Senckenbergiana lethaea	80	(1)	45 – 57	10 Text-figs, 3 Tabs	Frankfurt am Main, 31.05.2000

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A new basal galliform bird from the Middle Eocene of Messel (Hessen, Germany)

With 10 Text-figures and 3 Tables

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Abstract

A new basal galliform bird is described from the Middle Eocene of Messel (Hessen, Germany). *Paraortygoides messelensis* n. gen. n. sp. is one of the oldest galliform birds known so far and has been tentatively referred to the extinct family Gallinuloididae. This assignment is, however, not supported with derived characters, and in the presence of a very marked second fossa pneumotricipitalis on the humerus *P. messelensis* resembles the genus *Paraortyx* (Paraortygidae). The new taxon is clearly distinguished from all recent Galliformes by the absence of a transverse ridge at the beginning of the incisura capitis of the humerus, the cup-like cotyla scapularis on the coracoid, and by a very robust furcula. The latter feature and the far cranially situated apex carinae of the sternum might indicate that *Paraortygoides messelensis* had a less developed crop than recent Galliformes. If correctly referred to the Gallinuloididae, the cup-like cotyla scapularis of *Paraortygoides messelensis* shows that the Gallinuloididae branched off very early in the evolution of the Galliformes.

Key words: Eocene birds, Messel, Galliformes, Gallinuloididae, *Paraortygoides messelensis* n. gen. n. sp.

Kurzfassung

[Ein neuer basaler Vertreter der Galliformes aus dem mittleren Eozän von Messel (Hessen, Deutschland).] — Aus dem mittleren Eozän von Messel (Hessen, Deutschland) wird ein neuer basaler Vertreter der Galliformes beschrieben. *Paraortygoides messelensis* n. gen. n. sp. ist einer der ältesten bisher bekannten Hühnervögel und wurde unter Vorbehalt zu der ausgestorbenen Familie Gallinuloididae gestellt. Diese Zuordnung kann jedoch nicht mit abgeleiteten Merkmalen begründet werden, und in der Ausbildung einer sehr deutlichen zweiten Fossa pneumotricipitalis am Humerus ähnelt *P. messelensis* der Gattung *Paraortyx* (Paraortygidae). Durch das Fehlen einer querverlaufenden Knochenleiste am Beginn der Incisura capitis des Humerus, durch die schüsselförmige Cotyla scapularis am Coracoid und durch die sehr kräftige Furcula läßt sich das neue Taxon klar gegenüber allen rezenten Galliformes abgrenzen. Das letztgenannte Merkmal und der weit cranial gelegene Apex carinae des Sternums könnten darauf hinweisen, daß *Paraortygoides messelensis* einen weniger entwickelten Kropf als rezente Hühnervögel hatte. Falls *Paraortygoides messelensis* zu Recht den Gallinuloididae zugeordnet wurde, zeigt die schüsselförmige Cotyla scapularis, daß die Gallinuloididae sehr früh in der Evolution der Galliformes abzweigten.

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Introduction

There is consensus among most authors that the Galliformes comprise three monophyletic recent taxa (e. g. CRACRAFT 1981; SIBLEY & AHLQUIST 1990): the Australasian Megapodiidae (brush-turkeys, scrubfowl, megapodes), the neotropic Cracidae (guans, chachalacas, currasows), and the Phasianidae (including five subfamilies: Numidinae [guineafowl], Meleagrinae [turkeys], Odontophorinae [New World quails], Tetraoninae [grouse], Phasianinae [Old World quails, pheasants, partridges, etc.]). Traditionally Cracidae and Megapodiidae have been considered to be most closely related (e. g. WETMORE 1960; SIBLEY & AHLQUIST 1990), but CRACRAFT (1981) listed characters which support a sister group relationship between Cracidae and Phasianidae and this is also in concordance with a phylogenetic analysis undertaken by ERICSON (1997).

The earliest known fossil galliform species is *Gallinuloides wyomingensis* EASTMAN 1900 from the Lower Eocene Green River Formation (USA) which has been assigned to its own family, the Gallinuloididae, by LUCAS (1900). The type specimen of *G. wyomingensis* is a complete but not very well preserved skeleton on a slab (CROWE & SHORT 1992 reported another yet undescribed specimen of *Gallinuloides* sp.). Although the Gallinuloididae are very poorly diagnosed, three other early Tertiary galliform genera (*Taoperdix* MILNE-EDWARDS 1871, *Procrax* TORDOFF & MACDONALD 1957, and *Archaealectrornis* CROWE & SHORT 1992) ranging from Upper Eocene to Lower Miocene in age have been classified within this family (BRODKORB 1964; TORDOFF & MACDONALD 1957; BALLMANN 1969; MOURER-CHAUVIRÉ 1988; CROWE & SHORT 1992). So far the relationships between the Gallinuloididae and other galliform taxa are hardly understood. TORDOFF & MACDONALD (1957), BRODKORB (1964), and BALLMANN (1969) considered the Gallinuloididae to be closely related to recent Cracidae, but CROWE & SHORT (1992) believed them to be the sister taxon of the Phasianidae and the shared similarities with the Cracidae (sternum with small notches, limb proportions, hallux on same level as anterior toes) to be primitive within galliform birds. None of these classifications, however, has been established with derived characters and there seems to be evidence that the Gallinuloididae branched off very early in the evolution of the Galliformes (see discussion).

Revising the galliform birds from the fissure fillings of the Quercy (France), MOURER-CHAUVIRÉ (1992) described two other primitive galliform families, the Quercymegapodiidae (with the genera *Quercymegapodius* MOURER-CHAUVIRÉ 1992 and *Ameripodius* ALVARENGA 1995) and the Paraortygidae (including the genera *Paraortyx* GAILLARD 1908 and *Pirortyx* BRODKORB 1964). These two families are known from numerous isolated bones found in Upper Eocene and Lower Oligocene deposits of the Quercy, and obviously were substituted by the Phasianidae towards the end of the Lower Oligocene (MOURER-CHAUVIRÉ 1992). The Quercymegapodiidae also occur in the Upper Oligocene or Lower Miocene of Brazil (ALVARENGA 1995), remains of *Pirortyx* have been found in Oligocene deposits of Germany (FISCHER 1990). The presence of a cup-like cotyla scapularis, which according to outgroup comparison with primitive palaeognathous and Mesozoic birds very likely is primitive within neognathous birds (see MOURER-CHAUVIRÉ 1992), supports a basal position of Paraortygidae and Quercymegapodiidae within galliform birds.

