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New specimens of the early Eocene stem group galliform *Paraortygoides* (Gallinuloididae), with comments on the evolution of a crop in the stem lineage of Galliformes

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Abstract Two new specimens of the fossil stem group galliform *Paraortygoides messelensis* Mayr 2000 (Gallinuloididae) are described from the Middle Eocene of Messel in Germany, including a complete skeleton in which the hitherto unknown skull of this species is preserved. The shorter and more protruding crista deltopectoralis of the humerus, also for the first time visible in one of the new specimens, shows gallinuloidids to be the sister taxon of all other, extinct and extant, galliform birds. Gallinuloidids distinctly differ from modern Galliformes in several other plesiomorphic osteological features, mainly of the pectoral girdle, of which the absence of a spina interna on the sternum is here reported for the first time. It is assumed that major evolutionary transformations in the stem lineage of Galliformes are related to the evolution of a large crop, which appears to have been absent in gallinuloidids. The vegetarian food component of gallinuloidids thus probably mainly consisted of soft plant matter rather than coarse material such as seeds.

Keywords *Paraortygoides messelensis* · Galliformes · Phylogeny · Evolution · Fossil birds

Introduction

Galliformes (landfowl) today include the Australasian Megapodiidae (megapodes), the Neotropic Cracidae (guans, chachalacas, and curassows), and the Phasianidae (guineafowl, turkeys, grouse, pheasants, and allies), which have a worldwide distribution. There is strong morphological and molecular evidence that galliform birds are the sister taxon of Anseriformes (waterfowl) with which they form the taxon Galloanseres (Sibley and

Ahlquist 1990; Dzerzhinsky 1992; Mayr and Clarke 2003; Cracraft et al. 2004).

Fragmentary remains of putative galliform birds are known from the late Cretaceous of North America (Hope 2002; Clarke 2004), but the earliest well-preserved specimens are those of *Gallinuloides wyomingensis* from the Lower Eocene North American Green River Formation (Mayr and Weidig 2004) and *Paraortygoides messelensis* from the Middle Eocene of Messel in Germany (Mayr 2000). Both species belong to the Gallinuloididae and are outside the crown group of Galliformes, i.e. the clade including the last common ancestor of modern Galliformes and its descendants (Mayr 2000, 2005; Mayr and Weidig 2004).

Other fossil species were incorrectly assigned to the Gallinuloididae (Mayr and Weidig 2004), but further Paleogene stem group Galliformes, the Paraortygidae and Quercymegapodiidae, are known from the Middle Eocene to Upper Oligocene of the Quercy fissure fillings in France (Mourer-Chauviré 1992).

P. messelensis was hitherto known only from a single postcranial skeleton (Mayr 2000). Being among the earliest known galliform birds, a more detailed knowledge of its osteology is of significance for an understanding of the early evolution of Galliformes, and here I report on new specimens from Messel, which present previously unknown details of the osteology of this Paleogene stem group galliform. In addition, I comment on the evolution of a crop in the stem lineage of Galliformes.

Methods

Osteological terminology follows Baumel and Witmer (1993). The fossil specimens are deposited in the Forschungsinstitut Senckenberg, Frankfurt am Main, Germany (SMF); the Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (MCZ); and the Wyoming Dinosaur Center, Thermopolis, WY, USA (WDC).

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Results

Systematic paleontology

- Galliformes (Temminck 1820)
- Gallinuloididae (Lucas 1900)
- *Paraortygoides* (Mayr 2000)
- *P. messelensis* (Mayr 2000)

Referred specimens

SMF-ME 11112a + b (complete skeleton on two slabs; Fig. 1), SMF-ME 3663a + b (dissociated postcranial skeleton on two slabs).

Locality and horizon

Messel near Darmstadt, Germany; Middle Eocene (about 47 million years ago; Mertz et al. 2004).

Measurements

See Table 1.

Description and comparison (restricted to features not already described in Mayr 2000)

The new specimens measure only about 80% of the size of the holotype of *P. messelensis* (Table 1) and may represent female individuals, as there exists a marked sexual dimorphism in size within crown group Galliformes with males usually being distinctly larger than females.

In SMF-ME 11112a, the skull of *P. messelensis* is preserved for the first time, being visible in ventral view (Fig. 2). The tips of the praemaxilla and mandible are broadly rounded and resemble those of modern Galliformes. The mandibular pars symphyialis is also of similar extent to that of modern landfowl, which do not

show much variation in bill morphology. Fenestrae mandibulae are absent. The narial openings can be seen through the reverse of the transparent slab of SMF-ME 11112a and are of similar size to those of *G. wyomingensis* (Fig. 3 in Mayr and Weidig 2004). Processus retroarticularis, an apomorphic feature of Galloanseres (e.g., Cracraft and Clarke 2001; Mayr and Clarke 2003), cannot be discerned. On the X-ray photograph of specimen SMF-ME 11112a (Fig. 2), the pterygoid is visible, and is short as in extant *Alectura* (Megapodiidae), with a rostrally situated facies articularis basipterygoidea as in modern Galliformes. The processus postorbitalis is also short as in *Gallinuloides*. The condylus occipitalis exhibits a distinct incisura mediana condyli. The urohyale and cornu branchiale of the hyoid apparatus are preserved and resemble the corresponding bones of modern Galliformes.

