

A monodontid cetacean from the Early Pliocene of the North Sea

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Abstract

A partial skeleton from the Early Pliocene of Antwerp (north of Belgium), including a fragmentary skull, corresponds to the first record of a fossil member of the family Monodontidae in the North Sea. The vertex of the skull is lower than in the oldest known Monodontidae, the latest Miocene *Denebola brachycephala*, and the orbit is more anteriorly shifted. It differs from the two extant species of the family, the beluga *Delphinapterus leucas* and the narwhal *Monodon monoceros*, among others, in a shorter orbit and a shorter and wider antorbital notch. The anterior part of the temporal fossa is more elevated than in *D. leucas* and the rostrum lacked the modified pair of maxillary teeth of *M. monoceros*. Grooves observed at the surface of the skull bones are identified as shark teeth marks, either the result of a predation event or of scavenging.

Several isolated ear bones from the Neogene of Antwerp are similarly referred to Monodontidae. The new specimens described here imply that members of the family migrated towards colder water before or during earliest Pliocene, well before the first Pleistocene records of *Delphinapterus leucas* in the North Sea. The palaeobiogeography of fossil Delphinidae, Monodontidae and Phocoenidae further suggests a Pacific origin for the crown-Delphinoidea of the North Atlantic realm.

Keywords: beluga, narwhal, Monodontidae, Pliocene, North Sea, palaeobiogeography.

Résumé

Un squelette partiel découvert dans le Pliocène inférieur d'Anvers (nord de la Belgique), comprenant un crâne fragmentaire, constitue la première mention d'un membre fossile de la famille Monodontidae en Mer du Nord. Le vertex du crâne est plus bas que sur le plus ancien Monodontidae connu, *Denebola brachycephala*, Miocène terminal, et l'orbite est positionnée plus antérieurement. Ce crâne diffère des deux espèces actuelles de la famille, le bélouga *Delphinapterus leucas* et le narval *Monodon monoceros*, par, entre autres, l'orbite plus courte et l'encoche antéorbitaire plus courte et plus large. La partie antérieure de la

fosse temporale est plus élevée que chez *D. leucas* et le rostre ne comporte pas la paire de dents maxillaires modifiées de *M. monoceros*. Plusieurs sillons observés à la surface des os crâniens sont interprétés comme des marques de dents de requin, résultant soit d'un épisode de prédation, soit de l'action d'un charognard.

Plusieurs os de l'oreille isolés du Néogène d'Anvers sont également attribués à un Monodontidae. Les nouveaux spécimens décrits ici indiquent que des membres de cette famille ont migré vers des eaux plus froides avant ou durant le Pliocène précoce, bien avant les premières mentions pléistocènes de *Delphinapterus leucas* dans la Mer du Nord. De plus, la paléobiogéographie des Delphinidae, Monodontidae et Phocoenidae fossiles suggère une origine pacifique pour les 'crown-Delphinoidea' de l'Atlantique Nord.

Mots-clefs: bélouga, narval, Monodontidae, Pliocène, Mer du Nord, paléobiogéographie.

Introduction

The family Monodontidae includes two extant monospecific genera: the beluga *Delphinapterus leucas* (PALLAS, 1776) and the narwhal *Monodon monoceros* LINNAEUS, 1758, both geographically restricted to the cold Arctic Ocean and adjoining seas (BRODIE, 1989; HAY & MANSFIELD, 1989). The genus *Orcaella* GRAY, 1866 was occasionally placed in the family Monodontidae but most recent studies identify it as a Delphinidae (MUIZON, 1988a; ARNOLD & HEINSOHN, 1996; LEDUC *et al.*, 1999).

Except for non-diagnostic material (e.g., NEWTON, 1882), the only fossil Monodontidae described is *Denebola brachycephala* BARNES, 1984 from the latest Miocene of Mexico (BARNES, 1984). Following WHITMORE (1994), *Delphinapterus* sp. is a prominent member of the fauna of the Yorktown Formation, Early Pliocene of the east coast of North America (one undescribed skull and numerous ear bones). A periotic of Delphinapterinae is cited by MUIZON & DEVRIES (1985) from the Early Pliocene of Sacaco, Peru.

PILLERI (1986) and PILLERI *et al.* (1989) referred several ear bones from the Miocene of South Germany and Italy to Monodontidae. Later, BIANUCCI & LANDINI (2002) and BIANUCCI (1996) relocated these specimens in other odontocete families.

The purpose of this paper is the description of new monodontid material (a fragmentary skull and some post-cranial fragments) from the early Pliocene of Antwerp, North of Belgium. Predation/scavenging marks are observed on the specimen and their origin is briefly commented. Additionally, several ear bones from the Neogene of the Antwerp area are described and similarly referred to a monodontid. The palaeobiogeography of the monodontids and other crown-delphinoids is finally discussed.

Material and methods

Specimens. see Appendix.

Institutional abbreviations. IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels; M, Fossil mammal collection of types and figured specimens of the IRSNB; RMNH, Naturalis Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; ZMA, Zoologisch Museum Amsterdam, The Netherlands.

Systematic palaeontology

Order Cetacea BRISSON, 1762
Suborder Odontoceti FLOWER, 1867
Superfamily Delphinoidea GRAY, 1821
Family Monodontidae GRAY, 1821

Monodontidae indet.

Figs 3-8, Tables 1-2

Referred specimen. IRSNB M.1922, specimen including a partial skull, atlas and axis, vertebral epiphyses and rib fragments.

Locality. Eastern wall of Vrasene Dock, Kallo, western bank of Schelde River, NWW of Antwerp (Figs. 1, 2). Geographic coordinates: 51°15'N-04°14'E.

Horizon. Kattendijk Formation, about 6 m above the basis, Lower Pliocene (DE MEUTER & LAGA, 1976). The thin layer in which the specimen was found, rich in large bivalves, is mentioned by HERMAN (1975) at the level -13.50 m, located 2-4 m under the Oorderen Sands Member (Lillo Formation). Dinoflagellate

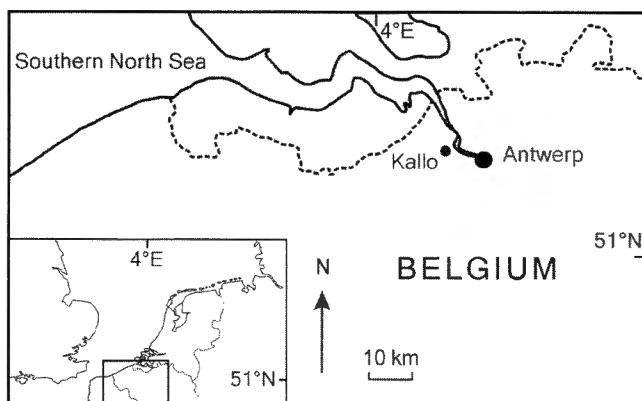


Fig. 1 — Map of the north of Belgium indicating the locality of Kallo, NW to Antwerp. Inset: map of the southern part of the North Sea Basin (mod. from LOUWYE *et al.*, 2004).

cysts from the Kattendijk Formation studied in two sections of the Verrebroek Dock and Deurganck Dock, less than 2 km from the Vrasene Dock, give an age between 5.0 Ma and 4.7-4.4 Ma, early Early Pliocene (LOUWYE *et al.*, 2004). Two isolated atlases, undoubtedly from the same species, were found in the same locality and level (Paul Gigase pers. comm.).

