

# Notes on the osteology and phylogenetic affinities of the Oligocene Diomedeoididae (Aves, Procellariiformes)

Gerald Mayr

Forschungsinstitut Senckenberg, Sektion Ornithologie, Senckenberganlage 25, 60325 Frankfurt am Main, Germany.  
E-mail: Gerald.Mayr@senckenberg.de

## Abstract

Received 16 September 2008

Accepted 10 October 2008

Published 3 August 2009

## Key Words

Fossil birds  
evolution

*Diomedeoides brodkorbi**Diomedeoides lipsiensis*

New specimens of the procellariiform taxon Diomedeoididae are reported from the early Oligocene (Rupelian) deposits of Wiesloch-Frauenweiler in southern Germany. Two skeletons belong to *Diomedeoides brodkorbi*, whereas isolated legs of larger individuals are tentatively assigned to *D. lipsiensis*, a species which has not yet been reported from the locality. The fossils allow the recognition of some previously unknown osteological features of the Diomedeoididae, including the presence of a vestige of the hallux. Diomedeoidids are characterized by extremely wide phalanges of the third and fourth toes, which also occur in some species of the extant procellariiform Oceanitinae (southern storm-petrels). The poorly developed processus supracondylaris dorsalis of the humerus supports a position of these Oligocene tubenoses outside a clade including the Diomedeidae (albatrosses), Procellariidae (shearwaters and allies), and Pelecanoididae (diving-petrels). It is hypothesized that like modern Oceanitinae, which have an equally short supracondylar process, diomedeoidids probably employed flap-gliding and used their immersed feet to remain stationary.

## Introduction

The Diomedeoididae are an extinct group of the Procellariiformes (tubenoses), which appears to have been widespread in the epicontinental seas covering parts of Europe in the Oligocene. A fair number of skeletons and isolated bones of these birds are known from Oligocene and early Miocene sediments of Central Europe (Cheneval 1995; Mayr et al. 2002; Fischer 2003). A record from early Oligocene deposits of Iran (Peters & Hamedani 2000) indicates that diomedeoidids were also part of the avifauna of the Paratethyan sea. Diomedeoidids are the only Paleogene procellariiform birds with a substantial fossil record, and three species have been named: the European *Diomedeoides brodkorbi* (Cheneval, 1995) and *D. lipsiensis* (Fischer, 1983), which mainly differ in size, and the Iranian *D. babaheydariensis* (Peters & Hamedani, 2000). The taxonomy of these birds is still in need of a revision, and the taxon name *Diomedeoides* Fischer, 1985 is likely to be a junior synonym of *Rupelornis* van Beneden, 1871, which was established for a diomedeoidid species from an early Oligocene locality in Belgium (Mayr et al. 2002).

Diomedeoidids are well characterized by their peculiar feet, whose phalanges, in particular those of the fourth toe, are greatly widened and flattened. To a striking extent, the foot morphology of these birds is paralleled by some species of the much smaller extant procellariiform Oceanitinae (southern storm-petrels), i.e., the Polynesian Storm-petrel *Nesofregetta fuliginosa* (Gmelin, 1789) (Oceanitinae; Mayr et al. 2002: fig. 5) and, to a lesser degree, the species of the taxon *Fregetta* and the White-faced Storm-petrel *Pelagodroma marina* (Latham, 1790). The pedal phalanges of other Oceanitinae are of usual proportions, but these have also very long legs as *Diomedeoides* and other southern storm-petrels. As detailed by Mayr et al. (2002), diomedeoidids lack derived features, which are shared by extant Oceanitinae, and there can be little doubt that the peculiar foot morphology evolved convergently in *Diomedeoides* and the above storm-petrels.

The counter slab of one of the best-preserved skeletons of these birds, from the early Oligocene of southern Germany, was recently donated to Forschungsinstitut Senckenberg. Study of this specimen has allowed phylogenetic affinities and way of living of diomedeoidids to be further examined. This skeleton and other

previously undescribed diomedeoidea specimens are reported in the present study, and allow the recognition of some new osteological details. Reassessment of other features, in concert with recent hypotheses on the interrelationships of extant tubenoses, makes it further possible to constrain the affinities of diomedeoidea, whose position within Procellariiformes was considered uncertain by Mayr et al. (2002).

## Material and methods

The osteological terminology follows Baumel & Witmer (1993), and the description focuses on features that were not already mentioned by previous authors (Fischer 1983, 1985, 1997, 2003; Cheneval 1995; Peters & Hamedani 2000; Mayr et al. 2002). In addition to the species listed by Mayr et al. (2002), skeletons of the following extant Procellariiformes were examined: Diomedeoidea: *Diomedea melanophris*, *D. antipodensis*, *D. epomophora*, *Phoebastria* sp.; Procellariidae: *Calonectris leucomelas*, *Halobaena caerulea*, *Macronectes giganteus*, *M. halli*, *Pachyptila belcheri*, *P. vittata*, *Procellaria aequinoctialis*, *P. cinerea*, *Pterodroma hypoleuca*, *P. incerta*, *P. lessoni*, *P. nigripennis*, *Puffinus creatopus*, *P. gavia*, *P. gravis*, *P. griseus*, *P. huttoni*, *P. tenuirostris*; Hydrobatinae: *Hydrobates pelagicus* (only legs), *Oceanodroma castro*, *O. leucorhoa*; Oceanitinae: *Pelagodroma marina*; Pelecanoididae: *Pelecanoides urinatrix*.

