Stratigraphical notes on *Macoma* (Bivalvia) in the southern part of the North Sea Basin and some remarks on the arrival of Pacific species

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Key words: Neogene, Quaternary, North Sea Basin, Pacific immigration, Bivalvia, *Macoma*.

The stratigraphical occurrence in the southern North Sea Basin of the marine bivalve genus *Macoma* is reviewed. New data concerning first and last appearances are presented. Especially the first appearance of *Macoma balthica* and the last appearances of *M. obliqua* and *M. praetenuis* are discussed. *M. balthica* appears in the late Middle Tiglian (Early Pleistocene). *M. obliqua* has been found in offshore deposits dating from the climatic optimum of the last interglacial, the Eemian. *M. praetenuis* occurs in deposits just underlying the Eemian deposits. The age of these underlying deposits is uncertain but may be Late Saalian/Early Eemian. Both latter species were previously considered to be extinct after the late Middle Tiglian. The age of the arrival of 'Pacific' species in the North Sea Basin in the Pliocene is briefly discussed.

Contents

Introduction

In Neogene and Quaternary deposits of the southern North Sea Basin the marine bivalve genus *Macoma* (s.s.) is represented with the following four species:

Macoma balthica (Linné, 1758)
Macoma calcarea (Gmelin, 1791)
Macoma obliqua (Sowerby, 1817)
Macoma praetenuis (Leathes in Woodward, 1833).

In the Atlantic Ocean species of *Macoma* s.s. are not observed in Miocene deposits, contrary to the Pacific Ocean where the subgenus was already present during those times (Coan, 1969a, b; Bernard, 1979). Therefore *Macoma* s.s. is considered to have originated in the Pacific Ocean. Representatives of this taxon should have immigrated into the Atlantic Ocean, most probably across the Bering Strait, at various moments after the Late Miocene. The successive appearances and ranges of the spe-

cies in Pliocene/Pleistocene deposits in the North Sea Basin are used in the regional molluscan biostratigraphy. Their biostratigraphical importance was already recognised in the nineteenth century. The literature concerning the biostratigraphical significance of *Macoma* in North Sea deposits is rather extensive, but nevertheless our knowledge appears to be still incomplete.

The stratigraphy of different parts of the basin was not always well understood. This led to wrong correlations and as a consequence first appearances of *Macoma* seemed to be diachronous. Much work has been done during the last 10-20 years. This resulted in better stratigraphical correlations in the Quaternary between Great Britain and The Netherlands (Gibbard et al., 1991) and in improvements in the taxonomy of the species under consideration (Spaink & Norton, 1967; Coan, 1969b).

Discussion of the species

Macoma balthica

General remarks — This low-boreal species is very common in shallow, near-coastal waters of the present-day North Sea. Also as a fossil in Middle and Late Pleistocene interglacial deposits *M. balthica* is commonly found at both sides of the basin. The strikingly abundant first occurrence in the youngest Early Pleistocene Crag deposits in eastern England, the so-called Weybourne Crag, was noted and discussed by the early workers (e.g. Wood & Harmer, 1872; Harmer 1877, 1906; Reid, 1890).

The correlation of the *M. balthica* occurrences in the British Crags with those in the Pliocene/Pleistocene beds of The Netherlands was initially hampered by taxonomical and stratigraphical misinterpretations (Heering, 1950; Zagwijn, 1975). The taxonomy was clarified by Spaink & Norton (1967), although as yet not everyone agrees completely, especially with regards to certain occurrences of *M. praetenuis* (cf. Janssen et al., 1984). The stratigraphical problems were only solved in the last few years (van Kolfschoten & de Boer, 1988; Gibbard et al., 1991).

British data — For the greater part the observations of the early British authors on the first appearance of *M. balthica* in the Early Quaternary of East Anglia are confirmed by the work of modern authors. The latter showed the presence of the species in the Weybourne Crag and in the possibly related 'Bure Valley Beds', and the absence in all underlying crags (Norton, 1967, 1980; Norton & Spaink, 1973). In this respect the section at Dobb's Plantation near Wroxham is significant. In Wroxham typical Norwich Crag, in which *Macoma balthica* does not occur, is overlain by a deposit with a typical Weybourne Crag assemblage in which that species is present (Cambridge, 1978). In the Weybourne Crag *Macoma balthica* co-occurs with e.g. *Mya arenaria* Linné, 1758 and the extinct fluvial species *Viviparus glacialis* (Wood, 1872). In the British Isles the latter species is confined to the Weybourne Crag and related deposits.

The Weybourne Crag is overlain by estuarine and freshwater deposits which are allotted to two younger interglacials: the Pastonian and the Cromerian (West, 1980). From the Pastonian deposits hardly any molluscs are known. In the younger Cromerian beds *Macoma balthica* occurs, however, without *Mya arenaria* and *Viviparus glacialis*, in the so-called '*Mya*-' [= *Mya truncata* (Linné, 1758)] or '*Leda myalis*-Bed' (Reid, 1890; Norton, 1980). In the Cromerian the fluvial species *Valvata goldfussiana* Wüst,

1901 is present. In the British Isles this latter species is not known from younger deposits (Meijer & Preece, in press).

