

Early Pleistocene bivalve *Mya arenaria* Linnaeus, 1758, from the ‘Kor en Bot’ expedition in the Eastern Scheldt estuary: a dinner course of the walrus *Ontocetus emmonsii* Leidy, 1859?

Peter W. Moerdijk^{1,3} & Klaas Post²

¹ Kingstraat 14, 4336 LG, Middelburg, The Netherlands

² Natural History Museum Rotterdam, Westzeedijk 345, 3015 AA Rotterdam, The Netherlands

³ Corresponding author: moerdijkpw@zeelandnet.nl

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Of 66 well-preserved early Pleistocene fossil shells of *Mya arenaria* L., 1758, sampled during the annual ‘Kor en Bot’ expeditions in 2013 and 2019 in Flauwers Pit I (Eastern Scheldt Estuary, The Netherlands), 65 specimens showed unusual damage. Judging the nature of the damage they were possibly victims of a large predator, presumably *Ontocetus emmonsii* Leidy, 1859. *O. emmonsii* may have used his incisors and/or canines to crack the shells before sucking in the animal. *M. arenaria* and *O. emmonsii* were most probably part of the same fauna. The origin of their fossil remains is the early Pleistocene (Gelasian) marine Maassluis Formation.

KEY WORDS: bivalve, *Mya arenaria*, predation, walrus, *Ontocetus emmonsii*

Introduction

The Eastern Scheldt (Oosterschelde) is a dammed estuary in the province of Zeeland (The Netherlands). Since 1951 a mussel cutter annually sets sail to collect fossils (Heuff, 2010) from the seafloor of this estuary; the ‘Kor & Bot’ expedition. Special attention is paid to the rich early Pleistocene (Gelasian) Oosterschelde Fauna comprising terrestrial mammals (De Vos *et al.*, 1998). From 2013 onwards the first author boarded the mussel cutter ZZ 10 with ‘Genootschap Kor en Bot’ on these annual expeditions. On the September 7, 2013 trip, 37 fossil shells of the sand gaper *Mya arenaria* Linnaeus, 1758 were collected from a single haul in Flauwers Pit I (Figs 1, 2). During the 2019 expedition, 29 *Mya* shells were found, very well preserved and showing no traces of wear by transport. On the other hand, all but one of the valves are fractured.

Nowadays, *M. arenaria* lives in large numbers in this estuary, therefore initially these finds were not identified as fossils. They also had not been expected as the species only lives in shallow water and is not found in the deeper water channels in which most of the drags of these expeditions are done. Another surprising observation was that 65 of the 66, otherwise well preserved, *Mya* shells showed an unusual and typical damage posteriorly, ventrally and/or anteriorly. Moreover, the chondrophore, which should be present on left valves, was broken or damaged in 10 of the 27 left valves (Fig. 4).

In this study we report the catch of these fossil shells,

analyse the unusual damage and propose a hypothesis for the cause of this damage.

Site and geological context

All shell specimens reported in this article were fished from the bottom of the Flauwers Pit 1 located at approximately N 51°40'; E 3°50', outside the dike of Moriaanshoofd on the island of Schouwen-Duiveland (province of Zeeland; southwest Netherlands) (Fig. 1). The fossils are found *ex situ*, at a depth of up to 40 m below sea level (Scager *et al.*, 2017).

A core drilling at Moriaanshoofd (TNO – Geological Survey of the Netherlands borehole number B42G0769, coordinates N 51°40'50'', E 3°50'09''; RDX = 047.740; RDY = 411.380), adjacent to the Eastern Scheldt dike south of Moriaanshoofd (Slupik *et al.*, 2013) provides detailed information about the deposits and their fossil content in the neighbourhood of Flauwers Pit 1. The Moriaanshoofd borehole lies ~100 metres N of Flauwers Pit 1 (Scager *et al.*, 2017).

All depths given in Slupik *et al.* (2013) for the Moriaanshoofd borehole are below ground surface, which is 4.19 m + N.A.P. For the sake of depth comparison of the Flauwers Pit 1 and Moriaanshoofd boreholes, in this paper the depths in the Moriaanshoofd borehole are also listed in m below N.A.P., increasing the depths given in Slupik *et al.* (2013) by ~4.19 m.