*Institutional abbreviations:* BSP – Bayerische Staatssammlung für Paläontologie und Historische Geologie, München, Germany; SMF – Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; SMNK – Staatliches Museum für Naturkunde, Karlsruhe, Germany.

## Systematic paleontology

**Aves** Linnaeus, 1758

**Procellariiformes** Fürbringer, 1888

**Diomedeoidea** Fischer, 1985

***Diomedeoidea*** Fischer, 1985

(= ?*Rupelornis* van Beneden, 1871)

***Diomedeoidea brodkorbi* (Cheneval, 1995)**

Figures 1A, 2A, 3A–B, 4A, 5B

*Referred specimens.* SMF Av 520 (nearly complete skeleton whose wing bones were, however, substantially reconstructed by the preparator; this specimen is the counter slab of SMNK-PAL.3812, which was described by Mayr et al. 2002), SMF Av 521 (partial dissociated skeleton lacking most of the skull, the pectoral girdle and sternum, left humerus, and left foot).

*Locality and horizon.* Frauenweiler south of Wiesloch (Baden-Württemberg, Germany), former clay pit of the Bott-Eder GmbH (“Grube Unterfeld”); Rupelian, early Oligocene (Micklich & Hildebrandt 2005).

*Measurements (maximum length in mm).* SMF Av 520. skull, 84.3; right carpometacarpus, 37.7; femur, 33.6 (left)/34.2 (right); right tibiotarsus, 83.1; tarsometatarsus, 50.6 (left)/52.1 (right).

SMF Av 521. right humerus, ~66; ulna, 72.0 (left)/~69 (right); right femur, ~35.5; right tibiotarsus, 84.0; right tarsometatarsus, ~54.

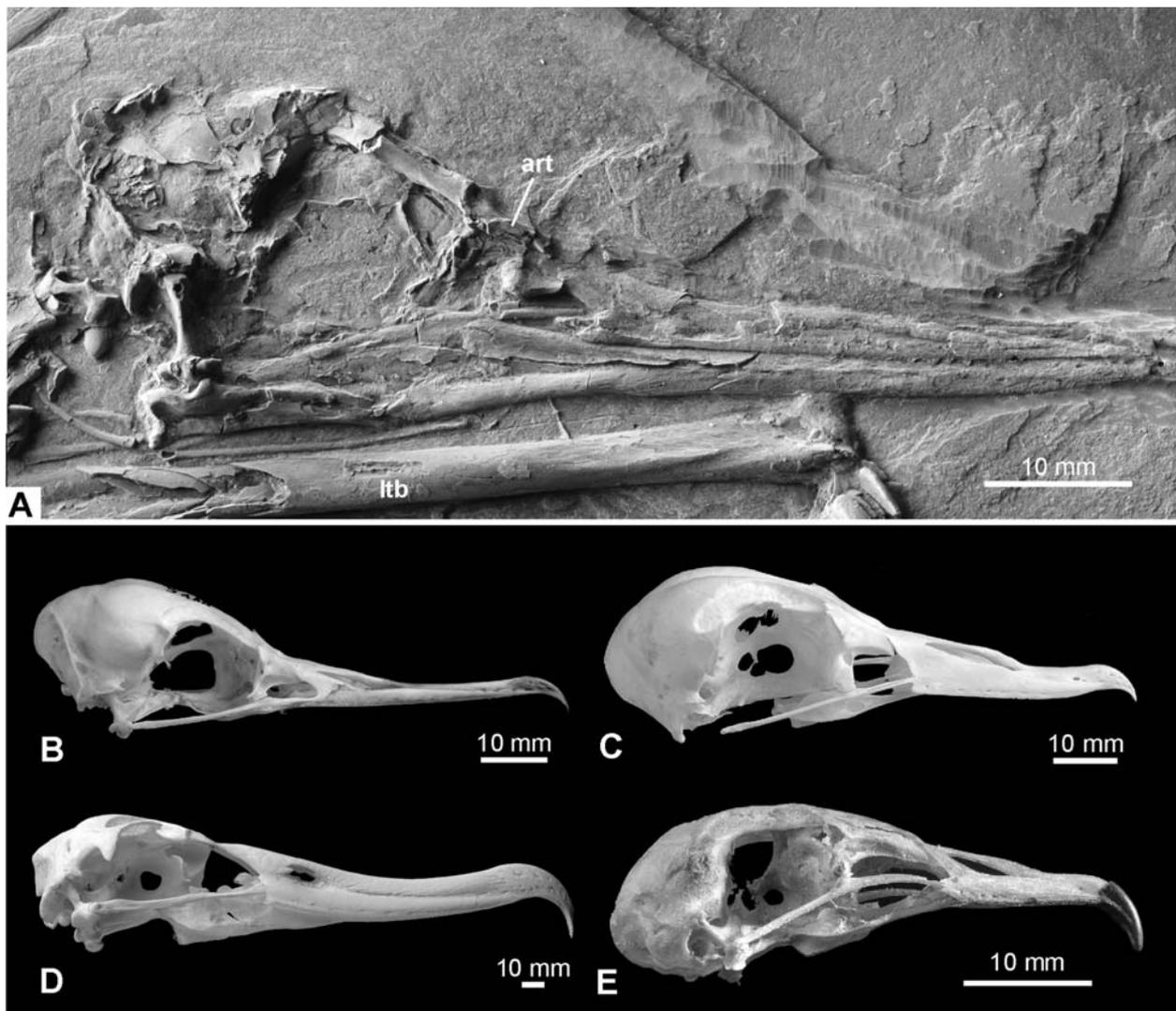
*Description and comparison.* Mayr et al. (2002) already noted that the narrow beak of *Diomedeoidea* most closely resembles that of the extant procellariiform taxon *Puffinus*, but that the tip is less strongly curved in the fossil. It has, however, not been adequately appreciated so far that the tip of the beak of *Diomedeoidea* is in fact less hooked than in all extant Procellariiformes (Fig. 1 and Mayr et al. 2002: fig. 3). As in the counter slab of this specimen (SMNK-PAL.3812), the praefrontal of SMF Av 520 is detached from the frontal, so that its articulation facet on the latter bone is visible. Clearly, thus, the praefrontal and frontal bones of *Diomedeoidea* were not fused (see also Mayr et al. 2002). Among the studied extant taxa such fusion occurs in the species of *Pterodroma*, *Fulmarus*, *Macronectes*, *Daption*, *Pachyptila*, and *Halobaena*.

