Journal of Vertebrate Paleontology 22(3):667–676, September 2002

PETREL-LIKE BIRDS WITH A PECULIAR FOOT MORPHOLOGY FROM THE OLIGOCENE OF GERMANY AND BELGIUM (AVES: PROCELLARIIFORMES)

GERALD MAYR[1], D. STEFAN PETERS[1], and SIEGFRIED RIETSCHEL[2]
[1]Forschungsinstitut Senckenberg, Division of Ornithology, Senckenberganlage 25, D-60325 Frankfurt a.M., Germany, gmayr@sng.uni-frankfurt.de
[2]Staatliches Museum für Naturkunde Karlsruhe, Erbprinzenstraße 13, D-76133 Karlsruhe, Germany

ABSTRACT—New specimens of procellariiform birds are described from the Oligocene of Germany and Belgium, including a virtually complete and extraordinarily well preserved articulated skeleton. These birds show a peculiar foot morphology which to a striking degree resembles that of the recent Polynesian Storm-petrel *Nesofregetta fuliginosa* (Oceanitinae, Hydrobatidae). The pedal phalanges are dorso-ventrally compressed and especially the proximal phalanx of the fourth toe is grotesquely widened. The Oligocene Procellariiformes trenchantly differ, however, from *Nesofregetta*, the closely related genus *Fregetta*, and all other taxa of recent Hydrobatidae in the remainder of the skeleton. Possibly the feet served as a brake for rapid stops in order to catch prey, and we consider the similarities to *Nesofregetta* to be a striking example of convergence among birds. The specimens described in this study are referred to *Diomedeoides brodkorbi*, *D. lipsiensis*, and to *Diomedeoides* sp. The genus *Frigidafons* is a junior synonym of *Diomedeoides*, and *Diomedeoides minimus* is a junior synonym of *Diomedeoides* (= ''*Gaviota*'') *lipsiensis*. An incomplete articulated specimen of *Diomedeoides brodkorbi* is of special taphonomic interest, since in the close vicinity of its left wing two fairly large shark teeth can be discerned which probably stuck in the soft tissues of the bird when it was embedded in the sediment.

INTRODUCTION

Today the avian order Procellariiformes (tubenoses or petrels) comprises four families of exclusively marine and highly pelagic birds, the Diomedeidae (albatrosses; two recent genera), Procellariidae (fulmars, petrels, shearwaters; 12 recent genera), Hydrobatidae (storm-petrels; eight recent genera in two subfamilies, Oceanitinae and Hydrobatinae), and Pelecanoididae (diving-petrels; a single recent genus). The members of this order greatly differ in size, with albatrosses being among the largest and storm-petrels the smallest seabirds. All Procellariiformes are characterized by more or less tubular nostrils which are associated with a well developed olfactory sense. All species either feed on marine invertebrates (mainly squid), or on fishes. The Procellariiformes are generally thought to be an ancient order which probably originated in the Southern Hemisphere where most of the recent species occur (see Carboneras, 1992 for general information on the order).

The early evolution of procellariiform birds is very poorly understood. Olson and Parris (1987) tentatively assigned an isolated humerus from the Upper Cretaceous or Paleocene (see Hope, 1999) of New Jersey to the Procellariiformes which, if correctly identified, would be the earliest fossil record of the order. In dire need of a revision are the fragmentary specimens described by Harrison and Walker (1977) from the Lower Eocene London Clay formation of England. The genus *Neptuniavis* Harrison and Walker, 1977, for example, most likely represents a pseudo-toothed bird of the extinct family Pelagornithidae, rather than a member of the Procellariidae as suggested by the authors. Panteleyev and Nessov (1987) described *Murunkus subitus*, a new genus and species which is based on an isolated carpometacarpus from the Middle Eocene of Uzbekistan and which was classified into the Diomedeidae. Feduccia and McPherson (1993) assigned an isolated distal tibiotarsus from the Late Eocene of Louisiana to the Procellariiformes, they found this specimen to be morphologically close to the recent genus *Pterodroma* (Procellariidae). ''*Larus*'' *raemdonckii* van Beneden, 1871 from the Rupelian of Belgium was classified into the genus *Puffinus* by Brodkorb (1962); this species is based on an isolated humerus.

The so far most complete record of a Paleogene procellariiform bird was studied by Cheneval (1995) (see also Cheneval and Pharisat, 1995). The specimen, a dissociated skeleton from the Rupelian of France, was assigned to *Frigidafons brodkorbi*, a new genus and species of the Procellariidae; due to its preservation, however, it allows the recognition of only few osteological details. A second species of the genus *Frigidafons*, *Frigidafons babaheydariensis*, was described by Peters and Hamedani (2000) from the Oligocene of the Iran. Fischer (1983, 1985, 1997) described various bones from the German site Espenhain (also Rupelian) as *Gaviota lipsiensis* Fischer, 1983 (distal humeri), *Diomedeoides minimus* Fischer, 1985 (femora), and *Frigidafons brodkorbi* (tarsometatarsi). Most likely these bones and a distal tibiotarsus assigned to *?Rupelornis definitus* by Fischer (1983) belong to a single species which is closely related to *Frigidafons brodkorbi* (see below).

In this study we present new or previously unrecognized material of procellariiform birds from the Oligocene of Germany and Belgium, including a virtually complete and extraordinarily well preserved articulated skeleton. These birds show a peculiar foot morphology which closely resembles that of the recent Polynesian Storm-petrel *Nesofregetta fuliginosa* (Oceanitinae, Hydrobatidae). Further, we undertake a taxonomic revision of the genus *Frigidafons* Cheneval, 1995 and of the above-mentioned taxa that were described by Fischer (1983, 1985, 1997).

Institutional Abbreviations—The specimens are deposited in the Bayerische Staatssammlung für Paläontologie und Historische Geologie, München, Germany (**BSP**), the Museum für Naturkunde, Berlin, Germany (**MB**), the Forschungsinstitut Senckenberg, Frankfurt a.M., Germany (**SMF**), the Staatliches Museum für Naturkunde, Karlsruhe, Germany (**SMNK**), and in the National Museum of Natural History, Washington, USA (**USNM**).

For comparisons, skeletons of the following recent procellariiform species were studied: Diomedeidae: *Diomedea* sp.; Hydrobatidae: *Fregetta tropica*, *Nesofregetta fuliginosa*,

Oceanites oceanicus, *Oceanodroma* sp.; Procellariidae: *Puffinus puffinus*, *P. lherminieri*, *Fulmarus glacialis*, *Daption capensis*, *Calonectris diomedea*, *Bulweria bulwerii*, *Pterodroma neglecta* (partial skeleton), *Procellaria aequinoctialis* (skull), *Macronectes* sp. (skull); Pelecanoididae: *Pelecanoides urinatrix*. In addition, representatives of all other higher avian taxa were investigated. If not indicated otherwise, the anatomical terminology used in this study follows Baumel and Witmer (1993); the dimensions are in millimeters.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758
PROCELLARIIFORMES Fürbringer, 1888
DIOMEDEOIDIDAE Fischer, 1985

Amended Diagnosis—The Diomedeoididae Fischer, 1985 differ from all extant procellariiform birds in the smaller processus supracondylaris dorsalis (humerus). The large processus supracondylaris dorsalis may suggest monophyly of recent Procellariiformes to the exclusion of the Diomedeoididae. Autapomorphic for the fossil family is the unique morphology of the feet: the pedal phalanges (including the ''nail-like'' claws) are dorso–ventrally flattened, the proximal phalanx of the fourth toe is greatly widened mediolaterally, a hallux is absent. The tarsometatarsus bears an unusually deep sulcus extensorius.

Diomedeoides Fischer, 1985

Remarks—The genus *Diomedeoides* is well characterized by the morphology of its femur. Diagnostic features are the very marked fovea ligamenti capitis, the proximo-distally narrow caput femoris and the cranio-caudally very narrow and in caudal view rectangularly-shaped trochanter femoris. We consider the genus *Frigidafons* Cheneval, 1995 a junior synonym of *Diomedeoides* Fischer, 1985. Although owing to the poor preservation of the specimen, details of the femur cannot be discerned in the holotype of *Frigidafons brodkorbi*, this element is well preserved in the referred specimens from Frauenweiler which perfectly match with the type specimen in size and osteological details (the holotype of *Frigidafons brodkorbi* also shows the highly characteristic flattened pedal phalanges which, however, for some reasons have not be mentioned by Cheneval, 1995).