In the Moriaanshoofd borehole, Holocene and upper Pleistocene deposits are present to a depth of 32.3 m -

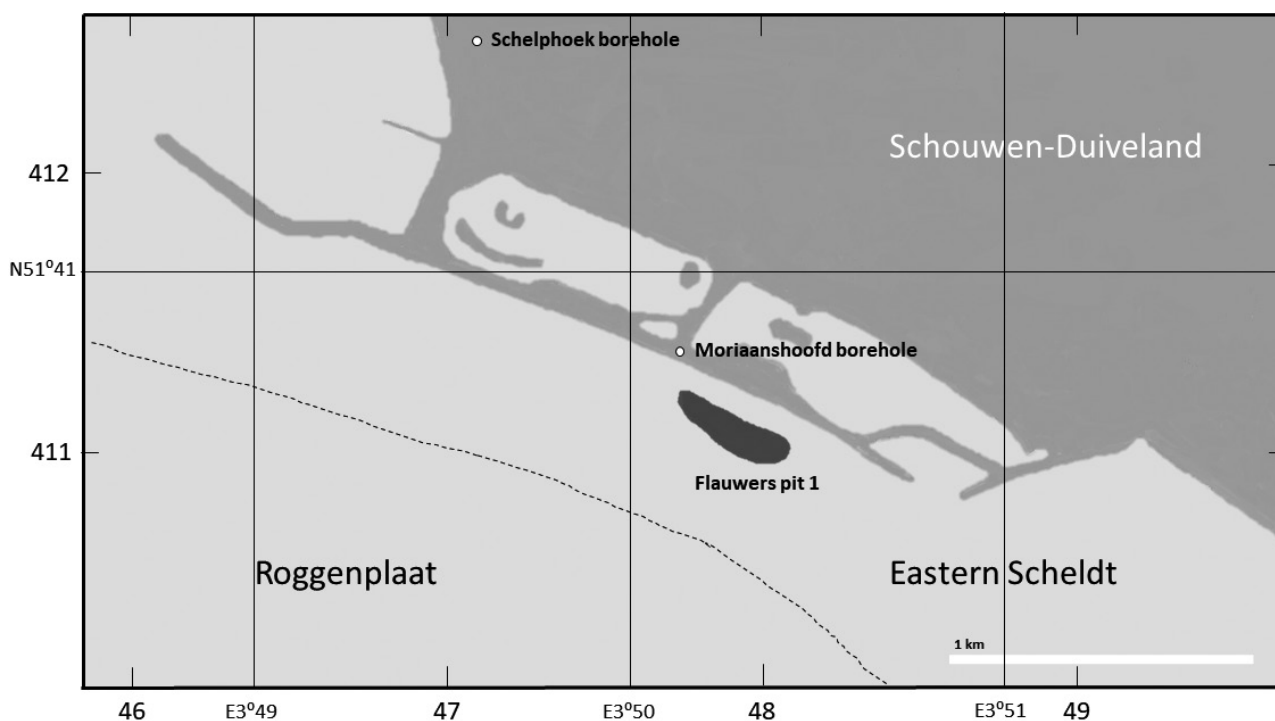


Figure 1. Map with localities Flauwers Pit 1, borehole Moriaanshoofd end borehole Schelphoek (Eastern Scheldt, The Netherlands).

