Aminornis excavatus AMEGHINO, 1899, p. 9.

HOLOTYPE: Coracoid, location of specimen unknown.

HORIZON AND LOCALITY: Lower Oligocene deposits, Deseado Formation; Rio Deseado, Santa Cruz, Argentina.

HYPODIGM: Holotype only.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: Unknown; not published by Ameghino (1899).

REMARKS: See above.

GENUS *LONCORNIS* AMEGHINO

Loncornis AMEGHINO, 1899, p. 9.

TYPE SPECIES: *Loncornis erectus* Ameghino.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Early Oligocene of Argentina.

DIAGNOSIS: Femur whose body is compressed transversely presenting a triangular cut [cross-section] so that the anterior face is constituted by a perpendicular sharp edge [ridge]. Position uncertain (translated from Ameghino, 1899, p. 9).

REMARKS: Ameghino (1899) did not express an opinion about the familial relationships of *Loncornis*. Lambrecht (1933) did not mention the genus, and Brodkorb (1967, p. 155) placed the genus in the Aramidae with the comment "position uncertain."

I have been unable to locate the holotype of the type species, and I place the latter in the Aramidae for convenience. There is no evidence that *Loncornis* belongs in this family.

Loncornis erectus Ameghino

Loncornis erectus AMEGHINO, 1899, p. 9.

HOLOTYPE: Femur, location of specimen unknown.

HORIZON AND LOCALITY: Lower Oligocene deposits, Deseado Formation; Rio Deseado, Santa Cruz, Argentina.

HYPODIGM: Holotype only.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: Anteroposterior depth of bone above condyles 12 mm.; breadth of bone above condyles 6 mm. (after Ameghino, 1899, p. 9).

REMARKS: See above.

GENUS *BADISTORNIS* WETMORE

Badistornis WETMORE, 1940, p. 30.

TYPE SPECIES: *Badistornis aramus* Wetmore.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Medial Oligocene of South Dakota.

DIAGNOSIS: Tarsometatarsus with inner trochlea projecting distally only to base of middle trochlea and turned very far posteriorly. In anterior view anteroposterior plane of middle trochlea inclined internally away from longitudinal axis of shaft.

REMARKS: In his description of *Badistornis* Wetmore (1940, p. 33) was of the opinion that the characters of the tarsometatarsus "leave no doubt almost at a glance that it is a species of the family Aramidae." He also listed five characters in which *Badistornis* resembled the Gruidae, not the Aramidae, and he suggested these characters indicate the "presupposed line of ancient connection" between the two families.

With regard to the distal end of the tarsometatarsus, *Grus* differs from *Aramus*, as follows: (1) inner trochlea not projecting so far distally relative to the middle trochlea (2) outer trochlea projecting slightly less distally relative to the middle trochlea (3) anterolateral surface of inner trochlea somewhat more bulbous, larger, and less flattened and trochlea turned more posteriorly (4) distal foramen situated somewhat less distally (i.e., intertrochlear bridge is deeper proximodistally), and (5) distal end of the bone is broader. *Badistornis* resembles *Grus* in characters (2) (3), and (4) and *Aramus* in character (5). *Badistornis* is intermediate in character (1). The gruid genus *Balearica* is very similar to *Aramus* in the relative positions of the trochleae but still retains the bulbous inner trochlea and broad distal end.

Although the proximal end of the tarsometatarsus of *Badistornis* is damaged posteriorly, the
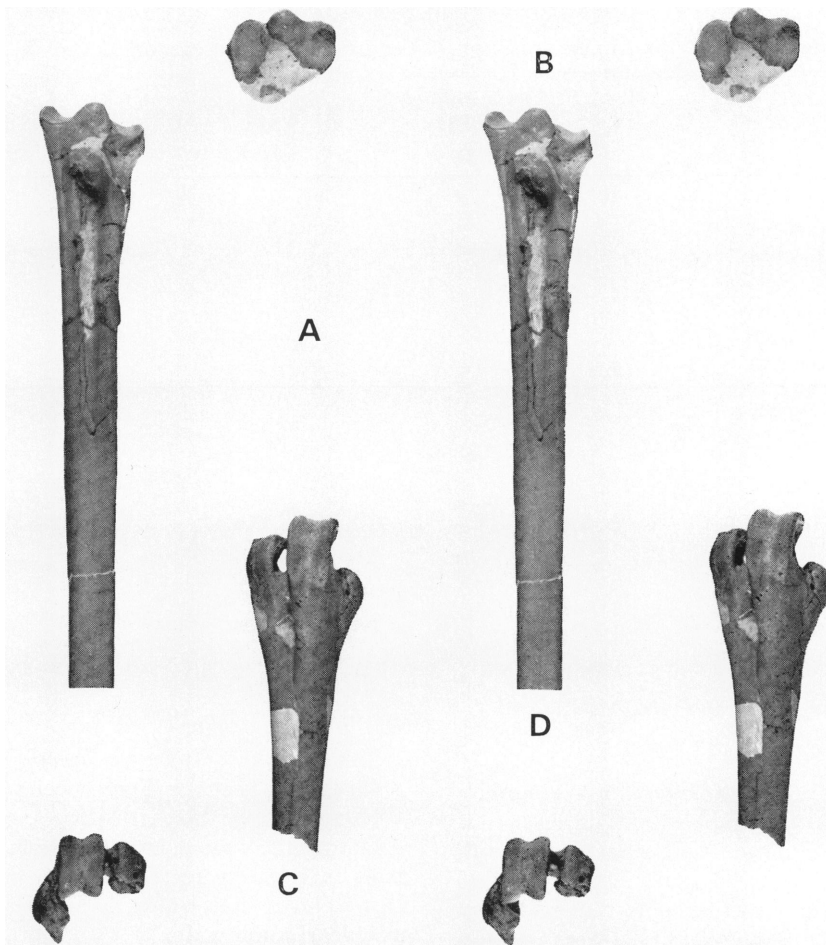
Fig. 43. *Badistornis aramus*, holotype, SDSM 3631, left tarsometatarsus. A. Anterior view of proximal end. B. Proximal end. C. Distal end. D. Anterior view of distal end. All stereo pairs. All about × 1.

shapes and positions of the cotylae and inter-cotylar prominence are unquestionably more similar to those of *Aramus* than those in gruids.

Badistornis is a very distinctive genus within the suborder Grui and appears to be an aramid that has become cranelike, presumably because of similar locomotor habits. This intermediate condition of *Badistornis* does not necessarily indicate that cranes and limpkins shared a more recent common ancestor with each other than either did with any other family, but it does suggest that they are relatively closely related, and, at least at the time of *Badistornis*, had developed the potential for a certain amount of parallel evolution. *Badistornis* is compared below with other aramid genera.

Badistornis aramus Wetmore

Figure 43

Badistornis aramus Wetmore, 1940, p. 30.

HOLOTYPE: SDSM 3631, almost complete left tarsometatarsus.

HORIZON AND LOCALITY: Middle Oligocene deposits, lower part of Brule Formation (*Metamynodon* zone), 35 miles southwest of Scenic, Shannon County, South Dakota.

HYPODIGM: Holotype only.

TABLE 34

Measurements (in Millimeters) of Tarsometatarsi of Species of Aramidae

	Badistornis aramus SDSM 3631 Holotype	Aramornis longurio[a] AMNH 6292 Holotype	Anisolornis excavatus BM(NH) A594 Holotype
Total length	155.0	—	—
Breadth across trochleae	17.1	15.6	17.1
Breadth of inner trochlea	4.7	4.5	4.2
Breadth of middle trochlea	6.7	5.8	6.9
Breadth of outer trochlea	5.4	4.9	5.2
Smallest breadth of shaft	6.5	5.9	—
Breadth of proximal end	14.9	—	—

[a] After Wetmore (1926).

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: See table 34.

REMARKS: See above.

GENUS *GNOTORNIS* WETMORE

Gnotornis WETMORE, 1942, p. 1.

TYPE SPECIES: *Gnotornis aramiellus* Wetmore.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Late Oligocene of South Dakota.

DIAGNOSIS: Humerus similar to that of *Aramus* but differs in that "entepicondylar area projecting only slightly laterally; ectepicondylar area relatively larger" (after Wetmore, 1942, pp. 1–2). To this can be added that the entepicondyle of *Gnotornis* projects more distally and that the internal contour of the distal end of the shaft is straighter.

REMARKS: See Wetmore (1942).

Gnotornis aramiellus Wetmore

Gnotornis aramiellus WETMORE, 1942, p. 1.

HOLOTYPE: SDSM 40158, distal end of left humerus.

HORIZON AND LOCALITY: Upper Oligocene deposits, Brule Formation, *Protoceras* Channel sandstones, *Leptauchenia* clays; 25 miles southeast of Scenic, 6 miles east of Rockyford, Shannon County, South Dakota.

HYPODIGM: Holotype only.

DIAGNOSIS: Same as for genus; only included species

MEASUREMENTS: Breadth across condyles, 10.4 mm.

REMARKS: See Wetmore (1942) and above.

GENUS *ARAMORNIS* WETMORE

Aramornis WETMORE, 1926, p. 1.

TYPE SPECIES: *Aramornis longurio* Wetmore.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Medial Miocene of Nebraska.

DIAGNOSIS: Tarsometatarsus with lower end of shaft moderately rounded on anterior surface. Distal end of shaft quite narrow. External intertrochlear notch wide.

REMARKS: *Aramornis* and *Badistornis* are very different structurally, the former being clearly closer to the living genus *Aramus*. As noted by Wetmore (1926) *Aramornis* differs from *Aramus* in having a more rounded anterior surface of the shaft, a more well-developed ala interna on the inner trochlea (this may be simply individual variation), and a relatively narrower shaft; also the external intertrochlear notch seems wider in *Aramornis*.

Aramornis longurio Wetmore

Figure 44

Aramornis longurio WETMORE, 1926, p. 1.

HOLOTYPE: AMNH 6292, distal end of left tarsometatarsus.

HORIZON AND LOCALITY: Middle Miocene deposits, lower Sheep Creek beds, *Merychippus primus* zone; Snake Creek quarries, Sioux County, Nebraska.
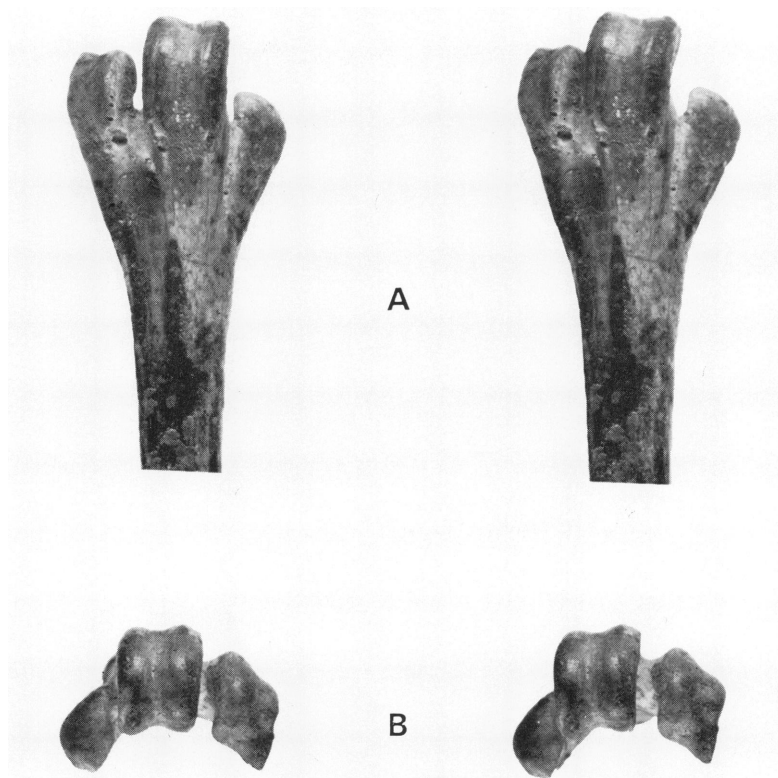
FIG. 44. *Aramornis longurio*, holotype, AMNH 6292, distal end of left tarsometatarsus. A. Anterior view. B. Distal end. Both stereo pairs. Both about ×2.

HYPODIGM: Holotype only.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: See table 34.

REMARKS: See Wetmore (1926) and above.

GENUS *ANISOLORNIS* AMEGHINO

Anisolornis AMEGHINO, 1891, p. 449.

Anissolornis AMEGHINO, 1899, p. 8; also LAMBRECHT, 1933, p. 442.

TYPE SPECIES: *Anisolornis excavatus* Ameghino.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Medial Miocene of Argentina.

DIAGNOSIS: Tarsometatarsus with inner trochlea not turned very far posteriorly. Outer trochlea almost on same level as middle trochlea. External intertrochlear notch narrow. Tendinal groove proximal to external distal foramen deep.

REMARKS: In his original description Ameg-hino (1891, p. 449) considered *Anisolornis* to be a phororhacoid, but later (1895, pp. 93–94) he changed his mind and tentatively referred the genus to the Phasianidae. Lambrecht (1933, p. 442) also considered *Anisolornis* as *incertae sedis* in the Phasianidae. Brodkorb (1964a, p. 305) placed the genus in the Cracidae with the comment that it "possibly belongs in the Tinamidae."

