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BONY-TOOTHED BIRDS (AVES: PELAGORNITHIDAE) FROM THE MIDDLE EOCENE OF BELGIUM

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Abstract: We describe well-preserved remains of the Pelagornithidae (bony-toothed birds) from the middle Eocene of Belgium, including a sternum, pectoral girdle bones and humeri of a single individual. The specimens are tentatively assigned to *Macrodontopteryx oweni* Harrison and Walker, 1976, which has so far only been known from the holotype skull and a referred proximal ulna. Another species, about two times larger, is represented by an incomplete humerus and tentatively identified as *Dasornis emuinus* (Bowerbank, 1854). The fossils provide critical new data on the osteology of the pectoral girdle of bony-toothed birds. For the first time, the sternum of one of the smaller species is preserved, and this bone exhibits a more plesiomorphic morphology than the recently described sternum of the giant Miocene taxon *Pelagornis*. The coracoid resembles that of the Diomedeidae (albatrosses) in overall morphology, but because bony-toothed birds lack apomorphies of the Procellariiformes, the similarities are almost certainly owing to convergence. Bony-toothed birds were often compared with the 'Pelecaniformes' by previous authors, who especially made comparisons with the Sulidae (gannets and boobies). However, the coracoid distinctly differs from that of extant 'pelecaniform' birds, and the plesiomorphic presence of a foramen nervi supracoracoidei as well as the absence of a well-delimited articulation facet for the furcula supports a position outside the Suloidea, the clade to which the Sulidae belong.

Key words: Fossil birds, *Macrodontopteryx*, *Dasornis*, Brussels Formation.

THE Pelagornithidae (bony-toothed birds) were most unusual marine birds, whose beak exhibits spiny osseous projections along the tomia. They occur in late Palaeocene to Pliocene deposits (about 58–2.5 million years ago) and had already achieved a global distribution in the Eocene (Olson 1985; Mayr 2009). Medium-sized to large species coexisted in the early Palaeogene, but only very large ones, with wingspans above four metres, are known from Neogene deposits. The phylogenetic relationships of bony-toothed birds are debated. Whereas earlier authors assumed affinities to the Procellariiformes (tubenoses) and 'Pelecaniformes' (pelicans, cormorants and allies), they were hypothesised to be most closely related to the Anseriformes (waterfowl) by Bourdon (2005).

Well-preserved bones of bony-toothed birds were reported by Bourdon (2005, 2006) from late Palaeocene/early Eocene sediments in Morocco, but detailed descriptions of these specimens have yet to be published. A mandible fragment from the late Paleocene of England was described as *Pseudodontornis tenuirostris* by Harrison (1985), and another mandible fragment of a bony-toothed bird from the late Palaeocene of Kazakhstan constitutes the holotype of *P. tshulensis* (Averianov *et al.* 1991). Three pelagornithid species can be distinguished in the early Eocene deposits of the London Clay Formation in England and are likewise mainly represented by cranial material, i.e. *Odontopteryx toliapica* Owen, 1873, *Macrodontopteryx oweni* Harrison and Walker, 1976, and the very large *Dasornis emuinus* (Bowerbank, 1854), which reached about twice the size of *O. toliapica* (Mayr 2008*a*, 2009). Postcranial elements of *O. toliapica* include the proximal end of an ulna and the proximal end of a tarsometatarsus (the holotype of the alleged procellariiform bird *Neptuniavis minor* Harrison and Walker, 1977; see Mayr *et al.* 2002; Bourdon 2006). Bones so far known of *D. emuinus* are distal humeri, the proximal end of an ulna and the distal and proximal ends of the tarsometatarsus (the latter bones were described as '*Neptuniavis miranda*' by Harrison and Walker 1977; see Mayr *et al.* 2002). The only postcranial bones that were assigned to *M. oweni* are a tentatively referred proximal end of an ulna from the type locality and a distal radius from the early Oligocene of England, which cannot be reliably identified without further material (Harrison and Walker 1977, 1979).

Although most of the named pre-Oligocene pelagornithid species come from the London Clay Formation, remains of these birds have also been found in Eocene

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deposits of other parts of the world. Some incomplete bones were identified in the early Eocene of Virginia (Olson 1999), and from the middle Eocene of Mexico González-Barba *et al.* (2002) reported a distal humerus of *Odontopteryx* sp. Fragmentary wing bones of *Dasornis* (‘*Argillornis*’) stem from the late Eocene of Oregon (Goedert 1989). From the middle Eocene of Nigeria, a partial sternum of a very large, *Dasornis*-sized species was described as *Gigantornis eaglesomei*, and as yet undescribed bony-toothed birds occurred in the middle Eocene of Togo (Harrison and Walker 1976; Bourdon 2006). A few remains of these birds were also discovered in middle and late Eocene deposits of the Antarctic region (Stilwell *et al.* 1998; Tambussi and Acosta Hospitaleche 2007).

Here, we describe pelagornithid fossils from the lower part of the middle Eocene of Belgium, including well-preserved wing and pectoral girdle elements of a single individual. Although these were already found in the late 19th/early 20th century and are among the most substantial Eocene records of the group, only one of the fossils has been briefly mentioned so far in the literature (Dollo 1909). Cranial remains are not preserved, but the bones are readily assigned to bony-toothed birds because of their large size, thin-walled bones and characteristic derived morphology. The fossils provide new data on the poorly known postcranial osteology of bony-toothed birds and add to our knowledge of the Paleogene avifauna of Belgium (Cheneval 1996; Mayr and Smith 2002).

MATERIAL AND METHODS

Osteological terminology follows Baumel and Witmer (1993). Measurements are in millimetres.

Institutional abbreviation. IRSNB, Institut royal des Sciences naturelles de Belgique, Belgium.

SYSTEMATIC PALAEONTOLOGY

AVES Linnaeus, 1758

PELAGORNITHIDAE Fürbringer, 1888

?MACRODONTOPTERYX Harrison and Walker, 1976

cf. *Macrodontopteryx oweni* Harrison and Walker, 1976
Text-figures 2–6

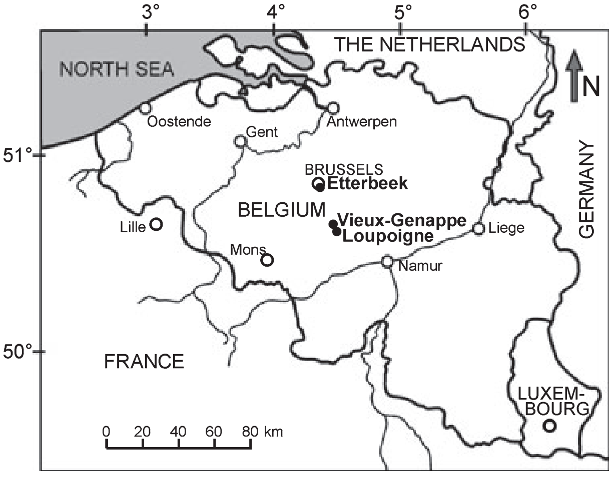
Referred specimens. IRSNB Av 86 (at least four incomplete thoracic vertebrae, two rib fragments, substantial portions of both humeri, a fragment of the proximal right ulna, a left coracoid and scapula, an incomplete furcula and sternum and a proximal end of a left tarsometatarsus); purchased in February 1913 from Emile Wauthier. IRSNB Av 87 (incomplete right humerus); Couturieaux collection, received in March 1894.

