

Late Quaternary environmental changes recorded in the Danish marine molluscan faunas

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GEOLOGICAL SURVEY OF DENMARK AND GREENLAND
MINISTRY OF THE ENVIRONMENT

Geological Survey of Denmark and Greenland Bulletin 3

Keywords

Bottom-communities, climate changes, Danish, environment, interglacial–glacial cycle, Late Quaternary, marine, mollusc faunas.

Cover

Donax vittatus on the sandy shores of northern France.

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Scientific editor of this volume: Svend Stouge

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Illustrations: Gurli E. Hansen Bengaard and Henrik Klinge Pedersen

Digital photographic work: Benny M. Schark and Jakob Laurrup

Graphic production: Knud Gr@phic Consult, Odense, Denmark

Printers: Schultz Grafisk, Albertslund, Denmark

Manuscript submitted: 9 January 1998

Final version approved: 11 December 2003

Printed: 15 July 2004

ISBN 87-7871-122-1

Geological Survey of Denmark and Greenland Bulletin

The series *Geological Survey of Denmark and Greenland Bulletin* replaces *Geology of Denmark Survey Bulletin* and *Geology of Greenland Survey Bulletin*.

Citation of the name of this series

It is recommended that the name of this series is cited in full, viz. *Geological Survey of Denmark and Greenland Bulletin*.

If abbreviation of this volume is necessary, the following form is suggested: *Geol. Surv. Den. Green. Bull.* 3, 268 pp.

Available from

Geological Survey of Denmark and Greenland
Øster Voldgade 10, DK-1350 Copenhagen K, Denmark
Phone: +45 38 14 20 00, fax: +45 38 14 20 50, e-mail: geus@geus.dk

or

Geografforlaget ApS
Rugårdsvej 55, DK-5000 Odense C, Denmark
Phone: +45 63 44 16 83, fax: +45 63 44 16 97, e-mail: go@geografforlaget.dk

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Abstract

Petersen, K.S. 2004: Late Quaternary environmental changes recorded in the Danish marine molluscan faunas. *Geological Survey of Denmark and Greenland Bulletin* 3, 268 pp.

Late Quaternary, marine deposits in Denmark have yielded 247 subfossil species of molluscs. The sites are presented, and comparisons are made between the subfossil mollusc assemblages and the 278 shell-bearing mollusc species presently living in the Danish seas. 184 species are common to the two groups. The 63 species no longer occurring around Denmark are used as indicators of changing environmental conditions, including temperature, salinity and depth, throughout the last 130 000 years. Seven modern faunal regional units are defined and considered: the Bælt, the Baltic, the Kattegat, the Limfjord, the North Sea and the Vendsyssel regions, and the Skagen area based on the Skagen III Well DGU File No. 1.287. The Late Quaternary, marine, shell-bearing molluscs, comprising 341 subfossil and recent species, are characterised from the point of view of climatic (i.e. Arctic, Subarctic, Boreal and Lusitanian) affinities and animal–sediment relationships. On this background the faunal and environmental evolution recorded in the 217 m long Skagen Well core is analysed and described. The mollusc assemblages in the Skagen sequence indicate a deeper-water facies during the Eemian, the Weichselian and the older Holocene in contrast to what hitherto was known in other parts of the Danish area during the Late Quaternary. For the Skagen Well the chronozones Preboreal/Boreal, Atlantic, Subboreal and Subatlantic can be identified by ^{14}C dating. The environmental changes within the seven regions through the Late Quaternary are evaluated by depicting the molluscan communities encountered in the seven Late Quaternary stages together with remarks on studies of the neighbouring areas. By following the marine communities through the Late Quaternary in the light of the classical bottom communities *sensu* C.G.J. Petersen, it is demonstrated how facies have changed both through time and space within the Danish marine realm. The well-established, more temperate Eemian marine fauna was closely associated with shallow-water environments. The inferred climatic changes reflect an interglacial–glacial cycle. However, the climatically induced changes during the Holocene in the marine environment were small and overshadowed by the facies changes. Out of the 341 species recorded in this study, 140 occur in the Eemian, 36 in the Early/Middle Weichselian and 41 in the Late Weichselian. The Holocene fauna is represented by 183 species of shell-bearing molluscs, of which the first recorded occurrence of 148 species has been radiocarbon-dated.

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Fig. 1. Location map with Late Quaternary marine localities and names of areas on land and of Danish waters.

Introduction

In the middle of 19th century, Denmark had its first 'Geology of Denmark' published by G. Forchhammer, in 1835. However, as Forchhammer expressed it in 1851 when making some notes on the work by the malacologist O.A.L. Mørch (1828–1878) at the Mineralogical Museum of Copenhagen. It has hitherto been enough for the geognost to establish formations using the characteristic fossils, but in the future we have to give a closer description from a zoological point of view (Petersen 1997, p. 5). Considering only the younger deposits, the efforts of the zoologist in geological works are highly significant and became important already in the 19th century. C.G.J. Petersen (1860–1928) is an outstanding example of such an influence with his work on the extent of shell-bearing molluscs in the Danish seas inside the Skagen (Petersen 1888, 1893). Here he points to the faunal conditions also in the Pleistocene and Holocene marine deposits compared to the recent distribution. In the description accompanying the geological map sheets of Vendsyssel (Jessen 1899), Jessen gives full credit to C.G.J. Petersen and A. Jensen (1866–1953) for their studies on the molluscan species recorded from that part of the country. Later both Petersen and Jensen contributed further to our knowledge of the marine molluscan fauna. Petersen formed the concept of the bottom communities (Petersen & Jensen 1911; Petersen 1913, 1914, 1915, 1918) that has been the tool for further work, not only within the Danish waters but all over the world with the so-called parallel bottom communities (Thorson 1957). Though the concept of parallel molluscan communities in the

sense of Thorson (1957) has been considerably modified in the last 30 years (Erwin 1983), there remains a recognition that particular molluscan assemblages are associated with various types of habitat. In 1899 the zoologist V. Nordmann (1872–1962) was engaged by the Geological Survey of Denmark to study the molluscs from the Quaternary deposits. Part of this work was already reflected in the next geological map sheet covering the southern part of Vendsyssel (Jessen 1905). Here Nordmann has identified the molluscs and given the faunal remarks on the Holocene marine fauna in the north-eastern part of the Limfjord (Fig. 1). In his work, the zoological considerations are given, elucidating the Holocene palaeoenvironments. However, from the beginning of the century Nordmann touched upon many other aspects within the Late Quaternary marine environments which form the most important base for the present study covering marine deposits from the Eemian, the Weichselian and the Holocene.

In the following chapter the presentation of some observed sites with marine sediments will be given as an introduction to an answer to the question raised by Petersen (1910, p. 29): "What I have often missed in the geological studies is a thorough or detailed comparison between the fossil faunas and the molluscan faunas now living before our eyes".

The aim of this work is to characterise the changing environments in the Danish waters through time as seen in the macrofaunas and bottom communities mainly based on molluscs.

Danish sites with marine sediments

Initially, the findings and descriptions of the Danish marine localities shown in Fig. 1 were part of the university studies pioneered by G. Forchhammer. However, since the start of the Geological Survey of Denmark in 1888, much of the information has come from the systematic mapping of Denmark, and the results have been published in the descriptions to the geological map sheets of Denmark (Fig. 2).

As seen from the plan for the geological mapping of Denmark (e.g. Sørensen & Nielsen 1978) it was decided to do the mapping first in the northern parts of Jylland and Sjælland and to present a record of the marine deposits from the areas mapped. Today, up to 80 per cent of the country has been mapped and descriptions for many map sheets have been published. The main information on the Holocene marine mol-

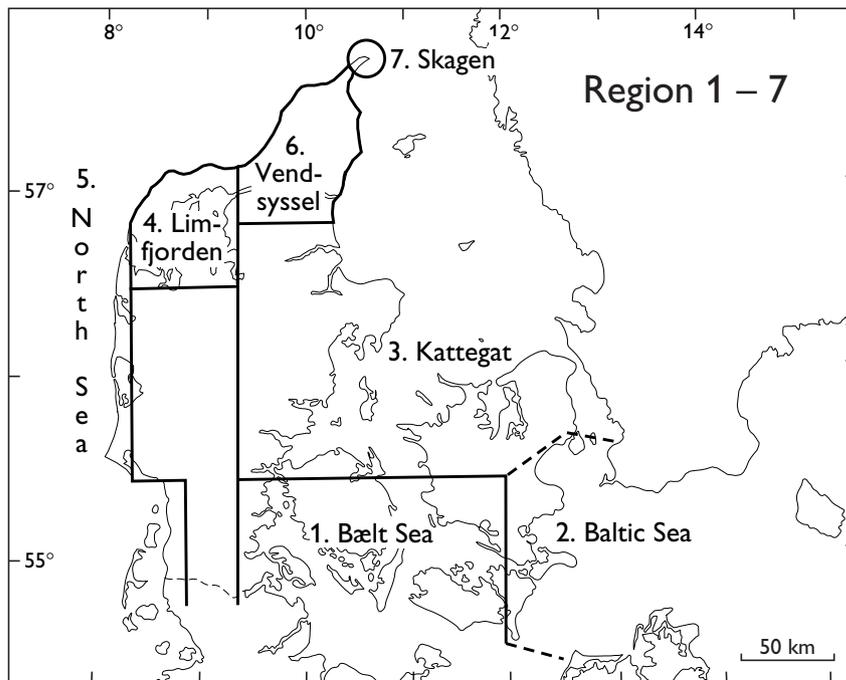


Fig. 2. The frame for the seven regions follows mainly the pattern of the old geological map sheets (Sørensen & Nielsen 1978, fig. 1) and partly the regions used in Jensen & Knudsen (1995, fig. 1).

1: The Bælt Sea covering the southern part of the Bælts. **2:** The Baltic covering the southern part of Øresund and east of Darss–Gedser. **3:** The Kattegat region covering the northern part of the Bælts and Øresund. **4:** The western Limfjord – except the North Sea coastal region. **5:** The North Sea with coastal regions and Skagerrak. **6:** Vendsyssel including former marine areas. **7:** Skagen, mainly the Skagen Well DGU File No. 1.287.

luscs is available in these publications and is used in the present description supplemented by specific molluscan studies within the areas.

Consequently, the frame will be the transition area between the North Sea and the Baltic and the descrip-

tion mainly based on the geological map sheets found in the following regions shown in Fig. 2: (1) The Bælt Sea; (2) The Baltic; (3) The Kattegat with bordering fjords; (4) The Limfjord; (5) The North Sea; (6) Vendsyssel and The Skagen Well III, DGU File No. 1, 287.

The Late Pleistocene

In 1841 Forchhammer found the *Cyprina* Clay to the southern part of Denmark, naming the unit after the dominating bivalve (Forchhammer 1842). First, however, Forchhammer referred the thick shell molluscs to *Glossus humanus* rather than to *Arctica islandica*. Consequently, he placed the deposits in the ‘Brunkulsformation’, viz. the Tertiary. When finally realising that the common species was *Arctica islandica*, he transferred the deposits to the so-called ‘Rullestensformation’, viz. the Quaternary. Along with the investigations of the *Cyprina* clay through the years since 1841, the actual stratigraphical position was very much under debate, and it was not until 1928 when Nordmann wrote his *La Position stratigraphique des Dépôts d’Eem* that the *Cyprina* clay attained its final position:

“appartenant à la dernière période interglaciaire” (Nordmann 1928, p. 65). Later the name ‘Eemian’ became the designation for the whole interglacial, according to Gripp (1964, pp. 215–216). Johnstrup (1882a) gave the first detailed description of the *Cyprina* Clay in Denmark and Slesvig. Also in the northern part of Denmark, Late Pleistocene deposits were studied by Johnstrup (1882b), but with references to the earlier works by Forchhammer (1822), Bredsdorff (1824), Faber (1828) and Pingel (1828). In 1908 Nordmann made his doctoral thesis on the molluscan fauna from the *Cyprina* Clay and other central European deposits, forming a part of the publication by Madsen *et al.* (1908).

The sequence of interglacial–glacial marine depos-

Fig. 3. Stratigraphic framework for the Late Quaternary deposits from Pedersen & Petersen (1997).

Period	Epoch	Age	Chron	Culture stage	Ice stream chronology	Calendar years BP	¹⁴ C years BP						
L a t e Q u a t e r n a r y	Holocene	Subatlantic		Historical age		1000	1050						
				Iron age		2000	2050						
				Bronze age		3000	2900						
		Subboreal					4000	3700					
							Neolithic	5000	4400				
		Atlantic					6000	5500					
							Mesolithic	7000	6100				
	8000							7200					
	Boreal					9000	8100						
	Preboreal					10000	9100						
	Pleistocene	Late Weichselian			Palaeolithic		11000	10000					
							Younger Dryas	12000	10200				
							Allerød	13000	11100				
							Older Dryas	14000	12100				
Bølling							15000	12800					
Middle Weichselian							16000	13400					
							Young Baltic	17000	14200				
								18000	15100				
							Swedish					19000	16100
												20000	17000
Norwegian					21000	17600							
					22000	18500							
Early Weich. Eemian						25000							
						Old Baltic					75000		
											115000		
						130000							

its is described from the well at Skærumhede (Jessen *et al.* 1910). Here the full Late Pleistocene record is found, although the stratigraphic position was not clear at that time. Later investigations, also with studies of the molluscan fauna, were published in 1974 and a Late Pleistocene age proposed (Bahnson *et al.* 1974). The difference between the Boreo-Lusitanian community in the boring and the typical Eemian community as found in southern Denmark was interpreted as difference in facies (Bahnson *et al.* 1974) (see Nilsson 1983).

In the study of the marine Late Pleistocene deposits in southern Denmark (Ødum 1933) based on the record of molluscan species as determined by V. Nordmann the finds point to two different deposits in time. One is regarded as Eemian and the other as the so-called Skærumhede fauna. However, later investigations at Strandegaards Dyrehave in southern Sjælland (Petersen & Konradi 1974) and at Holmstrup in central Sjælland (Fig. 1; Petersen & Buch 1974), revealed that the molluscan species found at Strandegaards Dyrehave, one of the localities of Ødum (1933) and regarded as

representing the Skærumhede fauna, could be Eemian but reflecting another facies than the typical Eemian on the islands south of Fyn. The Holmstrup fauna is to be correlated with the Arctic marine Weichselian in northern Jylland which is the upper part of the *Portlandia arctica* zone *sensu* Nordmann (Madsen *et al.* 1908) or the *Macoma calcarea* zone *sensu* Petersen (Bahnson *et al.* 1974, fig. 7), see Fig. 3 for stratigraphical position.

The aminostratigraphic investigations of the Danish Late Pleistocene deposits as published by Miller & Mangerud (1985) sustain only to some extent the above-mentioned correlations: “None of the sites regarded here as Eemian (Strandegaards Dyrehave) gave ratios as high as in Holsteinian deposits or as low as in Middle Weichselian deposits” (Miller & Mangerud 1985, p. 261). In the case of the Holmstrup Weichselian site, only three out of eleven individuals of *Macoma calcarea* gave Weichselian ratios (Miller & Mangerud 1985, p. 264).

The marine molluscan fauna of the Late Weichselian has been studied intensively only from the Vend-

syssel area recorded in the publications by Jessen (1899, 1936). Nearly 30 molluscan samples from these Late Weichselian – Younger *Yoldia* Sea deposits have been dated (Krog & Tauber 1974).

The evaluation of the molluscan communities in Vend-

syssel reveals the changing Late Weichselian sea level (Petersen 1984), and the highest marine shoreline, around 60 m a.s.l., in northern Denmark can be shown to develop between 14 000 and 13 000 B.P. (^{14}C years).

The Holocene

Forchhammer participated in the work of the so-called 'Lejrekomité', an interdisciplinary committee studying human remains along the shore. This commission gave the first – and now famous – description of the 'køkkenmødding' (kitchen midden), a mound consisting of shells of edible molluscs and other refuse, marking the site of a prehistoric human habitation (Hanks 1971). 'Køkkenmødding' is one of the few Danish international terms (Forchhammer *et al.* 1851). The work of the 'Lejrekomité' was concentrated on the marine molluscs in order to establish out whether the shell deposits were naturally based – oyster banks – or whether they were formed as waste deposits produced by men living at coastal sites.

The other members of the commission were J. Worsaae and J. Steenstrup, representing archaeology and zoology respectively. Consistently, the study of the molluscan elements was based mainly on Steenstrup's work. However, while working in the commis-

sion, Forchhammer continued his studies on the sea levels (Forchhammer 1838, 1840). This was essential for the discussion of whether the molluscs found belonged to raised marine deposits or were gathered by man. Forchhammer's study led to the concept of raised marine deposits north of a line from Nissum Fjord to south of Korsør in the Storebælt area (Fig. 1). This line still carries the name of Forchhammer and divides the country into two parts, with the raised marine areas to the north-east, and to the south-west the area where the land has been sinking. Together with the study of the Holocene molluscan fauna by Johnstrup (1882b), such observations on shorelines were also collected. It became one of the points specially mentioned in the instructions for the autographic geologists when the systematic geological mapping of Denmark was started in 1888 by the Geological Survey of Denmark (Sørensen & Nielsen 1978).

The recent fauna of shell-bearing molluscs compared to the subfossil fauna

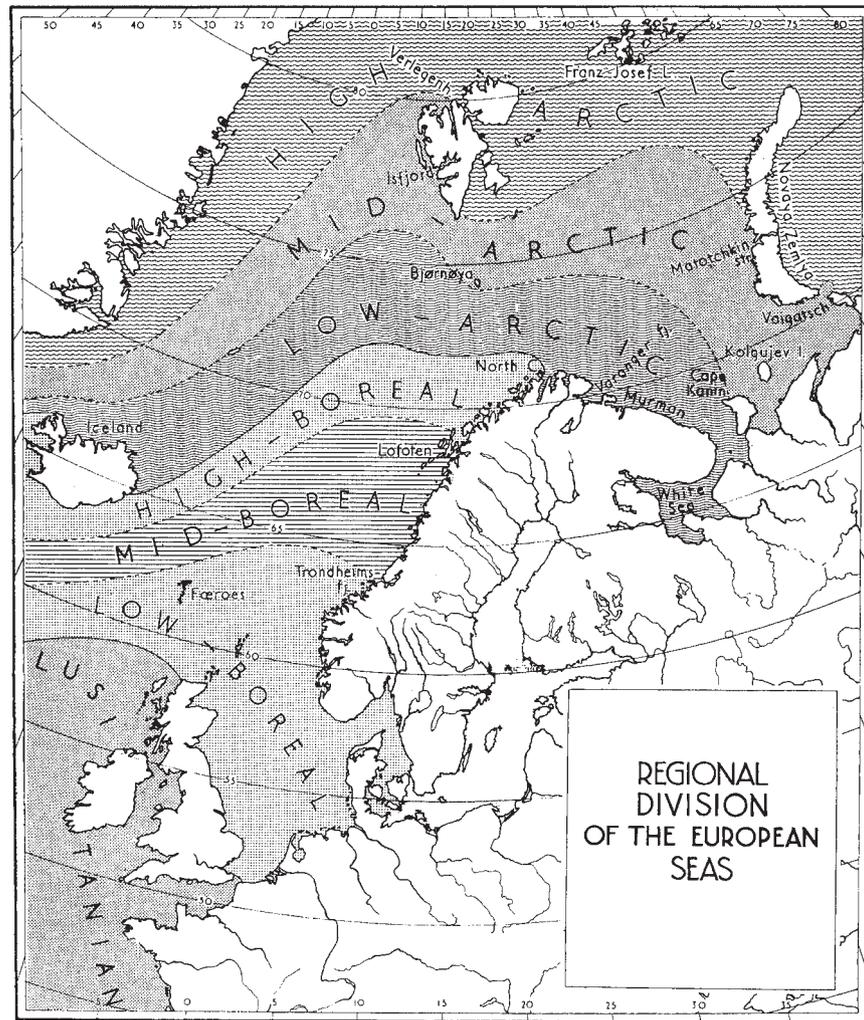
The record of recent Danish shell-bearing molluscs has been taken from the annotated check list of recent marine molluscs of Danish waters (Jensen & Knudsen 1995). In Appendix 1 the species are presented taxonomically following Jensen & Knudsen (1995). Late immigrants from the last centuries – transferred by man – have been omitted from the list, because the aim of the present study is to present the development in the subfossil Late Quaternary molluscan fauna also in Ap-

pendix 1 compared to the natural fauna of today. According to Fredén (1986), subfossil means that the weight of the object when found does not exceed its original weight, which is obviously the case for younger deposits seen geologically as shells from the Late Quaternary.

In all, 278 recent species of shell-bearing molluscs are recorded from the Danish waters:

The Class Polyplacophora is represented by seven

Fig. 4. Regional division of the Euro-
pean seas from Feyling-Hanssen (1955).



species forming 2.5% of the total number of known species.

The Class Gastropoda is represented by 151 species forming 54.3% of the total number of known species.

The Class Scaphopoda is represented by three species forming 1.1% of the total number of known species.

The Class Bivalvia is represented by 117 species forming 42.1% of the total number of known species.

The list of known finds of subfossil species amounts to 247 species. With regard to the classes, it appears that Polyplacophora is now represented by only one species, which formed 0.4% of the total subfossil molluscan species.

Within the Class Gastropoda 125 species occur, forming 50.6% of the total number of subfossil species, a figure which is nearly 5% lower than that for recent gastropods.

The Class Scaphopoda is represented by five fossil species which form 2.0% of the subfossil shell-bearing species which is a little higher than the ratio for the recent fauna.

The Class Bivalvia is represented by 116 species forming 47.0% of the total, which is a little more than 7% above the recent ratio.

The low number of subfossil Polyplacophora can be explained by the fact that the shells from those species are nearly always broken, and this excludes identification to species level, so to say, following the statement made by Knudsen (1970, p. 1): "Isolated and worn plates were neglected altogether".

Among the Gastropods, the subclasses and orders, except the Order Heterostropha within the subclass Heterobranchia, have a lower representation of subfossil finds than of recent ones. The Heterostropha, which has a 2.5% higher representation among the subfossil finds than among the recent ones, is a group



Fig. 5. Regional division of the European seas according to Simonarson *et al.* (1998).

of mostly tiny specimens which might be more looked for in the geological samples than in the recent bottom samples often used in the more practical work of evaluation benthos introduced by C.G.J. Petersen. However, many of these small species should be considered with the utmost care, with respect to the difficulty of identifying them to species level within subfossil material.

The reason why the Class Scaphopoda has a twice as great a representation within the subfossil material cannot be given, although it is tempting to regard the different palaeoenvironment back in the Late Quaternary as the explanation of the higher frequency. The greater variety of palaeoenvironment and different climate back in time is clearly the reason why the Bivalvia within all subclasses has a higher percentage than in the recent fauna.

However, as an overview, the total subfossil species could be compared to the recent ones arranged also after their climatic affinities, as will be thoroughly discussed in one of the following chapters. With respect to distribution of molluscan species within the North Atlantic – West European realm, four zones may be distinguished, viz.: the Arctic = a, the Subarctic = s, the Boreal = b and the Lusitanian = l (Figs 4, 5).

It appears from the comparison between subfossil species and recent species sorted after climatic affinity (Appendix 1) that the subfossil species have their dominance in the extreme groups, i.e. Arctic = a; Arctic/Subarctic = as; Arctic, Subarctic and Boreal = asb and

Subarctic/Boreal, while the species with a wide tolerance – Arctic, Subarctic, Boreal and Lusitanian = asbl – have a higher representation within the recent fauna.

Also the middle group, which is represented by faunal element from the Subarctic, Boreal and Lusitanian, the Boreal and Lusitanian (which is the most numerous group with 140 subfossil species) has a higher representation in the recent fauna. But the group of purely Lusitanian species has a clearly better representation among the subfossil species, as seen by the percentage figure 6.2% compared to 0.7% for the purely Lusitanian faunal elements among the subfossil and recent faunas respectively.

These observations reveal that the Late Quaternary fauna covers a period of 130 000 years with changing climatic conditions both with colder and warmer periods than at present.

So considering the totals of subfossil and recent species one has to discuss the difference not only quantitatively but qualitatively; because only 184 species are shared between the Late Quaternary and the recent finds, while 63 species have to be considered as particular ones occurring within the Late Quaternary during the Eemian, the Weichselian or the Holocene, in one, two or in all three groups but not the recent one.

Within the Bivalvia, the highest amount of subfossil species (31) found only in the Late Quaternary occur. Such species are also the species which must be focused on in the evaluation of the changing environment through time.

Molluscan finds within the seven regions during the Holocene

The molluscan finds within each region (see Fig. 2) from the Holocene, as appearing mainly from the descriptions accompanying the geological map sheets of Denmark, are presented.

The Bælt Sea area

From the Bælt Sea area the information on the occurrences of molluscs has been taken from the following map sheets: Madsen (1902) and Jessen (1907 (contributions by V. Nordmann), 1935, 1945); V. Milthers (1940) and K. Milthers (1959). Nordmann (1906) has a record of molluscs found in Skælskør Nor (SW Sjælland) and Petersen records from the areas south of Fyn, Storebælt and Lillebælt (1985c, 1989).

Subfossil Holocene species in the Bælt Sea area

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

- Littorina littorea* (Linnaeus 1758)
- Littorina obtusata* (Linnaeus 1758)
- Littorina saxatilis* (Olivi 1792)
- Littorina tenebrosa* (Montagu 1803)
- Lacuna pallidula* (da Costa 1778)
- Lacuna vincta* (Montagu 1803)
- Hydrobia ulvae* (Pennant 1777)
- Hydrobia ventrosa* (Montagu 1803)
- Onoba semicostata* (Montagu 1803)
- Rissoa albella* Lovén 1846
- Rissoa inconspicua* Alder 1844
- Rissoa membranacea* (J. Adams 1800)
- Bittium reticulatum* (da Costa 1778)

Order Heterogastropoda

- Triphora adversa* (Montagu 1803)

Order Neogastropoda

- Hinia reticulata* (Linnaeus 1758)

Subclass Heterobranchia

Order Heterostropha

- Omalogyra atomus* (Phillippi 1841)
- Odostomia conoidea* Winckworth 1932

Subclass Opisthobranchia

Order Anaspidea

- Retusa obtusa* (Montagu 1803)

Retusa truncatula (Bruguière 1792)

Akera bullata Müller 1776

Subclass Pulmonata

Order Basommatophora

Lymnaea peregra (Müller 1774)

Class Bivalvia

Subclass Pteriomorpha

Order Mytiloidea

- Mytilus edulis* Linnaeus 1758
- Modiolula phaseolina* (Phillippi 1844)
- Modiolus modiolus* (Linnaeus 1758)
- Musculus discors* (Linnaeus 1767)

Order Pterioidea

Ostrea edulis Linnaeus 1758

Subclass Heterodonta

Order Veneroidea

- Mysella bidentata* (Montagu 1803)
- Tridonta borealis* Schumacher 1817
- Parvicardium exiguum* (Gmelin 1791)
- Parvicardium ovale* (Sowerby 1840)
- Parvicardium scabrum* (Phillippi 1844)
- Cerastoderma edule* (Linnaeus 1758)
- Spisula subtruncata* (da Costa 1778)
- Angulus tenuis* (da Costa 1778)
- Macoma balthica* (Linnaeus 1758)
- Scrobicularia plana* (da Costa 1778)
- Abra alba* (Wood 1802)
- Arctica islandica* (Linnaeus 1767)
- Paphia aurea* (Gmelin 1791)
- Tapes decussatus* (Linnaeus 1758)
- Venerupis pullastra* (Montagu 1803)

Order Myoidea

- Mya arenaria* Linnaeus 1758
- Mya truncata* Linnaeus 1758
- Corbula gibba* (Olivi 1792)
- Hiatella arctica* (Linnaeus 1758)
- Barnea candida* (Linnaeus 1758)
- Zirfaea crispata* (Linnaeus 1758)

Total for the Holocene Bælt Sea: 47 (19.0%)

The Baltic area

The Baltic area is here restricted to the area east of Darss and south of Øresund at Saltholm, which must be considered the Baltic *sensu stricto* when regarding the present distribution of the marine fauna and also taking into consideration the subfossil Holocene molluscan fauna, as will be demonstrated by a following comparison with the other areas. The main map sheet published is by V. Milthers from 1908 with contributions by V. Nordmann on the Holocene molluscan fauna. The subfossil Holocene fauna has also been studied later in the western part by Petersen (1994b). In the description accompanying the map sheet Bornholm (Grönwall & Milthers 1916) there is no record of a mollusc fauna.

Subfossil Holocene species in the Baltic area

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Littorina littorea (Linnaeus 1758)

Littorina tenebrosa (Montagu 1803)

Hydrobia ulvae (Pennant 1777)

Hydrobia ventrosa (Montagu 1803)

Rissoa albella Lovén 1846

Rissoa inconspicua Alder 1844

Rissoa membranacea (J. Adams 1800)

Bittium reticulatum (da Costa 1778)

Aporrbais pespellicani (Linnaeus 1758)

Order Neogastropoda

Hinia reticulata (Linnaeus 1758)

Subclass Opisthobranchia

Order Anaspidia

Retusa truncatula (Bruguière 1792)

Subclass Pulmonata

Order Basommatophora

Lymnaea peregra (Müller 1774)

Class Bivalvia

Subclass Pteriomorpha

Order Mytiloida

Mytilus edulis Linnaeus 1758

Subclass Heterodonta

Order Veneroida

Parvicardium exiguum (Gmelin 1791)

Cerastoderma edule (Linnaeus 1758)

Cerastoderma glaucum (Poiret 1789)

Macoma balthica (Linnaeus 1758)

Scrobicularia plana (da Costa 1778)

Order Myoida

Corbula gibba (Olivi 1792)

Total for the Holocene Baltic: 19 (7.7%)

The Kattegat area with fjords

The Kattegat area *sensu lato* includes the fjords, i.e. the northern part of the Lillebælt area, Storebælt and Øresund. Therefore the following map sheets are taken within this area:

1. The north-eastern part of Sjælland described by Rørdam (1893), who published a detailed description of the Holocene marine deposits from north-east Sjælland already in 1891 and continued with the description of the map sheet København and Roskilde (1899) where the southernmost parts of the Roskilde Fjord and the Øresund are described in great detail for the marine Holocene part.
2. Furthermore, Rørdam & V. Milthers published the description for the geological map sheet of NW Sjælland in 1900 and Nordmann on the molluscs in Sidinge fjord (Westerby 1933).
3. From the north-western part of Fyn and the island of Samsø by Madsen (1897, 1900) and together with Ussing for the north-eastern part of Fyn (Ussing & Madsen 1897).
4. The map sheet of Fredericia (Nordmann 1958) covers the northern part of the Lillebælt and Vejle Fjord on the eastern coast of Jylland.
5. From the islands of Læsø and Anholt in the Kattegat the description was given by Jessen (1897) and Nordmann (1903a).
6. From Hobro by Nordmann (Jessen 1927).
7. From Mariager Fjord by Nordmann (Ødum 1929).
8. The peninsula of Djursland has been mapped during the last decades, and the description of the Holocene marine molluscan fauna is by Petersen (Pedersen & Petersen 1997) and Petersen (1993).

Subfossil Holocene species in the Kattegat

Class Gastropoda

Subclass Prosobranchia

Order Archaeogastropoda

Theodoxus fluviatilis (Linnaeus 1758)

Order Neotaenioglossa

Littorina littorea (Linnaeus 1758)

Littorina obtusata (Linnaeus 1758)

Littorina saxatilis (Olivi 1792)

Littorina tenebrosa (Montagu 1803)

Lacuna vincta (Montagu 1803)

Hydrobia ulvae (Pennant 1777)

Hydrobia ventrosa (Montagu 1803)

Skeneopsis planorbis (Fabricius 1780)

Onoba semicostata (Montagu 1803)

Onoba vitrea (Montagu 1803)

Rissoa albella Lovén 1846
Rissoa inconspicua Alder 1844
Rissoa membranacea (J. Adams 1800)
Bittium reticulatum (da Costa 1778)
 Order Heterogastropoda
 Triphora adversa (Montagu 1803)
 Order Neogastropoda
 Buccinum undatum Linnaeus 1758
 Hinia reticulata (Linnaeus 1758)
 Subclass Heterobranchia
 Order Heterostropha
 Omalogyra atomus (Phillippi 1841)
 Brachystomia eulimoides Hanley 1844
 Chrysallida spiralis (Montagu 1803)
 Subclass Opisthobranchia
 Order Anaspeida
 Retusa obtusa (Montagu 1803)
 Retusa truncatula (Bruguère 1792)
 Akera bullata Müller 1776
 Class Bivalvia
 Subclass Pteriomorpha
 Order Mytiloidea
 Mytilus edulis Linnaeus 1758
 Musculus discors (Linnaeus 1767)
 Order Pterioidea
 Heteranomia squamula (Linnaeus 1758)
 Ostrea edulis Linnaeus 1758
 Subclass Heterodonta
 Order Veneroidea
 Mysella bidentata (Montagu 1803)
 Acanthocardia echinata (Linnaeus 1758)
 Parvicardium exiguum (Gmelin 1791)
 Parvicardium scabrum (Phillippi 1844)
 Cerastoderma edule (Linnaeus 1758)
 Cerastoderma glaucum (Poiret 1798)
 Macoma balthica (Linnaeus 1758)
 Scrobicularia plana (da Costa 1778)
 Abra alba (Wood 1802)
 Arctica islandica (Linnaeus 1767)
 Paphia aurea (Gmelin 1791)
 Tapes decussatus (Linnaeus 1758)
 Venerupis pullastra (Montagu 1803)
 Order Myoidea
 Mya arenaria Linnaeus 1758
 Mya truncata Linnaeus 1758
 Corbula gibba (Olivi 1792)
 Hiatella rugosa (Linnaeus 1758)

Total for the Holocene Kattogat: 45 (18.2%)

The Limfjord area

From the Limfjord area (western part), excluding the part which falls within Vendsyssel, only one description for a map sheet has been published (Gry 1979). However, the molluscs are recorded in publications by Petersen (1976, 1981, 1985a, 1986a) and in Rasmussen & Petersen (1980). Furthermore, V. Nordmann collected Holocene marine shells from the western Limfjord in 1902–1903 which were further examined by Erna Nordmann and Leifur Símonarson in the sixties as mentioned in Petersen (1976, p. 78). It must be emphasised that C.G.J. Petersen in 1888 discussed the subfossil fauna also from the Limfjord, which was earlier the topic of Collin (1884).

