Online Journal of the Natural History Museum Rotterdam,
with contributions on all aspects of natural history
deinsea.nl

DEINSEA

Records of beaked whales *Ziphirostrum* and *Aporotus* (Odontoceti, Ziphiidae) from the Miocene of The Netherlands

Hidde Bakker & Klaas Post
Natural History Museum Rotterdam, Westzeedijk 345 (Museumpark), 3015 AA Rotterdam, the Netherlands

ABSTRACT
Beaked whales (Ziphiidae) are a diverse family of odontocetes (toothed whales) adapted to life in the open ocean. Their deep diving behavior and apparent low abundance make extant Ziphiidae hard to study resulting in a relatively poor understanding of their biology. Fossil data aid a better understanding of their evolution and lifestyle. The Miocene of the southern North Sea Basin is a rich source of fairly well preserved fossil ziphiid taxa. Here, we describe new ziphiid fossils from the Dutch part of the Westerschelde estuary: a well-preserved cranium of *Ziphirostrum marginatum* DU BUS, 1868 and some peculiar rostral fossils that represent the first Dutch record of *Aporotus recurvirostris* DU BUS, 1868.

Keywords biogeography, Cetacea, paleontology, rostrum, Westerschelde

Cite this article Bakker, H. & Post, K., 2020 - Records of beaked whales *Ziphirostrum* and *Aporotus* (Odontoceti, Ziphiidae) from the Miocene of The Netherlands - Deinsea 19: 17 - 26

Submitted 6 September 2020
Accepted 8 December 2020
Published 30 December 2020

Author for correspondence
H. Bakker
hiddecbakker@hotmail.com

Editors of this paper
Bram W. Langeveld
Jelle W.F. Reumer

DEINSEA online
ISSN 2468-8983

INTRODUCTION

With 23 extant species, the Ziphiidae (beaked whales) are among the most diverse, but also least-known large marine mammals due to their seclusive lifestyle and apparent low abundance which, even recently, led to recognition of new extant species (e.g. the North Pacific *Berardius minimus* YAMADA ET AL., 2019 (Yamada *et al.* 2019)). Well-preserved fossils of Ziphiidae are also quite rare (Ramassamy *et al.* 2018). Nevertheless, the area of Antwerp in Belgium offered a great number of important ziphiid specimens and is one of the richest locations in the world of fossil beaked whales (Lambert 2005). The earliest reported fossils of *Ziphirostrum* were described by Van Beneden (1860). He first described a skull (now lost) as *Diplodon d´Hemixem* but did not provide a drawing or reference number. Later he changed the genus name to *Ziphirostre* (Van Beneden 1864). Du Bus (1868) used the name *Ziphirostrum* for this taxon and presented a large number of new Ziphiidae taxa, including the aberrant genus *Aporotus* DU BUS, 1868. In his revision, Abel (1905) reduced the majority of (newly named) species to a single taxon: *Mioziphius belgicus* ABEL, 1905. More recently *Mioziphius* is classified as a junior synonym of *Ziphirostrum* (De Muizon 1984, Bianucci *et al.* 1992, McKenna & Bell 1998, Fordyce & de Muizon 2001). In his revision of Belgian ziphiids, Lambert (2005) recognized three clearly defined species in *Ziphirostrum* (*Z. marginatum* DU BUS, 1868, *Z. turniense* DU BUS, 1868, *Z. recurvus* DU BUS, 1868) and two

in *Aporotus* (*A. recurvirostris* DU BUS, 1868, *A. dicyrtus* DU BUS, 1868). In recent years additional in-depth research has been undertaken unravelling the complicated phylogenetic relationships among fossil and extant Ziphiidae (e.g. Lambert 2005, Bianucci & Post 2005, Bianucci *et al.* 2007, 2010, 2013, 2016, Buono & Cozzuol 2013, Lambert & Louwye 2016).

Contrary to the multitude of fossil beaked whale taxa found and described during the previous centuries from Belgium, only *Choneziphius planirostris* CUVIER, 1824 was reported from The Netherlands (Weber 1917). However, this century Post & Bosselaers (2010) recognized remains of *Ziphirostrum* trawled from the bottom of the Westerschelde (Western Scheldt), the most important estuary of the Scheldt river connecting the North Sea to the Port of Antwerp. Its relative proximity to the Antwerp region, from which most of the known *Ziphirostrum* specimens originate, is noteworthy. A few years later, Scager *et al.* (2017) also mention some fragmented fossils of *Ziphirostrum* sp. in their revision of the Eastern Scheldt (Oosterschelde) collection of Naturalis Biodiversity Center (Leiden, the Netherlands). In the meantime in nearby Denmark, beaked whale fossils were recognised and described: *Dagenodum mojnum* RAMASSAMY, 2016 (Ramassamy 2016).

Despite the multitude of described ziphiid fossils and taxa from neighbouring Belgium, still only a relatively small number of fossil ziphiid taxa is as yet reported from The Netherlands: *C. planirostris*, *Beneziphius brevirostrum* LAMBERT, 2005 and *Z. marginatum*. This article describes cranial fossils of two ziphiid taxa: the first well preserved cranium of *Ziphirostrum marginatum* from The Netherlands and the first record of *Aporotus recurvirostris* from the Dutch fossil record. These fossils help to understand the diversity and distribution of members of this family in the southern North Sea Basin.

