

On Miocene-Pleistocene Glycymerididae (Mollusca, Bivalvia) from the North Sea Basin, with the introduction of a new subspecies, *Glycymeris (Glycymeris) radiolyrata exaggerata*

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Glycymeridid bivalves of Miocene, Pliocene and Pleistocene age in the North Sea Basin are revised, and a new Pliocene subspecies, *Glycymeris (Glycymeris) radiolyrata exaggerata* nov. subsp., is erected. In addition, the earliest presence of *Glycymeris (Glycymeris) glycymeris* (Linnaeus, 1758) in the North Sea Basin is established as Early Pleistocene, and *Glycymeris (Glycymeris) bimaculata* (Poli, 1795) is recorded from the North Sea Basin for the first time. Lastly, the poorly known *Glycymeris (Glycymeris) auriculata* IJspeert, 1942 of Miocene age is reassessed and the subgenus *Glycymeris (Pseudaxinea)* di Monterosato, 1892 is revived.

KEY WORDS: North West Europe, Neogene, Quaternary, revision, new taxon

Introduction

Two decades ago, Moerdijk & Van Nieulande (1995, 2000) and Van Nieulande & Moerdijk (2002) published three papers on glycymeridids from Pliocene strata in the North Sea Basin. In addition to the designation of a lectotype for *G. (Chevronia) variabilis* (J. de C. Sowerby, 1824), those authors erected several new taxa, viz., the subgenus *Glycymeris (Chevronia)* Moerdijk & Van Nieulande, 2000 and the species and subspecies *G. (Glycymeris) radiolyrata* Moerdijk & Van Nieulande, 1995, *G. (Glycymeris) radiolyrata pseudodeshayesi* Van Nieulande & Moerdijk, in Marquet, 2002 (see below) and *G. (Chevronia) obovata ringelei* Moerdijk & Van Nieulande, 2000. Following recent studies, we here present new data on Miocene and Quaternary taxa, supply additional illustrations of *G. (Glycymeris) radiolyrata pseudodeshayesi* (inclusive of the holotype) and erect a new subspecies, *Glycymeris (Glycymeris) radiolyrata exaggerata* nov. subsp. The stratigraphical ranges of Neogene and Quaternary Glycymerididae in the North Sea Basin are shown in Figure 1.

Material and methods

Over recent years, we have studied specimens of glycymeridids that are housed in the collections of Naturalis Biodiversity Center (Leiden, The Netherlands) [which includes the collections of the former Rijksmuseum van

Geologie en Mineralogie (RGM), the former Zoölogisch Museum Amsterdam (ZMA), and the former Nederlands Instituut voor Toegepaste Geowetenschappen/Rijks Geologische Dienst (NITG/RGD)], the Senckenberg Naturmuseum Frankfurt (SMF; Frankfurt am Main, Germany), the Naturhistorisches Museum Basel (NMB; Basel, Switzerland), the Mayer-Eymar Collection, now housed at the Eidgenössische Technische Hochschule (ETH; Zürich, Switzerland), as well as the private collections of Messrs R. Marquet, M. Vervoenen, J. van der Voort and the authors. Information on and photographs of Glycymerididae from the Krinke Quarry at Werder (Germany) were kindly supplied by Mrs R. Husmann.

For the stratigraphical framework used here, reference is made to the Deutsche Stratigraphische Kommission (2016), King *et al.* (2016) and Vandenberghhe & Louwye (2020).

Systematic palaeontology

Class Bivalvia Linnaeus, 1758
Order Arcida Stoliczka, 1871
Superfamily Arcoidea Lamarck, 1809
Family Glycymerididae Dall, 1908

Remarks – Thomas (1975) noted that members of the family Glycymerididae showed a strong evolutionary conservatism in features of their general morphology; this explains why this group is generally considered dif-

ficult. To date, the genera *Axinactis* Mörch, 1861, *Glycymeris* Da Costa, 1778, *Glycymerita* Finlay & Marwick, 1937, *Melaxinaea* Iredale, 1930, *Nucunella* d'Orbigny, 1850, *Tucetona* Iredale, 1939 and *Tucetonella* Habe, 1961 are considered valid (MolluscaBase, 2023).

In Europe, the genus *Tucetona* is represented by *T. tarbelliana* Maestrati & Lozouet, 1996, from the Oligocene (Chattian) of the Adour Basin, France. Earlier, Glibert & Van de Poel (1965) had included the Oligocene *Pectunculus angusticostatus* Lamarck, 1805 in the genus *Axinactis* and subgenus *Tucetilla* Iredale, 1939. Indeed, *G. angusticostata* is generally reminiscent of *Pectunculus tenuicostatus* Reeve, 1843, the type species of *Tucetilla*. At present (MolluscaBase, 2023), *Tucetilla* is no longer considered valid, but treated as a subjective synonym of *Glycymeris*. Marquet *et al.* (2012) also assigned two Oligocene species, *G. tenuisulcata* (von Koenen, 1893) and *G. agnosta* R. Janssen, 1979 to *Axinactis*. However, in view of their subcircular shell and more or less equilateral and essentially smooth cardinal area these forms would provisionally match *Glycymeris*; for instance, their features are similar to those of *G. textus* (Dujardin, 1837) from the Miocene of western France. That species is characterised by a surface ornament of flat radial riblets, separated by narrow grooves. Members of this lot of species may be referred to as the *G. textus* group (*sensu* Cahuzac *et al.*, 1993).

Moerdijk & Van Nieulande (2000) proposed a new subgenus, *Chevronia*, thereby drawing attention to a combination of distinguishing features such as general morphology, surface ornament and, in particular, characters of the cardinal shell area. Considering the fact that 98 species of *Glycymeris* are currently accepted (MolluscaBase, 2023), the genus rather remains a 'waste basket' entity. Further generic and subgeneric subdivision of *Glycymeris* appears desirable. At the moment, *Pseudaxinea* di Monterosato, 1892 (type species: *Pectunculus violascens* Lamarck, 1819 = *P. nummaria* Linnaeus, 1758) is generally considered a subjective synonym of *Glycymeris* (MolluscaBase, 2021), but herein we propose to reinstall it as a subgenus of *Glycymeris*.

Genus *Glycymeris* Da Costa, 1778

Subgenus *Glycymeris* Da Costa, 1778

Type species – *Arca glycymeris* Linnaeus, 1758

Remarks – With the introduction of the subgenus *Chevronia* Moerdijk & Van Nieulande, 2000, the subgenus *Glycymeris* became applicable to species with a subcircular shell, a moderately developed surface ornament and an essentially smooth cardinal area. Here we erect a Pliocene subspecies, *G. (Glycymeris) radiolyrata exaggerata* nov. subsp., and discuss *G. (Glycymeris) glycymeris* (Pleistocene), *G. (Glycymeris) bimaculata* (Poli, 1795) (Miocene), and *G. (Glycymeris) auriculata* IJspeert, 1942 (Miocene).

Glycymeris (Glycymeris) glycymeris (Linnaeus, 1758)

Plate 1, figs 1-4

- 1758 *Arca glycymeris* Linnaeus, 1758, p. 695.
 ?1851 *Pectunculus glycymeris* – Wood, pp. 66-69 (*partim?*).
 ?1872 *Pectunculus glycymeris* – Wood jun. & Harmer, pp. xxii-xxiii.
 ?1874 *Pectunculus glycymeris* – Wood, pp. 116, 117 (*partim?*).
 ?1882 *Pectunculus glycymeris* – Wood, p. 15 (*partim?*).
 non 1851 *Pectunculus glycymeris* – Wood, pl. 9, figs 1a-i only.
 non 1879 *Pectunculus glycymeris* – Wood, pl. 6, fig. 5a only.

Description – Species of *Glycymeris* of moderate size, length up to c. 65 mm, with a globular outline, superficially equilateral, with opisthogyrate umbo. Outer shell surface with fine reticulate pattern; cardinal area smooth and clearly inequilateral, anterior part clearly longer than posterior.

Geographical and stratigraphical range – The stratigraphical range of this extant species is poorly known (see below); here we record it for the first time and without doubt from the Lower Pleistocene of the North Sea Basin. Its present distribution comprises the eastern Atlantic, from Norway to southern Morocco, the Canary Islands and Madeira, as well as the North Sea, albeit occurring rarely in the southern part. Also occasionally found in the Mediterranean. The species inhabits muds, sands or shelly gravels, especially in areas of high current. It can be found at sublittoral and shelf depths, just off-shore down to about 75 m or even deeper (1200 m) (Tebble, 1966, Nolf & Swinnen, 2013, Oliver *et al.*, 2016). Of note is the fact that this is the sole species of *Glycymeris* in western Europe to occur also under more boreal conditions.

