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MYTILUS ANTIQUORUM J. SOWERBY, 1821 AND OTHER PLIOCENE MUSSELS (MOLLUSCA, BIVALVIA) FROM THE SOUTHERN NORTH SEA BASIN

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Mytilus antiquorum J. Sowerby, 1821, is recorded from the Coralline Crag Formation of East Anglia (UK) and the Lillo Formation (Oorderen, Kruisschans and Merksem members) of the Antwerp area (Belgium). The species is diagnosed on the basis of newly collected material and differentiated from modern European mussel species. The presence of *M. antiquorum* in the southern North Sea Basin is restricted to the Middle (Piacenzian) and early Late Pliocene (Gelasian). A possible occurrence of the species in the latest Pliocene of northern Greenland is discussed. A second Middle- Late Pliocene North Sea Basin species, tentatively referred to as *M. edulis* forma *giganteus* Wood, 1874, is diagnosed and discussed. The systematic status of this species remains unresolved. In the Late Pliocene, a third mussel species occurs in the area, tentatively identified as *Mytilus ?trossulus* Gould, 1850.

Key words — Pliocene, North Sea Basin, Mollusca, Bivalvia, Mytilidae.

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INTRODUCTION

Since the late 1980s, several whole specimens and numerous fragments of *Mytilus* have been collected from the Middle Pliocene Oorderen Member (Lillo Formation) in the Antwerp area (Belgium). The Oorderen specimens were found to differ in various details from the modern European species *Mytilus edulis* Linné, 1758, *M. galloprovincialis* Lamarck, 1819 and *M. trossulus* Gould, 1850, and to resemble closely material recorded from the English crags under the names of *M. antiquorum* J. Sowerby, 1821 and *M. hesperianus* Lamarck, 1819.

Distinction of extant *Mytilus* species solely based on shell morphological characters is hazardous (McDonald *et al.*, 1991; Gosling, 1992; Seed, 1992; Carter & Seed, 1998). Comparing morphometric and DNA data, both Gosling (1992) and Seed (1992) found that up to 70% of *Mytilus* specimens were misidentified in cases where identification was based on a single shell character only. This percentage dropped to c. 15% when all morphologi-

cal characters were taken into account (Gosling, 1992; Seed, 1992). Much of the low diagnostic value of shell morphological characters in *Mytilus* is attributed to ecophenotypic plasticity. Furthermore, boundaries between the three extant European species of mussels (*M. edulis*, *M. galloprovincialis* and *M. trossulus*) are not always clear: the species are known to hybridise in some occasions (McDonald *et al.*, 1991; Gosling, 1992; Carter & Seed, 1998; Borsa *et al.*, 1999). In spite of these obvious drawbacks when dealing with fossil material, the newly collected Pliocene mussels have shells that in several aspects differ markedly from modern ones. The present paper aims to elucidate the taxonomic status of Pliocene North Sea Basin mussels, and to compare them to and differentiate them from extant European congeners.

Abbreviations – To denote the repositories of the material illustrated and/or referred to in the text the following abbreviations are used:

RGM- Nationaal Natuurhistorisch Museum (Department of Palaeontology, Cainozoic Mollusca), Leiden (the Netherlands, formerly Rijksmuseum van Geologie en Mineralogie).

RMNH- Nationaal Natuurhistorisch Museum (Department of Evertebrate Zoology, Mollusca), Leiden (the Netherlands, formerly Rijksmuseum van Natuurlijke Historie).

SYSTEMATIC PALAEONTOLOGY

Family Mytilidae Rafinesque, 1815
Genus *Mytilus* Linné, 1758

Type species – *Mytilus edulis* Linné, 1758, by monotypy.

Mytilus antiquorum J. Sowerby, 1821
Pl. 1, Figs 1-4, Pl. 2, Fig. 1.

