

## **Out of the Pacific: A Second Fossil Porpoise from the Pliocene of the North Sea Basin**

Authors: Colpaert, Wouter, Bosselaers, Mark, and Lambert, Olivier

Source: Acta Palaeontologica Polonica, 60(1) : 1-10

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.00115.2014>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](http://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# Out of the Pacific: A second fossil porpoise from the Pliocene of the North Sea Basin

WOUTER COLPAERT, MARK BOSSELAERS, and OLIVIER LAMBERT



Colpaert, W., Bosselaers, M., and Lambert, O. 2015. Out of the Pacific: A second fossil porpoise from the Pliocene of the North Sea Basin. *Acta Palaeontologica Polonica* 60 (1): 1–10.

Although modern porpoises (Phocoenidae, Odontoceti, Cetacea) occupy most oceanic regions of the world, their fossil record outside the Pacific Ocean remains extremely scarce. Based on a partial skull from lower Pliocene layers (Kattendijk Formation, Zandclean, 5–4.4 Ma) of the Antwerp harbour, a new genus and species of fossil phocoenid, *Brabocetus gigaseorum* gen. et sp. nov., is described. The new taxon is diagnosed by a unique combination of characters including an anterolaterally widely-open antorbital notch, the anteromedial sulcus being shorter than the posteromedial sulcus, the frontal boss being longer than wide, pronounced asymmetry of the vertex, and the possible presence of an additional longitudinal sulcus across the premaxillary eminence. The phylogenetic analysis indicates that *B. gigaseorum* is not closely related to extant phocoenids; it is included in a clade comprising most north-west Pacific fossil species, two north-east Pacific fossil species, and the only previously described North Sea fossil species *Septemtrioctetus bosselaersi*. Considering the paleobiogeographic distribution of phocoenids, an early Pliocene arrival from the North Pacific to the North Sea may be correlated to the early opening of the Bering Strait and migration via the Arctic. The presence of *S. bosselaersi* in younger deposits (Piacenzian) of the southern margin of the North Sea Basin could be the result of either a second dispersal event, or of local speciation in the North Sea, whereas an additional trans-Arctic migration from the North Pacific lead to the present occupation of the North Atlantic and North Sea by the phylogenetically distantly related harbor porpoise *Phocoena phocoena*.

**Key words:** Mammalia, Cetacea, Odontoceti, Phocoenidae, Pliocene, North Sea Basin, Belgium.

Wouter Colpaert [wouterjcolpaert@gmail.com], Research Unit Palaeontology, Universiteit Gent, Krijgslaan 281/S8, 9000 Gent, Belgium; current address: Populiereweg 16, 8680 Koekelare, Belgium.

Mark Bosselaers [mark.bosselaers@telenet.be] and Olivier Lambert [olivier.lambert@naturalsciences.be] (corresponding author), D.O. Terre et Histoire de la Vie, Institut royal des Sciences naturelles de Belgique, rue Vautier 29, 1000 Brussels, Belgium.

Received 5 August 2014, accepted 24 November 2014, available online 14 December 2014.

Copyright © 2015 W. Colpaert et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

## Introduction

Porpoises (Phocoenidae) are a family of small odontocetes (toothed whales) including six extant species in three genera (*Neophocaena*, *Phocoena*, and *Phocoenoides*). Nowadays, the family displays a worldwide distribution, in a high variety of habitats, from circumpolar Southern Hemisphere oceanic regions to shallow waters of the Gulf of California, from coastal, estuarine, and riverine habitats along the tropical to temperate Indian, South Pacific, and South Atlantic Oceans to the shelf temperate waters of the North Atlantic and North Pacific. As compared with the low modern species diversity and their wide geographic distribution, the study of the fossil record of the family resulted in the description of a growing

number of late Miocene and Pliocene species, predominantly from the North and South-East Pacific (11 species in 8 genera; Barnes 1984; Muizon 1984, 1988b; Ichishima and Kimura 2000, 2005, 2009; Murakami et al. 2012a, b; Racicot et al. 2014). Although a periotic from the middle Miocene (Serravallian) of Malta and isolated ear bones from the Pliocene of Italy were tentatively identified as belonging to phocoenids (Bianucci et al. 2009, 2011), the only well-founded and figured record of an extinct porpoise outside the Pacific Ocean is from the Pliocene of the southern margin of the North Sea Basin (Lambert 2008). This species is only distantly related to the modern inhabitant of the North Sea, *Phocoena phocoena*. The limited availability of marine rocks from the late Miocene and Pliocene outside the Pacific Ocean

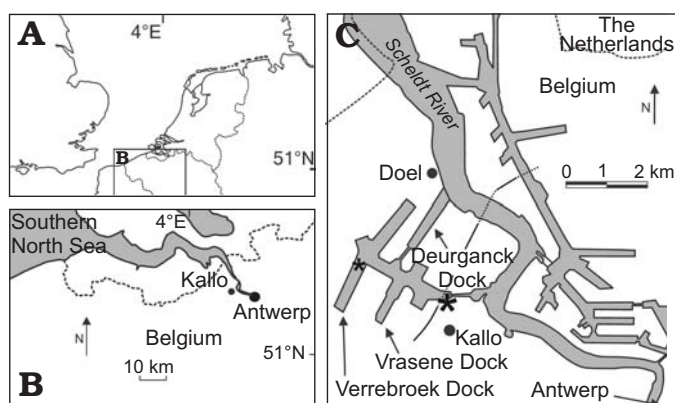


Fig. 1. Maps indicating the type localities of fossil phocoenids in the port of Antwerp, north-west of Antwerp, Belgium, southern margin of the North Sea Basin. **A.** Map of northern Belgium. **B.** Southern margin of the North Sea Basin. **C.** Port of Antwerp. The small asterisk indicates the type locality of *Septemtriocetus bosselaersi*, in the Verrebroek Dock, and the large asterisk indicates the type locality of *Brabocetus gigaseorum* gen. et sp. nov., at the entrance of the Beveren Tunnel. Modified from Lambert (2008).

does not fully explain this scarcity, as several localities, for example from the east coast of North America and the Mediterranean (e.g., Bianucci 1996; Bianucci and Landini 2002; Whitmore and Kaltenbach 2008), yielded rich cetacean assemblages. Another contributing factor may be the difficulty in identifying fragmentary remains of stem phocoenids, especially ear bones retaining similarities with other extant and extinct delphinids (Muizon 1988b; Bianucci et al. 2011). Indeed, all fossil phocoenids described to date fall outside the crown-clade Phocoenidae. And molecular data (Rosel et al. 1995) suggest a relatively recent radiation and dispersal for crown phocoenids, during the late Pliocene and Pleistocene for which fewer marine mammal fossil localities yielding phocoenid remains are available (e.g., Harington 1977; Post 2005). It is interesting to note that a rather similar process was recently proposed to account for the fossil record and extant diversity of delphinids (true dolphins; Bianucci 2013).

Based on a fragmentary skull from the early Pliocene of northern Belgium, we describe the second-known phocoenid species outside the Pacific Ocean. Furthermore, we report on our analysis of its phylogenetic affinities, and comment on dispersal scenarios accounting for the past and present geographic distribution of the family.

**Institutional abbreviations.**—IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.

## Material and methods

**Specimen.**—The fragmented skull IRSNB M. 2171 was discovered in the second half of the 1970s by Robert Marquet (volunteer palaeontologist at the IRSNB), in multiple detached fragments. Marquet was able to reassemble most of the elements into three large but separate regions of the skull. The first region preserves the rostrum base, the facial area, the

dorsal portion of the supraoccipital shield, and the palate. The second portion includes the left squamosal and exoccipital, part of the left alisphenoid, the occipital condyles, and elements of the basioccipital basin. The third reassembled cluster includes the right squamosal, exoccipital, and part of the right alisphenoid. The first and second fragments contact at the level of the internal sagittal crest dorsally and at the level of the vomer ventrally, just posterior to the choanae. The second and third fragments contact lateral to the right occipital condyle and along the medial margin of the right alisphenoid. However, due to slight approximations during assembling, these three parts cannot be precisely connected at each contact.

