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REVISION OF PLIOCENE GLYCYMERIDIDAE (MOLLUSCA, BIVALVIA) FROM THE NORTH SEA BASIN

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The systematic status of Pliocene glycymeridid bivalves from the North Sea Basin is discussed. *Chevronia* n. subgen., *Glycymeris (Chevronia) obovata ringelei* n. subspec., G. *(Glycymeris) radiolyrata* forma *pseudodeshayesi* n. forma, and *G. (G.) radiolyrata* forma *exaggerata* n. forma, are proposed as new. Lectotypes are designated for *G. (Ch.) obovata obovata* (Lamarck, 1819) and *G. (Ch.) variabilis* (J. de C. Sowerby, 1824).

Key words — Bivalvia, Glycymeridae, Pliocene, North Sea Basin, systematics, new taxa.

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INTRODUCTION

In the literature on Neogene molluscs from the North Sea Basin, there is little agreement over the systematic status of Pliocene Glycymeridae. Moerdijk & van Nieulande (1995) have recently noted that most previous authors had lumped *Glycymeris variabilis* and *G. radiolyrata*. In the present paper, results of a study of representatives of *Glycymeris* from the North Sea Basin Pliocene, originating from temporary excavations in Belgium (see Marquet, 1995 for details), borehole material from the Netherlands, dredged and beach fossil material as reworked from especially Pliocene strata in the province of Zeeland (the Netherlands), as well as from the Pliocene Coralline and Red crags (England). Specimens from the Miocene (Helvetian, Redonian) and Pliocene (Redonian) of France have been studied for comparison.

Moerdijk & van Nieulande (1995) concluded that, apart from external ornament, details of the ligament area are important within the Glycymeridae. In the present paper, a new subgenus, *Chevronia*, is introduced for those shells that show combined features of ligament and external ornament. Other fossil species from western, central and southern European localities have been studied; a few are here referred to the new subgenus. Stratigraphic data concerning Belgian material described in the present paper are according to De Meuter & Laga (1976).

The very common glycymeridids from the Lower Pliocene (Kattendijk Formation) of Belgium have turned out to be related to the Miocene *G. obovata baldii* Glibert & van de Poel, 1965 and are here described as a new subspecies, *G. obovata ringelei*. Lectotypes are designated for *G. obovata obovata* and *G. variabilis*.

SYSTEMATIC DESCRIPTIONS

Abbreviations — To denote the repositories of

specimens illustrated and/or referred to in the text the following abbreviations are used:

BMNH The Natural History Museum, London (Department of Palaeontology) (formerly British Museum of Natural History);
RGM Nationaal Natuurhistorisch Museum (Department of Palaeontology, Cainozoic Mollusca), Leiden (the Netherlands; formerly Rijksmuseum van Geologie en Mineralogie);
NITG Nationaal Instituut voor Toegepaste Geowetenschappen-TNO, Utrecht, the Netherlands;
KZGW Koninklijk Zeeuwsch Genootschap der Wetenschappen, Middelburg, the Netherlands.

Order Arcoida Stoliczka, 1871
Superfamily Limopsacea Dall, 1895
Family Glycymerididae Newton, 1922
Subfamily Glycymeridinae Newton, 1922

Remarks — Moerdijk & van Nieulande (1995) noted that two groups of glycymeridids were represented in the Pliocene North Sea Basin material, which could be distinguished by using the following characters:

- external ornament;
- ornament of ligament area.

Useful, but less important, characters are:

- shell form, *i.e.* outline and convexity;
- shell thickness;
- dimensions;
- form of ligament area;
- form and position of adductor muscle scars;
- characters of juvenile shells.

With respect to the importance of characters of external shell ornament, we agree with earlier authors, *e.g.* Nicol (1956); however, features of the ligament have only rarely been considered important. In our experience, however, these are very uniform within a species and quite constant in phylogenetic development. Combining external ornament and ligament area ornament leads to a good basis for (sub)generic divisions of glycymeridids.

Genus *Glycymeris* da Costa, 1778
Subgenus *Chevronia* n. subgen.

Type species — *Arca obovata* Lamarck, 1819. According to Janssen (1979), *Glycymeris obovata obovata* (see Pl. 1, Fig. 1) has often been misinterpreted, and is in need of nomenclatural stability. We here designate as lectotype of *G. o. obovata* the specimen illustrated in Favre (1918, pl. 34, fig. 230a-c). This valve has a label in Lamarck's handwriting associated.

Derivatio nominis — In allusion to chevrons on the ligament area.

Diagnosis — Glycymeridids with subcircular, subequilateral shells, external ornament almost obsolete to fine, and when present consisting mainly of radial elements, occasionally with distinct, distant, radial grooves; ligament area with well-developed, regular chevron-shaped ligamental grooves.

Other species — The following (sub)species (see Mayer-Eymar, 1868; Báldi, 1962; Maestrati & Lozouet, 1996) we have studied may be attributed to the new subgenus:

G. (Ch.) fichteli (Deshayes, 1852)
G. (Ch.) latiradiata latiradiata (Sandberger *in* Gümbel, 1861)
G. (Ch.) l. obovatoides Báldi, 1962
G. (Ch.) l. subfichteli Báldi, 1962
G. (Ch.) obovata baldii Glibert & van de Poel, 1965
G. (Ch.) poustagnacensis Maestrati & Lozouet, 1996
G. (Ch.) saucatsensis (Mayer-Eymar, 1868) (*non* Cossmann & Peyrot, 1914)
G. (Ch.) subterebratularis (d'Orbigny, 1852)
G. (Ch.) turonica (Mayer-Eymar, 1868)

We have not (yet) seen any Recent species.

Remarks — Other glycymeridid shells with well-developed ligament grooves have been referred to the genera *Melaxinaea* Iredale, 1930 and *Tucetona* Iredale, 1931. However, both of these show, in contrast with *Chevronia*, a pronounced external ornament.

Glycymeris (s. lat.) *cor* (Lamarck, 1805), which has also been described as *G. violascens* (Lamarck, 1819), *G. nummaria* (Linné, 1758) and *G. insubrica* (Brocchi, 1814), also has ligament grooves, but these are irregular, often intercalating under the beaks and start their development in varying stages of growth. In juveniles, the ligament area is always smooth. In addition, juvenile shells show a marked concentric ornament. The subgeneric classification of this species and its close relatives, will have to be revised.

Glycymeris (Chevronia) obovata ringelei n. subsp.
Pl. 1, Fig. 2

1878-81 *Pectunculus glycymeris* L., var. *transversa* — Nyst, p. 166 (*partim, non* Wood), pl. 17, fig. 8b?, e, g.
?1950 *Glycymeris (Gl.) pilosa* (Linné, 1767) — Heering, p. 33, pl. 8, figs 9, 10.
1957 *Glycymeris glycymeris* Linné sp. 1758 forme *variabilis* Sowerby, 1824 — Glibert, p. 16 (*partim*).
1962 *Glycymeris variabilis deshayesi* (Mayer, 1868) — van Regteren Altena *et al.*, p. 14, pl. 5, fig. 18a.

