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New skeleton from the early Oligocene of Germany indicates a stem-group position of diomedeoidid birds

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We report a new specimen of the extinct procellariiform species *Diomedeoides brodkorbi* (Aves, Diomedeoididae) from the early Oligocene (Rupelian) of Rheinweiler in southwestern Germany. The well-preserved partial skeleton allows the recognition and reassessment of new osteological details that bear on the phylogenetic affinities of diomedeoidids. The presence on the coracoid of a deeply excavated, cup-like facies articularis for the scapula suggests a stem group position of the Diomedeoididae within Procellariiformes, because this trait also occurs in stem-group representatives of several avian groups, as well as in Mesozoic non-neornithine birds, and is a plesiomorphic character. We hypothesize that the similarities of *Diomedeoides* to extant southern storm-petrels (Oceanitinae), such as the long mandibular symphysis, the small processus supracondylaris dorsalis and the long legs are plesiomorphic for Procellariiformes.

Key words: Aves, Diomedeoididae, phylogeny, stem-group, Oligocene, Rupelian, Upper Rhine Graben, Germany.

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Introduction

Procellariiformes (tubenoses) today include the albatrosses (Diomedidae), the shearwaters, prions and allies (Procellariidae), the diving petrels (Pelecanoididae), and the storm petrels (Hydrobatidae), which are divided into two sub-families, the Oceanitinae (southern storm petrels) and the Hydrobatinae (northern storm petrels). Some molecular data (e.g., Penhallurick and Wink 2004; Hackett et al. 2008) support the hypothesis of some 19th century authors (e.g., Forbes 1882) that the Hydrobatidae are not monophyletic. Indeed, Hackett et al. (2008) recovered the Oceanitinae as the sister taxon of the remaining taxa, and the Hydrobatinae resulted in a clade that includes all other Procellariiformes. Similarly, the monophyly of procellariids is unsure, as Pelecanoididae have been recovered nested within the Procellariidae in some molecular and morphological studies (Ericson et al. 2006; Ksepka et al. 2006).

For most procellariiforms, the Paleogene fossil record is scanty. *Tythostonyx glauconiticus* (Olson and Parris, 1987) from the Late Cretaceous or early Paleocene of North America has been tentatively assigned to the Procellariiformes.

Tythostonyx is known from a single humerus and is considered an early member of this order (Olson and Parris 1987; see, however, Bourdon et al. 2008). Apart from this taxon, whose exact age is uncertain, the earliest Paleogene remains are Eocene in age (Panteleyev and Nessonov 1993; Feduccia and McPherson 1993; Tambussi and Tonni 1998; Mayr 2009a) and, despite the fragmentary nature of the single bones, have all been assigned to extant families. So far no procellariiform has been assigned a stem-group position.

The only Paleogene procellariiform taxon of which substantial remains have been found are the Diomedeoididae, which comprise three species: *Diomedeoides brodkorbi* (Chenval, 1995), *D. lipsiensis* (Fischer, 1983) and *D. babaheydariensis* (Peters and Hamedani, 2000) (Mayr et al. 2002). The former two species are represented by multiple specimens, including complete articulated skeletons, with no such amount of fossil material being known for any other Paleogene procellariiform taxon. Several individuals and skeletal elements have been recovered in sediments that were deposited during the second Rupelian (early Oligocene) marine transgression from the North Sea that led to the formation in Europe of an epicontinental seaway connecting the