Younger occurrences of *M. balthica* are in the late Middle and Late Quaternary. These comprise the Hoxnian (= Holsteinian) and the Ipswichian (= Eemian) interglacials and the Holocene. In shallow marine Holocene deposits the species is very abundant. The extension of marine deposits of both interglacials is limited. Among the Hoxnian localities in which *M. balthica* occurs, Clacton (Baden-Powell, 1955) and the Nar Valley (Baden-Powell, 1967) may be mentioned. Ipswichian sites are: March (Baden-Powell, 1934) and Eye (Keen et al., 1990).

Dutch data — Since several decades the first appearance in The Netherlands has been known to occur in Middle Pleistocene estuarine deposits in the boreholes of Noord-Bergum-6D/38 and Exmorra-10B/168 (Tesch, 1942; ter Wee, 1976; Meijer & Preece, in press). From these beds the Interglacial of Noord-Bergum (Interglacial 4 of the 'Cromerian Complex') was introduced. In deposits of this interglacial *Valvata goldfussiana* is absent. The absence of this species in suitable assemblages indicates that the Interglacial of Noord-Bergum postdates the Cromerian s.s. After the investigation of borehole Zuurland-37C/554 (van Kolfschoten & de Boer, 1988) the first appearance of *M. balthica* in The Netherlands proved to have taken place much earlier. In Zuurland the species co-occurs with *Mya arenaria* and *Viviparus glacialis* in deposits of Late Tiglian age (Meijer, 1988a). Both latter species are extinct after the Late Tiglian. Later investigations of deeper strata in the same borehole showed the still earlier presence of *Macoma balthica* in late Middle Tiglian deposits. Additionally, in the same borehole the species was found in marine deposits of the subsequent Early Pleistocene interglacial, the Waalian (Meijer, 1987, 1988a). In these marine deposits *Mya arenaria* and *Viviparus glacialis* are lacking.

Marine deposits between the Waalian and the Interglacial of Noord-Bergum are as yet not known from The Netherlands. In deposits younger than the Interglacial of Noordbergum the species occurs in estuarine Holsteinian deposits (e.g. boring De Koog-9B/40 on the Isle of Texel) and in numerous boreholes penetrating Eemian deposits, e.g. Terschelling (Doeksen, 1975). In Holocene deposits the species is very commonly represented in tidal and shallow subtidal deposits.

Belgian data — From the Pliocene deposits of Belgium *Macoma balthica* is not known (Glibert, 1958a, b; Ringelé, 1974). The oldest known occurrences are from the so-called '*Cardium*-layers of Western Flanders', near Lo (Tavernier & de Heinzelin, 1962). The fauna which is present in these latter beds is very similar to the fauna of the deposits of the nearby locality at Herzeele in northern France (Meijer, 1988b). The age of both localities is considered to be Holsteinian. Examples of Eemian occurrences are in the neighbourhood of De Panne (Spaink & Sliggers, 1983), Zelzate (Janssen, 1965) and Meetkerke (Nolf, 1974). Also in Belgium *Macoma balthica* is very abundant in Holocene deposits.

Danish and German data — The earliest occurrences are of Holsteinian age, as for instance the stratotype of the Holsteinian at Hummelsbüttel (Germany; Spaink, 1975a). Eemian localities are at Stensigmose and Mandø Hølade (Denmark; Nordmann, 1908), and Offenbüttel-Schnittlohe (Germany; Hinsch, 1985).

Dutch offshore data — *Macoma balthica* has been found in deposits of Holocene and Eemian age in many offshore boreholes in the Dutch sector of the North Sea.

Older occurrences are less common and also less certain to date. Most of these are probably Holsteinian in age, the oldest may reach ages as old as the early Cromerian Complex. *M. balthica* is also present in Eemian deposits with an aberrant assemblage (Tables 1-2). These assemblages occur in several boreholes located rather close to the modern coast. The Eemian age of the assemblages is indicated by e.g.: *Gibbula cineraria* (Linné, 1758), *Hinia reticulata* (Linné, 1758), *Chlamys varia* (Linné, 1758), *Lucinella divaricata* (Linné, 1758), *Donax variegatus* (Gmelin, 1791), *Angulus distortus* (Poli, 1795) etc. These assemblages also show the presence of *Macoma obliqua* and other so-called Early Pleistocene species like *Acila cobboldiae* (Sowerby, 1817) and *Yoldia myalis* (Couthouy, 1838). Their occurrence is considered not to be the result of reworking from Early Pleistocene deposits, but to form part of the Eemian assemblage.

Icelandic data — In the Tjörnes sequence (Iceland), which ranges in age between Late Pliocene up to and including earliest Pleistocene, the species is lacking (Gladenkov et al., 1980).

Migration and first appearance in the North Sea Basin — The migration of *M. balthica* from the Pacific through the Bering Strait occurred with certainty before the Praetiglian: the species is known from the Alaskan Gubik Formation (Fish Creek near the coast of the Beaufort Sea), which has a latest Pliocene age predating the first cold Pleistocene stage (Repenning et al., 1987).

