Pliocene to Quaternary sinistral *Neptunea* species (Mollusca, Gastropoda, Buccinidae) from the NE Atlantic

Marcel Vervoenen[1], Freddy van Nieulande[2], Koen Fraussen[3], Frank P. Wesselingh[4, 6] & Ronald Pouwer[5]

[1] *Beekstraat 86A, B-9300 Aalst, Belgium*
[2] *Scheldepoortstraat 56, NL-4339 BN Nieuw- en Sint Joosland, The Netherlands; frvannieul@zeelandnet.nl*
[3] *Leuvensestraat 25, B-3200 Aarschot, Belgium; koenfraussen@skynet.be*
[4] *Naturalis Biodiversity Center, P.O. Box 9517, NL-2300 RA Leiden, The Netherlands; frank.wesselingh@naturalis.nl*
[5] *Naturalis Biodiversity Center, P.O. Box 9517, NL-2300 RA Leiden, The Netherlands; ronald.pouwer@naturalis.nl*
[6] *corresponding author.*

Received 29 April 2014, revised version accepted 23 May 2014

The taxonomy of sinistral *Neptunea* species from the Pliocene of the North Sea Basin and the Quaternary of NW Europe is investigated. All sinistral forms are considered to be part of a single clade. Morphological varieties from the Pliocene successions of the southern North Sea Basin are documented. A remarkable increase in the number of varieties occurs in a short stratigraphic interval in the latest Piacenzian (Lillo Formation, Kruisschans Member, Antwerp area, Belgium). The Pliocene morphs are for the moment grouped as forms within *Neptunea angulata* Harmer, 1914 (*non N. angulata* Wood, 1848). Several of the morphs appear to lack intermediate forms and thus the presence of sibling species may be demonstrated when more material will become available. During the Pleistocene, the sinistral species *N. inversa* Harmer, 1918, occurred in NW Europe. South of the North Sea Basin the last occurrence of the species is at least the Middle Pleistocene MIS 13. The extant *N. contraria* (Linné, 1771) (Bay of Biscay-Morocco) appeared in the Early Pleistocene of the Mediterranean Basin. We designate lectotypes for *Neptunea angulata* Harmer, 1914 and *N. inversa* Harmer, 1918.

Key words: Gastropoda, *Neptunea*, phylogeny, taxonomy, new forma, lectotype designation, Neogene, Pleistocene.

Introduction

The taxonomy of sinistral (left-coiled) *Neptunea* species in the Neogene and Quaternary of Europe has been a matter of debate (Nelson & Pain, 1986; Moerdijk & Rijken, 2002; Marquet, 1998). A single sinistral species, *N. contraria* (Linné, 1771), nowadays lives in the Lusitanian biogeographic province (from the Bay of Biscay to Morocco). Its relation to Pliocene species from the North Sea Basin is unclear and is of importance in order to establish the taxonomy of the latter. In this paper we document stratigraphic forms from Pliocene and Quaternary deposits in the North Sea Basin. After the first occurrence in the early Pliocene, sinistral forms developed a wide range of morphological variation near the end of the late Pliocene that were replaced by a single form in the Early Pleistocene. Aim of the current paper is to document the morphological variation of sinistral *Neptunea* in Pliocene to Quaternary material of the North Sea Basin and beyond, to establish the taxonomy and to discuss phylogenetic relationships.

Material and methods

This study is based on material mainly collected over the past four decades by the first author. Additionally, we studied material collected by the other authors and museum specimens as well as published accounts. Localities are shown in Fig. 1.

For the Pliocene succession of the Antwerp area the stratigraphic subdivision of Vandenberghe *et al*. (1998) and De Schepper *et al*. (2009) is followed. Age estimates of these successions and of the Crag deposits of East Anglia follow De Schepper *et al*. (2008), based on dinoflagellate data (Fig. 2), but age estimates in that paper based on the so-called 'Haq' curve are not considered (see comprehensive critique in Miall, 1997).

An additional unit (the Brown Clay Unit) is introduced for the standard Antwerp Pliocene stratigraphic succession. Specimens of *Neptunea* were found in the so-called 'basal shell bed' of the Oorderen Member showing a particular sediment infill and coloration of indurated brown-grey clay (becoming brown when oxidized) quite different from the usual Oorderen Member sediment. One particular specimen, when cleaned by the first

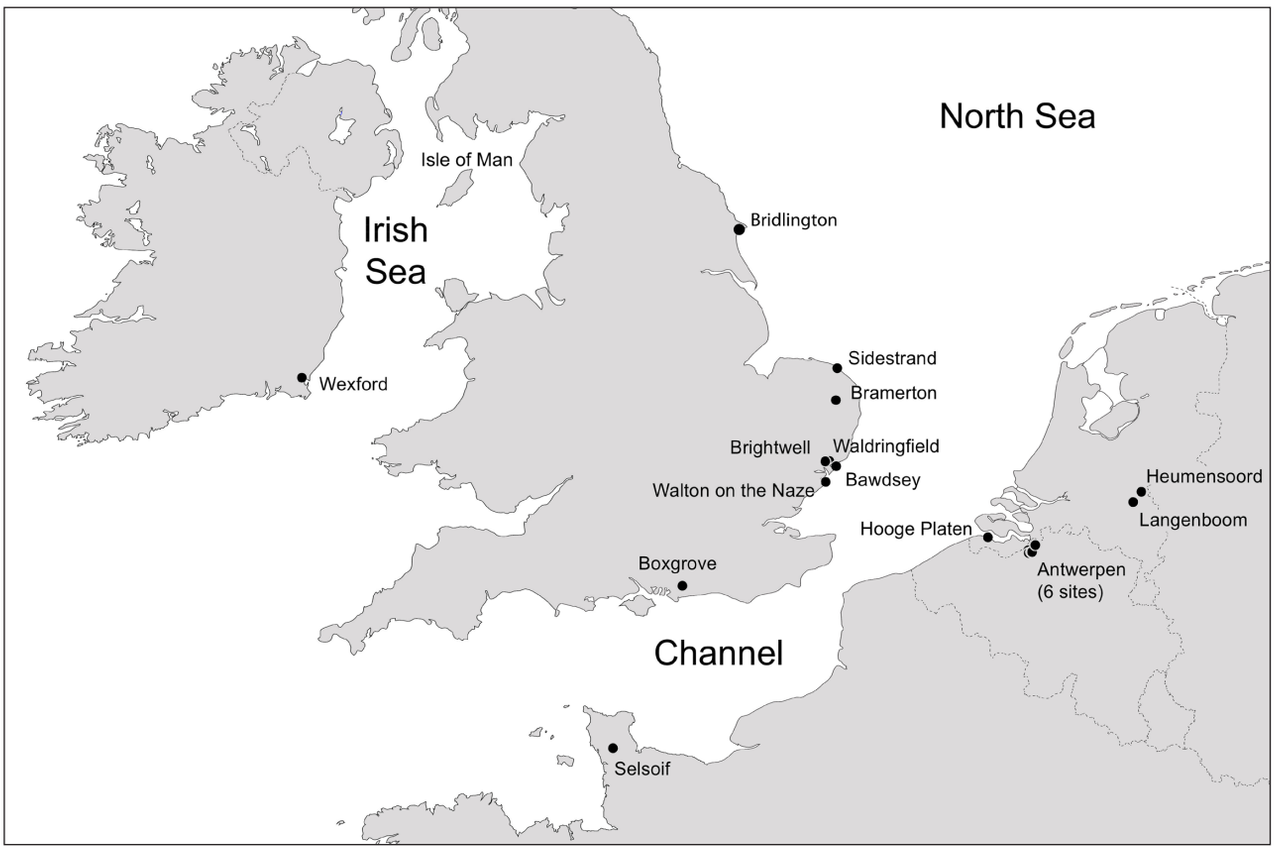


Figure 1. Localities mentioned in this paper.

author, demonstrated a stratigraphic succession *in situ*. The outer layer of the fill consisted of light grey quartz arenite with shell fragments as typical for the Oorderen Member. Below, a thin layer of yellow calcarenite typical for the Luchtbal Member was observed. The basal fill of the specimen, however, consisted of indurated brown clay. We consider specimens with such brown clay fill to be reworked from strata supposed to have been present between the early Pliocene Kattendijk Formation (that lacks sinistral *Neptunea*) and the early late Pliocene Luchtbal Member. Their age may correspond to the so-called 'Broechem fauna' (Marquet, 1980; van Bakel *et al*., 2003) that is known from phosphatic nodules found east of Antwerp. Another early record of sinistral *Neptunea* is from the lower part (Zanclean) of the Oosterhout Formation at Langenboom, Noord-Brabant, The Netherlands (Wijnker *et al*., 2008).

Neptunea is part of a faunal assemblage of Pacific origin that migrated through the Bering Strait into the northern Atlantic Ocean from between 4.8 and 5.5 Ma onwards (Marincovich, 2002; Gladenkov *et al*., 2002, 2004). Meijer (1993) provided an Sr-based age estimate of 4.7-4.8 Ma for the first arrival of Pacific immigrants in the North Sea Basin from borehole Heumensoord (The Netherlands). Geological units and their age estimates are shown in Fig. 2.

The Oorderen en Kruisschans members of the Lillo Formation are subdivided in several intervals (Vervoenen, 1995; Marquet, 1998). The former consists of the basal shelly lag, the *Atrina* Bed, the *Cultellus* Bed and the *Tellina* Bed, and the latter consists of the lower clayey part and the upper sandy part. These intervals are separated by disconformities (pers. obs.).

Buccinids in general and *Neptunea* in particular are notorious for their large morphological variability in shell characters complicating their taxonomy (*e.g.* Golikow, 1963; Fraussen & Terryn, 2007 and references therein). A number of characters, however, appear to be particularly useful in the identification of *Neptunea* species, including spiral ornament on early teleoconch whorls and size and shape of spiral interspaces. Yet, the value of certain morphological characters for the discrimination of species remains open to debate.

Below, we first characterize the various Pliocene North Sea Basin *Neptunea* forms. Second, we discuss further sinistral *Neptunea* forms from the Quaternary of Europe. Finally we outline implications for the taxonomy of sinistral *Neptunea* species from the European Neogene and Quaternary.

We have decided to describe the Pliocene morphotypes tentatively as infrasubspecific taxa (formae), rather than subspecies, because of the absence of obvious geographical or ecological barriers. We presume that naming those morphotypes will contribute to understanding the diverse fauna and will form a platform to build further studies on eventually.

