Swiss J Palaeontol (2016) 135:315–325
DOI 10.1007/s13358-016-0117-2

ORIGINAL ARTICLE

On the taxonomy and osteology of the Early Eocene North American Geranoididae (Aves, Gruoidea)

Gerald Mayr[1]

Received: 10 February 2016 / Accepted: 16 March 2016 / Published online: 12 April 2016

Abstract Whereas our knowledge of small arboreal Paleogene birds has greatly increased in the past years, that of the larger birds coexisting with them is far less detailed. Particularly poorly known and, hence, widely ignored are the North American Geranoididae, of which six species were described from the Early Eocene Willwood Formation. The published material of all of these consists only of incomplete leg elements, and previous descriptions and comparisons mainly focused on selected bones. Here, a revision of some geranoidids from the Willwood Formation is undertaken, and it is concluded that the taxon *Geranoides* Wetmore, 1933, the type genus of the Geranoididae, is a junior synonym of *Palaeophasianus* Shufeldt, 1913. *Eogeranoides campivagus* Cracraft, 1969 is poorly differentiated from *Paragrus prentici* (Loomis, 1906), and a synonymy of both species also seems likely. Complete leg bones of a large *Eogeranoides*/*Paragrus*-like species are reported, which constitute the most substantial record of a geranoidid from the Willwood Formation. It is detailed that geranoidids are likely to be stem group representatives of the Gruoidea, the clade including trumpeters, cranes, and allies, and the potential occurrence of geranoidids in the Eocene of Europe is discussed.

Keywords Fossil birds · Willwood formation · Wasatchian · *Palaeophasianus*

Editorial handling: D. Marty.

✉ Gerald Mayr
gerald.mayr@senckenberg.de

[1] Ornithological Section, Senckenberg Research Institute and Natural History Museum Frankfurt, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

Introduction

The Early Eocene (Wasatchian) strata of the Willwood Formation in Wyoming, USA, yielded various remains of medium-sized to large birds, which were assigned to the taxon Geranoididae. Despite the fact, however, that six species in four genus-level taxa are currently recognized (Cracraft 1969, 1973), the knowledge of these birds is rather poor.

The first species, which is now known as *Paragrus prentici*, was initially identified as a galliform bird by Loomis (1906). Another species from the Willwood Formation was described by Shufeldt (1913), who likewise identified the fragmentary bones available to him as those of a galliform bird, which he named *Palaeophasianus meleagroides*. Wetmore (1933) subsequently described comparatively well-preserved hindlimb bones as *Geranoides jepseni* and classified this species into the new taxon Geranoididae, as part of the Gruoidea, the clade including Psophiidae (trumpeters), Aramidae (limpkins), and Gruidae (cranes).

Cracraft (1968) revisited the holotype of *P. meleagroides* and assigned the species to the Aramidae. In a subsequent revision of the entire material of the crane-like birds from the Willwood Formation, Cracraft (1969) assigned *Palaeophasianus* and *Paragrus* to the Geranoididae and described three new geranoidid species, one each in the taxa *Paragrus* and *Palaeophasianus*, and a third in the new taxon *Eogeranoides*. Whereas Cracraft (1969) assumed gruoidean affinities of the Geranoididae, he later (Cracraft 1973) proposed closer affinities to the cariamiform Bathornithidae.

Although Cracraft (1969) is to be credited for recognizing the close relationships between the above species, some of his newly erected taxa are based on very

fragmentary remains and were not compared in detail with previously described species. In fact, the entire published material of all geranoidid species from the Willwood Formation consists only of incomplete leg elements, and previous descriptions and comparisons mainly focused on the distal ends of the tibiotarsus and tarsometatarsus.

Still, these birds are of considerable interest, because comparatively little is known of the larger birds that lived in Early Eocene avifaunas, with most of the numerous fossils described in the past years belonging to small arboreal forms (Mayr 2009). Geranoidids furthermore are of potential biogeographic significance, as they are considered to be most closely related to the Asian Eogruidae, a taxon that includes various species of long-legged birds from Eocene to Pliocene fossil sites of Eurasia (Cracraft 1969, 1973; Kurochkin 1981; Olson 1985; Karhu 1997).

During a visit at the American Museum of Natural History, I had the opportunity to study the geranoidid fossils housed in this institution. This led to the identification of a substantial specimen of these birds, which was not adequately appreciated by earlier authors, and raised some issues concerning the taxonomy of geranoidids that are discussed in the following.

Materials and methods

Institutional abbreviations: AMNH, American Museum of Natural History, New York, USA; YPM, Yale Peabody Museum of Natural History, New Haven, USA. In addition to the study of published illustrations, comparisons with the holotypes of *Geranoides jepseni* and *Eogeranoides campivagus* were based on photos in the online database of YPM (http://collections.peabody.yale.edu/search).

Taxonomy of the Willwood Formation Geranoididae

The type genus of the Geranoididae is *Geranoides* Wetmore, 1933. This taxon encompasses a single species, *Geranoides jepseni* Wetmore, 1933, the holotype and only known specimen of which consists of an incomplete tarsometatarsus (Fig. 1c, d), partial tibiotarsi, and some pedal phalanges. Unfortunately, it is just *Geranoides*, with which other geranoidids were only briefly compared by Cracraft (1969, 1973), and this lack of detailed comparisons is particularly true for the taxon *Palaeophasianus*.

In his reassessment of the holotype of *P. meleagroides*, Cracraft (1968: 285) remarked that "[t]he tibiotarsus of *P. meleagroides* shows some differences from the tibiotarsus of *Geranoides*, notably in the shape of the external condyle. Due to the fragmentary nature of the type material of *Palaeophasianus*, comments about its relationship with *Geranoides* are probably best kept at a minimum at this time." Later, he noted that "[a]s seen from the side, the external condyles of *Palaeophasianus* and *Geranoides* are very similar in their contours. However, the condyle is heavier in *Palaeophasianus*, the posterior intercondylar sulcus is more U-shaped […], and the anterior intercondylar fossa is apparently deeper" (Cracraft 1969: 21). Moreover, the condylus lateralis ("external condyle") is damaged in the holotype of *P. meleagroides* (AMNH 5128), and because the condylus medialis is missing in the holotype of *G. jepseni*, meaningful comparisons of the distal tibiotarsi of the two species are quite limited.

