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A new dolphin (Cetacea, Delphinidae) from the Plio-Pleistocene of the North Sea

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Hoekman's blunt-snouted dolphin *Platalearostrum hoekmani* gen. et sp. nov. is described from Plio-Pleistocene sediments of the North Sea (The Netherlands). It shows unique and bizarre features of the premaxilla that extends over the maxilla way beyond the lateral border of the rostrum. *Platalearostrum hoekmani* is compared to fossil and extant Delphinidae and similarities with extant *Globicephala* as well as functional implications of its strange morphology are discussed.

Hoekman's stompsnuitdolfijn *Platalearostrum hoekmani* wordt als een nieuwe Plio-Pleistocene dolfijn (nieuw genus en nieuwe soort) uit de Noordzee gemeld en beschreven. Deze dolfijn bezit een extreem kort rostrum waarop de premaxilla lateraal buiten de maxilla uitsteekt (en dat is uniek voor walvisachtigen). *Platalearostrum hoekmani* wordt vergeleken met fossiele en recente Delphinidae. Overeenkomsten met het recente genus *Globicephala* en mogelijke functionele implicaties van de bizarre morfologie van het rostrum worden besproken.

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Key words: *Platalearostrum hoekmani* gen. et sp. nov., pilot whales, Delphinidae, Orcininae, Pliocene, Pleistocene, premaxilla, North Sea, the Netherlands

INTRODUCTION

During the last decades our knowledge of cetacean evolution from the Eocene to the Pliocene has increased significantly (Bianucci & Landini 2007). However, fossils of and publications on Delphinidae (Late Miocene till recent) remain scarce and the phylogeny of extant and fossil members of this family has not yet been resolved (Bianucci 2005; Caballero *et al.* 2008; Aguire-Fernández *et al.* 2009; Kingston *et al.* 2009).

Although new cetacean genera and species should preferably be described based on fairly complete crania (ideally with adherent post crania), interesting but less complete fossils from little known families or genera, or fossils showing unique characters might be exempted from this unwritten rule. The fossil described in this article, trawled from the bottom of the North Sea, is represented by a large part of the rostrum which shows a highly peculiar morphology of the premaxilla allowing identification as a new delphinid genus. Moreover, its unusual morphological features have not been reported in cetacean studies so far and therefore justify publication.

ABBREVIATIONS

The following abbreviations are used to identify the institutions mentioned:

IRSNB - Institut royal des Sciences naturelles de Belgique, Brussels, Belgium

MSNTUP - Museo di Storia Naturale e del Territorio dell'Università di Pisa, Calci, Italy

MUSM - Museo de Historia Naturel, Universidad Nacional Mayor de San Marco, Lima, Peru
NMR - Natuurhistorisch Museum Rotterdam, Rotterdam, The Netherlands
RMNH - NCB Naturalis, Leiden, The Netherlands
ZMA - Zoölogisch Museum Amsterdam, Amsterdam, The Netherlands

MATERIAL AND METHODS

NMR 9991-00005362 (hereafter mentioned as NMR 5362) was collected by the crew of the fishing vessel GO 28, during bottom trawling in the North Sea at 52º 00' N - 02º 48' E (110 km west of Rotterdam) on November 11, 2008.

During the last four decades the North Sea has yielded tens of thousands of fossils through commercial bottom trawling (for demersal fish species). These *ex situ* finds have received considerable scientific attention and several authors have tried to offer a stratigraphic framework (e.g. Mol *et al.* 2008). From the area where NMR 5362 was collected, a Mid-Pliocene to Early Pleistocene marine mammal fauna (or mixture of faunas) with fossils of *Balaenoptera*-, *Delphinapterus*-, *Eubalaena*-, *Globicephala*-, *Hemisyntrachelus*-, *Mesoplodon*-, *Orcinus*-, *Physeter*-, *Stenella*/*Delphinus*- and *Tursiops*-like genera has been reported (Post & Bosselaers 2005). Apart from these cetaceans, the fossil walrus *Ontocetus emmonsoni* is frequently encountered, while phocids (close to extant genera and/or species) are recovered less frequently. The walrus is of stratigraphic importance as it roamed the North Sea from the Late Pliocene until the Early Pleistocene (Kohno & Ray 2008; K. Post, unpublished data). Based on the above, NMR 5362 is considered to be of Mid Pliocene to Early Pleistocene age.

For comparative material of extant Delphinidae, Monodontidae and Phocoenidae, the extensive collections of IRSNB, MSNTUP, MUSM, NMR, RMNH and ZMA were used.

SYSTEMATICS

Order Cetacea Brisson, 1762
Suborder Odontoceti Flower, 1867
Superfamily Delphinoidea Gray, 1821
Family Delphinidae Slijper, 1936
Subfamily Orcininae Wagner, 1846

Platalearostrum hoekmani gen. et sp. nov.

