

A diverse bird assemblage from the Ypresian of Belgium furthers knowledge of early Eocene avifaunas of the North Sea Basin

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With 12 figures

Abstract: We describe an assemblage of 54 avian bones from early Eocene marine sediments of the Ampe quarry near Egem in Belgium. The fossils belong to at least 20 species in more than 11 higher-level taxa. Well-identifiable specimens are assigned to the Odontopterygiformes, Galliformes, Messelornithidae, Apodiformes, Halcyornithidae, Leptosomiformes (cf. *Plesiocathartes*), and Coraciiformes (cf. *Septencoracias*). Further specimens are tentatively referred to the phaethontiform Prophaethontidae and to the Accipitridae, Masillaraptoridae, and Alcediniformes. The three-dimensionally preserved fossils from Egem provide new data on the osteology of taxa that are otherwise mainly known from compression fossils with crushed bones. The material also includes specimens that further knowledge of the composition of early Eocene avifaunas of the North Sea Basin. The comparatively well-represented small galliform species is clearly distinguished from the early Eocene Gallinuloididae and most closely resembles *Argillipes aurorum*, a largely ignored galliform species from the London Clay. The tentatively identified fossils of Accipitridae and Alcediniformes would represent the earliest fossil records of these clades. The bird assemblage from Egem includes relatively few seabirds (Odontopterygiformes, cf. Prophaethontidae) and is dominated by remains of terrestrial species (Galliformes, Messelornithidae). Arboreal birds (Halcyornithidae, Leptosomiformes, cf. Alcediniformes, Coraciiformes) are less abundant and aerial insectivores (Apodiformes) very scarce, which either indicates a taphonomic bias in the composition of the avifauna or particular paleoenvironmental characteristics of the nearshore habitats in that area of the southern North Sea Basin.

Key words: Aves, fossil birds, Paleogene, systematics, taxonomy

1. Introduction

The North Sea Basin features a number of early Eocene (Ypresian) localities, which yielded avian remains. The best known of these stem from the London Clay in southeastern England, whose strata are assigned to the nannoplankton zones NP10-12 and span an age of about 51.5–54.5 million years (RAYNER et al. 2009; COLLINSON et al. 2016; KING et al. 2016). Bird fossils from the London clay were already described in the 19th century, but many of these studies dealt with the remains of large marine birds (e.g., OWEN 1873; ANDREWS 1899). Being near-shore deposits, the

strata of the London Clay also include a diverse array of small landbirds, which lived in the paratropical forests along the coast. The first comprehensive survey of the avifauna of the London Clay was performed by HARRISON & WALKER (1977) and HARRISON (1980, 1982a, b, 1984a, b) described further avian remains. However, these authors made few attempts to assign isolated bones from different body parts to the same taxon and many fossil species were shoehorned into extant family-level clades, which produced an unrealistic picture of the diversity of the London Clay avifauna (MAYR 2009a).

Subsequent revisions have shown that the composition of the landbird fauna of the London Clay shows a great similarity to that of the latest early – earliest middle Eocene (between 48 and 47.5 million years ago [Ma]) lacustrine sediments of the Messel fossil site in Germany, which on a global scale is the most diverse and best studied early Eocene bird assemblage (MAYR 2009a; MAYR 2017a). Still, however, the identity of many species from the London Clay that are based on fragmentary material remains controversial, and some of the more recent descriptions are likewise flawed by erroneous identifications (see MAYR 2001; MAYR 2002a; MAYR 2009a).

Early Eocene sediments from the North Sea Basin are also exposed in the Fur Formation in Denmark, the strata of which have an age of about ~54–55.8 million years (BOURDON *et al.* 2016) and produced a number of well-preserved skeletons. A comprehensive revision of the avifauna of the Fur Formation has yet to be conducted and only the most spectacular specimens were described so far (e.g., KRISTOFFERSEN 2002; MAYR 2010a; MAYR 2011a; MAYR & BERTELLI 2011; BERTELLI *et al.* 2013; BOURDON & LINDOW 2015; BOURDON *et al.* 2016).

Early Eocene avifaunas with a similar composition to that of the London Clay are furthermore known from the North American Green River and Nanjemoy formations. Most bird fossils from the lacustrine sediments of the Green River Formation in Wyoming (USA) are from the Fossil Butte Member, which has an age of about 52 Ma (KSEPKA & CLARKE 2010). The bird-bearing marine strata of the Nanjemoy Formation in Virginia (USA) stem from the nannoplankton zone NP 11 and have an age of 53.7–54.2 Ma (OLSON 1999; WEEMS & GRIMSLEY 1999; ANTHONISSEN & OGG 2012; MAYR 2016b).

Here we describe avian remains from marine sediments of the Tielt Formation from the Egem locality in northwestern Belgium (Fig. 1). All fossils are three-dimensionally preserved bones and stem from the Ampe quarry (51° 00' 45" N, 3° 13' 56" E). They were found by amateur collectors in 20 to 80 centimeters thick layers of shelly glauconitic sands at the base of the Egemkapel Clay Member (STEURBAUT 1998; SMITH & SMITH 2013). Based on microfossil analyses, the Egemkapel Clay Member was referred to the Upper NP 12 nannoplankton zone (subzone VI; mid Ypresian, about 50.5–52 Ma; STEURBAUT 1998; KING *et al.* 2016). In addition to numerous elasmobranch teeth, the sediments yielded a few remains of mammals, which allowed a biochronologic referral of

the Egemkapel Clay Member to the reference-level MP8+9 of the Mammalian scale for the European Paleogene (SMITH & SMITH 2013; KING *et al.* 2016). So far, no bird fossils from Egem have been published and our study presents the first survey of the avifauna of the locality.

2. Material and methods

All bones described in the present study were found by amateur collectors, who screenwashed large amounts of sediment in the past two decades. For this study, we examined avian remains in seven private collections and selected all diagnostic avian remains, which are now deposited in the Royal Belgian Institute of Natural Sciences. Most of these fossils are major limb bones, of which all available specimens were included in the study; not considered were small numbers of vertebrae, pedal phalanges, and very fragmentary or undiagnostic bones (altogether about 30 specimens). Our sample is therefore representative for the relative abundance of these elements in the Egem material and we did not presort major limb bones. Not considered, however, were skeletal elements that were considered indeterminable, such as a few partial scapulae, as well as most pedal phalanges (other than a few raptor-like ungual phalanges described below) and vertebrae (other than a large atlas). Except for two bones, which are specified below and stem from the somewhat younger layer 5 (Egem Sand Member; subzones VII and VIII in STEURBAUT 1998), also belonging to the upper NP12 zone, all specimens described in the present study are from layer IV (Egemkapel Clay Member) of the Ampe quarry.

Throughout this study, we pursued a cautious taxonomic approach and rather than describing new taxa based on inadequate material, we tentatively assigned fossils to already known taxa even when minor differences are noticed. While we are therefore confident that our identification of higher-level taxa in the Egem material is likely to be conservative, we cannot be sure that our tentative referral of different isolated bones to these taxa is correct in all cases. In rich assemblages, an assignment of various skeletal elements to the same species can be guided by the relative abundance of the preserved bones, but this approach is not feasible in fossil samples of limited size, such as the one described in the present study. It is under these premises that the following account should be received.

In most instances, the higher-level taxonomy follows the IOC World Bird List (<https://www.worldbirdnames.org/>). However, instead of classifying the traditional “caprimulgid” and apodiform birds into an expanded “order” Caprimulgiformes, these birds are here assigned to the taxon Strisores, which was introduced by MAYR (2010). Based on the classification proposed by the latter author, the taxon Apodiformes is maintained for the clade including Aegothelidae, Apodidae, Hemiprocnidae, and Trochilidae.

Institutional abbreviations: IGWuG – Institut für Geologische Wissenschaften und Geiseltalmuseum of Martin-Luther-Universität Halle-Wittenberg, Halle/Saale, Germany.

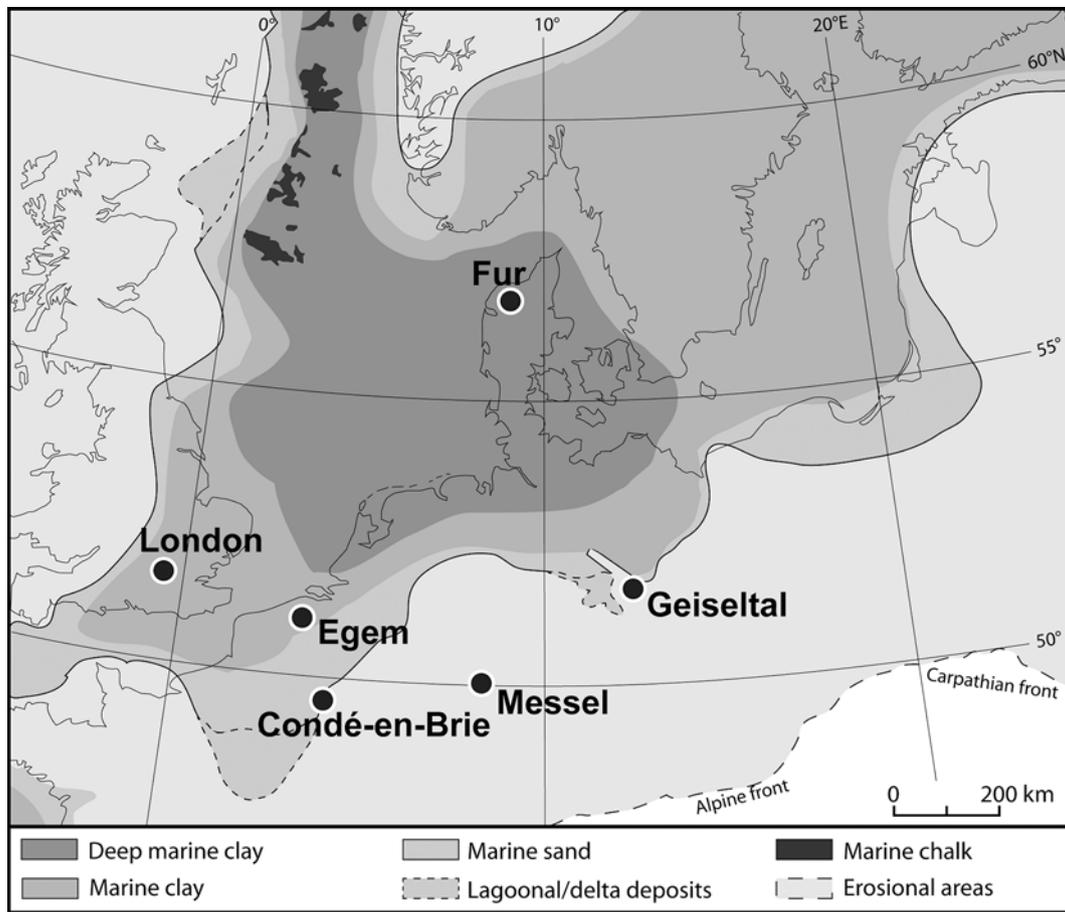


Fig. 1. Paleogeographic map of the North Sea Basin during the middle Ypresian, with the locations of Ypresian and Lutetian bird sites mentioned in the text (modified after GIBBARD & LEWIN 2016).

IRSNB – Royal Belgian Institute of Natural Sciences, Brussels, Belgium. MNHN – Muséum National d’Histoire Naturelle, Paris, France. NHMUK – Natural History Museum, London, UK. SMF – Senckenberg Research Institute Frankfurt, Germany. The anatomical terminology employed in this study follows BAUMEL & WITMER (1993).

3. Systematic paleontology

Odontopterygiformes HOWARD, 1957

Pelagornithidae FÜRBRINGER, 1888

Dasornis OWEN, 1870

Dasornis cf. *emuinus* (BOWERBANK, 1854)

Fig. 2A–C

Referred specimens: IRSNB Av 160: rostral section of right ramus mandibulae; collected by G. MARIËN. IRSNB Av 161: proximal end of right carpometacarpus; collected by G. VAN DEN ECKHAUT.

Measurements (in mm): Mandible fragment, length as preserved, 54.2. Carpometacarpus, length as preserved, 55.1.

Remarks: The mandible fragment (Fig. 2A) belongs to a large bony-toothed bird and exhibits the insertion sites of two large broken pseudoteeth; interspersed smaller pseudoteeth are absent. There is a marked furrow along the ventral section of the lateral surface of the bone and the ventral margin forms a sharp ridge. The specimen from Egem compares well with a mandible fragment from the London Clay, which was described as “*Pseudodontornis longidentata*” by HARRISON & WALKER (1976a), with this latter species having been synonymized with *Dasornis emuinus* by MAYR (2008a). Records of *D. emuinus* are also known from the late Paleocene and early Eocene of Morocco (BOURDON et al. 2010).

Based on its size, the proximal end of the carpometacarpus (Fig. 2B, C) is likely to be from the same species as the mandible fragment. The fossil has the characteristic shape of the carpometacarpus of Eocene bony-toothed birds, in which the trochlea carpalis and the os metacarpale alulare are proximodistally elongated, the processus extensorius has

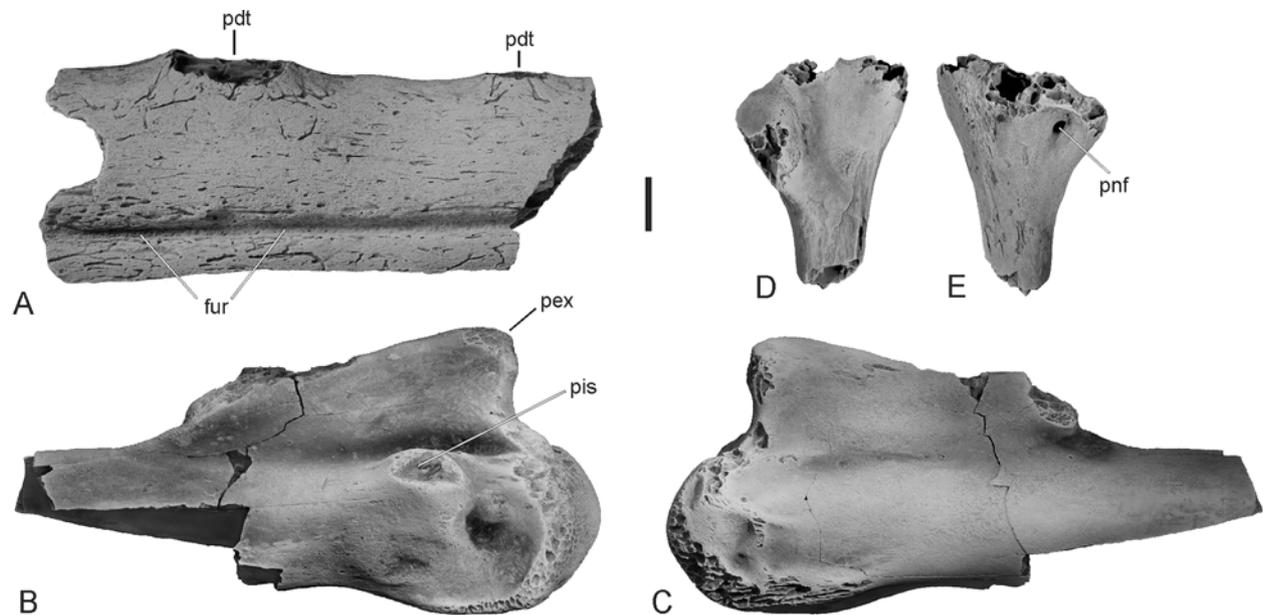


Fig. 2. Remains of bony-toothed birds (Odontopterygiformes) from Egem. **A** – rostral section of right ramus mandibulae of *Dasornis* cf. *emuinus* (IRSNB Av 160) in lateral view. **B**, **C** – proximal end of right carpometacarpus (IRSNB Av 161) in ventral (**B**) and dorsal (**C**) view. **D**, **E** – cranial end of left scapula of a smaller species (IRSNB Av 162) in lateral (**D**) and medial (**E**) view. Abbreviations: fur – furrow along ventral section of lateral mandibular surface; pdt – insertion site of pseudotooth; pex – processus extensorius; pis – processus pisiformis; pnf – pneumatic foramen. All specimens were coated with ammonium chloride. Scale bar equals 5 mm.

little cranial prominence, and the processus pisiformis forms a low bulge. In Neogene Pelagornithidae, the os metacarpale alulare is even more elongated and the processus extensorius less cranially prominent (MAYR & RUBILAR-ROGERS 2010).

