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# Galliformes, Upupiformes, Trogoniformes, and other avian remains (?Phaethontiformes and ?Threskiornithidae) from the Rupelian stratotype in Belgium, with comments on the identity of "*Anas*" *benedeni* Sharpe, 1899

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**Abstract** — We describe new avian fossils from the Boom Formation of Belgium, which almost double the number of bird taxa known from this part of the Rupelian stratotype. Three galliform species can, at least tentatively, be assigned to the paraortygid species *Paraortyx brancoi*, *P. lorteti*, and *Pirortyx major*. Among the fossils is a partial sternum, which shows that *Paraortyx* lacks a spina interna. The absence of this structure is plesiomorphic for Galliformes and probably related to the absence of a large crop, thus indicating that Paraortygidae were not yet adapted to the regular processing of coarse and dry food. Two distal humeri belong to Trogoniformes (trogons) and Upupiformes (hoopoes, woodhoopoes, and allies), respectively. A femur is tentatively assigned to Phaethontiformes (tropicbirds), and a carpometacarpus is, likewise tentatively, referred to Threskiornithidae (ibises and spoonbills). We finally comment on the affinities of "*Anas*" *benedeni* Sharpe, 1899 and detail that this species most likely belongs to Gaviiformes (loons).

**Key words:** fossil birds, early Oligocene, Boom Formation, Paraortygidae

## Introduction

The Lower Oligocene Boom Formation of the Rupelmonde area in Belgium was deposited in a shallow open sea in the southwestern part of the North Sea Basin, and is part of the Rupelian stratotype (*e.g.*, van Simaeys & Vandenberghe 2006). The formation is exposed at various localities in the Rupelmonde area near Antwerp and has yielded numerous avian remains, most of which were collected in the late 19th and early 20th century.

The majority of the bird fossils belongs to the diomedeoidid procellariiform *Rupelornis definitus* (Mayr & Smith 2012a). Remains of other marine birds are much rarer and were assigned to Diomedeidae (albatrosses; Mayr & Smith 2012b) and Gaviiformes (loons; Mayr 2009a). Lambrecht (1931) reported a large, putatively anseriform bird (*Cygnopterus affinis*), whose affinities are in need of a revision (Mayr 2009b). More recently, Mayr (2009a) identified a new species of Selenornithidae, an extinct and poorly known group of Strigiformes (owls), and fossils of the gruiform taxon Parvigruidae were described by Mayr (2013). Most of these species have been described after Cheneval's (1996) review of the Belgian avifauna, who at that time could mainly list various poorly established and largely incorrectly identified species described by van Beneden (1871).

Despite the progress made in recent years, our knowledge of the Rupelian avifauna of Belgium, and the North Sea Basin in general, is still

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anecdotal. Because of the marine origin of most fossil deposits the avian record is biased towards aquatic taxa, and very small birds are underrepresented in the old collections due to the fact that most fossils are surface finds. Here we report on further avian remains from the Boom clay, including the first remains of small land birds, and revise the affinities of "*Anas*" *benedeni* Sharpe, 1899, one of the species introduced by van Beneden (1871) under the preoccupied name "*Anas creccoides*".

## Material and methods

Osteological terminology follows Baumel & Witmer (1993). Measurements are in millimeters. Institutional abbreviations: IRSNB, Institut royal des Sciences naturelles de Belgique, Belgium; SMF, Senckenberg Research Institute and Natural History Museum Frankfurt.

## Systematic Palaeontology

### Galliformes Temminck, 1820
### Paraortygidae Mourer-Chauviré, 1992
### *Paraortyx* Gaillard, 1908

**Taxonomic remarks:** Paraortygidae is a taxon of stem group Galliformes, which was established by Mourer-Chauviré (1992) for fossils from the Quercy fissure fillings in France. In these deposits, three species can be distinguished, which occur in Late Eocene/Early Oligocene (*Paraortyx brancoi* and *P. lorteti*) and Late Oligocene (*Pirortyx major*) localities; Fischer (1990) further reported *P. major* from the Lower Oligocene of Germany.

Paraortygidae are distinguished from crown group Galliformes by plesiomorphic features of the humerus (lack of a transverse ridge at the beginning of the incisura capitis) and the coracoid (presence of an excavated cotyla scapularis). The Rupelmonde material includes remains of at least three paraortygid species, which can, at least tentatively, be assigned to the three species reported from the Quercy deposits.

#### *Paraortyx* cf. *lorteti* Gaillard, 1908
(Fig. 1A)

**Referred specimen:** IRSNB Av 115 (proximal end of right humerus; collection Delheid IG 8289, found in 1896).

**Locality and horizon:** Niel-Boom; Early Oligocene, between 30.5 and 31.5 Ma (lower part of the Boom Formation, Rupel Group, middle Rupelian).

**Measurements:** Length as preserved, 22.3; proximal width, 10.2 [9.2–11.2] (dimensions of Quercy specimens of *P. lorteti* in brackets, after Mourer-Chauviré 1992).

**Remarks:** The specimen is identified as a stem group galliform by the lack of a transverse ridge at the beginning of the incisura capitis. It exhibits a marked second (dorsal) fossa pneumotricipitalis (weakly developed in *Pirortyx*), and closely matches the Quercy specimens of *P. lorteti* in size and morphology (Mourer-Chauviré 1992: fig. 2). Assignment to this latter species is nevertheless tentative because of the fragmentary nature of the fossil.

#### *Paraortyx brancoi* Gaillard, 1908
(Fig. 1B–H)

**Referred specimens:** IRSNB Av 116a–c (cranial portion of corpus sterni, left coracoid, proximal end of right ulna; collection Delheid IG 8289, found in 1891).

