

The Early Eocene bird *Gallinuloides wyomingensis* —a stem group representative of Galliformes

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We identified a second, perfectly preserved skeleton of the earliest known galliform bird, *Gallinuloides wyomingensis* Eastman. The new specimen clearly shows that *G. wyomingensis* does not belong to crown group Galliformes as assumed by earlier authors. In particular, the primitive presence of a deeply excavated, concave facies articularis scapularis at the coracoid precludes the inclusion of *G. wyomingensis* into crown group Galliformes. *Gallinuloides wyomingensis* is morphologically very similar to *Paraortygoides messelensis* Mayr, a nearly contemporaneous galliform from Messel, Germany. The exclusive presence of stem group galliform birds in pre-Oligocene deposits does not support the Gondwanan origin of Galliformes as evidenced by the Southern Hemisphere distribution of basal crown group members (Megapodiidae and Cracidae).

Key words: Aves, Galliformes, *Gallinuloides*, *Paraortygoides*, Green River Formation, Eocene.

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Introduction

Extant Galliformes (landfowl) include the Australasian Megapodiidae (megapodes, “brush-turkeys”), which are the sister taxon of the Neotropic Cracidae (guans, chachalacas, and curassows) and the Phasianidae (guineafowl, turkeys, grouse, pheasants, and allies) (e.g., Cracraft 1988; Mayr 2000; Ericson et al. 2001; Livezey and Zusi 2001).

There is a growing consensus, from both molecular and morphological studies, that the Galliformes are the sister taxon of the Anseriformes (waterfowl) (e.g., Sibley and Ahlquist 1990; Dzerzhinsky 1995; Groth and Barrowclough 1999; van Tuinen et al. 2000; Cracraft and Clarke 2001; Livezey and Zusi 2001; see also Ericson et al. 2001).

Apart from fragmentary Late Cretaceous bones tentatively referred to the Galliformes (Hope 2002), the Early Eocene *Gallinuloides wyomingensis* Eastman, 1900 is the earliest known unquestionable galliform bird. To date, the taxon was known only from the holotype, a poorly preserved articulated specimen from the Green River Formation in Wyoming, USA (Fig. 1).

Lucas (1900) classified *G. wyomingensis* into its own family Gallinuloididae. Although Eastman (1900: 57) considered the species to be in “a position intermediate between the orders Paludicolae [= Gruiformes, i.e., rails, cranes, and allies] and Gallinae [= Galliformes]”, it was assigned to crown group Galliformes by subsequent authors—either to the Cracidae (Tordoff and Macdonald 1957; Brodkorb 1964; Ballmann 1969) or to the Phasianidae (Shufeldt 1915; Cracraft 1973; Crowe and Short 1992).

Mayr (2000) described a well-preserved skeleton of a galliform bird from the Middle Eocene of Messel (Germany) that exhibits a very similar osteology to that of *G. wyomingensis*. He assigned the Messel galliform to a new taxon, *Paraortygoides messelensis*, which he tentatively classified into the Gallinuloididae. Contrary to previous authors, Mayr (2000) considered the Gallinuloididae to be stem group galliforms. Dyke and Gulas (2002) reported another species of *Paraortygoides* from the Early Eocene London Clay in England and performed a cladistic analysis that supported placement of *Paraortygoides* outside the crown group Galliformes.

Most recently, however, the systematic affinities of *Gallinuloides wyomingensis* were evaluated by Dyke (2003) who, for this taxon, coded 39 of 102 osteological characters used in a phylogenetic analysis of extant Galliformes by Dyke et al. (2003). His analysis resulted in a sister group relationship between *Gallinuloides* and extant Phasianidae. Although the robustness of the resulting phylogeny was not evaluated and only few characters were listed as synapomorphies of *Gallinuloides* and Phasianidae (see below), Dyke (2003: 6) considered his analysis to be the “first clear character evidence that *Gallinuloides* is not in fact basal within the order”. He neither discussed the evidence for a basal position of the very similar and roughly contemporaneous *Paraortygoides* (Mayr 2000; Dyke and Gulas 2002), nor the fact that in Europe crown group Galliformes have not been identified in deposits earlier than Oligocene (Mourer-Chauviré 1992). In a calibration of galliform molecular clocks, van Tuinen and Dyke (2004) subsequently used *G.*

wyomingensis to estimate the divergence time between Numididae and Phasianidae some 50–54 million years ago.