A few other early Tertiary galliform birds have been described so far, but these are either known from very poorly preserved skeletons on slabs, or from fragmentary isolated bones. Under the first category comes *Ludiortyx hoffmanni* (GERVAIS 1852) from the Upper Eocene deposits of Montmartre, Paris, which has been assigned to the Galliformes by MILNE-EDWARDS (1867-1871) and which BRODKORB (1964) classified into the Gallinuloididae. Although BRUNET (1970) and CRACRAFT (1973) considered *L. hoffmanni* to belong to the Rallidae (rails), the species has not been compared in detail with the above-mentioned primitive galliform birds from the Upper Eocene of the Quercy so far and at least in size it corresponds with the species of the genus *Quercymegapodius*. HARRISON & WALKER (1977, 1979a, 1979b) described several "phasianid"±± genera from the Early Tertiary of England (*Argillipes* HARRISON & WALKER 1977, *Coturnipes* HARRISON & WALKER 1977, *Percolinus* HARRISON & WALKER 1977, *Litoripes* HARRISON & WALKER 1979a). Some of these remains are too fragmentary to be even sure that they are from galliform birds (let alone Phasianidae), and all should be restudied and compared with the extinct galliform families mentioned above.

In this study a new basal galliform taxon from the Middle Eocene of Messel near Darmstadt (Hessen, Germany) is presented (a detailed description of the site can be found in SCHAAL & ZIEGLER 1988). The specimen not only is one of the oldest but, though lacking the skull, also one of the best preserved skeletons of Early Tertiary galliform birds known so far.

Material and methods

The anatomical terminology follows BAUMEL & WITMER (1993), if not indicated otherwise. The dimensions represent the maximum length of the bone along its longitudinal axis, except for the claws where the distance between the tuberculum extensorium and the apex phalangis has been measured. The specimen described in this study is deposited in the Forschungsinstitut Senckenberg, Frankfurt am Main, Germany (SMF).

For osteological comparisons with recent birds, the collections of the SMF and the Museum für Naturkunde, Berlin, have been used.

Systematics

Galliformes TEMMINCK 1820

Diagnosis: All Galliformes including the new taxon described herein share the following characters: (1) thoracic vertebrae fused to a notarium, (2) coracoid with distinct impressio ligamenti acrocoracohumeralis, (3) furcula with very large and blade-like apophysis furculae, (4) humerus with more or less marked second fossa pneumotricipitalis and (5) distinct elongated attachment site for musculus supracoracoideus, (6) processus pisiformis of carpometacarpus shifted cranially, (7) plantar side of articular surface of trochlea metatarsi III asymmetric with lateral ridge protruding farther proximally than medial ridge. Outgroup comparison with the palaeognathous Lithornithiformes HOUDE 1988 suggests that at least characters (1), (3), (4), (5), and (7) are derived within neognathous birds.

?Gallinuloididae LUCAS 1900

Remarks: The galliform bird from Messel is easily distinguished from all recent galliform taxa by the much wider scapus claviculae (furcula) and the cup-like cotyla scapularis of the coracoid. The latter feature seems to be plesiomorphic within galliform birds (see MOURER-CHAUVIRÉ 1992), and so far has only been reported from the Paraortygidae and Quercymegapodiidae (MOURER-CHAUVIRÉ 1992; ALVARENGA 1995) from which the new taxon can, however, be clearly delimited (see differential diagnosis).

The conformation of the cotyla scapularis is unknown for *Gallinuloides wyomingensis* but given that a cup-like cotyla scapularis is plesiomorphic within galliform birds as assumed by MOURER-CHAUVIRÉ (1992), it is likely that it was also present in this species which is considerably older than the two above-mentioned families. As far as comparable the galliform bird from Messel is very similar in its osteology to *G. wyomingensis* and also corresponds well in the absolute and relative size of all major skeletal elements (tabs 1 and 2). Both taxa especially agree in the unusually slender carpometacarpus bearing a straight os metacarpale minus, the very robust, U-shaped furcula (which LUCAS 1900, listed as one of the diagnostic characters of the Gallinuloididae), the stout coracoid, the shape of the carina sterni (cranial margin concave, apex carinae reaching farther cranially than in recent galliform birds), and in the proportions of the pelvis. The small difference in age of about 2 million years between the deposits of the Green-River Formation and those of Messel (FEDUCCIA 1996: 168) and the high degree of concordance between the fossil avifauna of these sites (HESSE 1992; PETERS 1987; MAYR 1998; MAYR & PETERS 1998; MAYR 1999) might further justify a classification of the galliform bird from Messel into the Gallinuloididae. Yet, this assignment should be regarded as tentative since the type specimen of *G. wyomingensis* is only poorly preserved and since the above-mentioned similarities between the galliform bird from Messel and *Gallinuloides wyomingensis* might well be plesiomorphic (see discussion).

Paraortygoides n. gen.

Etymology: The name of the genus should express the similarities between the new taxon and both *Paraortyx* (Paraortygidae) and *Gallinuloides* (Gallinuloididae).

Diagnosis: *Paraortygoides* n. gen. exhibits the above-mentioned diagnostic characters of the Galliformes. The new genus is distinguished from all other galliform birds in the combination of the following features: (1) furcula U-shaped with very broad scapus claviculae; (2) coracoid with cup-like cotyla scapularis; (3) apex carinae of sternum not displaced caudally but sharply protruding in cranial direction; (4) humerus long and slender with (5) marked second fossa pneumotricipitalis which extends into the caput humeri and (6) without transverse ridge at the beginning of the incisura capitis; (7) carpometacarpus slender with straight os metacarpale minus and narrow spatium intermetacarpale, and (8) with an osseous arch for the tendon of musculus interosseus dorsalis on its distal end.