1821 *Mytilus antiquorum* Sowerby, p. 133, pl. 275, figs 1-3.
1845 *Mytilus antiquorum* Sowerby – Nyst, p. 267, pl. 21, fig. 1a, b.
1851 *Mytilus hesperianus* Lamarck – Wood, p. 55, pl. 8, fig. 10.
1878 *Mytilus edulis* Linné – Nyst, pl. 17, fig. 4.
1881 *Mytilus edulis* Linné – Nyst (*partim*), p. 161.
1957 *Mytilus edulis* Linné – Glibert, p. 21, pl. 1, fig. 10.

Material studied – Kallo, Vrasenedok, province of Oost-Vlaanderen, Belgium, Lillo Formation, Oorderen Member (Piacenzian), leg. F. van Nieulande (1988): RGM 456061 (LV, 3 def. LV); RGM 456062 (1 articulated specimen); RGM 456063 (1 articulated specimen); RGM 456064 (8 damaged pairs); Kallo, Verrebroekdok, Lillo Formation, Oorderen Member, *Atrina* bed (Piacenzian), leg. M. Vervoenen (1998): RGM 456065; (1 articulated specimen); RGM 456066 (3 fragments); RGM 456067 (1 damaged articulated speciemn); Kallo, Verrebroekdok, Lillo Formation, Oorderen Member, *Cultellus* bed (Piacenzian), leg. M. Vervoenen (1998): RGM 456068 (2 top fragments of a single articulated specimen); RGM 456069 (3 top fragments); Kallo, Verrebroekdok, Lillo Formation, Kruisschans Member (Gelasian), leg. M. Vervoenen (1987): RGM 456070 (1 top fragment); Kallo, Verrebroekdok, Lillo Formation, Oorderen Member, upper clayish interval (Piacenzian), leg. M. Vervoenen (1996): RGM 456071 (RV).

Diagnosis – Medium- to large-sized (L c. 75-82 mm), globose mytilid, with maximum semidiameter dorsal (or rarely medially); outer shell purple-brown, lacking radial stripes; shell lacking ventral ridge; ventral margin straight, rarely slightly concave; dorsal margin at ligament gently curved; lower margin evenly rounded; umbo broad, obtuse; anterior reductor muscle scar large, located almost below umbo, deeply impressed; anterior retractor muscle scar small, spatulate, located near umbo, deeply embedded in the nacre; well-developed hinge area with one to five dysodont teeth; ligament groove prominent and deep, sometimes resembling a (false) resilifer; base of ligament with well developed spongy bone-like open structures at its base; posterior byssal-pedal retractor narrow; nacre thick, covering the entire inner side up to the pallial region and markedly draped upon outer calcitic shell; nacre often pitted; no outer calcitic shell material present in a narrow zone between inner nacre and base of ligament groove.

Differentiation – Is it possible to distinguish *Mytilus antiquorum* from the three extant European *Mytilus* species on shell morphological characters? To determine this, we first used measurements on *Mytilus edulis* (n = 98), *M. galloprovincialis* (n = 95) and *M. trossulus* (n = 97) performed by J. McDonald (and used in analyses published by McDonald *et al.*, 1991). These measurements included 20 characters displayed by specimens collected in many different places spanning the northern hemisphere. Three valves of *M. antiquorum* were measured, and twelve out of twenty characters were scored. A principal component analysis was performed on these twelve characters of all specimens. Although *M. antiquorum* plotted outside the range of modern mussel species (being closest to *M. galloprovincialis*) in some ordination-plots, we found that much of the distinction could have been the result of the large size of these three fossil specimens. This influenced almost all characters used, and therefore challenged the outcome of the analysis. Furthermore, four characters not present in the database of modern mussels were found to be important discriminators, and no measurements for these were available in the database or from the literature. We therefore decided to discriminate between species qualitatively.

