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First European pontoporiid dolphins (Mammalia: Cetacea, Odontoceti) from the Miocene of Belgium and the Netherlands

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The description of two new partial skulls from the southern margin of the North Sea Basin, one from Antwerp, Belgium and the other from the Late Miocene of Neede, the Netherlands, allows a revision of the systematic affinities of the short-beaked dolphin species *Protophocaena minima*. The small species is placed in the family Pontoporiidae, subfamily Brachydelphininae. This new attribution greatly widens the paleogeographical distribution of the family, so far only known by cranial material from South America, and suggests that pontoporiid short-beaked taxa were probably more oceanic than long-beaked taxa such as the extant coastal to river species *Pontoporia blainvillei*. Several isolated periotics from Antwerp are also identified as belonging to pontoporiids.

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INTRODUCTION

The odontocete family Pontoporiidae (Mammalia, Cetacea) is currently known by one extant South American species, the coastal to river dolphin *Pontoporia blainvillei* GERVAIS & D'ORBIGNY, 1844 and three fossil genera with at least parts of the cerebral skull described: *Pontistes* BURMEISTER, 1885 from the Late Miocene of Argentina (figured by Muizon 1984, fig. 18), *Brachydelphis* MUIZON, 1988 from the late Middle Miocene of Peru, and *Pliopontos* MUIZON, 1983 from the Early Pliocene of Peru. Isolated periotics attributed to *Pontoporia* sp. and Pontoporiidae indet. were described by Cozzuol (1985) from the Neogene 'Mesopotamiense' of the Parana River, Argentina. An unnamed pontoporiid skull is reported from the Miocene of Maryland, USA (Godfrey 2001) and additional periotics assigned to the family are cited from the Early Pliocene Yorktown Formation, North Carolina, USA (Whitmore 1994) and the Late Miocene-Early Pliocene of Florida, USA (Morgan 1994). The attribution by Barnes (1984, 1985) of the latest Miocene and Pliocene *Parapontoporia*, from California and Baja California, to the Pontoporiidae was discussed by Muizon (1988a), who noticed more similarities with the Lipotidae. *Parapontoporia* was again linked to the Lipotidae by Fordyce & Muizon (2001), albeit with a question mark. An atlas from the Serravalian of Portugal was tentatively identified as belonging to a pontoporiid (Estevens & Antones 2002), but its identification needs further study (Estevens, pers. comm 2003).

The small odontocete *Protophocaena minima* was described by Abel (1905), based on a fragmentary and worn skull (IRSNB 3917-M.172) from the Neogene of Antwerp (northern Belgium). Its classification by that author in the porpoise subfamily Phocoeninae was probably related to its small size, the shortness of the rostrum, and the existence of premaxillary prominences antero-laterally to the bony nares. Winge (1921) questioned that attribution, suggesting that the anatomy of the face was more similar to *Lagenorhynchus* or *Grampus*. Much later, McKenna & Bell (1997) placed the genus in the superfamily Delphinoidea without familial attribution, and Fordyce & Muizon (2001) referred it to Odontoceti *incertae sedis* (genus name based on a non-diagnostic type specimen).

Recently, an additional specimen was found in a small museum (Boekenbergpark) in Antwerp, Belgium, without data about its locality and age. Another small skull, preserved in the Teylers Museum, Haarlem, the Netherlands, collected during June 1938 in the Late Miocene of the 'Needse Berg', Gelderland, eastern Netherlands, and provisionally identified as a baleen whale skull (Bosch 1999), is compared here to the two Belgian specimens of *Protophocaena minima*, and assigned to the same taxon. The two additional skulls provide information about the morphology of areas of the skull not preserved on the holotype, and about its systematic attribution to the Pontoporiidae. The taxonomic affinities of several periotics from the Neogene of the Antwerp area and the paleogeography of the Pontoporiidae are also discussed.

METHODS

Abbreviations

IRSNB : Institut royal des Sciences naturelles de Belgique, Brussels, Belgium.
M: Collection of types and figured specimens of fossil mammals from the IRSNB.
MNHN: Muséum National d'Histoire Naturelle, Paris, France.
NMB: Natuurhistorisch Museum Boekenberg, Antwerp, Belgium.
TM: Teylers Museum, Haarlem, The Netherlands.
UF: Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA.

Terminology

The terminology for cranial and ear bones anatomy is mainly taken from Fordyce (1994), Kasuya (1973) and Muizon (1984, 1988b). In the following descriptions, the orientations of the periotic are simplified relative to the anatomical position on the basicranium. The anterior direction of the periotic is given by the longitudinal axis of the anterior process and the horizontal ventral plane by the surface contacting the most ventral points of the pars cochlearis and the anterior process.

SYSTEMATIC PALAEONTOLOGY

Order Cetacea BRISSON, 1762
Suborder Odontoceti FLOWER, 1867
Superfamily Inioidea GRAY, 1846
Family Pontoporiidae GRAY, 1870
Subfamily Brachydelphininae MUIZON, 1988b

Type-genus *Brachydelphis* MUIZON, 1988b
Included genera *Brachydelphis* and *Protophocaena* ABEL, 1905

Protophocaena ABEL, 1905

Type and only included species *P. minima* ABEL, 1905

Diagnosis of the genus Same as for the only included species.