Cracraft (1969) tentatively referred another, better preserved specimen to *P. meleagroides*, which includes the distal and proximal ends of a tarsometatarsus as well as a distal tibiotarsus (AMNH 5156). Concerning this fossil, however, he noted that "[s]ome differences in size and morphology suggest that the referred specimen might represent a species distinct from *P. meleagroides*" (Cracraft 1969: 17). The distinguishing features especially concern a more strongly proximally directed eminentia intercotylaris of the proximal end of the tarsometatarsus of AMNH 5156, as well as the shape of the hypotarsus, which is much more plantarly prominent in the holotype of *P. meleagroides* (Fig. 2d) than in AMNH 5156 (Fig. 2e). Indeed, the hypotarsus of AMNH 5156 is so different from that of the holotype of *P. meleagroides* that both specimens are very unlikely to be conspecific, given the uniformity of hypotarsus shapes within avian species (Mayr 2016).

The proximal end of the tarsometatarsus is not preserved in the holotype of *Geranoides jepseni*, but the tarsometatarsus has a highly characteristic shape of the distal end, with unusually splayed trochleae, wide incisurae intertrochleares, a short trochlea metatarsi II, and a laterally deflected trochlea metatarsi III (Fig. 1c, d). Cracraft (1969: 7) interpreted this peculiar morphology as a probable taphonomic distortion of the fossil, but the *G. jepseni* holotype is one of the best preserved geranoidid fossils, and the shape of the distal tarsometatarsus is not too unusual to be real.

The distal end of the tarsometatarsus is poorly preserved in the holotype of *P. meleagroides* (Fig. 1a, b) and was not described by either Shufeldt (1913) or Cracraft (1968, 1969). Presumably because the *P. meleagroides* holotype includes a proximal tarsometatarsus from the left side, Cracraft (1969) considered the distal tarsometatarsus to be a left one, too. Actually, however, the morphology of the bone instead suggests that it is from the right side, which can be inferred from the direction in which the trochlea metatarsi III is slanted and the shortness of the more complete trochlea next to it (which identifies this

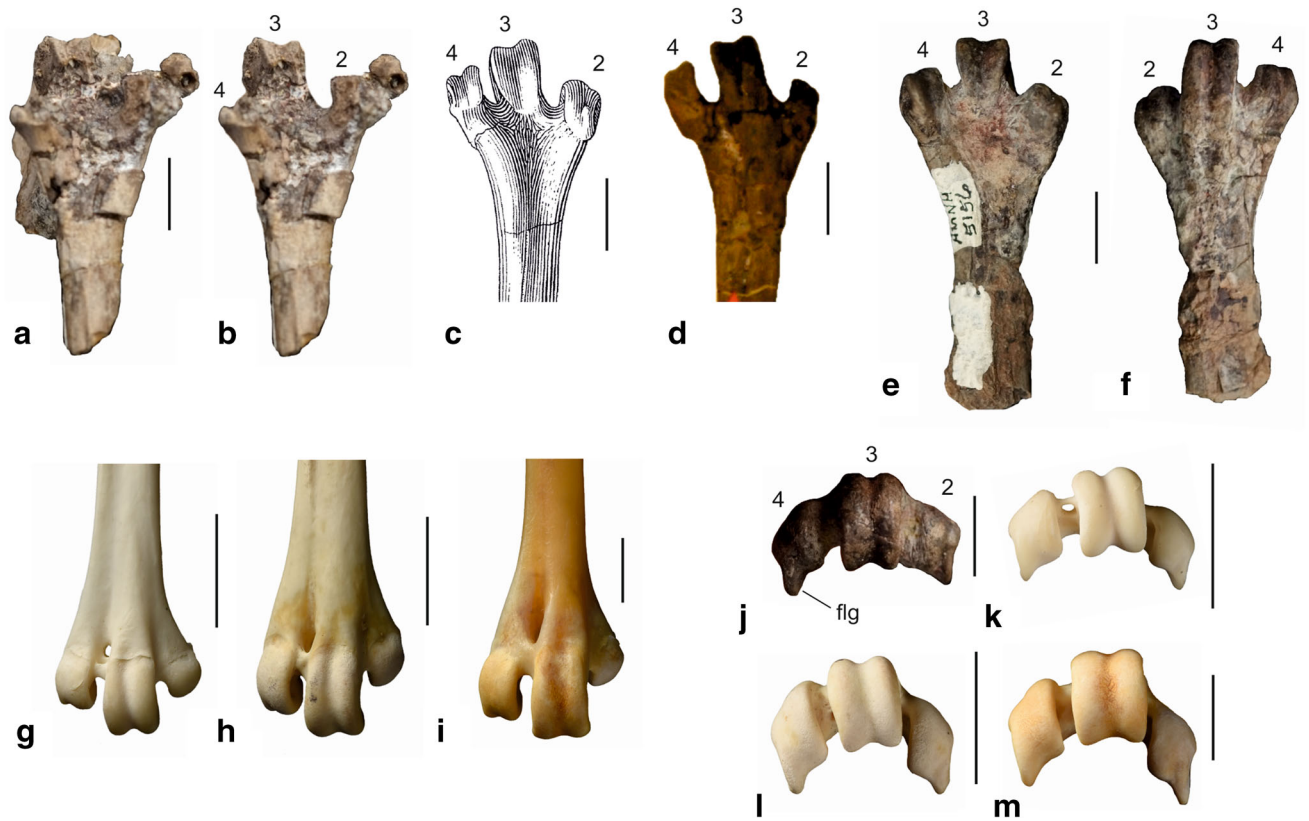

Fig. 1 Distal ends of the tarsometatarsi of *Palaeophasianus* ("*Geranoides*") in comparison with extant Gruoidea. **a**, **b** *Palaeophasianus meleagroides* (holotype, AMNH 5128), right tarsometatarsus in plantar view; in **b,** the matrix surrounding the bone was digitally removed. Holotype of *Geranoides jepseni* (YPM VP.PU.013257) in **c** plantar view (from Wetmore 1933, mirrored to ease comparisons) and **d** dorsal view. ?*Palaeophasianus* sp. (AMNH 5156) in **e** plantar and **f** dorsal view. Distal ends of right tarsometatarsi of extant Gruoidea in dorsal view: **g** *Psophia crepitans* (Psophiidae), **h** *Aramus guarauna* (Aramidae), and **i** *Balearica regulorum* (Gruidae). Distal ends of right tarsometatarsi (distal view) of **j** ?*Palaeophasianus* sp. (AMNH 5156), **k** *P. crepitans*, **l** *A. guarauna*, and **m** *B. regulorum*. The trochleae are numbered. *flg* plantar flange of trochlea metatarsi IV. *Scale bars* 10 mm