**Anatomical terminology.**—The terminology for the cranial features follows Mead and Fordyce (2009).

## Systematic palaeontology

Order Cetacea Brisson, 1762

Clade Neoceti Fordyce and Muizon, 2001

Suborder Odontoceti Flower, 1867

Infraorder Delphinida Muizon, 1984

Superfamily Delphinoidea Gray, 1821

Family Phocoenidae Gray, 1825

Genus *Brabocetus* nov.

*Type species:* *Brabocetus gigaseorum* sp. nov., monotypic, see below.

*Etymology:* From Silvius Brabo, a mythical character who liberated the city of Antwerp from the giant Antigoon, and Latin *cetus*, whale.

*Diagnosis.*—Same as for the only included species, *B. gigaseorum*.

*Brabocetus gigaseorum* sp. nov.

Figs. 2, 3, 5–7.

*Etymology:* Honouring Paul and Pierre Gigase (father and son) for their long-term effort in collecting fossil marine mammal remains in the area of Antwerp and for generously donating the specimen IRSNB M. 2171 to the IRSNB.

*Holotype:* IRSNB M. 2171, a partial skull in three fragments, lacking the anterior part of the rostrum, part of the left supraorbital process, the nasals, the pterygoids, and some elements of the cerebral cavity and basicranium.

*Type locality:* Beverentunnel, left bank of the River Scheldt, Antwerp Harbour, northern Belgium (Fig. 1). The locality is situated two kilometres north of the village of Kallo. Geographic coordinates: N 51°15'50", E 4°16'19".

*Type horizon:* The skull was found in the Kattendijk Formation, 2 m below the Oorderen Sands Member, Lillo Formation, in a layer of grey glauconitic sand without mollusc shells. The Kattendijk Formation is dated from the early Pliocene (Zanclean) based on dinoflagellates, foraminifers, and molluscs (Vandenberghe et al. 1998; Louwye et al. 2004), more precisely between 5 and 4.4 Ma (De Schepper et al. 2009). This unit represents a neritic deposition (30–50 m water depth) with open-marine influence, under a warm to temperate climate (De Schepper et al. 2009).

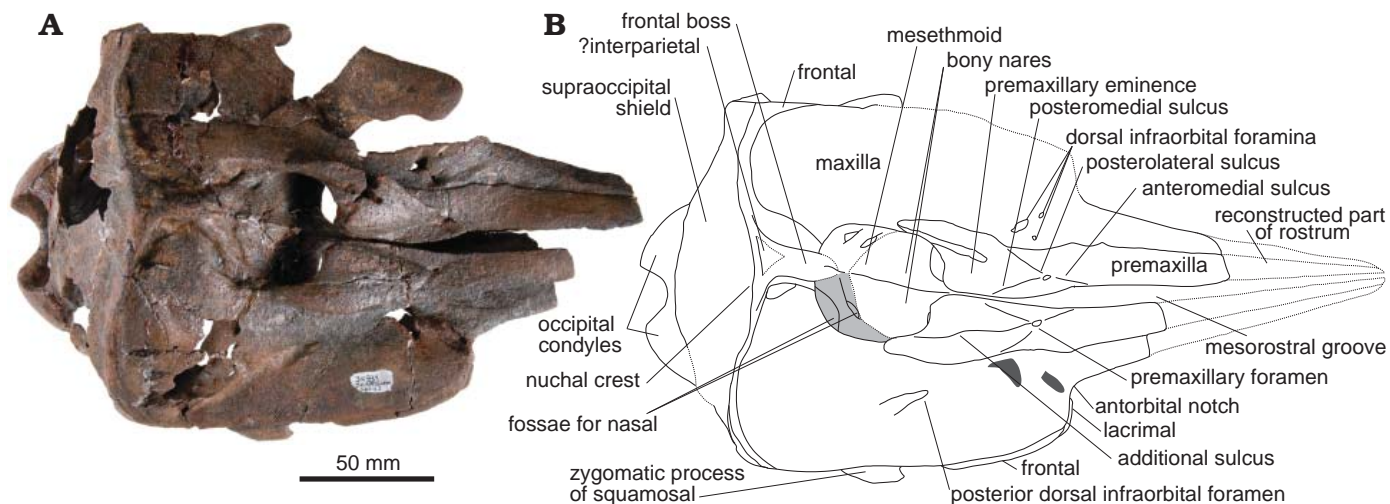


Fig. 2. Skull of the phocoenid cetacean *Brabocetus gigaseorum* gen. et sp. nov. from the Pliocene of northern Belgium IRSNB M. 2171 (holotype) in dorsal view. Photo (A) and corresponding line drawing (B). Dotted lines indicate reconstructed parts and poorly visible structures. Dark grey surfaces indicate fracture surfaces. Light grey surface indicates the original position of the lost right nasal.

**Diagnosis.**—*Brabocetus gigaseorum* sp. nov. has a cranium intermediate in size between that of the extant species *Neophocaena phocaenoides* and *Phocoenoides dalli*. It differs from all other phocoenids except *Septemtriocetus* in having a frontal boss that is longer than wide. It differs from all other phocoenids except *Haborophocaena* in the anteromedial sulcus being shorter than the posteromedial sulcus. It possibly differs from all extinct phocoenids except *Miophocaena* in the presence of an additional longitudinal sulcus across the premaxillary eminences. It differs from all phocoenids except *Haborophocaena*, *Miophocaena*, *Piscolithax tedfordi*, and *Septemtriocetus*, in that the level of the anterior margin of the bony nares is in line with the postorbital process of the frontal; from all other phocoenids except *Haborophocaena*, *Miophocaena*, *Neophocaena*, *Piscolithax tedfordi*, and *Septemtriocetus* in that the first anterior dorsal infraorbital foramen is distinctly posterior to the antorbital notch; from *Haborophocaena*, *Miophocaena*, *Numataphocaena*, *Piscolithax* spp., *Pterophocaena*, *Semirostrum*, and *Septemtriocetus* in the anterolaterally widely-open antorbital notch, not laterally limited by an extension of the antorbital process; and from extant phocoenids in a more pronounced asymmetry of the vertex, with medial sutures more distinctly shifted to the left side. It further differs from the other North Sea fossil phocoenid *Septemtriocetus* in that it possesses: an anteriorly longer pterygoid sinus fossa, reaching the level of the antorbital notch; a higher premaxillary eminence, overhanging the posterolateral sulcus; a significantly transversely narrower frontal boss; a lower, not dorsally pointed temporal fossa; a deeper and longer squamosal fossa; and a postglenoid process of the squamosal being thickened in lateral view.

### Description

Based on the anteriorly converging and rectilinear lateral margins of the maxillae at the rostrum base, a tentative reconstruction of the outline of the pointed rostrum of *Brabocetus gigaseorum* is provided (Fig. 2). This reconstruction

suggests a rostrum length shorter than the cranium length, a feature shared with extant phocoenids and possibly *Septemtriocetus*, but unlike the longer-snouted extinct phocoenids *Lomacetus*, *Piscolithax*, and probably *Salumiphocaena* (Wilson 1973; Barnes 1984; Muizon 1984, 1988b; Lambert 2008). However, a more complete specimen is needed to confirm this statement. The dimensions of the cranium (Table 1; pre- and postorbital widths, length from the antorbital notch to the nuchal crest) are roughly intermediate between those of the extant species *Neophocaena phocaenoides* and *Phocoenoides dalli*, and slightly smaller than in the holotype of *Septemtriocetus bosselaersi*. The small temporal fossa is still anteroposteriorly longer than the orbit and the roof of the former is slightly higher. The cranium displays a high degree of asymmetry that is especially developed in the region of the bony nares and vertex. This asymmetry is expressed as a shift to the left (ca. 15° in comparison to the sagittal plane of the skull), which is particularly conspicuous in anterior view (Fig. 3A). Differences in width and height of left and right elements are detailed below.