1965 *Glycymeris* (s.s.) *glycymeris variabilis* (Sowerby, 1824) — Glibert & van de Poel, p. 83 (*partim*).
1974 *Glycymeris glycymeris kattendijkensis* Ringelé (MS name).
1979 *Glycymeris glycymeris pilosatumida* (Bucquoy, Dautzenberg & Dollfus, 1891) — Geys & Marquet, pl. 14, fig. 4.

Diagnosis — Glycymeridid with a thick and inflated, subcircular, orthogyrate, equilateral shell, with external ornament consisting of very fine radial threads and often some distant radial grooves, with well-developed hinge teeth, an equilateral ligament area with distinct, rather coarse chevrons and adductor muscle scars of about equal height and width, in contact with hinge plate.
Locus typicus — Fifth harbour dock, Antwerp (Belgium).
Stratum typicum — base Kattendijk Formation, Pliocene.
Derivatio nominis — Named after A. Ringelé, who was the first to recognise it as a distinct taxon.
Types — Holotype is RGM 394 099 (a bivalved specimen) from Antwerp (5th harbour dock, 12 April 1971), base Kattendijk Formation (*ex* van Nieulande Colln); paratypes are four bivalved specimens (van Nieulande Colln, no. 108) from the type locality and level, and four bivalved specimens (van Nieulande Colln, no. 110) from Kallo (?tunnel construction pit).
Other material — **Kallo** (Beveren tunnel construction pit, Kattendijk Formation), 5 bivalved specimens, 1 valve (van Nieulande Colln, nos 106, 107); **Antwerp** (connection 5th harbour dock to Amerika dock), 14 valves, 2 bivalved specimens (RGM 494 115); **Kallo** (Beveren tunnel construction pit, base Oorderen Member, Lillo Formation), 4 bivalved specimens, 5 valves (van Nieulande Colln, nos 112, 113); **Kallo** (tunnel works, base Oorderen Member), 9 bivalved specimens (van Nieulande Colln, no. 109); **Antwerp** (Kaai 27, ?Luchtbal Member), 1 valve (van Nieulande Colln, no. 90, leg. A. Haandrikman); **Ellewoutsdijk/Baarland** (Western Scheldt, dredged, derived Pliocene), 47 valves (Moerdijk Colln); **Borsele** (de Kaloot, province of Zeeland, beach material, derived Pliocene), 2 valves (van Nieulande Colln, no. 102); **Sutton** (Suffolk, England, Coralline Crag, *ex* P. Cambridge Colln/L. van der Slik), 1 worn valve (cf. *Glycymeris o. ringelei*, RGM 394 116).
Description (holotype) — Height, width and semi-diameter of right valve are 54.2, 58.2 and 18.5 mm, respectively; of left valve 54.2, 58.3 and 18.7 mm, respectively. Thick and firm, inflated, almost orthogyrate, near-equilateral, broadly oval, posterior side slightly longer, transition from upper margins into ventral margin somewhat shorter rounded; umbones protruding. Shell surface almost smooth, with very fine, somewhat irregular, radial threads; with a few distant radial grooves, in this respect reminiscent of *G. latiradiata*. Hinge well developed with rather long teeth, continuing under ligament area (13 anterior, 12 posterior). Ligament area near equilateral, rather high, with incised chevrons (9 anterior, 8 posterior). Adductor muscle scars large, broad and callous, almost touching the hinge plate; pallial line parallel to the ventral shell margin, clear. Inner margin with well-developed crenulations.
Remarks — The present taxon has been considered by many authors to be related to *G. pilosa* Linné, 1758 and/or *G. glycymeris* Linné, 1758. Both these species have well-developed external ornament and smooth, inequilateral ligament areas, and are thus assignable to *Glycymeris* s. str., and are not closely related to *G. obovata ringelei*, which differs from *G. o. baldii* from the Antwerp Member (Berchem Formation, Miocene) by its smaller, thicker, relatively higher and more inflated shell with a better developed hinge with relatively longer hinge teeth.

The new subspecies differs in some respects from its Oligocene and Miocene relatives (see Dollfus & Dautzenberg, 1909); we follow Glibert & van de Poel (1965) in their treatment of Oligocene and Miocene representatives of *G. obovata* and rank it as a new subspecies. *Glycymeris o. ringelei* may be distinguished from *G. variabilis* in that it is more equilateral and orthogyrate, has a less accentuated radial ornament, a better developed hinge and its anterior adductor muscle scar is somewhat less slender and (almost) touches the hinge plate. Most specimens of *G. variabilis* are decidedly less inflated than those of *G. o. ringelei*.

Glycymeris (Chevronia) variabilis
(J. de C. Sowerby, 1824)
Pls 2, 3; Pl. 4, Figs 1, 2

*1824 *Pectunculus variabilis* J. de C. Sowerby, p. 111, pl. 471 (lower and central figures).
1845 *Pectunculus variabilis* — Nyst, p. 249, pl. 20, fig. 1a, b.
1851 *Pectunculus glycymeris* L. — Wood, p. 66, pl. 9, fig. 1g.
1851 *Pectunculus glycymeris* L. var. *subobliquus* Wood, p. 66, pl. 9, fig. 1h, i.
1878-81 *Pectunculus glycymeris*, L. var. *transversa* S. Wood — Nyst, p. 166 (*partim*), pl. 17, fig. 8a, c, f.
1879 *Pectunculus glycymeris* — Wood, p. 43, pl. 6, fig. 5a.
1879 *Pectunculus glycymeris* var. *nummarius* — Wood, p. 43, pl. 6, fig. 5b.
1937 *Glycymeris glycymeris variabilis* (J. Sow.) — van Regteren Altena, p. 55, pl. 3, fig. 50.
1950 *Glycymeris glycymeris variabilis* (Sowerby, 1824) — Heering, p. 30 (*partim*), pl. 8, figs 1-6.
1957 *Glycymeris glycymeris* Linné sp. 1758 forme *variabilis* Sowerby, 1824 — Glibert, p. 16 (*partim*).

1962 *Glycymeris glycymeris variabilis* — van Regteren Altena *et al.*, p. 55 (*partim*), pl. 4, fig. 50.
1965 *Glycymeris* (s.s.) *glycymeris variabilis* (Sowerby, 1824) — Glibert & van de Poel, p. 83.
1974 *Glycymeris glycymeris variabilis* (Sowerby, 1824) — Ringelé (MS), p. 96 (*partim*), pl. 4, fig. 5a, b.
1979 *Glycymeris glycymeris variabilis* (Sowerby, 1824) — Geys & Marquet, pl. 15, fig. 1.
1995 *Glycymeris (Glycymeris) variabilis* (J. de C. Sowerby, 1824) — Moerdijk & van Nieulande, pl. 4, fig. 1.

