Contr. Tert. Quatern. Geol. 30(3-4) | 83-103 2 figs, 4 pls. Leiden, December 1993

THE MOLLUSCAN FAUNA OF THE KRUISSCHANS MEMBER (LILLO FORMATION, LATE PLIOCENE) IN THE ANTWERP AREA (BELGIUM)

ROBERT T.C. MARQUET
Antwerp, Belgium

Marquet, Robert T.C. The molluscan fauna of the Kruisschans Member (Lillo Formation, Late Pliocene) in the Antwerp area (Belgium). — Contr. Tert. Quatern. Geol., 30(3-4): 83-103, 2 figs, 4 pls. Leiden, December 1993.

A list of all molluscan species recognised from the Kruisschans Member (Lillo Formation, Late Pliocene) as recently collected at Kallo and Antwerp (Belgium), is presented and commented upon. The molluscan fauna comprises 72 bivalve and 72 gastropod species, one of which is new (*Capulacmaea kalloensis* sp. nov.) and nine of which have not been recorded previously from the Belgian Pliocene. The occurrence of *Yoldia (Yoldia) myalis* (Couthouy, 1838) and *Admete viridula* (Fabricius, 1780) marks the incoming of a cooler climate molluscan fauna, although warm climate species still survive, albeit in lesser numbers.

Key words — Mollusca, Bivalvia, Gastropoda, Pliocene, Belgium, new species.

Dr R.T.C. Marquet, Constitutiestraat 50, B-2060 Antwerp, Belgium.

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INTRODUCTION

Between 1986 and 1989, a section exposing Pliocene deposits as accessible in a construction pit for elements of the Liefkenshoektunnel at Kallo, province of Oost Vlaanderen (Belgium), a few kilometres west of Antwerp, was studied. The exact location of the site and its measured section were published by Hoedemakers & Marquet (1992). Extensive samples were taken from the upper unit of the Lillo Formation, the Kruisschans Member, between 11.7 and 8.80 m. The molluscan fauna of these sands and clays was, amongst other Pliocene faunas, studied earlier by Nyst (1878/1881) and Glibert (1957a-c, 1958a-c, 1959a, b, 1960). The fauna recently collected at Kallo, however, proved to be far more diverse than those published by these authors. Therefore, a new species list is presented here; it has been complemented with material of identical age, collected in 1969 during construction of the Antwerp-Breda motorway, near the Noorderlaan at Antwerp, on the right bank of the River Scheldt, and during construction of the Sixth and Seventh Harbour Docks, Antwerp right bank. These localities and others mentioned in the text are shown in Fig. 1.

MATERIAL

All material from the Kallo and Antwerp sections is kept in the private collections of the author and of

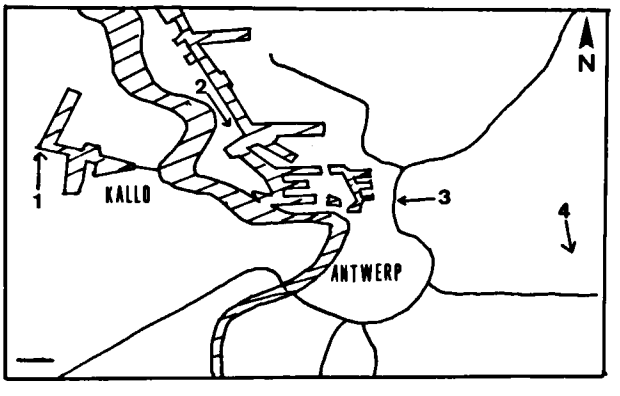

Fig. 1. Map showing location of the sections referred to in the text; 1 - construction pit, Kallo; 2 - harbour docks, Antwerp; 3 - Noorderlaan section; 4 - Wijnegem section, east of Antwerp (Austruweel Member). Scale bar equals 1.5 km.

Mr Albert Ratinckx (Antwerp), with the exception of all illustrated specimens and the holotype of the new taxon, which are deposited in the collections of the Koninklijk Belgisch Instituut voor Natuurwetenschappen (KBIN, Brussels). From the Kallo section, about 1,000 kg of 1 cm, 1 mm and 0.5 mm sieving residu was handpicked, yielding about 8,000 molluscan specimens. This material was taken from the basal shell bed of the Kruisschans Member and from a shell and sand layer, about 1.5 m above this basal bed (layers 11 and 15 to 17 of Hoedemakers & Marquet's [1992] section). Isolated shells were collected from the clayey parts of the section exposed.

The Noorderlaan and Harbour Dock sections were sampled less extensively, and only the larger species were collected. Specimens in older collections, made from the Kruisschans Member and kept at the KBIN were taken into consideration as well.

Species list and remarks

Abbreviations used are as follows: C - common (>10 specimens), R - rare (2-10 specimens), U - unique, F - fragments only, b - only from basal bed at Kallo, Nl - only from the Noorderlaan section, H - only from the Harbour Docks sections, KBIN - not found at Kallo, Noorderlaan nor at Harbour Docks sections, but present in older collections and recorded by Glibert (1957a-c, 1958a-c, 1959a, b, 1960). * - discussed below.

Bivalvia

1*	– *Nuculoma laevigata laevigata* (J. Sowerby, 1818)	C
2*	– *Nucula (Nucula)* aff. *trigonula* (Wood, 1851)	C b
3*	– *Nucula (Nucula)* aff. *nucleus* (Linné, 1767)	C
4*	*Yoldia (Yoldia) myalis* (Couthouy, 1838)	C
5*	– *Glycymeris variabilis* (J. de C. Sowerby, 1824)	C
6	– *Mytilus edulis* Linné, 1758	C
7*	– *Modiolula phaseolina* (Philippi, 1844)	R
8*	– *Atrina* sp.	F
9*	– *Pecten (Pecten) complanatus* J. de C. Sowerby, 1828	R
10*	– *Pecten (Pecten) grandis* J. de C. Sowerby, 1828	R
11	– *Aequipecten opercularis* (Linné, 1758)	C
12	– *Aequipecten radians* (Nyst, 1839)	KBIN
13	– *Palliolum tigerinum* (Müller, 1776)	U
14	– *Mimachlamys pusio harmeri* (van Regteren Altena, 1937)	R
15	– *Heteranomia squamula* (Linné, 1758)	C
16	– *Monia patelliformis* (Linné, 1767)	C
17*	– *Lima (Limatula) exilis* (Wood, 1839)	U Nl
18*	– *Lima (Limatula) loscombii* (J. de C. Sowerby, 1823)	U
19	– *Ostrea (Ostrea) edulis* Linné, 1758	C
20	– *Parvilucina scaldensis* Glibert & van de Poel, 1967	R
21	– *Lucinoma borealis borealis* (Linné, 1767)	C
22	– *Felaniella trigonula astartea* (Nyst, 1835)	C
23	– *Semierycina kautskyi* (Glibert, 1945)	C b
24	– *Mysella bidentata* (Montagu, 1803)	C
25	– *Mioerycina coarctata* (Wood, 1851)	R
26*	– *Pteromeris corbis* (Philippi, 1836)	C
27*	– *Cyclocardia orbicularis chamaeformis* (J. de C. Sowerby, 1825)	U b
28*	– *Cyclocardia scalaris* (J. de C. Sowerby, 1825)	C
29*	– *Glibertia prosperi* van der Meulen, 1951	R
30	– *Astarte fusca basteroti* de la Jonkaire, 1823	R
31	– *Astarte incerta* Wood, 1853	C
32	– *Astarte obliquata obliquata* J. Sowerby, 1817	R
33	– *Digitaria* aff. *excurrens* (Wood, 1853)	R
34*	– *Digitaria forbesi* (Wood, 1874)	R b
35	– *Digitaria digitaria* (Linné, 1758)	C
36	– *Goodallia triangularis* (Montagu, 1803)	C
37*	– *Laevicardium decorticatum* (Wood, 1840)	F
38*	– *Laevicardium parkinsoni* (J. Sowerby, 1814)	C
39	– *Cerastoderma edule hostiei* Chavan, 1941	R H
40*	– *Lutraria* sp.	F
41*	– *Spisula subtruncata triangulata* (Wood, 1857)	C
42*	– *Spisula inaequilatera* (Nyst, 1845)	KBIN
43*	– *Spisula arcuata* (J. Sowerby, 1817)	R
44*	– *Mactra glauca* Born, 1778	R
45*	– *Ensis complanatus* J. de C. Sowerby, 1844	R
46	– *Cultellus cultellatus* (Wood *in* Sowerby, 1844)	F
47*	– *Angulus benedeni* (Nyst & Westendorp, 1839)	R
48*	– *Angulus donacinus* (Linné, 1758)	R b
49	– *Gastrana laminosa* (J. de C. Sowerby, 1827)	F
50	– *Macoma obliqua* (J. Sowerby, 1817)	R
51*	– *Macoma praetenuis* (Leathes *in* Woodward, 1833)	C
52*	– *Abra alba* (Wood, 1802)	C
53	– *Abra prismatica* (Montagu, 1803)	KBIN
54	– *Gari fervensis* (Gmelin, 1791)	R
55	– *Arctica islandica islandica* (Linné, 1767)	C
56*	– *Pygocardia rustica rustica* (J. Sowerby, 1818)	R
57*	– *Dosinia lupinus lincta* (Pulteney, 1799)	R
58	– *Venerupis rhomboides striatella* (Nyst, 1843)	C
59	– *Timoclea ovata* Pennant, 1777)	R
60	– *Callista chione* (Linné, 1758)	KBIN
61*	– *Mya truncata gudmunduri* Strauch, 1972	R
62*	– *Arenomya arenaria* (Linné, 1758)	C
63	– *Lentidium complanatum* (J. Sowerby, 1822)	C
64	– *Corbula gibba gibba* (Olivi, 1792)	C
65	– *Hiatella arctica* (Linné, 1767)	R
66*	– *Panomya trapezoidis trapezoidis* Strauch, 1972	C
67	– *Cyrtodaria angusta* (Nyst & Westendorp, 1839)	R
68	– *Panopea faujasi* Ménard de la Groye, 1807	C
69	– Teredinidae indet.	R
70*	– *Zirfaea crispata* (Linné, 1758)	U
71*	– *Barnea cylindrica* (J. Sowerby, 1818)	F
72	– *Cochlodesma praetenue* (Pulteney, 1799)	KBIN

