

On the identity of *Mytilus edulis* forma *giganteus* Wood, 1874 (Pliocene, North Sea Basin), with implications for the generic assignment of other European Cainozoic mytilid bivalves

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Received 5 June 2001; revised version accepted 12 January 2002

A Middle to Late Pliocene mussel from the southern North Sea Basin referred to previously as *Mytilus edulis* forma *giganteus* Wood, 1874, is here reassigned to the genus *Perna* Retzius, 1788. The name of the forma *giganteus* has proved to be a junior homonym; hence the species is here renamed *P. woodi*. It is characterised by, amongst other features, a near-exclusively aragonitic shell, in contrast to species of *Mytilus*, which have a predominantly calcitic shell. Almost all Cainozoic mussels from Europe generally placed in *Mytilus* should be reassigned to *Perna*. Similarities of these to the Pacific genus *Crenomytilus* Soot-Ryen, 1955, and the use of specific shell characteristics in the generic placement of mussels are discussed.

KEY WORDS: Pliocene, North Sea Basin, Mollusca, Mytilidae, *Perna*, *Crenomytilus*, new name.

Introduction

A large mytilid bivalve from Pliocene strata in the southern North Sea Basin has recently been referred to by Vervoenen *et al.* (2000) as *Mytilus edulis* f. *giganteus*. New fossil and Recent material has since become available, and this demonstrates that this taxon cannot remain in the genus *Mytilus*. The aim of the present paper is to elucidate the taxonomic status of the North Sea Basin species and discuss implications for the generic placement of other European Cainozoic mussels.

Abbreviations used in the text are as follows:

- RGM Nationaal Natuurhistorisch Museum, Department of Palaeontology (Cainozoic Mollusca), Leiden (formerly Rijksmuseum van Geologie en Mineralogie)
- RMNH Nationaal Natuurhistorisch Museum, Department of Vertebrate Zoology (Mollusca), Leiden (formerly Rijksmuseum van Natuurlijke Historie)