Original diagnosis — 'Obliquely suborbicular, rather convex, finely striated longitudinally, becoming smooth or sulcated by wear; teeth of the hinge and lines upon the area of the ligament, numerous; beaks short nearly, close' (J. de C. Sowerby, 1824, p. 111).
Revised diagnosis — Moderately large, inequilateral, obliquely oval glycymeridid with a rather flat shell, a near-smooth external ornament with very fine, irregular radial threads, quite short hinge teeth, a ligament area with distinct chevrons and with the slender adductor muscle scars at some distance from the hinge plate.
Types — The original type series consists of three specimens; here we designate lectotype the specimen in J. de C. Sowerby's pl. 471 (bottom figure) (BMNH 43188a) (see Pl. 2, Fig. 1), since it most clearly represents the well-known, quite flat and inequilateral form. The right valve illustrated in the centre of this plate is heavily eroded and worn, rather inflated and more equilateral than the lectotype. However, it may be referred to the present species as well, and is designated paralectotype (BMNH 43188b) (see Pl. 2, Fig. 2). The specimen in pl. 471, top figure, may be assigned to *G. radiolyrata* forma *pseudodeshayesi* n. forma (see below; Pl. 5, Fig. 3).
Locus typicus — Suffolk (no additional locality data available).
Stratum typicum — Red Crag (no additional stratigraphic details available).
Description (lectotype) — Height, width and semi-diameter are 61.9, 64.9 and 17.6 mm, respectively; right valve, obliquely oval, inequilateral, the posterior side longer and drawn out ventro-posteriorly, anteriorly and ventrally regularly rounded, dorso-posteriorly straight (slightly damaged anteriorly above midline), umbo not very prominent, faintly opisthogyrate, shell rather flat and moderately thick shelled. External ornament consisting of very fine, irregular radial threads, because of wear only visible near ventral border; growth lines irregular, distinct, particularly posteriorly. As a result of wear, umbonal region is decorticated; four concentric growth zones are visible in this region, crossed by about 40 radial sulcae also prominent because of wear, running to about shell midline.

Below the beak is a broadly triangular ligament area, slightly inequilateral, anterior part somewhat longer, and almost reaching the inside border of the hinge plate; ornamented with incised ligament grooves in a regular roof-shaped pattern, anteriorly with 8, posteriorly with 7 grooves. Hinge not especially well developed, hinge teeth relatively short, 8 in number anteriorly as well as posteriorly. Below either end of hinge plate, callus of adductor muscle scars missing, as is inner shell layer which would have preserved the pallial line. Inner shell margin crenulate, 35 crenulations visible.
Material studied — **Antwerp area** (6th harbour dock construction pit, Oorderen Member), 14 valves (RGM 393 819, leg./don. M. van den Bosch); connection 5th harbour dock to Amerika dock, ?Luchtbal Member, 2 specimens (RGM 394 118), 3 valves (van Nieulande Colln, no. 111); **Stuyvenberg**, 1 bivalved specimen, 6 valves (NITG Colln); **Kallo** (sea sluice construction pit, Oorderen Member), 3 valves (Vervoenen Colln, no. F 251 B); **Kallo** (Waesland tunnel construction pit, Oorderen Member, level with *Angulus benedeni*), 1 valve (van Nieulande Colln, no. 17); **Kallo** (Beveren tunnel construction pit, Oorderen Member, level with *A. benedeni*), 1 valve (Moerdijk & van Nieulande, 1995, pl. 4, fig. 1; RGM 393 826); **Mill-St. Hubert**, borehole material, Pliocene, 24 valves (very inequilateral and thick-shelled form, van Nieulande Colln, no. 137); **Reek** (province of Noord-Brabant), auger drill 41 (45F/48), 18.00-31.80 mbs, Pliocene, *c.* 290 valves (juv., 1 fragment of an adult specimen, with very coarse radial lirae, NITG Colln, MOL 683); **Nijmegen** (province of Gelderland), 'Midden-Plioceen', 85 valves, 21 fragments (NITG Colln, MOL 686); **Borsele-Baarland**, dredged, reworked from Pliocene strata, 28 valves (Moerdijk Colln); **Baarland**, 5 valves (very inequilateral and thick-shelled form, Moerdijk Colln); **Veere-Domburg**, washed ashore, reworked from Pliocene strata, 23 valves (Moerdijk Colln); **Borsele-de Kaloot**, 7 valves (Moerdijk Colln); **Walton-on-the-Naze** (England, Red Crag, RGM 394 119, *ex* F.J. Janssen Colln), 11 valves.
Remarks — A borehole at Reek has yielded numerous juvenile valves with a remarkably coarse radial ornament, from sediments of Pliocene age. In reworked dregded material from the Western Scheldt a very inequilateral, oblique and thick-shelled forma of *G. variabilis* is known. From borehole Mill-St. Hubert, numerous similar specimens are available, but their adductor scars are markedly broader and almost touch the hinge plate, as in *G. obovata ringelei*.

Some specimens of *G. variabilis* are more inflated, often with a somewhat coarser radial ornament than in typical examples. The anterior adductor muscle scar is less slender as well. However, these shells are inequilateral and oblique as in typical *G. variabilis*, with a narrow hinge and short teeth, with similar characters of the ligament area and with the anterior adductor muscle scar at some distance from the hinge plate. In this respect, they differ from *G. obovata ringelei*, and seem to represent an early form of *G. variabilis*, possibly of stratigraphical significance.

Material of this inflated form of *G. variabilis* examined is from the following localities: **Sudbourn Hall** (Coralline Crag), 5 valves (NITG Colln, MOL 694); **Gedgrave** (Coralline Crag), 1 valve (RGM 394 117); **Kallo** (sea sluice construction pit, base Oorderen Member, probably reworked from older strata), 2 valves (Vervoenen Colln, no. F 251 B); **Bergen op Zoom** (borehole Vreederust, 49B/173, 81.30-95.70 mbs), 1 valve (Heering, 1950, pl. 8, figs 13, 14, 20, NITG Colln, MOL 678); **Western Scheldt** (province of Zeeland, dredged, reworked from Pliocene strata; **Terneuzen** (Put van Terneuzen, ZZ8 (Schot), 1 valve and 1 damaged valve (KZGW Colln, no. 3082 GM 98-03); **Ellewoutsdijk**, 1 valve (KZGW Colln, no. 648b, leg. C. Brakman); **Baarland**, 5 valves (Moerdijk Colln); **Schaar van de Spijkerplaat**, 1 valve.