Holotype NMR 9991-00005362, a partial rostrum consisting of an incomplete left maxilla with six alveoli, an incomplete left premaxilla and an incomplete vomer (Figs. 1, 2).

Type locality North Sea, 52º 00' N - 02º 48' E; 110 km west of Rotterdam, The Netherlands.

Diagnosis Medium to large sized delphinid with extremely short rostrum, differing from all other known fossil and extant delphinids by: (1) massive premaxilla protruding far beyond the lateral margins of the rostrum and creating a very broad and blunt apex of the rostrum, (2) concave outline of the rostrum in anterior view, (3) solid and massive vomer reaching the apex of the rostrum and (4) six maxillary teeth in the tooth row.

Etymology *Platalea* from Latin (spoon), because of the large spoon-shaped apex of the short rostrum characterising the genus; *hoekmani* after Mr. Albert Hoekman who discovered and donated the fossil. We propose the English name Hoekman's blunt-snouted dolphin.

DESCRIPTION

Dorsal view (Fig. 1a)

The anterior half of the dorsal exposure of rostrum is formed by the premaxilla. On the left side a massive 32 mm wide and 202 mm long straight segment of the left side of the vomer is visible along the complete length of the fossil. The premaxilla abruptly and bluntly widens laterally and dorsally until reaching a maximum width of 117 mm at 108 mm from the apex. After this point the premaxilla decreases sharply in width until reaching a minimum width of

81 mm, when the maxilla becomes visible and remains so till the damaged base of the rostrum. Towards the base the lateral border of the maxilla is somewhat curved and elevated and shows on the inner side a clear sulcus which was possibly reaching a ?dorsal infraorbital foramen (not preserved). The suture of maxilla and premaxilla remains clearly visible from the point where the maxilla protrudes under the premaxilla. On the dorsal side of the premaxilla a weak anteromedial sulcus (bordering the prenarial triangle) of c. 72 mm is traceable towards the broken base of the rostrum. When reaching this base the premaxillary foramen is visible, which supposedly at this point reached the dorsal surface of the rostrum (or was close to reach this surface). This point therefore marks - or was close to - the most anterior location of the premaxillary sacfossa (which is unfortunately not preserved). It seems clear that the rostrum is severed from the neurocranium along its basis, at or close to the location of the antorbital notch. The surface of the premaxilla from the apex to about a third of its length at the point where the premaxilla reaches its maximum width, is weathered (by erosion?), but, if so, on only a thin top layer appears to be eroded. Another possibility is that this area naturally showed a very open and rugose bone texture. The remainder of the dorsal surface shows a shiny, black and thin, but compact top layer in perfect state of preservation and numerous small foramina and sulci may be noted in the depressed central area of the premaxilla.

Anterior view (Fig. 1b)
The apex is formed by the anterior point of the vomer and by a heavy and up to 47 mm thick premaxilla. A few small foramina are visible and at 44 mm from the midline a large and prominent foramen protrudes from the middle of the premaxilla. The premaxilla extends laterally and dorsally until reaching its maximum width of 148 mm (measured from the midline of the rostrum), at which location the ventral border of the premaxilla is elevated c. 84 mm above the most ventral base of the rostrum. In anterior view and just below the large foramen the maxillary suture is visible and a hint of the alveolar groove may be noticed.

Lateral view (Fig. 2b)
The premaxilla appears as a 46 mm towards 42 mm thick wall which protrudes onwards from the apex in dorsal direction. A large foramen is located at 50 mm from the apex and the surface of most of the bony structure of the premaxilla is dotted with several small points and rugosities. Below the premaxilla the maxilla is clearly visible and starts at 11 mm from the apex. The prominent suture between maxilla and premaxilla moves more or less parallel with the main body of the premaxilla into a dorsal direction. At 171 mm from the apex this suture reaches the dorsal surface of the rostrum and from there the main body of the maxilla is visible till the point where the fossil is broken. Towards the ventral border of the maxilla an alveolar row is clearly visible over a length of 108 mm. The ventral border of the maxilla is more or less straight and proceeds to the distal surface of the fossil, at which point the maxilla is 41 mm thick. At this position traces of the suture with the palatine are located.

Ventral view (Fig. 2a)
The apex of the rostrum is made up at midpoint by a small portion of premaxilla which is wedged between maxilla and vomer for a maximum length of 115 mm and with a maximum width of 15 mm. The premaxilla is also visible laterally as a thick and large slice of bone (196 mm long and max. 41 mm wide). Wedged between both premaxillary surfaces the maxilla extends as a massive and smooth ventral surface. Both sutures between maxilla and the two views of the premaxilla are clearly noticeable, the largest of them (the one towards the lateral side of the fossil) is not straight and extends over a length of 182 mm. The maxilla reaches its maximum width of 129 mm at 131 mm from the apex (the maxilla at base is 120 mm wide). The maxilla appears to strengthen the massive premaxilla at its widest point. Six alveoli are present within a prominent and slightly laterally convex alveolar row which is