Protophocaena minima ABEL, 1905

Figures 1-4

Emended diagnosis Small pontoporiid with a cerebral skull larger than *Pontoporia blainvillei*, close to *Pliopontos littoralis* or

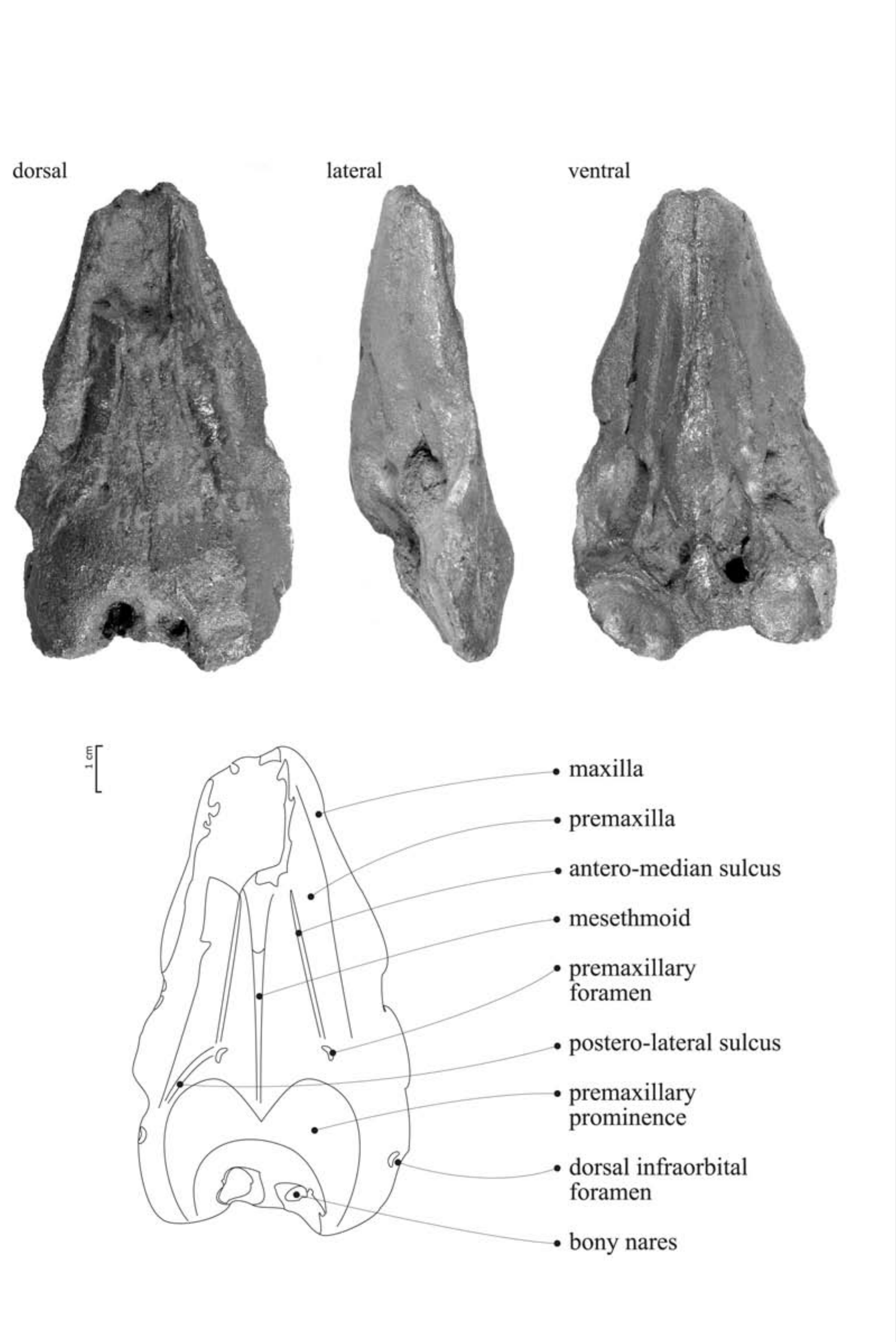

Figure 1 Dorsal, lateral and ventral view of the holotype of *Protophocaena minima* Abel, 1905 (IRSNB 3917-M.172).