Discussion — When we had just started our studies of Pliocene glycymeridids from the North Sea Basin, we assumed *G. variabilis* to be the direct descendant of what we now refer to as *G. obovata ringelei*. Shells of *G. (Ch.) turonica* (Pl. 4, Fig. 3) from the Miocene and Pliocene (Redonian) of the Nantes area (France), however, also have much affinity with *G. variabilis*. *Glycymeris turonica* is a common species from the Miocene (Helvetian) in the Tours area (France). Generally, but erroneously, this species is lumped with *G. bimaculata deshayesi* or with *G. texta* (Dujardin, 1837). The Helvetian form is quite small, with an almost equilateral, inflated shell, a very fine, mainly radial external ornament and many distinct chevrons on the ligament area. Specimens from the Redonian of the Nantes area are as a rule larger and clearly inequilateral; these were discussed by Lauriat-Rage (1981) and referred to as '*Glycymeris (Glycymeris) glycymeris* (Linné, 1758) sous-especes *pilosa* (Linné, 1758) et *variabilis* (Sowerby, 1824)'. The Redonian shells have many characters in common with *G. variabilis*, especially with the more inflated forms: clearly opisthogyrate, inflated, inequilateral and oblique shell, a moderately developed hinge and position of the adductor muscle scars. Juvenile specimens of *G. turonica* and *G. variabilis* are very similar; the external ornament in the former is similar to that of the more finely ornamented shells of the latter. In addition, *G. turonica* and *G. variabilis* have the concentric colour bands in common. The number of ligament chevrons in *G. turonica* is as a rule much higher. However, in a lot from St-Julien-de-Concelles (see Pl. 4, Fig. 3), the number of ligament chevrons is lower, as in some specimens of *G. variabilis*. The specimen illustrated in Lauriat-Rage (1981, Pl. 4, fig. 1), from Le Pigeon Blanc, also has fewer ligament chevrons than specimens collected at *e.g.* Sceaux d'Anjou. Judging from shell features, it seems plausible that *G. turonica* and *G. variabilis* are related.

At present, we are unable to decide whether *G. variabilis* is directly related either to *G. obovata ringelei* or to *G. turonica*. For the time being, it seems best to consider *G. obovata*, *G. turonica* and *G. variabilis* distinct taxa.

Genus and subgenus *Glycymeris* da Costa, 1778

Type species — *Arca glycymeris* Linné, 1758, by monotypy.

Diagnosis — 'Subcircular, subequilateral, with small umbones; teeth relatively short, transverse, becoming obsolescent medially; surface smooth or costate' (Newell *in* Moore, 1969, p. N267).

Revised diagnosis — Subcircular, subequilateral; teeth relatively short, transverse, effacing medially; external ornament fine to coarse, consisting of radial as well as concentric elements, all Recent species with a hairy periostracum, and a (near-)smooth ligament area.

Remarks — The subgenus is redefined here to distinguish it from *Chevronia* (see above).

Glycymeris (G.) radiolyrata
Moerdijk & van Nieulande, 1995
Pls 5, 6

Discussion — When we first described *G. radiolyrata*, a few valves of a form obviously related to it, but larger (up to 90 mm) and more inflated were before us. Now that we have seen additional material, the following features of this form may be added: a relatively thicker shell, with a better developed hinge, the adductor muscle scar rests on an internal buttress. The majority of valves may be subdivided further into two categories, viz. a principally equilateral form with fine and regular shell ornament, and an inequilateral form with very coarse and irregular ornament. Both ends of the continuum are clearly distinct, but some specimens are intermediate, suggesting them to be related. Below, we will refer to these forms as forma *pseudodeshayesi* n. forma, in view of their having similar strong shell inflation and fine reticulate ornament as *G. bimaculata deshayesi* (Mayer-Eymar, 1868) [Miocene (Helvetian) of Touraine and Redonian (Mio-Pliocene) of western France], and as forma *exaggerata* n. forma, since characters of external ornament are exaggerated in comparison to the typical form.

Forma *pseudodeshayesi* (Pl. 5, Figs 1-3) differs from the typical form in attaining larger dimensions, in being more inflated, in having a better developed hinge and in the position of the adductor muscle scars, close to the hinge plate. It may be distinguished from forma *exaggerata* (see below), as well as from the typical form, by the finer and more regular, reticulate shell ornament.

Forma *exaggerata* (Pl. 6, Figs 1-3) also differs from the typical form in being more inflated, in having a better developed hinge and in having the adductor muscle scars close to the hinge plate. It is distinguished

from both forma *pseudodeshayesi* and the typical form in having very coarse, reticulate shell ornament.

From boreholes at Ouwerkerk and Bergen op Zoom (the Netherlands), we have only seen f. *pseudodeshayesi*, based on excellently preserved material. The level which yielded the specimens at Ouwerkerk is an equivalent of the Luchtbal Member (Middle Pliocene). From the same borehole, samples from some metres above the level with this inflated and finely ornamented form have yielded the typical form. No specimens of f. *exaggerata* have been found in their original stratigraphical context in any of the outcrops/excavations studied. This complicates a satisfactory interpretation of the material. The only articulated specimen originates most probably from the upper part of the Kattendijk Formation, judging from sediment fill. These distribution patterns indicate that these formae may be of stratigraphical value. The bulk of the material from Belgian outcrops, as far as could be determined, originates from the base of the Oorderen Member (Lillo Formation), where the typical form of *G. radiolyrata* also occurs. Specimens showing features intermediate between f. *pseudodeshayesi*, f. *exaggerata* and the typical form do occur in our material, albeit rarely. Typical features of f. *pseudodeshayesi* in particular would suggest that *G. radiolyrata* evolved from *G. bimaculata* s. lat. Previously illustrated material that may be attributed to f. *pseudodeshayesi* includes:

1824 *Pectunculus variabilis* J. de C. Sowerby, pl. 471, top figure.
1950 *Glycymeris* spec. 1a Heering, p. 34, pl. 7, figs 15, 16, 19, 20.
1950 *Glycymeris (Gl.) pilosa* (Linné) var. *tumida* B.D.D. — Heering, p. 34, pl. 8, figs 11, 12.

Specimens illustrated by Wood (1851, pl. 9, fig. 1d), under the name *Pectunculus glycymeris* L. (pl. 9, fig. 1d), and Wood (1879, pl. 6, fig. 4a) as *P. pilosus* var. *insubricus* Brocchi, could also belong here.

Specimens recorded previously in the literature that may be referred to f. *exaggerata* include:

1957 *Glycymeris glycymeris* Linné sp. 1758, forme *tumida* B.D.D., 1891 — Glibert, pl. 1, fig. 4.
1992 *Glycymeris* cf. *bimaculata* (Poli, 1795) — Moerdijk & van Nieulande *in* Moerdijk *et al.*, p. 18 (*partim*), pl. 4, bottom right-hand figure.