Pelagornithidae FÜRBRINGER, 1888

Gen. et sp. indet.

Fig. 2D, E

Referred specimen: IRSNB Av 162: cranial end of left scapula; collected by G. VAN DEN EECKHAUT.

Measurements (in mm): Length as preserved, 21.4.

Remarks: In size and morphology, the bone resembles the scapula of a pelagornithid from the middle Eocene of Belgium, which was tentatively assigned to *Macrodontopteryx oweni* by MAYR & SMITH (2010). The specimen exhibits a large pneumatic foramen on the medial side of the extremitas cranialis, and appears to be from a smaller species than the above-described mandible fragment and proximal carpometacarpus.

Galliformes TEMMINCK, 1820

Family inc. sed.

aff. *Argillipes aurorum* HARRISON & WALKER, 1977

Fig. 3

Referred specimens: IRSNB Av 163: proximal end of right humerus; collected by F. MIGOM. IRSNB Av 164: proximal end of left ulna; collected by G. MARIËN. IRSNB Av 165: distal end of right tarsometatarsus; collected by S. MAILLIOT. IRSNB Av 166: proximal end of right tarsometatarsus; collected by F. MIGOM.

Tentatively referred specimens: IRSNB Av 167: right coracoid; collected by Y. CHRISTIANS. IRSNB Av 168: distal end of left tibiotarsus; collected by G. MARIËN.

Measurements (in mm): Coracoid, length as preserved, 21.6. Humerus, proximal width, 10.1. Ulna, proximal width across cotylae, 4.8. Tibiotarsus, distal width, 4.7. Tarsometatarsus, proximal width (IRSNB Av 166), 6.0. Tarsometatarsus, distal width (IRSNB Av 165), 5.4.

Description and comparisons: These specimens are from a small species about the size of the extant *Lophortyx gambelii* (Odontopterygidae). The proximal end of the humerus

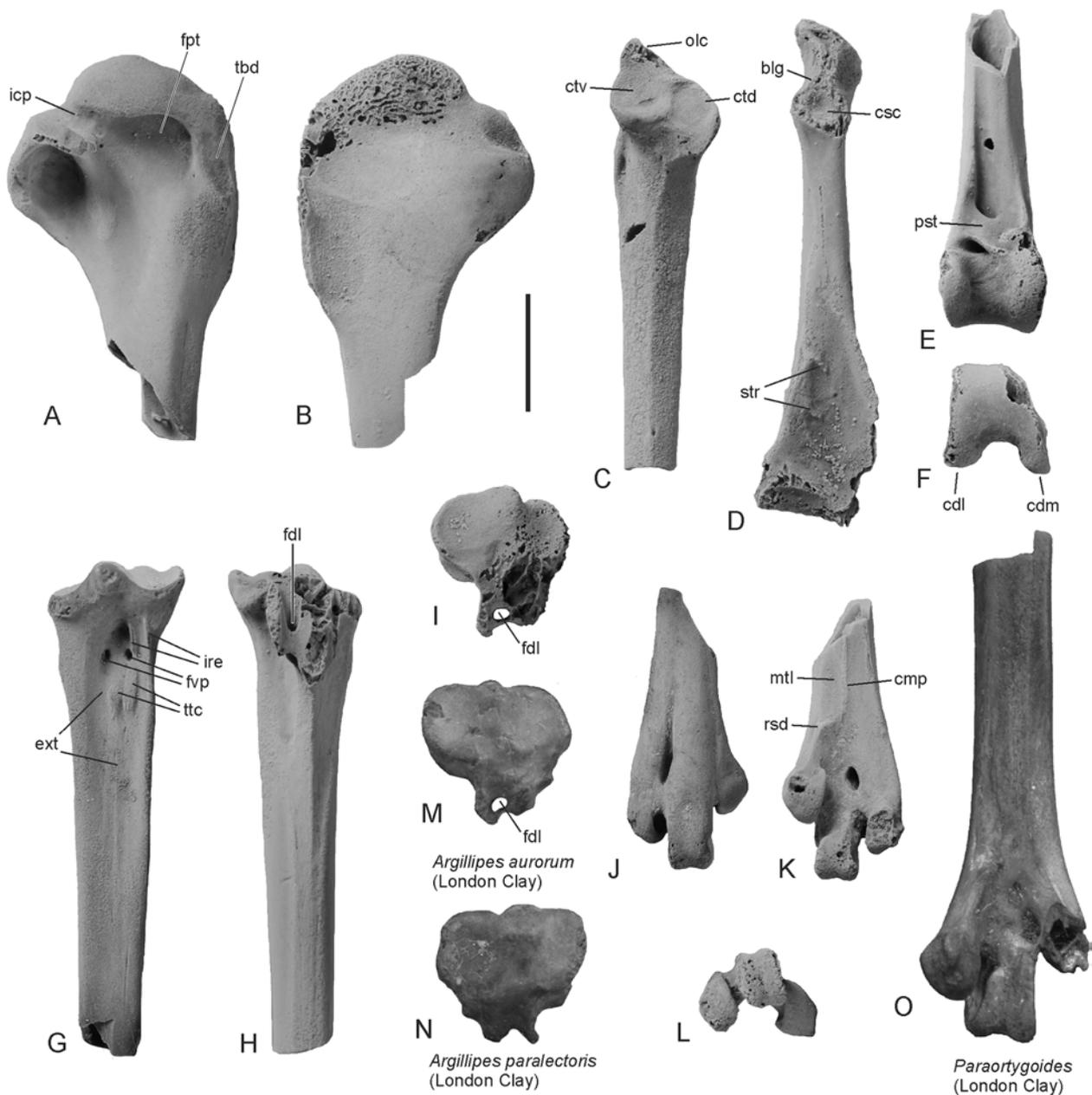


Fig. 3. Specimens of galliform birds from Egem. **A, B** – proximal end of right humerus (IRSNB Av 163) in caudal (**A**) and cranial (**B**) view. **C** – proximal end of left ulna (IRSNB Av 164) in cranial view. **D** – tentatively referred right coracoid (IRSNB Av 167) in dorsal view. **E, F** – tentatively referred distal end of left tibiotarsus (IRSNB Av 168) in cranial (**E**) and distal (**F**) view. **G–I** – proximal end of right tarsometatarsus (IRSNB Av 166) in dorsal (**G**), plantar (**H**), and proximal (**I**) view. **J–L** – distal end of right tarsometatarsus (IRSNB Av 165) in dorsal (**J**), plantar (**K**), and distal (**L**) view. **M** – proximal end of right tarsometatarsus of *Argillipes aurorum* from the London Clay (holotype; NHMUK A 3130). **N** – proximal end of left tarsometatarsus of *Argillipes paralectoris* from the London Clay (holotype; NHMUK A 3604). **O** – distal end of right tarsometatarsus of the gallinuloidid *Paraortygoides radagasti* from the London Clay (holotype; NHMUK A 6217). Abbreviations: blg – bulge in the sulcus supracoracoideus; cdl – condylus lateralis; cdm – condylus medialis; cmp – crista medianoplantaris; csc – cotyla scapularis; ctd – cotyla dorsalis; ctv – cotyla ventralis; ext – sulcus extensorius; fdl – hypotarsal canal for tendon of musculus flexor digitorum longus; fpt – second (dorsal) fossa pneumotricipitalis; fvp – foramina vascularia proximalia; icp – incisura capitis; ire – impressio retinaculi extensorii; mtl – fossa metatarsi I; olc – olecranon; pst – pons supratendineus; rsd – plantarly raised distal margin of fossa metatarsi I; str – muscle striae on dorsal surface of extremitas sternalis; tbd – tuberculum dorsale; ttc – tuberositas musculi tibialis cranialis. All fossil specimens except those in **M, N**, and **O** were coated with ammonium chloride. Scale bar equals 5 mm.

(Fig. 3A, B) features a proximodistally elongated tuberculum dorsale, which is a derived characteristic of Galliformes and other birds (e.g., Tinamiformes, Sphenisciformes) with a strong supracoracoideus muscle. Unlike in crown group Galliformes, but as in other early Paleogene stem group representatives, the incisura capitis plesiomorphically lacks a transverse ridge (MOURER-CHAUVIRÉ 1992). As in the early Eocene Gallinuloididae and other Paleogene Galliformes (MOURER-CHAUVIRÉ 1992; MAYR 2000), there is a second (dorsal) fossa pneumotricipitalis, which undercuts the caput humeri. This fossa is, however, shallower than in the early Eocene gallinuloid *Paraortygoides* (MAYR 2000) and the caput humeri is smaller than in the Gallinuloididae and most other galliform birds except for an unnamed species from the early Eocene of Mongolia (HWANG *et al.* 2010). The primary (ventral) fossa pneumotricipitalis lacks pneumatic foramina. The crista deltopectoralis is proximodistally short, only weakly protruding, and has a concave caudal surface. The sulcus transversus is very short. The humerus is proportionally larger than that of *L. gambelii*, but this difference would conform to the fact that early Eocene stem group Galliformes have proportionally longer forelimbs than the crown group taxa (MAYR 2000).

The tentatively referred coracoid (Fig. 3D) shows the characteristic derived morphology of galliform birds. However, based on comparisons with the coracoid of *Lophortyx gambelii* and unless the Egem galliform exhibited marked sexual size dimorphism, it appears to be from a smaller species than the other bones. The tip of the processus acroracoideus is broken, but the process appears to have been angled as in other galliform birds. It features the characteristic galliform morphology in that there is a marked bulge in the sulcus supracoracoideus, just omal of the cotyla scapularis. The tip of the short processus procoracoideus is broken. As in other Eocene stem group Galliformes (MOURER-CHAUVIRÉ 1992; MAYR 2000; MAYR & WEIDIG 2004), but unlike in the crown group taxa, there is a cup-like cotyla scapularis rather than a flat facies articularis scapularis. The shaft of the bone is narrow and the dorsal surface of the extremitas sternalis bears transverse muscle striae, as it does in other galliform birds.

The proximal end of the ulna (Fig. 3C) likewise corresponds with that of other galliform birds in that the olecranon is well developed, the cotyla dorsalis proximodistally long and the cotyla ventralis large and with a subcircular outline. The shaft of the bone is dorsoventrally compressed.

The tentatively referred tibiotarsus (Fig. 3E, F) agrees with that of galliform birds in that it has a mediolaterally narrow distal end with a proximodistally wide pons supratendineus and condyles of subequal proximodistal length. The condylus medialis is, however, mediolaterally narrower than in other Galliformes, and its low width does not conform to the mediolaterally wide cotyla medialis of the tarsometatarsus. For these reasons, our referral of the specimen is only tentative. An alternative assignment to the gruiform Messelornithidae conflicts with the fact that the condyles are of equal proximodistal length (in messelornithids, the condylus medialis is distinctly shorter).

The distal end of the tarsometatarsus (Fig. 3J–L) exhibits an autapomorphic feature of Galliformes, in which

the trochlea metatarsi III has an asymmetric plantar articulation surface, with the medial trochlear rim being distinctly shorter than the lateral one. Unlike in the early Eocene *Paraortygoides messelensis* from Messel, the crista medianoplantaris does not fork, and the trochleae are less splayed than in *P. messelensis*. The foramen vasculare distale is large and its dorsal opening has an elongate outline. The fossa metatarsi I is distinct and located near the medial margin of the bone; its distal margin is markedly raised. The trochlea metatarsi II is shorter than the trochlea metatarsi IV; the plantar surface of the latter trochlea is broken.

The proximal end of the tarsometatarsus (Fig. 3G–I) resembles that of *Argillipes aurorum* from the London Clay (Fig. 3M), which was described as a galliform bird by HARRISON & WALKER (1977). Compared with extant Galliformes, the hypotarsus corresponds to that of the Odonophorinae (MAYR 2016a: fig. 2H) and has a medially situated canal for the tendon of musculus flexor digitorum longus. The plantar surface of the lateral portion of the hypotarsus is broken, but a laterally facing shallow sulcus for the tendon of musculus flexor hallucis longus is visible. In plantar aspect, the lateral portion of the hypotarsus is reaching farther distally than the medial one. On the dorsal surface of the bone, the impressiones retinaculi extensorii form two distinct ridges. The foramina vascularia proximalia are large and widely spaced; the tuberositas musculi tibialis cranialis is bipartite. The wide sulcus extensorius extends over almost the entire dorsal surface of the bone. The lateral rim of the cotyla lateralis is damaged. On the lateral surface of the bone, there is a large and distinctive impressio ligamenti collateralis lateralis.

Remarks: A taxonomic assignment of the Egem galliform is impeded by the fragmentary condition of the bones and by the uncertainty of whether all skeletal elements belong to a single species. The proximal humerus and the proximal tarsometatarsus stem from the same collection, but it is unknown whether these bones were found in close association, and the same is true for the proximal ulna and the tentatively referred distal tibiotarsus. As detailed above, the coracoid may be too small to belong to the same species as the other bones.

HARRISON & WALKER (1977) distinguished four galliform species in the London Clay material they studied, and these were described as *Argillipes aurorum*, *A. paralectoris*, *Percolinus venablesi*, and *Coturnipes cooperi*. The holotypes of the former three species are proximal tarsometatarsi, whereas *C. cooperi* is based on a distal tarsometatarsus. A fifth galliform species from the London Clay was described as *Paraortygoides radagasti* by DYKE & GULAS (2002) and is represented by more substantial material (Fig. 3O); this species was referred to the early Eocene Gallinuloididae, which represent one of the earliest diverging branches of Galliformes (MAYR 2000). Other early and middle Eocene Galliformes are known from the early Eocene North American Green River Formation (MAYR & WEIDIG 2004), Messel (MAYR 2000; MAYR 2006a), Mongolia (HWANG *et al.* 2010), and Africa (MOURER-CHAUVIRÉ *et al.* 2011;

MOURER-CHAUVIRÉ et al. 2013; MOURER-CHAUVIRÉ et al. 2015). The named species include the gallinuloidids *Gallinuloides wyomingensis* from the Green River Formation (MAYR & WEIDIG 2004) and *Paraortygoides messelensis* from Messel (MAYR 2000; MAYR 2006a), as well as *Chambiortyx cristata* from the late early or early middle Eocene of Tunisia (MOURER-CHAUVIRÉ et al. 2013) and *Namaortyx sperrgebietensis* and *Scopelortyx klinghardtensis* from the middle Eocene of Namibia (MOURER-CHAUVIRÉ et al. 2011; MOURER-CHAUVIRÉ et al. 2015).

Compared with the putative Galliformes from the London Clay, the proximal tarsometatarsus of the Egem galliform most closely resembles that of *Argillipes aurorum* (Fig. 3M), the type species of the taxon *Argillipes*. It differs from the proximal tarsometatarsus of *Argillipes paralectoris* in that the hypotarsus has a canal for the tendon of musculus flexor digitorum longus (in *A. paralectoris* there is an open sulcus; Fig. 3N), and it is distinguished from *Percolinus venablesi* in the wider sulcus extensorius, which extends across nearly the entire dorsal surface of the bone in the Egem galliform, but is distinctly narrower in *P. venablesi* (compare Fig. 3I with HARRISON & WALKER 1977: pl. 8K). The distal tarsometatarsus of the Egem galliform is distinguished from *Coturnipes cooperi* in that the foramen vasculare distale has a longer dorsal opening, which is not continuous with a sulcus, and a farther distally situated plantar opening; the trochlea metatarsi II is furthermore more strongly plantarly deflected and the trochlea metatarsi III is mediolaterally narrower (compare Figs. 3K and 7H). Whereas galliform affinities of *Argillipes aurorum* are substantiated by the material from Egem, it is far from being certain that *A. paralectoris*, *P. venablesi*, and *C. cooperi* were correctly assigned to the Galliformes.