trochlea as the trochlea metatarsi II rather than the trochlea metatarsi IV, with the latter being broken in the *P. meleagroides* holotype). The distal end of the tarsometatarsus of the *P. meleagroides* holotype closely resembles that of the *G. jepseni* holotype, especially with regard to the very wide incisura intertrochlearis medialis and the marked splaying of the trochleae (Fig. 1a–d). Indeed, neither the distal tarsometatarsus nor the distal tibiotarsus of *P. meleagroides* can be differentiated from the corresponding elements of the *G. jepseni* holotype (the slight differences in Fig. 1 are due to somewhat different orientations of the bones). The holotypes of *G. jepseni* and *P. meleagroides* furthermore agree well in size and both stem from the Gray Bull fauna of the Willwood Formation in the Elk Creek of the Bighorn Basin. Accordingly, it is here concluded that *Palaeophasianus meleagroides* Shufeldt, 1913 and *Geranoides jepseni* Wetmore, 1933 are conspecific, with the former name having nomenclatural priority.

AMNH 5156, which was referred to *P. meleagroides* by Cracraft (1969), agrees with the latter species in that the incisurae intertrochleares are unusually wide, the trochlea metatarsi II is short, and the trochlea metatarsi III is laterally deflected (Fig. 1e, f). In the proportionally wider trochlea metatarsi II and the morphology of the hypotarsus (see above and Fig. 2d, e), AMNH 5156 is, nevertheless, distinguished from *P. meleagroides*, and the specimen should be classified as ?*Palaeophasianus* sp.

A very large putative geranoidid from the Willwood Formation was described as *Palaeophasianus incompletus* by Cracraft (1969). This species is only represented by a fragmentary distal end of a tarsometatarsus, and Cracraft himself was unsecure about the generic allocation of this species (i.e., whether it belongs to *Palaeophasianus* or to *Paragrus*). The fossil is, however, clearly distinguished from the tarsometatarsus of the much smaller *Palaeophasianus* ("*Geranoides*") in that the trochlea metatarsi III is not laterally deflected, the incisura intertrochlearis lateralis is narrower,