Material of f. *pseudodeshayesi* examined for the present paper is as follows:

Ouwerkerk (borehole 42H19-4(A40), 114.50-115.75 mbs, Luchtbal Member, 3 valves, 1 fragment (RGM 394 121, leg. Deltadienst); **Bergen op Zoom** (Vreederust, borehole 49B/173, 81.30-95.70 mbs), 1 valve (Heering, 1950, pl. 7, figs 15, 16, 19, 20, NITG Colln, MOL 690) and 3 fragments (NITG Colln, MOL 688); **Bergen op Zoom** (borehole Waterleiding 3, 49E/30, 87.60-94.50 mbs), 1 valve (Heering, 1950, pl. 8, figs 11, 12, NITG Colln, MOL 689); **Bergen op Zoom** (waterleiding Bergen op Zoom 3, 87-94 (?mbs), 1 valve, RGM 4326; **St. Jansteen** (borehole 55A/24, borehole A), 8.60-9.40 mbs), 1 fragment (NITG Colln, MOL 691); **Kallo** (Beveren tunnel construction pit, base Oorderen Member, 3 valves, van Nieulande Colln, nos 93, 93a, 114); **Antwerp** (Boudewijnsluis excavation, base Oorderen Member, 1 valve (Marquet Colln); **Kallo** (sea sluice construction pit, ?base Oorderen Member, 8 valves, Vervoenen Colln, no. F 717 Aa; 1 valve, van Nieulande Colln, no. 101; **Kallo** (Beveren tunnel construction pit, Oorderen Member, level with *Atrina*(?), 1 valve, van Nieulande Colln, no. 94; **Antwerp** (construction pit 5th harbour dock, level unknown, from sediment dump), 1 valve (RGM 2657); **Antwerp** (Oorderen polder, Pliocene, level unknown), 2 valves (RGM 56908); **Antwerp** (Ford plant north of Noordkasteel, level unknown, from sediment dump), 1 valve (RGM 394 097); **Antwerp** (5th harbour dock, level unknown, from sediment dump), 6 valves (RGM 100 394, 100 396-397, 100 401); **Antwerp** (level unknown), 1 valve and 1 specimen (RGM 56 896, 494 098). Dredged, reworked from Pliocene strata is material from **Baarland** (1 valve, Moerdijk Colln), **Ellewoutsdijk/Baarland** (4 valves, van Nieulande Colln, no. 103; Vervoenen Colln, no. F 717.

From the Red Crag is 1 valve (J. de C. Sowerby, 1824, pl. 471, top figure, BMNH 43188c) (see Pl. 5, Fig. 3 here).

Material of f. *exaggerata* examined for the present paper includes:

Antwerp? (original label stating, '*Pectunculus pilosus* uit het Diestien, in het Scaldisien gevonden; geremanieerd (gevuld met Diestien, ged. met *Ditrupa*)' (= '*Pectunculus pilosus* from the Diestian, found in the Scaldisian; reworked (filled with Diestian, part with *Ditrupa*'), 1 bivalved specimen (NITG Colln); **Kallo** (Vrasenedok excavation, base Oorderen Member, probably reworked from older strata), 1 valve (Marquet Colln); **Kallo** (Beveren tunnel construction pit, base Oorderen Member, probably reworked from older strata), 1 valve (van Nieulande Colln, no. 93b); **Verrebroek** (Liefkenshoektunnel construction pit, Oorderen Member, level with *Atrina*(?), probably reworked from older strata), 1 valve (van Nieulande Colln, no. 100, leg. G. Garding); **Kallo** (sea sluice construction pit, ?base Oorderen Member, probably reworked from older strata), 3 valves (Vervoenen Colln, no. F 717 A, A2); dredged, reworked from Pliocene strata are specimens from **Ellewoutsdijk**, 1 valve (Moerdijk Colln); **Baar-**

land, 1 valve (Moerdijk Colln); **Ellewoutsdijk/ Baarland**, 1 valve (van Nieulande Colln, no, 105b); washed ashore, reworked from Pliocene strata: **Nieuwesluis**, 1 valve (Simons Colln).

Additional data — As far as the stratigraphical distribution of the typical form is concerned, it should be noted that it has also been found in the Ouwerkerk borehole (province of Zeeland), at a level which is equivalent to the Luchtbal Member, as well as in the basal Oorderen Member during excavation of the Verrebroekdok, which levels have yielded well-preserved material. Data are as follows: **Kallo** (Verrebroekdok, base Oorderen Member, - 17.10-17.50 m, 1 valve (Moerdijk Colln); **Ouwerkerk** (borehole 42H-19-4(A40), 106-107 mbs, Luchtbal Member, 3 valves, 2 fragments (RGM 394 120, leg. Deltadienst).

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REFERENCES

Báldi, T., 1962. *Glycymeris* s. str. des europäischen Oligozäns und Miozäns. — Ann. hist.-nat. Musei nat. Hung., Mineral. Palaeont., 54: 85-153, 11 pls.

Dollfus, G. & Ph. Dautzenberg, 1909. Conchyliologie du Miocène moyen du Bassin de la Loire, 1. Pélécypodes. — Mém. Soc. géol. Fr. (Paléont.), 27(5): 1-500, 46 pls.

Favre, J., 1918. Catalogue illustré de la Collection Lamarck, Conchifères dimyaires fossiles, Première partie. Genève (Georg & Cie), 117 pls.

Geys, J.F. & R. Marquet, 1979. Veldatlas voor de cenozoische fossielen van België, 1. Neogeen. Rotterdam (Backhuys), 125 pp., 45 pls.

Glibert, M., 1957. Pélécypodes du Diestien, du Scaldisien et du Merxemien de la Belgique, première note. — Bull. Inst. r. Sci. nat. Belg., 33(9): 1-40, 1 pl.

Glibert, M. & L. van de Poel, 1965. Les Bivalvia fossiles du Cénozoïque étranger des collections de l'Institut Royal des Sciences Naturelles de Belgique, 1: Palaeotaxodontida et Eutaxodontida. — Mém. Inst. r. Sci. nat. Belg., (2)77: 1-112.

Heering, J., 1950. Pelecypoda (and Scaphopoda) of the Pliocene and older-Plistocene [*sic*] deposits of the Netherlands. — Meded. Geol. Sticht., (C)4(1)9: 1-225, 17 pls.

Janssen, R., 1979. Revision der Bivalvia des Oberoligozäns (Chattium, Kasseler Meeressand). — Geol. Abh. Hessen, 78: 1:118, 4 pls.

Lauriat-Rage, A., 1981. Les Bivalves du Rédonien (Pliocene Atlantique de France); signification stratigraphique et paléobiogéographique. — Mém. Mus. natn Hist. nat., n.s. (C: Sci. Terre), 45: 3-173, 18 pls.

Maestrati, Ph. & P. Lozouet, 1996. Les Glycymerididae (Mollusca, Bivalvia) de l'Oligocène Supérieur (Chattien) du Bassin de l'Adour, France. — Ann. Paléont. (Vert.-Invert.), 82(1): 3-25.