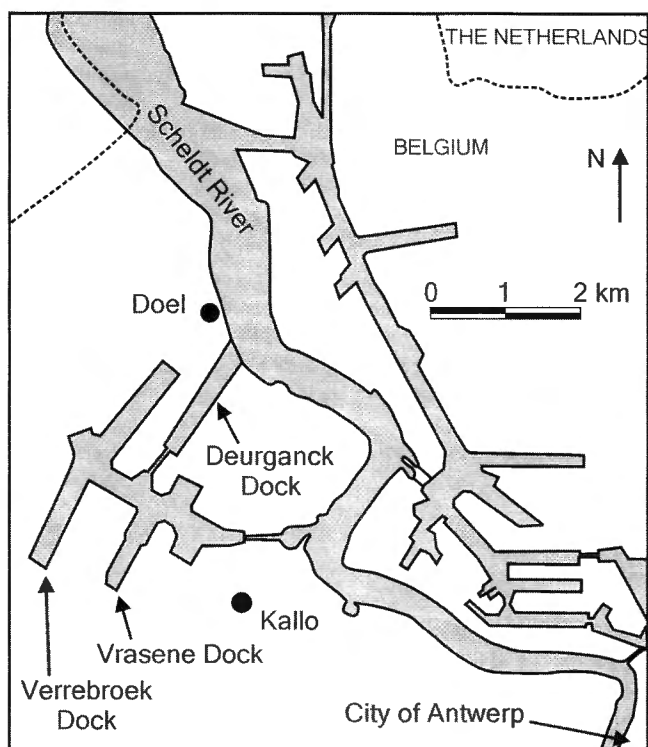


Fig. 2 — Map of the Scheldt River and main docks of the Antwerp Port giving the position of the Vrasene Dock where the main specimen was found (mod. from LOUWYE *et al.*, 2004).

width base rostrum	e2x90
width right premaxilla at base rostrum	35
width right maxilla at base rostrum	55
preorbital width of skull	e2x132
postorbital width of skull	e2x153
maximum width of right premaxilla	65
length of orbit (ventral tip preorbital-ventral tip postorbital)	68
vertical length of right postorbital process of frontal	42
longitudinal distance anterior margin naris - antorbital notch	109
horizontal length of temporal fossa	e158

Table 1 — Measurements (in mm) of the skull IRSNB M.1922, Monodontidae indet. from the Early Pliocene of Antwerp, North Sea Basin. (e) indicates estimate.

Description

Skull

The preserved elements of this fragmentary skull, lacking the basicranium and nearly the whole rostrum, are: most of the right premaxilla, maxilla and frontal on the cranium, a smaller part of the left side, two fragments of mesethmoid, the right lacrimal and jugal, an isolated portion of the supraoccipital shield, a fragment of the right squamosal and most of the right alisphenoid sutured to fragments of parietal, squamosal and basisphenoid.

The skull is somewhat smaller than adult *Delphinapterus leucas* (see Table 1), probably similar in size to the bottlenose dolphin *Tursiops truncatus*.

Premaxilla. The premaxillary foramen is located 55 mm posterior to the notch (Fig. 3); a similar posterior position of the foramen is observed in *Delphinapterus leucas*, *Denebola brachycephala* and *Monodon monoceros*. Among other extant delphinoids, only some phocoenids and *Orcaella* possess a premaxillary