Specimen SMF-ME 11112a confirms the observation of Mayr (2000) that there are two free thoracic vertebrae between the synsacrum and the notarium, whereas in crown group Galliformes, there is only a single free vertebra (Storer 1982). The pygostyle (Fig. 1) is small and slender as in modern Galliformes and is of similar shape to that of, e.g., *Rollulus roulroul* (Phasianidae).

As in *G. wyomingensis* (Fig. 4 in Mayr and Weidig 2004), there is no large pneumatic opening on the dorsal surface of the extremitas sternalis of the coracoid (SMF-ME 3663a, SMF-ME 11112b; Fig. 3). Such an opening occurs in some stem group Galliformes (e.g., Mourer-Chauviré 2000: pl. 1), many crown group representatives [e.g., *Crax*, *Nothocrax* (Cracidae), and *Phasianus*, *Chrysolophus*, Tetraoninae (Phasianidae)], as well as in the anseriform Anhimidae and Anseranatidae, and appears to be an underlying synapomorphy (Saether 1979) of Galloanseres. Also, as in *G. wyomingensis* (Fig. 4 in Mayr and Weidig 2004), the dorsal surface of the extremitas sternalis exhibits marked intermuscular lines (SMF-ME 11112b), which occur in modern Anatidae and the quercymegapodiid *Ameripodius* (Mourer-Chauviré 2000), but are fewer and less distinct in crown group Galliformes. There is a small processus lateralis (SMF-ME 11112a; Fig. 1), which is of similar shape to that of *Paraortyx lorteti* (Fig. 2d in Mourer-Chauviré 1992). Also as in *P. lorteti* and *G. wyomingensis* (Fig. 4 in

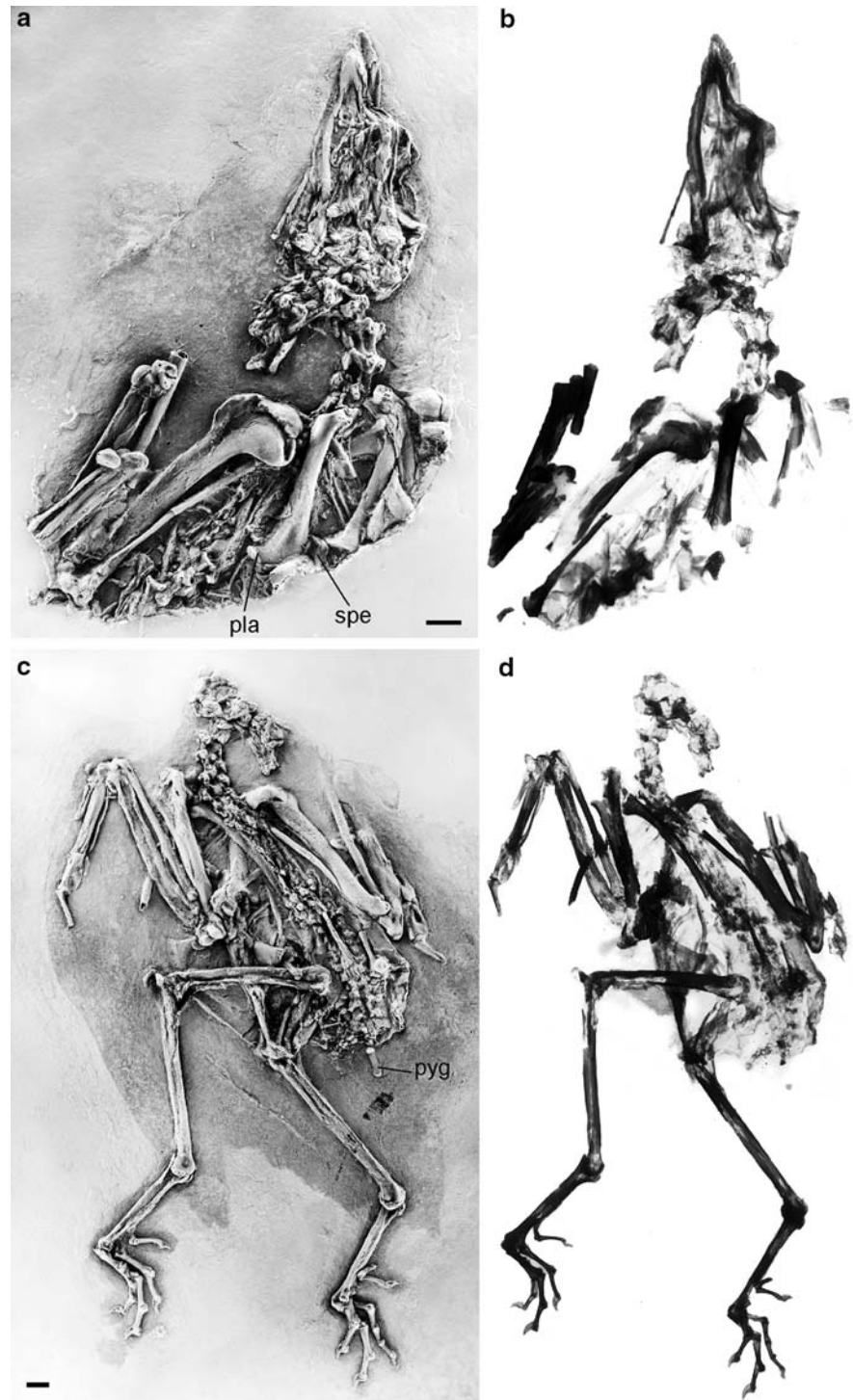
Table 1 Maximum length of the skull and major limb bones (*left/right*, in mm) of the described specimens of *P. messelensis* Mayr (2000) and *Gallinuloides wyomingensis* Eastman (1900)