Marquet, R., 1995. Pliocene gastropod faunas from Kallo (Oost-Vlaanderen, Belgium). Part 1. Introduction and Archaeogastropoda. — Contr. Tert. Quatern. Geol., 32(1-3): 53-85, 6 pls.

Mayer-Eymar, C., 1868. Catalogue systématique et descriptif des fossiles de terrains tertiaires qui se trouve au Musée fédéral de Zürich, 3. Mollusques; Famille des Arcides, Zürich, 124 pp.

Meuter, F.J. de & P.G. Laga, 1976. Lithostratigraphy and biostratigraphy based on benthonic Foraminifera of the Neogene deposits of Northern Belgium. — Bull. Soc. belge Géol., 85(4): 133-152, 1 pl.

Moerdijk, P.W. & F.A.D. van Nieulande, 1995. *Glycymeris (Glycymeris) radiolyrata* nov. sp. (Bivalvia, Glycymerididae) from the Pliocene of the North Sea Basin. — Contr. Tert. Quatern. Geol., 32(1-3): 3-17, 4 pls.

Moerdijk, P.W., R. Pouwer, R. Rijken & F.A.D. van Nieulande, 1992. Fossiele schelpen van Zeeuwse stranden en stromen, deel 1. — Werkgr. Geol. Kon. Zeeuwsch Gen. Wetensch., Publ. 2: 1-38, 10 pls.

Newell, N.D., 1969. Family Glycymerididae. *In*: Moore, R.C. (ed.). Treatise on Invertebrate Paleontology, Part N(2), Mollusca 6: N267-N269. Geol. Soc. Am., Boulder/Univ. Kansas Press, Lawrence.

Nicol, D., 1956. Distribution of living glycymeridids with a new species from Bermuda. — Nautilus, 70: 48-53.

Nyst, P.H., 1845. Description des coquilles et polypiers fossiles des terrains tertiaires de la Belgique. Bruxelles (Nyst), 675 + ii pp., 48 pls.

Nyst, P.H., 1878-1881. Conchyliologie des terrains tertiaires de la Belgique, 1: Terrain pliocène. — Ann. Mus. r. Hist. nat. Belg., 3: 1-263 (1878); 28 pls (1881).

Regteren Altena, C.O. van, 1937. Bijdrage tot de kennis der fossiele, sub-fossiele en recente mollusken, die op de Nederlandse stranden aanspoelen, en hunner verspreiding, Amsterdam (Universiteit van Amsterdam), 184 pp., 12 pls.

Regteren Altena, C.O. van, A. Bloklander & L.P. Pouderoyen, 1962. De fossiele schelpen van de Nederlandse stranden en zeegaten. Tweede serie, 1. — Basteria, 26: 5-16.

Ringelé, A., 1974. Bijdrage tot de systematiek, de evolutie en de paleoecologie van Bivalvia uit Neogene afzettingen van Noord-België, Deel 1. Systematiek. Leuven (Kath. Univ. Leuven), 136 pp. (unpubl. PhD).

Sowerby, J. de C., 1823-1829. The Mineral Conchology of Great Britain, or coloured figures and descriptions of those remains of testaceous animals or shells which have been preserved at various times and depths in the earth, 5. London (Arding/Richard Taylor), 160 pp., pls 408-503.

Wood, S.V., 1851-1860. A monograph of the Crag Mollusca, or, description of shells from the Middle and Upper Tertiairies of the east of England, 2. Bivalves. — Monogr. Palaeontogr. Soc. Lond., 1-150, pls 1-12 (1851); 151-216, pls 13-20 (1853); 217-342, pls 21-31 (1857), 1-2 (1860).

Wood, S.V., 1872-1874. Supplement to the monograph of the

Crag Mollusca, or, description of shells from the Middle and Upper Tertiairies of the east of England, 3. Univalves and Bivalves. — Monogr. Palaeontogr. Soc. Lond., 31 + 99 pp., pls 1-7 (1872); 99-231, pls 8-21 (1874).

Wood, S.V., 1879. Second supplement to the monograph of the Crag Mollusca, with descriptions of shells from the Upper Tertiairies of the east of England. Monogr. Palaeontogr. Soc. Lond., 1-58, 1 pl.

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PLATE 1

Fig. 1. *Glycymeris (Chevronia) obovata obovata* (Lamarck, 1819), interior of left valve, Dornberg, Ahnetal (Germany), Oligocene, Chattian, Kasseler Meeressand (A. Janse Colln), x 2.25

Fig. 2. *Glycymeris (Chevronia) obovata ringelei* n. subsp., RGM 394 099 (holotype), A - exterior of left valve (x 1.5), B - interior of right valve (x 1.5), C - interior of left valve (x 1.5); Antwerp, 5th harbour dock (province of Antwerp, Belgium), Pliocene, base Kattendijk Formation, *ex* van Nieulande Colln.