Locality. IRSNB Av 86: Vieux-Genappe, Belgium; IRSNB Av 87: Loupoigne, Belgium (Text-fig. 1).

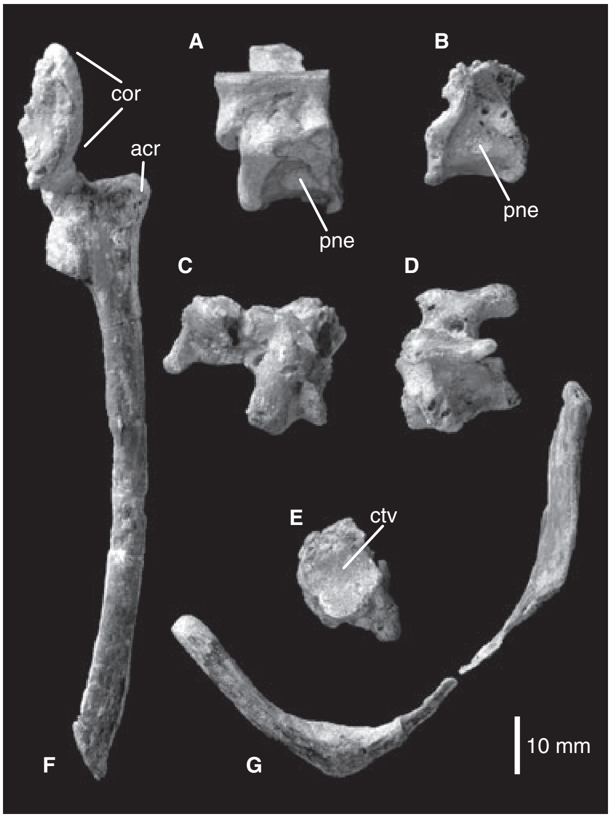
Horizon. Middle Eocene, lower Lutetian (Brussels Formation; see de Geyter *et al.* 2006).

Measurements. IRSNB Av 86: Coracoid, length from tip of processus acrocoracoideus to angulus medialis, 61.6; width of extremitas sternalis (angulus medialis to tip of processus lateralis), 55.8. Sternum, length of corpus, *c.* 159. Left humerus, length of large fragment, 274.8; length of small fragment, 57.4; estimated total length, *c.* 335; proximal width (tuberculum dorsale to tuberculum ventrale), 40.4; distal width, 28.3. Ulna, maximum diameter of cotyla ventralis, *c.* 11.8. Tarsometatarsus, proximal width, 17.7. IRSNB Av 87: Length as preserved, 283.

Remarks. The fossils can be assigned to the Pelagornithidae because of the derived morphology of the humerus, which has a craniocaudally narrow proximal end, a caput humeri that is markedly protuberant on the cranial surface of the bone and a weakly protruding tuberculum ventrale. The Belgian species represents a medium-sized pelagornithid, which was much smaller than *Dasornis emuinus*. The bones are larger than those of *Odontopteryx toliapica*, with the distal width of the humerus of IRSNB Av 86 being 28.3 mm vs 23–27.5 mm (Bourdon 2006, p. 27), and the proximal width of the tarsometatarsus 17.7 mm vs 15 (Bourdon 2006, p. 29) and 14.7 mm (Harrison and Walker 1977, p. 11 for ‘*Neptuniavis minor*’), respectively. The only postcranial element that was tentatively referred to *Macrodontopteryx oweni* is a proximal ulna (Harrison and Walker 1976). This bone is very fragmentary in IRSNB Av 86, but judging from the



TEXT-FIG. 1. Map of Belgium with the three localities (bold type) to show where pelagornithid remains have been found.



TEXT-FIG. 2. Skeletal elements of cf. *Macrodontopteryx oweni* Harrison and Walker, 1976 from the middle Eocene of Vieux-Genappe (IRSNB Av 86). A, B, thoracic vertebrae in right dorsolateral (A) and left lateral (B) view. C, D, cervicothoracic vertebra in dorsal (C) and left lateral (D) view. E, fragmentary proximal end of right ulna in cranial view. F, left scapula with attached portion of coracoid in lateral view. G, furcula in cranial view (note that the specimen consists of two portions that were assembled for the figure). Abbreviations: acr, acromion; cor, portion of coracoid; ctv, cotyla ventralis; and pne, pneumatic opening.

published figures (Harrison and Walker 1976, pl. 10D–H), its size matches that of the London Clay Formation specimen, with the dorsoventral width of the cotyla ventralis being *c.* 11.8 mm, vs about 12 mm in the London Clay Formation specimen. Because IRSNB Av 86 and IRSNB Av 87 are further of similar age and geographical provenance to the London Clay Formation fossils, they are here tentatively assigned to *M. oweni*. We note, however, that an unambiguous identification requires the discovery of more material, so much the more as morphological comparisons with *Pseudodontornis tshulensis* and *P. tenuirostris*, which are only known from mandible fragments, are not possible.

Description and comparisons. IRSNB Av 86 includes remains of at least four thoracic vertebrae, with the actual number being higher if four non-overlapping fragments belong to more than one vertebra. Two of these, which represent the caudalmost thoracic vertebrae, lack processus ventrales and have a mediolaterally narrow corpus, whose lateral surfaces bear pneumatic openings (Text-fig. 2). The articulation facets are poorly preserved but appear to have been only weakly heterocoelous. Another vertebra is identified as a cervicothoracic one; its corpus has a subrectangular cross section, with a flat ventral surface and concave lateral surfaces. The caudolateral angle of the processus transversus forms a caudally directing projection, the processus spinosus is short and knob-like; the processus ventralis is broken.

