A small galliform bird from the Lower Eocene Fur Formation, north-western Denmark

BENT E. K. LINDOW & GARETH J. DYKE

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A pair of fossilized imprints of feet represent the first published galliform (landfowl) specimen from the Lower Eocene Fur Formation of northwest Denmark. The specimen is referable to Galliformes due to the presence of a distinctly asymmetric trochlea metatarsi III. The specimen appears distinct from previously described Eocene Galliformes (e.g. Gallinuloididae, Quercymegapodiidae and Paraortygidae) and may represent a new taxon of Galliformes, increasing the diversity of this group in the Lower Eocene.

Key words: Galliformes, Landfowl, Lower Eocene, Fur Formation.

Bent E. K. Lindow [*lindow@snm.ku.dk*] *School of Biology and Environmental Science, University College Dublin, Belfield, Dublin 4, Republic of Ireland* & *Geological Museum, University of Copenhagen, Øster Voldgade 5-7, DK-1350 Copenhagen K, Denmark; Gareth J. Dyke* [*gareth.dyke@ucd.ie*] *School of Biology and Environmental Science, University College Dublin, Belfield, Dublin 4, Republic of Ireland.*

Along with Anseriformes (ducks, geese and relatives), the extant avian order Galliformes (landfowl) is considered by most systematists to occupy a basal position among modern birds (Mayr & Clarke 2003; Cracraft et al. 2004). Emerging consensus between recent molecular and morphological hypotheses places the two clades Anseriformes and Galliformes as sister taxa (sometimes referred to as Galloanserae) at the base of Neognathae (Groth & Barrowclough 1999; García-Moreno et al. 2003; Mayr & Clarke 2003; Cracraft et al. 2004; Pereira & Baker 2006). Despite this massive morphological and molecular evidence for the clade Gallonserae, a recent cladistic analysis by Bourdon (2005) challenged this view and instead placed Galliformes as the sister group to all other modern neognathous birds.

With the exception of a few incomplete and fragmentary bones from the Cretaceous (Brodkorb 1964; Hope 2002), the oldest certain records of Galliformes is the Lower Eocene taxon *Gallinuloides wyomingensis* (Eastman 1900; Lucas 1900; Shufeldt 1915; Crowe & Short 1992; Dyke 2003; Mayr & Weidig 2004). Together with the Lower – Middle Eocene genus *Paraortygoides* (Mayr 2000; Dyke & Gulas 2002), the taxon constitutes the single Lower Eocene family-level clade within Galliformes, the Gallinuloididae (Mayr, 2000; Mayr and Weidig, 2004). Other currently recognised Eocene family-level clades of Galliformes include the families Quercymegapodiidae (Middle – Upper Eocene) and Paraortygidae (Upper Eocene – Upper Oligocene) (Mourer-Chauviré 1992). Finally, the Middle Eocene *Amitabha urbsinterdictus* has been recognised as a stem-group 'phasianoid' (Gulas-Wroblewski & Wroblewski 2003).