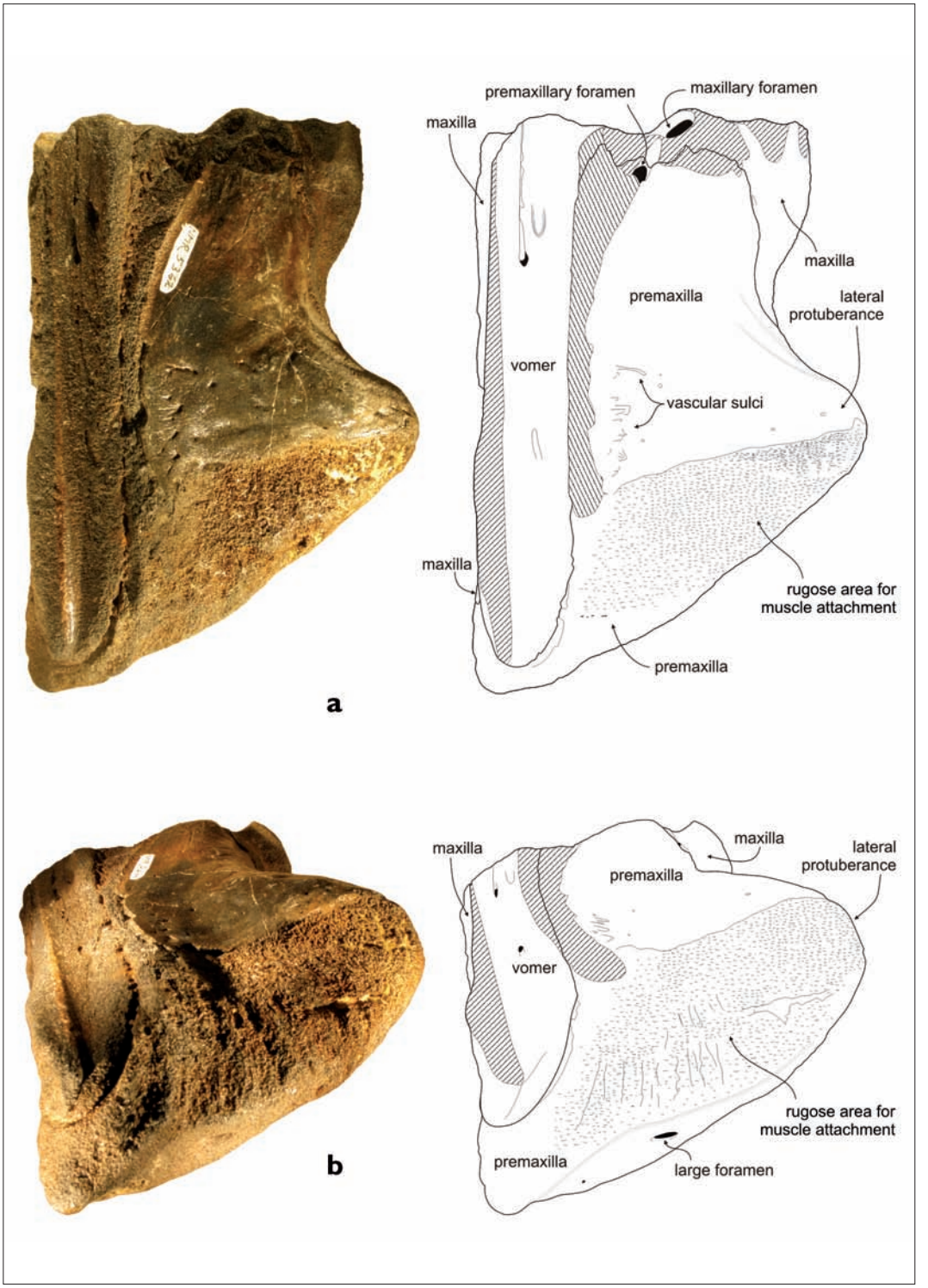

Figure 1 Dorsal (**a**) and anterior (**b**) view of rostrum (holotype) of *Platalearostrum hoekmani* (NMR 9991-00005362). Maximum length of the fossil is 221 mm.