Shell characteristics of extant European mussel species and the Pliocene *Mytilus antiquorum*

M. antiquorum
Largest shell semidiameter usually dorsal; aragonite/calcite ratio high (thick, pitted, aragonite in inner side of shell); outer shell smooth purple-brown, lacking radial rays; ventral ridge absent; umbo broad, obtuse; antero-dorsal margin evenly rounded; base of ligament area broad, with strongly developed spongy bone-like structure; ventral margin straight – slightly concave; anterior retractor scar spatulate, comparatively large, located near umbo; anterior reductor scar located below umbo.

M. trossulus
Largest shell semidiameter central-ventral; aragonite/calcite ratio very low (usually calcitic incursion below ligament area); outer shell usually smooth purple-brown (very rarely with radial stripes on adult specimens); ventral ridge very rare; umbo rather obtuse; antero-dorsal margin slightly curved; base of ligament area small, with small pits; ventral margin straight – slightly concave; anterior retractor scar small, elongate, located near umbo; anterior reductor scar located below or near umbo.

M. edulis
Largest shell semidiameter central-ventral; aragonite/calcite ratio intermediate; outer shell purple-blue, commonly with radial stripes (especially on juvenile specimens); ventral ridge common; umbo variable; antero-dorsal margin usually slightly curved but variable; base of ligament area very thin with small pits; ventral margin variable, convex-concave; anterior retractor scar very small, elongate, located at a little distance from umbo; anterior reductor scar comparatively large, located below or near umbo.

M. galloprovincialis
Largest shell semidiameter ventral; aragonite/calcite ratio intermediate; outer shell purple-blue, commonly with radial stripes (especially on juvenile specimens); ventral ridge common; umbo usually pointed; antero-dorsal margin straight or slightly curved; base of ligament area very thin with small pits; ventral margin straight or convex, only very rarely concave; anterior retractor scar very small, elongate, located at a little distance from umbo; anterior reductor scar located below umbo.

Wood (1856, p. 55) assigned Coralline Crag *Mytilus* from Sudbourne (Suffolk, UK) to *M. hesperianus* Lamarck, 1819; here we reassign them to *M. antiquorum*. *Mytilus hesperianus* is a species originally described from the Mediterranean; it is currently synonymised with *M. galloprovincialis* (Sabelli *et al.*, 1990). Wood's *M. edulis* var. *antiquorum* (Wood, 1856, p. 55) from the Red Crag is here reassigned to *M. ?trossulus* (see below). *Mytilus antiquorum* is known only from the Coralline Crag Formation (Piacenzian) of East Anglia, and from the Lillo Formation (Piacenzian-early Gelasian) in the Antwerp area. In the Antwerp harbour outcrops, fragments of *M. antiquorum* are not rare. Once a demolished block of sediment was found, containing a large, disintegrated piece of wood, crowded with these mussels. Thus, wood was a suitable substrate for *M. antiquorum*.

A mytilid recorded from the early Gelasian of North Greenland (Simonarson *et al.*, 1998) as *M. edulis* displays some similarities to *M. antiquorum*, such as the obtuse umbo, the apparent lack of a ventral ridge and the apparent dorsal location of the maximum shell semidiameter. Judging from the illustrations in Simonarson *et al.* (1998, figs 19h, 22), the shell is thick, and has a well-developed inner aragonitic layer, unlike modern *M. trossulus* from the same region (Pl. 2, Figs 3, 4 here). The Greenland specimen is very poorly preserved; its assignment to *M. antiquorum* is tentative.

Mytilus ?edulis forma **giganteus** Wood, 1874
Pl. 2, Figs 5, 6

1874 *Mytilus* ? *edulis* forma *giganteus* Wood – p. 52, pl 8, fig. 4.
1879 *Mytilus edulis* var. *galloprovincialis* Lamarck – Wood, p. 42, pl. 6, fig. 9a.
1879 *Mytilus edulis* var. *ungulatus* Linné – Wood, p. 43, pl. 6, fig. 9b.