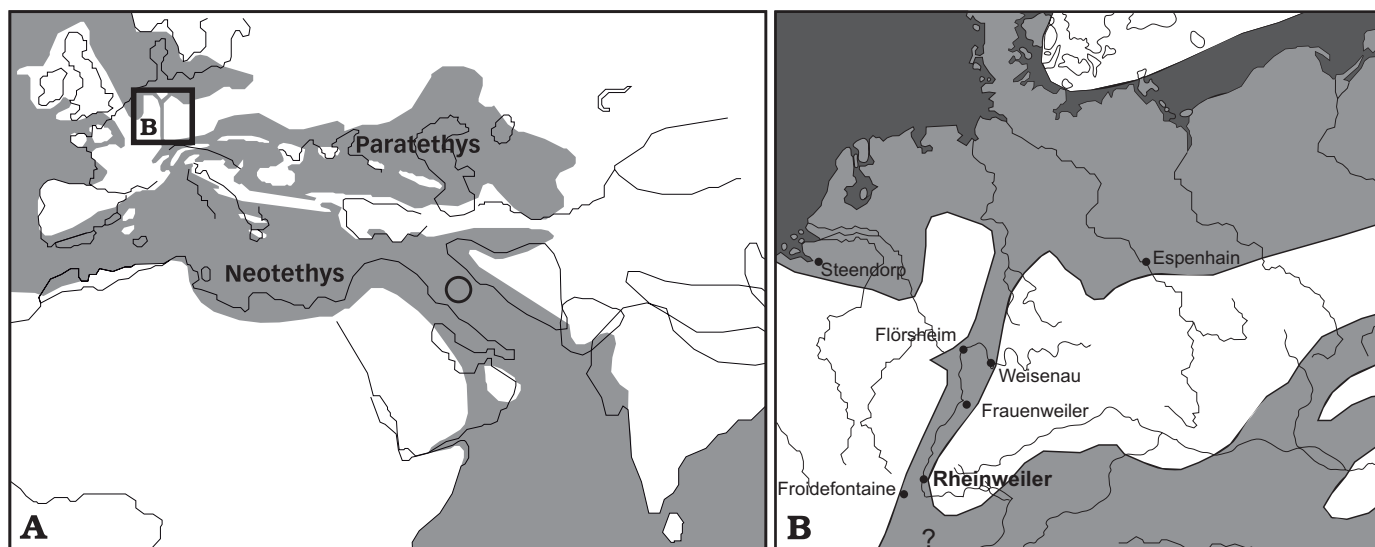


Fig. 1. **A.** Early Oligocene paleogeography, showing the configuration of the Paratethys and Neotethys Oceans. The circled area corresponds to the approximate paleo-location of the site at which the Iranian specimen, *Diomedeoides babaheydariensis*, was found. The squared area (enlarged in B) shows the known distribution of all other diomedeidids. Grey areas indicate the extent of the Oligocene sea. Redrawn and modified from Rögl 1999. **B.** The second Rupelian (Oligocene) marine transgression in Europe. The locations of diomedeid fossil sites are shown. The locality of Rheinweiler is framed. Redrawn and modified from Micklich and Hildebrandt 2005. Note that the connection between Upper Rhine Graben and Perialpine Sea is only hypothetical (see details in Pirkenseer 2007).

North Sea and Paratethys (Fig. 1). One specimen is known from the Zagros Mountains in Iran and was found in only slightly younger sediments (Peters and Hamedani 2000). The youngest appearance of the family, however, is in the early Miocene (MN 1, 23.8–22.4 Mya; Steininger 1999) of Weisenau, Mainz Basin, Germany (Cheneval 1995).

Diomedeidids are characterized by very long legs and greatly widened pedal phalanges, particularly those of the fourth toe. With regard to these features they strikingly resemble some species of extant Oceanitinae, most notably those of the taxa *Fregetta* and *Nesofregetta* (Mayr et al. 2002; Mayr 2009b), which are also the largest species of southern storm-petrels. It had already been noticed by Olson (1985) that within the Oceanitinae there is a trend towards greater size and increasing specialization of the tarsometatarsus and pedal phalanges. The smaller species possess pedal phalanges of regular proportions, but also have very long legs as in diomedeidids and other southern storm-petrels (Mayr 2009b).

The literature on diomedeidids is meanwhile fairly extensive (Fischer 1983, 1985, 1997, 2003; Cheneval 1995; Peters and Hamedani 2000; Mayr et al. 2002; Mayr 2009b), but although several suggestions have been made as to in which procellariiform lineage they ought to be placed (e.g., Fischer 1985; Cheneval 1995), no conclusive evidence has been presented until recently (Mayr 2009b).

We report a new and well-preserved specimen of *Diomedeoides brodkorbi* from the late Rupelian (early Oligocene) that was recovered from the small outcrop of Rheinweiler in southwestern Germany. The fossil is a partial disarticulated skeleton, which allows the recognition of new osteological details and a reassessment of previously de-

scribed elements. The new data obtained from the specimen allow clarification of the phylogenetic position of *Diomedeoides* within the Procellariiformes. Although a possible closer affinity between the Oceanitinae and Diomedeididae was proposed by Mayr (2009b) based on the size of the processus supracondylaris dorsalis of the humerus and, eventually, on

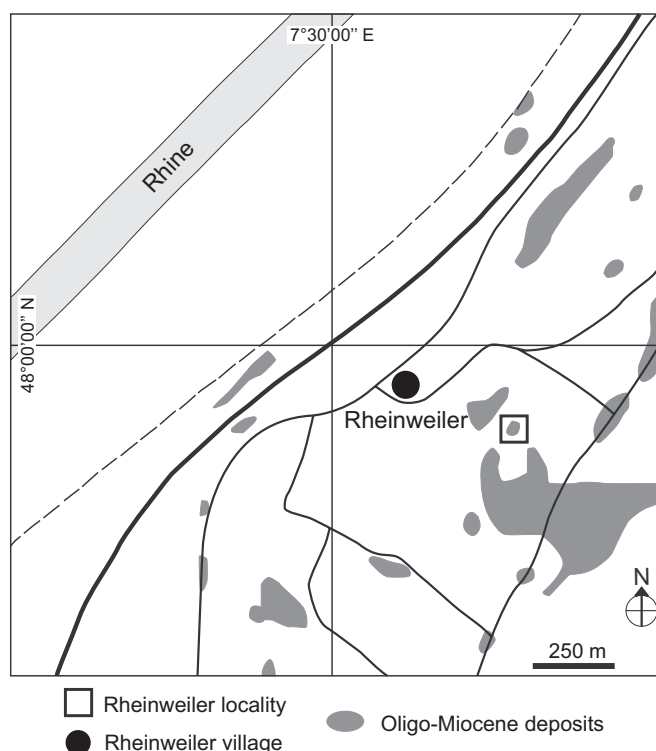


Fig. 2. Map of the immediate surroundings of the Rheinweiler locality.