PLATE 1

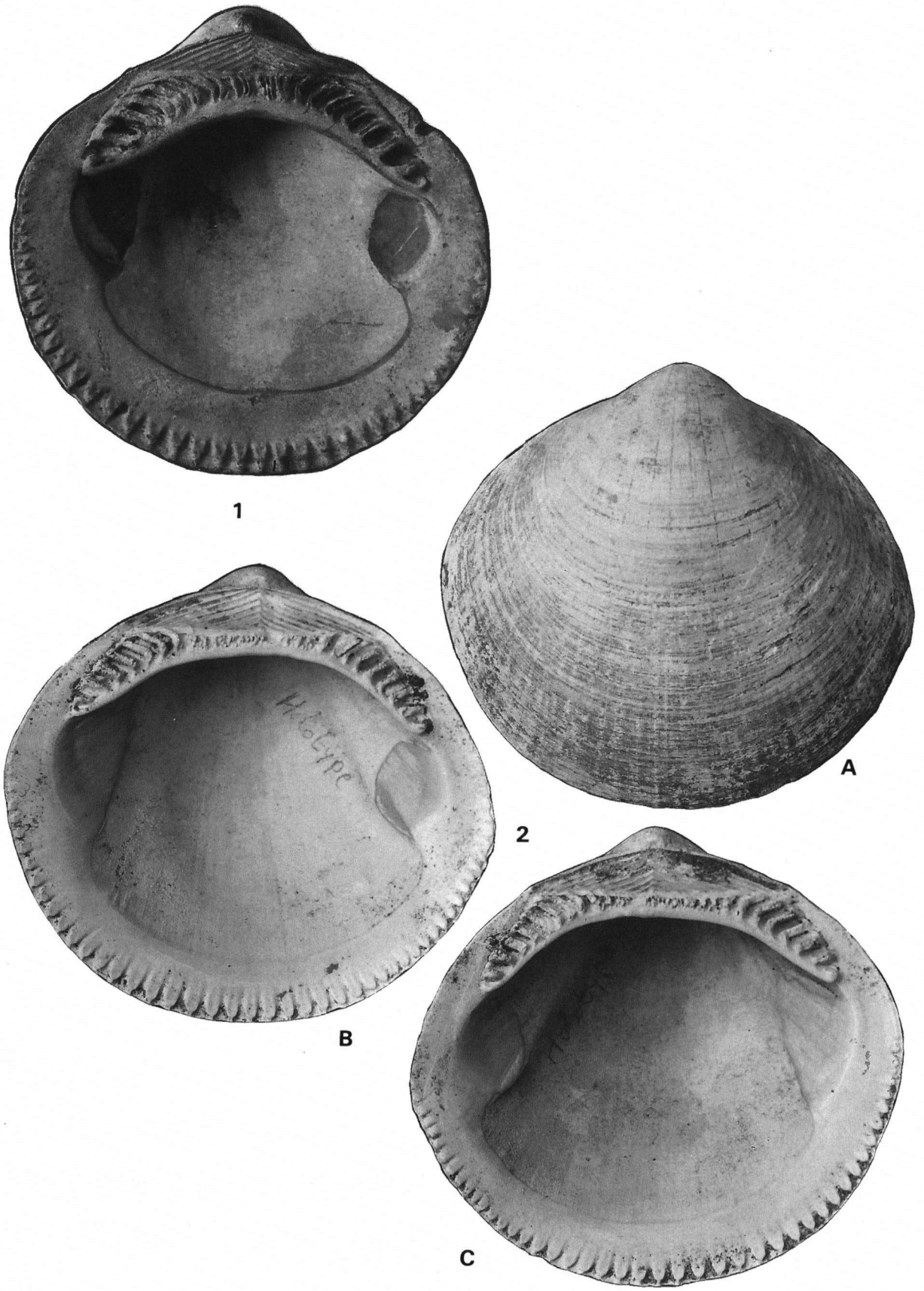

PLATE 2

Fig. 1. *Glycymeris (Chevronia) variabilis* (J. de C. Sowerby, 1824), BMNH 43188a (lectotype), right valve, A - exterior, B - interior views, Suffolk (England), Pliocene, Red Crag (previously illustrated by J. de C. Sowerby, 1824, pl. 471, bottom figure), x 1.3.

Fig. 2. *Glycymeris (Ch.) variabilis*, BMNH 43188b (paralectotype), right valve, A - exterior, B - interior views, Woodbridge (Suffolk, England), Pliocene, Red Crag (previously illustrated by J. de C. Sowerby, 1824, pl. 471, centra figure), x 1.4.

Fig. 3. *Glycymeris (Ch.) variabilis*, left valve of a juvenile specimen, somewhat eroded, x 10 (scale bar in mm). Borsele-de Kaloot (province of Zeeland), beach material, derived Pliocene (Moerdijk Colln).

PLATE 2

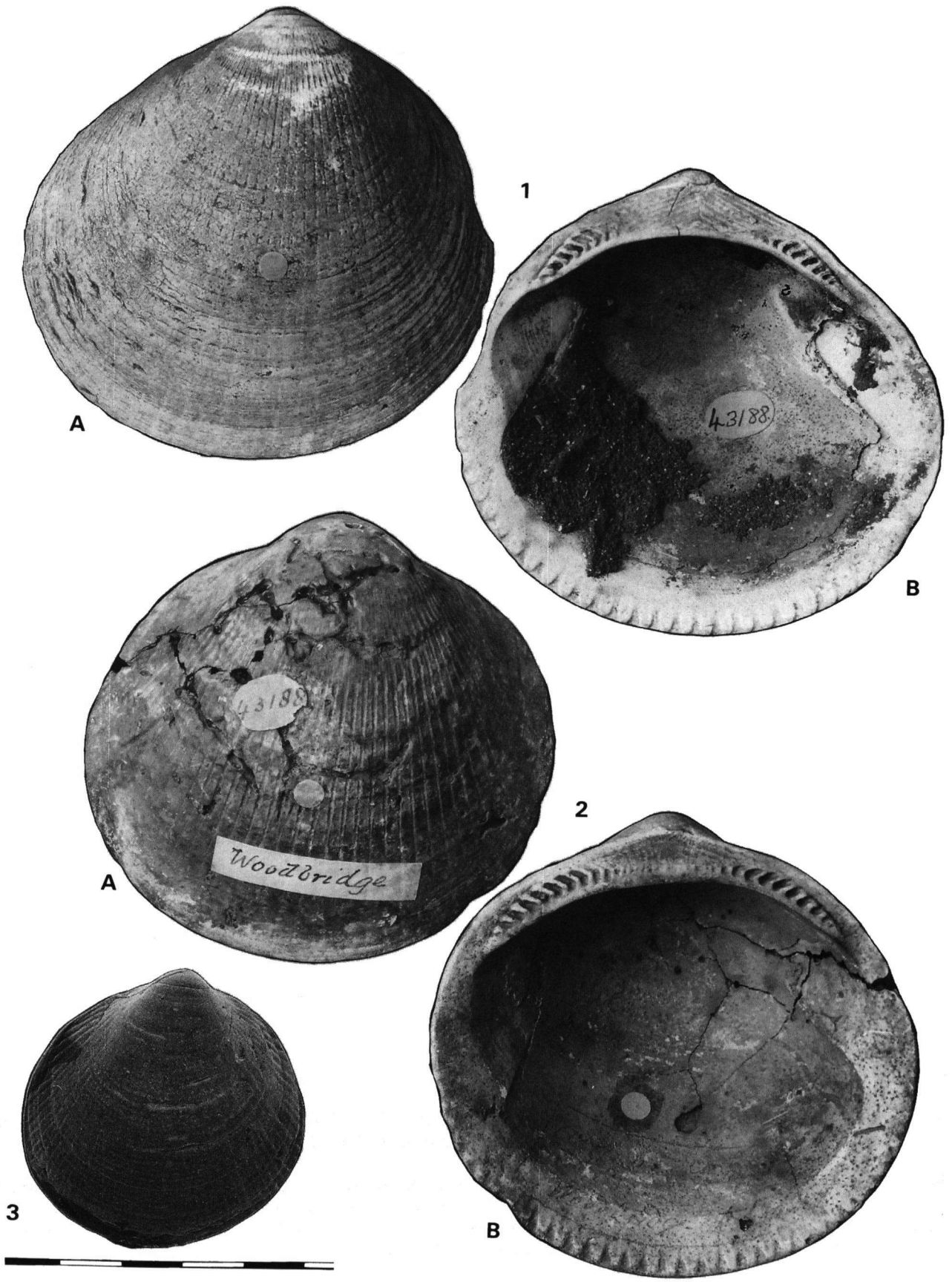

PLATE 3

Fig. 1. *Glycymeris (Ch.) variabilis*, right valve, A - exterior; B - interior views, Walton-on-the-Naze (England), Pliocene, Red Crag (van Nieulande Colln, leg. J. van der Voort), x 2.