A revision of the avifauna of the Green River Formation by one of us (IW) led to the identification of a second, perfectly preserved skeleton of *G. wyomingensis* from the type locality (Fig. 2). This specimen exhibits previously unknown osteological features that clearly show that *Gallinuloides* is not a member of crown group Galliformes and that are presented below; a detailed description of the new specimen will be presented elsewhere (Weidig in preparation). The osteological terminology used in this study follows Baumel and Witmer (1993).

Institutional abbreviations.—MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; WDC, The Wyoming Dinosaur Center, Thermopolis, USA.

Systematic paleontology

Galliformes Temminck, 1820

Gallinuloididae Lucas, 1900

Included genera: *Gallinuloides* Eastman, 1900, *Paraortygoides* Mayr, 2000.

Remarks.—Assignment of the Gallinuloididae to the Galliformes is supported by (1) the morphology of the caudal margin of the sternum (deep incisurae medialis and lateralis, trabeculae laterales and intermediae do not reach as far caudad as the trabecula mediana); (2) the presence of a very large and blade-like apophysis furculae; and (3) the great reduction of the processus procoracoideus and processus lateralis of the coracoid. Other derived galliform characters were listed by Mayr (2000) for the exceedingly similar (see below) Messel galliform *Paraortygoides messelensis* but are not preserved in the known specimens of *Gallinuloides wyomingensis*.

Emended diagnosis.—The Gallinuloididae are characterized by the combination of the following characters: (1) coracoid with deeply excavated, oval facies articularis scapularis; (2) scapula very long, with caudal end pointed; (3) sternum with apex carinae not shifted caudally; (4) humerus with well-developed second fossa pneumotricipitalis and (5) without transverse ridge at the beginning of the incisura capitis; (6) carpometacarpus very narrow and elongate, similar to that of extant Anatidae (Anseriformes); and (7) tarsometatarsus with trochleae metatarsorum splayed. Owing to preservation, characters (4) and (5) are not discernible in the known specimens of *Gallinuloides wyomingensis*; all characters, however, are present in *Paraortygoides messelensis* (see Mayr 2000). If its presence in *Gallinuloides* can be confirmed by future specimens, character (4) would distinguish the Gallinuloididae Lucas, 1900 from the very similar Quercymegapodiidae Mourer-Chauviré, 1992.



Fig. 1. *Gallinuloides wyomingensis*, holotype and hitherto only known specimen (MCZ 342221). Scale bar 20 mm.

Genus *Gallinuloides* Eastman, 1900

Remarks.—The new specimen of *G. wyomingensis* confirms the great similarity between this species and the Messel galliform *Paraortygoides messelensis*, which was already noted by Mayr (2000). In fact, all characters listed by Mayr (2000) in the diagnosis of *Paraortygoides* are also present in *Gallinuloides*. *Paraortygoides messelensis* has nearly the same size and limb bone proportions as *G. wyomingensis*. Some differences between the two taxa that were listed by Mayr (2002) are due to a misinterpretation of the poorly preserved holotype of *G. wyomingensis*, i.e., the purportedly shorter furcula and more protruding processus extensorius on the carpometacarpus of *Gallinuloides*. The proportionally shorter carina sterni of *P. messelensis* (Mayr 2000) needs to be verified in additional specimens of this species with a better preserved sternum. *Gallinuloides wyomingensis* differs from *P. messelensis* by having: (1) a proportionally longer ulna, which is slightly longer than the humerus in *G. wyomingensis* but slightly shorter than the hu-



Fig. 2. *Gallinuloides wyomingensis*, newly identified specimen from the Green River Formation (WDC CGR-012). Scale bar 20 mm.

merus in *P. messelensis* (the ratio ulna:tarsometatarsus is ~1.44 in *G. wyomingensis* and ~1.34 in *P. messelensis*); (2) a proportionally longer phalanx distalis digiti majoris which is longer than the phalanx proximalis digiti majoris in *Gallinuloides*, but only as long as this phalanx in *Paraortygoides*; and (3) proportionally longer anterior toes (third toe almost as long as tarsometatarsus in *G. wyomingensis* but distinctly shorter than tarsometatarsus in *P. messelensis*); and (4) claw of the third toe relatively longer and narrower.