**Locality and horizon:** Steendorp; Early Oligocene, between 30.5 and 31.5 Ma (lower part of the Boom Formation, Rupel Group, middle Rupelian).

**Measurements:** Coracoid, maximum length, 35.3; estimated length from processus acrocoracoideus to broken angulus medialis, ~32 [31.0]. Ulna, dorsoventral width across cotylae, 6.8 (dimensions of Quercy specimens of *P. brancoi* in brackets, after Mourer-Chauviré 1992).

**Remarks:** These three bones are from a single individual. In size and morphology, the coracoid (Fig. 1B) corresponds with that of *Paraortyx brancoi* from the Late Eocene (MP 18/19) of the Quercy fissure fillings in France (Mourer-Chauviré 1992). As in other stem group Galliformes

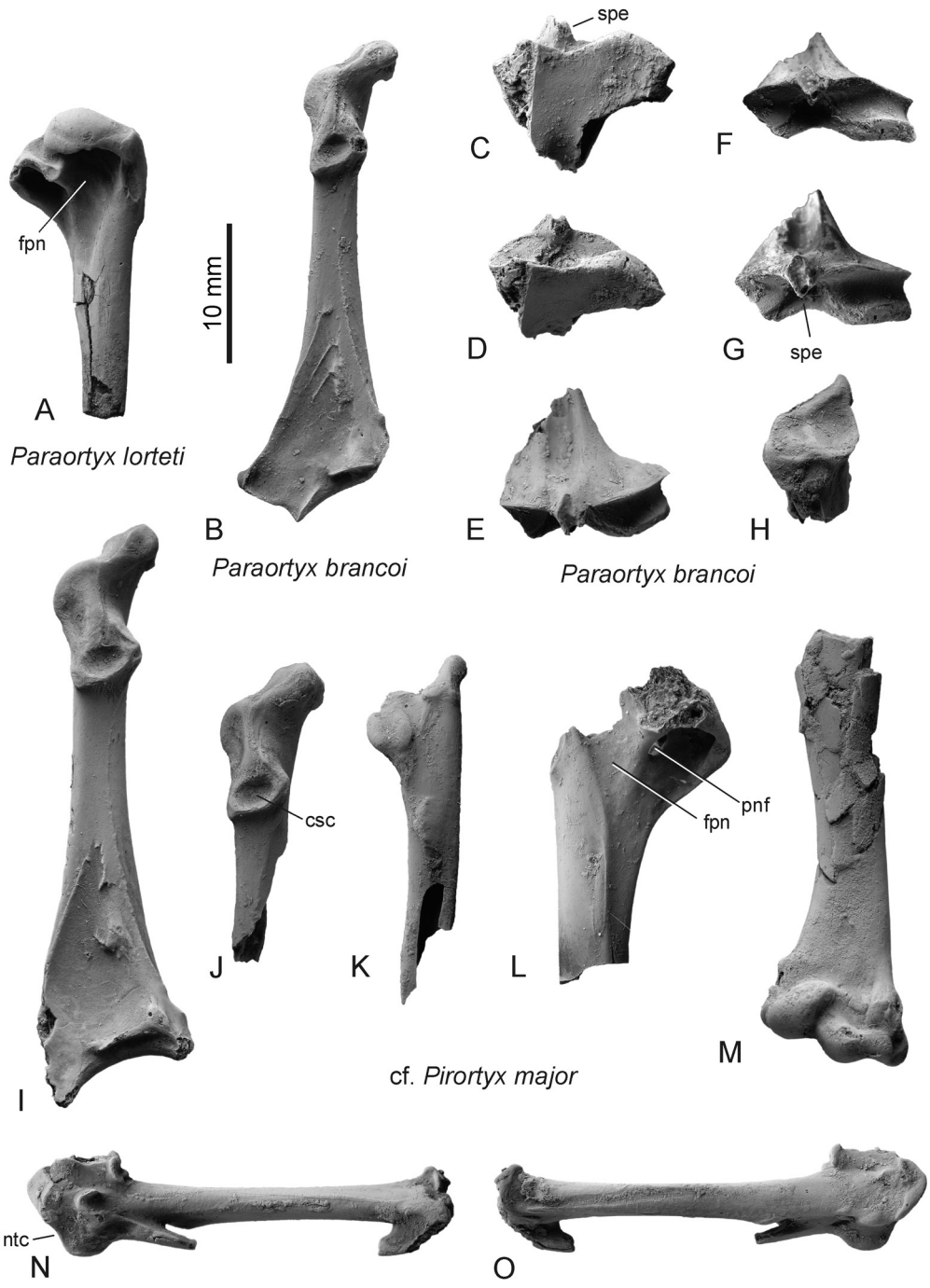


**FIGURE 1.** Galliformes from the Rupelian of Belgium. **A**, *Paraortyx* cf. *lorteti*, proximal end of right humerus (IRSNB Av 115) in caudal view. **B–H**, *P. brancoi*, **B**, left coracoid (IRSNB Av 116a) in dorsal view; **C–G**, cranial portion of corpus sterni (IRSNB Av 116b) in dorsal (**C**), craniodorsal (**D**), ventral (**E**), cranial (**F**), and cranioventral (**G**) view; **H**, proximal end of right ulna (IRSNB Av 116c) in cranial view. **I–O**, cf. *Pirortyx major*, **I**, left coracoid (IRSNB Av 117) in dorsal view; **J**, extremitas omalis of left coracoid (IRSNB Av 118a) in dorsal view; **K**, extremitas cranialis of left scapula (IRSNB Av 118b) in lateral view; **L**, proximal end of left humerus (IRSNB Av 119) in caudal view; **M**, distal end of right humerus (IRSNB Av 120) in cranial view; **N**, **O**, incomplete left carpometacarpus (IRSNB Av 122) in ventral (**N**) and dorsal (**O**) view. Abbreviations: csc, cotyla scapularis; fpn, second (dorsal) fossa pneumotricipitalis; ntc, notch in rim of ventral portion of trochlea carpalis; pnf, pneumatic foramen; spe, spina externa. Bones were coated with ammonium chloride.

it exhibits a cup-like cotyla scapularis. The ulna of *P. brancoi* has not been described, but, apart from being larger (proximal width 6.8 mm versus 4.4–4.9 mm; Mourer-Chauviré 1992), the Belgian ulna (Fig. 1H) matches that of *P. lorteti* (Mourer-Chauviré 1992).