**Premaxilla.**—In dorsal view, from the preserved anterior end of the rostrum, the premaxilla widens until the level of the antorbital notch, where its width equals the width of the maxilla (Fig. 2). From that level onwards, the lateral margin of the bone becomes slightly concave over 30–35 mm; it is followed backwards by the convex lateral margin of the premaxillary eminence. The maximum width of the mesorostral groove occurs at the level of the antorbital notches, from where the opening narrows backwards to terminate where the medial margins of the premaxillary eminences nearly abut.

Best preserved on the right side, the tiny elliptical premaxillary foramen (transverse diameter = 2 mm) is located posterior to the level of the antorbital notch. A short and shallow anteromedial sulcus originates from each premaxillary foramen; by contrast the posteromedial sulcus is longer. Consequently, the portion of the prenarial triangle posterior

Table 1. Measurements (in mm) on the skull of *Brabocetus gigaseorum* gen. et sp. nov. IRSNB M. 2171 (holotype). e, estimate; + incomplete.

Condylobasal length	e300
Rostrum length as preserved	+66
Distance between antorbital notch and posterior end of alveolar groove	33
Width of rostrum at base	e73
Width of premaxillae at rostrum base	40
Longitudinal distance between nuchal crest and antorbital notches	122
Longitudinal distance between anterior margin of bony nares and antorbital notches	57
Distance between premaxillary foramen and anterior margin of bony nares	44
Preorbital width of skull	e115
Postorbital width of skull	e148
Maximum width of premaxillae on cranium	52
Width of bony nares	40
Maximum width of fossae for nasals	37
Length of orbit	e50
Length of temporal fossa	e75
Distance between anterior tip of zygomatic process of squamosal and ventral tip of postglenoid process	42
Distance between jugular notches	e85
Width of occipital condyles	74
Maximum width of right occipital condyle	29
Width of foramen magnum	37
Height of foramen magnum	36

to the premaxillary foramen is longer than the portion anterior to the foramen. A roughly similar condition is seen only in *Haborophocoena*, whereas other phocoenids, including the extant species, display a longer anteromedial sulcus. Together with the long posterolateral sulcus, the posteromedial sulcus demarcates the anteriorly pointed and moderately elevated premaxillary eminence (Figs. 2, 3A). The left eminence is narrower (maximum width 22 mm for 25 mm on the right) and higher (maximum height relative to the lateral maxilla 7.5 mm for 6 mm on the right) than the right eminence. Each eminence is transversely and longitudinally convex, with the lateral margin distinctly overhanging the posterolateral sulcus (and part of the maxilla on the left side). The right eminence is crossed by a thin longitudinal groove, tentatively interpreted as the additional sulcus observed in extant phocoenids and *Miophocaena* (Murakami et al. 2012b). An alternative, but less likely interpretation would be that this groove is due to a longitudinal fracture of the eminence following the path of an underlying canal inside the premaxilla. A wider groove is exposed only on the posterior part of the left eminence, the dorsal exposure of which was possibly increased due to surface wear. The posteromedial corner of each eminence is truncated (slightly damaged on the left side), as it is in most extinct phocoenids and the fossil delphinoid *Albireo*. This feature most likely indicates the presence of maxillary ossicles on the anterior margin of the bony nares, as observed in extant

phocoenids (Barnes 1984; Muizon 1988a). Although wider on the right side of the skull, the portion of the premaxilla along the bony nares is narrow and ends before the posterolateral corner of the naris. A similar condition is observed in all phocoenids, except *Archaeophocaena*, *Haborophocoena minutus*, and *Miophocaena*, which display premaxillae wider and longer towards the vertex (Ichishima and Kimura 2009; Murakami et al. 2012b).

**Maxilla.**—Only the right antorbital notch is preserved. In dorsal view, the notch is anterolaterally widely open (Fig. 2). Consisting of the maxilla and lacrimal, the posterior wall is directed transversely, lacking an anterolateral projection. This major difference with *Septemtriocetus* is observed in most extant phocoenids, *Australithax*, *Lomacetus*, and possibly *Salumiphocaena*. Although incomplete in this area, the left maxilla bears three dorsal infraorbital foramina posteromedial to the corresponding notch: two small anterior foramina with a diameter not exceeding 2 mm and a larger posterior foramen with a transverse diameter of 6 mm. The anteromedial-most foramen is conjoined with a shallow groove anterolaterally. On the right side, a large opening posteromedial to the antorbital notch is probably due to damage of an area pierced by several dorsal infraorbital foramina. In the orbital region, the dorsal surface of the maxilla is smooth and moderately convex. Its lateral margin is thin. A large posterior dorsal infraorbital foramen is in line transversely with the level of the lost postorbital process of the frontal, and 12 mm lateral to the premaxilla. The left maxilla is exposed dorsally as a narrow strip medial to the corresponding premaxilla on the anterolateral corner of the bony naris, but this exposure may have been accentuated by wear of the overlying premaxilla. The dorsal surface of the maxilla is distinctly convex between the temporal fossa and the vertex. The maxilla reaches the nuchal crest over most of its posterior border, except in its posteromedial corner, where the concave dorsal surface of the frontal is exposed. The maxilla only contacts the frontal boss in the anterior part of the latter.

In lateral view, the medial part of the maxilla ascends gradually towards the vertex, although less abruptly than in *Phocoena* spp. and *Phocoenoides dalli*, whereas the bone slopes down posterolaterally from the orbit region to the postorbital process. The posterior end of the alveolar groove is preserved on the left side, beginning 33 mm anterior to the antorbital notch. However, the spongy bone of this area is partially worn and no detail of the alveoli (if originally present) is preserved. The palatal surface of the maxillae between the anterior tips of the palatines is wide and flat, as in other phocoenids and monodontids. On each maxilla, a longitudinal sulcus indicates the presence of a major palatine foramen anterior to the maxilla-palatine suture.

An anteroposteriorly directed thin groove on the lateral side of the maxilla originates medial to the jugal and extends for a short distance (25 mm) on the rostral base (Fig. 6). According to Mead and Fordyce (2009), this groove may correspond to the anterior extent of the zygomatic recess, the latter housing the maxillary process of the jugal. Ventromedial to this

groove, a broader and anteroposteriorly elongated depression is interpreted as a fossa for an anterior extent of the pterygoid sinus, possibly homologous to the anterior sinus fossa present in extant delphinids but presumably not in extant phocoenids (Fraser and Purves 1960; Mead and Fordyce 2009).

**Mesethmoid.**—Although the mesethmoid is not visible in dorsal view between the premaxillary eminences, it forms a thin and low nasal septum between the bony nares. Below the frontal boss, the transverse plate-like mesethmoid forms the posterior wall of the bony nares. This plate is proportionally wider and less erect than in extant phocoenids.

**Nasal.**—As in the holotype of *Septemtriocetus bosselaersi* and several other fossil phocoenid specimens, both nasals are lost. Anteroventrolateral to the frontal boss, a shallow fossa is observed above the mesethmoid on each side of the specimen (Fig. 2). This fossa is crossed by an oblique low ridge descending from the frontal boss ventrolaterally and the deepest portion of each fossa is located dorsolaterally. Similar features on a juvenile skull of *Phocoena phocoena*, of which one nasal could be removed (Fig. 4), indicate that these fossae in the frontals held the nasals in life. Consequently, originally each wide nasal extended much more laterally than the frontal boss, with a lateral limit in line with the lateral margin of the bony nares. The mesethmoid formed a dorsomedial projection between the nasals.