According to the British and Dutch data *Macoma balthica* appears in the southern North Sea as late as the second half of the Middle Tiglian Cold stage (=Prepastonian-a in the British sequence and late in palynostage TC4c in The Netherlands). This late arrival may have been the result of a long migration route. In that case the migration of this shallow marine species could well have followed the Siberian coasts. The absence of the species in the Icelandic deposits which range in age between the Late Pliocene Alaskan beds and the late Middle Tiglian North Sea deposits may be an indication for such a long migration route indeed.

Macoma calcarea

General remarks — At present this species shows a low-arctic/high-boreal distribution. This Recent distribution compares favourably with the fossil record where the species is met with in Pleistocene cold assemblages.

British data — In Britain the species appears in the Red Crag of Newbourn and remains present up to and including the Weybourne Crag (Wood, 1856; Norton, 1980). In Middle and Late Pleistocene strata *Macoma calcarea* is known from e.g. the Nar Valley (Holsteinian; Baden-Powell, 1967) and Powgavie in Scotland (Weichselian; Peacock, 1983).

Dutch data — In The Netherlands this species appears in Molluscan Zone B of the Neogene/Early Quaternary marine biozonation (Spaink, 1975b). Zone B is correlated with the Palynostage Praetiglian, which is considered to represent the first Quaternary cold stage in the region. In The Netherlands the species is not known later than the Middle Tiglian cold stage (palynostage TC4c) (Meijer, 1986).

Belgian data — In Belgium *Macoma calcarea* is not known, although the shallow marine facies of the youngest Pliocene strata seems suitable (Glibert, 1958a, b; Ringelé, 1974). The absence indicates that the highest Belgian Neogene marine deposits

Table 1. Occurrences of marine molluscan species in assemblages with *Macoma obliqua* and *Macoma praetenuis* present in boreholes in the Dutch sector of the North Sea. Details on boreholes A-S are given in Table 2.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S
Acila cobboldiae (Sowerby, 1817)	-	-	-	-	-	-	-	-	-	x	-	x	-	x	x	-	-	-	
Nucula nitidosa Winckworth, 1930	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	
Nucula nucleus (Linné, 1758)	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Leionucula tenuis (Montagu, 1808)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	
Yoldia myalis (Couthouy, 1838)	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	
Nuculana pernula (Müller, 1779)	x	-	-	-	-	-	-	-	-	-	-	-	x	-	-	x	-	-	
Portlandia arctica (Gray, 1824)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	
P. arctica or *intermedia* (Sars, 1858)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
Striarca lactea (Linné, 1758)	-	-	-	-	-	-	-	-	-	x	-	x	x	-	-	-	-	-	
Mytilus edulis Linné, 1758	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Modiolus modiolus (Linné, 1758)	x	x	x	x	x	x	-	x	-	x	x	x	x	-	-	x	x	-	-
Modiolula phaseolina (Philippi, 1844)	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Musculus discors (Linné, 1767)	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Crenella decussata (Montagu, 1808)	x	x	-	x	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-
Ostrea edulis Linné, 1758	x	x	x	x	x	x	x	x	x	x	x	x	x	-	x	-	-	-	
Flexopecten flexuosus (Poli, 1795)	-	-	-	-	-	-	-	-	-	x	-	-	x	-	-	-	-	-	
Aequipecten opercularis (Linné, 1758)	-	x	-	-	-	-	-	-	-	x	-	x	x	-	-	-	x	-	-
Chlamys varia (Linné, 1758)	x	-	x	-	-	x	x	x	x	x	x	x	x	-	x	-	-	-	
Similipecten similis (Laskey, 1811)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-
Pododesmus squamula (Linné, 1758)	-	-	x	x	x	-	-	-	-	-	-	x	-	-	-	-	-	-	
Anomia ephippium Linné, 1758	-	-	-	-	-	-	-	-	-	x	x	x	x	-	x	-	-	-	
Lucinoma borealis (Linné, 1767)	x	-	x	-	-	-	-	-	-	-	x	x	-	-	x	x	-	-	
Lucinella divaricata (Linné, 1758)	-	-	x	-	x	x	x	x	-	x	x	x	x	-	-	-	-	-	
Tridonta borealis (Schumacher, 1817)	-	x	x	-	-	-	x	x	-	x	x	x	x	-	x	-	x	-	-
Tridonta elliptica (Brown, 1827)	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Tridonta montagui (Dillwyn, 1817)	x	x	x	x	x	x	-	x	-	-	x	x	x	x	x	x	x	-	-
Goodallia triangularis (Montagu, 1853)	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	
Mysella bidentata (Montagu, 1803)	x	x	-	x	x	-	-	-	x	-	-	x	x	-	-	-	x	-	-
Tellimya ferruginosa (Montagu, 1808)	-	-	-	-	-	x	-	-	-	-	-	-	x	-	x	-	-	-	
Arctica islandica (Linné, 1767)	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x
Altenaeum dawsoni (Jeffreys, 1864)	x	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	
Diplodonta rotundata (Montagu, 1803)	-	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	
Cerastoderma edule (Linné, 1758)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-	-
Cerastoderma glaucum (Poiret, 1789)	-	x	x	-	x	x	x	x	-	x	x	x	x	-	x	x	x	-	-
Parvicardium scabrum (Philippi, 1844)	-	x	-	x	-	-	-	-	-	x	-	x	-	-	-	-	-	-	-
Sphaerocardium paucicostatum (Sowerby, 1839)	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Acanthocardia tuberculata (Linné 1758)	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clinocardium ciliatum (Fabricius, 1780)	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
Laevicardium crassum (Gmelin, 1791)	-	-	x	-	-	-	x	-	-	x	-	x	x	-	-	-	-	-	-
Serripes groenlandicus (Gmelin, 1791)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-
Spisula elliptica (Brown, 1827)	x	x	x	-	x	x	x	x	-	x	x	x	x	-	x	-	x	-	x
Spisula solida (Linné, 1758)	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Spisula subtruncata (da Costa, 1778)	x	-	x	x	x	x	x	x	x	x	x	x	x	-	-	-	x	-	-
Mactra corallina cinerea Montagu, 1803	-	-	x	-	x	-	-	x	-	x	x	x	x	-	-	-	-	-	-
Mactra glauca Born, 1778	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
Lutraria lutraria (Linné, 1758)	-	-	x	-	-	x	-	-	-	x	-	x	x	-	-	-	-	-	-