Discussion – Linked to the difficulties involved in identifying glycymeridids, the name *G. glycymeris* has been widely used for quite a number of different fossil and extant species. As a consequence, the geographical and stratigraphical range of extinct representatives of *G. (Glycymeris) glycymeris* is still largely unknown or imprecise. Wood (1851) lumped all glycymeridids from the Pliocene Coralline and Red crags in his '*Pectunculus glycymeris*'. In fact, genuine *G. (Glycymeris) glycymeris* appears not to have any close relationship with *G. (Chevronia) variabilis* from the Pliocene of the North Sea Basin. In that species the cardinal area shows clear grooves and ridges arranged in a chevron pattern; moreover, its average dimensions are larger and its shell surface is near smooth, covered merely by very fine, obsolete radial threads. *Glycymeris (Glycymeris) radiolyrata radiolyrata* Moerdijk & Van Nieulande, 1995 also attains larger sizes than *G. (Glycymeris) glycymeris*, has a more equilateral, yet smooth cardinal area and shows a coarser ornament consisting of irregular radial riblets, crossed by fine commarginal ridges (see also Moerdijk & Van Nieulande, 1995). Apparently, the last occurrence in the North Sea Basin of *Glycymeris (Chevronia) variabilis* and *G. (Glycymeris) radiolyrata* is during the Late Pliocene.

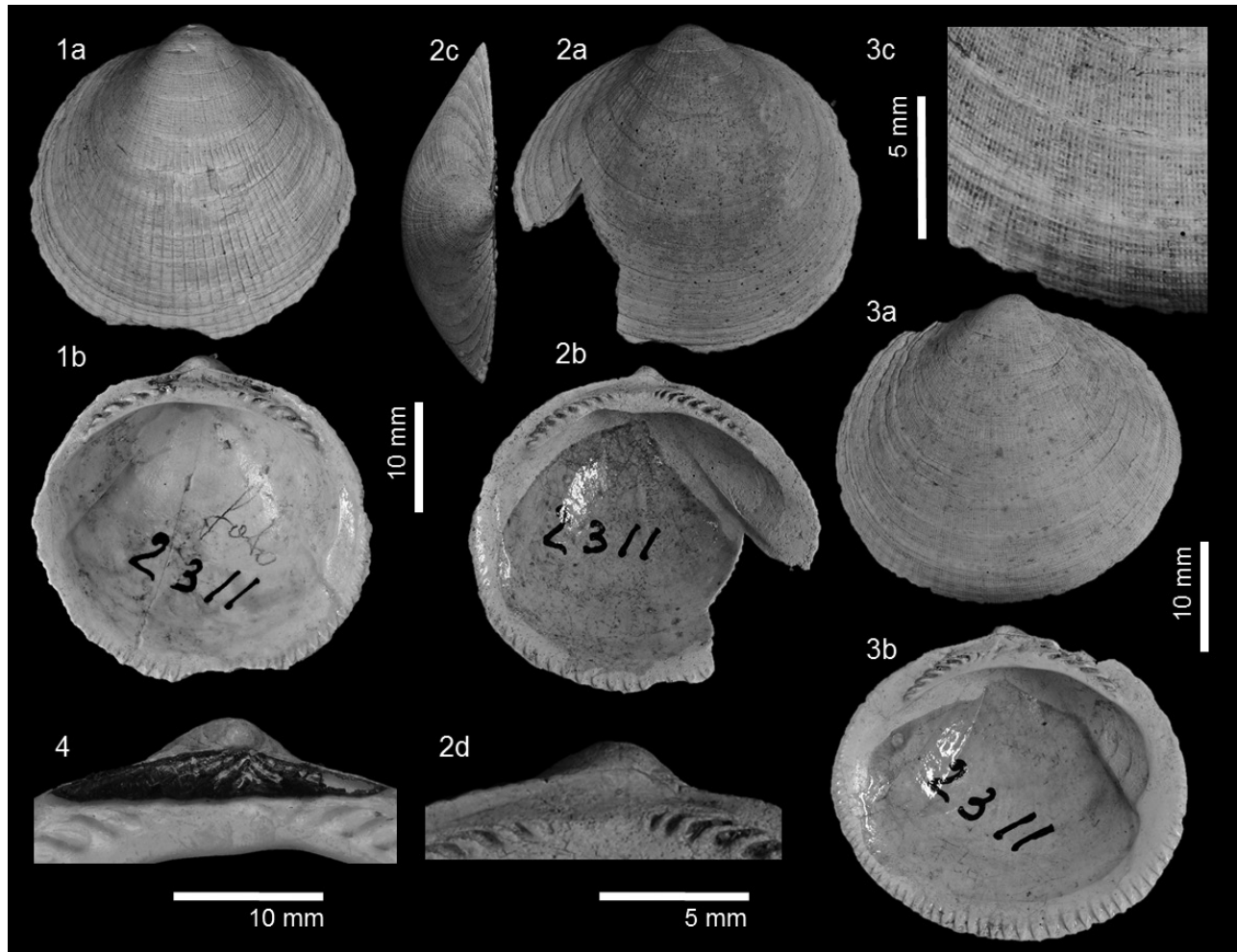


Plate 1. *Glycymeris (Glycymeris) glycymeris* (Linnaeus, 1758); 1-3. RGM.1379052, Haamstede (The Netherlands), borehole 576.5 B42B0005, O. 1070, depth 96.60-103.30 metres below surface, Lower Pleistocene; 1. Left valve, a. outer view, b. inner view; 2. Right valve, a. outer view, b. inner view, c. umbonal view, d. detail of cardinal area; 3. Left valve, a. outer view, b. inner view, c. detail of surface ornament near shell margin; 4. Detail of cardinal area with ligament of an extant specimen (coll. Moerdijk), French Atlantic coast, showing chevron arrangement of ligament sheets. Photographs: R. Pouwer (Naturalis, Leiden) (1-3) and the authors (4).

Extensive collecting in Pliocene strata at temporary outcrops in the Antwerp area (Belgium) has not yielded any specimen of *G. (Glycymeris) glycymeris*. Among samples from numerous boreholes in the south-west Netherlands, with exclusively Pliocene faunas, there is no trace of *G. (Glycymeris) glycymeris* either, nor is any unquestionable record of this species from Pliocene strata in East Anglia (England) known to us.

Records from the North Sea Basin of fossil forms of *Glycymeris* in general from deposits younger than Pliocene are quite rare. In two samples from a borehole at Haamstede (The Netherlands), shells and shell fragments of *Glycymeris* have been encountered. Eight of these are here identified as *G. (Glycymeris) radiolyrata* and one as *G. (Chevronia) variabilis*. Three well-preserved valves and three fragments clearly belong to *G. (Glycymeris) glycymeris* (see also Moerdijk & Van Nieulande, 1995). Most other molluscan species from this interval at Haamstede are definitely of Pliocene age, but some are

unknown from levels of this age in the North Sea Basin, namely the gastropod *Steromphala tumida* (Montagu, 1803) (see Beets, 1946) and the bivalves *Acila cobboldiae* (J. Sowerby, 1817), *Yoldia lanceolata* (J. Sowerby, 1817) and *Clausinella fasciata* (Da Costa, 1778) (see Heering, 1950a). Similar to *G. glycymeris*, the extant species *Steromphala tumida* and *Clausinella fasciata* are part of boreal faunas. At depths corresponding to the interval penetrated in the Haamstede borehole that yielded the material of *G. (Glycymeris) glycymeris*, no deposits younger than Early Pleistocene have been encountered.

In view of the fact that all specimens of *Glycymeris* of undoubted Pliocene age in the North Sea Basin that we have seen belong to *G. (Chevronia) obovata ringelei*, *G. (Chevronia) variabilis* or *G. (Glycymeris) radiolyrata* s. lat. and that shells of *G. (Glycymeris) glycymeris* from the Haamstede borehole are accompanied by some undoubtedly Early Pleistocene molluscan taxa, we assume

specimens and fragments of *G. (Glycymeris) glycymeris* to be of Early Pleistocene age.

Wood (1874, p. 117) recorded '*Pectunculus glycymeris*' from some Lower Pleistocene deposits, 'somewhat plentifully [*sic*] in a newly worked pit at Bramerton'. Wood (1851, 1874) also referred to rare specimens of '*Pectunculus glycymeris*' from the Lower Pleistocene Mammaliferous Crag of Thorpe and the Chillesford Bed of Aldeby in England, and finds from Bridlington were also added. Wood (1872) and Wood jun. & Harmer (1872) mentioned abundant specimens of *Glycymeris* of all sizes from the 'Middle Glacial' at Billockby and Hopton, where they are part of a fauna that consists mainly of rolled shells and debris. We have not been able to verify these records from the Pleistocene of East Anglia, but some, or all, of them may indeed refer to *G. (Glycymeris) glycymeris*.

Apparently, fossil valves of *G. (Glycymeris) glycymeris* are not uncommon among shells washed-up on beaches in the south of the Netherlands, where, in general, they are not accompanied by typical representatives of Early Pleistocene faunas. Although the species is not recorded from Eemian deposits (e.g., Spaik, 1958; Cleveringa *et al.*, 2000), these finds probably are not much older than Late Pleistocene.