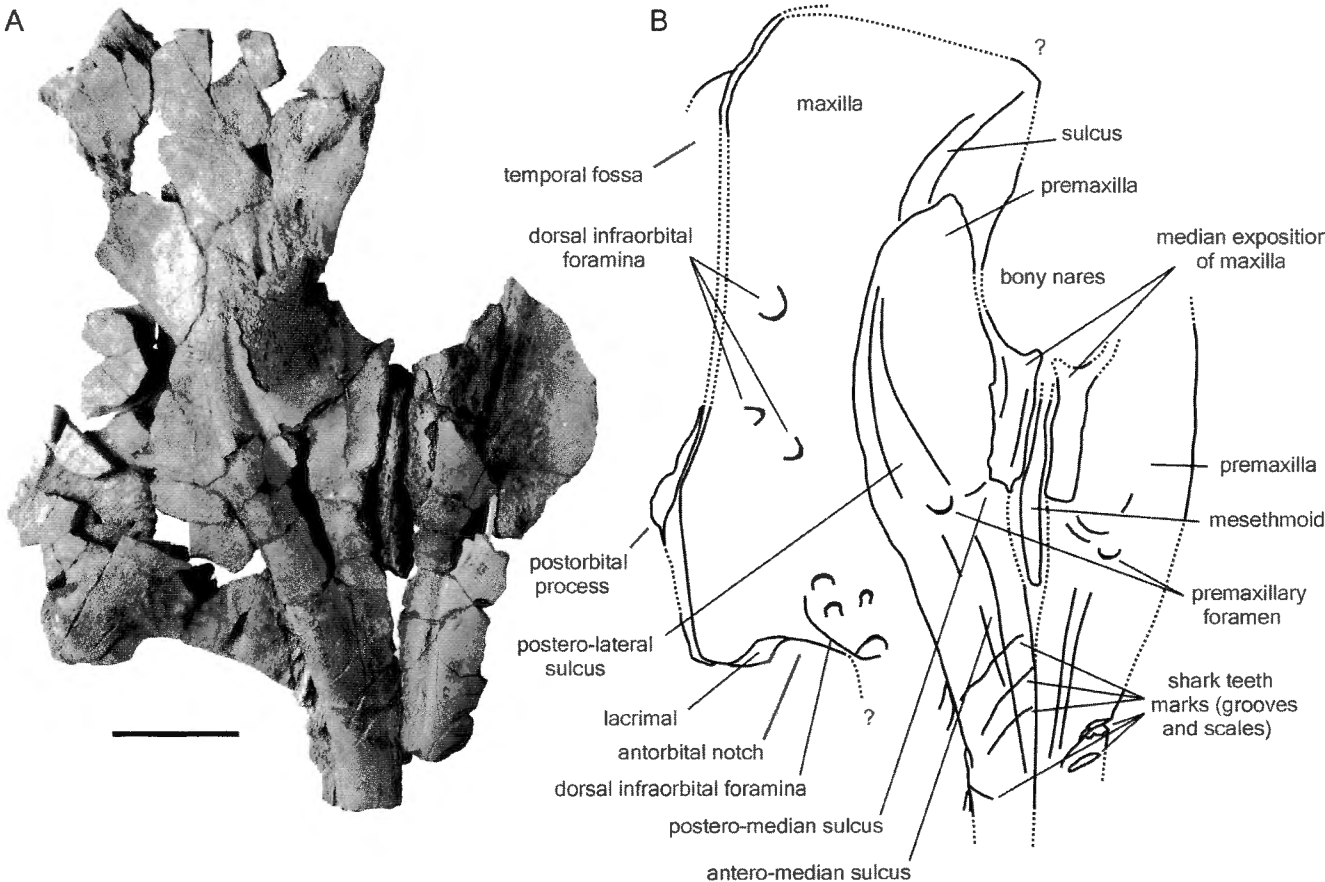


Fig. 3 — Skull of IRSNB M.1922, Monodontidae indet. from the Early Pliocene of Antwerp, North Sea Basin. **A** dorsal view. Note the shark teeth marks at the rostrum base. **B** schematic reconstruction of the preserved portion of the skull in dorsal view. Scale bar = 50 mm.

foramen somewhat posterior to the antorbital notch. A median triangular depression, made by the joined depressed median parts of the two premaxillae, extends from 60 mm anterior to the antorbital notch until the premaxillary foramen. In *Delphinapterus leucas* and *Monodon monoceros*, this area is convex and protuberant. The depression is margined by a shallow antero-median sulcus. Posterior to the premaxillary foramen, the convex premaxillary sac area is considerably swollen (Figs. 4A₁, 5B). This thickening is similar to the condition in *Monodon*

monoceros. It immediately follows the depression and gives the dorsal surface of the skull a more angulated lateral profile than in *D. leucas*. In the latter species, the thickening of the premaxilla increases with age, but it stays laterally located compared to IRSNB M.1922. The premaxillary sac fossa is bordered by a deeper postero-lateral sulcus and a shallow postero-median sulcus extending in the median exposition of the maxilla. The posterior apex of the right premaxilla is missing. However, considering the suture marks on the underlying maxilla, the premaxilla did not

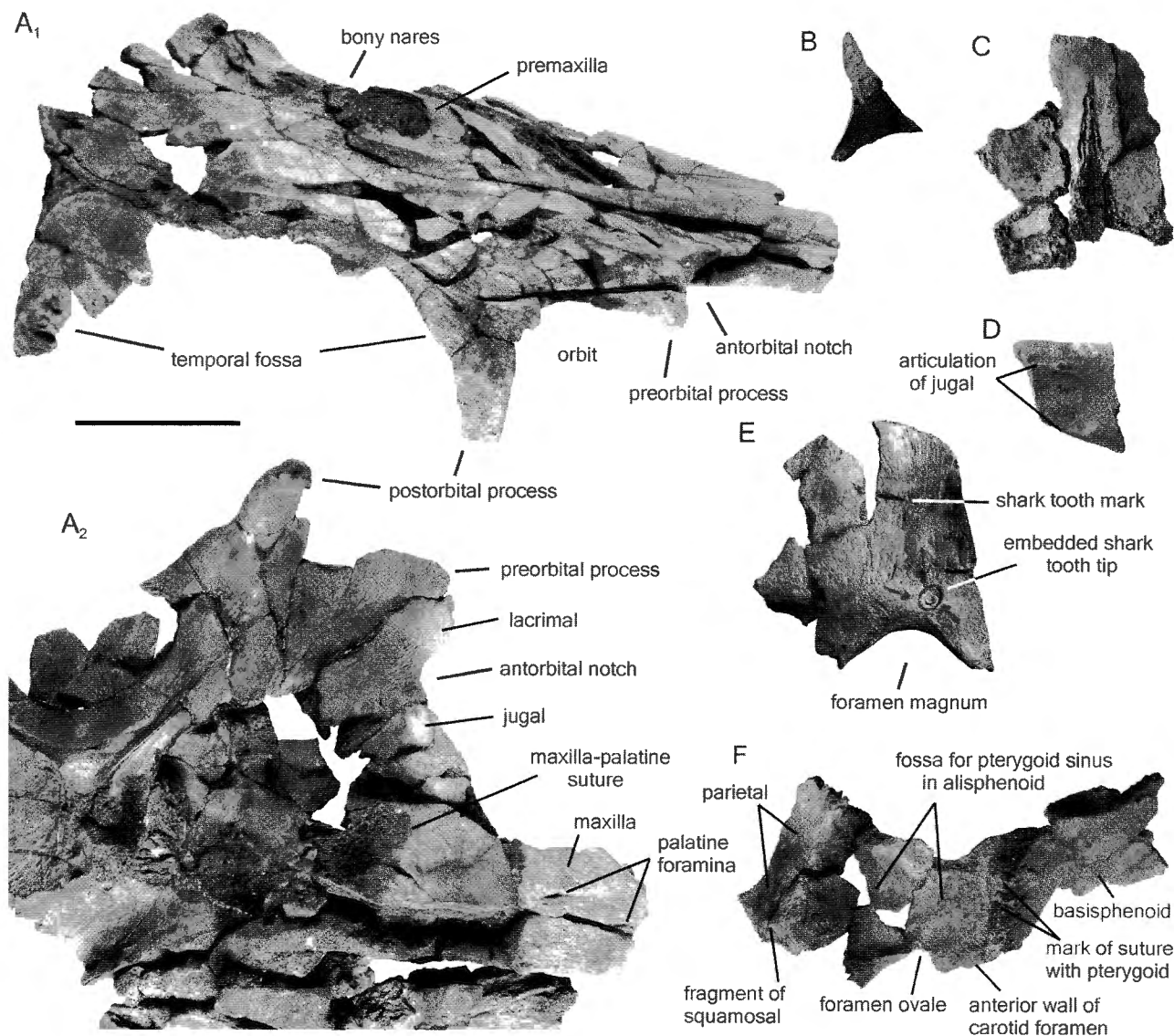


Fig. 4 — Skull of IRSNB M.1922, Monodontidae indet. from the Early Pliocene of Antwerp, North Sea Basin. A₁ lateral to dorsolateral view. A₂ detail of the right antorbital notch and orbit in ventral view. B fragment of crest formed by the joined supraoccipital and right frontal in lateral view. C fragment of the supraoccipital above the foramen magnum in posterior view, including the embedded tip of a shark's tooth. D zygomatic process of the right squamosal in medial view. E fragment of the mesethmoid forming the posterior wall of the bony nares in anterior view. F right alisphenoid with fragments of surrounding bones in ventral to anteroventral view. Scale bar for all elements = 50 mm.

border the bony naris and ended no more than 47 mm posterior to the anterior margin of the bony naris, before the maxilla-nasal contact.