Gastropoda

1	– *Diodora apertura* (Montagu, 1803)	F
2	– *Emarginula crassa* J. Sowerby, 1813	F
3	– *Emarginula reticulata* J. Sowerby, 1813	U
4*	– *Gibbula* aff. *beetsi* van Regteren Altena, 1954	U
5	– *Gibbula solarium* (Nyst, 1835)	U H
6	– *Gibbula gelriana* Beets, 1946	KBIN
7	– *Gibbula octosulcata* (Nyst, 1835)	F
8*	– *Calliostoma zizyphinum* (Linné, 1758)	F
9*	– *Calliostoma simile* (J. Sowerby, 1818)	C
10*	– *Lacuna suboperta* (J. Sowerby, 1813)	R

11*	– *Eulimene terebellata* (Nyst, 1835)	C
12	– *Cingula inusitata* (Beets, 1946)	R
13	– *Turboella obsoleta* (Wood, 1848)	C
14	– *Tornus belgicus* (Glibert, 1949)	R
15*	– *Potamides tricinctus* (Brocchi, 1814)	KBIN
16	– *Bittium robustum* Harmer, 1918	U
17	– *Haustator incrassata* (J. Sowerby, 1814)	R
18	– *Haustator tricarinata tricarinata* (Brocchi, 1814)	R
19	– *Petaloconchus intortus* (Lamarck, 1818)	R
20	– *Eulima glabra* (da Costa, 1778)	R
21	– *Epitonium clathratulum minutum* (J. de C. Sowerby, 1823)	F
22	– *Capulus unguis* (J. Sowerby, 1816)	C
23	– *Calyptraea chinensis* (Linné, 1758)	C
24	– *Aporrhais scaldensis* van Regteren Altena, 1954	F
25*	– *Capulacmaea kalloensis* n. sp.	R
26	– *Trivia coccinelloides* (J. de C. Sowerby, 1823)	C
27	– *Lunatia catenoides* (Wood, 1842)	R
28	– *Lunatia catena* (da Costa, 1778)	C
29	– *Euspira cirriformis* (J. de C. Sowerby, 1824)	C
30*	– *Natica multipunctata* Wood, 1842	C
31*	– *Polinices hemiclausus* (J. de C. Sowerby, 1824)	C
32	– *Polinices exvarians* (Sacco, 1891)	R
33	– *Galeodea bicatenata* (J. Sowerby, 1817)	F
34	– *Trophonopsis muricatus* (Montagu, 1803)	C
35	– *Trophonopsis alveolatus* (J. de C. Sowerby, 1829)	U
36	– *Spinucella tetragona* (J. de C. Sowerby, 1823)	R
37*	– *Nucella incrassata* (J. de C. Sowerby, 1823)	R
38	– *Liomesus dalei* (J. de C. Sowerby, 1825)	C
39	– *Sipho cordatus* (Bell, 1871)	R
40	– *Sipho curtus* (Jeffreys, 1867)	C
41*	– *Neptunea contraria* (Linné, 1771)	C
42*	– *Neptunea lyratodespecta striata* Strauch, 1972	C
43	– *Buccinum undatum* Linné, 1758	C
44*	– *Amyclina labiosa* (J. de C. Sowerby, 1824)	C
45*	– *Hinia consociata* (Wood, 1848)	C
46*	– *Hinia scaldensis* (Adam & Glibert, 1976)	C
47*	– *Hinia reticosa* (J. Sowerby, 1815)	C
48*	– *Hinia propinqua* (J. de C. Sowerby, 1824)	C
49*	– *Hinia elegans* (J. de C. Sowerby, 1824)	C
50*	– *Phrontis kennardi* (Harmer, 1914)	U
51	– *Narona jonkaireana* (Nyst, 1835)	U
52*	– *Admete viridula* (Fabricius, 1780)	C
53	– *Scaphella lamberti* (J. Sowerby, 1816)	R
54	– *Gemmula antwerpiensis* (Vincent, 1890)	U
55*	– *Haedropleura delheidi* Vincent, 1890	KBIN
56*	– *Cytharella* aff. *substriolata* (Harmer, 1918)	C
57*	– *Mangelia keepingi* (Etheridge & Bell, 1898)	C
58	– *Raphitoma hystrix* (Jan, 1832)	U
59	– *Terebra inversa* Nyst, 1835	R
60*	– *Chrysallida indistincta* (Montagu, 1808)	R
61	– *Pyramidella laeviuscula* Wood, 1842	R
62*	– *Odostomia (Odostomia) conoidea* (Brocchi, 1814)	R
63*	– *Odostomia (Odostomia) unidentata* (Montagu, 1803)	C
64*	– *Odostomia (Brachystomia) eulimoides* Hanley, 1844	R
65*	– *Turbonilla internodula* (Wood, 1848)	C
66*	– *Turbonilla senistriata* (Wood, 1879)	KBIN
67	– *Actaeon noae* J. Sowerby, 1822	C
68	– *Retusa elongata conoidea* (Wood, 1851)	R b
69*	– *Retusa* sp.	U
70	– *Cylichna cylindracea* (Pennant, 1777)	F
71	– *Scaphander lignarius* (Linné, 1758)	U
72	– *Philine* sp.	F

Remarks

— *Nuculoma laevigata laevigata* (J. Sowerby, 1818)

Specimens of this species are large, well preserved and often still articulated in the Kruisschans Member. Colour patterns are commonly preserved, consisting of a very light cream background with concentric, darker brown bands.

— *Nucula (N.)* aff. *trigonula* (Wood, 1851) and *Nucula (N.)* aff. *nucleus* (Linné, 1767)
(Pl. 1, Figs 1, 2)

In the Belgian Neogene, two species of the genus *Nucula* s. str. occur. The first, commoner type is represented by small shells (length usually less than 10 mm, in the Kruisschans Member 7 mm on average), with about eight teeth posterior and 14 to 16 teeth anterior of the umbo. The shell is fairly convex and has a short trigonal shape, with a rather pointed anterior margin. When the posterior dorsal margin is held vertical, the anterior dorsal line is not curved above a horizontal, and the umbonal angle is thus smaller than 90°. Ornament is variable, consisting firstly of a few growth lines, which may become more prominent, possibly as a result of growth halts. The growth lines may develop into ridges on the anterior and posterior margins. Radial ornament is less prominent to near-absent. When encountered in Recent faunas, this species would be assigned to *Nucula tumidula* (Malm, 1860), on account of small size, shell shape and number of teeth. In the fossil state, it has been described as *N. trigonula* (Wood, 1851). The author has not examined the type specimen of that species, which is why the Kruisschans specimens are assigned here with a query.

The second type is larger (12 to 15 mm in the Kruisschans Member), rather flat, with 11 to 12 anterior and 15 to 20 posterior hinge teeth. Shell shape is trigonal, with a rounded anterior margin. When the posterior margin is held vertical, the anterior dorsal margin curves above a horizontal, the umbonal angle thus being in excess of 90°. Ornament consists mainly of a few prominent growth lines, corresponding possibly to growth halts. Only on slightly worn specimens do radial lines become apparent. Of uneroded shells, the surface is smooth, especially in younger individuals. Although their size seems slightly larger than that of Recent representatives, the shape, teeth number and ornament suggest assignment of these shells to *N. nucleus*.

However, both these assignments are with a

query, in view of the importance of non-fossilising characters in the systematics of Nuculidae, such as the form of the faecal pellets (Winckworth, 1931; Arakawa, 1970) and the colour and gloss of the periostracum (Tebble, 1976). Furthermore, shell features, ornament in particular, are highly dependent of preservation, as stated above.

The occurrence of two species of *Nucula* s. str. in the Neogene of the Antwerp area appears unquestioned. Firstly, shell shape, ornament and teeth number allow to distinguish not only between adult, but also between juvenile specimens of both species. Secondly, both forms do not always co-occur. In the Miocene Berchem Formation, only the smaller type is represented. During deposition of the Oorderen Member (Lillo Formation) both types are present, with a slight dominance of *N.* aff. *trigonula*. In the basal layer of the Kruisschans Member, only the smaller species was found, and from the sandy layers 15 to 17 *N.* aff. *nucleus* was collected.

Wood (1851-81) also distinguished both types in the British Pliocene Crag faunas, referring to the larger species as *N. nucleus* (Wood, 1851-81, pl. 10, fig. 6) and the smaller as *N. trigonula* (pl. 10, fig. 7). In the Recent European fauna, *N. trigonula* is not distinguished. *Nucula turgidula* (Malm, 1862) closely resembles our smaller fossil type (see *e.g.* Nordsieck, 1969) and is here considered a synonym, *N. trigonula* having priority.

Heering (1950) also recorded two forms from Dutch borehole material, referring to the larger as *N. nucleus*. The smaller species was assigned to *Nucula proxima* Say, 1822, with *N. trigonula* as synonym. This is, however, an American species, which is slightly larger and has a green periostracum, in stead of a brown one as in *N. tumidula* (see Abbott, 1968).

Glibert (1957a) recorded the occurrence of a large and a small species of *Nucula* from the Belgian Neogene as well, and considered them conspecific, following Bucquoy *et al.* (1887-1898). The smaller type he considered to represent *N. nucleus* s. str., the larger forma *radiata* Forbes & Hanley, 1853. Glibert did not consider the possibility of a separate occurrence of these types.

Van Regteren Altena *et al.* (1962) also mentioned the occurrence of two types in Dutch fossil beach material, but did not name them.

In conclusion, the occurrence two separate species of *Nucula* now seems quite certain. To unravel their nomenclature and relationship with Recent congeners, further research is necessary.

— *Yoldia (Y.) myalis* (Couthouy, 1838)
(Pl. 1, Figs 3, 6)

Specimens from the Kruisschans Member differ clearly from *Yoldia* specimens occurring in the underlying Oorderen Member, in being rounded anteriorly, and having the posterior end drawn out into a well-defined rostrum. The shell is consequently strongly inequilateral, diminishing more rapidly in height posteriorly than anteriorly. The umbo lies closer to the anterior than to the posterior end. On the inside, under the umbo, is a triangular pit, the left and right margin of which make an angle in excess of 90°. The lower margin of this pit is regularly rounded. Anteriorly, about 23 hinge teeth are present, posteriorly about 18. The outer surface of the shell is near-smooth, glossy, with only growth lines present. These are clearest in the area immediately below the umbo.