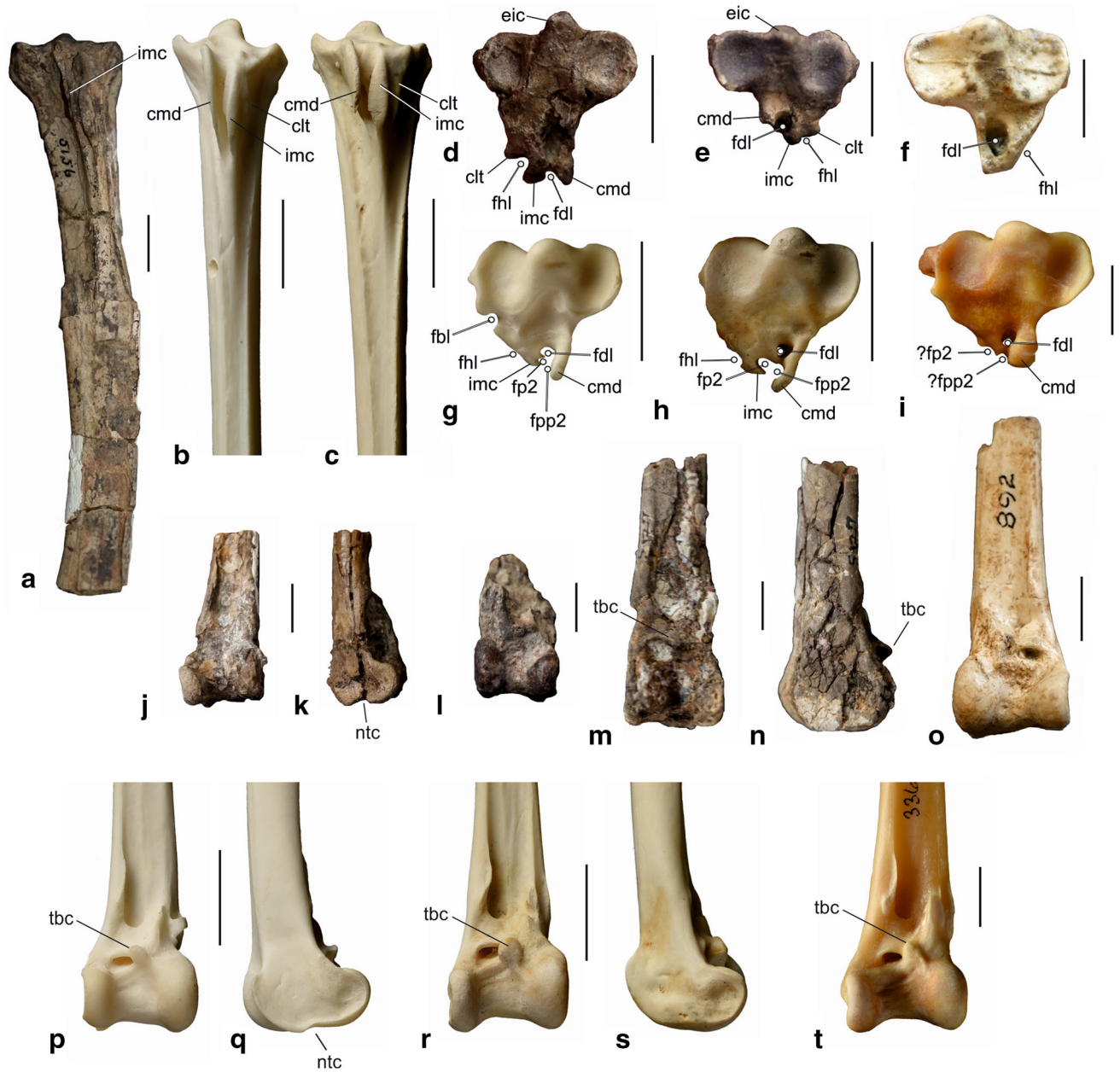

Fig. 2 Proximal tarsometatarsi and distal tibiotarsi of geranoidids from the Willwood Formation and extant Gruoidea. Proximal ends of right tarsometatarsi in plantar view: **a** ?*Palaeophasianus* sp. (AMNH 5156). **b** *Psophia crepitans* (Psophiidae). **c** *Aramus guarauna* (Aramidae). Proximal ends of tarsometatarsi in proximal view: **d** *Palaeophasianus meleagroides* (holotype, AMNH 5128), left tarsometatarsus. **e** ?*Palaeophasianus* sp. (AMNH 5156), right tarsometatarsus. **f** *Eogrus aeola* (holotype, AMNH 2936), right tarsometatarsus. **g** *P. crepitans*, left tarsometatarsus. **h** *A. guarauna*, left tarsometatarsus. **i** *Balearica regulorum* (Gruidae), left tarsometatarsus. Left tibiotarsus of *P. meleagroides* (holotype, AMNH 5128) in **j** cranial and **k** medial view. **l** Right tibiotarsus of ?*Palaeophasianus* sp. (AMNH 5156). Left tibiotarsus of AMNH 5127 (cf. "*Eogeranoides campivagus*") in **m** cranial and **n** medial view. **o** Right tibiotarsus of *Eogrus aeola* (AMNH 2946). Distal ends of left tibiotarsi of extant Gruoidea: **p**, **q** *P. crepitans*. **r**, **s** *A. guarauna*. **t** *B. regulorum*. *clt* crista lateralis, *cmd* crista medialis, *eic* eminentia intercotylaris, *fbl* sulcus for musculus fibularis longus, *fdl* sulcus/canal for tendon of musculus flexor digitorum longus, *fhl* sulcus for tendon of musculus flexor hallucis longus, *fp2* sulcus for tendon of musculus flexor perforatus digiti 2, *fpp2* sulcus for tendon of musculus flexor perforans et perforatus digiti 2, *imc* intermediate crest, *ntc* notch in distal rim of condylus medialis, and *tbc* tubercle laterodistal of pons supratendineus. *Scale bars* 10 mm

and in that the trochlea metatarsi IV lacks a well-developed plantarly directed flange (compare Cracraft 1969: fig. 9 with Fig. 1j). Although the specimen may belong to a species of the more similar *Paragrus*, it is too fragmentary for a definitive identification, and even its assignment to the Geranoididae needs to be further substantiated.

Paragrus was initially established for *Gallinuloides prentici* Loomis, 1906, whose holotype and only known specimen is the distal end of a tibiotarsus from a bird that was larger than any of the *Palaeophasianus* ("*Geranoides*") species. Another distal tibiotarsus that was initially also assigned to *P. prentici* (Loomis 1906) was described as a new species, *P. shufeldti*, by Cracraft (1969), although the features that distinguish this fossil from the *P. prentici* type are rather minor ones and difficult to trace on the published figures. Cracraft (1969) referred other bones to *P. shufeldti*, including a distal tarsometatarsus, which is distinguished from the distal tarsometatarsus of *Palaeophasianus* in that the incisurae intertrochleares are narrower, the trochleae metatarsi III is not laterally inclined, the trochlea metatatarsi II reaches farther distally, and the plantar flange of the trochlea metatarsi IV is less developed. Compared with *P. meleagroides*, the distal end of the tibiotarsus of *Paragrus shufeldti* furthermore bears a better developed tubercle next to the pons supratendineus. Unfortunately, the corresponding features are unknown for *P. prentici*, the type species of the taxon *Paragrus*, which aggravates a well-founded differentiation of *Paragrus* from *Palaeophasianus*.

The lack of detailed comparisons with *Paragrus prentici* also challenges the status of *Eogeranoides campivagus* Cracraft, 1969, which is based on fragmentary tibiotarsus and tarsometatarsus remains from the Willwood Formation. The tibiotarsus consists only of the distal section of the bone, which lacks the medial part. It was considered to be similar to the tibiotarsus of *Paragrus shufeldti*, from which it differs "in that anterior [=cranial] end of external condyle [=condylus lateralis] projects slightly more anterior" (Cracraft 1969: 14). However, Cracraft (1969: 10) listed an "external condyle decidedly less elongated in anteroposterior direction" as one of the diagnostic features distinguishing *P. shufeldti* from *P. prentici*, and *E. campivagus* has not been directly compared with the latter species. At least judging from the published illustrations, I cannot discern any significant differences between the distal tibiotarsi of *Eogeranoides campivagus* and *Paragrus prentici*, so much the more as parts of the distal end of the tibiotarsus of *P. prentici* are still covered with matrix. At present, *Eogeranoides campivagus* Cracraft, 1969 is, therefore, of doubtful validity, and may well turn out as a junior synonym of *Paragrus prentici* (Loomis, 1906).

In summary, it is here proposed to synonymize *Geranoides jepseni* Wetmore, 1933 with *Palaeophasianus meleagroides* Shufeldt, 1913. It is furthermore concluded that *Eogeranoides campivagus* Cracraft, 1969 is likely to be a junior synonym of *Paragrus prentici* (Loomis, 1906), although direct comparisons of the holotypes of these species are needed for a definitive taxonomic action. The holotype and only known specimen of "*Palaeophasianus*" *incompletus* is too fragmentary to be even sure about its correct assignment to the Geranoididae.

The first complete leg bones of a geranoidid from the Willwood Formation

In the collection of AMNH, there are a left femur, tibiotarsus, and tarsometatarsus from the Wasatchian of the Bighorn Basin (Wyoming), three miles southeast of Otto. The fossils (AMNH 5127; Fig. 3) are from a large bird with a femur length of ~140 mm, a tibiotarsus length of ~295 mm, and a tarsometatarsus length of ~250 mm. They were first mentioned by Shufeldt (1913: 290), who identified them as an indeterminate turkey-sized bird of probably galliform affinities. Since Shufeldt's publication, the specimens have been further prepared, but the various fragments remain disconnected and are here for the first time assembled (Fig. 3). The tarsometatarsus now lacks the trochlea metatarsi IV, but this trochlea was originally associated with the distal end of the bone, even though it seems to have been broken and detached from the distal tarsometatarsus (Shufeldt 1913: fig. 78).

AMNH 5127 is identified as *Palaeophasianus* cf. *incompletus* in the collection of AMNH, but was not included in the studies of Cracraft (1969, 1973). Whereas the holotype of *P. incompletus* consists only of a distal tarsometatarsus fragment that lacks the trochlea metatarsi II, it is the trochlea metatarsi IV that is now missing in AMNH 5127. Meaningful comparisons between the two specimens are, therefore, quite limited, and a referral of AMNH 5127 to *P. incompletus* can only be based on the large size of the fossil (the width of the trochlea metatarsi III is 10.4 mm in "*P.*" *incompletus* [Cracraft 1969] versus 9.6 mm in AMNH 5127). With regard to the laterally deflected trochlea metatarsi III, the fossil agrees with the much smaller *Palaeophasianus meleagroides*, but this feature distinguishes it from "*P.*" *incompletus*, in which the trochlea metatarsi III is not deflected and also appears to be mediolaterally wider.