All in all, *Glycymeris (Glycymeris) glycymeris* does not appear to be present in the North Sea Basin until the Early Pleistocene. Records of fossil (Neogene) specimens from beyond this basin referred to as *G. (Glycymeris) glycymeris* are erroneous or questionable, at best.

Material studied – Three valves and three fragments (RGM.1379052) from borehole Haamstede 576.5, B42B0005 (Boring O.1070), depth 96.60-103.30 metres below surface.

***Glycymeris (Glycymeris) radiolyrata exaggerata* nov. subsp.**

Plate 2, figs 4-6

- ?1851 *Pectunculus glycymeris* – Wood, pl. 9, fig. 1d ('elongated var.') only.
- ?1879 *Pectunculus pilosus* var. *insubricus* – Wood, p. 43, pl. 6, fig. 4a (*non* Brocchi).
- 1957 *Glycymeris glycymeris*, forme *pilosa-tumida* – Glibert, p. 17, pl. 1, fig. 4 (*non* Bucquoy, Dautzenberg & Dollfuss, 1891).
- 2000 *Glycymeris (Glycymeris) radiolyrata* forma *exaggerata* Moerdijk & Van Nieulande, pp. 7, 8, pl. 6, figs 1-3.

ZooBank registration – <https://zoobank.org/Nomenclatural-Acts/042347F4-F36C-4722-8705-D7EB43A39C96>

Type material – The holotype is RGM.607480, a right valve from Kallo (Antwerp area, Oost-Vlaanderen, Belgium), Beveren tunnel construction pit (*leg.* F.A.D. van Nieulande, April 18, 1975) from the basal Oorderen Member, probably reworked from older strata (*ex* Van Nieulande Collection, no. 93b).

Paratypes include the following: RGM.607476 (one right valve), Verrebroek (Antwerp area, Oost-Vlaanderen, Belgium), Verrebroekdok construction pit, Pliocene, Lillo Formation, Oorderen Member, level with *Atrina* (?), probably reworked from older strata (*leg.* G. Garding, c. 1989, *ex* coll. F.A.D. van Nieulande). RGM.607481 (one left valve), Kallo (Antwerp area, Oost-Vlaanderen, Belgium), sea sluice construction pit, Pliocene, Lillo Formation, Oorderen Member, basal layer, probably reworked from older strata (*leg./ex* coll. M. Vervoenen, F 717 A2). RGM.1364822 (three right valves), Kallo (Antwerp area, Oost-Vlaanderen, Belgium), sea sluice construction pit, Pliocene, Lillo Formation, Oorderen Member, *ex situ*, probably from basal transgressive level, reworked from older strata (one specimen with sediment from Luchtbal Member) (*leg./ex* coll. M. Vervoenen, F3176 = *ex* F 717 A). RGM.1364823 (one right valve), Kallo (Antwerp area, Oost-Vlaanderen, Belgium), Waaslandkanaal (= 1st dock). Pliocene, Lillo Formation, Oorderen Member, basal transgressive level, reworked from Luchtbal Member (*leg./ex* coll. M. Vervoenen, F 3176.A). RGM.1364824 (one right valve), Ramsholt, Suffolk (England), cliff outcrop near the River Deben, Ramsholt Cliff (*leg.* P. Cambridge).

Other material studied – Former NITG/RGD collections: 1 articulated specimen, labelled '*Pectunculus pilosus*' and originating from the 'Scaldisian' (= Oorderen Member), and originally filled with sediment containing the serpulid *Ditrupa* Berkeley, 1835 from the Diestien (= Kattendijk Member); Marquet Collection: 1 left valve, Kallo (Antwerp area, Vrasenedok excavation, base Oorderen Member, probably reworked from older strata; RGM.1364821, 13 valves, Yerseke, sucker dredged from Western Scheldt near Baarland province of Zeeland, The Netherlands), derived from Pliocene strata (*ex* coll. P. Moerdijk).

Diagnosis – A large, inflated and slightly oblique species of *Glycymeris* s. str., with posterior side slightly larger than anterior, with smooth, subsymmetrical, principally smooth ligamental area below umbo, and with initially about 20 regular radial riblets crossed by regular commarginal wrinkles on outer surface; during growth, ornament evolving into fine and regularly reticulate pattern.

Locus typicus – Kallo (Belgium), Beveren tunnel construction pit.

Stratum typicum – Base of Oorderen Member (Pliocene, Piacenzian), probably derived from the Kattendijk Member (Pliocene, Zanclean; see Discussion).

Geographical and stratigraphical range – Pliocene, Coralline Crag (Ramsholt Cliff, East Anglia, England) and probably Kattendijk Member, as well as derived within the Luchtbal and Oorderen members in north-west Belgium.

Derivatio nominis – In allusion to the coarser ornament which appears exaggerated in comparison to *G. (Glycymeris) radiolyrata* s. str.

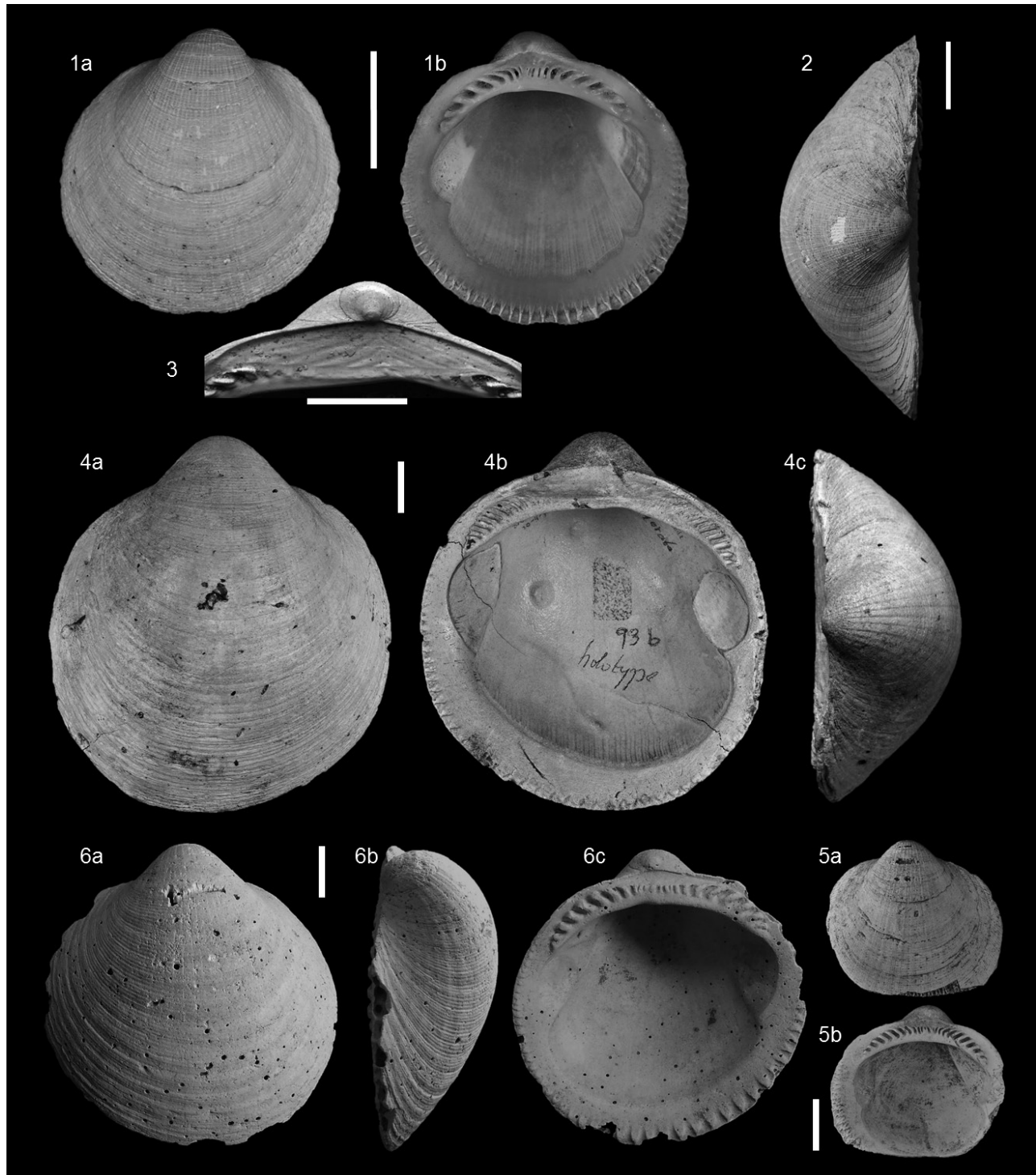


Plate 2. *Glycymeris (Glycymeris) radiolyrata pseudodeshayesi* Van Nieulande & Moerdijk, in Marquet, 2002; 1a, b. RGM.394121.a, holotype (left valve), Ouwerkerk (The Netherlands), borehole B42H0039, Deltadienst no. 42H19-4 (A40), depth 114.5-115.75 metres below surface, Pliocene, a. outer view, b. inner view; 2, 3. Moerdijk collection, Doel (Antwerp area, Oost-Vlaanderen, Belgium), Deurganckdok excavation, Pliocene, sediment from Luchtbal Sand Member: 2. umbonal view for comparison with Fig. 4c; 3. Cardinal area showing a superficial chevron pattern. Scale bars equal 10 mm.