The only previously described coracoids of bony-toothed birds are two very fragmentary specimens of *Odontopteryx* that were reported by Bourdon (2005, 2006), and it is thus an especially fortunate circumstance that the left coracoid is almost complete in IRSNB Av 86. The bone is very unlike the coracoid of crown group Anseriformes, and except for the larger processus acrocoracoideus and other details described below, it has similar overall proportions to the coracoid of the procellariiform Diomedeidae (albatrosses; Text-fig. 3). The dorsal surface of the processus acrocoracoideus including most of the facies articularis humeralis is broken and still attached to the scapula. The facies articularis scapularis is also broken, and it cannot be determined whether it was cup-like. The long processus acrocoracoideus is markedly angled and bent ventrally; its tip is mediolaterally narrow but very wide in proximo-distal direction. The facies articularis clavicularis does not overhang the sulcus supracoracoidei but smoothly merges into this sulcus, which exhibits no pneumatic openings. In contrast to all extant ‘pelecaniform’ birds except the Phaethontidae (tropicbirds), the processus acrocoracoideus does not bear a well-delimited articulation facet for the facies articularis acrocoracoidea of the furcula (in the Fregatidae (frigatebirds) coracoid and furcula are fused). Contrary to the Diomedeidae, the processus procoracoideus is well developed and sharply angled ventrally; development of this process in the ‘Pelecaniformes’ is variable, being long in the Phaethontidae, Sulidae (boobies and gannets) and Pelecanidae (pelicans), but very short in the Phalacrocoracidae (cormorants) and Anhingidae (anhingas). As in procellariiform birds but unlike all ‘Pelecaniformes’ except the Phaethontidae and Pelecanidae, there is a small foramen nervi supracoracoidei (Text-fig. 3). The dorsal surface of the midsection of the shaft is slanting laterally. As in the Diomedeidae but contrary to ‘pelecaniform’ birds, the impressio musculi sternocoracoidei on the dorsal surface of the extremitas sternalis is markedly excavated; its bottom has an irregular surface and appears to have borne pneumatic openings. Also as in the Diomedeidae, the processus lateralis is very long, whereas this process is short in all ‘Pelecaniformes’. The facies interna of the crista articularis sternalis is well developed and very prominent as in, e.g. the Diomedeidae and some ‘pelecaniform’ birds (e.g. Pelecanidae and Sulidae). Although part of the sternal margin of the extremitas sternalis is broken, it can be discerned that there was a notch next to the crista articularis sternalis, whose lateral margin forms a marked step as in extant Diomedeidae (Text-fig. 3).

The scapula of IRSNB Av 86 (Text-fig. 2F) is long and slender but quite small compared to the size of the coracoid and humerus. The acromion is longer than that of the Diomedeidae but not as long as in the Pelecanidae and Suloidea. The facies articularis humeralis is large and convex. The caudal end of the bone is broken, and its medial surface completely covered with matrix.

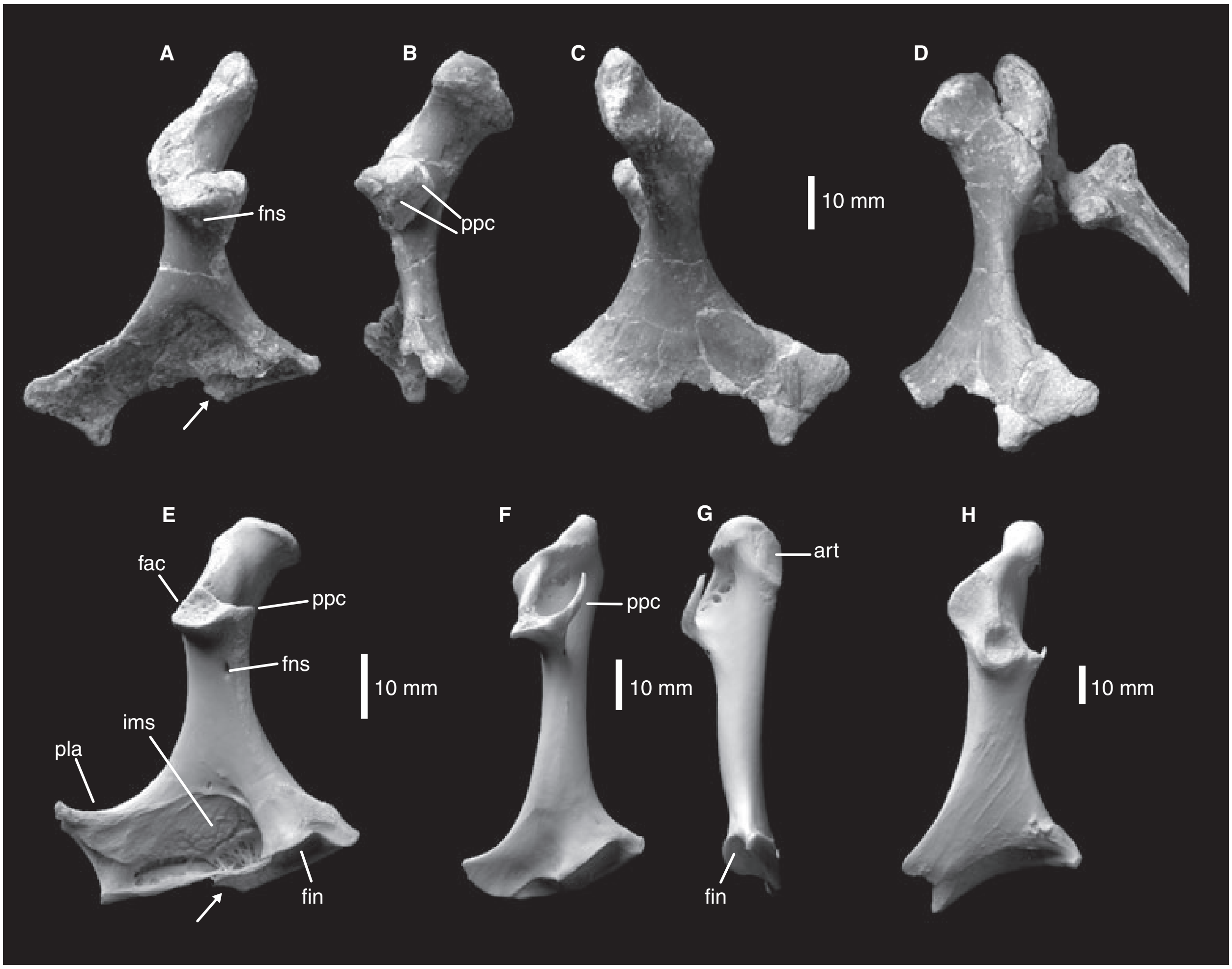
IRSNB Av 86 includes the extremitas sternalis of the widely U-shaped furcula, and a strap-like bone that we consider to be a portion of the left scapus claviculae (Text-fig. 2). If this interpretation is correct, the scapi claviculdarum were very wide and flat. The extremitas sternalis lacks an apophysis furculae; the extremitas omalis is not preserved.