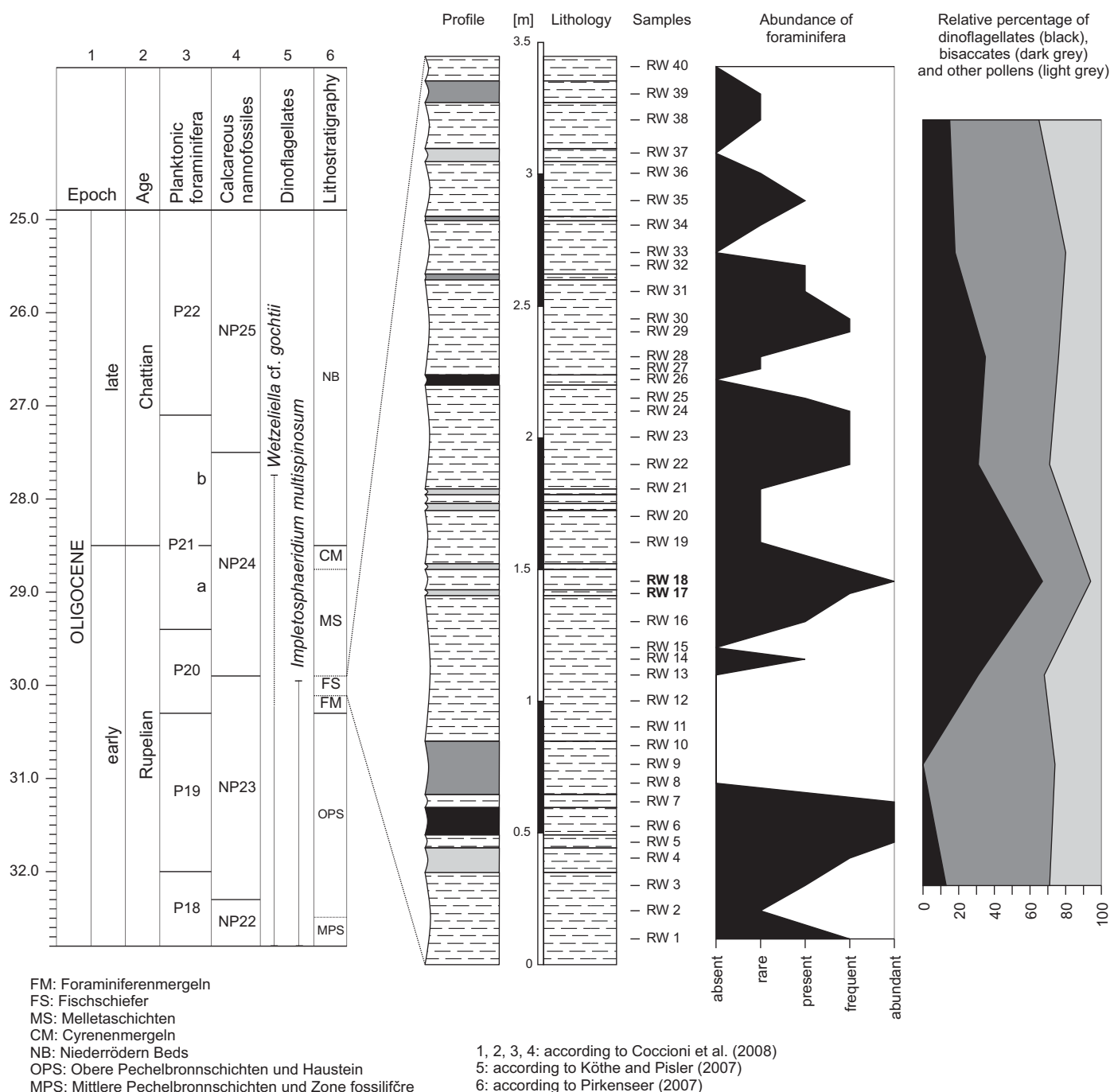


Fig. 3. Stratigraphy of the Rheinweiler locality. Note that the layers containing the bird are situated at about 1.5 m, between the samples RW17 and RW18 (shown in bold).

the length of the legs, it has not been clear whether the similarities between the Oceanitinae and Diomedoididae are derived for the two taxa or plesiomorphic within the Procellariiformes. Here, we present new osteological data that bear on this matter.

Institutional abbreviations.—MHNF, Musée d'Histoire naturelle de Fribourg, Switzerland; NMBE, Naturhistorisches Museum der Bürgergemeinde Bern, Switzerland; SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany.

Geological setting

The bird was found in July 2004 by a master student of the University of Basel, Sebastian Hinsken, during a field course organized by the Geoscience Department of the University Fribourg (Switzerland) under the direction of J-PB. The outcrop Rheinweiler (Fig. 2) has been studied in detail by Scherler (2005) and Pirkenseer (2007). It consists of about 3 m of schistoid black marls of the so-called “Fischschiefer” (Fish Shales) overlaid by 2–3 m of grey silty marls with small scale

turbiditic sand layers attributed to the lowermost “Meletta layers”.

As shown in Fig. 3, the age of the locality is well constrained by foraminifers (with *Planorbulina difformis*) as well as by dinoflagellates (*Wetzeliella* cf. *gochtii*, *Impletophaeridium multispinosum*) and can be correlated with the top of the Nannoplankton Zone NP23 and the Dinoflagellate Zone D14 (see Pross 1997; Koethe and Piesker 2007), i.e., about 30 Mya (see details on the stratigraphy of the Paleogene in the Upper Rhine Graben in Berger et al. 2005a, b and Pirkenseer 2007).