Specimens were collected in a number of localities in the Antwerp harbour area, located in the province of Oost-

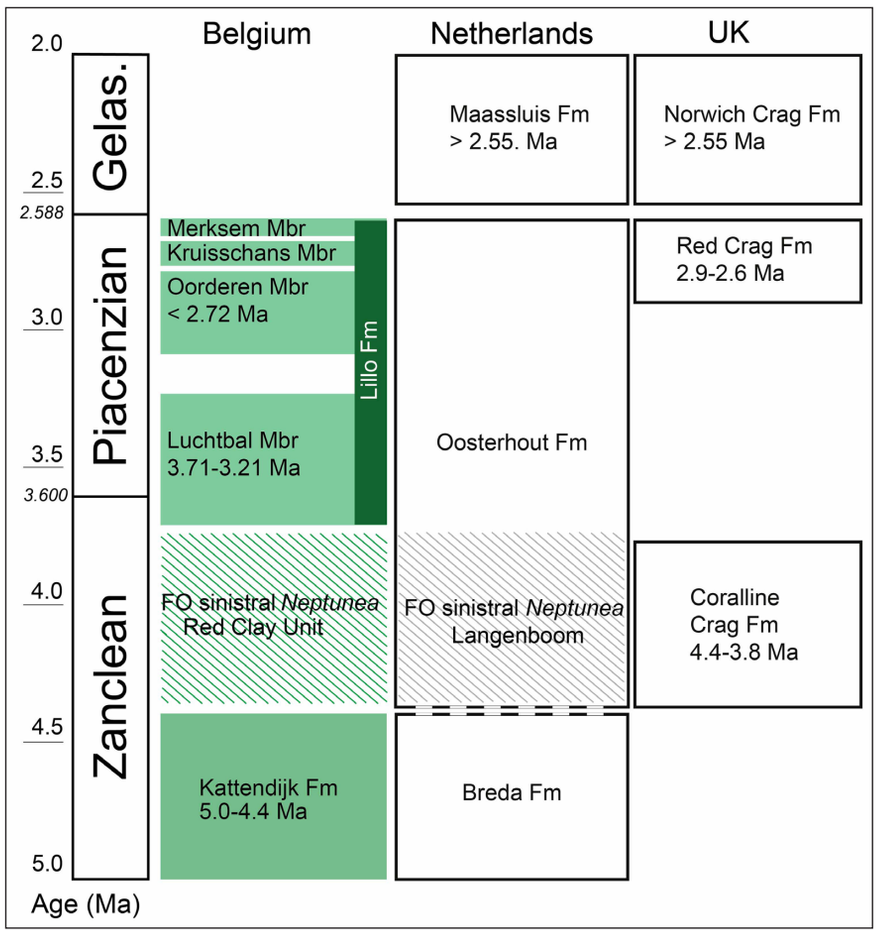


Figure 2. Approximate age for lithostratigraphical units discussed in text. Adapted mainly from dinoflagellate data presented by de Schepper et al. (2008, 2009).

Gelas.= Gelasian
Fm = Formation
FO = first occurrence datum
Mbr = Member

Vlaanderen, Belgium, unless stated otherwise. Locality details for the different 'doks' (like Verrebroekdok, Waaslanddok *etc.*), which are building sites for harbour docks, can be found in Vervoenen (1995). Samples listed below concern single specimens unless stated otherwise. Dimensions are given in mm.

Abbreviations

The following abbreviations are used: FN: Freddy van Nieulande collection (Nieuw- en Sint Joosland, The Netherlands); KF: Koen Fraussen collection (Aarschot, Belgium); KZGW: Koninklijk Zeeuwsch Genootschap der Wetenschappen collection (Middelburg, The Netherlands); MV: Marcel Vervoenen collection (Aalst, Belgium); RGM: Naturalis Biodiversity Center, fossil Mollusca collection (Leiden, The Netherlands). Material indicated with SMF and NHM will be donated to the Senckenberg Museum (Frankfurt am Main, Germany) and the Natural History Museum (London, United Kingdom), respectively.

Systematic palaeontology of Pliocene sinistral *Neptunea* from the North Sea Basin

Harmer (1914, 1918) introduced various names for species and forms. Ever since different opinions as to the attribution of the Pliocene material to the modern species *Neptunea contraria* exist. Later authors (*viz.* Nelson & Pain, 1986; Marquet, 1998) considered the Pliocene taxa to differ from the modern species especially by the nature of spiral ribs, allowing distinction.

The commonly applied name *Neptunea angulata* (Wood, 1848) for the Pliocene material, however, is not available (being a *nomen invalidum*) as it was introduced as 'a fourth name published as an addition to a trinomen' that according to article 45.5 (ICZN, 1999) automatically denotes an infrasubspecific entity. The first available name for the Pliocene species is *Neptunea contraria* var. *angulata* Harmer, 1914 (*non* Wood, 1848 = invalid name). Harmer's variety is valid under the rules of the code, even though it unfortunately is based on a specimen with unusual thick primary spirals.

Neptunea angulata Harmer, 1914

Figures 3-17

1848 *Trophon antiquum* var. *contrarium angulatum* Wood, pl. 5, fig. 1h (*nomen invalidum*).
1848 *Trophon antiquum* var. *contrarium sinistrorsum* Wood, pl. 5, fig. 1i (*nomen invalidum*).
1878 *Fusus contrarius* var. sénestre – Nyst, p. 44, pl. 1, fig. 9a.

1914 *Neptunea contraria* (Linné) Var. *typica* Harmer, p. 156 (*partim*), pl. 16, figs 1, 2.
1914 *Neptunea contraria* (Linné) Var. *sinistrorsa* Deshayes – Harmer, p. 159 (*partim*), pl. 16, fig. 3 (*non* Deshayes, *non* fig. 4).
*1914 *Neptunea contraria* (Linné) Var. *angulata* Wood, Harmer, p. 160, pl. 16, fig. 7.
1972 *Neptunea contraria* (Linné) – Strauch, pl. 3, figs 3, 4, 15 (*non* Linné).
1997 *Neptunea (Sulcosipho) angulata* (Wood, 1848) – Marquet, p. 94, pl. 7, figs 7a, b (*non* Wood = invalid name).
1998 *Neptunea (Sulcosipho) angulata* (Wood, 1848) – Marquet, p.140, figs a-d (*non* Wood = invalid name) (with extensive further synonymy).

Note – The specimen illustrated by Wood (1848, pl. 5, fig. 1h) as *Trophon antiquum* var. *contrarium angulatum* has an unusual form that appears not to fit the species *Neptunea angulata* Harmer (as interpreted herein). It is more or less smooth and has a heavy subsutural keel and shoulder. We encountered this type of morphology also in recent *Buccinum undatum* Linnaeus, 1758 from the North Sea (MV collection). The disfigurement in the modern *Buccinum* specimens is invariably linked to a severe crab predation in a juvenile stage and we suppose this to be the same for Wood's specimen.

Lectotype designation – We designate the specimen described by Harmer (1914, p. 160, pl. 16, fig. 7, housed at the Norwich Museum, United Kingdom) as *Neptunea contraria* Linné var. *angulata* from Little Oakley (Red Crag Formation) as the lectotype (Fig. 3 herein). Seven forms are recognized in the Antwerp material that are characterized below.

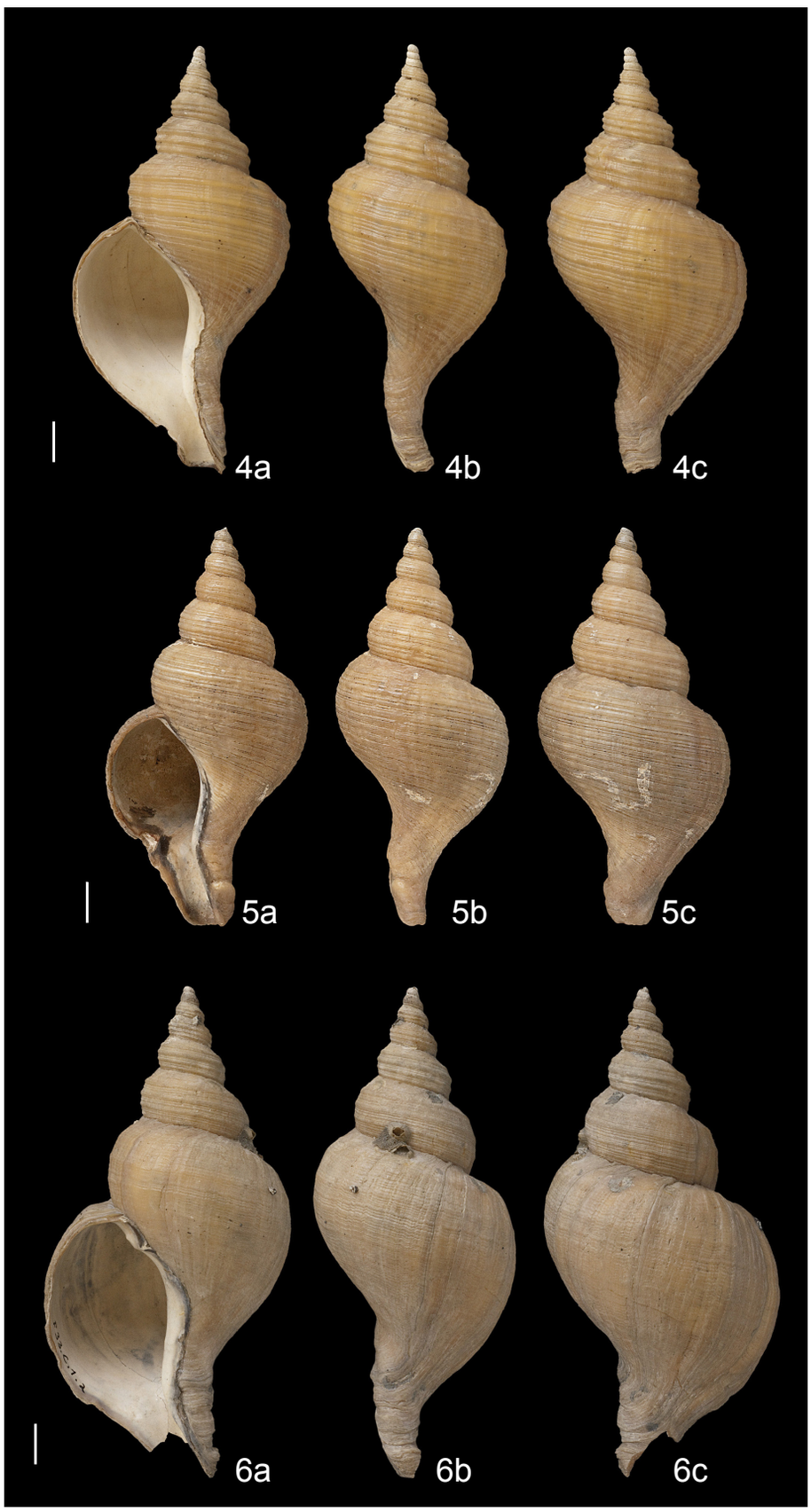
Figure 3. *Neptunea angulata* Harmer, 1914 (*non* Wood, 1848) as illustrated in Harmer (1914, pl. 16, fig. 7). Lectotype here designated. Little Oakley (UK), Red Crag Formation. H = 54.2 mm.

