Cetacean fossils from a 1961 expedition at the Schelde estuary, province of Zeeland, The Netherlands

Klaas Post[1] & Mark Bosselaers[2, 3]

[1] *Natuuurhistorisch Museum Rotterdam, Westzeedijk 345, 3015 AA Rotterdam, The Netherlands; klaaspost@fishcon.nl*
[2] *Koninklijk Belgisch Instituut voor Natuurwetenschappen, Vautierstraat 29, 1000 Brussels, Belgium*
[3] *Koninklijk Zeeuwsch Genootschap der Wetenschappen, Kousteensedijk 7, 4331 JE Middelburg, The Netherlands.*

During 2010-2015 the authors revisited the massive collection of marine mammal fossils in Naturalis Biodiversity Center, Leiden, The Netherlands. Between the thousands of postcrania collected by a single expedition at the Schelde estuary in 1961 they noted some fragmented but important toothed whale (Odontoceti) cranial specimens. This article reports on fossils of a narwhal (Monodontidae), a large beaked whale (Ziphiidae) and dolphins related to the Amazon river dolphins and the La Plata dolphin (Inioidea), which at times between the middle Miocene and early Pleistocene inhabited the North Sea realm.

KEY WORDS: fossil marine mammals, North Sea Basin, Inioidea, Monodontidae, Ziphiidae

Introduction

In 1961 G. Kortenbout van der Sluijs and C.J. Overweel, at the time curators of the National Museum of Geology and Mineralogy, at Leiden, The Netherlands (currently incorporated in Naturalis Biodiversity Center), were awarded the substantial Royal Dutch Shell Grant and used it to finance a collecting expedition to seafloor sediments of the Ooster- and Westerschelde estuaries in the SW part of the Netherlands, in search for fossils (Fig. 1). A musselcutter ZZ 8 (from Zierikzee) was hired. The

Figure 1. G. Kortenbout van der Sluijs (right) on board of the ZZ 8 in 1961.

survey yielded large amounts of both terrestrial and marine mammal fossils for the collections of their institute at Leiden. While the Plio-Pleistocene terrestrial fossils were adequately identified, the massive quantities of marine mammal remains - often isolated bones, without stratigraphic context - received little or no attention, and were stored in large stacks in the attics of the museum. During the beginning of this century preliminary identifications were made and all fossils were registered and stored in boxes. Recently Scager (2015) analysed the 1961 trip, re-located the various collecting sites, assessing their possible stratigraphic context and the faunal assemblages.

In this study we report on four fragmentary fossil remains of cetaceans supplying additional information to the composition of the North Sea Basin fossil marine mammal fauna, as well as to the paleogeographic distribution of fossil marine mammals.

Site and geological context

All specimens herein described were dredged from the seafloor during the 1961 expedition at the location 'Domburg', situated offshore opposite the city of Domburg on the Dutch coast (Scager, 2015, p. 9) (Fig. 2). According to Scager the seafloor consists of sediments of the terrestrial Waalre Formation (3.6-1.0 Ma), and/or the marine Maassluis Formation (2.0-1.8 Ma), both overlying the marine Oosterhout Formation (5.2-2.6 Ma). Scager suggested the Maassluis/Waalre formations as the source of the abundant fossils of an early Pleistocene terrestrial

Figure 2. The Domburg site.

fauna (biozone MN 17). The bulk of the fossil catch, however, consists of marine mammal remains, dominated by the walrus *Ontocetus emmonsi* Leydi, 1859 (Kohno & Ray, 2008). This walrus frequented the North Sea Basin from the late Pliocene until the early Pleistocene (KP, unpublished data) and its presence at the 'Domburg' location therefore indicates the presence of one or more late Pliocene to early Pleistocene marine mammal assemblages. Some fragmented fossil remains of middle to late Miocene marine mammals, such as rostra of the stem beaked whale *Ziphirostrum* sp. (Lambert, 2005), demonstrate that fossils of one or more Miocene assemblages are also present.

The lack of undisputed data, the *ex situ* character of the specimens, and the complicated stratigraphical context of the area urge us to consider any stratigraphic statement with utmost caution. Only middle to late Pleistocene marine mammal faunas may be with certainty excluded as being the origin of the heavily mineralised fossils from this locality, because marine middle Pleistocene strata are not known from the Netherlands, while fossils of the well-known late Pleistocene marine mammal fauna still contain collagen and are not markedly mineralised (Post, 2005). In conclusion, the here described fossils have to be considered as probably originating from middle Miocene to early Pleistocene marine strata.