The first four cervical vertebrae of SMF Av 520 are well preserved (Fig. 2). As far as details are visible, the morphology of these and the other cervical vertebrae closely resembles that of extant Procellariiformes. The atlas has a dorsally open incisura fossa. The arcus interzygapophysialis (terminology after Livezey & Zusi 2006) of the third cervical vertebra encloses a very small foramen (Fig. 2). Whether there were also such foramina on the fourth cervical vertebra cannot be discerned, as the corresponding area is damaged.

Although SMF Av 521 otherwise does not allow the recognition of new osteological features, in this specimen the ulna, whose morphology has only been incompletely known, is clearly visible. This bone does not depart from the typical procellariiform ulna as exemplified by, e.g., *Pterodroma* spp.

In SMF Av 520 the pelvis of *Diomedeoidea* is for the first time visible in dorsal view. As in the Diomedeoidea but in contrast to other extant procellariiform birds, the dorsal margins of the cristae iliacae dorsales of the ilium are not reduced but meet the crista spinosa of the synsacrum (Fig. 2). Also in this specimen, the proximal end of the tibiotarsus is much better visible than in the previously described skeletons (Fig. 2); its morphology corresponds with the description of Mayr et al. (2002). The hypotarsus bears a prominent crista medialis, a less protruding but much wider crista lateralis, and a very low crista intermedia. With regard to hypotarsus morphology, *D. brodkorbi* thus clearly differs from the Iranian *D. babaheydariensis*, which has three crests of roughly equal width and plantar extension (Peters & Hamedani 2000: fig. 7).

The articulated toes of SMF Av 520 are visible in ventral view, so that an in-situ examination of the interlocking system between them is possible (Fig. 3). The proximal ends of the basal phalanges of the second and fourth toes bear prominent medial projections, which were already noted by Mayr et al. (2002) and Fischer (2003) and about the trochlea metatarsi III. Similar, albeit less pronounced projections are present in all extant Procellariiformes (Fig. 4), and seem to serve as supports to facilitate spanning of the digital web. Because the tendon of the flexor muscle of the fourth toe of *Diomedeoidea* runs in a marked furrow on the lat-



**Figure 1.** Skulls in comparison. **A.** *Diomedeoides brodkorbi* (Cheneval, 1995) from the early Oligocene of Wiesloch-Frauenweiler (SMF Av 520). **B.** Fluttering Shearwater, *Puffinus gavia* (Forster, 1844) (Procellariidae). **C.** Cape Petrel, *Daption capense* (Linnaeus, 1758) (Procellariidae). **D.** Antipodean Albatross, *Diomedea antipodensis* (Robertson & Warham, 1992) (Diomedeidae; the os praefrontale is lacking in this specimen). **E.** Madeiran Storm-petrel, *Oceanodroma castro* (Harcourt, 1851) (Hydrobatinae). Abbreviations: **art** – articulation facet of praefrontale; **ltb** – left tibiotarsus. Note that the tip of the beak of the fossil is damaged (see Mayr et al. 2002: fig. 3 for the completely preserved bill of the counter slab).

eral, not plantar, surface of the proximal phalanx (Mayr et al. 2002; Fischer 2003), contraction of this muscle did not flex the toe, but led to its abduction. The shape of the interphalangeal articulations of the third and fourth toes, which are mere strap-like contact zones with little dorsoventral curvature, further indicates that these toes formed a stiff unit.