Yoldia shells from the Oorderen Member are rounded anteriorly as well as posteriorly. The posterior end may become bicarinate, but never pointed. The umbo is situated about halfway between anterior and posterior end. Consequently, the shell is much more equilateral. In addition, in specimens of the same size, the number of teeth is higher than in Kruisschans Member specimens, *viz.* 24 posteriorly and 27 anteriorly. The triangular pit under the umbo is faintly divided into two sections by a sinus in the lower margin. These Oorderen Member shells are assigned to *Y. (Y.) semistriata* (Wood, 1840) (Pl. 1, Figs 4, 5).

Yoldia myalis has not been recorded previously from the Belgian Neogene, where it is restricted to the Kruisschans Member, being not uncommon. Specimens are well preserved and occasionally found articulated. Left valves strongly outnumber right ones in the material before me.

The species was also recorded by Wood (1851-81) from the British Red and Chillesford Crags, while *Y. semistriata* appears to be confined to the Coralline Crag. Heering (1950) and van Regteren Altena *et al.* (1962) recorded it from Dutch boreholes and beach material, respectively.

The species survives to the present day and appears to inhabit cold waters, occurring in boreal-subarctic waters in Canada, the United States (down to Massachusetts Bay), Alaska (Ockelmann, 1954; Lubinsky, 1980) and Iceland. Nordsieck (1969) mentioned the species also from England, but this record was not confirmed by Tebble (1976).

— *Glycymeris variabilis* (J. de C. Sowerby, 1824)

This species is rather rare in the material studied and specimens are poorly preserved, looking worn. They belong to a form, described as *G. variabilis*, and differ from *G. glycymeris* (Linné, 1758) in being more flattened, and in having an obliquely oval outline. In addition, radial ornament is more pronounced. The ligament area possesses roof-like ridges, which are missing in the Recent species (Moerdijk *et al.*, 1992).

Specimens from the Kruisschans Member differ strongly from the *Glycymeris* shells occurring in the Oorderen Member, which have no ridges in the ligament area and a different radial as well as concentric ornament.

— *Modiolula phaseolina* (Philippi, 1844)

Glibert (1958b) recorded this species exclusively from the Miocene Edegem Member to the Pliocene Luchtbal Member. It is indeed much commoner in the Miocene and Early Pliocene than in younger deposits in the area.

— *Atrina* sp.

Only very small apical fragments have been collected, which cannot be identified to species.

— *Pecten (P.) grandis* J. de C. Sowerby, 1828 and *Pecten (P.) complanatus* J. de C. Sowerby, 1828

These species co-occur in the Kruisschans Member and are very similar, the latter differing mainly in having numerous, more regular and finer secondary ribs and a flatter right valve. Specimens of *Pecten grandis* are assigned to forma *grandis*, which is characterised by its high primary rib number (14) (see van Regteren Altena *et al.*, 1966).

— *Lima (Limatula) loscombii* (J. de C. Sowerby, 1823) and *Lima (Limatula) exilis* (Wood, 1839)

Of these species, a single valve has been collected from the Kruisschans Member at Kallo and at Antwerp-Noorderlaan, respectively. They are easily distinguished: the latter species has a flatter, larger and wider shell as well as stronger, more widely spaced ribs. Fossil specimens of the former species often have a dark bluish hue, which holds also true for the Kallo specimen.

Exactly which name should be applied to the latter species is an unresolved matter. Wood (1851-81), Glibert (1957c) and van Regteren Altena *et al.* (1969) recorded it as *Lima exilis*. Glibert (1957c), however, pointed out that *L. exilis* was a junior synonym of *Lima inflata* Chemnitz, 1784. Glibert & van de Poel (1965) referred to this species as *Limatula tuberculata* (Olivi, 1792), a name considered to be a junior synonym of *L. inflata* by Nordsieck (1969). As the Recent species, *L. inflata* is strongly inflated, rather narrow and clearly asymmetric, it is preferred to retain Wood's name for fossil specimens, which in general outline are close to the Recent *Lima hians* (Gmelin, 1790), but that species has a different ornament.

— Family Carditidae Fleming, 1828

Pteromeris corbis (Philippi, 1836) is not rare in the Kruisschans Member, but all specimens are eroded to such an extent that their ornament has virtually disappeared.

Two species of the genus *Cyclocardia* Conrad, 1867 have been found in the Kruisschans Member, *viz. C. orbicularis chamaeformis* and *C. scalaris*, the latter being the commoner one, and characterised by a flat shell with a superficial lunula, high rib number (21), narrow intercostal areas and flattened ribs, carrying quadrangular, rectangular or irregular block-like tubercles. Of the former taxon but a single eroded specimen has been collected from the basal layer. It has a more tumid shell with an excavated lunula, fewer and higher ribs (about 19) with wide intercostal areas. The taxonomic status of these species is still a matter of debate. Heering (1950) and Glibert (1957c) distinguished three species in the Belgian and Dutch Neogene, *viz. C. orbicularis*, *C. chamaeformis* and *C. scalaris*. Janssen & van der Slik (1972) united the first two under *C. orbicularis*, on account of their type specimens having the same number of ribs and identical size ratios. Both are indeed very similar, although *C. chamaeformis* is invariably much larger than typical *C. orbicularis*. They also seem to occur in different units, *C. orbicularis* being common especially in the Kattendijk Formation, and *C. chamaeformis* occurring mainly in the Lillo Formation. This is also the case for the type material of both taxa: *C. orbicularis* was described from the British Early Pliocene Coralline Crag, while *C. chamaeformis* was recorded from the overlying Red Crag (Janssen & van der Slik, 1972). These taxa are therefore considered as stratigraphic subspecies.

— *Glibertia prosperi* van der Meulen, 1951

A single valve of this diminutive, but very distinctive species has been collected from the basal bed of the Kruisschans Member, and two specimens from layer 15. It is known from the Luchtbal Member

onwards (Janssen & van der Slik, 1972) and occurs also in the Oorderen Member at Kallo.

— *Digitaria forbesi* (Wood, 1874)

Two specimens of this species, which resembles *D. digitaria* (Linné, 1758), occurring much more commonly in this member, have been collected from the Kruisschans Member basal bed. *Digitaria forbesi* has an oval outline, while *D. digitaria* is circular. The umbo occupies a posterior position in the former and a central one in the latter species. The ribs are strongly eccentric in the latter and less so in the former. In *D. forbesi* they are somewhat straightened in their middle part, while they are always ellipsoidal and gradually curved in *D. digitaria*, in which species furthermore an irregular transverse sculpture is present near the posterior dorsal margin.

Glibert (1957c, 1958b) did not record *D. forbesi* from Belgium. It appears to have been present, however, during much of the Antwerp Pliocene, from the Kattendijk Formation to the Kruisschans Member, but invariably in low numbers. It is also known from the British Pliocene, under the name *Astarte parva* Wood, 1848 (*non* Lea, 1833), and was also recorded from Dutch fossil beach material by Janssen & van der Slik (1974).

— *Laevicardium decorticatum* (Wood, 1840)

Only poorly preserved fragments of this species have been collected. It cannot be determined whether these are autochthonous elements or remanié specimens from the underlying Oorderen Member. Glibert (1958b) also classed the occurrence of this species in the Kruisschans Member as doubtful.

— *Laevicardium parkinsoni* (J. Sowerby, 1818)

This species is considered the most typical fossil of the Kruisschans Member, which was referred to as 'Sables à *Cardium parkinsoni*' by Glibert (1958c). However, specimens have also been collected by the present author from a site at Wijnegem, east of Antwerp, from sands also yielding the gastropods *Melampus pyramidalis* (J. Sowerby, 1822) and *Cepaea haesendoncki* (Nyst, 1844) and thus referable to the Austruweel Member (Lillo Formation). The species ranges up into the Merksem Member, but is much rarer in that unit.

Most adult specimens have been collected from the clayey intervals of the Kruisschans Member, where they are the most conspicuous and numerous biota and invariably well preserved.

— *Lutraria* sp.

Only a single fragment is known from Kallo, which appears to be reworked and cannot be identified precisely.

— *Spisula inaequilatera* (Nyst, 1845) and *Spisula subtruncata triangulata* (Wood, 1857)

The former species has not been collected at Kallo, where only the latter has been observed. The KBIN collections, however, contain specimens which possibly originate from the Kruisschans Member, one specimen from Antwerp-Boudewijnsluis labelled 'Merxemien zone à *C. parkinsoni* et falun cx à *Pecten complanatus*, 7-7,5 m' and 47 specimens from 'Anvers (6 darse)', labelled 'Scaldisien, zone à *Cardium parkinsoni*, 5-5,5 m'. However, both could also have come from the Merksem Member, for which this species is typical.

— *Mactra glauca* Born, 1778 and *Spisula arcuata* (J. Sowerby, 1817)
(Pl. 2, Figs 1-4)

The former species is recorded here for the first time from the Belgian Pliocene. The general outline and size of both species is variable but comparable. The former species seems more rounded at the anterior and posterior margins, the latter more pointed. Only details of the hinge differ, and these define the genera: the lateral teeth of the former are smooth, while those of the latter show striations, perpendicular to the length of the teeth. In addition, the resilium is separated from the lateral ligament pit in *M. glauca*, while these are continuous in *S. arcuata*. The hinge plate is strongly curved away from the umbo near the resilium in *S. arcuata* and hardly so in *M. glauca*.

Both species were found much more commonly at the Antwerp-Noorderlaan section than at Kallo; they were there equally abundant and could always be easily separated. Both have been recorded from the British Red Crag, and Janssen *et al.* (1984) recorded them from Dutch fossil beach material.

— *Ensis complanatus* J. de C. Sowerby, 1844

This species is typical of the upper part of the Lillo Formation in Belgium. It is rare at Kallo, but commoner at the Antwerp-Noorderlaan section.

— *Angulus benedeni* (Nyst & Westendorp, 1839)

Only fragments of this species have been found in the Kruisschans Member, which might have been

reworked from the underlying Oorderen Member, the top of which yields this species in abundance.

— *Angulus donacinus* (Linné, 1758)

Three valves have been collected from the Kruisschans Member basal layer at Kallo. They clearly differ from *Angulus distortus* (Poli, 1795) in having a more posteriorly situated umbo, flat right valve and absence of a keel and regular ornament. *Angulus distortus* was recorded by Glibert (1959b) under the name *Tellina pulchella* Lamarck, 1818 and, on account of the uncertainty about stratigraphic provenance, placed tentatively only in the Kruisschans Member.