Stratigraphic background

The fossils described here were collected during a paleontological survey of the Westerschelde in 2019. No datable sediments were recovered in direct correlation to the specimens. Previous finds retrieved from this general area (named 6D by Post & Reumer 2016, see Fig. 1) could be dated based on the presence of dinoflagellate cysts confirming the sea bottom exposure of the Breda Formation and Oosterhout Formation at the site (Post & Reumer 2016). These marine mammal fossils which are still embedded in their original sediments, are of Late Miocene age, but do not include the species described in this article.

We cannot prove that the fossils described here originated from a specific geological formation because mixing of eroded and reworked younger and older strata has been noted. For a more in-depth evaluation of the stratigraphy of the Westerschelde at location 6D see Post & Reumer (2016). *Z. marginatum* and *A. recurvirostris* specimens from Belgium originate from the Antwerp region. Sadly, the stratigraphical information of the majority of the specimens is lost. At least *A. recurvirostris* might originate from the middle Miocene Berchem Formation (pers. comm. O. Lambert, September 2020). Combined with the relative proximity of Antwerp (location 6D lays just 60 km north from Antwerp) a Middle to Late Miocene age may be hypothesized for the Westerschelde specimens.

MATERIAL AND METHODS

Our material consists of four specimens kept in the collection of the Natural History Museum Rotterdam (Rotterdam, The Netherlands; NMR). The specimens are: NMR 999100159956 (hereafter mentioned as NMR 159956): cranium with parts of premaxilla, maxilla, nasal, presphenoid, vomer, lacrimal, jugal, frontal and palatine; NMR 999100159960 (hereafter NMR 159960): partial left half of rostrum; NMR 999100159959 (hereafter NMR 159959): partial right half of rostrum; NMR 999100159958 (hereafter NMR 159958): posterior fragment of left half of rostrum.

Measurements were taken as per Ross (1984) and Lambert (2005) with calipers. Morphological terminology follows Mead & Fordyce (2009) and Ichishima (2016).

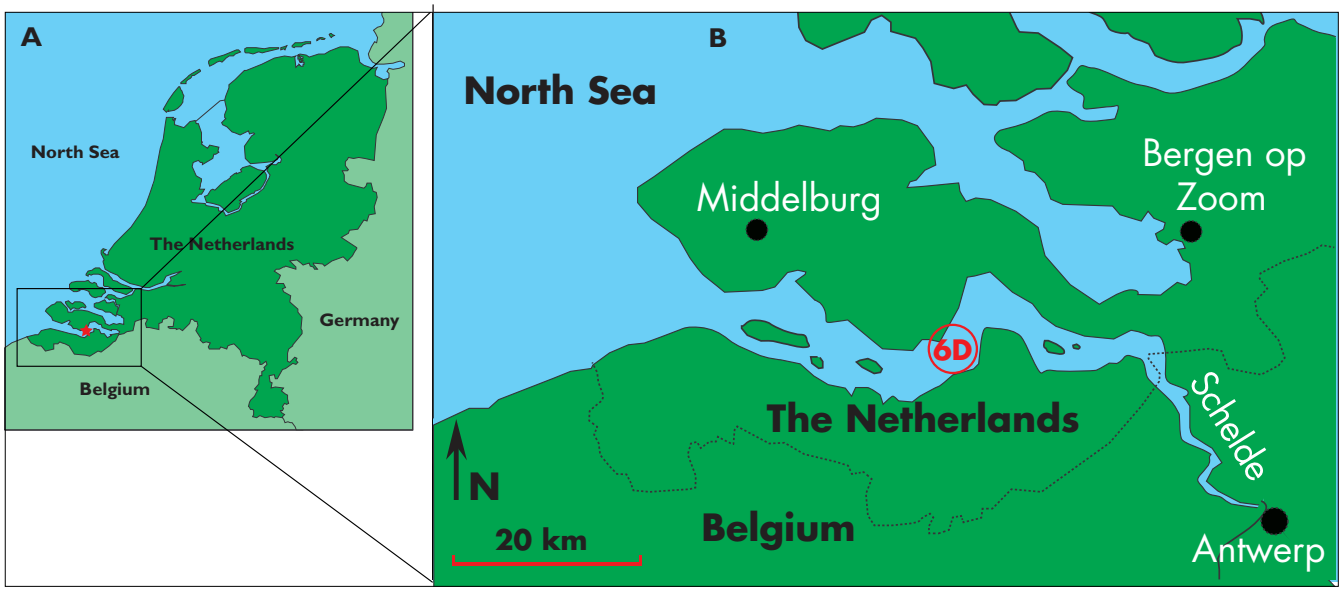

Figure 1 Locality 6D in the Westerschelde where *Ziphirostrum marginatum* and *Aporotus recurvirostris* specimens were recovered by bottom trawling. A: The Netherlands and neighboring Belgium and Germany. Red star: locality 6D. B: Close-up of the Westerschelde area with '6D' indicating the site. (Jaap van Leeuwen)

RESULTS

Class Mammalia Linnaeus, 1758
Order Cetacea Brisson, 1762
Suborder Odontoceti Flower, 1867
Family Ziphiidae Gray, 1865