Maxilla. The dorsal surface of the maxilla at the base of the rostrum is not fully preserved. However, several deep grooves, anterolaterally directed along the suture with the premaxilla, indicate the presence of at least two foramina anterior to the antorbital notch. More laterally, another foramen pierces the maxilla at the level of the notch, with a diameter of 5 mm. At least, three other foramina with a roughly similar size are present posterolaterally. Two additional small foramina are present 75 mm and 84 mm posterior to the antorbital notch and a larger maxillary foramen (width 10 mm) opens posterolaterally at the level of the anterior margin of the bony nares. This disposition is roughly similar to the condition in *Delphinapterus leucas*.

The lateral margin of the maxilla at the rostrum base is not complete but the aspect of the lacrimal on the antorbital notch and of the maxilla immediately anteromedially suggest that the rostral margin of the maxilla was originally directed anteromedially for some distance (more than 20 mm) before taking a more anteroposterior direction, a condition different from *D. leucas* and *M. monoceros*. The preorbital process is anteriorly shorter than in adult *D. leucas* and *M. monoceros*.

The median exposition of the maxilla between the premaxilla and the mesethmoid is 47 mm long until the anterior margin of the bony nares (Figs 3, 5A). At this point it is 17 mm wide. Along the bony naris, the width of the maxilla decreases until less than 4 mm. At the apex of the premaxilla, this smooth and thick plate of the maxilla widens and moderately raises towards the vertex (unpreserved). This plate is separated from the lateral part of the maxilla by a wide sulcus. Similarly to *D. leucas*, the sulcus originates from a foramen below the apex of the premaxilla.

Ventrally, the preserved palatal part of the maxilla is flat until the suture with the lost palatine, which nearly reaches the level of the antorbital notch. Two small palatine foramina pierce the maxilla 37 and 43 mm anteriorly to the antorbital notch (Fig. 4A₂). No alveolus is preserved on the maxilla. Considering the morphology and the posterior level of the large left tusk in the adult male *M. monoceros* and of the unerupted pair of modified maxillary teeth in the juvenile and adult female of this species (posterior to the antorbital notch, e.g., VAN BENEDEN & GERVAIS, 1880, pl. 45), there is no space for such elements on IRSNB M.1922. The pterygoid is lost.

Lacrimal. The lacrimal forms the outline of the shallow antorbital notch and the anteromedian part of the short preorbital process, where it is widely visible from a dorsal view. The lacrimal is nearly completely hidden by the frontal in lateral view.

Jugal. The jugal is at least anteriorly fused with the lacrimal. The section of the base of the zygomatic process of the jugal is subcircular.

Mesethmoid. The ossified mesethmoid is dorsally exposed between the premaxillae from 20 mm posterior to the antorbital notch. The extent of the exposition between the maxillae at the level of the premaxillary sac fossae might be overstated, due to reconstruction approximations.

An isolated fragment of the mesethmoid originates

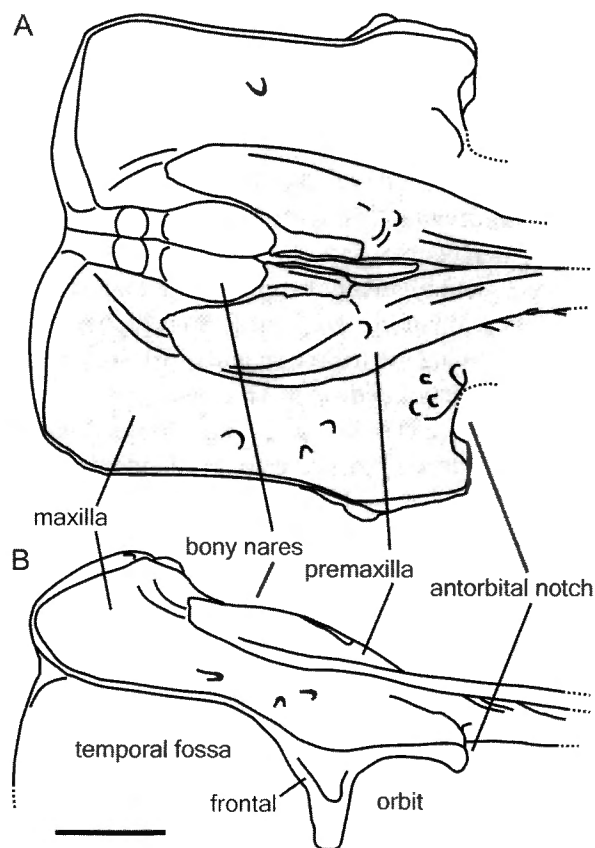


Fig. 5 — Reconstruction of the dorsal part of the cranium of IRSNB M.1922, Monodontidae indet. from the Early Pliocene of Antwerp, North Sea Basin. **A** dorsal, **B** right lateral view. The shaded area in dorsal view corresponds to the known elements of the skull. The morphology of the unpreserved vertex, specially the nasals, is inspired from *Delphinapterus leucas*. Scale bar = 50 mm.

from the posterior wall of the bony nares (Fig. 4E). The median keel is developed, separating distinctly concave lateral surfaces, while in *D. leucas* and in a lesser extent *Monodon monoceros*, the dorsal part of the plate is weakly keeled, with convex lateral surfaces. Two small (1 to 2 mm) foramina for the terminal nerve pierce the right surface and one the left. Limits of the bone are too damaged to compare its shape to the high and narrow mesethmoid of adult *D. leucas*. The left side of the plate is nevertheless thinner than the right side, a feature also observed in *D. leucas*.

In dorsal view, from the base of the rostrum to the posterior region of the nares, the sagittal plane of the skull is distinctly shifted to the left. However, the partial preservation precludes more precise quantification of the asymmetry of the premaxillae and the vertex.