Table 1 (continued).

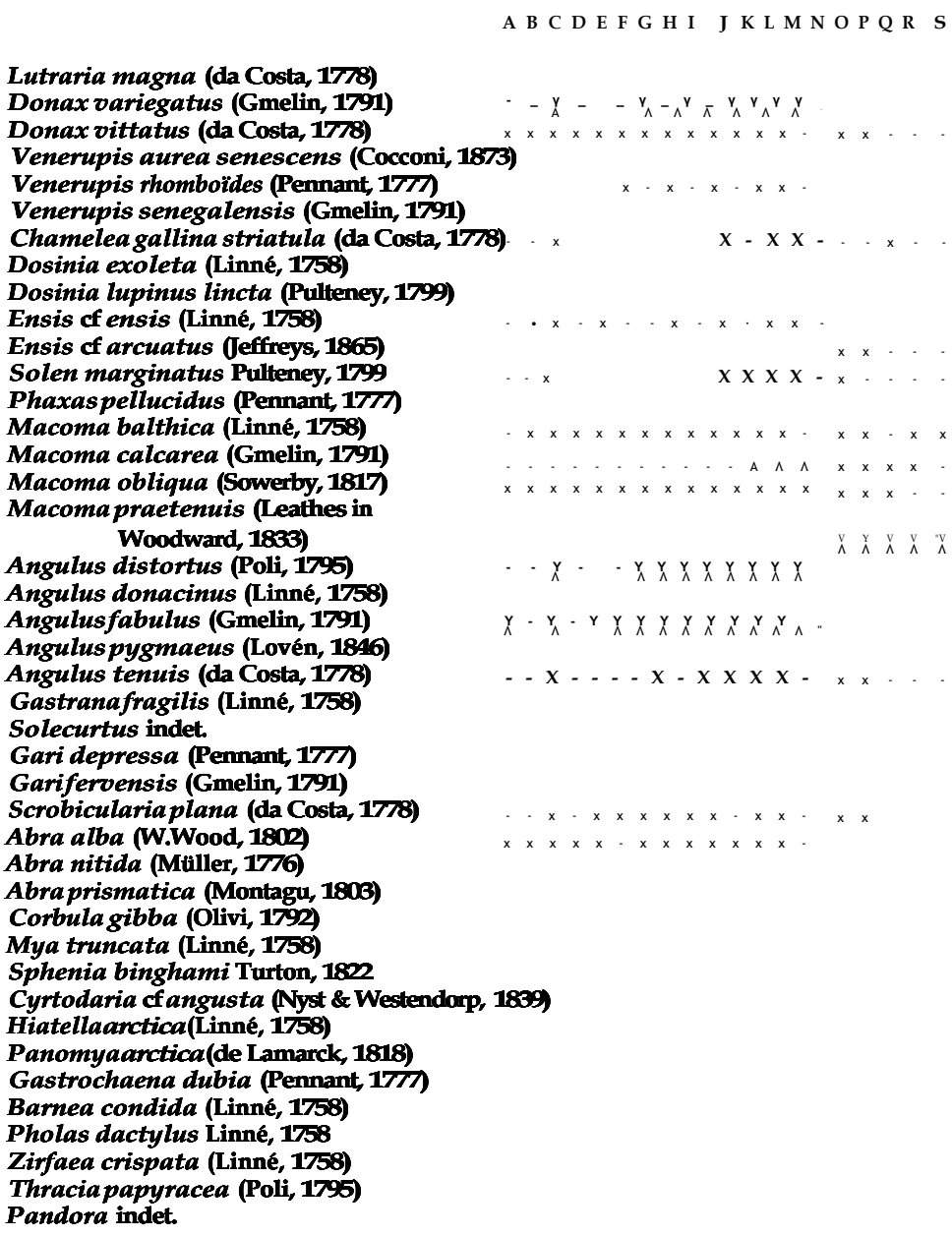

Table 1 (continued).