Genus *Ziphirostrum* du Bus, 1868

An extinct beaked whale genus which, following Lambert (2005), differs from:

- *Choneziphius* Duvernoy, 1851, *Tusciziphius* Bianucci, 1997, and *Ziphius* Cuvier, 1823 in: the absence of elevated longitudinal maxillary crest on the supraorbital process; less asymmetrical premaxillary sac fossae (ratio between maximum widths of left and right fossae higher or equal to 0.69); and anterodorsally shorter nasals;
- *Choneziphius* in: the excavation of a prenarial basin at the base of the rostrum margined by a wide strip of the maxillae elevated towards the antorbital notches; flat surface of the premaxillary sac fossa lacking a strong anterior concavity;
- *Aporotus* du Bus, 1868 in: fused premaxillae above the mesorostral groove; strip of the maxilla limiting the prenarial basin anterolaterally, without valley along the lateral side of the elevated premaxilla on the rostrum;
- *Beneziphius* Lambert, 2005 in: a relatively longer and less pointed rostrum; a deeper prenarial basin; the lack of excrescences on the dorsal surface of the maxilla along the prenarial basin;
- other known ziphiids in the fusion of the thickened premaxillae above the mesorostral groove and the presence of a prenarial basin.
- most of the characters defining *Ziphirostrum* are present in *Messapicetus* Bianucci et al., 1992, except the very dense rostrum, which is variable in *Ziphirostrum*. The prenarial basin is probably shallower in *Messapicetus*.

Ziphirostrum marginatum du Bus, 1868

Referred specimen: NMR 159956 (Fig. 2, Fig. 3, Table 1)
Diagnosis of *Ziphirostrum marginatum* as presented by Lambert (2005):
The species differs from *Ziphirostrum turniense* in: a deeper, longer and wider prenarial basin, bordered by relatively thicker and higher strips of the maxillae posterolaterally curving towards the antorbital notches; a more posterior position of the top of the premaxillae on the rostrum, at one quarter of its total