Subfossil Holocene species in the Limfjord

Class Gastropoda
 Subclass Prosobranchia
 Order Archaeogastropoda
 Patella vulgata Linnaeus 1758
 Helcion pellucidum (Linnaeus 1758)
 Iothia fulva (Müller 1776)
 Acmaea tessulata (Müller 1776)
 Acmaea virginea (Müller 1776)
 Margarites helicinus (Phipps 1774)
 Gibbula cineraria (Linnaeus 1758)
 Gibbula tumida (Montagu 1803)
 Skenea serpuloides (Montagu 1808)
 Skenea basistriata (Jeffreys 1877)
 Order Neotaenioglossa
 Littorina littorea (Linnaeus 1758)
 Littorina obtusata (Linnaeus 1758)
 Littorina saxatilis (Olivi 1792)
 Littorina tenebrosa (Montagu 1803)
 Lacuna pallidula (da Costa 1778)
 Lacuna parva (Montagu 1803)
 Lacuna vincta (Montagu 1803)
 Hydrobia ulvae (Pennant 1777)
 Hydrobia ventrosa (Montagu 1803)
 Skeneopsis planorbis (Fabricius 1780)
 Alvania lactea (Michaud 1830)
 Alvania punctura (Montagu 1803)
 Cingula semistriata (Montagu 1808)
 Onoba semicostata (Montagu 1803)
 Onoba proxima (Forbes & Hanley 1850)
 Onoba vitrea (Montagu 1803)
 Rissoa albella Lovén 1846
 Rissoa inconspicua Alder 1844
 Rissoa membranacea (J. Adams 1800)
 Rissoa parva (da Costa 1779)
 Rissoa violacea Desmarest 1814

- Caecum glabrum* (Montagu 1803)
Bittium reticulatum (da Costa 1778)
Turritella communis Risso 1826
Aporrhais pespelicani (Linnaeus 1758)
Lunatia alderi (Forbes 1838)
Lunatia catena (da Costa 1778)
Order Heterogastropoda
Triphora adversa (Montagu 1803)
Cerithiopsis barleei (Jeffreys 1867)
Cerithiopsis tubercularis (Montagu 1803)
Epitonium clathrus (Linnaeus 1758)
Epitonium turtonis (Turton 1819)
Aclis minor (Brown 1827)
Vitreolina philippii (Rayneval & Ponzi 1854)
Order Neogastropoda
Nucella lapillus (Linnaeus 1758)
Buccinum undatum Linnaeus 1758
Hinia incrassata (Ström 1768)
Hinia pygmaea (Lamarck 1822)
Hinia reticulata (Linnaeus 1758)
Oenopota turricola (Montagu 1803)
Raphitoma purpurea (Montagu 1803)
Raphitoma linearis (Montagu 1803)
Subclass Heterobranchia
Order Heterostropha
Omalogyra atomus (Phillippi 1841)
Brachystomia eulimoides Hanley 1844
Odostomia scalaris MacGillivray 1843
Chrysallida decussata (Montagu 1803)
Chrysallida eximia (Jeffreys 1849)
Chrysallida indistincta (Montagu 1808)
Chrysallida obtusa (Brown 1827)
Chrysallida spiralis (Montagu 1803)
Ebala nitidissima (Montagu 1803)
Eulimella laevis (Brown 1827)
Eulimella scillae (Scacchi 1835)
Ondina divisa (J. Adams 1797)
Ondina diaphana (Jeffreys 1848)
Odostomia acuta Jeffreys 1848
Odostomia conoidea Winckworth 1932
Odostomia turrita Hanley 1844
Odostomia albella Lovén 1846
Odostomia plicata (Montagu 1803)
Turbonilla crenata (Brown 1827)
Turbonilla delicata (Monterosato 1874)
Turbonilla lactea (Linnaeus 1758)
Subclass Opisthobranchia
Order Bullomorpha
Acteon tornatilis (Linnaeus 1758)
Cylichna cylindracea (Pennant 1777)
Cylichna alba (Brown 1827)
Philine aperta (Linnaeus 1767)
Philine punctata (Adams 1800)
Order Anaspidea
Diaphana minuta Brown 1827
Retusa obtusa (Montagu 1803)
Retusa truncatula (Bruguière 1792)
Retusa umbilicata (Montagu 1803)
Akera bullata Müller 1776
Class Bivalvia
Subclass Palaeotaxodonta
Order Nuculoida
Nucula nitidosa Winckworth 1930
Nucula nucleus (Linnaeus 1767)
Nuculoma tenuis (Montagu 1808)
Subclass Pteriomorpha
Order Mytiloida
Mytilus edulis Linnaeus 1758
Modiolula phaseolina (Philippi 1844)
Modiolus adriaticus (Lamarck 1819)
Modiolus modiolus (Linnaeus 1758)
Musculus discors (Linnaeus 1767)
Modiolaria tumida (Hanley 1843)
Order Pterioda
Aequipecten opercularis (Linnaeus 1758)
Chlamys varia (Linnaeus 1758)
Delectopecten vitreus (Gmelin 1791)
Palliolum striatum (Müller 1776)
Palliolum tigrinum (Müller 1776)
Pododesmus patelliformis (Linnaeus 1761)
Anomia ephippium Linnaeus 1758
Heteranomia squamula (Linnaeus 1758)
Ostrea edulis Linnaeus 1758
Subclass Heterodonta
Order Veneroida
Lucinoma borealis (Linnaeus 1758)
Thyasira flexuosa (Montagu 1803)
Mysella bidentata (Montagu 1803)
Tellimya ferruginosa (Montagu 1803)
Turtonia minuta (Fabricius 1780)
Lepton nitidum (Turton 1822)
Tridonta borealis Schumacher 1817
Acanthocardia echinata (Linnaeus 1758)
Parvicardium exiguum (Gmelin 1791)
Parvicardium ovale (Sowerby 1840)
Parvicardium scabrum (Philippi 1844)
Cerastoderma edule (Linnaeus 1758)
Cerastoderma glaucum (Poiret 1789)
Mactra stultorum (Linnaeus 1758)
Lutraria lutraria (Linnaeus 1758)
Spisula elliptica (Brown 1827)
Spisula solida (Linnaeus 1758)

Spisula subtruncata (da Costa 1778)
Ensis ensis (Linnaeus 1758)
Phaxas pellucidus (Pennant 1777)
Angulus tenuis (da Costa 1778)
Fabulina fabula (Gmelin 1791)
Macoma balthica (Linnaeus 1758)
Donax vittatus (da Costa 1778)
Gari fervensis (Gmelin 1791)
Scrobicularia plana (da Costa 1778)
Abra alba (Wood 1802)
Abra nitida (Müller 1776)
Abra prismatica (Montagu 1803)
Arctica islandica (Linnaeus 1767)
Chamelea striatula (da Costa 1778)
Clausinella fasciata (da Costa 1778)
Paphia aurea (Gmelin 1791)
Tapes decussatus (Linnaeus 1758)
Timoclea ovata (Pennant 1777)
Venerupis rhomboides (Pennant 1777)
Venerupis pullastra (Montagu 1803)
Mysia undata (Pennant 1777)
 Order Myoida
Mya truncata Linnaeus 1758
Corbula gibba (Olivi 1792)
Hiatella arctica (Linnaeus 1758)
Saxicavella jeffreysi Winckworth 1930
Barnea candida (Linnaeus 1758)
Pholas dactylus Linnaeus 1758
Zirfaea crispata (Linnaeus 1758)
 Subclass Anomalodesmata
 Order Pholadomyoida
Thracia phaseolina (Lamarck 1818)

Total for the Holocene Limfjord: 147 (59.5%)

The North Sea

In the North Sea region the map sheet Blaavands Huk (Fig. 1) forms the southernmost part of what is covered by the present presentation regarding the Holocene deposits, and this area was described by Jessen (1925). Nordmann (*in* Jessen 1925) contributed with the study of the molluscs.

1. In the work by Petersen (1985a) the molluscan fauna in the coastal region – the Aggertange – is recorded.
2. The geological map sheet from Ulfborg was published by Petersen *et al.* (1992a), and the molluscan fauna treated by Petersen, but not yet published, is included.

3. In 1994 the Holocene molluscs from the Jydske Rev were studied and reported in a work for the Danish Coastal Authority (Petersen 1994a), and with minor corrections published in Petersen (1998).

Subfossil Holocene species in the North Sea

Class Gastropoda

Subclass Prosobranchia

Order Archaeogastropoda

Gibbula cineraria (Linnaeus 1758)

Theodoxus fluviatilis (Linnaeus 1758)

Order Neotaenioglossa

Littorina littorea (Linnaeus 1758)

Littorina obtusata (Linnaeus 1758)

Littorina saxatilis (Olivi 1792)

Lacuna pallidula (da Costa 1778)

Lacuna parva (Montagu 1803)

Lacuna vincta (Montagu 1803)

Hydrobia ulvae (Pennant 1777)

Hydrobia ventrosa (Montagu 1803)

Cingula turgida (Jeffreys 1870)

Onoba vitrea (Montagu 1803)

Rissoa albella Lovén 1846

Rissoa inconspicua Alder 1844

Rissoa membranacea (J. Adams 1800)

Rissoa violacea Desmarest 1814

Caecum glabrum (Montagu 1803)

Bittium reticulatum (da Costa 1778)

Turritella communis Risso 1826

Aporrhais pespelicani (Linnaeus 1758)

Lunatia alderi (Forbes 1838)

Lunatia catena (da Costa 1778)

Order Heterogastropoda

Triphora adversa (Montagu 1803)

Epitonium clathrus (Linnaeus 1758)

Aclis ascaris (Turton 1819)

Aclis minor (Brown 1827)

Aclis walleri Jeffreys 1867

Order Neogastropoda

Nucella lapillus (Linnaeus 1758)

Buccinum undatum Linnaeus 1758

Hinia pygmaea (Lamarck 1822)

Hinia reticulata (Linnaeus 1758)

Subclass Heterobranchia

Order Heterostropha

Brachystomia eulimoides Hanley 1844

Chrysallida indistincta (Montagu 1808)

Chrysallida spiralis (Montagu 1803)

Eulimella laevis (Brown 1827)

Ondina diaphana (Jeffreys 1848)

Odostomia conoidea Winckworth 1932

Odostomia albella Lovén 1846
Turbonilla crenata (Brown 1827)
Turbonilla delicata (Monterosato 1874)
Turbonilla lactea (Linnaeus 1758)
 Subclass Opisthobranchia
 Order Bullomorpha
 Acteon tornatilis (Linnaeus 1758)
 Cylichna alba (Brown 1827)
 Order Anaspidea
 Retusa obtusa (Montagu 1803)
 Retusa truncatula (Bruguière 1792)
 Retusa umbilicata (Montagu 1803)
 Class Bivalvia
 Subclass Palaeotaxodonta
 Order Nuculoida
 Nucula nitidosa Winckworth 1930
 Nucula nucleus (Linnaeus 1767)
 Nucula sulcata (Bronn 1831)
 Nuculoma tenuis (Montagu 1808)
 Subclass Pteriomorpha
 Order Mytiloida
 Mytilus edulis Linnaeus 1758
 Musculus discors (Linnaeus 1767)
 Order Pterioidea
 Chlamys varia (Linnaeus 1758)
 Heteranomia squamula (Linnaeus 1758)
 Ostrea edulis Linnaeus 1758
 Subclass Heterodonta
 Order Veneroidea
 Thyasira flexuosa (Montagu 1803)
 Mysella bidentata (Montagu 1803)
 Tellimya ferruginosa (Montagu 1803)
 Lepton nitidum (Turton 1822)
 Acanthocardia echinata (Linnaeus 1758)
 Parvicardium exiguum (Gmelin 1791)
 Parvicardium ovale (Sowerby 1840)
 Parvicardium scabrum (Philippi 1844)
 Parvicardium minimum (Philippi 1836)
 Cerastoderma edule (Linnaeus 1758)
 Mactra stultorum (Linnaeus 1758)
 Spisula elliptica (Brown 1827)
 Spisula solida (Linnaeus 1758)
 Spisula subtruncata (da Costa 1778)
 Ensis ensis (Linnaeus 1758)
 Phaxas pellucidus (Pennant 1777)
 Angulus tenuis (da Costa 1778)
 Fabulina fabula (Gmelin 1791)
 Macoma balthica (Linnaeus 1758)
 Donax vittatus (da Costa 1778)
 Scrobicularia plana (da Costa 1778)
 Abra alba (Wood 1802)

Abra nitida (Müller 1776)
Arctica islandica (Linnaeus 1767)
Chamelea striatula (da Costa 1778)
Clausinella fasciata (da Costa 1778)
Paphia aurea (Gmelin 1791)
Tapes decussatus (Linnaeus 1758)
Timoclea ovata (Pennant 1777)
Venerupis pullastra (Montagu 1803)
Dosinia exoleta (Linnaeus 1758)
Dosinia lincta (Montagu 1803)
 Order Myoidea
 Mya truncata Linnaeus 1758
 Corbula gibba (Olivi 1792)
 Hiatella arctica (Linnaeus 1758)
 Saxicavella jeffreysi Winckworth 1930
 Barnea candida (Linnaeus 1758)
 Zirfaea crispata (Linnaeus 1758)
 Subclass Anomalodesmata
 Order Pholadomyoidea
 Cochlodesma praetenue (Pulteney 1799)
 Thracia phaseolina (Lamarck 1818)

Total for the Holocene North Sea: 95 (38.5%)

The Vendsyssel area

The Vendsyssel area includes the description accompanying the map sheets over the northern, central and southern parts, all by Jessen (1899, 1905), but with a contribution by V. Nordmann, who wrote the part on the Holocene molluscan fauna in the latter publication.

In this description by Nordmann he presents the different faunal communities as discovered in the sub-fossil assemblages. It was Nordmann's intention to continue the work further west into the western Limfjord area, but his first investigations were not used in the systematic geological mapping. They were, however, of great importance for the understanding of the development of the Holocene molluscan fauna (Nordmann 1910, 1918).

In 1928 in connection with the International Congress in Copenhagen a final overview by Nordmann of the Quaternary marine deposits in Denmark was given in the Summary of the Geology of Denmark (Madsen *et al.* 1928). Here Nordmann points to the *Dosinia* layers first described at the beginning of the century from Vendsyssel (Nordmann 1904), with a record of a fauna not found in the older *Tapes* beds originally demonstrated by Petersen (1888).

Later investigations by Lauersen (1937) and Petersen (1990, 1991a, b, 1992) on the *Dosinia* beds at Strandby are also included in the list of Holocene marine molluscs from Vendsyssel.

In Just Pedersen's thesis on Holocene molluscs from 1976 (unpublished), a new fauna element *Donax vittatus* in the *Dosinia* beds is recorded from Frederikshavn.

Subfossil Holocene species in the Vendsyssel

Class Gastropoda

Subclass Prosobranchia

Order Archaeogastropoda

- Helcion pellucidum* (Linnaeus 1758)
- Acmaea virginea* (Müller 1776)
- Gibbula cineraria* (Linnaeus 1758)
- Gibbula tumida* (Montagu 1803)

Order Neotaenioglossa

- Littorina littorea* (Linnaeus 1758)
- Littorina obtusata* (Linnaeus 1758)
- Littorina saxatilis* (Olivi 1792)
- Littorina tenebrosa* (Montagu 1803)
- Lacuna pallidula* (da Costa 1778)
- Lacuna parva* (Montagu 1803)
- Lacuna vincta* (Montagu 1803)
- Hydrobia ulvae* (Pennant 1777)
- Skeneopsis planorbis* (Fabricius 1780)
- Alvania lactea* (Michaud 1830)
- Alvania cimicoidea* (Forbes 1844)
- Alvania punctura* (Montagu 1803)
- Cingula semistriata* (Montagu 1808)
- Onoba semicostata* (Montagu 1803)
- Onoba vitrea* (Montagu 1803)
- Rissoa albella* Lovén 1846
- Rissoa inconspicua* Alder 1844
- Rissoa membranacea* (J. Adams 1800)
- Rissoa parva* (da Costa 1779)
- Rissoa violacea* Desmarest 1814
- Caecum glabrum* (Montagu 1803)
- Bittium reticulatum* (da Costa 1778)
- Turritella communis* Risso 1826
- Aporrhais pespellicani* (Linnaeus 1758)
- Trivia monacha* (da Costa 1778)
- Lunatia alderi* (Forbes 1838)
- Lunatia catena* (da Costa 1778)

Order Heterogastropoda

- Triphora adversa* (Montagu 1803)
- Epitonium clathrus* (Linnaeus 1758)
- Epitonium turtonis* (Turton 1819)
- Vitreolina philippii* (Rayneval & Ponzi 1854)

Order Neogastropoda

- Nucella lapillus* (Linnaeus 1758)
- Buccinum undatum* Linnaeus 1758
- Neptunea antiqua* (Linnaeus 1758)
- Hinia incrassata* (Ström 1768)
- Hinia pygmaea* (Lamarck 1822)
- Hinia reticulata* (Linnaeus 1758)
- Cytherea coarctata* (Forbes 1840)
- Oenopota turricola* (Montagu 1803)
- Raphitoma linearis* (Montagu 1803)

Subclass Heterobranchia

Order Heterostropha

- Omalogyra atomus* (Phillippi 1841)
- Brachystomia eulimoides* Hanley 1844
- Odostomia scalaris* MacGillivray 1843
- Chrysallida indistincta* (Montagu 1808)
- Chrysallida obtusa* (Brown 1827)
- Chrysallida spiralis* (Montagu 1803)
- Ebala nitidissima* (Montagu 1803)
- Eulimella laevis* (Brown 1827)
- Odostomia conoidea* Winckworth 1932
- Odostomia turrita* Hanley 1844
- Odostomia albella* Lovén 1846
- Odostomia plicata* (Montagu 1803)
- Turbonilla lactea* (Linnaeus 1758)

Subclass Opisthobranchia

Order Bullomorpha

- Acteon tornatilis* (Linnaeus 1758)
- Cylichna cylindracea* (Pennant 1777)
- Philine aperta* (Linnaeus 1767)
- Philine punctata* (Adams 1800)

Order Anaspidea

- Diaphana minuta* Brown 1827
- Retusa obtusa* (Montagu 1803)
- Retusa truncatula* (Bruguière 1792)
- Retusa umbilicata* (Montagu 1803)
- Akera bullata* Müller 1776

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

- Nucula nitidosa* Winckworth 1930
- Nucula nucleus* (Linnaeus 1767)

Subclass Pteriomorpha

Order Mytiloida

- Mytilus edulis* Linnaeus 1758
- Modiolula phaseolina* (Phillippi 1844)
- Modiolus adriaticus* (Lamarck 1819)
- Modiolus modiolus* (Linnaeus 1758)
- Musculus discors* (Linnaeus 1767)
- Modiolaria tumida* (Hanley 1843)

Order Pterioidea

- Aequipecten opercularis* (Linnaeus 1758)

Chlamys varia (Linnaeus 1758)
Pecten maximus (Linnaeus 1758)
Pododesmus patelliformis (Linnaeus 1761)
Anomia ephippium Linnaeus 1758
Heteranomia squamula (Linnaeus 1758)
Ostrea edulis Linnaeus 1758
 Subclass Heterodonta
 Order Veneroida
Lucinoma borealis (Linnaeus 1758)
Thyasira flexuosa (Montagu 1803)
Mysella bidentata (Montagu 1803)
Tellimya ferruginosa (Montagu 1803)
Turtonia minuta (Fabricius 1780)
Lepton nitidum (Turton 1822)
Kellia suborbicularis (Montagu 1803)
Acanthocardia echinata (Linnaeus 1758)
Parvicardium exiguum (Gmelin 1791)
Parvicardium ovale (Sowerby 1840)
Parvicardium scabrum (Philippi 1844)
Cerastoderma edule (Linnaeus 1758)
Laevicardium crassum (Gmelin 1791)
Mactra stultorum (Linnaeus 1758)
Lutraria lutraria (Linnaeus 1758)
Spisula elliptica (Brown 1827)
Spisula solida (Linnaeus 1758)
Spisula subtruncata (da Costa 1778)
Ensis ensis (Linnaeus 1758)
Phaxas pellucidus (Pennant 1777)
Angulus tenuis (da Costa 1778)
Fabulina fabula (Gmelin 1791)
Macoma balthica (Linnaeus 1758)
Macoma calcarea (Gmelin 1791)
Donax vittatus (da Costa 1778)
Gari depressa (Pennant 1777)
Gari fervensis (Gmelin 1791)
Scrobicularia plana (da Costa 1778)
Abra alba (Wood 1802)
Abra nitida (Müller 1776)
Abra prismatica (Montagu 1803)
Arctica islandica (Linnaeus 1767)
Chamelea striatula (da Costa 1778)
Clausinella fasciata (da Costa 1778)
Paphia aurea (Gmelin 1791)
Tapes decussatus (Linnaeus 1758)
Timoclea ovata (Pennant 1777)
Venerupis rhomboides (Pennant 1777)
Venerupis pullastra (Montagu 1803)
Dosinia exoleta (Linnaeus 1758)
Dosinia lincta (Montagu 1803)
Mysia undata (Pennant 1777)
 Order Myoida

Mya arenaria Linnaeus 1758
Mya truncata Linnaeus 1758
Corbula gibba (Olivi 1792)
Hiatella arctica (Linnaeus 1758)
Hiatella rugosa (Linnaeus 1758)
Saxicavella jeffreysi Winckworth 1930
Barnea candida (Linnaeus 1758)
Pholas dactylus Linnaeus 1758
Zirfaea crispata (Linnaeus 1758)
 Subclass Anomalodesmata
 Order Pholadomyoida
Thracia phaseolina (Lamarck 1818)

Total for Holocene Vendsysse: 133 (53.8%)

The Skagen Well area

The hitherto recorded molluscan assemblages from Danish deposits of Late Quaternary age are littoral to sublittoral – mostly – especially from the Holocene. The new information from the Skagen Well containing deeper-water deposits is presented below.

Subfossil Holocene species in the Skagen Well

Class Gastropoda
 Subclass Prosobranchia
 Order Neotaenioglossa
Lacuna pallidula (da Costa 1778)
Hydrobia ulvae (Pennant 1777)
Barleeia unifasciata (Montagu 1803)
Onoba vitrea (Montagu 1803)
Rissoa albella Lovén 1846
Rissoa violacea Desmarest 1814
Bittium reticulatum (da Costa 1778)
Turritella communis Risso 1826
Aporrhais pespellicani (Linnaeus 1758)
Lunatia alderi (Forbes 1838)
Lunatia montagui (Forbes 1838)
 Order Heterogastropoda
Epitonium trevelyanum (Johnston 1841)
Aclis minor (Brown 1827)
Polygireulima sinuosa (Sacco 1836)
Vitreolina collensi (Sykes 1903)
Vitreolina philippii (Rayneval & Ponzi 1854)
Graphis albida (Kanmacher 1798)
Melanella lubrica (Monterosato 1891)
Melanella alba (da Costa 1778)
Hemiaclis ventrosa (Jeffreys MS Fricke 1874)
 Order Neogastropoda
Buccinum undatum Linnaeus 1758

- Hinia pygmaea* (Lamarck 1822)
Hinia reticulata (Linnaeus 1758)
Oenopota turricola (Montagu 1803)
Mangelia brachystoma (Philippi 1844)
- Subclass Heterobranchia
- Order Heterostropha
- Chrysallida decussata* (Montagu 1803)
Eulimella scillae (Scacchi 1835)
Odostomia conoidea Winckworth 1932
Odostomia umbilicaris (Malm 1863)
Turbonilla delicata (Monterosato 1874)
Turbonilla sinuosa (Jeffreys 1884)
- Subclass Opisthobranchia
- Order Bullomorpha
- Cylichna alba* (Brown 1827)
- Order Anaspidea
- Retusa truncatula* (Bruguière 1792)
Retusa umbilicata (Montagu 1803)
- Class Bivalvia
- Subclass Palaeotaxodonta
- Order Nuculoida
- Nucula nitidosa* Winckworth 1930
Nucula nucleus (Linnaeus 1767)
Nuculana minuta (Müller 1776)
- Subclass Pteriomorpha
- Order Mytiloida
- Mytilus edulis* Linnaeus 1758
Musculus discors (Linnaeus 1767)
- Order Pterioidea
- Chlamys varia* (Linnaeus 1758)
Heteranomia squamula (Linnaeus 1758)
Ostrea edulis Linnaeus 1758
- Subclass Heterodonta
- Order Veneroida
- Thyasira flexuosa* (Montagu 1803)
Mysella bidentata (Montagu 1803)
Tellimya ferruginosa (Montagu 1803)
Turtonia minuta (Fabricius 1780)
Acanthocardia echinata (Linnaeus 1758)
Parvicardium minimum (Philippi 1836)
Mactra stultorum (Linnaeus 1758)
Spisula subtruncata (da Costa 1778)
Phaxas pellucidus (Pennant 1777)
Angulus tenuis (da Costa 1778)
Fabulina fabula (Gmelin 1791)
Tellina pygmaea (Lovén 1846)
Donax vittatus (da Costa 1778)
Gari fervensis (Gmelin 1791)
Abra alba (Wood 1802)
Abra nitida (Müller 1776)
Abra prismatica (Montagu 1803)
Arctica islandica (Linnaeus 1767)
Chamelea striatula (da Costa 1778)
Timoclea ovata (Pennant 1777)
- Order Myoida
- Mya arenaria* Linnaeus 1758
Corbula gibba (Olivi 1792)
Hiatella arctica (Linnaeus 1758)
Saxicavella jeffreysi Winckworth 1930
Barnea candida (Linnaeus 1758)
Pholas dactylus Linnaeus 1758
- Subclass Anomalodesmata
- Order Pholadomyoida
- Lyonsia norvegica* (Gmelin 1791)
Cochlodesma praetenue (Pulteney 1799)
Thracia phaseolina (Lamarck 1818)
- Total for Holocene Skagen Well: 71 (28.7%)

The Danish Late Quaternary marine molluscs

The record of shell-bearing Danish Late Quaternary marine molluscs has been established on the basis of finds made during the systematic geological mapping since 1888, as presented in the publications from the Geological Survey of Denmark, mainly in the I. Række covering the descriptions for the map sheets. Furthermore, special papers on Holocene and Late Pleistocene marine molluscs have been included. Most of them have been listed in one of the preceding chapters on works on Danish sites with marine sediments.

1. The Bælt Sea area
2. The Baltic Sea area
3. The Kattegat area with fjords
4. The Limfjord area
5. The North Sea coastal area
6. The Vendsyssel area
7. The Skagen area

The regions are figured on the map (Fig. 2) and follow the outline of the geological map sheets except the Skagen area. It should be especially noted that the southern limit during the Holocene of the North Sea coastal region is at Blåvands Huk. Although this area from Varde to the German border has been mapped, no descriptions have been published. However, studies of the Eemian from this region have been published and will be commented upon when presenting the Eemian records from the above-mentioned areas.

The Bælt Sea area has been taken as the region between the Kattegat region and the Baltic, here following Ekman (1953) saying that the boundary between the Bælt Sea and the Baltic proper is the threshold between Gedser and Darss and the southern end of the Øresund, see Fig. 1.

The reason for including the Øresund north of Saltholm (northern and middle Øresund *sensu* Jensen & Knudsen 1995) in the Kattegat region is that regarding the water from the Baltic the Øresund is a sound – a passage – for the brackish water flowing north, but regarding the salt-water from the Kattegat, the Øresund is a fjord down to the threshold between Amager and Limhamn, to quote Thorson (1944a, p. 42).

The subfossil shell-bearing molluscs are presented on the background of the annotated check list of recent marine molluscs of Danish waters by Jensen &

Knudsen (1995). Furthermore, general information has been taken from Jensen & Spärck (1934), Lemche (1948), Nordsieck (1968, 1969), Fretter & Graham (1976–1978, 1980–1982, 1984), Fretter *et al.* (1986) and Poppe & Goto (1991, 1993) (which will not be quoted throughout the text, listing the many species and their environment).

Only the synonyms mentioned in texts on Danish molluscan finds are included. A list of these synonyms is found heading the Index of species.

The investigations carried out by scientists in the northern Atlantic have given a good base for the evaluation of the Danish Late Quaternary molluscan fauna. These studies have been published mainly in papers on the Zoology of East Greenland, The Godthaab Expedition 1928, the Zoology of Iceland, and the Zoology of the Faeroes. However, the Zoology of Greenland has been supplemented by contributions from Macpherson (1971), Lubinsky (1980), the *6. og 7. Thule Expedition til Sydøstgrønland 1931–33* under the leadership of Knud Rasmussen and the *Trearssekspejitionen til Christian den X's Land 1931–34* under the leadership of Lauge Koch.

In the two last-mentioned contributions, especially the animal ecology and the Arctic communities have been treated, which form a very important part in the discussion of the Danish Late Quaternary molluscan assemblages. The following publications on molluscs can be mentioned:

1. From Greenland: Spärck (1933), Thorson (1933, 1944b, 1951), Thorson & Ussing (1934), Madsen (1936), Bertelsen (1937), Lemche (1941a, b), Ockelmann (1958), Kramp (1961, 1963).
2. From Iceland: Spärck (1937), Lemche (1938), Thorson (1941), Knudsen (1949a, b), Madsen (1949).
3. From the Faeroes: Lemche (1928), Thorson & Spärck (1928), Spärck & Thorson (1931), Petersen (1968), Knudsen (1970).

As to the community concept as worked out by C.G.J. Petersen, references have already been given to Petersen & Jensen (1911), Petersen (1913, 1914, 1915, 1918), and Thorson (1957). The regional division of the Northern European seas in to Arctic, Subarctic, Boreal and Lusitanian is from the zoogeographical division of the

northern European seas as given by Feyling-Hanssen (1955, fig. 5) and Símonarson *et al.* (1998), as seen on Figs 4 and 5 respectively.

The molluscan genera and species are presented in groups within Class, Subclass and Order mainly following the presentation of recent marine molluscs of Danish waters as given by Jensen & Knudsen (1995). When there is no subfossil record at hand the information is taken from the recent data as given by Poppe & Goto (1991, 1993), Jensen & Knudsen (1995) and others as listed previously. To facilitate the use of the index of all molluscan species, a list of synonyms is given as mentioned earlier including the species mentioned in Danish mollusc literature.

Class Polyplacophora

Order Neoloricata

Among the seven species recorded in the recent Danish fauna only one, *Tonicella marmorea*, has been found subfossil in the Vendsyssel area from the Younger Weichselian deposits. It is a circumBoreal species which in Europe is known from northern Scandinavia south to Denmark and recorded from around Iceland (Knudsen 1949a, b) down to Ireland (Poppe & Goto 1991). It is common in Danish waters, being known from the central part of the Kattegat and the Øresund region (Muus 1959), e.g. Subarctic–Boreal–Lusitanian species.

Habitat. Common in shallow water of less than 20 m, otherwise recorded from 0–183 m (Muus 1959).

The lack of information on subfossil finds may reflect difficulty in determination when the species is found in the subfossil state of preservation with the shell parts apart. Polyplacophora do occur as seen from the Skagen Well where finds have been recognised at the 70.10–70.30 m and the 37.0–37.25 m levels, viz. during the Subboreal and the Subatlantic respectively.

Among the other – only recent – finds of Polyplacophora, *Leptochiton asellus* is widely found from the Arctic to the Lusitanian. *Hanleya hanleyi*, *Ischnochiton albus* and the above-mentioned *Tonicella marmorea* are all found in the Subarctic, Boreal and Lusitanian regions. The last three species, *Callochiton septemvalvis*, *Lepidochitona cinereus* and *Tonicella rubra*, are all restricted to the Boreal–Lusitanian region.

Fig. 6. *Scissurella crispata* Fleming 1828. Anholt II, 78.06–78.09 m b.s. × 20. MGUH 25316.



Class Gastropoda

Subclass Prosobranchia

Order Archaeogastropoda

***Scissurella crispata* Fleming 1828**

Fig. 6

Distribution. W Greenland, S and W Iceland, Spitsbergen, Norway north of Lofoten, and south to the Mediterranean.