Material and methods

The material described and/or compared here is stored in the collections of Naturalis Biodiversity Center, Lei-

den, The Netherlands (RGM registration numbers) and the Natural History Museum, London, United Kingdom (NHMUK). Morphological terminology follows Mead & Fordyce (2009).
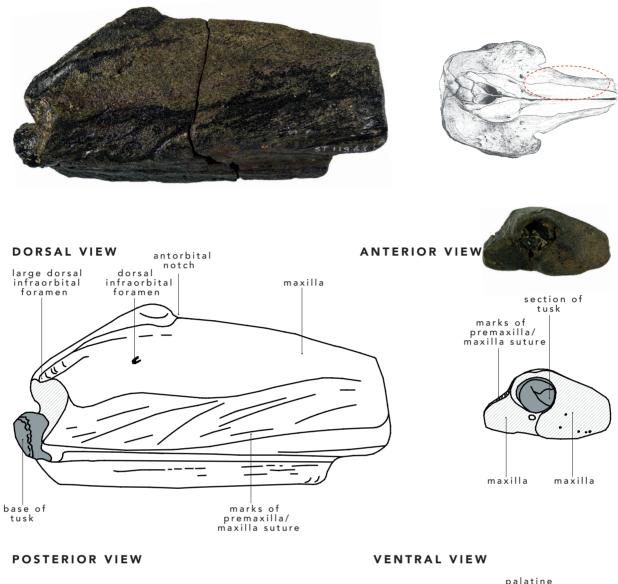
Systematic palaeontology

Order Cetacea Brisson, 1762
Suborder Odontoceti Flower, 1867
Family Monodontidae Gray, 1821

Monodon sp.
Figure 3

Material examined – Incomplete left maxilla with maxillary tusk embedded, RGM.119631.

Description – RGM.119631 is a 214 mm long fragment of the rostral and anterior neurocranial part of the left maxilla. Anteriorly and dorsally - at the fracture - the maxilla is 86 mm wide, while more posteriorly at its widest part the maxilla measures 114 mm. At this location a small lateral ridge marks the location of the left antorbital notch, while even more posteriorly an anterolaterally directed sulcus might indicate the anterior extension of a fairly large dorsal infraorbital foramen. On the whole length of the dorsal surface of the maxilla, the surface of the suture for the (lost) premaxilla is visible, transversally extending c. 30 mm from the midline of the skull. Ventrally three small, anterolaterally directed foramina are located in a worn area possibly corresponding to the posterior-
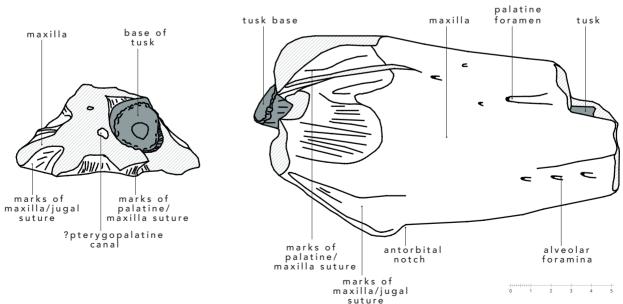
Figure 3. RGM.119631 *Monodon* sp., fragment of left maxilla with tusk. The fossil is indicated with a dashed ellipse on a line drawing of a cranium in dorsal view of *Monodon monoceros*.

most portion of the alveolar groove; these foramina may have been connected to vestigial posterior upper teeth. A larger, palatine canal or foramen is located more medially. At *c.* 80 mm from the posterior fracture, deep anteroposterior interdigitating grooves mark the palatine/maxilla suture. A deep channel situated just posteromedially to the antorbital notch marks the suture with the jugal.

Along the entire length of the maxilla, more or less lateromedially centred, and just under the dorsal surface, a 204 mm long tusk fragment is preserved. This root of a large tooth is broken and fractured at the anterior end, but it shows an undamaged oval posterior base with a maximum diameter of 29 mm, protruding some 20 mm out of the fractured posterior border of the maxilla.

Discussion – The family Monodontidae includes only two extant species, the enigmatic tusked narwhal, *Monodon monoceros* Linnaeus, 1758, and the beluga, *Delphinapterus leucas* (Pallas, 1776). The fossil history of the family is poorly known. The oldest reported fossil species is *Denebola brachycephala* Barnes, 1984 from the late Miocene of Mexico. Early Pliocene monodontids are recorded in Peru (Delphinapterinae indet.; Muizon & DeVries, 1985), the East Coast of North America (*Delphinapterus* sp.; Whitmore, 1994; Whitmore & Kaltenbach, 2008), *Bohaskaia monodontoides* Vélez-Juarbe & Pyenson, 2012), and the North Sea Basin (Monodontidae indet.; Lambert & Gigase, 2007). All fossil specimens for which cranial material is known are non-tusk-bearing members of the family. Remains of the extant monodontid species are reported from the late Pleistocene of the North Sea Basin (beluga, Post & Kompanje, 1995) and from the late Pleistocene and early Holocene of Canada (beluga and narwhal, Harrington, 2008). Van Deinse (1944, p. 188) reported a 1.64 m long tusk of *M. monoceros* dredged before 1919 from the Doggersbank (central North Sea). Carbon dating of the tusk at the University of Groningen resulted in an age of 710 ± 30 years BP (GrA-66668). Bearing in mind the reservoir adjustment and standard calibration, this date implies that between 1520 and 1645 either a narwhal vagrant died in the North Sea, or (more likely) that a 16th or 17th century ship lost its very precious cargo.