Material studied – Thames estuary, UK, exact locality and stratigraphic provenance unknown (dredged material), leg. M. Vervoenen: RGM 456072 (fragment LV), RGM 456073 (fragment RV); De Kaloot, Province of Zeeland, the Netherlands, exact locality and stratigraphic provenance unknown (collected from beach), leg. F. Wesselingh: RGM 456074 (fragment LV).
Other occurrences – Sutton, UK, Basal Red Crag Formation, Middle-Late Pliocene (Piacenzian-Gelasian), but possibly reworked from older strata (Wood, 1874, 1879); Boyton, UK, probably Coralline Crag Formation, Middle Pliocene (Piacenzian) (Wood, 1879).
Diagnosis – Large (H 12-15 cm), thick-shelled mytilid; shell elongate, low, with a well-defined ventral ridge; ventral side slightly concave or straight; dorsal side rounded, lacking a dorsal angle; shell almost entirely aragonitic; hinge area extremely thick, pointed, but

abraded in the material available; internal surface strongly pitted.

Differentiation – The species is easily differentiated from *M. antiquorum* and the extant European mytilids by its size and thickness, the prominence of aragonitic shell material and the pointed umbo. It resembles the Pliocene Italian *M. scaphoides* Bronn, 1831 (see Sacco, 1898, pl. 10, figs 12-14). The systematic status of this very large species deserves further study, pending additional finds.

DISCUSSION

In strata of Late Pliocene age in the southern North Sea Basin occurs a *Mytilus* species whose identity is uncertain. From the Red Crag Formation (East Anglia), this species was published as *M. edulis* var. *antiquorum* (Wood, 1856, pl. 8, fig. 9b). One valve of this form from the Merksem Member (Merksem Sands), of the Antwerp area was available for study (RGM 456075, Delwaidedok near Stabroek, province of Oost-Vlaanderen, Belgium, leg. F. van Nieulande, Pl. 2, Fig. 2), but only its exterior is exposed. The shell is flat and has its semidiameter centrally. The outer shell is smooth. A ventral ridge is lacking. The species resembles *M. trossulus*, but since we were not able to examine the shell's interior, the identification remains uncertain. Fragments of similar shells in matrix from 'De Kauter' (Nieuw Namen, province of Zeeland, the Netherlands; Oosterhout Formation, Late Pliocene) were available for study as well. Their general outline resembles the above-mentioned Merksem specimen, but the interior sides could not be studied either. For the moment the systematic status of these specimens remains unresolved. During this study, we have not seen any specimen in Pliocene strata from the North Sea Basin that could be attributed either to *M. galloprovincialis* or *M. edulis*.

CONCLUSIONS

During the Middle Pliocene, *Mytilus antiquorum* appeared in the southern North Sea Basin. It went extinct in the North Sea Basin in the Late Pliocene, but possibly survived until at least the latest Pliocene in the Arctic region. *Mytilus antiquorum* is easily differentiated from the three extant *Mytilus* species in NW Europe. The systematic status of a second North Sea Basin Pliocene mytilid, *M. edulis* forma *giganteus*, remains unresolved. In Late Pliocene strata of the Antwerp area a third mussel occurs that is tentatively identified as *M. ?trossulus*.

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REFERENCES

Borsa, P., C. Daguin, S.R. Caetano & F. Bonhomme, 1999. Nuclear-DNA evidence that northeastern Atlantic *Mytilus trossulus* mussels carry *M. edulis* genes.– J. moll. Stud. 65: 504-507.

Carter, J.G. & R. Seed, 1998. Thermal potential and mineralogical evolution in *Mytilus* (Mollusca; Bivalvia). *In*: Johnston, P.A. & J.W. Haggart (eds). Bivalves: an eon of evolution: 87-117. Calgary (Univ. Calgary Press).

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

Gosling, E., 1992. Systematics and geographic distribution of *Mytilus*. *In*: Gosling, E. (ed.). The Mussel *Mytilus*: Ecology, physiology, genetics and culture: 1-20. Amsterdam (Elsevier).

McDonald, J.H., R. Seed & R.K. Koehn, 1991. Allozymes and morphometric character of three species of *Mytilus* in the Northern and Southern Hemispheres.— Mar. Biol. 111: 323-333.