Systematic description

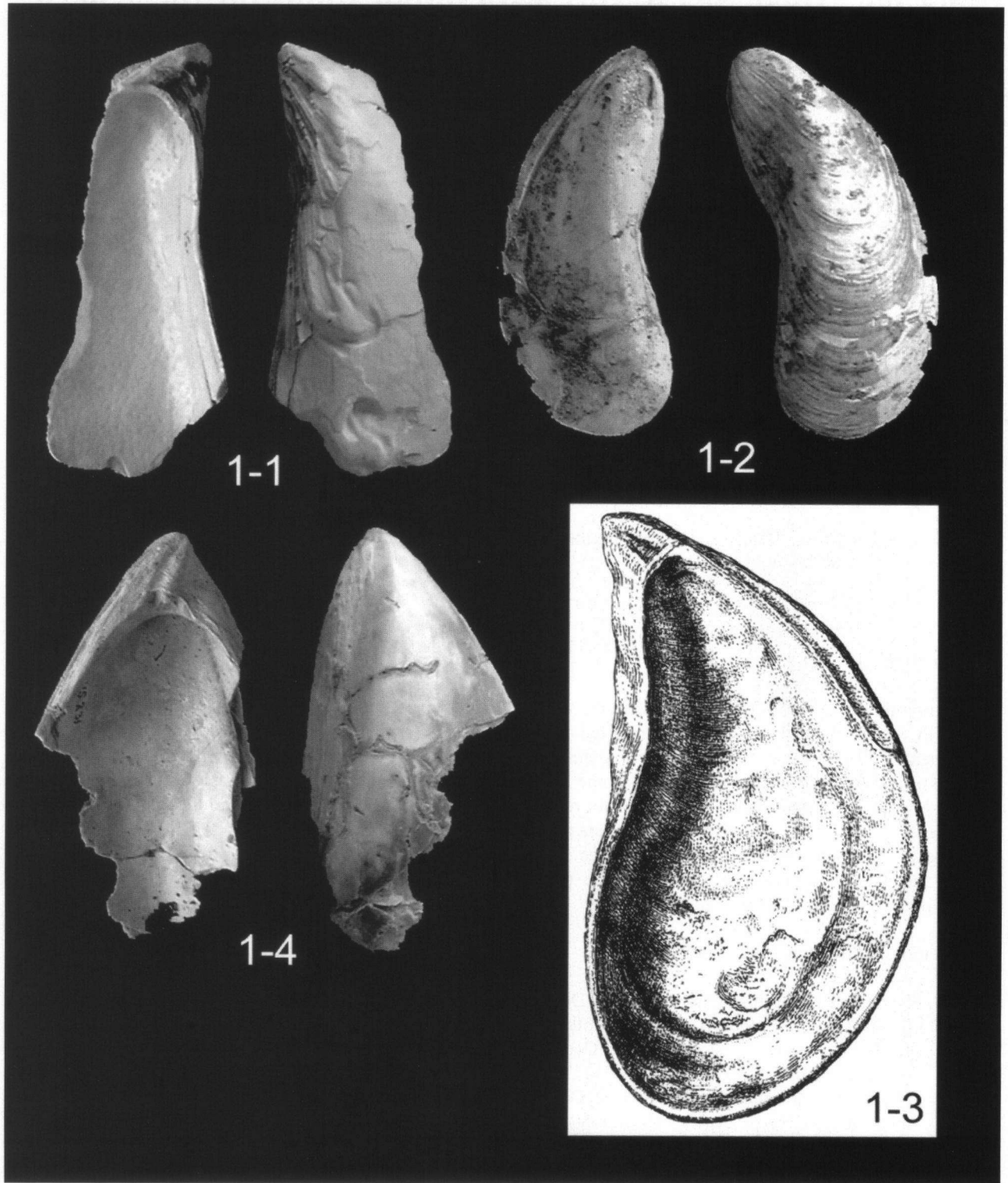
Family Mytilidae Rafinesque, 1815
Genus *Perna* Retzius, 1788