Glycymeris (Glycymeris) radiolyrata exaggerata nov. subsp. 4a-c. Holotype (right valve): RGM.607480, Kallo (Antwerp area, Oost-Vlaanderen, Belgium), Beveren tunnel construction pit, base Oorderen Member, probably derived from Kattendijk Member (Zanclean): a. outer view, b. inner view, c. umbonal view; 5a, b. Paratype (right valve): RGM.1364824, Ramsholt river cliff, Suffolk, East Anglia, Pliocene (Zanclean), Coralline Crag, Ramsholt Member (leg. P. Cambridge): a. outer view, b. inner view; 6. RGM.1364821, left valve, Western Scheldt near Baarland (Zeeland, The Netherlands): a. outer view, b. anterior/umbonal view; c. inner view. Scale bars equal 10 mm.

Photographs: R. Pouwer (Naturalis, Leiden) (1-5) and the authors (6).

Description – The holotype is a slightly worn right valve, measuring 73 mm in height, 66 mm in length and 26 mm in thickness. Large, solid and inflated, more or less inequilateral; posterior slightly higher and broader than anterior, with slightly opisthogyrate, protruding umbo. Umbo ornament consisting of about 20 regularly spaced ribs, crossed by commarginal wrinkles, during ontogeny developing into quite regular reticulate ornament; ribs weakening, becoming virtually inconspicuous towards shell margins. Hinge moderately well developed; centrally teeth absorbed by growth of cardinal area; cardinal area broad and becoming almost equilateral, surface virtually smooth, but faint, superficial chevron pattern observable. In smaller specimens cardinal area noticeably inequilateral. As in other glycymeridids, inner shell margin crenulated. Adductor muscle scars positioned close to hinge plate, posterior one resting on internal reinforcement.

Differentiation – *Glycymeris (Glycymeris) radiolyrata exaggerata* nov. subsp. differs from the nominal subspecies in being much more inflated, in having a better developed hinge with longer teeth and in having the adductor muscle scars close to the hinge plate. Its surface ornament is principally regular, whereas it is irregular in *G. (Glycymeris) radiolyrata radiolyrata*. It is distinguished from both subspecies, *i.e.*, *pseudodeshayesi* Van Nieulande & Moerdijk, in Marquet, 2002 and *radiolyrata* s. str. in being typically inequilateral, with about 20 equidistant ribs at the umbo.

The new subspecies differs from the extant *G. (Glycymeris) pilosa* (Linnaeus, 1767) in the presence of prominent radial ribs on the umbo, which are absent in the majority of specimens of the latter. However, in some shells of that species similarly prominent ribs are present. In addition, the overall shell morphology can be similar, but the extant species has a more opisthogyrate umbo and a clearly asymmetrical cardinal area.

Discussion – Wood (1874-1879) and Glibert (1957) noted the similarity to the extant Mediterranean *Glycymeris (G.) pilosa*, and in particular to the inflated forma *tumida* Bucquoy, Dautzenberg & Dollfuss, 1891. It is obvious that there is some relationship between these two taxa.

Wood (1851, 1879) illustrated a specimen of a *Glycymeris* of an ‘elongated variety’ (in outer view, 1851, pl. 9, fig. 1d; inner view, 1879, pl. 6, fig. 4a), originating from Ramsholt and in the 1879 paper referred to as ‘*Pectunculus pilosus* var. *insubricus*’. The sole specimen of *G. (Glycymeris) radiolyrata exaggerata* nov. subsp. from East Anglia that we have seen was collected *in situ* from the Lower Pliocene Coralline Crag of Ramsholt Cliff (Pl. 2, figs 5a-b). The similarity between specimens illustrated by Wood and the present taxon, plus its provenance, suggest that Wood most probably had this subspecies before him.

Glibert (1957, pl. 1, fig. 4) provided an image of a valve that without doubt belongs here; this was stated to have come from the Lower Pliocene Luchtbal Member, as exposed during excavation of the Afrikadok in Antwerp. Glibert (1957, p. 17) remarked on this valve, ‘Au début du

Pliocène (Horizons à *Isocardia cor* et à *Pecten gerardi*) l’on rencontre en petit nombre, aux environs d’Anvers, la forme *pilosa-tumida* B.D.D., 1891 ... qui est épaisse, globuleuse, dont les crochets sont gonflés et assez opisthogyres, dont la surface externe est ornée, surtout dans la jeune âge, de costules rayonnantes obsolètes et des cordonnets concentriques étroits’. This description matches both *pseudodeshayesi* and *exaggerata* nov. subsp. However, the valve’s provenance from the Horizon with ‘*Isocardia cor*’, which is part of the Lower Pliocene Kattendijk Sand Member, in particular, is of interest here. The taxon discussed is not found *in situ* within the younger Luchtbal Member that was extensively sampled during the excavation of the Deurganckdok at Antwerp around the year 2000. At that locality, *G. (Glycymeris) radiolyrata pseudodeshayesi* and *G. (Chevronia) variabilis* were found *in situ*, co-occurring with reworked, eroded and rolled valves of *G. (Chevronia) obovata ringelei*.

A single articulated, well-preserved specimen in the former NITG/RGD collection, labelled ‘*Pectunculus pilosus*’ (lapsus for *pilosus*) has been studied. According to the accompanying label, the specimen originated from the ‘Scaldisian’ (= Upper Pliocene Oorderen Member) and contained sediment with ‘*Ditrupe*’ from the ‘Diestien’ (= Kattendijk Member) (see also Moerdijk & Van Nieulande, 2000, p. 8). The provenance of this specimen is unknown, but from the mentions of ‘Scaldisien’ and ‘Diestien’ it can safely be assumed that this was somewhere in the Antwerp area (Belgium). We examined this specimen in 1998, but failed to photograph it at the time. Unfortunately, it could not be traced following transfer of the NITG/RGD collections to Naturalis, Leiden (R. Pouwer, email November 2, 2019). All other Belgian specimens of *G. (Glycymeris) radiolyrata exaggerata* nov. subsp. that we have studied to date comprise more or less eroded and/or rolled loose valves from the base of the Oorderen Member in the Antwerp area. These levels generally contain numerous reworked fossils originating from the underlying Luchtbal and Kattendijk members. In short, it may be assumed that these glycymeridid valves were reworked from underlying strata.

Loose valves of the present subspecies have also been dredged from the bottom of the Western Scheldt (The Netherlands), their state of preservation being typical of fossils found there that are without doubt derived from equivalents of the Kattendijk Member, such as *Glycymeris (Chevronia) obovata ringelei* and *Astarte omalii* De la Jonkaiere, 1823. Most of these shells of *G. (G.) radiolyrata exaggerata* nov. subsp. are infested by polychaete worms (presumably the ichnogenus *Maeandropolydora* Voigt, 1965; see Cadée & Wesselingh, 2005, fig. 17 for a specimen of *Glycymeris* sp. with that kind of infestation) and/or clionaid boring sponges (ichnogenus *Entobia* Bronn, 1937). It is clear that this infestation occurred *in vivo*, because the shell interior often show burrows produced by worms (see Pl. 2, fig. 4b), lacking entry and exit holes. Such a high degree of infestation and perforations (see Pl. 2, figs 6a-c) is indicative of a period of low sedimentation rates, or even no deposition at all.

Based on the Ramsholt specimen (NITG/RGD collections), material illustrated by Wood (1851, 1879), Glibert's (1957) remarks on his 'forme' *pilosa-tumida*, the fact that the articulated specimen in the NITG/RGD collections apparently contains Kattendijk Member sediment, plus the near-exclusive occurrence in the basal Oorderen Member and the state of preservation of shells from the Western Scheldt, we may safely deduce that *G. (Glycymeris) radiolyrata exaggerata* nov. subsp. is of Early Pliocene (Zanclean) age.

***Glycymeris (Glycymeris) radiolyrata pseudodeshayesi* Van Nieulande & Moerdijk, in Marquet, 2002**

Addendum – Van Nieulande & Moerdijk (in Marquet, 2002) erected this new subspecies. However, the section 'Type material' in that paper did not comprise a clear designation of a holotype and possible paratypes (see comments by A.W. Janssen, 2002), thus failing to meet all requirements of Article 16.4 of the International Code of Zoological Nomenclature. Nomenclatural stability seems best served with the following addendum to Van Nieulande & Moerdijk (in Marquet, 2002):

Text to be inserted to the description of *Glycymeris (Glycymeris) radiolyrata pseudodeshayesi* on page 30 under 'Type material', and in front of 'RGM 394121': 'We designate herewith as the holotype'; change 'RGM 394121' to 'RGM.394121.a' and add after '... NIEULANDE (2000)': ' '; and as paratype IRSeNB IST 6515 (Pl. 13, figs. 1 a-d).'