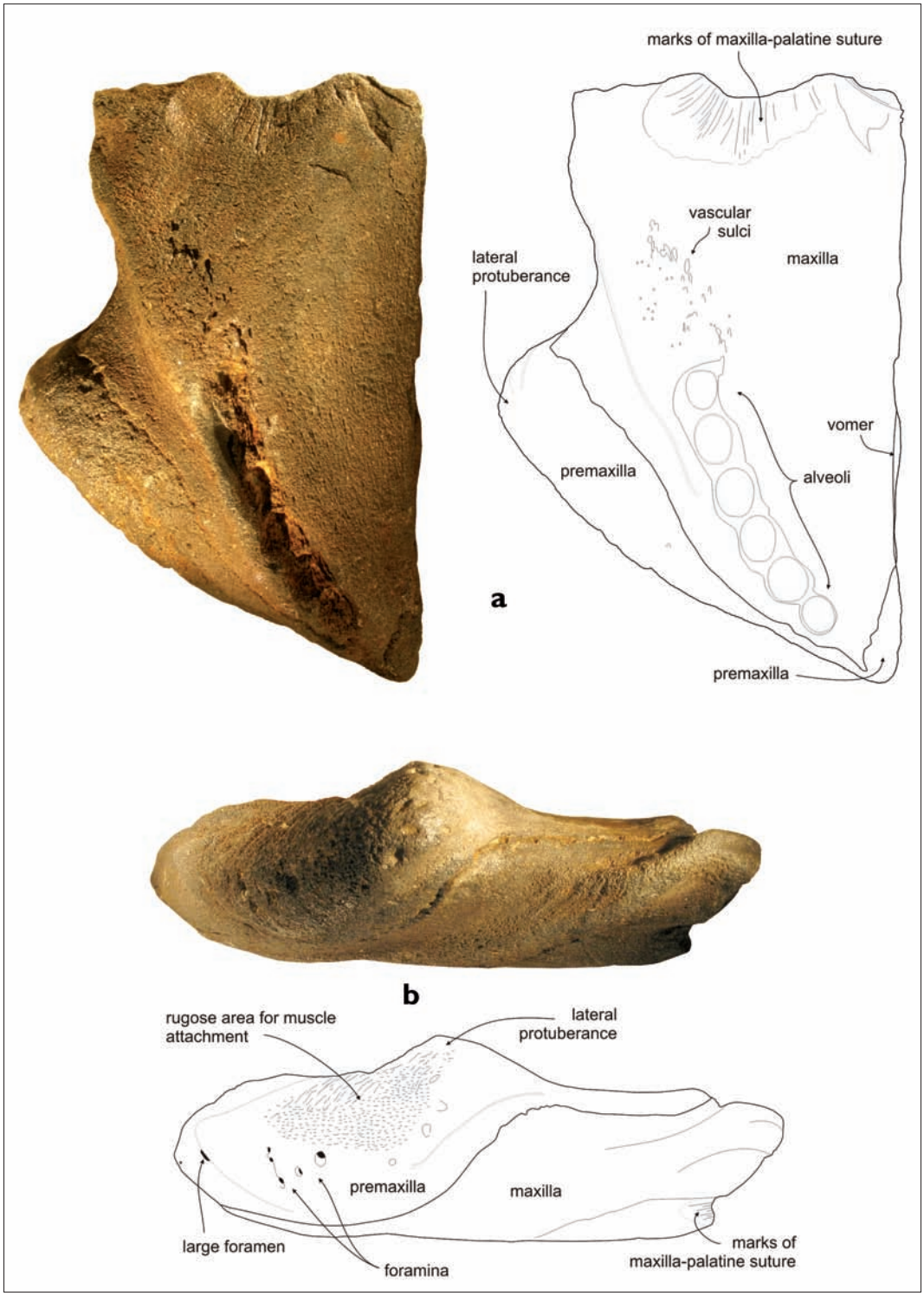

Figure 2 Ventral (**a**) and lateral (**b**) view of rostrum (holotype) of *Platalearostrum hoekmani* (NMR 9991-00005362). Maximum length of the fossil is 221 mm.

14 mm wide (on average) (and 108 mm long as mentioned previously). On the posterior part of the maxilla the wide suture with the palatine is visible and shows a blunt and square to semi-circular outline.

The fact that the rostral apex is formed by the premaxilla (visible in dorsal, anterior and ventral view); that - despite the somewhat eroded surface - the large anterior foramen is well preserved (and visible in anterior and lateral view) and that the alveolar row on the maxilla is situated well beyond the apex, may suggest that the maximum extent of the premaxilla on the apex represents fairly well the maximum extent of the rostrum itself. One may also assume that the most posterior left edge of the maxilla probably represents the location where the antorbital notch might have been located. The location of sutures of the palatine, and the posterior part of the vomer corroborate this assumption. Based on these assumptions the total length of the rostrum must have been just, or just over, 225 mm; whereas the maximum width of the rostrum at base must have been just c. 240 mm. Taking into account a maximum anterior width of c. 300 mm a bizarre, blunt, compact, and spoon shaped rostrum appears (Fig. 3).

PATHOLOGICAL IMPLICATIONS

Since structure and organization of osseous tissue in mammals can be subject to pathologic change, the possibility of the exceptional protruding premaxilla being the result of a pathologic condition should be considered. Pathologic changes may be due to (1) hereditary taints and/or developmental errors, (2) disorders of metabolism or endocrine function, (3) bacterial and non-bacterial inflammation, (4) degeneration and necrosis, and (5) primary or metastatic tumor formation (Marcove 1992). The features shown in NMR 5362 do not resemble any of the known hereditary and developmental disorders like hereditary multiple exostosis or osteopetrosis, which therefore can be excluded.