It is here considered more likely that AMNH 5127 belongs to *Eogeranoides campivagus* or *Paragrus prentici* (pending on the exact taxonomic status of the former species). The holotype of this latter species was found ten miles west of Otto (Wyoming), that is, close to the locality, from which AMNH 5127 comes from. The distal ends of the tibiotarsi of AMNH 5127 and the *P. prentici* holotype correspond well in size (width about 19.7 mm in *P. prentici* [Cracraft 1969] versus ~20 mm in AMNH 5127), but again close comparisons are impeded by the poor preservation of both specimens. A definitive assignment of


a
b
c
d
e
f
g
h
3
4
2
3
2
3
2
4

◀**Fig. 3** Left leg of a geranoidid from the Early Eocene (Wasatchian) Willwood Formation of the Bighorn Basin in Wyoming, USA (AMNH 5127; cf. "*Eogeranoides campivagus*"). The specimen consists of various fragments that were assembled for the photo. **a** Left tibiotarsus and femur. Left tarsometatarsus in **b** lateral and **c** dorsal view. The misalignment of the midsection of the shaft is due to the preservation of the fossil fragments. **d** Distal end of the tarsometatarsus of AMNH 5127 as figured by Shufeldt (1913: fig. 78). **e** Distal tarsometatarsus of AMNH 5127 as it is now after preparation. Right tarsometatarsus of *Eogrus aeola* (AMNH 2937) from the Middle Eocene Irdin Manha Formation of the Shara Murun region in Inner Mongolia (China) in **f** dorsal and **g** plantar view. **h** Detail of distal end in dorsal view. In **d**, **e,** and **h,** the trochleae are numbered. *Scale bars* 10 mm for **d**, **e,** and **h**, and 50 mm for **a**–**c**, **f,** and **g**

AMNH 5127 not only depends on direct comparisons with the *P. prentici* holotype, but also requires a reexamination of the *Eogeranoides campivagus* holotype, which, as detailed above, is likely to be a junior synonym of *Paragrus prentici*.

Irrespective of its still to be settled taxonomic identity, AMNH 5127 is the first North American geranoidid, of which complete leg elements are preserved. Although the poor preservation of the specimen precludes the description of many osteological details, some information on skeletal features can, nevertheless, be gained.

The femur is comparatively stout and appears to have had a slightly curved shaft. In its proportions, it is distinguished from the more slender femur of the Psophiidae and Aramidae, whereas the femur of the Gruidae has a straighter shaft (Fig. 4). Unlike in extant Gruoidea, there seems to have been no well-developed crista trochanteris. The distal end of the bone resembles the distal femur of extant Gruoidea, but adhering matrix obscures the recognition of osteological details.

Although the tibiotarsus is largely complete, the ends of the bone are very poorly preserved, which aggravates the recognition of osteological details. As in all extant Gruoidea, the crista cnemialis cranialis appears to be very large and cranially prominent. The distal end bears a fairly well-developed tubercle laterodistal of the pons supratendineus, but there is no marked notch in the distal rim of the condylus medialis; both features may, however, be a result of the abrasion of the specimen. In lateral view, the shape of the condylus lateralis resembles that of the holotypes of *Eogeranoides campivagus* and *Paragrus prentici* as figured by Cracraft (1969).

The tarsometatarsus is broken into several pieces, which were reassembled for Fig. 3b, c. The bone is long and slender, and the dorsal surface of its proximal end exhibits a very marked sulcus extensorius. In size and morphology, especially with regard to the relative position of the cotylae and the shape of the eminentia intercotylaris, the poorly preserved proximal end of the bone resembles the proximal tarsometatarsus of *E. campivagus* as figured by Cracraft (1969: fig. 6). Details of the hypotarsus are not discernible. The foramen vasculare distale is rather small, and the trochlea metatarsi II bears a distinct furrow. The distal tarsometatarsus of *E. campivagus* was not shown by Cracraft (1969), but, judging from a photo of the holotype in the online database of YPM, likewise shows a close resemblance to AMNH 5127.

Discussion

As detailed above, only two supraspecific taxa of the geranoidids from the Willwood Formation are here considered to be well established, that is, *Palaeophasianus* (including *Geranoides*) and *Paragrus* (possibly including *Eogeranoides*). An assignment of both taxa to the Gruoidea is supported by derived features of the tibiotarsus, especially a marked notch in the distal rim of the condylus medialis and a tubercle on the cranial surface of the distal tibiotarsus, laterodistal of the pons supratendineus (Fig. 2j–t), which serves as a support for the eminentia intercotylaris of the tarsometatarsus (both features occur in various other extant taxa and the latter may be functionally correlated with a very long tarsometatarsus). At least *Palaeophasianus* furthermore agrees with taxa of the Gruoidea in a derived morphology of the proximal end of the tarsometatarsus, which bears a proximodistally long hypotarsus with a well-developed central crest that separates the tendon of musculus flexor hallucis longus from that of musculus flexor digitorum longus (Fig. 2a–i; the hypotarsus of *Paragrus* is unknown).

Palaeophasianus is well characterized by the derived morphology of the distal end of its tarsometatarsus, in which the trochlea metatarsi II is short, the incisura intertrochlearis medialis very wide, and the trochlea metatarsi III laterally deflected (Fig. 1). Although the distal end of the tarsometatarsus of *Paragrus* resembles that of *Palaeophasianus* in overall shape, it lacks the aforementioned derived characteristics. So far, no apomorphies were identified that are exclusively shared by both taxa, and it is, therefore, anything but certain that *Palaeophasianus* and *Paragrus* are sister taxa.