***Neptunea angulata* Harmer, 1914 forma *kalloensis* new forma**
Figures 4-8

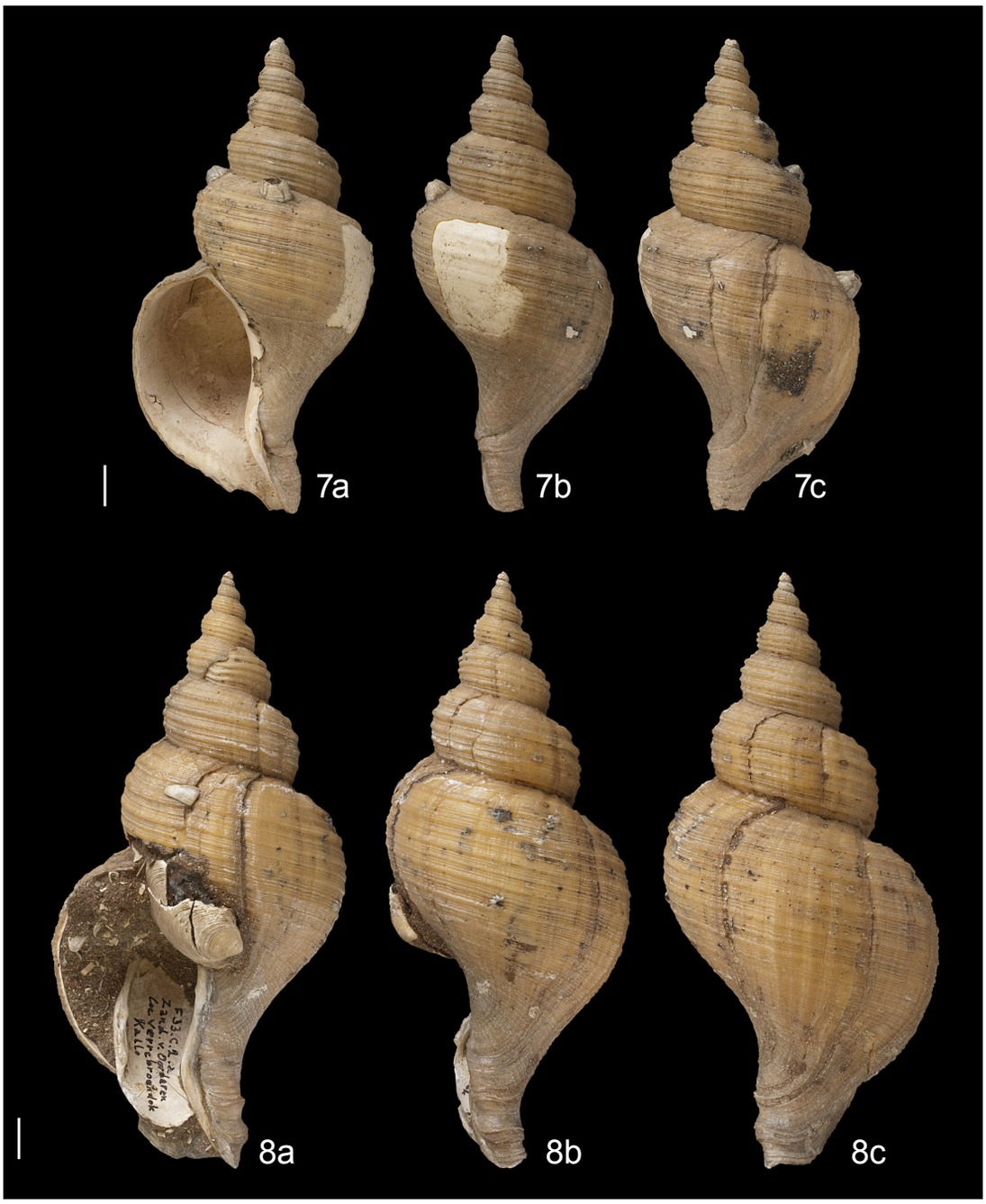
1914 *Neptunea contraria* (Linné) Var. *angulata* Wood – Harmer, p. 160, pl. 16, fig. 7 (*non* Wood, 1848 = invalid name).
1998 *Neptunea (Sulcosipho) angulata* (Wood, 1848) – Marquet, p.140, figs a-d (*non* Wood, 1848 = invalid name).

Description – Slender shell, 2nd to 4th teleoconch whorls with three prominent spiral ribs squarish in cross-section; subsutural depression slightly concave. The chalkish white protoconch (2-2.5 whorls) is blunt and smooth, slightly protruding. On the first teleoconch whorl there are 4-5 spiral ribs of equal strength, although the lower spiral rib may be slightly thinner and lower. On the second teleoconch whorl the upper spiral rib weakens and the second to fourth spiral become dominant. In cross sections also these three ribs are somewhat squarish. The lower spiral decreases further in strength and from the fourth teleoconch whorl onwards becomes located at or below the suture. Very fine spiral threads develop on the subsutural ramp. Between the spiral ribs a single secondary spiral thread develops on the third teleoconch whorl and further fine secondary and tertiary spiral threads occur on the fourth and fifth teleoconch whorl. In rare occasions the middle spiral rib disappears leaving the shell with two very robust primary ribs and a more angular whorl profile. On the sixth teleoconch whorl, only present in very large specimens (H >130 mm), almost all spiral ribs and threads smoothen and the ornamental elements become almost equal with numerous very fine spiral threads. From the first to fourth teleoconch whorl the ornamentation shows little variation, but on later teleoconch whorls the ribbing becomes very variable. Maximum shell height *c.*150 mm.

Material examined – **Verrebroekdok, Oorderen Member, basal shell bed.** Given the yellowish sediment infill the specimens must have been derived from the Luchtbal Member: RGM 794 414 (ex MV F33D1a) (leg. MV, 1990); RGM 794 415 (ex MV F33D1b); MV F33D1e; MV F33D1d (SMF). **Waaslanddok, Oorderen Member, basal shell bed:** RGM 794 416 (ex MV F33C4a) (leg. MV, 1983); MV F33C4b; MV F33C4d (SMF); MV F1738 (SMF). **Vrasenedok, Oorderen Member, basal shell bed.** Given the brown indurated clay infill, the specimens must have been derived from an eroded clay interval between the Kattendijk Formation and the Luchtbal Member: RGM 794 388 (Fig. 6) (ex MV F33C1a) (leg. MV, 1985); RGM 794 417 (ex MV F33Cb). **Verrebroekdok, Oorderen Member, lower sandy part:** RGM 794 386 (Fig. 4) (ex MV F33C2) (leg. MV, 1990-1998). **Verrebroekdok, Oorderen Member, *Atrina* Bed:** RGM 794 385 (Fig. 8) (ex MV F33C2a) (leg. MV, 1990-1998); RGM 794 418 (ex MV F33C2b) (leg. MV 1990 MV F33C2c (NHM); MV F33C7a (SMF); KF 5581 (ex MV F33A). **Vrasenedok, Oorderen Member, *Atrina* Bed:** RGM 794 401 (ex MV



Figures 4-6. *Neptunea angulata* Harmer, 1914 forma *kalloensis* new forma. **4.** Verrebroekdok, OordenMember, lower sandy part. RGM 794 386. H = 105.5 mm. Scale bar is 1 cm. **5.** Verrebroekdok, OordenMember, *Tellina* Bed. RGM 794 392. H = 97.3 mm. Scale bar is 1 cm. **6.** Vrasenedok, Oorderen Member, basal shell bed, from an eroded clay interval between Kattendijk Formation and Luchtbal Member. RGM 794 388. H = 119.0 mm. Scale bar is 1 cm.



Figures 7-8. *Neptunea angulata* Harmer, 1914 forma *kalloensis* new forma. **7.** Verrebroekdok, Kruisschans Member, lower clayey part. RGM 794 387. H = 115.7 mm. Scale bar is 1 cm. **8.** Verrebroekdok, Oorderen Member, *Atrina* Bed. RGM 794 385. H = 146.0 mm. Scale bar is 1 cm.

F33C1a) (leg. MV, 1990-1998). **Zeesluis en tunnelput, Beveren Tunnel, Oorderen Member, *Tellina* Bed:** RGM 794 419 (ex MV F33Ga) (leg. MV, 1972). **Verrebroekdok, Oorderen Member, *Tellina* Bed:** RGM 794 420 (ex MV F33Da) (leg. MV, 1986); RGM 794 392 (Fig. 5) (ex MV F33Db) (leg. MV, 1987) ; MV F33D. **Verrebroekdok, Kruisschans Member, lower clayey part:** RGM 794 387 (Fig. 7) (ex MV F1739C) (leg. MV 1987-1988).

Stratigraphical distribution – Lower part of Oosterhout Formation (Zanclean) at Langenboom, Noord-Brabant, The Netherlands (Wijnker *et al*., 2008); Lillo Formation (Luchtbal, Oorderen and Kruisschans members: Piacenzian) and reworked from eroded 'Brown Clay Unit' in the basal shell bed of the Oorderen Member in the Antwerp area, Belgium; Red Crag Formation (late Piacenzian) of East Anglia, UK. In the Antwerp region, this form dominates the sinistral *Neptunea* fauna of the Luchtbal Member and the lower part of the Oorderen Member (basal bed and *Atrina* Bed). It is rare in the upper Oorderen Member (*Tellina* Bed) and occurs very rarely in the overlying Kruisschans Member.

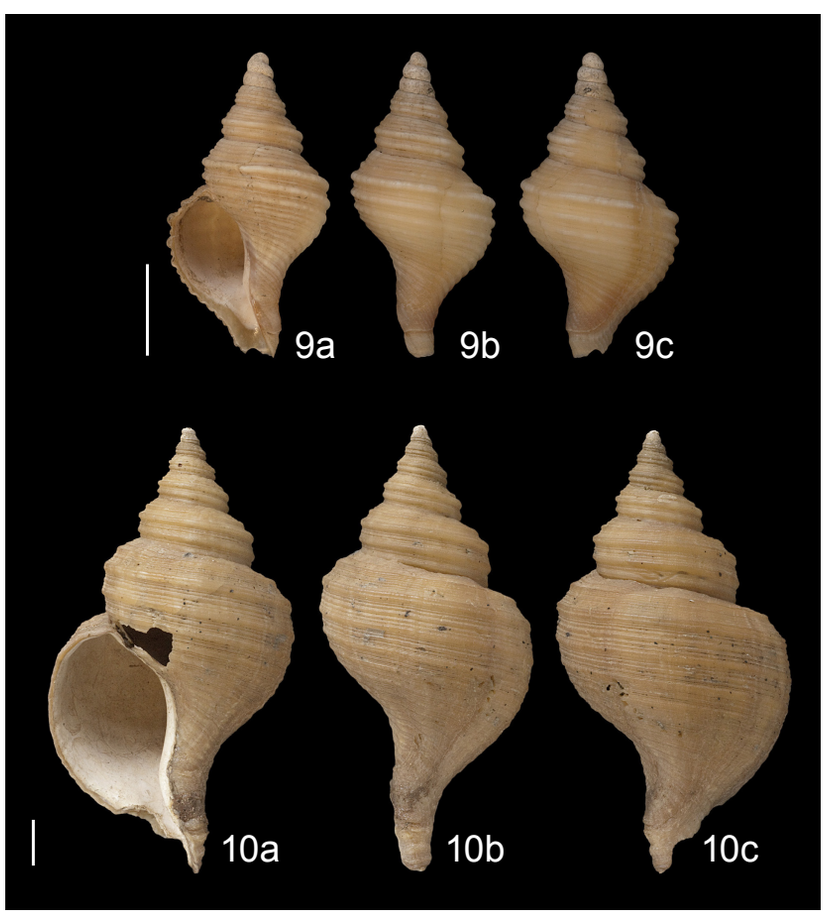
Discussion – This new form is named after the village of Kallo in the Antwerp harbour area, in which vicinity most material studied herein has been excavated.
Given its blunt protoconch we attribute a specimen illustrated by Harmer (1915, pl. 37, fig. 3) as *Neptunea contraria* Linné from the Zanclean Coralline Crag Formation of Boyton (East Anglia) to a sinistral *Liomesus dalei* (Sowerby, 1825).

***Neptunea angulata* Harmer, 1914 forma *strauchi* new forma**
Figures 9, 10

1872 *Trophon antiquus* var. *carinatus contrarius* Wood, p. 19, pl. 1, fig.10a (*nomen invalidum*).

Description – Slender shell with on early teleoconch whorls two very prominent spiral ribs with a squarish cross-section that give the shell in these early stages a distinctly keeled outline. The protoconch consists of 2.25 whorls. Two prominent spirals are situated on the basal half and two very thin spirals on the middle part of the first teleoconch whorl with a distinct straight subsutural ramp above. The finer upper ribs split into secondary spiral threads from the second teleoconch whorl onwards. On later teleoconch whorls finer secondary threads develop between the two lower primary ribs. Maximum shell height *c*. 96 mm.