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S
Calliostoma zizyphinum (Linné, 1758)	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Gibbula cineraria (Linné, 1758)	x	x	-	x	x	-	x	-	-	x	-	x	x	-	-	-	-	-	-
Gibbula tumida (Montagu, 1803)	x	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Moelleria costulata (Moeller, 1842)	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Littorina littorea (Linné, 1758)	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	x	-	-	-
Littorina saxatilis (Olivi, 1792)	-	-	-	-	x	-	x	x	x	x	x	-	x	-	-	-	-	-	-
Lacuna vincta (Montagu, 1803)	x	-	-	x	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-
Peringia ulvae (Pennant, 1777)	x	x	x	-	x	x	x	x	x	x	x	x	x	-	-	-	x	-	-
Hydrobia neglecta Muus, 1963	-	-	x	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Hydrobia ventrosa (Montagu, 1803)	-	-	-	-	x	-	x	-	-	-	-	x	x	-	-	x	-	-	-
Skeneopsis planorbis (Fabricius, 1780)	-	-	-	-	-	-	-	x	x	-	-	-	x	-	-	-	-	-	-
Tornus subcarinatus (Montagu, 1803)	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Turboella inconspicua (Alder, 1844)	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Turboella parva parva (da Costa, 1778)	x	-	-	x	-	-	x	x	-	-	-	-	x	-	-	-	-	-	-
Turboella parva interrupta (J.Adams, 1798)	x	x	-	x	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Cingula semistriata (Montagu, 1808)	-	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-
Cingula alderi (Jeffreys, 1858)	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Alvania lactea (Michaud, 1830)	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-
Triphora adversa -complex	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Cerithiopsis tubercularis (Montagu, 1803)	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Bittium reticulatum (da Costa, 1778)	-	-	-	-	-	-	x	-	x	-	-	-	x	-	-	-	-	-	-
Epitonium clathratulum (Kanmacher, 1798)	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epitonium clathrus (Linné, 1758)	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-
Epitonium turtonis (Turton, 1819)	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Turritella communis Risso, 1826	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
Euspira catena (da Costa, 1778)	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Euspira cf *pallida* (Broderip & Sowerby, 1829)	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Euspira poliana (delle Chiaje, 1830)	x	x	-	x	x	-	x	-	x	x	x	x	x	-	-	-	-	-	-
Capulus ungaricus (Linné, 1758)	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acrybia islandica (Gmelin, 1791)	-	x	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nucella lapillus (Linné, 1758)	x	-	-	-	x	-	-	-	-	-	x	-	x	-	x	x	-	-	-
Ocenebra erinacea (Linné), 1758)	-	-	x	-	-	-	-	-	x	x	-	x	x	-	-	-	-	-	-
Hinia incrassata (Ström, 1768)	-	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-
H. incrassata or *H. pygmaea*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
Hinia pygmaea (de Lamarck, 1822)	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-
Hinia reticulata (Linné, 1758)	-	-	x	x	-	-	x	x	-	x	-	x	x	-	-	-	-	-	-
Buccinum undatum Linné, 1758	x	x	-	x	x	-	x	-	-	x	-	x	x	-	-	-	-	-	-
Neptunea antiqua (Linné, 1758)	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	x	-	-	-
Boreotrophon truncatus (Ström, 1768)	x	-	-	-	x	-	-	-	-	x	-	-	-	-	-	-	-	-	-
Raphitoma linearis (Montagu, 1803)	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oenopota rufa (Montagu, 1803)	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oenopota turricula (Montagu, 1803)	-	x	x	x	x	-	-	-	x	x	-	x	x	-	-	-	-	-	-
Chrysallida spiralis (Montagu, 1803)	x	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Odostomia eulimoides (Hanley, 1844)	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Odostomia turrita Hanley, 1844	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Turbonilla lactea (Linné, 1758)	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Acteon tornatilis (Linné, 1758)	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Retusa obtusa (Montagu, 1803)	x	x	-	-	-	-	-	-	-	-	x	-	x	-	x	-	x	-	-

Table 2. Data on boreholes A-S in the Dutch sector of the North Sea.

Nr	boring	latitude	longitude	m below seabed	age	waterdepth in m
A	P07/007	03 15 48.0	52 32 24.0	9.00-10.00	Eemian	34.20
B	P14/007	03 31 00.0	52 20 00.0	7.00-10.00	Saalian	31.00
C	P17/056	03 24 59.0	52 00 31.0	4.00- 9.00	Eemian	33.00
D	S01/010	03 05 32.0	51 57 45.0	2.00- 3.00	Eemian	35.80
E	S01/013	03 02 15.0	51 55 12.0	6.00- 7.00	Eemian	34.20
F	S01/024	03 05 49.0	51 54 17.0	9.00-10.00	Eemian	28.00
G	S01/028	03 06 21.8	51 50 49.0	2.00- 4.50	Eemian	31.60
H	S01/114	03 20 03.9	51 50 57.5	6.00- 8.00	Eemian	26.50
I	S05/110	03 22 28.0	51 49 52.0	5.00- 6.00	Eemian	26.90
J	S01/111	03 07 02.8	51 56 08.0	4.00- 8.00	Eemian	35.00
K	S01/112	03 11 34.2	51 53 19.7	4.00- 5.00	Eemian	35.00
L	S01/110	03 08 04.5	51 59 43.8	1.00-10.00	Eemian	40.60
M	S01/113	03 06 20.4	51 50 39.9	1.00- 5.00	Eemian	34.50
N	F08/006	04 28 02.0	54 34 10.0	20.00-20.55	Saalian	49.50
O	S01/112	03 11 34.2	51 53 19.7	5.00- 9.00	Saalian	35.00
P	S01/113	03 06 20.4	51 50 39.9	7.00-10.00	Saalian	34.50
Q	F08/006	04 28 02.0	54 34 10.0	46.13-46.23	Saalian	49.50
R	F08/006	04 28 02.0	54 34 10.0	69.02-69.15	Saalian ?	49.50
S	A05/009	03 29 38.3	55 41 47.5	74.00-74.16	Saalian ?	46.30

predate the youngest Red Crag of England. This is confirmed by the absence of other molluscan taxa in the Belgian deposits, as for instance *Serripes groenlandicus* (Gmelin, 1791).