IRSNB Av 116a–c also includes the cranial portion of a sternum (Fig. 1C–G). This bone was unknown for *Paraortyx* and other Early Oligocene Galliformes before and distinctly differs from the sternum of crown group Galliformes in the absence of a spina interna, which in crown group Galliformes is fused with the spina externa to form a spina communis (see discussion).

**?*Pirortyx* Brodkorb, 1964**
**cf. *Pirortyx major* (Gaillard, 1939)**
(Fig. 1I–O)

**Referred specimens:** IRSNB Av 117 (Fig. 1I; left coracoid; collection Hasse IG 20664, found in 1904). IRSNB Av 118a+b (Fig. 1J, K; extremitas omalis of left coracoid, extremitas cranialis of left scapula; collection Delheid IG 8289, found in 1895). IRSNB Av 119 (Fig. 1L; proximal end of left humerus; collection Delheid IG 8289, found in 1901). IRSNB Av 120 (Fig. 1M; distal end of right humerus; collection Delheid IG 8289). IRSNB Av 121 (extremitas cranialis of right scapula; collection Delheid IG 8289). IRSNB Av 122 (Fig. 1N, O; incomplete left carpometacarpus; collection Delheid IG 8289, found in 1901).

**Locality and horizon:** Steendorp (IRSNB Av 119, IRSNB Av 118a+b), Niel-Boom (IRSNB Av 117), Rumst (IRSNB Av 120), Terhagen (IRSNB Av 122); all Early Oligocene, between 30.5 and 31.5 Ma (lower part of the Boom Formation, Rupel Group, middle Rupelian).

**Measurements:** Coracoid (IRSNB Av 117), maximum length, 41.0; length from tip of processus acrocoracoideus to angulus medialis, 38.5. Humerus (IRSNB Av 119), proximal width (est.), ~13.5 [13.5]. Humerus (IRSNB Av 120), distal width, 10.8 [9.7]. Carpometacarpus (IRSNB Av 122), length, 30.6 (in brackets the dimensions of Quercy specimens of *Pirortyx major*, after Mourer-Chauviré 1992).

**Remarks:** *Pirortyx major*, the only species of the taxon *Pirortyx*, is known from the holotype (a complete humerus from an unknown horizon of the Quercy fissure fillings), a referred proximal humerus from the Late Oligocene of the Quercy fissure fillings (Mourer-Chauviré 1992), as well as a proximal and another distal humerus from the Lower Oligocene of the Weißelster Basin in Germany (Fischer 1990). The proximal humerus IRSNB Av 119 agrees with *Pirortyx* and differs from *Paraortyx* in that the second fossa pneumotricipitalis is shallower, less extensive, and bears a pneumatic opening (Fig. 1L; Mourer-Chauviré 1992). The tentatively referred distal humerus IRSNB Av 120 is larger than that of previously reported *P. major* fossils (10.8 mm versus 9.7 mm in the *P. major* holotype and 8.7 mm in a specimen referred to the species by Fischer 1990), but a comparable range of individual size variation is known from humeri referred to *Paraortyx brancoi* (Mourer-Chauviré 1992: tab. 1).

The coracoid and scapula of *Pirortyx* have not been described before, and the above-listed specimens are referred to the taxon based on their large size. We note, however, that if our assignment is correct, *Pirortyx major* had a proportionally shorter humerus than the species of *Paraortyx*, as the ratio humerus length: coracoid length would then be 1.46 for *Pirortyx major* (holotype of *P. major*: IRSNB Av 117), whereas it is 1.62 in *Paraortyx lorteti* and 1.63 in *P. brancoi* (calculated after the mean dimensions given by Mourer-Chauviré 1992: tab. 1). Morphologically, the Belgian coracoids and scapulae closely resemble the corresponding bones of *Paraortyx lorteti*.

The carpometacarpus IRSNB Av 122 is too large to belong to either of the two *Paraortyx* species (the bone measures only 19.5–21.7 mm in the larger *P. brancoi*; Mourer-Chauviré 1992), but would correspond in size to *Pirortyx major*, with the ratio humerus length: carpometacarpus length being 1.84 (*P. major* holotype: IRSNB Av 122) and 1.90 in *Paraortyx brancoi* (calculated after the mean dimensions given by Mourer-Chauviré 1992: tab. 1). IRSNB Av 122 agrees with the carpometacarpus of *Paraortyx* in its proportions, and as in other stem group Galliformes the intermetacarpal tuberosity is only weakly developed. The ventral surface of the proximal portion of the os metacarpale minus does, however, not exhibit a well-developed tubercle, which is found in *Paraortyx* and some other taxa of stem group Galliformes (Mourer-Chauviré