After comparison of the holotype with almost all the nonpasseriform families, I conclude that the relationships of *Anisolornis* are almost certainly with the Aramidae. *Anisolornis* differs from *Aramus* in only a few characters: (1) the inner and outer trochleae are turned less posteriorly, and (2) the tendinal groove proximal to the external distal foramen is deeper. *Anisolornis* differs from *Aramornis* in the same characters as it does from *Aramus*, but in addition the external intertrochlear notch of *Anisolornis* is narrower.
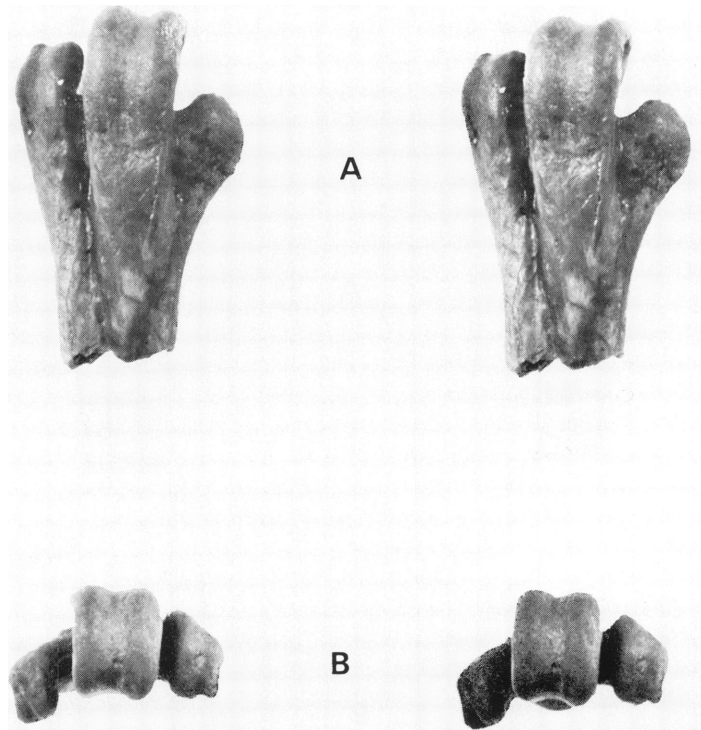
FIG. 45. *Anisolornis excavatus*, holotype, BM(NH) A594, distal end of left tarsometatarsus. A. Anterior view. B. Distal end. Both stereo pairs. Both about × 1.7.

Anisolornis excavatus Ameghino

Figure 45

Anisolornis excavatus AMEGHINO, 1891, p. 449.

HOLOTYPE: BM(NH) A594, distal end of left tarsometatarsus.

HORIZON AND LOCALITY: Middle Miocene deposits, Santa Cruz Formation; Karaihen, Patagonia, Argentina.

HYPODIGM: Holotype only.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: See table 34.

REMARKS: See above.

MORPHOLOGICAL VARIABILITY IN FOSSIL POPULATIONS

INFORMATION CONCERNING the amount of morphological variability of the skeleton in fossil bird populations (more correctly assemblages) is almost nonexistent; that for populations of recent birds is only slightly better. Moreover, those studies that are available (e.g., Simpson, 1946a; Goodge, 1951) have reported results only of the conventional osteological measurements such as bone length and width, and consequently they are of limited value in interpreting the details of skeletal form or of potential specific differences among fossil populations. Some fossil gruiform species have been recovered in sufficient numbers to provide a basis for a statistical analysis of variability of several skeletal elements. Three of the species discussed below—*Nesophalaris chathamensis* (Forbes), *Diaphorapteryx hawkinsi* (Forbes), and *Nesolimnas dieffenbachii* (Gray)—are extinct Quaternary rails from the Chatham Islands. A fourth species of rail, *Gallirallus australis* (Sparrman), is represented by material from Recent (or subrecent) cave deposits of New Zealand. One species of rail from Tertiary deposits was studied: *Paraortygometra porzanoides* from the Saint Gérand-le-Puy (Aquitanian in age) of France. The other three species include one bathornithid, *Bathornis celeripes*, from lower Oligocene deposits of Wyoming (Cracraft, 1968a, p. 4) and two species of idiornithids, *Elaphrocnemus phasianus* and *E. crex*, from the phosphorites du Quercy of France.

None of these eight fossil assemblages represents a random sample of a single breeding population. The four Quaternary and/or Recent rails do encompass, however, the narrowest stratigraphic range of the eight samples, and thus they are important in approaching the ideal case of preservation (that is, of a single breeding population) for studies of intrapopulational variability. The sample of *B. celeripes* was also preserved within a short span of time geologically speaking but probably involved more time than that of the rails. There are no reliable stratigraphic data on the samples of *E. phasianus* and *E. crex*, but since most of the specimens of *E. phasianus* apparently came from a small number of fissure-fillings, it is likely that they do not represent the entire time-span in which the phosphorites du Quercy were deposited. In any case, the samples of *E. phasianus* and *E. crex* almost certainly were accumulated over a much greater period of time than were those of the rails or *B. celeripes*.

SPECIMENS EXAMINED

Many of the individual elements, especially those of the rails, did not have separate catalogue numbers. In these cases it is only possible to give the inclusive numbers of the collection. The following specimens were measured for the variability study:

RALLIDAE

Diaphorapteryx hawkinsi: 40 tibiotarsi from BM(NH) R1489–R1521 and R3001–R3024; 28 tarsometatarsi from BM(NH) R1522–R1529, R6172, R6173, R2998–R3000, R2971–R2986, and A1533 (2 elements); 23 femora from BM(NH) R2127–R2151; and 28 humeri from BM(NH) R2165–R2192.

Nesophalaris chathamensis: 25 tibiotarsi from BM(NH) R2069–R2122; 25 humeri from BM(NH) R2193–R2244; 23 femora from BM(NH) R3025–R3036.

Nesolimnas dieffenbachii: 13 humeri, all numbered BM(NH) A965.

Gallirallus australis: 23 tibiotarsi from BM(NH) R6352–R6376; and 20 femora from BM(NH) R6459–R6506.

Paraortygometra porzanoides: 11 humeri, see systematic section for data on specimens.

IDIORNITHIDAE

Elaphrocnemus crex: 10 tarsometatarsi, see systematic section for data on specimens.

Elaphrocnemus phasianus: 45 tarsometatarsi and 25 tibiotarsi, see systematic section for data on specimens.

BATHORNITHIDAE

Bathornis celeripes: 58 tibiotarsi from MCZ 2286, 2234, 2503 (5 elements), 2502 (4 elements), 2285 (47 elements); and 50 tarsometatarsi from

TABLE 35

STATISTICAL ANALYSIS OF VARIABILITY IN HUMERI OF RAILS

	N	x̄±S.E.	Range	s±S.E.	V±S.E.
Total length					
Paraortygometra porzanoides	3	31.43	26.1– 29.2	—	—
Palaeolimnas chathamensis	24	93.68±0.72	87.2–100.7	3.54±0.51	3.78±0.55
Diaphorapteryx hawkinsi	25	63.10±0.65	57.0– 67.9	3.23±0.46	5.11±0.72
Nesolimnas dieffenbachii	13	43.57±0.40	41.5– 45.4	1.44±0.28	3.31±0.65
Breadth of distal end					
Paraortygometra porzanoides	7	4.67±0.05	4.5– 4.9	0.14±0.04	2.95±0.79
Palaeolimnas chathamensis	24	13.16±0.13	11.6– 14.2	0.64±0.09	4.83±0.70
Diaphorapteryx hawkinsi	23	11.00±0.22	9.1– 13.4	1.06±0.16	9.66±1.42
Nesolimnas dieffenbachii	13	6.69±0.06	6.4– 7.0	0.20±0.04	2.95±0.58
Depth of internal condyle					
Paraortygometra porzanoides	6	1.47±0.09	1.1– 1.8	0.22±0.06	15.28±4.41
Palaeolimnas chathamensis	20	3.88±0.06	3.4– 4.3	0.28±0.04	7.34±1.16
Diaphorapteryx hawkinsi	20	3.28±0.09	2.8– 3.8	0.42±0.07	12.90±2.04
Nesolimnas dieffenbachii	13	2.35±0.04	2.0– 2.6	0.15±0.03	6.41±1.26
Depth of external condyle					
Paraortygometra porzanoides	6	2.33±0.11	2.0– 2.6	0.27±0.08	11.40±3.29
Palaeolimnas chathamensis	20	7.40±0.09	6.8– 8.2	0.39±0.06	5.21±0.82
Diaphorapteryx hawkinsi	21	6.89±0.12	5.5– 8.2	0.55±0.08	8.00±1.23
Nesolimnas dieffenbachii	12	3.96±0.05	3.7– 4.3	0.17±0.03	4.26±0.87
Breadth of middle of shaft					
Paraortygometra porzanoides	7	2.10±0.03	2.0– 2.2	0.08±0.02	3.90±1.04
Palaeolimnas chathamensis	25	5.96±0.07	5.2– 6.6	0.37±0.05	6.15±0.87
Diaphorapteryx hawkinsi	27	5.30±0.09	4.5– 6.3	0.47±0.06	8.81±1.20
Nesolimnas dieffenbachii	12	2.94±0.02	2.9– 3.1	0.07±0.01	2.25±0.46
Depth of middle of shaft					
Paraortygometra porzanoides	7	1.96±0.03	1.9– 2.1	0.08±0.02	4.02±1.07
Palaeolimnas chathamensis	25	5.05±0.05	4.6– 5.5	0.26±0.04	5.11±0.72
Diaphorapteryx hawkinsi	27	4.53±0.07	3.9– 5.5	0.38±0.05	8.40±1.14
Nesolimnas dieffenbachii	12	2.71±0.03	2.5– 2.9	0.11±0.02	4.23±0.86
Breadth of proximal end					
Paraortygometra porzanoides	6	6.67±0.12	6.4– 7.2	0.29±0.08	4.41±1.27
Palaeolimnas chathamensis	23	19.61±0.17	18.0– 20.9	0.82±0.12	4.16±0.61
Diaphorapteryx hawkinsi	23	15.90±0.31	13.5– 18.5	1.51±0.22	9.49±1.40
Nesolimnas dieffenbachii	13	9.74±0.09	9.1– 10.4	0.33±0.06	3.40±0.67

Abbreviations: N, sample size; x̄, mean; s, standard deviation; V, coefficient of variation; measurements in millimeters.

MCZ 2234, 2235, 2286, 2287 (30 elements), 2285 (10 elements), 2502, 2503 (2 elements), and no number (4 elements).

ANALYSIS OF VARIATION

RALLIDAE

HUMERUS

Statistical data for seven measurements of the humerus are given in table 35; the coefficients of variation for these characters are summarized in table 36. Two points should be noted. First, the total length of the bone shows the least amount of variability of any measurement with an average coefficient of variation (V) of 4.07. Second, the depth of the external condyle and depth of the internal condyle have the highest amount of variability with respective average Vs of 7.22 and 10.48. The remaining four measurements have "normal" variability.

It is not immediately evident why the condylar depths should be more variable. A partial explanation is that these measurements are more

TABLE 36

COEFFICIENTS OF VARIATION FOR MEASUREMENTS OF HUMERI OF RAILS

	Paraortygometra porzanoides	Nesophalaris chathamensis	Diaphorapteryx hawkinsi	Nesolimnas dieffenbachii	Average
Total length	—	3.78	5.11	3.31	4.07
Lateromedial breadth across distal end	2.95	4.83	9.66	2.95	5.10
Depth of internal condyle	15.28	7.34	12.90	6.41	10.48
Depth of external condyle	11.40	5.21	8.00	4.26	7.22
Breadth of middle of shaft	3.90	6.15	8.81	2.25	5.28
Depth of middle of shaft	4.02	5.11	8.40	4.23	5.44
Breadth across proximal end	4.41	4.16	9.49	3.40	5.37
Average	6.99	5.23	8.91	3.83	—

difficult to take in a uniform manner. Thus, the high V of the condyles may not be due to intrinsic variability *per se* but to greater measurement error.

In all but two measurements *Diaphorapteryx hawkinsi* exhibits the greatest variability of the four rail species, and in all but one measurement *Nesolimnas dieffenbachii* has the lowest value of V. The other two species have intermediate values of V although *Paraortygometra porzanoides* averages somewhat higher Vs than does *Nesophalaris chathamensis*. The moderately high average variability shown by several characters of *P. porzanoides* may be the result of poor stratigraphic and geographic control of the small samples. The great variability of *D. hawkinsi* may be correlated, at least in part, with the advance state of wing reduction (relative to leg length) in this flightless species (Andrews, 1896a, pp. 83–84). It is a generally accepted assumption that when there is a tendency to lose certain structures through a lineage, the intensity of selection on that structure is reduced and an increase of variability follows. It is probable that *N. chathamensis* was capable of short powerful flight; the wings of *N. dieffenbachii* are reduced considerably but the species was likely capable of some flight (Andrews, 1896b).

FEMUR

Statistical data for eight measurements of rail femora are given in table 37; a summary of the coefficients of variation are shown in table 38. Of the eight measurements total length is the least variable (average V=4.80) and depth of the internal condyle the most variable (V=7.11). None of the measurements exhibits either a strikingly high or low degree of variability.

The femur of *G. australis* is somewhat more variable in all measurements than those of *D. hawkinsi* and *N. chathamensis* but reasons for this are not readily apparent.

TIBIOTARSUS

Statistical data on 10 measurements of the tibiotarsus of three species of rails are presented in table 39; the coefficients of variation of these measurements are summarized in table 40.

Table 40 shows that total length was the least variable character (V=4.85) for each species, and the depth of the anterior intercondylar fossa was the most variable (V=11.60). The high variability of the fossa is easily explained. I found it very difficult to take this measurement in a consistent manner and much of this variability must be due to measurement error. The depth of the middle of the shaft and depth of the proximal end were also somewhat more variable than most of the other characters. The magnitude of the depth of the proximal end is more dependent on the length of the cnemial crests than on the head of the tibiotarsus itself, and the development of these crests is especially variable (but broken and worn specimens were not measured).

All three species show about the same degree of variability although *G. australis* is again slightly more variable.