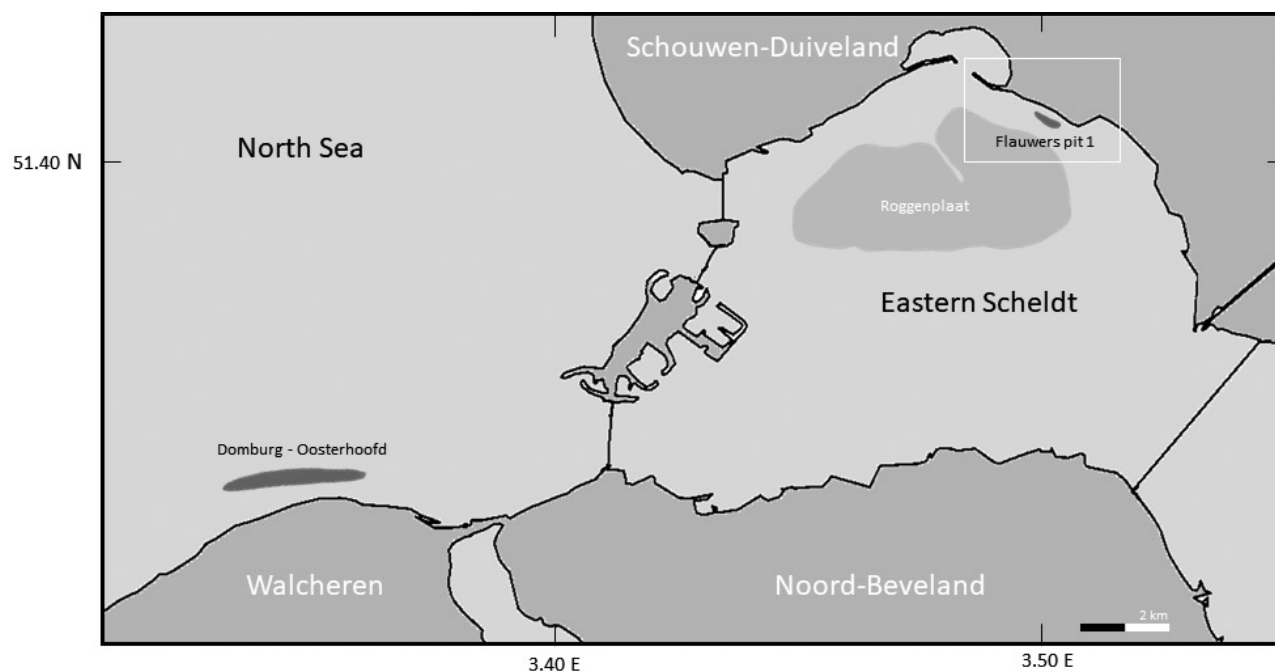


Figure 2. Map with localities Flauwers Pit 1 and Domburg Oosterhoofd (Eastern Scheldt, The Netherlands).

N.A.P. The borehole shows that a fossil-rich interval between 26.8 m and 32.3 m - N.A.P. was deposited by the Paleo-Scheldt comprising fossils washed out from both marine and terrestrial deposits of the entire Pleistocene interval. These fluvial sediments are referred to as the Koewacht Formation. It is almost certain that the well-known terrestrial so-called ‘Oosterschelde Fauna’ originated from this formation (Slupik *et al.*, 2013). In the Moriaanshoofd borehole the lower Pleistocene

Maassluis Formation is present at ~32.3 m – N.A.P. In Flauwers Pit 1, at depths of up to 40 m below mean sea level, therefore, not only the Koewacht Formation, but also the upper part of the Maassluis Formation is reached (Fig. 3). This Formation is deposited in a shallow marine, near shore environment and contains marine shells (TNO-GDN, 2021). In the Moriaanshoofd borehole and in the nearby Schelphoek borehole (Slupik *et al.*, 2007), at about 1 km N from the Moriaanshoofd

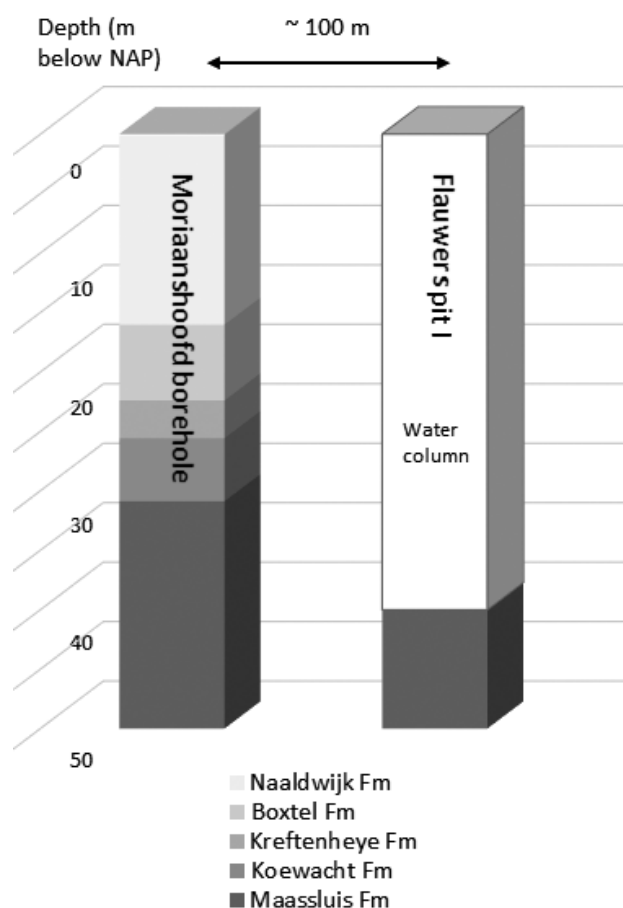


Figure 3. Schematic lithology of the Moriaanshoofd borehole after Slupik *et al.*, 2013, compared to presumed lithology of Flauwers Pit I.

borehole (N 51°41'12.0"; E 3°49'32.9"), the upper parts of the Maassluis Formation are present at respectively 36.5 (from 4.19 m + N.A.P.) and 38 m (from 3.16 + N.A.P.). The underlying Pliocene Oosterhout Formation was not reached in the Moriaanshoofd borehole. In the Schelphoek borehole the boundary between the Maassluis Formation and Pliocene Oosterhout Formation was reached at a depth of ~106 m – N.A.P. The channels in the Eastern Scheldt do not reach such depths, *i.e.* the Pliocene Oosterhout Formation is not exposed, and the fossils recovered from Flauwers Pit I are thus of early Pleistocene age or younger.