The assignation of RGM.119631 to *Monodon* sp. is based on clear morphological affinities with the extant *M. monoceros* and in particular on the presence of a relatively large tusk. RGM.119631 being a left maxilla, one would expect a large and heavy tusk fragment because the left tusk of extant narwhal is the tusk that usually protrudes in adult males and may reach a length up to 3.15 m (Born, 1994). The narwhal tusk is in fact an ever growing anteriorly directed canine and - because of its size - specimen RGM.119631 may have belonged to a juvenile individual, an assumption corroborated by the obviously non fused nature of the cranial bones (premaxilla, jugal and palatine were not fused with the maxilla and are lost), and especially by the shape and appearance of the base of the tusk (Nweeia *et al.*, 2009). However, the tusk (and especially its posteromedially oriented base) is also almost identical to non-erupted left tusks of sub-adult extant narwhals or of female narwhals, and to the general outline of the (almost always) non-protruding and non-developed right tusks of extant adult narwhals (Nweeia *et al.*, 2012; Van Beneden & Gervais, 1868-1879, p. xlv). Non-protruding tusks reach in extant narwhals lengths of 230 mm (female) to 290 mm (male) (Born, 1994); the tusk of the RGM.119631 specimen most likely originally attained, or even surpassed this latter length. Based on the presence of an enlarged maxillary tusk and similarities with *Monodon monoceros*, we tentatively identify this specimen as *Monodon* sp.

The preservation and colour of RGM.119631 is identical to late Pliocene to early Pleistocene marine mammal fossils originating from the same site (for example specimens belonging to *Ontocetus emmonsi*; KP, pers. obs.), but this observation is not conclusive. Another tusk-bearing right maxilla of a fossil narwhal is stored in the collection of the Natural History Museum, London (NHMUK 6137). Maxilla and tusk of that specimen seem to be morphologically very close to the RGM.119631 specimen. NHMUK 6137 was part of the famous Savin collection and has been collected at Overstrand, Norfolk, UK, in the Forest Bed. This 'aborted tusk *in situ'* was reported together with some more isolated tusk fragments (Newton, 1882). In Newton's time the (Cromer)/Forest Beds were assumed to be of late Pliocene age. However, recently marine (cold, arctic) stages of the Forest Beds were reported as late early Pleistocene or early middle Pleistocene (MIS 12-MIS 13) (Larkin *et al.*, 2014; N. Larkin, pers. com.). Whether or not specimen RGM.119631 and NHNUK 6137 belong to one and the same taxon remains to be studied, but both confirm the early Pleistocene or pre Pleistocene presence of at least one tusk-bearing monodontid in the North Sea Basin.

Family Ziphiidae Gray, 1850

Ziphiidae gen. et sp. indet.
Figure 4

Material examined – Mandible fragment of very large fossil beaked whale, RGM.117935 (Figure 4).

Description – Specimen RGM.117935 is a large and heavy fragment of the anterior part of the right mandible of a large-sized odontocete. The length of the specimen is 292 mm and the width 101 mm. Dorsally on the anterior fracture an oval cavity reveals a section of the mandibular canal. Smaller openings for branches of the mandibular canal are located just above and below the main canal. A 20-22 mm wide, shallow alveolar groove excavates the entire length of the dorsal surface of the mandible, which is pierced by several small foramina but lacks marks of post-apical alveoli. The dorsal margin of the fragment is slightly concave in lateral view. The lateral surface shows two mental foramina: a large and oval foramen on the anterior part of the specimen and a small foramen 58 mm more posteriorly. The medial side of the specimen exposes part of an at least 181 mm long and 99 mm deep man-
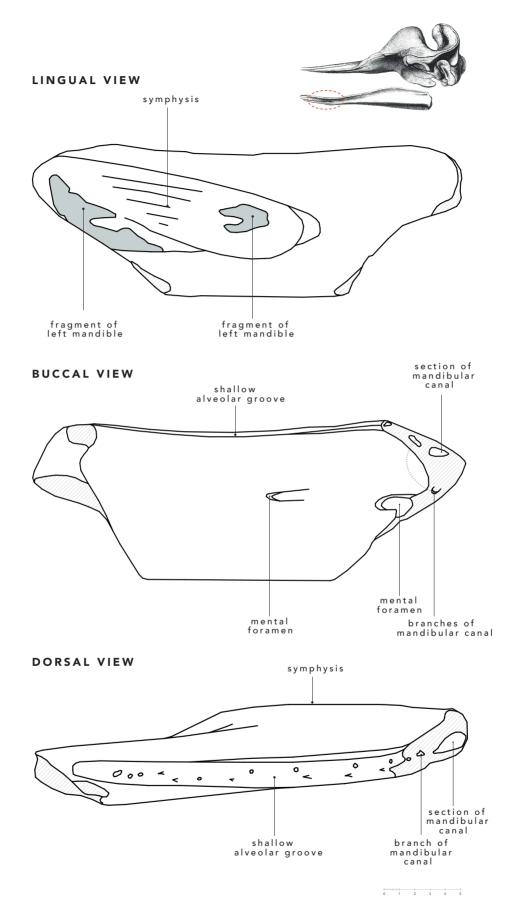
LINGUAL VIEW

symphysis

fragment of
left mandible

fragment of
left mandible

BUCCAL VIEW

section of
mandibular
canal

shallow
alveolar groove

mental
foramen

mental
foramen

branches of
mandibular canal

DORSAL VIEW

symphysis

section of
mandibular
canal

shallow
alveolar groove

branch of
mandibular
canal

Figure 4. RGM.117935 Ziphiidae indet., anterior portion of right mandible. The fossil is indicated with a dashed circle on a line drawing of a cranium in lateral view of *Hyperoodon ampullatus*.