TABLE 37

STATISTICAL ANALYSIS OF VARIABILITY IN FEMORA OF RAILS

	N	x̄±S.E.	Range	s±S.E.	V±S.E.
Total length					
Gallirallus australis	20	75.47±0.98	68.7– 82.9	4.38±0.69	5.81±0.92
Diaphorapteryx hawkinsi	23	96.56±0.92	87.5–104.0	4.41±0.65	4.57±0.67
Palaeolimnas chathamensis	21	84.82±0.74	80.7– 92.2	3.41±0.53	4.02±0.62
readth across condyles					
Gallirallus australis	20	14.72±0.29	12.8– 17.4	1.30±0.21	8.82±1.39
Diaphorapteryx hawkinsi	23	21.25±0.19	19.8– 22.9	0.91±0.13	4.28±0.63
Palaeolimnas chathamensis	22	18.43±0.20	17.0– 20.5	0.93±0.14	5.06±0.76
Depth of external condyle					
Gallirallus australis	18	12.37±0.22	10.8– 13.8	0.93±0.15	7.50±1.25
Diaphorapteryx hawkinsi	22	17.18±0.21	15.1– 18.8	0.98±0.15	5.68±0.86
Palaeolimnas chathamensis	23	14.67±0.17	13.3– 16.3	0.83±0.12	5.65±0.83
Depth of internal condyle					
Gallirallus australis	19	10.91±0.21	9.6– 12.3	0.90±0.15	8.22±1.33
Diaphorapteryx hawkinsi	21	15.43±0.24	13.0– 17.7	1.09±0.17	7.09±1.09
Palaeolimnas chathamensis	21	13.61±0.18	12.4– 15.9	0.82±0.13	6.02±0.93
Breadth of middle of shaft					
Gallirallus australis	20	6.16±0.11	5.4– 6.9	0.48±0.08	7.76±1.23
Diaphorapteryx hawkinsi	23	8.25±0.08	7.8– 9.1	0.37±0.05	4.47±0.66
Palaeolimnas chathamensis	23	7.38±0.08	6.7– 8.1	0.38±0.06	5.20±0.77
Depth of middle of shaft					
Gallirallus australis	20	6.61±0.12	5.5– 7.5	0.54±0.09	8.14±1.29
Diaphorapteryx hawkinsi	23	9.09±0.09	8.5– 9.7	0.41±0.06	4.50±0.66
Palaeolimnas chathamensis	23	8.00±0.08	7.4– 8.8	0.40±0.06	5.05±0.74
Breadth of proximal end					
Gallirallus australis	20	14.46±0.27	11.9– 15.9	1.22±0.19	8.42±1.33
Diaphorapteryx hawkinsi	23	22.73±0.26	20.3– 25.2	1.27±0.19	5.60±0.83
Palaeolimnas chathamensis	23	18.48±0.26	17.1– 21.4	1.27±0.19	6.89±1.02
Depth of head					
Gallirallus australis	19	6.37±0.10	5.8– 7.2	0.44±0.07	6.94±1.13
Diaphorapteryx hawkinsi	23	9.61±0.10	8.6– 10.7	0.48±0.07	4.99±0.74
Palaeolimnas chathamensis	23	8.05±0.11	7.1– 9.1	0.53±0.08	6.56±0.97

Abbreviations: N, sample size; x̄, mean; s, standard deviation; V, coefficient of variation; measurements in millimeters.

TABLE 38

COEFFICIENTS OF VARIATION FOR MEASUREMENTS OF FEMORA OF RAILS

	Gallirallus australis	Diaphorapteryx hawkinsi	Nesophalaris chathamensis	Average
Total length	5.81	4.57	4.02	4.80
Breadth across condyles	8.82	4.28	5.06	6.05
Depth of external condyle	7.50	5.68	5.65	6.28
Depth of internal condyle	8.22	7.09	6.02	7.11
Breadth of middle of shaft	7.76	4.47	5.20	5.81
Depth of middle of shaft	8.14	4.50	5.05	5.90
Breadth of proximal end	8.42	5.60	6.89	6.97
Depth of head	6.94	4.99	6.56	6.16
Average	7.70	5.15	5.56	—

TABLE 39

STATISTICAL ANALYSIS OF VARIABILITY IN TIBIOTARSI OF RAILS

	N	x̄±S.E.	Range	s±S.E.	V±S.E.
Total length					
Gallirallus australis	20	110.19±1.32	100.7–120.7	6.35±0.94	5.76±0.85
Palaeolimnas chathamensis	25	156.52±1.22	146.0–166.0	6.10±0.86	3.90±0.55
Diaphorapteryx hawkinsi	40	131.35±1.02	118.8–144.0	6.43±0.72	4.90±0.55
Depth of internal condyle					
Gallirallus australis	22	11.78±0.17	9.9– 12.9	0.80±0.12	6.81±1.03
Palaeolimnas chathamensis	25	15.37±0.18	13.8– 17.8	0.89±0.13	5.80±0.82
Diaphorapteryx hawkinsi	40	16.94±0.17	14.7– 18.9	1.06±0.12	6.27±0.70
Depth of external condyle					
Gallirallus australis	23	11.00±0.14	9.3– 12.0	0.69±0.10	6.27±0.92
Palaeolimnas chathamensis	25	13.70±0.13	12.5– 15.5	0.67±0.09	4.85±0.69
Diaphorapteryx hawkinsi	40	16.33±0.17	13.9– 18.0	1.10±0.12	6.71±0.75
Breadth across posterior end of condyles					
Gallirallus australis	23	8.40±0.12	7.3– 9.2	0.56±0.08	6.69±0.99
Palaeolimnas chathamensis	25	10.93±0.11	9.9– 11.8	0.52±0.07	4.73±0.68
Diaphorapteryx hawkinsi	40	12.79±0.15	10.3– 14.4	0.92±0.10	7.21±0.81
Breadth across anterior end of condyles					
Gallirallus australis	23	10.99±0.16	9.6– 12.2	0.75±0.11	6.84±1.01
Palaeolimnas chathamensis	25	14.87±0.15	13.5– 16.3	0.76±0.11	5.12±0.72
Diaphorapteryx hawkinsi	40	16.13±0.16	14.2– 17.8	1.03±0.12	6.37±0.71
Depth of anterior intercondylar fossa relative to external condyle					
Gallirallus australis	23	3.58±0.07	2.8– 4.4	0.33±0.05	9.12±1.34
Palaeolimnas chathamensis	25	3.90±0.10	3.1– 5.1	0.48±0.07	12.41±1.76
Diaphorapteryx hawkinsi	40	5.12±0.11	3.8– 6.4	0.68±0.08	13.27±1.48
Breadth of middle of shaft					
Gallirallus australis	23	5.96±0.11	5.0– 6.8	0.51±0.08	8.55±1.26
Palaeolimnas chathamensis	23	7.58±0.09	7.1– 9.1	0.45±0.07	5.92±0.87
Diaphorapteryx hawkinsi	40	7.50±0.09	6.4– 8.7	0.55±0.06	7.27±0.81
Depth of middle of shaft					
Gallirallus australis	23	5.17±0.10	4.1– 6.1	0.49±0.07	9.50±1.40
Palaeolimnas chathamensis	23	5.87±0.10	5.3– 7.0	0.46±0.07	7.82±1.15
Diaphorapteryx hawkinsi	40	7.54±0.08	6.7– 8.7	0.49±0.05	6.44±0.72
Breadth across proximal end					
Gallirallus australis	23	12.31±0.19	10.4– 13.4	0.91±0.13	7.36±1.09
Palaeolimnas chathamensis	23	14.97±0.15	13.2– 16.2	0.70±0.10	4.68±0.69
Diaphorapteryx hawkinsi	40	18.37±0.19	15.7– 20.5	1.19±0.13	6.48±0.72
Depth across proximal end					
Gallirallus australis	8	20.73±0.52	18.1– 22.8	1.48±0.37	7.14±1.79
Palaeolimnas chathamensis	9	24.37±0.69	19.5– 26.6	2.08±0.49	8.53±2.01
Diaphorapteryx hawkinsi	29	28.06±0.39	22.9– 31.5	2.09±0.27	7.43±0.98

Abbreviations: N, sample size; x̄, mean; s, standard deviation; V, coefficient of variation; measurements in millimeters.

TARSOMETATARSUS

Statistical data on 10 measurements of the tarsometatarsus of *N. chathamensis* and *D. hawkinsi* are shown in table 41; the coefficients of variability of the measurements are summarized in table 42.

The measurement with the least average variability is total length (V=4.17) and that with the greatest is breadth of inner trochlea (V= 8.01). The depth of the middle trochlea is also more variable (V=7.23) than most characters of the tarsometatarsus, but a considerable part

TABLE 40

COEFFICIENTS OF VARIATION FOR MEASUREMENTS OF TIBIOTARSI OF RAILS

	Gallirallus australis	Nesophalaris chathamensis	Diaphorapteryx hawkinsi	Average
Total length	5.76	3.90	4.90	4.85
Depth of internal condyle	6.81	5.80	6.27	6.29
Depth of external condyle	6.27	4.85	6.71	5.94
Breadth across posterior end of condyles	6.69	4.73	7.21	6.21
Breadth across anterior end of condyles	6.84	5.12	6.37	6.11
Depth of anterior intercondylar fossa relative to external condyle	9.12	12.41	13.27	11.60
Breadth of middle of shaft	8.55	5.92	7.27	7.25
Depth of middle of shaft	9.50	7.82	6.44	7.92
Breadth across proximal end	7.36	4.68	6.48	6.17
Depth of proximal end	7.14	8.53	7.43	7.70
Average	7.40	6.38	7.24	—

TABLE 41

STATISTICAL ANALYSIS OF VARIABILITY IN TARSOMETATARSI OF RAILS

	N	$\bar{x} \pm$S.E.	Range	$s \pm$S.E.	$V \pm$S.E.
Total length					
Palaeolimnas chathamensis	11	92.72±0.87	88.3–96.9	2.88±0.61	3.11±0.66
Diaphorapteryx hawkinsi	26	67.88±0.69	60.5–74.5	3.54±0.49	5.22±0.72
Distal breadth across trochleae					
Palaeolimnas chathamensis	11	15.81±0.28	13.9–17.0	0.94±0.20	5.93±1.26
Diaphorapteryx hawkinsi	26	17.74±0.15	15.9–19.5	0.77±0.11	4.36±0.60
Breadth of inner trochlea					
Palaeolimnas chathamensis	11	4.45±0.09	4.0– 4.9	0.30±0.06	6.67±1.42
Diaphorapteryx hawkinsi	27	5.48±0.10	4.7– 6.6	0.51±0.07	9.35±1.27
Breadth of middle trochlea					
Palaeolimnas chathamensis	11	5.89±0.13	5.2– 6.4	0.42±0.09	7.12±1.52
Diaphorapteryx hawkinsi	26	7.01±0.09	6.1– 7.9	0.47±0.07	6.66±0.92
Breadth of outer trochlea					
Palaeolimnas chathamensis	11	4.87±0.08	4.5– 5.4	0.28±0.06	5.69±1.21
Diaphorapteryx hawkinsi	28	5.28±0.06	4.5– 6.0	0.33±0.04	6.22±0.83
Depth of middle trochlea					
Palaeolimnas chathamensis	11	8.64±0.15	7.8– 9.3	0.49±0.10	5.69±1.21
Diaphorapteryx hawkinsi	26	9.23±0.16	6.4–10.5	0.81±0.11	8.77±1.22
Breadth of middle of shaft					
Palaeolimnas chathamensis	11	7.15±0.13	6.5– 7.8	0.42±0.09	5.87±1.25
Diaphorapteryx hawkinsi	28	8.66±0.09	7.9– 9.6	0.46±0.06	5.36±0.72
Depth of middle of shaft					
Palaeolimnas chathamensis	11	6.15±0.12	5.5– 6.8	0.39±0.08	6.37±1.36
Diaphorapteryx hawkinsi	28	6.11±0.08	5.5– 6.9	0.41±0.5	6.68±0.89
Proximal breadth across cotylae					
Palaeolimnas chathamensis	11	15.66±0.25	14.0–16.9	0.84±0.18	5.36±1.14
Diaphorapteryx hawkinsi	25	17.68±0.22	16.0–19.9	1.11±0.16	6.27±0.89
Depth of proximal end					
Palaeolimnas chathamensis	11	15.61±0.16	15.2–16.5	0.53±0.11	3.42±0.73
Diaphorapteryx hawkinsi	19	17.98±0.23	16.3–19.8	0.99±0.16	5.53±0.90

Abbreviations: N, sample size; x̄, mean; s, standard deviation; V, coefficient of variation; measurements in millimeters.

TABLE 42

COEFFICIENTS OF VARIATION FOR MEASUREMENTS OF TARSOMETATARSI OF RAILS

	Nesophalaris chathamensis	*Diaphorapteryx hawkinsi*	Average
Total length	3.11	5.22	4.17
Distal breadth across trochleae	5.93	4.36	5.15
Breadth of inner trochlea	6.67	9.35	8.01
Breadth of middle trochlea	7.12	6.66	6.89
Breadth of outer trochlea	5.69	6.22	5.96
Depth of middle trochlea	5.69	8.77	7.23
Breadth of middle of shaft	5.87	5.36	5.62
Depth of middle of shaft	6.37	6.68	6.53
Proximal breadth across cotylae	5.36	6.27	5.82
Depth of proximal end	3.42	5.53	4.48
Average	5.52	6.44	—

TABLE 43

STATISTICAL ANALYSIS OF VARIABILITY OF TIBIOTARSI OF *Bathornis* AND *Elaphrocnemus*

	N	$\bar{x}\pm$S.E.	Range	$s\pm$S.E.	$V\pm$S.E.
Total length					
Bathornis celeripes	—	—	—	—	—
Elaphrocnemus phasianus	1	101.8	—	—	—
Depth of external condyle					
Bathornis celeripes	55	12.63$\pm$0.07	11.7–13.5	0.51$\pm$0.05	4.02$\pm$0.38
Elaphrocnemus phasianus	17	8.82$\pm$0.11	8.1– 9.6	0.44$\pm$0.08	4.98$\pm$0.85
Depth of internal condyle					
Bathornis celeripes	47	13.77$\pm$0.09	12.2–15.3	0.65$\pm$0.07	4.75$\pm$0.49
Elaphrocnemus phasianus	17	9.65$\pm$0.09	9.2–10.3	0.37$\pm$0.06	3.88$\pm$0.67
Breadth across posterior end of condyles					
Bathornis celeripes	45	10.66$\pm$0.07	9.5–11.7	0.49$\pm$0.05	4.63$\pm$0.49
Elaphrocnemus phasianus	17	7.64$\pm$0.10	6.9– 8.7	0.43$\pm$0.07	5.60$\pm$0.96
Breadth across anterior end of condyles					
Bathornis celeripes	47	13.63$\pm$0.09	12.3–15.0	0.62$\pm$0.06	4.56$\pm$0.47
Elaphrocnemus phasianus	16	9.61$\pm$0.10	8.8–10.5	0.41$\pm$0.07	4.32$\pm$0.74
Depth of anterior intercondylar fossa relative to external condyle					
Bathornis celeripes	47	4.50$\pm$0.08	3.3– 5.6	0.52$\pm$0.05	11.63$\pm$1.20
Elaphrocnemus phasianus	16	3.11$\pm$0.12	2.0– 3.8	0.49$\pm$0.09	15.63$\pm$2.76
Breadth of middle of shaft					
Bathornis celeripes	—	—	—	—	—
Elaphrocnemus phasianus	11	5.35$\pm$0.16	4.6– 6.3	0.53$\pm$0.11	9.86$\pm$2.10
Depth of middle of shaft					
Bathornis celeripes	—	—	—	—	—
Elaphrocnemus phasianus	11	4.31$\pm$0.10	3.9– 5.0	0.32$\pm$0.07	7.38$\pm$1.57
Breadth across proximal end					
Bathornis celeripes	—	—	—	—	—
Elaphrocnemus phasianus	8	17.95$\pm$0.52	15.8–20.0	1.46$\pm$0.37	8.12$\pm$2.03
Depth of proximal end					
Bathornis celeripes	—	—	—	—	—
Elaphrocnemus phasianus	8	12.43$\pm$0.45	10.5–14.2	1.28$\pm$0.32	10.30$\pm$2.58

Abbreviations: N, sample size; x̄, mean; s, standard deviation; V, coefficient of variation; measurements in millimeters.