The Rheinweiler locality yielded a rich fossil fauna (29 fossiliferous samples) composed of foraminifers (*Aubignyna kiliani*, *Bolivina beyrichii*, *B. mellettica*, *Cibicides amphysiliensis*, *Globulina minuta*, *Guttulina communis*, *Gyroidina brockerti*, *Gyroidinoides girardanus*, *Melonis affinis*, *Planorbulina difformis*, *Porosonion subgranosum*, *Siphonodosaria ewaldi*, and *Globigerina praebuloides*), calcareous nannofossils (*Braarudosphaera bigelowii*, *Coccolithus crassipons*, *C. pelagicus*, *Dictyococcites bisectus filewiczii*, *Discoaster saipanensis*, *Pontosphaera multipora*, *Reticulofenestra celtica*, *R. dictyoda*, *R. minuta*, *Sphenolithus moriformis*, and *Zygrhablithus bijugatus*), fish fragments (with *Amphysile heinrichi* and *Cetorhinus parvus*), and one crocodylian tooth.

Palynomorphs have been studied by Andrea Storni (unpublished data) and include dinoflagellates (*Deflandrea phosphoritica*, *Palaeocystodinium golzowense*, *Wetzeliella* cf. *gochtii*, *Impletophaeridium multispinosum*, *Systematophora placantha*, and *Thalassiphora pelagica*) and pollen (bisaccates from *Pinus* type, taxads and rare angiosperms, see also Schüller 1990) as well as Prasinophyceae algae.

As shown in Fig. 3, the layer containing the bird corresponds to normal saline conditions with regular dysoxic and/or anoxic events deposited in the outer shelf; probably correlated with 100–300 m water depth.

Paleogeographically these sediments conform with the Série grise, known in the whole Upper Rhine Graben (URG). The URG may have been connected with the Perialpine Sea at times (Western Paratethys, see discussion in Berger et al. 2005a and Pirkenseer 2007).

Material and methods

The specimen is deposited at the Musée d'Histoire naturelle de Fribourg (MHNF), Switzerland.

The following skeletons of Recent procellariiforms were available for comparisons: Diomedidae: *Diomedea exulans*; Hydrobatidae: Hydrobatinae: *Oceanodroma leucorhoa*, *Oceanodroma* cf. *castro*, *Hydrobates pelagicus*, Oceanitinae: *Pelagodroma marina*; Procellariidae: *Puffinus tenuirostris*, *Puffinus lherminieri*, *Pachyptila desolata*, *Pterodroma lessonii*, *Pterodroma incerta*, *Fulmarus glacialis*, *Daption capense*, *Bulweria bulwerii*, *Procellaria aequin-*

octialis, *Macronectes halli*, *Macronectes giganteus*; Pelecanoididae: *Pelecanoides urinatrix*.

The anatomical terminology follows Baumel and Witmer (1993). Our description focuses on features not mentioned in previous publications (Fischer 1983, 1985, 1997, 2003; Cheneval 1995; Peters and Hamedani 2000; Mayr et al. 2002; Mayr 2009b).

Systematic paleontology

Aves Linnaeus, 1758

Procellariiformes Fürbringer, 1888

Diomedeoididae Fischer, 1985

Genus *Diomedeoides* Fischer, 1985

Type species: *Diomedeoides minimus* Fischer, 1985.

Type locality: Braunkohlentagebau Espenhain, south of Leipzig, Germany.

Age and horizon: Rupelian, early Oligocene; phosphorite nodules horizon.

Diomedeoides brodkorbi (Cheneval, 1995)

Fig. 4.

Type material: Froidefontaine specimen, three slabs; NP 23–24, Rupelian, early Oligocene; Froidefontaine, Territoire de Belfort, France (Cheneval 1995).

Locality: Rheinweiler near Bad Bellingen, Baden-Württemberg, Germany. This location is situated at the eastern shoulder of the Upper Rhine Graben, which stretches approximately 300 km in a north-south axis and represents the central part of the European Continental Rift system.

Horizon: Fischschiefer, Rupelian, early Oligocene (NP 23, D14).

Material.—MHNF 30877, disarticulated partial skeleton on three slabs, lacking sternum, most wing elements from the left side, and left leg.

Measurements (unless indicated otherwise, maximum length in mm).—Skull (as preserved), 73.6; mandible, 76.6; main body of hyoid, 8.3; left coracoid, 26.8; left scapula, 32.8 (broken); right humerus, 66.8; left humerus, 66.2; right ulna, 65.5; right carpometacarpus, 38.2; right phalanx proximalis digiti majoris, 22.1; right phalanx distalis digiti majoris, 25.5; right phalanx digiti minoris, 9.8; right femur, 35.4; left second pedal phalanx of third digit, 9.5; left proximal phalanx of fourth digit, 28; left second pedal phalanx of fourth digit, 11; ?left third phalanx of fourth digit, 7.5.

Description and comparisons.—In the new specimen, the skull of *Diomedeoides* is for the first time visible in dorsal view and presents a number of previously unknown osteological details (Fig. 5). In dorsal view, the overall shape of the skull resembles the Recent genus *Pelagodroma* the most.

Fig. 4. Partial disarticulated skeleton of the diomedeoidid bird *Diomedeoides brodkorbi* (Cheneval, 1995), MHNF 30877 from the early Oligocene of Rheinweiler, Germany (A); partial counterslab of MHNF 30877 (B); slab showing the proximal phalanx of the fourth digit and some ribs (C). →



The nasofrontal hinge area is nonetheless shorter, the proportions being like those of *Puffinus*. As noted by Mayr et al. (2002), the fossae glandularum nasales are narrow and shallow, showing no evident projections at their caudal end. The central part of the os frontale is thus wide and shows a shallow medial furrow. The beak, whose tip is broken in the specimen, is less curved than that of all extant procellariiforms. This can be appreciated in side view, and is also known from other diomedeoidid specimens (see figures in Cheneval 1995; Mayr et al. 2002). Both ossa lacrimalia have been lost, indicating that, in contrast to some Recent procellariids, they were not fused with the os frontale. Likewise, unfused lachrymals are present in members of the Hydrobatinae, Oceanitinae, and Diomedidae. The processus postorbitales are large and distinct; their tips project rostro-laterally. Large postorbital processes are known for several procellariid species, albeit in these they are usually related to broader fossae glandularum nasales.