The Egem galliform differs from the early Eocene Gallinuloididae (*Gallinuloides wyomingensis*, *Paraortygoides messelensis*, and *P. radagasti*) in the more gracile distal end of the tarsometatarsus, the proportionally shorter trochlea metatarsi II, and the narrower trochlea metatarsi III (compare Figs. 3K and 3O). The humerus furthermore has a smaller caput humeri and a shallower dorsal fossa pneumaticipitalis than the humerus of *P. messelensis*.

The species from Egem is distinguished from the African taxa *Chambiortyx* and *Namaortyx* in that the trochlea metatarsi II is distinctly shorter than the trochlea metatarsi IV. The tentatively referred coracoid from Egem differs from the holotype coracoid of *Scopelortyx klinghardtensis* in that the medial portion of the dorsal surface of the extremitas sternalis does not bear a marked fossa.

The distal end of the tarsometatarsus of the Egem galliform resembles that of *Nanortyx inexpectatus* from the late Eocene of Saskatchewan (Canada; WEIGEL 1963). This species is known from a fragmentary coracoid and a worn distal tarsometatarsus and is of comparable size to the Egem galliform (the distal tarsometatarsus of *N. inexpectatus* has a width of 5.2 mm; WEIGEL 1963). The tarsometatarsus of *N. inexpectatus* also agrees with that of the Egem galliform in being mediolaterally narrow, with a short trochlea metatarsi II, but these similarities are of rather general nature and do not constitute strong evidence for an assignment of the Egem fossil to *Nanortyx*.

The absence of a transverse ridge in the incisura capitis of the proximal humerus and the cup-shaped cotyla scapularis of the tentatively referred coracoid clearly indicate a position of the Egem galliform outside crown group Galliformes. However, a definitive phylogenetic placement of the species requires the discovery of more material not only to identify further characters of potential phylogenetic significance but also to confirm referral of the isolated bones to a single species.

Gruiformes BONAPARTE, 1854

Messelornithidae HESSE, 1988

Gen. et sp. indet.

Fig. 4

Referred specimens: IRSNB Av 169: left tarsometatarsus lacking proximal end; collected by G. MARIËN. IRSNB Av 170: distal half of left tarsometatarsus; collected by Y. CHRISTIANS.

Tentatively referred specimens: IRSNB Av 171: right carpometacarpus lacking most of os metacarpale minus; collected by F. MIGOM. IRSNB Av 172: distal half of right tarsometatarsus lacking trochleae metatarsorum II et IV; collected by Y. CHRISTIANS.

Measurements (in mm): Tarsometatarsus IRSNB Av 169, length as preserved, 42.5; estimated total length, 46–49; distal width, 6.3. Carpometacarpus, length, 21.1.

Description and comparisons: The long and slender tarsometatarsi, whose proximal end is missing in all specimens, closely resemble the tarsometatarsus of *Messelornis cristata* in size and proportions (Fig. 4A–G). The crista medianoplantaris forms a distinct crest, lateral and medial of which the plantar surface of the tarsometatarsus is sloping. In the distal portion of the bone, there is a low midline ridge along the plantar surface of the shaft, which extends onto the plantar surface of the trochlea metatarsi II; this ridge is likely to have been related to the presence of associated ossified tendons. The foramen vasculare distale is large and its dorsal opening has an ovate shape; proximal of the plantar opening there is a small neurovascular foramen. The fossa metatarsi I is shallow and very indistinct. The trochleae are best preserved in specimen IRSNB Av 170 (Fig. 4C–E). The plantarly deflected trochlea metatarsi II is much shorter than the trochlea metatarsi IV; its plantar surface bears a small, plantarly directed process. Unlike in the superficially similar galliform tarsometatarsus described above (IRSNB Av 165), the plantar rims of the trochlea metatarsi III have the same proximal extent. The tentatively referred tarsometatarsus IRSNB Av 172 (Fig. 4F) corresponds to specimens IRSNB Av 169 and IRSNB Av 170 in most of the above features but has a smaller foramen vasculare distale. Whether this indicates individual or interspecific variation is uncertain.

The carpometacarpus (Fig. 4J) resembles that of *Messelornis cristata* in its proportions and the length of the bone corresponds well with *M. cristata*, the carpometacarpus of

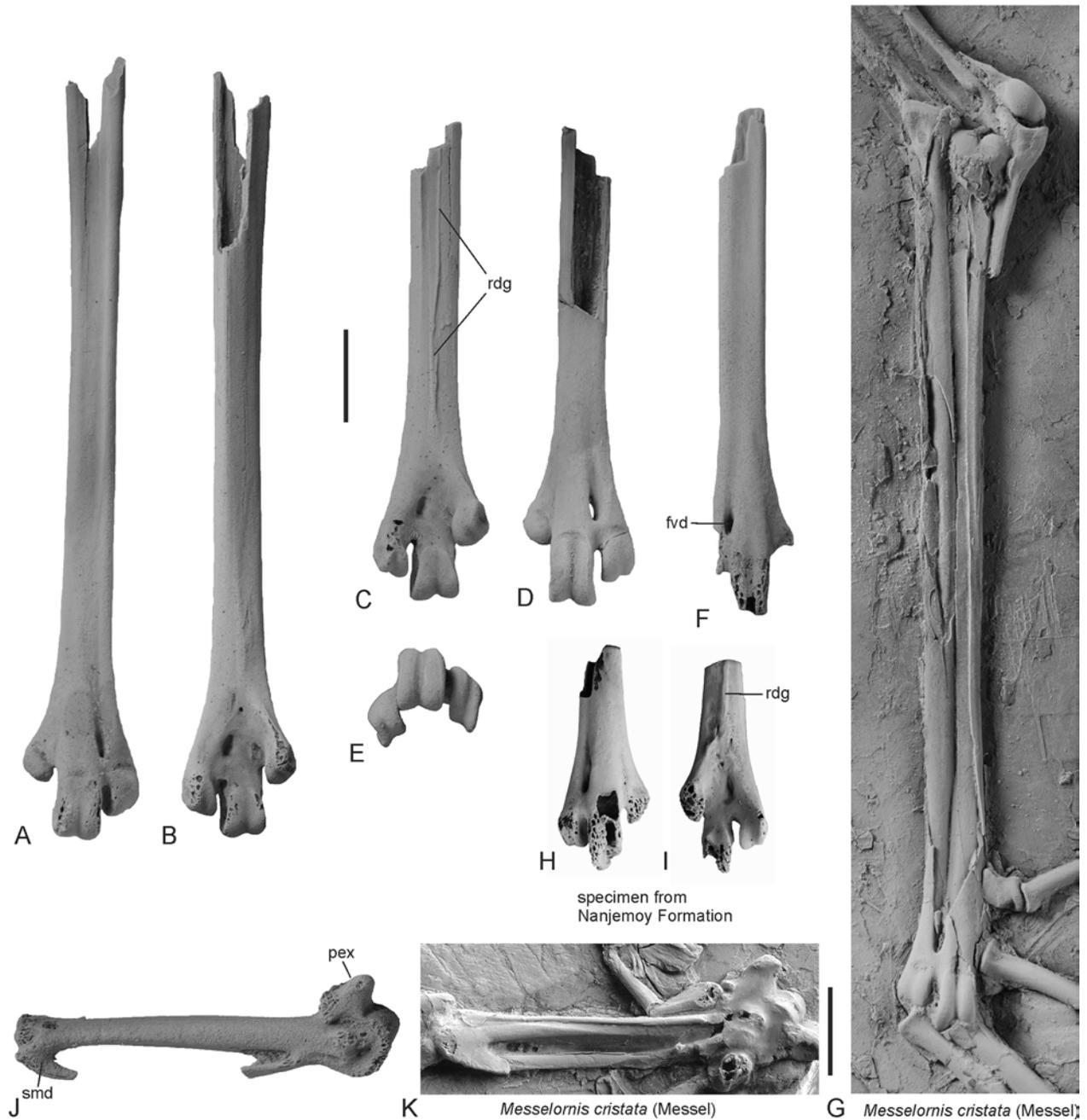


Fig. 4. Bones of the Messelornithidae from Egem. **A, B** – left tarsometatarsus lacking proximal end (IRSNB Av 169) in dorsal (**A**) and plantar (**B**) view. **C–E** – distal half of left tarsometatarsus (IRSNB Av 170) in plantar (**C**), dorsal (**D**), and distal (**E**) view. **F** – tentatively referred distal half of right tarsometatarsus (IRSNB Av 172) in dorsal view. **G** – right tarsometatarsus of *Messelornis cristata* from Messel, Germany (SMF, uncatalogued) in dorsal view. **H, I** – distal end of right tarsometatarsus of a putative messelornithid from the early Eocene Nanjemoy Formation in Virginia, USA (SMF Av 622) in dorsal (**H**) and plantar (**I**) view. **J** – cf. Messelornithidae, tentatively referred partial right carpometacarpus (IRSNB Av 171). **K** – right carpometacarpus of *M. cristata* from Messel (SMF-ME 782b). Abbreviations: fvd – foramen vasculare distale; pex – processus extensorius; rdg – ridge along plantar surface of tarsometatarsus shaft; smd – symphysis metacarpalis distalis. All specimens were coated with ammonium chloride. Scale bars equal 5 mm; same scale for **A–J**.

which measures 18.0–24.5 mm (HESSE 1990). The symphysis metacarpalis distalis is, however, proportionally shorter than in *M. cristata* (Fig. 4K).

Remarks: Fossils of the Messelornithidae are known from Messel (HESSE 1988; HESSE 1990; MAYR 2004a), the Fur Formation (BERTELLI et al. 2011), the Green River Formation (HESSE 1992), and the late Paleocene and late Eocene/early Oligocene of France (MOURER-CHAUVIRÉ 1995). Tentative records were also reported from the Nanjemoy Formation (MAYR 2016b; Fig. 4H, I).

The two named early Eocene genus-level taxa of the Messelornithidae are *Messelornis* from Messel, the Green River Formation, and the late Paleocene of France (HESSE 1988; HESSE 1992; MOURER-CHAUVIRÉ 1995), and *Pellornis* from the Fur Formation (BERTELLI et al. 2011). The bones from Egem are from a species the size of *Messelornis cristata*, which is the most abundant avian species in Messel. However, the Egem fossils are likewise of similar size to *Pellornis mikkelsenii*, of which the tarsometatarsus is unknown, and which cannot be distinguished from *M. cristata* in the bones known from Egem.

cf. Phaethontiformes SHARPE, 1891
 cf. Prophaethontidae HARRISON & WALKER, 1976
 cf. *Prophaethon* ANDREWS, 1899
 cf. *Prophaethon* sp.
 Fig. 5A–D

Referred specimens: IRSNB Av 173: distal half of right humerus; collected by Y. CHRISTIANS. IRSNB Av 174: distal end of left humerus; collected by L. KATTENWINKEL.

Measurements (in mm): IRSNB Av 174, maximum width of distal end, 13.1.

Description and comparisons: These humeri stem from a species about the size of the extant *Fulmarus glacialis* (Procellariidae). As in procellariiform birds, the shaft of the bone is straight and the dorsal margin of the distal end forms a low tuberculum dorsale that is distally continuous with a ridge along the dorsal surface of the bone. On the caudal surface, there is a narrow sulcus scapulotricipitalis and a deep sulcus humerotricipitalis. The large fossa musculi brachialis bears a deep depression in its ventral section. The processus flexorius is poorly developed and the ventral portion of the distal end of the bone slants caudally. The narrow condylus dorsalis tapers proximally into a ventrally deflected, pointed tip. The condylus ventralis is distally prominent and forms the distalmost point of the bone; its proximal base is slightly undercut by a distinct fossa, which extends from the fossa musculi brachialis to the condylus ventralis. The tuberculum supracondylare ventrale is dorsoventrally narrow and proximodistally elongate, reaching farther proximally than the tip of the condylus dorsalis.

Remarks: The shape of the distal end of the two humeri resembles that of some Paleogene procellariiform birds,

such as *Makahala mirae* from the latest Eocene or earliest Oligocene of Washington State, USA (Fig. 5F; MAYR 2015a). In contrast to the Procellariiformes, however, the humeri from Egem exhibit a well-developed sulcus scapulotricipitalis and here we consider it more likely that the specimens belong to the phaethontiform Prophaethontidae.

Prophaethontids were first reported from the London Clay (ANDREWS 1899; HARRISON & WALKER 1976b) and have subsequently also been identified in the middle Eocene of Belgium (MAYR & SMITH 2002), and the late Paleocene and early Eocene of Morocco (BOURDON et al. 2008). Putative Phaethontiformes are also known from the Paleocene of New Zealand, Asia and North America (MAYR & SCOFIELD 2016).

The humerus of *Prophaethon shrubsolei*, the prophaethontid species from the London Clay, is not preserved in the partial holotype skeleton, but MAYR (2015b: fig. S2) identified a humerus of this species in a private collection, which corresponds well with the Egem fossils. The distal humeri from Egem are likewise similar to the distal humerus of the Moroccan prophaethontid *Lithoptila abdounensis* (compare Fig. 5A with BOURDON et al. 2008: fig. 4).

As detailed by MAYR (2015b), the distal humerus of *Prophaethon* closely resembles that of *Proplegadis fisheri* from the London Clay (Fig. 5E). This latter species was described as an ibis (Threskiornithidae) by HARRISON & WALKER (1971) and is only known from the holotype distal humerus. A comparison of the distal humerus from Egem with that of *P. fisheri* supports the hypothesis that the latter species is likely to be a junior synonym of *Prophaethon shrubsolei* (see MAYR 2015b).

Aves indet. A (cf. Presbyornithidae)
 Fig. 5G, H

Referred specimen: IRSNB Av 175: distal end of right humerus and associated fragment of proximal portion of shaft of right humerus; collected by Y. CHRISTIANS (layer 5).

Measurements (in mm): Length as preserved, 18.6; distal width, 13.1.

Remarks: This bone stems from layer 5 of the Egem quarry and resembles the above-described putative prophaethontid humeri in size and morphology. However, the fossa musculi brachialis is less deep and more centrally located, the tuberculum supracondylare ventrale is less elongated (its proximal end does not reach farther proximally than the tip of the condylus dorsalis), the sulcus humerotricipitalis is proportionally wider, and the processus flexorius is more prominent.

Because of these differences, we do not consider IRSNB Av 175 to be from a species of the Prophaethontidae. The bone resembles the distal humerus of the anseriform Presbyornithidae (compare Fig. 5G, H with KUROCHKIN & DYKE 2010: fig. 12), but without further skeletal elements, a well-based classification is not possible.