The sternum has so far only been described for *Gigantornis* and the equally large Miocene *Pelagornis* (Mayr *et al.* 2008). IRSNB Av 86 for the first time allows its examination in one of the smaller pelagornithid species. The specimen is broken into three pieces that are reassembled in Text-figure 4. The carina and most of the left half of the corpus are preserved; the ventral surface of the bone (facies visceralis) is completely embedded in matrix. The carina is restricted to the cranial half of the sternum and proportionally lower and longer than that of *Gigantornis*. As in the latter, the strongly cranially protruding apex carinae bears a concave notch, which probably served as a bearing for the extremitas sternalis of the furcula (note that this notch is filled with sediment in the specimen). Also as in *Gigantornis*, the cranial margin of the carina bears a sharp ridge along its midline, and along its lateral surfaces there are lineae intermusculares. The corpus of the bone is elongate and narrow as in the Anseriformes and most 'Pelecaniformes', whereas it is shorter in the Procellariiformes. As in *Pelagornis*, the cranial portion of the corpus sterni of IRSNB Av 86 is markedly projecting, although it is proportionally somewhat wider in the Belgian fossil (compare Text-fig. 4 with Mayr *et al.* 2008, fig. 2). In *Gigantornis*, only a very small part of the corpus sterni is preserved, and meaningful comparisons are not possible. The labrum externum of the very long sulcus articularis coracoidei is reduced to a small lip-like projection (Text-fig. 4); the sulci articulares coracoidei do not cross in the midline of the sternum. Whether a spina externa was present as in *Gigantornis* and *Pelagornis* cannot be discerned, as the cranial tip of the bone is damaged. The processus craniolateralis is short and situated far caudally. The margo costalis is partly covered with matrix, so that the exact number of processus costales (probably four or five) cannot be counted; fragments of two sternal ribs are preserved in articulation. The caudal end of the corpus exhibits a moderately deep semicircular incision. Judging from its position and the general proportions of the preserved parts of the bone, there was only one such incision in each half of the sternum. The lateral margin of this incision bears a small caudomedially directing projection, which may represent a trabecula intermedia (Text-fig. 4). The trabecula mediana is short and has a straight end, the trabecula lateralis is broad and slightly curved. In *Pelagornis* (Mayr *et al.* 2008), there is a much deeper incision in the caudal margin of the sternum, and the trabecula lateralis is longer and straighter. In contrast to the sternum of *Pelagornis*, the corpus sterni of IRSNB Av 86 is further not strongly vaulted, and the carina sterni does not bear a marked cranial projection.

The very long and slender humeri exhibit the characteristic derived morphology of pelagornithid birds (Text-fig. 5). The proximal end is narrow and craniocaudally flat. The elongate caput humeri merges into the convex and almost hemispherical tuberculum dorsale; on the cranial surface of the bone, the caput humeri is markedly protuberant, which was considered an apomorphy of the Pelagornithidae by Bourdon (2005, caption of fig. 1). The tuberculum ventrale is only weakly protruding. The far distally situated crista deltopectoralis is well preserved in IRSNB Av 87 and has a rounded margin; its caudal surface is concave. The crista deltopectoralis of the Diomedeidae is proportionally shorter, more protruding and has a triangular outline (Text-fig. 5G), whereas it is much lower in the Suloidea. An elongated fossa on the caudal surface of the shaft of the left humerus of IRSNB Av 86, adjacent to the crista bicipitalis (Text-fig. 5A), probably represents a muscular attachment scar. The humerus shaft is slightly sigmoidally curved in dorsoventral view and its distal section is craniocaudally flattened and wide as in the Diomedeidae. The distal end of the bone resembles the distal humeri of *Odontopteryx* described by González-Barba *et al.* (2002) and Bourdon (2005, 2006). As in the Diomedeidae but in contrast to crown group Anseriformes, its ventral surface is markedly slanted cranioventrally and the processus flexorius very short. There is a marked ovate fossa next to the narrow tuberculum supracondylare ventrale and proximal of the condylus ventralis. The fossa musculi brachialis appears to have been shallow, but only small portions of it are visible on the damaged distal end of the left humerus of IRSNB Av 86. The large and globular condylus ventralis has a similar shape to that of the Sulidae. The proximal end of the small condylus dorsalis is rounded, and the incisura intercondylaris is shallow. In both humeri of IRSNB Av 86, the dorsal portion of the distal end is damaged, but it can still be seen that the dorsal margin of the shaft is narrow and ridge-like just before the distal end of the bone.

The fragment of the proximal end of the right ulna of IRSNB Av 86 (Text-fig. 2E) has a shallow cotyla ventralis and lacks a well-delimited tuberculum ligamenti collateralis ventralis. The cotyla dorsalis and the olecranon are broken.

The proximal end of the left tarsometatarsus of IRSNB Av 86 (Text-fig. 6) corresponds well in its morphology with the tarsometatarsi that were referred to the allegedly procellariiform taxon *Neptuniavis* by Harrison and Walker (1977). It is larger than the proximal tarsometatarsus of *Odontopteryx toliapica* ('*Neptuniavis minor*'), but much smaller than that of *Dasornis emuinus* ('*N. miranda*'). Although the cotylae are covered by hard matrix, it can be discerned that the cotyla lateralis is slanting dorsally. The fossa infracotylaris dorsalis is very deep and also partly filled with matrix. Only the large lateral foramen vasculare proximale is visible. The prominent tuberositas musculi tibialis cranialis is bipartite; next to its medial portion there is a sharp ridge, which borders a well-marked, narrow sulcus, presumably for the tendon of musculus extensor digitorum longus (Text-fig. 6A). Matrix also adheres to the hypotarsus, but it is clearly visible that it did not enclose bony canals. The cristae medialis et lateralis hypotarsi are prominent, and the former is slightly wider than the latter. There are two hypotarsal sulci, which are separated by low crista intermedia (Text-fig. 6E); the medial sulcus, which presumably was for the tendon of musculus flexor digitorum longus, is deeper than the lateral one. Fossae parahypotarsales are absent. The hypotarsi of the London Clay Formation specimens are worn and