	Skull	Humerus	Ulna	Carpometacarpus	Femur	Tibiotarsus	Tarsometatarsus
<i>P. messelensis</i>							
SMF-ME 1303 (type) ^a	–	48.5/48.5	46.3/47.2	26.0/–	~41.3/41.3	55.6/55.1	–/34.9
SMF-ME 11112	~37	41.0/41.3	~40.0/–	21.7/–	~35.6/–	46.8/–	~26.1/~26.1
SMF-ME 3663	–	–/~39.5	–/~40.6	22.3/~22.5	–/~32.5	~46.9/~46.0	~30.3/~29.7
<i>Gallinuloides wyomingensis</i>							
MCZ 342221 (type) ^b	~47	46.7/47.3	49.1/–	26.2/–	41.0/–	57.4/56.7	34.5/33.9
WDC-CGR-012 ^b	~44	–/~47	~48.4/~49	25.5/~27.1	–/39.7	56.4/56.0	34.2/34.0

^a After Mayr (2000)

^b After Mayr and Weidig (2004)

Fig. 1a–d *P. messelensis* Mayr (2000). **a** Specimen SMF-ME 11112a, coated with ammonium chloride. **b** Specimen SMF-ME 11112a, X-ray photograph. **c** Specimen SMF-ME 11112b, coated with ammonium chloride. **d** Specimen SMF-ME 11112b, X-ray photograph. *pla* Processus lateralis (coracoid), *pyg* pygostyle, *spe* spina externa (sternum). Scale bars equal 5 mm