Gallinuloides wyomingensis Eastman, 1900

Figs. 1–6.

Referred specimen: WDC CGR-012 (complete articulated skeleton on a slab).

Locality and horizon: Green River Formation, Upper Fossil Butte Member of Fossil Lake (18-inch-layer), Kemmerer, Wyoming, USA, Early Eocene; see Grande (1980) for a detailed description of the locality.

Measurements (in mm, measurements of the holotype in brackets): Humerus: ~47 (right) [46.7 (left), 47.3 (right)]. Ulna: ~48.4 (left), ~49 (right) [49.1 (left)]. Carpometacarpus: 25.5 (left), ~27.1 (right) [26.2 (left)]. Femur: 39.7 (right) [41.0 (left)]. Tibiotarsus: 56.4 (left), 56.0 (right) [57.4 (left), 56.7 (right)]. Tarsometatarsus: 34.2 (left), 34.0 (right) [34.5 (left), 33.9 (right)]

Characters bearing on the phylogenetic position of *Gallinuloides*

(1) The skull has a well-developed os ectethmoidale (Fig. 3) which is reduced in extant Cracidae and Phasianidae (see also Cracraft 1968). The presence of a well developed os ectethmoidale almost certainly is plesiomorphic within galliform birds.

(2) The skull has poorly developed processi postorbitales (Fig. 3) and lacks ossified aponeuroses zygomaticae, which are a characteristic derived feature of all extant Galliformes (see Zusi and Livezey 2000).

(3) The coracoid bears a cup-like, concave facies articularis scapularis (Fig. 4) which also occurs in *Paraortygoides* (Mayr 2000) and the Paleogene Quercymegapodiidae and Paraortygidae (Mourer-Chauviré 1992, 2000; Alvarenga 1995), but is absent in all crown group Galliformes in which the facies articularis scapularis is flat or slightly convex (Fig. 5C₁). A cup-like facies articularis scapularis is present in the Anseriformes, the sister taxon of Galliformes, as well as in Mesozoic non-neornithine birds and thus unquestionably primitive within Neornithes (Mourer-Chauviré 1992; Mayr 2000; Clarke 2002).

(4) The scapula is proportionally much longer than that of any extant galliform bird and pointed. The caudal end of this

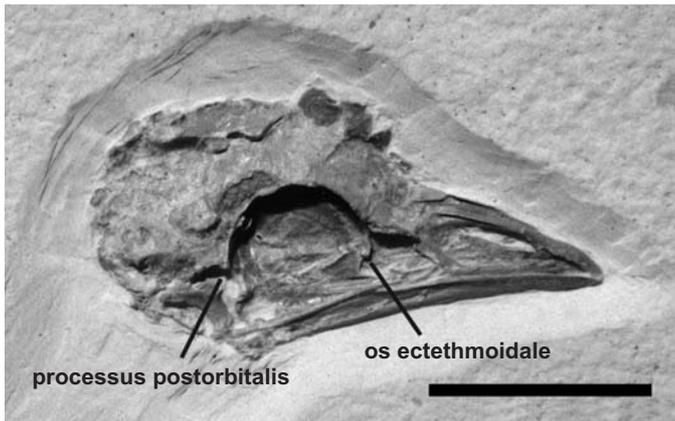


Fig. 3. *Gallinuloides wyomingensis*, skull (WDC CGR-012). Scale bar 20 mm.