***Glycymeris (Glycymeris) bimaculata* (Poli, 1795)**

Plate 3, figs 1a-c

- 1795 *Arca bimaculata* – Poli, 1795, p. 143, pl. 25 figs 17-18
 2017 *Glycymeris (Glycymeris) bimaculata* – Kopp & George (online).

Remarks – Both Kautsky's (1925) and IJspeert's (1942) records of *Pectunculus (Axinea) bimaculatus* actually refer to *G. (Chevonia) obovata baldii* Glibert & Van de Poel, 1965.

Description – This extant species may attain a large size; Sacco (1898) noted a maximum shell length of 145 mm; extant material may reach up to c. 115 mm in length. The larger of the two specimens discussed here measures 27.8 mm in length, *i.e.*, is immature. *Glycymeris (G.) bimaculata* is characterised by a globular shell with a typically orthogyrate umbo, finely reticulated outer surface and smooth cardinal area. In juvenile specimens the cardinal area is still inequilateral, but during growth it becomes typically equilateral. Large specimens may be very thick shelled.

Geographical and stratigraphical range – From the Early Miocene onwards, *G. (Glycymeris) bimaculata* s. lat. has

become widespread in the Mediterranean, Aquitaine and Loire basins. From Pliocene to present day, it has been confined to the Mediterranean and adjacent Atlantic Ocean. Two specimens from the Krinke Quarry at Werder (northern Germany), collected by Mrs R. Husmann, constitute the first confirmed record to date of *G. (Glycymeris) bimaculata* from the North Sea Basin. The fauna from the Krinke Quarry is of late Burdigalian/Langhian (Hemmoorian) age.

Discussion – Kautsky (1925) and IJspeert (1942) confused the superficially similar *Glycymeris (Chevonia) obovata baldii* with this well-known extant species. In fact, the two species co-occur in the Miocene fauna of the Krinke Quarry. The latter is recognised by a cardinal area which is sculptured by grooves and ridges arranged in chevrons whereas the shell surface is almost smooth. The subspecies *Glycymeris (G.) bimaculata deshayesi* (Mayer-Eymar, 1868) typically is more inflated; it has been recorded from the Miocene of the Loire Basin (France).

***Glycymeris (Glycymeris) auriculata* IJspeert, 1942**

Plate 3, figs 2-4

- 1942 *Glycymeris auriculata* IJspeert, pp. 53-55, pl. 4, figs 1a-b, 2a-c.
 1950b *Glycymeris* spec. 2 – Heering, pp. 35-36, pl. 8, figs 15, 16, 23.

Remarks – This species should not be confused with *Pectunculus auriculatus* Bronn, 1831, which currently is known as the limopsid *Limopsis* (s. lat.) *auriculata* (Bronn, 1831) (see also Bronn, 1848). Only three specimens of *Glycymeris (G.) auriculata* are known to date; the species appears to belong to the *G. textus* group of *Glycymeris* s. str.

Description – The lectotype, designated here (see Type material), measures 45.5 mm in height, 49.5 mm in length and 15.5 mm in thickness. Moderately convex species of *Glycymeris*, subequilateral, with perceptibly opisthogyrate umbo. Dorsal shell margin sloping downwards, and over short distance more or less straight to concave, especially anteriorly, giving shell an auriculated appearance. Surface ornament of large number of slightly irregular, flattened riblets, separated by narrow grooves and at umbo crossed by commarginal wrinkles. Ribs tending to split during ontogeny. Hinge moderately developed; extreme shell margins far from row of hinge teeth. Cardinal area narrow and clearly inequilateral, virtually smooth, except for some faint, superficial scars reflecting chevron structure of ligament. Inner shell margin crenulate; adductor muscle scars lying close to hinge plate.

Type material – Two left valves, Maasbree (The Netherlands), borehole Maasbree-Helden DB13, MAB-13 (B58B0004), coordinates 51.3453°N, 6.0130°E, 130-198.60 metres below surface; RGM.607694 (lectotype, desig-

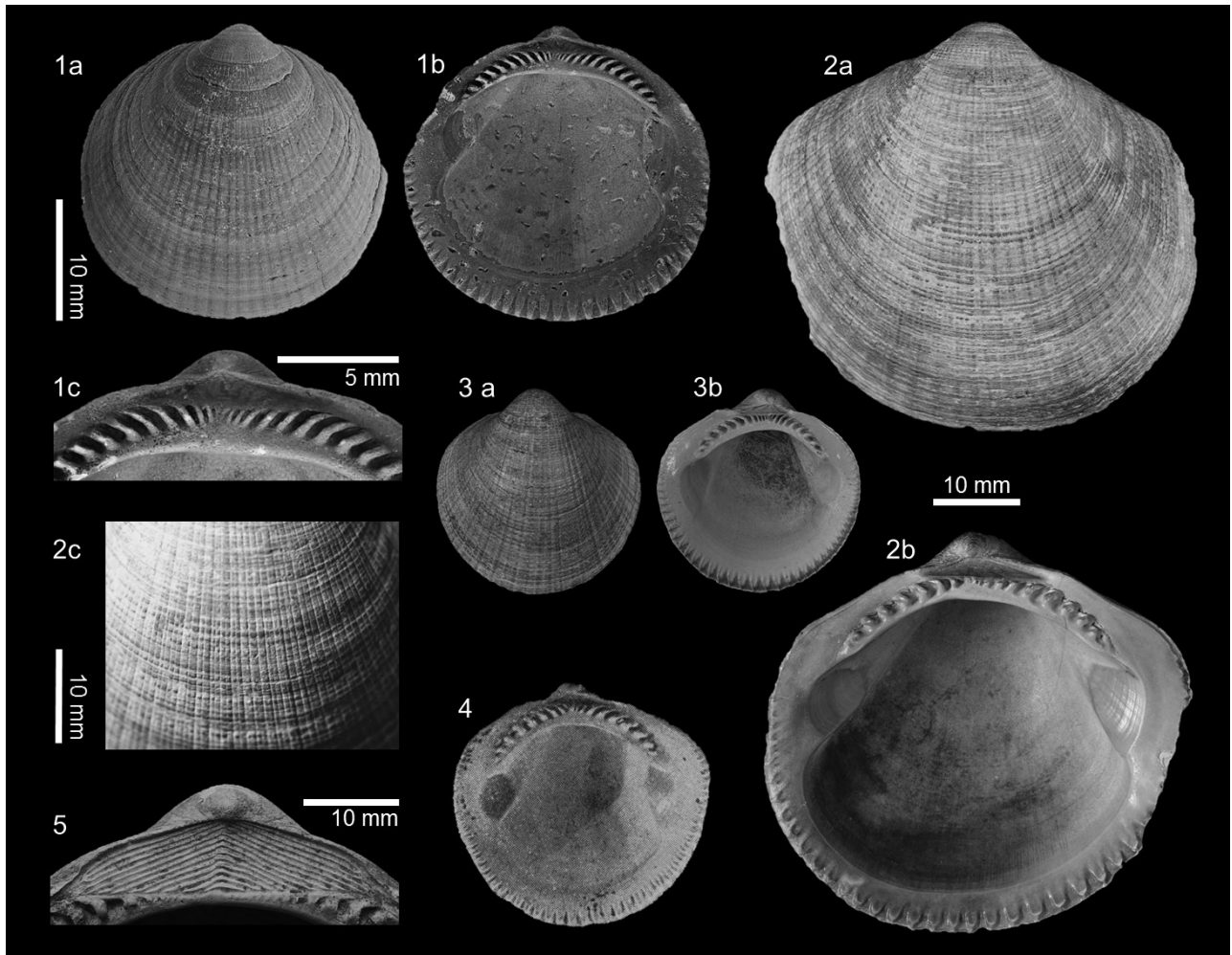


Plate 3. *Glycymeris (Glycymeris) bimaculata* (Poli, 1795), 1. R. Husmann Collection, Krinke Quarry, Werder (near Bremen, Germany), Miocene, Hemmoorian: a. outer view, b. inner view, c. cardinal area.

Glycymeris (Glycymeris) auriculata IJspeert, 1942; 2-4. Maasbree (The Netherlands), borehole Maasbree-Helden DB13, MAB-13 (B58B0004), Miocene: 2. RGM.607694, lectotype, left valve: a. outer view, b. inner view, c. detail of surface ornament; 3. RGM.1357588, right valve: a. outer view, b. inner view; 4. Paralectotype, left valve, inner view (copied from IJspeert, 1942).

Glycymeris (Chevronia) obovata baldii Glibert & Van de Poel, 1965; 5. Moerdijk Collection, Antwerp-Berchem (Belgium), Miocene, *ex situ*, cardinal area of left valve.