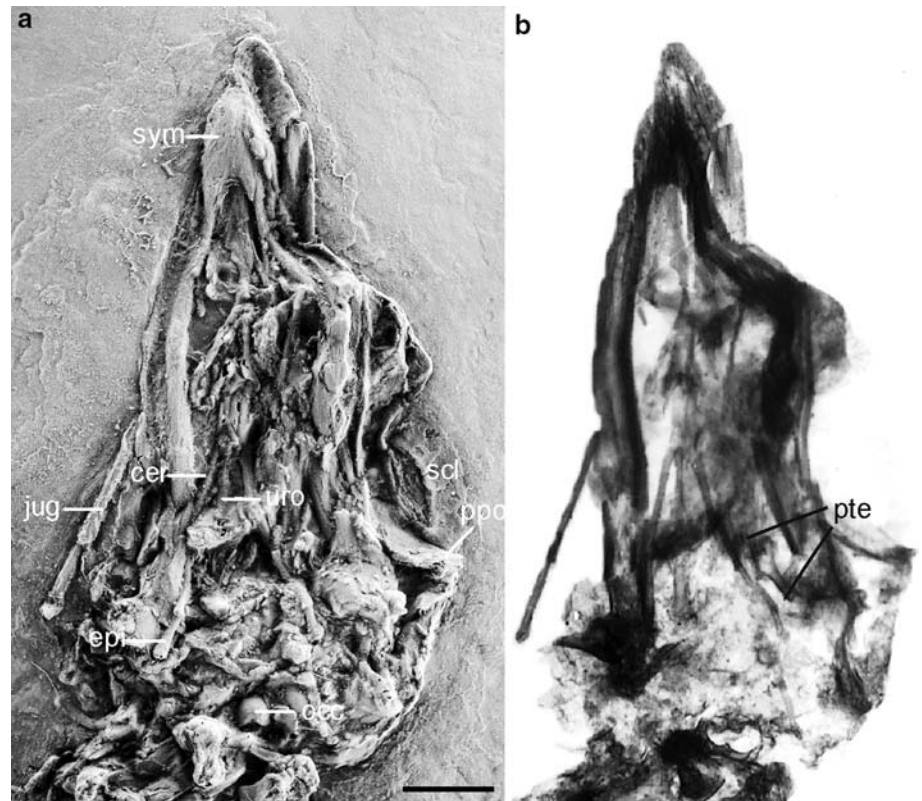


Mayr and Weidig 2004), there is a small indentation on the medial side of the sternal end of the bone (SMF-ME 3663a; Fig. 3) and the angulus medialis is protruding and pointed. The presence of a cup-like cotyla scapularis (Mayr 2000) can be verified in SMF-ME 3663a and through the reverse of the transparent slab of SMF-ME 11112a.

P. messelensis resembles *G. wyomingensis* in the shape of the carina sterni (SMF-ME 11112b, contra Mayr

2000). The sulcus carinae is very wide as in modern Galliformes (SMF-ME 3663b). The spina externa is well developed (SMF-ME 11112a; Fig. 1), but, contrary to crown group Galliformes, there is no spina interna (SMF-ME 3663a, SMF-ME 11112a; Fig. 3). A spina interna is also absent in anseriform birds and thus apparently evolved in the stem lineage of Galliformes; in crown group Galliformes, it fuses with the spina externa to form a spina communis (Fig. 4). The caudal margin

Fig. 2 a, b *P. messelensis* Mayr (2000) skull (SMF-ME 11112a). **a** Coated with ammonium chloride. **b** X-ray photograph. *cer* Os ceratobranchiale, *epi* os epibranchiale, *jug* os jugale, *occ* condylus occipitalis, *ppo* processus postorbitalis, *pte* os pterygoideum, *scl* scleral ring, *sym* pars symphyialis of mandible, *uro* os urohyale. Scale bar equals 5 mm



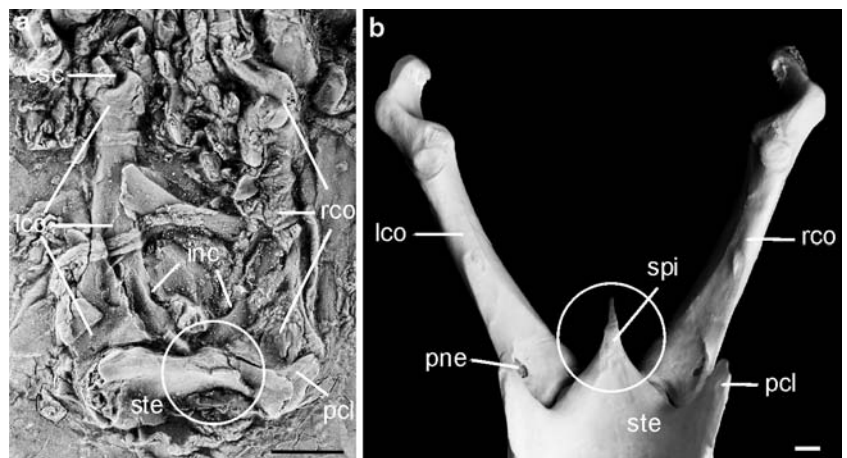
of the sternum (SMF-ME 11112b) is similar to that of the referred specimen of *G. wyomingensis* figured by Mayr and Weidig (2004; Fig. 2); as in the latter the trabeculae are shorter than those of the holotype of *G. wyomingensis*, which may, however, be an artifact of preservation. Compared to modern Galliformes and as noted by earlier authors (Lucas 1900), the sternum of gallinuloidids most closely resembles that of the Craciidae in the morphology of its caudal end, whereas the incisions are much deeper in the Phasianidae, and the trabecula lateralis much wider in the Megapodiidae.

For the first time the cranial surface of the humerus of *P. messelensis* is visible (SMF-ME 11112) and again

this aspect of the bone is very similar to the humerus of *G. wyomingensis*. In both species, the crista deltopectoralis is proportionally shorter, more protruding, and with a more convex margin than in Quercymegapodiidae, Paraortygidae, and crown group Galliformes (Fig. 5). Also as in modern Anatidae, the crista bicipitalis meets the shaft of the humerus at a steeper angle than it does in other, extinct and extant, Galliformes. The distal end of the bone is similar to the distal humerus of *G. wyomingensis* (Fig. 6 in Mayr and Weidig 2004) and other Paleogene stem group Galliformes.