Materials and methods

For the ‘Kor en Bot’ expeditions, mussel dredges are used, which harvest – due to mesh size – predominantly coarser sediment and objects. In order to catch and sample smaller objects two tubes are attached to the dredges. The focus here is particularly on vole teeth, which can provide good clues about the age of the fossil terrestrial faunas, but also fossil mollusc shells can be present in the sediment from these so called ‘mouse tubes’. The sediment samples collected with these tubes are sifted out on a

sieve table. The 66 fossil shells reported in this article are stored in the collections of Naturalis Biodiversity Center Leiden (RGM.1364022, RGM.1364023, RGM.1364024, RGM.1364025 & RGM.1364026) and the Natural History Museum Rotterdam (NMR993000184669). Ten specimens are stored in the private collection of Herman Nijhuis, seven specimens are provisionally housed in the private collection of the first author. Morphological terminology of shells follows Moerdijk *et al.* (2010), of marine mammals follows Mead & Fordyce (2009).

N.A.P. = Nieuw Amsterdams Peil = Normal Amsterdam Level, the reference plane for height in the Netherlands. RD(X,Y) = Rijks Driehoek = coordinates of the national Dutch geodetic measurement system.

Mya arenaria from the Kor and Bot expeditions

M. arenaria shells from Zeeland province are either recent, not older than the thirteenth century AD (Essink & Oost, 2017), or fossil. In the latter case they are not younger than of an early Pleistocene, Gelasian age (Moerdijk *et al.*, 2010). Recent shells always allow light to pass through from a powerful light source. Fossil shells can be identified by the fact that they do not transmit any light and are completely recrystallised (Cadée & Wesselingh, 2005). On fresh fractures, these shells are chalky white. Since the fished shells are opaque and chalky white at fresh fractures, it is evident that these are fossils, *i.e.* no younger than the early Pleistocene.

The following fossil molluscs of the 2013 and 2019 expeditions that indicate an early Pleistocene (Gelasian) age of the fauna:

Species	2013	2019
<i>Mya arenaria</i>	37	29
<i>Arctica islandica</i> (Linnaeus, 1758)	12	8
<i>Macoma obliqua</i> (Sowerby, 1817)	4	5
<i>Macoma calcarea</i> (Gmelin, 1791)	2	1
<i>Macoma praetenuis</i> (Leathes in Woodward, 1833)	5	4
<i>Acila cobboldiae</i> (Sowerby, 1817)	1	
<i>Littorina littorea</i> (Linnaeus, 1758)	1	
<i>Potamides tricinctus</i> (Brocchi, 1814)	1	
<i>Nucella spec.</i>	1	

Most ‘Kor en Bot’ expeditions yielded far fewer early Pleistocene shells than those caught in 2013 and 2019, and these fossil shells were all heavily worn. This is in accordance with the experience of Wesselingh *et al.* (2002), who also sampled 10 valves and *c.* 20 fragments of *M. arenaria* shells. They state that the majority of the early Pleistocene shells collected during the ‘Kor en Bot’ expeditions are fragmentary, moderately preserved, and often worn.

Regarding the shells sampled in 2013 and 2019, it is striking that almost all *M. arenaria*, three of the *Arctica*'s and most of the early Pleistocene *Macoma*'s are excellently preserved and without any trace of wear. Many of them are partially or almost completely encrusted with present-day bryozoans. This indicates that they were washed from the Maassluis Formation sediment on the spot and prior to being fished up laid exposed on the seabed for some time.

Damage on *Mya arenaria*

Despite their very sturdy shells and their surprisingly good preservation, 65 of the 66 *Mya* shells collected and examined show typical damage posteriorly, ventrally and/or anteriorly (Fig. 4 A). Also, the chondrophore, which should be present in left valves, is broken or damaged in 10 of the 27 left valves (Fig. 4 B). Some fractures are fresh, clearly caused by the dredge or the dumping on the deck of the vessel. But most fractured surfaces, however, correspond in patina to the undamaged parts of the shell and are completely or partially encrusted with bryozoans. So most probably the shells were washed out of the sediment in this damaged state.

The fractures could have been caused by pressure (compaction) exerted by the layers of sediment accumulated in time above the shells. Although theoretically possible, the shells appear firm and offer a lot of resistance when such force is applied. Also, there are numerous long fractures; while shells broken by compaction fracturing and damage would have affected the entire shell. As several intact valves of the fragile *Macoma praetenuis* were col-

lected simultaneously, compaction is not likely the cause of the damage.

A second possibility is that the fractures were caused by predators. Cadée & Wesselingh (2005) mention crabs and benthic fish as possible predators of *M. arenaria*, and illustrate some damaged shells. In the growth lines of some of the *Mya*'s, indentations are present that may have been the result of predation by crabs. However, the long fractures of the *Mya*'s and the fractures of the chondrophore can hardly be caused by bottom fish or crabs. One of the shells (Fig. 4 A) has a large repaired fracture on the anterior, which cannot be caused by a small animal. The nature of the damage, such as the fractures of the chondrophore suggests the application of significant force which cannot be caused by compaction or smaller predators such as fish and crabs, so the damage to the shells of *Mya arenaria* must be caused by a large and powerful predator.