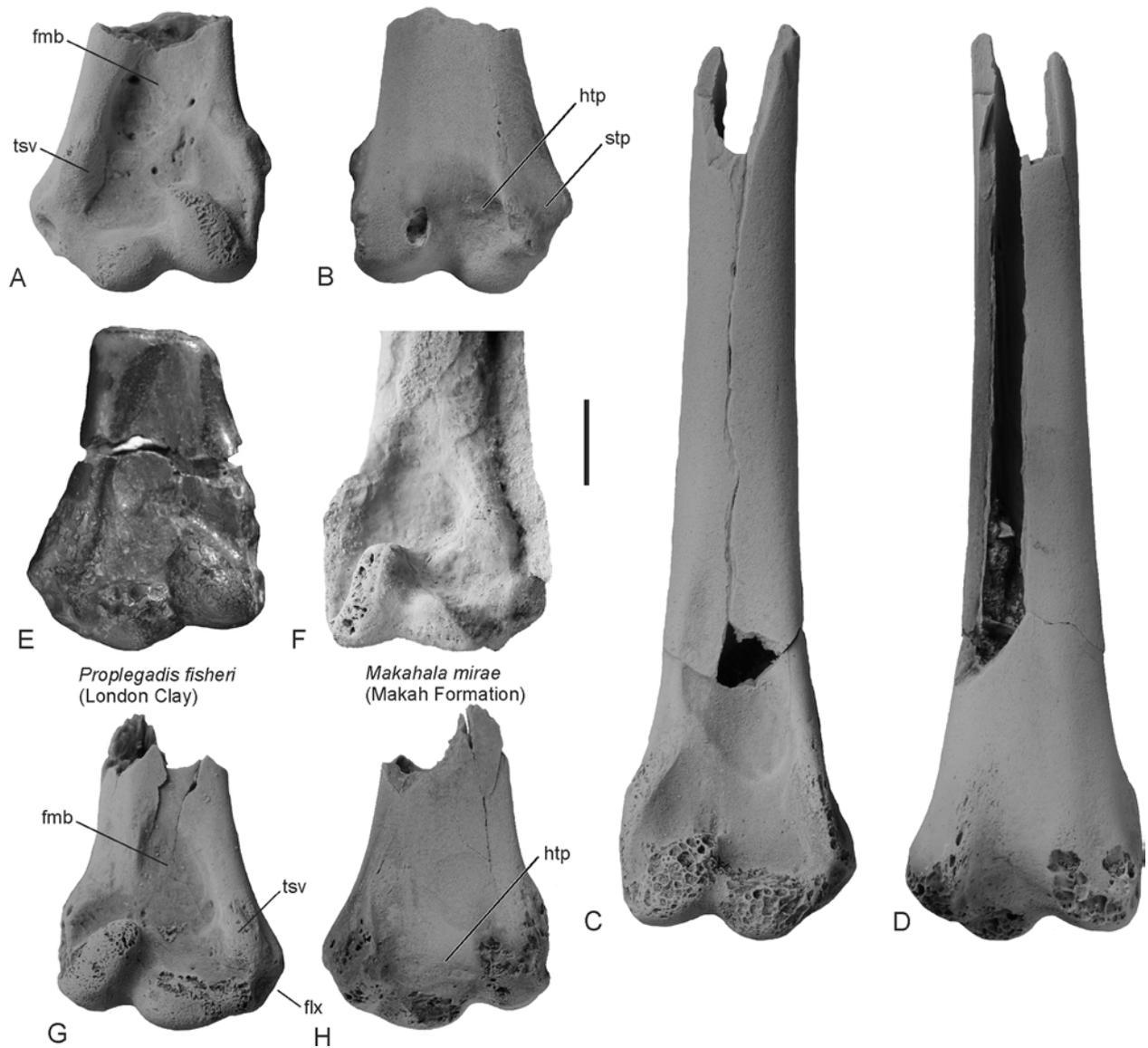


Fig. 5. **A–D** – humeri from Egem, which are tentatively referred to the phaethontiform taxon *Prophaethon* (Prophaethontidae). **A, B** – distal end of left humerus (IRSNB Av 174) in cranial (**A**) and caudal (**B**) view. **C, D** – distal half of right humerus (IRSNB Av 173) in cranial (**C**) and caudal (**D**) view. **E** – distal end of left humerus of *Proplegadis fisheri* from the early Eocene of the London Clay (holotype, NHMUK A 10) in cranial view. **F** – distal end of right humerus of the procellariiform species *Makahala mirae* from the late Eocene Makah Formation of Washington State, USA (holotype, SMF Av 603) in cranial view. **G, H** – Aves indet. A, distal end of right humerus (IRSNB Av 175) in cranial (**G**) and caudal (**H**) view. Abbreviations: flx – processus flexorius; fmb – fossa musculi brachialis; htp – sulcus humerotricipitalis; stp – sulcus scapulo-tricipitalis; tsv – tuberculum supracondylare ventrale. All specimens except **E** were coated with ammonium chloride. Scale bar equals 5 mm.

Apodiformes PETERS, 1940

Family inc. sed.

Gen. et sp. indet.

Fig. 6A

Referred specimen: IRSNB Av 176: partial left coracoid lacking part of extremitas omalis and the extremitas sternalis; collected by W. ZANDERING.

Measurements (in mm): Length as preserved, 8.2.

Remarks: This fragmentary coracoid stems from a tiny bird and has a morphology, which allows an unambiguous referral to the Apodiformes. Characteristic features include a cup-like cotyla scapularis, a foramen nervi supracoracoidei, which is widely separated from the cotyla scapularis and shifted situated towards the extremitas sternalis, as well as a wide shaft with a crista procoracoidei.

In size, the bone corresponds with the coracoid of the early Eocene stem group apodiform *Eocypselus* (Fig. 6B), which is known from the London Clay (HARRISON 1984a) and from the Fur Formation (MAYR 2010a), as well as the North American Nanjemoy and Green River formations (KSEPKA et al. 2013; MAYR 2016b). However, the shaft of the coracoid from Egem is wider than in *Eocypselus* and does not show the medial constriction found in *Eocypselus*, and the cotyla scapularis of IRSNB Av 176 is more cup-shaped than in *Eocypselus*. The coracoid is unknown of another early Eocene apodiform bird from the London Clay, which was described as *Primapus lacki* by HARRISON & WALKER (1975), and a definitive taxonomic assignment of the fragmentary specimen from Egem is not possible.

Telluraves (sensu YURI et al. 2013) inc. sed.

Halcyornithidae HARRISON & WALKER, 1972

Gen. et sp. indet.

Fig. 6G–L

Referred specimens: IRSNB Av 177: right coracoid; collected by Y. CHRISTIANS (layer 5). SMF Av 507: distal end of left humerus; collected by S. MAILLIOT.

Tentatively referred specimens: IRSNB Av 178: left carpometacarpus; collected by G. VAN DEN EECKHAUT. IRSNB Av 179: right femur; collected by F. MIGOM.

Measurements (in mm): Humerus SMF Av 507, distal width, 5.1. Coracoid, length as preserved, 17.8. Carpometacarpus, length, 16.6. Femur, length as preserved, 20.1.

Description and comparisons: The coracoid (Fig. 6G), which unlike most other specimens described in the present study stems from layer 5 of the Egem quarry, shows a distinctive morphology that is only matched by the Halcyornithidae. The elongate bone has a narrow shaft with a well-developed foramen nervi supracoracoidei, which opens medially into an elongate fossa. The processus acrocoracoideus

is short and dorsoventrally narrow. The cotyla scapularis is only weakly excavated. The facies articularis clavicularis has a flat medial surface and its dorsal section forms a sternal projection; the ventral portion is damaged. The processus procoracoideus is broken. Compared with the described Halcyornithidae, the specimen is most similar to species from the London Clay and Messel (MAYR 1998a; MAYR 2002a; MAYR 2007), whereas the coracoid of the taxon *Cyrlavis* from the Green River Formation has a more deeply excavated, cup-like cotyla scapularis (KSEPKA & CLARKE 2012).

The distal end of the humerus (Fig. 6H, I) closely corresponds to the distal humerus of a halcyornithid (“pseudasturid”) from the London Clay, which was figured by MAYR (2002a: fig. 2H). The bone has a well-developed fossa musculi brachialis. The dorsal surface of the distal end forms a ridge-like bulge. The cranial surface of the condylus ventralis bears an elongate depression. The condylus dorsalis is proximodistally short. The processus flexorius is caudally projected.

The carpometacarpus (Fig. 6J, K) is tentatively referred to the Halcyornithidae based on its size and overall morphology. In its proportions, the bone resembles carpometacarpus of the Halcyornithidae from Messel, the London Clay, and the Green River Formation (MAYR 1998a; KSEPKA & CLARKE 2012), but there are no specific derived features that support an assignment to the Halcyornithidae.

The tentatively referred femur (Fig. 6L) resembles a halcyornithid femur from the London Clay that was figured by MAYR (2002a: fig. 2L). The bone has a well-defined linea intermuscularis caudalis and a marked ridge-like tuberosity proximal of the fossa poplitea.

Remarks: The Halcyornithidae are parrot-like birds that are a common element in early and middle Eocene avifaunas, with fossils having been reported from the London Clay (MAYR 1998a), Messel (MAYR 1998a), Geiseltal (MAYR 2002b), and the North American Nanjemoy and Green River formations (KSEPKA & CLARKE 2012; MAYR 2016b). Halcyornithids are part of Telluraves, the “landbird clade”, but the exact affinities of these arboreal birds are uncertain and a recent analysis challenged their previous classification as stem group Psittaciformes (MAYR 2015c). Several halcyornithid genus-level taxa have been described (*Halcyornis*, *Pulchrapollia*, *Pseudasturides*, *Serudaptus*, *Cyrlavis*; see MAYR 2017b), but the bones preserved in the Egem material do not allow a classification beyond the family level. It is likewise uncertain, whether all of the referred bones belong to a single species.

cf. Masillaraptoridae MAYR, 2009b

Gen. et sp. indet.

Fig. 7A–E

Tentatively referred specimens: IRSNB Av 180: symphyseal part of mandible; collected by Y. CHRISTIANS. IRSNB Av 181: distal end of left tarsometatarsus; collected by W. ZANDERING.

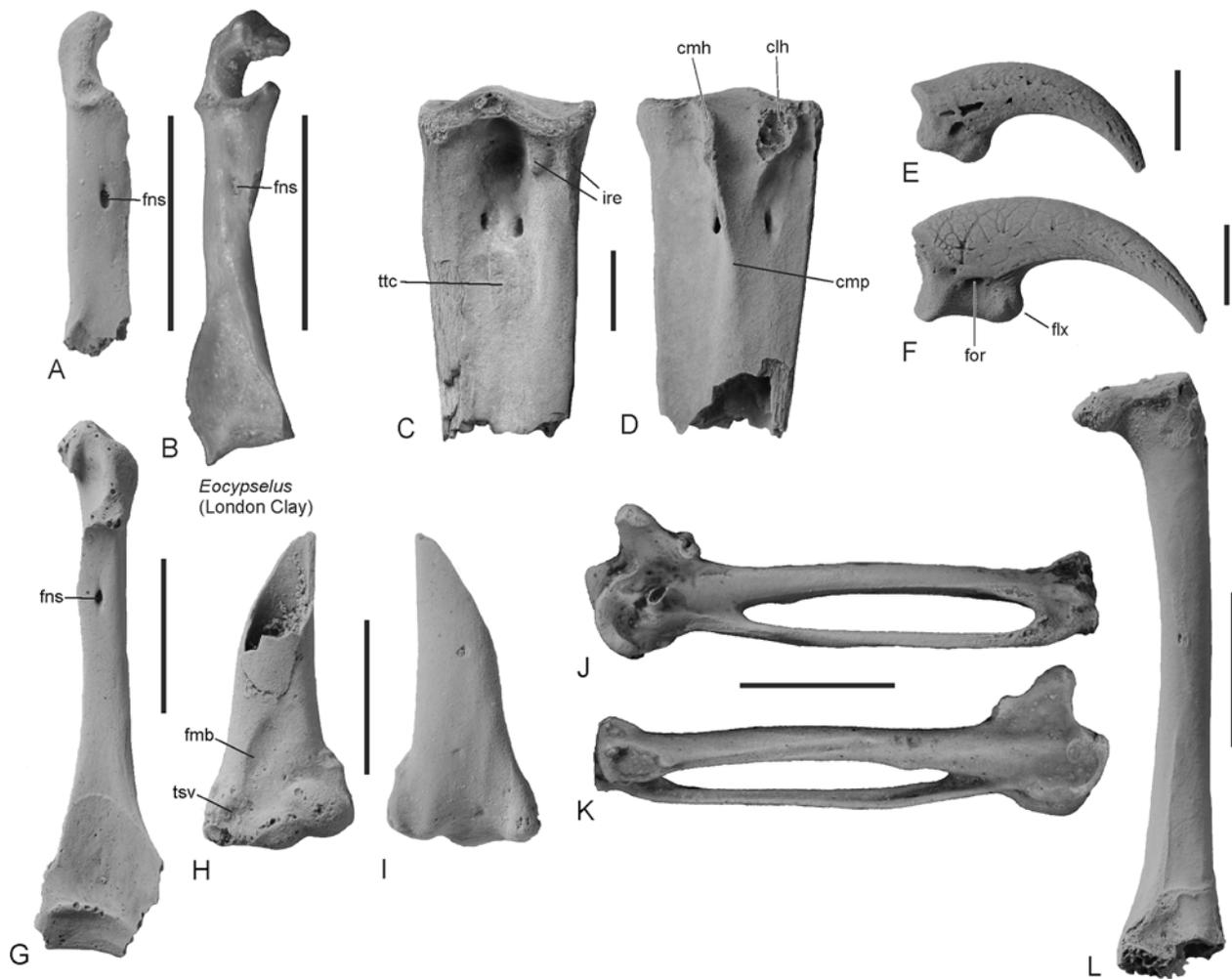


Fig. 6. Apodiformes (A), cf. Accipitriformes (C–F), and Halcyornithidae (G–L) from Egem. A – partial left coracoid of an apodiform bird (IRSNB Av 176) in dorsal view. B – left coracoid of the apodiform species *Eocypselus vincenti* (Eocypselidae) from the London Clay in dorsal view (holotype; NHMUK A 5429). C, D – cf. Accipitridae, gen. et sp. indet., proximal end of right tarsometatarsus (IRSNB Av 182) in dorsal (C) and plantar (D) view. E, F – cf. Accipitridae, gen. et sp. indet., ungual pedal phalanges in lateral view (E: IRSNB Av 184; F: IRSNB Av 183). G – right coracoid of a halcyornithid species (IRSNB Av 177) in cranial (H) and caudal (I) view. J, K – tentatively referred left carpometacarpus of a halcyornithid (IRSNB Av 178) in ventral (J) and dorsal (K) view. L – tentatively referred right femur of a halcyornithid (IRSNB Av 179) in caudal view. Abbreviations: clh – crista lateralis hypotarsi; cmh – crista medialis hypotarsi; cmp – crista medianoplantaris; flx – tuberculum flexorium; fmb – fossa musculi brachialis; fns – foramen nervi supracoracoidei; for – foramen of sulcus neurovascularis; ire – impressio retinaculi extensorii; tsv – tuberculum supracondylare ventrale; ttc – tuberositas musculi tibialis cranialis. All specimens except for B were coated with ammonium chloride. Scale bars equal 5 mm.

Measurements (in mm): Mandible, length as preserved, 27.1. Tarsometatarsus, distal width, 6.4.

Description and comparisons: The partial mandible preserves most of the symphyseal part, but lacks the tip (Fig. 7A, B). The pars symphysealis is very long, mediolaterally narrow, and dorsoventrally deep. The tomia are straight and the lateral surfaces of the bone exhibit numerous large foramina neurovascularia.