TABLE 44

COEFFICIENTS OF VARIATION FOR MEASUREMENTS OF TIBIOTARSI OF *Bathornis* AND *Elaphrocnemus*

	Bathornis celeripes	*Elaphrocnemus phasianus*	Average
Total length	—	—	—
Depth of internal condyle	4.75	3.88	4.32
Depth of external condyle	4.02	4.98	4.50
Breadth across posterior end of condyles	4.63	5.60	5.12
Breadth across anterior end of condyles	4.56	4.32	4.44
Depth of anterior intercondylar fossa relative to external condyle	11.63	15.63	13.63
Breadth of middle of shaft	—	9.86	—
Depth of middle of shaft	—	7.38	—
Breadth across proximal end	—	8.12	—
Depth of proximal end	—	10.30	—
Average	5.92	7.79	—

of this average is contributed by the high variability in *D. hawkinsi* (V=8.77). The remaining characters exhibit intermediate degrees of variability.

In most features of the tarsometatarsus *D. hawkinsi* is slightly more variable than *N. chathamensis*, the average V for all features being 6.44 and 5.52 respectively.

BATHORNITHIDAE AND IDIORNITHIDAE

TIBIOTARSUS

Statistical data about variability of the tibiotarsi of *Bathornis* and *Elaphrocnemus* are given in table 43, and the coefficients of variation for the 10 measurements are summarized in table 44.

Many measurements of the tibiotarsus of *B. celeripes* were not possible, so it is difficult to make comparisons with *E. phasianus* in the same way as it was among the rails. Again the depth of the anterior intercondylar fossa and the depth of the proximal end of the bone are the two most variable characters. The reasons already given for this high variability in rail tibiotarsi are also true for those of *B. celeripes* and *E. phasianus*. In both species the depths of the internal and external condyles have comparatively little variability.

Although not enough data are available on *B. celeripes* it does appear that *E. phasianus* shows a greater variability for most characters sampled. Since the time span of the sample of *E. phasianus*

is probably greater than that of *B. celeripes*, this difference in variability is not wholly unexpected.

TARSOMETATARSUS

Table 45 presents the statistical data on the variability of 10 characters of the tarsometatarsus. Table 46 summarizes the coefficients of variability for these characters.

Of the 10 characters the breadths of the outer and inner trochleae have the greatest amount of variability (average Vs of 10.50 and 10.19, respectively) whereas the breadth across the cotylae has the lowest V (4.36). The depth of the middle of the shaft in *E. phasianus* shows a high variability with a V of 10.14. No character exhibits a particularly low value of V.

As might be expected *E. crex* and *E. phasianus* have greater overall variability than *B. celeripes*, and this is almost certainly correlated with the larger time span of the sample.

DISCUSSION

The above data on fossil gruiforms can be compared with the studies of Simpson (1946a) and Goodge (1951) in order to ascertain whether there exist possible generalities about variability of the avian skeleton. Simpson (1946a, pp. 65–67) presented some statistical data on variability of seven elements of the King Penguin (*Aptenodytes patagonicus*). His samples of each element were small, the largest being 12 for the femur and the remainder consisting of seven or eight individuals. The skeletons Simpson measured

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TABLE 45

STATISTICAL ANALYSIS OF VARIABILITY OF TARSOMETATARSI OF *Bathornis* AND *Elaphrocnemus*

</div>

	N	x̄ ±S.E.	Range	s±S.E.	V±S.E.
Total length					
Bathornis celeripes	4	96.50	85.5–104.7	—	—
Elaphrocnemus phasianus	17	69.58±1.11	63.1– 75.8	4.58±0.79	6.59±1.13
E. crex	3	81.63	79.3– 86.2	—	—
Distal breadth across trochleae					
Bathornis celeripes	20	15.64±0.15	14.5– 16.7	0.66±0.10	4.21±0.67
Elaphrocnemus phasianus	32	11.23±0.10	10.0– 12.0	0.54±0.07	4.84±0.61
E. crex	8	12.60±0.28	11.9– 14.4	0.80±0.20	6.35±1.59
Breadth of inner trochlea					
Bathornis celeripes	24	4.27±0.05	3.8– 4.9	0.25±0.04	5.86±0.85
Elaphrocnemus phasianus	33	2.69±0.05	2.1– 3.2	0.28±0.03	10.53±1.30
E. crex	8	2.84±0.14	2.2– 3.5	0.40±0.10	14.19±3.55
Breadth of middle trochlea					
Bathornis celeripes	34	6.09±0.05	5.4– 6.8	0.30±0.04	4.91±0.60
Elaphrocnemus phasianus	35	4.50±0.05	4.0– 5.0	0.29±0.03	6.33±0.76
E. crex	9	5.14±0.15	4.6– 6.1	0.46±0.11	8.87±2.09
Breadth of outer trochlea					
Bathornis celeripes	28	4.56±0.07	4.0– 5.5	0.35±0.05	7.60±1.02
Elaphrocnemus phasianus	30	3.06±0.06	2.2– 3.5	0.32±0.04	10.61±1.37
E. crex	7	3.27±0.16	2.8– 4.1	0.43±0.11	13.29±3.55
Depth of middle trochlea					
Bathornis celeripes	32	8.38±0.07	7.5– 9.4	0.41±0.05	4.94±0.62
Elaphrocnemus phasianus	34	6.06±0.06	5.3– 6.6	0.34±0.04	5.53±0.67
E. crex	9	6.92±0.16	6.5– 7.9	0.49±0.12	7.10±1.67
Breadth of middle of shaft					
Bathornis celeripes	3	6.3	6.0– 6.6	—	—
Elaphrocnemus phasianus	25	4.52±0.05	4.1– 4.9	0.24±0.03	5.30±0.75
E. crex	4	5.60	5.1– 6.3	—	—
Depth of middle of shaft					
Bathornis celeripes	3	7.10	6.5– 8.3	—	—
Elaphrocnemus phasianus	25	4.01±0.08	3.5– 4.9	0.41±0.06	10.14±1.43
E. crex	4	4.88	4.5– 5.0	—	—
Breadth across cotylae					
Bathornis celeripes	18	15.50±0.17	14.5– 17.0	0.72±0.12	4.66±0.78
Elaphrocnemus phasianus	24	10.51±0.09	9.8– 11.4	0.43±0.06	4.05±0.58
E. crex	3	12.57	11.5– 14.0	—	—
Depth of proximal end					
Bathornis celeripes	10	13.85±0.33	12.0– 15.5	1.03±0.23	7.44±1.66
Elaphrocnemus phasianus	26	9.46±0.16	8.5– 10.9	0.59±0.08	6.27±0.87
E. crex	3	10.77	9.8– 12.3	—	—

Abbreviations: N, sample size; x̄, mean; s, standard deviation; V, coefficient of variation; measurements in millimeters.

are in the American Museum of Natural History, and because they were collected over a number of years they cannot represent a single breeding population. Goodge (1951, pp. 99–100) studied the variability of eight elements of the Common Murre (*Uria aalge*). Goodge had very large sample sizes for each element; all the bones came from Indian middens on Southeast Farallon Island off the coast of California. Unfortunately both Simpson and Goodge only measured the length and width of each element and did not attempt to characterize the elements in any more detail. Nevertheless, some interesting comparisons can be made with the

TABLE 46

COEFFICIENTS OF VARIATION FOR MEASUREMENTS OF TARSOMETATARSI OF *Bathornis* AND *Elaphrocnemus*

	Bathornis celeripes	*Elaphrocnemus phasianus*	*Elaphrocnemus crex*	Average
Total length	—	6.59	—	—
Distal breadth across trochleae	4.21	4.84	6.35	5.13
Breadth of inner trochlea	5.86	10.53	14.19	10.19
Breadth of middle trochlea	4.91	6.33	8.87	6.70
Breadth of outer trochlea	7.60	10.61	13.29	10.50
Depth of middle trochlea	4.94	5.53	7.10	5.86
Breadth of middle of shaft	—	5.30	—	—
Depth of middle of shaft	—	10.14	—	—
Proximal breadth across cotylae	4.66	4.05	—	4.36
Depth of proximal end	7.44	6.27	—	6.86
Average	5.66	7.02	9.96	—

TABLE 47

COEFFICIENTS OF VARIATION ($\pm$S.E.) FOR SKELETAL ELEMENTS OF COMMON MURRE AND KING PENGUIN

	Common Murre[a] (*Uria aalge*)	King Penguin[b] (*Aptenodytes patagonicus*)
HUMERUS		
Length	2.10$\pm$0.10	2.40$\pm$0.60
Width above distal end	—	2.10$\pm$0.60
FEMUR		
Length	2.55$\pm$0.21	2.10$\pm$0.40
Distal width	—	1.60$\pm$0.30
Shaft width	4.68$\pm$0.42	—
TIBIOTARSUS		
Length	2.84$\pm$0.36	2.90$\pm$0.80
Distal width	3.62$\pm$0.62	3.20$\pm$0.80
TARSOMETATARSUS		
Length	3.49$\pm$0.40	2.10$\pm$0.50
Proximal width	—	2.10$\pm$0.50
Distal width	—	4.10$\pm$1.0
Shaft width	4.26$\pm$0.51	—

[a] Data from Goodge, 1951, p. 100.
[b] Data from Simpson, 1946a, p. 65.

gruiform data. Coefficients of variation (V) for the skeletal characters measured by Simpson and Goodge are summarized in table 47.

The skeletal elements of the murre and penguin consistently show less variability than those of the rails, *B. celeripes* or of the idiornithids. The highest variability of the Common Murre

was a V of 4.68 for the shaft width of the femur and the highest V of the King Penguin was 4.10 for the distal width of the tibiotarsus. Most of the measurements of the two species had Vs between 2.00 and 3.00. In general the King Penguin had a lower overall variability than the Common Murre. There are several possible explanations for the striking differences in variability between the Recent species and the fossil gruiforms. It is possible that the murre and penguin have less intrinsic variability. One can argue that murres and penguins are subject to strong stabilizing selection associated with their rather narrow breadth of adaptation to an aquatic environment. This strong stabilizing selection would result in a lowering of variance for many features, no doubt including the skeletal elements. In contrast, rails and other birds such as the bathornithids are probably not subject to as strong stabilizing selection as are aquatic birds like the murres and penguins. If this is true it may explain some of the differences in variability. As might be expected, if the above argument has some validity, the King Penguin shows somewhat less variability than the Common Murre.

Another factor influencing differences in variability between the fossil and Recent species is the time-span over which the bones were accumulated. The skeletons of the penguins represent only a few years of collecting, and the murre skeletons were apparently all taken by the Indians within about 30 years (Goodge, 1951). The skeletons of the Quaternary-subrecent rails

were probably accumulated over a longer time span than either the murres or penguins, and the Tertiary rail, bathornithid, and idiornithids certainly were. The amount of temporal variability being introduced into the fossil samples is probably significant.

Another major generalization about skeletal variability is that the lengths of the skeletal elements, with few exceptions, tend to be less variable than other measurements of the same element. The only examples that did not follow this pattern were the humerus and femur of the King Penguin, the humerus of *Nesolimnas dieffenbachii*, the femur and tarsometatarsus of *Diaphorapteryx hawkinsi*, and the tarsometatarsus of *Elaphrocnemus phasianus*. However, in all of these elements except the last the V for the length was among the lowest of the Vs for that element. A partial explanation for the difference in variability between length and the other measurements may lie with the relationship between growth rate and the mechanical problems of supporting body weight. Cock (1963) has shown for chickens (*Gallus gallus*) that body weight is still increasing after tarsometatarsal length is attained. Because the magnitude of widths and depths of shafts and distal ends of bone tend to have an allometric relationship to the amount of weight that must be supported, the measurements can be expected to vary with differences in body size (in this case, weight). There may be stronger selection for an optimum bone length than for an optimum body weight and hence more variability in weight and those linear measurements which are related to mechanical support.

Goodge (1951) found that in the Common Murre there was an increase in variation from the distal to the proximal elements; adjacent elements were not significantly different, however. The data of Simpson (1946a) and those collected here for some fossil gruiforms do not parallel the results of Goodge. In general, rail tibiotarsi tend to be slightly more variable than femora, but tarsometatarsi are less variable than both femora and tibiotarsi. Simpson's data suggest that the tibiotarsus may be the most variable element of the hindlimb in the King Penguin. The tibiotarsus of *B. celeripes* and *E. phasianus* are more variable than the tarsometatarsi.

The above considerations demonstrate that considerable intraspecific variation exists in the skeletal elements of many species of fossil gruiforms. It therefore becomes necessary to consider this variation when interpreting species limits within fossil assemblages. An analysis of the rail and *Bathornis* assemblages can be used as a guideline in determining the probable species limits within the idiornithids. By recognizing four species of *Idiornis* and three species of *Elaphrocnemus*, and by assuming the presence of sexual size dimorphism, the variability of each species is close to those of the rails and *Bathornis*. If the assumption of sexual size dimorphism were rejected and additional species were recognized, the variability of the idiornithids would be much lower than the rails and *Bathornis*.