In specimen SMF-ME 3663a, the previously unknown morphology of the ventral side of the carpo-

Fig. 3 a *P. messelensis* Mayr (2000), coracoid and cranial margin of the sternum in ventral view (SMF-ME 3663a) in comparison to **b** modern *Pavo cristatus* (Phasianidae). *csc* Cotyla scapularis, *inc* incision in medial margin of extremitas sternalis (coracoid), *lco* left coracoid, *pcl* processus craniolateralis, *pne* pneumatic opening, *rco* right coracoid, *spi* spina interna, *ste* sternum. The circled areas indicate the medial section of the cranial end of the sternum. Fossil coated with ammonium chloride, scale bars equal 5 mm



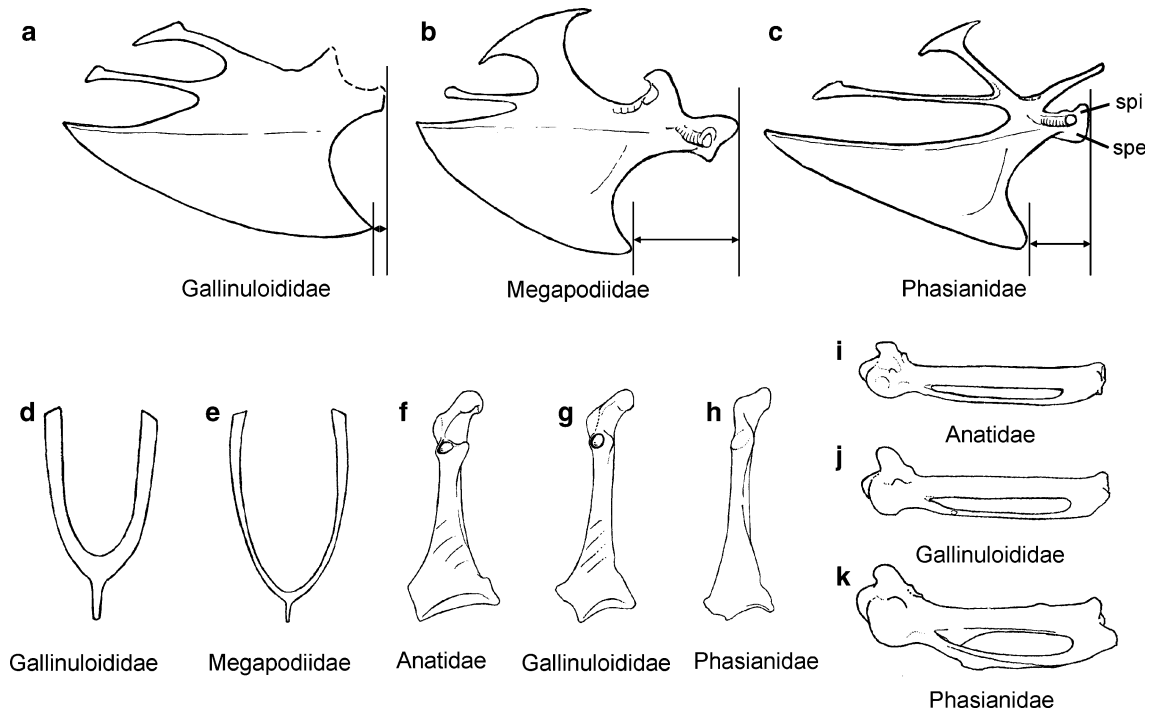


Fig. 4 Sternum (a–c), furcula (d, e), left coracoid (f–h), and left carpometacarpus (i–k) of Gallinuloididae in comparison to crown group Galliformes and Anseriformes. **a, d, g, j** *Gallinuloides wyomingensis* (Gallinuloididae; sternum after holotype, other bones after WDC-CGR-012). **b, e** *Alectura lathamii* (Megapodiidae). **c** *Rollulus roulroul* (Phasianidae). **f, i** *Anas crecca* (Anatidae, Anseriformes; modified from Mayr and Weidig 2004). **h, k** *Lophortyx gambelii* (Phasianidae; modified from Mayr and Weidig 2004). Note the caudally displaced apex carinae of the sternum in modern Galliformes, which is indicated by the vertical lines in a–c. *spe* Spina externa, *spi* spina interna. Not to scale

metacarpus of *P. messelensis* can be seen, and this bone also closely resembles the carpometacarpus of *G. wyomingensis*. Most notably, the os metacarpale minus bears a distinct tubercle on its ventral surface (Fig. 5) which also occurs in *Quercymegapodius*, *Paraortyx*, and some extant Megapodiidae (Mourer-Chauviré 1992) but is absent in Cracidae and Phasianidae and thus appears to be a plesiomorphic trait of galliform birds (its reduction may be related to the bowing of the os metacarpale minus and the width of the intermetacarpal space). The processus extensorius is more protruding than in modern Galliformes. As in other Galliformes, the processus pisiformis is shifted towards the cranial margin of the bone.