Nyst, P.-H., 1845. Description des coquilles et des polypiers fossiles des terrains tertiaires de la Belgique. Bruxelles (M. Hayez), 675 + ii pp. (misdated 1843).

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

Sabelli, B., R. Giannuzzi-Savelli & D. Bedulli, 1990. Annotated checklist of Mediterranean marine molluscs, 1. Bologna (Edizioni Libreria Naturalistica Bolognese), 1-348.

Sacco, F., 1898. I molluschi dei terreni terziarii del Piemonte e della Liguria, 25. Torino (Carlo Clausen), 1-54.

Seed, R., 1992. Systematics, evolution and distribution of mussels belonging to the genus *Mytilus*: an overview.— Am. Malac. Bull. 9: 123-137.

Simonarson, L.A., K.S. Petersen & S. Funder, 1998. Molluscan palaeontology of the Pliocene-Pleistocene Kap København Formation, North Greenland.— Meddr. Grønl., Geoscience, 36: 1- 104.

Sowerby, J., 1821. The mineral conchology of Great Britain, 3. London (W. Arding), 1-306.

Wood, S.V., 1851. A monograph of the Crag Mollusca, 2: Bivalves. – Monogr. Palaeontogr. Soc. Lond. (1851), 1-150.

Wood, S.V., 1874. Supplement to the monograph of the Crag Mollusca, or, description of shells from the Middle and Upper Tertiaries of the east of England, 3: Univalves and Bivalves.— Monogr. Palaeontogr. Soc. Lond., 99-231.

Wood, S.V., 1879. Second supplement to the monograph of the Crag Mollusca, with description of shells from the Upper Tertiaries of the east of England, 4: Univalves and Bivalves.— Monogr. Palaeontogr. Soc. Lond., 1-58.

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PLATE 1

Figs 1-4. *Mytilus antiquorum* J. Sowerby, 1821. Kallo, Verrebroekdok, province of Oost-Vlaanderen, Belgium, Lillo Formation, Oorderen Member, *Atrina* bed (Piacenzian), leg. M. Vervoenen (1998): RGM 456067: 1a LV interior, 1b LV exterior, 2a RV interior, 2b RV exterior; RGM 456065: 3a RV exterior; 3b LV exterior; RGM 456066: *Cultellus* bed (Piacenzian), leg. M. Vervoenen (1998): 4a RV interior, 4b RV exterior, 4c RV interior, detail of apical region.

All shells natural size (except photographs of details).