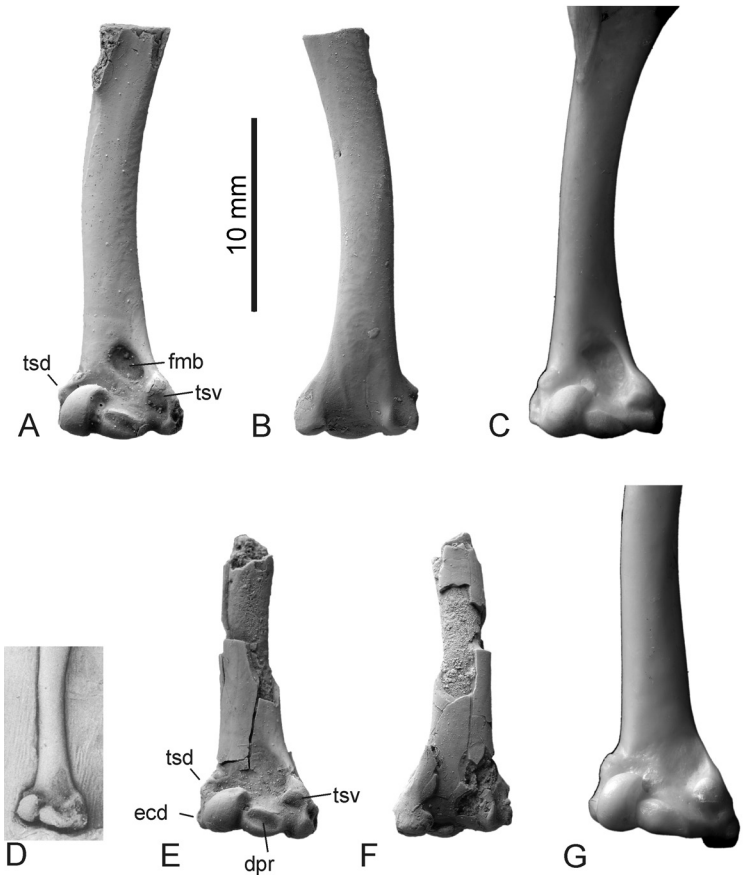


**FIGURE 2.** Trogoniformes and Upupiformes from the Rupelian of Belgium. **A**, **B**, ?*Primotrogon* sp., distal end of right humerus (IRSNB Av 123) in cranial (**A**) and caudal (**B**) view, in comparison to **C**, the distal humerus of the Orange-breasted Trogon, *Harpactes oreskios* (Trogonidae). **D**, distal end of right humerus of *Messelirrisor halcyrostris* (Messelirrisoridae) from the early Eocene of Messel in Germany (from Mayr 1998: pl. 6). **E**, **F**, Upupiformes, gen. et sp. indet., distal end of right humerus (IRSNB Av 124) in cranial (**E**) and caudal (**F**) view, in comparison to the distal humerus of **G**, the Green Woodhoopoe, *Phoeniculus purpureus* (Phoeniculidae). Abbreviations: dpr, depression on cranial surface of condylus ventralis; ecd, epicondylus dorsalis; fmb, fossa musculi brachialis; tsd, tuberculum supracondylare dorsale; tsv, tuberculum supracondylare ventrale. Fossil bones were coated with ammonium chloride.

1992: pl. 2; Mayr 2006: fig. 5d). Further unlike *Paraortyx*, the caudal rim of the ventral portion of the trochlea carpalis is distinctly notched (Fig. 1N).

**Trogoniformes American Ornithologists' Union, 1886**
**?Primotrogon Mayr, 1999**

**?*Primotrogon* sp.**
(Fig. 2A, B)

**Referred specimen:** IRSNB Av 123 (distal right humerus; collection Delheid IG 8289).

**Locality and horizon:** Steendorp; Early Oligocene, between 30.5 and 31.5 Ma (lower part of the Boom Formation, Rupel Group, middle Rupelian).

**Measurements:** Length as preserved, 21.9; distal width, 6.5.

**Remarks:** IRSNB Av 123 is from a species about the size of the extant Orange-breasted Trogon, *Harpactes oreskios*. It is identified as a trogon by its stout overall proportions and by the marked and sharply delimited fossa musculi brachialis; this latter fossa is very distinct in most of the studied species of *Harpactes* (*oreskios*, *diardii*, *ardens*) as well as in *Trogon rufus*, whereas it is shallower in *H. erythrocephalus*, *Apalharpactes reinwardtii*, *Trogon viridis*, and

*Pharomachrus* spp. The tuberculum supracondylare dorsale of IRSNB Av 123 is more marked and dorsally protruding than in all studied crown group Trogoniformes (specimens of *Apaloderma* were not available for comparisons) (Fig. 2). In this latter, possibly plesiomorphic feature, the Belgian fossil is also distinguished from *Paratrogon gallicus* from the Lower Miocene of France (Milne-Edwards (1869–71: pl. 177). The tuberculum supracondylare ventrale is large as in *Trogon* and *Pharomachrus*, whereas it is proximodistally less elongate in *Harpactes*.

IRSNB Av 123 is tentatively assigned to *Primotrogon*, which is the only trogoniform taxon from the Lower Oligocene of Europe that has been named (Mayr 1999, 2001, 2005, 2009b). It is larger than an Early Oligocene trogon fossil from the German locality Frauenweiler (the distal width of the humerus of SMF Av 498, described by Mayr 2005, is only 4.7 mm), but corresponds well in size with *Primotrogon wintersteini* from the Early Oligocene of the Luberon in southern France (the distal width of SMF Av 423, described by Mayr 2001, is 6.1 mm).

**Upupiformes sensu Mayr (2000)**

**Upupiformes gen. et sp. indet.**
(Fig. 2E, F)

**Referred specimen:** IRSNB Av 124 (distal right humerus; IG 17702).

**Locality and horizon:** Steendorp; Early Oligocene, between 30.5 and 31.5 Ma (lower part of the Boom Formation, Rupel Group, middle Rupelian).