Material examined – **Vrasenedok, Oorderen Member, *Tellina* Bed, clay interval:** RGM 794 402 (Fig. 9) (ex MV F33C3a) (leg. MV, 1985-1986). **Vrasenedok, *ex situ***, judged from sediment infill originating from Oorderen Member, *Atrina* Bed: RGM 794 391 (Fig. 10) (ex MV F33C1) (leg. MV 1985-1987). **Verrebroekdok, Oorderen Member, *Atrina* Bed:** MV F33C2d (NHM), leg. MV 1987; MV F33C2e (SMF). **Waaslanddok, *ex situ***, judged from sediment infill originating from Oorderen Member, *Atrina* Bed: RGM 794 421 (ex MV F33K: 3 specimens) (leg. MV 1983-1984). **Verrebroekdok, Oorderen Member, *Atrina* Bed:** MV F33C2e, leg. MV 1987-1998; MV F33C2d. **Vrasenedok, Oorderen Member, *Tellina* Bed:** KF 5579 (ex MV F33C3) (leg. MV 1985-1986). **Verrebroekdok, Kruisschans Member, lower clayey part:** RGM 794 422 (ex MV 1739Ma) (leg. MV, 1987-1998); RGM 794 423 (ex MV 1739Mb); RGM 794 424 (ex MV 1739Mc: 2 juveniles); RGM 794 425 (ex MV 1739Md); RGM 794 426 (ex MV 1739Me). **Verrebroekdok, Kruisschans Member, upper sandy**



Figures 9-10. *Neptunea angulata* Harmer, 1914 forma *strauchi* new forma. **9.** Vrasenedok, Oorderen Member, *Tellina* Bed, clay interval. RGM 794 402. H = 32.8 mm. Scale bar is 1 cm. **10.** Vrasenedok, *ex situ*, judged from sediment infill originating from Oorderen Member, *Atrina* Bed. RGM 794 391. H = 95.7 mm. Scale bar is 1 cm.

part: RGM 794 427 (ex MV 1739Da) (leg. MV, 1987-1998); RGM 794 428 (ex MV 1739Db).

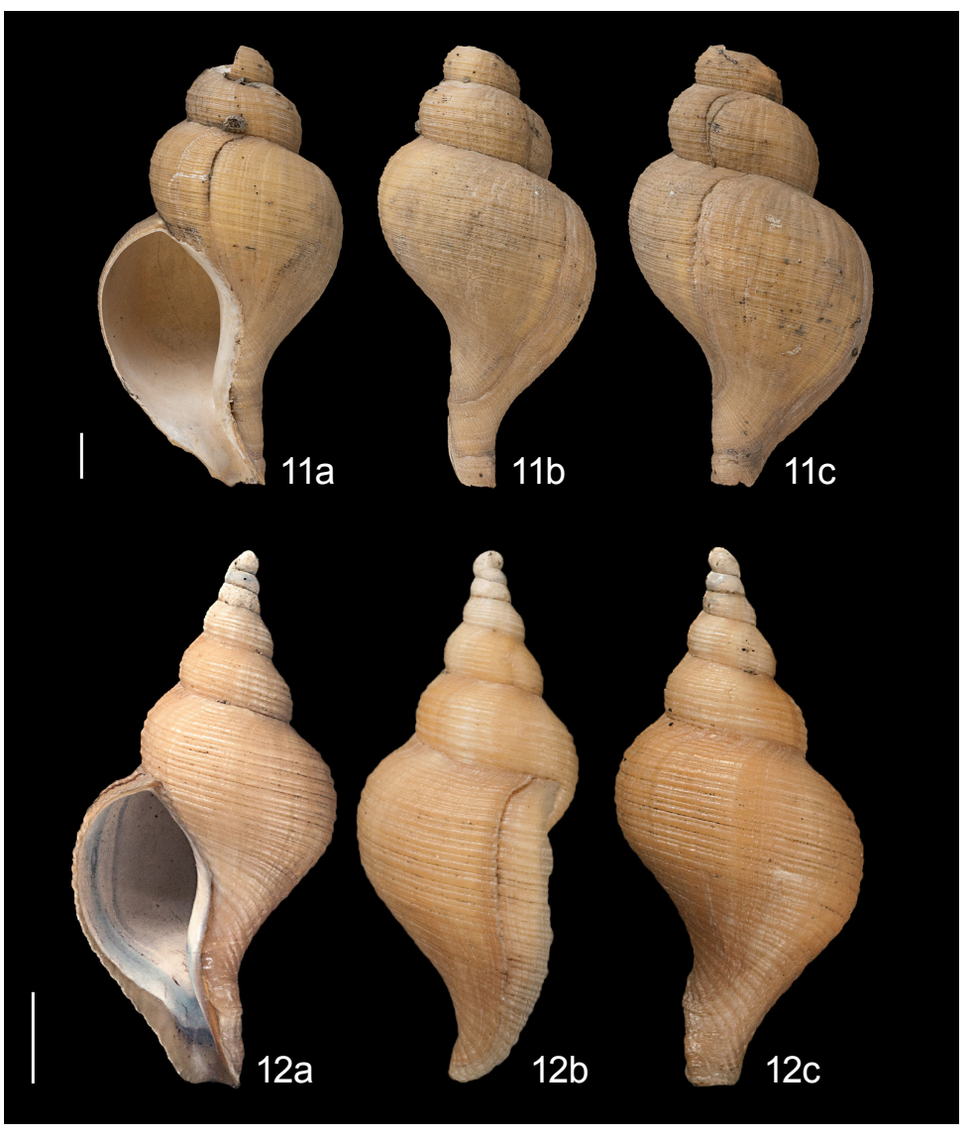
Stratigraphical distribution – This new form is very rare in the *Atrina* and *Tellina* beds of the Oorderen Member (Piacenzian) and in the Kruisschans Member (late Piacenzian), Antwerp area, Belgium.

Discussion – This form is readily differentiated from other sinistral *Neptunea* forms by the presence of the two very prominent spiral ribs on the lower half of early teleoconch whorls that in conjunction with the straight subsutural ramp give it a distinctly keeled outline.
Sinistral *Neptunea angulata* forma *strauchi* closely resembles dextral *N. lyratodespecta lyratodespecta* Strauch, 1972, from the Pliocene of Tjörnes, North Iceland.
A Pleistocene specimen from Bridlington, Yorkshire that resembles forma *strauchi* is discussed below under *N. inversa*.
This new form is named in honor of Friedrich Strauch (Havixbeck, Germany) for his contributions to paleontology and especially to the knowledge of fossil *Neptunea*.

***Neptunea angulata* Harmer, 1914 forma *contrariaeformis* new forma**
Figures 11, 12

1914 *Neptunea contraria* (Linné) Var. *sinistrorsa* Deshayes – Harmer, p. 159 (*partim*), pl. 16, fig. 3 [*non* Deshayes; *non* fig.4 = *Neptunea contraria* (Linné, 1771)].

Description – Thin-shelled form with relatively regularly convex whorl profile and rather deep suture. On the first



Figures 11-12. *Neptunea angulata* Harmer, 1914 forma *contrariaeformis* new forma. **11.** Verrebroekdok, Kruisschans Member, upper sandy part. RGM 794 393. H = 96.3 mm. Scale bar is 1 cm. **12.** Waaslanddok, *ex situ*, judged from sediment infill originating from Kruisschans Member, upper sandy part. RGM 794 203. H = 56.1 mm. Scale bar is 1 cm.

1.5 teleoconch whorls are five primary spirals, where after secondary ones develop in between. Spiral ribs are slightly flattened and broad, interspaces are relatively narrow, almost groove-like. Adult specimens are all broken, but probably maximum shell height is *c*. 110 mm.

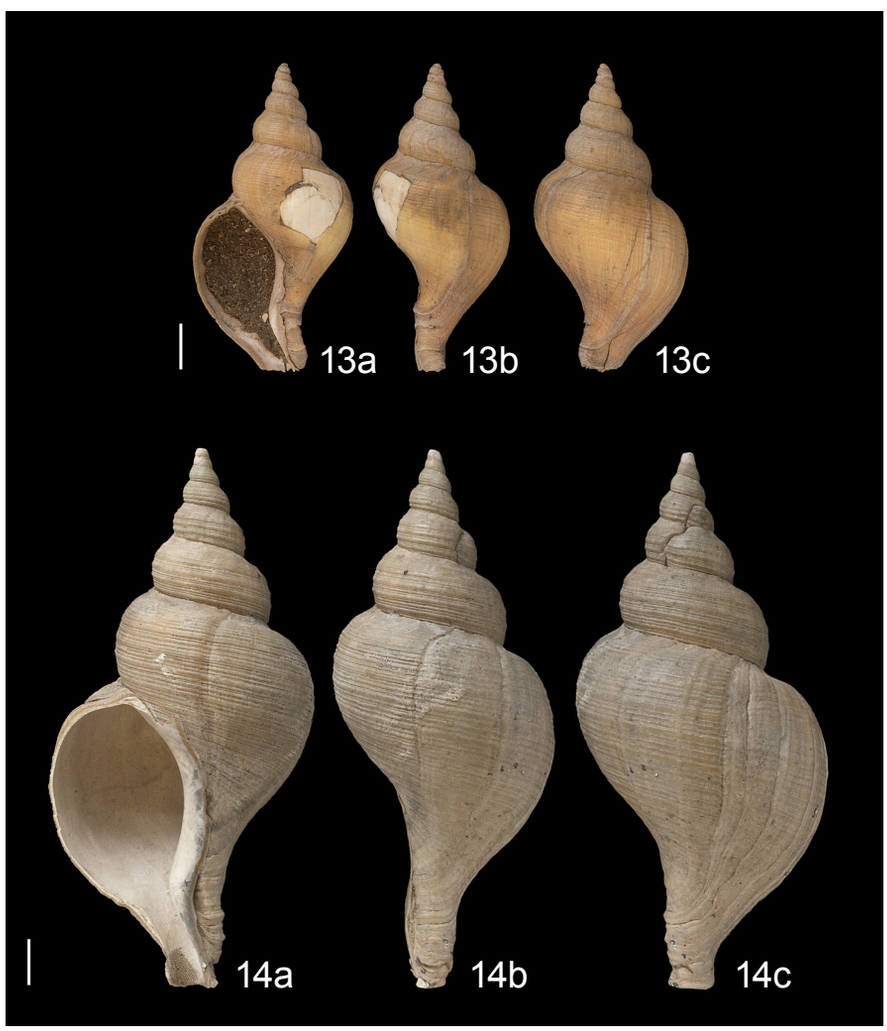
Material examined – **Verrebroekdok, Kruisschans Member, lower clayey part:** RGM 794 429 (ex MV F1739C: 2 specimens), (leg. MV, 1987-1998); same sample (1 SMF, 1 NHM). **Waaslanddok, *ex situ***, judged from sediment infill originating from Kruisschans Member, upper sandy part: RGM 794 203 (Fig. 12) (ex MV F1739I2) (leg. MV, 1983-1984); MV F1739C; MV F1739C. **Verrebroekdok, Kruisschans Member, upper sandy part:** RGM 794 393 (Fig. 11) (ex MV F1739Da) (leg. MV, 1987-1998). **Verrebroekdok, *ex situ***, judged from sediment infill originating from Kruisschans Member, upper sandy part: RGM 794 430 (ex MV F1739C3) (leg. MV, 1987). **Vrasenedok, *ex situ***, judged from sediment infill originating from Kruisschans Member: RGM 794 431 (ex MV F1739K) (leg. MV 1986).

Stratigraphical distribution – Kruisschans Member (late Piacenzian), Antwerp area, Belgium.

Discussion – This form has a thin-walled shell, a convex whorl profile and five primary spiral ribs on the initial teleoconch whorls. This combination of characters is not found in other Pliocene forms from the North Sea Basin. It resembles most the recent species *Neptunea contraria* (Linné, 1771) (see below), but the latter has more regular ribbing with interspaces as grooves and secondary ribs forming on the bodywhorl.
This form is named after the recent *N. contraria* for the similarities in shell ornamentation.

***Neptunea angulata* Harmer, 1914 forma *elongata* (Wood, 1848)**
Figures 13-15

*1848 *Trophon antiquum* var. *contrarium elongatum* Wood, p. 44, pl. 5, fig. 1j.



Figures 13-14. *Neptunea angulata* Harmer, 1914 forma *elongata* (Wood, 1848). **13.** Verrebroekdok, Kruisschans Member, lower clayey part. RGM 794 403. H = 65.2 mm. Scale bar is 1 cm. **14.** Waaslanddok, *ex situ*, judged from sediment infill originating from Kruisschans Member, lower clayey part. RGM 794 389. H = 110.3 mm. Scale bar is 1 cm.