There is a small claw on the phalanx digiti alulae as in many modern Galliformes (Stephan 1992). The phalanx proximalis digiti majoris bears a deep depression in the proximocaudal part of its ventral surface.

The plantar surface of the hypotarsus (tarsometatarsus, SMF-ME 11112b) bears three shallow crests separated by two sulci and resembles the hypotarsus of modern Cracidae (e.g., *Pipile jacutinga*).

The hallux is much more elevated than in Megapodiidae and Cracidae (see also the text of Fig. 9 in Mayr 2000), which indicates that the incumbent hallux in the latter two taxa is probably derived for Galliformes in adaptation to mound-building (Megapodiidae) and roosting in trees (Cracidae). The claws are shorter than

in the referred specimen WDC CGR-012 of *G. wyomingensis* figured by Mayr and Weidig (2004; Fig. 2).

In both specimens, poorly preserved feather remains are visible. In SMF-ME 11112, the outermost primary measures about 79 mm and appears to be not significantly shorter than the following primary; tail feathers cannot be discerned.

Discussion

Although unquestionably outside crown group Galliformes (Mayr 2000; Mayr and Weidig 2004; contra Dyke 2003 and earlier authors), the exact phylogenetic position of the Gallinuloididae, especially with respect to the morphologically similar Paraortygidae, has hitherto been uncertain (Mayr 2000; Mayr and Weidig 2004). The shorter, more protruding, and more rounded crista deltopectoralis that is visible on the humerus of specimen SMF-ME 11112a now indicates that gallinuloidids are the sister group of a clade including Paraortygidae, Quercymegapodiidae, and crown group Galliformes, which share a much more reduced deltopectoral crest. A similarly shaped crista deltopectoralis to that of the Gallinuloididae is also found in anseriform birds and thus considered plesiomorphic for Galliformes.

The Gallinuloididae are also distinguished from crown group Galliformes in other plesiomorphic fea-

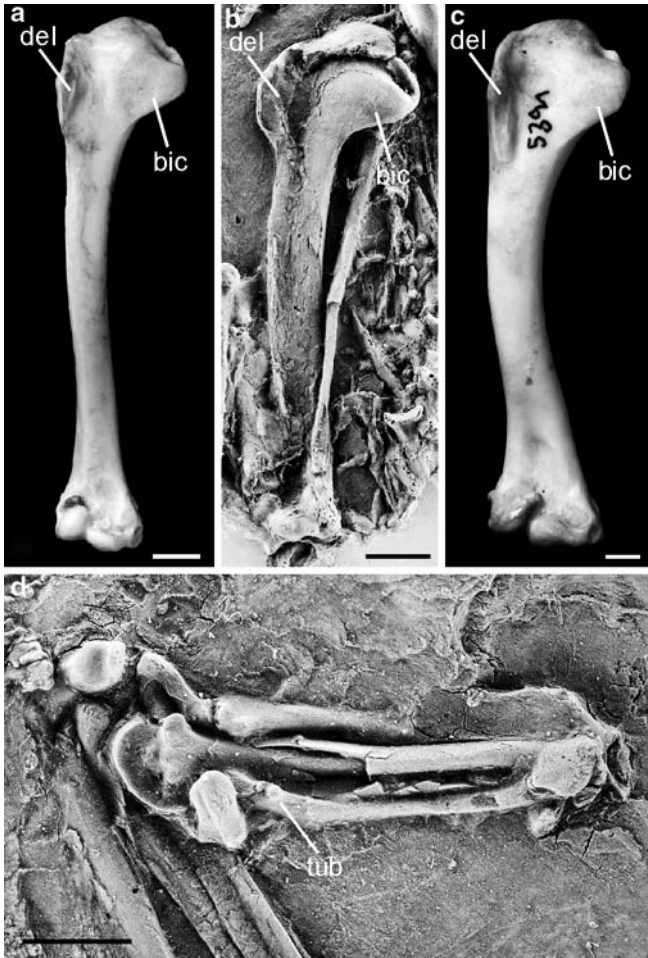


Fig. 5 Cranial view of right humerus (a–c), and ventral view of left carpometacarpus (d) in comparison. **a** *Nettapus auritus* (Anseriformes, Anatidae). **b** *P. messelensis* Mayr 2000 (SMF-ME 11112a, Gallinuloididae). **c** *Nothocrax urumutum* (Cracidae). **d** *P. messelensis* Mayr 2000 (SMF-ME 3663a). *bic* Crista bicipitalis, *del* crista deltopectoralis, *tub* tubercle on proximal end os metacarpale minus. Fossils coated with ammonium chloride, scale bars equal 5 mm

tures. Dyke and Gulas (2002), for example, noted the presence of marked lateral depressions on the thoracic vertebrae (concauitates laterales of Baumel and Witmer 1993). Such depressions occur in the early Tertiary anseriform Presbyornithidae (Ericson 1997), the supposed anseranatid *Anatalavis* (Olson 1999: 241), and modern Anhimidae, but are absent in extant Galliformes and Anatidae (ducks).