Occurrence. The Subarctic (not in true Arctic water), Boreal and Lusitanian regions (according to Thorson 1941).

Habitat. In the waters around Iceland (Thorson 1941, p. 4), the living specimens have often been found at depths greater than 500 m on clay bottom. However, Poppe & Goto (1991, p. 64) write that the species lives on stones, shelly sand and clay bottoms between 15 and 600 m. Fretter & Graham (1976, pp. 2–4) stated that the species is always sublittoral, even in the extreme northerly limits of its range, and occurs from 8–2000 m. It is not recorded from Danish waters although Fretter & Graham mentioned it from the Norwegian and Swedish coasts of the Skagerrak.

Only subfossil finds. During the Eemian in the Kattegat region.

***Patella vulgata* Linnaeus 1758**

Distribution. Faeroes, Norway off the Lofoten islands, and south to the Straits of Gibraltar (Thorson 1941).

Occurrence. Boreal–Lusitanian.

Habitat. Intertidal, rocky shores or man-made hard substrates. However, it also occurs with seaweed. Only one recent individual has been found at Løkken, while empty shells are often found on the Skagerrak coast (Knudsen 1993).

Subfossil finds. The Limfjord region, Holocene, in a 'køkkenmødding' (kitchen midden) at Bulbjerg (Petersen 1888).

***Helcion pellucidum* (Linnaeus 1758)**

Distribution. West and South Iceland, northern Norway north of Lofoten, and south to Portugal (Thorson 1941). Also found in the Øresund, but absent from the Baltic and the Limfjord.

Occurrence. Boreal and Lusitanian.

Habitat. Lives on seaweeds at depths from 0 to 27 m. Petersen (1888) points to this habitat as a reason why it is rarely found.

Subfossil finds. The Limfjord region and Vendsyssel, Holocene.

***Lepeta caeca* (Müller 1776)**

Distribution. From northern Scandinavia, N and S Iceland and Spitsbergen (Thorson 1941) south to Scotland. It is not present in the Baltic, the North Sea and the Channel, but occurs in the Azores. This species, according to Poppe & Goto (1991), prefers cold temperatures and lives at greater depths in the southern part of its range. In this way it exemplifies the tropical submerge. It is present in the Øresund region and has been reported from single finds in the Kattegat (Petersen 1888).

Occurrence. Subarctic and Boreal.

Subfossil finds. None.

***Iotbia fulva* (Müller 1776)**

Distribution. Northern Scandinavia and S and W Iceland south to the Irish Sea, and like *Lepeta caeca* in deep water off the Azores. It is found in the Øresund region, but with rare and single finds in the Kattegat (Petersen 1888).

Occurrence. Boreal and Lusitanian.

Habitat. Offshore between 5 and 600 m on hard substrates like *Lepeta caeca*.

Subfossil finds. The Limfjord region, Holocene.

***Acmaea tessulata* (Müller 1776)**

Distribution. East Greenland, around Iceland (Thorson 1941) and in Scandinavia according to Petersen (1888). The Limfjord (Petersen 1986a). Common in the Øresund, but absent in the Baltic. Extends southwards to the north of the British Isles and Northern Ireland.

Occurrence. Arctic, Subarctic, Boreal, and Lusitanian.

Habitat. Lower part of the intertidal zone. In the south connected with *Zostera*.

Subfossil finds. The Limfjord region, Holocene.

***Acmaea virginea* (Müller 1776)**

Distribution. Northern Scandinavia and around Iceland (Thorson 1941), south to the Cape Verde Islands. Common in the Kattegat and Øresund, but not found in the Baltic.

Occurrence. Subarctic, Boreal, Lusitanian.

Habitat. On hard substrate at depths from 0 to 100 m.

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene.

***Emarginula fissura* (Linnaeus 1758)**

Distribution. Scandinavia and south to the Mediterranean, according to Petersen (1888) taken alive from the Øresund, dead shells in the northern Kattegat.

Occurrence. Boreal and Lusitanian.

Habitat. From the low tide line to a depth of 700 m on hard substrate.

Subfossil finds. None.

***Puncturella noachina* (Linnaeus 1771)**

Distribution. Spitsbergen and around Iceland (Thorson 1941), Scandinavia south to Portugal. Also found in the Skagerrak and Kattegat including Øresund.

Occurrence. Arctic, Subarctic, Boreal and Lusitanian.

Habitat. Between 10 and 200 m on rock and stones.

Subfossil finds. None.

***Margarites belicinus* (Phipps 1774)**

Distribution. From northern Scandinavia, Spitsbergen and around Iceland (Thorson 1951) south to the British Isles. A few records from the Skagerrak and Kattegat.

Occurrence. Arctic, Subarctic, Boreal and northern part of the Lusitanian region.

Habitat. From the intertidal zone to 400 m deep on seaweeds and under stones.

Subfossil finds. The Limfjord region, Holocene.

***Gibbula cineraria* (Linnaeus 1758)**

Distribution. From northern Scandinavia north of Lofoten, and W and S Iceland (Thorson 1941) south to Morocco. According to Petersen (1888) known from the Kattegat including Øresund, the Bælt Sea and the Limfjord area.

Occurrence. Boreal–Lusitanian.

Habitat. Intertidal to 130 m deep on rocks and seaweeds.

Subfossil finds. The Limfjord, the North Sea and Vendsyssel, Holocene. Recorded from the North Sea during the Eemian.

***Gibbula tumida* (Montagu 1803)**

Distribution. From northern Norway north of Lofoten, and S and W Iceland (Thorson 1941), south to Spain. Known from the Kattegat, including the Øresund, but not so common as *Gibbula cineraria*. The species does not occur in the Limfjord (Petersen 1986a, table 1).

Occurrence. Boreal–Lusitanian.

Habitat. On gravel bottoms from below low tide to depths of 1200 m.

Subfossil finds. The Limfjord and Vendsyssel area, Holocene.

***Jujubinus clelandi* (W. Wood 1828)**

Distribution. From the Lofoten Islands south into the Mediterranean. Found in the Kattegat region, including the Øresund, but rare.

Occurrence. Boreal–Lusitanian.

Habitat. On various types of bottom from depths of 35 m to 800 m.

Subfossil finds. None.

***Calliostoma formosa* (Mighels 1842)**

Distribution. Along the Norwegian coast, W and S Iceland (Thorson 1941), and south to the British Isles but not on the west side.

Occurrence. Boreal.

Habitat. Dredged at depths between 19 and 1000 m – the species is never littoral.

Subfossil finds. None.

***Calliostoma zizyphinum* (Linnaeus 1758)**

Distribution. From the Lofoten islands south to the Azores. In the Skagerrak.

Occurrence. Boreal–Lusitanian.

Habitat. Intertidal to 300 m deep – lives on all types of bottoms.

Subfossil finds. None.

***Skenea serpuloides* (Montagu 1808)**

Distribution. From the British Isles south to Portugal and into the Mediterranean.

Occurrence. Lusitanian.

Habitat. From the intertidal zone down to 50 m deep. Intertidal on weeds and stones, and sublittoral dredged from shelly and gravelly sand.

Only subfossil finds. The Limfjord area, Holocene.

***Skenea basistriata* (Jeffreys 1877)**

Distribution. Atlantic coast of Europe, but not in the North Sea and the Baltic.

Occurrence. Boreal–Lusitanian.

Habitat. On soft bottom – never in shallow water or littoral sequences, deep water 90–2400 m.

Subfossil finds. The Limfjord region, Holocene.

***Theodoxus fluviatilis* (Linnaeus 1758)**

Distribution. From the Pyrenees and the British Isles east towards the Caucasus, including northern Sweden and the coasts of Finland.

Occurrence. Lusitanian–Boreal.

Habitat. The primary habitat of this species is rivers. In the Baltic Sea the form *littoralis* becomes a common littoral animal (Fretter & Graham 1978a, p. 105). The species is also recorded from the fjords bordering the Kattegat region today.

Subfossil finds. The Kattegat and Limfjord regions, Holocene.

The Archaeogastropoda are represented by 16 species in the recent marine fauna, out of which ten have been recorded from the past. Only two species, *Skenea serpuloides* and *Scissurella crispata*, are not found in the

recent fauna. There is a total number of subfossil finds among the Archaeogastropoda of 12 species, with two from the Eemian and ten from the Holocene.

Order Mesogastropoda

***Littorina littorea* (Linnaeus 1758)**

Distribution. From northern Norway north of Lofoten, and south to Spain. Common along all the Danish coasts but not in the Baltic and on the more exposed sandy coasts (Petersen 1888). Recent records from the Baltic as far as Bornholm (Fretter & Graham 1980, p. 256).

Occurrence. Boreal and Lusitanian.

Habitat. The intertidal zone, abundant on rocky shores, might be found to a depth of 60 m.

Subfossil finds. The Bælt Sea, Baltic, Kattegat, Limfjord, the North Sea and Vendsyssel regions, Holocene. The Bælt Sea, Baltic, Kattegat and North Sea regions in the Eemian.

***Melaraphe (Littorina) neritoides* (Linnaeus 1758)**

Distribution. From western Norway south to Morocco and the Mediterranean. A scattered occurrence in the Kattegat (Jensen & Knudsen 1995). The species is recorded from the Limfjord (Petersen 1986a).

Occurrence. Boreal and Lusitanian.

Habitat. Lives high on the rocky shores (splash zone).

Subfossil finds. None.

***Littorina mariae* Sacchi & Rastelli 1966**

Distribution. From northern Scandinavia south to the Mediterranean, extending through the Kattegat into the Bælt Sea.

Occurrence. The Boreal and Lusitanian.

Habitat. In the tidal zone on weeds.

Subfossil finds. None. (The species may have been confused with *Littorina obtusata*.)

***Littorina obtusata* (Linnaeus 1758)**

Distribution. W Greenland, S and W Iceland (Thorson 1941), northern Scandinavia north of Lofoten, and south to the Mediterranean. The species extends through the Limfjord and Kattegat into the Bælt Sea (Fretter & Graham 1980).

Occurrence. Subarctic, Boreal and Lusitanian.

Habitat. Intertidal, lives on weeds.

Subfossil finds. The Bælt Sea, Kattegat, Limfjord, North Sea and Vendsyssel regions, Holocene. During the Eemian recorded from the North Sea.

***Littorina saxatilis* (Olivier 1792)**

Distribution. From Greenland, Spitsbergen, around Iceland and the Atlantic coasts of Europe. Common in the fjords bordering the Kattegat, including the Limfjord (Petersen 1986a).

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian.

Habitat. Intertidal.

Subfossil finds. The Bælt Sea, Kattegat, Limfjord, North Sea and Vendsyssel regions, Holocene. The North Sea during the Eemian, and the Vendsyssel area in the Late Weichselian.

***Littorina tenebrosa* (Montagu 1803)**

Distribution. Off southern Iceland and the Atlantic coasts of Europe. The species is found in the Limfjord, and penetrates also into the Baltic, with finds off Møn and Stevns (Petersen 1888).

Occurrence. The Boreal and Lusitanian.

Habitat. Intertidal.

Subfossil finds. The Bælt Sea, Baltic, Kattegat, Limfjord and Vendsyssel regions, Holocene.

***Lacuna pallidula* (da Costa 1778)**

Fig. 7a, b

Distribution. From Spitsbergen, around Iceland and along the Atlantic coast down to the Gulf of Biscay. Enters the Danish waters, including the Limfjord, the Øresund and the Bælt Sea.

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian.

Habitat. Intertidal to 70 m deep on weeds.

Subfossil finds. The Bælt Sea, Limfjord, North Sea and Vendsyssel regions, Holocene. In the Skagen Well from the Subatlantic.

***Lacuna crassior* (Montagu 1803)**

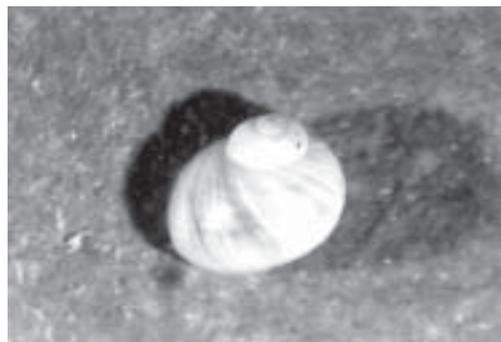
Distribution. From the Arctic Seas to the British Isles. Only records from the North Sea and from the NW coast of Sweden.

Occurrence. The Arctic, Subarctic and Boreal.

Habitat. Sublittoral to 90 m deep on soft bottoms with stones and shells (Fretter & Graham 1980, p. 248).

Subfossil finds. None.

Fig. 7. **a, b:** *Lacuna pallidula* (da Costa 1778). Skagen 4, 30.8–30.5 m b.s., lab. no. 355,93. × 20. MGUH 25317.



***Lacuna parva* (Montagu 1803)**

Distribution. From Norway off the Lofoten, and south to Spain, found in the Kattegat region with fjords, but few records, and not found in the Limfjord.

Occurrence. Boreal and Lusitanian.

Habitat. Intertidal extending sublittorally to around 50 m as *Lacuna vincta* (Fretter & Graham 1980, p. 250) and living on seaweeds.

Subfossil finds. The Limfjord, North Sea and Vendsyssel regions, Holocene. From the North Sea during the Eemian.

***Lacuna vincta* (Montagu 1803)**

Distribution. From W Greenland around Iceland, Norway and south to Spain. In the Danish waters, including the Limfjord, found into the Bælt Sea (Fretter & Graham 1980).

Occurrence. Subarctic, Boreal and Lusitanian.

Habitat. Intertidal to 60 m deep living on seaweeds.

Subfossil finds. The Bælt Sea, Kattegat, Limfjord, North Sea and Vendsyssel regions, Holocene. In the North Sea region found during the Eemian. In the Vendsyssel area recorded from the Eemian, and also from the Early/Middle and Late Weichselian (Older and Younger Yoldia Sea respectively).

***Hydrobia neglecta* Muus 1963**

Distribution. The British Isles, Ireland and the North Sea.

Occurrence. Boreal and Lusitanian.

Habitat. Shallow-water environments on the soft substratum or the vegetation.

Subfossil finds. None.

***Hydrobia ulvae* (Pennant 1777)**

Fig. 8

Distribution. Norway off Lofoten south to the Mediterranean. In all the Danish waters including the Baltic.

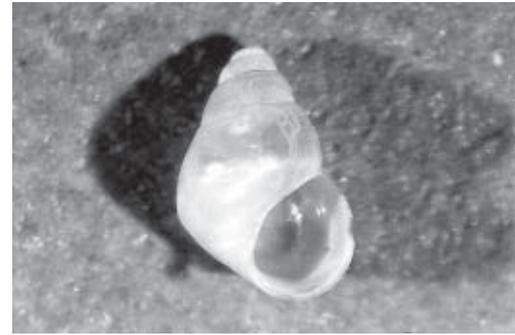


Fig. 8. *Hydrobia ulvae* (Pennant 1777). Skagen 4, 25.0–25.5 m b.s., lab. no. 350,93. × 20. MGUH 25318.

Occurrence. The Boreal and Lusitanian.

Habitat. The intertidal zone, but has been found as deep as 20 m, on soft substrate, most often on intertidal banks of firm mud or muddy sand (Fretter & Graham 1978a, p. 122).

Subfossil finds. The Bælt Sea, Baltic, Kattegat, Limfjord, North Sea and Vendsyssel regions, Holocene. In the Skagen Well from the Subatlantic. During the Eemian recorded from the Bælt Sea, Baltic, Kattegat and the North Sea regions.

***Hydrobia ventrosa* (Montagu 1803)**

Distribution. Norway off Lofoten, south to the Mediterranean. In all the Danish waters including the Baltic.

Occurrence. The Boreal and Lusitanian regions.

Habitat. The intertidal zone, on soft substratum like *Hydrobia ulvae*, but prefers lower salinities (Fretter & Graham 1978a, p. 126). The two species may occur together, so quantitative analyses must be undertaken to designate any changes in the environment (Petersen 1993).

Subfossil finds. The Baltic, Kattegat, Limfjord and the North Sea regions, Holocene.

***Potamopyrgus antipodarum* (Gray 1853)**

Distribution. From Scandinavia to Spain and in Danish waters into the Baltic, a late immigrant according to Jensen & Knudsen (1995).

Occurrence. The Boreal and Lusitanian regions.

Habitats. In all kinds of brackish and freshwater habitats. Much like the distribution of *Hydrobia ventrosa* in brackish waters (Fretter & Graham 1978a, p. 132).

Subfossil finds. None.

***Skeneopsis planorbis* (Fabricius 1780)**

Distribution. W Greenland, around Iceland and Norway, south to the Mediterranean. Known from few places in Danish waters.

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. Intertidal down to a depth of 70 m, lives on seaweeds.

Only subfossil finds. The Limfjord and the Vendsyssel regions, Holocene.

***Barleeia unifasciata* (Montagu 1803)**

Fig. 9

Distribution. From the Shetlands south into the Mediterranean.

Occurrence. The Boreal and Lusitanian regions.

Habitat. Shallow waters, intertidal, lives on seaweeds on rocky shores.

Only subfossil finds. The Skagen Well from the Subatlantic.

***Alvania abyssicola* (Forbes 1850)**

Distribution. From northern Norway to the Mediterranean. The species extends into the Skagerrak and Kattegat, including the Øresund.

Occurrence. The Boreal and Lusitanian regions.

Habitat. On muddy bottom in sublittoral areas at depths of 15–100 m.

Subfossil finds. The Vendsyssel area from the Eemian.



Fig. 9. *Barleeia unifasciata* (Montagu 1803). Skagen 3, 33.90–34.20 m b.s., lab. no. 709,93. × 20. MGUH 25319.

***Alvania jeffreysi* (Waller 1864)**

Distribution. S and W Iceland, Norway, south to the Mediterranean. Found in the Skagerrak, but not in the North Sea.

Occurrence. The Boreal and Lusitanian regions.

Habitat. Always sublittoral from 50 to 600 m on sandy bottom.

Subfossil finds. None.

***Alvania lactea* (Michaud 1830)**

Distribution. From the Channel Islands south to Morocco and the Mediterranean.

Occurrence. The Lusitanian region.

Habitat. Sublittorally under stones and amongst algae.

Only subfossil finds. The Limfjord and Vendsyssel areas, Holocene.

***Alvania cimicoides* (Forbes 1844)**

Distribution. SW and NW Iceland (empty shells), Norway, north of Lofoten, and south to the Mediterranean; probably absent from the Channel and the North Sea.

Occurrence. The Boreal and Lusitanian regions.

Habitat. Sublittoral, from the laminarian zone downwards, but mainly in deeper water down to 500 m.

Usually found on soft bottoms (Fretter & Graham 1978b).

Only subfossil finds. The Vendsyssel area, Holocene.

***Alvania punctura* (Montagu 1803)**

Distribution. Norway south of Lofoten (including Lofoten) and south to the Mediterranean. It extends to the Swedish west coast, but is absent from the Øresund, the Baltic, the eastern shores of the North Sea and the eastern basin of the Channel (Fretter & Graham 1978b). However, according to Jensen & Knudsen (1995) *Alvania punctura* is found in the northern and central parts of the Øresund.

Occurrence. The Boreal and Lusitanian regions.

Habitat. Sublittoral to depths of *c.* 100 m, on both finer and coarser substrata.

Subfossil finds. The Limfjord and the Vendsyssel regions, Holocene.

***Alvania cruenta* Odhner 1915**

Distribution. Arctic Canada, West Greenland and Svalbard (Thorson 1951; Macpherson 1971).

Occurrence. The Arctic and Subarctic.

Habitat. From 19 to 234–254 m on mud (Macpherson 1971).

Only subfossil finds. The Early/Middle Weichselian in the Vendsyssel region.

***Alvania jan mayeni* (Friele 1886)**

Distribution. E and W Greenland, Spitsbergen, NE Iceland, and Norway north of Lofoten (Thorson 1941).

Occurrence. The Arctic and Subarctic with Boreal outposts.

Habitat. Off Iceland between 94–442 m in deep on clay with many stones (Thorson 1941).

Only subfossil finds. The Early/Middle Weichselian (Older *Yoldia* Clay) in Vendsyssel.

***Alvania scrobiculata* (Möller 1842)**

Distribution. E and W Greenland, Spitsbergen, N and E Iceland, and Norway north of Lofoten (Thorson 1941).

Occurrence. The Arctic and Subarctic with Boreal outposts.

Habitat. From 22 m at E Greenland to 342 m in the northern Arctic Sea on a bottom of sand and with algae (Thorson 1941).

Only subfossil finds. From the Early/Middle Weichselian (Older *Yoldia* Clay) in Vendsyssel.

***Cingula semistriata* (Montagu 1808)**

Distribution. From Lofoten and south along the West coast of Norway to the Mediterranean (rare in the north). It extends into the Kattegat, but is absent from the eastern shores of the southern North Sea and the Limfjord.

Occurrence. The Boreal and Lusitanian regions.

Habitat. On rocky shores in the intertidal zone and sublittorally to 100 m, fond of silty places (Fretter & Graham 1978b).

Subfossil finds. The Limfjord and the Vendsyssel areas, Holocene.

***Cingula turgida* (Jeffreys 1870)**

Distribution. From Norway north of Lofoten to the south into Kattegat.

Occurrence. The Boreal region.

Habitat. On muddy bottoms down to *c.* 1000 m.

Subfossil finds. The North Sea region, Holocene.

***Obtusella alderi* (Jeffreys 1858)**

Distribution. From Norway to Spain, not on the eastern shores of the North Sea and in the Baltic; however, found in the Kattegat, including the northern part of the Øresund.

Occurrence. The Boreal and Lusitanian regions.

Habitat. Sublittoral to a depth of 60 m amongst algae and on sandy or gravelly bottoms.

Subfossil finds. None.

***Onoba aculeus* (Gould 1841)**

Distribution. From Spitsbergen, W Greenland, around Iceland and along the coast of Norway into the Kattegat, including the Øresund. Also found at localities off Ireland.

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian regions.

Habitat. Found to about 200 m on algae.

Subfossil finds. None.

***Onoba semicostata* (Montagu 1803)**

Distribution. Around Iceland, along the coast of Norway and south to the Mediterranean. Absent from the eastern North Sea coasts, but extends through the Limfjord and Kattegat, including the Øresund, into the Bælt Sea and the most saline parts of the Baltic (Fretter & Graham 1978b).

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. From the intertidal region to depths of 100 m. Found under stones, amongst weeds, mussels and tunicates in shelly gravel, but only where there are quantities of silt (Fretter & Graham 1978b).

Subfossil finds. The Bælt Sea, Kattegat, Limfjord and Vendsyssel regions, Holocene.

***Onoba proxima* (Forbes & Hanley 1850)**

Distribution. From the western coast of Britain south to the Mediterranean.

Occurrence. The Lusitanian region.

Habitat. From 10 to 170 m on bottoms of muddy sand.

Only subfossil finds. The Limfjord region, Holocene.



Fig. 10. *Onoba vitrea* (Montagu 1803). Skagen 3, 67.0–67.25 m b.s., lab. no. 720,93. × 9.6. MGUH 25320.

***Onoba vitrea* (Montagu 1803)**

Fig. 10

Distribution. From Norway off Lofoten and south to the Mediterranean, extends through Skagerrak into the Kattegat, including the Øresund, but absent from the Limfjord.

Occurrence. The Boreal and Lusitanian regions.

Habitat. Muddy bottoms at depths of 10–50 m in the northern parts of its range, but extending to 120 m in the south. Further notes on *Onoba* species in Fretter & Graham (1978b, p. 170).

Subfossil finds. The Kattegat, Limfjord, North Sea, Vendsyssel and Skagen areas, Holocene. In the Skagen Well recorded from the Atlantic, the Subboreal and the Subatlantic. During the Eemian recorded from the North Sea.

***Rissoa albella* Lovén 1846**

Fig. 11

Distribution. From Norway off the Lofoten islands, and south to the Mediterranean, extending into the Limfjord and the Kattegat with the Danish fjords, including the Øresund and the Bælt Sea.

Occurrence. The Boreal and Lusitanian regions.

Habitat. On rocky shores amongst weeds, sublittoral to 15 m. It is tolerant of some brackishness (Fretter & Graham 1978b).

Subfossil finds. The Bælt Sea, Baltic, Kattegat, Limfjord, North Sea, Vendsyssel and Skagen Well from the Sub-

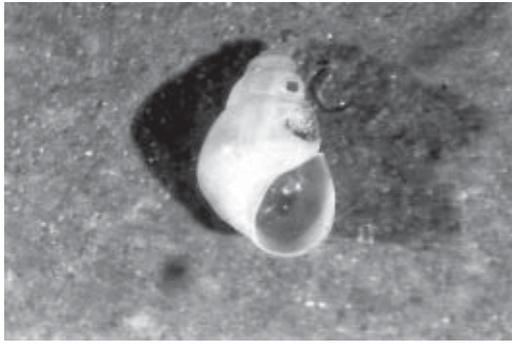


Fig. 11. *Rissoa albella* Lovén 1846. Skagen 4, 30.0–30.5 m b.s., lab. no. 355,93. × 20. MGUH 25321.

atlantic, Holocene. From the Eemian recorded from the North Sea.

***Rissoa inconspicua* Alder 1844**

Distribution. From northern Norway, north of Lofoten, and south to the Mediterranean. Occurring in the Limfjord, Øresund and Bælt Sea.

Occurrence. The Boreal and Lusitanian regions. Fretter & Graham (1978b, p. 200) indicate that the species is found to the Arctic. However, it is not recorded from Iceland and the Faroes but only from Norway north of Lofoten (Thorson 1941, table II, p. 141).

Habitat. Typically sublittoral living on algae, and on sandy gravel to depths of about 100 m. Tolerant of slightly brackish conditions.

Subfossil finds. The Bælt Sea, Baltic, Kattegat, Limfjord, North Sea and Vendsyssel, Holocene. During the Eemian recorded from the Bælt Sea, Kattegat and North Sea regions.

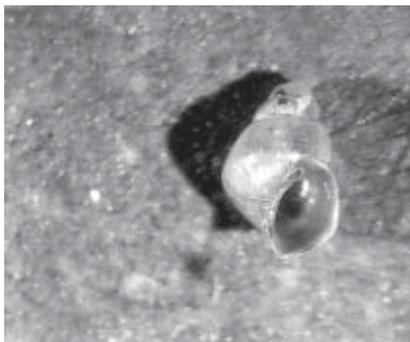


Fig. 12. *Rissoa violacea* Desmarest 1814. Skagen 4, 27.0–27.5 m b.s., lab. no. 352,93. × 20. MGUH 25322.

***Rissoa membranacea* (J. Adams 1800)**

Distribution. From Norway off Lofoten and south to the Canary Islands. Extends into the Limfjord, Kattegat, Bælt Sea and the westernmost part of the Baltic (the Rügen Island).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone sublittorally to about 15 m associated with *Zostera* or on weeds with the same habit, extending into brackish water.

Subfossil finds. The Bælt Sea, Baltic, Kattegat, Limfjord, North Sea and Vendsyssel areas, Holocene. During the Eemian in the Bælt Sea and North Sea regions.

***Rissoa parva* (da Costa 1779)**

Distribution. From Norway, north of Lofoten and the Faeroes, south to the Mediterranean, found in the Limfjord (Petersen 1986a) and the northern part of the Øresund but not in the Baltic according to Fretter & Graham (1978b). However, Bondesen (1975) includes the species in the Baltic, but excludes it from the Bælt Sea. Petersen (1888, p. 93) regarded the species as being limited to the central part of the Kattegat, depending on sufficient salt content – therefore the information of the occurrences in the Baltic given by Bondesen (1975) is surprising.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone to about 25 m on fronds, smaller weeds and under stones. In the Faeroes from the rock pools and the beach to a depth of 20 m (Spärck & Thorson 1931).

Subfossil finds. The Limfjord and Vendsyssel areas, Holocene. During the Eemian recorded from the Bælt Sea, North Sea and Vendsyssel regions.

***Rissoa violacea* Desmarest 1814**

Fig. 12

Distribution. *Rissoa violacea* is not at all recorded from Iceland (Thorson 1941) and the Faroes (Spärck & Thorson 1931) but from Norway off the Lofoten islands and south. Both of the recent subspecies are recorded from the Kattegat, including the Øresund region. Bon-

desen (1975) has *Rissoa violacea sensu lato* from the Skagerrak, the Kattegat and the Limfjord regions.

Occurrence. The Boreal and Lusitanian regions.

Habitat. In the tidal zone to about 50 m on weeds and amongst sandy gravel.

Subfossil finds. The Limfjord, North Sea, Vendsyssel and Skagen areas, Holocene. In Skagen recorded from the Subatlantic. The species occurred during the Eemian in the Kattegat region.

***Assiminea grayana* Fleming 1828**

Distribution. The species is confined to the North Sea coasts. In Danish waters it extends south to Blāvands Huk.

Occurrence. The Boreal region.

Habitat. The species is limited to the upper parts of the salt-marsh areas on the vegetation.

Subfossil finds. None.

***Caecum glabrum* (Montagu 1803)**

Distribution. From Norway off Lofoten south to the Mediterranean. It extends into Kattegat, where it has been reported from the northern part (Jensen & Knudsen 1995), but not from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Sublittorally to about 250 m on sandy and sandy-muddy bottoms.

Subfossil finds. The Limfjord, North Sea and Vendsyssel regions, Holocene. Recorded from the Bælt Sea and the North Sea during the Eemian.

***Tornus exquisitus* (Jeffreys 1883)**

Distribution. Within the Danish waters recorded from northern Kattegat (Jensen & Knudsen 1995), but no record is given by Fretter & Graham (1978b, p. 232) so the species is not treated further.

Habitat. Unknown for this species.

Subfossil finds. None.

Fig. 13. *Bittium reticulatum* (da Costa 1778). GEUS collection. Vejlager XIV, Denmark. × 9.6. MGUH 25323.



***Bittium reticulatum* (da Costa 1778)**

Fig. 13

Distribution. From off Lofoten in Norway south to the Mediterranean. It is found through the Skagerrak, Limfjord, Kattegat, including the Øresund, and into the Bælt Sea, but not from the southern coastal part of the North Sea.

Occurrence. The Boreal and Lusitanian regions.

Habitat. Common in shallow sublittoral water, but recorded to 250 m. Found on soft bottoms in association with weeds.

Subfossil finds. The species is recorded from all regions during the Holocene. From Skagen recorded from the Subatlantic. From the Eemian found in the Bælt Sea, Kattegat, North Sea, and Vendsyssel regions.

***Turritella communis* Risso 1826**

Fig. 14

Distribution. From the Lofoten Islands south to the Mediterranean. The species extends into all the Danish waters as far as the Øresund.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 10 to 200 m depths on soft bottoms.

Subfossil finds. The Limfjord, North Sea, Vendsyssel and Skagen areas, Holocene. In the Skagen area re-

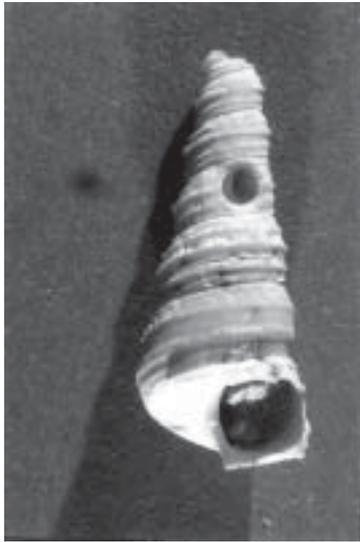


Fig. 14. *Turritella communis* Risso 1826. Skagen 3, 73.10–73.30 m b.s., lab. no. 722,93. × 4.8. MGUH 25324.



Fig. 15. *Aporrbais pespelicani* (Linnaeus 1758). Skagen 3, 0.0–30.0 m b.s. (washed sample). × 4.8. MGUH 25325.

corded from the Subboreal and Subatlantic. During the Eemian recorded from the Baltic, Kattegat, North Sea and Vendsyssel regions.

***Turritella erosa* Couthouy 1838**

Distribution. West and East Greenland (Thorson 1944b, p. 40), Svalbard and on the northern coast of Russia (Macpherson 1971).

Occurrence. The Arctic and subarctic regions.

Habitat. From 10 to 350 m on soft bottoms.

Subfossil finds. Recorded from the Vendsyssel region in Early/Middle Weichselian.

***Aporrbais pespelicani* (Linnaeus 1758)**

Fig. 15

Distribution. On the southern and western part of Iceland, Norway off Lofoten with a questionable occurrence north of Lofoten (Thorson 1941), and south to the Mediterranean. It does not occur off the west coast of Denmark nor in its fjords, except the Limfjord. It extends through the Kattegat, including Øresund (Fretter & Graham 1981, p. 297). Empty shells are found in Kieler Bucht (Arntz *et al.* 1976).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Sublittoral to depths of 180 m on mud, muddy sand and sand.

Subfossil finds. The Baltic, Limfjord, North Sea, Vendsyssel and Skagen areas, Holocene. In the Skagen region from the Subatlantic. During the Eemian recorded from the Bælt Sea, Baltic, North Sea, and Vendsyssel regions.