dibular symphyseal surface, the posterior part of which does not reach the ventral margin of the mandible. Bone remnants at the anterior most and posterior most surfaces of the symphysis indicate that both left and right mandibles might have been at least partly fused.

Discussion – The shape of the edentulous mandible fragment is typical for most members of the family Ziphiidae. Since the apex of the mandible is not preserved it is impossible to decide if one or more apical and subapical tusks were present. The size of RGM.117935, together with the absence of post-apical teeth, and the short mandibular symphysis, most likely making much less than one third of the mandible length, do not match with *Chavinziphius*, *Dagonodum*, *Messapicetus*, *Nazcacetus* or *Ninoziphius*, which are the fossil ziphiid genera of which the mandible is known (Bianucci *et al.*, 2010, 2016; Lambert *et al.*, 2009, 2013; Ramassamy, 2016). These characteristics do not match either with any of the extant *Mesoplodon* species of which the mandibular tusk is positioned on or beyond the posterior part of the symphysis (Dalebout *et al.*, 2008; Mead, 1989). *Mesoplodon mirus* True, 1913 and *Indopacetus pacificus* Longman, 1926 do have a single apical tusk, but their mandible size is smaller than in RGM.117935, and the same is true for all extant species of *Mesoplodon* and for the fossil species known from crania only. In fact only the extant genera *Berardius*, *Hyperoodon* and *Ziphius* combine single or double apical teeth, absence of post-apical teeth, and large body (and mandible) size. Mandibles of large individuals of extant North Atlantic *Hyperoodon ampullatus* (Forster, 1770), which may reach up to 9-10 meters of body length (Christensen, 1995), seem to be morphologically close to specimen RGM.117935, considering the presence of a large mental foramen usually followed by a more posteriorly located smaller foramen and the comparable mandible size (Table 1). Fossil beaked whale mandibles of this size and shape have not yet been reported in literature. Specimen RGM.117935 confirms the presence of a very large beaked whale in the early Pleistocene or pre-Pleistocene North Sea Basin. Together with the record of a fossil vertex of *Ziphius* sp. from Neogene deep-sea deposits off South Africa, which might have belonged to an animal reaching a body length of 8-10 meters (Bianucci *et al*., 2008), specimen RGM.117935 demonstrates the past occurrence of giant beaked whales. An occurrence which seems to corroborate a possible link of large sized beaked whales with colder waters of high latitudes (Bianucci *et al*., 2016).

Superfamily Inioidea Muizon, 1988

Inioidea gen. et spec. indet.
Figures 5, 6

Material examined – Cranial vertices of Inioidea, RGM. 118856 (Fig. 5) and RGM.145349 (Fig. 6).

Description – Both RGM.118856 and RGM.145349 are

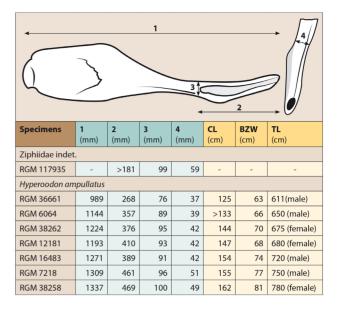| Specimens	1 (mm)	2 (mm)	3 (mm)	4 (mm)	CL (cm)	BZW (cm)	TL (cm)
Ziphiidae indet.							
RGM 117935	-	>181	99	59	-	-	-
Hyperoodon ampullatus							
RGM 36661	989	268	76	37	125	63	611(male)
RGM 6064	1144	357	89	39	>133	66	650 (male)
RGM 38262	1224	376	95	42	144	70	675 (female)
RGM 12181	1193	410	93	42	147	68	680 (female)
RGM 16483	1271	389	91	42	154	74	720 (male)
RGM 7218	1309	461	96	51	155	77	750 (male)
RGM 38258	1337	469	100	49	162	81	780 (female)

Table 1. Comparison of mandible RGM.117935 with *Hyperoodon ampullatus* (Forster, 1770) (CL= condylobasal length of cranium, BZW = bizygomatic width of cranium, TL = total body length).