**Frontal.**—Posterior to the fossae for the nasals, the frontal boss is longer than wide (Fig. 2), as in *Septemtriocetus*, and transversely narrower than in any other phocoenid, somewhat more similar to the monodontid *Delphinapterus*. It should be noted that this area is unknown in *Pterophocaena* and poorly known in *Archaeophocaena* and *Numataphocoena* (Ichishima and Kimura 2000; Murakami et al. 2012b). The right wall of this transversely pinched frontal boss is relatively high, with a dorsal margin forming the top of the skull and slightly overhanging the rest of the wall. This right wall is located far beyond the sagittal plane of the skull on the left side, as is also seen in *Haborophocaena* and *Septemtriocetus*. The left wall slopes more gradually towards the corresponding maxilla. Although the interfrontal suture is visible on the anterior surface of the frontal boss, the state of preservation of the posterior part of the boss precludes a detailed description, including the potential presence of an interparietal (Fig. 2).

In lateral view, the preorbital process of the frontal is barely thickened, roughly continuous with the supraorbital portion (Fig. 5). Although no postorbital process is preserved, the broken surface at the base of the right process indicates a process in line with the anterior half of the bony nares.

In ventral view of the orbit region, a deep fossa for the postorbital lobe of the pterygoid sinus excavates the frontal medial to the infratemporal crest (Fig. 6). This fossa is deeper than in the holotype of *Septemtriocetus bosselaersi*, but its extent is variable in extant phocoenids (OL personal observations). The fossa for the preorbital lobe of the pterygoid sinus extends posterodorsally for a short distance above the frontal groove, close to the configuration of the same in *Septem-*

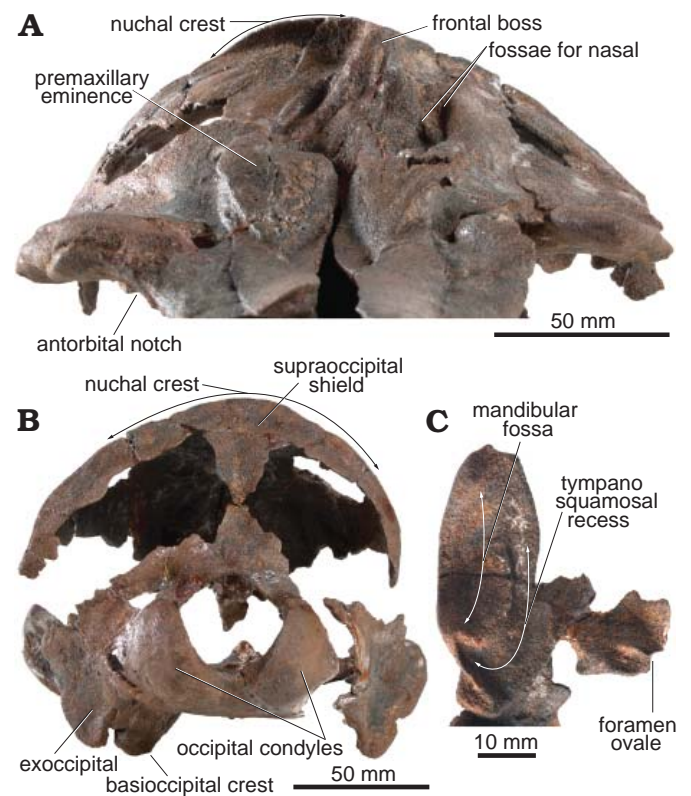


Fig. 3. Skull of the phocoenid cetacean *Brabocetus gigaseorum* gen. et sp. nov. from the Pliocene of northern Belgium IRSNB M. 2171 (holotype). A. Anterior view of the facial region. B. Posterior view. C. Ventral view of the right squamosal.

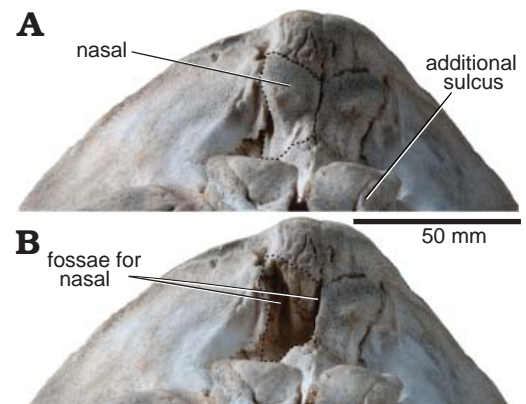


Fig. 4. Anterior view of the facial region of the skull of the extant porpoise *Phocoena phocoena* (Linnaeus, 1758) with both nasals present (A) and right nasal removed (B), to show the corresponding fossae on the corresponding frontal and maxilla. Dotted lines indicate the outline of the right nasal, both when present and when removed.

*triocetus*. This feature is also present in some extinct phocoenids, as well as some extant delphinids, whereas it is more developed in extant phocoenids (Fraser and Purves 1960). The roof of the temporal fossa extends for two thirds of the length of the fossa. This roof is proportionally longer anteroposteriorly than in extant phocoenids (most likely linked to the proportionally less transversely inflated cerebral hemispheres), but transversely narrower than in *Septemtriocetus*.

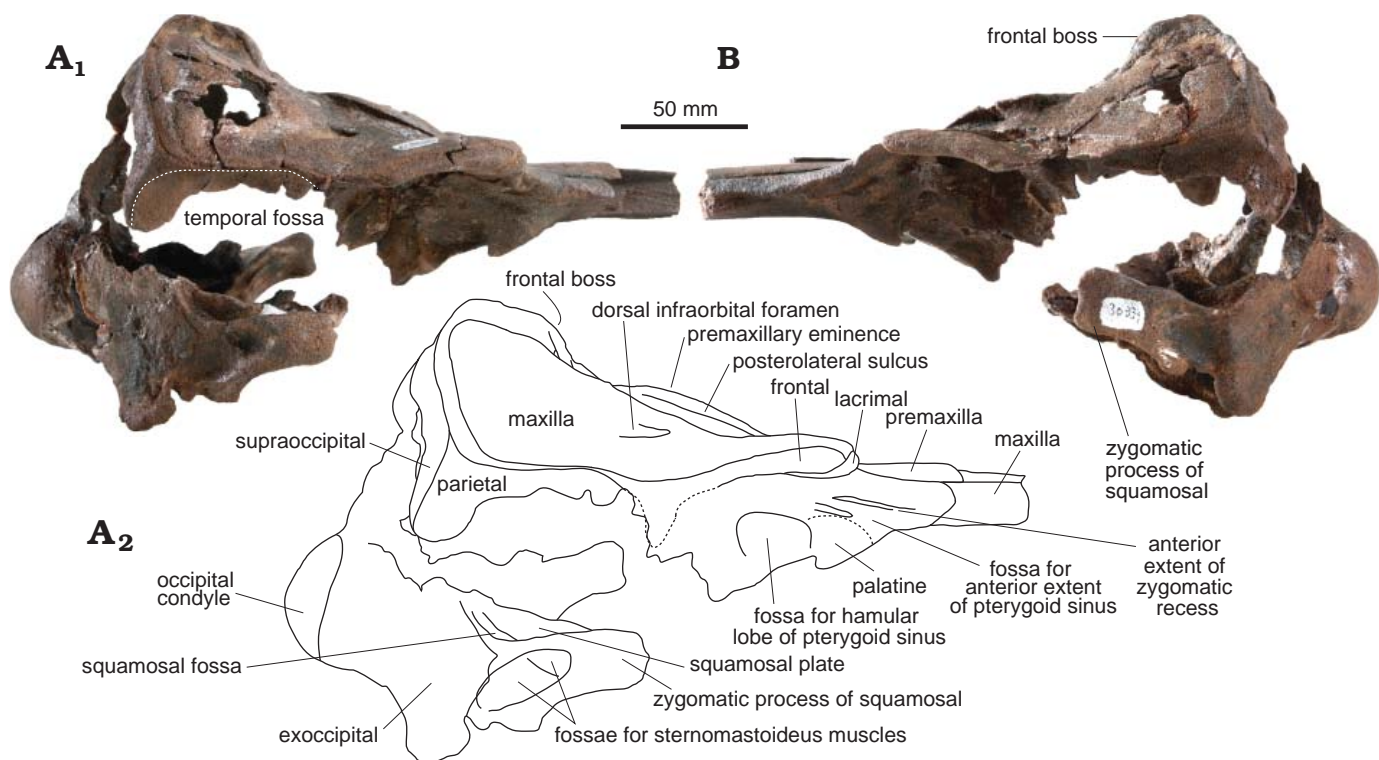


Fig. 5. Skull of the phocoenid cetacean *Brabocetus gigaseorum* gen. et sp. nov. from the Pliocene of northern Belgium IRSNB M. 2171 (holotype). **A.** Right lateral view, photo ( $A_1$ ) and corresponding line drawing ( $A_2$ ). Dotted lines indicate the dorsal margin of the temporal fossa ( $A_1$ ), the reconstructed right postorbital process, and poorly visible sutures ( $A_2$ ). **B.** Left lateral view.