**Measurements:** Length as preserved, 15.9; distal width, 6.3.

**Remarks:** This specimen is identified as an upupiform bird by the shape of the small condylus dorsalis, which is proximodistally low and oriented at a very oblique angle towards the longitudinal humerus axis, and by the protruding epicondylus dorsalis. In these features it differs from the humerus of the otherwise similar coraciiform Geranopteridae (Mayr & Mourer-Chauviré 2000). The tuberculum supracondylare dorsale is low but distinct. There is a marked depression on the cranial surface of the condylus ventralis. This depression is less marked in crown group Upupiformes, but present in middle Eocene stem group representatives (Mayr 1998: fig. 10A–C). The tuberculum supracondylare ventrale is situated far distally, with its proximal margin being on a level with the proximal margin of the condylus dorsalis. The processus flexorius is not protruding distally and somewhat shorter than in crown group Upupiformes (Fig. 2G); again the shape of this process is more similar to middle Eocene stem group Upupiformes (Fig. 2D; Mayr 1998: fig. 10A–C) than to the extant representatives. The fossa brachialis is shallow and ventrally situated.

Stem group representatives of Upupiformes are already known from the Early Eocene of Europe and were classified in the extinct taxon Messelirrisoridae (Mayr 1998, 2009b). Upupiform birds have not yet been described from lower Oligocene localities, but there exist fossils from the Luberon (southern France) in private collections (Mayr 2009b). An undescribed upupiform species occurs also in the Late Eocene of the Quercy fissure fillings (Mourer-Chauviré 2006). Two upupiform species of the taxon *Laurillardia* were further reported from the Late Eocene of the Paris Basin in France (Mayr 1998, 2009b), but the very poor preservation of the fossils does not allow for closer comparisons with IRSNB Av 124. The latter is slightly larger than the Early Miocene *Phirriculus pinicola* (distal width of humerus 6.3 mm versus 4.9–5.2 mm; Mlíkovský & Göhlich 2000), from which it further differs in the less strongly distally protruding processus flexorius. The small size of IRSNB Av 124, as well as its close similarity to the humerus of messelirrisorids (Fig. 2D), suggest that the fossil is from a stem group representative of Upupiformes.

**?Phaethontiformes Christidis & Boles, 2008**

**?Phaethontiformes gen. et sp. indet.**
(Fig. 3A, B)

**Referred specimen:** IRSNB Av 125 (right femur; collection Hasse IG 20664, found in 1904).

**Locality and horizon:** Niel-Boom; Early Oligocene, between 30.5 and 31.5 Ma (lower part of the Boom Formation, Rupel Group, middle Rupelian).