As detailed by Mayr (2000) and Mayr and Weidig (2004), gallinuloidids further distinctly differ from modern Galliformes in the morphology of the pectoral girdle. Most notably, the scapi clavicularum are much wider than those of crown group Galliformes, the apex carinae of the sternum reaches farther craniad, and the cotyla scapularis of the coracoid is cup-like, not shallow as in crown group Galliformes (Fig. 4). Wide scapi clavicularum and a cup-like cotyla scapularis also occur in Anseriformes and are plesiomorphic for galliform birds (Mourer-Chauviré 1992; Mayr 2000; Mayr and Weidig 2004).

The weak furcula and caudally displaced apex carinae of the sternum of modern Galliformes are functionally related to the large crop of these birds (Stegmann 1964), which indicates that Paleogene stem group Galliformes had a less voluminous crop than their modern relatives (Mayr 2000; Mayr and Weidig 2004).

A large crop is absent in Anseriformes and most other birds and certainly evolved in the stem lineage of Galliformes, i.e. was absent in the stem species of Galloanseres. It either occurs in birds which get food only occasionally but then in great quantities [e.g., Accipitridae (hawks)], or in birds which feed on dry and coarse plant matter, such as roots and seeds [Columbidae (doves), parrots (Psittaciformes)]. Although there is a great intraspecific and seasonal variability in food composition within galliform birds, with Megapodiidae apparently being rather omnivorous (del Hoyo et al. 1994), the crop of modern Galliformes certainly also evolved to soak and ferment plant matter for improvement of later digestion in the stomach, as it is often filled even if the stomach is empty and thus does not serve as a mere receptacle of food (Stresemann 1927–34: 158).

Because anseriform birds are also predominantly herbivorous, the stem species of Galloanseres most likely already was a herbivorous bird. For this reason and as there is no difference in bill structure between gallinuloidids and modern Galliformes, the diet of the Gallinuloididae certainly also included a fair amount of plant matter. Because of the presumed absence of a large crop, however, the vegetarian food component of gallinuloidids probably consisted of fruits and other easily digestible plant matter, rather than coarse material such as seeds. This assumption is in concordance with the fact that in none of the known specimens of the Gallinuloididae is grit preserved in the region of the former stomach, though it is regularly ingested by modern Galliformes to mechanically break down coarse plant matter in the muscular gizzard (Schifferli 1985).

There is no pre-Oligocene fossil record of crown group Galliformes (Mayr 2005), and the evolution of a large crop in galliform birds may thus have occurred in the mid-Paleogene, possibly because of competition with other herbivorous birds or mammals for food after the opening of Paleogene forests and the spread of grasslands towards the Oligocene and Miocene (e.g., Jacobs et al. 1999).

Zusammenfassung

Neue Exemplare des mitteleozänen Stammlinien-Hühnervogels/*Paraortygoides*/(Gallinuloididae) und Anmerkungen zur Evolution eines Kropfes in der Stammlinie der Galliformes

Zwei neue Exemplare von *P. messelensis* Mayr, 2000, eines fossilen Stammgruppenvertreterers der Hühnervögel (Galliformes, Gallinuloididae), werden aus dem mittleren Eozän von Messel in Deutschland beschrieben. Das neue Material beinhaltet ein vollständiges Skelettes,

an dem der bisher unbekannte Schädel dieser Art erhalten ist. Die kürzere und stärker vorspringende Crista deltopectoralis des Humerus, auch zum ersten Mal an einem der neuen Exemplaren sichtbar, zeigt, dass die Gallinuloididae das Schwestertaxon aller anderen Hühnervögel sind. Gallinuloididae unterscheiden sich deutlich in mehreren plesiomorphen Merkmalen, vor allem des Schultergürtels, von modernen Hühnervögeln. Das Fehlen einer Spina interna am Sternum wird zum ersten Mal beschrieben. Es wird angenommen, dass Hauptveränderungen in der Stammlinie der Galliformes mit der Evolution eines großen Kropfes zusammenhängen, welcher den Gallinuloididae noch zu fehlen scheint. Eher als z.B. Körner dürfte der pflanzliche Nahrungsanteil der Gallinuloididae daher noch einen großen Anteil an weichen Bestandteilen enthalten haben.