**Supraoccipital.**—The nuchal crest is only poorly elevated against the frontal boss, unlike that in *Piscolithax* spp. and several extant phocoenids (Muizon 1984; Lambert 2008). Lateral to the vertex, the nuchal crest is higher and more acute on the right side (Fig. 3A, B), overhanging the maxilla and frontal. At the top of the right nuchal crest lies the weakly developed external occipital protuberance. A shallow groove extends from the protuberance towards the foramen magnum. The supraoccipital shield slopes more steeply posteroventrally (mean angle of ca.  $50^\circ$  to the horizontal plane over the first 45 mm, taken mediodorsally in lateral view) than in extant phocoenids, due to its less posteriorly developed cerebral hemispheres (Fig. 5).

**Lacrimal and jugal.**—Only the right lacrimal and part of the corresponding jugal are preserved. In dorsal and lateral views (Figs. 2, 5), the lacrimal is visible on the anterior margin of the antorbital process. In ventral view, the triangular lacrimal occupies about 50% of the surface of the orbit region (Fig. 6). The suture with the jugal is not visible. Only the base of the styliform portion of the jugal is preserved, located medial to the antorbital notch and displaying a concave lateral surface.

**Palatine and pterygoid.**—The maxilla-palatine suture is difficult to follow, only discernable in its medial portion where the suture is directed anterolaterally (Fig. 6). The anterior tips of right and left palatines are widely separated (54 mm) as in most other extant delphinoids. The robust ridge of the palatine directed posteromedioventrally and marking the limit between the palate and the orbit/pterygoid sinus region

is keeled and more prominent than in extant phocoenids, although it is not as sharp as in *Septemtriocetus*. In the latter, this ridge has been proposed to correspond to the anterior limit of a lobe of the pterygoid sinus (Lambert 2008). Considering the presence of this oblique ridge in extant monodontids, which are known to lack an anterior sinus (Fraser and Purves 1960), alternatively it may mark the origin of part of the pterygoid muscles involved in the closure of the mandibles (for delphinids see Seagers 1982). Only a small part of the lateral lamina of the palatine is preserved. Although both pterygoids are lost, the well-preserved medial part of the right palatine provides a rough estimate of the palatine-ptyergoid suture and of the extent of the pterygoid sinus in this area. The pterygoid sinus fossa excavates the palatine up to the level of the antorbital notch, whereas the sinus is more posterior in extant phocoenids (and some extinct taxa like *Septemtriocetus*). A few small pockets in the dorsal plate of the palatine anterior to each choana presumably correspond to extensions of the pterygoid sinus system.

**Parietal.**—Only a short portion of the thin parietal is preserved on the mediodorsal wall of each temporal fossa. The wider dorsal exposure of the left parietal in this area (Fig. 2) is almost certainly an artefact introduced during reconstruction of the skull and/or post-mortem deformation.

**Squamosal.**—The zygomatic process is proportionally longer than in extant phocoenids and the extinct *Salumiphocaena*. In lateral view, this process has a rectangular outline (Fig. 5). The fossae for the sternomastoideus muscles, deeper than in

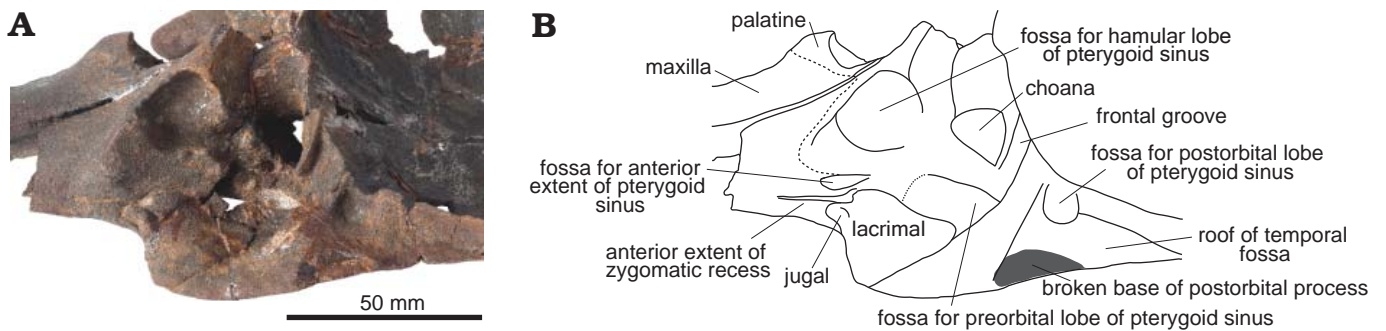


Fig. 6. Skull of the phocoenid cetacean *Brabocetus gigaseorum* gen. et sp. nov. from the Pliocene of northern Belgium IRSNB M. 2171 (holotype). Right ventrolateral view of the palate and orbital regions. Photo (A) and corresponding line drawing (B). Dotted lines indicate poorly visible sutures. Dark grey surface indicates fracture surfaces.

extant phocoenids, occupy more than two thirds of the lateral surface of the process. The postglenoid process is a short and rounded protuberance, more prominent than in *Septemtriocetus*. The distance between the postglenoid process and the spiny process is longer in the latter, corresponding to a posterior portion of the tympanosquamosal recess (for the middle sinus see Fraser and Purves 1960) that is larger than in *Brabocetus gigaseorum*. The mandibular fossa is proportionally narrower, less rounded than in *Septemtriocetus*, and medially margined by a wider and longer anterior part of the tympanosquamosal recess, on a broad medial flange along the zygomatic process (Figs. 3C, 7). Between the zygomatic process and the squamosal plate, a deep and narrow squamosal fossa forms the floor of the temporal fossa. In extant phocoenids, the shallower squamosal fossa is more open laterally, and not, or only slightly concave longitudinally. Present in the holotype of *Septemtriocetus bosselaersi*, the fossa is nevertheless posteriorly shorter than in *Brabocetus gigaseorum*.

**Exoccipital.**—The occipital condyles protrude only weakly from the posterior wall of the braincase and a shallow dorsal condyloid fossa is present (Fig. 3B). The long axis of the left condyle diverges more from the sagittal plane than on the right side (difference of ca. 5°). In addition, the left exoccipital is wider than the right exoccipital along its ventral margin. Not due to reconstruction approximations, this asymmetry may indicate either an asymmetrical position, or even preferential directions of movement, for the head relative to the vertebral column (a hypothesis that should be tested with a larger sample, including extant phocoenids). The foramen magnum is subcircular. As in *Septemtriocetus* and most other fossil phocoenids, a shallow depression is present on the anterior surface of the paroccipital process, probably corresponding to the fossa for the posterior sinus. The fossa is deeper in *Haborophocoena minutus* (Ichishima and Kimura 2009) and extant phocoenids, in which it is sometimes only closed posteriorly by a thin, translucent plate of exoccipital.

**Basioccipital.**—The left basioccipital crest is preserved. In lateral view, a shallow notch cuts the crest before a transversely swollen region anterior to the jugular notch. As in *Septemtriocetus*, a subcircular depression is present on the medial wall of the basioccipital crest, next to the jugular

notch (Fig. 7), probably for the scalenus medius muscle, which when activated draws the head downward (Lambert 2008). In ventral view, the angle drawn by the two basioccipital crests is roughly estimated at 45–50°.