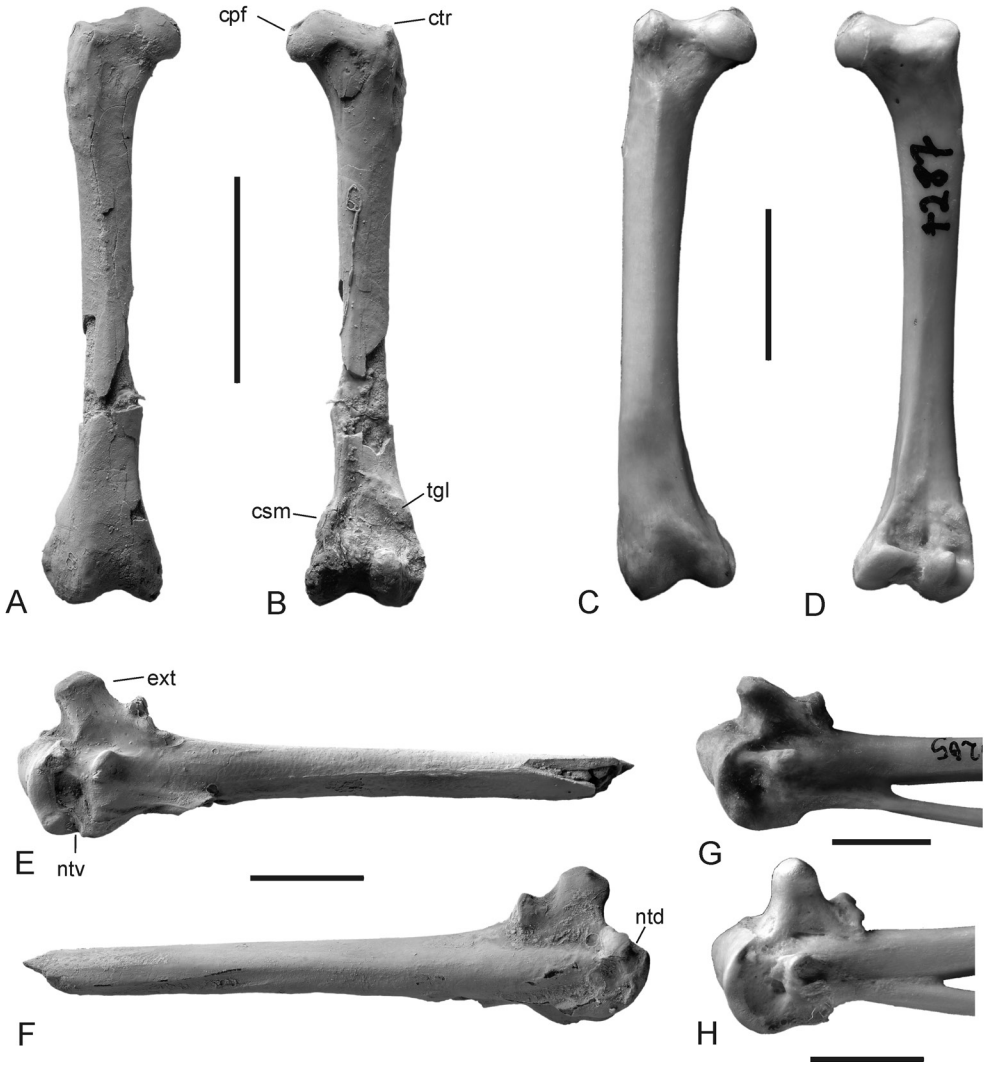


**FIGURE 3.** ?Phaethontiformes and ?Threskiornithidae from the Rupelian of Belgium. **A**, **B**, ?Phaethontiformes, gen. et sp. indet., right femur (IRSNB Av 125) in cranial (**A**) and caudal (**B**) view, in comparison to **C**, **D**, the right femur of the Red-tailed Tropicbird, *Phaethon rubricauda*, in cranial (**C**) and caudal (**D**) view. **E**, **F**, ?Threskiornithidae, gen. et sp. indet., proximal portion of left carpometacarpus (IRSNB Av 126) in ventral (**E**) and dorsal (**F**) view, in comparison to the left carpometacarpus of **G**, the Northern Bald Ibis, *Geronticus eremita*, and **H**, an immature Madagascar Ibis, *Lophotibis cristata*. Abbreviations: cpf, caput femoris; csm, crista supracondylaris medialis; ctr, crista trochanteris; ext, processus extensorius; ntd, notch in dorsal portion of trochlea carpalis; ntv, notch in ventral portion of trochlea carpalis; tgl, tuberculum musculi gastrocnemialis lateralis. Fossil bones were coated with ammonium chloride. Scale bars equal 10 mm.

**Measurements:** Length, 29.0; proximal width, 6.2; distal width, 5.9.

**Remarks:** This femur exhibits a characteristic morphology in that the caput femoris is proximomedially directed, *i.e.*, oriented obliquely to the shaft and not perpendicular as in most other birds. The facies articularis acetabularis is large and globular. The crista trochanteris is very low in proximal direction, but distally continuous with a ridge along the craniolateral margin of the bone. The shaft of the bone is straight and the distal end narrow. At the beginning of its distal third, the bone is broken in two pieces, which were glued together at a slightly inaccurate angle. The crista supracondylaris medialis on the distal end is well-developed (Fig. 3B). The tuberculum musculi gastrocnemialis lateralis is moderately developed, the sulcus patellaris is shallow and wide.

A similar femur morphology is found in some pelecaniform birds, of which only the femora of Phaethontidae are, however, as small as the fossil one, with IRSNB Av 125 being slightly smaller than the femur of the extant White-tailed Tropicbird, *Phaethon lepturus*, which in the one individual available to us measures 32.1 mm. Despite a similar overall morphology, the fossil differs, however, from extant Phaethontidae in the more proximomedially directed caput femoris, the less proximally projecting crista trochanteris, and the more marked fossa poplitea.

The earliest fossils assigned to Phaethontiformes belong to the Prophaethontidae, which occur in the Late Paleocene of Maryland (USA; Olson 1994) and Kazakhstan (Bourdon *et al.* 2008), the Early Eocene of England (Harrison & Walker 1976a) and Morocco (Bourdon *et al.* 2008a), and the Middle Eocene of Belgium (Mayr & Smith 2002a). The earliest unambiguous fossil record of true Phaethontidae dates from the Miocene, with *Heliadornis ashbyi* having been reported from the middle Miocene of Maryland (USA) and Belgium (Olson 1985, Olson & Walker 1997), and *H. paratethydicus* from the Late Miocene of Austria (Mlíkovský 1997). Another record of putative Phaethontidae, *Phaethusavis pelagicus* from the Early Eocene of Morocco (Bourdon *et al.* 2008b), needs confirmation of its affinities within Phaethontiformes by more material (Mayr 2009b).

Among the fossil species, the femur is only known from the prophaethontid *Lithoptila abdounensis* (Bourdon *et al.* 2008a: fig. 2). In this species the crista trochanterica is as low as in IRSNB Av 125, but the caput femoris is not proximally directed, the distal end more medially inflected, the condylus medialis larger, and the crista supracondylaris medialis more prominent.

**?"Ciconiiformes" sensu Christidis & Boles (2008)**
**?Threskiornithidae Richmond, 1917**

**?Threskiornithidae gen. et sp. indet.**
(Fig. 3E, F)

**Referred specimen:** IRSNB Av 126 (proximal portion of left carpometacarpus; collection Hasse IG 20664).

**Locality and horizon:** Steendorp; Early Oligocene, between 30.5 and 31.5 Ma (lower part of the Boom Formation, Rupel Group, middle Rupelian).

**Measurements:** Length as preserved, 54.8; estimated total length, ~65; proximal width, 14.5.

**Remarks:** This fossil is from a medium-sized bird and, compared to extant taxa, most similar to the carpometacarpus of Threskiornithidae (ibises). The bone is characterized by a distinct notch in the caudal rim of the ventral portion of the trochlea carpalis, and another notch in the proximocranial rim of the dorsal portion of this trochlea (Fig. 3E, F). In these features it differs from extant Threskiornithidae and other taxa with a similar carpometacarpus shape. The processus extensorius is straight and protrudes perpendicular to the long axis of the bone; in most extant Threskiornithidae it is lower and with a more proximally directed tip (Fig. 3G), but a similar shape of the processus extensorius is found in the Madagascar Ibis, *Lophotibis cristata* (Fig. 3H).