The distal tarsometatarsus (Fig. 7C–E) has a moderately developed fossa metatarsi I, which is situated at the medial margin of the bone. The dorsal opening of the large foramen vasculare distale forms a distal recess, which houses the proximal opening of the canalis interosseus distalis. The trochlea metatarsi II reaches as far distally as the trochlea metatarsi IV and is not strongly plantarly deflected; its plantar surface forms a plantarly directed projection. The plantar surface of the trochlea metatarsi III is slightly asymmetric,

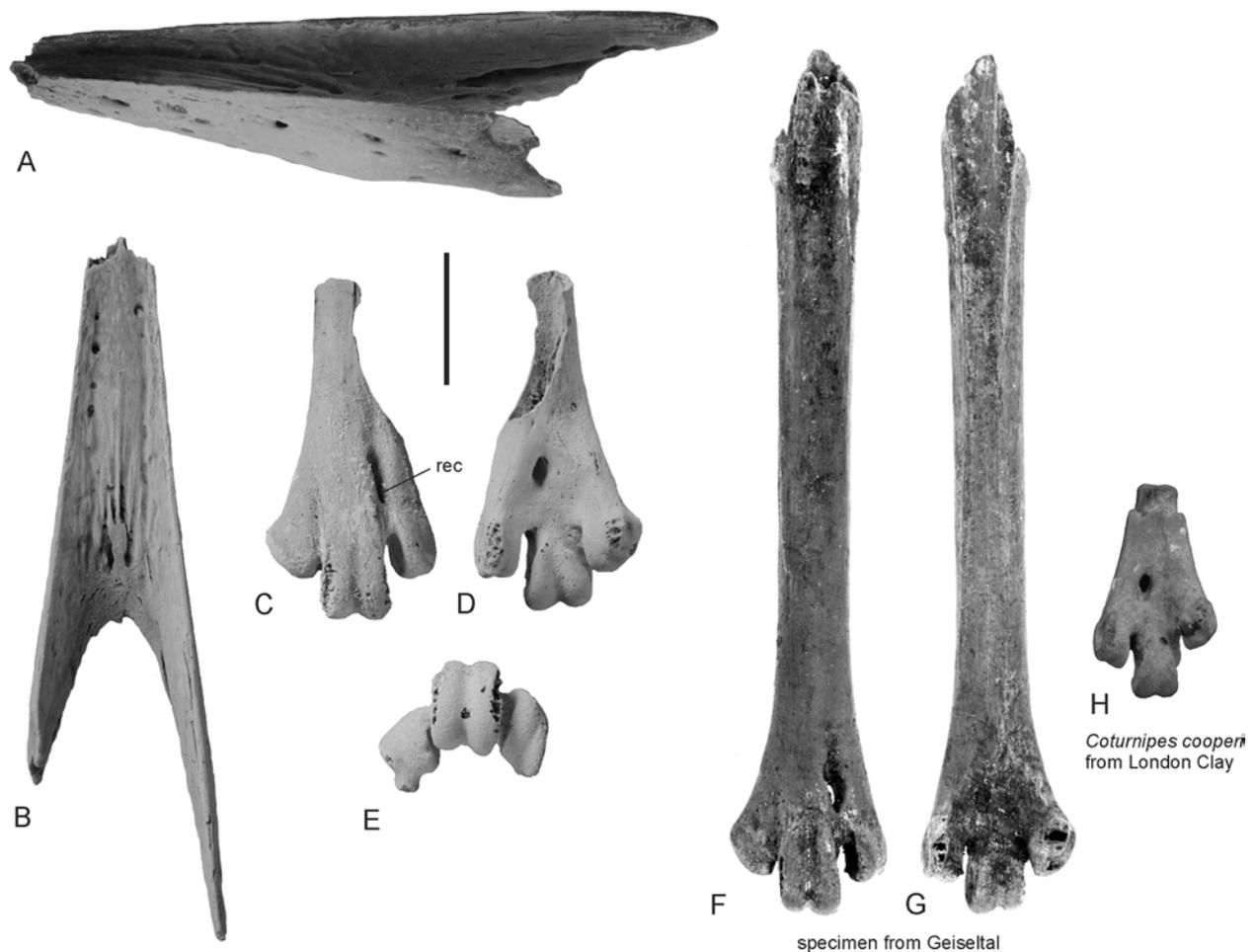


Fig. 7. A–E – partial mandible and distal tarsometatarsus from Egem, which are tentatively referred to the Masillaraptoridae. A, B – partial mandible (IRSNB Av 180) in laterodorsal (A) and dorsal (B) view. C–E – tentatively referred distal end of left tarsometatarsus (IRSNB Av 181) in dorsal (C), plantar (D), and distal (E) view. F, G – partial left tarsometatarsus from the middle Eocene of Geiseltal in Germany (IGWuG NW XIV), which closely resembles the specimen from Egem (F: dorsal view; G: plantar view). H – distal end of left tarsometatarsus of *Coturnipes cooperi* from the London Clay (holotype; NHMUK A 3706) in plantar view. Abbreviation: rec – recess distal of foramen vasculare distale. Specimens in A–E were coated with ammonium chloride. Scale bar equals 5 mm.

with the medial rim being somewhat shorter than the lateral one. The trochlea metatarsi IV is mediolaterally narrow.

Remarks: The distinctive proportions of the mandible are not matched by any extant bird and correspond best with the mandible of *Masillaraptor parvunguis* from Messel (MAYR 2006b; MAYR 2009b), even though the tomia of IRSNB Av 180 appear to be straighter than in *Masillaraptor*. The tentatively referred distal tarsometatarsus is very similar to a tarsometatarsus from the middle Eocene of the German locality Geiseltal (Fig. 7F, G), which was described by MAYR (2002b). MAYR (2002b) noted that the Geiseltal tarsometatarsus corresponds well with the tarsometatarsus of a Messel fossil, which was later described as *Masillaraptor parvunguis* (MAYR 2006b). It is this taxonomic history,

upon which we base our referral of the mandible and the distal tarsometatarsus to the same species.

In addition to noting a resemblance to the Messel fossil, MAYR (2002b) also considered close affinities between the Geiseltal tarsometatarsus and *Coturnipes cooperi* from the London Clay, which is only known from a distal tarsometatarsus. MAYR (2002b) based his conclusion on the published figures of the specimen, but direct examination of the holotype and only known specimen of *C. cooperi* by one of the authors (GM) has shown that the trochlea metatarsi II of the London Clay species (Fig. 7H) is more strongly plantarily deflected than in the Geiseltal tarsometatarsus and the specimen from Egem. Close affinities between *Coturnipes* and *Masillaraptor* are therefore considered unlikely. The phylogenetic position of *Masillaraptor* is uncertain, but the

species may represent an early stem group representative of the Falconiformes (falcons and allies; MAYR 2009b).

cf. Accipitriformes VIEILLOT, 1816

cf. Accipitridae VIGORS, 1824

Gen. et sp. indet.

Fig. 6C–F

Referred specimens: IRSNB Av 182: proximal end of right tarsometatarsus; collected by L. KATTENWINKEL. IRSNB Av 183: unguis pedal phalanx; collected by G. MARIËN. IRSNB Av 184: unguis pedal phalanx; collected by G. MARIËN.

Measurements (in mm): Tarsometatarsus, length as preserved, 22.3; proximal width, 11.6. Unguis phalanx IRSNB Av 183, length from tuberculum extensorium to tip (apex phalangis), 19.6. Unguis phalanx IRSNB Av 184, length from tuberculum extensorium to tip (apex phalangis), 15.6.

Description and comparisons: The tarsometatarsus (Fig. 6C, D) is from a large species about the size of the extant *Buteo buteo* (Accipitridae). The hypotarsus corresponds to that of extant Accipitridae in that it formed two widely separated crests, with the lateral one being mediolaterally broader than the medial crest (although the crests themselves are broken, the remaining portions allow inferences on their position and size). The small foramina vascularia proximalia are situated close together in the deep sulcus extensorius, with the dorsal opening of the lateral foramen being positioned slightly farther proximally than that of the medial foramen. The impressiones retinaculi extensorii form two low and short ridges. The tuberositas musculi tibialis cranialis is centrally positioned as in extant Accipitridae, but it is much less prominent in the fossil. The crista medianoplantaris is better developed than in extant Accipitridae. The preserved section of the shaft gradually narrows towards the distal end of the bone. The dorsoplantarily flat shaft forms a very narrow medial margin and a much deeper lateral one.

The phalanges (Fig. 6E, F) correspond to the tarsometatarsus fragment in size and resemble the unguis phalanges of extant Accipitridae. Even though the specimens are of different size and are distinguished in some morphological features (IRSNB Av 184 is distinctly smaller than the other two fossils and has a less pronounced tuberculum flexorium), we cannot exclude the possibility that they stem from different toes of the same species. All three phalanges differ from the unguis phalanges of strigiform birds in that the plantar surface of the corpus is flat (rounded in Strigiformes). The sulcus neurovascularis is laterally closed and exits with a foramen next to the tuberculum flexorium.

Remarks: If correctly assigned to the Accipitridae, the fossils would constitute the earliest record of the clade (MAYR 2009a; MAYR 2017b) and the above-described differences to the tarsometatarsus of extant Accipitridae are likely to

be due to the retention of plesiomorphic features in the fossil. The next-oldest record, *Milvovides kempi* from the middle Eocene of England, is based on a fragmentary distal tarsometatarsus, which is of a similar size to the Egem fossil but is too incomplete for a reliable identification (HARRISON & WALKER 1979). HARRISON (1984b) described a distal tarsometatarsus from the London Clay as a putative falconid (*Stintonornis mitchelli*), but although the species is of a size comparable to the Egem tarsometatarsus, the shaft of the bone is much narrower in *S. mitchelli* (5.5 versus 9.1 mm).

Leptosomiformes SHARPE, 1891

Plesiocathartes GAILLARD, 1908

Plesiocathartes sp.

Fig. 8

Referred specimen: IRSNB Av 185: left tarsometatarsus lacking trochlea metatarsi II, collected by L. KATTENWINKEL.

Measurements (in mm): Length, 32.2.

Tentatively referred specimens: IRSNB Av 186: distal end of left humerus; collected by G. VAN DEN EECKHAUT. IRSNB Av 187: distal end of left humerus; collected by Y. CHRISTIANS.

Description and comparisons: The tarsometatarsus (Fig. 8A, B) is a moderately long bone with a mediolaterally narrow shaft. The proximal end is damaged and the hypotarsus is broken, but it can be discerned that the eminentia intercotylaris is well developed. The tuberositas musculi tibialis cranialis is situated in the medial portion of the sulcus extensorius and is cranially prominent. Only the small lateral foramen vasculare proximale is preserved. The low crista medianoplantaris reaches to about the midsection of the bone. Cristae plantares lateralis et medialis are well-developed. The small fossa metatarsi I is located at the medial side of the bone and is essentially flat, with a semicircular outline. The foramen vasculare distale is small and opens distally into a canalis interosseus distalis. The trochlea metatarsi II is broken, but appears to have not been plantarily deflected. The trochlea metatarsi IV forms a distinct, plantarily directed flange, whose tip is broken in the fossil.

The distal humerus IRSNB Av 186 (Fig. 8F, G) and the very similar and probably conspecific specimen IRSNB Av 187 (Fig. 8E) resemble the distal humeri of extant Accipitriformes and Leptosomiformes. Even when a sexual size dimorphism is taken into account, the bones are too small to belong to the same species as the above-described accipitrid-like tarsometatarsus IRSNB Av 182. The specimens are here tentatively referred to the Leptosomiformes. This assignment has to be regarded as provisional, because isolated distal humeri of *Plesiocathartes* are unknown, and the articulated skeletons from Messel and the Green River Formation do not allow meaningful comparisons with the specimens from Egem.

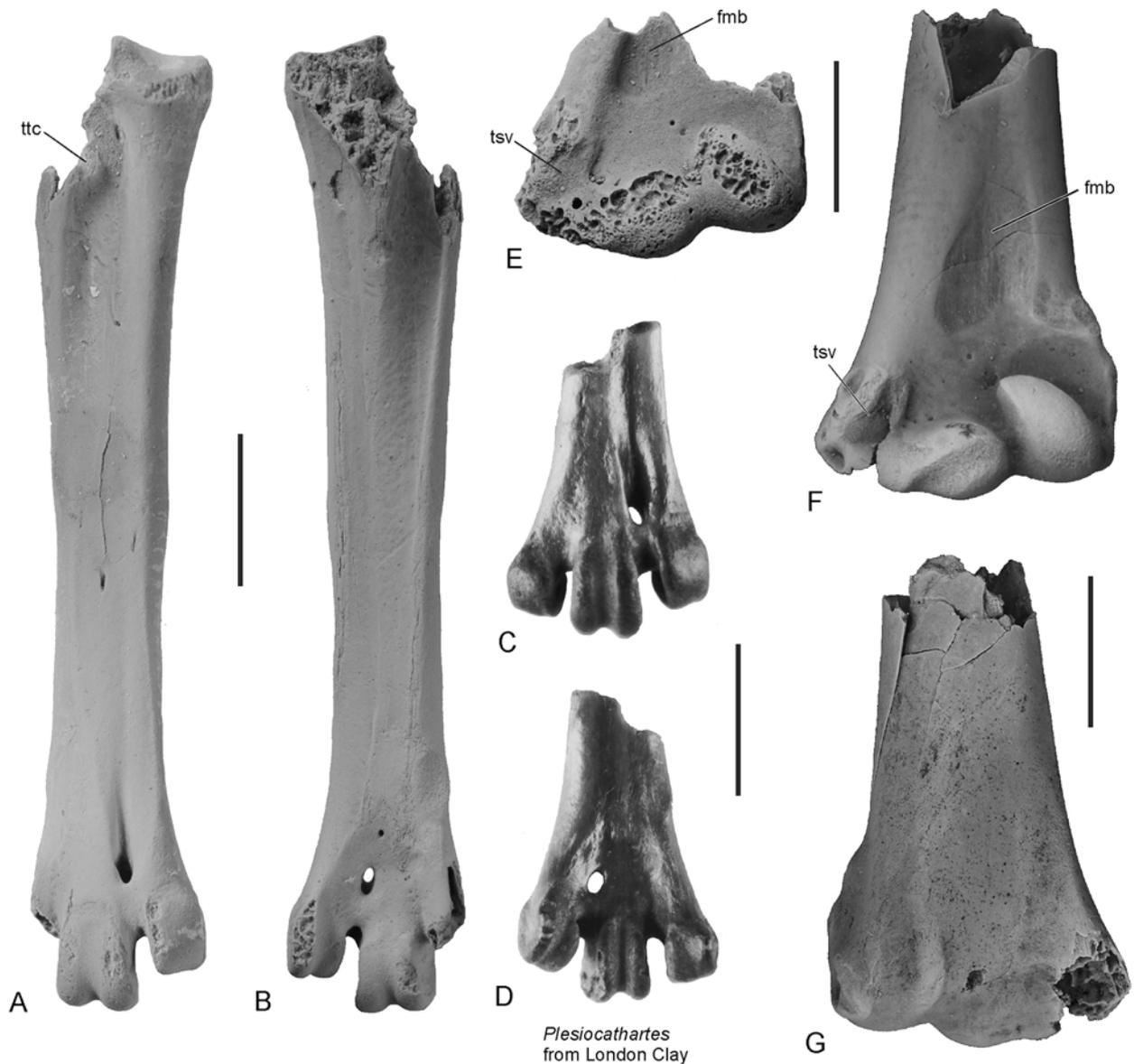


Fig. 8. Tarsometatarsus and tentatively referred humeri of the leptosomiform taxon *Plesiochathartes* from Egem. **A, B** – incomplete left tarsometatarsus of *Plesiochathartes* sp. (IRSNB Av 185) in dorsal (**A**) and plantar (**B**) view. **C, D** – distal end of the left tarsometatarsus of a species of *Plesiochathartes* from the London Clay (NHMUK A 6178) in dorsal (**C**) and plantar (**D**) view. **E**, tentatively referred distal end of a left humerus (IRSNB Av 187) in cranial view. **F, G** – tentatively referred distal end of a left humerus (IRSNB Av 186) in cranial (**F**) and caudal (**G**) view. Abbreviations: fmb – fossa musculi brachialis; tsv – tuberculum supracondylare ventrale; ttc – tuberositas musculi tibialis cranialis. Specimens in **A, B**, and **E–G** were coated with ammonium chloride. Scale bars equal 5 mm.

Remarks: Eocene stem group representative of the Madagascan Leptosomifomes were first identified by MAYR (2002c; see also MAYR 2008b) and are known from the London Clay and Messel (MAYR 2002c), Geiseltal (MAYR 2002b), and the Green River Formation (WEIDIG 2006). All of these fossils were assigned to the taxon *Plesiochathartes*, which was originally based on tarsometatarsi from an unknown horizon of the middle Eocene to late Oligocene exposures of the Quercy fissure fillings in France (MOURER-CHAUVIRÉ 2002). A *Plesiochathartes*-like

tarsometatarsus was also reported from the early Eocene of India (MAYR et al. 2010).