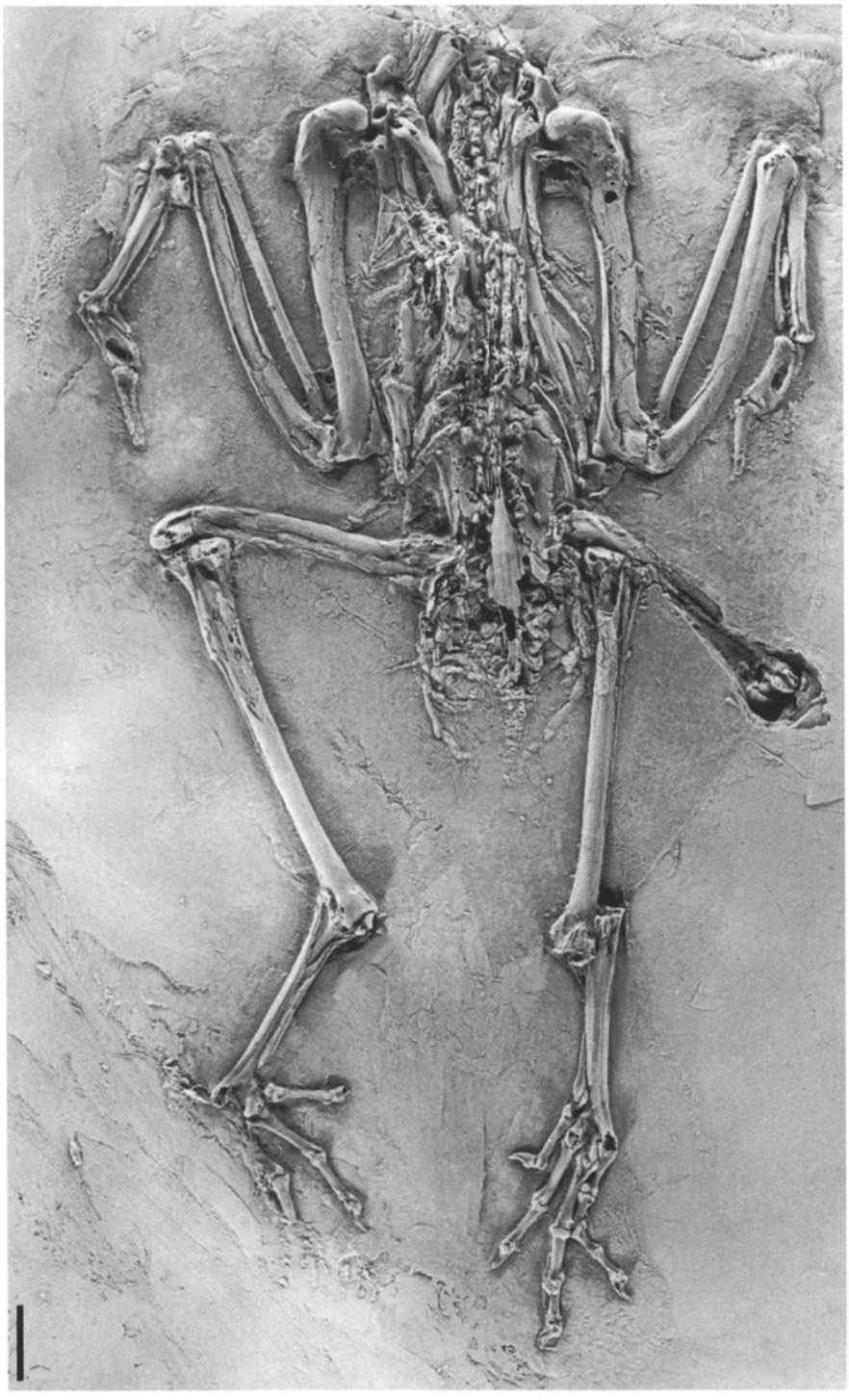
Characters (1)-(4), (6), and (7) very likely are plesiomorphic within Galliformes (see discussion). Probably autapomorphic for the new genus are characters (5) and (8).

Differential Diagnosis:
Paraortygoides n. gen. differs from:
- all genera of the Megapodiidae, Cracidae, and Phasianidae in: scapus claviculae (furcula) much wider, cotyla scapularis of the coracoid cup-like, and humerus without transverse ridge at the beginning of the incisura capitis.
- the Quercymegapodiidae MOURER-CHAUVIRÉ 1992 in: presence of a very marked second fossa pneumotricipitalis (humerus), absence of a ridge which interrupts the incisura capitis of the humerus (although this ridge is rather weak in the Quercymegapodiidae), oval cotyla scapularis of the coracoid (circular in Quercymegapodiidae), and presence of a short processus procoracoideus.
- the Paraortygidae MOURER-CHAUVIRÉ 1992 in: coracoid stouter with straighter and more rounded processus acrocoracoideus and less developed tuberculum brachiale, carpometacarpus more slender and with larger and more protruding processus extensorius of os metacarpale alulare, fossa metatarsi I (tarsometatarsus) more marked, trochlea metatarsi II less strongly turned plantad, trochlea metatarsi III narrower, and wing bones relatively longer (these differences are between *Paraortyx* and *Paraortygoides*, from *Pirortyx* only the humerus is known, which has a shallower second fossa pneumotricipitalis).
- *Gallinuloides* EASTMAN 1900 in: furcula relatively longer with scapus claviculae becoming wider towards extremitas omalis (of equal width in *Gallinuloides*, proximal width of scapus claviculae 3.6 mm in *Paraortygoides* vs. 2.4 mm in *Gallinuloides* [*Gallinuloides wyomingensis* has the same overall size like the species of *Paraortygoides* described herein]), carina sterni cranio-caudally shorter and with more concave cranial margin (text-figs 3H, 3I), ulna shorter than humerus (according to TORDOFF & MACDONALD 1957, slightly longer than humerus in

Gallinuloides), processus extensorius of os metacarpale alulare more protruding, tibiotarsus somewhat shorter in relative length (tab. 1).

- *Taoperdix* MILNE-EDWARDS 1871 in: furcula with wider scapus claviculae (3.6 mm vs. 1.3 mm in *Taoperdix pessieti*), pelvis medio-laterally much narrower (24 mm vs. 40 mm in *Taoperdix pessieti*) (*Taoperdix pessieti* has the same overall size like the species of *Paraortygoides* described herein).
- *Procrax* TORDOFF & MACDONALD 1957 in: corpus scapulae narrower, humerus more slender and with marked second fossa pneumotricipitalis, carpometacarpus with less bowed os metacarpale minus and more protruding processus extensorius of os metacarpale alulare.
- *Archaealectrornis* CROWE & SHORT 1992 in: humerus more slender and with marked second fossa pneumotricipitalis.
- *Ludiortyx* BRODKORB 1964 in: humerus more slender and with marked second fossa pneumotricipitalis, tibiotarsus relatively shorter.
- *Litoripes* HARRISON & WALKER 1979a in: tarsometatarsus stouter.

The putatively galliform genera *Argillipes* HARRISON & WALKER 1977 and *Percolinus* HARRISON & WALKER 1977 are known from proximal tarsometatarsi only and cannot be compared with *Paraortygoides* n. gen. in detail; the distal end of the tarsometatarsus of *Coturnipes cooperi* HARRISON & WALKER 1977 is wider (6.8 mm vs. 4.7 mm).



Text-fig. 1. *Paraortygoides messelensis* n. gen. n. sp. – Type specimen (SMF-ME 1303a). The skeleton is seen in dorsal view and has been coated with ammonium chloride to enhance contrast. – Natural size, scale bar = 10 mm.

Paraortygoides messelensis n. sp.

Text-figs 1-9

Etymology: The specific name refers to the type locality.

Holotype and only known specimen: SMF-ME 1303 a+b: articulated postcranial skeleton on a slab with parts of the left foot on a counter slab; the proximal end of the right carpometacarpus and the right os carpi ulnare are preserved as isolated bones.

Type locality: Grube Messel (Hessen, Germany).

Type horizon: Lower Middle Eocene.

Dimensions: See tabs 1 and 2.

Diagnosis: Only species of the genus, therefore diagnosis same as for genus.

Description and comparison

Vertebrae: About 11-13 praesacral vertebrae are preserved. Like in other galliform birds four or five vertebrae cranially of the synsacrum are fused to a notarium, and there seem to be two free thoracic vertebrae between the latter and the synsacrum. The exact number of caudal vertebrae cannot be discerned. The pygostyle seems to have been very small.