#### *Diomedeoides* cf. *lipsiensis* (Fischer, 1983)

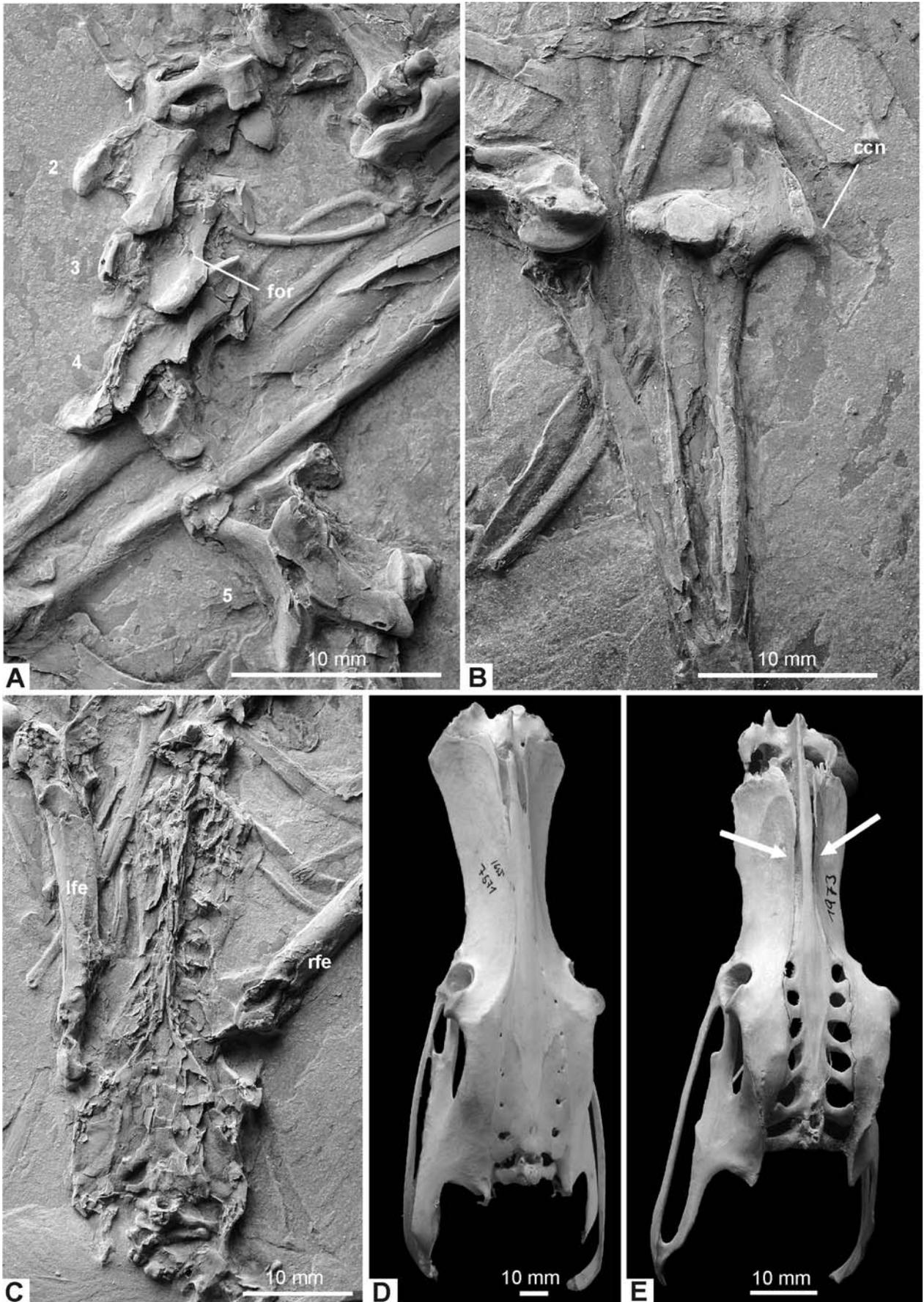
Figures 3C, 4B

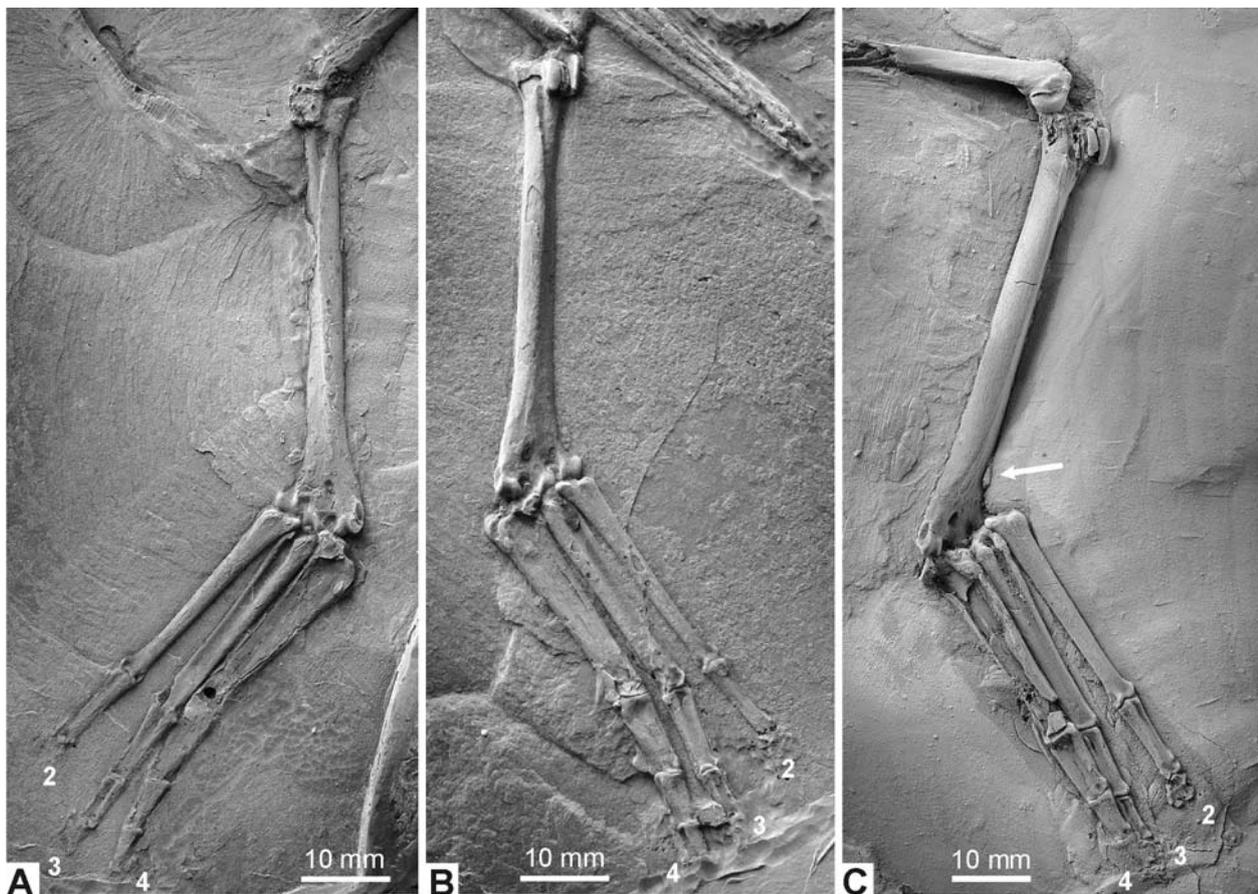
*Referred Specimens.* SMF Av 523 (incomplete left and right legs), SMF Av 524 (incomplete left and right legs).

*Locality and horizon.* Frauenweiler south of Wiesloch (Baden-Württemberg, Germany), former clay pit of the Bott-Eder GmbH (“Grube Unterfeld”); Rupelian, early Oligocene.

*Measurements (maximum length in mm).* SMF Av 523: left tibiotarsus, ~85.5 (length as preserved, without cristae cnemiales); left tarsometatarsus, ~58. Meaningful measurements of SMF Av 524 are not possible.

*Description and comparison.* The tarsometatarsi of these specimens are distinctly larger than those referred to *D. brodkorbi*. Based on this size difference, the fossils are tentatively referred to the larger *D. lipsiensis*, which has not yet been reported from the Frauenweiler fossil site. Because *D. brodkorbi* and *D. lipsiensis* also occur together at the type locality of the latter species (Fischer 2003), there remains a possibility that both represent size classes of a sexually dimorphic species. Such a variation in size is, however, the very exception in extant Procellariiformes (according to P. Scofield,





**Figure 3.** Right (A) and left (B) foot of *Diomedeoides brodkorbi* (Cheneval, 1995) from the early Oligocene of Wiesloch-Frauenweiler (SMF Av 520). C. Left foot of *D. cf. lipsiensis* (Fischer, 1983) from the early Oligocene of Wiesloch-Frauenweiler (SMF Av 523). The toes are numbered; the arrow points to the vestige of the hallux. All specimens coated with ammonium chloride.

pers. comm., a size variation up to 10 % occurs in *Macronectes* spp.), and for the moment I prefer to keep both species separate.