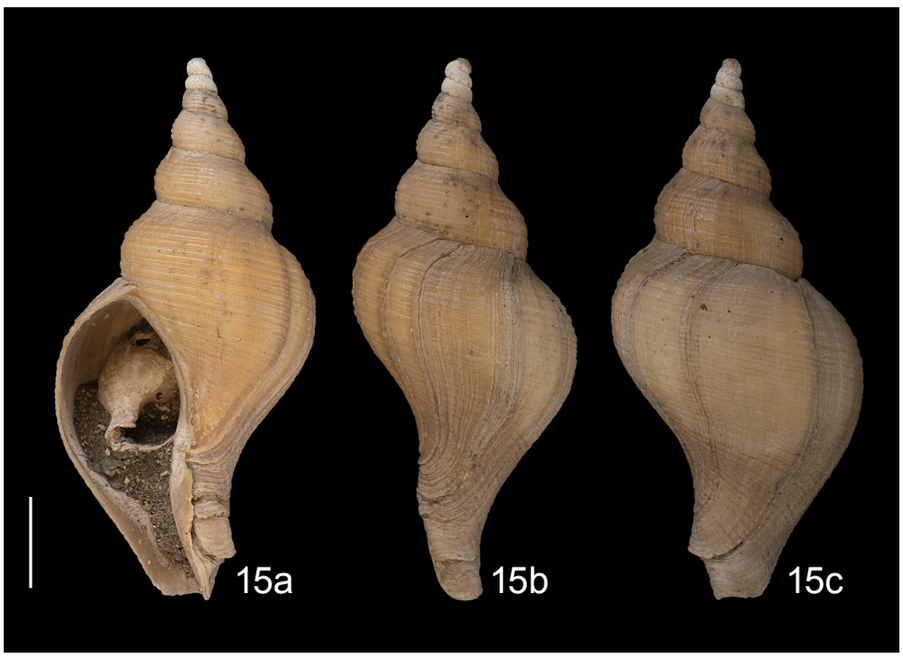


Figure 15. *Neptunea angulata* Harmer, 1914 forma *elongata* (Wood, 1848). Delwaidedok, *ex situ*, probably from Kruisschans Member, upper sandy part. RGM 794 401. H = 57.5 mm. Scale bar is 1 cm.

1957 *Neptunea contraria* (Linnaeus, 1771) – van Regteren Altena *et al*., pl. 14, fig. 130c *non* (Linné, 1771).

Description – Protoconch consists of 2.25 whorls; first and second teleoconch whorls with 5-7 spiral ribs (round in cross-section) of equal strength on the lower two-thirds of the whorl; uppermost two ribs are low and becoming subdivided in four obsolete spirals; from the third teleoconch whorl onwards the lower five ribs split into numerous, very low and fine, somewhat irregular spiral ribs. Subsutural ramp slightly concave. Maximum shell height 113 mm.

Material examined – **Verrebroekdok, Kruisschans Member, lower clayey part:** RGM 794 403 (Fig. 13) (ex MV F1739C) (leg. MV, 1987-1998). **Waaslanddok, *ex situ***, judged from sediment infill originating from Kruisschans Member, lower clayey part: RGM 794 389 (Fig. 14) (ex MV F1739I3a) (leg. MV, 1983). **Delwaidedok (Antwerpen province), *ex situ***, probably from Kruisschans Member, upper sandy part: RGM 794 401 (Fig. 15) (ex MV F1739B).

Stratigraphical distribution – Kruisschans Member (late Piacenzian), Antwerp area, Belgium; Red Crag Formation (late Piacenzian), East Anglia, UK.

Discussion – The round cross section of the ribs as well as the slightly concave nature of the subsutural ramp distinguishes this forma readily.

***Neptunea angulata* Harmer, 1914 forma *harmeri* new forma**

Figures 16, 17.

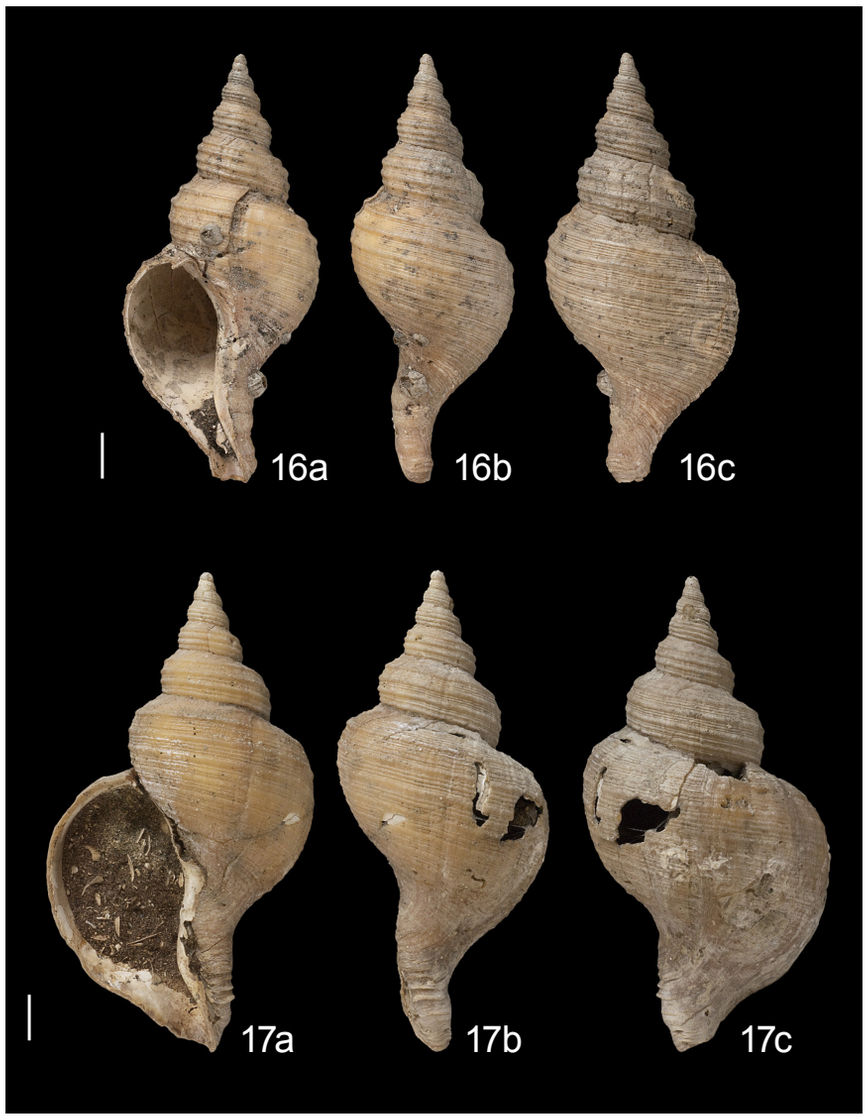
1914 *Neptunea contraria* (Linné) Var. *typica* Harmer, p. 156 (pars), pl. 16, fig. 2 (*non* fig. 1 = *Neptunea angulata* forma *elongata*).

Description – Slender shell, with a regular fine thread-like, narrowly spaced spiral rib ornament among which are four regularly spaced more prominent spirals. Protoconch of 2.25 whorls; first and second teleoconch whorls with four regularly spaced spiral ribs of equal strength (sometimes a fifth rib is visible at the lower suture). On the third teleoconch whorl two very fine spiral threads develop in between the five stronger spiral ribs. On the ultimate two teleoconch whorls the two fine threads each split up into 4-5 still finer elements. The shoulder on the ultimate whorl is slightly concave. Maximum H 104 mm.

Material examined – **Verrebroekdok, *ex situ***, judged from sediment infill originating from Kruisschans Member, upper sandy part: RGM 794 394 (Fig. 16) (ex MV F1739c4) (leg. MV, 1987-1998); RGM 794 390 (Fig. 17) (ex MV F1739F3).

Stratigraphical distribution – Kruisschans Member (late Piacenzian), Antwerp area, Belgium. The exact stratigraphic origin of the specimen illustrated in Harmer that was indicated as 'Scaldisien, Antwerp' cannot be established.

Discussion – *Neptunea angulata* forma *harmeri* resembles *N. angulata* forma *kalloensis*. However, the latter has only



Figures 16-17. *Neptunea angulata* Harmer, 1914 forma *harmeri* new forma. **16.** Verrebroekdok, *ex situ*, judged from sediment infill originating from Kruisschans Member, upper sandy part. RGM 794 394. H = 94.2 mm. Scale bar is 1 cm. **17.** Verrebroekdok, *ex situ*, judged from sediment infill originating from Kruisschans Member, upper sandy part. RGM 794 390. H = 104.2 mm. Scale bar is 1 cm.

four strong ribs occuring on the lower two-thirds of the whorl on initial teleoconch whorls and three prominent spirals on later teleoconch whorls whereas forma *harmeri* has five prominent ribs on the ultimate whorls.

This new form is named after Frederic William Harmer who was the first to illustrate it. Harmer himself named the form variety '*typica*' indicating that he considered it to be a genuin *Neptunea contraria*. Although one could argue the name '*typica*' might be available for naming this variety we find it against the opinion of Harmer himself and thus choose to introduce a new name for this form instead.

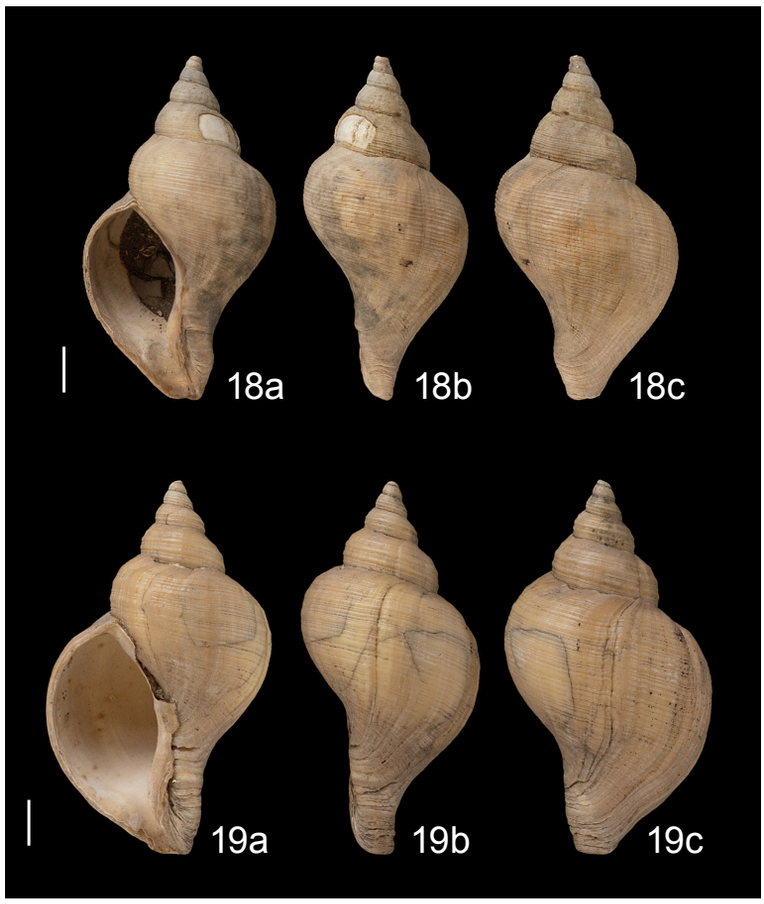
***Neptunea angulata* Harmer, 1914 forma *informis* Harmer, 1914**

Figures 18, 19

*1914	*Neptunea contraria* (Linné) Var. *informis* Harmer, p. 160, pl. 16, fig. 6.
1915	*Neptunea contraria* (Linné) Var. *informis* Harmer – Harmer, pl. 36, fig. 30. *non* 1918 (see below under *Neptunea inversa*)

Description – Relatively short and broad, fusiform shell. Protoconch missing in all specimens. On the lower two-third part of the first teleoconch whorl five irregularly developed low spirals with a rounded cross-section are present. The number of spirals increases on the second teleoconch whorl by splitting up into various finer threads of the lower two ribs. From the third teleoconch whorl onwards up to 18 fine, low, more or less regularly developed spiral riblets are present. Maximum shell height 82 mm.