Danish and German data — In Denmark and northern Germany the species occurs in Late Glacial deposits of Elsterian, Saalian and Weichselian ages. Examples of these are the Skærumhede-2 borehole (Denmark, Weichselian; Bahnson et al., 1974), Esbjerg (Denmark, 4th Cromerian Interglacial; Miller & Mangerud, 1985), Itzehoe and Rensing (Germany, Late Elsterian; Grahle, 1936). From these countries no older occurrences are known.

Dutch offshore North Sea data — *Macoma calcarea* is a common species in Weichselian and Saalian marine deposits of the North Sea. Several localities are listed in Table 1.

Icelandic data — The species is known from the *Serripes* Zone in the Tjörnes section and from the younger Breidavik Beds. It is not present in the underlying *Tapes* and *Mactra* zones (Gladenkov et al., 1980; Gladenkov, 1981). According to Gladenkov (1981) the *Serripes* zone ranges in age between c. 2-3.5 Ma, and the Breidavik Beds 0.7-1.8 Ma.

Migration and first appearance in the North Sea Basin — Appearance in North Sea deposits occurs in the Praetiglian (Newbourn Crag/Molluscan Zone B). This is also the case in the Icelandic deposits. No data of this or earlier age are known from the Alaskan/Beringian coasts.

Macoma obliqua

General remarks — This species is not present in the modern fauna of the North

Sea. It was long thought to be extinct, but Coan (1969b) recognised the conspecificy with the still extant east Pacific *Macoma incongrua* (auct., non von Martens, 1865).

British data — In England *Macoma obliqua* rarely occurs in the Coralline Crag whilst it is abundant in the overlying Red Crag. It remains present, up to and including the Weybourne Crag (Norton & Spaink, 1973; Norton, 1980). From younger strata, the species is reported from the March Gravels, exposed in and south of the Wash, which are assumed to have an Ipswichian age (Baden-Powell, 1934; Keen et al., 1990). Although the specimens from the March Gravels were considered to be reworked from Pliocene/Early Pleistocene strata, recent discoveries may shed new light on these occurrences (see below).

Dutch data — In The Netherlands the first appearance occurs early in Molluscan Zone D1 of the Neogene marine biozonation. It remains present up to and including the late Middle Tiglian cold stage.

Belgian data — In Belgium, the species is present in all Pliocene deposits, with the exception of the oldest, the Kattendijk Sands (Glibert, 1958a, b; Ringelé, 1974). From Quaternary deposits the species is not known.

Danish and German data — From these countries *Macoma obliqua* is not known.

Dutch offshore North Sea data — As indicated in the discussion on *M. balthica* the species occurs in Eemian assemblages in which Lusitanian and Mediterranean species are present. *Macoma obliqua* is further known from Saalian and Weichselian deposits associated with the above mentioned Eemian beds. These colder deposits are known in boreholes more offshore. A selection of the assemblages is listed in Table 1. In Holocene deposits and in the modern fauna of the North Sea, *Macoma obliqua* is not present.

Icelandic data — *M. obliqua* is only present in the lower part of the *Serripes* Zone (Gladenkov et al., 1980; Gladenkov, 1981).

Migration and first appearance in the North Sea Basin — The first appearance of this species coincides, in England, Belgium and The Netherlands, with other first appearances of taxa with a Pacific origin. There are indications that the arrival of Pacific species in the North Sea occurred in more than one wave. *Macoma obliqua* belongs to the earliest observed taxa, and is considered to belong to the first Pliocene wave of Pacific arrivals. The species remains present during the Late Pliocene and the Early Pleistocene up to and including the Eemian, probably Early Weichselian. Onshore the species is not known younger than late Middle Tiglian, with a probable exception of the March Gravels (England).

The absence in the lowermost Icelandic deposits apparently indicates that the early migration is not documented in the Northern region. According to Coan (1969a, b) the precursor of *M. obliqua* was present during the Miocene in the North Pacific.

Macoma praetenuis

General remarks — For the moment this seems to be the only extinct species of post-Miocene North Sea *Macoma*. According to Coan (1969a) very related species, which may even be conspecific with *Macoma praetenuis*, do occur in the modern Pacific.

British data — In England the species appears in the oldest Red Crag ('Waltonian')

and remains present in the overlying Norwich Crag. The last occurrence is in deposits with a Baventian age. Deposits of this age are supposed to be slightly older than the Weybourne Crag, although both are assigned to the same stage (Gibbard et al., 1991; Zalasiewicz et al., 1991).