Photographs: R. Husmann (1), R. Pouwer (Naturalis, Leiden) (2 and 3) and the authors (5). Scale bars equal 10 mm.

nated herein); the paralectotype (designated herein) is the specimen illustrated by IJspeert (1942, pl. 4, figs 1a-b), the present whereabouts of which are unknown to us.

Other material studied – RGM.1357588, a subadult right valve, from the same borehole at Maasbree and discussed in open nomenclature by Heering (1950a), who apparently did not recognise this as belonging to IJspeert's species.

Geographical and stratigraphical range – The three specimens of *G. (Glycymeris) auriculata* known to date all originate from Diepboring 13 at Maasbree, in which they co-occur with other Miocene molluscan species (IJspeert, 1942; Van Voorthuysen, 1944; Heering, 1950b), such as the bivalves *Yoldia glaberrima* (Münster, in Goldfuss, 1835), *Anadara diluvii* (Lamarck, 1805),

Limopsis aurita (Brocchi, 1814), *Hinnites ercolianus* Cocconi, 1873, *Glossus lunulatus* (Nyst, 1835), *Venus nux* (Gmelin, 1791) (= *Cytherea multilamella* Lamarck, 1818) and the gastropods *Turritella subangulata* (Brocchi, 1814) and *Aporrhais dingdenensis* Marquet, Grigis & Landau, 2002. According to Van Voorthuysen (1944), the fauna of these boreholes consisted almost exclusively of Middle Miocene ('Hemmoor Stufe') species. The Hemmoorian corresponds to the upper Burdigalian and lower Langhian (DSK, 2016).

Discussion – Wagner & Abbott (1982) listed '*Pectunculus auriculatus* Bronn, 1831' without any specific motivation as a species of *Glycymeris*, so that IJspeert's name would appear to be preoccupied. However, Bronn (1831) described his new species as, 'Ganz die Form von *P. auritus*', the latter which is *Limopsis aurita* (Broc-

chi, 1814) in current nomenclature. Bronn (1848) subsequently transferred *P. auriculatus* to *Limopsis*. Thus the attribution by Wagner & Abbott of *Pectunculus auriculatus* to *Glycymeris* is erroneous and IJspeert's name *Glycymeris auriculata* IJspeert, 1942 must be retained.

Subgenus *Chevronia* Moerdijk & Van Nieulande, 2000

Type species – *Pectunculus obovatus* Lamarck, 1805, by original designation.

Remarks – Moerdijk & Van Nieulande (2000) introduced this subgenus for glycymeridids in which the cardinal area had an incised repetitive chevron pattern of grooves and ridges and a slightly developed surface ornament consisting of fine, predominantly radial threads, although shells are occasionally notched with distant radial grooves. To date, no extant representative of this subgenus is known to us.

The duplivincular cardinal area in the subgenus *Chevronia* is of the regular symmetrical type (Malchus, 2004), consisting of a regular repetitive pattern of chevron-shaped, alternating grooves and ridges, starting at the earliest growth stage of the dissoconch. Of note is the fact that, in addition to the regular chevrons, there is always one additional ridge in the anterior part of the cardinal area in *Chevronia*.

Characteristics of the periostracum have not been observed. Judging from the modestly developed (often obsolete) surface ornament in *Chevronia*, it may be inferred that the periostracum in this subgenus was thin and could easily be abraded. Another hypothesis is that the distant radial grooves present in some species represent the base of radial rows of better-developed periostracal hairs.

In well-preserved specimens of *G. (Chevronia) variabilis*, the fibrous tissue of the ligament is occasionally preserved, while the lamellar elastic tissue is invariably missing. In such specimens it can be observed that the plane of adherence of the fibrous ligament layers is tilted towards the dorsal side of the shell. Thus, the lamellar tissue apparently adhered to the ventrally directed part of the ridges.

For Late Oligocene (Chattian) species of *Chevronia* the names *G. lunulata* (Nyst, 1836) and *G. philippii* (Deshayes, 1860) have been used. Here we follow A.W. Janssen (1984), who preferred the name *G. obovata*, but it must be stressed that taxonomic and nomenclatural issues relating to Oligocene representatives of *Chevronia* have not yet been solved satisfactorily. The subgenus can be traced back to at least the Palaeocene *G. (Chevronia) terebratularis* (Lamarck, 1805).

For illustrations and descriptions of and discussions on *Glycymeris (Chevronia) variabilis* and *Glycymeris (Chevronia) obovata ringelei*, reference is made to Moerdijk & Van Nieulande (2000).

Glycymeris (Chevronia) obovata baldii Glibert & Van de Poel, 1965

Plate 3, fig. 5

- (?)1845 *Pectunculus variabilis* – Nyst, p. 249 (*partim*).
- 1925 *Pectunculus (Axinea) bimaculatus* – Kautsky, pp. 18, 19, pl. 2, fig. 2 (*non* Poli).
- 1942 *Glycymeris (Glycymeris) bimaculata* – IJspeert, pp. 49-53, pl. 3, figs 4-6 (*non* Poli).
- 1945 *Glycymeris (Glycymeris) pilosa deshayesi* – Glibert, p. 44, pl. 1, fig. 13 (*non* Mayer-Eymar).
- 1959 *Glycymeris (Glycymeris) pilosa deshayesi* – Anderson, p. 83, pl. 13, fig. 7a-c (*non* Mayer-Eymar).
- 1962 *Glycymeris (Glycymeris) pilosa deshayesi* – Baldi, pp. 115-120 (*partim non* Mayer-Eymar).
- 1964 *Glycymeris (Glycymeris) pilosa deshayesi* – Anderson, pp. 131, 132 (*non* Mayer-Eymar).
- 1965 *Glycymeris (Glycymeris) lunulata baldii* – Glibert & Van de Poel, p. 85.
- 1984 *Glycymeris (Glycymeris) obovata baldii* – A.W. Janssen, pp. 47, 48, pl. 22, fig. 8a, b.
- 2005 *Glycymeris (Chevronia) obovata baldii* – Schnetler, p. 73, pl. 1, fig. 11a, b.
- 2010 *Glycymeris (Chevronia) obovata baldii* – Moths *et al.*, p. 11, figs 8a, 9e.
- 2020 *Glycymeris (Chevronia) baldii* – Everaert *et al.*, pl. 2, figs 1-6.

Description – Relatively large shell, length up to at least 90 mm, rather longer than high and, as a rule, posteriorly longer than anteriorly. Surface almost smooth, with very fine radials. In some specimens, distant radial grooves. Hinge teeth moderately developed. Cardinal area equilateral, with up to 11 grooves and ridges in chevron arrangement, typical of subgenus.

Geographical and stratigraphical range – In strata of late Burdigalian, Langhian and Serravalian age in Germany, Belgium and the Netherlands, *G. (Chevronia) obovata baldii* is a common to dominant endemic faunal element. It is particularly abundant in the Antwerp Member (Miocene) in the vicinity of Antwerp (Belgium), where it occurs in near-monospecific coquinas (Glibert, 1945). It has also been recorded from the upper Miocene (Tortonian) of Antwerp (Bosselaers *et al.*, 2004) and of Gram, Denmark (Schnetler, 2005).

Discussion – This subspecies is not closely related to *G. (Glycymeris) bimaculata* nor to *G. (Glycymeris) bimaculata deshayesi* (which is not a subspecies of *pilosa*) from which it can be easily differentiated by the clear chevrons on the cardinal area. Its supposed descendant, *G. (Chevronia) obovata ringelei*, is smaller and typically equilateral with an orthogyrate umbo and has relatively longer hinge teeth.

We here opt to maintain *G. (Chevronia) obovata baldii* as subspecies of its presumed ancestor, *G. (Chevronia) obovata obovata*, rather than as separate species. The only feature to discriminate between both subspecies is that *G. (Chevronia) obovata baldii* attains larger sizes.

The shell variability among material from a range of Miocene strata in the Antwerp area has recently been discussed by Everaert *et al.* (2020).

Subgenus *Pseudaxinea* di Monterosato, 1892

Type species – *Pectunculus violacescens* Lamarck, 1819 (= *P. nummaria* Linnaeus, 1758), by original designation.

Remarks – Van Nieulande (2009) referred to *Glycymeris* (*Intercalaria*?), but this is a junior synonym of *Intercalaria* Filatova & Schileyko, 1984, which is a subgenus of *Parayoldiella* Filatova, 1971 (Bivalvia, Nuculanidae).

Description – Shells rounded to subtrapezoid; posterior part of ventral margin often tending to be straight. Outer ornament predominantly commarginal, most marked in young shells and at umbo in adult shells. During ontogeny, shells often becoming gradually smooth. In juvenile shells, ligament of simple duplivincular type; during growth irregular alternating sheets added, leading to irregularly intercalating, imbricated ligament grooves and ridges in cardinal area.