Material examined – **Verrebroekdok, Kruisschans**



Figures 18-19. *Neptunea angulata* Harmer, 1914 forma *informis* Harmer, 1914. **18.** Verrebroekdok, Kruisschans Member, lower clayey part. RGM 794 396. H = 76.8 mm. Scal bar is 1 cm. **19.** Verrebroekdok, Kruisschans Member, lower clayey part. RGM 794 395. H = 82.2 mm. Scale bar is 1 cm.

Member, lower clayey part: RGM 794 396 (Fig. 18) (ex MV F1739Ca) (leg. MV, 1987-1998); RGM 794 395 (Fig. 19) (ex MV F1739Cb), same locality, *ex situ*; RGM 794 432 (ex MV F1739F3), same locality.

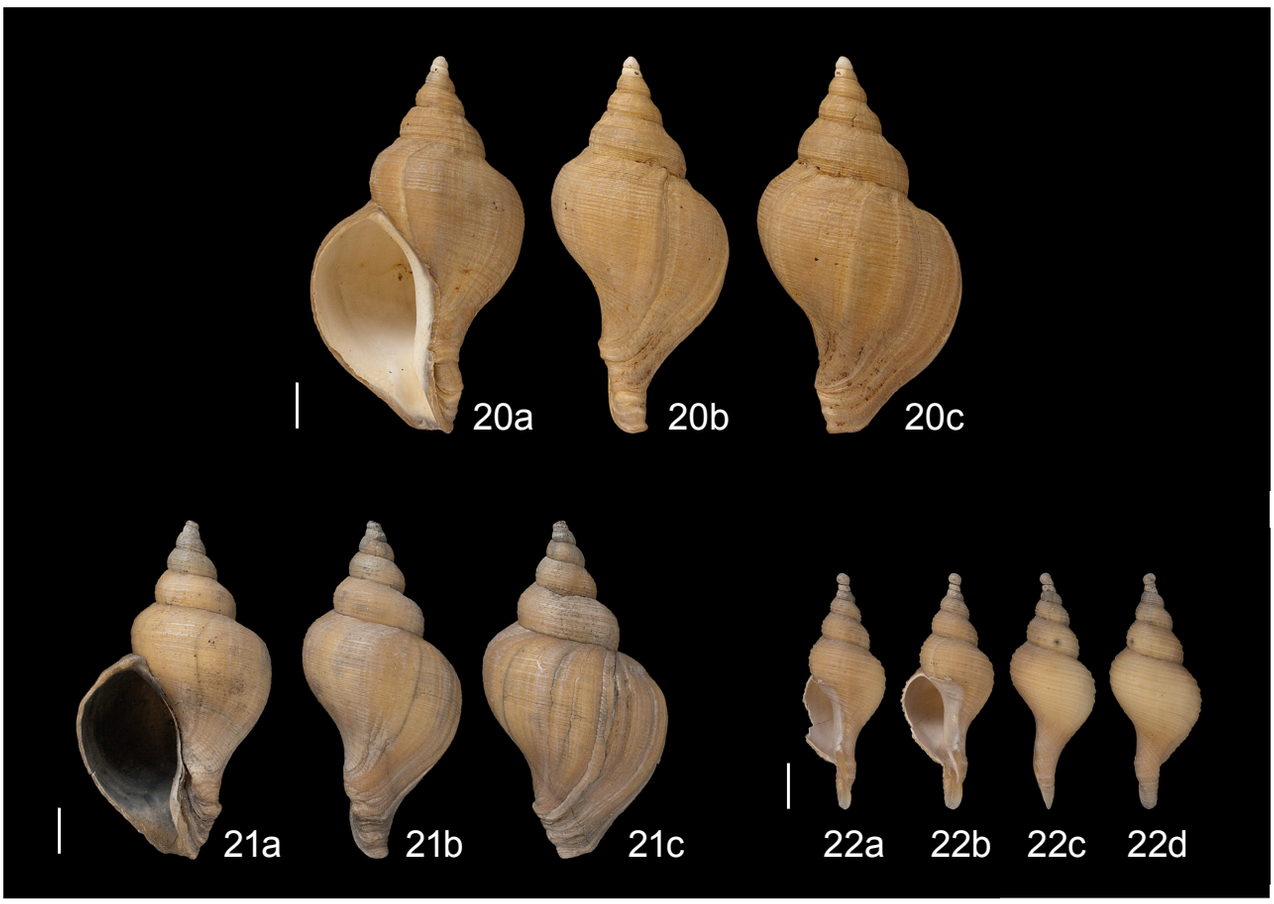
Stratigraphical distribution – Kruisschans Member (late Piacenzian), Antwerp area, Belgium.

Discussion – The broad fusiform shape and relatively fine ornament distinguish this form from other Pliocene forms of the North Sea Basin with the exception of forma *multicincta* (see below). The latter contains more pronounced spiral ribs lacking in forma *informis*. The present form resembles the modern *Neptunea contraria* from the Biskay-Morocco Atlantic. The latter, however, has more inflated whorls and a deeper suture, is more slender and has more regularly developed flat ribs on later teleoconch whorls with interspaces that appear like grooves. It also lacks the common secondary spiral threads found in *N. angulata* forma *informis*.
Harmer's material from the Red Crag (like all *Neptunea* from the Red Crag) has thick-walled shells with most of the spiral ribbing often abraded or poorly developed compared to the Pliocene material from Belgium and the Netherlands. The difference between thin- and thick-walled specimens is also seen in modern *Neptunea* species from the North Sea, with the latter common in the coarse-grained environments of the English coastal zone. Erroneously, Harmer (1918) named another form of this species from the Middle Pleistocene Wexford gravels from Ireland var. *informis* as well. This latter form is treated below as *N. inversa*.

***Neptunea angulata* Harmer, 1914 forma *multicincta* new forma**
Figures 20-22

Description – Relatively slender form with a marked bulbous body whorl. Protoconch consisting of 2.25 whorls; first teleoconch whorl initially with four spirals, but within 0.2 whorls the upper spiral splits into two thread-like ones that in turn split within a few mm into 3 threads each. From the third teleoconch whorl onwards the lower two spiral ribs become lower and have a triangular cross-section. Sometimes they are divided into two even finer spirals. In between these ribs 3-4 very fine threads are present. Maximum shell height 82 mm.

Material examined – **Beveren Tunnel construction pit,**



Figures 20-22. *Neptunea angulata* Harmer, 1914 forma *multicincta* new forma. **20.** Beveren Tunnel construction pit, Kruisschans Member, upper sandy part. RGM 794 397. H = 81.7 mm. Scale bar is 1 cm. **21.** Verrebroekdok, Kruisschans Member, upper sandy part. RGM 794 398. H = 74.9 mm. Scale bar is 1 cm. **22.** Verrebroekdok, Kruisschans Member, upper sandy part. RGM 794 400. H = 51.6 mm. Scale bar is 1 cm.

Kruisschans Member, upper sandy part: RGM 794 397 (Fig. 20) (ex MV F1739a) (leg. MV, 1978); RGM 794 433 (ex MV F1739b); RGM 794 434 (ex FN 60-01). **Verrebroekdok, Kruisschans Member, upper sandy part:** RGM 794 398 (Fig. 21) (ex MV F1739Dc) (leg. MV, 1987-1999); RGM 794 399 (ex MV F1739Dd); RGM 794 400 (Fig. 22) (ex MV F1739D); MV F1739Da (NHM); MV F1739Db (NHM); MV F1739De (SMF); MV F1739Df (SMF); KF 5584 (ex MV F1739).

Stratigraphical distribution – Kruisschans Member (late Piacenzian), Antwerp area, Belgium.

Discussion: At first sight this new forma more or less resembles *Neptunea angulata* forma *informis* Harmer, 1914, that differs, however, in having only threadlike spirals from its first teleconch whorl onwards, a short, relatively broad shell and its siphonal canal being much shorter than that of forma *multicincta*.
The usually worn nature of many of the specimens suggests them to have been transported in the high energy environments of the upper sandy part of the Kruisschans Member. It cannot be excluded that specimens are derived from the underlying clay bed of the same member.

Summary of Pliocene sinistral *Neptunea angulata* forms

The stratigraphical distribution of the Antwerp forms of *Neptunea angulata* Harmer, 1918 is summarized in Fig. 23. In the larger part of the Pliocene succession only the forma *kalloensis* is present, and the very rare second form, forma *strauchi*, occurs within the Oorderen Member. Both forms extend until the Kruisschans Member, but there they are accompanied by an additional five forms making the Kruisschans a hotbed of *Neptunea* forms that cannot be considered subspecies because they co-occur within a single paleohabitat. Within the Antwerp succession intermediate specimens are absent, yet in the *ex situ* collected material from the Schelde estuary in the nearby province of Zeeland, The Netherlands, within reworked material intermediates do seem to occur (P. Moerdijk, pers. comm.). For the moment we classify the Antwerp material as forms for scientific discussion, but the possibility exists that study of further material with well documented stratigraphical origin will enable to elevate the rank of some of these forms to species.

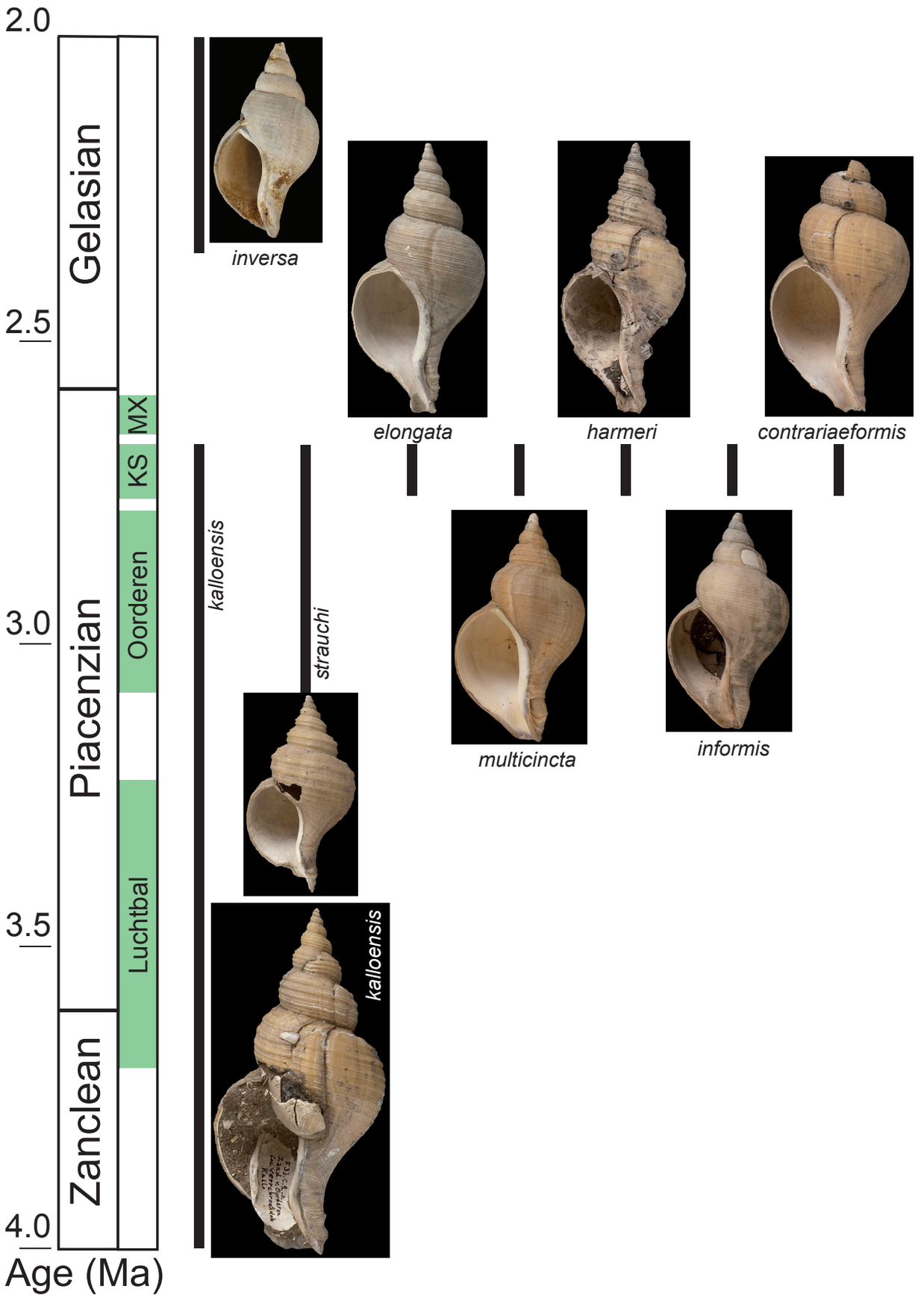


Figure 23. Summary of stratigraphic distribution of *Neptunea angulata* formae in the North Sea Basin. KS = Kruisschans Member, MX = Merksem Member.