Walrus and *Mya*

Such a large and powerful predator of *Mya* is the walrus *Odobenus rosmarus* (Linnaeus, 1758) (Vibe, 1950, Levermann et al., 2003). Walruses preferably eat bivalve molluscs (Fay, 1982). The siphon and foot of the blunt gaper *Mya truncata* Linnaeus, 1758 are an important element of the walrus diet (Fisher & Stewart, 1997). But other molluscs such as *Hiattella arctica* (Linnaeus, 1767) and *Serripes groenlandicus* (Mohr, 1786) are on the menu as well. In captivity *M. arenaria* is also accepted (Kastelein & Mosterd, 1989).

During the late Pleistocene, the extant walrus migrated

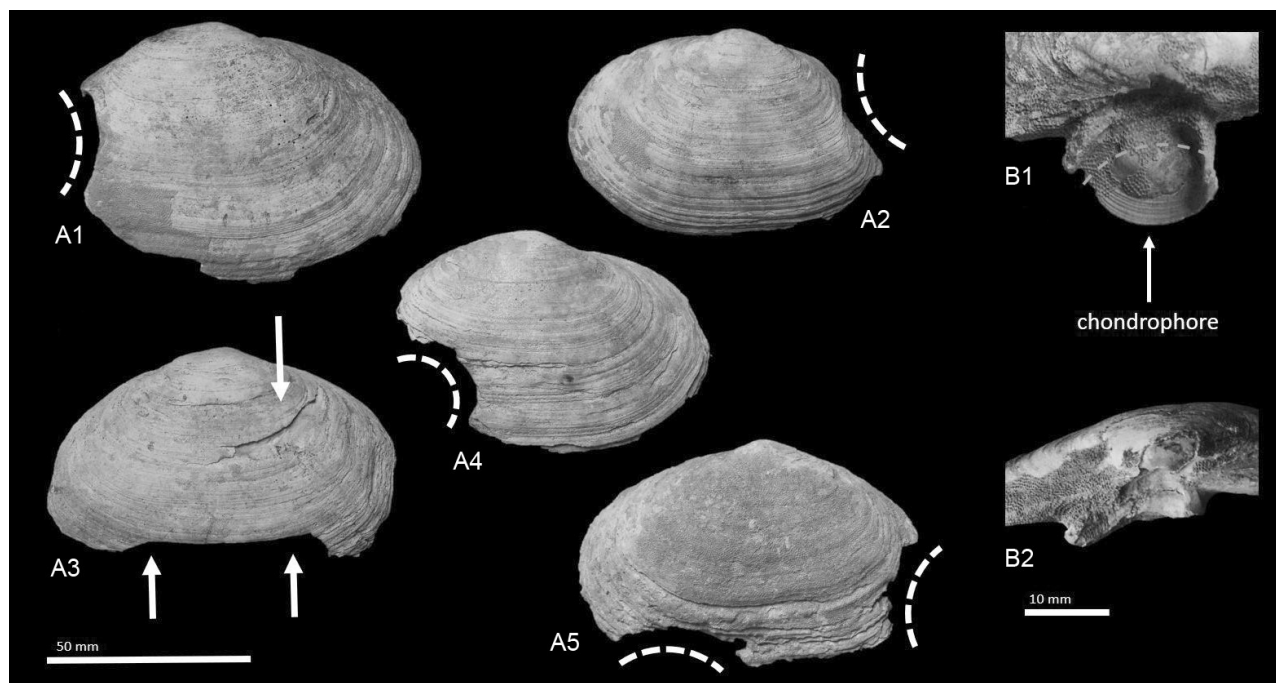


Figure 4. Damage on some shells of *Mya arenaria* collected during the 2013 and 2019 'Kor en Bot' expeditions at Flauwers Pit 1. A. Damage that could be caused by predation; white arrow: a large repaired fracture along the ventral edge (A1-A3: RGM.1364022-RGM.1364024; A4-A5 = NMR993000184669); B. Intact (B1: RGM.1364025) and broken (B2: NMR993000184669) chondrophores.

from the Pacific to the Atlantic Ocean and subsequently reached the coasts of North West Europe (Kohn & Ray, 2008). The youngest Pleistocene occurrence of *M. arenaria* in the North Sea Basin is in the sediments of the Weybourne Crag in East Anglia (United Kingdom), dated to 2.1-2.2 Ma (Preece *et al.*, 2020). The oldest confirmed remnants of *O. rosmarus* from the North Sea Basin are dated at c. 50 Ka (Post, 2005). So, *M. arenaria* had been extinct for more than 2 Ma when the first *O. rosmarus* arrived in the North Sea. *Mya arenaria* returned however in the North Sea Basin in the 13th century, probably reintroduced by Vikings from the West coast of America (Petersen *et al.*, 1992; Essink & Oost, 2017). Consequently, *Odobenus rosmarus* can be excluded as a possible predator responsible for the damage to the *Mya* shells.