**Basisphenoid.**—The basisphenoid crest is damaged by erosion. Its lateral wall is slightly excavated at its base, but not as much as in *Septemtriocetus* and extant phocoenids. If present, the basisphenoidal sinus (sensu Mead and Fordyce 2009; basisphenoid lobe of the pterygoid sinus sensu Ichishima and Kimura 2005, 2009; Lambert 2008) was poorly developed. A deeper fossa is reported in *Piscolithax longirostris*, and the condition in *Brabocetus gigaseorum* more closely matches the condition in *Australithax*, *Haborophocoena toyoshimai*, *Lomacetus*, and *Piscolithax tedfordi* (Barnes 1984; Muizon 1984, 1988b; Ichishima and Kimura 2005).

**Alisphenoid.**—Better preserved on the left side of IRSNB M.2171, the foramen ovale is small (maximum diameter 7 mm). It is bordered laterally by a short trough that held the mandibular nerve V3 (Fig. 7). The anterior ridge of the aforementioned trough corresponds to the posterior limit of a wide and shallow fossa for the pterygoid sinus.

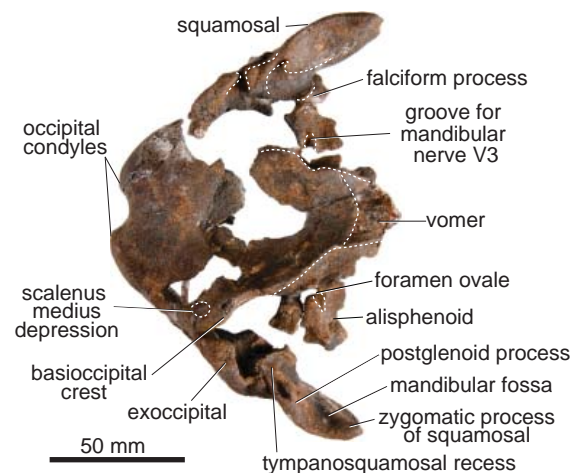


Fig. 7. Skull of the phocoenid cetacean *Brabocetus gigaseorum* gen. et sp. nov. from the Pliocene of northern Belgium IRSNB M. 2171 (holotype). Fragmentary basicranium in ventral view. Dotted lines indicate poorly visible sutures, the right tympanosquamosal recess, the groove for the mandibular nerve V3, and the presumed area of origin for scalenus medius.



## Phylogeny

In order to explore the phylogenetic relationship of *Brabocetus gigaseorum* with other phocoenids (extant and extinct), a cladistic analysis was carried out using Paup 4.0 b10 (Swofford 2001). The character-taxon matrix of Lambert (2008) was used as a starting point, with the addition of 9 characters from a subsequent analysis (Murakami et al. 2012b) and of recently published taxa from the North Pacific (Murakami et al. 2012a, b; Racicot et al. 2014). The Miocene kentriodontines *Kentriodon pernix* and *Delphinodon dividum* were considered a priori as outgroups. The list of characters and the character-taxon matrix can be found as Supplementary Online Material (available at [http://app.pan.pl/SOM/app60-Colpaert\\_etal\\_SOM.pdf](http://app.pan.pl/SOM/app60-Colpaert_etal_SOM.pdf)). All characters were treated as unweighted and unordered, as in recent cladistic analyses on phocoenids (Fajardo-Mellor et al. 2006; Lambert 2008, Murakami et al. 2012a, b). The heuristic search provided 27 shortest trees with a length of 91 steps. The consistency index (CI) is 0.53 and the retention index (RI) is 0.69. The consensus tree of the 27 most parsimonious trees is shown in Figure 8. Several nodes are unresolved among extant phocoenids and fossil North Pacific species. Furthermore, the support is generally low, due to the high number of taxa and fragmentary and/or poorly preserved specimens, resulting in a relatively low number of characters and many question marks in the matrix. Therefore, these results should be considered tentative.

For the paleobiogeography discussion, we optimized on the consensus tree the geographic range of each fossil and extant phocoenid included in the phylogenetic analysis, simply dividing the taxa into two sets: absent from the North Atlantic or North Sea (0) and present in the North Atlantic or North Sea (1). As discussed above, the selection of the Pacific Ocean as the most likely origin for Phocoenidae is strongly supported by the fossil record of the family, as well as by the fact that the earliest members of the related delphinoid families (Albireonidae, Delphinidae, Monodontidae, and Odobenocetopsidae) are all found along the coasts of the Pacific Ocean (Barnes 1984, 2008; Muizon and Domning 2002; Murakami et al. 2014). Optimization was performed with the software Mesquite (version 2.75; Maddison and Maddison 2011) under Parsimony Ancestral States reconstruction method. The results of this simple optimization are summarized in Figure 8 (with numbers 1, 1', 1'' and 2, 2', 2'' illustrating the successive dispersal events towards and from the North Atlantic/North Sea) and discussed below.

As in previous analyses by Murakami et al. (2012b) and Racicot et al. (2014), *Pterophocaena* is the most stemward phocoenid. The next node suggests the existence of two major clades, as partly proposed in a past analysis (Lambert 2008), one including all the extant species, all the south-east Pacific fossil species, and two north-east Pacific fossil species, and the other including most north-west Pacific fossil species, two north-east Pacific fossil species, and the two North Sea fossil species. As in all recent analyses, and con-

trary to early works (Barnes 1985; Muizon 1988a), no fossil species falls within crown Phocoenidae. Focusing on the North Sea taxa, the new genus *Brabocetus* branches after the Californian *Salumiphocaena*, and before the other North Sea taxon *Septemtriocetus*. Given the addition of new North Pacific taxa, the latter is sister-group to a larger clade than in Lambert (2008), including *Haborophocaena* spp., *Archaeophocaena*, *Miophocaena*, and *Semirostrum*. Finally, the genera *Haborophocaena*, *Phocoena*, and *Piscolithax*, the only ones including more than one species, are not monophyletic in the present analysis. However, the addition/deletion of one character or one taxon can change their relationships, and no decision should be taken considering the attribution or not of the different species to the corresponding genera before a better-supported phylogenetic tree is obtained.

## Concluding remarks

*Brabocetus gigaseorum* is a member of the family Phocoenidae for the following combination of morphological features of the skull: (i) well developed premaxillary eminences; (ii) shortened and narrow posterior end of both premaxillae along the bony nares; (iii) frontal boss on the vertex; (iv) anterior apices of palatines and corresponding pterygoid sinus fossae widely separated by a flat surface on the palate; (v) posterodorsal extension of the fossa for the preorbital lobe of the pterygoid sinus above the frontal groove.

Some of these derived characters are not present in all phocoenids (i, ii, v), and/or occur in a few other delphinidans (i, iii–v), and/or are more developed in extant phocoenid species (i, v). Nevertheless, their combination occurs only in phocoenids (Barnes 1985; Ichishima and Kimura 2005; Muizon 1988a; Lambert 2008) and strongly supports a phocoenid attribution for this new taxon. Furthermore, *B. gigaseorum* is thought to have possessed an additional sulcus on the premaxillary eminence, a feature present in many extant phocoenids and absent in non-phocoenid odontocetes.

Within the family, *B. gigaseorum* falls outside the crown group, for now only occupied by the six short-snouted extant species. Despite some similarities with the latter (reduction of the antorbital notch, possible presence of an additional sulcus on the high premaxillary eminence), *B. gigaseorum* is proposed to belong to another, even if poorly defined, phocoenid clade. Although closely related to the other Pliocene North Sea species *Septemtriocetus bosselaersi*, *B. gigaseorum* is not the sister-group of the latter in our analysis; it differs in, among others, the shallower antorbital notch not limited anterolaterally, the higher premaxillary eminence overhanging the posterolateral sulcus, the narrower frontal boss, and the pterygoid sinus fossa reaching anteriorly the level of the antorbital notch. *B. gigaseorum* is therefore the second pre-Pleistocene phocoenid species described outside the Pacific Ocean.