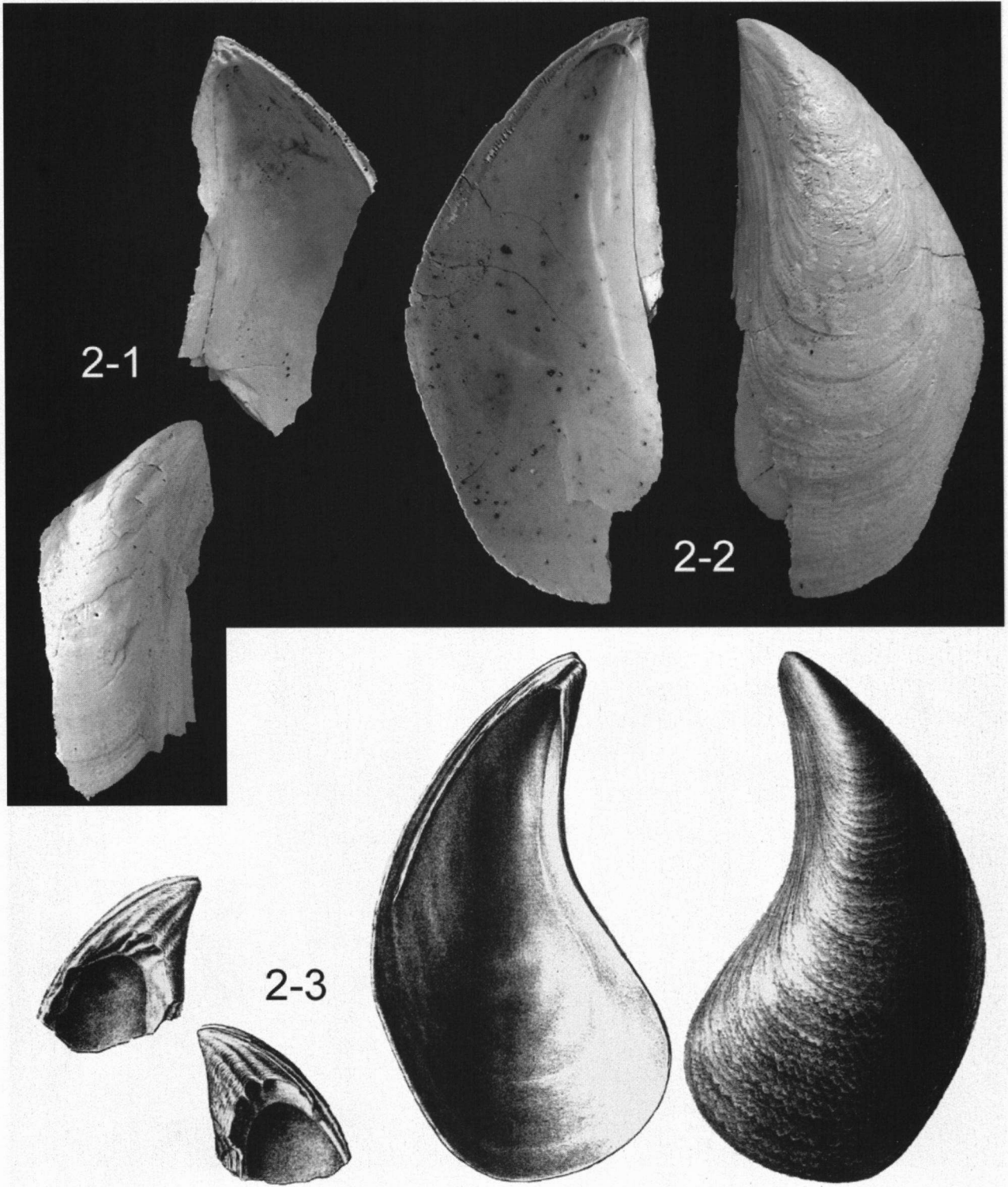
Type species — *Perna magellanica* Retzius, 1788 (= *Mya perna* Linné, 1758), by monotypy.

Distribution — Species of *Perna* are known from tropical and subtropical seas bordering the Atlantic and Indian oceans, and from temperate seas in southern South America. Alleged Recent introductions have been reported from the Indo-Pacific.

Remarks — European mytilids attributed to *Perna*, and discussed below, have several features in common with the extant North Pacific genus *Crenomytilus*. In having thick shells with a massive subumbonal shelf, European fossil mytilids are unlike modern species of *Perna*, which usually have thin and delicate shells. The range of variation seen in the Miocene *P. aquitanica* (Mayer-Eymar, 1858) from the Aquitaine, France (see Figures 2-1, 2-2) and the Vienna Basin (see Figure 2-3), illustrates the fact that within that particular species there occur thin as well as thick shells. Quaternary specimens of *Perna picta* (Born, 1780) from the Moroccan coast also range from thin to thick shells. A strong byssal inflection at the ventral margin found in most of the larger European Cainozoic specimens is atypical of extant *Perna*.

The Recent *Crenomytilus grayanus* (Dunker, 1853), from the northwest Pacific (see Figure 3-1) is strikingly similar in outline to some of the thicker-shelled fossil European *Perna*.