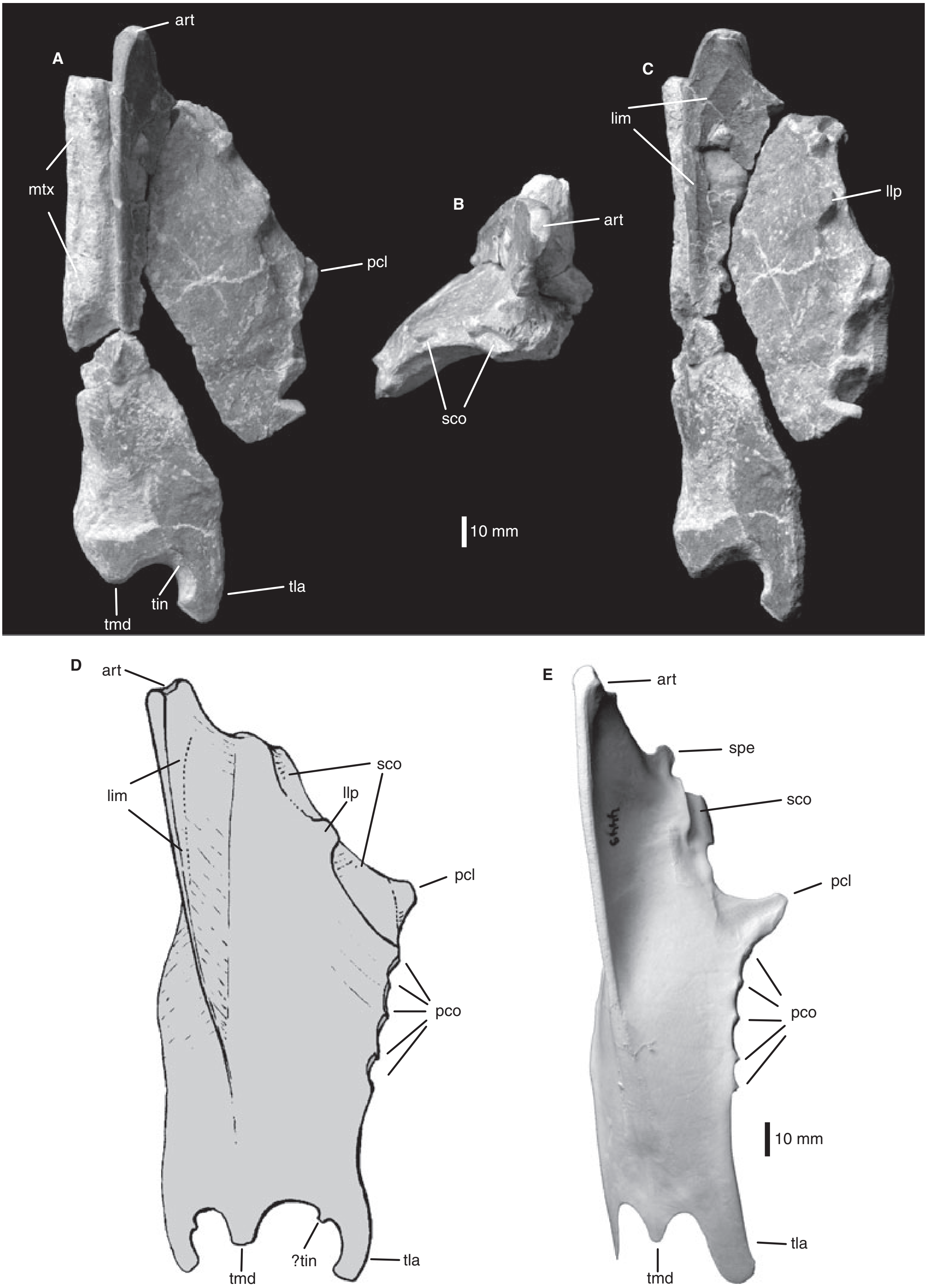
TEXT-FIG. 3. A–D, Left coracoid of cf. *Macrodontopteryx oweni* Harrison and Walker, 1976 from the middle Eocene of Vieux-Genappe (IRSNB Av 86). A, dorsal view. B, medial view. C, ventral view. D, ventrolateral view with scapula and attached portion of coracoid in articulation to show the size of the processus acrocoracoideus. E–G, Coracoids of extant birds for comparison. E, Black-browed Albatross, *Diomedea melanophris* (Diomedeidae). F, G, Northern Gannet, *Sula bassana* (Sulidae). H, Mute Swan, *Cygnus olor* (Anseriformes). Abbreviations: art, articulation facet for facies articularis acrocoracoidea of furcula; fac, facies articularis clavicularis; fin, facies interna of crista articularis sternalis; fns, foramen nervi supracoracoidei; ims, impressio musculi sternocoracoidei; pla, processus lateralis; and ppc, processus procoracoideus (surrounded by matrix in the fossil). The arrows indicate the step in the margin of the extremitas sternalis (see text). Same scale bars for A–D and F, G, respectively.

do not allow for close comparisons. The proximal tarsometatarsus of the *Odontopteryx* species described by Bourdon (2006, pl. 21G) from the late Palaeocene/early Eocene of Morocco differs from that of IRSNB Av 86 in the presence of a distinct sulcus lateral to the hypotarsus. The hypotarsus of IRSNB Av 86 is also distinguished from that of a very large pelagornithid from the late Miocene to early Pliocene of Chile (Walsh and Hume 2001), which encloses at least one bony canal. The hypotarsus of *Cyphornis magnus* Cope, 1894 from the early Miocene (Olson 1985) of British Columbia, Canada, is broken. Compared to the extant taxa that were considered closely related to the Pelagornithidae, the hypotarsus of IRSNB Av 86 resembles that of the Diomedeidae but has more protruding cristae (Text-fig. 6). The hypotarsus of anseriform birds has either four cristae (Anatidae) or only two, with a reduced lateral one (Anhimidae). The hypotarsus of the Suloidea encloses bony canals (Text-fig. 6). IRSNB Av 86 includes a piece of matrix that contains a bone that may be the distal end of the left tarsometatarsus but does not allow the recognition of any morphological details.

DASORNIS Owen, 1870

cf. *Dasornis emuinus* (Bowerbank, 1854)
Text-figure 7

1909 *Argillornis longipennis* Dollo, p. 111.
1933 *Argillornis longipennis* Lambrecht, p. 284.
1958 *Argillornis longipennis* Misonne, p. 9.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Referred specimen. IRSNB Av 88 (right humerus lacking distal end and crista bicipitalis).

Locality. Etterbeek near Brussels, Belgium (Text-fig. 1).

Horizon. Middle Eocene, lower Lutetian (Brussels Formation).

Measurements. Length as preserved, 465; estimated total length, *c.* 570.

Remarks. This specimen was mentioned by Dollo (1909, p. 111), Lambrecht (1933, p. 284), who incorrectly identified it as an ulna, and Misonne (1958, p. 9). It comes from a species that was much larger than *Odontopteryx toliapica* and *Macrodontopteryx oweni*, and is here tentatively referred to *Dasornis emuinus* because of its very large size, similar age and geographic provenance. No other similar-sized pelagornithids are known from the Eocene of Europe. The estimated width of the proximal end is about 60 mm, which is somewhat more than that of a proximal humerus of *D. emuinus* ('*Argillornis emuinus*') from the London Clay Formation, whose width is about 50 mm (Harrison and Walker 1976, pl. 6A–C). The species '*Argillornis longipennis*', as which IRSNB Av 88 was identified by earlier authors (Dollo 1909; Lambrecht 1933; Misonne 1958), was synonymised with *D. emuinus* by Mayr (2008*a*).