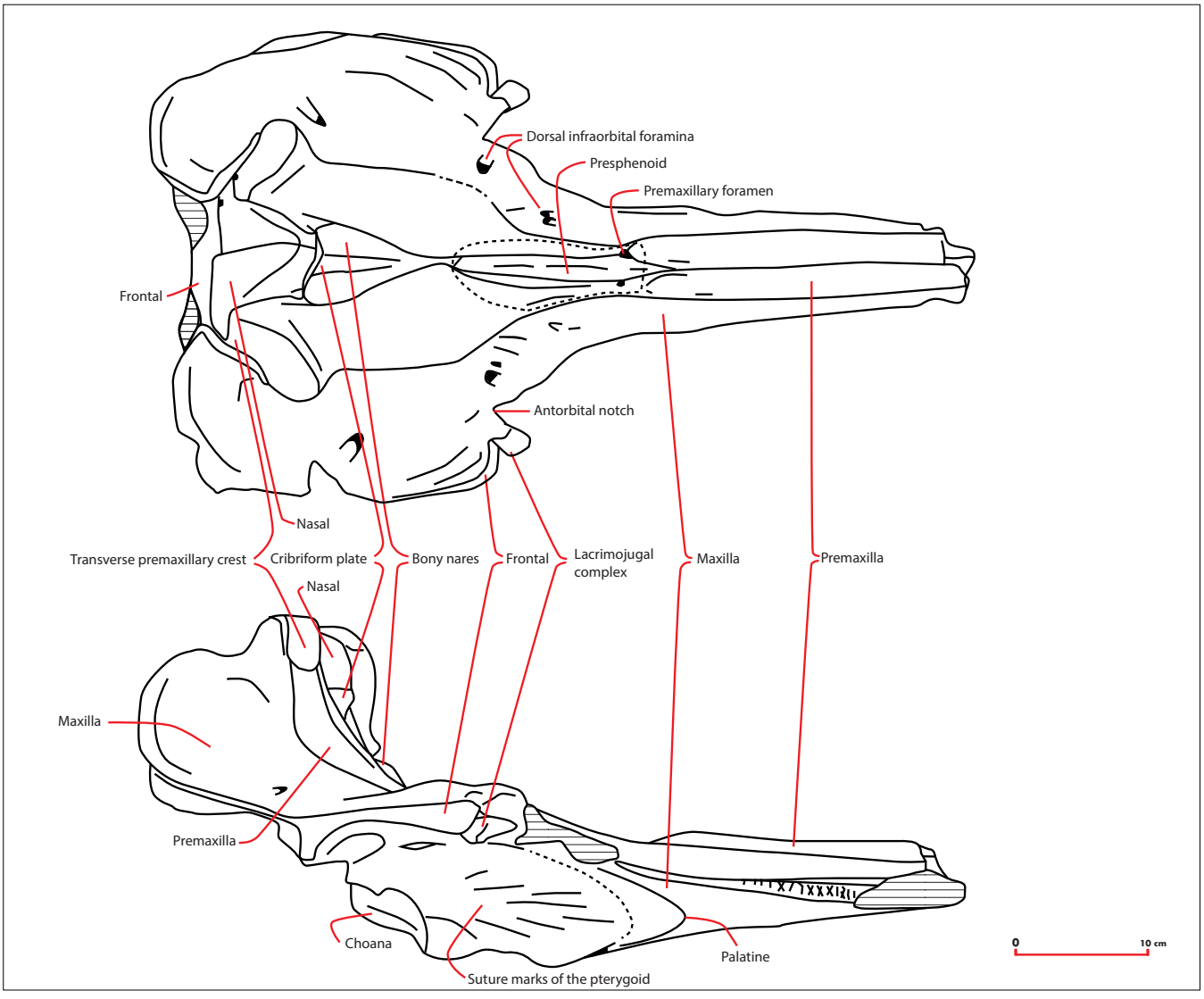

Figure 2 Generalised line drawing based on Lambert (2005) of the cranium of *Ziphirostrum marginatum* in dorsal and right lateral view.

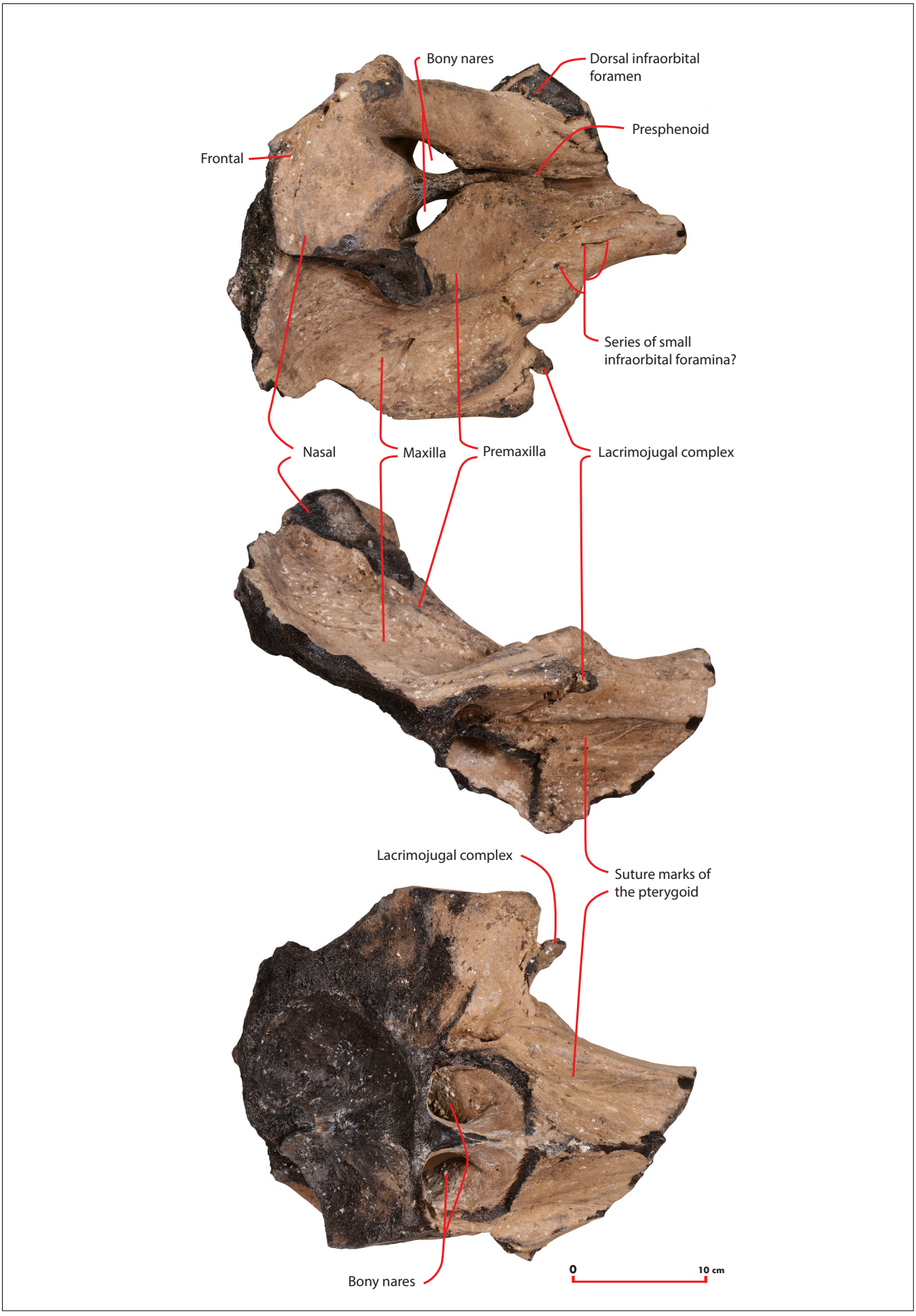

Figure 3 Cranium of *Ziphirostrum marginatum* NMR 159956 in dorsal, lateral and ventral view.

Table 1 Measurements (in millimetres) taken from NMR 159956 *Ziphirostrum marginatum*. Estimated measurements are indicated with E.