Rupelornis definitus van Beneden, 1871, the type and only species of the genus *Rupelornis*, was based on a distal end of a tibiotarsus from the Rupelian of Belgium which is similar in its morphology to the distal tibiotarsus of *Diomedeoides* (see below and Fischer, 1983). Unfortunately, van Beneden (1871) neither indicated where he deposited the type specimen (probably the Institut Royal des Sciences Naturelles de Bruxelles, Belgium) nor gave a detailed description. It is possible that future studies will show the genus *Diomedeoides* Fischer, 1985 to be a junior synonym of *Rupelornis* van Beneden, 1871. However, until the type specimen of *R. definitus* is directly compared to the specimens treated in this study, we maintain classification of the latter into the genus *Diomedeoides*.

Diomedeoides brodkorbi (Cheneval, 1995) (Figs. 1–5)

Frigidafons brodkorbi Cheneval, 1995:189–197:figs. 1–4.

Referred Specimens—SMNK.PAL.3812 (nearly complete skeleton; the distal left carpometacarpus, the distal right humerus, and the proximal right ulna were fabricated by the preparator of the specimen, Fig. 1); SMNK.PAL.3811 (incomplete articulated skeleton lacking the left leg and the distal part of the left wing, Fig. 2).

Locality—Frauenweiler south of Wiesloch (Baden-Württemberg, Germany), clay pit of the Bott-Eder GmbH (''Grube Unterfeld'') (for information on the site see Micklich and Parin, 1996; Trunkó and Munk, 1998; Mayr, 2000).

Horizon—Rupelian, Early Oligocene (MP 22) (Micklich and Parin, 1996; Legendre and Lévêque, 1997).

Dimensions (Maximum Length in mm)—See Tables 1 and 2.

Description and Comparison—The beak (Fig. 3) is very slender and, apart from the less hooked tip, most similar to that of the recent genus *Puffinus* in shape. In other recent Procellariiformes it is either much shorter (all Hydrobatidae) or more robust. The narial openings measure about 1/3 of the entire length of the beak and are positioned near its dorsal side. There is a groove from the distal end of the narial openings towards the ventral margin of the beak which is also present in recent Procellariiformes. Like in the latter, the rami mandibulae are high at the level of the orbitae (contrary to Cheneval, 1995, who based his observation on a poorly preserved specimen). The os praefrontale has been lost in SMNK.PAL.3812 and obviously was not fused with the os frontale like in some recent Procellariidae (e.g., *Macronectes*, *Procellaria*). Due to preservation it cannot be discerned if, like in recent Hydrobatidae, the frontal part of the os praefrontale was separated by a wide gap from the os frontale. The fossae glandularum nasales (impressions of the ''salt glands'') are narrow like in *Puffinus*, though they appear to have been much shallower. In the recent genera *Fregetta* and *Nesofregetta* (Hydrobatidae), these fossae are very shallow, too, but much wider than in *Diomedeoides*. There are no conspicuous projections at the caudal end of the fossae glandularum nasales, contrary to recent Hydrobatidae and some Procellariidae (e.g., *Bulweria bulwerii*). Like in recent *Puffinus* and *Calonectris*, the septum interorbitale is perforated by a large fenestra. The processus postorbitales are distinct, similar in size to those of *Calonectris diomedea*; they direct ventrally. The fossae temporales are marked like in most recent Procellariidae except, for example, *Bulweria*; in recent Hydrobatidae they are shallow and much smaller.

The cervical vertebrae are fairly long and bear rather short processus costales. Recent Procellariiformes have 15 cervical vertebrae (Forbes, 1882), and a similar number seems to have been present in *Diomedeoides* (although the exact number cannot be discerned). In SMNK.PAL.3812 seven or eight free caudal vertebrae can be counted, at least one of which bears a large processus ventralis. The pygostyle (visible in SMNK.PAL.3812) is large, the lamina pygostyli has a rounded tip.

In its overall morphology, the coracoid is similar to the corresponding bone of recent Procellariiformes. The facies articularis clavicularis does not protrude far medially. The cotyla scapularis is cup-like, a small foramen nervi supracoracoidei is situated near the medial margin of the bone. Cheneval (1995: 189) mentioned a ''slightly developed sterno–coracoidal process [=processus lateralis],'' but in the specimens from Frauenweiler this process appears to be fairly long. Like in some recent Procellariiformes (e.g., *Calonectris diomedea*), the ventral side of the extremitas sternalis bears a marked depression (SMNK.PAL.3812, right side).

The furcula is very widely U-shaped, wider than in all recent Procellariiformes we investigated. Due to preservation, the apophysis furculae is not visible in any of the specimens; it is large in some recent Procellariiformes (e.g., *Fregetta*, *Nesofregetta*), but small in others (e.g., *Puffinus*).

The scapula resembles that of recent Procellariiformes (e.g., *Calonectris diomedea*), the acromion is very short. The sternum is similar to that of *Fulmarus glacialis* in its general outline but is peculiar in that its caudal margin apparently only had one pair of small incisurae laterales. Within recent Procellariiformes, the configuration of the caudal margin of the sternum shows great variation (Forbes, 1882; Pycraft, 1899). Most Procellariidae have two pairs of notches, if incisions are reduced,

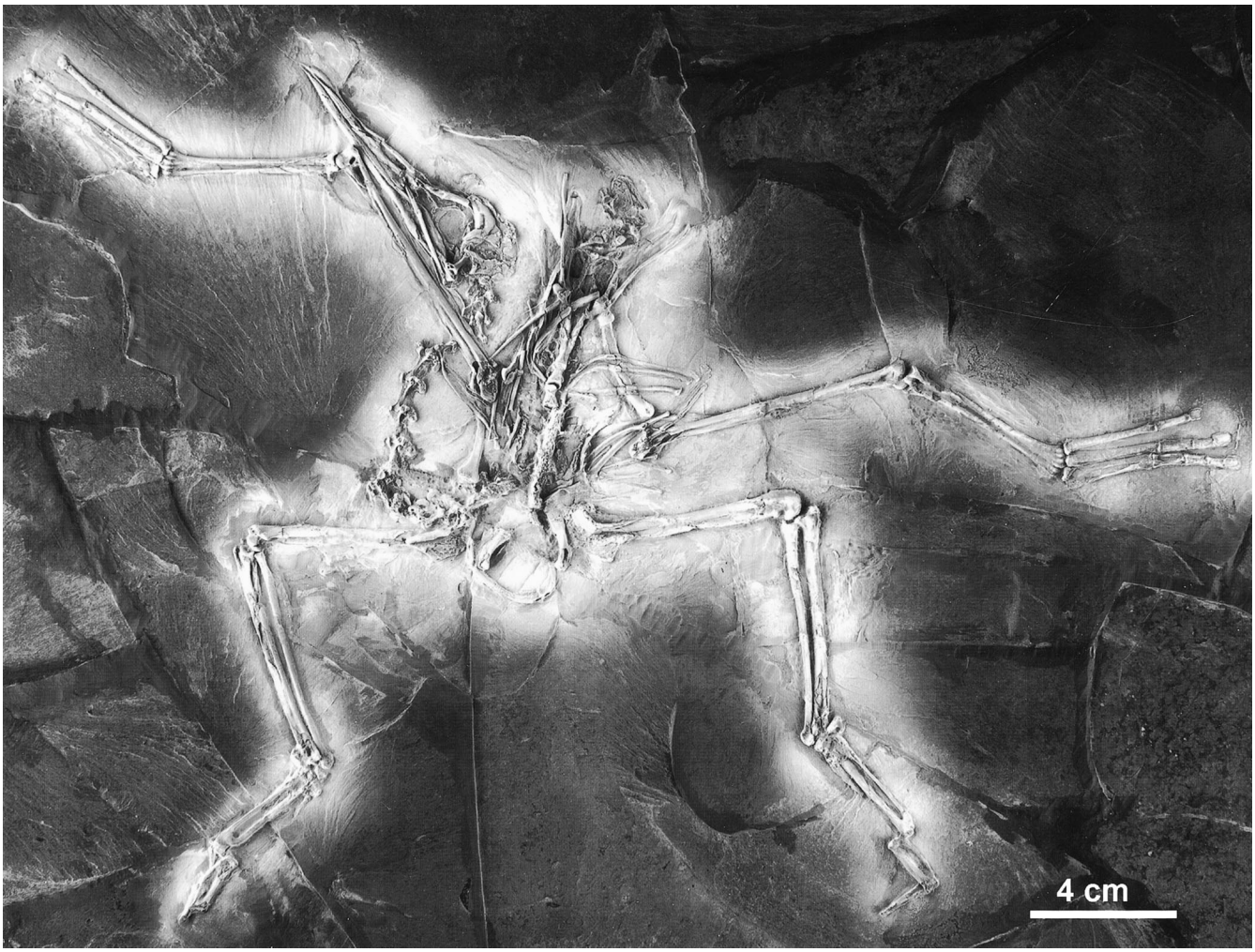

FIGURE 1. Complete articulated skeleton of *Diomedeoides brodkorbi* from the Rupelian of Frauenweiler, Germany (SMNK.PAL.3812). The specimen was coated with ammonium chloride to enhance contrast.

these are the lateral not the medial ones. The caudal margin of the sternum of recent Hydrobatidae completely lacks incisions.