— *Macoma praetenuis* (Leathes *in* Woodward, 1833)

This species is typical of the Kruisschans and Merksem members, and is absent from any of the underlying units in the Antwerp area, as previously mentioned by Glibert (1958b). It is also known from the British Red and Chillesford Crags (Wood, 1851-81).

— *Abra alba* (Wood, 1802)

This species occurs commonly in the Kruisschans Member, but is not restricted to this unit, occurring also in older strata as indicated by Glibert (1958b).

— *Pygocardia rustica rustica* (J. Sowerby, 1818)

Although fragments are abundant in the Kruisschans Member, entire specimens are rare; all are assignable to the typical form, the forma *extensa* Janssen *et al.*, 1984 has not been found.

— *Dosinia lupinus lincta* (Pulteney, 1799)

This taxon was referred to by Glibert (1958b) as *Dosinia exoleta* (Linné, 1758). In having an escutcheon, most Antwerp Pliocene specimens of the genus *Dosinia* Scopoli, 1777 should be assigned to the present subspecies.

— *Mya truncata gudmunduri* Strauch, 1972

Only a single, juvenile specimen is available. It is rather elongate, with an oblique posterior margin, which is why it is referred to this subspecies with a query.

— *Arenomya arenaria* (Linné, 1758)

The occurrence of this species in fossil faunas from Belgium was mentioned in a list by Glibert (1958b), but not in the text. Its first occurrence is in the Late Pliocene, from the Austruweel Member onwards, and it is common in the Kruisschans Member at Kallo, but absent from other localities.

— *Panomya trapezoidis trapezoidis* Strauch, 1972

This species is comparatively common and has also been found articulated in clay layer 12 of Hoedemakers & Marquet's (1992) section, in which no other molluscan species were observed. The occurrence of this taxon in the Belgian Pliocene was mentioned already by Glibert (1959b) under the name of *Panomya arctica* Lamarck, 1818, but from the basal layer of the Oorderen Member. Strauch (1972) considered this to be a deep-burrowing species, which probably explains why it is the sole molluscan species occurring in layer 12.

— *Zirfaea crispata* (Linné, 1758) and *Barnea cylindrica* (J. Sowerby, 1818)
(Pl. 3, Figs 1, 2)

A single valve of the former species has been collected from shell layer 15, and it represents the first record as a Pliocene fossil from Belgium. The latter species appears to be also restricted to the Kruisschans Member. These species can be distinguished easily by the much larger size and relatively shorter shell of the former. Both are borers; they could have lived in the clay, but they were found as isolated valves and no traces of their boring activities have been observed in the clay.

— *Gibbula* aff. *beetsi* van Regteren Altena, 1954

This species, recorded by Glibert (1957b) to be typical of the Luchtbal Member, has been found in a single specimen in the Kruisschans Member at Kallo. It lacks the larger part of the outer shell layer, so that identification is with a query. However, it does certainly lack the granulose spiral ornament which characterises *G. gelriana* Beets, 1946, considered more typical of the upper part of the Lillo Formation by Glibert (1957b).

— *Calliostoma zizyphinum* (Linné, 1758) and *Calliostoma simile* (J. Sowerby, 1818)

The former species is, as Glibert (1957b) noted previously, present in the older part of the Belgian Pliocene. During deposition of the Oorderen Member, only the latter species appears to have been present. In the Kruisschans Member, *C. zizyphinum* re-appears. Provided that reworking can be excluded, their co-occurrence in the same unit would indicate that they are real species, not subspecies, as van Regteren Altena *et al.* (1965) thought.

Calliostoma multigranus (Wood, 1848), recorded tentatively by Glibert (1957b) from the Kruisschans Member, was not encountered at Kallo.

— *Eulimene terebellata* (Nyst, 1835) and *Lacuna suboperta* (J. Sowerby, 1813)

Although Glibert (1958b) did not list the former species for the Kruisschans Member, it is much commoner in this unit than the latter species. The former seems to be highly typical of the Kruisschans Member.

— *Potamides tricinctus* (Brocchi, 1814)

This species has not been collected at Kallo from the Kruisschans Member, but exclusively from the overlying Merksem Member. In the KBIN collections there are 15 specimens from the Kruisschans sea lock at Antwerp, but these lack indication of exact provenance. A single, very worn fragment from the Boudewijn sea lock (Antwerp) is assigned to the 'Merxemien zone à *Cardium parkinsoni*' and may have come from the Kruisschans Member. However, its presence in this unit needs confirmation. The species occurs in underlying units and is known from the Austruweel Member at Wijnegem.

— *Capulacmaea kalloensis* sp. nov.
(Pl. 3, Figs 3-5)

1965 *Capulacmaea radiata* (M. Sars, 1850) — van Regteren Altena *et al.*, p. 26, pl. 10, fig. 98 (*non* Sars).

Diagnosis — Small, somewhat flattened patelliform shell, comprising $1^1/_2$ whorls, with left-pointing umbo positioned close to the centre.
Derivatio nominis — This species is named after its type locality.
Locus typicus — Kallo, province of Oost-Vlaanderen (Belgium), topographical map of Belgium, 1:25,000, sheet 15/1-2, co-ordinates x = 139 611, y = 219 504, 250.
Stratum typicum — Kruisschans Member, Lillo Formation, Late Pliocene [layer 15 of Hoedemakers & Marquet's (1992) section].
Type — Holotype is specimen no. 6129 (KBIN, section Tertiary Invertebrates Type Collection).
Additional material — Kruisschans Member at Kallo: five specimens; Oorderen Member (*Atrina* layer) at Kallo: 9 specimens; Oorderen Member (*Cultellus* layer) at Kallo: 2 specimens; Oorderen Member (*Atrina* layer) at Kallo-Vrasenedok: 8 specimens (all Marquet Collection).

Description — The shell is very thin, patelliform and consists of $1^1/_2$ whorls. The umbo is slightly eccentric and is situated near the centre. The last half whorl is much larger than the remainder of the shell, giving it a flattened, oval shape. No ornament is present, except for irregular concentric growth lines. The interior of the shell is smooth and glossy. Muscular impressions are not visible in the material studied. The largest specimen measures 9 mm across. No specimens preserving colour patterns are known, although such specimens have been recorded from Dutch fossil beach material.
Discussion — This species had not previously been recorded from the Belgian Pliocene; it cannot be confused with the only other representative of the lamellariid genus *Capulacmaea* Sars, 1859 [type species *C. radiata* (Sars, 1850)] in the Belgian Pliocene, *viz. C. virgata* (Wood, 1848), which has a much higher, less patelliform shell and comprises about $2^1/_2$ whorls. Recent specimens of *C. radiata*, from Hornafjordmidum (Iceland; Fraussen Collection) differ from the fossil species in having a higher shell, which may grow to a much larger size, and in the umbo, which is positioned more eccentrically above the shell margin. Some taxa, belonging to utterly different groups, resemble the present species. *Williamia gussonii* (O.G. Costa, 1829), which occurs in the Pliocene of Italy is smoother exteriorly, with the apex pointing very slightly to the right and with an interior with typical muscular impressions (Bucquoy *et al.*, 1887-1898; Cavallo & Repetto, 1992). *Capulacmaea kalloensis* has possibly been lumped with *Calyptraea chinensis* (Linné, 1758) previously from which it is easily distinguished by the absence of an internal septum.

The Recent *C. radiata* has an arctic distribution: Norway, northern Russia, Iceland, Greenland and Canada (Macpherson, 1971).

— *Natica multipunctata* Wood, 1842
(Pl. 3, Fig. 6)

This is one of the commonest species in the Kruisschans Member, specimens with preserved opercula occurring not uncommonly. Most specimens are typical in outline, some, however, have a slightly higher spire, with the outer lip attached nearly halfway the penultimate whorl. Their umbilical ridge is not noticeably weaker than in the typical form. Such specimens are reminiscent of *Natica bevelandensis* Pouderoyen, 1956. The fact that the range of variation of *N. multipunctata* is quite wide makes it difficult to delimit it sharply. I consider *N. bevelan-*

densis to represent but a forma of *N. multipunctata*, rather than a separate species.

— *Polinices hemiclausus* (J. de C. Sowerby, 1824)

Rather low-spired specimens [forma *proxima* (Wood, 1848)], as well as higher-spired forms [forma *woodi* Harmer, 1921] occur in the Kruisschans Member, the characters of the callus separating these formae. The stratigraphic range of this species is much wider than assumed by Glibert (1958b), who considered it to be confined to the Kattendijk Formation.

— *Nucella incrassata* (J. de C. Sowerby, 1823)

This species is confined to the Kruisschans Member in the Belgian Pliocene, where it co-occurs with *Spinucella tetragona* (J. de C. Sowerby, 1823). The shells of the former differ strongly from Recent *N. lapillus* (Linné, 1758) by being larger, and having a subsutural keel, fewer spirals, which are narrower than or as wide as the interspaces, a relatively lower aperture and a higher spire. Specimens of *Nucella* differing from Recent representatives only in being larger were illustrated by van Regteren Altena *et al.* (1965) as *N. lapillus vulgaris* (Wood, 1848). At Kallo, these occur in the Oorderen Member. As the ranges of both taxa overlap, *N. incrassata* might better be considered a species, rather than a subspecies of *N. lapillus*.

— *Neptunea contraria* (Linné, 1771)

This species is very common in the Kruisschans Member. Glibert (1959a) assumed the forma *sinistrosa* (Deshayes, 1830) to be typical of this unit. Strauch (1972) considered this forma to be a separate species, but found its distribution limited to southern Europe and the Mediterranean.

In the Kruisschans Member, the shell shape of this species is very variable, with taller, slender shells co-occurring with broad, tumid specimens, along with every possible transition between these two extremes. The ornament is also variable, consisting of a large number (invariably over 50) primary and secondary spirals. The same holds true for specimens from the Oorderen Member, although their range of variation appears more limited. It appears inappropriate to distinguish two species in this material.