***Aporrbais serresianus* (Michaud 1828)**

Distribution. From southern and western Iceland, Norway off Lofoten and south to the Mediterranean. According to Fretter & Graham (1981) absent from the Skagerrak and all Danish seas; however, Jensen & Knudsen (1995) note a single record from the central Kattegat.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From Sublittoral (as *Aporrbais pespelicani*) down to 1000 m on finer muds.

Subfossil finds. None.

***Crepidula fornicata* (Linnaeus 1758)**

Distribution. *C. fornicata* is a late immigrant to Europe (first recorded in the British Isles late in the 19th century). The present distribution is from Norway south to Portugal. It reached the Limfjord in 1934. In 1949–50 it was found in the northern part of Kattegat but has not spread further south (Jensen & Knudsen 1995).

Occurrence. The Boreal–Lusitanian regions within its European distribution. *Crepidula fornicata* was transferred by man as seen also for species like *Mya arenaria*.

Habitat. Sublittoral to depths of *c.* 10 m. The animals live in chains, the oldest attached to a substrate which might be an oyster. The species was actually transported to Europe with oysters (Fretter & Graham 1981, p. 311).

Subfossil finds. Obviously none.

***Capulus ungaricus* (Linnaeus 1758)**

Distribution. Empty shells recorded from SW and NW Iceland and living specimens from Norway north of Lofoten south to the Mediterranean. The record from Greenland mentioned in Fretter & Graham (1981) cannot be sustained in the literature (Thorson 1944b, 1951).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Usually sublittorally to 805 m attached to stones or the host animal.

Subfossil finds. None (young date from the North Sea).

***Lamellaria perspicua* (Linnaeus 1758)**

Distribution. SW and NW Iceland, Norway from Lofoten and south to the Mediterranean. It occurs in the Skagerrak but not on the Danish coasts.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone and downwards to depths of 1200 m, especially in the southern parts of its range on rocky shores and under stones.

Subfossil finds. None.

***Velutina plicatilis* (Müller 1776)**

Distribution. From East Greenland and Spitsbergen, southern and western Iceland, Norway north of Lofoten and south to northern Spain. It extends into the Skagerrak, Kattegat and the northern part of the North Sea.

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian regions.

Habitat. From 10 to *c.* 375 m deep on hard bottoms, usually in association with ascidians and hydroids.

Subfossil finds. None.

***Velutina velutina* (Müller 1776)**

Distribution. From Spitsbergen, E and W Greenland, around Iceland and Norway south to the Mediterranean. It extends into the Skagerrak and Kattegat, including Øresund.

Occurrence. Arctic, Subarctic, Boreal and Lusitanian regions.

Habitat. Sublittoral extending to 1000 m on hard bottoms associated with tunicates.

Subfossil finds. None.

***Trivia arctica* (Pulteney 1799)**

Distribution. From Norway off Lofoten and south to the Mediterranean. It extends into the Skagerrak and Kattegat (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Sublittoral to about 100 m, in southerly latitudes to about 1000 m. It is associated with ascidians.

Subfossil finds. None.

***Trivia monacha* (da Costa 1778)**

Distribution. From the British Isles south to the Mediterranean. The recent distribution in the North Sea is questioned, and the species is not recorded from Scandinavia (Fretter & Graham 1981, p. 329).

Occurrence. The Lusitanian region.

Habitat. On rocky shores and under stones associated with ascidians.

Subfossil finds. The Vendsyssel region, Holocene.

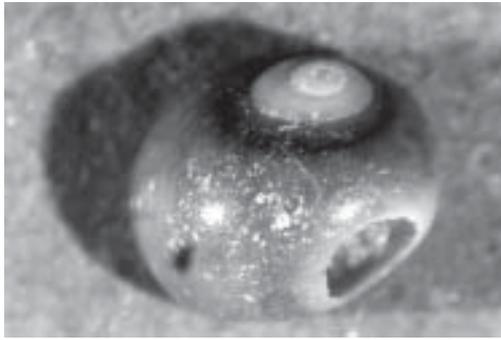


Fig. 16. *Lunatia alderi* (Forbes 1838). Skagen 4, 26.0–26.5 m b.s., lab. no. 351,93. × 20. MGUH 25326.



Fig. 17. *Lunatia montagui* (Forbes 1838). Skagen 4, 20.0–20.5 m b.s., lab. no. 345,93. × 4.8. MGUH 25327.

***Amauropsis islandicus* (Gmelin 1791)**

Distribution. From Spitsbergen, E and W Greenland, around Iceland and Norway. It extends into the Skagerrak and Kattegat, including Øresund, although it is rare there (Jensen & Knudsen 1995).

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. Sublittorally to about 80 m deep on sandy clay bottoms.

Subfossil finds. None (late date from the North Sea).

***Lunatia alderi* (Forbes 1838)**

Fig. 16

Distribution. From southern and western Iceland and Norway off the Lofoten islands south to the Mediterranean (Thorson 1941). It extends into the Skagerrak, Kattegat and Øresund, but the species is not recorded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Sublittoral between 10 and 50 m, extending to 2000 m. Infaunal on sandy shores, clean sand and some admixture of mud. According to Petersen (1888), it is common on mixed bottoms in the Kattegat.

Subfossil finds. The Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen area recorded from the Atlantic, Subboreal and Subatlantic. From the Eemian recorded from the Baltic, Kattegat, North Sea, Vendsyssel and Skagen regions.

***Lunatia catena* (da Costa 1778)**

Distribution. From the Skagerrak and Kattegat, including Øresund but not the Limfjord, south to the Mediterranean (Fretter & Graham 1981, p. 339).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone down to about 125 m on sandy bottoms.

Subfossil finds. The Limfjord, North Sea and Vendsyssel regions, Holocene.

***Lunatia montagui* (Forbes 1838)**

Fig. 17

Distribution. From W and S Iceland, Norway north of the Lofoten islands, and south to the Mediterranean. It occurs in the Skagerrak and Kattegat, including Øresund, however, rare in the Sound as the presiding species according to Jensen & Knudsen (1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 15 to 200 m depth on sandy and muddy bottoms.

Subfossil finds. Recorded from the Skagen Well from the Subatlantic.

***Lunatia pallida* (Broderip & Sowerby 1829)**

Distribution. From Spitsbergen, E and W Greenland, around Iceland and Norway, south to the North Sea, Skagerrak and the Kattegat, including the Øresund.

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. From 10 to 2000 m on clay bottoms – the greatest depths in the most southerly parts of its range (Fretter & Graham 1981). In Greenland waters common in the Arctic *Macoma* community (Thorson 1944b).

Subfossil finds. The Vendsyssel region during the Early/Middle Weichselian and Late Weichselian (the Older and Younger *Yoldia* Sea respectively).

***Natica affinis* (Gmelin 1790)**

Distribution. From Spitsbergen, W and E Greenland, around Iceland and Norway south to the Mediterranean. However, within the Lusitanian region the species lives in deep water (Fretter & Graham 1981, p. 345). The species is recorded from Danish waters (Jensen & Knudsen 1995).

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian regions.

Habitat. From about 4 m depth in high latitudes to well over 2000 m in low ones on sandy, muddy and clay bottoms. As mentioned for other species with a wide geographical distribution this is a ‘tropical submerge’ which is quite common for cold-water animals which in the northern regions inhabit the surface water to occur mainly or exclusively in deeper zones in the southern seas (Ekman 1953, p. 112).

The species is found in the Arctic *Macoma* community (Spärck 1937).

Subfossil finds. Recorded from the Vendsyssel area during the Early/Middle Weichselian (the Older *Yoldia* Sea), and the Late Weichselian (the Younger *Yoldia* Sea).

Order Heterogastropoda

***Tripbora adversa* (Montagu 1803)**

Distribution. From Norway off the Lofoten islands and south to Spain. It extends into the Kattegat, including Øresund and the Bælt Sea, but not recorded from the Limfjord.

Occurrence. The Boreal and Lusitanian regions.

Habitat. Sublittorally to 100 m under stones, algae or associated with sponges.

Subfossil finds. The Bælt Sea, Kattegat, Limfjord, North Sea and Vendsyssel areas, Holocene. Recorded from the Bælt Sea and the North Sea during the Eemian.

***Cerithiella metula* (Lovén 1846)**

Distribution. S and W Iceland, Norway north of Lofoten, and south to the Mediterranean. Recorded from the Danish waters (Jensen & Knudsen 1995), although rare in the Skagerrak and not occurring in the Kattegat (Fretter & Graham 1982, p. 377).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 40 to 400 m depth on soft bottoms.

Subfossil finds. None.

***Cerithiopsis barleei* Jeffreys 1867**

Distribution. According to Fretter & Graham (1982), from SW England south to the Mediterranean. However, the species is recorded from Danish waters, i.e. the Øresund area, although as rare (Jensen & Knudsen 1995), but is not found in the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Sublittorally associated with sponges.

Subfossil finds. The Limfjord region, Holocene.

***Cerithiopsis tubercularis* (Montagu 1803)**

Distribution. From Norway off the Lofoten islands and south to the Mediterranean. Recorded from the Swedish west coast, but not in Danish waters (Fretter & Graham 1982).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone and sublittorally to 100 m. The species is found on sponges.

Only subfossil finds. The Limfjord region, Holocene, and the North Sea during the Eemian.

***Epitonium clatratulum* (Kanmacher 1797)**

Distribution. From Norway and south to the Mediterranean. It extends into the Kattegat, including the Øresund.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 30 to 100 m deep on sandy–muddy bottoms.

Subfossil finds. None.

***Epitonium clatrus* (Linnaeus 1758)**

Distribution. From Norway off the Lofoten islands and south to the Mediterranean. The species extends into the Kattegat and Øresund (Jensen & Knudsen 1995), but does not enter the Danish fjords (Fretter & Graham 1982, p. 387).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Sublittorally from 5 to 70 m on sandy–muddy bottoms.

Subfossil finds. The Limfjord, North Sea and Vendsyssel regions, Holocene. Recorded from the Bælt Sea and the North Sea during the Eemian.

***Epitonium trevelyanum* (Johnston 1841)**

Fig. 18

Distribution. From Norway off the Lofoten islands and south to the Mediterranean. The species extends into the Kattegat, including the Øresund.

Fig. 18. *Epitonium trevelyanum* (Johnston 1841). Skagen 3, 58.5–60.0 m b.s., lab. no. 98,93. × 9.6. MGUH 25328.



Occurrence. The Boreal and Lusitanian regions.

Habitat. From 30 to 200 m depth on sandy–muddy bottoms.

Subfossil finds. The Skagen area, Holocene, recorded from the Subboreal and the Subatlantic.

***Epitonium turtonis* (Turton 1819)**

Distribution. From Norway off the Lofoten islands (Thorson 1941) and south to the Mediterranean. Occurring in the Kattegat (Fretter & Graham 1982) and Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 5 to 20 m deep on sandy–muddy bottoms.

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene.

***Aclis ascaris* (Turton 1819)**

Distribution. From Norway off Lofoten and south to the Mediterranean. The species extends into the Skagerrak and Kattegat, including the Øresund.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 10 to 50 m deep on soft sandy bottoms.

Subfossil finds. The North Sea, Holocene.



Fig. 19. *Aclis minor* (Brown 1827). Skagen 3, 55.1–55.3 m b.s., lab. no. 716,93. × 20. MGUH 25329.

***Aclis minor* (Brown 1827)**

Fig. 19

Distribution. From Norway off the Lofoten islands and south to the Mediterranean. The species is recorded from the southern Kattegat and Øresund.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 15 to 150 m deep on bottoms of sand, muddy sand or gravel.

Subfossil finds. The Limfjord, North Sea and Skagen areas, Holocene; in the Skagen Well recorded from the Atlantic, Subboreal and Subatlantic.

***Aclis walleri* Jeffreys 1867**

Distribution. From Norway off the Lofoten islands and south to the Mediterranean. Recorded from north of Skagen (Petersen 1888) and the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. According to Fretter & Graham (1982), at greater depths than the other *Aclis* ssp. – down to 550 m on soft bottoms.

Subfossil finds. The North Sea, Holocene.

***Eulima bilineata* (Alder 1848)**

Distribution. From Norway north of Lofoten, south to the Mediterranean. In the Danish waters recorded from the southern Kattegat.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 20 to 250 m deep on soft bottoms associated with ophiuroids.

Subfossil finds. None.

***Haliella stenostoma* (Jeffreys 1858)**

Distribution. Off West Greenland, around Iceland, Norway off the Lofoten islands, and south to the Mediterranean.

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. Sublittoral from about 70 to 3000 m on soft bottoms. The species has its main occurrence at rather great depths (Thorson 1941), but is also recorded from Danish waters (Jensen & Knudsen 1995).

Subfossil finds. None.

***Polygireulima sinuosa* (Sacco 1836)**

Fig. 20

Distribution. From the Kattegat and south to the Mediterranean.

Occurrence. The Boreal and Lusitanian regions.

Habitat. Sublittoral from 30 to 150 m on soft bottoms.

Subfossil finds. The Skagen area, Holocene, recorded from the Subatlantic.

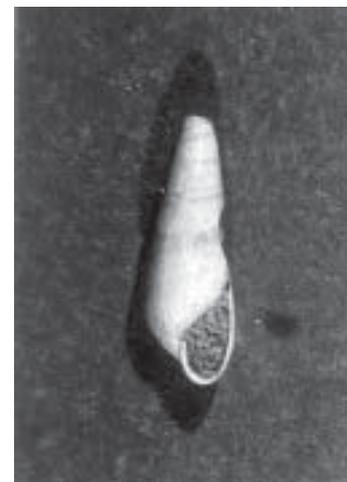


Fig. 20. *Polygireulima sinuosa* (Sacco 1836). Skagen 3, 38.19–38.24 m b.s., core sample K-6. × 9.6. MGUH 25330.



Fig. 21. *Vitreolina collensi* (Sykes 1903). Skagen 3, 70.10–70.30 m b.s., lab. no. 721,93. × 20. MGUH 25331.

***Polygireulima monerosatoi* (Monterosato 1890)**

Distribution. Norway south of the Lofoten islands, and south to the Mediterranean.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 20 to 120 m deep on sandy muddy or gravelly bottoms. However, as Fretter & Graham (1982, p. 421) say: “presumably these animals attack echinoderms like their relatives, but which is not known”.

Subfossil finds. None.

***Vitreolina collensi* (Sykes 1903)**

Fig. 21

Distribution. From the west coast of Britain and Ireland to the Mediterranean.

Occurrence. The Lusitanian region.

Habitat. Sublittorally to 35–40 m on soft bottoms.

Only subfossil finds. The Skagen area, Holocene, recorded from the Subboreal and the Subatlantic.

***Vitreolina philippii* (Reyneval & Ponzi 1854)**

Fig. 22a, b

Distribution. From Norway off the Lofoten islands and south to the Mediterranean. According to Petersen (1888), very common in Danish waters from the Skagerrak, the Kattegat and the Øresund, and the Bælt Sea, but not recorded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the lowest part of the tidal zone to a depth of 200 m on soft bottoms. Fretter & Graham (1982, p. 422) hold it as perhaps the most common local eulimid and like other eulimids an intermittent parasite of echinoderms.

Subfossil finds. The Limfjord, Vendsyssel and Skagen areas, Holocene, recorded from the Subatlantic in the Skagen Well. Occurring in the Eemian in the Vendsyssel region.

***Graphis albida* (Kanmacher 1798)**

Fig. 23

Distribution. From southern Norway south to the Mediterranean. The species has a record from the Limfjord (Petersen 1986a).



Fig. 22. **a, b:** *Vitreolina philippii* (Rayneval & Pouzi 1854). Skagen 4, 21.0–21.5 m b.s., lab. no. 346,93. × 20. MGUH 25332.

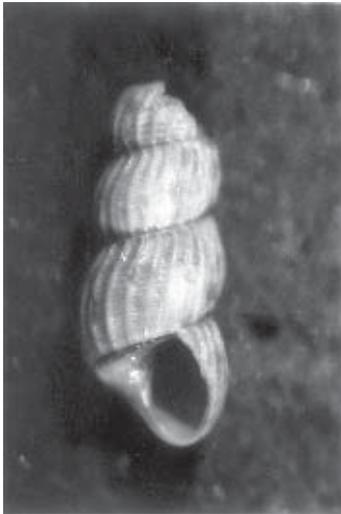


Fig. 23. *Graphis albida* (Kanmacher 1798). Skagen 4, 25.0–25.5 m b.s., lab. no. 350,93. × 40. MGUH 25333.

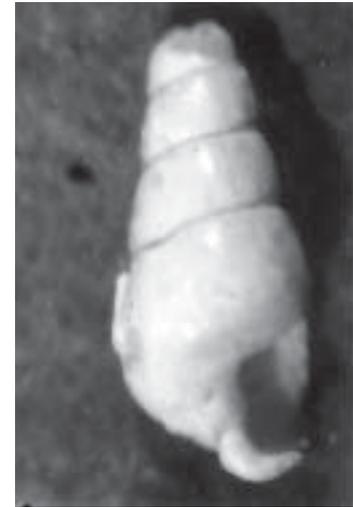


Fig. 25. *Melanella alba* (da Costa 1778). Skagen 3, 74.89–75.00 m b.s., lab. no. 509,93. × 40. MGUH 25335.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From low in the tidal zone to 30 m deep on muddy and sandy bottoms.

Only subfossil finds. The Skagen Well area, Holocene, recorded from the Subatlantic.

***Melanella lubrica* (Monterosato 1891)**

Fig. 24

Distribution. From Norway south to Iberia. The species is recorded from the Danish waters south into the Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 14 to 100 m on soft bottoms of muddy



Fig. 24. *Melanella lubrica* (Monterosato 1891). Skagen 3, 83.73–83.83 m b.s., lab. no. 512,93. × 40. MGUH 25334.

sand and gravel. The species is an intermittent ectoparasite (Fretter & Graham 1982).

Subfossil finds. The Skagen area, Holocene, recorded from the Atlantic and Subatlantic.

***Melanella alba* (da Costa 1778)**

Fig. 25

Distribution. From Norway off the Lofoten islands and south to the Mediterranean.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 16 to 135 m deep on muddy sand and gravel bottoms, an ectoparasite of holothurians.

Only subfossil finds. The Skagen Well area, Holocene, recorded from the Subboreal.

***Hemiacclis ventrosa* (Jeffreys MS Fricke 1874)**

Fig. 26

Distribution. From west and south Iceland, Norway off the Lofoten islands, and south to the Bay of Biscay.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 100 to 300 m deep on soft bottoms.

Only subfossil finds. The Skagen Well area, Holocene, recorded from the Subatlantic.



Fig. 26. *Hemiaclis ventrosa* (Jeffreys MS Fricle 1874). Skagen 4, 30.0–30.5 m b.s., lab. no. 355,93. × 20. MGUH 25336.

***Pelseneeria stylifera* (Turton 1826)**

Distribution. From Norway off the Lofoten islands and south to the Mediterranean. Few recorded from the Skagerrak and Kattegat, including Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. The animals are confined to the surface of regular sea urchins (Fretter & Graham 1982, p. 431).

Subfossil finds. None.

***Enteroxenos oestergreni* Bonnevie 1902**

Distribution. Recorded from Scandinavia, a single Danish record (Jensen & Knudsen 1995).

Occurrence. The Boreal region.

Habitat. A parasite in the holothurian *Stichopus tremulus* (Jensen & Knudsen 1995).

Subfossil finds. None.

Order Neogastropoda

***Nucella lapillus* (Linnaeus 1758)**

Distribution. W Greenland, around Iceland, Norway from north of Lofoten, and south to the Straits of Gibraltar. The species reaches into the Skagerrak, but it

is uncommon in Danish waters (Fretter & Graham 1984). However, it occurs on breakwaters along the North Sea and Skagerrak coasts. There are a few records from the southern Kattegat and Øresund (Jensen & Knudsen 1995).

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. Intertidal on rocky shores and extends, albeit rarely, to depths of 30 to 40 m. It avoids very weedy shores and seems to stand only limited reduction of salinity (Fretter & Graham 1984, p. 445).

Subfossil finds. The Kattegat, Limfjord (exposed towards the Skagerrak), North Sea and Vendsyssel regions, Holocene.

***Boreotrophon clatbratus* (Linnaeus 1767)**

Distribution. Spitsbergen, E and W Greenland, around Iceland, the Faroes and the coast of Norway south to the Skagerrak and Kattegat.

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. From 8 m to over 1000 m on soft bottoms.

Subfossil finds. The Vendsyssel area, Late Weichselian (the Younger *Yoldia* Sea).

***Boreotrophon truncatus* (Ström 1768)**

Distribution. Spitsbergen, E and W Greenland, around Iceland, Norway south to the Biscay. The species extends in to Danish waters south to the Øresund.

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian regions.

Habitat. From the laminarian zone to depths of about 200 m on bottoms of a stony, gravelly or muddy nature.

Subfossil finds. None.

***Ocenebra erinacea* (Linnaeus 1758)**

Distribution. From the southern coasts of Britain south to the Mediterranean. However, the few records from

Danish waters might have been introduced with oysters (Jensen & Knudsen 1995).

Occurrence. The Lusitanian region.

Habitat. Sublittoral to 150 m deep on stony bottoms.

Subfossil finds. None.

***Trophonopsis barvicensis* (Johnston 1825)**

Distribution. W and S Iceland, Norway and south to the British Isles, and further south (France) at greater depths. In Danish waters from the Kattegat, including the Øresund, although rare (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Sublittoral at a few metres' depth at the northern end of its range to 300–400 m at the southern end.

Subfossil finds. None.

***Buccinum undatum* Linnaeus 1758**

Fig. 27

Distribution. Spitsbergen, W Greenland, around Iceland, Norway and south to the Bay of Biscay (Thorson 1944b). The species extends into the Kattegat, Limfjord, and the Bælt Sea with the Mecklenburger Bucht as the easternmost position.



Fig. 27. *Buccinum undatum* Linnaeus 1758. GEUS collection. Limfjord, Denmark. Height 70 mm. MGUH 25337.

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. Sublittorally to about 1200 m deep usually on soft bottoms.

Subfossil finds. The Kattegat, Limfjord, North Sea, Vendsyssel and Skagen areas, Holocene, recorded as a fragment from the Skagen Well from the Subatlantic. During the Eemian in the Kattegat, North Sea, and Vendsyssel regions. From the Vendsyssel area found during the Late Weichselian (the Younger *Yoldia* Sea).

***Buccinum cyaneum* Bruguière 1792**

Distribution. Spitsbergen, W and E Greenland around Iceland and Norway north of Lofoten.

Occurrence. The Arctic, Subarctic and northern part of the Boreal regions.

Habitat. From 0 to 392 m on all sorts of bottoms – sand, clay, stones and algae (Thorson 1944b).

Only subfossil finds. From the Vendsyssel area recorded during the Late Weichselian (the Younger *Yoldia* Sea).

***Colus gracilis* (da Costa 1778)**

Distribution. S and W Iceland (empty shells), Norway off the Lofoten islands and south to Portugal. The species extends into the Kattegat.

Occurrence. The Boreal and Lusitanian regions.

Habitat. Usually from 30 to 800 m deep (less common and deeper in the south).

Subfossil finds. None.

***Colus jeffreysianus* (Fischer 1868)**

Distribution. From Norway south to the Mediterranean. The species extends through the Skagerrak to the Kattegat, including the northern part of the Øresund.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 30 to 2000 m deep on soft bottoms.

Subfossil finds. None.

***Colus sabini* (Gray 1824)**

Distribution. From W Greenland (empty shells) and S and W Iceland, northern North Sea and extending into the Skagerrak (Jensen & Knudsen 1995).

Occurrence. The Boreal region. (A Subarctic extension is not considered, since only empty shells have been found off W Greenland and no occurrences on N and E Iceland (Thorson 1941, 1944b).)

Habitat. From 35 to 1500 m deep on muddy bottoms.

Subfossil finds. None.

***Liomesus ovum* (Turton 1825)**

Distribution. From Greenland, the Faeroes and the coasts of Norway. According to Fretter & Graham (1984, p. 465), the species is not recorded from the Skagerrak or Kattegat; however, Jensen & Knudsen (1995) mentioned this species as occurring in Danish waters. Furthermore, the species *Liomesus ovum* cannot be found in Thorson (1944b), who has *Buccinum ovum* Middendorff, which is not the same according to Fretter & Graham (1962), and the occurrence off the Faeroes cannot be confirmed in Spärck & Thorson (1931).

Occurrence. The Boreal region with only uncertain outposts into the Subarctic and Lusitanian regions.

Habitat. From 70 to 400 m deep on soft bottoms.

Subfossil finds. None.

***Neptunea antiqua* (Linnaeus 1758)**

Distribution. From southern Norway south to the Bay of Biscay. The species extends into the Kattegat, Øresund (Jensen & Knudsen 1995), and the Bælt Sea as far east as Lübecker Bucht. The species has also been recorded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 15 to 1200 m on all kinds of bottom, mainly soft.

Subfossil finds. The Vendsyssel area, Holocene.

***Neptunea despecta* (Linnaeus 1758)**

Distribution. From Spitsbergen, E and W Greenland, around Iceland and the coasts of Norway, south to the seas off Denmark according to Fretter & Graham (1984), but not mentioned by Jensen & Knudsen (1995) in their annotated check list of recent marine molluscs of Danish waters.

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. From 6 to 1400 m on soft bottoms.

Only subfossil finds. The Vendsyssel region during the Late Weichselian (the Younger *Yoldia* Sea).

***Turrisipho moebii* (Dunker & Metzger 1874)**

Distribution. From the coasts of northern and southern Norway and the Faeroes (*Sipho sarsi* in Spärck & Thorson 1931). The species extends into the Skagerrak.

Occurrence. The Boreal region.

Habitat. From 200 m to 1000 m deep on soft bottoms.

Subfossil finds. None.

***Hinia incrassata* (Ström 1768)**

Distribution. S and W Iceland, Norway north of Lofoten, and south to the Mediterranean (Thorson 1941). The species extends into the Kattegat and Øresund, although rare in this place (Jensen & Knudsen 1995), and it has not been found in the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Rocky coasts in the lower part of the tidal zone. Mainly found in the shallow sublittoral, but may extend to about 200 m.

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene. Recorded from the Vendsyssel region during the Eemian.

***Hinia pygmaea* (Lamarck 1822)**

Fig. 28

Distribution. From Norway off the Lofoten islands and



Fig. 28. *Hinia pygmaea* (Lamarck 1822). Skagen 4, 12.0–12.5 m b.s., lab. no. 337,93. × 9.6. MGUH 25338.



Fig. 29. *Hinia reticulata* (Linnaeus 1758). Skagen 3, 55.10–55.30 m b.s., lab. no. 716,93. × 4.8. MGUH 25339.

south to the Mediterranean. It extends into Danish waters such as the Skagerrak, Limfjord and Kattegat and Øresund.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 1 m to about 200 m on sandy bottoms.

Subfossil finds. The Limfjord, North Sea, Vendsyssel and Skagen areas, Holocene. Recorded from the Subatlantic in the Skagen Well material. Found in the Bælt Sea, Kattegat and North Sea regions during the Eemian.

***Hinia reticulata* (Linnaeus 1758)**

Fig. 29

Distribution. From Norway off Lofoten and south to the Mediterranean. In Danish waters within the Limfjord and Kattegat with fjords, the Øresund and the Bælt Sea.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone to about 15 m deep on soft bottoms.

Subfossil finds. The Bælt Sea, Baltic, Kattegat, Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. In the Skagen Well material recorded from the Subatlantic. From the Bælt Sea, Baltic, Kattegat, North Sea and Vendsyssel regions recorded from the Eemian.

***Troschelia bernicensis* (King 1846)**

Distribution. From Norway north of Lofoten and south to the west coast of Scotland and the Dogger Bank. Recorded from Danish waters by Jensen & Knudsen (1995).

Occurrence. The Boreal and Lusitanian (northern part) regions.

Habitat. Lives on the continental shelves and upper slopes, between 90 and 2700 m (Poppe & Goto 1991).

Subfossil finds. None.

***Cytherea coarctata* (Forbes 1840)**

Distribution. From Norway off the Lofoten islands (Thorson 1941: *Mangelia costata*) and south to the Mediterranean. The species is recorded from the Skagerrak and Kattegat where it extends into the Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone to 250 m deep on sandy bottoms.

Subfossil finds. The Vendsyssel area, Holocene. During the Eemian in the North Sea region.

***Oenopota incisula* (Verrill 1882)**

Distribution. The species is known from the Boreal zone of the east coast of North America, and is com-

mon off West Greenland (Posselt & Jensen 1898), but it is not recorded from Iceland or the coasts of the north-east Atlantic (Thorson 1941).

Occurrence. The Arctic, Subarctic, and in North America into the Boreal regions.

Habitat. In the Canadian north-east region the species has been collected from 6–7 to 140 m deep on clay (Macpherson 1971).

Only subfossil finds. From the Vendsyssel region recorded during the Eemian and Early/Middle Weichselian (the Older *Yoldia* clay).

***Oenopota trevelliiana* (Turton 1834)**

Distribution. Spitsbergen, E and W Greenland, around Iceland (Thorson 1941: *Bela trevelliiana* (Turton)), Norway from north of Lofoten, and south to the British Isles. The species extends south to the Kattegat, including Øresund.

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian (northern part) regions.

Habitat. Sublittorally from 25 m to depths over 300 m on fine sand.

Subfossil finds. The Vendsyssel area during the Eemian.

***Oenopota turricola* (Montagu 1803)**

Fig. 30

Distribution. Greenland, Iceland, Faeroes, Norway south to Scotland (Spärck & Thorson 1931). The species extends into the Limfjord and Kattegat (Fretter & Graham 1984) and the Øresund (Jensen & Knudsen 1995).

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. Sublittoral from 20 to 200 m on sandy bottoms.

Subfossil finds. The Limfjord, Vendsyssel and Skagen areas, Holocene. From the Skagen Well recorded from the Subatlantic. Found in the Vendsyssel area from the Late Weichselian (the Younger *Yoldia* Sea).

Fig. 30. *Oenopota turricola* (Montagu 1803). Skagen 4, 21.0–21.5 m b.s., lab. no. 346,93. × 9.6. MGUH 25340.



***Oenopota violacea* (Mighels & Adams 1842)**

Distribution. E and W Greenland, Spitsbergen, around Iceland and south along the coast of Norway, but not reaching the British Isles (Thorson 1941).

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. From 1 m to 761 m on mud and stones.

Only subfossil finds. The Vendsyssel area during the Eemian.

***Bela exarata* G.O. Sars 1878**

Distribution. E and W Greenland, Spitsbergen, around Iceland, the Faeroes, and Norway from north of Lofoten and west of Ireland. The species is also recorded west of Iceland, where it has been found at depths down to 2214 m (Thorson 1941).

Occurrence. The Arctic, Subarctic, Boreal regions with Lusitanian outposts.

Habitat. In the northern part of its range it belongs to the shallow-water species (Norway and E Greenland from 3 m) (Thorson 1941).

Only subfossil finds. From the Eemian in the Vendsyssel area.

***Mangelia attenuata* (Montagu 1803)**

Distribution. From Norway off the Lofoten islands and



Fig. 31. *Mangelia brachystoma* (Philippi 1844). Skagen 3, 58.04–58.25 m b.s., lab. no. 717,93. × 9.6. MGUH 25341.

south to the Mediterranean. The species extends into the Skagerrak and Kattegat, including the Øresund.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 5 to 150 m deep on sand or clay bottoms.

Subfossil finds. None.

***Mangelia brachystoma* (Philippi 1844)**

Fig. 31

Distribution. From Norway off the Lofoten islands and south to the Mediterranean. The species extends into the Skagerrak and Kattegat, including the Øresund.

Occurrence. The Boreal and Lusitanian regions.

Habitat. Sublittorally from 4 m to 60 m deep on bottoms of sand and sandy mud.

Subfossil finds. The Skagen area, Holocene, recorded from the Subatlantic in the Skagen Well cores. During the Eemian found in the Vendsyssel region.

***Mangelia nebula* (Montagu 1803)**

Distribution. Norway off the Lofoten islands and south to the Mediterranean. The species is recorded a few times from the Kattegat and extends into the Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 10 to 50 m deep on sandy bottoms.

Subfossil finds. None.

***Raphitoma purpurea* (Montagu 1803)**

Distribution. From northern Norway off the Lofoten islands south into the Mediterranean.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 10 to 100 m deep on sandy, gravelly and stony bottoms.

Only subfossil finds. The Limfjord region, Holocene.

***Raphitoma asperrima* (Brown 1827)**

Distribution. From the coast of Norway south to the Mediterranean, extending into the Kattegat, including the Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 20 to 100 m deep on sandy bottoms.

Subfossil finds. None.

***Raphitoma leufroyi* (Michaud 1821)**

Distribution. From the coast of Norway off the Lofoten islands and south to the Mediterranean, extending into the Skagerrak and with a few records from the northern Kattegat (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone to 150 m deep on sandy, shelly and stony bottoms.

Subfossil finds. None.

***Raphitoma linearis* (Montagu 1803)**

Distribution. SW and NW Iceland, Norway from north of Lofoten and south to the Mediterranean. The species extends into the Skagerrak and Kattegat and Øresund, although rare (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 10 to 200 m deep on sandy, shelly and stony bottoms.