In the Paleogene of Europe, Threskiornithidae were reported from the Early Oligocene of the Luberon in France (Roux 2002) and the Late Eocene of England (Harrison & Walker 1976b), but meaningful comparisons with the Belgian fossil are not possible because the carpometacarpus is either poorly preserved (in the case of the Luberon fossil) or unknown (in the case of the Late Eocene *Actiornis anglicus*).

## Discussion

By adding six new species to the seven previously described ones, the present study almost doubles the number of bird species known from the Rupelian stratotype (Table 1). Mayr (2009a) already commented on biogeographic affinities between the Rupelmonde avifauna and those of other Lower Oligocene localities in Europe, and Table 2 provides an updated overview of some taxa and localities. In Belgium, Early Oligocene avifaunas are also known from Hoogbutsel and Boutersem, some 60 km southeast of the Rupelmonde area. The fluvio-lacustrine deposits of these fossil sites yielded several taxa so far unknown from the Boom Formation, including duck-like Anseriformes, Charadriiformes, Ral-

lidae, Picidae, and Coliiformes (Mayr & Smith 2001, 2002b). In part this probably reflects different palaeohabitats (marine versus fluviolacustrine) and depositional environments, but a collection bias towards larger fossils may have also contributed to the scarcity of very small bird remains in the Rupelmonde avifauna.

Diomedeoidid Procellariiformes and other aquatic birds that occur in the Boom Formation were widespread in the Rupelian epicontinental sea system, which covered Europe in the Early Oligocene (Mayr 2009b). Some of the terrestrial taxa also appear to have had a wide distribution across Europe, and the newly reported fossils add Paraortygidae and Trogoniformes to those avian groups, which are also known from Lower Oligocene localities in southern Europe.

As detailed above, the sternum of *Paraortyx* lacks a spina interna. A spina interna is likewise absent in the Early Eocene Gallinuloididae (Mayr 2006: fig. 3a, 2009b), which further differ from crown group Galliformes in a much more robust furcula and a more cranially prominent apex of the carina sterni. These differences in the morphology of the pectoral girdle bones were ascribed to the presence of a large crop in crown group Galliformes, which, through the shift of the center of gravity and the caudal displacement of the pectoral muscles, led to modifications in the morphology of the pectoral girdle bones (Stegmann 1964; Mayr 2006). The plesiomorphic sternum morphology found in *Paraortyx* indicates that a large crop, one of the key innovations of crown group Galliformes, was not developed in Paraortygidae, and these birds were thus probably not yet adapted to regular processing of very coarse and dry plant matter (Mayr 2006).

Trogons are predominantly frugivorous or insectivorous birds with poor migration capabilities and are today only found in subtropical and tropical regions. However, these birds had a long evolutionary history in Europe (Mayr 2009b), and in the Early Eocene they even occurred in the northern part of Denmark (Fig. 4A; Kristoffersen 2002). The Belgian fossil reported here is the so far northernmost occurrence of trogons in post-Eocene deposits (Fig. 4A), and indicates the presence of forests or at least woodlands in the

**TABLE 1.** List of avian taxa reported from the Rupelian of the Boom Formation

| Order | Family | Species | References |
|---|---|---|---|
| ?Anseriformes | family inc. sed. | *Cygnopterus affinis* | Lambrecht (1931) |
| Procellariiformes | Diomedeidae | *Tydea septentrionalis* | Mayr & Smith (2012b) |
| | Diomedeoididae | *Rupelornis definitus* (incl. *Vanellus selysii* van Beneden, 1871) | Mayr, 2009b; Mayr & Smith (2012a) |
| Gaviiformes | Gaviidae | "*Anas*" *benedeni* (= *Anas creccoides* van Beneden, 1871) | Mayr (2009a); this study |
| Galliformes | Paraortygidae | *Paraortyx* cf. *lorteti* | this study |
| | | *Paraortyx brancoi* | this study |
| | | cf. *Pirortyx major* | this study |
| "Gruiformes" | Parvigruidae | cf. *Parvigrus pohli* | Mayr (2013) |
| | | *Rupelrallus* (?) *belgicus* | Mayr (2013) |
| Strigiformes | Selenornithidae | *Selenornis steendorpensis* | Mayr (2009a) |
| Trogoniformes | Trogonidae | ?*Primotrogon* sp. | this study |
| Upupiformes | family inc. sed. | gen. et sp. indet. | this study |
| ?Phaethontiformes | family inc. sed. | gen. et sp. indet. | this study |
| ?"Ciconiiformes" | ?Threskiornithidae | gen. et sp. indet. | this study |
| **species of doubtful affinities** | | | |
| order inc. sed. | family inc. sed. | "*Puffinus*" ("*Larus*") *raemdonckii* | van Beneden (1871) |
| order inc. sed. | family inc. sed. | "*Fulica*" *dejardinii* | van Beneden (1871) |

palaeoenvironment of the Boom Formation.

We finally comment on the affinities of "*Anas*" *benedeni* Sharpe, 1899, a species originally described by van Beneden (1871) under the preoccupied name "*Anas creccoides*". The original material assigned to "*A.*" *benedeni* includes a humerus lacking the proximal end, a proximal humerus, and two proximal ulnae. Brodkorb (1962) removed the species from Anseriformes, considering its affinities uncertain and designating the more complete humerus as the lectotype. Whereas other material referred to "*A. creccoides*" by van Beneden (1871) belongs to the procellariiform Diomedeoididae (Mayr 2009b; Mayr & Smith 2012a), the lectotype humerus closely resembles a humerus of a gaviiform bird from the Boom Clay, which was assigned by Mayr (2009a) to *Colymboides* (?) *metzleri*, a species originally described from the Early Oligocene Rhine Graben locality Frauenweiler (Mayr 2004) (Fig. 4B, C). Based on the published figure of the lectotype humerus, we consider it most likely that "*Anas*" *benedeni* is a gaviiform bird. However, because the condylus dorsalis shows slight differences to *Colymboides* (?) *metzleri* in size and orientation (Fig. 4B, C), we refrain from any taxonomic action until the "*Anas*" *benedeni* lectotype, which is not in the collection of IRSNB, is located.