PHYLOGENY OF THE INFRAORDER GRUI

INTRODUCTION

PRESENT EVIDENCE suggests that two distinct phyletic lines evolved within the infraorder Grui during the Cenozoic. Furthermore, because of the presence of these two lineages in the Eocene, it seems highly probable that they had a common ancestor sometime in the Cretaceous, although this ancestor is unknown. One lineage includes the Geranoididae, Bathornithidae, and Idiornithidae (superfamily Geranoidea), and the other lineage consists of the Eogruidae, Gruidae, Ergilornithidae, Aramidae, and Psophiidae (superfamily Gruoidea). The probable phyletic relationships of these families are shown in figure 46.

The Geranoididae and Eogruidae share numerous features that suggest their derivation from a common ancestor. With respect to characters of the tibiotarsus (fig. 47), the internal condyles are very similar in shape, the external and internal condyles are almost parallel and in the same relative positions, the external condyles are both elongated (at least in some genera of the geranoidids), and the areas of the supratendinal bridge have similar configurations. There is also evidence for this relationship in some of the features of the tarsometatarsus (figs. 48–50). The cotylae are of the same relative sizes and the hypotarsus is in the same position (toward the external side in proximal view). The distal ends of the tarsometatarsi have the trochleae in the same relative positions and with a slight curve as seen from the distal end. Of importance is the fact that the inner (second) trochlea is reduced in the Eogruidae. When compared with morphological data on the other
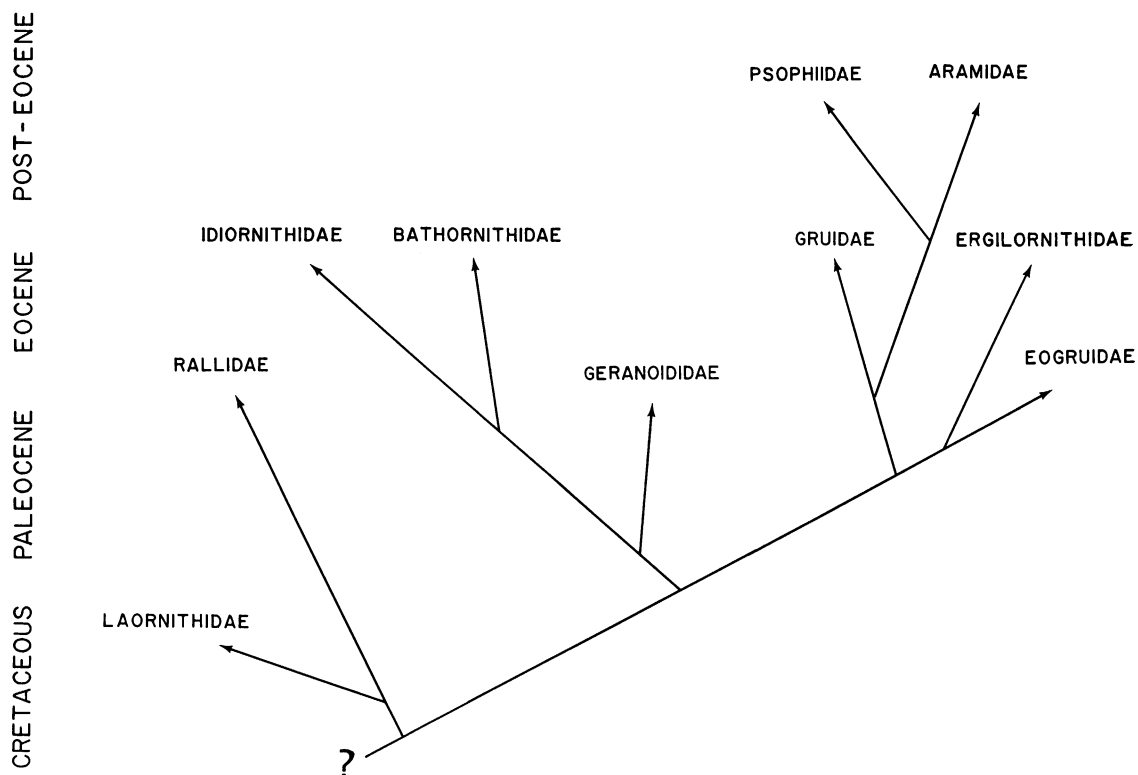
FIG. 46. Proposed phylogeny for the families discussed in the text. Vertical scale represents approximate time of first known occurrence.

108

FIG. 47. Possible evolutionary pathways of some gruiform tibiotarsi (right distal end). This is not a phylogeny. A. *Paragrus shufeldti* (Geranoididae). B. *Eogrus aeola* (Eogruidae). C. *Urmiornis maraghanus* (Ergilornithidae). D. *Palaeogrus excelsus* (Gruidae). E. *Grus primigenia* (Gruidae). F. *Psophia crepitans* (Psophiidae). G. *Aramus guarauna* (Aramidae). H. *Bathornis celeripes* (Bathornithidae). I. *Elaphrocnemus phasianus* (Idiornithidae). Abbreviations: aif, anterior intercondylar fossa; ec, external condyle; ic, internal condyle; ilp, internal ligamental prominence; pis, posterior intercondylar sulcus; tu, tubercle on supratendinal bridge.

families in the two lineages and in other suborders of the Gruiformes (see below), the comparison between the Geranoididae and Eogruidae suggests that most of the characters of the geranoidids are probably primitive within the Grui and the features of the eogruids represent a more derived condition.

THE SUPERFAMILY GERANOIDEA

Table 48 summarizes a morphological comparison of the Geranoididae, Bathornithidae, and Idiornithidae. The bathornithids and idiornithids are more similar to each other in almost all the characters than either is to the geranoidids. Although it is not possible to be certain of the primitive-derived sequences in each case, characters 1, 3, 4, 7, 9, and 12 are undoubtedly derived within the bathornithids–idiornithids (see discussion in systematic section). Several other characters (e.g., 2, 6, 8, and 10) are probably also derived for these two families. Thus, I think there is little question that the Bathornithidae and Idiornithidae originated

TABLE 48

MORPHOLOGICAL COMPARISON OF THE GERANOIDIDAE, BATHORNITHIDAE, AND IDIORNITHIDAE

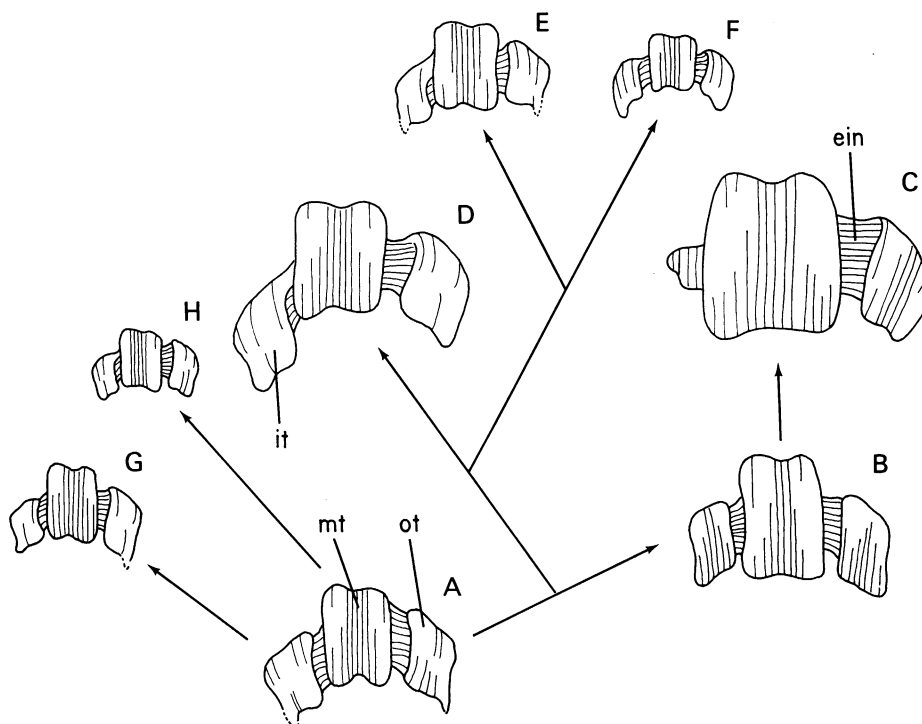|	GERANOIDIDAE[a]	BATHORNITHIDAE	IDIORNITHIDAE
TIBIOTARSUS			
External condyle	Flat distally, not raised posteriorly	Posterior portion raised distally	Posterior portion raised distally; tends to be rounded more
Internal condyle	Noticeable notch in distal margin; anterior end thick lateromedially; internal ligamental prominence moderately well developed	Notch in margin barely present (*B. veredus*) or absent; condyle less heavy, thin lateromedially; internal ligamental prominence poorly developed or absent	Notch in margin poorly developed; condyle only moderately heavy, intermediate in anterior thickness; internal ligamental prominence moderately to poorly developed
Supratendinal bridge	Broad proximodistally; tubercle present on distoexternal edge	Narrow proximodistally; tubercle poorly developed or absent	Narrow to broad proximodistally; tubercle poorly developed or absent
Depth of condyles	About equal in anteroposterior depth	Internal condyle always deeper than external	Internal condyle invariably deeper than external
Anterior intercondylar fossa	Tends to be shallow relative to depth of external condyle	Tends to be deep	Tends to be shallow
External wall (ridge) of tendinal groove	Tends to be long, extending proximally well beyond supratendinal bridge	Tends to be short, extending slightly beyond bridge	Tends to be short
TARSOMETATARSUS			
Hypotarsus	Relatively long proximodistally; apparently a single canal located externally	Relatively short; single canal located centrally	Relatively short; single canal (*Gypsornis*); canal absent (*Idiornis* and *Elaphrocnemus*); see table 26
Intercotylar prominence	Pointed; triangular in shape	Blunter, rounder; not as triangular in shape	Blunter, rounder; not as triangular in shape
Cotylae	Internal situated slightly more proximally relative to external	Internal situated noticeably more proximally	Internal situated noticeably more proximally
Shaft at proximal end of bone	Attachment for ligament on internal side well developed	Ligamental attachment relatively low	Ligamental attachment relatively low
Outer trochlea	Turned little posteriorly; extends distally about 70% the length of middle trochlea; large, robust; intertrochlear notch wide	Turned little posteriorly; extends distally about 50% (in *B. cursor*) to about 60% (in *B. celeripes*) the length of middle trochlea; moderate in size, somewhat less robust; intertrochlear notch narrow	Turned little posteriorly; extends distally about 50% the length of middle trochlea; moderate in size; intertrochlear notch narrow
Inner trochlea	About ⅓ of trochlea turned posteriorly beyond level of middle trochlea; extends distally about 60% the length of middle trochlea; large, robust; intertrochlear notch narrow	About ⅓ of trochlea turned posteriorly; in *B. celeripes* extends distally about 30% the length of middle trochlea (45% in *B. geographicus*, 35% in *B. cursor*); small, less developed; intertrochlear notch narrow to moderately wide	About ½ of trochlea turned posteriorly; extends distally only to base of middle trochlea in *Elaphrocnemus*, about 50% in *Idiornis*; small, less developed; notch moderate

[a] Except *Geranodornis*.

FIG. 48. Possible evolutionary pathways of some gruiform tarsometatarsi (left) as seen in distal view. This is not a phylogeny. A. *Paragrus shufeldti* (Geranoididae). B. *Eogrus aeola* (Eogruidae). C. *Proergilornis minor* (Ergilornithidae). D. *Pliogrus pentelici* (Gruidae). E. *Anisolornis excavatus* (Aramidae). F. *Psophia crepitans* (Psophiidae). G. *Bathornis celeripes* (Bathornithidae). H. *Elaphrocnemus phasianus* (Idiornithidae). Abbreviations: ein, external intertrochlear notch; it, inner trochlea; mt, middle trochlea; ot, outer trochlea.

from a common ancestor, and I suggest that the latter was probably very similar morphologically to the Geranoididae.

Despite the numerous similarities between bathornithids and idiornithids, each evolved certain "specializations" within their own radiation. The evolutionary trends within the idiornithids have been discussed above in the systematic section of this paper, and the transition to the bathornithids is discussed below. The major differences between the bathornithids and idiornithids are found in the structure of the tarsometatarsus. The hypotarsus of the idiornithids underwent considerable modification from the primitive geranoidid-like condition, whereas that of the bathornithids changed much less (fig. 50). In some features (e.g., the detailed shapes of the trochleae) the distal tarsometatarsus of the idiornithids is less like that of the geranoidids than that in the bathornithids. But the general proportions of

the idiornithids (i.e., short and stubby) seem closer to the geranoidids than the more slender distal end of the bathornithids (at least in the later members of the family).

THE GERANOIDID-BATHORNITHID TRANSITION

The recent discovery of a new genus and species of gruiform that is apparently intermediate between the bathornithids and the geranoidid-like condition permits a more detailed analysis of the origin of the Bathornithidae. The new form, *Eutreptornis uintae*, is from the Uintan (late Eocene) of Utah and therefore is also temporally intermediate between the two families (Cracraft, 1971).

Eutreptornis is allocated to the Bathornithidae because it possesses numerous distinctive features that represent the derived character-states within this lineage. Among these derived characters are a tibiotarsus with the posterior portion of

TABLE 49

RATIOS OF THE TIBIOTARSAL CHARACTERS OF THE GERANOIDIDAE, BATHORNITHIDAE, AND *Eutreptornis*

	Depth Internal Condyle / Depth External Condyle	Depth Fossa[a] / Depth External Condyle	Depth Fossa[a] / Depth Internal Condyle
GERANOIDIDAE			
Paragrus shufeldti (ACM 6619)	1.10	0.36	0.34
P. shufeldti (PU 18871)	—	0.30	—
P. prentici (ACM 3626)	0.96	0.38	0.39
Palaeophasianus meleagroides (AMNH 5156)	0.99	0.36	0.36
Eogeranoides campivagus (PU 16179)	—	0.30[b]	—
Geranodornis aenigma (AMNH 2628)	—	0.37	—
Geranoides jepseni (PU 13257)	—	0.29	—
EUTREPTORNIS UINTAE (AMNH 2092)	1.10	0.37	0.33
BATHORNITHIDAE			
Bathornis geographicus (SDSM 4030)	1.07	0.45	0.42
B. veredus (SDSM 5815)	1.05	0.48	0.46
B. veredus (PU 14400)	1.12	0.48	0.43
B. fricki (AMNH 2100)	1.17	0.40	0.35
B. celeripes (MCZ 2285)	1.10	0.42	0.38
B. celeripes (MCZ 422)	1.04	0.39	0.38

[a] Anterior intercondylar fossa.
[b] Ratio approximate.

the external condyle raised distally, a thin internal condyle, a poorly developed tubercle on the supratendinal bridge, the internal condyle deeper than the external, and a short external wall of the tendinal groove; and a tarsometatarsus with the internal cotyla situated noticeably more proximally than the external cotyla.