Fig. 4. *Gallinuloides wyomingensis* furcula and coracoids (WDC CGR-012). The arrow at the left coracoid indicates the cup-like cotyla scapularis which distinguishes *Gallinuloides* from crown group Galliformes. Scale bar 20 mm.

bone is pointed only in the Megapodiidae but blunt in the extant Cracidae and Phasianidae. The scapula of anseriform

birds also is very long, and thus the long scapula of *Gallinuloides* is probably plesiomorphic for galliform birds.

(5) As in *Paraortygoides*, the furcula has very robust scapi claviculae that are much weaker in crown group Galliformes. Anseriform birds also have robust scapi claviculae and the weak scapi claviculae of extant galliform birds are derived relative to the condition seen in *Gallinuloides* and probably due to the large crop of galliform birds (Stegmann 1964).

(6) The apex carinae of the sternum protrudes much farther cranially than in extant Cracidae and Phasianidae. The apex carinae is shifted caudally in extant Cracidae and Phasianidae, which is a derived feature probably correlated with the large crop of these birds (Stegmann 1964).

(7) The carpometacarpus (Fig. 6) is very elongate and the spatium intermetacarpale is narrow as in Megapodiidae, Anseriformes (Fig. 5A₂), and basal non-neornithine birds (e.g., Clarke 2002). The morphology of the carpometacarpus of *Gallinuloides* strongly differs from the proportionally shorter and wider carpometacarpus of extant Cracidae and Phasianidae (Fig. 5C₂) and certainly reflects the primitive condition in galliform birds. The narrow intermetacarpal space of *Gallinuloides* is clearly visible in the holotype (Mayr 2000: 54), which makes it hard to understand why Dyke (2003: 10) considered the carpometacarpus of *Gallinuloides* to be wide.

(8) As in *Paraortygoides* and extant Megapodiidae, the trochleae metatarsorum are splayed, whereas they are situated more closely together in extant Cracidae and Phasianidae.

(9) There are no ossified tendons along the leg and wing bones. In *Paraortygoides* there is only a single ossified tendon along the plantar surface of the tarsometatarsus (which, owing to preservation is not visible in the *Gallinuloides* specimens). In extant Cracidae and Phasianidae, the tendons along the wing and leg bones usually are heavily ossified, which unquestionably is a derived condition within neornithine birds.

Discussion

The new specimen described in this study clearly shows that *Gallinuloides wyomingensis* is not a member of crown group Galliformes, let alone the sister taxon of the Phasianidae. In particular, the primitive presence of a deeply excavated facies articularis scapularis on the coracoid precludes the inclusion of *Gallinuloides* into crown group Galliformes (see above, Mourer-Chauviré 1992; Mayr 2000). *Gallinuloides* further lacks several synapomorphies of the clade (Cracidae + Phasianidae) of which especially the primitive morphology of the very “anseriform” carpometacarpus precludes assignment of the fossil taxon to either Cracidae or Phasianidae (Fig. 7).

As also noted by Crowe and Short (1992), the similarities shared by *Gallinuloides wyomingensis* and extant Cracidae,