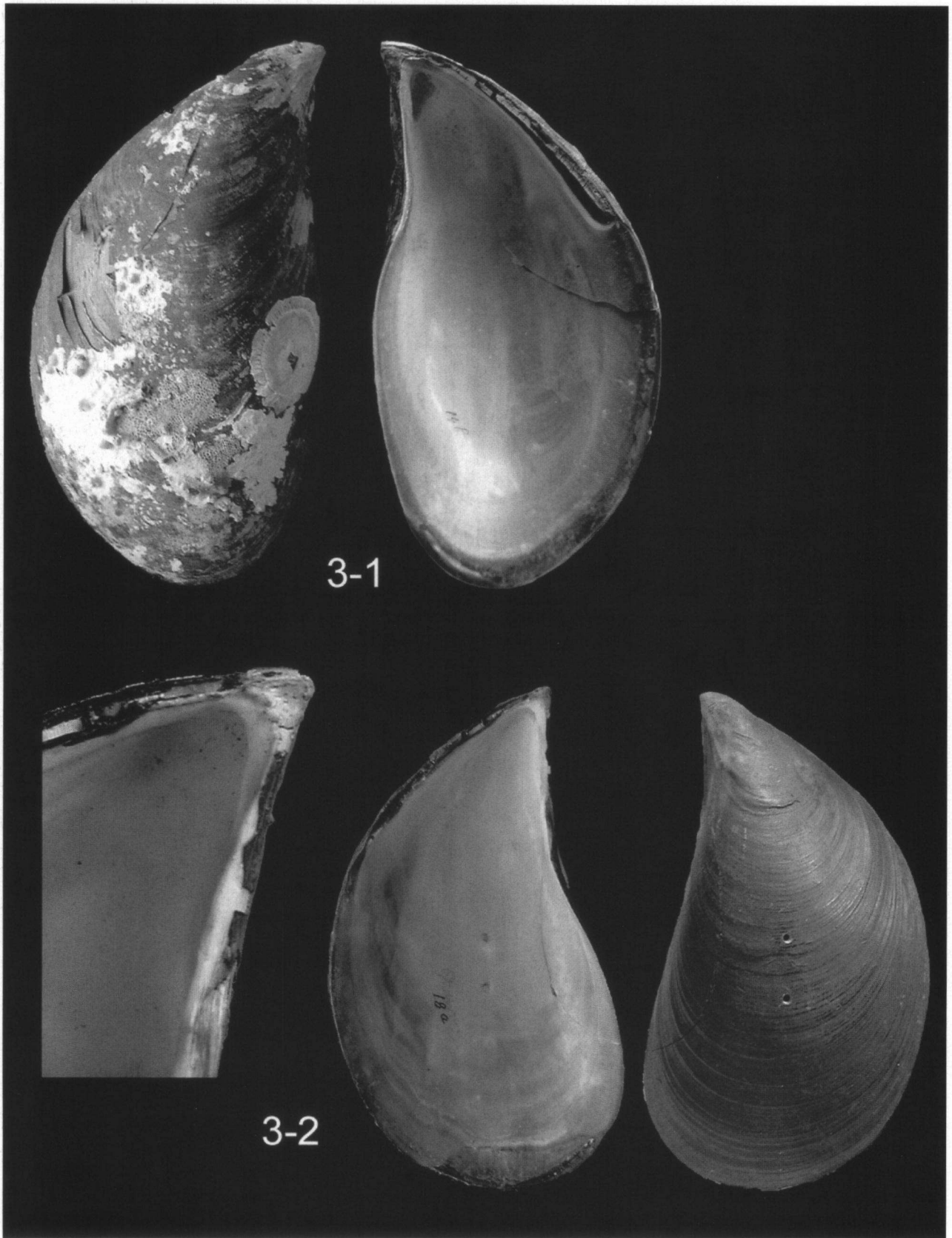


Figure 1. *Perna woodi* nom. nov. (1-3) and *Perna scaphoides* (Bronn, 1831) (4):

1. RGM 456 074, fragmentary left valve; washed ashore at 'de Kaloot', Borsele (province of Zeeland, the Netherlands), interior and exterior views, respectively (height, as preserved, 67 mm);
2. RGM 456 086, left valve; 9th harbour dock, Lillo (province of Antwerpen, Belgium), Lillo Formation (Kruisschans Member), interior and exterior views, respectively (height 65 mm);
3. Boyton, Suffolk (United Kingdom), right valve; Coralline Crag Formation (copy of Wood, 1879, pl. 6, fig. 9b, as *Mytilus edulis* var. *ungulatus* Linné), interior view (height 121 mm);
4. RGM 115 231, right valve; Valle Andona (province of Asti, Italy), unnamed Pliocene (Piacenzian) beds, interior and exterior views, respectively (height, as preserved, 74 mm).