Quaternary European sinistral *Neptunea* species beyond the North Sea Basin

Two species are recognized in Quaternary deposits. One of these, whose oldest records are from the late Early Pleistocene (Calabrian) of the Mediterranean, is indistinguishable from and attributed to the modern *Neptunea contraria* that lives from the Gulf of Biskay to Morocco. The second one (*N. inversa* Harmer, 1918) occurred in the Pleistocene of NW Europe (see below) with a confirmed record ranging from the Gelasian (North Sea Basin, Channel region) to Middle Pleistocene (Irish Sea region). This second species is closely related to *N. contraria*, but nonetheless clearly distinct.

***Neptunea inversa* Harmer, 1918**
Figures 24-26.

*1918	*Neptunea antiqua* (Linné) Var. *inversa* Harmer (*partim*), p. 368, pl. 36, fig. 27 [*non* fig. 28 = *Neptunea contraria* (Linné, 1771)].
1918	*Neptunea contraria* (Linné) Var. *informis* Harmer (*non* Harmer, 1914) – Harmer (*partim*), p. 367, pl. 36, figs 30, 31 [*non* pl. 16, fig. 6 = *Neptunea contraria* (Linné, 1771) forma *informis* Harmer, 1914].

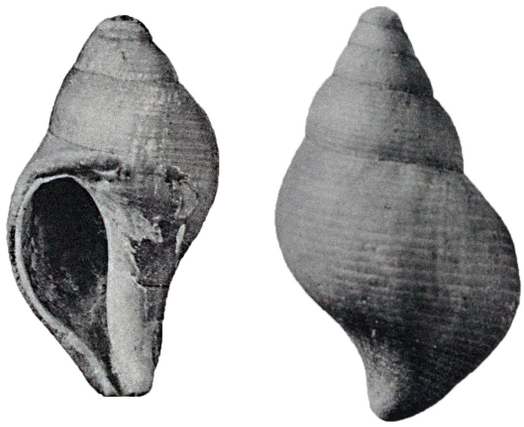
Description – Small robust species with relatively flat whorls, a shallow suture and regularly developed spiral ribs (8-9 on early teleconch whorls) with groove-like interspaces. Maximum H 70 mm.

Lectotype designation – We designate the specimen of *Neptunea antiqua* (Linnaeus) var. *inversa*, as illustrated by Harmer (1918, p. 368, pl. 36, fig. 27: CAMSM C.6870, Sedgwick Museum, Cambridge, United Kingdom) from the Wexford gravels (Ireland) as lectotype.

Material examined – **Selsoif (Manche, France), sand dredging, unnamed beds, Gelasian:** RGM 794 435 (> 30 juvenile specimens and fragments); **Hooge Platen (Zeeland, The Netherlands), washed ashore, reworked from unknown beds:** KZGW NHG0 4917 (Fig. 26) (ex FN), (leg. FN 1983). **Further records** are from Maasvlakte-2 beach (1 damaged specimen, leg. A.C. Janse (Den Briel), 2012 and two specimens dredged from the Thornton Bank, southern North Sea (ex coll. FN).

Stratigraphical distribution – Norwich Crag and Weybourne Crag Formation, East Anglia (Gelasian); unnamed Early to Middle Pleistocene beds, Channel Region (France, United Kingdom); Holderness Formation, Bridlington Member, Early Pleistocene, Bridlington, UK; Wexford Gravels, Middle Pleistocene, Wexford (Ireland); unnamed locality Isle of Man; various localities washed ashore on Dutch beaches and from off shore dredgings, The Netherlands (Pleistocene).

Discussion – The regular type of ribbing at later adult stages with relatively flat ribs, very little development of secondary ribs and interspaces in the form of grooves is shared with *Neptunea contraria*. The latter, however, has convex whorls, a deeper suture and is taller.



Figures 24-25. *Neptunea inversa* Harmer, 1918. **24 (left).** Lectotype, H = 43.3 mm. **25 (right).** Another specimen, H = 48.7 mm. Wexford (Ireland), Middle Pleistocene. Both illustrated in Harmer (1918), pl. 36, figs 27 and 31, respectively.

Figure 26. *Neptunea inversa* Harmer, 1918. Hooge Platen (Zeeland, The Netherlands), washed ashore, reworked from unknown beds. KZGW NHG0 4917. H = 46 mm. Scale bar is 1 cm.

Harmer's specimen from Wexford has two characters in common with other NW European Pleistocene material: its regular ribbing on early teleoconch whorls and the relatively robust shell with a flat whorl profile and shallow suture. The presence of irregular ribs on the last whorl of his damaged specimen is only rarely seen in other specimens from NW Europe but does occur. The Gelasian specimens from Selsoif and the one from Bramerton illustrated in Harmer (1918, fig. 30) have slightly more inflated adult whorls than specimens from Middle and Late Pleistocene localities. The name *informis* proposed by Harmer (1918) is preoccupied by Harmer's 1914 paper in which it was attributed to a Pliocene form (see above).

A sinistral *Neptunea* specimen from the Pleistocene of

Bridlington, *Trophon antiquum* var. *contrarium carinatum* Wood (1848, p. 45, pl. 5, fig. 1k), referred in Harmer (1918, p. 366 [*partim*] pl. 37, fig. 4) as *Neptunea contraria* var. *carinata* (Wood), poses us with a dilemma. The apical fragment has two very clear spiral ribs in early teleoconch stages, strongly resembling *Neptunea angulata* forma *strauchi* (described above) from the Antwerp Pliocene. Such pronounced spiral ribs are not seen in *N. inversa*, thus the incomplete Bridlington specimen might either represent another sinistral *Neptunea* species or may represent an aberrant sinistral specimen of the dextral *Neptunea antiqua* group. Further material is required to establish the identity of the Bridlington specimen. According to Catt (2001) the Bridlington Crag flora and fauna is Early Pleistocene. Pollen and dinoflagelates point to a Pastonian age and amino acid data on *Mya truncata* Linnaeus, 1758 indicates an Early Pleistocene age as well. With the exception of a find in Sidestrand (T. Meijer, pers. comm.), other occurrences in the North Sea Basin are of unknown age: the origin of the Pleistocene material washed ashore in the Netherlands is uncertain. The species has never been found in boreholes onshore nor offshore in Eemian or Late Pleistocene deposits (T. Meijer, pers. comm.). So, with certainty the species is only known from the Early Pleistocene in the North Sea Basin. It is well possible that *N. inversa* became extinct in the North Sea Basin after the Early Pleistocene, although the good preservation of some of the Dutch offshore material suggests a relative "young" Pleistocene age.

Another site with *Neptunea inversa* is Boxgrove on the English Channel coast (Preece & Bates, 1999) which has an age of MIS 13 preceeding the first breach of the Dover Strait in MIS 12. Wexford and the Isle of Man sites probably also are of Middle Pleistocene age predating the Strait of Dover. From both Wexford and Isle of Man no reliable dating is available and exact localities are uncertain although the Wexford material figured by Harmer probably derived from Wexford Blackwater (McMillan, 1964).

***Neptunea contraria* (Linné, 1771)**
Figures 27, 28.

*1771	*contrarius, Murex* Linné, p. 551.
1914	*Neptunea contraria* (Linné) Var. *sinistrorsa* Deshayes – Harmer, p. 159 (*partim*), pl. 16, fig. 4 (*non* fig. 3).
1918	*Neptunea antiqua* (Linné) Var. *inversa* Harmer (*pars*) – Harmer, p. 368, pl. 36, fig. 28 (*non* fig. 27).
1972	*Neptunea sinistrorsa* (Deshayes 1830) – Strauch, p. 20, pl. 3, figs 1, 2.
1986	*Neptunea (Sulcosipho) contraria* (Linnaeus, 1771) – Nelson & Pain, p. 300, figs 5,6 (Figure 27 herein) (with extensive further synonymy).

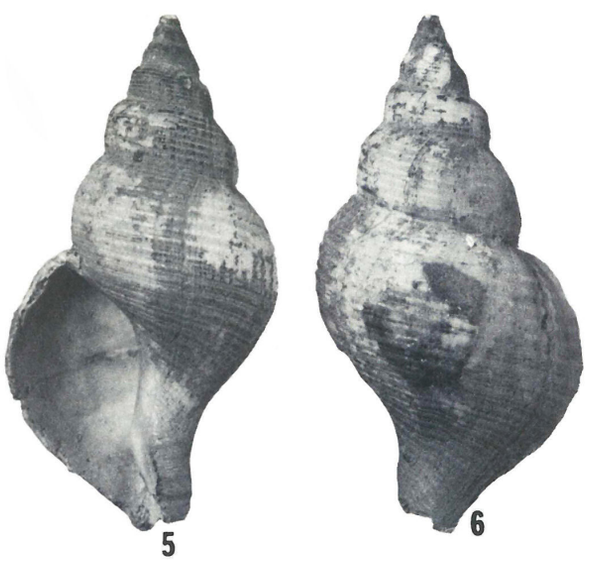


Figure 27. *Neptunea contraria* (Linné, 1771). Lectotype, as illustrated in Nelson & Pain (1986, figs 5, 6). Recent, Vigo Bay (Spain). H = 80.75 mm.

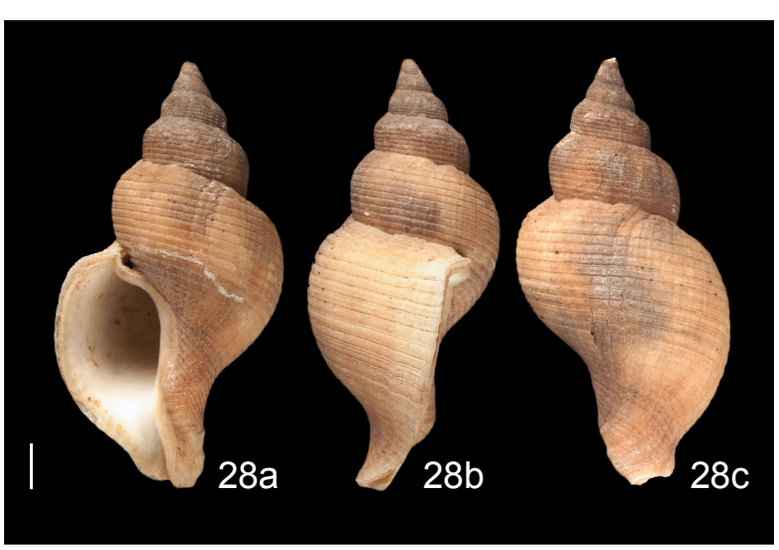


Figure 28. *Neptunea contraria* (Linné, 1771). RGM 794 202. Recent, Vigo (Spain). H = 89.6 mm. Scale bar is 1 cm.