Subfossil finds. The Limfjord and Vendsyssel area, Holocene. During the Eemian found in the Vendsyssel area (the *Turritella terebra* zone in the Skærumhede sequence).

***Taranis borealis* Bouchet & Warén 1980**

Distribution. So far as known, this species is confined to waters off western Norway and the Skagerrak (Fretter & Graham 1984, p. 548).

Occurrence. The Boreal region.

Habitat. From 150 m to nearly 2000 m deep on soft bottoms.

Subfossil finds. None.

***Taranis moerchi* (Malm 1861)**

Distribution. From Norway north of Lofoten south to the Mediterranean, extending into the Kattegat.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 80 m deep near the northern limits of its range to over 2000 m elsewhere on soft bottoms.

Subfossil finds. None.

***Admete viridula* (Fabricius 1780)**

Distribution. Spitsbergen, E and W Greenland, around Iceland, empty shells from off the Faeroes, Norway from north of the Lofoten islands, and south to the northern borders of the North Sea. Included in the recent Danish fauna (Jensen & Knudsen 1995).

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. From a few metres to depths of 1000 m, the greatest depths in the south of its range (Fretter & Graham 1984, p. 507) on soft bottoms.

Subfossil finds. Recorded from the Early/Middle Weichselian (The *Portlandia arctica* zone in the Skærumhede sequence) in the Vendsyssel region.

**Subclass Heterobranchia
Order Heterostropha**

***Omalogyra atomus* (Philippi 1841)**

Distribution. W Greenland, around Iceland and Norway, south to the Mediterranean. Known from only a few places in Danish waters.

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. From the lower part of the shore to a depth of 20 m, occurring on seaweeds.

Only subfossil finds. The Limfjord region, Holocene.

***Brachystomia carozzai* van Aartsen 1987**

Distribution. From the southern part of Norway (Spärck & Thorson 1931) and south to the Mediterranean. The species extends into the Kattegat and Limfjord. As commented on by Fretter *et al.* (1986, p. 605) and Jensen & Knudsen (1995), the determination of these small snails living ectoparasitically on other marine organisms is still in progress, so the actual situation for the record of subfossil material should be taken with great precaution.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone, where it occurs in crevices, to depths of about 70 m.

Subfossil finds. None.

***Brachystomia eulimoides* Hanley 1844**

Distribution. From Norway off the Lofoten islands and south to the Mediterranean. Recorded from the Limfjord, according to Jensen & Knudsen (1995) the only Danish record, following Fretter *et al.* (1986, p. 602).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Most frequently found on living animals of *Pecten*, *Chlamys*, oysters and *Turritella* to depths of 120 m.

Subfossil finds. The Kattegat, Limfjord, North Sea and

Vendsyssel regions, Holocene. From the North Sea region during the Eemian.

***Odostomia scalaris* MacGillivray 1843**

Distribution. From southern Norway south to the Mediterranean. The species extends into the Limfjord, through the Kattegat, including the Øresund, and the Bælt Sea into the Kiel Bay (Fretter *et al.* 1986, p. 600).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Associated primarily with banks of *Mytilus edulis*, but also recorded from other hosts (Fretter *et al.* 1986, p. 600).

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene. From the Bælt Sea and North Sea during the Eemian.

***Cbrysallida decussata* (Montagu 1803)**

Fig. 32

Distribution. Mainly southern distribution, with the Shetlands as the northernmost post, but recorded from the Øresund (Jensen & Knudsen 1995) and there are older records from east of Scotland (Fretter *et al.* 1986).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 14 to 40 m deep on sandy and shelly bottoms.

Subfossil finds. The Limfjord and Skagen areas, Holocene, in the Skagen Well recorded from the Subatlantic.



Fig. 32. *Cbrysallida decussata* (Montagu 1803). Skagen 4, 15.0–15.5 m b.s., lab. no. 340,93. × 20. MGUH 25342.

***Cbrysallida eximia* (Jeffreys 1849)**

Distribution. SW and NW Iceland, Norway north of Lofoten, and south to western Scotland. There is no record from Danish waters.

Occurrence. The Boreal and Lusitanian (northernmost) region.

Habitat. From 20 m to more than 1000 m, the greater depths in the southern part of its range, on soft gravelly bottoms.

Only subfossil finds. The Limfjord region, Holocene. From the Vendsyssel area during the Eemian.

***Cbrysallida indistincta* (Montagu 1808)**

Distribution. From Norway off the Lofoten islands (Thorson 1941) and south to the Mediterranean. It extends into the Kattegat and Øresund (Jensen & Knudsen 1995), but is not recorded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 7 to 100 m deep on sandy bottoms.

Subfossil finds. The Limfjord, North Sea and Vendsyssel areas, Holocene. Recorded from the North Sea during the Eemian.

***Cbrysallida obtusa* (Brown 1827)**

Distribution. From Norway off the Lofoten islands and south to the Mediterranean. The species extends into the Limfjord and through the Kattegat into the Øresund (Fretter *et al.* 1986, p. 562).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone in rock pools to 90 m deep in stony places, associated with oysters (Fretter *et al.* 1986, p. 562).

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene. From the Bælt Sea and North Sea regions during the Eemian.

***Chrysallida spiralis* (Montagu 1803)**

Distribution. From Norway north of Lofoten and south to the Mediterranean. According to Fretter *et al.* (1986, p. 574), the species extends into the Kattegat and Øresund, but it is absent from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone to about 120 m deep, often abundant in the neighbourhood of tubes of sedentary polychaetes (Fretter *et al.* 1986).

Subfossil finds. The Kattegat, Limfjord, North Sea and Vendsyssel regions, Holocene. The Bælt Sea, Kattegat, and North Sea regions during the Eemian.

***Ebala nitidissima* (Montagu 1803)**

Distribution. From south of Norway to the Mediterranean. Recorded from the Kattegat region with fjords and the Øresund and the Bælt Sea regions as far as Kiel Bay (Fretter *et al.* 1986, p. 630), but absent from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 5 to 50 m deep on muddy sand or shelly bottoms.

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene. From the Bælt Sea and North Sea areas during the Eemian.

***Eulimella laevis* (Brown 1827)**

Distribution. From Norway off the Lofoten islands and south to the Mediterranean. It has not been recorded from Danish waters except the Øresund region (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 20 to 400 m deep on muddy sand.

Subfossil finds. The Limfjord, North Sea and Vendsyssel regions, Holocene.

***Eulimella scillae* (Scacchi 1835)**

Fig. 33

Distribution. From Norway off the Lofoten islands, but empty shells only off SW Iceland (Thorson 1941), and south to the Mediterranean. It extends into the Kattegat along the Swedish west coast (Fretter *et al.* 1986), but occurs in the Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 20 to 400 m deep on muddy sand or sand.

Subfossil finds. The Limfjord and Skagen areas, Holocene, recorded in the Skagen Well from the Atlantic and Subboreal. From the Vendsyssel area found during the Eemian.

***Ondina divisa* (J. Adams 1797)**

Distribution. From S and W Iceland, northern Norway (W Finmarken) (Thorson 1941) and south to the Biscay. The species extends through the Kattegat to the Øresund (Fretter *et al.* 1986, p. 582).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 18 to 200 m deep on sandy and gravelly mud.

Subfossil finds. The Limfjord region, Holocene. From the Vendsyssel area found during the Eemian.



Fig. 33. *Eulimella scillae* (Scacchi 1835). Skagen 3, 82.34–82.50 m b.s., lab. no. 729,93. × 9.6. MGUH 25343.

***Ondina obliqua* (Alder 1884)**

Distribution. According to Fretter *et al.* (1986, p. 586) from southern Scandinavia to Biscay. However, Spärck & Thorson (1931) only mentioned Scotland. Furthermore, only western localities have been reported from the British Isles (Fretter *et al.* 1986), and it is doubtful whether the Danish records actually refer to this species. Therefore, the species is here considered to be Lusitanian and should not be taken as present in the recent Danish fauna, although recorded by Jensen & Knudsen (1995).

Habitat. From 30 to 60 m deep in gravelly or sandy mud.

Subfossil finds. None.

***Ondina diaphana* (Jeffreys 1848)**

Distribution. According to Spärck & Thorson (1931), present from southern Norway and south to the Mediterranean. In Danish waters the Kattegat and the Øresund.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 20 to 90 m deep on soft bottoms.

Subfossil finds. The Limfjord and North Sea regions, Holocene.

***Liostomia clavula* (Lovén 1846)**

Distribution. From southern Norway south to the Mediterranean. Extends through the Kattegat to the Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 30 to 90 m deep on soft bottoms associated with *Pennatula* (Fretter *et al.* 1986, p. 590).

Subfossil finds. None.

***Liostomia afzelii* Warén 1991**

This species, newly established, will not be considered further.

***Odostomia acuta* Jeffreys 1848**

Distribution. From Norway north of Lofoten and south to the Mediterranean. The species is found in the Skagerrak, Kattegat and Øresund (Fretter *et al.* 1986, p. 613).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 20 to 30 m deep. Perhaps associated with bryozoans.

Subfossil finds. The Limfjord region, Holocene.

***Odostomia conoidea* Winckworth 1932**

Fig. 34

Distribution. From Norway off the Lofoten islands and south to the Mediterranean. Recorded from the Skagerrak (Fretter *et al.* 1986) and the Øresund (Jensen & Knudsen 1995), but not from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 10 to 150 m deep, usually in association with the starfish *Astropecten irregularis* (Fretter *et al.* 1986, p. 617).

Subfossil finds. The Bælt Sea, Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. In the Skagen area recorded from the Subatlantic.



Fig. 34. *Odostomia conoidea* Winckworth 1932. Skagen 3, 48.90–49.10 m b.s., lab. no. 714,93. × 40. MGUH 25344.

***Odostomia turrita* Hanley 1844**

Distribution. From Norway north of Lofoten and south to the Mediterranean. The species extends through the Kattegat to the Øresund (Fretter *et al.* 1986, p. 612), but is not recorded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone to 100 m deep on weed and clay bottoms.

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene. Recorded from the Vendsyssel area during the Eemian.

***Odostomia albella* Lovén 1846**

Distribution. Empty shells recorded from Spitsbergen, SW and NW Iceland, Norway north of Lofoten and south to the Mediterranean. The species occurs in the Skagerrak (Fretter *et al.* 1986), the Øresund area (Jensen & Knudsen 1995), and the Limfjord region (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone to depths of about 100 m on boulders, associated with growth of *Pomatoceros* (Fretter *et al.* 1986).

Subfossil finds. The Limfjord, North Sea and Vendsyssel regions, Holocene. From the North Sea region during the Eemian.

***Odostomia plicata* (Montagu 1803)**

Distribution. From the southern part of Scandinavia (not southern Norway (Spärck & Thorson 1931)) and south to the Mediterranean (Fretter *et al.* 1986, p. 610). The species extends into the Kattegat, including the Øresund (Jensen & Knudsen 1995), but is not recorded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. In the tidal zone associated with *Pomatoceros triqueter* (Fretter *et al.* 1986).

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene.

***Odostomia umbilicaris* (Malm 1863)**

Fig. 35

Distribution. From southern Norway (Spärck & Thorson 1931) to the British Isles. The species extends to the Swedish west coast but not further into the Kattegat (Fretter *et al.* 1986, p. 620).

Occurrence. The Boreal and Lusitanian (northern part) regions.

Habitat. From 20 to 275 m deep, found on the bivalve *Mytilus adriaticus* (Fretter *et al.* 1986).

Subfossil finds. The Skagen area, Holocene, recorded from the Atlantic and Subatlantic.

***Turbonilla crenata* (Brown 1827)**

Distribution. From Norway off the Lofoten islands (Thorson 1941) and south to the Mediterranean. The species extends into the Kattegat and Øresund (Fretter *et al.* 1986), but is absent from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 15 to 350 m deep on fine sand.

Subfossil finds. The Limfjord and North Sea regions, Holocene. Recorded from the Bælt Sea and North Sea during the Eemian.



Fig. 35. *Odostomia umbilicaris* (Malm 1863). Skagen 3, 82.34–82.50 m b.s., lab. no. 725,93. × 20. MGUH 25345.

***Turbonilla delicata* Monterosato 1884**

Fig. 36

Distribution. From the south-western part of the British Isles to the Mediterranean (Fretter *et al.* 1986, p. 636). However, recorded from the northern Kattegat and northern Øresund although, rare (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. On soft bottoms, but at uncertain depths (Fretter *et al.* 1986, p. 636).

Subfossil finds. The Limfjord, North Sea and Skagen regions, Holocene. From the Skagen area recorded from the Subatlantic.

***Turbonilla lactea* (Linnaeus 1758)**

Distribution. From northern Norway and south to the Mediterranean. Present although uncommon in Danish waters (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone to depths of about 80 m, occurring under stones in silty places in the tidal zone and on soft, muddy and sandy bottoms sublittorally (Fretter *et al.* 1986, p. 634).

Subfossil finds. The Limfjord, North Sea and Vendsyssel regions, Holocene. Recorded from the Bælt Sea, Kattegat, and North Sea regions during the Eemian.



Fig. 36. *Turbonilla delicata* (Monterosato 1874). Skagen 4, 20.0–20.5 m b.s., lab. no. 345,93. × 20. MGUH 25346.

Subclass Opisthobranchia
Order Bullomorpha

***Acteon tornatilis* (Linnaeus 1758)**

Distribution. W and S Iceland, Norway off the Lofoten islands and south to the Mediterranean (Lemche 1938). The species extends into the Kattegat, including the Øresund (Petersen 1888, p. 78), but it is not recorded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone down to 250 m in sand, usually in sheltered areas (Poppe & Goto 1991, p. 192).

Subfossil finds. The Limfjord, North Sea and Vendsyssel regions, Holocene. Recorded from the North Sea and Vendsyssel areas during the Eemian.

***Haminoea navicula* (da Costa 1778)**

Distribution. From the British Isles south to the Mediterranean.

Occurrence. The Lusitanian region.

Habitat. Lives in the *Zostera* beds in sheltered areas (Poppe & Goto 1991, p. 196).

Only subfossil finds. The Bælt Sea, Kattegat, and North Sea regions during the Eemian.

***Cylichna cylindracea* (Pennant 1777)**

Distribution. W and S Iceland, Norway off the Lofoten islands and south to the Mediterranean. The species extends into the Limfjord and Kattegat, including Øresund (Petersen 1888, p. 78; Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 40 to 200 m deep, in sand. According to Lemche (1938) associated with the Boreal *Amphiura filiformis* community in deeper water south of Iceland, corresponding to its occurrence in Danish waters.

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene.



Fig. 37. *Cylichna alba* (Brown 1827). Skagen 3, 44.88–45.00 m b.s., lab. no. 499,93. $\times 9.6$. MGUH 25347.

***Cylichna alba* (Brown 1827)**

Fig. 37

Distribution. W and E Greenland, around Iceland, Norway north of Lofoten and south to the Bay of Biscay at greater depth (Lemche 1938, p. 9). The species extends into the North Sea and Skagerrak (Lemche 1928, p. 4).

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian regions.

Habitat. According to Lemche (1928), this species is also widely distributed in depth, being found in low water to depths down to 2700 m, on clay bottom (Faeroes).

Subfossil finds. The Limfjord, North Sea and Skagen areas, Holocene. In the Skagen Well recorded from the Subatlantic. Also found in the Vendsyssel area from the Early/Middle and Late Weichselian (the Older and Younger *Yoldia* Sea respectively).

***Cylichna occulta* (Mighels 1841)**

Distribution. E and W Greenland, N and E Iceland, Norway north of Lofoten (Lemche 1938).

Occurrence. The Arctic, Subarctic and Boreal (northernmost part) regions. Will be referred as an Arctic and Subarctic species.

Habitat. From 10 to 388 m deep (Iceland), especially found within the *Macoma calcarea* community, and

might also occur within the *Yoldia hyperborea* community (Lemche 1938).

Only subfossil finds. Recorded from the Kattegat region during the Early/Middle Weichselian and the Vendsyssel region during the Early/Middle and Late Weichselian (the Older and Younger *Yoldia* Sea respectively).

***Scaphander lignarius* (Linnaeus 1758)**

Distribution. From S and W Iceland, the Faeroes, Norway off the Lofoten islands and south to the Mediterranean.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 60 to 700 m deep. The species is associated with the Boreal *Spisula elliptica* community on sandy plateaus south and west of Iceland (Lemche 1938, p. 7).

Subfossil finds. None.

***Scaphander punctostriatus* (Mighels & Adams 1841)**

Distribution. E and W Greenland, S and W Iceland, the Faeroes, Norway north of Lofoten and south to the Mediterranean.

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian regions.

Habitat. Recorded from depths between 10 and 3000 m, this probably having some relation to its wide horizontal distribution. Around the Faeroes the species may be expected to be found on the great, sandy plateaus (Lemche 1928, p. 4).

Subfossil finds. None.

***Philine aperta* (Linnaeus 1767)**

Distribution. From the Faeroes, western Norway off Lofoten, and south to the Mediterranean (Lemche 1928). The species extends through Kattegat and Øresund, into the Bælt Sea as far as Kieler Bugt (Petersen 1888, p. 83), and it is also recorded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. The species prefers shallow water but has been found at depths down to 100 m off the Faeroes (Lemche 1928) on sandy bottoms. In Danish waters recorded from 10 to 30 m, also on sandy bottoms (Petersen 1888).

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene. Recorded from the Bælt Sea and the North Sea during the Eemian.

***Philine angulata* Jeffreys 1867**

This species is mentioned by Jensen & Knudsen (1995), but only on the basis of one broken shell found in the Zoological Museum in Copenhagen; difficult to identify; occurrence uncertain. So in the light of “the difficult problem of the relation between *punctata* and *angulata*”, as treated by Lemche (1948, p. 67), this find will be omitted, also that no subfossil species have been found.

***Philine catena* (Montagu 1803)**

Fig. 38

Distribution. From Norway off the Lofoten islands and south to the Mediterranean.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From low water-mark to 76 m (Forbes & Hanley 1853)

Subfossil finds. The Skagen region during the Eemian.

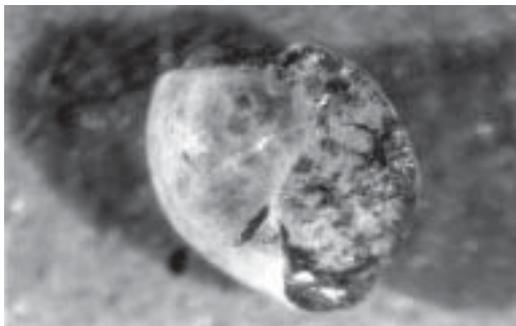


Fig. 38. *Philine* cf. *catena* (Montagu 1803). Skagen 3, 180.77–180.89 m b.s., lab. no. 798,93. × 40. MGUH 25348.

***Philine denticulata* (Adams 1800)**

Distribution. From Norway south to the Mediterranean.

Occurrence. The Boreal and Lusitanian regions.

Subfossil finds. None.

***Philine punctata* (Adams 1800)**

Distribution. The Faeroes, southern part of the west coast of Norway, and south to the Mediterranean. Lemche (1928) also mentioned occurrences from Greenland, which, however, was not repeated in later papers (Lemche 1941a, b). Jensen & Knudsen (1995) report occurrences from the Øresund, although rare, and Petersen (1888) has a single find from the Bælt Sea and Petersen (1986a) from the Limfjord.

Occurrence. The Boreal and Lusitanian regions.

Habitat. At the Faeroes the species is recorded from depths down to 240 m (Lemche 1928).

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene.

***Philine quadrata* (Wood 1839)**

Distribution. W Greenland, around Iceland, Norway north of Lofoten, and south to the Mediterranean. Recorded from the Øresund, but rare (Jensen & Knudsen 1995).

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. The vertical range of the species is about 35 m down to 2150 m (Lemche 1938).

Subfossil finds. None.

***Philine scabra* (Müller 1776)**

Distribution. S and W Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean. The species extends into the Kattegat, including the Øresund (Petersen 1888, p. 84).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Off the coasts of W and S Iceland from 20–216 m on sandy bottom (Lemche 1938, p. 11); however, in Danish waters (Kattegat) from 20–40 m on mixed bottom (Petersen 1888, p. 84).

Subfossil finds. None.

***Philinoglossa belgolandica* Hertling 1932**

Distribution. From the North Sea – Helgoland – and south to the Mediterranean, the species might occur in Danish waters (Jensen & Knudsen 1995, p. 29).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Probably in shell gravel (Jensen & Knudsen 1995).

Subfossil finds. None.

Order Anaspidea

***Diaphana minuta* Brown 1827**

Distribution. E and W Greenland, around Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean. The species extends into the Kattegat and Øresund (Petersen 1888; Jensen & Knudsen 1995).

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian regions.

Habitat. In general from the tidal zone to 770 m, but is said to prefer sandy clay at depths of 20–40 m (Lemche 1928). This is very much the same as for the Kattegat, where Petersen (1888) says that the species prefers mixed bottom at a depth of about 19–38 m.

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene.

***Retusa obtusa* (Montagu 1803)**

Distribution. E and W Greenland, around Iceland, the Faeroes, Norway north of Lofoten, and south to the British Isles (Shetland and Scotland) (Lemche 1928). The species is found in the Limfjord and is common in the fjords and bays bordering the Kattegat, including the Øresund, and extends into the Bælt Sea and the western part of the Baltic (Petersen 1888, p. 81).

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. From the intertidal zone down to 300 m deep in mud or fine sand. In Danish waters Petersen (1888) points to the observed differences in depth, i.e. in the Kattegat region around 20 m while 60 m deep in the Baltic. The species is connected with the Arctic *Macoma* community (Lemche 1941a, b).

Subfossil finds. The Bælt Sea, Kattegat, Limfjord, North Sea and Vendsyssel regions, Holocene. Also recorded from the Vendsyssel area during the Early/Middle Weichselian and the Late Weichselian (the Older *Yoldia* Sea and the Younger *Yoldia* Sea respectively).

***Retusa truncatula* (Bruguière 1792)**

Fig. 39

Distribution. The Faeroes, Norway north of Lofoten, and south to the Mediterranean (Lemche 1928, 1938). The species extends through the Kattegat, including the Øresund, and into the Bælt Sea, and it is also recorded from the Limfjord (Petersen 1888, p. 80).

Occurrence. The Boreal and Lusitanian regions.

Habitat. In general the species lives from the tidal zone down to 200 m (Poppe & Goto 1991). However, in Danish waters, according to Petersen (1888), it lives in shallow water down to only about 20 m deep on sandy bottoms with *Zostera*.

Subfossil finds. The Bælt Sea, Baltic, Kattegat, Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene.

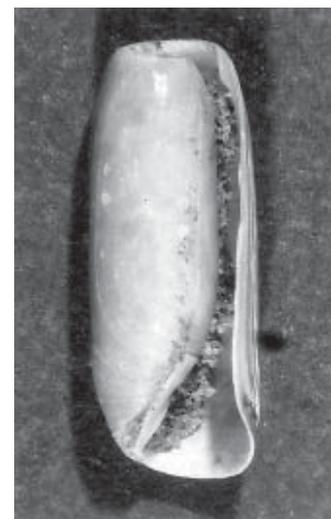


Fig. 39. *Retusa truncatula* (Bruguière 1792). Skagen 3, 67.34–67.39 m b.s., core sample K-25. × 9.6. MGUH 25349.

Recorded from the Skagen area from the Subboreal and Subatlantic. From the Bælt Sea and the North Sea recorded during the Eemian.

***Retusa umbilicata* (Montagu 1803)**

Fig. 40

Distribution. From Norway north of Lofoten (Lemche 1928) and south to the Mediterranean (Poppe & Goto 1991). The species extends into the Kattegat and Øresund (Petersen 1888; Jensen & Knudsen 1995), but is not recorded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From depths of about 20 to 30 m on mixed bottoms (Petersen 1888).

Subfossil finds. The Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded from the Subboreal and Subatlantic. From the Bælt Sea, North Sea, and Vendsyssel regions found during the Eemian.

***Rhizorus acuminatus* (Bruguière 1792)**

Distribution. From western and southern Norway south to the Mediterranean, in Danish waters from the southern Kattegat.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone to 800 m deep.

Subfossil finds. None.



Fig. 40. *Retusa umbilicata* (Montagu 1803). Skagen 3, 70.10–70.30 m b.s., lab. no. 721,95. × 20. MGUH 25350.

***Akera bullata* O.F. Müller 1776**

Distribution. The Faeroes, Norway north of Lofoten, and south to the Mediterranean (Lemche 1928). The species extends into the Limfjord, the Kattegat, including the Øresund, and the Bælt Sea as far as the Kieler Bugt (Petersen 1888).

Occurrence. The Boreal and Lusitanian regions.

Habitat. In sheltered bays down to 370 m deep (Poppe & Goto 1991). Common in shallow water with *Zostera* (Petersen 1888).

Subfossil finds. The Bælt Sea, Kattegat, Limfjord and Vendsyssel regions, Holocene. In the Bælt Sea and Kattegat regions recorded from the Eemian.

Order Thecosomata

***Limacina retroversa* (Fleming 1823)**

Fig. 41

Distribution. E and W Greenland, around Iceland, Norway north of Lofoten, and south to Ireland (Lemche 1938). It is common in the North Sea and Skagerrak, penetrating into the Kattegat, occasionally even into the Bælt Sea (Kramp 1961).

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian (northernmost) regions.

Habitat. Pelagic.

Subfossil finds. Recorded from the Vendsyssel and Skagen regions during the Eemian and from the Vendsyssel region during the Late Weichselian (the Younger Yoldia Sea).



Fig. 41. *Limacina retroversa* (Fleming 1823). Skagen 3, 180.57–180.70 m b.s., lab. no. 797,93. × 20. MGUH 25351.

Order Gymnosomata

Clione limacina (Phipps 1774)

Fig. 42

Distribution. E and W Greenland, around Iceland, the Faeroes, Norway north of Lofoten (Lemche 1938), and south to the west coast of England. Common in the northern part of the North Sea and in the Skagerrak, occasionally penetrating into the Kattegat (Kramp 1961). Rare occurrences in the Øresund (Jensen & Knudsen 1995).

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian (northern part) regions.

Habitat. Pelagic.

Subfossil finds. Recorded (imprint) from the Skagen Well during the Late Weichselian (the Younger Yoldia Sea).

Subclass Pulmonata

Order Basommatophora

Ovatella myosotis (Draparnaud 1801)

Distribution. From Scandinavia along the coast of western Europe, south to the Mediterranean (Steenberg 1911, p. 204). In Danish waters recorded from the Bælt Sea and the Baltic (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Lives on sea wrack along the coasts (Steenberg 1911).

Subfossil finds. None.



Fig. 42. *Clione limacina* (Phipps 1774). Skagen 3, 115.07–115.15 m b.s., lab. no. 749,93. × 20. MGUH 25352.

Lymnaea (Radix) peregra (Müller 1774) f. *baltica* Linné

Distribution. *Lymnaea peregra* is found all over Europe: Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean (Mandahl-Barth 1938). The species occurs in the Baltic and southern Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. *Lymnaea peregra* f. *baltica* Linné and *L. p.* f. *succinea* Nilsson are brackish water forms tolerating up to 8‰ salt (Mandahl-Barth 1949, p. 74).

Subfossil finds. The Bælt Sea and Baltic regions, Holocene.

Class Scaphopoda

Order Siphonodentalioida

Cadulus subfusiforme (M. Sars 1865)

Fig. 43

Distribution. Western Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean (Knudsen 1949b). In Danish waters taken in the Skagerrak (Muus 1959).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 80 to 1300 m deep on mud bottoms. In Danish waters at a depth of 230 m on clay bottom (Muus 1959).

Subfossil finds. Recorded from the Skagen Well during the Eemian.



Fig. 43. *Cadulus subfusiforme* (M. Sars 1865). Skagen 3, 180.77–180.89 m b.s., lab. no. 798,93. × 20. MGUH 25353.



Fig. 44. *Siphonodentalium lobatum* (Sowerby 1860). Skagen 3, 114.64–? m b.s., core sample K-57. × 9.6. MGUH 25354.

***Siphonodentalium lobatum* (Sowerby 1860)**

Fig. 44

Distribution. E and W Greenland, N and E Iceland (Knudsen 1949b), the Faeroes, Norway north of Lofoten, and south to Portugal. The species might be found in Norske Rende. In Norway often found in glacial deposits (Muus 1959).

Occurrence. The main areas are the Arctic, Subarctic and Boreal regions, but the species extends into the Lusitanian region.

Habitat. From 36 to 3116 m on mud (Knudsen 1949b).

Only subfossil finds. Recorded from the Skagen Well in the Late Weichselian (the Younger *Yoldia* Sea) and from the Eemian.

***Entalina tetragona* (Brocchi 1814)**

Fig. 45

Distribution. From northern Norway south to the Bay of Biscay and the Mediterranean. From Danish waters in the North Sea and Skagerrak (Muus 1959).

Occurrence. The Boreal and Lusitanian regions.

Habitat. It is a deep-water species preferring mud bottoms (Poppe & Goto 1993). In the Danish waters known from 100 to 480 m on mixed bottom (Muus 1959) connected with the *Amphihilipis norvegica*/*Pecten vitreus* community at depths of 250–700 m.

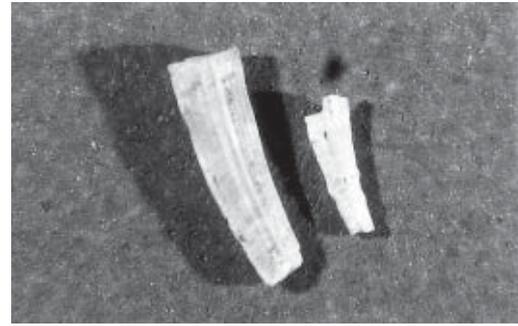


Fig. 45. *Entalina tetragona* (Brocchi 1814). Skagen 3, 183.77–184.00 m b.s., lab. no. 799,93. × 9.6. MGUH 25355.

Subfossil finds. Recorded from the Skagen Well during the Eemian.

Order Dentalioida

***Antalis agile* G.O. Sars 1878**

Distribution. S and W Iceland, Norway off the Lofoten islands, and south to the Mediterranean. In the Danish waters the species extends from the North Sea into the Skagerrak and Kattegat.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 55 m down to 1250 m. In Scandinavian waters rarely at depths less than 70 m (Muus 1959).

Subfossil finds. None.

***Antalis entalis* (Linnaeus 1758)**

Distribution. W Greenland, Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean (Knudsen 1949b). Common in the Danish waters, extending into the Kattegat (Muus 1959) although rare in the Øresund (Jensen & Knudsen 1995).

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. From 20 to 400 m in the Kattegat region, and in the North Sea between 30 and 200 m (Muus 1959). However, the vertical range in general goes from 6–3200 m (Knudsen 1949b).

Subfossil finds. The Skagen Well during the Eemian.

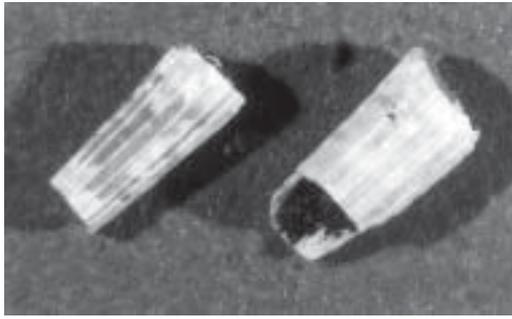


Fig. 46. *Dentalium vulgare* da Costa 1778. Skagen 3, 181.17–181.21 m b.s., core sample K-99. × 9.6. MGUH 25356.

***Dentalium vulgare* da Costa 1778**

Fig. 46

Distribution. From the British Isles and south to the Mediterranean. Might be found in the southern North Sea.

Occurrence. Mainly the Lusitanian region.

Habitat. Sublittorally from 1 m and down to 50 m on mud and sandy bottoms.

Only subfossil finds. Recorded from the Skagen Well during the Eemian.

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

***Nucula nitidosa* Winckworth 1930**

Fig. 47

Distribution. From Norway off the Lofoten islands and

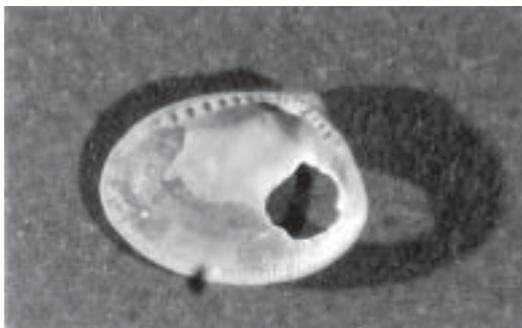


Fig. 47. *Nucula nitidosa* Winckworth 1930. Skagen 4, 21.0–21.5 m b.s., lab. no. 346,93. × 9.6. Right valve. MGUH 25357.

south to the Mediterranean (Madsen 1949). The species extends from the more shallow part of the North Sea and Skagerrak into the Kattegat, including the Øresund. Very common in the western part of the Limfjord (Jensen & Spärck 1934, p. 23).

Occurrence. The Boreal and Lusitanian regions.