In its proportions, the humerus is similar to the corresponding bone of recent Procellariidae whereas it is shorter and stouter in the Oceanitinae (southern storm-petrels: *Oceanites*, *Pelagodroma*, *Garrodia*, *Fregetta*, and *Nesofregetta*). The shaft is nearly straight, the crista deltopectoralis has a triangular shape. The attachment site of the musculus latissimus dorsi is a marked scar (SMNK.PAL.3811). Apart from being smaller, the distal end is very similar to the distal humerus of *Diomedeoides lipsiensis* which is described below. The humerus of *Diomedeoides* differs from that of recent Procellariiformes in the smaller processus supracondylaris dorsalis. The dorsal margin of the sulcus humerotricipitalis exhibits a ventrally protruding edge (SMNK.PAL.3811), like in some recent Hydrobatidae (e.g., *Fregetta*, *Nesofregetta*).

The ulna resembles that of recent Procellariidae in its proportions. In the Oceanitinae this bone is much shorter and stouter. As far as comparable, the morphology of the proximal and distal end is similar to that of *Fulmarus* and *Calonectris*; in *Puffinus* (which is a wing-propelled diver) the proximal end is more compressed dorso–ventrally and the distal margin of the cotyla ventralis protrudes more cranially.

The carpometacarpus resembles that of recent *Fulmarus* in its proportions; again, it is proportionally shorter in recent Oceanitinae. Judging from the illustrations in Panteleyev and Nessov (1987), the bone also resembles the carpometacarpus of *Murunkus subitus*. Like in some recent Procellariiformes (e.g., *Fulmarus*), the processus pisiformis is only a low elevation. The os metacarpale minus bears a ventrally projecting tubercle at its proximal end (SMNK.PAL.3812).

The phalanx proximalis digiti majoris has a similar shape like that of recent Procellariiformes, a short processus internus indicis (terminology after Stegmann, 1963) is present. Like in many recent Procellariiformes, the phalanx distalis digiti majoris bears a small projection at its caudal margin (SMNK.PAL.3812). The phalanx digiti minoris is long and slender. The crus longum of the os carpi ulnare exceeds the crus breve in length.

The pelvis is narrow like in all recent Procellariiformes, in its proportions it is similar to the pelvis of recent *Calonectris diomedea*. The crista spinosa synsacri is very distinct and raised above the cristae iliacae dorsales. The alae praeacetabulares ilii are medio-laterally narrow. The foramina obturata are not completely closed. Contrary to recent Procellariiformes, the processus terminales ischii do not meet the ossa pubes in specimen SMNK.PAL.3812 (in SMNK.PAL.3811 they are not completely preserved).

In hindlimb proportions, *Diomedeoides* closely resembles recent southern storm-petrels (Oceanitinae) in having very long

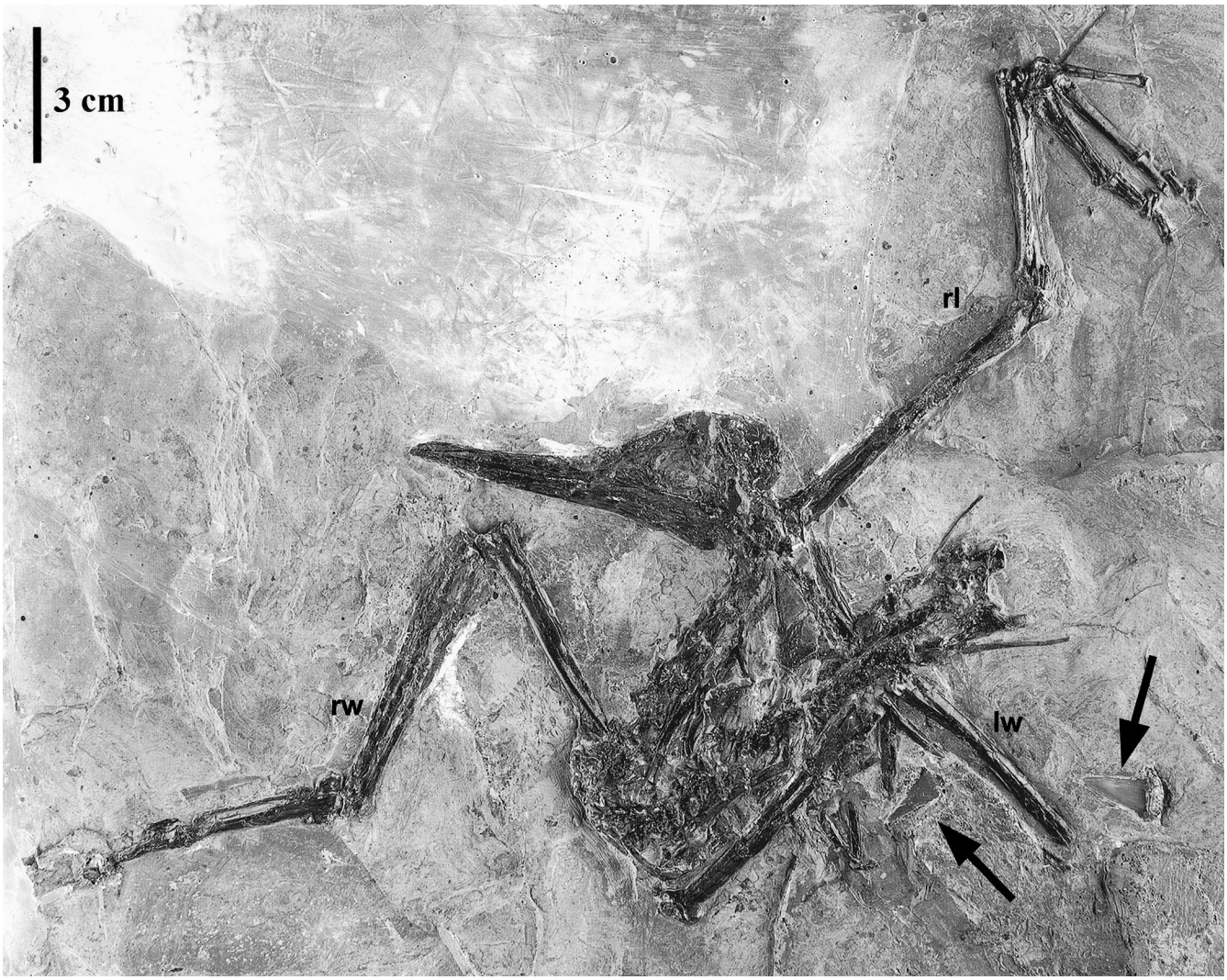

FIGURE 2. Incomplete articulated skeleton of *Diomedeoides brodkorbi* from the Rupelian of Frauenweiler, Germany (SMNK.PAL.3811). Note the two shark teeth next to the left wing (arrows). **Abbreviations**: **lw**, left wing; **rw**, right wing; **rl**, right leg.

tibiotarsi and tarsometatarsi (see Cheneval, 1995). The femur is slightly curved like in *Fulmarus* and *Calonectris* (not as strongly as in *Puffinus*). The caput femoris is very narrow in proximo–distal direction, the fovea ligamenti capitis marked (SMNK.PAL.3812).