small cranial fragments: vertices on which the nasals with the surrounding parts of maxillae, premaxillae, frontals, and supraoccipital are preserved. Along the anterior margin as preserved, specimen RGM.118856 displays two triangular cavities for the most posterior points of the premaxillae, demonstrating that each premaxilla was originally contacting the anterolateral border of the nasal. In line with the premaxilla, and alongside the nasal, some small remnants of the maxilla are preserved. Deeply serrated grooves of the maxilla/frontal suture are exposed on the underlying frontal. The nasal is elongate (10 mm wide and 46 mm long) and posterodorsally directed; the anterior part of the upper surface of the nasal is approximately horizontal, but the posterior half makes a much steeper angle. The nasal therefore shows - in lateral view - an unusual dorsal concavity. On top of the vertex triangular frontals are exposed over a fairly broad surface. Clear observations, however, are difficult because sutures of nasal, frontal, and supraoccipital are completely fused (suggesting a fully grown adult individual). In posterior view the dorsal border of the supraoccipital is located markedly below the frontal, resulting in a significant and broad posterior exposure of the medial parts of the frontal. Compared to the sagittal plane as seen inside the brain cavity, the vertex bones are strongly shifted to the left side, with the internasal suture being directed markedly posterolaterally towards the left.

Vertex RGM.145349 shows the same distinctive features observed in RGM.118856 (sharply uprising posterior part of the elongated slender nasals, cavities for the premaxilla that might suggest premaxilla/nasal contact, triangular broad exposure of frontals on top of the vertex, and top of the supraoccipital much lower than the frontal on the vertex). On the frontal, and alongside of the vertex, some
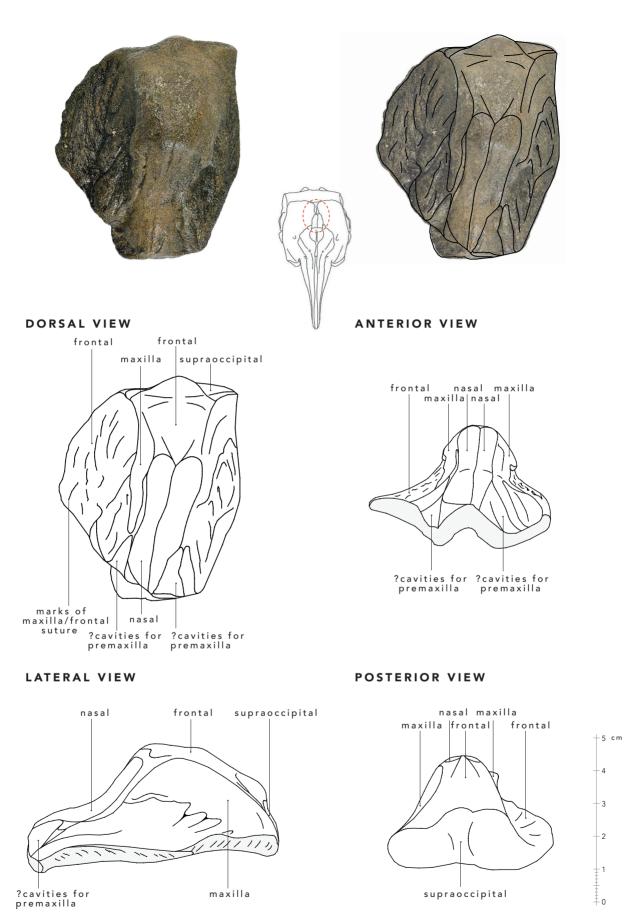
DORSAL VIEW

ANTERIOR VIEW

LATERAL VIEW

POSTERIOR VIEW

Figure 5. RGM.118856 Inioidea indet., vertex of cranium. The fossil is indicated with a dashed circle on a line drawing of a cranium in dorsal view of *Brachydelphis mazeasi*.
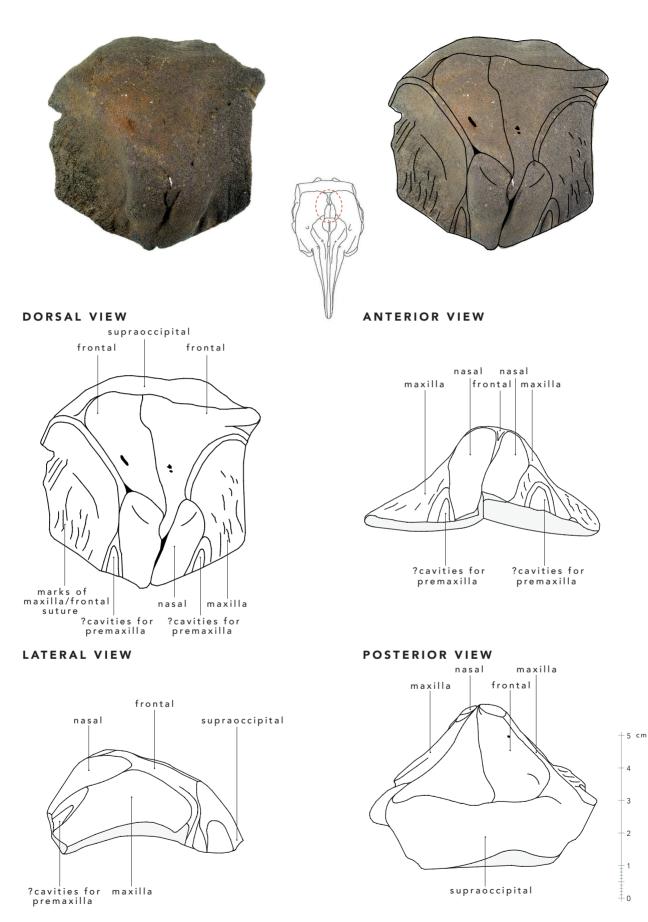
DORSAL VIEW

supraoccipital

frontal   frontal

marks of
maxilla/frontal
suture
?cavities for   nasal   maxilla
premaxilla   ?cavities for
premaxilla