Differentiation – Both *Glycymeris* s. str. and *Chevronia* are principally orbicular and the dorsal margins in young specimens are shorter and tend to merge gradually with the anterior and posterior sides. Their ligament is of the regular repetitive duplivincular type (see Malchus, 2004), in which the development of the repetitive pattern starts at the earliest stage of growth of the dissoconch and covers the entire ligament area. In *Chevronia* the sheets of the ligament cause an incised regular pattern of grooves and ridges in the cardinal area, whereas in *Glycymeris* s. str. the cardinal area remains more or less smooth. *Glycymeris* s. str. and *Chevronia* show a predominantly reticulate or radial surface ornament, respectively, that tends to become obsolete in the latter subgenus.

Discussion – It was di Monterosato (1892) who noted that the extant *G. nummaria* differed from congeners in overall morphology as well as in surface ornament. However, the main difference is in the ligament and the cardinal area to which the ligament is attached. In early developmental stages, the angle of the cardinal area with the hinge plate (in lateral view) is rather small and the ligament can be described as simply duplivincular, with an anterior and posterior elastic lamella bordering the dorsal sides of the cardinal area. The remainder of this area is covered with fibrous tissue. In a more advanced growth stage some deep, irregularly intercalating ligamental grooves cut into the cardinal area. The grooves reflect the development of secondary elastic lamellae within the ligament. The first one of these lamellae appears on the anterior side of the area. This kind of ligament pattern is of the irregular alternating type (according to Malchus, 2004). We have seen specimens of *G. nummaria* not smaller than 40 mm with the basal duplivincular kind of ligament, while in other specimens a second groove has been seen to be inserted

when it is not larger than *c.* 25 mm. In large individuals the arrangement of grooves often tends to become regular and at first glance may resemble that of *Chevronia*. However, in *Pseudaxinea* these grooves do not occur at the earliest stage of growth of the dissoconch.

It are not only shell characters that turn *G. nummaria* into an outsider within the family Glycymerididae. Combosch & Giribet (2016) and Purroy *et al.* (2016) conducted molecular genetic research on both of Linnaeus's species, *Pectunculus nummaria* and *P. glycymeris*; Purroy *et al.* (2016) also included the extant European species *G. pilosa* and *G. bimaculata* in their analysis. Both research teams recorded deep genealogical divergence between *G. nummaria* on the one hand and other species of *Glycymeris* analysed on the other. The estimated divergence time for the *G. nummaria* clade is Early Cretaceous.

A related species of *Glycymeris* with this kind of irregularly alternating ligament is *G. obtusata* (Parsch, in Hörnes, 1864), a compact triangular species from the Miocene of the Vienna Basin in Austria (see Pl. 4, fig. 5). An extant species that appears to be related as well is *G. concentrica* (Dunker, 1853) (see Pl. 4, figs 6a-c), which belongs to the West African fauna. As far as ligament type is concerned, *G. nummaria*, *G. obtusata* and *G. concentrica* differ from all other glycymeridids known to us to date. They share this particular type with some representatives of the families Arcidae and Cucullaeidae. The irregularly alternating ligament in *Pseudaxinea* is consistent with the conclusion reached by Nicol (1950) that glycymeridids most probably evolved from cucullaeids.

Considering the conservatism within this family (Thomas, 1975), the deep genealogical divergence time of *G. nummaria* from *Glycymeris* s. str. inferred from molecular genetic data as well as specific shell traits that differ from those of *Glycymeris* s. str., *G. nummaria*, *G. obtusata* and *G. concentrica* would appear to deserve at least subgeneric rank. The subgeneric name *Pseudaxinea* di Monterosato, 1892 is available for this lot.

Material studied – *Glycymeris* (*Pseudaxinea*) *concentrica* (Dunker, 1853): ZMA.MOLL.8944, (1 left valve; ex N. Koekkoek Collection, 1998), Senegal, Baie de Harin, 5-10 metres, 1985. *Glycymeris* (*Pseudaxinea*) *obtusata* (Parsch in Hörnes, 1864): ETH Zürich (1 left valve, Mayer-Eymar Collection, lot G 17119), Buituri (Romania), Middle Miocene (Badenian); Senckenberg Naturmuseum Frankfurt, 4 valves, Ritzing, Burgenland, Austria, Middle Miocene (Badenian); H.P.J. Keukelaar Collection (now in Naturalis, Leiden), 2 valves, Ritzing, Burgenland, Austria, Middle Miocene (Badenian).

***Glycymeris* (*Pseudaxinea*) *nummaria* (Linnaeus, 1758)**
Plate 4, figs 1-4

- 1758 *Arca nummaria* Linnaeus, p. 695.
- 1997 *Glycymeris cor* (Lamarck, 1805) – Moerdijk & Van Nieulande, p. 60.
- 1999 *Glycymeris* (*Subgenus* 2) *cor* (Lamarck, 1805) – Van Nieulande & Moerdijk, p. 21, pl. 27, figs 2a-b.

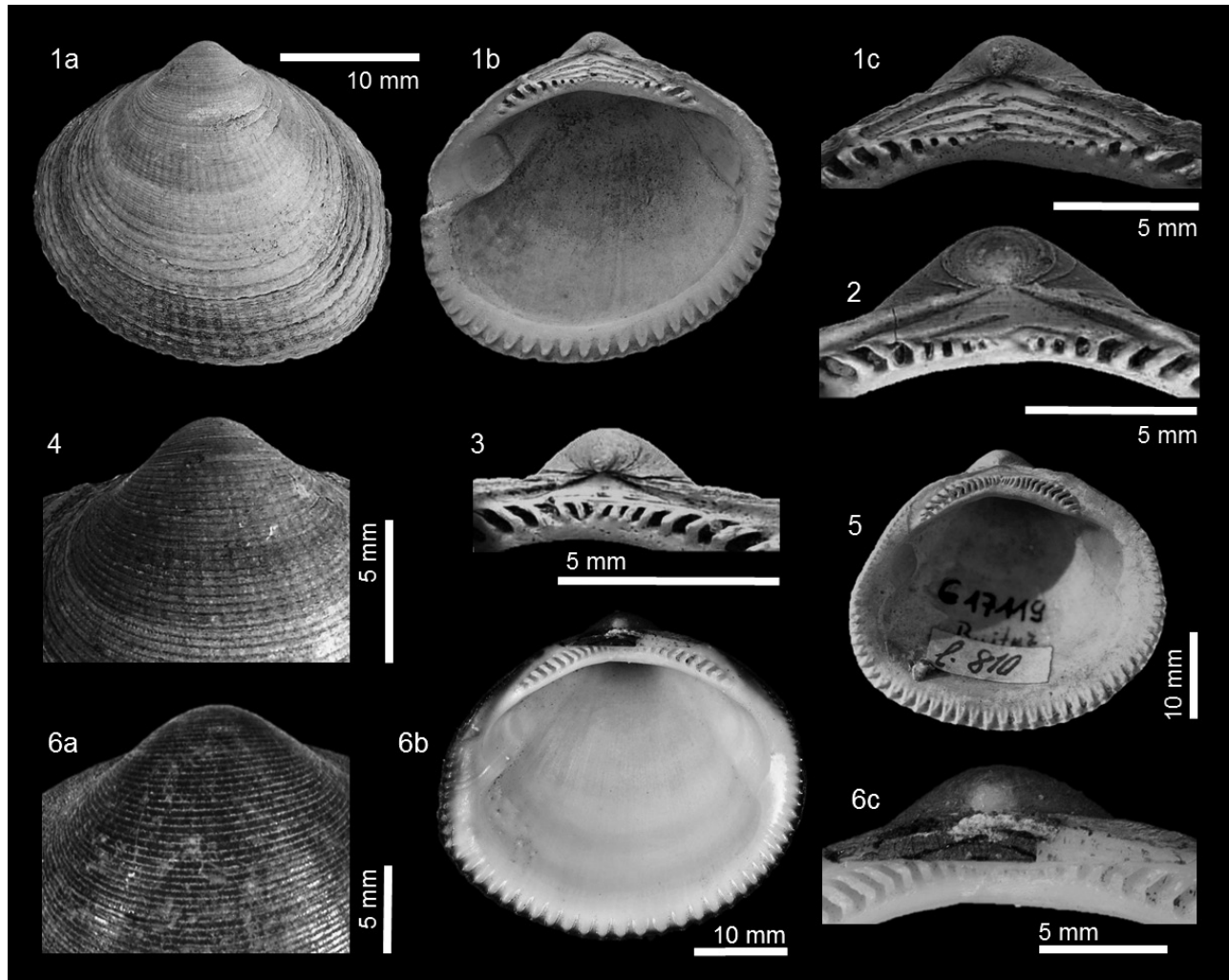


Plate 4. *Glycymeris (Pseudaxinea) nummaria* (Linnaeus, 1758); 1-4. R. Husmann Collection, Krinke Grube, Werder (northern Germany), Miocene, Hemmoorian: 1a. outer view, b. inner view, c. cardinal area with four additional ligament grooves; 2. cardinal area with first and second irregular ligament groove; 3. cardinal area of young specimen with basically duplivincular ligament; 4. detail of surface ornament at umbo.