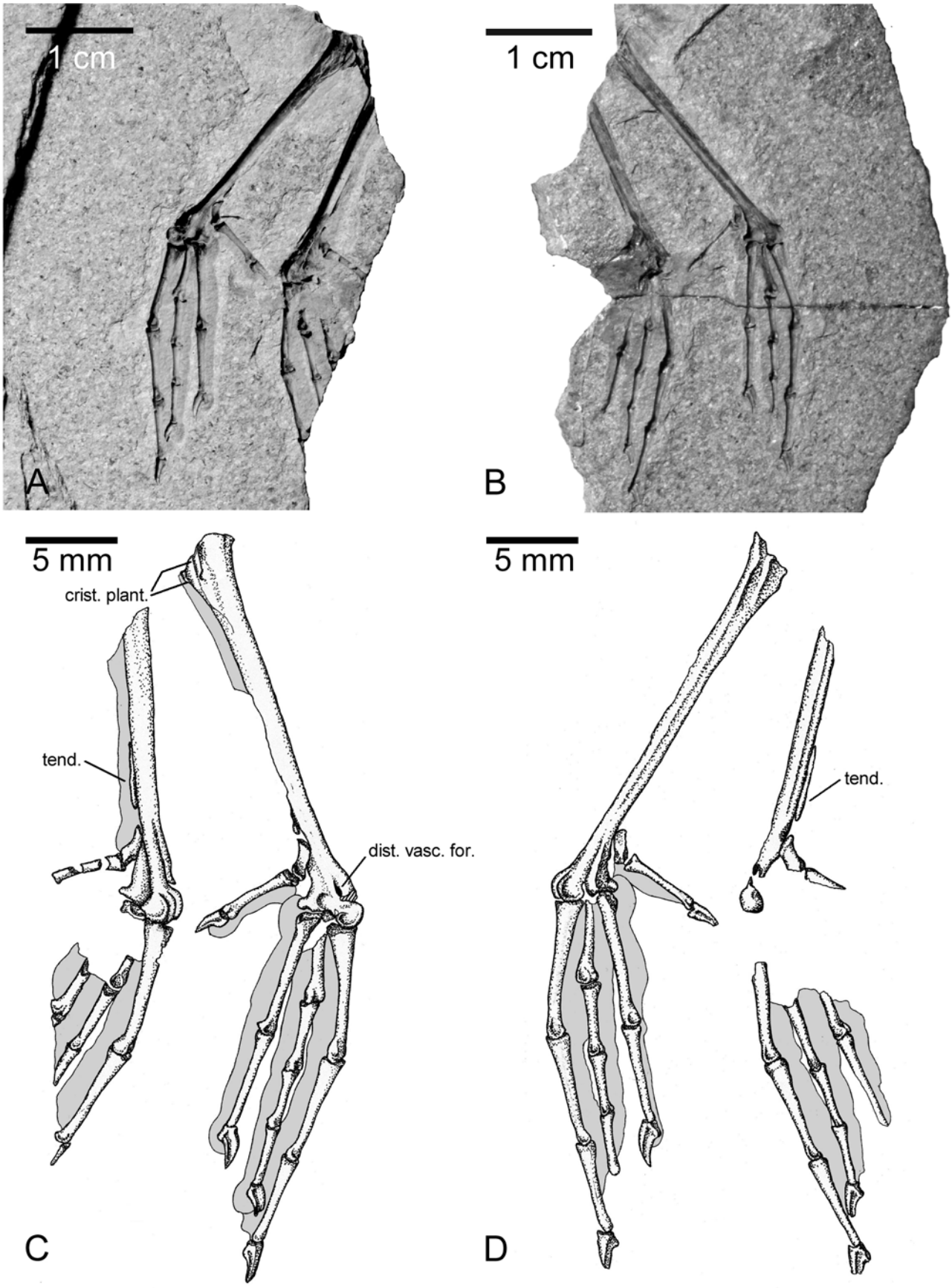
This paper describes the first record of a galliform bird from the Lower Eocene Fur Formation of Denmark; a pair of fossilized imprints of feet, which increases the Early Eocene diversity of Galliform birds.

Institutional abbreviations. MCZ

Museum of Comparative Zoology, Harvard University, Cambridge, USA; MGUH: Palaeontological type collection of Geological Museum, University of Copenhagen, Denmark; SMF: Forschungsinstitut Senckenberg, Frankfurt-am-Main, Germany.

Material and methods

Overall photos of the specimen were made with a Canon® Powershot A75 digital camera (Figs 1A-B).


1 cm
A
1 cm
B
5 mm
crist. plant.
tend.
dist. vasc. for.
C
5 mm
tend.
D

The extremely fine-grained diatomite (typically 40–70 wt% in the grain size fraction 2–20 µm; Pedersen *et al.* 2004: Table 1) allows details down to 1/20 of an mm to be discerned (B. Lindow, pers. obs.) and an extremely detailed reconstruction of the original morphology of the specimen (Figs 1C-D). This was done by combining information from a series of highly magnified, overlapping photos in low-angle light were made with an Olympus® DP12 Digital Image Acquisition System camera linked to an Olympus® SZ40 Binocular Microscope, with direct studies of the specimen in a binocular microscope with low-angle light from various directions.

Systematic Palaeontology

Order Galliformes Temminck, 1820
Incertae sedis

Referred specimen

MGUH 28385, part and counterpart of impression in diatomite of right and left tarsometatarsi, digits and soft tissue (Figs 1A-B).

Locality and horizon

MGUH 28385 was collected from a large diatomite pit north of Stendal Høje, on the Island of Fur, Denmark. The Fur Formation is of Lower Eocene (Ypresian) age, based on the presence of the Palaeocene-Eocene boundary in the underlying Stolleklint Clay (Ølst Formation) (Heilmann-Clausen & Schmitz 2000, Beyer et al. 2001), and $^{39}Ar/^{40}Ar$-dating of two ash layers within the formation to 54.5 and 54.0 Ma, respectively (Chambers et al. 2003).

Description

Specimen and comparative measurements are given in Table 1. Both feet are visible in MGUH 28385, preserved as impressions in the diatomite. The right tar-

Table 1. Longitudinal measurements (left/right, in millimeters) of DK 251, *Gallinuloides wyomingensis* holotype (Eastman 1900), *Paraortygoides messelensis* holotype (Mayr 2000), *Paraortyx lorteti* and *Quercymegapodius depereti* (Mourer-Chauviré 1992). **Tmt**, tarsometatarsus; **I1**, first phalange of first digit; **I2**, second phalange of first digit, etc.