ANTERIOR VIEW

nasal   nasal
maxilla   frontal   maxilla

?cavities for   ?cavities for
premaxilla   premaxilla

LATERAL VIEW

frontal

nasal   supraoccipital

?cavities for   maxilla
premaxilla

POSTERIOR VIEW

nasal   maxilla
maxilla   frontal

5 cm

4

3

2

1

supraoccipital   0

Figure 6. RGM.145349 Inioidea indet., vertex of skull. The fossil is indicated with a dashed circle on a line drawing of a cranium
in dorsal view of *Brachydelphis mazeasi*.

small traces of maxilla are preserved (as in RGM.118856, showing the same strongly serrated marks). However, RGM.145349 most likely represents a younger individual because the sutures between the cranial bones are more open than in RGM.118856. The premaxilla possibly reached the nasal at a more posterior level than in RGM.118856, and the posterior part of the frontal on the vertex is significantly wider than in RGM.118856 (40 versus 26 mm). The vertex is shifted to the left side as in RGM.118856.

Discussion – The anteroposteriorly directed, narrow and anteroposteriorly long nasals suggest pontoporiid affinities for both specimens described above (see for example Muizon, 1988). However, the broad exposure of frontals on the vertex above the supraoccipital is more reminiscent of the iniids *Inia* and *Ischyrorhynchus* (both belonging, together with the Pontoporiidae, to the superfamily Inioidea (Marx *et al.*, 2016, p. 133). The combination of the markedly concave dorsal surface of the nasal in lateral view, the premaxilla reaching the nasal, the presence on the vertex of wide and triangular frontals of which the posterior parts are significantly lower than the anterior parts, the broad posterior exposure of medial parts of the frontal over the dorsal border of the supraoccipital, and the marked cranial asymmetry, distinguish RGM.118856 and RGM.145349 from all the known fossil Inioidea.

The extant iniid *Inia geoffrensis* (de Blainville, 1817) occupies freshwater habitats in the Amazon region. Undisputed fossils of *Inia* are not yet described, but lately two fossil species were tentatively attributed to the Iniidae family: *Isthminia panamensis* Pyenson *et al.*, 2015, from Panama, and *Meherrinia isoni* Geisler, Godfrey & Lambert, 2012, from the NW Atlantic (North Carolina, USA). Both confirm that unambiguous osteological differences between the inioid lineages are as yet difficult to demonstrate. Together with the other fossil inioid taxa, most of them being collected from marine strata, those new taxa confirm that, contrary to extant *Inia* and fossil *Ischyrorhynchus*, fossil inioids were not restricted to freshwater habitats.

In addition to the South Atlantic extant *Pontoporia blainvillei* (Gervais & d'Orbigny, 1844), pontoporiid fossil species are known from the South Pacific and the South Atlantic: *Pontistes rectifrons* (Bravard, 1858) from Argentina; *Pliopontos littoralis* Muizon, 1984 from Peru; and *Brachydelphis mazeasi* Muizon, 1988 and *B. jahuayensis* Lambert & Muizon, 2013 from Chile and Peru (Gutstein *et al.*, 2009). More recently it became evident that also the North Atlantic had accommodated a surprising variety of Miocene and Pliocene pontoporiids: *Protophocaena minima* Abel, 1905 (Lambert & Post, 2005) (from Belgium and The Netherlands), *Stenasodelphis russellae* Godfrey & Barnes, 2008 (from Maryland, USA), *Auroracetus bakerae* Gibson & Geisler, 2009 (from North Carolina, USA); and Inioidea gen. et sp. indet. (Pyenson & Hoch, 2007) (from Denmark). Whether or not RGM.118856 and RGM.145349 belong to different species will be difficult to decide because of their different ontogenetic stage and fragmentary state of

preservation.

Both fossils described herein demonstrate that at least one enigmatic and as yet unidentified inioid was present in the North Sea Basin during the early Pleistocene or before.

Conclusions

On the basis of specimens housed in Naturalis Biodiversity Center, Leiden, The Netherlands, three as yet formally undescribed odontocete taxa are demonstrated to have been present between the middle Miocene and early Pleistocene in the North Sea Basin:
• A tusked monodontid (*Monodon* sp.)
• A large ziphiid (Ziphiidae indet.)
• At least one inioid (Inioidea indet.).
Further observations and more complete specimens are needed to resolve the true identity and age of these marine mammals and the assemblage(s) they once belonged to.

Acknowledgements

References

Barnes, L.G., 1984. Fossil odontocetes (Mammalia: Cetacea) from the Almejas Formation, Isla Cedros, Mexico. *Paleobios* 42: 1-46.