The topology of our consensus tree (Fig. 8) suggests that: a complex series of dispersal events occurred between north-

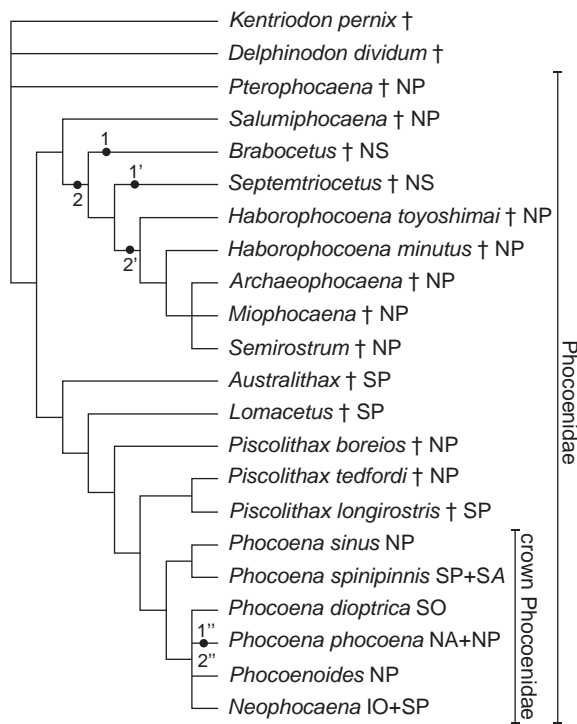


Fig. 8. Consensus tree of the 27 most parsimonious trees, showing the phylogenetic relationships of *Brabocetus gigaseorum* gen. et sp. nov. with other extinct and extant phocoenids. † indicates extinct taxon. IO, Indian Ocean; NA, North Atlantic; NP, North Pacific; NS, North Sea; SA, South Atlantic; SO, southern oceans; SP, South Pacific; 1, 1', and 1'' correspond to a first trans-Arctic migration scenario with three successive dispersals to the North Sea. 2, 2', and 2'' correspond to a second scenario with two dispersals to the North Sea (2, 2'') and a dispersal back to the North Pacific (2').

east, north-west, and South Pacific during the late Miocene and Pliocene; the origin of the crown Phocoenidae has to be found in the south-east or north-east Pacific, two areas displaying diversified fossil phocoenid faunas (e.g., Barnes 1984; Muizon 1984, 1988b; Boessenecker 2013). The two Pliocene North Sea species probably arrived in the North Atlantic realm from the North Pacific via the Bering Strait, as proposed elsewhere (see discussion in Lambert 2008 and arguments for other groups of marine organisms in Grant and Stahl 1988; Vermeij 1991; Marinovich 2000; Deméré et al. 2003; Verhoeven et al. 2011). Because the holotype of *B. gigaseorum* was found in layers considerably older (5–4.4 Ma) than the holotype of *S. bosselaersi* (3.5–2.6 Ma; Lambert 2008), its arrival in the North Sea better matches the early stages of the opening of the Bering Strait (5.5–4.8 Ma). A main trans-Arctic dispersal from the North Pacific to the North Atlantic, related to changes in oceanic circulation, was recorded for molluscs at ca. 3.6 Ma (Marinovich 2000), and new data from Iceland suggest a somewhat older major mollusc invasion, at ca. 4.5 Ma (Verhoeven et al. 2011), an event still younger than the geological age of *B. gigaseorum*. The presence of *S. bosselaersi* in younger deposits could be the result of either a second, later dispersal event, or of speciation in the North Sea, with a subsequent return to the North Pacific, both scenarios being equally parsimonious

(Fig. 8). Therefore, taking into account the late Pleistocene to Recent occupation of the North Sea (and the North Atlantic) by the distantly related *Phocoena phocoena*, at least two, and possibly three, trans-Arctic dispersal events account for the North Sea distribution of the family from the early Pliocene to Recent.

## Acknowledgements

We wish to thank Paul Gigase (Berchem, Belgium) and Pierre Gigase (Zandvliet, Belgium) for generously donating the holotype of *Brabocetus gigaseorum* to the IRSNB, Robert Marquet (IRSNB, Brussels, Belgium) for providing accurate information on the locality and level where he discovered the specimen, Wilfried Miseur (IRSNB) for the photographic work, Christine Argot, and Christian de Muizon (Muséum national d'Histoire naturelle, Paris, France), Lawrence G. Barnes, Samuel A. McLeod, and Vanessa R. Rhue (Natural History Museum of Los Angeles County, USA), James G. Mead and Charley Potter (US National Museum of Natural History, Washington DC, USA), Georges Lenglet and Sébastien Bruaux (IRSNB), Adri Rol (Zoological Museum, Amsterdam, The Netherlands), and Hein van Grouw (Naturalis, Leiden, The Netherlands) for the access to the collections under their care. We also thank Stephen Louwe (Ghent University, Ghent, Belgium) for his support and advice during the Master thesis of WC at Ghent University. The constructive comments of the reviewers Giovanni Bianucci (Università degli Studi di Pisa, Pisa, Italy), Stephen J. Godfrey (Calvert Marine Museum, Solomons Island, USA), and Rachel A. Racicot (Howard University, Washington DC, USA), and the editor Mark D. Uhen (George Mason University, Fairfax, Virginia, USA) considerably improved our manuscript, for both the content and form. The research of OL at the IRSNB from 2012 to April 2013 was carried out within the framework of “Mandats de retour 2011” of the Belgian Federal Science Policy.

## References

- Barnes, L.G. 1984. Fossil odontocetes (Mammalia: Cetacea) from the Almejas Formation, Isla Cedros, Mexico. *PaleoBios* 42: 1–46.
- Barnes, L.G. 1985. Evolution, taxonomy and antitropical distributions of the porpoises (Phocoenidae, Mammalia). *Marine Mammal Science* 1: 149–165.
- Barnes, L.G. 2008. Miocene and Pliocene Albireonidae (Cetacea, Odontoceti), rare and unusual fossil dolphins from the eastern North Pacific Ocean. *Natural History Museum of Los Angeles County Science Series* 41: 99–152.
- Bianucci, G. 1996. The Odontoceti (Mammalia Cetacea) from Italian Pliocene. Systematics and phylogenesis of Delphinidae. *Palaeontographia italica* 83: 73–167.
- Bianucci, G. 2013. *Septidelphis morii*, n. gen. et sp., from the Pliocene of Italy: New evidence of the explosive radiation of true dolphins (Odontoceti, Delphinidae). *Journal of Vertebrate Paleontology* 33: 722–740.
- Bianucci, G. and Landini, W. 2002. Change in diversity, ecological significance and biogeographical relationships of the Mediterranean Miocene toothed whale fauna. *Geobios* 35: 19–28.
- Bianucci, G., Sorbi, S., Vaiani, S., and Landini, W. 2009. Pliocene marine mammals from Italy: a systematic and stratigraphic overview. In: Fanti, F. and Spalletta, C. (editors), *International Conference on Vertebrate Palaeobiogeography and Continental Bridges Across Tethys, Mesogea, and Mediterranean Sea. Bologna, Italy*, 9–12. Museo Geologico Giovanni Capellini, Bologna.
- Bianucci, G., Gatt, M., Catanzariti, R., Sorbi, S., Bonavia, C.G., Curmi,