Frontal. The orbit is short. The preorbital process of the frontal is barely thickened (Figs. 4A₁, 5B). The postorbital process is positioned at a level distinctly anterior to the bony nares, more elongated (43 mm) and less robust than in *D. leucas* and *M. monoceros*. The posterior wall of the postorbital process is erected, limiting a long temporal fossa. The fossa is more elevated dorsoventrally than in *D. leucas* and *M. monoceros* and relatively longer than in the latter. The anterior portion of the temporal fossa is higher than in *D. leucas*, giving the fossa a roughly oval shape rather than anteriorly pointed, as in *M. monoceros*.

The orbit canal is deep and posteromedially elongated, forming an angle of ca. 43 degrees with

the longitudinal axis of the skull, close to *D. leucas* and differing from the more right angle orientation of the canal seen in *Denebola brachycephala* (BARNES, 1984).

On this specimen, there is no extension of the pterygoid sinus fossa on the frontal. In *D. leucas* and *M. monoceros*, the undivided pterygoid sinus fossa (FRASER & PURVES, 1960) extends shortly on the base of the ventral surface of the frontal, immediately posterior to the optic canal (a process linked to ontogeny at least in *D. leucas*). There, a thin plate of the frontal limits the fossa laterally and joins the lateral lamina of the palatine forwards. The absence of this feature on IRSNB M.1922 probably indicates a less dorsally developed pterygoid sinus fossa.

An isolated fragment of the posterior margin of the right frontal sutured to the supraoccipital forms an acute and high crest laterally to the vertex, only partly dorsally covered by the maxilla, similar to largest *D. leucas*.

Alisphenoid. The ventral surface of the alisphenoid is hollowed by a wide fossa for the pterygoid sinus, posteriorly margined by the foramen ovale and laterally by the parietal (Fig. 4F). The fossa is better anteriorly delimited than in *Delphinapterus leucas*, supporting the hypothesis of a fossa not extending in the orbit roof. The squamosal is briefly wedged between parietal and alisphenoid on the posterolateral corner of the latter.

Supraoccipital. A fragment of the supraoccipital

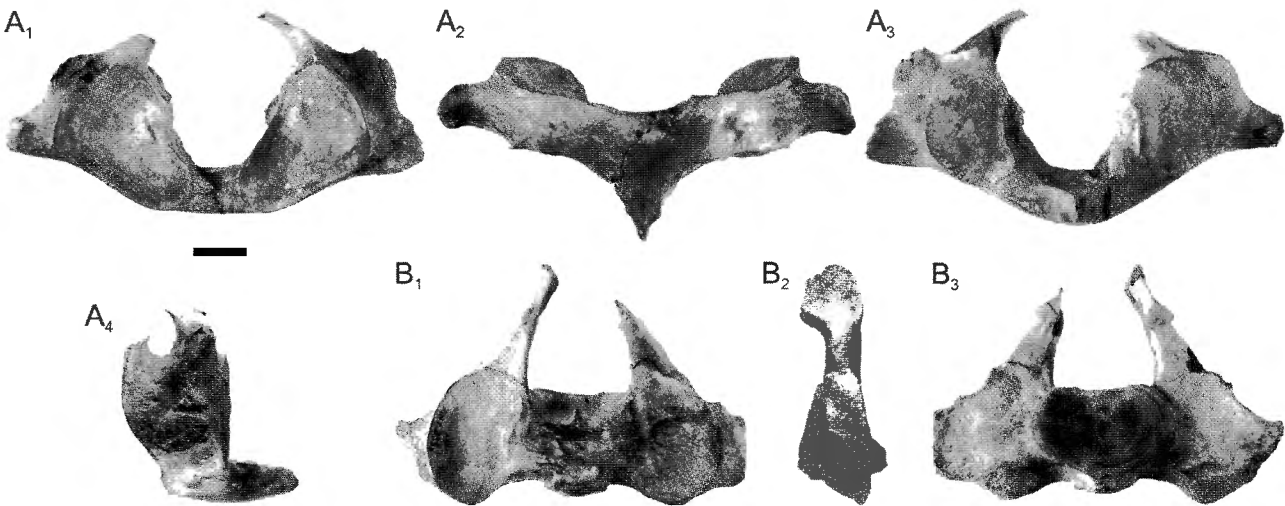


Fig. 6 — Atlas and axis of IRSNB M.1922, Monodontidae indet. from the Early Pliocene of Antwerp, North Sea Basin. **A** atlas. A₁ anterior, A₂ ventral, A₃ posterior, A₄ left lateral view. **B** axis. B₁ anterior, B₂ right lateral, B₃ posterior view. Scale bar = 20 mm.

above the foramen magnum (containing the tip of a shark tooth, see predation/scavenging section) indicates a rather pointed dorsal edge of the foramen magnum (Fig. 4C).

Squamosal. A fragment of the zygomatic process of the right squamosal shows a smooth, slightly concave and partly demarcated ventral part of the medial surface, corresponding to the surface of articulation of the jugal (Fig. 4D). The zygomatic process is lower than in *Denebola brachycephala*.

Postcranial elements

Atlas. The free atlas is robust; the width across the ventral transverse processes is 159 mm (nearly complete, see Table 2); the maximum length between anterior and posterior articular facets is 35 mm (Fig. 6A). The anterior articular facets are wide and concave, with a dorsolateral edge distinctly projecting anteriorly, but to a lesser extent than in *Monodon monoceros*. A short and thin spine leaves the top of the left articular facet (probably broken on the right side) in a dorsomedial direction, parallel to the incomplete neural arch for 6 mm. The asymmetrical subhorizontal ventral transverse process, shorter, more robust and positioned lower on the left side, bears a distinct dorsolateral muscular insertion surface, origin of the rectus capitis lateralis (see MUIZON, 1984). The dorsal transverse process, best preserved on the left side, is reduced to a knob, more than in *Delphinapterus leucas*. The triangular ventral spine is robust, thick and longer than in *D. leucas* and *M. monoceros*, extending on the whole length of the axis when articulated.

Axis. This bone is 131 mm wide across the ventral transverse processes. The ventral transverse process is less postero-laterally elongated than in *D. leucas*, and, similarly to the atlas, the left process is somewhat shorter, less pointed than the left and more developed dorsoventrally (Fig. 6B). As in *D. leucas*, the dorsal transverse process is nearly absent, contrary to the condition in *M. monoceros*. The facets of articulation with the atlas are reniform and poorly concave, ventrally narrower than in *D. leucas*. The odontoid apophysis is short and blunt, giving the bone a maximum ventral length of 37 mm. The incomplete vertical neural arch is slender and less posteriorly directed than in *D. leucas*.