Beneden, [M.] van & Gervais, P., 1868-1879. *Ostéographie des cétacés vivants et fossiles, comprenant la description et l'iconographie du squelette et du système dentaire de ces animaux, ainsi que des documents relatifs à leur histoire naturelle*. Paris (Bertrand): 666 pp., atlas 64 pls.

Bianucci, G., Lambert, O. & Post, K., 2010. High concentration of long-snouted beaked whales (genus *Messapicetus*) from the Miocene of Peru. *Palaeontolog*y 53(5): 1077-1098.

Bianucci, G., Post, K. & Lambert, O., 2008. Beaked whale mysteries revealed by seafloor fossils trawled off South Africa. *South African Journal of Science* 104: 140-142.

Bianucci, G., Di Celma, C., Urbina, M. & Lambert, O., 2016. New beaked whales from the late Miocene of Peru and evidence for convergent evolution in stem and crown Ziphiidae (Cetacea, Odontoceti). *PeerJ 4:e2479; DIO 10.7717/ peerj.2479*: 1-55.

Born, E.W., 1994. *Monodon monoceros* Linnaeus, 1758. Narwal. *In*: Robineau, D. *et al*. (eds). *Handbuch der Säugetiere Europas,* 6(1). *Meeressäuger*, 1a. *Wale und Delphine*, 1. Wiesbaden (Aula Verlag): 209-240.

Christensen, V.I., 1995. *Hyperoodon ampullatus* (Forster, 1770) - Nördlicher Entenwal (auch Dögling). *In*: Robineau, D. *et al*. (eds). *Handbuch der Säugetiere Europas,* 6(1). *Meeressäuger*, 1b. *Wale und Delphine*, 2. Wiesbaden (Aula Verlag): 509-525.

Dalebout, M.L., Steel, D. & Baker, C.S., 2008. Phylogeny of the beaked whale genus *Mesoplodon* (Ziphiidae: Cetacea) revealed by nuclear introns: implications for the evolution of male tusks. *Systematic Biology* 57: 857-875.

Deinse, A.B. van, 1944. *De fossiele en recente Cetacea van Nederland*. Amsterdam (H.J. Paris): xi + 304 pp.

Geisler, J.H., Godfrey, S.J. & Lambert, O., 2012. A new genus and species of late Miocene inioid (Cetacea: Odontoceti) from the Meherrin River, North Carolina. *Journal of Vertebrate Paleontology* 32: 198–211.

Gibson, M.L. & Geisler, J.H., 2009. A new Pliocene dolphin (Cetacea: Pontoporiidae) from the Lee Creek Mine, North Carolina. *Journal of Vertebrate Paleontology* 29: 966–971.

Godfrey, S. & Barnes, L.G., 2008. A new genus and species of late Miocene pontoporiid dolphin (Cetacea: Odontoceti) from the St. Marys Formation in Maryland. *Journal of Vertebrate Paleontology* 28: 520–528.

Gutstein, C.S., Cozzuol, M.A., Vargas, A.O., Suarez, M.E., Schultz, C.L. & Rubilar-Rogers, D. 2009. Patterns of skull variation of *Brachydelphis* (Cetacea, Odontoceti) from the Neogene of the southeastern Pacific. *Journal of Mammalogy* 90: 504–519.

Harrington, C.R. 2008. The evolution of arctic marine mammals. *Ecological Applications* 18(2) Supplement: S23–S40.

Kohno, N. & Ray, C.E., 2008. Pliocene walruses from the Yorktown Formation of Virginia and North Carolina, and a systematic revision of the North Atlantic Pliocene walruses. *In*: Ray, C.E. *et al*. (eds). Geology and Paleontology of the Lee Creek Mine, North Carolina, 4. *Virginia Museum of Natural History Publication* 14: 39-80.

Lambert, O., 2005. Systematics and phylogeny of the fossil beaked whales *Ziphirostrum* du Bus, 1868 and *Choneziphius* Duvernoy, 1851 (Cetacea, Odontoceti), from the Neogene of Antwerp (North of Belgium). *Geodiversitas* 27: 443-497.

Lambert, O., Bianucci, G. & Post, K., 2009. A new beaked whale (Odontoceti, Ziphiidae) from the middle Miocene of Peru. *Journal of Vertebrate Paleontology* 29, 3: 910-922.

Lambert, O. & Post, K., 2005. First European pontoporiid dolphins (Mammalia: Cetacea, Odontoceti), from the Miocene of Belgium and the Netherlands. *Deinsea* 11: 7–20.

Lambert, O. & Gigase, P., 2007. A monodontid cetacean from the early Pliocene of the North Sea. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 77: 197-210.

Lambert, O. & Muizon, C. de, 2013. A new long-snouted species of the Miocene pontoporiid dolphin *Brachydelphis* and a review of the Mio-Pliocene marine mammal levels in the Sacaco Basin, Peru. *Journal of Vertebrate Paleontology* 33: 709-721.

Lambert, O., Muizon, C. de & Bianucci, G., 2013. The most basal beaked whale *Ninoziphius platyrostris* Muizon, 1983: clues on the evolutionary history of the family Ziphiidae (Cetacea: Odontoceti). *Zoological Journal of the Linnean Society* 167: 569–598.