Glycymeris (Pseudaxinea) obtusata (Parsch in Hörnes, 1864); 5. 'Bujtur, Siebenbürgen' (= Buituri, Romania), Miocene, Badenian, ETH Zürich, Mayer-Eymar Collection, lot G 17119: inner view of left valve.

Glycymeris (Pseudaxinea) concentrica (Dunker, 1853); 6. ZMA.MOLL.8944, Senegal, Baie de Harin, 5-10 metres depth, 1985, left valve: a. detail of surface ornament at umbo; b. inner view, c. cardinal area with ligament.

Photographs: R. Husmann (1-4), the authors (5) and R. Pouwer (Naturalis, Leiden) (6).

- 2010 *Glycymeris (?Intercalaria) cor* (Lamarck, 1805) – Moths *et al.*, pp. 11-12, figs 8b, c, 9a-d; pl. 2, fig. 3a, b.
- 2017 *Glycymeris (Glycymeris) nummaria* (Linnaeus, 1758) – Kopp & George [online, GLY02, GLY03]
- non 1845 *Pectunculus nummarius?* – Nyst, p. 253, pl. 26, figs 3a-b.
- non 1879 *Pectunculus pilosus* var. *insubricus* – Wood, p. 43, pl. 6, figs 4a-b.
- non 1879 *Pectunculus glycymeris* var. *nummarius* – Wood, p. 43, pl. 6, fig. 5b.

Description – Well-known, extant species, currently primarily occurring in the Mediterranean and adjacent Atlantic Ocean, in well-sorted sands at depths ranging between

2 and 40 m (Legac & Hrs-Brenko, 1999). Shells rounded to subarcoid, with largest diameter well behind shell middle. Juvenile specimens orbicular, with dorsal margins showing marked angle to lateral margins. Adult specimens with posterior part of ventral margin often tending to be straight. External ornament predominantly commarginal, most marked in young shells. During ontogeny shell often becoming gradually smooth. In juvenile shells, ligament of simple duplivincular type; during growth irregular alternating sheets added, leading to irregularly intercalating, imbricated ligamental grooves and ridges in cardinal area.

Geographical and stratigraphical range – In the Aquitaine Basin, this species occurs in Aquitanian, Burdigalian, Langhian and Serravallian strata (Cahuzac *et al.*,

1993). It is also well-known in the Neogene of the Mediterranean (e.g., Sacco, 1898). In the Nantes area (France), it has been found in outcrops of Redonian (Upper Miocene) strata (Lauriat-Rage, 1981).

During the Miocene, *Glycymeris (Pseudaxinea) nummaria* appears to have been confined within the North Sea Basin to the Hemmoorian (upper Burdigalian/lower Langhian), occurring at the Krinke quarry near Werder, northern Germany (Moerdijk & Van Nieulande, 1997; Moths *et al.*, 2010) and to the Burdigalian Edegem Sand Member in north-west Belgium (see Moerdijk & Van Nieulande, 1997). According to Moths *et al.* (2010), *G. (Pseudaxinea) nummaria* was very common and outnumbered *G. (Chevronia) obovata baldii* at the Krinke quarry.

Discussion – Another name used for the present-day species is *G. insubrica* (Brocchi, 1814), which appears to be a junior synonym; for fossil specimens the name *G. cor* (Lamarck, 1805) is often found in the literature. Although Miocene material from Aquitaine is polymorphous and some extreme morphs might be designated (see Cahuzac *et al.*, 1993), specimens that cannot be distinguished from extant ones are common. Material from the North Sea Basin shows no essential differences with Miocene specimens of Aquitaine and recall those of the “morphé aplatie” (*sensu* Cahuzac *et al.*, 1993) in particular.

The name *Pectunculus nummarius* is used with a query by Nyst (1845) for a small specimen from Vliermaal (Belgium), of Oligocene age. This obviously does not belong to this taxon and probably is a juvenile individual of *G. (Chevronia) caproensae* Marquet, Lenaerts & Laporte, 2012. Neither *Pectunculus pilosus* var. *insubricus*, nor *Pectunculus glycymeris* var. *nummarius* from the Coraline Crag illustrated in Wood (1879) can be recognised as the present species.

Material studied – Two valves (R. Marquet Collection) from Wilrijk (Belgium), Edegem Sand Member, Miocene; two valves (J. van der Voort Collection) from Krinke Quarry, Werder, near Bremen (Germany), Miocene.

Concluding remarks on Neogene and Pleistocene Glycymerididae of the North Sea Basin

Prior to the onset of the Neogene, during the Late Oligocene (Chatthian), there were two glycymeridids present in the North Sea region, namely *G. (Glycymeris) agnosta* and *G. (Chevronia) obovata obovata* (Lamarck, 1819). The latter is undoubtedly the precursor of the Miocene *G. (Chevronia) obovata baldii*, which ranged throughout the Miocene in the North Sea Basin.

The brief appearance of *G. (Pseudaxinea) nummaria* and *G. (Glycymeris) bimaculata* in this basin once again provides evidence of a connection between the North Sea Basin and the Aquitaine Basin in south-west France during the Late Burdigalian and Langhian (Moths *et al.*, 2010). In view of the fact that both *G. (Pseudaxinea) nummaria* and *G. (Glycymeris) bimaculata* are restricted mainly to the Mediterranean at the present day, this is evidence of a tem-

porarily subtropical climate in the North Sea area during this part of the Miocene. We cannot exclude that *G. (Glycymeris) auriculata* is closely related to *G. (Glycymeris) textus* and thus also an example of this North Sea/Aquitaine connection. However, features of the ornament and cardinal area could also hint at a relationship with the Chattian North Sea Basin species, *G. (Glycymeris) agnosta*.

In the Lower Pliocene (Zanclean) Kattendijk Member, *G. (Chevronia) obovata ringelei* is the common glycymeridid, and undoubtedly a descendant of the Miocene *G. (Chevronia) obovata baldii*. *Glycymeris (Glycymeris) radiolyrata exaggerata* nov. subsp. makes its first appearance during the Early Pliocene, and is uncommon. It certainly is of Zanclean age and appears to be an immigrant from a more southerly origin, possibly having a common ancestry with *G. (Glycymeris) pilosa*. The younger subspecies, *G. (Glycymeris) radiolyrata pseudodeshayesi* appears in the Lower Pliocene (upper Zanclean) Luchtbal Member in Belgium and is probably the descendant of *G. (G.) radiolyrata exaggerata* nov. subsp.

Glycymeris (Chevronia) obovata ringelei probably evolved into *G. (Chevronia) variabilis*. Thus, during the entire Neogene the phylogenetic species *G. (Chevronia) obovata* s. lat. was present in the North Sea Basin. The earliest appearance of *G. (Chevronia) variabilis* is in the upper Zanclean (Lower Pliocene) Coraline Crag (Sudbourne Member) in England and the Luchtbal Member in Belgium; the species ranges into the Upper Pliocene (Piacenzian), where it co-occurs with *G. (Glycymeris) radiolyrata radiolyrata*, which descended from *G. (Glycymeris) radiolyrata pseudodeshayesi*. Both Pliocene taxa (*G. (Chevronia) variabilis* and *G. (Glycymeris) radiolyrata radiolyrata*) appear to have been endemic to the North Sea Basin. At the beginning of the Pleistocene they had already gone extinct. During the Early Pleistocene (Gelasian), *G. (Glycymeris) glycymeris* appears in the North Sea Basin. There seems to be no close relationship to either *G. (Chevronia) variabilis* or *G. (Glycymeris) radiolyrata* s. lat. The species appears to occur also in deposits from Middle and/or Late Pleistocene age and is still a member of the extant fauna of the North Sea. The species is the only extant representative of *Glycymeris* in western Europe north of Portugal and is evidently adapted to more boreal conditions than the other extant western European Glycymerididae.

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		<i>Glycymeris s.s.</i>	<i>Chevronia</i>	<i>Pseudaxinea</i>
Pleistocene	Late Pleistoc			
	Gelasian			
Pliocene	Piacenzian	<i>r. radiolyrata</i>	<i>variabilis</i>	
	Zanclean	<i>r. pseudodeshayesi</i> <i>r. exaggerata</i>	<i>obovata ringelei</i>	
Miocene	Messinian			
	Tortonian			
	Serravallian		<i>obovata baldii</i>	
	Langhian	<i>auriculata</i> <i>bimaculata</i>		<i>nummaria</i>
	Burdigalian			
	Aquitanian	?		
Oligocene	Chattian	<i>agnosta</i>	<i>obovata obovata</i>	

Figure 1. Stratigraphical ranges of Neogene and Quaternary (Pleistocene) glycymeridids in the North Sea Basin.

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