The tibiotarsus is the longest limb element. The cristae cnemiales are large and protrude proximally, though not as strongly as in the recent genus *Puffinus*; they do not taper to a point. The crista cnemialis cranialis does not bear a distal hook (like, for example, in *Fulmarus*). The sulcus extensorius is strongly marked as in the unnamed procellariiform bird described by Feduccia and McPherson (1993). The condylus medialis is slightly narrower than the condylus lateralis. The incisura intercondylaris is wide. The fibula measures 2/3 of the length of the tibiotarsus.

The tarsometatarsus of *Diomedeoides* (Fig. 4A) has already been described in some detail by Cheneval (1995), Fischer (1997), and Peters and Hamedani (2000); a few additional descriptive notes are made below. The bone is stouter than the tarsometatarsus of *Diomedeoides* (=''*Frigidafons*'') *babaheydariensis* (which has about the same length but a minimum width of 3.5 vs. 4.2). Its distal end is a nearly identical but larger replica of the distal tarsometatarsus of *Nesofregetta fuliginosa* (Oceanitinae, Hydrobatidae). A characteristic feature of the tarsometatarsus of *Diomedeoides* is the strongly marked sulcus extensorius which, to a slightly lesser degree, is very

TABLE 1. Maximum length of the major bones of *Diomedeoides brodkorbi* (Cheneval, 1995) (left/right).

	Skull	Humerus	Ulna	Carpometacarpus	Femur	Tibiotarsus	Tarsometatarsus
SMNK.PAL.3811	~83	~67/	/65.6	/36.3		/~81	/54.8
SMNK.PAL.3812	85.8	~66.0/	66.9/	36.3/36.8	/~32	84.3/~82.5	51.0/52.3
holotype[a]		69.0	70.7/71.7	40.0/40.2	37.7/38.0	81.6/83.0	55.4/56.4

[a]After Cheneval (1995).

TABLE 2. Length of the pedal phalanges of *Diomedeoides brodkorbi* (Cheneval, 1995).

	I1	I2	II1	II2	II3	III1	III2	III3	III4	IV1	IV2	IV3	IV4	IV5
SMNK.PAL.3811	—	—	26.7			26.3	9.4	6.0		26.3	9.7	6.1	4.9	
SMNK.PAL.3812	—	—	27.0	10.5	5.0	27.0	9.6	6.6	5.0	26.5	9.1	6.7	4.6	4.1

distinct in *Nesofregetta*, too. The distal tarsometatarsus of *Fregetta* does not exhibit this unique morphology and more closely resembles that of other procellariiform birds.

To a striking degree, the peculiar feet of *Diomedeoides* resemble those of the extant *Nesofregetta fuliginosa* (Figs. 4B, 5). The distal phalanges and the proximal phalanges of the third and fourth toe are dorso-ventrally compressed; the proximal phalanx of the second toe is flattened only in its distal third. As is the case in *Nesofregetta*, the proximal phalanx of the fourth toe is grotesquely widened, just distally of its proximal end it strongly projects laterally. A more detailed description of the proximal pedal phalanges is given below. Like in recent Hydrobatidae, the proximal phalanx of the third toe is longer than that of the next two phalanges taken together (in recent Procellariidae it is always shorter, see Forbes, 1882). The fourth toe exceeds the third and second in length. Like in *Fregetta* and *Nesofregetta*, the ungual phalanges are dorso-ventrally flattened, and appear somewhat ''nail-like'' with a blunt distal end. They are medio-laterally wider than the adjacent phalanges. A hindtoe cannot be discerned in any of the specimens of *Diomedeoides brodkorbi*, within recent Procellariiformes it is absent in *Pelecanoides* and extremely vestigial in many other taxa (especially most *Diomedeidae* and Hydrobatidae). The feet of *Diomedeoides* differ from those of *Nesofregetta* in that the proximal ends of the distal phalanges of the fourth toe lack distinct laterally protruding tubercles, the distal phalanges are dorso-ventrally compressed (in *Nesofregetta*, this compression has a stronger medio-lateral component and it is rather the lateral [fourth toe] respectively medial [second and third toe] surface which directs dorsally), and in that the claws are symmetric (asymmetric in *Nesofregetta*). As already noted by Olson (1985), the feet of *Fregetta* are less specialized than those of *Nesofregetta*, the phalanges are less flattened and the proximal phalanx of the fourth toe is less widened. Flattened pedal phalanges also occur in recent grebes (Podicipediformes), but in this taxon the proximal phalanges are medio-laterally compressed not dorso-ventrally like in *Diomedeoides* (grebes are adapted to foot-propelled diving and medio-laterally compressed phalanges reduce drag when the feet are moved forwards).

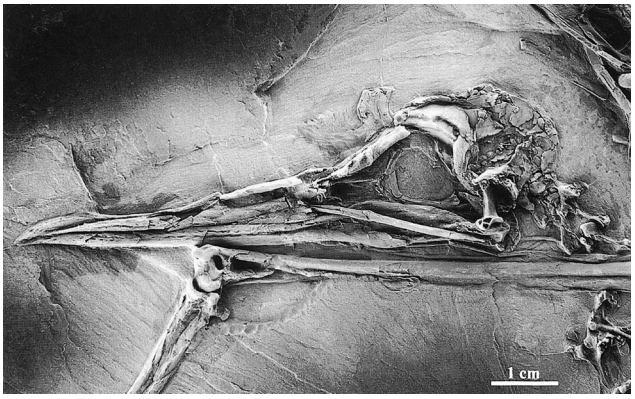

FIGURE 3. Skull of *Diomedeoides brodkorbi* (SMNK.PAL.3812). The specimen was coated with ammonium chloride to enhance contrast.

Diomedeoides lipsiensis (Fischer, 1983)
(Figs. 6–7)

Gaviota lipsiensis Fischer, 1983:152–153, figs. 1, 2.
?*Rupelornis definitus* Fischer, 1983:153, fig. 5.
Diomedeoides minimus Fischer, 1985:113–118, figs. 1–6, 12, 13, 15, 16.
Frigidafons brodkorbi Fischer, 1997:278–280, figs. 17–23.

Referred Specimen—BSP 1973 VII 226 (incomplete right humerus lacking the proximal end).

Locality—Steendorp, Belgium.

Horizon—Rupelian, Early Oligocene (MP? 23–24) (see Cheneval, 1996).

Dimensions (in mm)—Length as preserved, 73.3; estimated total length, ~85; minimum width of shaft, 5.5; distal width, 11.3.

Differential Diagnosis—*Diomedeoides lipsiensis* (Fischer, 1983) differs from *Diomedeoides brodkorbi* (Cheneval, 1995)

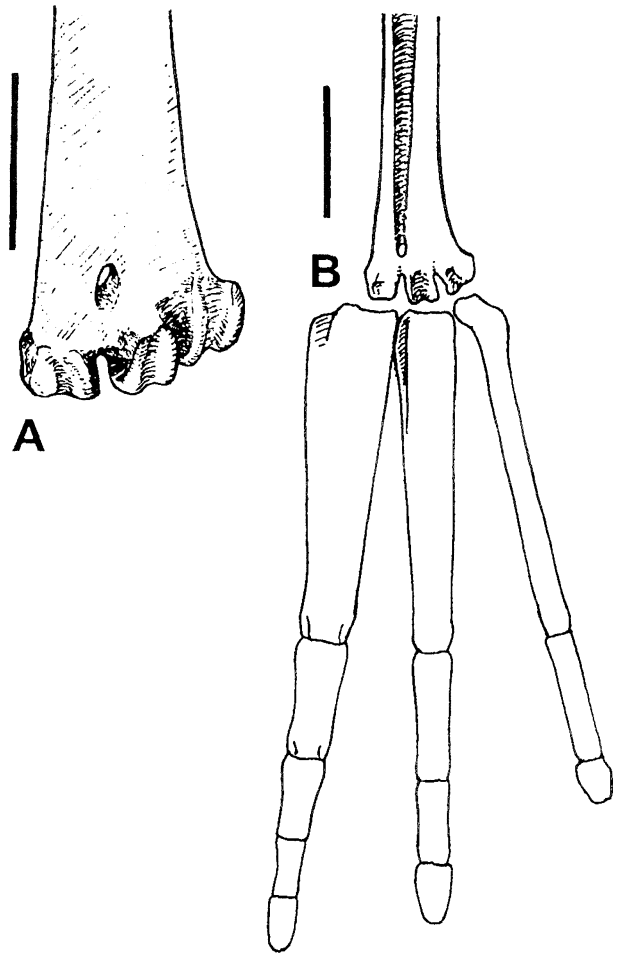

FIGURE 4. A. Distal end of left tarsometatarsus of *Diomedeoides* sp. in plantar (ventral) view (SMF Av 307o). B. *Diomedeoides brodkorbi*, reconstruction of the right foot in dorsal view (after SMNK.PAL.3812). Scale bars equal 10 mm.