The distal end of the tarsometatarsus from Egem closely resembles that of an unnamed stem group leptosomiform from the London Clay (NHMUK A 6178; Fig. 8C, D), which was described by MAYR (2002c). The tarsometatarsus from Egem is longer than the tarsometatarsus of *P. kelleri* from Messel (tarsometatarsus length: 26.2–28.2 mm; MAYR 2002c) and *P. wyomingensis* from the Green River Formation (tarsometatarsus length: 26–27 mm; Weidig 2006),

but it is shorter than the tarsometatarsi of *P. geiselen-sis* from Geiseltal (tarsometatarsus length: 40.8 mm; MAYR 2002b) and *P. major* from the Green River Formation (tarsometatarsus length: 36.2–36.6 mm; WEIDIG 2006). In size, the specimen corresponds best with the tarsometatarsus of *P. europaeus*, the type species of *Plesiocathartes* from the Eocene-Oligocene Quercy fissure fillings in France, whose tarsometatarsus has a length of 43.2 mm (MOURER-CHAUVIRÉ 2002). The exact age of the *P. europaeus* fossils is unknown, but like most Quercy fossils they probably are from late Eocene or early Oligocene exposures, so that we consider a specific identity with the specimen from Egem to be unlikely.

Picocoraciae sensu MAYR (2011b)
cf. Alcediniformes sensu MAYR (1998b)
Gen. et sp. indet. A
Fig. 9

Referred specimen: IRSNB Av 188: left tarsometatarsus; collected by W. ZANDERING. IRSNB Av 189: left humerus lacking proximal end; collected by W. ZANDERING.

Measurements (in mm): Humerus, length as preserved, 17.4; estimated total length ~19–20; distal width, 4.1. Tarsometatarsus, length, 10.5; proximal width, 2.4; distal width, 2.4.

Description and comparisons: The humerus (Fig. 9A, B) has a sigmoidally curved shaft. Overall, it most closely resembles the corresponding bone of extant alcediniform birds (Fig. 9E), but the preserved portion of the crista deltopectoralis shows that it is proportionally shorter. The fossa musculi brachialis (Fig. 9C) is shallow and extends to the medial margin of the bone. The distally located tuberculum supracondylare ventrale is proximodistally short and has a subtriangular outline. The cranial surface of the condylus ventralis bears a depression. The condylus dorsalis is proximodistally short and has a broadly rounded proximal margin. The processus flexorius is well developed. The dorsal surface of the distal end bears a ridge that extends distally from the tuberculum supracondylare dorsale.

The short tarsometatarsus (Fig. 9F, G) has a narrow shaft and its proportions correspond best with the tarsometatarsus of some Alcedinidae (e.g., *Ceyx*, Fig. 9I) and the early Eocene taxon *Quasisyndactylus* (MAYR 1998b; MAYR 2004b). The dorsal openings of the foramina vascularia proximalia are situated in a fossa, the medial foramen vasculare proximale is distinctly larger than the lateral one. The medially located tuberositas musculi tibialis cranialis is large but not very prominent (Fig. 9J). The eminentia intercotylaris is low. The hypotarsus is broken, but the preserved portion indicates that there was a medially situated sulcus or canal for the tendon of musculus flexor digitorum longus (Fig. 9K). Distally, the hypotarsus is continuous with a distinct crista medianoplantaris. The foramen vasculare distale is large and has an elongate-ovate shape (Fig. 9M). The large and distinct fossa metatarsi I extends onto the medial surface of the shaft. The trochlea metatarsi IV reaches

as far distally as the trochlea metatarsi III. The trochlea metatarsi II is slightly shorter than the trochlea metatarsi III and is only slightly plantarly deflected; the plantar surface of the trochlea is broken. The incisurae intertrochleares are short and a canalis interosseus distalis is present.

Remarks: These two specimens belong to a very small species, which had about the size of the extant *Ceyx lepidus* (Alcedinidae). Our assignment of both fossils to the same species is based on their matching size and resemblance to the corresponding bones of the Alcedinidae. Both specimens are from the same collection, but it is unknown whether they were found together and therefore possibly stem from a single individual.

The shape of the trochleae supports an assignment of the fossil to the Picocoraciae sensu MAYR (2011b), that is, the clade including upupiform, coraciiform, alcediniform, and piciform birds. Compared with the extant representatives of this clade, the tarsometatarsus most closely resembles the corresponding bone of the Alcedinidae, whereas the tarsometatarsus of the closely related (e.g., PRUM et al. 2015) Momotidae and Todidae is proportionally longer and that of the Meropidae stouter. The shorter incisurae intertrochleares and the more cylindrical and less plantarly deflected trochlea metatarsi II distinguish the specimen from the tarsometatarsus of coraciiform birds (rollers). The Egem tarsometatarsus also shows a resemblance to that of the upupiform Meselirrisoridae (Fig. 9H) in its proportions, but unlike in the Upupiformes, the hypotarsus includes only a single sulcus/canal, for the tendon of musculus flexor hallucis longus (in Upupiformes there is also a canal for m. flexor hallucis longus; MAYR 2016a). The humerus is likewise clearly distinguished from that of upupiform birds in that the bone is less stout and lacks a prominent epicondylus dorsalis, and in that the tuberculum supracondylare dorsale is situated farther distally (compare Figs. 9C and 9D).

The only previously described Eocene alcediniform species is *Quasisyndactylus longibrachis* from Messel (MAYR 1998b). This species is represented by several individuals and its tarsometatarsus resembles that of the Egem fossil in proportion. However, osteological features of the ends of the bone are obscured in the Messel fossils, so that detailed comparisons with the fossil from Egem are not possible. With an estimated humerus length of 19–20 mm and a tarsometatarsus length of 10.5 mm, the Egem fossil is, however, distinguished in its size from *Q. longibrachis*, which has a humerus length of 15.8–20.6 mm and a tarsometatarsus length of 7.6–9.8 mm (MAYR 1998b; MAYR 2004b). The exact affinities of *Quasisyndactylus* within Alcediniformes, the possibly paraphyletic (e.g., PRUM et al. 2015) taxon including Meropidae, Alcedinidae, Momotidae, and Todidae, are uncertain (MAYR 1998b, MAYR 2004b). The Egem fossil resembles the tarsometatarsus of some extant Alcedinidae in its proportions, whereas the tarsometatarsus of Momotidae and Todidae is proportionally longer and that of the Meropidae stouter, but the similarities between the Egem fossil and extant Alcedinidae are likely to be due to the retention of plesiomorphic tarsometatarsus proportions in the latter.

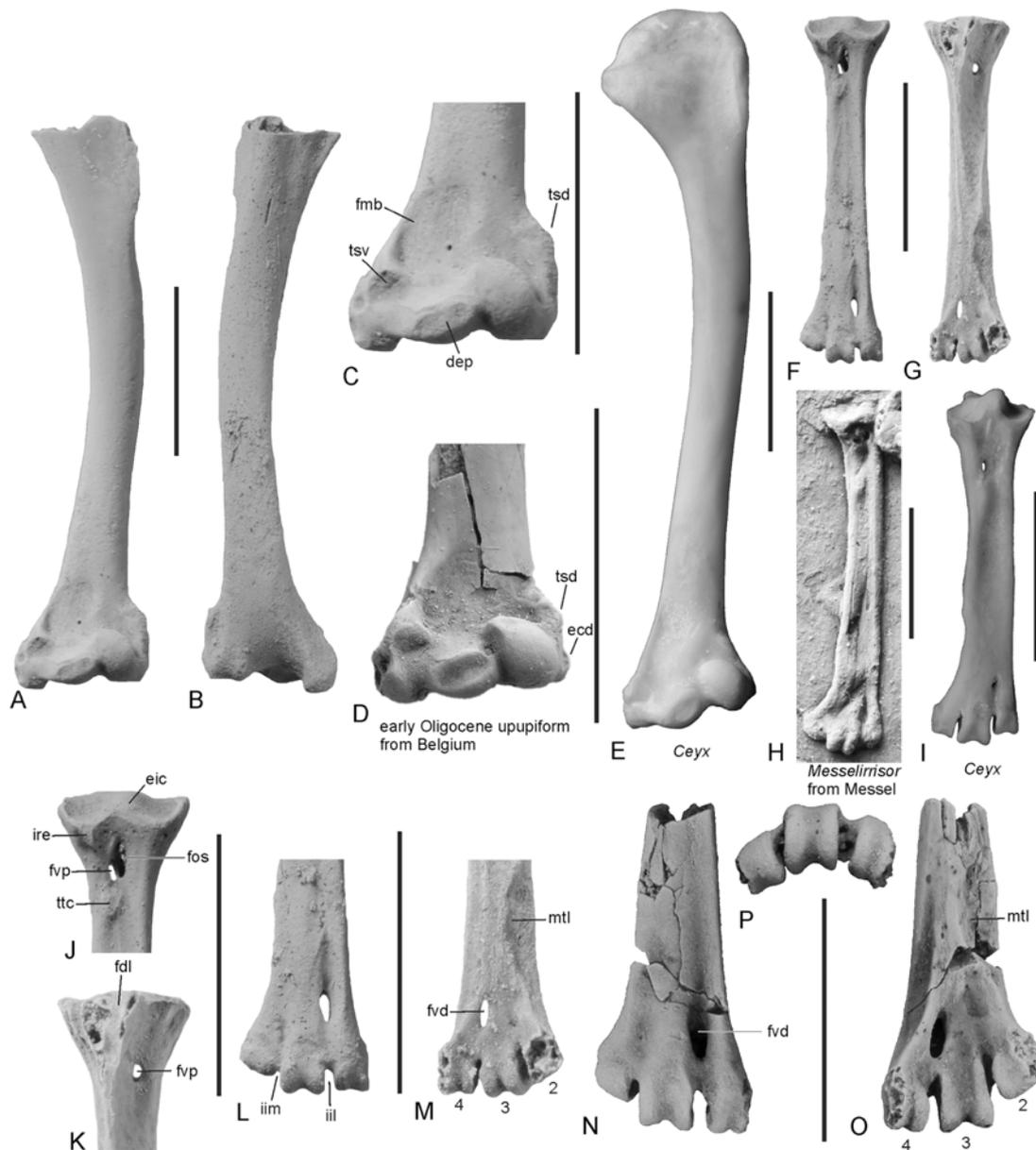


Fig. 9. Humerus (A–C) and tarsometatarsus (F, G, J–M) of a small alcediniform-like bird from Egem (cf. Alcediniformes, gen. et sp. indet. A). A, B – incomplete left humerus (IRSNB Av 189) in cranial (A) and caudal (B) view; C – detail of distal end in cranial view. D – distal humerus (cranial view) of an unnamed upipiform bird from the early Oligocene of Belgium (IRSNB Av 124, right side, reversed to ease comparisons; from MAYR & SMITH 2013). E – left humerus of the extant *Ceyx lepidus* (Alcedinidae) in cranial view. F, G – left tarsometatarsus of the alcediniform-like bird from Egem (IRSNB Av 188; gen. et sp. indet. A) in dorsal (F) and plantar (G) view. H – left tarsometatarsus of the upipiform species *Messelirrisor grandis* (Messelirrisoridae) from the early Eocene of Messel (SMF-ME 10833) in dorsal view. I – left tarsometatarsus of the extant *C. lepidus* in dorsal view. J–M – details of proximal (J, K) and distal (L, M) ends of the tarsometatarsus of the alcediniform-like bird (gen. et sp. indet. A) from Egem (J, L: dorsal view; K, M: plantar view). N–P – cf. Alcediniformes, gen. et sp. indet. B, distal end of left tarsometatarsus (IRSNB Av 190) in dorsal (N), plantar (O), and distal (P) view. Abbreviations: dep – depression on cranial surface of condylus ventralis; ecd – epicondylus dorsalis; eic – eminentia intercotylaris; fdl – hypotarsal canal for tendon of musculus flexor digitorum longus; fmb – fossa musculi brachialis; fos – dorsal fossa encompassing foramina vascularia proximalia; fvd – foramen vasculare distale; fvp – medial foramen vasculare proximale; iil – incisura intertrochlearis lateralis; iim – incisura intertrochlearis medialis; ire – impressio retinaculi extensorii; mtl – fossa metatarsi I; tsd – tuberculum supracondylare dorsale; tsv – tuberculum supracondylare ventrale; ttc – tuberositas musculi tibialis cranialis. In M and O, the trochleae are numbered. All fossil specimens were coated with ammonium chloride. Scale bars equal 5 mm.

cf. Alcediniformes sensu [MAYR \(1998b\)](#)

Gen et sp. indet. B

Fig. 9N–P

Referred specimen: IRSNB Av 190: distal end of left tarsometatarsus; collected by G. VAN DEN EECKHAUT.

Measurements (in mm): Distal width, 3.0.

Remarks: This tiny specimen resembles the above-described, putatively alcediniform tarsometatarsus IRSNB Av 188 (gen. et sp. indet. A), but is somewhat larger (distal width 3.0 versus 2.4 mm) and differs in several morphological features. Unlike in IRSNB Av 188, the trochlea metatarsi IV of IRSNB Av 190 reaches slightly farther distally than the trochlea metatarsi III. The foramen vasculare distale of IRSNB Av 190 is furthermore proportionally larger than in IRSNB Av 188 and the bony section between the distal end of this foramen and the incisura intertrochlearis lateralis is proportionally shorter. The trochlea metatarsi II is only slightly plantarly deflected and a foramen interosseus distalis is present.

Picocoraciae sensu [MAYR \(2011b\)](#)

Coraciiformes FORBES, 1884

(sensu [MAYR & MOURER-CHAUVIRÉ 2000](#))

cf. Primobucconidae FEDUCCIA & MARTIN, 1976

cf. *Septencoracias* BOURDON et al., 2016

cf. *Septencoracias* sp.

Fig. 10A–C

Referred specimen: IRSNB Av 191: right tarsometatarsus lacking trochlea metatarsi IV; collected by G. MARIËN.

Measurements (in mm): Tarsometatarsus, length, 16.1, proximal width, 4.1.

Description and comparisons: This tarsometatarsus is relatively short and has similar proportions to that of the early Eocene coraciiform taxa *Primobucco* ([MAYR et al. 2004](#)) and *Septencoracias* ([BOURDON et al. 2016](#)). The hypotarsus encloses a single canal, for the tendon of musculus flexor digitorum longus, which, unlike in extant rollers, is not completely closed plantarly. There are two hypotarsal crests, with the medial one bearing a shallow sulcus, presumably for the tendon of musculus flexor perforans et perforatus digiti II ([MAYR 2016a](#)). One of the most characteristic features of the bone is a very large medial foramen vasculare proximale, which has about the same size as the foramen vasculare distale. The large tuberositas musculi tibialis cranialis is cranially prominent and medially located. The crista medianoplantaris is well developed. The medial margin of the proximal end forms a narrow ridge. The fossa metatarsi I is large and situated near the medial margin of the bone; its proximal section bears a circular articulation facet for the processus articularis tarsometatarsalis of the os metatarsale I. The foramen vasculare distale is

very large. The mediolaterally wide and medially directed trochlea metatarsi II is wider than the trochlea metatarsi III and reaches less far distally than the latter trochlea. Most of the trochlea metatarsi IV is broken, but the remaining proximalmost portion preserves remnants of a small, plantarly directed flange. As in other coraciiform birds, the canalis interosseus distalis is plantarly open, so that there is a distinct sulcus between the bases of the trochleae metatarsorum III et IV.

Remarks: The tarsometatarsus can be unambiguously assigned to the Coraciiformes, because of the plantarly open canalis interosseus distalis, which is an apomorphy of rollers (Coraciiformes; [MAYR et al. 2004](#)). In overall morphology, the bone also closely corresponds to the tarsometatarsus of coraciiform birds.