Figure 2. *Perna aquitanica* (Mayer-Eymar, 1858):

1. RGM 456 087, fragmentary right valve; Saucats (Pont-Pourquey, département Gironde, France), Faluns de Pont-Pourquey (Miocene, Burdigalian), interior and exterior views, respectively (height, as preserved, 89 mm);
2. RGM 456 088, left valve; same locality and stratigraphy, interior and exterior views, respectively (height 102 mm);
3. left valve and apical fragments of both valves, Vienna Basin (Austria), Miocene (copy of Hoernes, 1870, pl. 46, figs 1-3) (height of complete shell 190 mm).

Figure 3. *Crenomytilus grayanus* (Dunker, 1853) (1) and *C. coruscus* (Gould, 1861) (2):

1. RMNH colln, right valve; Akashi (Japan), exterior and interior views, respectively (height 144 mm);
2. RMNH colln, right valve; 'Philippines' (probably incorrect indication for Japan), detail of hinge, and interior and exterior views, respectively (height 131 mm).

Both the shell and subumbonal shelf are thick, the structure of the hinge area being similar in these groups, the byssal inflection at the ventral margin well defined and the inner shell composed of thick and pitted nacre. However, this European material is not attributed to *Crenomytilus* for the following reasons:

- * *Crenomytilus grayanus* has a more or less distinct calcitic outer shell;
- * the European and north Pacific populations are wide apart, although faunal exchange between these realms during the Cainozoic has been documented;
- * most European material consists of valves which easily decompose into sheet-like fragments, closely similar to modern *Perna*, and quite unlike sturdier valves of *Crenomytilus*.

***Perna woodi* nom. nov.**

pro *Mytilus edulis* forma *giganteus* Wood, 1874, non *Mytilus edulis* forma *gigantea* von Nordmann, 1862 = *Mytilus californianus* Conrad, 1837 (see Coan *et al.*, 2001)

Figures 1-1, 1-2 and 1-3

- 1874 *Mytilus edulis* forma *giganteus*? Wood, p. 110, 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.
 2000 *Mytilus edulis* forma *giganteus* Wood — Vervoe-
 nen *et al.*, p. 75, pl. 2, figs 5, 6.

Type — Holotype, by monotypy, is a fragment from the 'Nodule Pits in the Red Crag at Sutton' (see Wood, 1874, p. 110), originating from the basal Red Crag For-

mation (Pliocene), and possibly derived from 'some older formation'. So far, we have not been able to relocate the type in various English collections. At the moment of writing, substantial portions of the Wood Collection are being recovered at the British Geological Survey, but, at present, we do not know whether these include the type of *M. edulis* f. *giganteus* or not.

Derivatio nominis — Named after Searles Valentine Wood (1798-1880).

Material studied — From the Thames estuary (United Kingdom), exact locality and stratigraphic provenance unknown (dredged material): RGM 456 072 (fragment of left valve, leg. M. Vervoe-
 nen), RGM 456 073 (fragment of right valve), and RGM 456 085 (4 fragments); from de Kaloot (province of Zeeland, the Netherlands), exact locality and stratigraphic provenance unknown (washed ashore): RGM 456 074 (fragment of left valve, leg. F. Wesselingh); from Lillo (9th harbour dock, province of Antwerpen, Belgium), Lillo Formation, Kruisschans Member (Late Pliocene, Gelasian): RGM 456 086 (right valve, leg. M. Vervoe-
 nen).