Metabolic osteoporosis is known in dolphins (e. g. *Tursiops truncatus*) (E.J.O. Kompanje, unpublished data). However, skeletal changes due to disorders of metabolism and of endocrine function do not result in excessive and massive growth of bone in a localized spot, but usually result in loss of structure and bone tissue (like osteoporosis). Therefore we can exclude a metabolic causation.

Pyogenic osteomyelitis has been recognized and described in several cetaceans (Kompanje 1995, 1999). Infectious and infectious-like disorders of bone usually result in severe bone destruction, formation of cloacae and new and very irregular bone formation. It never results in smooth and bulky new bone formation as present in the protruding premaxilla in NMR 5362. Furthermore, severe destructive pyogenic infection will not leave the sutures untouched. In the rostrum NMR 5362 they are clearly and sharply visible between maxilla and premaxilla rostrum, as described above.

Degenerative destruction of bone is very common in cetacean species (Kompanje 1995, 1999), but has only be found in the vertebrae and long bones.

Benign and malignant bone tumors can result in expanded bone growth. Leontiasis ossea (fibrous dysplasia) can result in disfigurement of the head resulting from more or less symmetrical hyperostotic thickening of the bones of the craniofacial skeleton (Lee *et al.*, 1996). Although determined in humans and higher primates, it has never been described in cetaceans and the features as we know them from human cases look very dissimilar from the protruding premaxilla in NMR 5362. Hence we exclude this possible cause. The most common sites for osteogenic malignant sarcomas are the long bones, but they have also been found in facial bones and can result in reactive new bone formation (Yamaguchi *et al.* 2004), which is irregular and highly destructive. Therefore, we exclude a malignant tumor as possible cause. Since none of the known pathological conditions can be linked to the features seen in the protruding premaxilla of NMR 5362, we conclude that these features are the result of normal structure and organization of bone tissue.

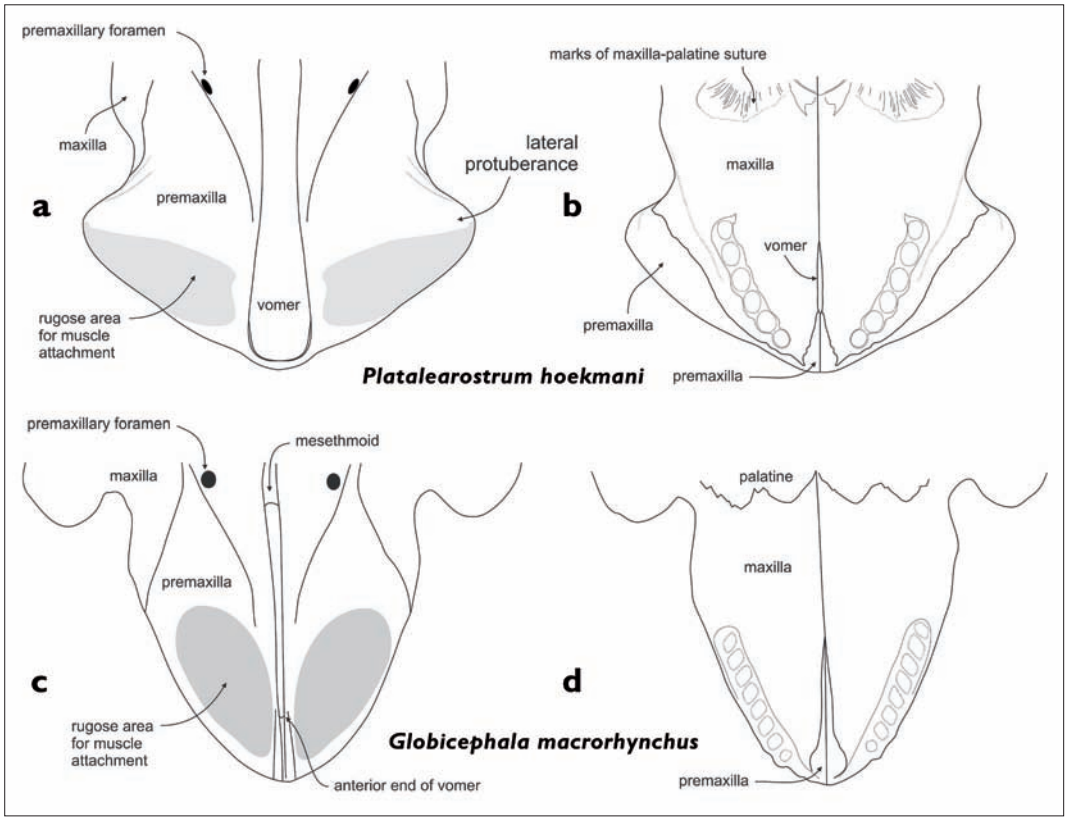

Figure 3 Comparison of rostrum of *Platalearostrum hoekmani* (**a** dorsal - **b** ventral) with rostrum of *Globicephala macrorhynchus* (**c** dorsal - **d** ventral).