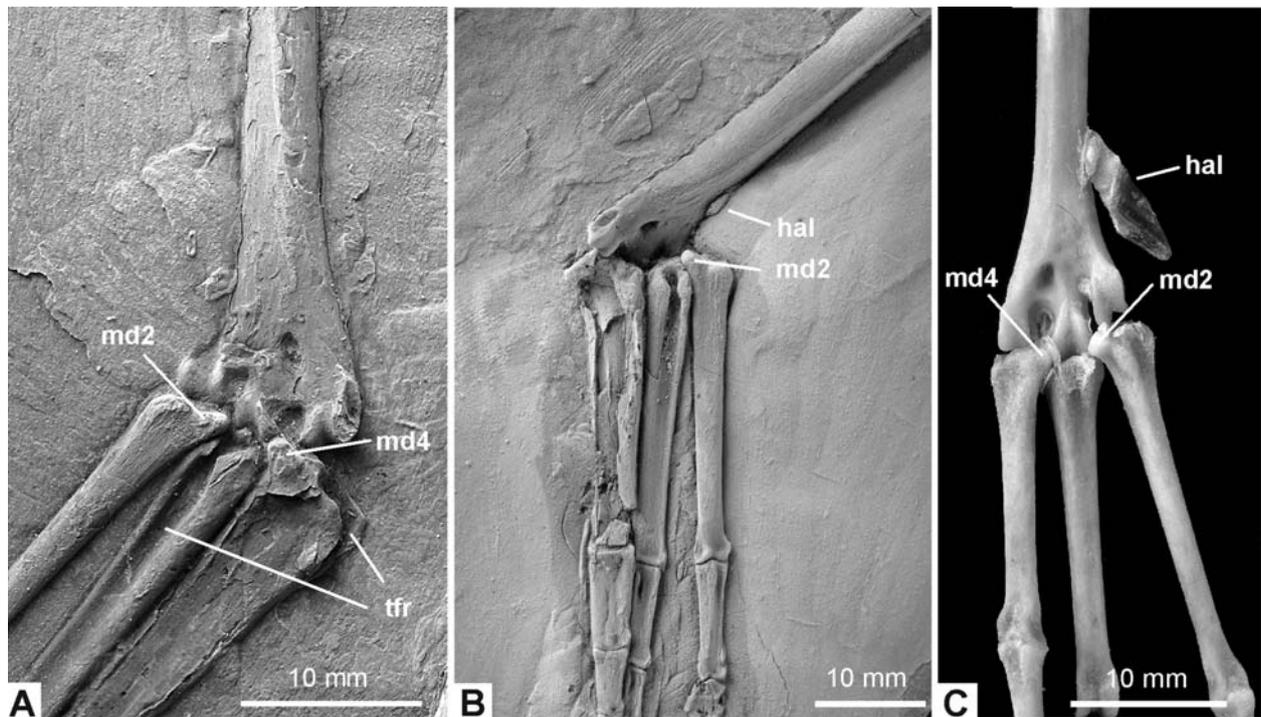
In both specimens the condylus lateralis of the tibiotarsus is well-preserved, and the articular surface is more rounded and more laterally sloping than in extant Procellariiformes; the epicondylus lateralis is more protruding and the depressio epicondylus lateralis very shallow.

The second and third toes of SMF Av 523 are visible in ventral view, whereas the fourth toe is flipped over so that its dorsal surface is exposed, and the lateral margin directed medially. The specimens of the Diomedeoididae known so far did not allow an unambiguous assessment whether a hallux was completely absent or vestigial. Specimen SMF Av 523 now clarifies this issue, as a very small ossicle is preserved on the left tar-

sometarsus, which, based on its position and shape, probably represents a vestige of the os metatarsale I (Figs 3, 4). Traces of digital phalanges of the hallux are not visible. Accordingly, the hindtoe of the Diomedeoididae was almost completely reduced, similar to that of extant Diomedeidae (Forbes 1882). The Pelecanoididae lack a hallux altogether. In other Procellariiformes the hallux is better developed, but consists only of a single, unguis, phalanx; the hallux of the Oceanitinae is very small. The larger ossicle associated with the holotype of *D. babaheydariensis*, which was identified as a phalanx of the hallux by Peters & Hamedani (2000), is here interpreted as a fish tooth, based on its shape and the enameloid-like structure of the bone surface. The unguis phalanx of the second toe of SMF Av 523 is well preserved and has irregularly-shaped margins.



**Figure 2.** Selected skeletal elements of *Diomedeoides brodkorbi* (Cheneval, 1995) from the early Oligocene of Wiesloch-Frauenweiler (SMF Av 520). A. First five cervical vertebrae (numbered). B. Proximal end of right tibiotarsus. C. Pelvis in dorsal view. D. Pelvis of the extant Antipodean Albatross, *Diomedea antipodensis* (Robertson & Warham, 1992) (Diomedeidae). E. Pelvis of the extant Northern Fulmar, *Fulmarus glacialis* (Linnaeus, 1761) (Procellariidae). Abbreviations: **ccn** – cristae cnemiales; **for** – foramen enclosed by arcus interzygapophysialis; **lfe** – left femur; **rfe** – right femur. The arrows indicate the reduced cristae iliacae dorsales. Fossil specimens coated with ammonium chloride.