Coracoid: The coracoid (text-fig. 3A) appears to have been fairly stout. Its most distinctive feature is that the cotyla scapularis is cup-like as in the Paraortygidae and Quercymegapodiidae (text-fig. 3A: 1), whereas it is shallow in all recent galliform families (see MOURER-CHAUVIRÉ 1992 – the cotyla scapularis is not visible in the type specimen of *Gallinuloides wyomingensis*). Contrary to the circular cotyla scapularis of *Quercymegapodius*, the cotyla scapularis of SMF-ME 1303 is oval like in *Paraortyx*. The processus procoracoideus is very short (absent in *Quercymegapodius*). The processus acrocoracoideus appears to have been more rounded and straighter than is usual among Galliformes. The tuberculum brachiale hardly overhangs the sulcus musculi supracoracoideus. The impressio ligamenti acrocoracohumeralis is distinct. The sternal end is only shadowyly visible on the x-ray photograph (text-fig. 2).

Furcula: The furcula (text-fig. 3C) can be seen through the reverse of the transparent slab. It is U-shaped like in *Gallinuloides wyomingensis* (V-shaped in many extant Galliformes) and differs from the furcula of all recent galliform birds in its much stouter scapus claviculae which becomes slightly wider towards the extremitas omalis. The scapus claviculae is also very wide in *Gallinuloides wyomingensis* where it, however, has an equal width. A long blade-like apophysis furculae is visible on the x-ray photograph (text-fig. 3C: 2). The extremitas omalis is not preserved.

Scapula: The scapula (text-fig. 3G) is very long, slender, and fairly straight. It measures 52 mm and is thus nearly as long as the tibiotarsus. The dorsal side of the corpus scapulae bears a distinct tubercle at the end of its proximal fifth (text-fig. 3G: 3), similar to many Anseriformes (e. g. *Aix sponsa*, *Aix galericulata*, *Anas platyrhynchos*, *Callonetta leucophrys*). In recent Galliformes this tubercle is situated on the lateral margin of the corpus scapulae. The distal end of the bone tapers off to a point whereas it is blunt in recent galliform birds. The facies articularis humeralis is more oval than in recent Galliformes. The acromion is long, slightly curved, and narrow.

Text-fig. 2. *Paraortygoides messelensis* n. gen. n. sp. – X-ray photograph of the type specimen (SMF-ME 1303a). – Natural size.

Table 1. *Paraortygoides messelensis* n. gen. n. sp. – Length of the limb bones in comparison with *Gallinuloides wyomingensis* EASTMAN 1900 (left/right, in mm):

	hum	uln	cmc	fem	tbt	tmt
Paraortygoides messelensis SMF-ME 1303	48.5 / 48.5	46.3 / 47.2	26.0 /	~41.3 / 41.3	55.6 / 55.1	/ 34.9
Gallinuloides wyomingensis type specimen[a]	46.8	49.2	25.8	40.8	57.6	33.8

[a] after TORDOFF & MACDONALD (1957)

Table 2. *Paraortygoides messelensis* n. gen. n. sp. – Length of the pedal phalanges in comparison with *Gallinuloides wyomingensis* EASTMAN 1900, in mm:

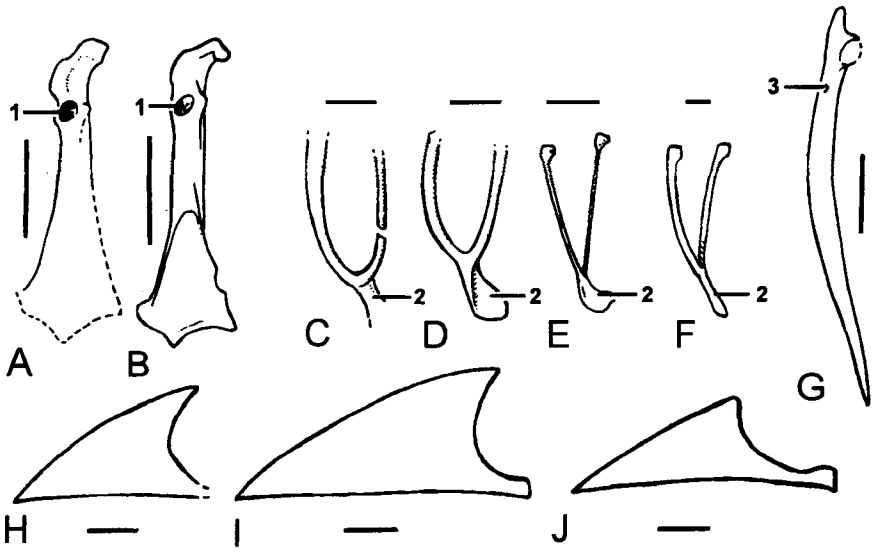
	I1	I2	II1	II2	II3	III1	III2	III3	III4	IV1	IV2	IV3	IV4	IV5
Paraortygoides messelensis SMF-ME 1303	7.7	3.9	9.8	7.5	5.0	10.1	9.1	7.7	5.0	7.1	~4.4	4.4	4.6	4.4
Gallinuloides wyomingensis type specimen[a]	7	4	11	8	6	12	10	8	6	7.5	5.5	4	4	4

[a] after EASTMAN (1900).

Ribs: At least six pairs of vertebral ribs can be counted.

Sternum: The carina sterni (text-fig. 3H) can be seen through the reverse of the transparent slab. It is very high and in its shape resembles the carina sterni of the extant *Macrocephalon maleo* (Megapodiidae). The carina sterni of *Paraortygoides* is relatively shorter than that of *Gallinuloides* (text-fig. 3I), its cranial margin is more concave. The apex carinae is pointed and reaches farther cranially than in recent Cracidae and Phasianidae (text-fig. 3J). Details of the corpus sterni (especially the shape of the margo caudalis and the spina externa) are not visible. The margo costalis appears to have been fairly long (as preserved it measures 8 mm).

Humerus: The humerus (text-fig. 5A) is slender with a small proximal end and a slightly sigmoidally curved shaft.