Within Gruoidea, geranoidids are considered to be closely related to the Eogruidae, the earliest representatives of which belong to *Eogrus aeola* from the Middle and Late Eocene Eocene of China, Mongolia, and Kazakhstan (Fig. 3; Wetmore 1934; Mayr 2009). Later geranoidids, that is, the taxa *Sonogrus*, *Amphipelargus*, and *Urmiornis*, are characterized by a progressive reduction of the trochlea metatarsi II of the tarsometatarsus, which ultimately led to the complete loss of this trochlea and, hence, the second

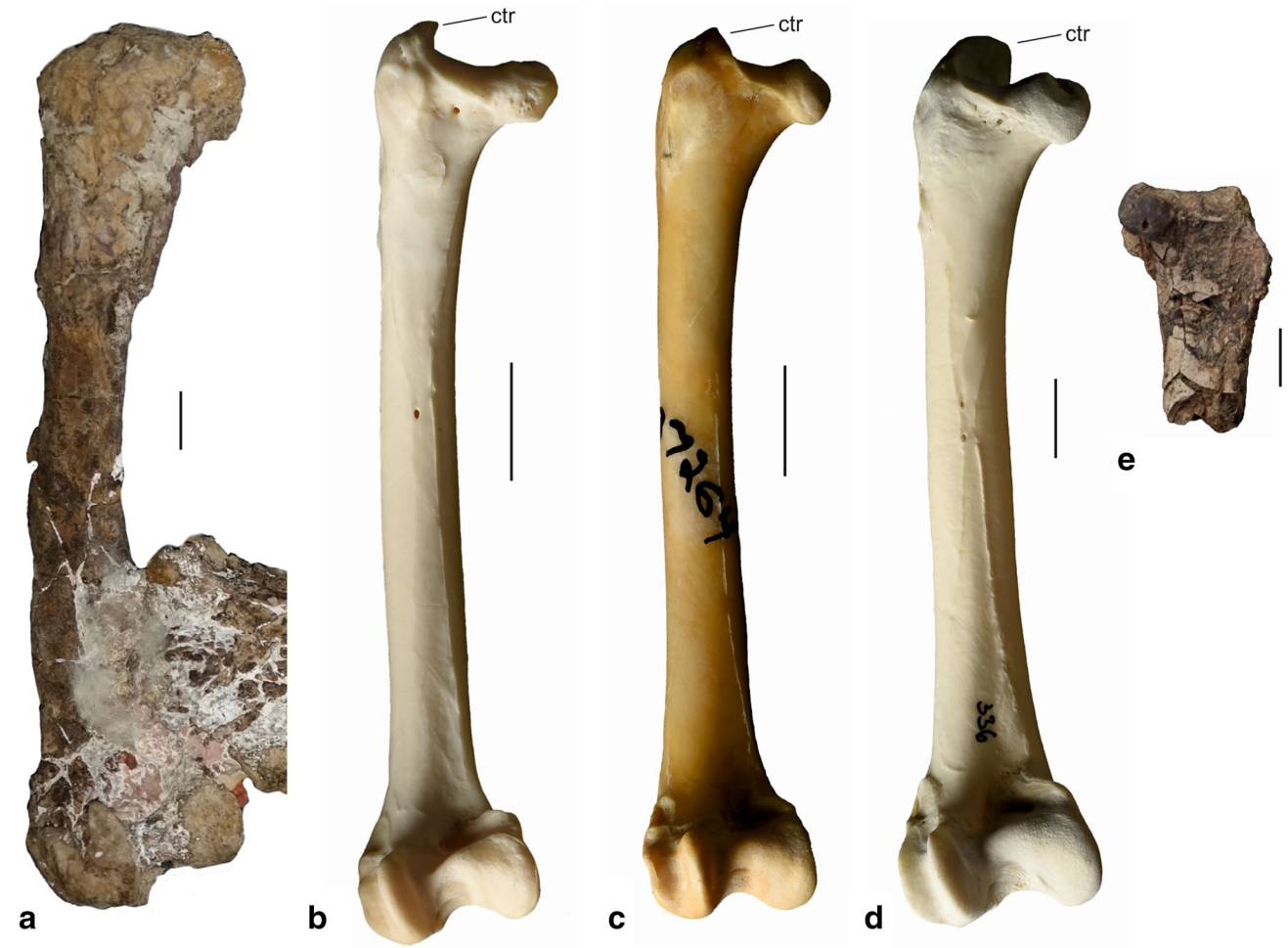

Fig. 4 Femora of geranoidids from the Willwood Formation and extant Gruoidea. **a** Left femur of AMNH 5127 (cf. "*Eogeranoides campivagus*") in caudal view. Left femora (caudal view) of **b** *Psophia crepitans* (Psophiidae), **c** *Aramus guarauna* (Aramidae), and **d** *Balearica regulorum* (Gruidae). **e** Proximal end of left femur of ?*Palaeophasianus* sp. (AMNH 5156) in cranial view. *crt* crista trochanteris. *Scale bars* 10 mm

toe. Because of this remarkable case of didactyly, Olson (1985: 153) considered geranoidids to be stem group representatives of the palaeognathous Struthioniformes, the only other taxon in which the second toe is lost. The single phylogenetic analysis in which eogruids were included, by contrast, resulted in a sister group relationship between Eogruidae and a clade including Aramidae and Gruidae, and, therefore, established the traditional assignment of these birds to the Gruoidea (Clarke et al. 2005).

Whereas close affinities between Geranoididae and Eogruidae are very likely, the exact interrelationships between both taxa are not well established. Species of the Geranoididae were not considered in the analysis of Clarke et al. (2005), and although Cracraft (1973: 108) noted that "Geranoididae and Eogruidae shared numerous features that suggest their derivation from a common ancestor," the evidence for a sister group relationship between both taxa is actually quite limited. Most characters listed by Cracraft (1973) refer to similar overall shapes of osteological structures, and among the more specific features are a parallel orientation of the condyles of the distal tibiotarsus and a lateral placement of the hypotarsus. Newly added here is a long and slender tarsometatarsus, which occurs in at least *Palaeophasianus* (as evidenced by the *Geranoides jepseni* holotype) and *Eogeranoides* (both the *E. campivagus* holotype and AMNH 5127).