—*Neptunea lyratodespecta striata* Strauch, 1972

The systematics of dextral species of *Neptunea* from the Pliocene of the North Sea Basin is in a state of confusion, due to a plethora of specific names and varieties applied to them in the past. The first name to be employed for dextral species of *Neptunea* from the British Crags is *Murex striatus* J. Sowerby, 1813. Wood (1848) united dextral and sinistral British shells under the name *Trophon antiquum* Müll., mentioning *M. striatus* as a synonym. In a supplement, Wood (1851-81) split this species into several varieties, two sinistral and two dextral (*Trophon antiquus striatus* and *T. antiquum carinatus*). Harmer (1914-25) divided the dextral species into *N. antiqua* (with four varieties) and *N. despecta* (with 10 varieties), and considered the fossil specimens to be conspecific with Recent ones. Nyst (1878/81) recorded from the Belgian Pliocene *Fusus antiquus* (= *Murex striatus*) and var. *jugosum* Wood, 1848. Glibert (1959a) split the same material into two subspecies, *viz. N. despecta carinata* and *N. antiqua striata.* Van Regteren Altena *et al.* (1965), however, considered all Dutch Pliocene dextral forms to represent a single, variable species, *N. antiqua carinata.* Strauch (1972) was of the same opinion, but he gave the species a new name, *N. lyratodespecta*, with three subspecies, *viz. N. l. lyratodespecta* (Iceland, England, Belgium), *praedecemcostata* (Iceland) and *striata* (England, Belgium, The Netherlands). Nelson & Pain (1986), however, reunited *N. lyratodespecta* with *N. antiqua.*

In the material studied no sharp distinctions between the different forms can be made. Comparisons should be based on average specimens, not on exceptional ones, which in this case easily overlap with the invariably considerable variation of related species. Furthermore, every population studied shows its own characteristics, which would, however, be too cumbersome to formalise in nomenclature.

I agree with Strauch (1972) in distinguishing the Pliocene specimens from Recent European dextral species of *Neptunea. Neptunea antiqua* (Linné, 1758) is always more finely ornamented, without distinction between primary and secondary spirals. This species is certainly not conspecific with Pliocene fossils, as Nelson & Pain (1986) suggested. *Neptunea despecta* (Linné, 1758) from the North Sea possesses primary and secondary spirals. Mostly, there is however only one primary spiral on each whorl, instead of more as in fossil specimens. Often this spiral shows notches, which may develop into spines, as figured by Poppe & Goto (1991, fig. 29.1). Few specimens possess spirals without spines and are close to the Pliocene form (Poppe & Goto, 1991, fig. 29.2). However, notches are never present in Pliocene forms. So their range of variation overlaps with

Recent North Sea *N. despecta*, but average specimens are clearly different.

All specimens of undoubted or doubtful Oorderen Member age from Kallo in the author's collection or from other localities in the KBIN collections show clearly dominant primary spirals and a strongly angular shape. They belong to *N. lyratodespecta lyratodespecta* Strauch, 1972. A single specimen has four very prominent primary and very unclear secondary spirals and is assigned to var. *subspitzbergensis* Harmer, 1919. All Kruisschans Member specimens have much fewer prominent primary spirals, compared with the secondary ones, although both never become equally strong. Kallo specimens have a very high slender spire, and may be referred to *N. l. striata.* A single specimen from the Merksem Member of Antwerp-Berendrecht in the author's collection shows very weak spirals; primary and secondary ones are indistinguishable. Although the ornament is still slightly coarser, this specimen is close to *N. antiqua.*

— *Amyclina labiosa* (J. de C. Sowerby, 1824)

This species, which is very typical of the Oorderen Member at Kallo, is rare in the Kruisschans Member, from which only incomplete, apparently reworked, specimens are known.

— *Hinia elegans* (J. de C. Sowerby, 1824) and *Hinia consociata* (Wood, 1848)
(Pl. 4, Figs 1-4)

These species are similar. The former has, however, a slightly wider apical angle than the latter and a different ornament, consisting also of spirals and longitudinal ribs, but the ribs are clearly more widely spaced. Both co-occur in the Kruisschans Member, but the former species is much commoner. In the Oorderen Member, *H. consociata* only is found. Nyst (1878/81) recorded only *H. elegans* from Belgium, but Glibert (1959a) considered all Belgian Pliocene material to belong to *H. consociata. Hinia elegans* has also been recognised in Dutch beach material by van Regteren Altena *et al.* (1965), while Beets (1946) did not distinguish it. Both are also known from the British crags.

— *Hinia reticosa* (J. Sowerby, 1818) and *H. scaldensis* (Adam & Glibert, 1976)

The former species is one of the most abundant in the Kruisschans Member, reaching an acme in this unit and in the underlying *Angulus benedeni* unit (no. 10) of the Oorderen Member. Two types may be distinguished: the typical form having rather weak longitudinal costae and broad primary spirals alternating with secondary ones. The forma *tiara* (Wood, 1848) has much stronger longitudinal costae and fewer, broader spirals, which may be lacking on the upper half of the last whorl. No distinction between primary and secondary spirals can be made. Intermediates between these forms occur commonly, while specimens with initial *tiara*-like whorls, may have a *reticosa*-type ultimate whorl.

A few shells are smaller than *H. reticosa* and have more spirals, which are always equal and as narrow as the interspaces. There is a variable number of costae; in some specimens these are nearly absent, and, if present, narrow. Their protoconch is not clearly separated from the teleoconch, and they most closely agree with *H. scaldensis*, although their general shape is variable: some individuals have very narrow, very shallow sutures, others have broader, more tumid whorls. Some, but not all, have a parietal knob. Shell form and whorl shape appear to be unreliable features in separating the various species of this genus.

The number of costae per whorl is invariably fewer than 25 and the protoconch is, in the few specimens preserving it, not clearly delimited. These characteristics separate *H. scaldensis* from *H. ligustica* (Bellardi, 1882) (see Adam & Glibert, 1976). Part of the material, mentioned under that name by van Regteren Altena *et al.* (1965) and Moerdijk *et al.* (1992) from Dutch beaches probably belongs to *H. scaldensis.*

— *Hinia propinqua* (J. de C. Sowerby, 1824)

This species is abundant in the Kruisschans Member at Kallo, but is absent from the Oorderen Member. Glibert (1959a) found this species also in the Austruweel Member.

— *Phrontis kennardi* (Harmer, 1914)

This species is easily distinguished on account of its small aperture, shallow sutures and distinctive ornament, consisting of fine spirals and a few, broad and unclear ribs, which run obliquely against the shell's longitudinal axis. This is a very rare Kruisschans Member species, only a single specimen being available. Glibert (1959a) recorded specimens from the Austruweel Member.

— *Admete viridula* (Fabricius, 1780)
(Pl. 3, Fig. 7)

This is a very common species in the Kruisschans

Member at Kallo, where it is confined to this unit. Nyst (1878/81) recorded it from the 'Scaldisien jaune de Doel', a locality nearby Kallo. Glibert (1960) also recorded Nyst's three original specimens from that locality and referred them to the 'Scaldisien (Sables à *Melampus pyramidalis*)' or 'Sables d'Austruweel de Doel'. Nyst (1878/81) did not record *M. pyramidalis* in his list for Doel. It may well be that the indication 'Sables d'Austruweel' is a later addition, which is why I consider this species to be confined to the Kruisschans Member.

Admete viridula is in Recent faunas an arctic, circumpolar species, inhabiting soft-bottom settings from a few metres to 1,000 m depth in the southern part of its geographic distribution (Graham, 1988). In Europe, the species occurs off Iceland and Scandinavia, ranging to the Faroes and the British Isles (Poppe & Goto, 1991); and it thus seems to be associated with colder climates. However, Harmer (1914-25) recorded it already from the Coralline Crag. This occurrence is not entirely convincing, as Wood (1848) typified the Coralline Crag material as 'few, small and very imperfect'.

— *Haedropleura delheidi* Vincent, 1890

This species has not been found at Kallo, and its presence in the Kruisschans Member is not beyond doubt. It was originally recorded from the 'Couche à *Corbulomya complanata* (Poederlien)' at Austruweel (bassin America), Antwerp by Vincent (1890). *Lentidium complanatum* (J. Sowerby, 1822) occurs in the Kruisschans Member, but is also known from the Austruweel Member.

The type specimen of the present species in the KBIN collections is labelled as coming from the 'Couche à *Conovulus pyramidalis*, Bassin America'. This suggests the Austruweel Member, which is characterised by this species, rather than the Kruisschans Member. Glibert (1958b) referred this species to the 'gravier du Bassin America', at the base of the Kruisschans Member. Thus its exact provenance is still not fully known.

— *Cytharella* aff. *substriolata* (Harmer, 1918)

The identification of this and related Pliocene-Recent species is rendered difficult by the fact that the species, in their original descriptions, were mostly distinguished solely on their gross morphology, while later systematic generic interpretations involved the protoconch rather than the teleoconch, which resulted in disparate definitions of species. In addition, protoconch features are hardly ever preserved in fossils.

Harmer (1914-25) described *Mangelia substriolata* from the British Red Crag. *Mangelia altenai* Brakman, 1938 was described from Dutch beach material. Van Regteren Altena (1959) and van Regteren Altena *et al.* (1965) united both species under Harmer's name, and distinguished it from *M. smithi* (Forbes, 1840) by the larger, more slender and narrower shell of that species. Glibert (1960) distinguished *M. altenai* from *M. smithi* by the smaller protoconch of the latter, while the spiral ornament on the first teleoconch whorl is coarser than later spirals in *M. altenai* and equal in *M. smithi.*

Kallo material from the Oorderen Member appears slightly more slender than that of the Kruisschans Member, with more tumid whorls. The ornament of the protoconch and first teleoconch whorl are like that described for *M. altenai* (= *M. substriolata*). Kruisschans Member shells only very rarely preserve an intact protoconch, but seem closer to *M. smithi.* Their sizes are not different, seldom exceeding 10 mm, and never as large as the Recent species *M. smithi.* Not having been able to study the type material of both species, it is impossible for me to decide to refer the Kruisschans Member specimens to either species; the name *C. substriolata* is employed for the fossil material here.