The left os pterygoideum is situated between the rami of the lower jaw and is visible in dorsal view. This bone is not preserved in any of the previously known diomedeoidid specimens and most closely resembles the pterygoid of taxa in the Hydrobatinae and Oceanitinae. The medial wing of the fossil, however, is broader than in these two taxa. Within procellariiforms, the procellariids and the pelecanoidids possess ossa pterygoidea with a rostral wing that articulates with the basiptyergoid process only caudally (these processes are often vestigial; Pycraft 1899). The ossa pterygoidea are rod-shaped in species in Oceanitinae, Hydrobatinae, and Diomedidae. In these taxa they lack an articulation facet for the basiptyergoid processes, which are absent in the Diomedidae and absent or vestigial in species in Oceanitinae and Hydrobatinae (Pycraft 1899). The pterygoid of *Diomedoides* likewise does not seem to bear any basiptyergoid facets, so that basiptyergoid processes either were absent or vestigial. It should be noted that the pterygoid of the fossil specimen shows an awkward rostro-lateral projection. Upon closer inspection there is a clear separation between the main body of the pterygoid and this protuberance, which also shows rugged edges, and this protuberance may possibly be an artefact of preservation.

The quadrate (Figs. 4 and 5) does not significantly differ from that of extant procellariiforms, which is quite uniform throughout the group. The tip of the processus orbitalis is broken and most features have been poorly preserved. The caudal margin of the bone between the processus oticus and the condylus caudalis is more markedly concave in the fossil than in the examined extant species.

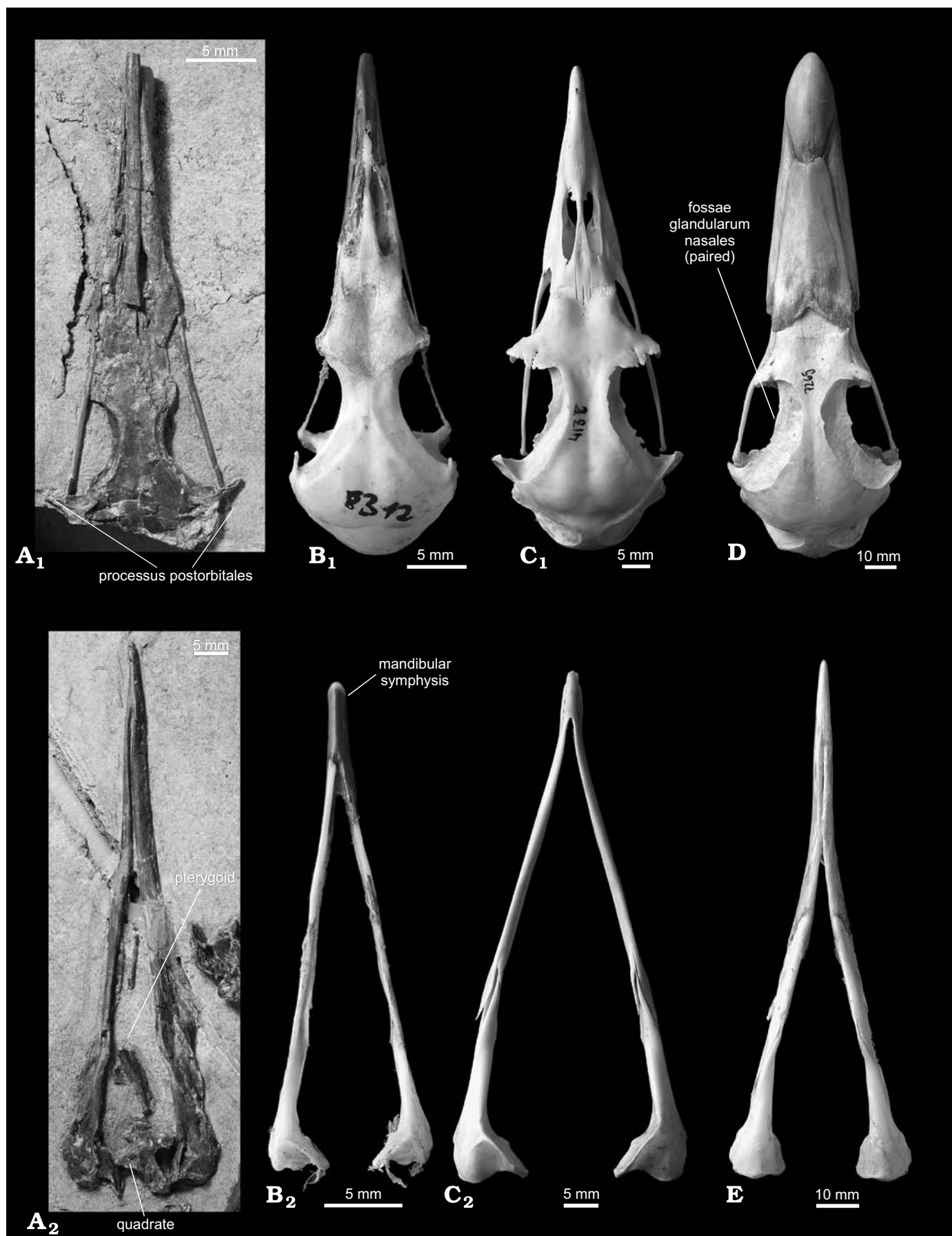
For the first time, the lower jaw can be fully appreciated in ventral view (Fig. 5). The rami mandibulae do not diverge as strongly as in other procellariiforms; the symphysis is of