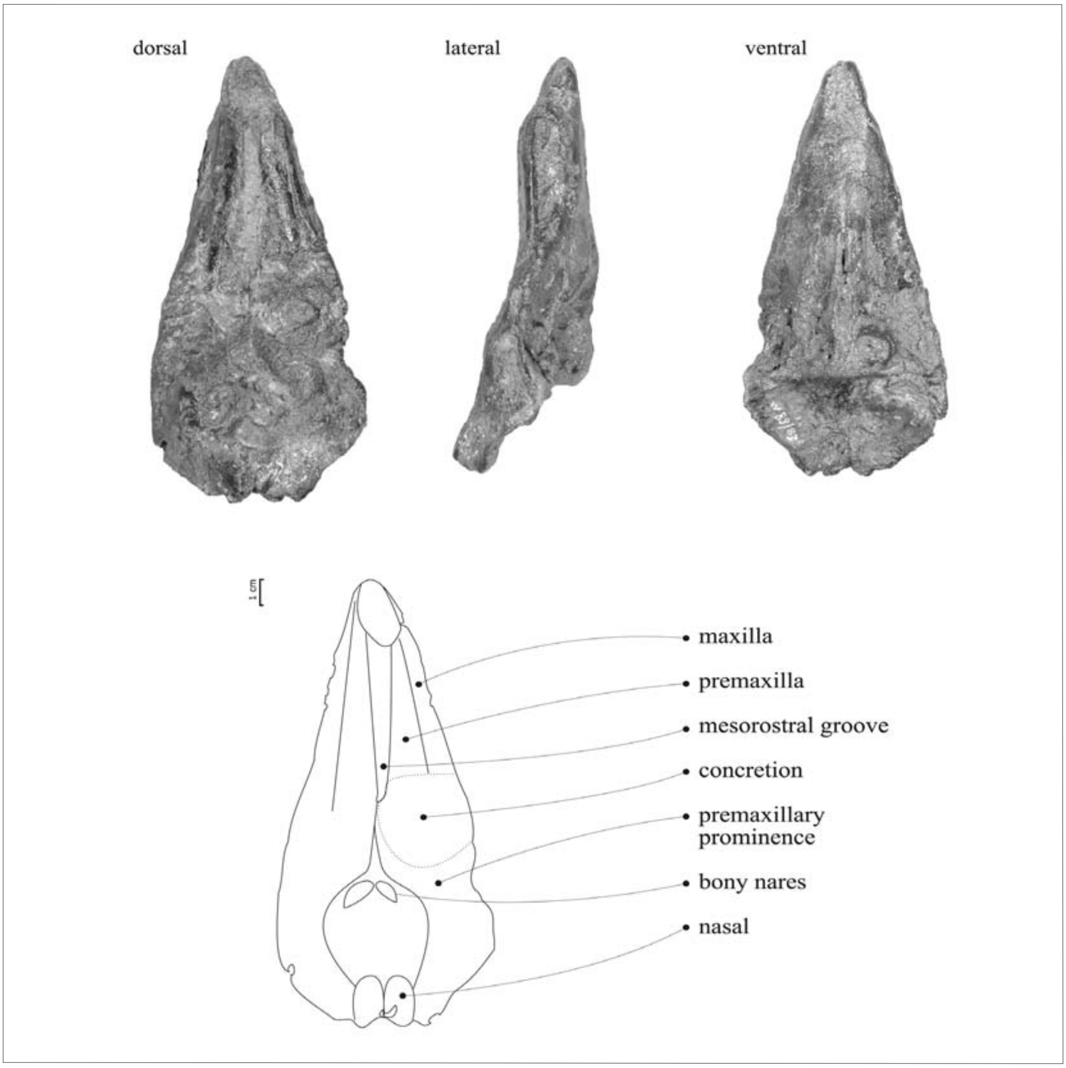

Figure 2 Dorsal, lateral and ventral view of the second Belgian specimen of *Protophocaena minima* (NMB 001).

Brachydelphis mazeasi, and smaller than *Pontistes rectifrons*, with a shortened and pointed rostrum, differing from *Brachydelphis* in: longer contact between premaxilla and nasal relative to the length of the nasal; shorter exposure of the frontals on the vertex; and more median and pointed apices of the palatines.

Holotype IRSNB 3917-M.172, a partial skull including the anterior portion of the face and the base of the rostrum (figured by Abel 1905, figs. 22 and 23).

Locus typicus Antwerp.

Stratum typicum 'Boldérien d'Anvers' following Abel (1905). This stratigraphic information is of reduced interest; most of the odontocetes of Antwerp cited in the works of Abel (1901, 1905) are placed in that old stratigraphic unit while they were more probably found in different levels of the Miocene and even Pliocene. The two Belgian skulls are strongly worn, a characteristic that might indicate a phase of reworking, and a probable origin in the post-Miocene base gravel present in several places around Antwerp (see Vandenberghe *et al.* 1998). This gravel usually contains reworked fossils from the underlying Deurne Sands, Late Miocene, and from older layers (see for example De Meuter *et al.* 1976). The Dutch skull TM 25112 was found in situ in an Upper Miocene bed, Formation of Breda, Upper North Sea Group (Late Miocene).

Referred specimens NMB 001, an eroded partial skull including most of the rostrum, the face, and a part of the vertex, found in Antwerp, Belgium; TM 25112, another partial skull including a worn part of the rostrum, the face and a major part of the vertex, collected in June 1938 by H.C.J. Bosch in a quarry near Neede (Needse Berg), Gelderland, eastern Netherlands.

DESCRIPTION

The holotype IRSNB 3917-M.172 is a worn partial skull of 104 mm (Fig. 1). The anterior part of the rostrum is missing and the face is only preserved until the posterior margin of the bony nares. The second Belgian specimen, NMB 001, is a little bit larger, with a similar type of preservation. It is even more eroded, bearing more concretions, but it is preserved over a greater length, 177 mm (Fig. 2). The rostrum is nearly complete, with probably no more than 10 mm lacking. Posteriorly, the face is preserved until the anterior margin of the frontals on the vertex. The Dutch skull TM 25112 is preserved over a length of 184 mm, including the basal part of the rostrum, the face and a portion of the vertex, on which the nasals are lost (Fig. 3). The length of the short and pointed rostrum is estimated around 100-110 mm on NMB 001, with a width at its base of more than 61 mm (see Table 1). The dorsal and ventral margins of the rostrum stay parallel for more than two-thirds of its length. The apical narrowing is not preserved.