Habitat. In general from 7 to 250 m deep on fine sand or sand/mud bottoms (Poppe & Goto 1993). However, according to Jensen & Spärck (1934) the species is often found at depths of 6–10 m in the Limfjord and 10–30 m in the Kattegat region.

Subfossil finds. The Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded from the Subatlantic. During the Eemian found in the Bælt Sea, Baltic and North Sea regions.

***Nucula nucleus* (Linnaeus 1767)**

Fig. 48

Distribution. From Norway off the Lofoten islands, the Faeroes, and south to the Mediterranean (Madsen 1949). Posselt & Jensen (1898) have but few records from West Greenland. The species extends from the North Sea into the Kattegat, including the Øresund (Jensen & Spärck 1934), and is recorded from the Limfjord (Pettersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Lives from the tidal zone down to 150 m on gravel and mud bottoms. In Danish waters common between 20 and 100 m.

Subfossil finds. The Limfjord, North Sea, Vendsyssel

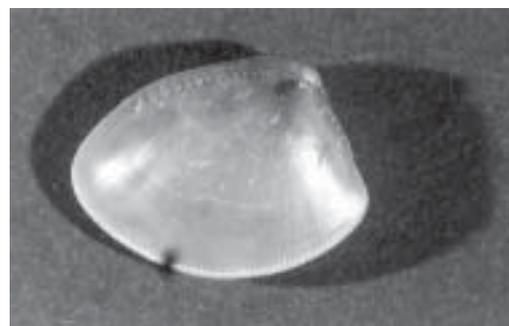


Fig. 48. *Nucula nucleus* (Linnaeus 1767). Skagen 4, 9.0–9.5 m b.s., lab. no. 334,93. × 4.8. Right valve. MGUH 25358.

and Skagen regions, Holocene. Recorded in the Skagen Well from the Subatlantic. In the Eemian recorded from the Baltic and Vendsyssel regions.

***Nucula sulcata* (Bronn 1831)**

Distribution. Norway off the Lofoten islands and south to the Mediterranean. In Danish waters common in the deeper parts of the Kattegat and Øresund (Jensen & Knudsen 1995), and it is also recorded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 10 to 400 m deep, on mud or clay bottoms, and down to 2250 m (Poppe & Goto 1993). In Kattegat from 50 to 100 m deep on silty bottom (Jensen & Spärck 1934).

Subfossil finds. The North Sea, Holocene. From the Bælt Sea, North Sea and Vendsyssel regions recorded from the Eemian.

***Nuculoma banleyi* Winckworth 1931**

Distribution. From the British Isles south to Spain (Poppe & Goto 1993). Recorded from the northern Kattegat (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 30 to 90 m deep on mud and gravel bottoms.

Subfossil finds. None.

***Nuculoma tenuis* (Montagu 1808)**

Distribution. W and E Greenland, Spitsbergen, around Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean (Madsen 1949). The species extends from the deeper part of the Skagerrak into the Kattegat, Øresund, and Bælt Sea (Jensen & Spärck 1934).

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian regions.

Habitat. From off-shore down to 300 m on muddy bottoms (Poppe & Goto 1993). The species is more

littoral in the northern latitudes than in the south (Jensen & Spärck 1934).

Subfossil finds. From the Limfjord and North Sea regions, Holocene. Recorded from the Vendsyssel area during the Eemian, and from the Kattegat and Vendsyssel area during the Early/Middle Weichselian (the Older *Yoldia* Sea), and furthermore from the Vendsyssel region during the Late Weichselian (the Younger *Yoldia* Sea).

***Nuculana minuta* (Müller 1776)**

Fig. 49

Distribution. SE and W Greenland, around Iceland, the Faeroes, Norway north of Lofoten, and south to the British Isles. According to Ockelmann (1958), lacking in the most high-Arctic seas. In south-western Europe only at depths greater than 400 m (Madsen 1949). The species extends from the North Sea and Skagerrak into the Kattegat and Øresund (Jensen & Spärck 1934).

Occurrence. The Subarctic and Boreal regions.

Habitat. From 10 to 190 m. However, recorded from 2000 m on mud, sand and gravel bottoms (Poppe & Goto 1993). In Danish waters common on silty bottom (Jensen & Spärck 1934).

Subfossil finds. The Skagen region, Holocene. Recorded from the Skagen Well during the Subboreal and Subatlantic. From the Vendsyssel region found during the Eemian and in the Skagen area during the Late Weichselian (the Younger *Yoldia* Sea).



Fig. 49. *Nuculana minuta* (Müller 1776). GEUS collection. Læsø, Denmark. × 4.8. Right valve. MGUH 25359.

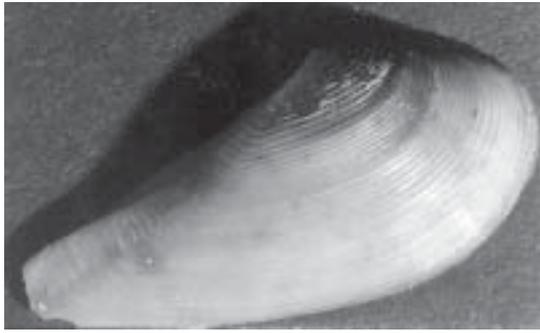


Fig. 50. *Nuculana pernula* (Müller 1776). GEUS collection. Læsø, Denmark. × 4.8. Right valve. MGUH 25360.

***Nuculana pernula* (Müller 1776)**

Fig. 50

Distribution. E and W Greenland, around Iceland, the Faeroes, Norway north of Lofoten, and south to the Bay of Biscay. However, in SW Europe only at depths greater than 400 m (Madsen 1949). In Danish waters the species extends from the North Sea, Skagerrak, and into the Kattegat, Øresund, and Bælt Sea region north of Femern (Jensen & Spärck 1934).

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. Lives off-shore between 80 and 900 m deep, especially in mud bottoms (Poppe & Goto 1993). However, in Danish waters the species is found from a depth of 20 m (Kattegat) to 200 m (Skagerrak) according to Jensen & Spärck (1934), and in the Arctic (East Greenland) from 3–9 m (Ockelmann 1958), being mostly littoral in the Arctic.

Subfossil finds. Recorded from the Vendsyssel and Skagen regions during the Eemian. From the Kattegat, Vendsyssel and Skagen regions during the Early and Middle Weichselian (the Older *Yoldia* Sea). From the Vendsyssel and Skagen regions during the Late Weichselian (the Younger *Yoldia* Sea).

***Yoldia hyperborea* Lovén 1859**

Fig. 51

Distribution. E and W Greenland, Spitsbergen, around Iceland and Norway north of Lofoten (Madsen 1949).

Occurrence. The Arctic, Subarctic and Boreal (northern part – High-Boreal) regions.



Fig. 51. *Yoldia hyperborea* Lovén 1859. GEUS collection. Nordre Strømfjord, Greenland. × 4.8. Right valve. MGUH 25361.

Habitat. From about 5 to 675 m on clay or mud, in few cases sand (Madsen 1949).

Only subfossil finds. Recorded from the Vendsyssel and Skagen areas during the Early and Middle Weichselian (the Older *Yoldia* Sea) and from the Skagen Well also during the Late Weichselian (the Younger *Yoldia* Sea).

***Portlandia arctica* (Gray 1824)**

Fig. 52

Distribution. According to Ockelmann (1958, p. 26): “Widely distributed in high-Arctic seas”.

Occurrence. North Greenland, East Greenland, Spitsbergen, the Barents Sea, Novaya Zemlya, the Kara Sea, The Siberian Ice Sea, viz: Arctic and Subarctic regions.

Habitat. From 2 m to 340 m deep, however, the species is most common at depths between 10 and 50 m on a muddy or clayey bottom (Ockelmann 1958, p. 25).



Fig. 52. *Portlandia arctica* (Gray 1824). GEUS collection. Disko, Greenland, 46 m a.s.l. × 4.8. Specimen seen from the right. MGUH 25362.

Only subfossil finds. Recorded from the Kattegat, Vendsyssel, and Skagen areas during the Early and Middle Weichselian (the Older *Yoldia* Sea) and from the same areas during the late Weichselian (the Younger *Yoldia* Sea).

***Yoldiella lucida* (Lovén 1846)**

Distribution. W Greenland, around Iceland, Norway north of Lofoten (Madsen 1949), and south over the British Isles to the Mediterranean. In the Danish waters found in the deeper part of the Skagerrak (Jensen & Spärck 1934).

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. From about 20 m to about 1400 m (Iceland), in the Skagerrak from about 200 m to more than 600 m on clayey bottoms.

Subfossil finds. From the Vendsyssel area during the Eemian.

***Yoldiella lenticula* (Möller 1842)**

Fig. 53

Distribution. E and W Greenland, Spitsbergen, Siberian Sea, Norway north of the Lofoten Islands, south to the British Isles. Further south only at depths greater than 400 m (Madsen 1949).

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. Most common at depths between 20 and 200 m (East Greenland) on rather pure clay or mud (Ockelmann 1958).



Fig. 53. *Yoldiella lenticula* (Möller 1842). Skagen 3, 121.39–121.50 m b.s., lab. no. 759,93. × 20. Specimen seen from the left. MGUH 25363.

Only subfossil finds. Recorded from the Vendsyssel area during the Eemian, Early/Middle Weichselian (the Older *Yoldia* Sea) and Late Weichselian (the Younger *Yoldia* Sea). Found in the Skagen area from the Late Weichselian (the Younger *Yoldia* Sea).

***Yoldiella frigida* (Torell 1859)**

Fig. 54

Distribution. E and W Greenland, Spitsbergen, around Iceland, Norway from north of Lofoten, and south to the Mediterranean (Madsen 1949). In the Danish waters found in the deeper parts of the Skagerrak (Jensen & Spärck 1934). However, this is questioned by Ockelmann (1958), who says that the main distribution is high-Arctic and therefore the recent finds in Danish waters should be referable to *Yoldiella nana*. However, according to the old information, the species must have a wide distribution.

Occurrence. The Arctic and Subarctic regions, Boreal and Lusitanian.

Habitat. Most common at depths between 30 and 150 m on bottoms consisting of clay, mud, and clay mixed with sand and gravel (Ockelmann 1958).

Subfossil finds. Following the distribution of *Portlandia frigida sensu* Jensen & Spärck (1934), the species has been recorded from the Vendsyssel and Skagen areas during the Eemian and from the Early and Middle Weichselian (the Older *Yoldia* Sea) and the Late Weichselian (the Younger *Yoldia* Sea).



Fig. 54. *Yoldiella frigida* (Torell 1859). Skagen 3, 127.39–127.50 m b.s., lab. no. 763,93. × 20. Specimen seen from the right. MGUH 25364.

***Yoldiella philippiana* (Nyst 1845)**

Distribution. From Norway off the Lofoten islands and south to the Mediterranean.

Occurrence. The Boreal and Lusitanian regions.

Habitat. Lives to a depth of about 135 m (Poppe & Goto 1993); however, found at depths of 2500 m (Jensen & Spärck 1934).

Only subfossil finds. Recorded from the Vendsyssel area during the Eemian.

***Yoldiella nana* (M. Sars 1846)**

Distribution. Considering the discussion by Ockelmann (1958) on distinguishing between *Portlandia frigida* and *Yoldiella nana*, where the latter “at least in part” should be referable to *P. fraterna*, it is not possible to give any information on the distribution of *Yoldiella nana* mentioned by Jensen & Knudsen (1995) as being part of the recent Danish fauna.

Subfossil finds. None.

***Malletia obtusa* (G.O. Sars 1872)**

Distribution. From Norway off the Lofoten islands and south to SW Europe. The occurrences around the British Isles and in the Mediterranean are at depths greater than 400 m (Madsen 1949).

Occurrence. The Boreal and Lusitanian regions.

Habitat. This species has a wide range of depths according to Madsen (*op. cit.*) from 20–3200 m deep. In Danish waters only from the deeper part (> 300 m), and in the Skagerrak mostly at a depth of 600 m (Jensen & Spärck 1934).

Subfossil finds. None.

**Subclass Pteriomorpha
Order Arcoida**

***Acar nodulosa* (Müller 1766)**

Distribution. S and W Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean. The

species has been taken on the Dogger Bank, but not in the inner Danish waters.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone down to 1000 m fixed with its byssus to hard substrates (Poppe & Goto 1993).

Subfossil finds. None.

***Bathyarca glacialis* (Gray 1824)**

Fig. 55

Distribution. W and E Greenland, Spitsbergen, and around Iceland. The occurrences from SW Europe are of dead shells and from deep water (Ockelmann 1958).

Occurrence. Mainly the Arctic and Subarctic regions; however, the occurrences from southern Iceland imply extension into the Boreal region as well.

Habitat. From 6–10 m down to 425 m (East Greenland), but most abundant below 40 m on clay bottoms with stones and gravel, where the *Astarte crenata* community occurs.

Only subfossil finds. Recorded from the Vendsyssel (not in the Skærumhede sequence) and Skagen regions during the Early/Middle Weichselian and the Late Weichselian respectively.

***Bathyarca pectunculoides* (Scacchi 1834)**

Distribution. W and E Greenland, around Iceland, Norway north of Lofoten, and south to the Mediterranean. In the Danish waters the species is rather common in the deeper part of the Skagerrak between 300–700 m (Jensen & Spärck 1934).

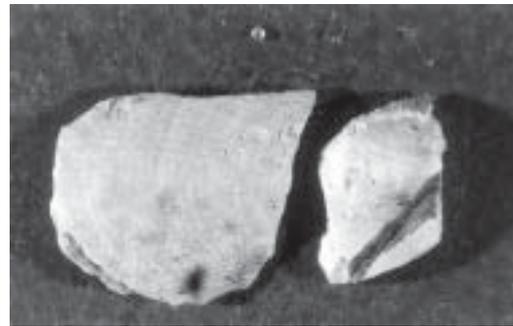


Fig. 55. *Bathyarca glacialis* (Gray 1824). Skagen 3, 114.64–? m b.s., core sample-57. × 9.6. Fragments of left valve. MGUH 25365.

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian regions.

Habitat. From 50 m (the Shetland Isles) to more than 2000 m (the Mediterranean) (Madsen 1949).

Subfossil finds. None.

Order Mytiloida

Mytilaster lineatus (Gmelin 1791)

Distribution. A Mediterranean species according to Jensen & Spärck (1934) but also found in the neighbouring Atlantic (Poppe & Goto 1993).

Occurrence. The Lusitanian region.

Habitat. Intertidal, attached to rocks.

Only subfossil finds. The Eemian in the Kattegat and North Sea regions.

Mytilaster solidus form minimus (Poli 1795)

Distribution. From Bretagne and south into the Mediterranean.

Occurrence. The Lusitanian region.

Habitat. Intertidal, attached to rocks or algae.

Subfossil finds. Recorded from the Bælt Sea during the Eemian.

Mytilus edulis Linnaeus 1758

Fig. 56

Distribution. W and E Greenland, but only along the south-eastern coast (Ockelmann 1958), around Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean. Known from all parts of the Danish waters, including the Baltic.

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. Intertidal to 40 m deep, but in Danish waters common as an epifaunal element down to a depth of

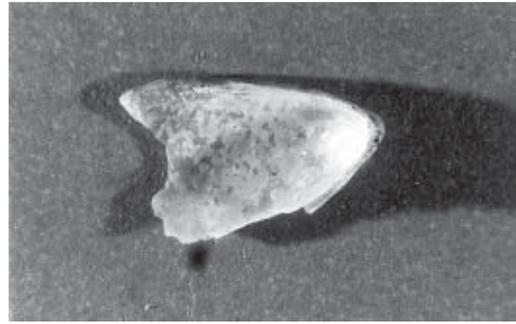


Fig. 56. *Mytilus edulis* Linnaeus 1758. Skagen 4, 18.7–18.8 m b.s., lab. no. 311,95. $\times 4.8$. Fragment of left valve. MGUH 25366.

10 m; however, in the Baltic as deep as 40 m (Jensen & Spärck 1934).

Subfossil finds. The Bælt Sea, Baltic, Kattegat, Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. Recorded in the Subatlantic from the Skagen Well. In the Eemian records from the Bælt Sea, Baltic, Kattegat, North Sea and Vendsyssel regions. In the Late Weichselian also recorded from the Vendsyssel region (the Younger Yoldia Sea).

Modiolula phaseolina (Philippi 1844)

Distribution. From SW and NW Iceland, the Faeroes, Norway north of Lofoten, and south to the British Isles (Petersen 1968) and the Mediterranean. The species extends from the North Sea and Skagerrak into the Kattegat and Øresund (Jensen & Knudsen 1995), but is not recorded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone and down to 160 m, attached by its byssus to rocks or on the base of the larger seaweeds (Poppe & Goto 1993), but also recorded from depths of 1000 m.

Subfossil finds. The Bælt Sea, Limfjord and Vendsyssel regions, Holocene. Recorded from the Bælt Sea and the North Sea regions during the Eemian.

Modiolus adriaticus (Lamarck 1819)

Distribution. Recorded from the southern part of the British Isles and Denmark (Petersen 1968) south to the Mediterranean. In Danish waters taken in the Kattegat, including the Øresund (Jensen & Spärck 1934), but

not observed in the Limfjord (Petersen 1986a). It might have been passed over in many places, as mentioned by Petersen (1888, p. 127).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Sublittoral between 14 and 75 m on mud bottoms.

Subfossil finds. The Limfjord and Vendsyssel region, Holocene.

***Modiolus modiolus* (Linnaeus 1758)**

Distribution. Around Iceland, the Faeroes, Norway north of Lofoten, and south to the British Isles (Petersen 1968) and the Bay of Biscay (Poppe & Goto 1993). In Danish waters, including the Limfjord, the species extends into the Bælt Sea (Jensen & Spärck 1934) and the Øresund (Jensen & Knudsen 1995).

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. From the extreme low tide down to 150 m attached with its byssus to rocks or gravel (Poppe & Goto 1993). In Danish waters the species replaces *Mytilus edulis* as the dominating epifaunal element in deeper water (Jensen & Spärck 1934).

Subfossil finds. The Bælt Sea, Limfjord and Vendsyssel regions, Holocene. Recorded from the Baltic and North Sea during the Eemian.

***Musculus discors* (Linnaeus 1767)**

Fig. 57

Distribution. E and W Greenland, around Iceland and Spitsbergen (Madsen 1949), Norway from north of Lofoten (Petersen 1968) and south to the Mediterranean. In Danish waters the species extends into the Bælt Sea and Øresund (Jensen & Spärck 1934), but it has not been observed in the Limfjord (Petersen 1986a).

Occurrence. The Arctic, Subarctic, Boreal, and Lusitanian regions.

Habitat. From the intertidal zone on algae (Poppe & Goto 1993) and rarely on water deeper than about 200 m (Jensen & Spärck 1934).



Fig. 57. *Musculus discors* (Linnaeus 1767). Skagen 4, 28.0–28.5 m b.s., lab. no. 353,93. × 20. Left valve. MGUH 25367.

Subfossil finds. The Bælt Sea, Kattegat, Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded from the Subatlantic.

***Musculus laevigatus* (Gray 1824)**

Distribution. E and W Greenland, around Iceland and Norway north of Lofoten.

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. From the infralittoral zone down to 83 m (Poppe & Goto 1993).

Only subfossil finds. Recorded from the Early/Middle Weichselian (the Older *Yoldia* Sea, but not in the Skærumhede sequence) and the Late Weichselian (the Younger *Yoldia* Sea) in the Vendsyssel region.

***Musculus niger* (Gray 1824)**

Distribution. E and W Greenland, around Iceland, the Faeroes, Norway north of Lofoten, and south to the North Sea and the Irish Sea (Madsen 1949; Petersen 1968). In Danish waters the species extends from the North Sea into the Kattegat, Øresund and Bælt Sea as far as Warnemünde (Jensen & Spärck 1934; Jensen & Knudsen 1995).

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. Most often found in Danish waters at water depths of more than 25 m (Jensen & Spärck 1934). Poppe & Goto (1993) indicate from 7 m deep down to about 135 m. However, off the East Greenland coast the species is rarely met with at depths exceeding 40 m (Ockelmann 1958).

Subfossil finds. Recorded from the Vendsyssel region during the Eemian, the Early and Middle Weichselian (the Older *Yoldia* Sea) and the Late Weichselian (the Younger *Yoldia* Sea).

***Modiolaria tumida* (Hanley 1843)**

Distribution. The British Isles and the Shetlands, and south to the Mediterranean (Madsen 1949). In Danish waters the species is very common in the Limfjord, but also in the other fjords, and it extends into the Bælt Sea (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. It is a common shallow-water species in Danish waters (Jensen & Spärck 1934), but goes down to 60 m (Poppe & Goto 1993) associated with tunicates and echinoderms.

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene. Recorded from the North Sea region during the Eemian.

***Crenella decussata* (Montagu 1803)**

Distribution. E and W Greenland, around Iceland, Norway north of Lofoten and south to the British Isles (Madsen 1949; Petersen 1968). In Danish waters the species is found in the Kattegat, including the Øresund.

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. From 4 to 200 m deep on all kinds of bottoms (Poppe & Goto 1993). According to Jensen & Spärck (1934), most common in Danish waters between 15 and 30 m.

Subfossil finds. Recorded in the Kattegat during the Holocene and from the Early and Middle Weichselian (the Older *Yoldia* Sea) in the Vendsyssel region.

***Adipicola simpsoni* (Marshall 1900)**

Distribution. From southern Iceland and south to Portugal and the Mediterranean. Might be found in Danish waters (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. As mentioned by Poppe & Goto (1993, p.

48): “The species has been collected repeatedly on the skulls of whales, where it lies, attached in the sutures, by its byssus”.

Subfossil finds. None.

Order Pteroida

***Chlamys islandica* (O.F. Müller 1776)**

Distribution. SE and W Greenland, around Iceland, Spitsbergen, Norway north of Lofoten, and south to the Shetlands and the Orkney Islands (rare) (Petersen 1968).

Occurrence. The Subarctic and Boreal regions.

Habitat. Around Iceland one of the most common bivalves present from nearly all localities along the NW, N and E coast, both in the fjords and on the outer part of the shelf, at depth from a few metres to 300 m (Madsen 1949). Common in Danish waters from 10 to 100 m (Jensen & Spärck 1934) on rocks and gravel bottoms. Lives attached to hard substrates with its byssus (Poppe & Goto 1993).

Only subfossil finds. Recorded from the Vendsyssel region during the Early and Middle Weichselian (the Older *Yoldia* Sea) and the Late Weichselian (the Younger *Yoldia* Sea).

***Aequipecten opercularis* (Linnaeus 1758)**

Distribution. Norway from north of Lofoten, and south to the Mediterranean (Petersen 1968). In Danish waters the species extends into the Kattegat and Øresund, but is not recorded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone down to 400 m on all types of bottoms except rocky ones (Poppe & Goto 1993).

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene. Recorded from the North Sea region during the Eemian.

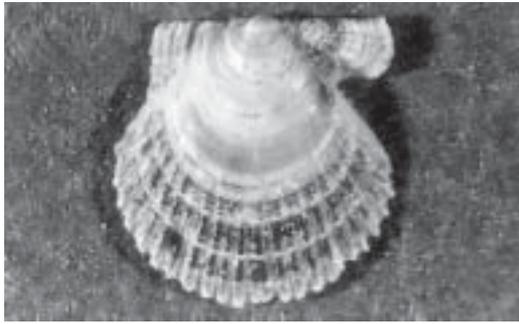


Fig. 58. *Chlamys varia* (Linnaeus 1758). Skagen 3, 32.85–32.90 m b.s., core sample-2. $\times 20$. Right valve. MGUH 25368.

***Chlamys varia* (Linnaeus 1758)**

Fig. 58

Distribution. Norway off the Lofoten islands, and south to the Mediterranean (Petersen 1968). In Danish waters the species occurs in the Limfjord (Jensen & Spärck 1934) and has been recorded juvenile from the Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Intertidal to 83 m, attached by its byssus (Poppe & Goto 1993).

Subfossil finds. The Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded from the Subatlantic. Recorded from the North Sea during the Eemian.

***Delectopecten vitreus* (Gmelin 1791)**

Fig. 59

Distribution. W Greenland, W Iceland, Spitsbergen, Norway north of Lofoten, and south to the British Isles

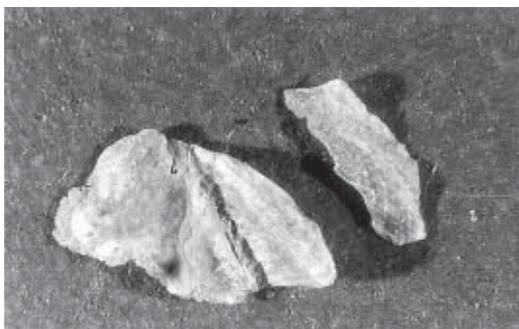


Fig. 59. *Delectopecten* cf. *vitreus* (Gmelin 1791). Skagen 3, 183.17–183.40 m b.s., lab. no. 9E+05. $\times 9.6$. MGUH 25369.

(Madsen 1949), and according to Poppe & Goto (1993) also into the Mediterranean. In Danish waters from the Skagerrak (Jensen & Spärck 1934).

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. Between 30 and 600 m, fixed by its byssus to hard substrates (Poppe & Goto 1993). The species lives in the deeper part of the Skagerrak, from 400 to 600 m, according to Jensen & Spärck (1934).

Subfossil finds. The Limfjord, Holocene. Recorded from the Eemian in the Skagen Well.

***Palliolium greenlandicum* (Sowerby 1842)**

Fig. 60

Distribution. E and W Greenland, N and E Iceland, Spitsbergen, and Norway north of Lofoten (Madsen 1949). However, at depths greater than 400 m the species has been found off the Faeroes and the British Isles.

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. In the Arctic seas living in shallow water from 5 m, but most common between 20 and 70 m on clay bottoms containing stones or shells (Ockelmann 1958).

Only subfossil finds. Recorded from the Vendsyssel region and the Skagen Well during the Early/Middle Weichselian (the Older *Yoldia* Sea).

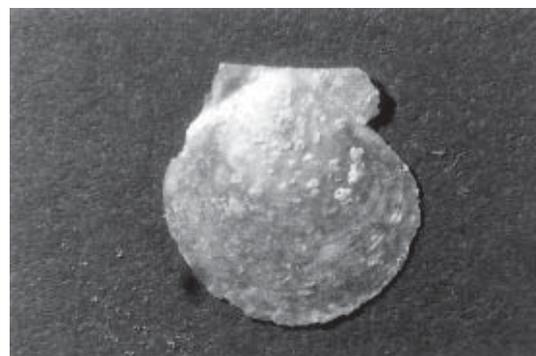


Fig. 60. *Palliolium greenlandicum* (Sowerby 1842). GEUS collection. East Greenland. $\times 4.8$. Right valve. MGUH 25370.

***Palliolium striatum* (Müller 1776)**

Distribution. From S and W Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean. The species extends from the North Sea and Skagerrak into the Kattegat, including Øresund.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From shallow water around 5 m to more than 800 m deep on all types of bottom (Poppe & Goto 1993). The vertical range off Iceland is indicated to lie between 100 and 260 m (Madsen 1949).

Subfossil finds. The Limfjord region, Holocene.

***Palliolium tigrinum* (Müller 1776)**

Distribution. From NW, W and S Iceland, the Faeroes, Norway north of Lofoten, and south to Morocco. In Danish waters from the North Sea and Skagerrak into the Kattegat, including the Øresund.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone down to 400 m, but deeper in the southern part of its range on sandy bottoms (Poppe & Goto 1993).

Subfossil finds. The Limfjord region, Holocene.

***Pecten maximus* (Linnaeus 1758)**

Distribution. Norway off the Lofoten islands and south to Spain. In Danish waters rarely found living in the Kattegat and only shells have been recovered from the Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone down to 250 m on sand and gravel bottoms (Poppe & Goto 1993).

Subfossil finds. Recorded from the Vendsyssel region, Holocene.

***Pseudamussium septemradiatum* (Müller 1776)**

Distribution. S Iceland, Norway from north of the Lofoten islands, and south to the Mediterranean. In Danish waters the species extends from the Skagerrak and

becomes common in the southern Kattegat with finds also in the Øresund (Jensen & Spärck 1934; Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. In general living between 60 and 600 m deep on muddy bottoms (Poppe & Goto 1993). In Danish waters often found between 30 and 60 m.

Subfossil finds. Recorded from the Vendsyssel region during the Eemian.

***Similipecten similis* (Laskey 1811)**

Distribution. S and W Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean (Pettersen 1968). The species extends into the Kattegat from Skagerrak.

Occurrence. The Boreal and Lusitanian regions.

Habitat. Sublittorally between 4 and 250 m deep on sand and fine gravel bottoms (Poppe & Goto 1993). In Danish waters from 30 to 80 m deep (Jensen & Spärck 1934). However, the vertical range around Iceland is 200–320 m (Madsen 1949).

Subfossil finds. Recorded from the Vendsyssel area during the Eemian.

***Pododesmus patelliformis* (Linnaeus 1761)**

Distribution. S and W Iceland, the Faeroes, Norway off the Lofoten islands, and south to the Mediterranean (Madsen 1949). The species extends from the North Sea into the Kattegat, including the Øresund, and occurs also in the Limfjord (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Intertidal to 50 m deep on gravel or rock bottoms, often attached to shells (Poppe & Goto 1993).

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene.

***Pododesmus squama* (Gmelin 1791)**

Distribution. Around the British Isles and from Danish waters the occurrences in the Kattegat and Øresund

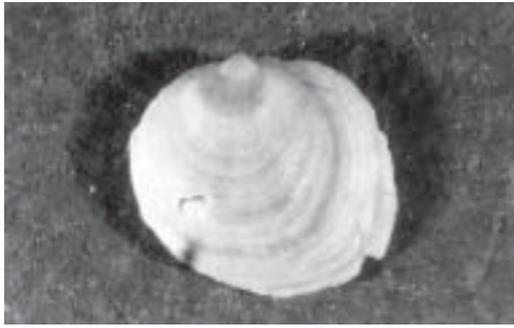


Fig. 61. *Heteranomia squamula* (Linnaeus 1758). Skagen 4, 21.0–21.5 m b.s., lab. no. 346,93. × 20. Left valve. MGUH 25371.

are questioned, although larvae occur (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone to 75 m deep on all types of bottoms attached to hard substrates (Poppe & Goto 1993).

Subfossil finds. None.

***Anomia ephippium* Linnaeus 1758**

Distribution. From the British Isles, including the Orkney Islands, and south to the Mediterranean.

Occurrence. Mainly the Lusitanian region.

Habitat. From the intertidal zone down to 150 m on all kinds of hard substrates.

Only subfossil finds. The Limfjord and the Vendsyssel region, Holocene.

***Heteranomia squamula* (Linnaeus 1758)**

Fig. 61

Distribution. Around Iceland, the Faeroes, Norway north of Lofoten, and south to the Bay of Biscay. The species extends into the Kattegat, Øresund, and occurs in the Limfjord (Jensen & Spärck 1934).

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. From 5 to 110 m deep fixed on hard substrates, but also on algae and crustaceans (Poppe & Goto 1993).

Subfossil finds. The Kattegat, Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded from the Subatlantic. During the Eemian recorded from the Bælt Sea and the North Sea regions.

***Crassostrea gigas* (Gmelin 1791)**

This oyster species from the Portuguese–Spanish region (Poppe & Goto 1993) has been introduced in 1972 as spat for commercial production (Jensen & Knudsen 1995) and is not considered here, although mentioned as now part of the Danish molluscan fauna. No subfossil records either.

***Ostrea edulis* Linnaeus 1758**

Fig. 62a, b

Distribution. From the southern part of the west coast of Norway south to the Mediterranean. In Danish waters only common in the western part of the Limfjord, although stray specimens are found in the northern North Sea, Skagerrak and northern Kattegat (Jensen & Spärck 1934; Jensen & Knudsen 1995).

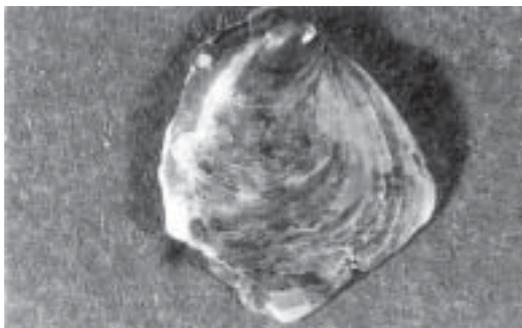


Fig. 62. **a, b:** *Ostrea edulis* Linnaeus 1758. Skagen 4, 8.0–8.5 m b.s., lab. no. 333,93. × 9.6. Left valve of juvenile specimen (exterior and interior, respectively). MGUH 25372.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone down to 90 m on all types of bottoms. In Danish waters the species can be found at depths of 3 to 7 m in the Limfjord, but also deeper elsewhere (Jensen & Spärck 1934).

Subfossil finds. The Bælt Sea, Kattegat, Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. Recorded from the Subatlantic in the Skagen Well. Finds from the Bælt Sea, Kattegat, and North Sea regions during the Eemian.

***Limaria bians* (Gmelin 1791)**

Distribution. Norway north of Lofoten, the Orkney islands and south to the Mediterranean (Petersen 1968). A few records from the northern and central parts of the Kattegat (Jensen & Knudsen 1995). Already Jensen & Spärck (1934) mentioned that the species then known from the deeper parts of the North Sea might occur in Danish waters.