COMPARISON TO KNOWN EXTANT AND FOSSIL DELPHINID GENERA

Semi circular or convex maxillary tooth rows are supplementary to mandibles with short to extremely short symphyseal contact. Contrary to concave, parallel or straight V-shaped tooth rows, these features are rarely seen in odontocetes and are non-existent in archaic delphinoids. In fact, convex maxillary and mandibulary tooth rows are only present within the Delphinoidea and - more precisely - only within the Phocoenidae and Delphinidae (K. Post pers. obs.).

If rostrum NMR 5362 should have belonged to a member of the Phocoenidae then its robust teeth and low tooth count isolate it from all the known fossil and extant porpoises. Besides this observation, the width of the rostrum indicates a dolphin of a size considerably larger than any of the known fossil and extant porpoises.

The short and wide rostrum, the wide premaxilla covering the main part of the rostral surface, the rugose area of the anterior dorsal surface of the rostrum, and the low number of teeth suggest that NMR 5362 did belong to a member of the subfamily Orcininae of the Delphinidae (*sensu* Bianucci 2005 = Globicephalinae *sensu* Aguirre-Fernandez *et al*. 2009). Extant Orcininae (*Feresa*, *Globicephala*, *Grampus*, *Pseudorca*, *Orcinus*) possess wide and/or anteriorly widening premaxilla overlapping significant parts of the maxilla. In *Globicephala*, this is one of the major cranial features identifying the two extant species *G. melas* TRAILL, 1809 and *G. macrorhynchus* GRAY, 1846. The premaxilla of the latter is almost covering the complete dorsal surface of

the rostrum and often reaching the lateral wall of the rostrum. NMR 5362 resembles this condition, but its premaxilla extents way beyond the lateral border of the maxilla, a condition which is shared by none of the known fossil and extant Delphinidae (nor any other odontocete).

Another striking feature of extant *Globicephala* is the extremely rounded short beak with a very convex arrangement of the teeth (in maxilla and mandible). The tooth row of NMR 5362 shows a curve similar to that in *Globicephala* (Fig. 3). *Globicephala* is characterised by 7-9 (*G. macrorhynchus*) and 9-12 (*G. melas*) feeble and forward protruding teeth embedded in shallow alveoli (Van Bree 1971), while NMR 5362 shows just six alveoli. NMR 5362 shows a very anteriorly located rugose area of attachment of the nasal plug retractor muscle combined with an extremely rugose anterior premaxillary surface of the rostrum. Both conditions are present in extant *Globicephala*; the first feature is typical for Globicephalinae (= Orcininae *sensu* Bianucci 2005) (Aguirre-Fernandez *et al.* 2009), while the latter feature (rugose anterior dorsal surface of the premaxilla) is considered a synapomorphy of *Globicephala* and fossil *Protoglobicephala mexicana* (Aguirre-Fernández *et al.* 2009).

Among fossil Orcininae, only few fossil pilot whale-like cetaceans have been described or mentioned in literature. The geologically oldest pilot whale was recovered from the ocean bottom near Chile, identified as *Globicephala* sp. and reported to be 5.2-4.2 Ma (Valenzuela & Brito 1994). No obvious differences with the recent species were noted. From the Pliocene Yorktown Formation of the Lee Creek Mine (North Carolina, USA) 16 fragments of mandibles and numerous teeth and periotics have been reported, but larger cranial remains are lacking and these fossils cannot be distinguished with certainty from extant *Globicephala* (Whitmore & Kaltenbach 2008). Pilleri (1984) described a partial mandible from the Italian Pliocene as *Globicephala etruriae*. This mandible possesses at least thirty teeth and both rami are completely fused at the symphysis, lacking teeth in their apical portions. Although this fossil clearly represents a delphinid, its assignment to *Globicephala* is debatable (Bianucci 1996). Bianucci (1996) assigned several periotics of Delphinidae from the Pliocene of Italy to a '*Globicephala* group' and described them as robust periotics close to, but in several features slightly different from extant *Globicephala*. Aguirre-Fernández *et al.* (2009) described *Protoglobicephala mexicana* from the Late Pliocene of Mexico and referred it to Globicephalinae (= Orcininae *sensu* Bianucci 2005) because of the relatively broad rostrum, the wide premaxilla occupying the major part of dorsal surface of the rostrum, the large antorbital process and the reduced (10) tooth count. These authors also suggested a close link with *Globicephala* because of the large premaxillary sac fossae, the significantly wider premaxilla than the maxilla on the dorsal surface of the rostrum and the rugosities present on the anterior dorsal part of the premaxilla. Their preferred phylogenetic analysis shows *Protoglobicephala* as the sistergroup of *Globicephal*a. A fossil cranium with cervical complex from the Late Pleistocene from Taiwan was considered indistinguishable from extant *G. macrorhynchus* (Chang 1996). *G. baereckeii* (with dental count 7) was described from the Pliocene or Pleistocene of Florida (Sellards 1916), however Morgan (1994) considered this a younger synonym of *G. macrorhynchus*.