Fig. 2. *Glycymeris (Ch.) variabilis*, left valve of inequilateral and thick-shelled form, A - interior, B - exterior views, Mill-St. Hubert, Langenboom (province of Noord-Brabant, the Netherlands), Pliocene, van Nieulande Colln, no. 137), x 2.5.

PLATE 3

PLATE 4

Fig. 1. *Glycymeris (Ch.) variabilis*, left valve of inflated form, A - exterior, B - interior views, Kallo, sea sluice construction pit, base Oorderen Member (probably reworked from older strata), Vervoenen Colln, no. F.25B, x 1.25.

Fig. 2. *Glycymeris (Ch.) variabilis*, left valve of inflated form, A - interior, B - exterior views, Sudbourn Hall (England), Coralline Crag, Pliocene, NITG Colln, MOL 694, x 1.4.

Fig. 3. *Glycymeris (Ch.) turonica* (Mayer-Eymar, 1868) s. lat., interior of left valve, St-Julien-de-Concelles (Nantes area, France), Mio-Pliocene, Redonian, van Nieulande Colln, x 1.4.

PLATE 4

PLATE 5

Fig. 1. *Glycymeris (G.) radiolyrata* f. *pseudodeshayesi* n. forma, left valve, A - exterior, B - interior views, borehole 42H19-4(A40), 114.50-115.75 mbs, Pliocene, 'Luchtbal Member', leg. Deltadienst, RGM 394 121, x 5 (photographs by W. Krull, Oostburg).

Fig. 2. *Glycymeris (G.) radiolyrata* f. *pseudodeshayesi* n. forma, right valve, Antwerp, Boudewijnsluis, base Oorderen Member, Marquet Colln, x 1.6.

Fig. 3. *Glycymeris (G.) radiolyrata* f. *pseudodeshayesi* n. forma, BMNH 43188c, right valve, A - exterior, B - interior views, x 1,C - detail of hinge plate, x 2, ?Suffolk (England), Red Crag (previously illustrated by J. de C. Sowerby, 1824, pl. 471, top figure).

PLATE 5

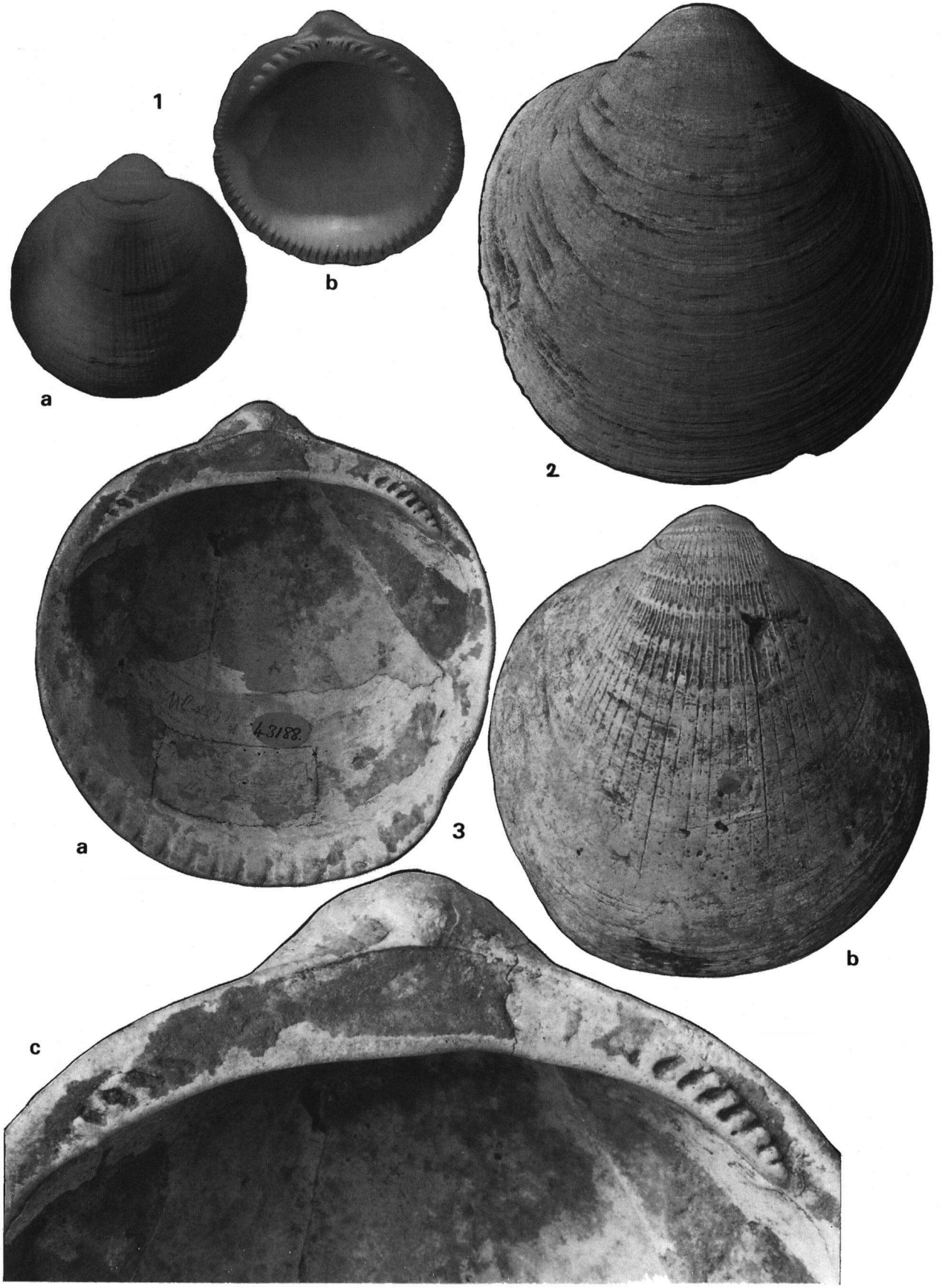

PLATE 6

Fig. 1. *Glycymeris (G.) radiolyrata* f. *exaggerata* n. forma, A - interior, B - exterior views, x 1.15, C - detail of umbonal region, Kallo, Beveren tunnel construction pit, base Oorderen Member (probably reworked from older strata), 10 April 1975, van Nieulande Colln, no. 93b.

Fig. 2. *Glycymeris (G.) radiolyrata* f. *exaggerata* n. forma, Kallo, sea sluice construction pit, ?base Oorderen Member (probably reworked from older strata), Vervoenen Colln, no. F 717 A2, x 1.75.

Fig. 3. *Glycymeris (G.) radiolyrata* f. *exaggerata* n. forma, left valve, Kallo, Vrasenedok excavation, base Oorderen Member (probably reworked from older strata), Marquet Colln, x 1.

PLATE 6