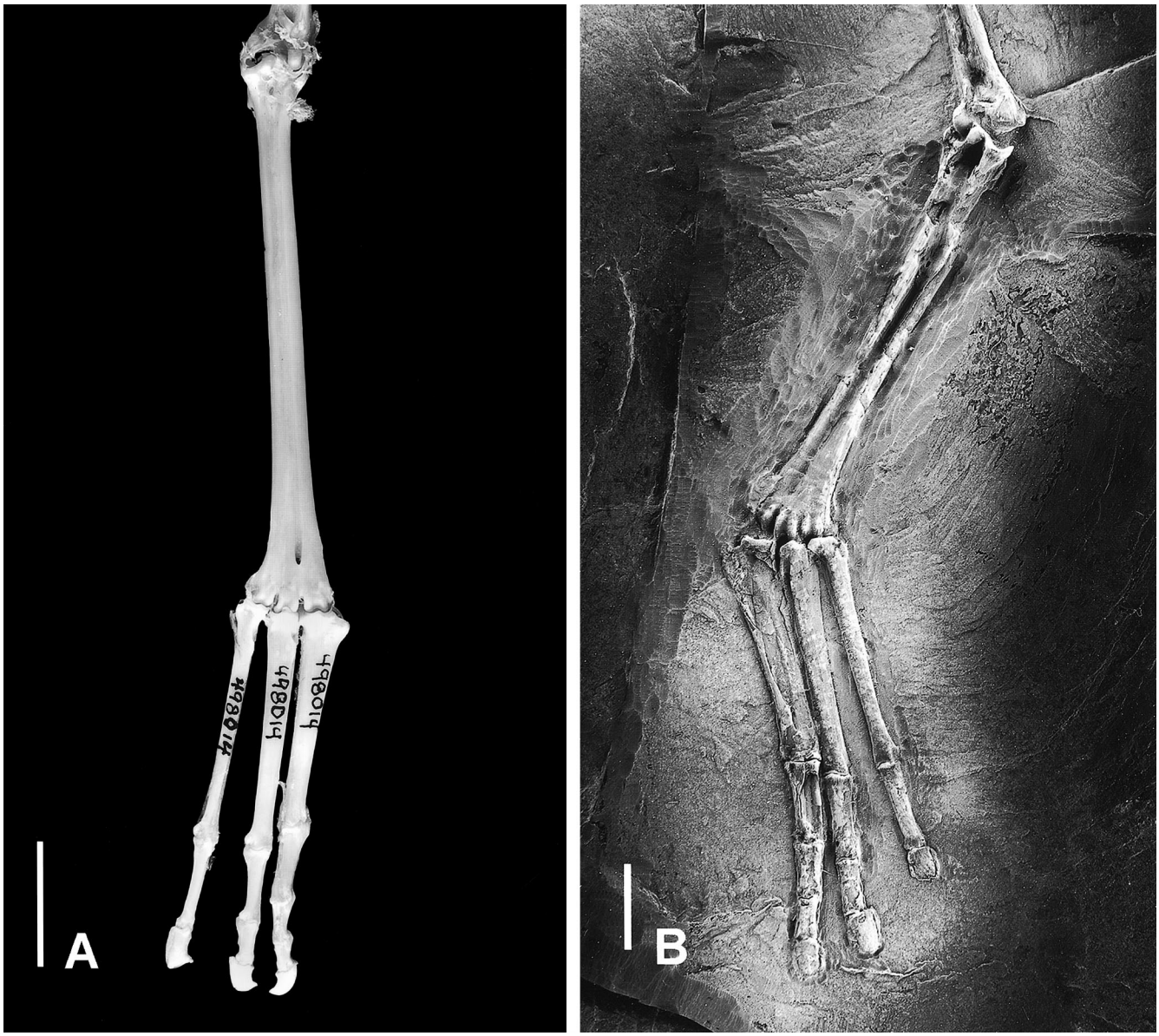

FIGURE 5. **A**, left foot of recent *Nesofregetta fuliginosa* (USNM 498014) in dorsal view. **B**, right foot of *Diomedeoides brodkorbi* (SMNK.PAL.3812) in dorsal view. Scale bars equal 10 mm.

in its larger size (Table 3). It further has a somewhat straighter femur than the Frauenweiler specimens of *Diomedeoides brodkorbi*.

Taxonomic Remarks—This species has a fairly complex taxonomic history because Fischer (1983, 1985, 1997) assigned four different skeletal elements from the same early Oligocene site (Espenhain near Leipzig, Germany) to four different species. ''*Gaviota*'' *lipsiensis* Fischer, 1983 was based on five distal humeri (Figs. 6A, C, 7) and was considered to be a gull (Laridae, Charadriiformes). This species trenchantly differs, however, from recent gulls in the shorter processus supracondylaris dorsalis, and apart from being much smaller and much older (early Oligocene vs. Upper Miocene) it differs from *Gaviota niobara* Miller and Sibley, 1941 in the presence of a ventrally protruding edge at the dorsal margin of the sulcus humerotricipitalis, the smaller fossa musculi brachialis, and the more pronounced epicondylus ventralis. As revealed by the new specimens described above, the humeri referred to ''*Gaviota*'' *lipsiensis* are identical to the corresponding bone of *Diomedeoides brodkorbi*. A distal tibiotarsus from Espenhain was assigned to *?Rupelornis definitus* van Beneden, 1871 by Fischer (1983); this bone is very similar to the distal tibiotarsus of *D. brodkorbi*, too, and also exhibits a marked sulcus extensorius. Fischer (1983) considered the possibility that the tibiotarsus be-

TABLE 3. Comparison of major long bone dimensions between *Diomedeoides brodkorbi* (Cheneval, 1995) and *D. lipsiensis* (Fischer, 1983).

	Humerus, distal width	Femur, maximum length
Diomedeoides brodkorbi[a]	~8.5	~32–38
Diomedeoides lipsiensis[b]	9.3–11.2	44.0

[a]After the holotype, SMNK.PAL.3811, and SMNK.PAL.3812.
[b]After Fischer (1983, 1985).

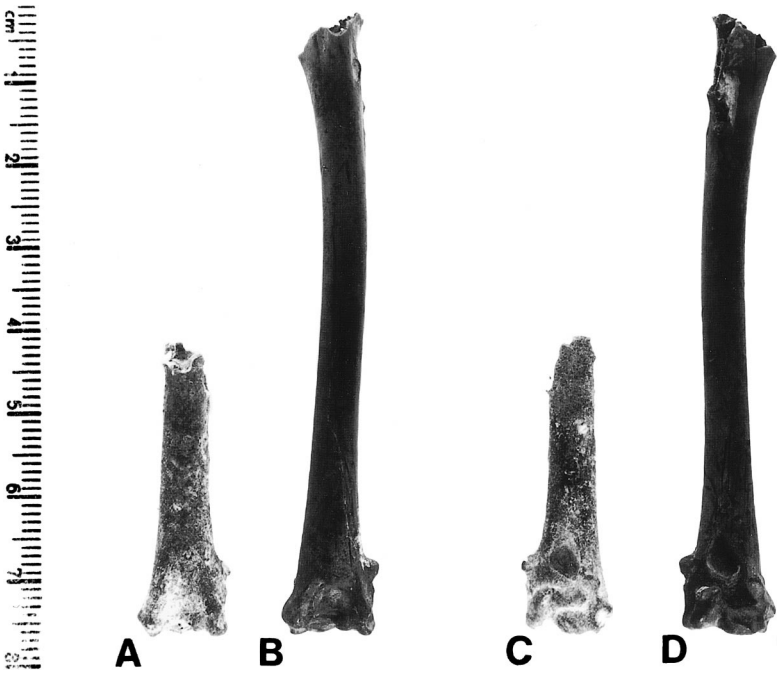

FIGURE 6. **A**, **C**, holotype (distal right humerus) of *Diomedeoides lipsiensis* (Fischer, 1983) (MB.Av.732). **B**, **D**, referred specimen from the early Oligocene of Steendorp, Belgium (BSP 1973 VII 226). **A**, **B**, caudal view. **C**, **D**, cranial view.

longed to the same species as the humeri, but found it to be proportionally too large (taking the proportions of recent gulls as a basis). Also from the Rupelian of Espenhain, Fischer (1985) described three femora as *Diomedeoides minimus*, a new genus and species of the Procellariiformes which he believed to be closely related to recent albatrosses, and for which he erected the new family Diomedeoididae. Apart from being larger, these bones closely resemble the femora of the articulated specimens from Frauenweiler in the proximo-distally narrow caput femoris and in the marked fovea ligamenti capitis. In 1997, Fischer finally assigned 15 isolated tarsometatarsi from Espenhain to *Frigidafons brodkorbi*, but for some reasons did not consider the possibility that these bones belonged to one of the species he described in his earlier studies.