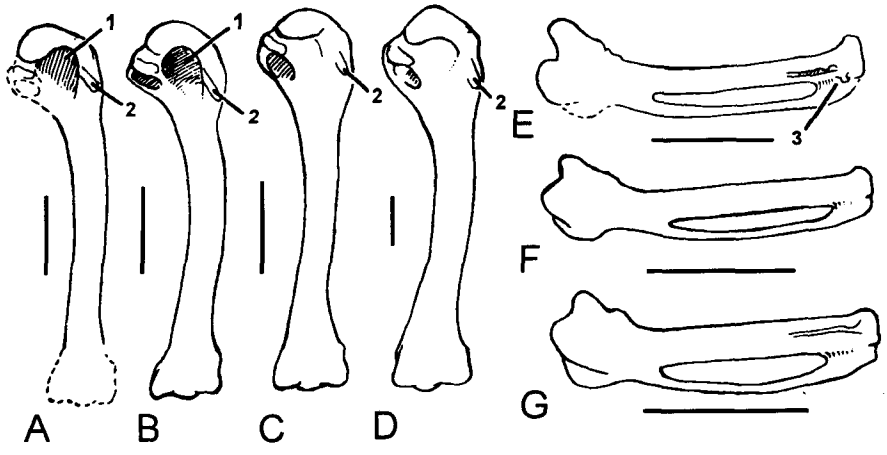
Text-fig. 3. Elements of the pectoral girdle in comparison: coracoid (A, B), furcula (C-F), scapula (G), and carina sterni (H-J, slightly schematic). – A) *Paraortygoides messelensis* n. gen. n. sp. (?Gallinuloididae); B) *Paraortyx lorteti* GAILLARD 1908 (Paraortygidae); C) *Paraortygoides messelensis* n. gen. n. sp. (?Gallinuloididae); D) *Gallinuloides wyomingensis* EASTMAN 1900 (Gallinuloididae, after LUCAS 1900); E) *Lophortyx californica* (SHAW 1798) (Phasianidae, Odontophorinae); F) *Nothocrax urumutum* (SPIX 1825) (Cracidae); G) *Paraortygoides messelensis* n. gen. n. sp. (?Gallinuloididae); H) *Paraortygoides messelensis* n. gen. n. sp. (?Gallinuloididae); I) *Gallinuloides wyomingensis* EASTMAN 1900 (Gallinuloididae); J) *Lophortyx californica* (SHAW 1798) (Phasianidae, Odontophorinae). – 1 = cotyla scapularis; 2 = apophysis furculae; 3 = tubercle on dorsal side of scapula. – Scale bar = 10 mm.

Text-fig. 4. *Paraortygoides messelensis* n. gen. n. sp. – Pectoral region, dorsal aspect (SMF-ME 1303a). Coated with ammonium chloride to enhance contrast. – 1 = left scapus claviculae; 2 = left scapula; 3 = left coracoid, 4 = left humerus. – Scale bar = 10 mm.

As far as comparable, it closely resembles the corresponding bone of *Paraortyx*. The fossa pneumotricipitalis is separated into two fossae with the very marked second fossa (= fossa tricipitalis of BALLMANN 1969) extending under the caput humeri. Contrary to all recent galliform taxa there is no transverse ridge at the beginning of the incisura capitis which connects the caput humeri with the tuberculum ventrale (see MOURER-CHAUVIRÉ 1992: text-fig. 3). This ridge is also absent in the Paraortygidae and in *Archaealectrornis* (Gallinuloididae). The humerus is too poorly preserved for detailed comparison in the type specimen of *G. wyomingensis*, but CROWE & SHORT (1992) reported an undescribed specimen of *Gallinuloides* sp. in which the ridge is absent, too. The tuberculum dorsale is separated from the caput humeri by a shallow furrow. The accessory attachment site of the musculus supracoracoideus (= crista musculi supracoracoidei of BAUMEL & WITMER 1993) is elongated and runs obliquely to the longitudinal axis of the bone; like in *Paraortyx* it extends to the second fossa pneumotricipitalis. Only the caudal surface of the distal humerus is visible, and like in other galliform birds the sulcus scapulotricipitalis is very shallow. The sulcus humerotricipitalis is wide. The processus flexorius reaches about as far distally as the condylus ventralis.

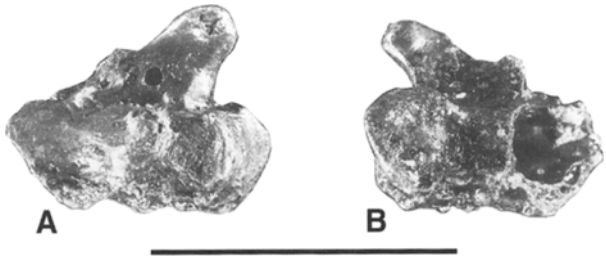
Ulna: Like in recent Phasianidae, but contrary to *Gallinuloides wyomingensis*, and most recent Megapodiidae and Cracidae, the ulna is shorter than the humerus. The olecranon is short and blunt. The processus cotylaris dorsalis hardly protrudes dorsally. The proximal end of the ulna bears a distinct depression on its dorsal side below the processus cotylaris dorsalis (this depression, which is not found in recent Galliformes, is visible at the right and the left bone and thus probably not of diagenetic origin). The incisura tendinosa of the distal end is distinct.

Radius: The radius is fairly straight, details of its proximal and distal ends are, however, not visible.



Text-fig. 5. Humerus (A-D) and carpometacarpus (E-G) in comparison: A) *Paraortygoides messelensis* n. gen. n. sp. (?Gallinuloididae); B) *Paraortyx lorteti* GAILLARD 1908 (Paraortygidae); C) *Quercymegapodius depereti* (GAILLARD 1908) (Quercymegapodiidae); D) *Archaealectrornis sibleyi* CROWE & SHORT 1992 (?Gallinuloididae); E) *Paraortygoides messelensis* n. gen. n. sp. (?Gallinuloididae); F) *Quercymegapodius depereti* (GAILLARD 1908) (Quercymegapodiidae); G) *Paraortyx lorteti* GAILLARD 1908 (Paraortygidae). 1 = second fossa pneumotricipitalis; 2 = attachment site of musculus supracoracoideus; 3 = osseous arch for the tendon of musculus interosseus dorsalis. – Scale bar = 10 mm.

Carpometacarpus: The carpometacarpus (text-fig. 5E) is more slender and has a straighter os metacarpale minus than that of all other galliform birds except *G. wyomingensis* (LUCAS 1900 noted that in *Gallinuloides wyomingensis* "the third metacarpal [= os metacarpale minus] appears to have been much straighter than is usual among gallinaceous birds"), the Quercymegapodiidae (text-fig. 5F), and some recent Megapodiidae. The spatium intermetacarpale is narrow, a processus intermetacarpalis (which is characteristic for most Phasianidae) is absent. The processus extensorius of the os metacarpale alulare is fairly long like in *Nothocrax* (Cracidae); its tip points proximo-cranially. The processus extensorius appears to have been distinctly lower in *G. wyomingensis* (and it is also lo-



Text-fig. 6. *Paraortygoides messelensis* n. gen. n. sp. – A) ventral and B) dorsal aspect of the proximal end of the right carpometacarpus (SMF-ME 1303). – Scale bar = 10 mm.