— *Mangelia keepingi* (Etheridge & Bell, 1898)
(Pl. 4, Figs 5, 6)

This species has not been recorded previously from Belgium. The protoconch consists of three smooth whorls, followed by a whorl, on which equally strong spiral and radial elements are present. The shell is high, fairly slender, with height 2.9 times the width. Height never exceeds 10 mm, being mostly *c* 9 mm. Five to seven teleoconch whorls are present. Aperture occupies about 40% of total height of shell. Whorls are not tumid, with shallow sutures. Ornament of teleoconch consists of eight to nine costae on each whorl, which are especially pronounced in immature specimens and may become obsolete on the youngest whorl. They do not reach the adapical suture, but end on a more or less accentuated subsutural depression. Below this, on the body whorl are found twelve to fifteen primary spirals, much weaker than the costae and continuing over these. Between the primary spirals, some specimens possess two to four weaker secondary spirals. These may form the only ornament on the subsutural depression; in other specimens, the remains of earlier anal sinuses cause the formation of a regular lattice sculpture in the depression.

Outer lip forms a regular circle segment, with a shallow broadly v-shaped anal sinus.

The species most closely resembling the present one is *M. neerlandica* (Beets, 1946), which has a similar protoconch, but has more and lower costae and more regular spirals, which cannot be separated into primary and secondary ones. The shell is also more slender, with even shallower sutures. It is common in the Oorderen Member at Kallo.

The present species was first described from the St Erth Beds of Cornwall (SW England). Harmer (1914-25, pl. 39) illustrated specimens under various names, *viz. Raphitoma compacta* (Etheridge & Bell, 1898) (smaller specimens, *e.g.* fig. 7), *R. hoernesi non* Mayer, 1858 (fig. 8) and *R. keepingi* (Etheridge & Bell, 1898) (fig. 17), all from the same locality. *Raphitoma consimilis* Harmer, 1918 from the Coralline Crag could also belong here, but study of the type material is necessary to decide this; the illustrated specimen is worn.

Beets (1946) figured the species from *in situ* material from The Netherlands. Van Regteren Altena *et al.* (1965, pl. 17, fig. 166a) listed it also for Dutch beach material: their forma *consimilis* of *M. keepingi* (pl. 17, fig. 166b) represents a specimen of *M. neerlandica* (Beets, 1946).

— *Chrysallida indistincta* (Montagu, 1808)
(Pl. 4, Figs 7, 8)

This species is new to the Belgian Pliocene. The specimens collected are all small, their maximum height being *c* 3 mm. The visible part of the protoconch is smooth, and the teleoconch consists of *c* five to six flattened whorls (earlier ones) or slightly tumid whorls. The sutures are not deep. Ornament consists of about 25 to 30 costae on the ultimate whorl, slightly sigmoid. Between the costae, four to six spirals may be seen on the abapical half of the body whorl, the base of the shell being smooth. A small umbilical slit is present. The columellar tooth is rarely visible.

The species is easily distinguished from *Chrysallida jeffreysi* (Bellardi, 1871), the only other representative of the genus from the Belgian Pliocene, which has much more tumid whorls and a spiral ornament extending over the entire whorl. *Chrysallida obtusa* (Brown, 1827), known from Dutch beach material, has only two to three spirals and the columellar tooth is usually clearly visible.

Chrysallida indistincta is unknown as a fossil from England. It has been recorded from Dutch beach material, but van Regteren Altena *et al.* (1965) considered such specimens to be of Eemian age. Its Recent distribution is from the Mediterranean to off northern Norway (Graham, 1988).

— *Odostomia (O.) conoidea* (Brocchi, 1814) and *Odostomia (O.) unidentata* (Montagu, 1803)
(Pl. 4, Figs 9-12)

The latter species is new to the Belgian Pliocene. Both species are small, up to three millimetres in height. The protoconch's axes lie perpendicular to the shell length, so that the apices are exposed. Both species have five to six whorls, which are nearly straight sided, but slightly more convex in the former. The shells are smooth, with only very weak, slightly prosocline growth lines. The body whorl is regularly rounded in the former species, but shows a slight keel in the latter. Both have a narrow umbilical groove. The clearest difference is the presence of five to seven spiral ridges on the inside of the outer lip in the former.

Odostomia unidentata is much commoner than *O. conoidea* in the Kruisschans Member; it is also known from the Oorderen Member and part of the material listed by Glibert (1958a) under the name *O. conoidea* should probably be assigned to *O. unidentata.* This species has been recorded from Dutch beach material (van Regteren Altena *et al.*, 1965) and from the British crags (Harmer, 1914-25). The systematics of this group, comprising a vast number of species, are however, in a state of confusion due to the poor knowledge of the type material as well as the lack of distinguishing features.

— *Odostomia (Brachystomia) eulimoides* Hanley, 1844
(Pl. 4, Figs 13, 14)

This species is also new to the Belgian Pliocene. Its protoconch is sunken, the shell being high spired, about two millimetres high, with six rather flat whorls. The body whorl is broad, about half or more of the total shell height. Only a small umbilical slit is present. The ornament consists of straight, prosocline growth lines. The aperture shows a prominent columellar tooth.

This species can be distinguished from both species of *Odostomia (Odostomia)* co-occurring with it in the Kruisschans Member easily by its sunken protoconch, the different shell shape and slightly more tumid whorls. It differs from *O. scalaris* (MacGillivray, 1843), as found in Dutch beach material (van Regteren Altena *et al.*, 1965), by its less tumid whorls, shallower sutures and different aperture. It

is not known from the British Pliocene. In The Netherlands, it has been found in beach material of supposedly Eemian age. In Recent faunas, it occurs from the Mediterranean to the Arctic (Graham, 1988).

— *Turbonilla internodula* (Wood, 1848) and *Turbonilla senistriata* (Wood, 1879)

Only the former species has been encountered in the Kruisschans Member at Kallo. Specimens of the latter from the Kruisschans Member are present in the KBIN collections. They are easily differentiated by the absence of costae in the latter species.

— *Retusa* sp.

Only a single, incomplete specimen has been collected (A. Ratinckx Collection). The upper part of the aperture is damaged, which is why it is impossible to decide whether it should be assigned to *Retusa obtusa* (Montagu, 1803) or *R. truncatula* (Bruguière, 1792). These species differ primarily in the shape of this upper part which is as high as or lower than total shell height in the former, and higher in the latter (Thompson, 1988). Only the latter species has so far been recorded from the Belgian Pliocene (Glibert, 1960), exclusively from the Luchtbal Member.

The molluscan fauna of the Kruisschans Member as collected at Kallo comprises a total of 125 species, 67 bivalves and 68 gastropods. This fauna is thus more diverse than previously observed: Glibert (1958b) listed a total of 53 bivalves and 28 gastropods. Of his species, nine have not been encountered in the present study, which brings the total number of the species present at 134 (72 bivalves and 72 gastropods).

A few species are new to the Belgian Pliocene, *viz. Nucula* aff. *trigonula*, *Yoldia myalis*, *Mactra glauca*, *Zirfaea crispata*, *Capulacmaea kalloensis*, *Hinia elegans*, *Mangelia keepingi*, *Chrysallida indistincta*, *Odostomia eulimoides* and *O. unidentata*. Species recorded previously from the Kruisschans Member, but not collected during the present study include *Aequipecten radians*, *Spisula inaequilatera**, *Abra prismatica*, *Callista chione*, *Cochlodesma praetenue*, *Gibbula gelriana*, *Potamides tricinctus**, *Haedropleura delheidi**, and *Turbonilla senistriata*. However, it is still doubtful whether these species marked with * really did originate from the Kruisschans Member. Some have been recorded from the basal gravel of the Americadok, which does not appear to be present at Kallo.

Stratigraphy

The Kruisschans Member was defined (as Kruisschans Sands) by de Heinzelin de Braucourt (1955a, b) in a temporary section at the Boudewijnsluis at Antwerp. De Meuter & Laga (1976) included it as a member in the Pliocene Lillo Formation and presented a description of this unit (Fig. 2). From this, it appears that this member is often sandier than seen at Kallo, consisting of fine- to coarse-grained sands with intercalated dark clay layers. In the Kallo section, the reverse was seen, the unit consisting there mainly of clay with intercalated sands.

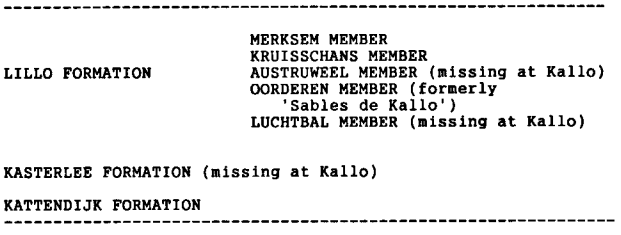

Fig. 2. Lithostratigraphic units of the Belgian Pliocene/early Pleistocene (the former Scaldisien), modified after Glibert (1958b) and de Meuter & Laga (1976).

The Kruisschans Member has previously been defined mainly by the occurrence of *Laevicardium parkinsoni* and *Nucella incrassata* and the absence of *Ellobium pyramidale* (J. de C. Sowerby, 1824). The first-mentioned species, although being common in this unit, extends to the overlying Austruweel Member. *Abra alba*, *Arenomya arenaria*, *Spisula inaequilatera* and *Macoma praetenuis* have also been listed as typical faunal elements by Laga (1973). The two first-named species occur also in underlying strata and the occurrence of *S. inaequilatera* in the Kruisschans Member is doubtful. Apparently confined to this unit are the following species: *Yoldia myalis*, *M. praetenuis*, *Neptunea lyratodespecta striata*, *Hinia elegans*, *Admete viridula*, *Mangelia keepingi*, *Chrysallida indistincta* and *Odostomia unidentata*. The presence of *Y. myalis* and *A. viridula* may be of significance, these species being typically arctic in their present-day distribution. Their presence might indicate a considerable climatic cooling, but caution is called for. Limited numbers of fairly warm-water species are still present in the Kruisschans Member, such as *Galeodea bicatenata*, *Narona jonkaireana* and *Scaphella lamberti*.

In England, the Norwich Crag as well as the Red Crag are now considered to be of Pliocene age

(Gibbard & Zalasiewicz, 1988). The Norwich Crag fauna appears to be younger than that of the Kruisschans Member, yielding amongst other species, abundant *Nucella lapillus lapillus* (Linné, 1758) rather than *N. incrassata*. The Red Crag yields much more species than the Kruisschans Member. At a number of localities, *e.g.* Buckanaye Farm Pit (East Anglia) a fauna showing some similarities to the Kruisschans Member is found, and occurring in both are *A. viridula*, *Lacuna suboperta*, *N. incrassata* and *Pteromeris corbis* (Gibbard & Zalasiewicz, 1988).