Description – Tall, thin-walled species with markedly convex whorls and therefore a relatively deep suture. On early teleoconch whorls 8-9 spiral ribs. Secondary ribs absent on early teleoconch whorls and only very thin on body whorl. Spiral ribs on later teleoconch whorls regularly spaced and equal in size, flat, with groove-like interspaces. Clear, flat sutural ramp is separated from the lower part of the whorls by an edgy bend. Height between 80-110 mm off northern Spain, occasionally up to 184 mm off Morocco (KF collection).

Material examined – **Vigo (Galicia, Spain):** RGM 794 202, Recent. (Figure 28),

Stratigraphical distribution **–** Living: Bay of Biscay in the north to the Atlantic Morrocan coast to the south (Nelson & Pain, 1986); Calabrian (Early Pleistocene), Sicily.

Discussion – The regular organization of the spiral ribs on later teleoconch whorls distinguishes this species from Pliocene *Neptunea* of the North Sea Basin. The size, convex shape of the whorls and deeper suture distinguishes the species from *Neptunea inversa*.

Pliocene versus modern sinistral *Neptunea*: taxonomic implications

In the successive Pliocene forms of *Neptunea angulata* in the North Sea Basin, the morphology of the shells develops towards the modern *Neptunea contraria*. Especially the increasing number of ribs and their organization on the early teleoconch whorls comes close to the modern species. Yet the habitus of the latest Pliocene specimens as well as the nature of ornament on later teleoconch whorls (with abundant irregular secondary and tertiary spiral generations) differ and show no overlap between Pliocene and modern specimens. Since no other sinistral *Neptunea* species are known from the late Neogene of Europe other than *N. angulata*, and morphologies are similar, it is likely that the Pliocene North Sea Basin species is the ancestor of the modern *N. contraria*.

Origin of sinistral European *Neptunea*

We can only speculate about the origin of sinistral *Neptunea angulata* in the European Pliocene. *Neptunea* is part of a northern Pacific fauna that immigrated into the northern Atlantic in the Pliocene through the Bering Strait and across the arctic seas (*e.g.* Vermeij, 1991). We are not aware of an early Pliocene sinistral *Neptunea* species in the Pacific that may be the ancestor of the Atlantic species, thus assume the latter to be derived from a dextral *Neptunea* species within the Atlantic. The dextral species *N. lyratodespecta* Strauch, 1972 from the Pliocene deposits of Tjörnes (north Iceland) is the oldest record in the Atlantic.

The evolution of the strength of the spiral sculpture in sinistral *Neptunea*, from well pronounced but few spiral cords in the Pliocene to more numerous but finer spiral cords at recent times, follows the same trend of Atlantic dextrally coiled *Neptunea* in which the strongly sculptured *N. lyratodespecta* in the Pliocene gave rise to progressively weaker sculptured *N. despecta* (Linnaeus, 1758) and even smoother *N. antiqua* (Linnaeus, 1758).

Pliocene diversification in the North Sea Basin

A 'sudden' increase in morphological variability of sinistral *Neptunea* took place in the Kruisschans Member/ 'Waltonian' Red Crag Formation in the latest Piacenzian of the North Sea Basin. This morphological diversification co-occurred with large changes in the faunal composition. Warm temperate species disappeared including several North Sea Basin endemics (Marquet, 1998). The interval is further characterized by the short occurrence of several temperate North Sea endemics, like the bivalve species *Cerastoderma parkinsoni* (Sowerby, 1814) and *Yoldia heeringi* Marquet & Moerdijk *in* Marquet, 2002 (see Marquet, 2002, pp. 21, 77) as well as the ongoing introduction of Pacific species, like *Mytilus trossulus* Gould, 1850 and *Mactromeris polynyma* (Stimpson, 1860) (*e.g.* Moerdijk, 2003).

Although local speciation in the North Sea might explain some of the variability in sinistral *Neptunea* during the Kruisschans/Red Crag interval, we think it more likely that the populations are an assembly of forms that originated further north and west in the northeastern Atlantic Ocean. During the late Pliocene, the British Islands formed a peninsula that acted as a wedge between temperate Atlantic regions and the North Sea Basin that at the time was a '*cul de sac*'. An increased overall cooling trend in the glacial climate cycles at the same time must have caused range displacement of species and may have driven north Atlantic forms that lived separated from each other to the south of the North Sea Basin where they were trapped. There they co-occurred and became fossilized.

Acknowledgments

Extensive discussions with Peter Moerdijk (Middelburg, The Netherlands) have been essential to elucidate the nomenclatural and some of the taxonomic issues in this paper. Dr M. Riley (Sedgewick Museum, Cambridge, United Kingdom) provided information on the material described by Harmer. Comments and suggestions from reviewers F. Strauch and T. Meijer considerably improved our manuscript. We also thank Tom Meijer for providing Fig. 1.

References

Bakel, B.W.M. van, Jagt, J.W.M. & Fraaije, R.H.B. 2003. A new Pliocene cancrid crab from Oelegem, province of Antwerpen (NW Belgium). *Cainozoic Research* 2: 79-85.

Catt, J.A., 2001. Day 1: The Holderness Coast. Dimlington Cliff (TA 386224 – TA 399205). – The Quaternary of East Yorkshire and North Lincolnshire. *Field Guide Q.R.A*. pp. 53-67.

De Schepper, S. & Head, M.J. 2008. New dinoflagellate cyst and acritarch taxa from the Pliocene and Pleistocene of the eastern North Atlantic (DSDP Site 610). *Journal of Systematic Palaeontology* 6: 101–117.

De Schepper, S., Head, M.J. & Louwye, S. 2009. Pliocene dinoflagellate cyst stratigraphy, palaeoecology and sequence stratigraphy of the Tunnel-Canal Dock, Belgium. *Geological Magazine* 146: 92–112.

Fraussen, K. & Terryn, Y. 2007. *The family Buccinidae, Genus Neptunea. A conchological iconography.* Hackenheim (Conchbooks), 166 pp.

Gladenkov, A.Y., Oleinik, A.E., Marincovich, L. Jr. & Barinov, K.B. 2002. A refined age for the earliest opening of Bering Strait. *Palaeogeography, Palaeoclimatology, Palaeoecology* 183: 321-328.

Gladenkov, A.Y. & Gladenkov, Y.B, 2004. Onset of Connections between the Pacific and Arctic Oceans through the Bering Strait in the Neogene. *Stratigraphy and Geological Correlation* 12: 175-187.

Golikov A.N. 1963. Gastropod mollusks of the genus *Neptunea*. *Fauna of the USSR, Mollusks* 5: 1-183 (in Russian).

Harmer, W.F. 1914-1918. The Pliocene Mollusca of Great Britain, being supplementary to S.V. Wood's Monograph of the Crag Mollusca, 1-3. *Monograph Palaeontographical Society* 67: 1-200, 1914 (1); 68: 201-302, 1915 (2); 70: 303-461, 1918 (3).

ICZN (International Commission on Zoological Nomenclature) 1999. *International Code of Zoological Nomenclature*. London (International Trust for Zoological Nomenclature): i-xxix, 1-306.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines,genera, species, cum characteribus, differentiis, synonymis, locis*, 1. Editio decima, reformata. Holmiae (Laurentii Salvii): 824 pp.

Linné, C. a 1771. *Mantissa plantarum altera generum editionis* VI. & *specierum editionis* II. Holmiæ (Laurentii Salvii): i-vi, 143-588.

MacMillan, N.F. 1964. The Mollusca of the Wexford Gravels (Pleistocene), South-East Ireland. *Proceedings of the Royal Irish Academy* 63B: 265-289.

Marincovich Jr, L., Barinov, K.B. & Oleinik, A.E. 2002. The *Astarte* (Bivalvia: Astartidae) that document the earliest opening of Bering Strait. *Journal of Paleontology*, 76: 239-245.

Marquet, R. 1980. De stratigrafie van Neogene afzettingen in een bouwput voor een waterreservoir te Broechem (prov. Antwerpen, België). *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie* 17: 57-64.

Marquet, R. 1997. Pliocene gastropod faunas from Kallo (Oost-Vlaanderen, Belgium), 4: Buccinidae to Helicidae. *Contributions to Tertiary and Quaternary Geology* 34: 69-149.

Marquet, R. 1998. De Pliocene gastropodenfauna van Kallo (Oost-Vlaanderen, België). *Belgische Vereniging voor Paleontologie* (Antwerpen), publicatie 17: 246 pp.

Marquet, R. 2002. The Pliocene Amphineura and Bivalvia (Palaeotaxodonta and Pteriomorphia) from Kallo and Doel (Oost-Vlaanderen, Belgium). *Paleontos* 2 : 1-100.

Meijer, T. 1993. Stratigraphical notes on *Macoma* (Bivalvia) in the southern part of the North Sea Basin and some remarks on the arrival of Pacific species. *Scripta Geologica, Special Issue* 2: 297-312.

Miall, A.D. 1997. *The geology of stratigraphic sequences*. Berlin (Springer): 433 pp.

Moerdijk, P. & Rijken, R. 2002. Fossiele noordhorens van de Steenbanken, Westerschelde en Roompot/Onrust. *Voluta* 8(2): 5-11.

Moerdijk, P.W. 2003. *Mactromeris polynyma* (Stimpson, 1860) (Mollusca, Mactridae) from the Upper Pliocene of the Netherlands and Belgium. *Cainozoic Research* 2: 135-137.

Nelson, C.M. & Pain, T. 1986. Linnaeus' *Neptunea* (Mollusca: Gastropoda). *Zoological Journal of the Linnean Society* 88: 291-306.

Nyst P.-H. 1878: Conchyliologie des terrains tertiaires de la Belgique; 1. *Annales du Musée Royal d'Histoire Naturelle de Belgique* 3: 1-262.

Preece, R.C. & Bates, M.R. 1999. Mollusca. *English Heritage Archaeological Report* 17: 169-175.

Regteren Altena, C. O. van, Bloklander, A. & Pouderoyen, L.P. 1957. De fossiele schelpen van de Nederlandse stranden en zeegaten, 4. *Basteria* 21: 67-73.

Strauch, F. 1972. Phylogenese, adaptation und migration einiger nordischer mariner molluskengenera *(Neptunea, Panomya, Cyrtodaria* und *Mya). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 531: 1-211.

Vandenberghe, N., Laga, P., Steurbaut, E., Hardenbol, J. & Vail, P.R. 1998. Tertiary sequence stratigraphy at the southern border of the North Sea basin in Belgium. *SEPM Special Publication* 60: 119-154.

Vermeij, G. J. 1991. Anatomy of an invasion: The trans-Arctic interchange. *Paleobiology* 17: 281-307.

Vervoenen, M. 1995. Taphonomy of some Cenozoic seabeds from the Flemish region, Belgium. *Professional Paper Geological Survey of Belgium* 1994/5(272): 1-115.

Wijnker, E., Bor, T.J., Wesselingh, F.P., Munsterman, D.K., Brinkhuis, H., Burger, A.W., Vonhof, H.B., Post, K., Hoedemakers, K., Janse, A.C. & Taverne, N. 2008. Neogene stratigraphy of the Langenboom locality (Noord-Brabant, The Netherlands). *Netherlands Journal of Geosciences* 87: 165-180.

Wood, S.V. 1848. *A monograph of the Crag Mollusca with descriptions of shells from the upper Tertiaries of the British Isles*, 1. Univalves. London (The Palaeontographical Society): 208 pp.

Wood, S.V. 1872. Supplement to the Crag Mollusca, with descriptions of shells from the upper Tertiaries of the British Isles, 1 (Univalves). *Monograph of the Palaeontographical Society London* 25: 1-98.