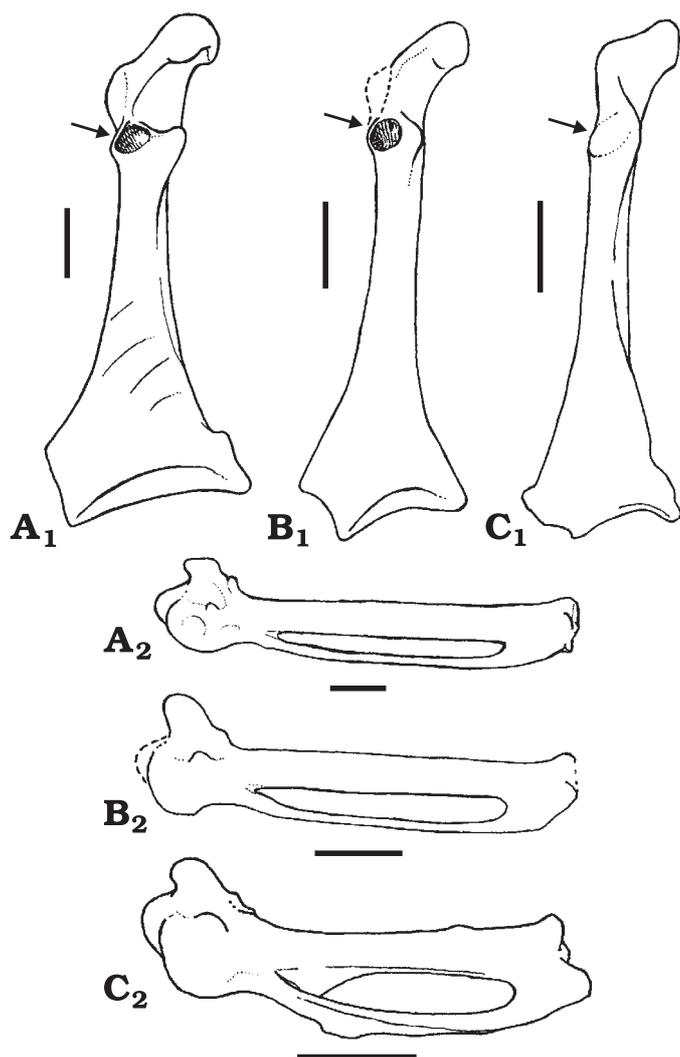


Fig. 5. Left coracoid (A₁, B₁, C₁) and carpometacarpus (A₂, B₂, C₂) of anseriform and galliform birds in comparison. A. *Anas crecca* (Anatidae, Anseriformes; SMF 851). B. *Gallinuloides wyomingensis* (Gallinuloididae, stem group Galliformes; WDC CGR-012). C. *Lophortyx gambelii* (Phasianidae, crown group Galliformes; SMF 1604). The arrows indicate the facies articularis scapularis of the coracoid which is shallow in crown group Galliformes. Scale bars 5 mm.

such as the morphology of the caudal margin of the sternum, similar limb proportions, hind toe articulating at same level as anterior toes (see Tordoff and Macdonald 1957), are plesiomorphic within Galliformes and also present in the Megapodiidae, the sister group of the clade (Cracidae + Phasianidae).

Crowe and Short (1992) based their assignment of *Gallinuloides wyomingensis* to the Phasianidae on an undescribed proximal end of a humerus from the Oligocene of North America, which they referred to *Gallinuloides* sp. Our examination of this specimen (MCZ 342506), which is considerably larger than *G. wyomingensis*, indicates that it is not referable to *Gallinuloides*. The proximal end of the humerus of the holotype of *G. wyomingensis* is badly crushed and even

the better preserved new specimen does not show any diagnostic characters that would permit reliable assignment of an isolated proximal humerus to *Gallinuloides*. Besides, a second pneumatic fossa, which is listed as evidence for the phasianid affinities of MCZ 342506 by Crowe and Short (1992), also occurs in basal Galliformes such as *Paraortyx* (Mourer-Chauviré 1992) and *Paraortygoides* (Mayr 2000), and thus seems to have evolved independently several times within Galliformes. This character is also found in gulls (Laridae) and many songbirds (Passeriformes).

Dyke (2003: 4) listed two characters in order to support his assignment of *Gallinuloides* to the clade (Cracidae + Phasianidae): “(1) trochlea [sic] of tarsometatarsus pinched [sic] together; and (2) carpometacarpus with a wide spatium intermetacarpale”. As detailed above, both character states are absent in *Gallinuloides wyomingensis*. The single character Dyke (2003) listed as synapomorphy of the clade (*Gallinuloides* + Phasianidae), the “presence of a large and well-developed foramen pneumaticum on the proximal end of the humerus” is not discernible either in the holotype of *G. wyomingensis* (the only specimen studied by Dyke) or in the new specimen described in this study.

Several other features coded by Dyke (2003) as present in *G. wyomingensis* also cannot be seen in the holotype or the new specimen described in this study because of the preservation of both specimens, including a moderately developed “secondary fossa pneumaticum [sic]” (his character 56), a ridge enclosing the incisura capitis distally from the crus dorsale fossae (his character 61), and a distinctly asymmetric trochlea metatarsi III (his character 83).