Width at rostrum base	132.0
Width at prominental notch	183.7
Width of premaxillary sac fossae	143.0
Width at preorbital process	332.0 E
Width of nasals	77.2
Anteroposterior thickness of premaxillary crest at vertex	61.0
Mediolateral width of premaxillary crest at vertex	150.2 E
Total length of fossil as preserved	325.5
Total height of fossil as preserved	288.5

length. It differs from the more fragmentarily known *Z. recurvus* in a relatively lower rostrum, wider than high in its anterior portion, and the open mesorostral tunnel.

Description

General

The cranium NMR 159956 is medium sized compared to other ziphiid taxa. It consists of the rostrum base and facial region including vertex and right orbit. Most of the rostrum is missing and it shows in anterior cross-section a transversely concave dorsal surface of the rostrum base. In anterior view the premaxilla is enclosed laterally by the upheaved maxilla bearing a thick rostral maxillary crest. On the left side this crest is incomplete due to mechanical damage. On the surface of the nasal septum a color pattern of white branches is present, most likely caused by marine plant- and/or invertebrate life. The vertex is a prominent and elevated structure, even if compared to some extant medium sized ziphiids, and is dominated by massive triangular shaped nasals. Moreover, it is markedly directed to the left side of the cranium.

Premaxilla

In anterior view, on the broken cross-section, the premaxillae are thickened and enclosed by the swollen maxillae, hiding the premaxillae from lateral view. Two (left and right) large, 1.8 mm wide, canals are present at the cross-section underlaying the premaxillae anteroventrally. Just before descending into the prenarial basin the anteriormost preserved portion of the premaxillae are present as two very slender strips of bone, the left one smaller than the right one. They are almost obscured from dorsal view by the bulbous maxillae and are positioned along a prominent, deep and dorsally open mesorostral groove contributing to a deep prenarial basin. The basin is located at the posterior part of the rostrum base as a deep and wide depression. It consists of the floor of premaxillae laterally bordered by upheaved maxillae and posteriorly by the premaxillary sac fossae. The premaxillary sac fossae are asymmetrical with a considerably smaller but much more elevated left fossa (max. width 54 mm) compared to the right fossa (max. width 77 mm). The premaxillary sac fossae are dorsally separated by a prominent presphenoid, which is present from the level of the rostrum base till the bony nares. The suture of the premaxilla and maxilla along the prenarial basin is pierced with small foramina which may represent small dorsal infraorbital foramina. The left ascending process of the premaxilla runs to the vertex into an almost vertical position and terminates in a not prominent, laterally directed, premaxillary crest. The right crest is severely damaged but is supposed to show the same features. Posteriorly the crest shows three dominant dorsoventrally directed foramina in the suture of the premaxilla and maxilla.

Maxilla

At the damaged surface of the rostrum, the maxilla appears laterally and dorsally as a thick and swollen crest which is laterally thickest at the position of the prominental notch. From the prominental notch to the antorbital notch the maxilla forms a moderately elevated rostral maxillary crest. This portion of the maxilla (from the antorbital notch to the preserved anterior end of the specimen) is pierced by a series of dorsal infraorbital foramina. Just anterior of the notch the right maxilla reaches its maximum dorsal elevation. The left maxilla is damaged and therefore missing the dorsally elevated part, but still at least four infraorbital foramina can be observed piercing the broken surface of the maxilla. After forming a prominent and deep antorbital notch the maxilla extends laterally, forming the slightly domed dorsal surface of the antorbital process. Anteriorly it bends around the jugal and posteriorly it dorsally covers the frontal contribution of the preorbital process. The frontal is laterally wider than the maxilla at this position and the suture is clearly visible in dorsal view. The supraorbital process is a slightly hollowed portion with one large dorsal infraorbital foramen in its centre, which shows a sulcus pointing in a posterolateral direction. Further posteriorly the maxilla contributes to the transverse premaxillary crest by covering its posterolateral side.

Presphenoid, cribriform plate and ectethmoid

The presphenoid is exposed dorsally at the level between the prominental notch and the antorbital notch, and separates the premaxillary sac fossae until it forms a robust nasal septum. More posteriorly the presphenoid is followed by the cribriform plate, which is a thin and elevated plate of bone that contacts laterally the ectethmoid, posterolaterally the premaxilla and most posteriorly the suture with the nasal. Some vertically directed foramina are present at the upper most level of the contact of the premaxilla, nasals and cribriform plate; the right ones being somewhat bigger than the left ones.

Vomer
The vomer underlays the presphenoid, which hides its posteriormost part completely from dorsal view. Posteriorly the vomer ends in two laminae contacting the ectethmoid. Ventrally the vomer shows as a solid and robust part of the nasal septum. It is anteriorly enclosed by the palatine and posteriorly broken before the suture with the basisphenoid.

Nasal
The triangular shaped massive nasals (the right one larger than the left one) are located between the premaxillary crests and contact the crests only at their posterolateralmost corner. They are longer (left 64.2 mm) than wide (left 35.8 mm) and slightly overhang the bony nares. Their joint dorsal surface shows a longitudinal depression following the internasal suture. Posteriorly the nasals are bordered by the frontals.

Frontal
In dorsal view the preorbital process of the frontal partly extends laterally beyond the maxilla. In lateral view the right orbit (consisting of the preorbital process and an almost completely preserved postorbital process) is 95 mm long. Some portions of the frontal are visible beyond the most posterior part of the maxilla and are preserved on the vertex as a 8 mm thick wall. On the vertex the left and the right frontal are separated by a tiny, almost totally fused, suture. The frontal parts of the vertex are slightly less elevated and smaller compared to the massive nasals.