similar relative length to that of *Pelagodroma*, being longer than in all other extant procellariiforms examined. In lateral view, the rostrum mandibulae is straight. The anterior parts of the rami mandibulae are unusual in that they are more closely aligned than in most of the Recent procellariiforms we have examined, the exception being some *Puffinus* species. This condition can also be observed in the Froidefontaine specimen of *D. brodkorbi* described by Cheneval (1995), and a similar morphology occurs in Phaethontidae (tropicbirds; Fig. 5E) and the early Eocene *Prophaethon shrubsolei* Andrews, 1899 (Prophaethontidae; see Harrison and Walker 1977: pl. 5), as well as in some members of other avian orders (e.g., some “pelecaniforms” [pelicans and allies] and some “gruiforms” [cranes, rails, and allies]). The processus mandibulae medialis resembles that of extant procellariiforms in size, shape and orientation. The processus mandibulae lateralis likewise does not differ from that of extant species. The fossae caudales are deep and very well defined, so that there is a deep incision between the processus mandibulae lateralis and medialis. This incision is quite shallow in *Oceanodroma* and tends to be deeper in the procellariids. A small ossicle next to the extremitas ventralis of the scapula may represent the basihyale, but this identification needs further verification.

Ten presacral vertebrae can be counted on the slab, at least two of which are thoracic ones. Overall, they resemble those of extant procellariiforms, although the poor preservation of these elements does not allow for any sensible interpretation. On the other hand, three out of five caudal vertebrae have been nicely preserved, and do not differ from those of extant procellariiforms.

The morphology of the coracoid of the Diomedoididae has so far been only poorly known. In the new specimen the bone is completely exposed and well preserved (Fig. 6). In overall proportions it most closely resembles that of *Pterodroma*. The facies articularis clavicularis is short and does not protrude far medially as in the Diomedidae and in some procellariids (e.g., *Puffinus*). *Diomedoides* further differs from these two families in having a less developed processus procoracoideus. As in species of Hydrobatinae and Oceanitinae, the processus acrocoracoideus does not protrude medially beyond the processus procoracoideus. Most notably and in contrast to all Recent procellariiforms, the cotyla scapularis is cup-shaped, circular and deeply excavated. The circular outline is most similar to *Pelagodroma*, and to a lesser extent to *Oceanodroma*, although it is much shallower in these two genera. The processus lateralis is broken from the main part of the coracoid, but preserved on the counter slab. It has a similar overall shape to that of extant procellariiforms, but its tip is less pointed and upwardly curved than in extant tubenoses. The impressio muscoli sternocoracoidei is well marked.

Fig. 5. Skull and mandible of *Diomedoides brodkorbi* from the early Oligocene of Rheinweiler, Germany, in comparison to extant Procellariiformes. →
A. *Diomedoides brodkorbi* (MHNF 30877), with caudal portion of skull missing: skull (A₁), lower jaw (A₂). **B.** *Pelagodroma marina* Latham, 1790 (SMF 8312): skull (B₁), lower jaw (B₂). **C.** *Pterodroma incerta* Schlegel, 1863 (SMF 4138) skull (C₁), lower jaw (C₂). **D.** Skull of *Macronectes giganteus* Gmelin, 1789 (SMF 7265). **E.** Lower jaw of *Phaethon rubricauda* Boddaert, 1783 (SMF 7287).





The furcula (seen as right clavicle, caudal view) is widely U-shaped; Mayr et al. (2002) mentioned that it is wider than in all Recent procellariiforms investigated by them. The scapus clavicularae has the same width throughout. The facies articularis acrocoracoidea has a smooth angle. The processus acromialis does not appear to be as pointed as in *Puffinus*, being rather like in other procellariids (e.g., *Pterodroma*).

The short acromion of the scapula agrees with that of Recent procellariiforms. The facies articularis humeralis does not project as far ventrally as in *Puffinus*. The overall proportions are like those of procellariids (e.g., *Procellaria*), and not like *Pelagodroma*, whose scapula is much shorter. The thin sheet of bone at the dorsal end has broken off, and therefore its total length is unknown.