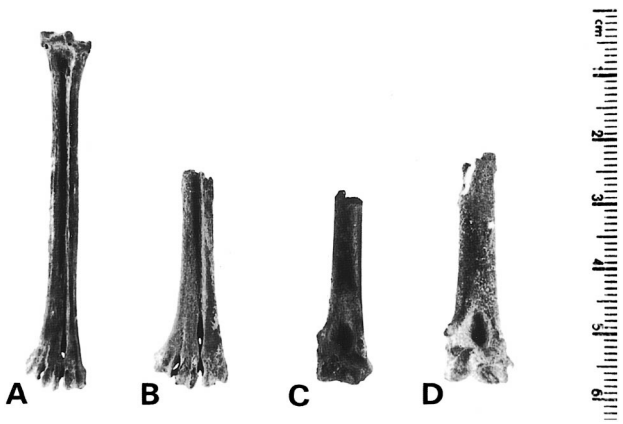

FIGURE 7. Original material of *Diomedeoides lipsiensis* (Fischer, 1983) described by Fischer (1983, 1997), from the early Oligocene of Espenhain near Leipzig (Germany). **A**, complete left tarsometatarsus (MB.Av.896); **B**, distal end of left tarsometatarsus (MB.Av.898); **C**, distal end of right humerus (MB.Av.733); **D**, distal end of right humerus (MB.Av.732, holotype). Note the great difference in size between the specimens.

The above-mentioned specimens from Espenhain greatly differ in size (Fig. 7) and might represent more than one species. The type specimens of ''*Gaviota lipsiensis*'' and ''*Diomedeoides minutus*,'' however, are compatible and from the upper size range. We consider these specimens to be from a single species for which the earliest available name is *Diomedeoides lipsiensis* (Fischer, 1983). *Diomedeoides minimus* Fischer, 1985 is a junior synonym of *Diomedeoides lipsiensis*. For the remains assigned to ''*Gaviota lipsiensis*,'' ''*Diomedeoides minimus*,'' and ''*Frigidafons brodkorbi*'' which are represented by a fair number of specimens, a specific identity is also supported by statistical reasons since avian remains in general are rare at the Espenhain site (other taxa described so far include a rail, a galliform bird, and an owl, see Fischer, 1997).

We identified several other previously unrecognized skeletal elements of *Diomedeoides lipsiensis* in the collection of the Museum für Naturkunde in Berlin: a left carpometacarpus lacking the os metacarpale minus (MB.Av.1141, maximum length: 39.3), a proximal phalanx of the third toe (MB.Av.1148), and three proximal phalanges of the fourth toe (MB.Av.1146 [two specimens with the same number], MB.Av.1154). A complete right ulna (MB.Av.1152, maximum length: 60.5) and a distal right ulna (MB.Av.1145) probably also belong to this species.

Description and Comparison—The specimen from Steendorp, BSP 1973 VII 226, almost perfectly matches with the holotype of ''*Gaviota lipsiensis*'' (Fig. 6), the slightly shorter tuberculum supracondylare ventrale and the slightly less marked ventral margin of the fossa musculi brachialis probably are due to individual variation. Apart from being larger, BSP 1973 VII 226 also corresponds well with the humeri of the known specimens of *Diomedeoides brodkorbi* from Frauenweiler (see above). Compared to recent Procellariiformes, it most closely resembles the humerus of *Fulmarus glacialis* in overall morphology. The attachment site of the musculus latissimus dorsi is a marked scar. The shaft of the humerus is nearly straight and slightly flattened cranio-caudally like in *Fulmarus* (not as strongly as in *Puffinus*). The processus supracondylaris

dorsalis is smaller than in recent Procellariiformes (this process is especially large in *Puffinus*, including the Oligocene *P. raemdonckii*). Condylus dorsalis and condylus ventralis also resemble those of the recent genus *Fulmarus* in shape. The incisura intercondylaris is very shallow. The tuberculum supracondylare ventrale is large and its proximal end protrudes cranially. The distal end of the bone is not compressed in cranioventral-caudodorsal direction as in recent wing-propelled divers like *Puffinus*. The fossa musculi brachialis is of similar depth as in *Fulmarus*. There are two distinct depressions on the epicondylus ventralis and on the epicondylus dorsalis each. The dorsal margin of the sulcus humerotricipitalis bears a ventrally protruding edge, like in recent Hydrobatidae (*Oceanodroma, Fregetta, Nesofregetta*).

Diomedeoides sp.
(Figs. 8–9)

Referred Specimens—SMF Av 302a (right tarsometatarsus lacking distal end); SMF Av 303 (complete left tarsometatarsus); SMF Av 305a (proximal phalanx of left fourth toe); SMF Av 305d (various fragments on a slab, including proximal right humerus and both coracoids); SMF Av 305f (incomplete distal end of right tarsometatarsus); SMF Av 305l (distal right tarsometatarsus); SMF Av 307a (fragmentary articulated skeleton on a slab, including distal part of the beak); SMF Av 307c (distal left tibiotarsus and proximal left tarsometatarsus); SMF Av 307g (articulated thorax on a slab); SMF Av 307h (distal tibiotarsus on a slab); SMF Av 307j (left carpometacarpus); SMF Av 307k (incomplete distal end of left tarsometatarsus); SMF Av 307l (proximal phalanx of right third toe); SMF Av 307o (distal left tarsometatarsus); SMF Av 307p (several pedal phalanges including the proximal phalanx of the right second toe).

Locality—Flörsheim (Hessen, Germany).

Horizon—Late Oligocene (MP 30) (see Mlíkovský and Hesse, 1996).

Dimensions (in mm)—SMF Av 303. Maximum length, 51.0; distal width, 11.0. SMF Av 305a. Maximum length, about 29. SMF Av 307c. Distal width of tibiotarsus, 8.2. SMF Av 307j. Maximum length, 40.5. SMF Av 307l. Maximum length, 30.2. SMF Av 307o. Length as preserved, 48.2; estimated total length, approximately 60–65; distal width, 11.8.

Remarks—The remains from Flörsheim were mentioned by Lambrecht (1933); however, Mlíkovský and Hesse (1996) considered their whereabouts to be unknown. Like the specimens from Espenhain (see above), the tarsometatarsi from Flörsheim greatly differ in size, the estimated length of SMF Av 307o, for example, is nearly 20% longer than that of SMF Av 303. Recent Procellariiformes do not show such an extreme variation in size (neither by individual variation nor by sexual dimorphism) and there might be more than one species represented by the material. The tarsometatarsi SMF Av 302a and SMF Av 303 correspond with those of *Diomedeoides brodkorbi* in size. The tarsometatarsus SMF Av 307o, however, is distinctly larger than that of the type of *D. brodkorbi*. It matches with a tarsometatarsus from the early Miocene of Weisenau (Germany) which—despite its much larger size—was referred to *D. brodkorbi* by Cheneval (1995). Like the latter, the bones from Flörsheim are from younger deposits than the specimens of *Diomedeoides* from Espenhain, Frauenweiler, and Froidefontaine (the type locality of *Diomedeoides brodkorbi*).

Description and Comparison—The tarsometatarsi from Flörsheim are much stouter than the tarsometatarsus of *Diomedeoides babaheydariensis*: SMF Av 303 has the same length as the tarsometatarsus of the type of *D. babaheydariensis*, its distal width, however, is 11.0 vs. 8.0, the minimum width of the shaft is 5.0 vs. 3.5. The specimens have a dorso-ventrally wider shaft than the tarsometatarsi of *Diomedeoides lipsiensis* from Espenhain (with which they compare best in size). The trochlea metatarsi IV reaches as far distally as the trochlea metatarsi III. The latter directs medially and is asymmetric in plantar view (Fig. 4A). A fossa metatarsi I is absent. The incisura intertrochlearis lateralis is much wider than the incisura intertrochlearis medialis.