Dutch data — This species was found in boreholes near Macharen and Oss (van der Burg, 1987). From these boreholes this author described two biozones from Pliocene deposits: an upper *Cerastoderma edule hostiei* Range Zone and a lower *Pseudamussium gerardi* Range Zone. In my opinion these zones may be correlated with the Molluscan (Assemblage) Zones C and D1 (Spaink, 1975), respectively. In the boreholes near Macharen and Oss *Macoma praetenuis* only occurs in the *Cerastoderma edule hostiei* Range Zone. Older occurrences are unknown in The Netherlands. Apparently the species appears for the first time in Molluscan Zone C of the marine biozonation, which correlates with the palynostage Reuverian-C. It remains present during the Early Pleistocene. In borehole Zuurland *Macoma praetenuis* has its last appearance in late Middle Tiglian deposits, in which it co-occurs with *Macoma balthica*. As already mentioned the latter species has its first appearance in these beds. In onshore deposits *Macoma praetenuis* is not known from younger deposits.

Belgian data — In Belgium *Macoma praetenuis* appears in the Kruisschans Sands and is still present in the overlying Merksem Sands which are the top of the regional Neogene marine shell-bearing succession (Glibert, 1958a, b; Ringelé, 1974).

Danish and German data — From these countries *Macoma praetenuis* is not known.

Dutch offshore data — *Macoma praetenuis* has very recently been found in late Middle to Late Pleistocene deposits in boreholes in the central part of the present North Sea (boreholes A5/009, F8/006), and in several near-coastal boreholes. The species is present in samples in which no reworking in the molluscan assemblages can be noticed. Remarkably, the species occurs in cold assemblages with e.g. *Yoldia myalis*, *Nuculana pernula* (Müller, 1779), *Portlandia arctica* (Geray, 1824), and *Macoma calcarea* (Table 1). The *Macoma praetenuis* bearing deposits are in some cases directly overlain by Eemian deposits of the climatic optimum. There is no clear lithological break between the cold deposits and the Eemian beds and therefore it is assumed they represent Saalian late glacial or Eemian early interglacial deposits. In several boreholes *M. praetenuis* is also found together with *M. obliqua* (Table 1). Like *M. obliqua*, *M. praetenuis* is not known from younger strata.

Icelandic data — The species is present in the *Serripes* Zone in the Tjörnes section and in the younger Beidavik Beds (Gladenkov et al., 1980; Gladenkov, 1981).

Migration and first appearance in the North Sea Basin — The species appears in the North Sea during the latest Pliocene (Walton Red Crag, Kruisschans Sands, Molluscan Zone C). From Iceland the species is only known from the *Serripes* Zone. Apparently, also from this species the earliest migration is not documented.

Conclusions

A correlation scheme of English, Belgian and Dutch Neogene-Early Pleistocene deposits, and the arrivals of *Macoma* in the North Sea Basin is given in Figs. 1-2.

First appearance dates — From all available data the succession of the first appearances is as follows: in the Pliocene *M. obliqua* arrives first, followed by *M. praetenuis*

and *M. calcarea*. The last species to arrive is *M. balthica*, in the Early Pleistocene. This succession is essentially according to Norton & Spaink (1973). The arrival of *M. obliqua* is well documented and occurs in this part of the North Sea in more or less time-equivalent deposits: the Coralline Crag, the Luchtbal Sands and the lower part of Molluscan Zone D1.

A similar pattern exists for the first appearance of *M. praetenuis*. This species appears in the Walton Crag, the Kruisschans Sands and Molluscan Zone C. The other two species differ from the foregoing ones, because of the large hiatus in the marine succession of Belgium. *M. calcarea* appears in the Newbourn Red Crag and the Molluscan Zone B. This species is absent in Belgium. The youngest species, *M. balthica*, is observed in the Weybourne Crag and late in Molluscan Zone A, more precisely in a late part of the Middle Tiglian cold stage. In Belgium the species appears first in the Holsteinian interglacial. The last two species are the only species known from Denmark and Germany. There, *M. calcarea* appears in the Elsterian and *M. balthica* in a late Cromerian interglacial, most probably correlative with the Interglacial of Noord-Bergum (Miller & Mangerud, 1985).

Last appearance dates — Both *M. balthica* and *M. calcarea* are still living in the North Sea, whereas the other two species are extinct there. Onshore, *M. obliqua* and *M. praetenuis* are not known younger than the Late Tiglian warm stage. However, offshore the species are known from much younger deposits. *M. obliqua* occurs in Eemian, and possibly Weichselian deposits. Recently this species was reported also from Late Emilian and Sicilian strata in the Mediterranean (Bellomo & Raffi, 1991). The observations in both basins point to a persistent occurrence of the species after the Tiglian at the eastern side of the Atlantic Ocean at least up to and including the Eemian.

M. praetenuis is present in deposits predating the Eemian. The probable age of these deposits is Saalian, but a much older age cannot be excluded.