Diagnosis — Large (height 120-150 mm), usually thick-shelled mytilid; subadult shells elongate, slightly bilobed modioliform, thin-shelled, but with terminal beak; adult shell broadly elongate, low, with a well-defined marginally located ventral ridge; disc markedly flat, lined with broad concentric growth lines; ventral side slightly concave or straight; dorsal side slightly curved, lacking a dorsal angle; shell thick, almost entirely nacreous (a few traces only of thin calcite in RGM 456 074 and RGM 456 086); beaks terminal; hinge area extremely thick, pointed; interior subumbonal shelf unguulate with two very low and ill-defined radial ridges, bounding a very low, elongate depression; base of hinge area arcuate;

anterior adductor and byssal retractor scars near the umbo at equal distance, deeply entrenched in nacre, obsolete in adult specimens; internal surface strongly pitted.

Remarks — RGM 456 086 (see Figure 1-2) from the Upper Pliocene of the Antwerp area is a complete, subadult valve, with a distinct modioliform outline, and two transverse ridges and a byssal inflection on the ventral margin of the shell. However, the structure of the hinge area, with a well-developed interior umbonal shelf, the terminal position of the beaks and the thick nacreous shell demonstrate that this specimen cannot be assigned to *Modiolus*. In spite of the fact that the beaks appear to be subterminal, *i.e.* typical of *Modiolus*, on the shell's exterior the hinge, when viewed from the inside, is clearly terminal. We are not entirely certain whether this specimen should be seen as a subadult *P. woodi*, or as a distinct species. Juvenile and subadult stages of adult specimens of *P. woodi* are modioliform, and the thick shells probably are a gerontic feature, just as we have observed in a larger series of *P. aquitanica*. On this evidence, we assign RGM 456 086 to *P. woodi*.

Differentiation — Many, if not all, European Cainozoic species previously referred to *Mytilus*, with the exception of *M. antiquorum* and *M. ?rossulus* (see Vervoenen *et al.*, 2000), should be reassigned to *Perna*. The oldest occurrences we have been able to check ourselves involve *P. acutangula* (Deshayes, 1824) and *P. rimosa* (Lamarck, 1823), both from the Middle Eocene of the Paris Basin (Cossmann & Pissarro, 1905, pl. 37, figs 112-1, 112-2). A number of species, attributable to *Perna*, have been recorded in the literature from Oligocene and Miocene strata throughout Europe. The taxonomy of these species is in need of clarification (Harzhauser & Mandic, 2001). Those authors synonymised *Crenomytilus* (= *Perna*) *rissoi* (Mayer-Eymar, 1858) from the Miocene of Italy, and *C. haidingeri* (Hoernes, 1848) from the Oligo-Miocene of the Paratethys, with *Crenomytilus aquitanicus* (Mayer-Eymar, 1858), originally described from the Miocene of the Aquitaine Basin (France).

Perna aquitanica is a highly variable species. In particular, the hinge area in subadult specimens is characterised by the presence of two arc-shaped incursions with a small drop-like 'tooth' at the base of the umbonal shelf (Figures 2-1 and 2-3). French populations studied by ourselves and Italian material referred to in the literature consist of thin-shelled specimens, whereas Paratethyan populations comprise a range of thin- to extremely thick-shelled valves. *Perna aquitanica* differs from *P. woodi* in having a more clearly pointed umbo and in lacking a well-defined ventral byssal inflection. The former species also occurred in the North Sea Basin during the Miocene. Glibert (1945, p. 54, pl. 2, fig. 6) recorded it, as *Mytilus fuscus* Hoernes, 1870, from the 'Horizon de Houthaellen', which according to A.W. Janssen (pers. comm.) is of

'Hemmoorian' age. In larger specimens, the delicate hinge of *P. aquitanica* is closer to the more flattened and robust structure typical of species of *Crenomytilus*.