Currently, most of our knowledge about the osteology of eogruids and geranoidids is restricted to features of the major leg bones. However, in the collection of the AMNH, there is a left coracoid from the Middle Eocene type locality of *Eogrus aeola*, which was initially assigned to the Falconiformes by Wetmore (1934). Olson (1985: 154) was the first to propose that the specimen (AMNH 2941) actually belongs to *Eogrus aeola*, and this identification is followed here. As noted by Olson (1985) and Mayr (2009), this coracoid differs in several features from the

corresponding bone of extant Gruoidea. In particular, the extremitas omalis is more medially inflected, the processus procoracoideus shorter, and the cotyla scapularis more excavated than in extant Gruoidea, and unlike in the latter, there is a deep fossa in the sulcus supracoracoideus, just below the cotyla scapularis (Fig. 5b). In further contrast to extant Gruoidea, the dorsal surface of the extremitas sternalis is smooth and does not exhibit marked ridge-like scars (Fig. 5). Some of these differences were taken by Olson (1985) as evidence for a possible flightlessness of *Eogrus*. Alternatively, however, they may be genuinely plesiomorphic, and especially the absence of ridge-like scars on the extremitas sternalis of the coracoid, the cup-like cotyla scapularis, and the less pronounced tubercle on the distal tibiotarsus support a position of *Eogrus* outside crown group Gruoidea. Clarke et al. (2005) identified one character that suggests a sister group relationship between Eogruidae and the clade (Aramidae + Gruidae), that is, "trochlea metatarsi II subequal to IV in distal projection, distal end reaching approximately middle of trochlea metatarsi IV" (Clarke et al. 2005: 10). Actually, however, the trochlea metatarsi II is shorter than the trochlea metatarsi IV in Eogruidae, Aramidae, and Gruidae (see Figs. 1h, i, 3h), but the polarity of this feature is uncertain, because a short trochlea metatarsi II also occurs in many Ralloidea, which are the sister taxon of the Gruoidea (e.g., Ericson et al. 2006; Prum et al. 2015), as well as in the extinct Parvigruidae, which are another group of stem group Gruoidea (Mayr 2013 and below).

The morphology of *Palaeophasianus meleagroides* ("*Geranoides jepseni*") likewise does not support its position within crown group Gruoidea. The crista medialis of the hypotarsus of *Palaeophasianus* is less developed in extant Gruoidea, and unlike in the latter, the femur of geranoidids, as exemplified by AMNH 5156 (cf. *Palaeophasianus)* and AMNH 5127 (cf. "*Eogeranoides*"), lacks a well-developed crista trochanteris (Fig. 4). These plesiomorphic features suggest a position of at least *Palaeophasianus* outside crown group Gruoidea. The hypotarsus of *Palaeophasianus meleagroides* differs from that of all extant Gruoidea, with the most notable characteristics being its marked plantar prominence and the presence of a distinct sulcus for the tendon of musculus flexor hallucis longus (Fig. 2). This peculiar morphology may be an autapomorphy of *P. meleagroides* related to a specialized use of the hindlimbs of this species. Indeed, the hypotarsus of AMNH 5156, the specimen that was referred to *P. meleagroides* by Cracraft (1969), better conforms with that of *Eogrus* in that it is less plantarly prominent, and the sulcus for the tendon of musculus flexor hallucis longus is much less marked (Fig. 2e, f).

The presence of a tubercle on the distal end of the tibiotarsus may indicate that geranoidids are more closely related to crown group Gruoidea than are the Parvigruidae from the Early Oligocene of Europe, which were also considered to be stem group representatives of the Gruoidea (Mayr 2013). However, before a meaningful analysis of the interrelationships of these and other Paleogene Gruoidea can be performed, it would be desirable to revisit collections of bird fossils from the Willwood Formation and to identify further skeletal elements of geranoidids. In this regard, it may be particularly rewarding to restudy the

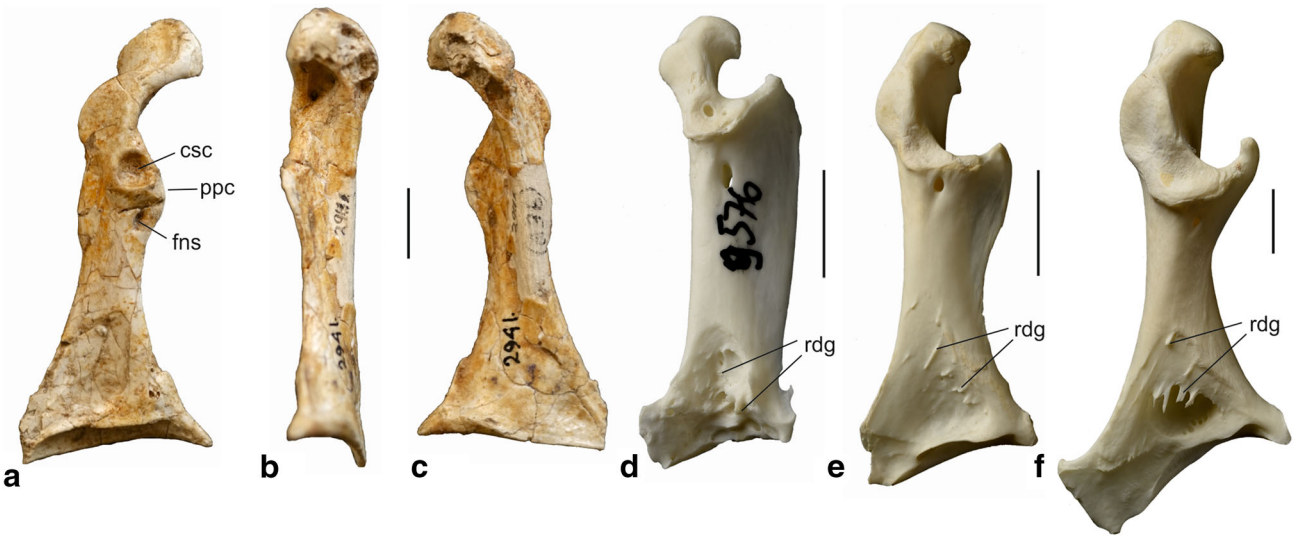

Fig. 5 *Eogrus aeola* (Eogruidae), tentatively referred left coracoid (AMNH 2941) from the Middle Eocene of the Irdin Manha Formation of the Shara Murun region in Inner Mongolia (China), in **a** dorsal, **b** medial, and **c** ventral view. Coracoids of extant Gruoidea in dorsal view: **d** *Psophia crepitans* (Psophiidae). **e** *Aramus guarauna* (Aramidae). **f** *Balearica regulorum* (Gruidae). *csc* cotyla scapularis, *fns* foramen nervi supracoracoidei, *ppc* processus procoracoideus, and *rdg* ridge-like scars. *Scale bars* 10 mm

holotype of the alleged heron *Calcardea junnei* from Clark's Fork Basin of the Willwood Formation (Gingerich 1987). The specimen consists of partial coracoids, fragmentary tarsometatarsi, as well as a sternum fragment, and two incomplete vertebrae. Unfortunately, no photographs of these fossils were published, but at least judging from the published drawing, the coracoid resembles the just mentioned bone that is likely to belong to *Eogrus*. A reexamination of the *Calcardea junnei* holotype may, therefore, be worthwhile and may shed further light on the osteology and affinities of geranoidids.