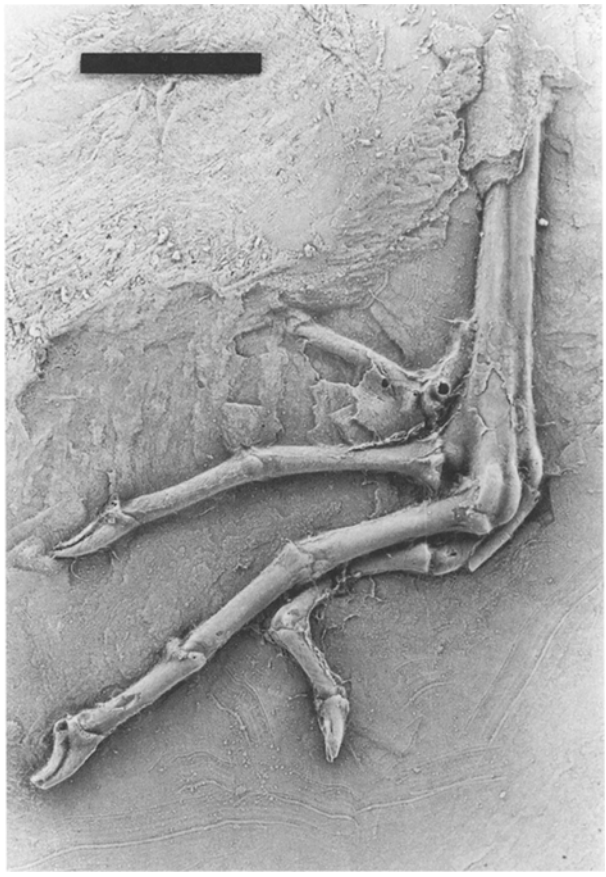
wer in *Quercymegapodius* and *Paraortyx*). The processus pisiformis is shifted cranially and widened cranio-caudally (text-fig. 6). The depressio muscularis interna (BALLMANN 1969) is less distinct than in most recent Phasianidae. The sulcus tendinosus is shallow, below its distal end there is an osseous arch for the tendon of musculus interosseus dorsalis (text-fig. 5E: 3; STEGMANN 1978: text-fig. 7) which is also found in some recent Phasianidae (e. g. *Lagopus lagopus* and *Bonasa umbellus* [Phasianidae, Tetraoninae] – in many other galliform birds this arch is imperfectly closed). The distal end of the os metacarpale majus protrudes cranially, the symphysis metacarpalis distalis is fairly wide.

Other elements of the wing: The phalanx distalis digiti majoris is large and as long as the phalanx proximalis digiti majoris. The right os carpi radiale is preserved as an isolated bone. In its general shape it resembles the corresponding ossicle of some Anseriformes (e. g. *Callonetta leucophrys*) whereas the os carpi radiale of recent Galliformes is more square. The facies articularis metacarpalis is concave, the facies articularis radialis rather shallow. The facies articularis ulnaris bears a large depression, the surface opposite to it exhibits a small tubercle. The dorsal surface bears a distinct furrow.

Pelvis: The pelvis is about half as wide as long and corresponds well in its proportions with the pelvis of *Gallinuloides wyomingensis* and the extant *Lophortyx californica* (Phasianidae, Odontophorinae). The praeacetabular portion has about the same length as the postacetabular portion and becomes medio-laterally slightly wider towards the cranial end of the pelvis. The lateral margin of the alae praeacetabulares ilii is slightly concave. Due to preservation it cannot be discerned if canales iliosynsacrales (which are characteristic for recent Galliformes) were present. Tuberculi praeacetabulares seem to be absent. The os pubis is long, extending well beyond the processus terminalis ischii (which itself is not well preserved).

Femur: The femur appears to have been stouter than in other galliform birds, although this impression might be caused by the flattening of the bone. The trochlea fibularis is distinctly grooved and bordered by two cristae of equal height. The ansae musculi iliofibularis are small but distinct.

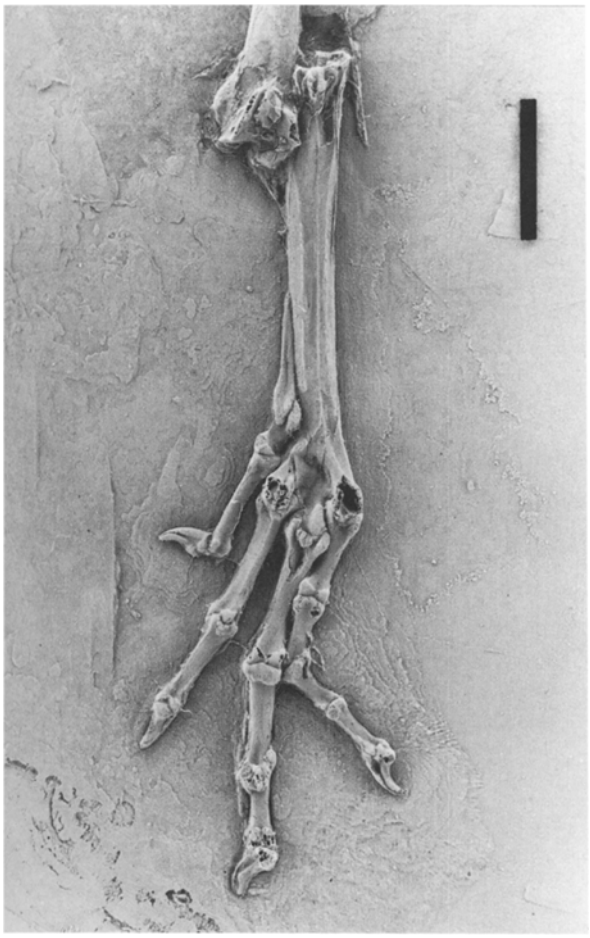
Tibiotarsus: The tibiotarsus is the longest limb element. Details of the proximal end cannot be discerned. The



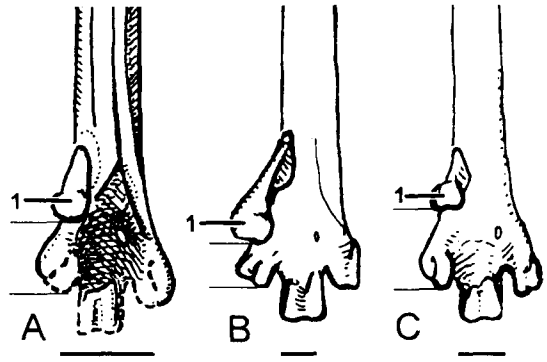
Text-fig. 7. *Paraortygoides messelensis* n. gen. n. sp. – Left foot (SMF-ME 1303b), dorsal aspect. Coated with ammonium chloride to enhance contrast. – Scale bar = 10 mm.

trochlea cartilaginis tibialis is shallow and slightly asymmetric. The cranial surface of the distal end of the bone is visible through the reverse of the transparent slab. The condyli have about equal size, the incisura intercondylaris is fairly wide. A pons supratendineus is present. The sulcus extensorius runs along the medial side of the bone. The fibula is long and reaches about two thirds of the entire length of the tibiotarsus.

Tarsometatarsus: The tarsometatarsus (text-figs 7-9) measures about two thirds of the length of the tibiotarsus and is similar to that of *Quercymegapodius* in its proportions. The hypotarsus is low and resembles that of other galliform birds in its general shape, closer details of its morphology, however, are not discernible. The fossae parahypotarsales are shallow. There are three low but sharp ridges on the palmar side of the tarsometatarsus: lateral and medial cristae plantares, and a crista medianoplantaris which forks on the level of the fossa metatarsi I. The foramen vasculare distale is of average size and oval. The distal end of the tarsometatarsus most closely resembles the distal tarsometatarsus of the Quercymegapodiidae. Like in the latter the trochleae are widely splayed. The trochlea metatarsi II reaches only slightly less far distally than the trochlea metatarsi IV which extends to the midst of the trochlea metatarsi III (the trochlea metatarsi II is distinct-



Text-fig. 8. *Paraortygoides messelensis* n. gen. n. sp. – Right foot (SMF-ME 1303a), plantar aspect. Coated with ammonium chloride to enhance contrast. – Scale bar = 10 mm.