Perna fusca (Hoernes, 1870), from the Miocene of the Vienna Basin (Austria) and the Loire Basin (France; see Dollfus & Dautzenberg, 1902), differs from *P. woodi* in being small and thick-shelled and in containing irregularly concentric shell thickenings and folds. *Perna woodi* most closely resembles *P. scaphoides* (Bronn, 1831) (see Figure 1-4) from the Middle Pliocene of northern Italy, which has a more clearly pointed umbo when viewed from the inside, brought about by a constriction just below the umbo on the ventral side. The ventral region below the umbo is slightly convex to straight in adult specimens, whereas it is concave in adult *P. woodi*.

The extant northwest Pacific *Crenomytilus grayanus* (Figure 3-1) differs from *Perna woodi* in various respects.

For instance, the shell of the former is more calcitic. On the inner side of the shell, the aragonite is pitted in the area below the umbo only. The umbonal shelf is smaller than that of *P. woodi*. In addition, the base of the ligament groove is not pitted. Finally, marginal crenulations, common in *C. grayanus*, are not seen in *P. woodi*. '*Mytilus*' *coruscus* Gould, 1861 (Figure 3-2) of Japan is lower and broader than *P. woodi*, with the largest width abapical, and also wedge-shaped (see below).

Occurrence — Sutton (United Kingdom), basal Red Crag Formation, Middle-Late Pliocene (Piacenzian-Gelasian), but possibly reworked from older strata (Wood, 1874, 1879); Boyton (United Kingdom), probably Coralline Crag Formation, Middle Pliocene (Piacenzian) (Wood, 1879).

Discussion and conclusions

While studying *Crenomytilus* material, we came across a second species from Asia, generally referred to as *Mytilus coruscus* (see Figure 3-2). This bears a striking resemblance to both *C. grayanus* and *P. aquitanica*. *Mytilus coruscus*, known from Japan, has been reported to be karyotypically very close to *Crenomytilus grayanus* (Ieyama, 1984). However, on account of the smooth, *i.e.* non-pitted, base of the ligament groove, and in the absence of marginal crenulations, previous authors have not considered the former to represent a species of *Crenomytilus*. We think that the general shell structure (*e.g.*, thick, strongly developed aragonitic inner shell, rather weakly developed calcitic outer shell and structure of subumbonal shelf) is indicative of a close relationship between *C. grayanus* and *M. coruscus*. The marginal crenulations in *C. grayanus* have been observed in some, but not in all specimens studied, and thus are another variable, and unreliable, feature in generic classification. We doubt if the structure of the base of the ligament may

serve as a reliable characteristic in distinguishing mytilid genera and suspect that *Mytilus coruscus* is in fact a species of *Crenomytilus*. Although both in general shell outline and hinge structure Pacific species of *Crenomytilus* are strikingly similar to some European Cainozoic mytilids, notably *P. aquitanica*, slight differences in shell mineralogy and structure as well as the disjunct distribution of Pacific and European mytilids, appear to justify generic separation.

Perna woodi nom. nov. is currently known from the Pliocene of the southern North Sea Basin. It shows a number of features that are similar to those of species of the genus *Crenomytilus*, as do other European Cainozoic mussels here attributed to *Perna*. The oldest European species of *Mytilus* occurs in the Middle Pliocene (Vervoenen *et al.*, 2000). It is quite conceivable that *Mytilus* was amongst the group of Pacific-Arctic taxa that migrated into northwest Europe during the Middle and Late Pliocene.

Acknowledgements

We thank Koen Fraussen (Aarschot) for supplying material of *C. grayanus* (Russian Pacific), Arie W. Janssen (Xewkija, Malta) for discussing material of *Mytilus* with us and for reviewing an earlier typescript, Geerat Vermeij (Davis, USA) for providing data important for the generic assignment, for making relevant Russian literature (and translations) available and for reviewing an earlier typescript, Oleg Mandic and Matias Harzhauser (Vienna) for helping us clarify the generic assignment of the various Miocene mussels from Europe, and John W.M. Jagt (Maastricht) for his linguistic input.

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