Asymmetry is also observed on the transverse processes of the axis of the tusk-bearing male *M. monoceros* and on the atlas of the Pliocene walrus-like

delphinoid *Odobenocetops leptodon* MUIZON *et al.*, 1999, with an additional crest and a more developed transverse process on the left side, possibly related to the weight of the elongated right tusk (MUIZON & DOMNING, 2002). These connections between cervical asymmetry and tusk-like development of one tooth make attractive the hypothesis of a similar feature in IRSNB M.1922. However, atlas and axis of *D. leucas*, which lacks any tusk, are both distinctly asymmetric (proportions, length and level of the processes and articular surfaces).

The free atlas and axis quite similar to *D. leucas* and the well-developed supraoccipital crest are elements supporting the idea of a flexible neck region which would have permitted a high degree of vertical head movement, as is the case in *D. leucas* (BRODIE, 1989; MUIZON & DOMNING, 2002).

atlas	
width across transverse processes	+159
width across anterior articular facets	115
width across posterior articular facets	108
height posterior articular facets (left/right)	44/45
maximum width neural canal	53
maximum length between anterior and posterior articular facets	35
axis	
width across transverse processes	131
width across anterior articular facets	118
width posterior articular facets	53
height posterior articular facet	37
width neural canal	38
width across postzygapophyses	53
maximum ventral length	37

Table 2 — Measurements (in mm) of the atlas and axis IRSNB M.1922, Monodontidae indet. from the Early Pliocene of Antwerp, North Sea Basin. (+) indicates nearly complete.

Vertebral epiphyses. The maximum width of the four unfused vertebral epiphyses (indicating a not fully mature individual) ranges from 44 to 49 mm.

Rib fragments. Three rib fragments include the double-headed proximal extremity, two of them with an important enlargement of the bone from the level of the reduced capitulum, indicating more anterior

ribs (between first and fourth when compared to *D. leucas*) (Fig. 7). Another fragment is probably a part of sternal rib.

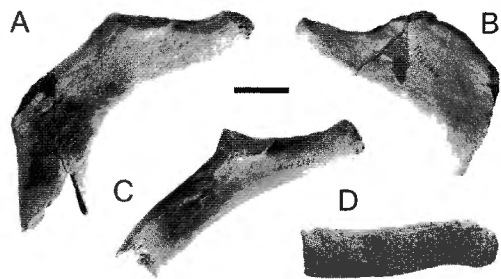


Fig. 7 — Rib fragments of IRSNB M.1922, Monodontidae indet. from the Early Pliocene of Antwerp, North Sea Basin. A-C anterior double-headed ribs, D ?sternal rib. Scale bar = 20 mm.

Systematic discussion

Among the four characters listed by MUIZON (1988a) to diagnose the family Monodontidae, only the dorsal exposition of the maxilla along the bony naris can be distinctly observed in IRSNB M.1922. The alisphenoid is not significantly thickened laterally to the foramen ovale and because of the incompleteness of the specimen (pterygoid and palatine not preserved) the two other features (morphology of the lateral lamina of the palatine, loss of the lateral lamina of the hamular process) cannot be observed. From the preserved elements, the deepening of the pterygoid sinus fossa in the lateral wall of the cranium noted by FRASER & PURVES (1960) in *Delphinapterus leucas* and *Monodon monoceros* is either absent or less developed in IRSNB M.1922. Whatever, the pterygoid sinus is probably undivided (see discussion in ARNOLD & HEINSOHN, 1996) in IRSNB M.1922, as no trace of pre- or postorbital fossa is visible. In the phylogenetic analysis of HEYNING (1989), this character of extant monodontids is considered as a reversion.

Another synapomorphy of the Monodontidae is the anterior shift of the orbit compared to the rest of the cranium (ARNOLD & HEINSOHN, 1996). This character, also present in the presumably closely related and deeply modified *Odobenocetops* MUIZON, 1993, is linked to the development of a long temporal fossa; the shift is more pronounced in IRSNB M.1922 than in *Denebola brachycephala*, with the postorbital process of the frontal much anterior to the bony

nares. IRSNB M.1922 is also more derived than *D. brachycephala* in the flattening of the dorsal surface of the cranium and the barely elevated vertex, more similar to *D. leucas* and *M. monoceros*. However, the temporal fossa of IRSNB M.1922 is higher than in the two extant monodontids, probably closer to *D. brachycephala*, and the premaxilla is depressed anteromedially to the premaxillary sac fossa.

No clear apomorphy could relate IRSNB M.1922 more closely to one of the two extant monodontids. Similarities with both species are noted (less flattened anterior part of the temporal fossa and swelling of the premaxillary sac fossa, as in *M. monoceros*; lower vertex and longer temporal fossa, as in *D. leucas*). IRSNB M.1922 lacks the enlarged tooth of *M. monoceros*, a character that should exclude it from the genus *Monodon*.

Several characters differentiate IRSNB M.1922 from the other monodontids: the shorter orbit with a more elongated and more slender postorbital process of the frontal (partly known in *Denebola brachycephala*) and the shorter and wider antorbital notch. These features might constitute autapomorphies of a new monodontid taxon, but the fragmentary preservation of IRSNB M.1922 does not allow to precise their status.

Predation/scavenging

Description

Several scratches are observed on the well-preserved surface of the skull, especially on the premaxillae at the base of the rostrum (Fig. 8A). The right premaxilla presents three parallel grooves ca. 25 mm long, with a maximum space of 10 mm between distal and second groove and 14 mm between second and proximal groove. A similarly directed groove, 26 mm long, marks the left premaxilla, 22 mm distant from the distal groove on the right premaxilla. On the lateral portion of the groove, a fragment of the premaxilla has been scaled off. At the preserved end of the left premaxilla, an additional larger scale of bone has been similarly removed. Another small groove (7 mm) on the right premaxilla is differently oriented, with an angle of 65° to the main orientation of the other grooves. On the fragment of supraoccipital, a wider and deeper horizontal groove, 18 mm long, marks the outer surface 40 mm above the foramen magnum (Fig. 8B). Furthermore, the apex of a shark tooth is slightly obliquely embedded in the supraoccipital 8 mm above the foramen magnum. The largest diameter of the fragment is 4.2 mm.

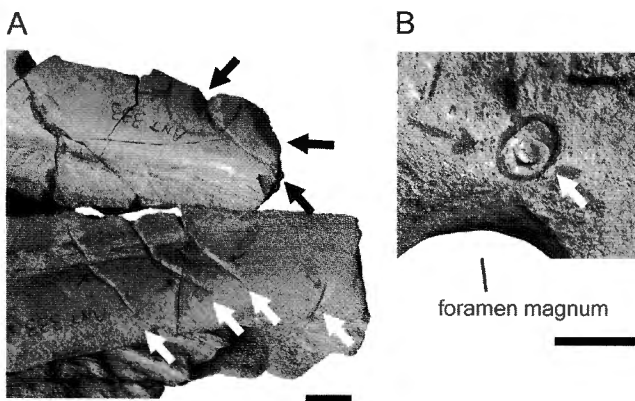


Fig. 8 — Predation/scavenging marks on the skull of IRSNB M.1922, Monodontidae indet. from the Early Pliocene of Antwerp, North Sea Basin. **A** detail of the dorsal surface of the rostrum base (arrows indicate marks). **B** detail of the posterior surface of the supraoccipital with the tip of a shark's tooth embedded (arrow). Scale bars = 10 mm.