In addition to the above derived characters *Eutreptornis* retains some morphological features found in the more primitive geranoidids. These primitive characters include a tibiotarsus with the supratendinal bridge broad, and the anterior intercondylar fossa shallow; and a tarsometatarsus with a long hypotarsus and a triangular-shaped, pointed intercotylar prominence.

The proportions of the distal end of the tibiotarsus further substantiate the intermediate nature of *Eutreptornis* (table 49). With respect to the ratios of internal condyle depth/external condyle depth, *Eutreptornis* resembles the bathornithids more than the geranoidids. However, *Eutreptornis* is closer to the geranoidids in the ratios of the anterior intercondylar fossa depth to the depths of the internal and external condyles. In terms of the fossa depth/external

condyle depth ratio, *Eutreptornis* is very nearly intermediate.

Eutreptornis does not provide any information about the morphological transition in the distal end of the tarsometatarsus, but some important changes did take place. In the bathornithids the outer trochlea became somewhat less robust and shorter relative to the length of the middle trochlea, and the external intertrochlear notch became narrower. The most significant changes took place in the inner trochlea which became much smaller and separated slightly more from the middle trochlea. In general, the distal end of the tarsometatarsus became more slender in the Bathornithidae.

Whereas the total morphology of *Eutreptornis* is clearly intermediate between the Geranoididae and the Bathornithidae, few individual features themselves are intermediate in form, that is, they either resemble the primitive or derived condition and not something intermediate. The poorly developed notch on the distal margin of the internal condyle and the slightly developed internal ligamental attachment of the tarsometatarsus might fall into this latter category.
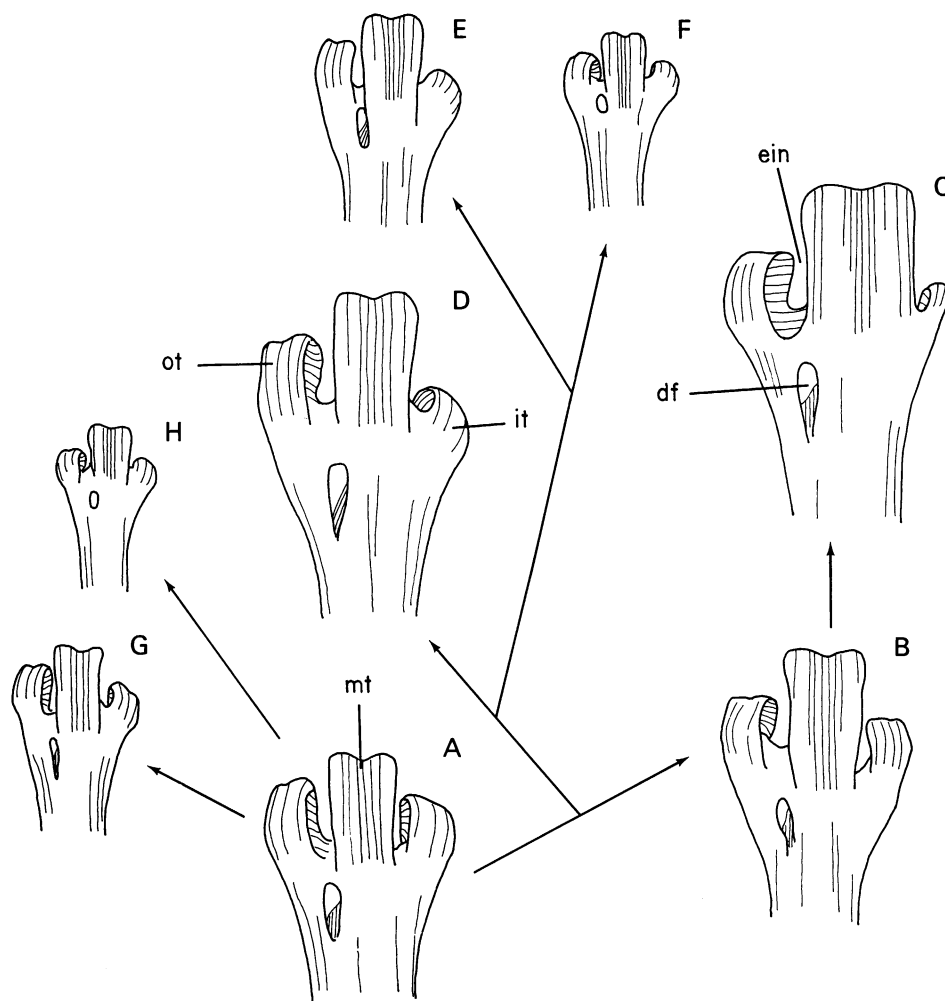
FIG. 49. Possible evolutionary pathways of some gruiform tarsometatarsi (left distal end) as seen in anterior view. This is not a phylogeny. A. *Paragrus shufeldti* (Geranoididae). B. *Eogrus aeola* (Eogruidae). C. *Proergilornis minor* (Ergilornithidae). D. *Pliogrus pentelici* (Gruidae). E. *Anisolornis excavatus* (Aramidae). F. *Psophia crepitans* (Psophiidae). G. *Bathornis celeripes* (Bathornithidae). H. *Elaphrocnemus phasianus* (Idiornithidae). Abbreviations: df, distal foramen; ein, external intertrochlear notch; it, inner trochlea; mt, middle trochlea; ot, outer trochlea.

THE SUPERFAMILY GRUOIDEA

As mentioned above, the Eogruidae and Geranoididae share many characters that suggest their derivation from a common ancestor.[1] *Eogrus* possesses numerous features that have

[1] This statement does not preclude the idea that the Eogruidae had a more recent common ancestry with the Gruidae. Furthermore, although the eogruids have many derived character-states when compared to the geranoidids many of these character-states can be considered primitive when compared to the gruids (see below).

been modified from the geranoidid condition, which is presumably close to that of the ancestor of the two families. Some of these derived features are maintained within the lines leading to the Ergilornithidae and to the Gruidae, another family closely related to the Eogruidae (see below). Compared with the geranoidid condition, the inner and outer (but especially the inner) trochleae of the tarsometatarsus have become reduced in *Eogrus*, and the middle trochlea has become elongated (fig. 49). The

external condyle of the tibiotarsus became deeper anteroposteriorly, developed a slight notch in its distal margin, and became elevated posteriorly. The internal condyle also deepened but did not change its basic shape from the geranoidid condition. The supratendinal bridge of *Eogrus* is narrower, and the external wall of the supratendinal groove is shorter and stubbier.

ORIGIN OF THE ERGILORNITHIDAE

All the available morphological evidence indicates that the Ergilornithidae are more closely related to the Eogruidae than to any other gruiform family. Whether the ergilornithids were derived directly from the eogruids or whether both came from some as yet unknown ancestor is difficult to say. The time gap between *Eogrus* and the ergilornithids *Ergilornis* and *Proergilornis* was from seven to 15 million years (extrapolated from Evernden et al., 1964). If rates of morphological change comparable with those postulated in the geranoidid-bathornithid lineage (see below) are assumed, then it is entirely possible for *Eogrus* or an allied genus to have been the direct ancestor. Regardless of the actual historical events, the ergilornithids exhibit numerous morphological characteristics derived from the more primitive condition of the eogruids.

The most marked changes within the eogruid-ergilornithid lineage involved the distal ends of the tarsometatarsus and tibiotarsus. With respect to the tarsometatarsus, the ergilornithids lost or greatly reduced the inner trochlea, developed a wider external intertrochlear notch, and enlarged the middle trochlea (figs. 48 and 49). The ergilornithid tibiotarsus is known only for *Urmiornis*, and its characters show the marked exaggeration of morphological trends begun in the Eogruidae. In the ergilornithids both condyles became much heavier; the notch in the distal margin of the internal condyle raised more distally; the tubercle on the supratendinal bridge enlarged greatly and, along with the external ridge of the supratendinal groove, moved internally away from the external margin of the shaft; the distal opening of the supratendinal canal became rounder, faced more anteriorly, and shifted more anteriorly because of the enlarged tubercle; the external condyle came to project more posteriorly and less anteriorly relative to the internal condyle; the

internal condyle became more flared posteriorly and came to meet the shaft at a sharper angle; and the contour of the external condyle (in distal view) became angular rather than remaining straight (fig. 47). The tibiotarsi of *Ergilornis* and *Proergilornis* are unknown, but the prediction can be made that when found they will be a mosaic of *Urmiornis* and *Eogrus* characters (see discussion of *Eutreptornis* above).

Because of the close relationship of the cranes (Gruidae) to the eogruids (Wetmore, 1934; see below), it is necessary to make a comparison between the gruids and ergilornithids to demonstrate that the latter family has a closer relationship to the eogruids than to the gruids.

In the characters of the distal end of the tarsometatarsus, *Ergilornis* differs from *Grus* in that (1) the outer intertrochlear notch is wider (2) the hallux and inner trochlea are lacking and the outer trochlea is relatively smaller (3) the middle trochlea is heavier and more robust and projects more distally beyond the outer trochlea (4) the outer trochlea is flatter anteroposteriorly (5) the anterior metatarsal groove is slightly less deep (6) the shaft is heavier, and (7) the external face of the shaft flares more externally rather than passes more directly posteriorly. *Urmiornis* differs from the gruids in the characters of the proximal end of the tarsometatarsus, as follows: (1) the intercotylar prominence projects less (is blunter and not raised so much) (2) in anterior view, the slope from the intercotylar prominence to the internal cotyla is more gradual, less steep (3) the external ridge of the hypotarsus is larger than the internal (internal largest in gruids) and the hypotarsus is situated more externally, and (4) in anterior view, the internal cotyla is situated slightly less proximally relative to the external cotyla (cotylae thus more nearly on the same level).

With few exceptions, the differences between the Ergilornithidae and Gruidae are the same as those between the Eogruidae and Gruidae. Characters such as the reduction of the inner and outer trochleae, the configuration of the cotylae and intercotylar prominence, and the structure of the hypotarsus unite the Eogruidae and Ergilornithidae and at the same time separate them from the Gruidae.

ORIGIN OF THE GRUIDAE

Wetmore (1934) first noted the close relation-

ship of the Eogruidae and Gruidae. However, it is difficult to find many derived characters that unite the two families. Wetmore called attention to the similarities of the tibiotarsi, but most if not all, of these similarities are primitive characters and cannot be used to indicate relationships. Several shared similarities in the distal ends of the tarsometatarsi appear to be derived and thus provide some evidence for relationship: (1) the distal ends are slender (2) the middle trochleae are elongate proximodistally, and (3) the external intertrochlear notches are wide. We can assume that the lineage leading to the Gruidae and several other recent families (see below) probably separated from the Eogruidae line sometime in the late Cretaceous or, less likely, in the Paleocene. This time of origin is suggested by the presence of both gruids and eogruids in the Eocene.

The phyletic line leading to the Gruidae developed a number of advanced characters in the tibiotarsus and tarsometatarsus. Several of the tibiotarsal characters were present soon after the origin of the line as evidenced by the structure of *Palaeogrus hordwelliensis* of the late Eocene: (1) anterior end of internal condyle became thin lateromedially, (2) the internal condyle became longer than the external, and (3) the condyles separated anteriorly so that they were no longer parallel (fig. 47). Several other characters developed later in the Cenozoic (apparently by the Miocene or Pliocene): (1) the external condyle developed a notch in its distal margin, and (2) the supratendinal bridge became very broad proximodistally. The Gruidae retained several primitive characters of the tibiotarsus including the presence of a tubercle on the supratendinal bridge, the long external wall of the supratendinal groove, and in having the external condyle not very elongated anteroposteriorly.

The tarsometatarsus also shows some derived characters leading to the Gruidae: (1) the inner trochlea enlarged and turned posteriorly (2) the internal cotyla became located much more proximally relative to the external, and (3) the intercotylar prominence became inflated, blunter and rounder (figs. 48, 49). The latter two characters are much less strongly developed in the Aquitanian species, *Palaeogrus excelsus*, thus suggesting they are probably a post-Miocene development.

ORIGIN OF THE ARAMIDAE

The close relationship of the Aramidae to the Gruidae has been known for a long time. Only a few authors (e.g., Clay, 1950; Sibley, 1960) have suggested relationships to the rails. Some workers (e.g., Hendrickson, 1969, p. 88, who cited other papers) have talked about the intermediate nature of the Aramidae, but this only promulgates ambiguous statements about relationships and begs the issue. In terms of skeletal features the aramids are unequivocally closer to the cranes than to the rails, and this conclusion is based on the sharing of derived characterstates. Not only has the evidence supporting a rail-limpkin relationship been poorly analyzed, some of it is highly questionable as systematic data in the first place. Thus, one might question whether it is valid systematic theory to base the relationships of two avian families not on the similarities of their morphology but instead on the morphology of their parasites (e.g., Clay, 1950). It seems preferable to determine the relationships of the hosts and parasites separately and then attempt to explain any conflicts that arise.

The aramids possess the following characters of the tibiotarsus, all of which are derived within the lineage leading to the gruids: (1) a thin anterior end of the internal condyle (2) a tendency toward a broad supratendinal bridge (3) an internal condyle longer than the external, and (4) a separation of the anterior ends of the condyles (fig. 47). Compared with cranes the aramids did not develop a notch in the distal margin of the external condyle, which was a late Tertiary development of the cranes. Instead, the external condyle became somewhat rounded and thus exhibits a slight similarity to rails; however, the morphology of the condyle is still closer to cranes than to rails. The similarities of *Aramus* and the Gruidae are more apparent when comparison is made to a crane with a more primitive skeleton such as that of *Balearica*.