Early Eocene stem group rollers are known from the London Clay ([MAYR & WALSH 2018](#)), the Fur Formation ([BOURDON et al. 2016](#)), the locality of Cond en-Brie in France (Fig. 10D; [MAYR et al. 2004](#)), the Green River Formation ([MAYR et al. 2004](#); [CLARKE et al. 2009](#); [KSEPKA & CLARKE 2010](#)), and Messel ([MAYR & MOURER-CHAUVIR  2000](#); [MAYR et al. 2004](#)). The coraciiform species from Egem is smaller than *Eocoracias brachyptera* from Messel (tarsometatarsus length 18.1–18.2; [MAYR & MOURER-CHAUVIR  2000](#)) and *Paracoracias occidentalis* from the Green River Formation (19.2 mm; [CLARKE et al. 2009](#)). It is larger than the species of the taxon *Primobucco* from Messel and the Green River Formation, the tarsometatarsi of which measure 11.5–14 mm ([MAYR et al. 2004](#); [KSEPKA & CLARKE 2010](#)). The tarsometatarsus from Egem differs from the superficially similar tarsometatarsus of *Microena goodwini* from the London Clay, for which possible coraciiform affinities were assumed by [MAYR \(2009a\)](#), in that the canalis interosseus distalis is plantarly open (closed in *Microena*) and in that the medial foramen vasculare proximale is much larger.

In size and morphology, the bone from Egem corresponds best to the tarsometatarsus of *Septencoracias morsensis* from the Fur Formation, which was described by [BOURDON et al. \(2016\)](#). With a tarsometatarsus length of 16.1 mm, the species from Egem is, however, slightly larger than *S. morsensis*, the tarsometatarsus of which measures 15.5 mm ([BOURDON et al. 2016](#)). A similarly-sized unnamed roller species has also been reported from the London Clay ([MAYR & WALSH 2018](#)).

The coraciiform from Egem is distinguished from all extant coraciiform birds in that the hypotarsus has an incompletely closed canal for the tendon of musculus flexor digitorum longus (compare Fig. 10C with [MAYR 2016a](#): fig. 6H, I). Judging from the smooth surface of the proximal end of the bone, the Egem tarsometatarsus is from an adult bird, and the incompletely closed hypotarsal canal is therefore likely to be a true morphological feature of the species. Incomplete closure of the canal for the tendon of musculus flexor digitorum longus may represent the plesiomorphic condition for Coraciiformes. However, the fact that a closed canal for this tendon occurs in Alcediniformes and Bucerotes ([MAYR 2016a](#)), which are the closest extant relatives of rollers, indi-

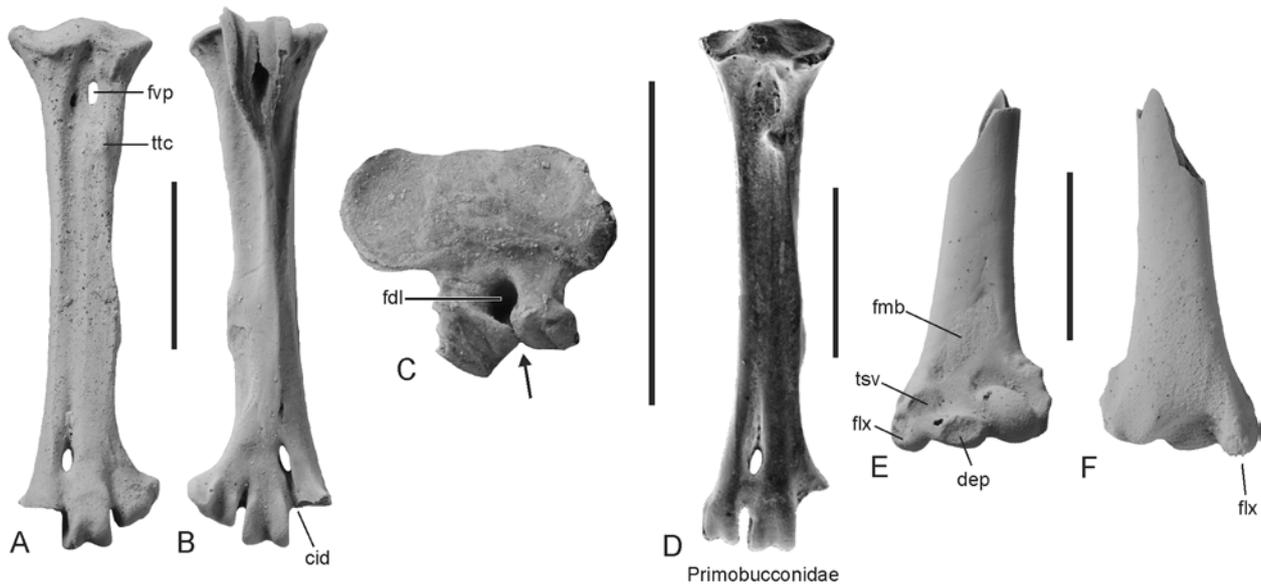


Fig. 10. A–C – incomplete right tarsometatarsus of a small coraciiform bird from Egem (cf. *Septencoracias* sp.; IRSNB Av 191) in dorsal (A), plantar (B), and proximal (C) view. D – tarsometatarsus of a unnamed species of the coraciiform Primobuconidae from the early Eocene of France (MNHN-CB-17346, the specimen is a left tarsometatarsus, which was digitally reversed to ease comparisons; from MAYR et al. 2004). E, F – distal end of left humerus of an undetermined species of the Picocoraciae (IRSNB Av 192) in cranial (E) and caudal (F) view. Abbreviations: cid – plantarly open canalis interosseus distalis; dep – depression on cranial surface of condylus ventralis; flx – processus flexorius; fmb – fossa musculi brachialis; fdl – hypotarsal canal for tendon of musculus flexor digitorum longus; fvp – medial foramen vasculare proximale; tsv – tuberculum supracondylare ventrale; ttc – tuberositas musculi tibialis cranialis. The arrow in C indicates the incomplete plantar fusion of the canal for the tendon of musculus flexor digitorum longus. Specimens in A–C and E, F were coated with ammonium chloride. Scale bars equal 5 mm.

cates homoplasy in the evolution of the hypotarsus of coraciiform birds.

Picocoraciae sensu MAYR (2011b)

Gen. et sp. indet.

Fig. 10E, F

Referred specimen: IRSNB Av 192: distal end of left humerus; collected by L. KATTENWINKEL.

Measurements (in mm): Humerus IRSNB Av 192, distal width, 5.0.

Remarks: This distal humerus has a shallow fossa musculi brachialis and a well-defined processus flexorius. The cranial surface of the condylus ventralis bears an elongate depression. Among others, the bone differs from the superficially similar but smaller alcediniform-like humerus IRSNB Av 189 in the shape of the fossa musculi brachialis, the more distally located tuberculum supracondylare ventrale, and the

presence of a dorsally projecting tubercle distally of the tuberculum supracondylare dorsale. IRSNB Av 192 resembles the distal humerus of the (much larger) late Eocene coraciiform *Geranopterus* (MAYR & MOURER-CHAUVIRÉ 2000), but is too small to be from the same species as the above-described tarsometatarsus IRSNB Av 191. The specimen also shows a resemblance to the distal humerus of upupiform birds, especially with regard to the presence of an elongate depression on the condylus ventralis and the dorsally projecting tubercle distally of the tuberculum supracondylare dorsale (compare Figs. 10E and 9D). In Upupiformes, the latter tubercle is, however, situated farther distally and the processus flexorius is less prominent.

Indeterminate species

Aves indet. B

Fig. 11A–C

Referred specimens: IRSNB Av 193: distal end of left tarsometatarsus lacking most of trochlea metatarsi II; collected by S. MAILLIOT.

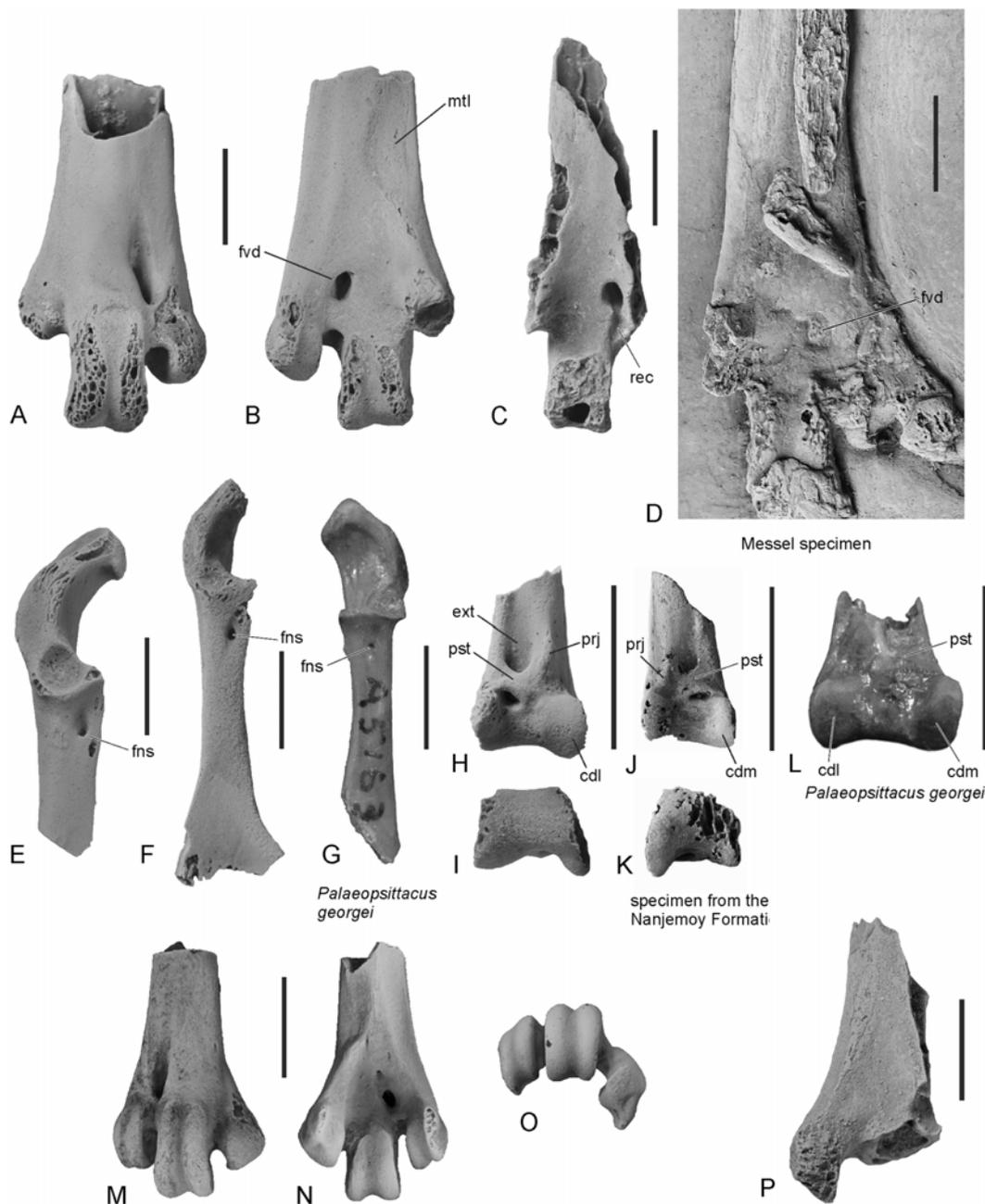


Fig. 11. Undetermined avian remains from Egem. **A, B** – Aves indet. **B**, distal end of left tarsometatarsus (IRSNB Av 193) in dorsal (**A**) and plantar (**B**) view. **C** – Aves indet. **B**, tentatively referred distal end of right tarsometatarsus (IRSNB Av 194) in plantar view. **D** – distal end of incomplete right tarsometatarsus of an undetermined bird from Messel, Germany (SMF-ME 11607). **E** – Aves indet. **C**, extremities omalis of left coracoid (IRSNB Av 195) in dorsal view. **F** – Aves indet. **D**, partial left coracoid (IRSNB Av 196) in dorsal view. **G** – right coracoid (dorsal view) of *Palaeopsittacus georgei* from the London Clay (holotype; NHMUK A 5163). **H, I** – Aves indet. **E**, distal end of left tibiotarsus (IRSNB Av 197) in cranial (**H**) and distal (**I**) view. **J, K** – distal end of right tibiotarsus of an undetermined bird from the early Eocene Nanjemoy Formation in Virginia, USA (SMF Av 623) in cranial (**J**) and distal (**K**) view. **L** – distal end of right tibiotarsus of *P. georgei* from the London Clay (holotype; NHMUK A 5163). **M–O** – Aves indet. **F**, distal end of right tarsometatarsus (IRSNB Av 198) in dorsal (**M**), plantar (**N**), and distal (**O**) view. **P** – fragmentary distal end of right tarsometatarsus (IRSNB Av 212) in plantar view. Abbreviations: cdm – condylus medialis; cdl – condylus lateralis; ext – sulcus extensorius; fns – foramen nervi supracoracoidei; fvd – foramen vasculare distale; mtl – fossa metatarsi I; prj – cranial projection for attachment of retinaculum extensorium; pst – pons supratendineus; rec – plantar recess distal of foramen vasculare distale. All specimens except those in **G** and **L** were coated with ammonium chloride. Scale bars equal 5 mm.

Tentatively referred specimen: IRSNB Av 194: distal end of right tarsometatarsus lacking trochleae metatarsorum II et IV, collected by L. KATTENWINKEL.

Measurements (in mm): IRSNB Av 193: Length as preserved, 19.0; mediolateral width of trochlea metatarsi III, 4.1; estimated width of distal end, ~10.0.

Remarks: These two tarsometatarsi are from a medium-sized bird and have a similar morphology, but only the more complete specimen IRSNB Av 193 allows a meaningful description. Even though the trochlea metatarsi II is broken in this fossil, the remaining portion indicates that it was slightly plantarly deflected. The trochlea metatarsi III reaches much farther distally than the trochlea metatarsi IV. The latter trochlea is mediolaterally narrow and appears to have had a plantarly directed wing, which is, however, broken in IRSNB Av 193. The dorsal opening of the foramen vasculare distale is large and elongate with an asymmetric outline, because its medial margin is overhung by a ledge that runs obliquely to the longitudinal axis of the tarsometatarsus. The fossa metatarsi I is large but shallow and situated on the plantar surface of the bone near its medial margin.

As far as comparisons are possible, the fragmentary tentatively referred specimen IRSNB Av 194 is similar to the more complete tarsometatarsus IRSNB Av 193 in size and morphology. Unlike in IRSNB Av 193, however, the plantar opening of the foramen vasculare distale of IRSNB Av 194 is distally continuous with a plantarly open recess.

The specimens from Egem resemble the distal end of a tarsometatarsus from Messel (Fig. 11D), which was described as “unknown genus and species C” by MAYR (2016c). The Messel bird is represented by a foot, but its affinities are indeterminate. Although the fossils from Egem and Messel resemble some gruiform (e.g., Psophiidae) and cariamiform birds, these similarities are rather unspecific and a definitive classification has to await the discovery of more material.

Aves indet. C
Fig. 11E

Referred specimen: IRSNB Av 195: extremitas omalis of left coracoid; collected by J. TAK (received via Y. CHRISTIANS).

Measurements (in mm): Length as preserved, 17.1.

Remarks: This partial coracoid is characterized by a large and deeply excavated cotyla scapularis with a semicircular outline. The facies articularis clavicularis overhangs the sulcus supracoracoideus. The bone resembles coracoids of two undetermined ornithurine birds from the latest Cretaceous of North America (“ornithurines B and C”; LONGRICH *et al.* 2011: figs. 3B, C). It also shows a similarity to the coracoid of the early Paleogene anseriform taxon *Presbyornis* (KUROCHKIN & DYKE 2010: fig. 7), but appears to be too small to belong to the same species as

the above-described presbyornithid-like humerus IRSNB Av 175 (Aves indet. A).

Aves indet. D
Fig. 11F

Referred specimen: IRSNB Av 196: left coracoid; collected by Y. CHRISTIANS.

Measurements (in mm): Length as preserved, 20.7.