Discussion

All these marks correspond to interactions with one or several sharks. The four parallel grooves grouped at the rostrum base suggest a single movement of the shark's jaw directed *ca.* 55 degrees from the longitudinal axis of the skull, probably from the right side to the left side if we consider the scaling off on the lateral margin of the left premaxilla. Because the grooves continue on the depressed area of the right premaxilla, they were made by the tip of the shark's teeth more than by the cutting edge. In both extant monodontids *D. leucas* and *M. monoceros*, the melon and facial musculature are voluminous, protuberant nearly until the apex of the rostrum. Considering a similar condition in IRSNB M.1922, only a particularly powerful bite could have reached the premaxillae of the living animal. However, it is also possible that the grooves were made during the next steps of the predation, after death and removal of a part of the soft tissues, or even during scavenging on a partly decomposed carcass. This possibility very likely applies to the groove and tooth fragment on the supraoccipital shield. The musculature of the neck is indeed also voluminous, and a bite on the living animal would hardly contact the bone just above the foramen magnum.

Contrary to the specimens from the Italian Pliocene studied by CIGALA-FULGOSI (1990) and BIANUCCI *et al.* (2000), the morphology of the few simple marks recorded does not allow the identification of the predator/scavenger. The depth of the grooves and the

deeply embedded tooth extremity suggest a powerful, large shark, maybe from the genus *Cosmopolitodus* (Mako sharks, isurids). *Cosmopolitodus hastalis* (AGASSIZ, 1843) is for example common in the Pliocene of the area of Antwerp (LERICHE, 1926; J. Herman pers. comm. 2005). The spacing of the four grooves gives the minimum spacing of the teeth on the shark's jaw, suggesting a shark several meters long. BIANUCCI *et al.* (2000) similarly suggest an isurid shark attack for a specimen of the Italian Pliocene delphinid *Astadelphis gastaldii*.

Besides killer whales and polar bears, the extant Greenland shark *Somniosus microcephalus*, with a body length often exceeding 4 m, is known to feed on dead or moribund narwhals (BECK & MANSFIELD, 1969).

Isolated monodontid periotics from the Neogene of Antwerp (Fig. 9)

This series of roughly complete isolated Mio-Pliocene periotics, four right and one left, has a total length ranging from 32 to 35 mm (the posterior process is usually somewhat abraded) and a maximum medio-lateral height across the pars cochlearis from 24 to 26.5 mm, somewhat smaller than in *Delphinapterus leucas* (respectively measurements 13 and 15 in KASUYA, 1973).

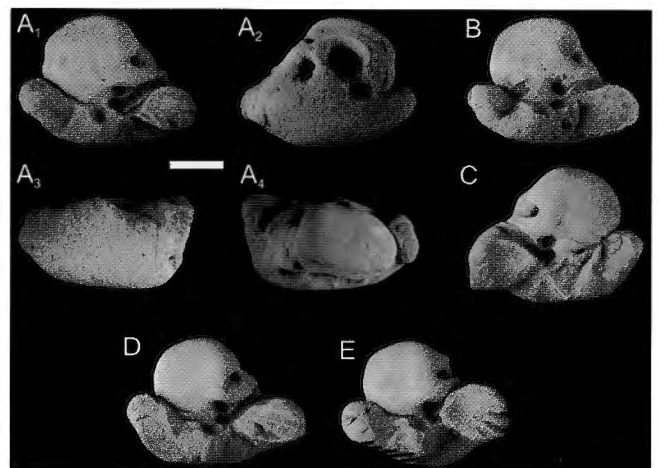


Fig. 9 — Isolated periotics of Monodontidae indet. from the Mio-Pliocene of the area of Antwerp, North Sea Basin. **A** IRSNB M.1923 in **A**₁ ventral, **A**₂ dorsal, **A**₃ lateral, **A**₄ medial view. **B-E** in ventral view. **B** IRSNB M.1924. **C** IRSNB M.1925. **D** IRSNB M.1926. **E** IRSNB M.1927. All periotics from right side except **C**. Scale bar = 10 mm.

The anterior process is short, with a blunt apex stuck to the pars cochlearis, as in *D. leucas*, shorter than in *Monodon monoceros* and *Orcaella brevirostris*, and less pointed than in *Denebola brachycephala* and *M. monoceros*. The anterior process, otherwise similar to *D. leucas*, lacks the pointed medial projection of the anterior process seen in the latter. Main monodontid characteristics are: the elevation of the pars cochlearis; its dorsoventral flattening (a feature mainly marked on the ventral surface, which is only slightly convex); the dorsal process thickened lateral to the dorsal aperture for the endolymphatic duct (better seen in medial view). In the Pliocene delphinid *Astadelphis gastaldii* (BRANDT, 1874) and in *O. brevirostris*, the pars cochlearis is similarly high, but less dorsoventrally flattened. And the dorsal process of *A. gastaldii* is not expanded. The fenestra rotunda is here relatively smaller than in *D. leucas*.

The posterior process is shorter than in *M. monoceros* and, to a lesser extent, than in *D. brachycephala*, with a dorsal margin more abruptly ventrally turning than in *D. leucas*. The process is posteriorly more than laterally directed, differing in this respect from *M. monoceros* (KASUYA, 1973). The concave posterior bullar facet bears deep ridges and grooves.

In general these periotics are closer to *Delphinapterus* than to *Monodon*, suggesting delphinapterine affinities, but the similarities with the periotic of the more archaic (based on cranial characters: vertex and orbit) *Denebola* preclude a definitive subfamilial attribution. Furthermore, because the stratigraphic information associated to these periotics is no more precise than Late Miocene-Pliocene, it cannot be asserted that they belong to the same taxon as the Lower Pliocene skull described above. They only further support the presence of monodontid taxon/taxa before the Pleistocene in the North Sea Basin.

Palaeobiogeographic considerations

Monodontids are the only extant odontocetes to be strictly distributed in the cold Arctic Ocean and adjoining seas. *Monodon monoceros* has only occasionally been recorded as far south as Britain and Germany and *Delphinapterus leucas* as far south as Japan, New Jersey, Washington, Ireland, Scotland, the Rhine River, and the Baltic Sea (BRODIE, 1989; HAY & MANSFIELD, 1989; references herein).