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**TABLE 2.** Comparison of the Rupelmonde avifauna with other early Oligocene (MP 21–23) European localities (after Mayr 2009b and references listed in the reference list); entries for the middle Eocene to late Oligocene Quercy fissure fillings include only records with a proven early Oligocene age (after Mourer-Chauviré 2006).

| | Belgium | | Germany | | France | |
|---|---|---|---|---|---|---|
| | Rupelmonde | Boutersem/ Hoogbutsel | Weißelster Basin | Frauenweiler | Luberon | Quercy |
| Paraortygidae | + | – | + | – | – | + |
| Diomedeidae | + | – | – | – | – | – |
| Diomedeoididae | + | – | + | + | – | – |
| Gaviiformes | + | + | – | + | – | – |
| Parvigruidae | + | – | + | – | + | – |
| Selenornithidae | + | – | – | – | – | + |
| Upupiformes | + | – | – | – | +[b] | – |
| Trogoniformes | + | – | – | + | + | – |
| Pelecanidae | – | – | – | – | + | – |
| Phalacrocoracidae | – | – | – | – | +[b] | – |
| Anatidae | – | + | – | – | – | – |
| Charadriiformes | – | + | – | + | + | – |
| Rallidae | – | + | – | – | – | – |
| Idiornithidae | – | ?[a] | – | – | – | + |
| Archaeotrogonidae | – | – | – | – | – | + |
| Coliiformes | – | + | – | + | – | – |
| Todidae | – | – | – | + | – | + |
| Sylphornithidae | – | + | – | – | – | – |
| Piciformes | – | + | – | + | – | – |
| Passeriformes | – | – | – | + | + | – |

[a] a fragmentary distal tarsometatarsus was tentatively identified by Mayr & Smith (2001)

[b] unpublished fossils in private collections (Mayr 2009b)

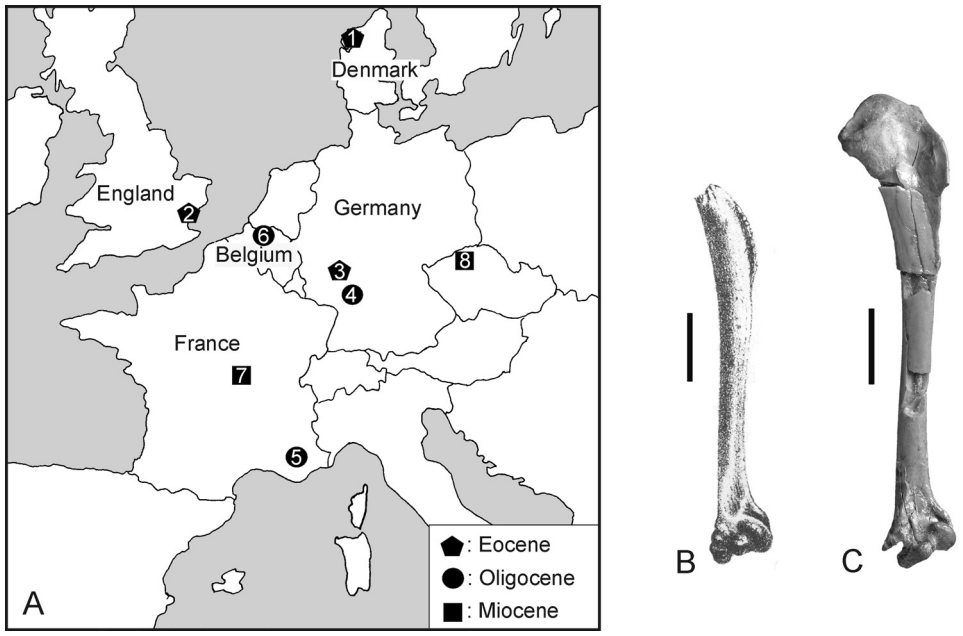


**FIGURE 4. A**, Map of Central Europe with localities where fossil Trogoniformes were found (after Mlíkovský 2002; Mayr 2009b, 2011): 1 – Fur Formation, Denmark (Early Eocene); 2 – London Clay (Clacton-on-Sea), England (Early Eocene); 3 – Messel, Germany (Middle Eocene); 4 – Frauenweiler, Germany (Early Oligocene); 5 – Luberon, France (Early Oligocene); 6 – Steendorp, Belgium (Early Oligocene); 7 – Saint-Gérand-le-Puy, France (Early Miocene); 8 – Dolnice, Czech Republic (Early Miocene; undescribed record mentioned by Mlíkovský 2002: 227). **B**, **C**, Humeri of loons (Gaviiformes) from the Boom Formation. **B**, lectotype of *Anas benedeni* Sharpe, 1899 (from van Beneden 1871: fig. 3). **C**, right humerus (reversed as to appear from the left side to facilitate comparison) from the Rupelian of Niel-Boom (IRSNB Av 85), which was assigned to *Colymboides* (?) *metzleri* by Mayr (2009a). Scale bar in B and C equals 10 mm; scale for *A. benedeni* based on the assumption that figures in van Beneden (1871) represent the natural size of the bones.

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