Owing to the fact that the bone is very fragmentary, only few morphological details are discernible. The most notable feature is a prominent tubercle on the cranial surface of the proximal end, on the level of the broken crista bicipitalis (Text-fig. 1A). This structure probably served for the insertion of the caput humerale of musculus biceps brachii and also occurs in the Miocene *Pelagornis miocaenus* (Harrison and Walker 1976, pl. 10B) but is absent in small Pelagornithidae (Bourdon 2006, pl. 7). Among extant birds, such a prominent tubercle is present in, e.g. the Diomedeidae and Pelecanidae, weakly developed in the Fregatidae, and absent in other 'pelecaniform' birds. The corresponding area of the known proximal humeri of the London Clay Formation specimens of *D. emuinus* is broken (Harrison and Walker 1976, pl. 6), but as far as comparisons are possible, these otherwise closely resemble IRSNB Av 88. The other features of the bone, e.g. the shape of the caput humeri and tuberculum dorsale, are as in the smaller pelagornithid species described earlier.

DISCUSSION

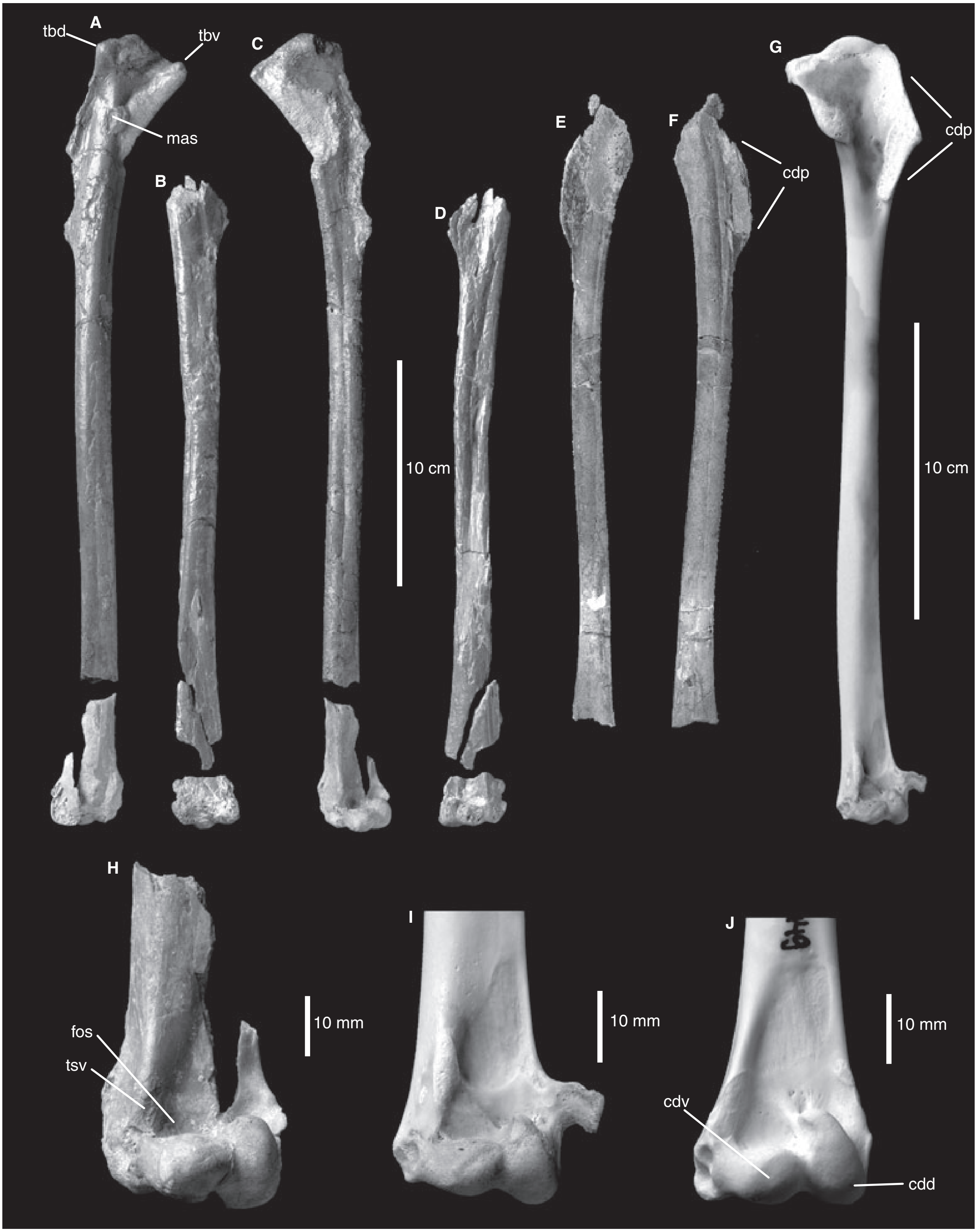
The fossils reported in the present study indicate that the diversity of bony-toothed birds was similar in the middle Eocene of Belgium and the early Eocene of England, with medium-sized and very large species coexisting in the same area. The humerus of the smaller species of the Belgian Pelagornithidae (cf. *Macrodontopteryx oweni*) is about 1.3 times longer than that of the Black-browed Albatross (*Diomedea melanophris*), which has a humerus length of about 265 mm and a wingspan of 240 cm (Carboneras 1992). Because the feathering of the fossil species is unknown, its exact wingspan cannot be determined, but it was certainly more than in *D. melanophris*. The larger species (cf. *Dasornis emuinus*) was nearly twice as large and had a wingspan of more than four metres, thus being larger than any extant volant bird (see also Mayr 2008*a*).