The aramids also show some derived characters of the tarsometatarsus, including: (1) the inner trochlea being enlarged and turned posteriorly (2) a large, well-developed outer trochlea (3) internal cotyla situated much more proximally than the external, and (4) an intercotylar prominence inflated and rounded (but much less so than in the gruids) (figs. 48, 49). The aramids also possess a hypotarsus that can be considered derived within the superfamily

Gruoidea (see below) and which is very different from that evolved within the Ralli.

The aramids evolved some specializations of their own in the structure of the tarsometatarsus, notably: (1) the external ridge of the hypotarsus enlarged to help form deep hypotarsal grooves between the external and internal ridges (2) the internal and external sides of the shaft adjacent to the hypotarsus became depressed and excavated for muscle attachments (3) the inner trochlea became less bulbous and situated more distally relative to the middle trochlea, and (4) the distal end of the bone became more slender.

The only important derived feature of the aramid tibiotarsus was the development of a more rounded external condyle.

In addition to the above evidence the affinities of the Aramidae to the infraorder Grui (and not to the Ralli) are also apparent in a number of skeletal characters, but because these characters are primitive they cannot be used for determining relationships within the infraorder but can be used as evidence of a relationship to the Grui. Among these are the structure of the distal end of the humerus, the absence of posterior lateral processes on the sternum, and some features of the pelvis.

It seems reasonable to suggest that the Aramidae probably had their origin in the late Eocene or early Oligocene. We know that the family is at least as old as the medial Oligocene, and because of the phylogenetic relationships and the degree of divergence of related lines, the family probably did not go as far back as the early Eocene. Of course, only additional fossil evidence will provide a better estimate.

ORIGIN OF THE PSOPHIIDAE

Most workers have considered the relationships of the Psophiidae to be with the cranes and their allies, although some have suggested affinities to rails. Beddard (1890, p. 340) considered the psophiids closest to the Cariamidae, but he also postulated a close relationship to the rails. Shufeldt (1915b) placed the family in the same superfamily as the Gruidae and Aramidae. Verheyen (1957) recognized affinities to both rallids and aramids but later (1960) apparently decided the evidence was strongest for an aramid-gruid relationship. Using egg-white proteins Sibley (1960) considered *Psophia* to be somewhat intermediate between the cranes and

rails, but he still believed that the relationship to both "at best is a distant one." Recent work on egg-white proteins (Hendrickson, 1969, p. 89) has prompted a fairly strong assertion that the "Eurypygidae, Heliornithidae, Rallidae, Turnicidae and Psophiidae form a natural group with common ancestry."

As noted elsewhere (Cracraft, 1972b) I think we must seriously question most of the above kinds of evidence as being inconclusive and without strongly reliable systematic information. None of these workers provides any basis for deciding whether the similarities they use in suggesting relationship to a particular taxon are primitive or derived. Also, to treat the psophiids, like the aramids, as an "intermediate" family is basically nothing more than an admission of failure to resolve the relationships.

On the basis of skeletal evidence it appears that the Psophiidae have a much closer relationship to the cranes and limpkins than to the rails. The psophiids possess numerous derived character-states of the lineage leading to the gruids (see above): (1) characters of the sternum, (2) pelvic characters, (3) tibiotarsal characters, and (4) tarsometatarsal characters.

More specifically, the psophiids appear to be closer to the aramids than to the gruids. The tibiotarsus provides little support for this conclusion, for although the two families are exceedingly similar in this element, all the characters appear to be derived for the gruid-aramid-psophiid lineage and thus primitive within the aramid-psophiid lineage.

In contrast to the tibiotarsus, the tarsometatarsus of the psophiids possesses characters that can be considered derived with the Aramidae (see above): (1) external ridge of the hypotarsus is enlarged to help form several deep hypotarsal grooves between the external and internal ridges (fig. 50) (2) the internal and external sides of the shaft adjacent to the hypotarsus are depressed and excavated for muscle attachments, and (3) the inner trochlea is less bulbous and situated more distally relative to the middle trochlea (figs. 48, 49). The psophiids further modified some of these characters, but the pattern of the aramids is unmistakable. Thus in the psophiids, the excavations on either side of the hypotarsus are deeper (consequently so is the posterior metatarsal groove) and the inner trochlea has become smaller and turned less posteriorly.

FIG. 50. Possible evolutionary pathways of some gruiform tarsometatarsi (proximal end of right). This is not a phylogeny. A. *Palaeophasianus meleagroides* (Geranoididae). B. *Eogrus aeola* (Eogruidae). C. *Urmiornis maraghanus* (Ergilornithidae). D. *Palaeogrus excelsus* (Gruidae). E. *Psophia crepitans* (Psophiidae). F. *Aramus guarauna* (Aramidae). G. *Bathornis minor* (Bathornithidae). H. *Gypsornis cuvieri* (Idiornithidae). I. *Orthocnemus cursor* (Idiornithidae). J. *Elaphrocnemus phasianus* (Idiornithidae). *Abbreviations:* ec, external cotyla; hr, hypotarsal ridge; ic, internal cotyla; icp, intercotylar prominence; tc, tendinal canal; tg, tendinal groove.

The Psophiidae evolved numerous other advanced features, for example, in the wing skeleton. But the present evidence supports a close relationship to the aramids. I am not convinced that Beddard's suggestion (1890) that the psophiids have close affinities with the cariamids is incorrect. Indeed, the psophiids may be closer phylogenetically to the cariamids than to the aramids. At the present time I am unwilling to make a commitment and will have to study the problem in greater detail as it necessitates comparisons with numerous non-gruiform families. If cariamids are closer to the psophiids, this will entail only a slight modification of my dendrogram.

Unfortunately there is no fossil record for the Psophiidae. The South American Miocene genus *Anisolornis* is an aramid, not a psophiid. It is possible that the psophiids originated at about the same time as did the aramids, that is, probably in the late Eocene or early Oligocene.

EVOLUTIONARY CONSIDERATIONS

CONVERGENCE OF THE ERGILORNITHIDAE AND STRUTHIONIDAE

RECENTLY BRODKORB (1967, p. 154) suggested that the ergilornithids might be closely related to the ostriches (Struthionidae), and indeed since the evolution of two digits has been previously unknown in birds except for the ostriches and is obviously a derived condition, this is not an unreasonable preliminary suggestion. However, comparison of the two taxa with each other and with other families clearly shows that they are quite different despite the structural convergence of the trochleae. The ergilornithids differ from the struthionids and agree with the Gruoidea in many features of the tarsometatarsus, as follows: (1) the outer trochlea is turned more posteriorly (2) the external intertrochlear notch is much wider (3) the middle trochlea is elongated proximodistally and flattened much more lateromedially (5) the external distal foramen is situated much more proximally relative to the external intertrochlear notch (6) the shaft is very different in shape in that (a) the external face is much flatter, not rounded, nor as developed into a noticeable flair posteriorly (b) the anterior metatarsal groove is less developed, and (c) the internal side of the shaft is much less rounded and more squared-off posteriorly, (7) the ridge which extends distally from the hypotarsus is more on the external side of the bone rather than more in the middle (8) the hypotarsus is very different with two posterior ridges instead of one and with the presence of a canal (lacking in *Struthio*) (9) the intercotylar prominence is present and well developed (essentially lacking in *Struthio* since it is low and broad), and (10) the cotylae are rounded rather than square-shaped.

On the basis of these differences with *Struthio* and the similarities with other gruiforms, especially the eogruids and gruids, there can be no doubt that the affinities of the ergilornithids lie with the gruiforms and not with the ostriches or other ratites. Thus, the Ergilornithidae and Struthionidae provide one of the better examples of structural convergence seen in the avian hindlimb.

RATES OF MORPHOLOGICAL CHANGE

During a transition from one level of organization to another, evolutionary rates will not be constant for all morphological features. Consequently, intermediate taxa will necessarily share both primitive and derived features. I noted above (also Cracraft, 1971) that the evidence indicates that the Uintan genus *Eutreptornis* is structurally intermediate between the Geranoididae and the Bathornithidae. There is no evidence that *Eutreptornis* was directly ancestral to any of the known bathornithids. However, if one assumes that the genus is representative of the advanced geranoidids or primitive bathornithids of the late Eocene, then it is possible to arrive at a general idea of the relative evolutionary rates of a few morphological features.[1] Although the fossil record is not complete, I am aware of no other example for birds in which the rate of morphological (skeletal) change has been (or perhaps can be) estimated, even in a general way. Such an excerise also provides some insight into the specific manner in which these morphological changes might have taken place.

All the geranoidids, except the peculiar *Geranodornis aenigma* and a fragmentary tarsometatarsus tentatively assigned to *Palaeophasianus*, are from deposits that are early Wasatchian (Graybull) in age (Cracraft, 1969). Evernden et al. (1964, p. 165) have given a potassium-argon (KA) date from the late Wasatchian Wind River Formation (KA1012) of 49.2 million years (m.y.). The geranoidids, then, are slightly older, and for purposes of discussion, I will assume their age to be approximately 53 m.y. (this date is extrapolated from fig. 1 of Evernden et al., 1964, p. 167). *Eutreptornis uintae* was collected at the base of the Myton Member of the Uinta Formation, which would be late Eocene. A late Bridgerian/early Uintan date (KA1021) of 45.4 m.y. has been recorded from

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[1] In this argument *Eutreptornis* is not considered "intermediate" between the geranoidids and bathornithids in the same sense as other workers have talked about the "intermediate" families. *Eutreptornis* is clearly a bathornithid as discussed earlier.

unit 1 of Wagonbed Springs, Wyoming (Evernden et al., 1964). I will assume that the age of *Eutreptornis* is about 45 m.y. The earliest bathornithids are Chadronian (early Oligocene), and KA dates for this Mammal Age range from 33 to about 37 m.y. (the latter date is from the Clarno Formation near the Duchesnean-Chadronian boundary). The earliest bathornithids, then, are first known to appear about 35 m.y. ago. In summary, approximately eight m.y. elapsed between the known geranoidids and *Eutreptornis*, and the first "true" bathornithids appeared about 10 m.y. after *Eutreptornis*.

Using the above time scale, it can be noted that it took eight m.y. or less for the following morphological features to evolve from the geranoidid condition to one like the bathornithids: (1) the posterior portion of the external condyle was raised posteriorly from a flat condition (2) the internal condyle became thinner lateromedially (3) the ligamental prominence was reduced in size (4) the tubercle on the supratendinal bridge was lost (5) the internal condyle elongated relative to the external (6) the external wall of the supratendinal groove and bridge shortened (7) the tendinal canal came to occupy a more central position in the hypotarsus (8) the internal cotyla of the tarsometatarsus became somewhat larger (relative to external) and became more proximal relative to the external, and (9) the shaft of the tarsometatarsus narrowed and the external side became less depressed.

Other features of the tibiotarsus and tarsometatarsus apparently did not begin to change to the bathornithid condition until the very end of the Eocene. On the basis of the structure of *Eutreptornis* the following morphological changes leading to the bathornithids had not taken place by Uintan times but were evolved in the succeeding 10 m.y.: (1) the distal margin of the internal condyle became flat, not raised posteriorly (2) the supratendinal bridge shortened proximodistally (3) the anterior intercondylar fossa became deeper relative to the condyles (4) the intercotylar prominence of the tarsometatarsus became blunter and less triangular in shape, and (5) the hypotarsus shortened.

Many of these changes are either difficult to quantify or are based on insufficient material to allow quantification. However, several characters of the tibiotarsus lend themselves to more detailed analysis and the results for six ratios

are presented in figure 51. The ratio showing the greatest average difference between the geranoidids and bathornithids was the depth of the anterior intercondylar fossa/depth of external condyle, which changed about 28 percent over 18 m.y. or about 1.25 percent/m.y. The rate of change in this ratio was slightly greater after the late Eocene, as evidenced by *Eutreptornis*. The ratio showing the least total change was the depth of internal condyle/depth of external condyle which had an average rate of change of about 0.56 percent/m.y. However, this ratio attained the bathornithid condition before the late Eocene (average rate approximately 1.25 percent/m.y.) and remained stable thereafter. Several ratios showed relatively rapid evolution between *Eutreptornis* and the bathornithids. The depth of the intercondylar fossa/depth of internal condyle ratio changed as much as 2.1 percent/m.y. between *Eutreptornis* and the bathornithids, and the height (proximodistal)/width ratio of the supratendinal bridge changed about 2.5 percent/m.y.

Although the above data are only approximate, they provide a general idea as to the rate of change in the avian tibiotarsus. But because these data were derived from some bathornithids that were post-Chadronian in age, the above rates must be considered as maximums. The discovery of additional Bridgerian and Uintan fossils will help document the timing of the changes more accurately and possibly will tell us whether the other lineages of the transition were paralleling *Eutreptornis* in the sequence of morphological changes.

PALEOCLIMATOLOGY AND PALEOGEOGRAPHY

EOCENE-OLIGOCENE ENVIRONMENTS AND ORIGIN OF SOME GRUIFORM TAXA

It can be inferred from various kinds of evidence—including morphology, paleoclimatology, and the history of other vertebrates, particularly mammals—that the origins of some gruiform taxa, for example the Bathornithidae and Ergilornithidae, involved the development of new adaptations associated with (or perhaps caused by) broad changes in their environments.