PLATE 1

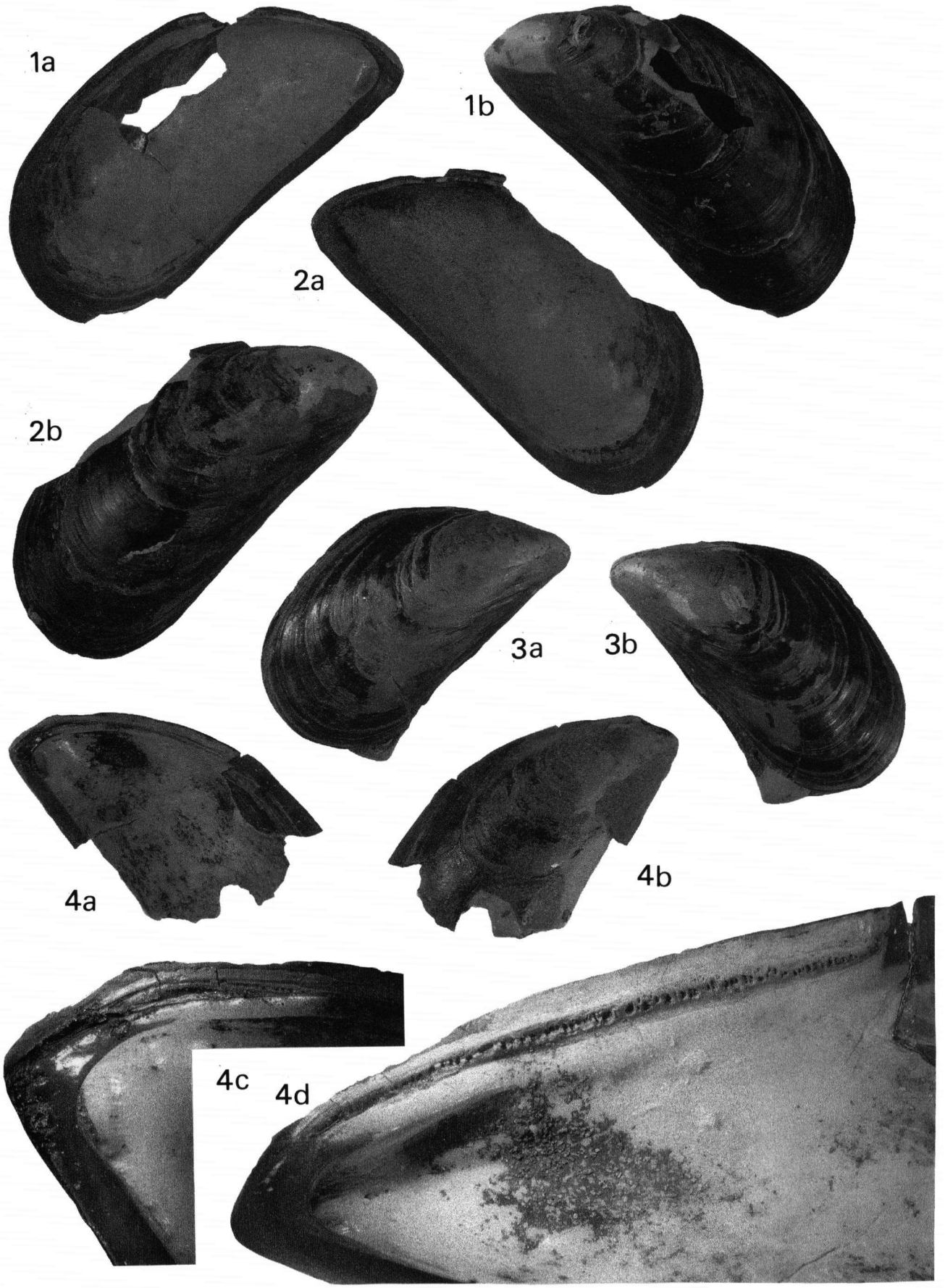

PLATE 2

Fig. 1. *Mytilus antiquorum* J. Sowerby, 1821. Kallo, Verrebroekdok, province of Oost-Vlaanderen, Belgium, Lillo Formation, Oorderen Member, *Cultellus* bed (Piacenzian), leg. M. Vervoenen (1998): RGM 456066: 1a LV interior, 1b LV exterior, 1c LV interior, detail of apical region, 1d LV interior, detail of ligament area..

Fig. 2. *Mytilus ?trossulus* Gould, 1850. Stabroek, Delwaidedok, province of Oost-Vlaanderen, Belgium, Lillo Formation, Merksem Member (Gelasian), leg. F. van Nieulande (1976): RGM 456715 LV.

Fig. 3. *Mytilus trossulus* Gould, 1850. RV. Hopedale, Labrador, Canada. Coll. RMNH. Leg. W.W. Berret.

Fig. 4. *Mytilus trossulus* Gould, 1850. LV. Angmaksalik, Greenland. Coll. RMNH. Leg. J.J. ter Pelkwijk.

Figs 5, 6. *Mytilus ? edulis* forma *giganteus* Wood, 1874. Thames estuary, UK, exact locality and stratigraphic provenance unknown (dredged material), leg. M. Vervoenen: RGM 456073: 5a internal view of fragment RV, 5b exterior; RGM 456072: 6a external view of fragment LV, 6b interior.

All shells natural size.

PLATE 2