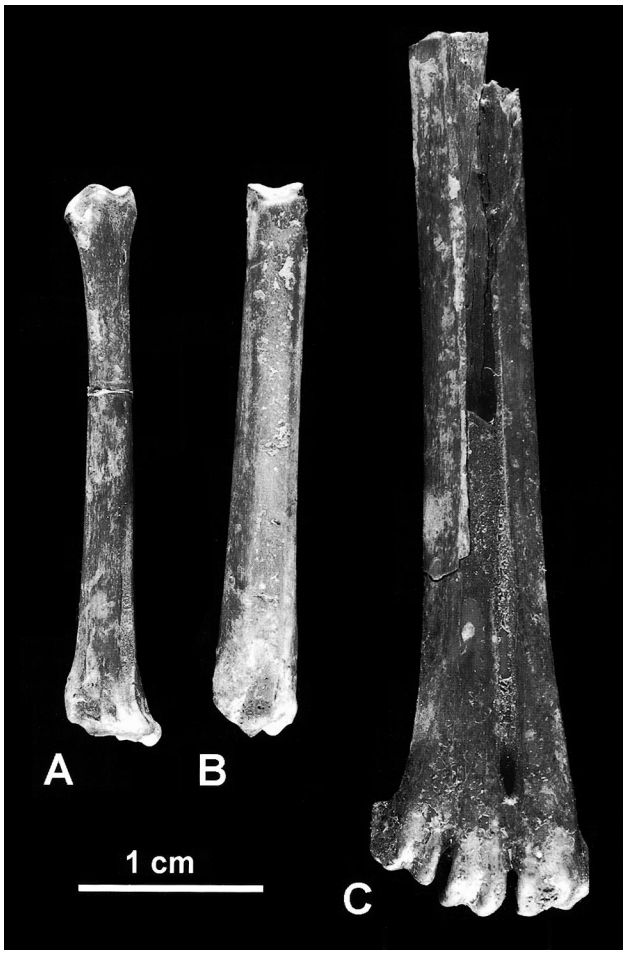

FIGURE 8. Various skeletal elements of *Diomedeoides* sp. from the late Oligocene of Flörsheim (Hessen, Germany). **A**, proximal phalanx of the right second toe, dorsal view (SMF Av 307p); **B** proximal phalanx of right third toe, ventral view (SMF Av 307l); **C**, distal end of left tarsometatarsus, dorsal view (SMF Av 307o).

The proximal pedal phalanges closely resemble those of *Nesofregetta fuliginosa*. The proximal phalanx of the second toe (SMF Av 307p; Figs. 8A, 9A) is dorso–ventrally flattened only in its distal third end, the proximal part of the shaft has a trapezoid cross section. The distal articular surface is asymmetric. The proximal end bears a distinct tendinal groove on its ventromedial side and is strongly protruding laterally. Like in *Nesofregetta*, the lateral projection probably interlocked the phalanx with the adjacent phalanx of the third toe.

The proximal phalanx of the third toe (SMF Av 307l; Figs. 8B, 9B) is greatly flattened dorso-ventrally, only the proximal articular surface is widened. In distal view, the distal articular surface merely is a narrow stripe. In medio-lateral width the phalanx slightly tapers towards its distal end. Along the lateral margin of the dorsal surface there is a narrow but deep sulcus for the tendon of the extensor muscle; in *Nesofregetta* this sulcus is situated more laterally. Along the ventral side of this

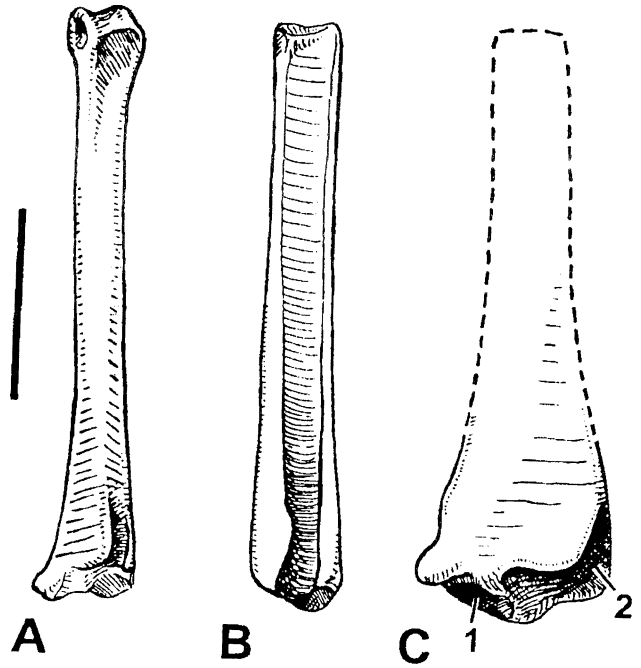

FIGURE 9. *Diomedeoides* sp., proximal pedal phalanges in ventral view. **A**, right second toe (SMF Av 307p); **B**, right third toe (SMF Av 307l); **C**, left fourth toe (SMF Av 305a); **1**, cotyla articularis; **2**, fossa on lateral side of phalanx. Scale bar equals 10 mm.

phalanx there is a very marked groove for the tendon of the flexor muscle which extends over the whole length of this phalanx (although in its distal half it is only very shallow). In proximal view, the proximal articular surface is symmetric with two cotylae for the rims of the trochlea metatarsi III.

The proximal phalanx of the fourth toe (SMF Av 305a; Fig. 9C) is greatly flattened dorso-ventrally and becomes gradually narrower towards its distal end. Especially the proximal end has a very weird morphology: Like in *Nesofregetta* and *Fregetta*, there is a distinct medially projecting process on its ventro-medial side which probably interlocked this phalanx with the adjacent one of the third toe. Situated directly next to this process is the small, oval cotyla articularis (Fig. 9C, no. 1). The phalanx is greatly expanded laterally and most part of its proximal end was not in direct articulation with the rather small trochlea metatarsi IV. Like in *Nesofregetta* there is a strongly marked sulcus on the lateral side of the proximal end (Fig. 9C, no. 2).

DISCUSSION

If only the feet of *Diomedeoides* were known, this genus would certainly have been described as an extinct giant species of the genus *Nesofregetta* (Oceanitinae, Hydrobatidae). The similarities between *Nesofregetta* and *Diomedeoides* are so much the more astonishing since the two taxa greatly differ in size (the fossil genus is about two times larger). Yet whereas the peculiar feet of *Diomedeoides* resemble those of *Nesofregetta fuliginosa* even in detail, the Oligocene genus trenchantly differs from *Nesofregetta*, the closely related genus *Fregetta*, and all other taxa of recent Hydrobatidae in the remainder of its skeleton. The wing proportions of *Diomedeoides* are like those of recent Procellariidae (see Cheneval, 1995); in the Oceanitinae the wing is much shorter and the tibiotarsus is at least two times longer than the humerus. Apart from being larger, *Diomedeoides* further differs from all recent Hydrobatidae in its longer and more slender, *Puffinus*-like beak, the absence of conspicuous projections at the caudal end of the fossae glandularum nasales, the much more marked fossae temporales, the presence of lateral incisions in the caudal margin of the sternum (which is entire in all recent Hydrobatidae), and in the conformation of the hypotarsus (see Cheneval, 1995). Of these characters at least the short wing, the wing-like projections at the caudal end of the fossae glandularum nasales, and the entire caudal margin of the sternum are derived characters, shared by *Fregetta*, *Nesofregetta* and the other Oceanitinae, but absent in *Diomedeoides*.

As already noted by Olson (1985), *Fregetta* is intermediate in its foot morphology between the highly specialized *Nesofregetta* and the other Oceanitinae (see also above). Although being strikingly similar, the feet of *Nesofregetta* and *Diomedeoides* do differ in some details (see description), and we consider the congruences to be one of the more striking examples of parallelism within birds.