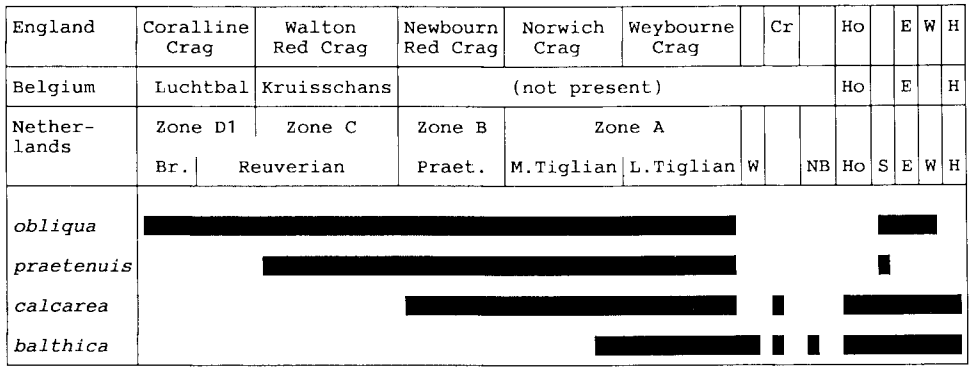

Fig. 1. Stratigraphical ranges of *Macoma* in the southern North Sea. Pliocene and Early Pleistocene stages in which no first or last appearances occur, are omitted. Br. = Brunssumian; Praet. = Praetiglian.; W = Waalian; Cr = Cromerian s.s.; NB = Interglacial of Noordbergum; Ho = Holsteinian/Hoxnian; S = Saalian/Wolstonian; E = Eemian/Ipswichian; W = Weichselian/Devensian; H = Holocene.

Macoma arrivals	England (East Anglia)		Belgium	The Netherlands	
	Crags	Pollen	Lithostratigraphy	Molluscan Zone	Pollen
		(Pastonian)		A	Tiglian C5
balthica	Weybourne	Prepastonian-a			Tiglian C4
	Chillesford Clay	Baventian			
	Norwich	Antian/Bramertonian			Tiglian C1/3
		Thurnian			(Tiglian B)
	Butley	Ludhamian			(Tiglian A)
calcarea	Newbourne	(Preludhamian)		B	Praetiglian
praetenuis	Walton		Merksem Kruisschans	C	Reuverian
			Oorderen	D1	
obliqua	Coralline		Luchtbal		Brunsumian
			Kattendijk	D2	

Fig. 2. Arrivals of *Macoma*-species in the southern North Sea, and stratigraphical correlations between England, Belgium and The Netherlands. Stratigraphic names in parentheses: no molluscan data available.

Remarks on the first appearance of Pacific species in the North Sea

The first wave of Pacific arrivals in the North Sea, from which *Macoma obliqua* forms part, is an important datum level in the Late Neogene of the basin. Conventially, this event is considered to have taken place in the British Red Crag and the Belgian Oorderen Sands. Indeed 'Pacific' representatives are very common in these deposits. However, in the underlying deposits, which are the Coralline Crag and the Luchtbal Sands respectively, the following 'Pacific' species already (rarely) occur: *Mytilus edulis* Linné, 1758, *Modiolus modiolus* (Linné, 1758), *Macoma obliqua*, *Mya truncata*, *Trichotropis borealis* Broderip & Sowerby, 1829, *Nucella tetragona* (Sowerby, 1823), *Buccinum undatum* Linné, 1758, and *Neptunea angulata* (Wood, 1848)(= *N. contraria* auct.) (of these the Mytilidae should be handled with care, because other Mytilidae are present in Miocene strata and most species are very difficult to identify if only fragmentary material is available). In The Netherlands the same species are present in lower parts of the Molluscan Zone D1. These deposits are assigned to foraminiferal zone FB (Doppert et al., 1979; Doppert, 1985; Beets, 1992), and the Brunssumian palynostage (Andrew & West, 1977).

According to Zagwijn & Suc (1983) the age-limits of the Brunssumian are 3.3-5.2 Ma. Jenkins & Houghton (1987) and Jenkins et al. (1988) inferred an age-range of 2.3-4.2 Ma for the Coralline Crag based upon planktonic foraminifera [FAD of *Globorotalia puncticulata* (Deshayes, 1832) and LAD of *Neogloboquadrina atlantica* (Berggren, 1972)] and nannoplankton (LAD of *Sphenolithes* sp.). However, according to the same authors, the most probable age of this deposit is c. 3.5 Ma which is late in the Brunssumian. This age coincides with the supposed age of the opening of the Bering Strait at c. 3.5 Ma (Vermey, 1989).

Beets (1992) measured Sr-isotopes on Pliocene and Late Miocene shells from several boreholes in The Netherlands in order to obtain absolute ages. With this method, also beds in which first appearances of 'Pacific' species occur, were dated. In borehole Heumensoord-46A/260, at depths between 87.00 and 94.00 m, the following FAD's of 'Pacific' species are observed: *Mytilus edulis*, *Modiolus modiolus*, *Mya truncata*, *Buccinum undatum*, and *Neptunea angulata*. From the measurements of Beets an age-range of 4.7-4.8 Ma may be inferred. This age falls within the assumed age-limits of the Brunssumian but seems to be too high for the first arrival of Pacific immigrants. Based upon faunal evidence e.g. Cohen (1968) suggested an earlier opening occurring briefly during the Late Miocene, predating the longer lasting opening of the Bering Strait in the Pliocene. More absolute dating in the North Sea Basin may shed more light on this important stratigraphical event.

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