Remarks: This specimen is characterized by a straight processus acrocoracoideus, a fossa in the dorsal portion of the sulcus supracoracoideus, and a large foramen nervi supracoracoidei. The cotyla scapularis is shallow, the facies articularis humeralis has little lateral prominence; the tip of the processus procoracoideus is broken. The remaining omal portion of the extremitas sternalis has a flat dorsal surface. The bone shows a resemblance to the coracoid of *Palaeopsittacus georgei* from the London Clay (Fig. 11G; HARRISON 1982a) and to the coracoid of the Leptosomiformes, but these similarities are likely to be due to the retention of plesiomorphic features. The fossil is much too small to be from the same species as the tarsometatarsus referred to the leptosomiform *Plesiocathartes* (see above).

Aves indet. E
Fig. 11H, I

Referred specimen: IRSNB Av 197: distal end of left tibiotarsus; collected by L. KATTENWINKEL.

Measurements (in mm): Distal width, 3.4.

Remarks: This distal tibiotarsus stems from a small bird. The sulcus extensorius runs in the medial portion of the bone. The condyli are proximodistally low and widely separated; the condylus medialis, whose medial surface is damaged, seems to be proximally displaced relative to the condylus lateralis. A distinctive feature of the bone is the presence of a marked cranial projection lateral of the distal end of the sulcus extensorius, which is likely to represent the lateral attachment site of the retinaculum extensorium.

The bone resembles a distal tibiotarsus from the Nanjemoy Formation (Fig. 11J, K, which was compared with the tibiotarsus of the Trogoniformes (MAYR 2016b: fig. 2l–n). In the specimen from the Nanjemoy Formation, the cranial projection for the attachment of the retinaculum extensorium is, however, less prominent. The specimen from Egem is also similar to the distal tibiotarsus of *Palaeopsittacus georgei* from the London Clay, which represents, however, a distinctly larger species and lacks the cranial projection (Fig. 11L). Unlike in the Halcyornithidae, which have similarly splayed condyli, the sulcus extensorius is positioned in the medial portion of the bone.

Aves indet. F
Fig. 11M–O

Referred specimen: IRSNB Av 198: distal end of right tarsometatarsus; collected by G. VAN DEN EECKHAUT.

Measurements (in mm): Distal width, 7.4.

Remarks: This specimen resembles the distal tarsometatarsus, which we tentatively referred to the Masillaraptoridae, but it is somewhat larger and differs in the proportions of the trochlea metatarsi III and the more plantarly deflected trochlea metatarsi II. The fossil shows an overall resemblance to the distal tarsometatarsus of the extant gruiform Psophiidae and Rallidae, but the similarities are too un-specific for a definitive identification. It differs from the distal tarsometatarsus of the Messelornithidae in that the trochlea metatarsi II reaches as far distally as the trochlea metatarsi IV.

Miscellaneous further indeterminate avian remains

Fig. 12

Material: IRSNB Av 199: atlas; collected by G. MARIËN. IRSNB Av 200: cranialmost portion of sternum; collected by Y. CHRISTIANS. IRSNB Av 201: left coracoid; collected by F. MIGOM. IRSNB Av 202: right coracoid; collected by Y. CHRISTIANS. IRSNB Av 203: extremitas omalis of left coracoid; collected by W. ZANDERING. IRSNB Av 204: extremitas omalis of right coracoid; collected by L. KATTENWINKEL. IRSNB Av 205: left humerus lacking portion of proximal end; collected by Y. CHRISTIANS. IRSNB Av 206: distal end of left humerus; collected by Y. CHRISTIANS. IRSNB Av 207: distal end of left ulna; collected by W. ZANDERING. IRSNB Av 208: distal portion of left ulna; collected by G. MARIËN. IRSNB Av 209: proximal end of left ulna; collected by collected by J. TAK (received via Y. CHRISTIANS). IRSNB Av 210: proximal end of left carpometacarpus; collected by W. ZANDERING. IRSNB Av 211: fragmentary proximal portion of left carpometacarpus; collected by G. MARIËN. IRSNB Av 212: distal end of right tarsometatarsus lacking trochleae metatarsorum III et IV; collected by Y. CHRISTIANS.

Remarks: Our study faces the problems associated with the analysis of isolated Eocene bird bones, and although our identifications were guided by comparisons with more complete fossils known from other localities, such as Messel (in the case of, e.g., the halcyornithid and leptosomiform remains) and the London Clay (concerning the putative Prophaethontidae), a number of well-preserved bones from the Egem material defied a reliable classification. These fossils are from miscellaneous, differently-sized species and some are likely to belong to one of the above-described taxa.

The atlas (Fig. 12A) has a widely open incisura fossae, a craniocaudally broad arcus atlantis, and short processus articulares caudales. The size of the bone is comparable to the atlas of a larger species of the Threskiornithidae (e.g.,

Platalea leucorodia). Similarly-sized species in the Egem material include the putative prophaethontid, the putative accipitrid, and the indeterminate species A and B.

The cranial fragment of the sternum (Fig. 12B) features a very long, blade-like spina externa and overlapping sulci coracoidei. In size, the specimen would correspond to the small galliform or to the messelornithid. The labrum internum is, however, not as deep as in Galliformes and the spina externa is proportionally longer than in *M. cristata* (HESSE 1990: pl. 6). Unlike in crown group Galliformes, the fossil lacks a spina interna, but this spine is plesiomorphically absent in Paleogene stem group Galliformes (MAYR & SMITH 2013).

The partial right coracoid IRSNB Av 204 (Fig. 12C) has a foramen nervi supracoracoidei and shows a resemblance to the coracoid of the Messelornithidae (Fig. 12D). Unlike *Messelornis*, however, IRSNB Av 204 lacks a crista procoracoidei, and the specimen appears to be too small to be from one of the above-described messelornithids from Egem.

The three coracoids IRSNB Av 201, IRSNB Av 202, and IRSNB Av 203 (Fig. 12E–G) are of similar size (maximum length as preserved 17.7 in IRSNB Av 201 and 18.1 in IRSNB Av 202) and at first glance they show a resemblance in their morphology. Close examination suggests, however, that they are from three different species. The two largely complete bones (Fig. 12E, G) are comparatively stout, with a fairly long extremitas omalis and a wide shaft. The facies articularis scapularis is shallow and slightly concave. The processus procoracoideus is not completely preserved but has a sterno-omally broad base. A foramen nervi supracoracoidei is absent. The medial margin of the extremitas sternalis forms a small notch. Specimen IRSNB Av 201 has a somewhat smaller extremitas sternalis than IRSNB Av 202, the sulcus supracoracoideus exhibits a fossa in its dorsal portion, and unlike in IRSNB Av 202 the dorsal surface of the extremitas sternalis bears muscular striae. IRSNB Av 203 is distinguished from the other two coracoids in that the facies articularis clavicularis is longer and the processus acrocoracoideus has a more hook-like outline. Especially the two nearly complete coracoids show a coraciiform-like morphology, and one of these specimens may belong to the above-described coraciiform species (cf. *Septencoracias*). However, not least because the coracoid of *Septencoracias* is unknown, it cannot be determined which of the bones, if any, actually belongs to the above-described tarsometatarsus.

Among the Egem material there are two morphologically different humeri, one of which may belong to the Messelornithidae. The more complete humerus IRSNB Av 205 (Fig. 12H, I) has a slightly sigmoidally curved shaft and a short and dorsally projected crista deltopectoralis with a rounded dorsal margin and a convex caudal surface. The ventral portion of the proximal section of the shaft exhibits a shallow fossa along its caudal surface, which may indicate the presence of a second fossa pneumotricipitalis. The fairly deep fossa musculi brachialis is sharply delimited and extends obliquely across the humerus shaft. The small tuberculum supracondylare ventrale has a slightly convex cranial surface. The processus flexorius appears to have had little ventral prominence, but its tip is broken in the spec-



Fig. 12. Miscellaneous undetermined avian remains from Egem. **A** – atlas (IRSNB Av 199) in cranial view. **B** – cranialmost portion of sternum (IRSNB Av 200) in ventral view. **C** – extremitas omalis of a right coracoid (IRSNB Av 204) in dorsal view. **D** – extremitas omalis of right coracoid of *Messelornis cristata* from Messel (SMF-ME 2614a) in dorsal view. **E** – left coracoid (RSNB Av 201) in dorsal view. **F** – extremitas omalis of left coracoid (IRSNB Av 203) in dorsal view. **G** – right coracoid (IRSNB Av 202) in dorsal view. **H, I** – incomplete left humerus (IRSNB Av 205) in cranial (**H**) and caudal (**I**) view. **J** – distal end of right humerus from the Nanjemoy Formation in Virginia, USA (SMF Av 621) in cranial view. **K** – distal end of left humerus (IRSNB Av 206) in cranial view. **L** – proximal end of left ulna (IRSNB Av 209) in cranial view. **M** – distal end of left ulna (IRSNB Av 207) in ventral view. **N** – distal portion of left ulna (IRSNB Av 208) in ventral view. **O** – fragmentary proximal portion of left carpometacarpus (IRSNB Av 211) in ventral view. **P** – proximal end of left carpometacarpus (IRSNB Av 210) in ventral view. Abbreviations: cdp – crista deltopectoralis; cpc – crista procoracoidei; dep – depression on cranial surface of condylus ventralis; fmb – fossa musculi brachialis; fos – ?dorsal pneumotricipital fossa; spe – spina externa; tsv – tuberculum supracondylare ventrale. All specimens were coated with ammonium chloride. Scale bar equals 5 mm.

imen. The condyles are abraded and damaged. The distal end of the bone resembles a distal humerus from the early Eocene Nanjemoy Formation (Fig. 12J), which was tentatively referred to the gruiform Messelornithidae by MAYR (2016b). With a preserved length of 37.2 mm, the bone from Egem corresponds well with the humerus of the messelornithid *Messelornis cristata* in size, but the convex caudal surface of the crista deltopectoralis conflicts with messelornithid affinities. The incipient second (dorsal) pneumotricipital fossa and the convex caudal surface of the crista deltopectoralis may suggest that the fossil is from a galliform bird, but the shaft of the bone is narrower than in other Galliformes. The crista deltopectoralis is furthermore more dorsally protruding and less cranially deflected than in most other fossil and extant Galliformes, even though the shape of the crest corresponds well with the crista deltopectoralis of the gallinuloidid *Paraortygoides messelensis* from Messel.

The distal humerus IRSNB Av 206 (Fig. 12K) is from a different species and resembles the distal humerus of *Messelornis russelli* from the late Paleocene of France (MOURER-CHAUVIRÉ 1995), from which it, however, differs in that the distal margin is oriented less obliquely relative to the longitudinal axis of the bone and in that the cranial surface of the condylus ventralis bears a shallow depression. As in *M. russelli*, the tuberculum supracondylare ventrale is dorsoventrally extensive, the shallow fossa musculi brachialis extends obliquely across the humerus shaft, and the processus flexorius protrudes ventrally. Clearly, only one (if any) of the above humeri – i.e., either IRSNB Av 205 or IRSNB Av 206 – belongs to the Messelornithidae, but without more complete material an unambiguous identification of either bone is not possible.

The proximal ulna IRSNB Av 209 (Fig. 12L) has a dorsoventrally compressed shaft. The specimen appears to be too large to be from the messelornithid and may or may not belong to the same species as the above-described partial coracoid IRSNB Av 195 (indeterminate species C), which was found by the same collector.

The two distal ulnae are of different size (Fig. 12M, N). The smaller one (IRSNB Av 207) has a long condylus dorsalis and a small tuberculum carpale and is from a species the size of the halcyornithid. Possible halcyornithid affinities are also suggested by the presence of a distinct depressio radialis (MAYR 1998a). The larger ulna (IRSNB Av 208) has a proximodistally longer tuberculum carpale and is from a species the size of the messelornithid.

The carpometacarpi (Fig. 12O, P) are from two different species, but a reliable identification of the bones is not possible. In size, the larger specimen IRSNB Av 210 would correspond with the tarsometatarsus of the indeterminate species B and with the putative accipitrid tarsometatarsus.

The fragmentary distal tarsometatarsus IRSNB Av 212 (Fig. 11P) is too incomplete for a well-based identification. In size, the specimen corresponds with the tarsometatarsi of the undetermined species B, but the trochlea metatarsi II appears to be mediolaterally wider and there is no canalis interosseus distalis. A fossa metatarsi I is not clearly discernible.

4. Discussion

The above-described avian assemblage consists of 54 bones, which belong to a minimum of 20 species representing more than 11 higher-level taxa, with this high taxonomic diversity corresponding well with coeval Central European avifaunas (MAYR 2017a). By comparison, the mammalian record from Egem is more depauperate and includes only six species: a multituberculate, a marsupial, an erinaceomorph insectivore, a nyctitheriid, a chiropteran, and a perisodactyl (SMITH & SMITH 2013). This dominance of birds in the Egem material is in concordance with the composition of fossil assemblages of other sites of the North Sea Basin, especially the London Clay and the Fur Formation, and is likely to be a taphonomic artefact: not only are volant animals more likely to be blown into the open sea, but feathered bird carcasses also drift for a longer time on the surface before they sink down to the sea floor.

The early Eocene avifauna from Egem corresponds to that of the London Clay and the Fur Formation in that the majority of the fossils represents landbirds, despite the fact that the sediments originated in a marine environment. Concerning the seabirds, the Egem avifauna agrees with that of the London Clay in the presence of Odontopterygiformes and Prophaethontidae (even though our identification of the latter taxon in the Egem material is tentative). The composition of the Egem avifauna likewise shows a resemblance to that of the slightly older (53.7–54.2 Ma) Nanjemoy Formation in Virginia (USA).

Terrestrial taxa dominate among the landbirds from Egem, but there are also several remains of arboreal birds (Halcyornithidae, Leptosomiformes, Coraciiformes), whereas aerial insectivores (Apodiformes) are only represented by a single bone. Notable absences among the arboreal landbirds in the Egem material concern Coliiformes, Upupiformes, and Zygodactylidae, which are abundantly represented in the Messel fossil site and were also reported from the London Clay (MAYR 2009a). The fact that these forest-dwelling taxa have not yet been found in Egem indicates either a taphonomic bias in the composition of the avifauna (arboreal birds may have been less likely to become embedded into the sea sediments) or particular paleoenvironmental characteristics of the nearshore habitats in that area of the southern North Sea Basin.

Except for the seabirds, most of the birds from Egem represent relatively small species, which indi-

cates a taphonomic bias in the assemblage. A taphonomic bias towards smaller landbirds may also explain the absence of remains of the palaeognathous Lithornithidae in Egem, with these birds being comparatively abundant in the London Clay and the Fur Formation (MAYR 2009a; BOURDON & LINDOW 2015). Small-sized species also dominate among the mammals from Egem (SMITH & SMITH 2013).

The Egem avifauna includes a few taxa that have not yet been reported from coeval sites. Particularly noteworthy are the specimens, which we tentatively assigned to the Alcediniformes, and which would constitute the earliest fossil record of this clade. Alcediniformes are unknown from the London Clay and the Fur Formation, and the next-oldest record stems from Messel in Germany (about 48.0–47.5 Ma). If correctly assigned to the Accipitridae, the above-described tarsometatarsus fragment and pedal phalanges from Egem likewise are among the earliest fossil records of this avian clade. The small galliform species finally constitutes evidence for the presence of a galliform higher-level taxon in the early Eocene of Europe, which is distinguished from the Gallinuloididae.

We note, however, that the significance of our study does not mainly lie in the recognition of new taxa or earliest occurrences, but in the identification of well-preserved isolated bones of key groups that are otherwise mainly known from compression fossils. The fact that even the relatively small assemblage described in the present study reveals new insights into the composition of early Eocene avifauna of the North Sea Basin furthermore exemplifies how incomplete our knowledge of early Eocene avifaunas still is. Studies of the past years have added much to an improved understanding of the bird diversity in that period. However, even with regard to the comparatively well-researched early Eocene avian fossil record from Europe much work still has to be conducted for a reasonably comprehensive inventory, and the fair proportion of unidentifiable albeit diagnostic bones in our sample documents the need of increased research efforts to close the many existing gaps in our knowledge.

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