- R., and Varola, A. 2011. Systematics, biostratigraphy and evolutionary pattern of the Oligo-Miocene marine mammals from the Maltese Islands. *Geobios* 44: 549–585.
- Boessenecker, R.W. 2013. A new marine vertebrate assemblage from the Late Neogene Purisima Formation in Central California, part II: Pinnipeds and cetaceans. *Geodiversitas* 35: 815–940.
- Brisson, M.-J. 1762. *Regnum Animale in classes IX distributum, sine synopsis methodica*. 296 pp. Theodorum Haak, Paris.
- Deméré, T.A., Berta, A., and Adam, P.J. 2003. Pinnipedimorph evolutionary biogeography. *Bulletin of the American Museum of Natural History* 279: 32–76.
- De Schepper, S., Head, M.J., and Louwey, S. 2009. Pliocene dinoflagellate cyst stratigraphy, palaeoecology and sequence stratigraphy of the Tunnel-Canal Dock, Belgium. *Geological Magazine* 146: 92–112.
- Fajardo-Mellor, L., Berta, A., Brownell, R.L. Jr., Boy, C.C. and Goodall, N.P. 2006. The phylogenetic relationships and biogeography of true porpoises (Mammalia: Phocoenidae) based on morphological data. *Marine Mammal Science* 22: 910–932.
- Flower, W.H. 1867. Description of the skeleton of *Inia geoffrensis* and the skull of *Pontoporia blainvillii*, with remarks on the systematic position of these animals in the Order Cetacea. *Transactions of the Zoological Society of London* 6: 87–116.
- Fordyce, R.E. and Muizon, C. de. 2001. Evolutionary history of cetaceans: a review. In: J.-M. Mazin, and V. de Buffrénil (eds.), *Secondary Adaptation of Tetrapods to Life in Water*, 169–233. Verlag Dr. Friedrich Pfeil, München.
- Fraser, F.C. and Purves, P.E. 1960. Hearing in cetaceans: Evolution of the accessory air sacs and the structure of the outer and middle ear in recent cetaceans. *Bulletin of the British Museum (Natural History), Zoology* 7: 1–140.
- Grant, W.S. and Stahl, G. 1988. Evolution of Atlantic and Pacific cod: loss of genetic variation and gene expression in Pacific cod. *Evolution* 42: 139–146.
- Gray, J.E. 1821. On the natural arrangement of vertebrate animals. *London Medical Repository* 15: 296–310.
- Gray, J.E. 1825. An outline of an attempt at the disposition of Mammalia into tribes and families, with a list of the genera apparently appertaining to each tribe. *Annals of Philosophy* 26: 337–344.
- Harington, C. 1977. Marine mammals in the Champlain Sea and the Great Lakes. *Annals of the New York Academy of Sciences* 288: 508–537.
- Ichishima, H. and Kimura, M. 2000. A new fossil porpoise (Cetacea; Delphinoidea; Phocoenidae) from the early Pliocene Horokaoshirika Formation, Hokkaido, Japan. *Journal of Vertebrate Paleontology* 20: 561–576.
- Ichishima, H. and Kimura, M. 2005. *Haborophocoena toyoshimai*, a new early Pliocene porpoise (Cetacea: Phocoenidae) from Hokkaido, Japan. *Journal of Vertebrate Paleontology* 25: 655–664.
- Ichishima, H. and Kimura, M. 2009. A new species of *Haborophocoena*, an Early Pliocene phocoenid cetacean from Hokkaido, Japan. *Marine Mammal Science* 25: 855–874.
- Lambert, O. 2008. A new porpoise (Cetacea, Odontoceti, Phocoenidae) from the Pliocene of the North Sea. *Journal of Vertebrate Paleontology* 28: 863–872.
- Louwey, S., Head, M.J., and De Schepper, S. 2004. Dinoflagellate cyst stratigraphy and palaeoecology of the Pliocene in northern Belgium, southern North Sea Basin. *Geological Magazine* 141: 353–378.
- Maddison, W.P. and Maddison, D.R. 2011. *Mesquite: a Modular System for Evolutionary Analysis*. Version 2.75. <http://mesquiteproject.org>
- Marincovich, L. Jr. 2000. Central American palaeogeography controlled Pliocene Arctic Ocean molluscan migrations. *Geology* 28: 551–554.
- Mead, J.G. and Fordyce, R.E. 2009. The therian skull: a lexicon with emphasis on the odontocetes. *Smithsonian Contributions to Zoology* 627: 1–248.
- Muizon, C. de 1984. Les Vertébrés de la Formation Pisco (Pérou). Deuxième partie: Les Odontocètes (Cetacea, Mammalia) du Pliocène inférieur du Sud-Sacaco. *Travaux de l'Institut Français d'Etudes Andines* 27: 1–188.
- Muizon, C. de 1988a. Les relations phylogénétiques des Delphinida. *Annales de Paléontologie* 74: 159–227.
- Muizon, C. de 1988b. Les Vertébrés fossiles de la Formation Pisco (Pérou). Troisième partie: Les Odontocètes (Cetacea, Mammalia) du Miocène. *Travaux de l'Institut Français d'Etudes Andines* 42: 1–244.
- Muizon, C. de and Domning, D.P. 2002. The anatomy of *Odobenocetops* (Delphinoidea, Mammalia), the walrus-like dolphin from the Pliocene of Peru and its palaeobiological implications. *Zoological Journal of the Linnean Society* 134 (4): 423–452.
- Murakami, M., Shimada, C., Hikida, Y., and Hirano, H. 2012a. A new basal porpoise, *Pterophocaena nishinoi* (Cetacea, Odontoceti, Delphinoidea), from the upper Miocene of Japan and its phylogenetic relationships. *Journal of Vertebrate Paleontology* 32: 1157–1171.
- Murakami, M., Shimada, C., Hikida, Y., and Hirano, H. 2012b. Two new extinct basal phocoenids (Cetacea, Odontoceti, Delphinoidea), from the upper Miocene Koetoi Formation of Japan and their phylogenetic significance. *Journal of Vertebrate Paleontology* 32: 1172–1185.
- Murakami, M., Shimada, C., Hikida, Y., Soeda, Y., and Hirano, H. 2014. *Eodelphis kabatensis*, a new name for the oldest true dolphin *Stenella kabatensis* Horikawa, 1977 (Cetacea, Odontoceti, Delphinidae), from the upper Miocene of Japan, and the phylogeny and paleobiogeography of Delphinoidea. *Journal of Vertebrate Paleontology* 34: 491–511.
- Post, K. 2005. A Weichselian marine mammal assemblage from the southern North Sea. *Deinsea* 11: 21–27.
- Racicot, R.A., Deméré, T.A., Beatty, B.L., and Boessenecker, R.W. 2014. Unique feeding morphology in a new prognathous extinct porpoise from the Pliocene of California. *Current Biology* 24: 774–779.
- Rosel, P.E., Haygood, M.G., and Perrin, W.F. 1995. Phylogenetic relationships among the true porpoises (Cetacea: Phocoenidae). *Molecular Phylogenetics and Evolution* 4: 463–474.
- Seagers, D.J. 1982. *Jaw Structure and Functional Mechanics of Six Delphinids (Cetacea, Odontoceti)*. 179 pp. Unpublished M.Sc. thesis, San Diego State University, San Diego.
- Swofford, D.L. 2001. *PAUP\*: Phylogenetic Analysis Using Parsimony (\*and Other Methods)*. Version 4b. Sinauer Associates, Sunderland.
- Vandenbergh, N., Laga, P., Steurbaut, E., Hardenbol, J., and Vail, P.R. 1998. Tertiary sequence stratigraphy at the southern border of the North Sea Basin in Belgium. *Special Publication SEPM* 60: 119–154.
- Verhoeven, K., Louwey, S., Eiriksson, J., and De Schepper, S. 2011. A new age model for the Pliocene–Pleistocene Tjörnes section on Iceland: its implication for the timing of North Atlantic–Pacific palaeoceanographic pathways. *Palaeogeography, Palaeoclimatology, Palaeoecology* 309: 33–52.
- Vermeij, G.J. 1991. Anatomy of an invasion: the trans-Arctic interchange. *Paleobiology* 17: 281–307.
- Whitmore, F.C. Jr. and Kaltenbach, J.A. 2008. Neogene Cetacea of the Lee Creek Phosphate Mine, North Carolina. *Virginia Museum of Natural History Special Publication* 14: 181–269.
- Wilson, L.E. 1973. A delphinid (Mammalia, Cetacea) from the Miocene of Palos Verdes Hills, California. *University of California Publications in Geological Sciences* 103: 1–34.