From the end of the early Pliocene into the early Pleistocene, the walrus *Ontocetus emmonsii* Leidy, 1859, lived in the North Sea (Wijnker *et al.*, 2008; Bakker & Post, 2020). A large quantity of fossil remains of this Plio-Pleistocene walrus has been recovered by the 'Kor en Bot' expeditions. Most of the fossils of *O. emmonsii* were fished at the Domburg–Oosterhoofd site (Fig. 2), but substantial remains of *O. emmonsii* were also recovered from the same locality as the fossil *Mya*'s, the Flauwers Pit I (Scager, 2015; Scager *et al.*, 2017).

Were *Mya arenaria* and *Ontocetus emmonsii* part of the same fauna – at some point in time?

In Flauwers Pit I the upper parts of the Maassluis Formation are exposed. This is the only possible source of the fossils of *M. arenaria*: the excellent conservation of the

shells excludes reworking. Drees (1986) indicated that there is no reason to assume that the marine fossils from the Eastern Scheldt estuary would originate from other strata than the Maassluis and Oosterhout formations. As indicated previously, at the Flauwers Pit I locality the Oosterhout Formation is not exposed, so this formation cannot be the source of the fossils. Fossils of *Ontocetus emmonsii* are only expected in marine sediments, and the species was already extinct in western Europe before or near the end of the Baventian (Bakker & Post, 2020), a regional (British) substage of the Gelasian, which is of a similar age as the Maassluis Formation. Therefore, it is most likely that the Maassluis Formation is also the source of fossils of *Ontocetus*.

The absolute age of the Maassluis Formation in the Mori-aanshoofd borehole is estimated at 2.25 - 2.35 Ma based on the vole fauna and the absence of the younger 'Concurrent range zone' of *Macoma balthica* and *Mya arenaria* (Mayhew *et al.*, 2014; Preece *et al.*, 2020). The youngest absolute age of the Maassluis Formation almost coincides with the youngest in situ finds of *Ontocetus* in Western Europe, i.e. in the early Pleistocene deposits of Easton Bavents (Bakker & Post, 2020). According to Preece *et al.* (2020) the Baventian is considered to be a cold stage pre-dating the 'Weybourne Crag' and thus older than 2.1 Ma. The fossils of *M. arenaria* and of *O. emmonsii* from Flauwers Pit I are therefore estimated between 2.25 Ma and 2.35 Ma old (Fig. 5).

Deméré *et al.* (2003) noted the coincidence of the migration of Pacific molluscs and *Ontocetus* to the Atlantic region. *Mya arenaria* is one of the molluscs that during the Pliocene migrated from the Pacific to the Atlantic Ocean (Vermeij, 1989). In the North Sea basin the earliest oc-

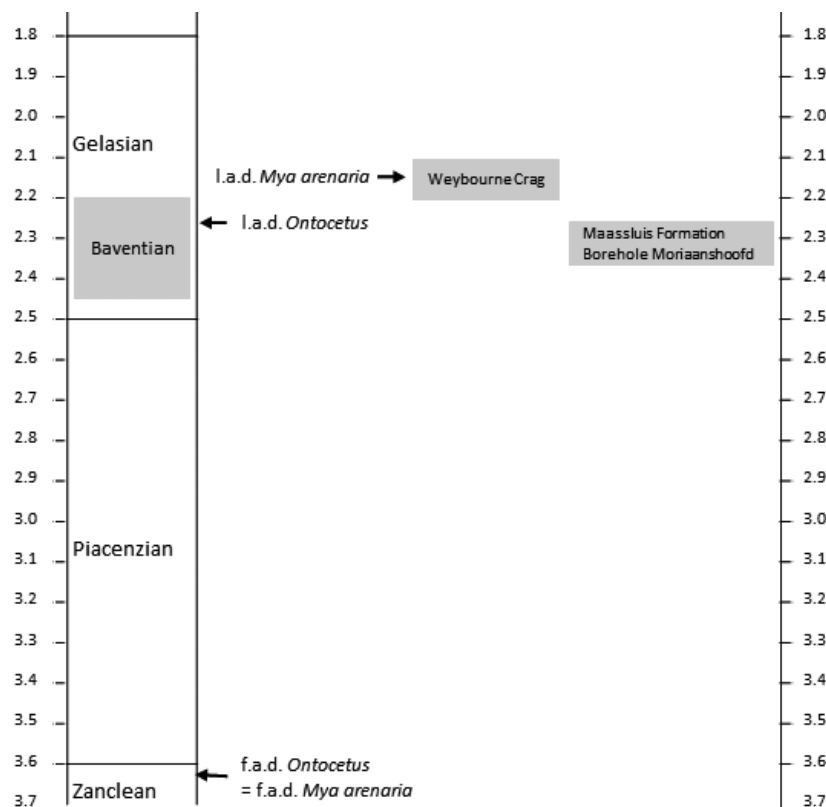


Figure 5. Geology and stratigraphy related to the first appearance dates (f.a.d.) and last appearance dates (l.a.d.) of *Mya arenaria* and *Ontocetus emmonsii*.