Palaeoenvironment and taphonomy

At Kallo, the Kruisschans Member consists mainly of clay layers, with some intercalated sands. The first are indicative of either a low-energy environment or a slow rate of sedimentation, and contain rather few shells, mainly *L. parkinsoni* and *Panomya trapezoidis*. Most of the described species originate from the sandy intervals, which are often composed of complete and fragmentary shells. Many of the gastropods, such as *Sipho cordatus*, *S. curtus*, *Neptunea contraria*, *N. lyratodespecta striata*, and *Hinia reticosa* are commonly found empty instead of filled with sand. They may have been deposited rapidly and buried half alive by storm surges. Other species, such as *Lutraria* sp. and *Laevicardium decorticatum* seem to have been reworked. Possibly part of the clay layers was removed before rapid sedimentation, leaving fragments and disarticulated valves of boring pholadids in the sandy intervals.

The fauna of the Kruisschans Member is clearly holomarine, no terrestrial or estuarine species being represented. Such species are common in the underlying Austruweel Member. The absence of estuarine influences at Kallo may explain the absence of *Potamides tricinctus*, which is found in underlying as well as in overlying strata.

Acknowledgements

Mr K. Hoedemakers assisted me during the field work sessions and provided numerous samples from the Kruisschans Member, Mr A. Ratinckx also contributed to the field work and made his collection available for study; Drs A.V. Dhondt and P. Bultynck (Brussels) allowed access to collections in their care and to photographic and SEM facilities. Photomicrographs have been prepared by Mr J. Cillis, other photographs by Messrs W. Miseur (Brussels) and M. Wagenaar. Mr A.W. Janssen is thanked for suggesting improvements to an earlier draft.

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PLATE 1

Unless indicated otherwise, all specimens are from the Kruisschans Member (Lillo Formation) as exposed at Kallo (Belgium).

Fig. 1. *Nucula* aff. *nucleus* (Linné, 1758), interior of left valve, x 3.4 (KBIN Collections, Brussels).

Fig. 2. *Nucula* aff. *trigonula* (Wood, 1851), interior of left valve, x 5.8 (KBIN Collections, Brussels).

Figs 3, 6. *Yoldia (Yoldia) myalis* (Couthouy, 1838), interior of right valves, x 4.8 and 9.6, respectively (KBIN Collections, Brussels).

Figs 4, 5. *Yoldia (Yoldia) semistriata* (Wood, 1840), Kallo, Oorderen Member (Lillo Formation), interior of right valves, x 4.6 and 9.6, respectively (Marquet Collection).

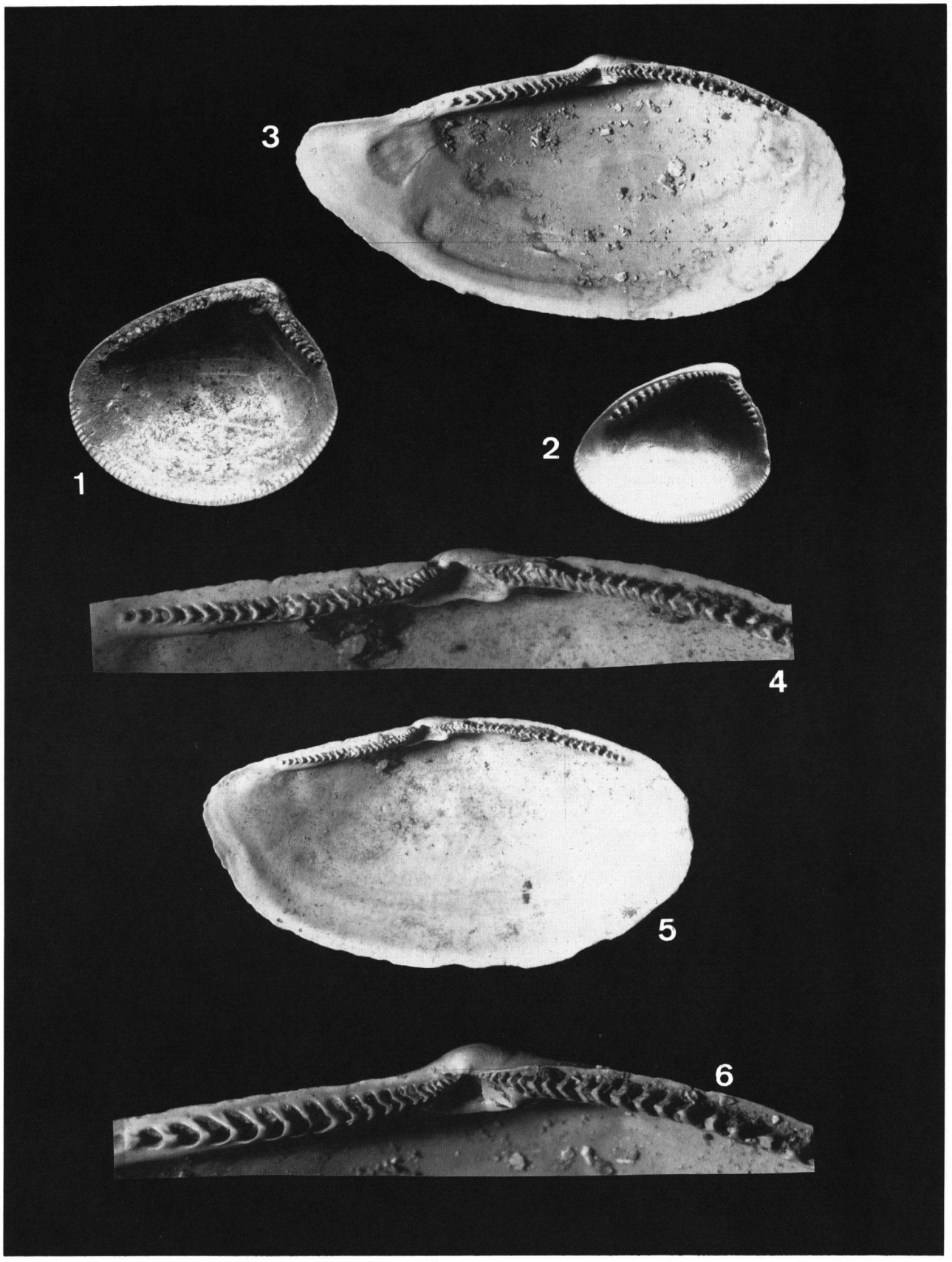
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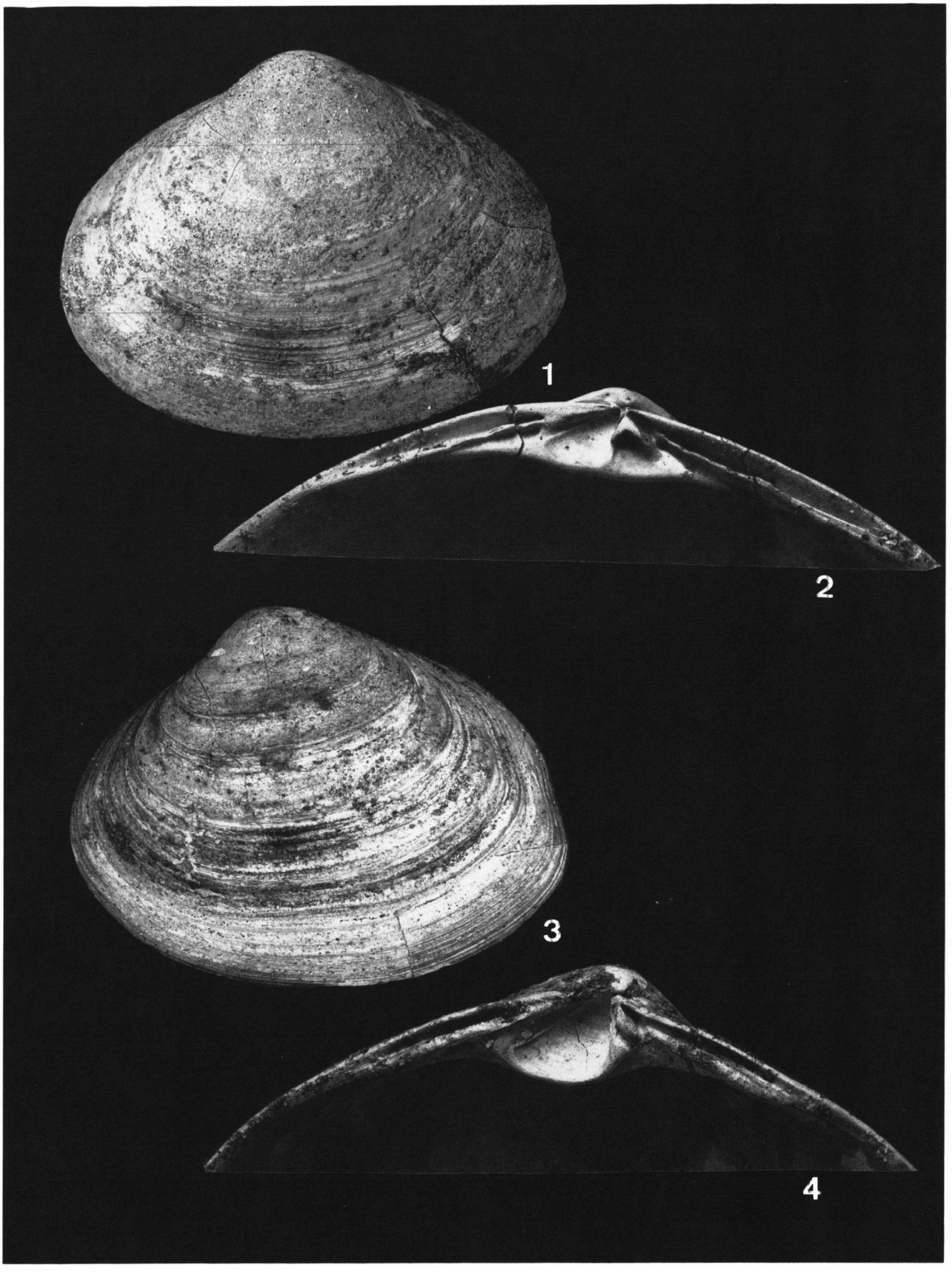
PLATE 2

All specimens are from the Kruisschans Member (Lillo Formation) as exposed at Antwerp.