The morphology of the ulna of the diomedeidids has so far only been incompletely known. The bone resembles that of some extant procellariids (Fig. 6), but markedly differs from the much stouter and proportionally shorter ulna of the oceanitines. The proportions of the bone resemble those of Recent procellariids. Unlike in species of Oceanitinae, the ulna is slightly longer than the humerus. As in most extant procellariiforms, the olecranon is low. The proximal end is very much like that of *Fulmarus*, the main differences residing in the shape of the tuberculum ligamenti collateralis ventralis, which is narrower in MHNF 30877, and in the depth of the impressio brachialis, which is deeper in the fossil. The processus cotylaris dorsalis of *Diomedeoides* is less protruding than in procellariids, a condition also present in *Pelagodroma* and *Oceanodroma*. Nevertheless, the ulna of *Pelagodroma* is highly derived and very different from that of the Rheinweiler specimen (Fig. 6). The tuberculum ligamenti collateralis ventralis of *Diomedeoides* is well developed and, as in most procellariids (e.g., *Daption*, *Procellaria*), situated farther distally than that of *Pelagodroma*. On the distal end of the bone, the tuberculum carpale appears to be proportionally smaller than in most procellariids examined, its shape being like that of *Pelagodroma* and *Oceanodroma*, where it is quite small. The depressio radialis is very well marked in the fossil specimen. Both the condylus ventralis ulnaris and the dorsal edge of the condylus dorsalis ulnaris of *Diomedeoides* resemble those of *Fulmarus*.

The left os carpi radiale is situated on the slab above the ulna and the phalanx proximalis digiti majoris; the articular surface with the carpometacarpus faces up. It does not differ from that of extant Procellariiformes.

In the new specimen, the carpometacarpus is for the first time well preserved (Fig. 6). The shape of the processus extensorius is peculiar in that it (gradually) slopes in a dorso-

ventral direction rather than pointing slightly cranially as in other tubenoses. To a lesser extent, this feature can be observed in *Pterodroma*. The proportions of the carpometacarpus resemble those of extant procellariids; although the bone is slightly longer in the fossil than in the members of this family (see also Cheneval 1995). The ventral rim of the carpal trochlea is less rounded and lower compared to other procellariiforms. The os metacarpale minus is straight, whereas it is more bent in *Pelagodroma* (Fig. 6). The sulcus tendineus is very well marked, as in *Oceanodroma* and *Pelagodroma*, being less so in most procellariids (e.g., *Puffinus*, *Bulweria*, *Procellaria*, *Daption*). Mayr et al. (2002) mentioned that *Murunkus*, a fossil from the Eocene of Kazakhstan which is known from a carpometacarpus, could be a member of the Diomedeididae. The processus extensorius of *Murunkus*, however, has a very different shape from that of *Diomedeoides*, making a position of *Murunkus* within the Diomedeididae unlikely. Furthermore, the cranially directing tuberosity on the distal end of the os metacarpale majus of *Murunkus* seems less protruding, unlike that of *Diomedeoides*. The carpometacarpus of *Murunkus* is also smaller (34.4 mm) than that of MHNF 30877.

The shape of the phalanx proximalis digiti majoris closely resembles that of *Pelagodroma*, whereas it is narrower and more elongated, with a less curved cranial margin in other examined procellariiforms (Fig. 6). The similar shape of this bone in *Diomedeoides* and *Pelagodroma* could be related to more rounded wings (see Mayr 2009b concerning presumed flight and foraging strategies of these birds). As in all Procellariiformes, the processus internus indicis is well-developed, but seems to point slightly more ventrally in *Diomedeoides*.

Discussion

As noted in the introduction, the affinities of *Diomedeoides* within the Procellariiformes have remained uncertain. Cheneval (1995) confidently assigned *Diomedeoides* to the Procellariidae although he did not present derived characters supporting this classification, which was mainly based on overall limb proportions. Fischer (1985) proposed a close relationship between *Diomedeoides* and *Diomedea* based on a single femur. Better preserved specimens have enabled refined hypotheses regarding the affinities of the Diomedeididae, and most recently it has been hypothesized that the poorly developed processus supracondylaris dorsalis of the humerus suggests a position of the Diomedeididae outside a

← Fig. 6. Wing and pectoral girdle elements of *Diomedeoides brodkorbi* from the early Oligocene of Rheinweiler, Germany, in comparison to extant Procellariiformes. **A.** *Diomedeoides brodkorbi* (MHNF 30877); right ulna in ventral view (A₁), right carpometacarpus in dorsal view (A₂), right phalanx proximalis digiti majoris in ventral view (A₃), left coracoid in dorsal view (A₄). **B.** *Pelagodroma marina* Latham, 1790 (SMF 8312); right ulna in ventral view (B₁), right carpometacarpus in dorsal view (B₂), right phalanx proximalis digiti majoris in ventral view (B₃), left coracoid in dorsal view (B₄). **C.** *Fulmarus glacialis* Linnaeus, 1761 (SMF 7181); right ulna in ventral view (C₁), right phalanx proximalis digiti majoris in ventral view (C₂), left coracoid in dorsal view (C₃). **D.** *Pterodroma incerta* Schlegel, 1863 (SMF 4138); dorsal view of right carpometacarpus. **E.** *Oceanodroma castro* Harcourt, 1851 (SMF 5641); dorsal view of left coracoid.

clade including the Diomedidae, Procellariidae, Pelecanoididae, and Hydrobatinae (Mayr 2009b). Their exact phylogenetic position with respect to the Oceanitinae, however, remained unresolved.

An assessment of the affinities of these birds is complicated by the fact that molecular studies have returned ambiguous results bearing on the early divergences within crown group Procellariiformes. Whereas some analyses of molecular data either support the Oceanitinae (Hackett et al. 2008) or the Diomedidae (Ericson et al. 2006) as the sister taxon of all remaining procellariiforms, some other analyses indicate that the Hydrobatinae split first, followed by the Oceanitinae (Nunn and Stanley 1998; note that in Fig. 2 of this paper the names Oceanitinae and Hydrobatinae are interchanged). Likewise, the analysis of morphological features has yielded unclear results: a basal monophyletic Hydrobatidae was recovered by Bertelli and Giannini 2005, a basal Diomedidae by Ksepka et al. 2006 and a basal Pelecanoididae by Livezey and Zusi 2007. However, it is worth mentioning that none of these studies have focused on Procellariiformes exclusively. Forbes's (1882) anatomical study on the procellariiforms endorses the position of the Oceanitinae as sister taxon to all other members of this order.