Premaxilla On NMB 001, the premaxillae are medially separated for most of their rostral portion; the maximal width of the opening is around 6 mm. From at least 50 mm before the bony nares, the space between the premaxillae is filled by the ossified mesethmoid - a feature only clearly visible on the holotype. This space progressively narrows, with a width of no more than 1 mm just anteriorly to the bony nares. Starting from the premaxillary foramen, at 24 mm from the bony nares on the holotype, shallow antero-median, postero-lateral, and postero-median sulci separate three main areas of the premaxilla at the base of the rostrum: an elongated triangular medio-anterior surface is more irregular than the smooth lateral part of the bone, and clearly depressed relatively to the rounded eminence that borders the bony nare

Table 1 Measurements (in mm) on the skulls of several pontoporiid species. The measurements on *Pontistes* are taken from the pictures of Muizon (1984, fig. 18); small differences are noticed relatively to the drawing in Burmeister (1885, pl. 2). The measurements of *Pliopontos littoralis* are a mean between the measurements taken on the three skulls MNHN SAS 931, SAS 953 and SAS 193. The measurements of *Brachydelphis mazeasi* are taken on the skull MNHN PPI 121, and of *Pontoporia blainvillei* on the skull IRSNB 6804-1506. e = estimation; + = nearly complete; - = no data.

Measurements on the skulls of different pontoporiid taxa	*P. minima* IRSNB 3917-M.172	*P. minima* NMB 001	*P. minima* TM 3880	*Pontistes rectifrons*	*Pliopontos littoralis*	*Brachydelphis mazeasi*	*Pontoporia blainvillei*
1. width base rostrum	+49	+61	-	e98	63.6	57	39
2. width premaxillae base rostrum	e31	e37	-	54	34.8	e35	20
3. width bony nares	+20	28	29	32	27.8	25	22
4. maximal posterior premaxillary width	46	+52	e71	63	61.3	65	41
5. minimal posterior distance between maxillae	-	11	-	12	18.3	6	6