**Figure 4.** Details of the feet of diomedeoidids and extant Procellariiformes to show the interlocking system between the toes. **A.** Right foot of *Diomedeoides brodkorbi* (Cheneval, 1995) from the early Oligocene of Wiesloch-Frauenweiler (SMF Av 520). **B.** Left foot of *D. cf. lipsiensis* (Fischer, 1983) from the early Oligocene of Wiesloch-Frauenweiler (SMF Av 523). **C.** The left foot of the extant Northern Fulmar, *Fulmarus glacialis* (Linnaeus, 1761) (Procellariidae). Abbreviations: **hal** – vestige of the hallux; **md2** – medial process of basal phalanx of second toe; **md4** – medial process of basal phalanx of fourth toe; **tfr** – tendinal furrows. Fossil specimens coated with ammonium chloride.

## Discussion

Extant Procellariiformes are presently classified into four taxa, the Hydrobatidae (storm-petrels), Diomedeidae (albatrosses), Procellariidae (fulmars, petrels, shearwaters, and allies), and Pelecanoididae (diving-petrels). Analyses of molecular data, however, support hypotheses of some 19th century authors (e.g., Forbes 1882) that the Hydrobatidae, which encompass the Oceanitinae and Hydrobatinae (northern storm-petrels), are not monophyletic. These analyses further congruently indicate a position of the Oceanitinae outside a clade comprising the Diomedeidae, Procellariidae, and Pelecanoididae (Nunn & Stanley 1998; Kennedy & Page 2002; Hackett et al. 2008). The Oceanitinae resulted as the sister taxon of all other extant Procellariiformes in the analysis of Hackett et al. (2008), whereas the Hydrobatinae were placed within the Diomedeidae / Procellariidae / Pelecanoididae clade in this study. A position of northern storm-petrels within the latter clade was also obtained in an analysis of nuclear gene sequences by Ericson et al. (2006), whereas a study based on mitochondrial sequences (Nunn & Stanley 1998) supported sister group relationship between the Hydrobatinae and a clade (Oceanitinae + (Diomedeidae + Pelecanoididae + Procellariidae)).

The Diomedeidae and Procellariidae share a very prominent processus supracondylaris dorsalis on the distal end of the humerus (Fig. 5). This process serves

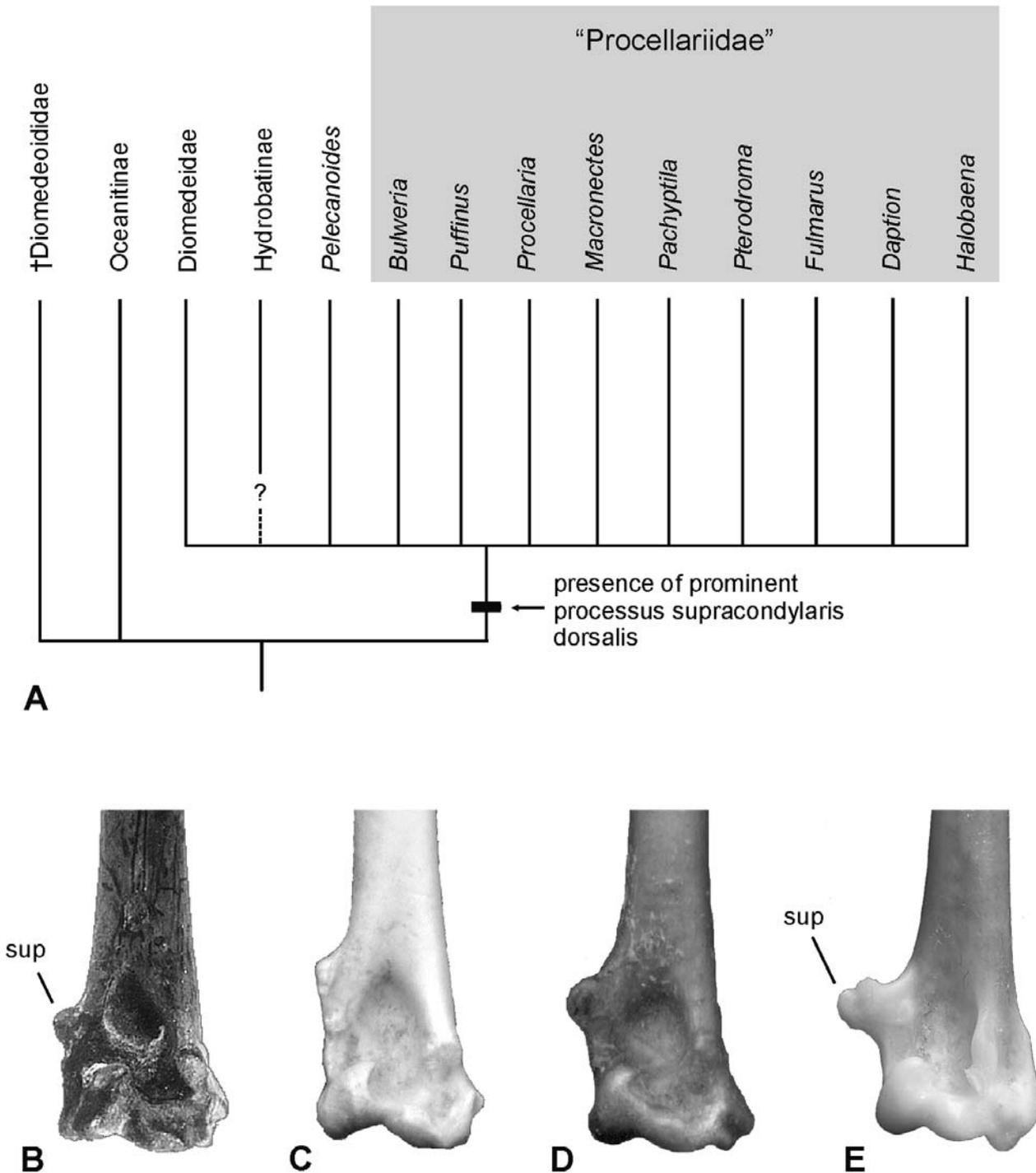
as the attachment site of ligaments, which are connected with the ligamentum propatagiale. In most representatives of the just-mentioned two extant taxa its enlargement is correlated with the formation of a large sesamoid bone, which possibly acts as a strut to stabilize the propatagium (Brooks 1937; Kaiser 2007). By contrast, the processus supracondylaris dorsalis is weakly developed in the Diomedeoididae, Oceanitinae, and Pelecanoididae, and of intermediate development in the Hydrobatinae (Fig. 5). Its small development in the Pelecanoididae probably represents a secondary reduction, because diving-petrels are nested within the Procellariidae (Kennedy & Page 2002; Ericson et al. 2006; Hackett et al. 2008), and their humerus is modified for underwater propulsion. I thus consider a prominent processus supracondylaris dorsalis to be an apomorphy of a clade including the Diomedeidae, Procellariidae, and Pelecanoididae. The small processus supracondylaris dorsalis of the Oceanitinae and Diomedeoididae supports their position outside this clade (Fig. 5).