Text-fig. 9. Distal tarsometatarsus in comparison. A) *Paraortygoides messelensis* n. gen. n. sp. (?Gallinuloididae); B) *Crax alector* LINNÉ 1766 (Cracidae); C) *Catreus wallichi* (HARDWICKE 1827) (Phasianidae, Phasianinae). The two horizontal lines mark the distal end of the os metatarsale I and the distal end of the trochlea metatarsi II. 1 = os metatarsale I. – Scale bar = 5 mm.

ly shorter in the Phasianidae). It is not as abbreviated and not turned as far plantad as the trochlea metatarsi II of *Paraortyx*. The trochlea metatarsi III is longer than wide, like in all other Galliformes the plantar side of its articular surface is asymmetric with the lateral ridge protruding farther proximally than the medial ridge.

Toes: In their relative length the toes correspond with those of *G. wyomingensis*. The third toe is the longest and somewhat shorter than the tarsometatarsus. The fourth toe slightly exceeds the second in length. The hallux is moderately long and appears to have been slightly elevated, although not as much as in most recent Phasianidae (text-fig. 9C). The distal end of the os metatarsale I does not reach the level of the foramen vasculare distale (in the Cracidae and Megapodiidae the hallux is incumbent, i. e. on the level of the three anterior toes; text-fig. 9B). The claws are short, medio-laterally compressed, and bear a sulcus neurovascularis. The processus articularis tarsometatarsalis of the os metatarsale I is short like in recent Phasianidae, an ossified tendon (of musculus flexor hallucis brevis ?) is attached to its proximal end (the processus articularis tarsometatarsalis of the Cracidae and Megapodiidae is fairly long).

Feathers: Remains of both, remiges and rectrices, are visible. As preserved the wing measures about 110 mm from the carpal joint to the tip of the longest feather. It has thus a similar overall length like the wing of recent Galliformes of comparable size (e. g. *Lophortyx californica*). The tail appears to have been very short (25 mm) but might not be preserved in its entire length.

Discussion

Palaeobiology

The foot structure, especially the slightly elevated hallux and the very short and fairly straight claws, indicates that *Paraortygoides messelensis* n. gen. n. sp. was rather terrestrial. Certainly it was less adapted for an arboreal way of life than recent Cracidae where the hallux inserts almost on the level of the three anterior toes and the claws are longer and more curved. The Eocene species most trenchantly differs from recent Galliformes in the morphology of the pectoral girdle and the wing skeleton. Whereas it has a similar overall size like the extant *Lophortyx californica* (taking the length of pelvis, hindlimbs, and furcula as reference), its forelimbs are proportionally much longer than in the latter and most other recent galliform birds (tab. 3). Possibly, *P. messelensis* was thus capable of a more sustained active flight than the great majority of recent Galliformes which are rather adapted for short bursts of flight in order to escape enemies (tab. 3 shows that the few recent migratory or semi-migratory genera, e. g. *Coturnix* and *Lagopus*, also have a comparatively longer wing than the other species).

Paraortygoides messelensis distinctly differs from recent Galliformes in the uncommonly robust furcula (concerning *G. wyomingensis*, LUCAS 1900, too, recognized that the furcula "is unusually stout for a gallinaceous bird, exceeding in this respect any species with which is has been compared"), and both *Paraortygoides* and *Gallinuloides* are further distinguished from all recent Galliformes except the Megapodiidae in that the apex carinae of the sternum is situated farther cranially. Both features, the weak scapus claviculae and the

Table 3. Length proportions of limb elements of galliform birds in comparison. Abbreviations: hum = humerus, uln = ulna, cmc = carpometacarpus, tbt = tibiotarsus, tmt = tarsometatarsus; "wing" = hum+uln+cmc, "leg" = femur+tbt+tmt.

	hum:tmt	uln:tmt	cmc:tmt	hum:tbt	uln:tbt	cmc:tbt	tbt:tmt	wing:leg
			Gallinuloididae inc. sed.					
Paraortygoides messelensis	1.39	1.34	0.74	0.88	0.84	0.47	1.59	0.92
Taoperdix pessieti[a]	~1.43	~1.37	~0.71	~0.81	~0.77	~0.40	~1.77	~0.86
Procrax brevipes[b]	1.20	1.22	0.67	0.78	0.80	0.44	1.53	0.85
			Gallinuloididae					
Gallinuloides wyomingensis	1.38	1.46	0.76	0.81	0.85	0.45	1.70	0.92
			Paraortygidae					
Paraortyx lorteti[c]	1.19	1.10	0.63	0.77	0.71	0.41	1.55	0.77
			Quercymegapodiidae					
Quercymegapodius depereti[c]	1.33		0.75					
			Megapodiidae					
Leipoa ocellata	1.41	1.52	0.73	0.85	0.91	0.44	1.66	0.95
Macrocephalon maleo	1.00	1.10	0.56	0.69	0.76	0.39	1.44	0.77
			Cracidae					
Nothocrax urumutum	0.95	1.01	0.51	0.64	0.68	0.34	1.49	0.70
Crax alector	1.03	1.13	0.55	0.68	0.73	0.35	1.53	0.76
			Phasianidae					
Lophortyx californica	1.05	0.96	0.57	0.61	0.56	0.33	1.74	0.65
Catreus wallichi	0.98	0.93	0.52	0.61	0.58	0.32	1.61	0.63
Coturnix coturnix	1.32	1.15	0.74	0.78	0.68	0.44	1.68	0.79
Lagopus lagopus	1.60	1.54	0.90	0.80	0.78	0.45	1.99	0.88

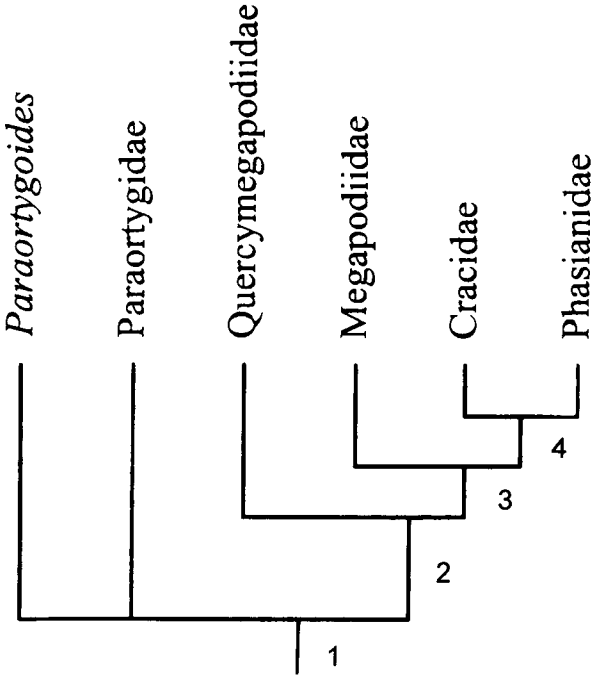
[a] after measurements in EASTMAN (1905)
[b] after measurements in TORDOFF & MACDONALD (1957)
[c] after measurements (mean of different individuals) in MOURER-CHAUVIRÉ (1992).