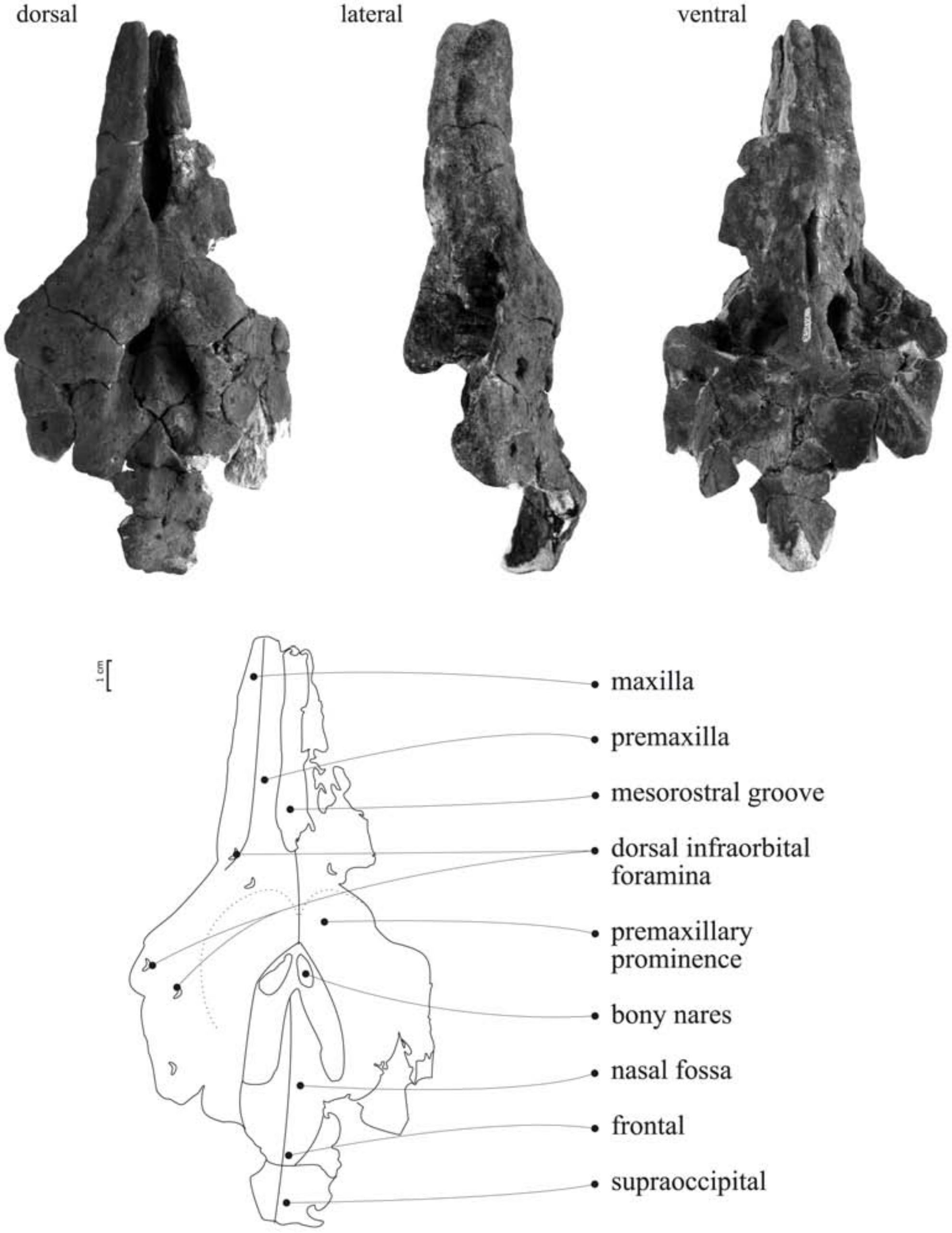

Figure 3 Dorsal, lateral and ventral view of the Dutch specimen of *Protophocaena minima* (TM 25112).

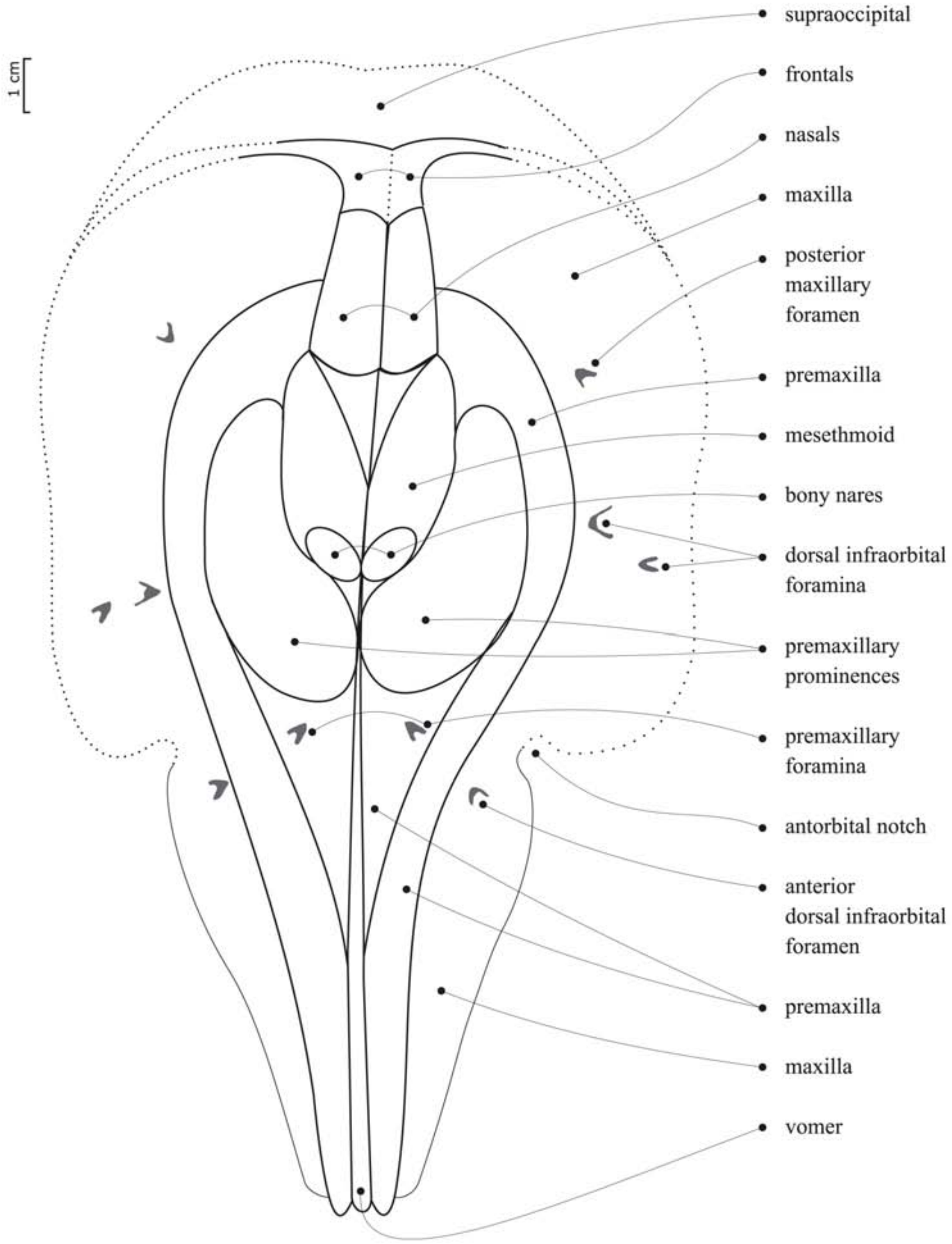

Figure 4 Reconstruction of the skull of *Protophocaena minima*.

antero-laterally. This rounded elevated area is partially eroded on NMB 001, but it is 7 mm higher than the lateral portion of the bone on the holotype, and slightly more developed on TM 25112. The lateral slope of the eminence is moderate, much less pronounced than in fossil and extant phocoenids with a vertical or even overhanging lateral wall. The right prominence is higher than the left on TM 25112 but this condition might be due to a local deformation. From the base of the rostrum, the elevation towards the vertex is achieved in two steps: a first rise for the premaxillary prominences, followed by a plateau, and a second rise, no more pronounced than the first, until the top of the frontals on the vertex.