currence of *Ontocetus* has been demonstrated at Langenboom (Brabant, The Netherlands), where material has been found in a deposit of early Pliocene (Zanclean > 3.6 Ma) age (Wijnker *et al.*, 2008). Although at Langenboom *Ontocetus* and *M. arenaria* have not been found in layers of the same age, *M. arenaria* has been found at nearby Balgoy in sediments with an age that corresponds to the earliest occurrence of *Ontocetus* at Langenboom (Peters & Wesselingh, 2009). The earliest occurrences of *Ontocetus* and *M. arenaria* in the North Sea therefore coincide.

Was *Mya arenaria* on the menu of *Ontocetus emmonsi*?

The damaged *Mya* shells collected from the 'Kor en Bot' expeditions, combined with the contemporaneous occurrence of *Ontocetus* and *M. arenaria*, make way for the hypothesis that *M. arenaria* was on the menu of *O. emmonsi*. Could *Ontocetus* have preyed on *M. arenaria* in the same way as *Odobenus* does on *M. truncata*? Based on the dental characteristics and the morphology of the jaws of *Ontocetus* (especially the coronoid process), Post (2004) noted that the *Ontocetus* dentary allowed some form of biting or chewing (at least to a higher extent than the suction feeder *Odobenus*). This suggests that *Ontocetus* was a more opportunistic predator, less specialised than *Odobenus*.

The extant walrus *Odobenus* searches for *M. truncata* in the seabed, flushes them out of the sediment with a jet of water, then takes the shellfish between its lips, draws a vacuum in the oral cavity with its tongue, and sucks the meat out of the shell. The empty shells remain on the seabed (Adam & Berta, 2002). Vibe (1950) made the observation that the discarded empty bivalve shells were always intact and connected.

Kastelein & Mosterd (1989), associated with the dolphinarium at Harderwijk in The Netherlands, made detailed observations on the feeding habits of the walrus in captivity, using *M. arenaria* as food. Piet Mosterd (pers. comm.; mail 14 October 2013) states that the walruses cracked the shells of *M. arenaria* by crushing them against the bottom of the basin, or (if cracking was not achieved) they only ate the foot. This suggests that *Odobenus* is unable to suck the animal out of the *Mya arenaria* shell as it does with *Mya truncata*.

The dentition of *Odobenus* differs from *Ontocetus* in the absence of upper incisors I1 and I2, the absence of all lower incisors, the reduction of the lower canine, and by less, larger and more rounded post canines of the upper and lower jaw (Fig. 6). Adam & Berta (2002) state that the lack of incisors likely facilitates the emptying of molluscs within Pinnipedimorpha. The incisors of *O. emmonsi* are quite large, peglike and protrude well beyond the canines (Fig. 7)

As stated before, almost all *M. arenaria* shells that have been fished are damaged to some degree. In addition, some of the *Mya* shells have a conspicuous inwardly curved outline (Fig. 4 A). One hypothesis to explain this typical damage is that *Ontocetus* used its incisors to crack the shells in order to get to the soft tissues. The inward bending damage to the *Mya* shells could then be the results of bite

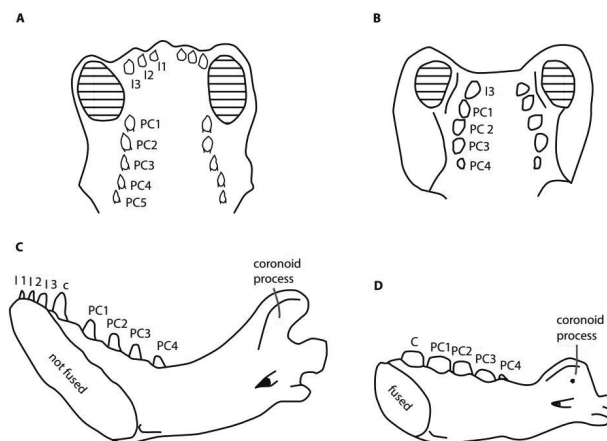


Figure 6. Schematic comparison dentition *Ontocetus* and *Odobenus*. A = *Ontocetus* upper jaw, B = *Odobenus* upper jaw, C = *Ontocetus* mandibula, D = *Odobenus* mandibula. I = incisor, PC = postcanine.