Not yet described and unidentified, but present in fairly large numbers in Dutch and Belgian collections, are Pliocene periotics that are difficult to distinguish from extant *Globicephala* (K. Post, pers. obs.). From shell heaps in Yerseke, province of Zeeland, (harvested in the North Sea at or close to the site of NMR 5362) one fragment of a *Globicephala*-like mandible is known. Cetacean fossils collected on these shell heaps are identical to the Mid-Pliocene to earliest Pleistocene fauna(s) as noted by Post & Bosselaers (2005). The fossil is catalogued as number NMR 9991-00006785 (hereafter

mentioned as NMR 6785) and indentified as Delphinidae indet. aff. *Globicephala* (Fig. 4).

This apex of a mandible clearly shows the *Globicephala*-like downward and inward curve and other typical *Globicephala* mandibular features, such as multiple small mandibular foramina and the - for a delphinid unusual - rounded cross-section just after the symphysis. However, it differs clearly from the mandible of extant *Globicephala* in the extreme circular surface of the symphysis, the almost completely circular cross-section of the mandibular ramus after the symphysis, and the significantly smaller dimensions. Six alveoli are visible and when comparing the curve and size of these alveoli with those of *Platalearostrum hoekmani* (NMR 5362), the taxonomic affinity of both fossils is striking (Table 1).

FUNCTIONAL MORPHOLOGY

The peculiar morphology of this extremely short rostrum invites speculations about the function of such a strange and blunt apex. As observed above most (if not all) crania of fully grown extant pilot whales expose unusual and large rugose areas anteriorly on the dorsal