The extension of the premaxillae towards the vertex is not clear on NMB 001; they are thin and relatively wide until the posterior margin of the bony nares, differing from the narrow and thick posterior projection of the premaxilla in phocoenids. On TM 25112, the posterior portion of the right premaxilla seems the best preserved. The bone stays wide until the posterior margin of the bony nare. From there it narrows until a pointed apex at mid-length along the fossa for the nasal.

Maxilla The maxillae are poorly preserved along the premaxillae on the rostrum. Only one dorsal supraorbital foramen is visible on the left side of the holotype, 8 mm anteriorly to the premaxillary foramen, and another one on the right side, 17 mm posteriorly to the premaxillary foramen, in a position roughly homologous to the one noticed by Muizon (1988b, fig. 53) on *Brachydelphis mazeasi*. The antorbital notches are lost on the three skulls. The alveolar groove has a position similat to *Brachydelphis* (seen on the left side of TM 25112). No teeth alveoli could be identified. On the supraorbital process of TM 25112, the maxilla is pierced by a large dorsal infraorbital foramen 11 mm posteriorly to the anterior apex of the bony nares. The presence of two additional smaller foramina is suggested, one antero-laterally to this larger one, and one 19 mm posteriorly. In ventral view, the maxillae of NMB 001 are separated on the apical portion of the rostrum by the premaxillae or the vomer, with a maximal width of the fenestra of more than 7 mm, in a way similar to *Brachydelphis*.

Palatine The suture between maxilla and palatine is partially visible and a part of the right palatine is preserved on NMB 001. The palatines have a roughly pointed apex, distant one from the other by 9-10 mm, more than 20 mm anteriorly to the antorbital notches. The pterygoid is lacking but the anteriorly narrowing pterygoid sinus fossa hollows the palatine on most of its length.

Nasal On the low vertex of NMB 001, the main posterior part of the nasals is preserved as two posteriorly pointed thick bones with a maximal total width of 25 mm. The length of the nasals could be estimated, by the extension of their fossa on the frontals of TM 25112, at roughly 32 mm. The bony nares are best preserved on TM 25112, they are relatively anteriorly pointed between the premaxillary prominences.

Frontal The frontals appear on the vertex of TM 25112 on a length of more or less 15 mm between the nasal fossae and the supraoccipital, intermediary for that point between *Pliopontos* with very short frontals and *Brachydelphis/Pontoporia* with longer frontals.

Supraoccipital The supraoccipital of TM 25112 shows an anterior part, weakly posteriorly sloping, of 10 mm in length. This area, which was probably originally subhorizontal, is separated from the nearly vertical dorsal portion of the supraoccipital shield by a distinct angulation.

DISCUSSION

The skulls NMB 001 and TM 25112 are distinctly larger than the holotype of *Protophocaena minima*, but the similarities at the level of the base of the rostrum lead us to refer them to the same taxon. *Protophocaena*