The Diomedeidae and Procellariidae are capable of slope-soaring and dynamic gliding. By contrast, the predominant flight technique of the Oceanitinae, which have broader and more rounded wings than other extant procellariiform birds, is flap-gliding, i.e., a regular alternation between short periods of flapping and gliding (e.g., Pennycuik 1982). The weakly developed processus supracondylaris dorsalis of the Diomedeoididae

indicates that these birds also had a different flight mode than albatrosses and shearwaters and allies, and were possibly less well adapted to sustained gliding.

Southern storm-petrels and diomedeoidids have proportionally longer legs than other Procellariiformes, and there may be a functional correlation between the leg and wing morphology of these birds. As noted by Carbo-

neras (1992: 261), southern storm-petrels employ a peculiar foraging strategy, “which involves the bird facing into the wind with its wings spread open and its feet tucked into the water acting as anchors, as it sails about gazing down and picking out prey”. By contrast, most other Procellariiformes usually feed by surface seizing while sitting on the water, or by shallow plunges and sur-



**Figure 5.** A. Hypothesis on the phylogenetic interrelationships between the Diomedeoidea and extant Procellariiformes. B–E. Distal end of right humerus in comparison: B. *Diomedeoidea lipsiensis* from the early Oligocene of Steendorp in Belgium (BSP 1973 VII 226). C. White-faced Storm-petrel, *Pelagodroma marina* (Latham, 1790) (Oceanitinae, left side, reversed to facilitate comparisons). D. Madeiran Storm-petrel, *Oceanodroma castro* (Harcourt, 1851) (Hydrobatinae). E. Bonin Petrel, *Pterodroma hypoleuca* (Salvin, 1888) (Procellariidae). Abbreviation: **sup** – processus supracondylaris dorsalis. Not to scale.

face-dives. To remain stationary if prey was located, diomedoidids could have also used their feet as an anchor. The striking differences in the foot morphology of extant Oceanitinae seem to be due to the different size of these species, as *Pelagodroma*, *Fregetta*, and *Nesofregetta*, which have widened pedal phalanges, are larger than *Oceanites* and *Garrodia*, whose phalanges are not widened (see also Olson 1985). Although the flattened pedal phalanges certainly evolved convergently in the Oceanitinae and *Diomedoides* (Mayr et al. 2002), it is less clear whether this is also true for the long legs shared by these taxa, and there remains a possibility that long legs are either plesiomorphic for the Procellariiformes or an apomorphy of a clade including the Diomedoididae and Oceanitinae.

## Acknowledgements

I am indebted to Manfred Keller for donating specimens SMF Av 520 and 521 to Forschungsinstitut Senckenberg. I further thank Jutta Oelkers-Schaefer and Rainer Brocke (both SMF) for their loan, Walter Boles (Australian Museum, Sydney) for enabling examination of a skeleton of *Pelagodroma*, and P. Scofield and B. Lindow for reviewing the manuscript. The photographs were taken by Sven Tränkner.

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