Occurrence. The Boreal and Lusitanian regions.

Habitat. Lives from the low tide mark zone down to 100 m on coarse sand and gravel bottoms (Poppe & Goto 1993).

Subfossil finds. None.

***Limaria loscombi* (Sowerby 1832)**

Distribution. Norway off the Lofoten islands, the Faeroes and south to the Mediterranean (Petersen 1968). Poppe & Goto (1993) mentioned occurrences of *L. bians* and *L. loscombi* off Iceland which, however, cannot be found in the other literature. In Danish waters the species has been found in the Kattegat, including the Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Lives from 35 to 100 m deep on fine sand and sand–mud bottoms (Poppe & Goto 1993). In Danish waters it is characteristic in the south-eastern part of Kattegat together with *Pseudamussium septemradium* (Jensen & Spärck 1934).

Subfossil finds. None.

***Limatula subauriculata* (Montagu 1808)**

Distribution. SE and W Greenland, N and E Iceland, Norway north of Lofoten, and south to the Mediterranean (Petersen 1968). In the Danish waters only shells have been recorded from the northern Kattegat (Jensen & Knudsen 1995).

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. Especially living on the continental shelves. However, records ranges from 4 to 2000 m (Poppe & Goto 1993).

Subfossil finds. None.

Subclass Heterodonta

Order Veneroida

***Chama gryphoides* Linnaeus 1767**

This Lusitanian species (up to the coasts of Portugal) has only one record from Danish waters (Jensen & Knudsen 1995), and this is considered to have been dropped by a ship. Therefore it will not be discussed. No subfossil records.

***Lucinella divaricata* (Linnaeus 1758)**

Distribution. From the English Channel and southern part of the North Sea south to the Mediterranean.

Occurrence. Mainly the Lusitanian region.

Habitat. From the tidal zone down to a depth of 60 m in fine sand and/or mud (Poppe & Goto 1993).

Only subfossil finds. The Eemian in the Bælt Sea, Kattegat, and North Sea regions.

***Lucinoma borealis* (Linnaeus 1758)**

Distribution. The Faeroe islands, Norway from off Lofoten, and south to the Mediterranean (Petersen 1968). In Danish waters the species occurs in the Kattegat, including the Øresund, but is not recorded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone down to 500 m deep on gravel bottoms and in pure sand and/or mud (Poppe & Goto 1993). In Danish waters between 20 and 50 m (Jensen & Spärck 1934).

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene.

***Myrtea spinifera* (Montagu 1803)**

Distribution. From Norway south to Morocco. In Danish waters recorded from the northern Kattegat (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 7 to 250 m deep on sand, mud and gravel bottoms (Poppe & Goto 1993).

Subfossil finds. None.

***Axinopsida orbiculata* (G.O. Sars 1878)**

Distribution. E and W Greenland, around Iceland, the Faeroes, and Norway north and just south of the Lofoten Islands (Petersen 1968). The species occurs off the north western part of Scotland.

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. From 2 to 50 m deep on sand, clay and mud around Iceland (Madsen 1949). North of the Hebrides occurring at depths down to 900 m (Jensen & Spärck 1934).

Only subfossil finds. The Vendsyssel region from the Early and Middle Weichselian (the Older *Yoldia* Sea) and the Late Weichselian (the Younger *Yoldia* Sea).

***Thyasira croulinensis* (Jeffreys 1847)**

Distribution. W Greenland, around Iceland, the Faeroes, Norway north of Lofoten (Petersen 1968), and south to the Mediterranean (Poppe & Goto 1993). In Danish waters taken in the North Sea and Skagerrak.

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. About 40 to 2500 m off the Faeroes on gravel

and clay (Petersen 1968). In Danish waters the species is found in the deeper water (Jensen & Spärck 1934).

Subfossil finds. None.

***Thyasira equalis* (Verrill & Bush 1898)**

Distribution. It is questioned by Nordsieck (1969, p. 79) if *T. equalis* should be *Thyasira flexuosa* var. *rotunda*. There are no subfossil finds under the name of *T. equalis*, so this species will not be considered any further. However, as discussed by Ockelmann (1958, p. 100) a species, *T. equalis*, does occur in the Arctic, while *T. flexuosa* has a Boreo-Lusitanian main distribution.

***Thyasira flexuosa* (Montagu 1803)**

Fig. 63

Distribution. E and W Greenland, Spitsbergen, around Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean. In the Danish waters it is very common and extends into the Øresund (Jensen & Knudsen 1995), but is not recorded from the Limfjord (Petersen 1986a).

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian regions (see comments under *T. equalis*).

Habitat. From 10 to 2000 m deep on sand and mud bottoms (Poppe & Goto 1993). In Danish waters from 20 m to around 100 m deep on clay bottoms (Jensen & Spärck 1934). From the North Sea recorded at 30 to 200 m depths on mixed bottom in the trenches around the Dogger Bank (Petersen 1977).

Subfossil finds. The Limfjord, North Sea, Vendsyssel



Fig. 63. *Thyasira flexuosa* (Montagu 1803). Skagen 3, 35.90–36.00 m b.s., lab. no. 496,93. × 9.6. Left valve. MGUH 25373.

and Skagen regions, Holocene. From the Skagen Well recorded from the Subatlantic. From the North Sea during the Eemian and in the Vendsyssel region recorded from the Late Weichselian (the Younger *Yoldia* Sea).

***Thyasira sarsi* (Philippi 1845)**

Distribution. From Novaja Semlja along the coast of Norway south to the Skagerrak region. The species extends into the Kattegat, including the Øresund (Jensen & Knudsen 1995).

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. From 100 m to deep water.

Subfossil finds. None.

***Leptaxinus ferruginosus* (Forbes 1844)**

Distribution. W Greenland, W Iceland, Spitsbergen, Norway off the Lofoten islands, and southwards to Madeira (Madsen 1949). Jensen & Spärck (1934) mentioned the species from the deeper part of the Skagerrak, but Jensen & Knudsen (1995) have no further record of this species as belonging to the recent Danish fauna.

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian regions.

Habitat. About 20 m to more than 3000 m. The vertical range off Iceland is 320–560 m. So here is another example of tropical submerge (see Order Mesogastropoda *Natica affinis*).

Subfossil finds. Recorded from the Vendsyssel region during the Eemian.

***Mysella bidentata* (Montagu 1803)**

Fig. 64

Distribution. Around Iceland, the Faeroes, Norway from north of Lofoten, and south to West Africa (Petersen 1968). The species has a common distribution in Danish waters, including the Limfjord, south to the Bælt Sea by Warnemünde (Arntz *et al.* 1976), and the Øresund (Jensen & Spärck 1934). Also found in the North Sea (Petersen 1977).

Occurrence. The Subarctic, Boreal and Lusitanian regions.

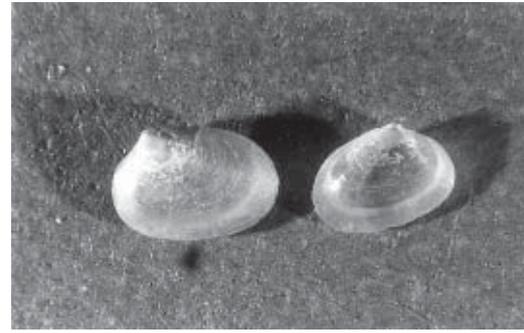


Fig. 64. *Mysella bidentata* (Montagu 1803). Skagen 4, 27.0–27.5 m b.s., lab. no. 352,93. × 9.6. To the left a specimen seen from the right, and to the right a left valve. MGUH 25374.

Habitat. Intertidal zone down to 2500 m, often in commensal association with other animals. In the North Sea it is recorded from 20 to 90 m as a commensal on for example, *Acrocnida brachiata* (Petersen 1977).

Subfossil finds. The Bælt Sea, Kattegat, Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen Well, records from the Preboreal–Boreal, Subboreal and Subatlantic. From the Bælt Sea, Baltic, North Sea and Vendsyssel regions also recorded from the Eemian.

***Mysella tumidula* (Jeffreys 1867)**

Distribution. This species is recorded by Jensen & Knudsen (1995) as being part of the Danish fauna, although it seems to have a purely Lusitanian distribution (Poppe & Goto 1993). The species has no subfossil occurrence.

***Montacuta substriata* (Montagu 1803)**

Distribution. W Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean. In Danish waters rarely found in the North Sea, Skagerrak and Kattegat.

Occurrence. The Boreal and Lusitanian regions.

Habitat. Off Iceland the vertical range is between 31 and 165 m (Madsen 1949). In Danish waters out to depths of around 700 m (Skagerrak) reported as a commensal on *Spatangus purpureus* (Jensen & Spärck 1934) and from the North Sea also on *Echinocardium flavescens* at depths from 30 to 100 m (Petersen 1977).

Subfossil finds. None.



Fig. 65. *Tellimya ferruginosa* (Montagu 1803). Skagen 4, 27.0–27.5 m b.s., lab. no. 352,93. $\times 9.6$. To the left interior of a right valve, and to the right a specimen seen from the left. MGUH 25375.

***Tellimya ferruginosa* (Montagu 1803)**

Fig. 65

Distribution. Around Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean. In Danish waters the species extends from the North Sea, Limfjord, and Skagerrak into the Kattegat and Øresund (Jensen & Spärck 1934).

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. In general the species is most common just below the tidal zone, which according to Poppe & Goto (1993) is the preferred habitat of *Echinocardium* with which *T. ferruginosa* is often associated. However, the species is also found on *Brissopsis lyrifera* or living by itself (Jensen & Spärck 1934). Accordingly, the depth range may vary, around Iceland being between 32 and 80 m (Madsen 1949).

Subfossil finds. The Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. The records from the Skagen Well are from the Subboreal and Subatlantic. Furthermore, the species has been recorded from the Bælt Sea and North Sea during the Eemian.

***Mysella dawsoni* (Jeffreys 1864)**

Distribution. Petersen (1888, p. 154) mentioned a single find from the Limfjord, and the species is mentioned by Petersen (1986a) on the basis of the tables on molluscan finds in the Limfjord from Danmarks Fiskeri- og Havundersøgelser (Petersen 1976). However, it is not cited among the recent Danish species

by Jensen & Knudsen (1995). The species is mentioned from W Greenland (Thorson 1951) and south to the Mediterranean (Poppe & Goto 1993), and also from Spitsbergen and the west coast of Norway (Jensen & Spärck 1934).

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian regions.

Habitat. Deep-living species, but mentioned from a depth of 5 m by Posselt & Jensen (1898) and in sandy bottom in West Greenland.

Subfossil finds. None.

***Tellimya tenella* (Lovén 1846)**

Cited only from the Kattegat, including the Øresund, by Jensen & Knudsen (1995). No subfossil finds. Will not be considered further.

***Turtonia minuta* (Fabricius 1780)**

Fig. 66

Distribution. W Greenland, around Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean.

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. Lives in the tidal zone among plants and algae on rocks (Poppe & Goto 1993). Off Iceland in the tidal zone all around the island, but also down to a depth of 50 m (Petersen 1968).

Only subfossil finds. The Limfjord, Vendsyssel and



Fig. 66. *Turtonia minuta* (Fabricius 1780). Skagen 3, 39.85–40.02 m b.s., lab. no. 711,93. $\times 40$. Right valve. MGUH 25376.

Skagen regions, Holocene. Recorded from the Subatlantic in the Skagen Well.

***Lepton nitidum* (Turton 1822)**

Distribution. From the Faeroes, western Norway, and south to the Mediterranean (Jensen & Spärck 1934; Madsen 1949). Only recently recorded from the northern Kattegat and Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 18 to 216 m, commensal on the crustaceans *Upogebia deltaura* and *Gebia stellata* (Nordsieck 1969, p. 89).

Subfossil finds. The Limfjord, North Sea and Vendsyssel regions, Holocene. Recorded from the Eemian in the Bælt Sea and North Sea areas.

***Lepton squamosum* (Montagu 1803)**

Distribution. From the west coast of Norway and south to Spain. Only shells have been found in Danish waters (northern Kattegat) mentioned by Jensen & Knudsen (1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 10 to 120 m deep it lives in and around the burrows of the crustaceans (*Upogebia deltaura* and *U. stellata*) on mud or gravel bottoms (Poppe & Goto 1993).

Subfossil finds. None.

***Devonia perrieri* (Malard 1904)**

Distribution. From the British Isles south to Spain. In Danish waters recorded from the northern Kattegat (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. This species is a commensal on *Leptosynapta inbaerens* (Nordsieck 1969, p. 95).

Subfossil finds. None.

***Kellia suborbicularis* (Montagu 1803)**

Distribution. S and W Iceland, the Faeroes, Norway off the Lofoten islands and south to the Mediterranean. In Danish waters recorded from the northern Kattegat and Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Intertidal to 120 m deep in crevices, shells or in borings made by other species (Poppe & Goto 1993).

Subfossil finds. Recorded from the Vendsyssel region, Holocene.

***Potidoma dorkiae* (Clark 1852)**

This species has been recorded only in a single find by Jensen & Knudsen (1995), and there are no subfossil finds from the literature, so it will not be considered further.

***Astarte sulcata* (da Costa 1778)**

Distribution. SE and W Greenland, S and W Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean. The species extends from the North Sea into the Kattegat, but is not common (Jensen & Spärck 1934).

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. Sublittorally from 20 m and deeper on sand, mud and gravel bottoms.

Subfossil finds. None.

***Tridonta borealis* Schumacher 1817**

Distribution. This species is found in all regions of the north Atlantic except the British Isles (Madsen 1949). However, according to Petersen (1968) the species has not been recorded from the Faeroes. In the Danish waters the species extends from the deeper part of the northern North Sea (single finds) into the Kattegat, including the Øresund and the Bælt Sea, becoming very common in the Baltic (Jensen & Spärck 1934).

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. From below the tidal zone down to 250 m on mud, sand and gravel bottoms. The species is “a common member of all the zones of the Arctic *Macoma* community, and the *Gomphina fluctuosa* community” (Ockelmann 1958, p. 83).

Subfossil finds. The Bælt Sea and Limfjord regions, Holocene. Recorded from the Vendsyssel region both in the Early/Middle Weichselian (not in the Skærumhede sequence) and the Late Weichselian (the Older *Yoldia* Sea and the Younger *Yoldia* Sea respectively).

***Tridonta elliptica* (Brown 1827)**

Distribution. This species is found in all regions of the north Atlantic, including the British Isles (Madsen 1949). Petersen (1968) specified the occurrence of this species to be in the Clyde Sea and off the Isle of Man only. In the Danish waters it occurs in the Kattegat, Øresund, the Bælt Sea and the Baltic, where it becomes as common as *T. borealis* (Jensen & Spärck 1934).

Occurrence. The Arctic, Subarctic and Boreal regions. Considering the occurrences on the west coast of Britain it is also in the northern part of the Lusitanian region, but here probably mostly in deeper water.

Habitat. The vertical range for this species is off Iceland 6 to 300 m (Madsen 1949), and off the East Greenland coast it is most often taken between about 5 and 50 m, being abundant locally within the Arctic *Macoma* community (Ockelmann 1958).

Subfossil finds. Recorded from the North Sea during the Eemian, and in Vendsyssel during the Early/Middle Weichselian, being part of the Older *Yoldia* Sea found in the Skærumhede sequence (Jessen *et al.* 1910).

***Tridonta montagui* (Dillwyn 1817)**

Distribution. E and W Greenland, around Iceland, Spitsbergen, the Faeroes, Norway from north of Lofoten, and south to the Clyde Sea and Isle of Man (Petersen 1968), also recorded from the Bay of Biscay. It is present in the north western part of the North Sea (Petersen 1977) and common in the Kattegat, Øresund and extending into the Bælt Sea (Jensen & Spärck 1934).

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian regions.

Habitat. The vertical range off Iceland is 7–150 m (Madsen 1949) and in the North Sea sampled at depths between 40 and 75 m on mixed bottom in the trenches around the Dogger Bank (Petersen 1977, p. 226).

Subfossil finds. Recorded from the North Sea region during the Eemian and from the Vendsyssel area during the Early/Middle Weichselian (the Older *Yoldia* Sea).

***Acanthocardia echinata* (Linnaeus 1758)**

Fig. 67

Distribution. S and W Iceland, Norway north of Lofoten, and south to the Mediterranean (Madsen 1949). In Danish waters the species extends from the North Sea (Petersen 1977) into the Skagerrak, Limfjord, and Kattegat regions and the Øresund (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 4 to 350 m deep on mud, sand and gravel bottoms (Poppe & Goto 1993).

Subfossil finds. The Kattegat, Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded from the Subboreal and Subatlantic. There are Eemian records from the Bælt Sea, Kattegat, North Sea and Vendsyssel regions.

***Parvicardium exiguum* (Gmelin 1791)**

Distribution. Norway north of Lofoten and south to the Mediterranean (Madsen 1949). In Danish waters common in bays and fjords, including the Limfjord. Considering all the variations belonging to the same species it extends into the Bælt Sea (Petersen 1888).

Occurrence. The Boreal and Lusitanian regions.



Fig. 67. *Acanthocardia echinata* (Linnaeus 1758). Skagen 4, 27.0–27.5 m b.s., lab. no. 352,93. × 20. Right valve. MGUH 25377.

Habitat. In general occurring from low tide to about 55 m deep (Poppe & Goto 1993); however, according to Rasmussen (1973) the species has its main occurrence along the shores and is associated with vegetation.

Subfossil finds. The Bælt Sea, Baltic, Kattegat, Limfjord, North Sea and Vendsyssel regions, Holocene. Recorded also from the Bælt Sea, Kattegat, and North Sea regions during the Eemian.

***Parvicardium hauniense* (Petersen & Russell 1971)**

Distribution. This newly established species has been recorded from recent Danish waters, but no subfossil records are at hand.

***Parvicardium ovale* (Sowerby 1840)**

Distribution. Around Iceland, Norway north of Lofoten, and south to the Mediterranean (Madsen 1949). In Danish waters the species is found in all the regions except the Baltic extending only to Darss (Jensen & Spärck 1934).

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. According to the Icelandic records (Madsen 1949) found between 5 to 350 m on bottoms such as mud, sand, clay and shell gravel with stones.

Subfossil finds. The Bælt Sea, Limfjord, North Sea and Vendsyssel regions, Holocene. From the North Sea and Vendsyssel regions also recorded from the Eemian.

***Parvicardium scabrum* (Philippi 1844)**

Distribution. From Norway north of the Lofoten islands, and south to the Mediterranean (Madsen 1949). In Danish waters common in the Limfjord (Jensen & Spärck 1934) and recorded from the Kattegat, but questioned, as there may be two separate species (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone to several hundred metres deep on sand, mud and gravel bottoms (Poppe & Goto 1993).

Subfossil finds. The Bælt Sea, Kattegat, Limfjord, North Sea and Vendsyssel regions, Holocene. Recorded from the North Sea during the Eemian.

***Plagiocardium papillosum* (Poli 1795)**

Distribution. From the English Channel south into the Mediterranean (Poppe & Goto 1993).

Occurrence. The Lusitanian region.

Habitat. From 1 to 60 m deep on rough sand and gravel bottoms.

Only subfossil finds. Recorded from the Eemian in the North Sea region.

***Parvicardium minimum* (Philippi 1836)**

Fig. 68

Distribution. S and W Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean at greater depths. In Danish waters common in the deeper part of the Skagerrak extending into the Kattegat, including the Øresund (Petersen 1888). The occurrence in the Limfjord is questioned (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 4 to 161 m on mud, sand and gravel bottoms (Poppe & Goto 1993). However, according to Madsen (1949) the species has around Iceland only been found at depths of more than 75 m, and the bottoms are recorded as sand with shells and stones or as ooze and clay. In Danish waters the species prefers



Fig. 68. *Parvicardium minimum* (Philippi 1836). GEUS collection. North of Skagen, Denmark. × 9.6. Specimen seen from the right. MGUH 25378.

depths of more than about 30 m, and it occurs at the greatest depth (Petersen 1888).

Subfossil finds. The North Sea and Skagen regions, Holocene. Recorded from the Skagen Well during the Preboreal–Boreal, the Atlantic, Subboreal and Subatlantic. From the Vendsyssel region recorded from the Eemian.

***Cerastoderma edule* (Linnaeus 1758)**

Distribution. Norway north of the Lofoten islands, and south to the Mediterranean (Madsen 1949). In Danish waters found in all regions (Petersen 1888, p. 136 – who already stressed that it is a very variable species).

Occurrence. The Boreal and Lusitanian regions.

Habitat. This is a shallow-water infaunal species – intertidal to few metres deep, but in the Baltic occurring also at 20–30 m depths (Jensen & Spärck 1934) on sandy bottoms.

Subfossil finds. The Bælt Sea, Baltic, Kattegat, Limfjord, North Sea and Vendsyssel regions, Holocene. From the Eemian recorded in the Bælt Sea, Baltic, Kattegat and North Sea regions.

***Cerastoderma glaucum* (Poiret 1789)**

Distribution. From the west coast of Norway south to the Mediterranean (Poppe & Goto 1993, pp. 95–96). In Danish waters the species extends into the Baltic (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. This is a shallow-water species on sand and mud bottoms. However, according to studies on subfossil material (Rasmussen 1973, p. 298–302), the associated fauna indicates a tidal estuarine environment for the Danish material of an Ertebølle age in the Isefjord.

Subfossil finds. The Baltic, Kattegat and Limfjord regions, Holocene. However, the species identifications on the subfossil material recorded through time should be taken with some reservation on the basis of the great difficulties connected with recent species identifications.

***Clinocardium ciliatum* (Fabricius 1780)**

Distribution. W and E Greenland, Spitsbergen, around Iceland and Norway north of the Lofoten islands. From the Faeroes only at depths exceeding 400 m (Petersen 1968).

Occurrence. The Arctic, Subarctic and Boreal (High-Boreal) regions.

Habitat. From the tidal zone down to 700 m, off Iceland occurring on ooze, mud, clay, sand and mixed bottoms (Madsen 1949). Mainly found in the Arctic *Macoma* community (Ockelmann 1958).

Only subfossil finds. From the Vendsyssel region recorded both from the Eemian and from the Early/Middle Weichselian (the Older *Yoldia* Sea).

***Laevicardium crassum* (Gmelin 1791)**

Distribution. From Norway north of the Lofoten islands and south to the Mediterranean. In Danish waters only recorded from the North Sea (Petersen 1977) and the northern part of the Kattegat (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone down to 183 m deep on sand, mud or gravel bottoms.

Subfossil finds. The Vendsyssel region, Holocene. From the Eemian recorded in the Kattegat region.

***Serripes groenlandicus* (Bruguère 1798)**

Distribution. W and E Greenland, Spitsbergen, around Iceland and Norway north of Lofoten. From the Faeroes only at depths exceeding 400 m (Petersen 1968).

Occurrence. The Arctic, Subarctic and Boreal (High-Boreal) regions.

Habitat. From 0 to 1 m to 120 m deep on clay and mud, but also sand and gravel are recorded (Madsen 1949).

Subfossil finds. From the Vendsyssel area during the Eemian and Early/Middle Weichselian.

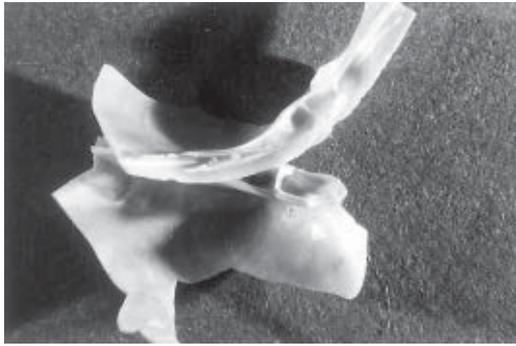


Fig. 69. *Mactra stultorum* (Linnaeus 1758). Skagen 4, 15.0–15.5 m b.s., lab. no. 340,93. $\times 4.8$. Hinges of two right valves. MGUH 25379.

***Mactra stultorum* (Linnaeus 1758)**

Fig. 69

Distribution. From the British Isles and Denmark south to the Mediterranean (Petersen 1968). In the Danish waters the species is common in the North Sea and Skagerrak, extending into the Limfjord (Petersen 1986a), Kattegat and Øresund, although here only juveniles are present (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone down to 60 m in clean sand.

Subfossil finds. The Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded from the Subatlantic. During the Eemian recorded from the Bælt Sea region.

***Lutraria lutraria* (Linnaeus 1758)**

Distribution. Norway off the Lofoten islands and south to the Mediterranean. Since 1990 live specimens have been taken in Danish waters near Frederikshavn and at the Skagerrak coast (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Intertidal down to 100 m, lives at depths up to 35 cm, burrowing in sand, sand–mud or gravel bottoms (Poppe & Goto 1993).

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene.

***Spisula elliptica* (Brown 1827)**

Distribution. Around Iceland, the Faeroes, Norway north of Lofoten, and south to the English Channel and Gibraltar. The species occurs in the North Sea, extending into the Limfjord and Kattegat and the Øresund (Jensen & Knudsen 1995).

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. Between 20 and 200 m deep in mud, sand and gravel bottoms.

Subfossil finds. The Limfjord, North Sea and Vendsyssel regions, Holocene. From the Bælt Sea region recorded during the Eemian.

***Spisula solida* (Linnaeus 1758)**

Distribution. S and W Iceland, and south to the Mediterranean (Petersen 1968). In Danish waters very common offshore from the west coast of Jylland (Jensen & Knudsen 1995 – as recorded by Petersen 1977, fig. 25). The species extends into the Limfjord (Petersen 1986a) and Kattegat, including the Øresund and the Bælt Sea regions (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone down to 100 m on sandy bottoms. In the North Sea found at 15–40 m depths in coarse sand (Petersen 1977).

Subfossil finds. The Limfjord, North Sea and Vendsyssel regions, Holocene. Recorded from the Kattegat during the Eemian.

***Spisula subtruncata* (da Costa 1778)**

Fig. 70a, b

Distribution. Norway north of the Lofoten islands, and south to the Mediterranean (Petersen 1968). In Danish waters the species extends from the North Sea into the Kattegat, where it is also common. The species has been recorded both from the Øresund and the Bælt Sea (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the Intertidal zone down to 200 m deep

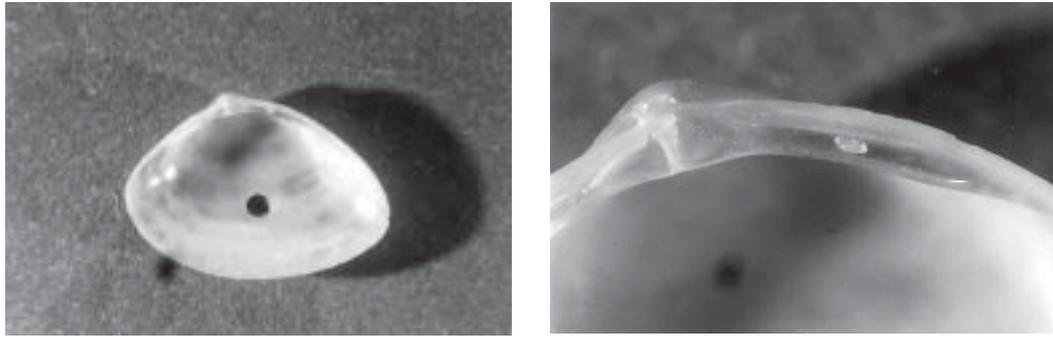


Fig. 70. **a:** *Spisula subtruncata* (da Costa 1778). Skagen 4, 15.0–15.5 m b.s., lab. no. 340,93. $\times 4.8$. Right valve interior. MGUH 25380. **b:** *Spisula subtruncata* (da Costa 1778). Skagen 4, 15.0–15.5 m b.s., lab. no. 340,93. $\times 20$. Serrated surfaces of paired right valve laterals. MGUH 25380.

in mud and sand (Poppe & Goto 1993). In Danish waters common at depths out to 20–30 m in sand (Jensen & Spärck 1934).

Subfossil finds. The Bælt Sea, Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded from the Atlantic, Subboreal and Subatlantic; in the Subatlantic occurring in huge quantities. From the Eemian recorded from the Bælt Sea, Baltic and Kattegat regions.

***Solecurtus chamasolen* (da Costa 1778)**

Distribution. Norway off the Lofoten islands, and south to the Mediterranean. In the Danish waters shells have been found near Frederikshavn (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 5 to 400 m deep on muddy bottoms.

Subfossil finds. None.

***Solecurtus scopula* (Turton 1822)**

Distribution. From the British Isles and south to the Mediterranean. Shells recorded from the northern Kattegat (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Mainly offshore to 110 m deep in muddy sand and on clean gravel bottoms (Poppe & Goto 1993).

Subfossil finds. None.

***Ensis americanus* Gould 1870**

Distribution. At present occurring down to the Øresund. However, the species has recently accidentally been transported to western Europe from the east coast of North America (Jensen & Knudsen 1995), so it will not be further considered.

***Ensis arcuatus* (Jeffreys 1865)**

Distribution. The Faeroes, the British Isles and south to Spain. In Danish waters shells have been recorded from the Kattegat region, including the Øresund.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone to 40 m deep in sand and gravel bottoms.

Subfossil finds. None.

***Ensis ensis* (Linnaeus 1758)**

Distribution. The Faeroes, Norway north of Lofoten, and south to the Mediterranean (Petersen 1968). The species extends from the North Sea east to the Limfjord and Kattegat regions, including the Øresund (Jensen & Spärck 1934; Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone to about 80 m deep, burrowing in fine sand (Poppe & Goto 1993). From the North Sea mainly recorded from depths of 20–30 m on the Dogger Bank and along the west coast of Jylland (Petersen 1977, fig. 40).



Fig. 71. *Phaxas pellucidus* (Pennant 1777). Skagen 4, 27.0–27.5 m b.s., lab. no. 352,93. × 9.6. View of the inside of a left valve above and a right valve below (valves not paired). MGUH 25381.

Subfossil finds. The Limfjord, North Sea and Vendsyssel areas, Holocene. During the Eemian recorded from the Bælt Sea, North Sea and the Vendsyssel regions.

***Ensis siliqua* (Linnaeus 1758)**

Distribution. Norway from north of Lofoten, and south to the Mediterranean. In Danish waters, the species is recorded from the North Sea, Kattegat and Øresund (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone to about 70 m deep in fine sand.

Subfossil finds. None.

***Phaxas pellucidus* (Pennant 1777)**

Fig. 71

Distribution. Norway off the Lofoten islands, and south to the Mediterranean (Madsen 1949). In Danish waters the species extends into the Limfjord and Kattegat, Øresund and Bælt Sea regions (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Found offshore between 4 and 150 m deep in sand, mud and gravel bottoms (Poppe & Goto 1993). In the North Sea it is abundant in the whole area, mainly from depths of 30–50 m (Petersen 1977).

Subfossil finds. The Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded from the Subboreal and Subatlantic. During

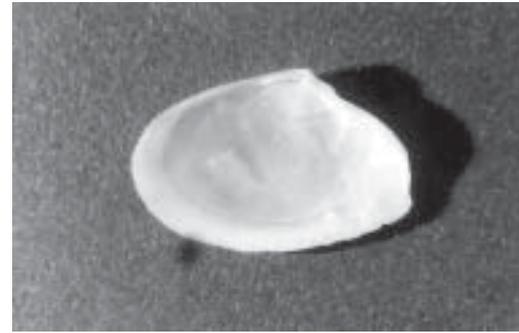


Fig. 72. *Angulus tenuis* (da Costa 1778). Skagen 4, 6.0–6.5 m b.s., lab. no. 331,93. × 4.8. View of the inside of a right valve. MGUH 25382.

the Eemian found in the North Sea and Vendsyssel regions.

***Angulus tenuis* (da Costa 1778)**

Fig. 72

Distribution. Norway off the Lofoten islands, and south to the Mediterranean (Madsen 1949). In Danish waters the species extends from the North Sea, where it is common in shallow waters, into the Kattegat and Limfjord regions (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Common in shallow water down to 10–20 m deep in fine sand.

Subfossil finds. The Bælt Sea, Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded from the Subatlantic. During the Eemian found in the Bælt Sea and North Sea regions.

***Arcopagia crassa* (Pennant 1778)**

Distribution. From Norway south to West Africa. Only one record from Danish waters other than empty shells (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone down to 150 m deep in sand, mud and shell gravel bottoms (Poppe & Goto 1993).

Subfossil finds. None.

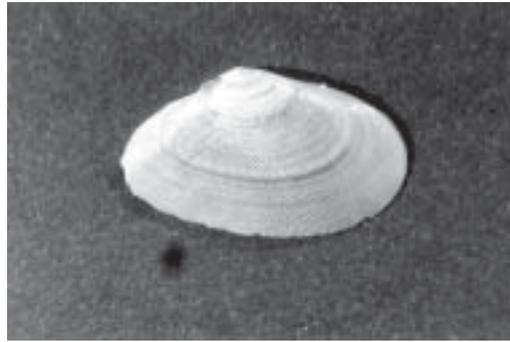
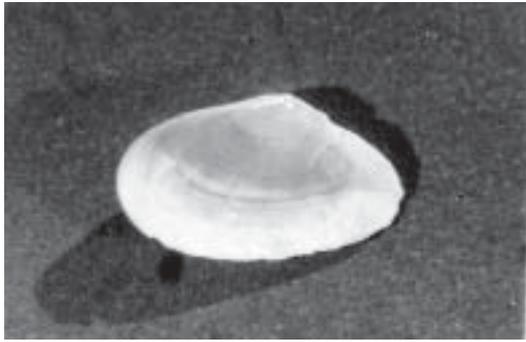


Fig. 73. **a:** *Fabulina fabula* (Gmelin 1791). Skagen 4, 6.0–6.5 m b.s., lab. no. 331,93. $\times 4.8$. View of the inside of a right valve. MGUH 25383. **b:** $\times 4.8$. Right valve exterior with diagonal lines running from the upper right to the lower left superimposed upon sculpture of concentric lines. MGUH 25383.