Lacrimal and jugal
The right lacrimal is present in front of the preorbital process and is completely fused with the base of the styliform process of the jugal.

Palatine
Ventrally the palatine is present as two large and wide palatine surfaces, extending anteriorly beyond the preserved part of the rostrum and posteriorly to the bony nares. The lateral side of the palatine is marked by a prominent longitudinal ridge which might correspond with the lateral border of a large pterygoid sinus fossa. The palatine surface exhibits suture marks consisting of shallow longitudinal grooves probably indicating the position of the pterygoid which is not preserved. The palatine ends posteriorly at the position of a prominent ventral infraorbital foramen.

Identification of NMR 159956
The wide transverse premaxillary crests at the vertex and the distinct, deep and long prenarial basin bordered by laterally thickened and dorsally prominently elevated maxillae posterolaterally curving towards the antorbital notches are both characteristics of *Z. marginatum*. Moreover, the wide open mesorostral groove at the rostrum base separates NMR 159956 from *Z. turniense* and corroborates its identification as *Z. marginatum*.

Genus *Aporotus* du Bus, 1868
An extinct beaked whale genus which, following Lambert (2005), differs from:

- *Ziphirostrum*, *Messapicetus*, *Choneziphius*, and *Beneziphius* in the unfused elevated premaxillae covering the mesorostral groove. It further differs from:
- *Ziphirostrum* and *Messapicetus* in: longer and higher longitudinal maxillary crest on the preorbital process; a longitudinal wide valley between this maxillary crest and the more elevated premaxilla on the rostrum;
- *Choneziphius* in: excavation of a prenarial basin at the base of the rostrum; flat surface of the premaxillary sac fossae;
- *Tusciziphius* in: flat surface of the premaxillary sac fossae; thinner transverse premaxillary crests;
- all the other known ziphiid genera by the dorsal roofing of the mesorostral groove by the thickened premaxillae.

Aporotus recurvirostris du Bus, 1868
Referred specimens: NMR 159960, NMR 159959, NMR 159958

Diagnosis of rostral characters of *A. recurvirostris*:
The rostrum of *Aporotus* is dominated by an extremely swollen, but medially unfused longitudinal premaxillary crest covered with numerous vascular sulci (Fig. 4). The elevated massive premaxillae hide the mesorostral groove from dorsal view. The maxillae are dorsally hardly exposed on the rostrum. Differing from *Aporotus dicyrtus* in: the longer, slightly anterodorsally curved rostrum and a more elevated premaxilla on the rostrum forming a high longitudinal crest with a top more posteriorly positioned and with a steeper posterior slope (modified from Lambert 2005).

Description
NMR 159960 (Fig. 5, Table 2)
NMR 159960 is a well preserved partial left half of a rostrum of which the swollen and extremely developed premaxilla is the most peculiar feature. Numerous small vascular sulci are present on both the lateral and medial side of the premaxilla and maxilla, most numerous on the anterolateral side of the premaxilla. The tip of the rostrum is missing due to postmortem damage. In lateral view the premaxilla is very high with a maximum height

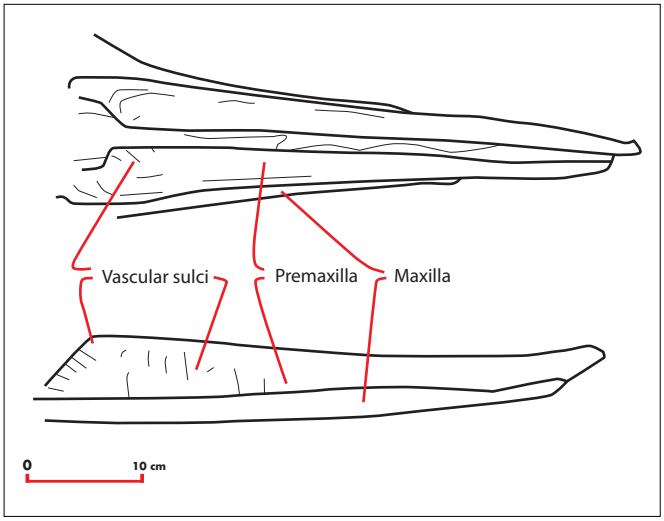

Figure 4 Generalised line drawing based on Lambert (2005) of the rostrum of *Aporotus recurvirostris* in dorsal and right lateral view.

Figure 5 Rostral portions of *Aporotus recurvirostris* NMR 159960, NMR 159959 and NMR 159958 in dorsal, lateral and medial view.

posteriorly (43 mm), followed by a steep lowering of the most posterior part. Posteriorly the premaxilla is mechanically damaged and shows its very compact, almost glassy bone structure. Dorsomedially there is no sign of a suture line or connection remains of the left premaxilla with the right premaxilla, which confirms that the for ziphiids common rostral fusion is absent. Five large, circular holes can be observed on the medial side of the maxilla, like the *'aborted? molluscan drillings'* as observed by Lambert (2005) on one of the Belgian crania of *Z. marginatum*. Dorsally and laterally the maxilla is present as a thin strip of bone, widening posteriorly in dorsal view. Ventrally it is slightly transversely convex showing an anteroposterior canal leading to a small vascular foramen (palatine foramen?) near the midline of the fossil.