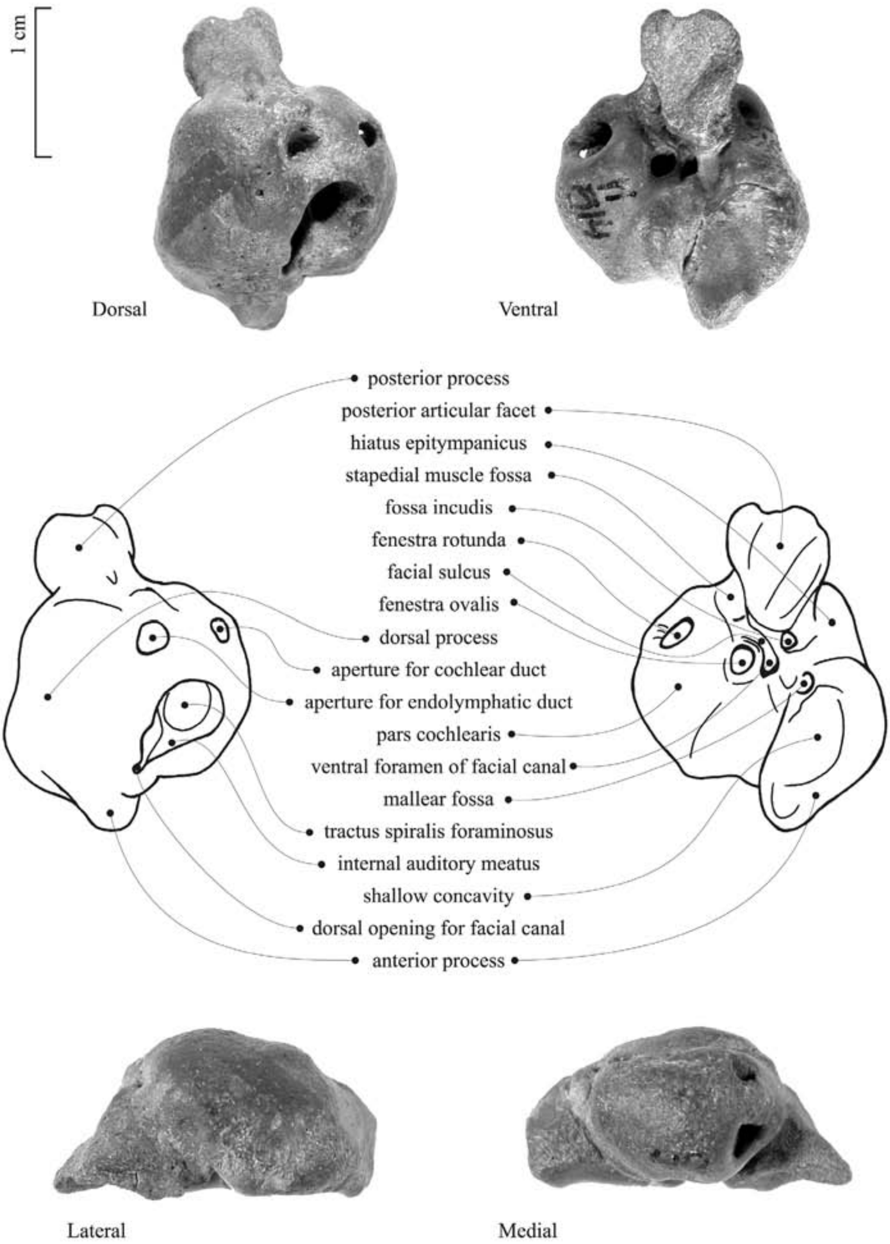

Figure 5 Dorsal, ventral, lateral and medial view of the right periotic of Pontoporiidae cf. *Protophocaena* (IRSNB M1890) from Doel, Belgium.

differs from the Phocoenidae, contradicting the hypothesis of Abel (1905), by the more median apices of the palatines, a less erected lateral wall of the premaxillary prominence antero-lateral to the bony nare, wider and thinner posterior projection of the premaxilla along the bony nare and a particularly low vertex.

The last feature, added to strong morphological similarities at the level of the premaxillary eminences and to long nasals, clearly suggests pontoporiid affinities.

The most striking feature of *Protophocaena minima* is the very short and pointed rostrum (see reconstruction, Fig. 4), comparable to the condition in *Brachydelphis mazeasi*. In that species, the ratio between width of the rostrum at its base and length of the rostrum is around 0.56. On NMB 001, the ratio is estimated to more than 0.54. *Protophocaena minima* differs from *Brachydelphis mazeasi* in the following characters: the premaxilla has a longer contact with the nasal in *P. minima*, the exposed part of the frontals on the vertex is shorter than in Brachydelphis; the palatine is relatively more pointed. Because of the fragmentary state of the three specimens, it seems prudent not to merge them (yet) in the genus *Brachydelphis*, even if the similarities seem significant. Nevertheless, since the subfamily Brachydelphininae Muizon, 1988 - until now only containing the monotypic genus *Brachydelphis* - is mainly defined by the shortness of the rostrum, we suggest to include *Protophocaena minima* in that subfamily, keeping in mind that the development of an ecologically constrained short rostrum occurs in parallel in several families of usually long-snouted dolphins (see Bianucci & Landini 2002, fig. 5).

Pontoporiidae cf. Protophocaena
Figure 5

Referred specimen IRSNB M 1890, a right periotic collected by M. Bosselaers in piles of moved Neogene sands at Doel (near the Indaver factory), north of Antwerp.

Discussion The complete right periotic has a total length of 23 mm. (Fig. 5). The antero-medially pointed anterior process is short: just 4 mm. from the apex of the process to te anterior margin of the pars cochlearis. The ventral face of the anterior process is only weakly concave, lacking a distinct epitubarian fossa for the accessory ossicle of the tympanic. The hiatus epitympanicus is deep, isolating the posterior process from the rest of the bone, a condition specially visible in dorsal view. The posterior articular facet is markedly concave. The pars cochlearis is distinctly dorso-ventrally flattened. The internal auditory meatus is elongated towards the base of the anterior process by the anterior shift of the dorsal opening for the facial canal. The aperture for the endolymphatic duct is rounded, a little more lateral than the internal auditory meatus. The aperture for the cochlear duct is also circular, but smaller, on the medio-postero-dorsal corner of the pars cochlearis. In lateral view, the outline of the dorsal process is elevated on its whole length.

The much shortened anterior process, the constriction at the base of the posterior process, and the thick dorsal process are characters present on the few known pontoporiid periotics - *Pontoporia*, *Brachydelphis* and *Pliopontos*. Apart from the more circular dorsal opening of the endolymphatic duct in IRSNB M 1890, the similarities with *Brachydelphis mazeasi* are particularly striking, with a relatively low pars cochlearis and a well developed posterior process. Furthermore, the size of the periotic is nearly equal (total length of 24 mm. in *B. mazeasi* MNHN PPI 121).