The new specimen of *Gallinuloides wyomingensis* provides evidence that the Early Oligocene *Procrax* Tordoff and Macdonald, 1957 is not closely related to *Gallinuloides* (contra Tordoff and Macdonald 1957). *Procrax* distinctly differs from *Gallinuloides* at least in the morphology of the carpo-

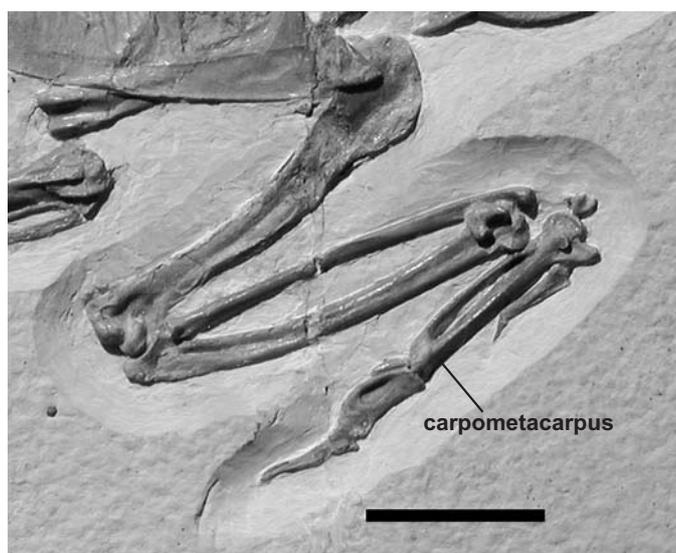


Fig. 6. *Gallinuloides wyomingensis*, left wing (WDC CGR-012). Note the slender, “anseriform” carpometacarpus. Scale bar 20 mm.

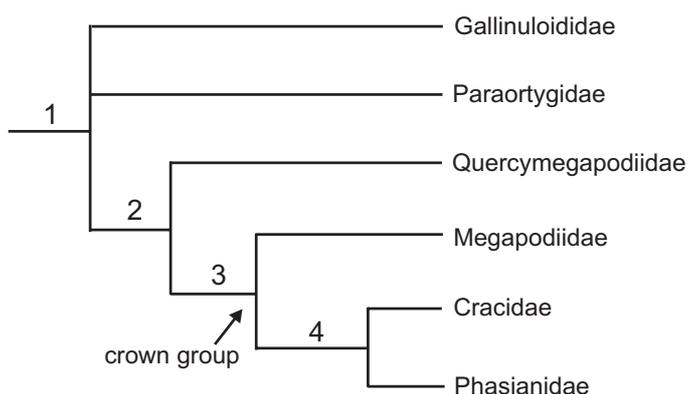


Fig. 7. Relationships between Gallinuloididae Lucas, 1900, Paraortygidae Mourer-Chauviré, 1992, Quercymegapodiidae Mourer-Chauviré, 1992, and crown group Galliformes. The nodes are characterized as follows: 1, humerus with marked elongated tuberculum dorsale; plantar side of articular surface of trochlea metatarsi III asymmetric with lateral ridge protruding farther proximally than medial ridge; 2, humerus with transversal ridge at the beginning of the incisura capitis (weakly developed in Quercymegapodiidae); 3, cotyla scapularis of coracoid shallow; 4, carpometacarpus with wide spatium intermetacarpale and bowed os metacarpale minus. Other derived characters that are present in the crown group but absent in the Gallinuloididae (see text) are unknown for the Paraortygidae and Quercymegapodiidae.

metacarpus (which in *Procrax* is relatively shorter, with a wide intermetacarpal space) and coracoid (which in *Procrax* has a shallow facies articularis scapularis). These two characters indicate that *Procrax* is a member of crown group Galliformes. *Procrax* may possibly be closely related to the Cracidae, as assumed by its original describers, but its exact systematic position can only be determined by direct comparison with the various more advanced Galliformes from the Oligocene of Europe (e.g., Mourer-Chauviré 1992).