NMR 159959 (Fig. 5, Table 2)

NMR 159959 is a partial right half of a rostrum. The premaxilla is extremely high (62 mm), higher than in NMR 159960, and is missing most of the vascular sulci shown by NMR 159960. Mechanical damage resulted in the absence of the anterior part of the rostrum but reveals a cross-section of the premaxilla in which the compact, osteosclerotic bone and bone layers that probably correspond to growth layer groups can be observed. The surface of the section shows a high compactness and layers paralleling each other and the outer contour of the premaxilla. These are growth layers (also mentioned in Lambert *et al.* 2011) (Fig. 6). An opposed situation is observed on the section of the broken maxilla, which shows a more cancellous bone construction as revealed by Buffrénil & Lambert (2011) in another specimen of *A. recurvirostris*. The premaxilla reaches its maximum height in the posterior part, just before an abrupt lowering at its posterior most margin. There is no clue for a suture on the dorsomedial side of the premaxilla with the opposite premaxilla.

The maxilla widens posteriorly in dorsal view and can be observed as a small, thin piece of bone underlying the premaxilla.

Table 2 Measurements (in millimetres) taken from NMR 159960, NMR 159959 and NMR 159958 *Aporotus recurvirostris*.

NMR 999100159960	
Maximum width of premaxilla	31.8
Maximum height of premaxilla	49.7
Maximum width of maxilla	52.4
Maximum height of maxilla	17.0
Total length of fossil	377.8
NMR 999100159959	
Maximum width of premaxilla	33.8
Maximum height of premaxilla	61.4
Maximum width of maxilla	49.7
Maximum height of maxilla	11.2
Total length of fossil	365.2
NMR 999100159958	
Maximum width of premaxilla	29.2
Maximum height of premaxilla	54.8
Maximum width of maxilla	52.1
Maximum height of maxilla	34.7
Total length of fossil	127.5