Specimen	Tmt	I1	I2	II1	II2	II3	III1	III2	III3	III4	IV1	IV2	IV3	IV4	IV5
DK 251	/ 25.3	/ 5	/ 2.4	/ 8.3	/ 6.2	/ 3.1	8.2 / 8.5	6.8 / 6.9	5.4 / 5.3	2.5 / 3.0	/ 5.1	4.6 / 4.6	3.7 / 3.8	3.7 / 3.7	2.1 / 2.2
Gallinuloides wyomingensis MCZ 2221	34.5 / 33.9		7	4	11	8	6	12	10	8	6	7.5	5.5	4	4
Paraortygoides messelensis SMF-ME1303	/ 34.9	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
Paraortyx lorteti	33.48														
Quercymegapodius depereti	30.0														

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Fig. 1. A-D, Galliformes *incertae sedis* from the Lower Eocene Fur Formation of Denmark, MGUH 28385. A. Part, impression of left and right tarsometatarsi, digits and skin; B, counterpart. C. Reconstruction of part (A). D. Reconstruction of counterpart (B). Abbreviations: crist. plant., cristae plantares; dist. vasc. for., distal vascular foramen; tend., ossified tendon.

sometatarsus and digits are almost complete, but the trochlea for digit IV is missing. The left foot lacks the proximal end of the tarsometatarsus, part of the distal end, the proximal phalanges of digits II and IV, distal phalanges of digits II, III and IV and claws of digit III.

The right tarsometatarsus of MGUH 28385 is approximately equal in length to the third toe and slender. On the proximal end of this bone the hypotarsus eminentia intercondylaris is raised medially, and two cristae plantares are visible on the palmar surface (Fig. 1C). The shaft is straight and remnants of an ossified tendon extending from the hypotarsus to the proximal surface of digit I are present (Figs. 1C-D). The foramen vasculare distale is situated beyond the distal end of metatarsal I (Fig. 1C). The trochleae metatarsorum are splayed, and the trochlea for digits II and III are approximately equally extended distally. The trochlea for the third digit is distinctly asymmetric with the medial ridge extending further distally (Fig. 1C).

The digits of MGUH 28385 are typical for Galliformes in general; the third toe is the longest (four phalanges and a claw), almost as long as the tarsometatarsus, and the second toe only slightly shorter than the fourth. Digit I consists of one phalanx and a small claw, the hallux appears to have been incumbent. The claws of MGUH 28385 are compressed and have prominent sulci.

Traces of soft tissue are visible as faint shadows of slightly darker sediment beneath the digits and below the tarsometatarsus (Figs 1A-D).

Systematic Placement

MGUH 28385 is referred to the order Galliformes based on the presence of a distinctly asymmetric trochlea metatarsi III of the tarsometatarsus (Mayr, 2000; Dyke et al. 2003; Mayr and Weidig, 2004). This character is seen in all living and fossil representatives of the order (Mayr, 2000; Dyke et al., 2003). Kristoffersen (2002: 30) referred specimen MGUH 28385 to "?Family Gallinuloididae" in her unpublished Ph.D.-thesis, but it is not immediately referable to any of the described Eocene families of Galliformes. The specimen shares the presence of splayed trochleae metatarsorum with the two other Eocene families Gallinuloididae and Quercymegapodiidae, but tarsometatarsus of MGUH 28385 is much more slender. The tarsometatarsus and relatively smaller claws of MGUH 28385 also differ from the two other genera in the Gallinuloididae, as does the presence of strongly ossified tendons, which the Gallinuloididae lack (Mayr & Weidig, 2004). Finally, MGUH 28385 differs from known members of the Upper Eocene family Paraortygidae by its much smaller size and slender tarsometatarsus.

While MGUH 28385 is clearly a Galliform bird, it cannot readily be assigned to one of the extinct Eocene family, nor does it contain enough character information which allows it to be referred to a particular lineage of early phasanids with certainty. It is therefore referred to Galliformes *incertae sedis*.

Conclusion

The specimen represents the first published occurrence of Galliformes from the Fur Formation. The morphological differences between this specimen and hitherto described Eocene Galliformes (e.g. Gallinuloididae, Quercymegapodiidae and Paraortygidae) may indicate the presence of a new family-level taxon of Galliformes in the Lower Eocene. More complete specimens displaying information on the rest of the skeleton are needed, before such a conclusion can be confirmed, however. The new Danish specimen is significantly distinct from the galliform *Paraortygoides radagasti* (Dyke & Gulas 2002) from the London Clay deposits of same age across the North Sea Basin, and indicates the wide diversity achieved by modern birds in the Lower Eocene.

Dansk sammendrag

Det fossile aftryk af et par fuglefødder i moler (diatomit) repræsenterer den første publicerede hønsefugl (Orden Galliformes) fra den nedre eocæne (Ypresien) Fur Formation. Stykket kan bestemmes til at være en hønsefugl på grund af tilstedeværelsen af et par asymmetriske rygge på tarsometatarsus' mellemste ledflade. Stykket kan ikke henføres til hverken nogle af de tidligere beskrevne familier af eocæne hønsefugle (Gallinuloididae, Quercymegapodiidae og Paraortygidae) eller til de tidlige phasanider, og repræsenterer muligvis en ny gruppe af hønsefugle. Der kræves dog yderligere, mere komplet materiale for at understøtte denne hypotese.

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