far caudally displaced apex carinae of (most, see below) recent Galliformes have been considered by STEGMANN (1964) to be functionally related to the large crop of these birds. He argued that, being predominantly ground-dwelling, Galliformes are dependent on a rapid and steep take off, to which a cranially situated center of gravity (i. e. a filled crop) is obstructive. According to STEGMANN (1964) the weak furcula and the caudally displaced apex carinae can be explained as a functional requirement to shift the crop and thus the center of gravity farther caudally. Unfortunately, STEGMANN (1964) did not include the Megapodiidae in his study, and in this taxon the apex carinae is not displaced caudally although the furcula is weak like in other Galliformes (I investigated specimens of *Macrocephalon maleo*, *Leipoa ocellata*, and *Megapodius laperouse*). The internal anatomy of Megapodiidae is rather poorly known and future studies will have to show if the crop of these birds differs in relative size and extension from other Galliformes. Given that the pectoral morphology of recent Galliformes is indeed connected with a large crop, it is near at hand to assume that *Paraortygoides messelensis* and *G. wyomingensis* had a less well developed crop than at least recent Cracidae and Phasianidae.

Phylogeny

Text-fig. 10 depicts a possible phylogeny of recent and fossil galliform birds. The polarity of the characters rests upon outgroup comparisons with the Anseriformes (which most recent authors consider to be the sister taxon of the Galliformes, e. g. DZERZHINSKY 1995; WEBER & HESSE 1995; CRACRAFT 1988; SIBLEY & AHLQUIST 1990; LIVEZEY 1997), and with the palaeognathous Lithornithiformes HOUDE 1988. Except for the position of the Megapodiidae the topology of this cladogram is in concordance with that proposed by MOURER-CHAUVIRÉ (1992). Since most of the characters supporting the nodes are unknown for *Gallinuloides wyomingensis*, this species has not been included.

Paraortygoides messelensis has been referred to the Gallinuloididae in this study, but this classification should be regarded as tentative since many of the similarities between *G. wyomingensis* and the new species obviously are plesiomorphic. For example the very slender carpometacarpus of *Paraortygoides* and *Gallinuloides* is also characteristic for the Quercymegapodiidae and many Megapodiidae, and that a narrow and elongated carpometacarpus might be primitive



Text-fig. 10. Relationships between *Paraortygoides* n. gen., the Paraortygidae MOURER-CHAUVIRÉ 1992, Quercymegapodiidae MOURER-CHAUVIRÉ 1992, and recent galliform taxa. The nodes are characterized as follows: 1 - humerus with distinct elongated accessory attachment site for musculus supracoracoideus, 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 - ectethmoidale greatly reduced or lost (CRACRAFT 1981), processus orbitalis of quadratum long and thin (CRACRAFT 1981), apex carinae of sternum displaced caudally, carpometacarpus with wide spatium intermetacarpale and bowed os metacarpale minus.

within neognathous birds in general is further supported by outgroup comparison with the palaeognathous Lithornithiformes which have a carpometacarpus of similar proportions like the mentioned galliform taxa (see HOUDE 1988). As outlined above, the robust furcula and the far cranially situated apex carinae of the sternum might well be primitive within galliform birds, too.

An assignment of *P. messelensis* to the Gallinuloididae is further aggravated by the fact that this family is only poorly diagnosed and that the four genera currently classified within it are morphologically quite heterogeneous. *Procrax* for example differs from *Gallinuloides* (and *Paraortygoides*) in the much wider corpus scapulae and the more bowed os metacarpale minus; *Taoperdix pessieti*, the type species of the genus *Taoperdix*, has about the same size like *G. wyomingensis* but a much narrower scapus claviculae and a medio-laterally considerably wider pelvis than both *G. wyomingensis* and *P. messelensis*. Both in *Procrax* and *Archaealectrornis* the fossa pneumotricipitalis is much shallower than in *Paraortygoides*, and at least *Procrax* seems to lack a cup-like cotyla scapularis (these differences are of course only significant if *Paraortygoides* is correctly assigned to the Gallinuloididae). Although *Paraortygoides*, *Gallinuloides*, *Taoperdix*, and *Procrax* have similar limb proportions, these might well be plesiomorphic within the Galliformes since they also occur within some Megapodiidae and Cracidae (tab. 3 and MOURER-CHAUVIRÉ 1992: text-fig. 7).

With regard to the other higher galliform taxa described so far, an alternative classification of *Paraortygoides* could only be an assignment to the Paraortygidae, since Quercymegapodiidae and recent Galliformes have a transverse ridge at the beginning of the incisura capitis of the humerus which certainly is derived within neognathous birds (see MOURER-CHAUVIRÉ 1992). Especially in the presence of a marked second fossa pneumotricipitalis the humerus of *Paraortygoides* strikingly resembles the corresponding bone of *Paraortyx* (Paraortygidae). Yet, although this feature certainly is derived within neognathous birds (see BOCK 1962), it obviously evolved independently more than once within the Galliformes. A distinct second fossa pneumotricipitalis for example also occurs in the genus *Palaeortyx* MILNE-EDWARDS 1879, one of the earliest known taxa of the Phasianidae (BALLMANN 1969; MOURER-CHAUVIRÉ 1992), in the recent Odontophorinae, and in some Phasianinae (e. g. *Ammoperdix*, *Coturnix*). Moreover, the second fossa pneumotricipitalis of *Pirortyx* (Paraortygidae) is much shallower than that of *Paraortyx* and also suggests that the marked second fossa of *Paraortyx* is autapomorphic for this taxon (given that *Pirortyx* is correctly referred to the Paraortygidae). The oldest record of the Paraortygidae (from the locality La Bouffie) has an absolute age of 38 million years, and is thus some 10 million years younger than the deposits of Messel which are about 48 million years old (see LEGENDRE & LÉVÊQUE 1997).

Further preparation of the type specimen of *G. wyomingensis* might reveal the morphology of the proximal humerus and the cotyla scapularis of the coracoid in this species, and thus either confirm or refute the classification proposed herein. If correctly referred to the Gallinuloididae, the cup-like cotyla scapularis of *Paraortygoides messelensis* shows that the Gallinuloididae branched off very early in the evolution of the Galliformes. This is also supported by the fact that the humeri of *Archaealectrornis* and *Gallinuloides* lack a transverse ridge at the beginning of the incisura capitis of the humerus (CROWE & SHORT 1992) which is characteristic for the recent galliform taxa and which is derived within neognathous birds (MOURER-CHAUVIRÉ 1992).

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