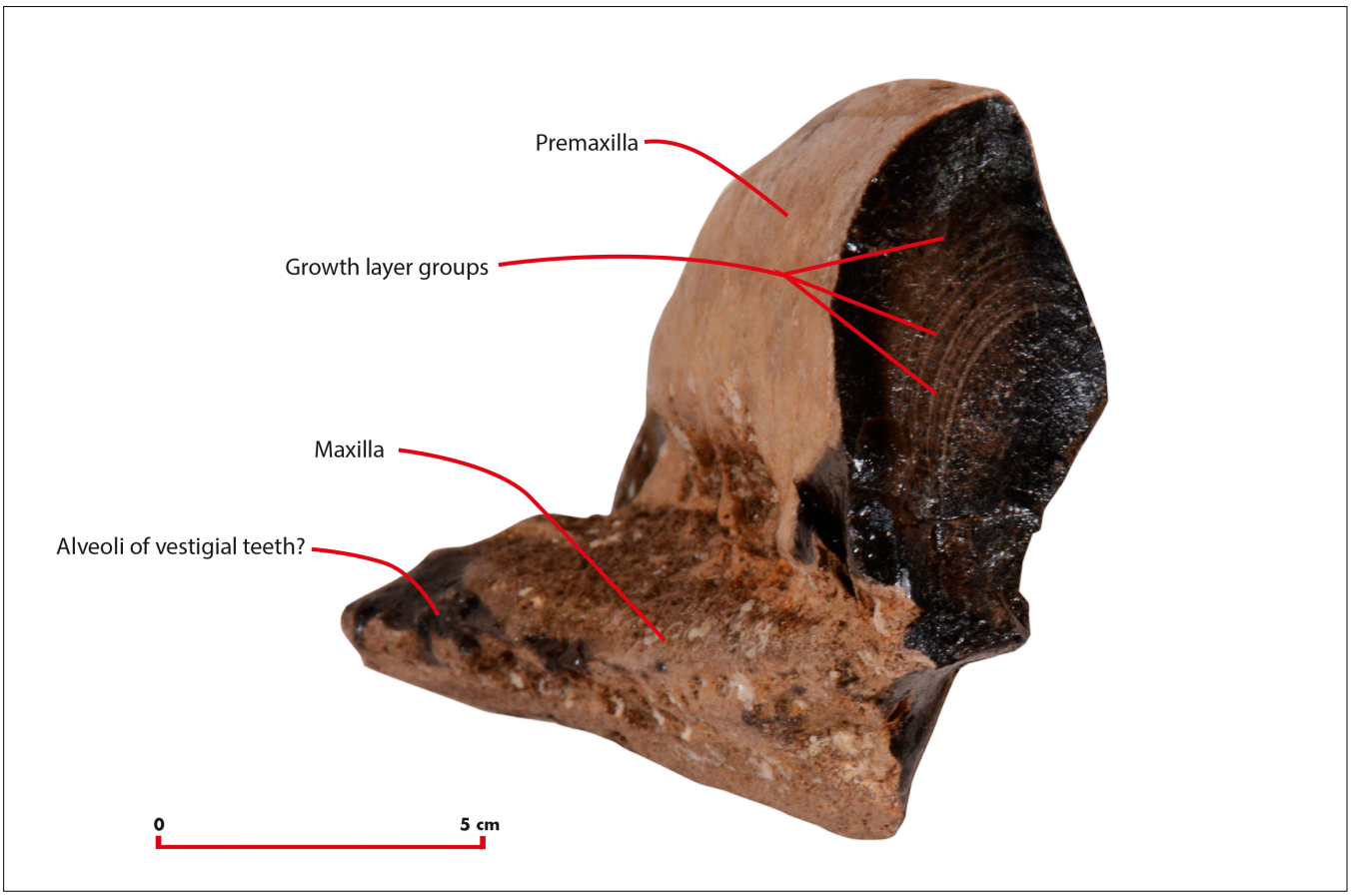

Figure 6 Transverse fracture plane of the proximal rostrum portion showing growth layer groups on *Aporotus recurvirostris* NMR 159958.

The ventral side is severely damaged but shows at the posterior break surface remnants of an anteroposterior directed canal.

NMR 159958 (Fig. 5, Table 2)

NMR 159958 is a fragment of the right half of a rostrum. It shows the posteriormost part of the typical high longitudinal premaxillary crest, which exhibits some small anastomosed vascular sulci at its surface. At the transverse break surface the very compact bone mass is showing multiple growth layer groups, as observed in NMR 159959 and mentioned in Lambert et al. (2011) and Buffrénil & Lambert (2011) (Fig. 6). The posterior part of the premaxilla shows the position of the premaxillary foramen.

The maxilla is present as a small flat ventrolateral surface, covered by remnants of an equally flat palatine, which is completely fused with the maxilla and showing the possible presence of the pterygoid suture. At the posterior break surface the maxilla shows an anteroposteriorly directed small longitudinal canal. Laterally the maxilla might show some alveoli for vestigial teeth.

Identification of NMR 159960, NMR 159959, NMR 159958

All three specimens are (large parts of) heavily mineralized rostrum halves, which clearly were not dorsally fused with their corresponding side of the rostrum, and which show a marked and typical longitudinal dorsal elevation (crest) of the premaxilla. Both features are characteristics of the genus *Aporotus*. Furthermore all specimens show a steep posterior slope of the elevated premaxillary crest in which they differ from *A. dicyrtus* and which is present in *A. recurvirostris*. The rostra NMR 159960 and NMR 159959 show in lateral view a slight curve in anterodorsal direction, another feature present in *A. recurvirostris*. Therefore NMR 159960, 159959 and 159958 may be with certainty identified as belonging to *A. recurvirostris*.

CONCLUSION

For centuries, the fossil record of Miocene ziphiids from the North Sea (and on a larger scale from the eastern North Atlantic Ocean) was dominated by a multitude of fossil taxa from Belgium. But, even if during parts of the Miocene beaked whales found exceptionally favorable conditions in the southern North Sea Basin near what is now the Belgian coast, it seems plausible that they must have reached other parts of the North Sea Basin (and the eastern North Atlantic). In this respect the first report of *Aporotus recurvirostris* (this paper), the first report of *Beneziphius brevirostrum* (Bosselaers 2014) and repeated finds of *Choneziphius planirostris* and *Ziphirostrum marginatum* from the southern provinces of The Netherlands (nearby the Antwerp area) are only logical and indicate that fossils of other beaked whale taxa described from Belgium might be found as well in The Netherlands. The recent reports of a new genus and species of a fossil beaked whale (*Dagonodum mojnum*) and an undescribed taxon from the Gram Formation of Denmark (Ramassamy 2016, Ramassamy & Lauridsen 2019); of *Chon-*

eziphius leidyi Bianucci et al., 2013, a new species of the genus *Beneziphius* (*B. cetariensis* Miján et al., 2017), and other new genera from Portugal and Spain (Bianucci *et al*. 2013, Miján *et al*. 2017); a report of *Choneziphius planirostris* from the Faroe Islands (Post & Jensen 2013), and fossils from *Choneziphius leidyi* from the north of Germany (pers. obs. authors) do confirm that at least some of beaked whale genera historically found only in Belgium occurred throughout the entire eastern North Atlantic Ocean. This conclusion also implies that in the future more new species will certainly be added to the already significant number and variety of Miocene beaked whale taxa from the coastal European countries bordering the East Atlantic and North Sea.

ACKNOWLEDGEMENTS

Captain Jan van Dokkum and his crew of fishing vessel UK 12 are thanked for their hard work in difficult circumstances at the strong currents of the Westerschelde estuary. Bram Langeveld (NMR), is thanked for access to comparative material and additional information. We thank the reviewers Dr. Olivier Lambert and Dr. Giovanni Bianucci for their most valuable remarks and suggestions, which considerably improved the manuscript.

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DEINSEA - the online open-access Journal of the Natural History Museum Rotterdam publishes contributions on all aspects of natural history
editor-in-chief Jelle W.F. Reumer | editors Bram W. Langeveld & Cornelis W. Moeliker
design TANK | layout Jaap van Leeuwen | content, back-issues & guidelines www.deinsea.nl

submissions deinse@hetnatuurhistorisch.nl