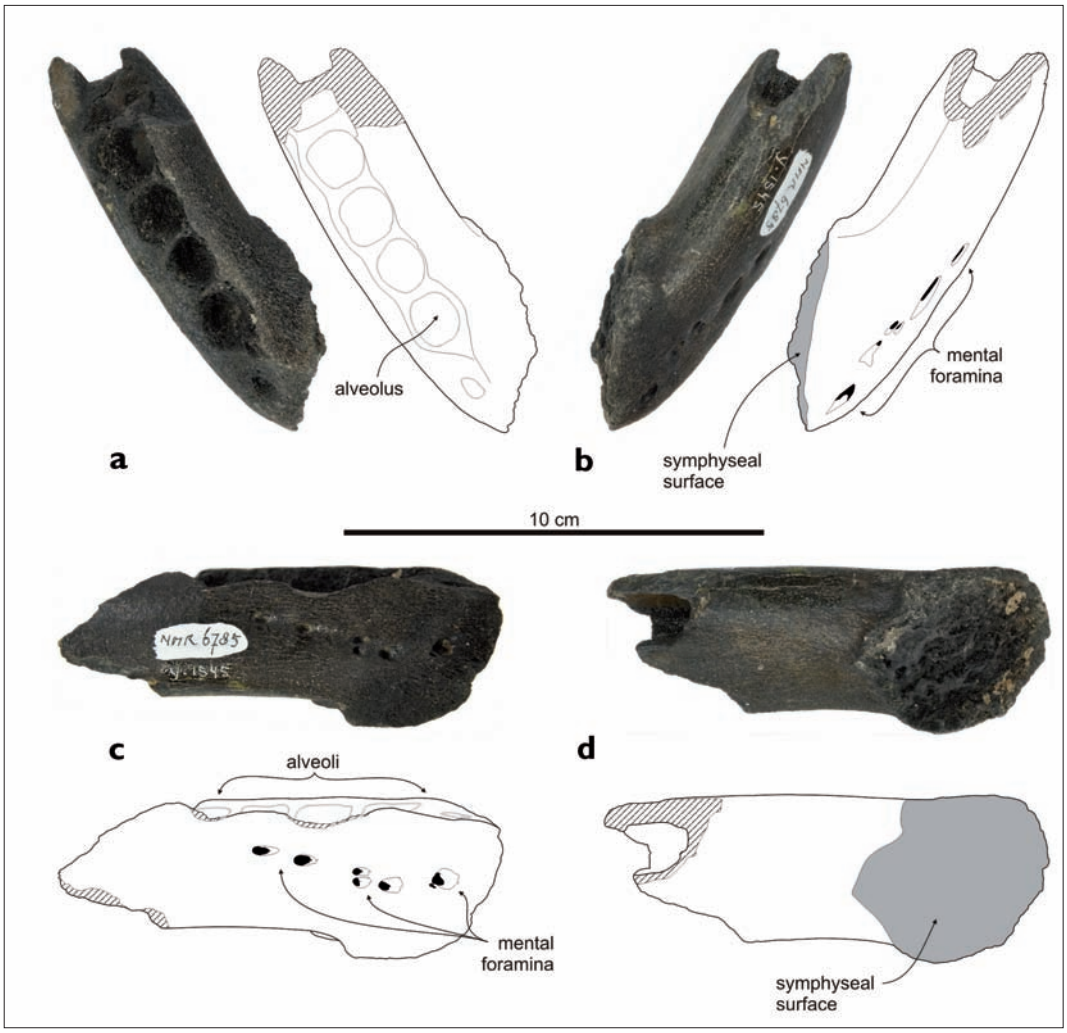

Figure 4 Mandible fragment NMR 9991-00006785: dorsal (**a**), ventral (**b**), buccal (**c**) and lingual (**d**) view.

Table 1 Measurements (in mm) of rostrum (holotype) of *Platalearostrum hoekmani* (NMR 9991-00005362) and mandible fragment NMR 9991-00006785.

	NMR 5362	NMR 6785
maximum length of fossil	221	98
preserved length of vomer	202	-
largest width of rostrum	156	-
largest width premaxilla	117	-
length alveolar groove	111	-
length largest alveolus	9	9
width largest alveolus	6	9
length symphysis	-	46
height symphysis	-	38
diameter ramus after symphysis	-	32

surface of the premaxilla. The fossil Chilean cranium seems to lack this feature (although precise details were not available), but the Late Pliocene *Protoglobicephala mexicana* and the Late Pleistocene Taiwanese skull do show these rugose areas and Aguirre-Fernández et al. (2009) considered these rugosities to constitute a synapomorphy of *Globicephala* and *Protoglobicephala*. It is worth noting that an Early Pleistocene and as yet unpublished delphinid from Italy, referred to Orcininae, also shows rugose dorsal areas of the rostrum (and even fusion of parts of its premaxillas) at more or less the same position as in extant *Globicephala* and NMR 5362 (G. Bianucci pers. comm.).

Apart from the important work of Mead (1975), little has been published about the attachment of muscles and their tendons on the dorsal surface of the rostrum (and the melon) of Delphinidae. Extant pilot whales are characterised by a short, blunt, high and bulky forehead which in mature individuals exceeds over the apex of the snout. Werth (2006) stated that the combination of rostral shortening, blunt heads, wide jaws (and corresponding dental reduction) facilitates suction feeding abilities and noted that especially globicephaline delphinids show blunter cranial profiles. The blunt forehead of pilot whales is caused by the large melon being housed on a relatively short rostrum and/or specific melon/sonar use. Sexual dimorphism may also be linked to this feature (Mead 1975). A study on *Tursiops truncatus* (Harper *et al.* 2008) confirms that the oblique rostral muscle and the

Figure 5 Hypothetical reconstruction of Hoekman's blunt-snouted dolphin (*Platalearostrum hoekmani*). [Remie Bakker | Manimal Works]

nasal plug muscle are secured to the premaxilla surface and act as an important vehicle to continuously shape and reshape the melon and thereby allowing for secure and efficient sonar use. As in *Tursiops*, the melon and the musculus maxillonasolabialis must maintain strong and continuous interaction and the pars labialis of this muscle is secured on the rugose area of the distal surface of the premaxilla (Harper *et al*. 2008). It seems that the size of melon and rostrum in fully grown (presumably male) *Globicephala* require a rough and open surface on the distal parts of the premaxilla to ensure extra strength and stability of the musculus maxillonasolabialis. It may not be too farfetched to conclude that the strange and very short rostrum of *Platalearostrum hoekmani* was housing a large melon which exceeded the rostrum laterally and frontally and needed very firm rostral muscle attachments. This hypothesis has also been suggested for *Protoglobicephala mexicana* by Aguirre-Fernández *et al.* (2009). Therefore, *P. hoekmani* may have shown an extremely large, high and dome-like forehead which probably greatly exceeded the limits of the rostrum (Fig. 5). The strongly concave dorsal surface of the rostrum of NMR 5362 (unique for delphinids, but possible analogous structures are known in Physeteridae and, by high maxillary crests, in *Hyperoodon*) seems to corroborate this configuration. More fossils and further studies must confirm or reject this image.

CONCLUSION

In summary, we conclude that NMR 5362, NMR 6785 and the numerous isolated periotics in Dutch and Belgian collections corroborate the presence of *Globicephala*-like species in the Plio-Pleistocene North Sea. We also conclude that *Platalearostrum hoekmani* can be placed within the Orcininae (*sensu* Bianucci 2005). However, its position within the Orcininae and the putative link with *Globicephala*-like delphinids can only be determined through phylogenetic analysis based on more complete specimens of *Platalearostrum* and a larger sample of fossil Delphinidae.

ACKNOWLEDGEMENTS

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APPENDIX

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