IRSNB M 1890 is actually even closer to the periotic MNHN PPI 236 of the unnamed new species of *Brachydelphis* (Muizon 1988b, fig. 38). Because *Protophocaena* is close to *Brachydelphis* and is, so far, the only known pontoporiid from the Neogene of Belgium and The Netherlands, this periotic probably belongs to that genus, but we cannot prove that the periotic comes from the same stratigraphic horizon as the skulls. The periotic IRSNB M 1890 is therefore placed in Pontoporiidae cf. *Protophocaena*.

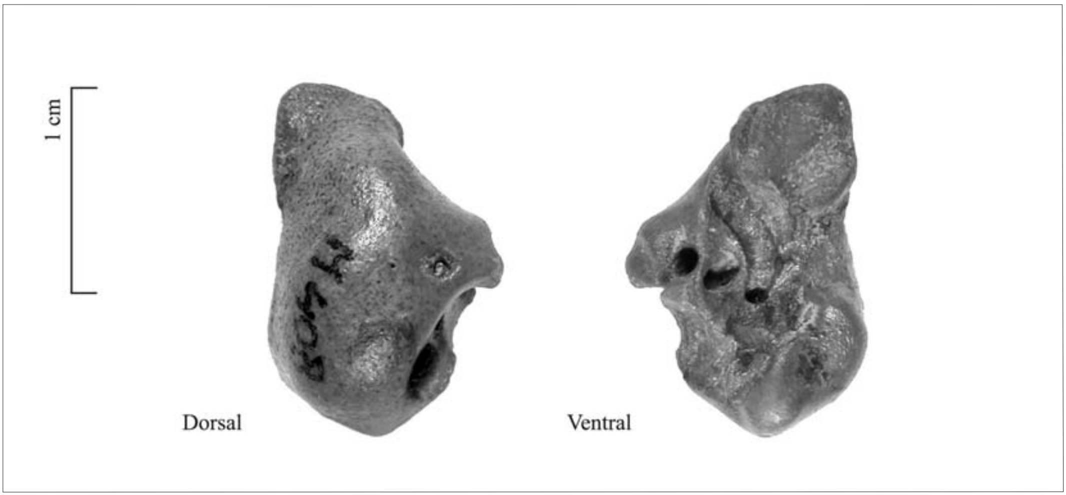

Figure 6 Dorsal and ventral view of the fragmentary right periotic of an indeterminate Pontoporiidae (IRSNB M1891) from Doel, Belgium.

Pontoporiidae indet.

Figure 6

Referred specimen IRSNB M 1891, a fragmentary right periotic collected by J. Tak, in the same piles of moved Neogene sands as IRSNB M 1890, at Doel, north of Antwerp.

Discussion This more fragmentary right periotic (Fig. 6), lacking a part of the pars cochlearis and smaller than IRSNB M 1890 (total length of 18 mm) also shares with the pontoporiids the short anterior process, the posteriorly extented posterior process, and the thick dorsal process. It is identified as Pontoporiidae indet. and might represent a taxon different from IRSNB M 1890.

The pontoporiid periotic UF 135935, from the Late Miocene-Early Pliocene of Florida, figured by Morgan (1994, fig. 6a-b), is larger than IRSNB M 1890. It has a relatively more elevated pars cochlearis, a more distinctly separated dorsal aperture for the facial canal, and a dorsal aperture for the endolymphatic duct more distant from the internal auditory meatus. In these characters, it is more similar to extant *Pontoporia* than to the fossil taxa. The pontoporiid periotics from the Early Pliocene of North Carolina, mentioned by Whitmore (1994) were not figured.

PALEOGEOGRAPHY OF THE FAMILY PONTOPORIIDAE

Except for the periotics from Florida and North Carolina, cranial parts of fossil and extant pontoporiid dolphins were previously only described from both coasts of South America (Fig. 7). The systematic revision of *Protophocaena minima* allows an important extension of the geographic range of the family into the North Sea Basin. Furthermore, these records are among the oldest for the family (Late Miocene for the Dutch specimen). Even if, judging by current knowledge, South America seems to be the area where the Pontoporiidae have reached their highest taxonomic diversity, its origin around that continent is no longer obvious.

It is also interesting to note that the North Sea specimens belong to a short-rostrum genus, probably closely related to the Late Miocene Peruvian *Brachydelphis*, while the known long-rostrum taxa are limited to the coasts of South America; the extant *Pontoporia blainvillei* is geographically limited to waters not deeper than 30 m. on the eastern coast of South America (Culik 2001), and is relatively common in the La Plata river (Brownell 1989). This might suggest more oceanic abilities for the species with a shorter ros-

Figure 7 World distribution of pontoporiids. **a** = Mid-Late Miocene; **b** = Early Pliocene; **c** = Recent.

trum, allowing a more widespread subfamily Brachydelphininae.

Small extant odontocetes with a shortened rostrum are the phocoenids *Phocoena*, *Neophocaena* and *Phocoenoides*. The rostrum of *Phocoenoides dalli*, Dall's porpoise, is particularly short and pointed, with a length usually less than 1.5 times its basal width. It is known to inhabit both neritic and oceanic zones, although the major populations are oceanic and individuals rarely come close to shore (Houck & Jefferson 1999). This comparison might help us to understand the records of pontoporiids far from South American coasts.

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