I would like to conclude this revision of some North American geranoidids with some notes on the possible occurrence of these birds in the early Paleogene of Europe. The avifaunas of Europe and North America were very similar in the Early Eocene, and intermittent land connections allowed even the dispersal of flightless birds (Mayr 2009). It would therefore not be unexpected to find geranoidids in the Early Eocene of Europe. Indeed, it was recently suggested that fossils from the Early Eocene of France may represent such remains (Bourdon et al. 2016). These specimens were described as *Galligeranoides boriensis* Bourdon et al., 2016, and the referred material includes a tibiotarsus and a tarsometatarsus. However, some differences to the North American Geranoididae were already noted by Bourdon et al., (2016), and especially in distal view, the tarsometatarsus of *Galligeranoides* is clearly distinguished from that of *Palaeophasianus* ("*Geranoides*"), with the mediolateral width of the trochlea metatarsi III of *G. boriensis* exceeding its dorsoplantar depth, but being much deeper than wide in *Palaeophasianus* (including "*Geranoides*") and *Paragrus* (compare Bourdon et al. 2016: fig. $6B_4$ with Fig. 1j). The hypotarsus of *Galligeranoides* furthermore consists of a single large crest, and there are no marked sulci for the tendons of either musculus flexor digitorum longus or musculus flexor hallucis longus. The distal end of the tibiotarsus is distinguished from that of *Palaeophasianus* and *Paragrus* in that the condylus medialis does not bear a notch in its distal rim, and the pons supratendineus is much wider. Accordingly, it is here considered doubtful that *Galligeranoides* belongs to the Geranoididae, and it was already previously suggested that the taxon is more likely to be a representative of the palaeognathous Palaeotididae (Mayr 2015). Still, however, eogruids may well have occurred in the Early Eocene of Europe, and, at least judging from the published figures, the distal end of the tibiotarsus of *Paragrus prentici* is remarkably similar to that of *Palaeogrus princeps* from the Middle Eocene of Italy. This latter species was described by Portis (1884) and is only known from the holotype distal tibiotarsus. *P. princeps* is currently assigned to the Gruidae (Cracraft 1973; Mlíkovský 2002), but has not yet been compared with geranoidids. Because of its comparable age and morphological alikeness, I consider an assignment to the Geranoididae more likely than its current referral to the Gruidae.

Acknowledgments I thank Carl Mehling (AMNH) for access to fossil specimens and Christopher Norris (YPM) for permission to use a photo of the *Geranoides jepseni* holotype. Sven Tränkner took the photos of the extant comparative material. Comments from two reviewers, Vanesa De Pietri and Trevor Worthy, improved the manuscript.

References

Bourdon, E., Mourer-Chauviré, C., & Laurent, Y. (2016). Early Eocene birds from La Borie, southern France. *Acta Palaeontologica Polonica, 61*, 175–190.

Clarke, J. A., Norell, M. A., & Dashzeveg, D. (2005). New avian remains from the Eocene of Mongolia and the phylogenetic position of the Eogruidae (Aves, Gruoidea). *American Museum Novitates, 3494*, 1–17.

Cracraft, J. (1968). Reallocation of the Eocene Fossil *Palaeophasianus meleagroides* Shufeldt. *The Wilson Bulletin, 80*, 281–285.

Cracraft, J. (1969). Systematics and evolution of the Gruiformes (Class, Aves). 1, The Eocene family Geranoididae and the early history of the Gruiformes. *American Museum Novitates, 2388*, 1–41.

Cracraft, J. (1973). Systematics and evolution of the Gruiformes (Class Aves). 3. Phylogeny of the suborder Grues. *Bulletin of the American Museum of Natural History, 151*, 1–127.

Ericson, P. G. P., Anderson, C. L., Britton, T., Elzanowski, A., Johansson, U. S., Källersjö, M., et al. (2006). Diversification of Neoaves: Integration of molecular sequence data and fossils. *Biology Letters, 2*, 543–547.

Gingerich, P. D. (1987). Early Eocene bats (Mammalia, Chiroptera) and other vertebrates in freshwater limestones of the Willwood Formation, Clark's Fork Basin, Wyoming. *Contributions from the Museum of Paleontology, University of Michigan, 27*, 275–320.

Karhu, A. (1997). A new species of *Urmiornis* (Gruiformes: Ergilornithidae) from the early Miocene of western Kazakhstan. *Paleontological Journal, 31*, 102–107.

Kurochkin, E. N. (1981). New representatives and evolution of two archaic gruiform families in Eurasia. *Trudy Sovmestnaja Sovetsko-Mongolskaja Paleontologicheskaja Ekspeditsija, 15*, 59–85. **(in Russian)**.

Loomis, F. B. (1906). A fossil bird from the Wasatch. *American Journal of Science*, *22*, *series 4*, 481–482.

Mayr, G. (2009). *Paleogene fossil birds*. Heidelberg: Springer.

Mayr, G. (2013). Parvigruidae (Aves, core-Gruiformes) from the early Oligocene of Belgium. *Palaeobiodiversity and Palaeoenvironments, 93*, 77–89.

Mayr, G. (2015). The middle Eocene European "ratite" *Palaeotis* (Aves, Palaeognathae) restudied once more. *Paläontologische Zeitschrift, 89*, 503–514.

Mayr, G. (2016). Variations in the hypotarsus morphology of birds and their evolutionary significance. *Acta Zoologica*, *97*, 196–210.

Mlíkovský, J. (2002). *Cenozoic birds of the world. Part 1: Europe*. Praha: Ninox Press.

Olson, S. L. (1985). The fossil record of birds. In D. S. Farner, J. R. King, & K. C. Parkes (Eds.), *Avian biology* (Vol. 8, pp. 79–238). New York: Academic Press.

Portis, A. (1884). Contribuzioni alla ornitolitologia italiana. *Memorie della Reale Accademia delle Scienze di Torino, 36*, 361–384.

Prum, R. O., Berv, J. S., Dornburg, A., Field, D. J., Townsend, J. P., Moriarty Lemmon, E., & Lemmon, A. R. (2015). A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature, 526*, 569–573.

Shufeldt, R. W. (1913). Further studies of fossil birds with descriptions of new and extinct species. *Bulletin of the American Museum of Natural History, 32*, 285–306.

Wetmore, A. (1933). Fossil bird remains from the Eocene of Wyoming. *Condor, 35*, 115–118.

Wetmore, A. (1934). Fossil birds from Mongolia and China. *American Museum Novitates, 711*, 1–16.