Geographically the oldest described monodontid is

known from the latest Miocene of Mexico (BARNES, 1984). During the Early Pliocene, a member of the family is cited from the other side of the equator, on the coast of Peru (MUIZON & DEVRIES, 1985). The migration of monodontids in the North Atlantic occurred before 5.0–4.4 Ma (Kattendijk Formation; LOUWYE *et al.*, 2004), time of their appearance in the North Sea Basin. At roughly the same time or slightly later (ca. 4.8–3 Ma; DOWSETT & WIGGS, 1992), *Delphinapterus* sp. is first recorded from the east coast of North America (Virginia and North Carolina, Yorktown Formation; WHITMORE, 1994). From the Pacific Ocean to the North Sea Basin, two major geographic features potentially affected the migrations of marine mammals: the Panama Seaway and the Channel (between Atlantic Ocean and southern North Sea). The former remained open until mid-Pliocene (HAUG *et al.*, 2001 and references herein), after the entrance of monodontids in the North Atlantic. The latter did probably not open before late Zanclean (ca. 4.4–4.3 Ma, VAN VLIET-LANOË *et al.*, 2002); monodontids had therefore to go even further north, around the British Islands, to reach the southern North Sea.

From an ecological point of view, the sands of the Kattendijk Formation, in which IRSNB M.1922 was found, were deposited in a near coastal environment, with a water depth of 30–50 m and cool-temperate sea-surface conditions (less than 7.2°C for April sea-surface temperatures) (GAEMERS, 1988; LOUWYE *et al.*, 2004). This is colder than on the coast of Virginia and North Carolina during Early Pliocene (between 12.9–14°C and 22.2–23.7°C, CRONIN, 1991) and much colder than the warm tropical waters off Peru during the same interval of time (MUIZON & DEVRIES, 1985). Early Pliocene monodontids were therefore distributed in environments more diverse than nowadays. Furthermore, the shift to colder areas as discussed by WHITMORE (1994) was already partly made at that time, before or during the first steps of the strengthening of the Gulf Stream related to the formation of the Isthmus of Panama (from ca. 4.7 Ma, HAUG *et al.*, 2001) and much before the first Late Pleistocene records of *Delphinapterus leucas* in the North Sea (e.g., POST & KOMPANJE, 1995; MOL *et al.*, 2006). The subtle warming of the climate occurring during the Early Pliocene, locally and worldwide (BUCHARDT, 1978; ZACHOS *et al.*, 2001) might have been a factor facilitating the northward migration of monodontids.

The late Middle to Late Miocene is a crucial time in the evolutionary history of the odontocetes. This

interval is marked by a profound climatic cooling and sea level drop, related to the development of the East Antarctic Ice Sheet (HAQ *et al.*, 1987; FLOWER & KENNETT, 1994; ZACHOS *et al.*, 2001) and implying a reduction of the underwater part of the continental shelves. During the same time, several mostly long-snouted odontocete families originating in the Oligocene became extinct (Eurhinodelphinidae, Kentriodontidae and Squalodontidae), while the Platanistidae disappeared from the marine record (FORDYCE & MUIZON, 2001; BIANUCCI & LANDINI, 2002). The Late Miocene provides the first records of members of the living Delphinoidea families (crown-Delphinoidea: Delphinidae, Monodontidae, Phocoenidae), competing with the last members of the archaic families cited above and/or filling the ecological niches left empty. However, this process is until now only recorded at low latitudes along the east coast of the Pacific Ocean: Delphinidae, Monodontidae and Phocoenidae from California and Mexico (BARNES, 1977, 1984; BARNES *et al.*, 1985) and Delphinidae and Phocoenidae from Peru (MUIZON, 1988b). Even if the Late Miocene fossil record is poorer in several major North Atlantic localities (GOTTFRIED *et al.*, 1994; pers. obs.), no crown-Delphinoidea is identified in the North Atlantic realm before the Early Pliocene (GOTTFRIED *et al.*, 1994; MORGAN, 1994; BIANUCCI & LANDINI, 2002; work in progress for the North Sea). This delayed appearance of the North Atlantic crown-Delphinoidea might indicate a Pacific origin for the three families, as suggested by BARNES (1985) for the Phocoenidae, and a subsequent migration across the progressively restricted Panama Seaway. As a matter of fact, a biogeographic barrier between Pacific and Atlantic Oceans has been proposed by COLLINS *et al.* (1996) by 8-6 Ma, on the basis of shallow water benthic foraminifera. Such a feature did probably not facilitate the passage of crown-Delphinoidea to the North Atlantic.

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APPENDIX

Specimens and preparation

The main specimen IRSNB M.1922 was found by P. G. on June 2, 1984 during the excavation for the eastern wall of the Vrasene Dock, on the territory of the village of Kallo, western bank of the Scheldt River, NWW of the city of Antwerp (Figs. 1, 2). The bones were discovered in the upper part of the Kattendijk Formation, Lower Pliocene (DE MEUTER & LAGA, 1976). This layer contains numerous bones of marine mammals, mostly well preserved, often in anatomical connection. From the fragments partly removed from the wall by the excavation machines, several bones could be reconstructed: nearly complete atlas and axis, five vertebral epiphyses belonging to at least four vertebrae and six rib fragments. With more than 60 fragments of a completely crushed skull, P. G. was able to reconstruct a large portion of the dorsal surface of the cranium. About ten smaller cranial fragments remained isolated. Abraded margins of several fragments indicate that the skull has been

fragmented prior to its discovery. On the basis of the morphology of the atlas-axis complex, P. G. and his father Paul Gigase referred the specimen to an unknown monodontid and offered it to the IRSNB.

Additionally, five isolated monodontid periotics were recently found in the Neogene of the area of Antwerp, without stratigraphic data, but probably mostly from the Pliocene: IRSNB M.1923, sands dredged from the Scheldt estuary, collected by C. Riemslag, 2004; IRSNB M.1924, sands removed from the Liefkenshoektunnel, Antwerp; IRSNB M.1925, Antwerp area, no precise locality; IRSNB M.1926, sands dredged from Doeldok, Antwerp Port, collected by M. Bosselaers, July 6, 2004; IRSNB M.1927, sands dredged from Doeldok, Antwerp Port, collected by M. Bosselaers, September 1, 2004.

Comparison material of the extant monodontid species *Delphinapterus leucas* and *Monodon monoceros* mainly comes from the collections of IRSNB, RMNH and ZMA, with a large series of animals from both sexes and different ages.