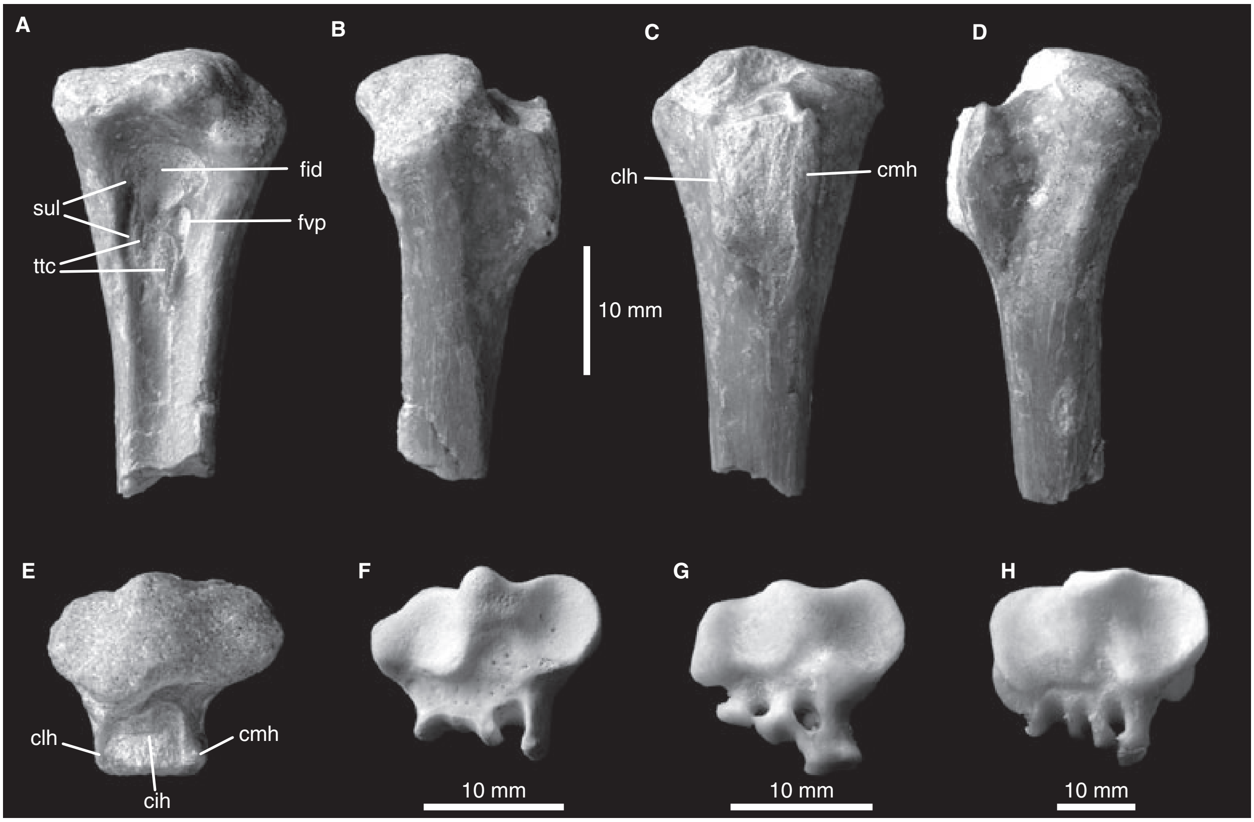
It is assumed that the very large Pelagornithidae, in which the proximal end of the humerus has a highly peculiar, derived morphology, were not capable of sustained flapping flight (Olson 1985). IRSNB Av 86 provides critical new data on the very poorly known pectoral girdle of the smaller bony-toothed birds. The sternum exhibits a more plesiomorphic morphology than that of the Miocene taxon *Pelagornis*, which reached a wingspan of five to six metres, and neither is the corpus strongly vaulted as in *Pelagornis* nor is there are marked cranial projection on the carina. There can be little doubt that these unusual features of *Pelagornis* are derived, and owing to the greater stresses the sternum is exposed to (Mayr *et al.* 2008). Compared to the *Dasornis*-sized *Gigantornis*, the sterna of IRSNB Av 86 and *Pelagornis* have a proportionally lower and longer carina sterni. The sternum thus differs in all three pelagornithid species of which this bone is known, and the high variability in sternal morphology indicates that these birds employed somewhat different flight techniques.

As noted in the introduction, the Pelagornithidae were mainly compared with the 'Pelecaniformes' and Procellariiformes by earlier authors (e.g. Howard 1957; Harrison and Walker 1976), whereas the only cladistic analysis, in which bony-toothed birds were included, resulted in a sister group relationship to the Anseriformes (Bourdon

TEXT-FIG. 4. A–C, Sternum of cf. *Macrodontopteryx oweni* Harrison and Walker, 1976 from the middle Eocene of Vieux-Genappe in Belgium (IRSNB Av 86; note that the specimen consists of three pieces that were assembled for the figure). A, ventrolateral view. B, cranial view. C, lateral view. D, schematic reconstruction in ventrolateral view. E, Sternum of the extant Northern Gannet, *Sula bassana* (Sulidae) for comparison. Abbreviations: art, articulation facet for furcula (filled with matrix in the fossil); lim, linea intermuscularis; llp, lip-like projection of labrum externum of sulcus articularis coracoidei; mtx, matrix; pcl, processus craniolateralis; pco, processus costales; sco, sulcus articularis coracoidei; spe, spina externa; tin, trabecula intermedia; tla, trabecula lateralis; and tmd, trabecula mediana. Same scale bar for A–C.

2005). A detailed character analysis is beyond the scope of the present study and would require the consideration of the abundant material reported by Bourdon (2006), but we also do not consider 'pelecaniform' or procellariiform affinities of the Pelagornithidae to have been convincingly established.