Black and Dawson (1966) have summarized the changes in the geology and the mammalian faunas between the Eocene and Oligocene of North America. Basically, the early Eocene was
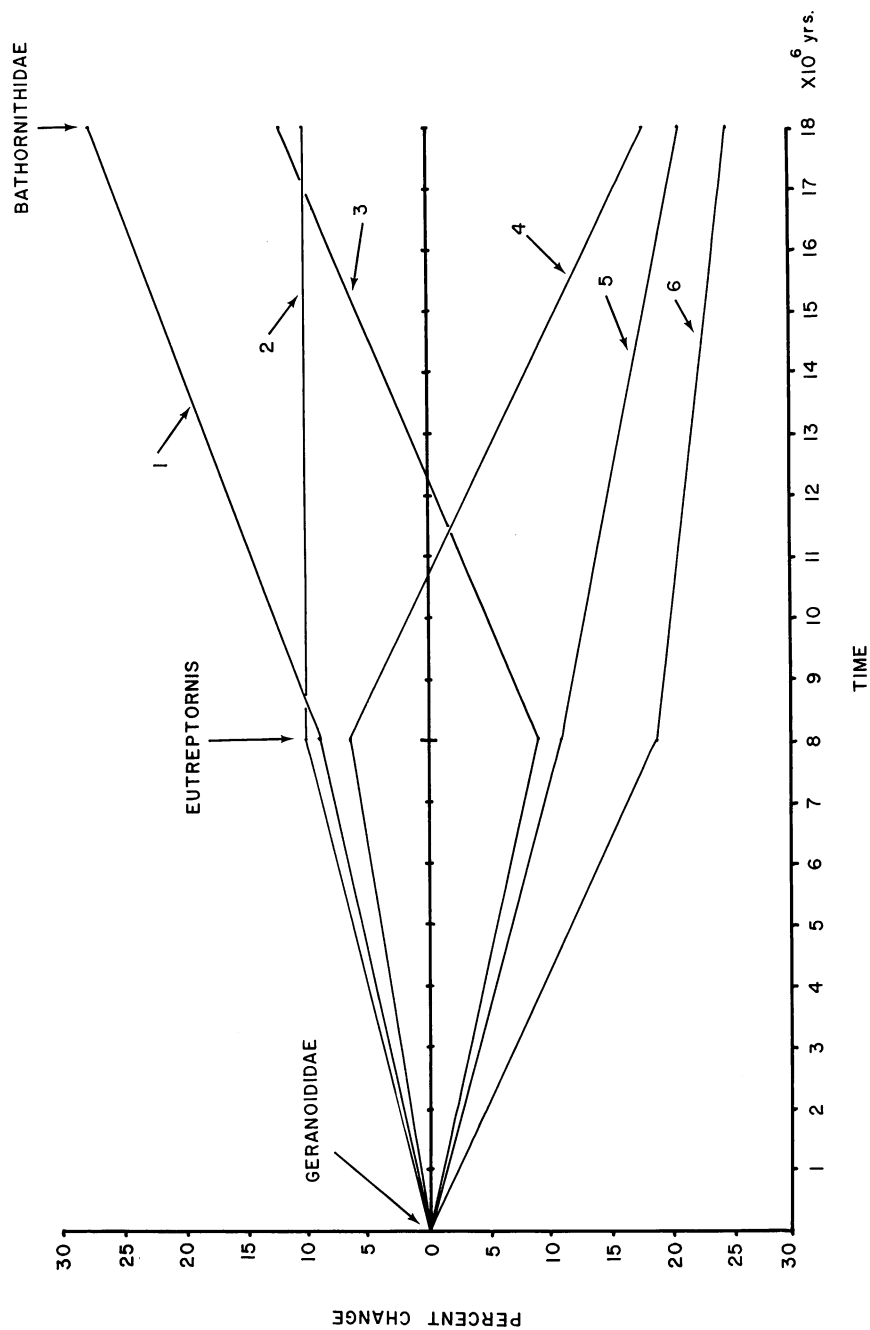
FIG. 51. Estimated rates of morphological change for certain characters (ratios) of the tibiotarsus during the geranoidid-bathornithid transition. See text. Characters: 1, depth of anterior intercondylar fossa/depth of external condyle; 2, depth of internal condyle/depth of external condyle; 3, depth of anterior intercondylar fossa/depth of internal condyle; 4, height/width of supratendinal bridge; 5, width/height of anterior end of internal condyle; 6, length of external wall of supratendinal bridge/depth of external condyle.

a time of broad basin deposition, whereas large flood plain deposits predominated in the Oligocene. The change in the composition of the mammal faunas around the Eocene-Oligocene boundary is striking. For example, perissodactyls greatly declined in number and the artiodactyls became the dominant ungulates. The late Eocene-early Oligocene was also a time of change in the rodent faunas, protrogomorphs being replaced (faunistically) by myomorphs. In addition, a change in the types of carnivores occurred in late Eocene times with many new groups making their first appearance (Black and Dawson [1966] and Simpson [1946b] document additional cases of this change in the mammalian faunas).

The mammals exhibit a pattern that suggests a response to significant changes in the environment rather than adaptive modifications in the absence of accompanying environmental (in this sense, climatological and vegetational) shifts. Numerous simultaneous (geologically speaking) replacements across diverse taxonomic groups would not be expected if the environment remained more or less constant. Indeed, paleobotanical evidence exists for such an environmental change.

North America during the Eocene was covered by widespread tropical, subtropical, and warm temperate forests (MacGinitie, 1958; Dorf, 1959). A subtropical forest found along the Pacific Coast extended far northward into British Columbia and eastward to Wyoming (Dorf, 1953). The Green River Flora (medial Eocene) of Colorado and Wyoming was subtropical or warm temperate in its composition (Chaney, 1947; MacGinitie, 1958). With the beginning of the Oligocene the warm, moist climates of the Eocene became cooler and drier. Species of the Arcto-Tertiary Flora became more prevalent in the previously subtropical-warm temperate floras, and by the end of the Oligocene the climatic zones of the Eocene were pushed southward possibly 10 to 15 degrees. Although the paleobotanical evidence for climatic changes during the Tertiary has been misinterpreted frequently (see Axelrod and Bailey, 1969, and Wolfe, 1971, for critical analyses of previous work), there can be little doubt that distinct changes in the composition of lowland forests took place between the early and medial Oligocene.

In regard to the geranoidid-bathornithid transition, it can be noted that in the late Eocene the boundary between the subtropical and warm temperate forests was probably situated near the area in which these families lived (see figs. in Dorf, 1953). Because of the southward shift of the boundary at the beginning of the Oligocene, the subsequent environmental change was probably an important influence on the origin of the Bathornithidae. It can only be speculated as to how the bathornithids differed adaptively from the geranoidids. Adaptive shifts of higher taxa almost always involve modifications of the feeding and/or locomotor mechanisms. In the case of the former no evidence is presently available for the Geranoididae or Bathornithidae. The striking differences in hindlimb morphology are undoubtedly a reflection of a change in the locomotor mechanism and probably involved adaptations for a more cursorial habit in the bathornithids.

Similar climatic changes also took place in the Old World (Kobayashi and Shikama, 1961; Schwarzbach, 1961) and presumably had a parallel effect on the origin of the ergilornithids. I suggest that this family originated in response to a more arid environment that probably facilitated a more cursorial mode of life, and evolution of the advanced ergilornithids such as *Urmiornis* may have involved adaptation to a grassland habitat.

DISPERSAL OF THE GRUI

The geranoidids in North America and the eogruids in eastern Asia are postulated to have had a common ancestor sometime in the late Cretaceous. The geographic distribution of this ancestor is unknown but the least demanding hypothesis is that it was in both North America and eastern Asia. Because the geranoidids are probably closer to the ancestor in terms of morphology than are the eogruids, perhaps a stronger argument can be made for a North American origin.

It is a reasonable hypothesis that the Geranoidea had their origin in North America. One phyletic line dispersed to Europe in the Eocene and gave rise to the Idiornithidae, whereas the other line gave rise to the bathornithids in North America. I think it very plausible that the idiornithid ancestor dispersed to Europe via the North Atlantic intercontinental connections of the early Eocene (Szalay and McKenna, 1971;

Le Pichon, 1968; Cracraft, In press). The isolation of the idiornithids from the geranoidid-like ancestors in North America after the opening of the North Atlantic around medial Eocene times would explain their relatively greater degree of morphological divergence when compared with the bathornithids. The latter family seems to show relatively less differentiation from the geranoidid-like ancestor.

The ergilornithids undoubtedly originated in Asia, particularly if the ancestor was close to the eogruids. The absence of the eogruids and the early ergilornithids from Europe is explainable on the assumption that Europe and Asia were separated north to south by the Turgai Straits during part of the Eocene (Kurtén, 1966). With the closing of the straits it was then possible for later genera such as *Urmiornis* to spread westward.

The Aramidae and Psophiidae are obviously of New World origin but present evidence does not allow a more specific statement. Fossil evidence suggests either a North or South American origin for the Aramidae. Present distribution patterns argue for a South American origin for the Psophiidae.

COMMENTS ON CLASSIFICATION

The above phylogeny allows us to make some comments on the classification of the suborder Grues. Not unexpectedly the systematic information presented here leads to a classification that differs somewhat from those of previous workers, who proposed various arrangements in the absence of critical or extended discussion of phylogenetic relationships. Consequently none of these classifications gives an adequate representation of the relationships of these families, at least as envisioned in this paper.

It is pertinent to discuss several of these classifications, and I will concentrate on those of Wetmore (1960) and Brodkorb (1967) principally because they included fossil families. The taxonomic arrangements below include those groups I have discussed in the systematic section above. My citations of other workers' classifications sometimes omit taxa that I did not treat, but in several instances I have included taxa that I did not discuss to make it easier for the reader to understand these workers' opinions about relationships.

Perhaps the most widely recognized classification is that of Wetmore (1960):

Suborder Grues
    Superfamily Gruoidea
       Family Geranoididae
       Family Eogruidae
       Family Gruidae
       Family Aramidae
       Family Psophiidae
    Superfamily Ralloidea
       Family Idiornithidae
       Family Rallidae
Suborder Cariamae
    Superfamily Cariamoidea
       Family Bathornithidae
       Family Cariamidae

Several aspects of Wetmore's arrangement require comment. First, he has included a linear arrangement of related families (but lacking the family Ergilornithidae which was described in the same year, 1960) within the superfamily Gruoidea, but there is no way of interpreting more precisely the degrees of relationship. Second, he placed the Idiornithidae in the superfamily Ralloidea but noted that this

decision was provisional. And third, he included the Bathornithidae in the suborder Cariamae. At the time of his work the evidence seemed to support a relationship between the bathornithids and cariamids, and indeed I also thought this in my revision of the fossil family (1968a). However, new fossil discoveries and better comparative analysis renders the relationship of the bathornithids to the cariamids to be untenable (Cracraft, 1969; present paper).

Brodkorb's arrangement (1967) of the gruiform taxa is more complex because of the detailed consideration of the fossil groups. In fairness it should be stressed that Brodkorb was not presenting a classification per se (unlike Wetmore), but his arrangement will have a strong influence on future workers simply because of the importance of his catalogue to paleontologists and systematists. It therefore seems valid to examine it closely:

Suborder Ralli
    Family Rallidae
    Family Idiornithidae
Suborder Grues
    Family Gruidae
       Subfamily Geranoidinae
       Subfamily Balearicinae
       Subfamily Eogruinae
       Subfamily Gruinae
    Family Ergilornithidae
    Family Aramidae
    Family Psophiidae
Suborder Cariamae
    Family Cunampaiidae
    Family Phororhacidae
    Family Cariamidae
       Subfamily Bathornithinae
       Subfamily Psilopterinae
       Subfamily Prophororhacinae
       Subfamily Cariaminae

Like Wetmore, Brodkorb provisionally includes the Idiornithidae with the Rallidae, but unlike Wetmore he has placed these families in their own suborder Ralli. Within the suborder Grues, Brodkorb has considered the geranoidids and eogruids as subfamilies of the Gruidae but has recognized the ergilornithids, aramids, and psophiids as of family rank. Finally, he placed the bathornithids in the suborder Cariamae but

relegated them to a subfamily of the Cariamidae, which also includes a portion of the phoror-hacoids (this has profound implications about the relationships of the phororhacoids, which will be discussed at a later date).

Both of these arrangements have some similarities and differences, but they express relationships quite differently, if in fact they were constructed on the assumption that monophyletic taxa should be classified together. Quite clearly, both authors placed strong emphasis on morphological divergence in determining rank.

As mentioned in the introduction, the relationships of the taxa discussed in this paper have been determined by using a cladistic approach. If this same systematic theory is followed in the construction of a classification, then most information is contained in a classification that expresses phylogenetic relationships in a dichotomous fashion. Such a classification might be the following:

Suborder Grues
  Infraorder Ralli
    Superfamily Ralloidea
      Family Rallidae
    Superfamily Laornithoidea
      Family Laornithidae
  Infraorder Grui
    Superfamily Geranoidea
      Family Geranoididae
      Family Bathornithidae
        Subfamily Bathornithinae
        Subfamily Idiornithinae
    Superfamily Gruoidea
      Family Eogruidae
        Subfamily Eogruinae
        Subfamily Ergilornithinae
      Family Gruidae
        Subfamily Gruinae
        Subfamily Psophiinae
          Tribe Psophiini
          Tribe Aramini

This arrangement has distinct advantages and, in some workers' opinions, disadvantages over those of Wetmore and Brodkorb. Certainly it expresses relationships in a more precise manner, assuming my phylogeny (fig. 46) is correct. By examining the classification it is possible to identify the "sister-group" (taxon sharing the most recent common ancestry) of any taxon. This is quite important for many kinds of evolutionary studies such as biogeographic problems. On the other hand, in order to attain this classification, it was necessary to employ additional ranks in the hierarchy and to reduce some family-rank taxa to subfamily or tribal status. I doubt whether this will upset many systematists once the advantages are realized. Probably few would be disturbed with recognizing the bathornithids, idiornithids, eogruids, and ergilornithids as subfamily-rank taxa, because these groups are fossil and unfamiliar to most ornithologists. More controversy might be expected with recognizing gruids as a subfamily and the psophiids and aramids as tribes of another subfamily, because systematists and ornithologists have always thought of them as families and not as taxa to be assigned a rank.

A major problem of this cladistic arrangement is that the addition of other gruiform taxa will create difficulties in maintaining a dichotomous classification. If, for example, the cariamids (and possibly the phororhacoids) are more closely related to the psophiids than to other gruiform families, there simply will not be enough ranks to accommodate this radiation. It will then become necessary to express this divergence by abandoning the strictly dichotomous approach. However, it seems preferable to follow this type of classification as much as possible. Obviously this arrangement cannot reach a final form until other gruiform families are studied and their relationships determined. What I am trying to emphasize here is that our classifications can and should become more precise in expressing phylogenetic relationships.

In the systematic section of this paper I have compromised somewhat and recognized all the taxa at least at the family rank. This was done mainly for convenience, because (a) I believe it best to wait until the relationships of the other gruiform families have been ascertained before trying to settle on a classification, and (b) the emphasis in this paper has been on phylogeny and evolution rather than on classification.

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