The new osteological data obtained from specimen MHNF 30877 indicates that *Diomedoides* is outside crown group Procellariiformes (Fig. 7). The critical feature that strongly argues for a stem-group position of the Diomedoididae is the deeply excavated, cup-like cotyla scapularis of the coracoid by which diomedoidids are clearly distinguished from all extant procellariiform taxa, in which the facies articularis scapularis of the coracoid is shallow. Such a deeply excavated, cup-like articulation facet for the scapula is also present in Mesozoic non-neornithine birds such as *Ichthyornis* Marsh, 1872 and *Hesperornis* Marsh, 1872, and is without a doubt a primitive character for Neornithes (Mourer-Chauviré 1992a; Mayr and Weidig 2004). A cup-like cotyla scapularis of the coracoid occurs in stem group representatives of several other avian lineages, whose extant relatives have a flat facies articularis scapularis, such as the Galliformes (Mourer-Chauviré 1992a) and Psittaciformes (Mourer-Chauviré 1992b; Mayr 2000). Within all extant procellariiform taxa, the facies articularis

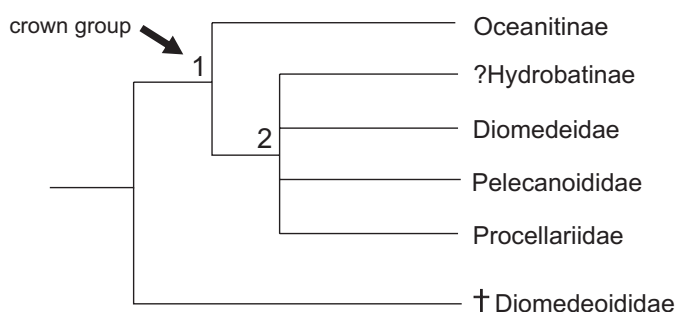


Fig. 7. Relationships between crown group Procellariiformes and the Diomedoididae. The two nodes are characterized by the characters: 1, cotyla scapularis of coracoid shallow; 2, mandibular symphysis short; processus supracondylaris dorsalis large; legs short (note that the Hydrobatinae are intermediate in the last two characters mentioned).

scapularis of the coracoid is shallow (Fig. 6). A shallow facies articularis scapularis may serve to increase the movability of the scapula relative to the coracoid, but the exact functional significance of this feature remains unknown.

As noted in the introduction, diomedoidids share several striking features with some members of extant Oceanitinae. Most notable among these are the long legs and greatly widened pedal phalanges (Mayr et al. 2002; Mayr 2009b). The new specimen adds to these similarities in the long mandibular symphysis, the circular outline of the cotyla scapularis of the coracoid, and in the wider phalanx proximalis digiti majoris. Whereas the long legs and similar length of the pars symphysialis of the mandible may be plesiomorphic for Procellariiformes, the extraordinary similarities in the morphology of the pedal phalanges certainly evolved convergently (Mayr et al. 2002; Mayr 2009b). Whether the same is true for the shape of the phalanx proximalis digiti majoris is less clear.

Procellariiform birds are today among the most diversified and numerically abundant groups of pelagic birds. Unambiguous remains of representatives of crown group Procellariiformes are, however, unknown from pre-Oligocene fossil sites, and the most abundant medium-sized seabirds in the late Paleocene and Eocene were the Prophaethontidae and the Pelagornithidae (bony-toothed birds) (Mayr 2009a). Prophaethontidae are unknown from post-Eocene sediments, whereas late Paleogene and Neogene pelagornithids are giant forms with a wingspan above four meters (Mayr 2009a). Because even early Oligocene procellariiforms appear to have been stem group representatives, we consider it well possible that the radiation of crown group Procellariiformes was in some way connected with the demise of the Prophaethontidae and small Pelagornithidae. Whether, however, tubenoses occupied ecological niches that became vacant after extinction of prophaethontids and bony-toothed birds, or whether the latter became extinct owing to competition with tubenoses can only be said once more data on the temporal occurrences of these birds become available.

The abundance of diomedoidids in Central Europe during the Mid-Oligocene marine transgression may be related to the seasonal productivity of these waters. Detailed analysis from the clay pit of the Bott-Eder GmbH ("Grube Unterfeld", Frauenweiler, Germany), which yielded several specimens of the Diomedoididae (Mayr et al. 2002; Mayr 2009b), indicates that primary producers appear regularly in abundance (Grimm et al. 2002). Planktonic blooms were caused by the seasonal upwelling of bottom nutrients, triggered by differences in salinity between surface and bottom waters as a result of enhanced evaporation during the summer months (Grimm et al. 2002; see also Micklich and Hildebrandt 2005). Phytoplankton blooms were the reason for the very diverse ichthyofauna of the area (its deposition is known as the "fish shales"), and provided the basis for a complex food web, thus supporting the presence of numerous predators such as sharks and procellariiform birds. The presence of large amounts of dinoflagellates in the layers where the bird was found confirms this hypothesis.

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