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References

- Baumel JJ, Witmer LM (1993) Osteologia. In: Baumel JJ, King AS, Breazile JE, Evans HE, Van den Berge JC (eds) Handbook of avian anatomy: nomina anatomica avium. Publ Nuttall Ornithol Club 23:45–132
- Clarke JA (2004) The morphology, phylogenetic taxonomy and systematics of *Ichthyornis* and *Apatornis* (Avialae: Ornithurae). Bull Am Mus Nat Hist 286:1–179
- Cracraft J, Clarke JA (2001) The basal clades of modern birds. In: Gauthier J, Gall LF (eds) New perspectives on the origin and early evolution of birds. Peabody Museum of Natural History, New Haven, pp 143–156
- Cracraft J, Barker FK, Braun M, Harshman J, Dyke GJ, Feinstein J, Stanley S, Cibois A, Schikler P, Beresford P, Garcia-Moreno J, Sorenson MD, Yuri T, Mindell DP (2004) Phylogenetic relationships among modern birds (Neornithes): toward an avian tree of life. In: Cracraft J, Donoghue M (eds) Assembling the tree of life. Oxford University Press, New York, pp 468–489
- del Hoyo J, Elliott A, Sargatal J (1994) Handbook of the birds of the world, vol 2. New World vultures to guineafowl. Lynx Edicions, Barcelona
- Dyke GJ (2003) The phylogenetic position of *Gallinuloides* Eastman (Aves: Galliformes) from the Tertiary of North America. Zootaxa 199:1–10
- Dyke GJ, Gulas BE (2002) The fossil galliform bird *Paraortygoides* from the Lower Eocene of the United Kingdom. Am Mus Novit 3360:1–14
- Dzerzhinsky FY (1992) Evidence for common ancestry of the Galliformes and Anseriformes. Cour Forsch-Inst Senckenberg 181:325–336
- Ericson PGP (1997) Systematic relationships of the Palaeogene family Presbyornithidae (Aves: Anseriformes). Zool J Linn Soc 121:429–483
- Hope S (2002) The Mesozoic radiation of Neornithes. In: Chiappe LM, Witmer LM (eds) Mesozoic birds: above the heads of dinosaurs. University of California Press, Berkeley, pp 339–388
- Jacobs BF, Kingston JD, Jacobs LL (1999) The origin of grass-dominated ecosystems. Ann Missouri Bot Gard 86:590–643
- Lucas FA (1900) Characters and relations of *Gallinuloides wyomingensis* Eastman, a fossil Gallinaceous bird from the Green River Shales of Wyoming. Bull Mus Comp Zool 36:79–84
- Mayr G (2000) A new basal galliform bird from the Middle Eocene of Messel (Hessen, Germany). Senck leth 80:45–57
- Mayr G (2005) The Paleogene fossil record of birds in Europe. Biol Rev 80 DOI 10.1017/S1464793105006779
- Mayr G, Clarke J (2003) The deep divergences of neornithine birds: a phylogenetic analysis of morphological characters. Cladistics 19:527–553
- Mayr G, Weidig I (2004) The early Eocene bird *Gallinuloides wyomingensis*—a stem group representative of Galliformes. Acta Palaeont Pol 49:211–217
- Mertz DF, Harms F-J, Gabriel G, Felder M (2004) Arbeitstreffen in der Forschungsstation Grube Messel mit neuen Ergebnissen aus der Messel-Forschung. Nat Mus 134:289–290
- Mourer-Chauviré C (1992) The Galliformes (aves) from the phosphorites du quercy (France): Systematics and biostratigraphy. In: Campbell KE (ed) Papers in avian paleontology honoring Pierce Brodkorb. Nat Hist Mus Los Angeles Cty Sci Ser 36:67–95
- Mourer-Chauviré C (2000) A new species of *Ameripodius* (Aves: Galliformes: Quercymegapodiidae) from the lower Miocene of France. Palaeontology 43:481–193
- Olson SL (1999) The anseriform relationships of *Anatalavis* Olson and Parris (Anseranatidae), with a new species from the Lower Eocene London Clay. In: Olson SL (ed) Avian paleontology at the close of the 20th century: proceedings of the 4th international meeting of the Society of Avian Paleontology and Evolution, Washington, DC, 4–7 June 1996. Smithsonian Contr Paleobiol 89:231–243
- Saether OA (1979) Underlying synapomorphies and anagenetic analysis. Zool Scr 8:305–312
- Schifferli L (1985) Grit. In: Campbell B, Lack E (eds) A dictionary of birds: 256. Poyser, Calton
- Sibley CG, Ahlquist JE (1990) Phylogeny and classification of birds: a study in molecular evolution. Yale University Press, New Haven
- Stegmann B (1964) Die funktionelle Bedeutung des Schlüsselbeines bei den Vögeln. J Ornithol 105:450–463
- Stephan B (1992) Vorkommen und Ausbildung der Fingerkrallen bei rezenten Vögeln. J Ornithol 133:251–277
- Storer RW (1982) Fused thoracic vertebrae in birds: their occurrence and possible significance. J Yamashina Inst Ornithol 14:86–95
- Stresemann E (1927–34) Aves. In: Kükenthal W, Krumbach T (eds) Handbuch der Zoologie. de Gruyter, Berlin, pp 1–899