Likewise, the Late Oligocene *Taoperdix pessieti* (Gervais, 1862) is not a member of the Gallinuloididae (*contra* Brodkorb 1964) as it lacks a robust, U-shaped furcula and an elongate and narrow carpometacarpus (Milne-Edwards 1867–1871: pl. 127) as do crown group Galliformes. Assignment of the Oligocene *Archaelectornis* to the Gallinuloididae (Crowe and Short 1992) was based on comparisons with the isolated humerus MCZ 342506, which is not referable to *Gallinuloides* (see above).

Gallinuloides wyomingensis is of considerable interest concerning the biogeography of galliform birds, as the distributions of extant Megapodiidae (mainly Australian continental plate) and Cracidae (South America) have been considered as evidence for a Southern Hemisphere (Gondwanan) origin of galliform birds (Cracraft 1973, 2001). This hypothesis implies a Cretaceous origin of crown group Galliformes which is not supported by the exclusive presence of stem group Galliformes in pre-Oligocene deposits (Mourer-Chauviré 1992; Mayr 2000; Dyke and Gulas 2002; this study; *contra* van Tuinen and Dyke 2004). The earliest (Late Oligocene or Early Miocene) galliform birds from South

America also belong to stem group Galliformes (Alvarenga 1995; Mourer-Chauviré 2000). Moreover, if *Procrax* is indeed a member of the Cracidae, as assumed by Tordoff and McDonald (1957), it would suggest a Northern Hemisphere origin of the Cracidae, as this taxon was found in North American deposits. The earliest record of the Megapodiidae is from the Late Oligocene of Australia (Boles and Ivison 1999; van Tuinen and Dyke 2004 erroneously referred the stem group galliform Quercymegapodiidae to crown group Megapodiidae, see Mourer-Chauviré 1992, 2000; Mayr 2000).

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Addendum

After this paper has been accepted for publication, Gulas-Wroblewski and Wroblewski (2003) described a purportedly crown-group galliform from the middle Eocene of North America. The new taxon, *Amitabha urbsinterdictensis* Gulas-Wroblewski and Wroblewski, 2003 is known from a proximal end of a humerus and few associated bones, including a scapula and partial sternum. A phylogenetic analysis performed by the authors resulted in placement of *A. urbsinterdictensis* within the Phasianidae. The results of this analysis are, however, considerably flawed by the fact that only galliform birds were included in the ingroup and, except for the new taxon, no fossil galliform taxa were considered. Moreover, of the 96 included characters only 27 could be coded for *A. urbsinterdictensis*, owing to the fragmentary preservation of the single known specimen.

Two characters were listed as evidence for galliform affinities of the new taxon: “double, and open, incisurae laterales on the sternum” and “incisura capitis of proximal humerus enclosed from crus dorsale fossa [sic] by a distinct ridge” (Gulas-Wroblewski and Wroblewski 2003: 1272). The first

character is not diagnostic of Galliformes and occurs in a number of other avian taxa, including pigeons (Columbidae) and many charadriiform birds. The transversal ridge at the beginning of the incisura capitis is much less pronounced in *A. urbsinterdictensis* than in crown group Galliformes (a similar shallow ridge occurs in many charadriiform birds). Likewise, the single character listed in order to support assignment of *A. urbsinterdictensis* to the Phasianidae, the “lack of extensive pneumaticity in the sternal plate” (Gulas-Wroblewski and Wroblewski 2003: 1272), is found in many other avian taxa (including, e.g., most diving birds).

We consider referral of *A. urbsinterdictensis* to crown group Galliformes not to be supported by the morphology of the fossil and even the galliform affinities of this taxon to be far from being certain.

Reference

- Gulas-Wroblewski, B.E. and Wroblewski, A.F.-J. 2003. A crown-group galliform bird from the Middle Eocene Bridger Formation of Wyoming. *Palaeontology* 46: 1269–1280.