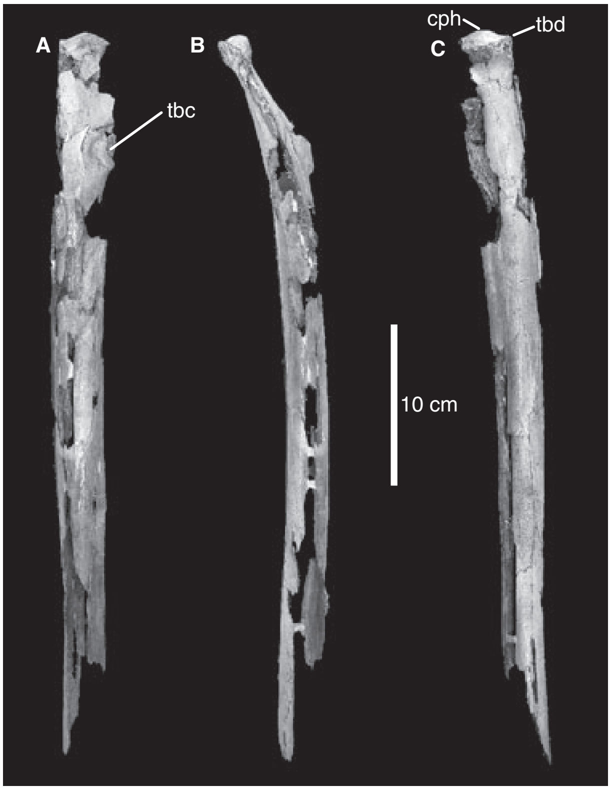




TEXT-FIG. 6. A–E, Proximal end of left tarsometatarsus of cf. *Macrodontopteryx oweni* Harrison and Walker, 1976 from the middle Eocene of Vieux-Genappe (IRSNB Av 86). A, dorsal view. B, lateral view. C, plantar view. D, medial view. E, proximal view. F–H, proximal tarsometatarsi of extant birds for comparison. F, Black-browed Albatross, *Diomedea melanophris* (Diomedeidae). G, Northern Gannet, *Sula bassana* (Sulidae). H, Mute Swan, *Cygnus olor* (Anseriformes). Abbreviations: cih, crista intermedia hypotarsi; clh, crista lateralis hypotarsi; cmh, crista medialis hypotarsi; fid, fossa infracotylaris dorsalis; fvp, lateral foramen vasculare proximale; sul, sulcus (presumably for tendon of musculus extensor digitorum longus); and ttc, tuberositas musculi tibialis cranialis. Note that the hypotarsus is filled with matrix in the fossil. Same scale bar for A–E.

Olson (1985) cited the position of the fossae glandulae nasales within the orbits as evidence for ‘pelecaniform’ affinities of bony-toothed birds. The nasal glands of neornithine birds are, however, primitively situated within the orbits, and their position on the dorsal surface of the cranium, as in procellariiform birds, is a derived trait (see Technau 1936). Molecular analyses congruently support polyphyly of the ‘Pelecaniformes’, which in traditional classifications include the Phaethontidae, Pelecanidae, Fregatidae, Sulidae, Anhingidae and Phalacrocoracidae (Ericson *et al.* 2006; Mayr 2008*b*; Hackett *et al.* 2008). Previous authors mainly compared bony-toothed birds with the Sulidae (Harrison and Walker 1976, p. 58; Olson and Rasmussen 2001, pl. 11), which are shown to be within a clade including the Fregatidae, Anhingidae and Phalacrocoracidae in the above studies. As evidenced by the new Belgian specimen, the coracoid of bony-toothed birds is very different from that of all ‘pelecaniform’ taxa. The plesiomorphic presence of a foramen nervi supracoracoidei and the absence of a derived articulation facet for the facies articularis acrocoracoidea of the furcula support a position of bony-toothed birds outside the Suloidea, i.e. the clade including the Fregatidae, Sulidae, Phalacrocoracidae and Anhingidae. In contrast to the representatives of this clade,

TEXT-FIG. 5. Humeri of cf. *Macrodontopteryx oweni* Harrison and Walker, 1976 from the middle Eocene of Belgium. A–D, left (A, C) and right (B, D) humeri of IRSNB Av 86 from Vieux-Genappe in caudal (A, B) and cranial (C, D) view. E, F, right humerus of IRSNB Av 87 from Loupoigne in cranial (E) and caudal (F) view. G, left humerus of the Black-browed Albatross, *Diomedea melanophris* (Diomedeidae). H–J, distal end of left humerus in comparison. H, IRSNB Av 86. I, *D. melanophris*. J, Northern Gannet, *Sula bassana* (Sulidae). Abbreviations: cdd, condylus dorsalis; cdp, crista deltopectoralis; cdv, condylus ventralis; fos, fossa (see text); mas, muscle attachment scar; tbd, tuberculum dorsale; tbv, tuberculum ventrale; and tsv, tuberculum supracondylare ventrale. Same scale bar for A–F.



TEXT-FIG. 7. Right humerus of cf. *Dasornis emuinus* (Bowerbank, 1854) from the middle Eocene of Etterbeek (IRSNB Av 88). A, cranial view. B, ventral view. C, caudal view. Abbreviation: cph, caput humeri; tbc, tubercle; and tbd, tuberculum dorsale.

the hypotarsus of at least the Eocene Pelagornithidae does not enclose bony canals, and the trochlea metatarsi II of the tarsometatarsus does not protrude farther distally than the other trochleae (see also Olson 1985, p. 199).

The coracoid of bony-toothed birds resembles that of the Diomedeidae in overall shape, but there are some distinct differences in detail (see description and Text-fig. 3). Albatrosses are shown to be nested within the Procellariiformes by recent analyses (e.g. Hackett *et al.* 2008). Because bony-toothed birds lack derived features of crown group Procellariiformes, most notably well-developed fossae glandulae nasales on the dorsal surface of the skull and strongly protruding cristae cnemiales of the tibiotarsus (Mayr 2003; Bourdon 2006), the similarities between these very large gliding birds most likely are because of convergence.

Bourdon (2005) listed 12 putative synapomorphies of the Pelagornithidae and Anseriformes, including a derived morphology of the rostropterygoid articulation and the presence of only two condyles on the processus mandibularis of the quadratum. In contrast to virtually all other recent analyses (e.g. Ericson *et al.* 2006; Livezey and Zusi 2007; Hackett *et al.* 2008), her study did, however, not result in a monophyletic Galloanseres, and it still has to be shown whether anseriform affinities of the Pelagornithidae are also maintained in analyses that support sister group relationship between Galliformes (landfowl) and Anseriformes.

The palatinum of bony-toothed birds lacks a well-developed crista ventralis (Mayr 2008*a*), which has been considered a derived characteristic of Neoaves, i.e. all neognathous birds except the Galloanseres, by Mickoleit (2004). This feature was, however, not identified as a neoavian apomorphy in the analysis of Livezey and Zusi (2007), and is also absent in few taxa within Neoaves, e.g. the Caprimulgidae (nightjars) and Nyctibiidae (potoos). The fronto-parietal suture of Palaeogene bony-toothed birds is further incompletely fused, a trait which is plesiomorphically present in Mesozoic non-Neornithes and some palaeognathous birds, but does not occur in the adults of neoavian taxa (although this suture fuses very late in the Spheniscidae (penguins); Elzanowski and Galton 1991; Milner and Walsh 2009). Certainly more data have to be gathered for a well-supported placement of bony-toothed birds outside Neoaves, whose sole unambiguous apomorphy remains the derived reduction of the phallus (Mayr 2008*b*). However, Milner and Walsh (2009, p. 211) also concluded from a study of the brain morphology of *Odontopteryx* that ‘the long anastomosis intercarotica and enclosure of the carotid rami (…) seem to provide some support for Bourdon’s (2005) hypothesis of a sister group relationship between Odontopterygiformes [=Pelagornithidae] and Anseriformes’, and that the ‘the mosaic of braincase characters (…) provides no clear evidence of a closer relationship with either Pelecaniformes or Procellariiformes’. It is to be hoped that future studies of little known aspects of the morphology of these fascinating birds provide further data that bear on their phylogenetic affinities.

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