Both *Fregetta* and *Nesofregetta* mainly feed on the wing, by ''pattering and dipping'' (Carboneras, 1992:268) and ''use their feet to bound rapidly across the [water] surface, often against strong head winds'' (Olson, 1985:125). According to Stresemann (1927–1934), some small recent storm-petrels, including *Fregetta*, further use their feet as a brake for rapid stops when they catch sight of prey near the water surface. Perhaps a similar habit could also be assumed for *Diomedeoides*, the obviously well developed extensor muscles of the digits probably prevented the toes from swinging back once they were dipped into the water.

In all recent procellariiform birds the three anterior toes are connected by webs, and this certainly was also true in *Diomedeoides*, so much the more since in the articulated skeletons from Frauenweiler the toes cluster close together. As noted by Olson (1985:125) the feet of *Nesofregetta* are ''fused by the skin of the web into a nearly inflexible paddle.''

Crucial for our understanding of the functional and adaptive significance of the feet of *Nesofregetta* (and thus also *Diomedeoides*) is the question why the similarly-sized species of the genus *Fregetta* differ so distinctly in details of their feet morphology. Whether this is, for example, related to a different immersion depth of the feet or to different flight speeds (which effects the resulting forces on the immersed feet) can, however, not be said without further observations of these birds in life.

Specimen SMNK.PAL.3811 is of special taphonomic interest, because in the close vicinity of its left wing two fairly large shark teeth can be discerned (Fig. 2). Isolated shark teeth are very rare in the deposits of Frauenweiler and hence this association is unlikely to be a postmortal accumulation as a result of sea-floor currents. The position of these fossil teeth next to the incomplete left wing further suggests, that either the living bird or its drifting carcass was attacked by a shark. Shark teeth are easily shed and the fossil ones obviously stuck in the feathering or musculature of the bird whilst it was embedded in the sediment.

ACKNOWLEDGEMENTS

We thank the collectors M. Keller and K. Weiß for leaving the excellently prepared fossil specimens from Frauenweiler to SMNK. We are further indebted to S. Olson and J. Dean (National Museum of Natural History, Washington/D.C.) for providing recent comparative material of *Fregetta* and *Nesofregetta*, and to U. Göhlich (BSP), J. Oelkers-Schaefer (SMF), and W. Munk (SMNK) for the loan of the fossil specimens. D. Unwin and S. Frahnert (Museum für Naturkunde, Berlin) made fossil and recent comparative material under their charge available for study. The photographs for Figures 6 and 7 were taken by W. Harre (Museum für Naturkunde, Berlin), all others by S.

Tränkner (SMF). Comments by Cécile Mourer-Chauviré and Gareth Dyke improved the manuscript.

LITERATURE CITED

Baumel, J. J., and L. M. Witmer. 1993. Osteologia; pp. 45–132 *in* J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans, and J. C. Vanden Berge (eds.), Handbook of Avian Anatomy: Nomina Anatomica Avium. Publications of the Nuttall Ornithological Club 23.

Brodkorb, P. 1962. The systematic position of two Oligocene birds from Belgium. Auk 79:706–707.

Carboneras, C. 1992. Order Procellariiformes; pp. 197–278 *in* J. del Hoyo, A. Elliott, and J. Sargatal (eds.), Handbook of the Birds of the World, Vol. 1. Lynx Edicions, Barcelona.

Cheneval, J. 1995. A fossil Shearwater (Aves: Procellariiformes) from the Upper Oligocene of France and the Lower Miocene of Germany. Courier Forschungsinstitut Senckenberg 181:187–198.

——— 1996. Tertiary Avian Localities of Belgium; pp. 535–540 *in* J. Mlíkovský (ed.), Tertiary Avian Localities of Europe. Acta Universitatis Carolinae, Geologica 39.

———, and A. Pharisat. 1995. Contribution de l'avifaune à la taphonomie et au paléonenvironnement du gisement rupélien de Froidefontaine (Territoire de Belfort, France). Geobios, Mémoire spécial 18:87–92.

Feduccia, A., and A. B. McPherson. 1993. A petrel-like bird from the late Eocene of Louisiana: earliest record for the order Procellariiformes. Proceedings of the Biological Society of Washington 106: 749–751.

Fischer, K. 1983. Möwenreste (Laridae, Charadriiformes, Aves) aus dem mitteloligozänen Phosphoritknollenhorizont des Weisselsterbeckens bei Leipzig (DDR). Mitteilungen aus dem Zoologischen Museum in Berlin 59, Supplement: Annalen für Ornithologie 7: 151–155.

——— 1985. Ein albatrosartiger Vogel (*Diomedeoides minimus* nov. gen., nov. sp., Diomedeoididae nov. fam., Procellariiformes) aus dem Mitteloligozän bei Leipzig (DDR). Mitteilungen aus dem Zoologischen Museum in Berlin 61, Supplement: Annalen für Ornithologie 9:113–118.

——— 1997. Neue Vogelfunde aus dem mittleren Oligozän des Weißelsterbeckens bei Leipzig (Sachsen). Mauritiana 16:271–288.

Forbes, W. A. 1882. Report on the Anatomy of the Petrels (Tubinares), collected during the Voyage of H.M.S. Challenger. Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–1876, zoology, vol. 4:1–64.

Harrison, C. J. O., and C. A. Walker. 1977. Birds of the British Lower Eocene. Tertiary Research Special Paper 3:1–52.

Hope, S. 1999. A new species of *Graculavus* from the Cretaceous of Wyoming (Aves: Neornithes); pp. 261–266 *in* S. L. Olson (ed.), Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington, D.C., 4.–7. June 1996. Smithsonian Contributions to Paleobiology 89.

Lambrecht, K. 1933. Handbuch der Palaeornithologie. Gebrüder Borntträger, Berlin.

Legendre, S., and F. Lévêque. 1997. Etalonnage de l'échelle biochronologique mammalienne du Paléogène d'Europe occidentale: vers une intégration à l'échelle globale; pp. 461–473 *in* J.-P. Aguilar, S. Legendre, and J. Michaux (eds.), Actes du Congrès BiochroM'97. Mémoires et Travaux de l'Ecole Pratique des Hautes Etudes, Institut de Montpellier, 21.

Mayr, G. 2000. A new mousebird (Coliiformes: Coliidae) from the Oligocene of Germany. Journal für Ornithologie 141:85–92.

Micklich, N., and N. Parin. 1996. The fishfauna of Frauenweiler (Middle Oligocene, Rupelian; Germany): first results of a review. Instituto Español de Oceanografía, Publicaciones Especiales 21:129–148.

Mlíkovský, J., and A. Hesse. 1996. Tertiary Avian Localities of Germany; pp. 619–647 *in* J. Mlíkovský (ed.), Tertiary Avian Localities of Europe. Acta Universitatis Carolinae, Geologica 39.

Olson, S. L. 1985. Early Pliocene Procellariiformes (Aves) from Langebaanweg, South-Western Cape Province, South Africa. Annals of the South African Museum 95:123–145.

———, and D. C. Parris. 1987. The Cretaceous Birds of New Jersey. Smithsonian Contributions to Paleobiology 63:1–22.

Panteleyev, A. V., and L. A. Nessov. 1987. A small tubinare (Aves: Procellariiformes) from the Eocene of Middle Asia. Trudy zoologicheskogo Instituta 252:95–103.

Peters, D. S., and A. Hamedani. 2000. *Frigidafons babaheydariensis* n. sp., ein Sturmvogel aus dem Oligozän des Irans (Aves: Procellariidae). Senckenbergiana lethaea 80:29–37.

Pycraft, W. P. 1899. Contributions to the Osteology of Birds. Part III. Tubinares. Proceedings of the Zoological Society of London 1899: 381–411.

Stegmann, B. 1963. Der Processus internus indicis im Skelett des Vogelflügels. Journal für Ornithologie 104:413–423.

Stresemann, E. 1927–1934. Aves; pp. 1–899 *in* W. Kükenthal and T. Krumbach (eds.), Handbuch der Zoologie. Walter de Gruyter, Berlin and Leipzig.

Trunkó, L., and W. Munk. 1998. Geologische Beobachtungen in drei tertiären Aufschlußkomplexen im Randbereich des Mittleren Rheingrabens. Carolinea 56:9–28.

Van Beneden, P. J. 1871. Les oiseaux de l'argile rupélienne. Bulletin de l'Académie Royale des Sciences, Lettres et Beaux-Arts de Belgique, série 2, 32:256–261.

Received 3 July 2001; accepted 16 October 2001.