Larkin, N.R., Coope, G.R., Lee, J.R. & Silva, B., 2014. Early middle Pleistocene sediments at Sidestrand, northeast Norfolk, yield the most extensive preglacial cold stage beetle assemblage from Britain. *Quaternary International*: 1-14. http://dx.doi.org/10.1016/j.quaint.2014.0

Mead, J.G., 1989. Beaked whales of the genus Mesoplodon. *In*: Ridgway S., H. & Harrison R., (eds.), *Handbook of marine mammals, vol. 4: River dolphins and the larger toothed whales*, 349-430.

Mead, J.G. & Fordyce R.E., 2009. The therian skull: a lexicon with emphasis on the odontocetes. *Smithsonian Contributions to Zoology*, 627: 1-248.

Marx, F.G., Lambert, O. & Uhen, M.D., 2016. *Cetacean Paleobiology*. Blackwell (Wiley): 1-319.

Muizon, C. de 1984-1988. Les vertébrés de la Formation Pisco (Pérou), 2. Les odontocètes (Cetacea, Mammalia) du Pliocène inférieur du Sud-Sacaco; 3. Les odontocètes (Cetacea, Mammalia) du Miocène. *Travaux de l'Institut Français d'Études Andines* 27: 1–188 (2); 42: 1-244 (3).

Muizon, C. de & Vries, T.J. de, 1985. Geology and paleontology of late Cenozoic marine deposits in the Sacaco area (Peru). *Geologische Rundschau* 74: 547-563.

Newton, E.T., 1882. The Vertebrata of the Forest Bed Series of Norfolk and Suffolk. *Memoirs of the Geological Survey of Great Britain: England and Wales*: 1-143.

Nweeia, M.T., Eichmiller, F.C., Nutarak, C., Eidelman, N., Giuseppetti, A.A., Quinn, J., Mead, J.G., Kíssuk, K., Hauschka, P.V., Tyler, E., Potter, C., Orr, J.R., Avike, R., Nielsen, P. & Angnatsiak, D., 2009. Considerations of anatomy, morphology, evolution, and function for narwhal dentition. *In*: Krupnik I., Lang M.A. & Miller, S.E, (eds). *Smithsonian at the Poles: Contributions to International Polar Year Science*: 223-240.

Nweeia, M.T., Eichmiller, F.C., Hauschka, P.V., Tyler, E., Mead, J.G., Potter, C.W., Angnatsiak, D.P., Richard, P.R., Orr J.R. & Black S.R., 2012. Vestigial tooth anatomy and tusk nomenclature for *Monodon monoceros. The Anatomical Record* 295: 1006-1016.

Pyenson, N.D. & Hoch, E., 2007. Tortonian pontoporiid odontocetes from the eastern North Sea. *Journal of Vertebrate*

Paleontology 27: 757–762.

Pyenson, N.D., Vélez-Juarbe, J., Gutstein, C.S., Little, H., Vigil, D & O'Dea, A., 2015. *Isthminia panamensis*, a new fossil inioid (Mammalia, Cetacea) from the Chagres Formation of Panama and the evolution of 'river dolphins' in the Americas. *PeerJ* 3:e1227; DOI 10.7717/peerj.1227.

Post, K., & Kompanje, E.J.O., 1995. Late Pleistocene white whales *Delphinapterus leucas* from Dutch coastal waters. *Lutra* 38: 67-76.

Post, K., 2005. A Weichselian marine mammal assemblage from the southern North Sea. *Deinsea* 11: 21-27.

Ramassamy, B., 2016. Description of a new long-snouted beaked whale from the Late Miocene of Denmark: evolution of suction feeding and sexual dimorphism in the Ziphiidae (Cetacea, Odontoceti). *Zoological Journal of the Linnean Society*. DOI: 10.1111/zoj.12418: 1- 29.

Scager, D.J., 2015. Kor en Bot: 65 jaar en 2000 fossielen later,

een inventarisatie en interpretative van de collectie. *Cranium* 32: 6-18.

Vélez-Juarbe, J., & Pyenson, N.D. 2012. *Bohaskaia monodontoides*, a new monodontid (Cetacea, Odontoceti, Delphinoidea) from the Pliocene of the western North Atlantic Ocean. *Journal of Vertebrate Paleontology* 32: 2, 476-484.

Whitmore, F.C. 1994. Neogene climatic change and the emergence of the modern whale fauna of the North Atlantic Ocean. *In*: Berta, A. & Deméré T.A. (eds). Contributions in marine mammal paleontology honoring Frank. C. Whitmore Jr.. *Proceedings of the San Diego Society of Natural History* 29: 223-227.

Whitmore, F.C., & Kaltenbach, J.A. 2008. Neogene Cetacea of the Lee Creek phosphate mine, North Carolina. *In*: Ray, C.E. *et al*. (eds). Geology and Paleontology of the Lee Creek mine, North Carolina, 4 , *Virginia Museum of Natural History Publication* 14: 181-269.