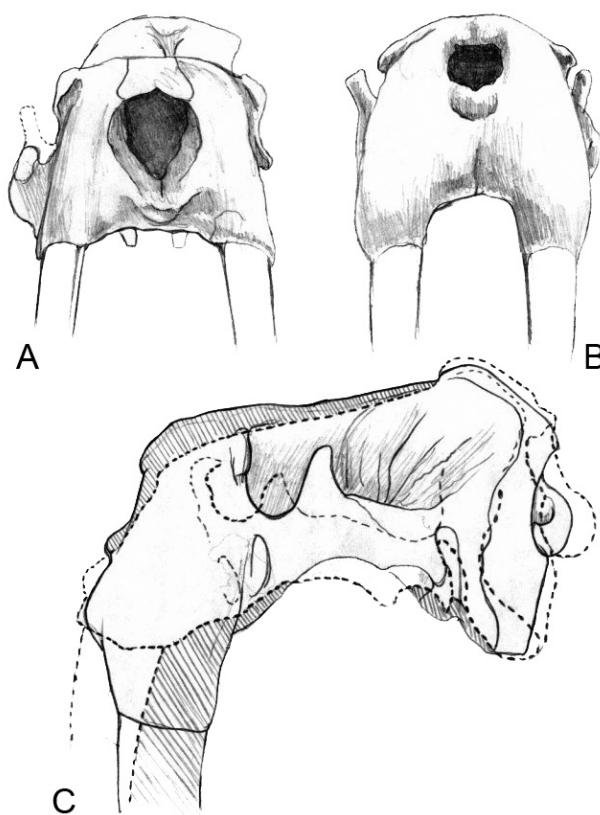


Figure 7. Crania of *Ontocetus* and *Odobenus*. A = *Ontocetus*, anterior view, B = *Odobenus*, anterior view, C = comparison *Ontocetus* and *Odobenus* in lateral view (hatched figure = *Odobenus*). Illustration A. Kennis & A. Kennis.

marks. *Mya* is a filter feeder that lives in the seabed with the anterior side down at depths of about 20 cm (Zwarts & Wanink, 1989). Its posterior end faces the bottom surface and the large and fleshy siphon is the connection to seawater with food. Whereas the shell of *M. truncata* gapes strongly at the back and the posterior edges are straight,

the posterior edges of *M. arenaria* form two closely located sharp points (Fig. 8) The sucking feeding mode which *Odobenus* uses with *M. truncata* is therefore not suitable for *M. arenaria*. Moreover, the sandy and muddy soils in which *Mya* lives offer little support for crushing the shells (as living walrus were observed to do in the basin of the dolphinarium at Harderwijk). Cracking the shells with the incisors and/or mandibular canines therefore seems a good alternative to harvest the meat of *M. arenaria*.

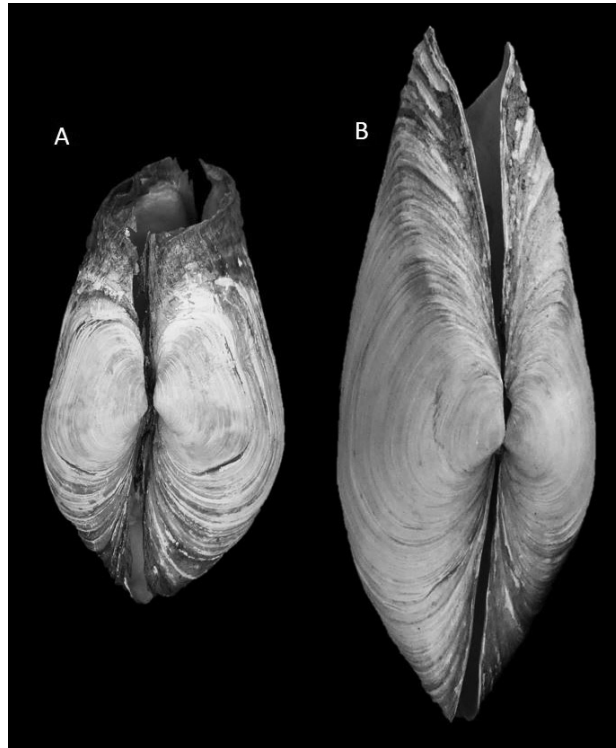


Figure 8. Comparison of present-day specimens of *Mya truncata* and *M. arenaria* in life position: A. *Mya truncata* showing the truncate posterior end and oval gape, Hammen, Eastern Scheldt, Zeeland, Netherlands, 7/9/2013 (Kor en Bot), coll. P.W. Moerdijk; B. *Mya arenaria* showing the sharp, pointed posterior of the shell, Kattendijke ("Gebroken Dijk"), Zeeland, Netherlands, 7/6/2003, coll. P.W. Moerdijk

Conclusions

- The fossils of *Ontocetus emmonsii* and *Mya arenaria* fished up at Flauwers Pit I by the 'Kor and Bot' expeditions originate from (part of) the Maassluis Formation, are of the same age, and must be considered to belong to one and the same contemporaneous marine fauna.
- *M. arenaria* was most probably part of the diet of *O. emmonsii*.

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