Figs 1, 2. *Mactra glauca* Born, 1778, exterior of left valve and hinge, x 1.3 and 2.6, respectively (Marquet Collection).

Figs 3, 4. *Spisula arcuata* (J. Sowerby, 1818), exterior of left valve and hinge, x 1.4 and 3.1, respectively (Marquet Collection).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Manuscript received 11 June 1993, revised version accepted 11 October 1993.

PLATE 3

Unless indicated otherwise, all specimens are from the Kruisschans Member (Lillo Formation) as exposed at Kallo (Belgium).

Fig. 1. *Barnea cylindrica* (J. Sowerby, 1818), Antwerp, exterior or right valve, x 2.1 (Marquet Collection).
Fig. 2. *Zirfaea crispata* (Linné, 1758), exterior of right valve, x 1.2 (Marquet Collection).
Figs 3-5. *Capulacmaea kalloensis* sp. nov. Holotype (KBIN Collections, no. 6129); 3 - lateral view (x 3.9), 4 - top view (x 3.9), 5 - protoconch (x 11.5). SEM.
Fig. 6. *Natica multipunctata* Wood, 1842, apertural view, x 3.1 (Marquet Collection).
Fig. 7. *Admete viridula* (Fabricius, 1780), apertural view, x 4.9 (Marquet Collection).

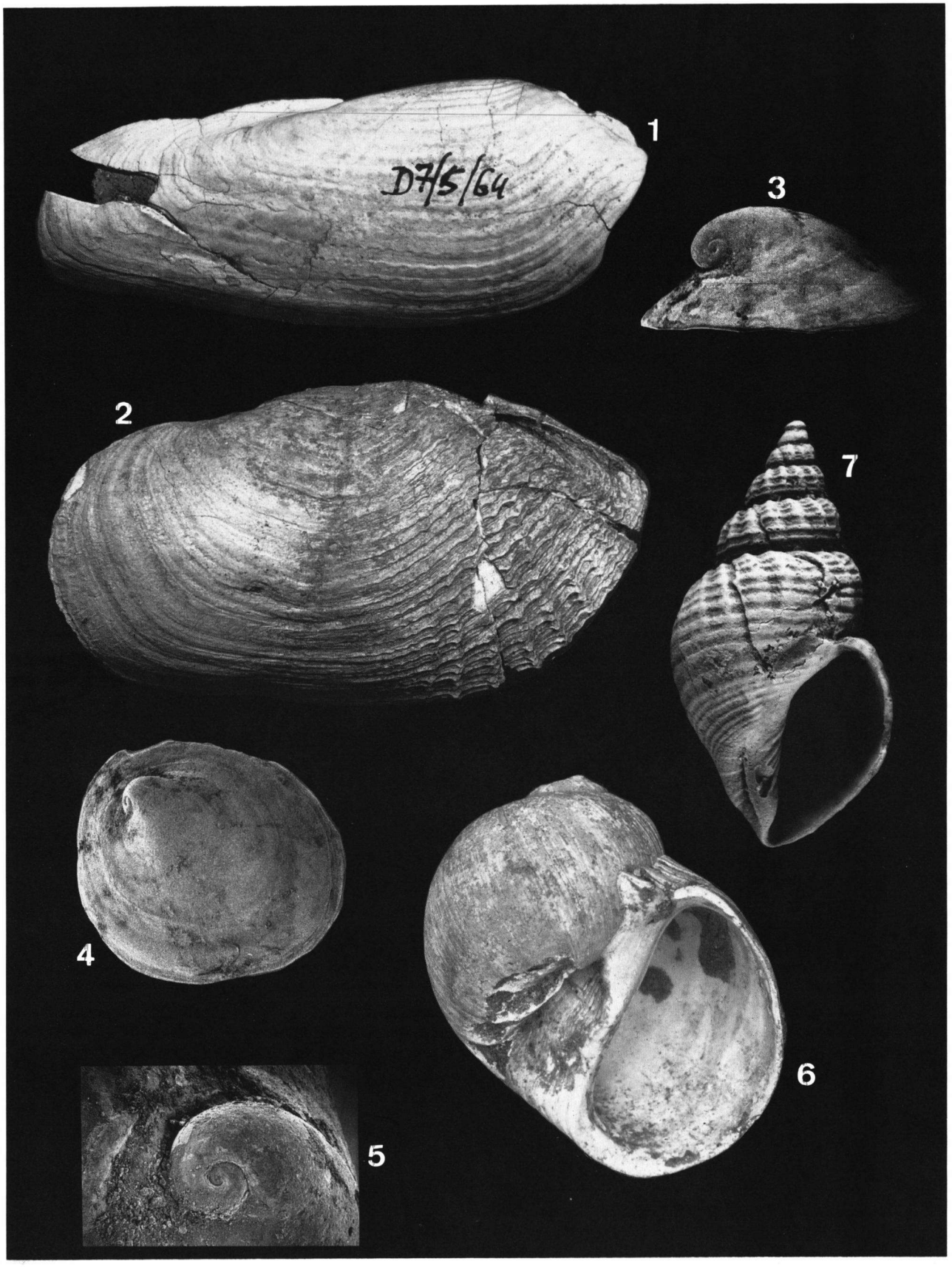
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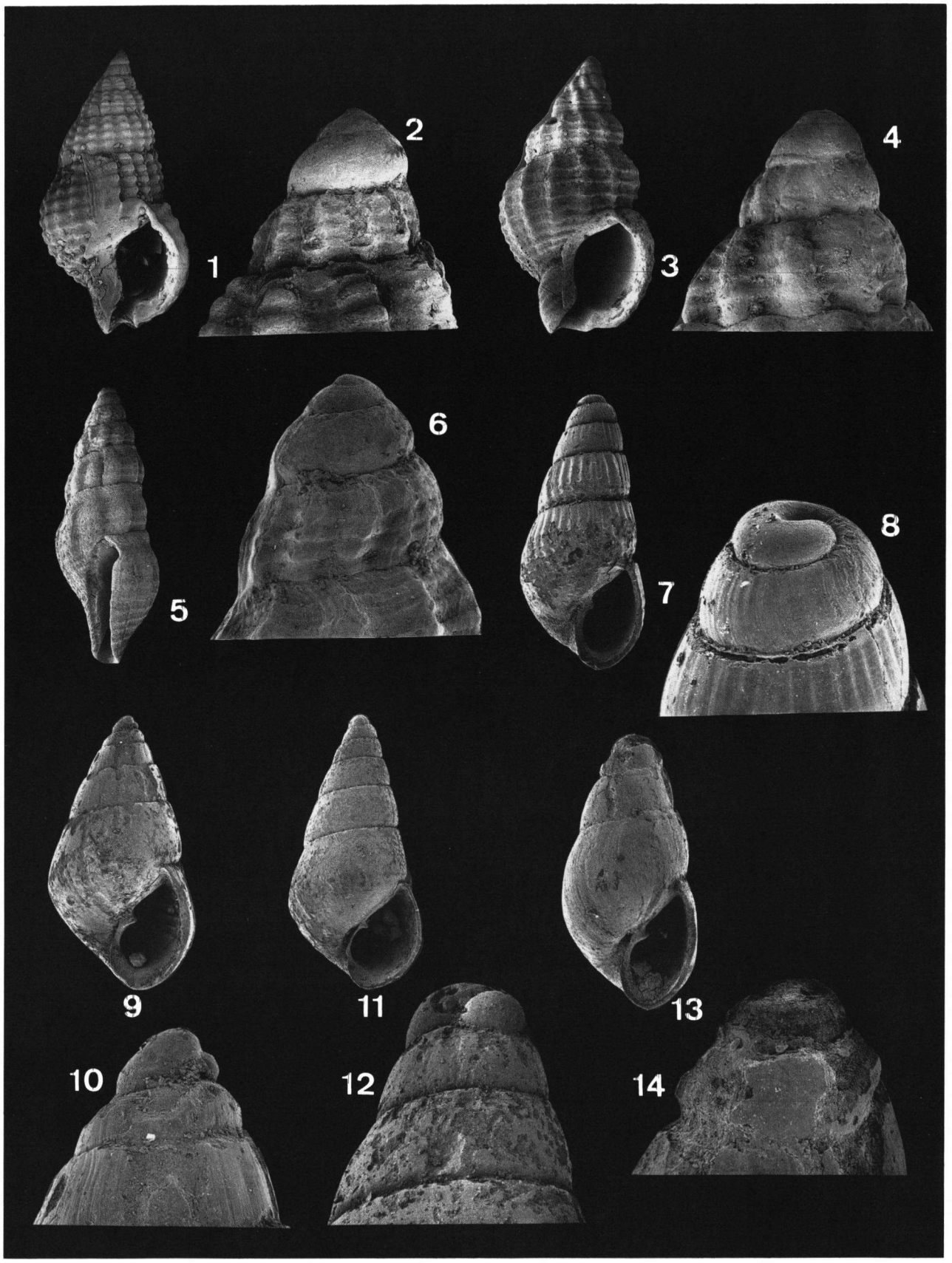
PLATE 4

All specimens are from the Kruisschans Member (Lillo Formation) as exposed at Kallo (Belgium). All SEM photographs.

Figs 1, 2. *Hinia consociata* (Wood, 1848), apertural view (x 2.2) and protoconch (x 16) (KBIN Collections, Brussels).
Figs 3, 4. *Hinia elegans* (J. de C. Sowerby, 1824), apertural view (x 2.8) and protoconch (x 13.5) (KBIN Collections, Brussels).
Figs 5, 6. *Mangelia keepingi* (Etheridge & Bell, 1898), apertural view (x 2.7) and protoconch (x 30.7) (KBIN Collections, Brussels).
Figs 7, 8. *Chrysallida indistincta* (Montagu, 1808), apertural view (x 12.6) and protoconch (x 47.4) (KBIN Collections, Brussels).
Figs 9, 10. *Odostomia (O.) conoidea* (Brocchi, 1814), apertural view (x 9.4) and protoconch (x 38.9) (KBIN Collections, Brussels).
Figs 11, 12. *Odostomia (O.) unidentata* (Montagu, 1803), apertural view (x 9.4) and protoconch (x 38.9) (KBIN Collections, Brussels).
Figs 13, 14. *Odostomia (Brachystomia) eulimoides* Hanley, 1844, apertural view (x 11.4) and protoconch (x 33) (KBIN Collections, Brussels).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