***Tellina donacina* Linnaeus 1758**

Distribution. From the Shetlands over the British Isles and south into the Mediterranean (Poppe & Goto 1993). The species occurs in the southern North Sea and has been recorded off Edinburgh (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the low-tide mark to 200 m deep in sand, mud and gravel bottoms.

Only subfossil finds. Recorded from the North Sea during the Eemian.

***Fabulina fabula* (Gmelin 1791)**

Fig. 73a, b

Distribution. Norway of the Lofoten islands, and south to the Mediterranean (Madsen 1949). The species extends into Danish waters from the North Sea to the Kattegat and Limfjord regions (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone to 50 m deep in fine sand. In Danish waters common on sand between 5–25 m, but it has been taken at depths of 40 m (Jensen & Spärck 1934).

Subfossil finds. The Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded from the Subatlantic. From the Eemian recorded from the North Sea.

***Tellina pygmaea* (Lovén 1846)**

Fig. 74

Distribution. The Faeroes, Norway north of Lofoten, and south to the Mediterranean (Madsen 1949). The species extends from the North Sea into the Kattegat and Øresund (Jensen & Knudsen 1995). Uncertain in the records from the Limfjord (Collin 1884, p. 113).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone to depths of 100 m. In the North Sea found at depths of 30–50 m on hard bottoms (Petersen 1977).

Subfossil finds. From the Skagen Well recorded from the Subatlantic.

***Gastrana fragilis* (Linnaeus 1758)**

Distribution. From the British Isles including the Shetlands, and south to the Mediterranean.

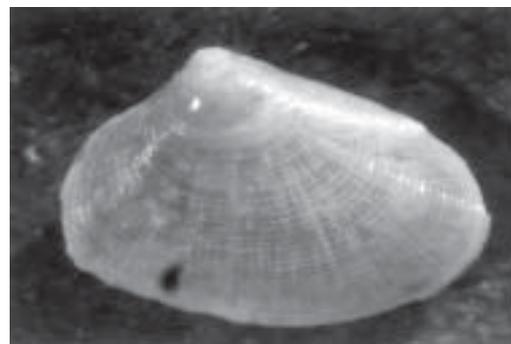


Fig. 74. *Tellina pygmaea* (Lovén 1846). Skagen 4, 27.0–27.5 m b.s., lab. no. 352,93. $\times 40$. Right valve. MGUH 25384.

Occurrence. Mainly the Lusitanian region.

Habitat. From below the tidal zone to a depth of 750 m in sand, mud and gravel bottoms (Poppe & Goto 1993).

Subfossil finds. Recorded from the Bælt Sea, Kattegat and the North Sea during the Eemian.

***Macoma balthica* (Linnaeus 1758)**

Distribution. W Greenland, Norway from north of Lofoten, and south to the British Isles (Petersen 1968) and Spain (Poppe & Goto 1993). The species is found in all the regions and extends far into the Baltic, but it is not common in the North Sea region from Blåvandshuk and north to Skagen (Jensen & Spärck 1934).

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. This is a shallow-water species, but in the Baltic occurs also at depths of more than 50 m on soft bottoms (Muus 1967, p. 163). The species is also the characterising animal of the Petersen *Macoma balthica* community so often found in the inner Danish waters. However, Muus (*op. cit.*, pp. 215–217) discussed the problem concerning this community in further detail and concluded that Petersen's community can be considered a serviceable way of giving a brief description of a faunal region for other marine biologists.

Subfossil finds. The Bælt Sea, Baltic, Kattegat, Limfjord, North Sea and Vendsyssel regions, Holocene. Recorded from the Bælt Sea, Baltic, and the North Sea during the Eemian, and from the Vendsyssel area during the Late Weichselian.

***Macoma calcarea* (Gmelin 1791)**

Distribution. W and E Greenland, Spitsbergen, around Iceland, the Faeroes, Norway from north of Lofoten (Madsen 1949), and south into the North Sea, Kattegat, Bælt Sea and Baltic (Jensen & Spärck 1934).

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. From the intertidal zone down to several hundred metres in the southern part of the distribution area. The species is the characteristic animal of the Arctic *Macoma* community (Thorson 1957).

Subfossil finds. From the Vendsyssel region, Holocene. Recorded from the Baltic and the Vendsyssel regions during the Eemian, from the Kattegat and Vendsyssel regions during the Early/Middle Weichselian (the Older *Yoldia* Sea stage), and finally from the Vendsyssel region also during the Late Weichselian (the Younger *Yoldia* Sea stage).

***Macoma torelli* (Steenstrup) Jensen 1904**

Distribution. E and W Greenland and Spitsbergen. According to Ockelmann (1958) this species is regarded as having a high-Arctic main distribution and being restricted to the N Atlantic sector.

Occurrence. The Arctic region.

Habitat. Recorded rarely from Greenland sublittorally out to 90 m deep on clay and gravel (Ockelmann 1958).

Subfossil finds. Recorded from the Vendsyssel region during the Late Weichselian (the Younger *Yoldia* Sea).

***Macoma loveni* (Steenstrup) Jensen 1904**

Distribution. W and E Greenland and Spitsbergen. According to Ockelmann (1958), the main distribution is high-Arctic with low-Arctic outposts.

Occurrence. The Arctic and Subarctic regions.

Habitat. At East Greenland the vertical range of the species has been recorded from 4–5 m to 207 m, and the species has been taken from various types of bottoms: clay, mud, sand, gravel and stony ones (Ockelmann 1958).

Subfossil finds. The Vendsyssel region during the Late Weichselian (the Younger *Yoldia* Sea).

***Donax vittatus* (da Costa 1778)**

Fig. 75

Distribution. Norway off the Lofoten islands, and south to the Mediterranean (Madsen 1949). This species is found on the southern part of the Dogger Bank and along the west coast of Jylland (Petersen 1977) but not in the inner Danish waters (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.



Fig. 75. *Donax vittatus* (da Costa 1778). GEUS collection. Hol-land. × 4.8. View of the inside of a right valve. MGUH 25385.

Habitat. From the tidal zone down to 20 m in clean sand. One of the few molluscan species well suited to live in the coastal zone of sandy beaches.

Subfossil finds. The Limfjord on old beach ridges facing the Skagerrak (Petersen 1976), North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded from the Subatlantic. Found in the North Sea during the Eemian.

***Gari depressa* (Pennant 1777)**

Distribution. Norway off the Lofoten islands, and south to the Mediterranean.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone down to about 50 m in sand, mud and gravel bottoms.

Subfossil finds. The Vendsyssel region, Holocene.

***Gari fervensis* (Gmelin 1791)**

Fig. 76

Distribution. W Greenland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean (Petersen 1968). In the North Sea the species is most common on the Dogger Bank (Petersen 1977) and extends through the Skagerrak into the Kattegat and Øresund (Jensen & Spärck 1934).

Occurrence. The Subarctic, Boreal and Lusitanian regions.

Habitat. From the tidal zone to a depth of 110 m in coarse sand and shell gravel bottoms (Poppe & Goto



Fig. 76. *Gari fervensis* (Gmelin 1791). Skagen 4, 23.0–23.5 m b.s., lab. no. 348,93. × 4.8. Right valve. MGUH 25386.

1993). In Danish waters on mixed bottoms and sand at depths of 15–40 m (Jensen & Spärck 1934).

Subfossil finds. The Limfjord, Vendsyssel and Skagen regions, Holocene. Recorded from the Subatlantic in the Skagen Well.

***Gari tellinella* (Lamarck 1818)**

Distribution. S and W Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean. The species has been taken from the northern Kattegat (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone to a depth of 460 m in coarse sand, gravel and stone bottoms.

Subfossil finds. None.

***Scrobicularia plana* (da Costa 1778)**

Distribution. Norway off the Lofoten islands, and south to the Mediterranean (Madsen 1949). The species extends into the Bælt Sea at Kiel and Warnemünde (Jensen & Spärck 1934), and is also recorded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone to about 30 m in clay or muddy bottoms, often in estuaries (Poppe & Goto 1993). Jensen & Knudsen (1995) point to the occurrences in the Wadden Sea and to the sensitivity to severe winters, living in such shallow-water environments.

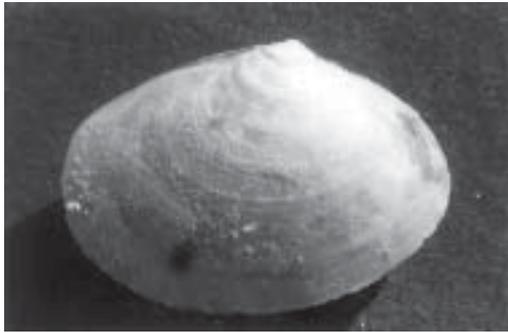


Fig. 77. *Abra alba* (Wood 1802). GEUS collection. Storebælt, Denmark. × 4.8. Specimen seen from the left. MGUH 25387.

Subfossil finds. The Bælt Sea, Baltic, Kattegat, Limfjord, North Sea and Vendsyssel regions, Holocene. During the Eemian recorded from the Bælt Sea, Baltic, Kattegat, and North Sea regions.

***Abra alba* (Wood 1802)**

Fig. 77

Distribution. Norway off the Lofoten islands, and south to the Mediterranean (Madsen 1949). In Danish waters it is found most abundantly in the shallow-water parts of the North Sea (Petersen 1977) and extends through the Skagerrak, Limfjord and Kattegat and Øresund into inner Danish waters such as the Bælt Sea and the Baltic to Neustadt, where it is the typical bottom animal (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the infralittoral zone to a depth of 65 m in sand, mud or muddy gravel (Poppe & Goto 1993). In Danish waters common at depths of 3–8 m and out to 15–20 m in soft bottoms (Jensen & Spärck 1934).

Subfossil finds. The Bælt Sea, Kattegat, Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. In the Skagen Well recorded from the Subboreal and Subatlantic. During the Eemian recorded from the Bælt Sea, North Sea and Vendsyssel regions.

***Abra nitida* (Müller 1776)**

Fig. 78

Distribution. Recorded from S and W Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean (Madsen 1949). In Danish waters recorded from the North Sea, Skagerrak, Limfjord and Kattegat



Fig. 78. *Abra nitida* (Müller 1776). GEUS collection. Hellebæk, Denmark. × 4.8. Specimen seen from the left. MGUH 25388.

(Jensen & Spärck 1934), including the Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Mainly offshore to depths of 200 m in sandy mud, mud or gravel bottoms (Poppe & Goto 1993). However, in Danish waters such as the North Sea on soft to mixed bottoms at depths of 40–70 m (Petersen 1977) and in the Skagerrak at depths of 100–300 m extending into the Kattegat, including the Øresund, on soft bottoms (Jensen & Spärck 1934).

Subfossil finds. The Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. In the Skagen Well recorded from the Subboreal and Subatlantic. During the Eemian recorded from the Vendsyssel region.

***Abra prismatica* (Montagu 1803)**

Fig. 79

Distribution. S and W Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean (Madsen 1949). In the Danish waters the species extends from the North Sea and Skagerrak into the Kattegat and Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the infralittoral zone to 400 m deep in sand or muddy sand (Poppe & Goto 1993). In the North Sea most abundant at depths deeper than 50 m on mixed bottoms (Petersen 1977).

Subfossil finds. The Limfjord, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded from the Subboreal and Subatlantic. During the Eemian re-

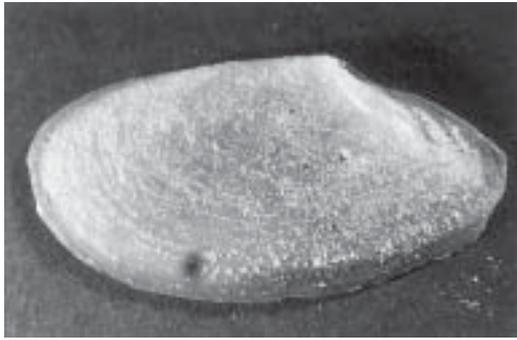


Fig. 79. *Abra prismatica* (Montagu 1803). GEUS collection. Iceland. $\times 4.8$. Specimen seen from the left. MGUH 25389.

corded from the Bælt Sea, Kattegat, North Sea, and Vendsyssel regions.

***Abra segmentum* (Récluz 1843)**

Distribution. From the west coast of France into the Mediterranean.

Occurrence. The Lusitanian region.

Habitat. In the infralittoral zone in sandy mud (Poppe & Goto 1993). It seems to be connected with the shallow-water environment, also with brackish water (Jensen & Spärck 1934).

Only subfossil finds. Recorded from the Bælt Sea and the North Sea during the Eemian.

***Arctica islandica* (Linnaeus 1767)**

Fig. 80

Distribution. Around Iceland, the Faeroes, Norway



Fig. 80. *Arctica islandica* (Linnaeus 1767). GEUS collection. Læsø Rende, Denmark. $\times 4.8$. Juvenile specimen, beaks directed forwards. MGUH 25390.

north of Lofoten, and south to the Bay of Biscay. In the Danish waters, including the Limfjord, the species extends from the North Sea and Skagerrak as far as the Baltic (to Bornholm) (Jensen & Spärck 1934).

Occurrence. The Subarctic, Boreal and (Lusitanian) regions. However, the species tends to live more deeply in the southern part of its range (Poppe & Goto 1993).

Habitat. Intertidal to 482 m in mud, sand or gravel bottoms. In the North Sea mainly from depths deeper than 40 m and from mixed bottoms (Petersen 1977). In inner Danish waters often at depths from 10–15 to 50–60 on clay or clayey bottoms (Jensen & Spärck 1934). According to Badarsson (1920), fishermen say that the species occurs in very shallow water, just below the low-water mark, in winter living deeply burrowed in the substrate, but in the summer often lying in abundance on the bottom.

Subfossil finds. The Kattegat, Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded in the Subatlantic. In the Bælt Sea, Baltic and North Sea (there are (single find) records from the Eemian and the Vendsyssel region during the Late Weichselian (the Younger *Yoldia* Sea).

***Kelliella miliaris* (Philippi 1844)**

Fig. 81

Distribution. From Norway off the Lofoten islands, and south to the Mediterranean. From Danish waters recorded from the Skagerrak. According to Jensen & Spärck (1934), very common in the deeper part of the Skagerrak. Jensen & Knudsen (1995) mentioned a single finding from the southern Kattegat.



Fig. 81. *Kelliella miliaris* (Philippi 1844). Skagen 3, 185.04–185.06 m b.s., core sample-102. $\times 20$. Two specimens seen from the left. Inside the corroded specimen to the left, pyrite is seen. MGUH 25391.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 134 to 700 m deep (Nordsieck 1969).

Subfossil finds. Recorded from the Eemian in the Vendsyssel and Skagen regions.

***Glossus humanus* (Linnaeus 1758)**

Distribution. S and W Iceland, Norway off the Lofoten islands, and south to the Mediterranean. In Danish waters recorded from the North Sea and Kattegat, where shells are common (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Offshore beyond 7 m on bottoms of sand, sandy mud or soft mud (Tebble 1966).

Subfossil finds. None.

***Chamelea striatula* (da Costa 1778)**

Fig. 82

Distribution. The Faeroes, Norway north of Lofoten, and south to the Mediterranean (Madsen 1949). In Danish waters the species extends from the North Sea, Limfjord and Skagerrak into the Kattegat and Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the infralittoral zone to 55 m deep on sand and mud bottoms (Poppe & Goto 1993). In the North Sea mainly from 20 to 40 m on sand to mixed bottoms (Petersen 1977). In the Skagerrak at depths of more than 100 m, but in the Kattegat at depths of less



Fig. 82. *Chamelea striatula* (da Costa 1778). Skagen 4, 21.0–21.5 m b.s., lab. no. 346,93. × 4.8. Left valve. MGUH 25392.

than 50 m, since the sand bottom is not to be found at deeper levels (Jensen & Spärck 1934).

Subfossil finds. The Limfjord, North Sea, Vendsyssel and Skagen areas, Holocene. From the Skagen Well recorded from the Subboreal and Subatlantic. During the Eemian recorded from the Bælt Sea, North Sea and Vendsyssel regions.

***Clausinella fasciata* (da Costa 1778)**

Distribution. The Faeroes, Norway off the Lofoten islands, and south to the Mediterranean. From the North Sea the species extends into the Kattegat (Petersen 1888).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 4 to 110 m deep in sand, mud and gravel bottoms (Poppe & Goto 1993). In the North Sea in hard sand (Petersen 1977), and in the Kattegat in gravel and sand between 15 and 30 m (Petersen 1888, p. 143).

Subfossil finds. The Limfjord, North Sea and Vendsyssel areas, Holocene.

***Paphia aurea* (Gmelin 1791)**

Distribution. Norway off the Lofoten islands, and south to the Mediterranean. The finds closest to Danish waters are from southern Norway (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone down to 36 m deep in sand, mud and gravel bottoms.

Only subfossil finds. The Bælt Sea, Kattegat, Limfjord, North Sea and Vendsyssel regions, Holocene. Recorded from the Kattegat region during the Eemian.

***Paphia aurea senescens* (Cocconi 1873)**

Distribution. The only one of our Quaternary molluscs which does not live at present. Also found in Quaternary deposits in Italy (Jensen & Spärck 1934). Regarded as a Lusitanian species according to Nordmann (1913). However, Poppe & Goto (1993) regard the fossil valves found, for example along the coast of the Netherlands and Belgium, as a subspecies in which the differences

from extant ones are minimal, and they propose that the relationship between the fossil and recent shells be restudied. From Nordmann (1913) and Cerulli-Irelli (1908) it seems right that *Tapes senescens* Doederl. and *Tapes aureus* var. *eemiensis* are identical. But as the relationship between *T. senescens* and *T. aureus sensu stricto* at the time of Nordmann (1913) was not clear, the position as a not extant subspecies given by Poppe and Goto is followed here.

Only subfossil finds. The Bælt Sea, Kattegat, and North Sea regions during the Eemian.

***Tapes decussatus* (Linnaeus 1758)**

Distribution. Norway off the Lofoten islands, and south to the Mediterranean. Closest to Danish waters the species occurs off western Norway (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the tidal zone to a depth of few metres in sand or muddy-gravel bottoms.

Only subfossil finds. The Kattegat, Limfjord, North Sea and Vendsyssel regions, Holocene. Recorded from the North Sea region during the Eemian.

***Timoclea ovata* (Pennant 1777)**

Fig. 83a, b

Distribution. S and W Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean (Madsen 1949). In Danish waters the species extends from the North Sea into the Kattegat and Øresund (Jensen &

Knudsen 1995), but has not been recorded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. At depths between 4 and 200 m on all types of bottoms (Poppe & Goto 1993). In the North Sea usually deeper than 50 m and on soft bottoms (Petersen 1977).

Subfossil finds. The Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. In the Skagen Well recorded from the Subatlantic. During the Eemian found in the Bælt Sea, Kattegat and North Sea regions.

***Venerupis rhomboides* (Pennant 1777)**

Distribution. The Faeroes, Norway off the Lofoten islands (Madsen (1949) does not mention any Norwegian occurrence), and south to the Mediterranean (Petersen 1968). One pair of united valves recorded from the northern Kattegat (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone to 180 m deep (Poppe & Goto 1993) in gravel and mud bottoms.

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene.

***Venerupis pullastra* (Montagu 1803)**

Distribution. Norway from north of the Lofoten islands, and south to the Mediterranean (Madsen 1949). From Danish waters recorded from the Limfjord and Katte-



Fig. 83. **a:** *Timoclea ovata* (Pennant 1777). Skagen 4, 27.0–27.5 m b.s., lab. no. 352,93. × 40. Left valve. MGUH 25393. **b:** *Timoclea ovata* (Pennant 1777). GEUS collection. Herthas Flak, Denmark. × 4.8. Right valve. MGUH 25394.

gat regions (Jensen & Spärck 1934) and the Øresund (Jensen & Knudsen 1995). The species has a common occurrence in the Isefjord (Rasmussen 1973).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone to 40 m deep in hard sand and muddy gravel (Poppe & Goto 1993). Rasmussen (1973, p. 303): considers “its present common occurrence there [in the Isefjord] to be a result of the disappearance of the *Zostera* since 1933–45, as the lack of a continuous vegetation caused a change in the bottom conditions to the benefit of *Venerupis pullastra*. Undoubtedly the species has lived in interior Danish waters since the Stone Age, being, however, rare in recent times up to 1933–34”.

Subfossil finds. The Bælt Sea, Kattegat, Limfjord, North Sea and Vendsyssel regions, Holocene. Recorded from the North Sea region during the Eemian.

***Dosinia exoleta* (Linnaeus 1758)**

Distribution. Norway off Lofoten, and south to the Mediterranean. The species extends from the North Sea (Petersen 1977) into the northern Kattegat (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone to 73 m deep, burrowing deeply in sand, mud and gravel bottoms (Poppe & Goto 1993). In the North Sea found at depths of 30–100 m, on hard bottoms around the Dogger Bank (Petersen 1977).

Subfossil finds. The North Sea and Vendsyssel regions, Holocene.

***Dosinia lincta* (Montagu 1803)**

Distribution. S and W Iceland, the Faeroes, Norway north of Lofoten, and south to the Mediterranean (Petersen 1968). The species extends from the North Sea into the Kattegat and Øresund (Petersen 1888).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone to 200 m deep in pure sand and fine gravel bottoms (Poppe & Goto 1993). In the North Sea sampled at 10–100 m on soft to

mixed bottoms (Petersen 1977). From the Kattegat recorded on mixed bottoms between 18 and 56 m (Petersen 1888).

Subfossil finds. The North Sea and Vendsyssel regions, Holocene. Recorded from the Bælt Sea and the North Sea during the Eemian.

***Gouldia minima* (Montagu 1803)**

Distribution. The Faeroes, Norway off the Lofoten islands, and south to the Mediterranean (Petersen 1968).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From below the tidal zone to depths of over 200 m in sand, mud and fine gravel bottoms (Poppe & Goto 1993).

Only subfossil finds. Recorded from the Bælt Sea and the North Sea during the Eemian.

***Petricola pholadiformis* (Lamarck 1822)**

Distribution. This species in an immigrant introduced in to Europe, probably with oysters, at the end of the last century (Poppe & Goto 1993). According to Jensen & Knudsen (1995), the species occurred in 1906 in the Wadden Sea; the Skagerrak 1905; the Kattegat 1931; and the Bælt Sea 1943. It will not be considered any further in this work.

***Mysia undata* (Pennant 1777)**

Distribution. The Faeroes, Norway north of the Lofoten islands, and south to the Mediterranean (Petersen 1968). In Danish waters the species extends from the North Sea (Petersen 1977) into the Kattegat and Øresund (Jensen & Knudsen 1995). It is not recorded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From below the tidal zone to depths of 55 m in muddy sand and gravel bottoms (Poppe & Goto 1993). In the North Sea found at depths of 40–70 m on soft to mixed bottoms (Petersen 1977).

Subfossil finds. The Limfjord and Vendsyssel regions, Holocene. During the Eemian recorded from the North Sea region.

Order Myoida

Mya arenaria Linnaeus 1758

Distribution. Norway from north of the Lofoten islands, south to the British Isles (Petersen 1968). The species extends from the North Sea into the Limfjord and the inner Danish waters, including the Baltic (Jensen & Spärck 1934). It is a late immigrant, known from Europe in the Plio-Pleistocene (Strauch 1972, pp. 135–137) having been transferred from North America by man, presumably the Vikings, and dated back to the 13th century, i.e. well before Columbus (Petersen *et al.* 1992b).

Occurrence. Mainly in the Boreal region, but with new finds further to the south on the east coast of North America (Rasmussen & Heard 1994).

Habitat. From the tidal zone down to 6–7 m deep in sandy bottoms, the species avoids high-energy coastal environments (Jensen & Spärck 1934).

Subfossil finds. The records from the Bælt Sea and Vendsyssel might be of recent dates; only the occurrences at Jerup halfway up to the Skagen Spit have been dated and included in the Skagen area from the Subatlantic.

Mya truncata Linnaeus 1758

Distribution. W and E Greenland, Spitsbergen, around Iceland, the Faeroes, Norway from north of Lofoten, and south to the Bay of Biscay (Madsen 1949; Poppe & Goto 1993). The species extends from the North Sea into the Limfjord and the inner Danish waters as far as the Bælt Sea (Kiel and Warnemünde) (Jensen & Spärck 1934).

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian regions.

Habitat. From the intertidal zone down to about 75 m deep (Poppe & Goto 1993). However, in Danish waters often at depths between 10 and 20 m (Jensen & Spärck 1934). In the North Sea found at depths of 37–70 m on soft mixed bottoms (Petersen 1977). In East Greenland the species belongs to the Arctic *Macoma* community (Ockelmann 1958). However, according to Jensen (1900) the typical *Mya truncata* is not found in the Arctic (G.H. Petersen, personal communication 1998).



Fig. 84. *Corbula gibba* (Olivi 1792). Skagen 3, 37.00–37.25 m b.s., lab. no. 710,93. $\times 9.6$. To the upper left a specimen seen from the left, and to the right a view of the inside of a right valve. MGUH 25395.

Subfossil finds. The Bælt Sea, Kattegat, Limfjord, North Sea and Vendsyssel regions, Holocene. Recorded from the Eemian in the Bælt Sea, Baltic, North Sea and Vendsyssel areas. From the Early/Middle Weichselian in the Kattegat and Vendsyssel regions, and from the Vendsyssel region also in the Late Weichselian.

Corbula gibba (Olivi 1792)

Fig. 84

Distribution. Norway north of Lofoten, and south to the Mediterranean (Petersen 1968). The species extends from the North Sea into the inner Danish waters, including the Limfjord, as far as the westernmost part of the Baltic region at Møn (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the low intertidal zone to 250 m deep anchored by a byssus on silty sand and muddy-gravel bottoms (Poppe & Goto 1993). However, in Danish waters rarely at depths of more than about 50 m (Jensen & Spärck 1934). In the North Sea sampled at 35–50 m depths on mixed bottoms (Petersen 1977).

Subfossil finds. The Bælt Sea, Baltic, Kattegat, Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded from the Subboreal and Subatlantic. During the Eemian recorded from the Bælt Sea, Baltic, Kattegat, North Sea and Vendsyssel regions.



Fig. 85. *Hiatella arctica* (Linnaeus 1758). Skagen 3, 37.00–37.25 m b.s., lab. no. 710,93. × 20. Left valve. MGUH 25396.

***Hiatella arctica* (Linnaeus 1758)**

Fig. 85

Distribution. W and E Greenland, Spitsbergen, around Iceland, the Faeroes, Norway from north of Lofoten, and south to the Mediterranean (Madsen 1949). Following Jensen & Spärck (1934) who regard the records of *Hiatella* as one species, it is widely spread but not always common in all the Danish waters, it extends to Kiel in the Bælt Sea.

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian regions.

Habitat. “From the intertidal zone down to almost 1400 m fixed by its byssus on or in all kinds of substrate on all types of bottoms. Also found in holes previously bored by other species” (Poppe & Goto 1993, p. 130). However, Petersen (1977, p. 228) states: “Both the systematics and nomenclature are insufficiently investigated for this genus”. So with regard to the subfossil finds, the questions on species are even more difficult, as seen from Petersen (1986b, figs 2, 3), where forms with different habitat such as *Hiatella* cf. *byssifera* are found fixed on a stone taken as a grab sample in Kejser Franz Josephs Fjord, East Greenland, and as traces of *Hiatella arctica* in the *Saxicava* Sand of Late Weichselian age in Vendsyssel. However, here Simonarson *et al.* (1998) is followed, relating the more widely used and less specific name *Hiatella arctica*.

Subfossil finds. The Bælt Sea, Limfjord, North Sea, Vendsyssel and Skagen areas, Holocene. From the Skagen Well records from the Subboreal and Subatlantic. From the Eemian recorded from the Kattegat, North Sea, Vendsyssel and Skagen regions. In the Kattegat and Vendsyssel regions finds from the Early/Middle Weich-

selian (the Older *Yoldia* Sea) and in the Vendsyssel region from the Late Weichselian (the Younger *Yoldia* Sea).

***Hiatella rugosa* (Linnaeus 1758)**

Distribution. Jensen & Knudsen (1995) include this as a separate species and take it as part of the recent Danish shell-bearing fauna. Records from the literature on subfossil finds are therefore considered here. According to Poppe & Goto (1993), found from Norway south to the Mediterranean. Ockelmann (1958, p. 135 ff.), discussing the *Hiatella* taxonomy at some length, concludes that reservations must be made as to future separations of the *Hiatella* forms (*H. arctica* incl. of *H. gallicana* and *H. pholadis*) occurring in the northern hemisphere into valid species.

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian regions.

Subfossil finds. The Kattegat and Vendsyssel regions, Holocene.

***Saxicavella jeffreysi* Winckworth 1930**

Fig. 86

Distribution. Norway off the Lofoten islands, and south to the Mediterranean (Madsen 1949). The species extends into the Kattegat and Øresund, although rare (Jensen & Knudsen 1995). It has been recorded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Offshore between 7 and 240 m deep in sand, mud or gravel bottoms (Poppe & Goto 1993). In the



Fig. 86. *Saxicavella jeffreysi* Winckworth 1930. Skagen 4, 20.0–20.5 m b.s., lab. no. 345,93. × 4.8. Right valve. MGUH 25397.

Danish waters often at depths between 25–50 m (Jensen & Spärck 1934).

Subfossil finds. The Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. In the Skagen Well recorded from the Subatlantic. During the Eemian recorded from the North Sea region.

***Panomya arctica* (Lamarck 1818)**

Distribution. S and W Iceland, Norway from north of Lofoten, and south to the British Isles and Denmark (Madsen 1949). However, Petersen (1968) refers to empty shells from N Iceland and occurrences in the Clyde Sea and off the Isle of Man. In Danish waters only once taken alive near Skagen, otherwise shells only, but found as far south as Øresund (Jensen & Knudsen 1995).

Occurrence. Mainly Boreal, but outposts into the Subarctic (subfossil?) and Lusitanian regions (Strauch 1972).

Habitat. From the intertidal zone down to 300 m buried in mud or sand (Poppe & Goto 1993).

Subfossil finds. None.

***Barnea candida* (Linnaeus 1758)**

Fig. 87

Distribution. Norway off the Lofoten islands, and south to the Mediterranean (Madsen 1949). In the Danish waters, including the Limfjord, the species extends into the Bælt Sea as far as Kiel (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

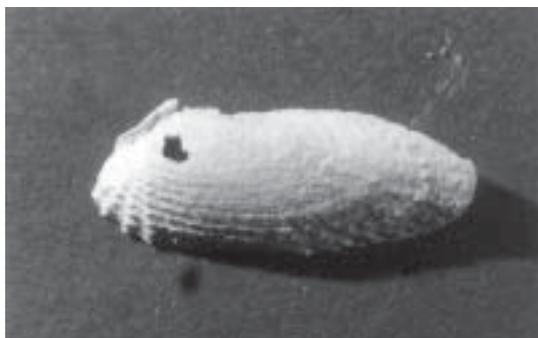


Fig. 87. *Barnea candida* (Linnaeus 1758). GEUS collection. Off Rubjerg Knude, Denmark. × 4.8. Left valve. MGUH 25398.

Habitat. From the low intertidal zone to about 30 m deep, the species bores in semi-hard substrates such as clay (Poppe & Goto 1993).

Subfossil finds. The Bælt Sea, Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded from the Subatlantic. During the Eemian found in the Bælt Sea and North Sea regions.

***Pholas dactylus* Linnaeus 1758**

Fig. 88a, b

Distribution. Norway off the Lofoten islands, and south to the Mediterranean (Madsen 1949). In Danish waters only found to Frederikshavn and the Limfjord (Petersen 1986a; Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone to a depth of 10 m boring in different substrates, preferring clay bottoms (Poppe & Goto 1993).

Subfossil finds. The Limfjord, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded from the Subatlantic.

***Zirfaea crispata* (Linnaeus 1758)**

Distribution. Around Iceland, Norway from north of the Lofoten islands, and south to the Bay of Biscay (Madsen 1949). In the Danish waters, including the Limfjord, extending into the Bælt Sea as far as Kiel (Jensen & Spärck 1934).

Occurrence. Mainly Boreal with outposts into the Lusitanian region.

Habitat. From the low tide line to about 7 m deep, boring in semi-hard substrates (Poppe & Goto 1993). In the Danish waters the species has a wide extension, depending on the bottom substrates (Jensen & Spärck 1934): In the North Sea and Skagerrak peat and chalk; in the Limfjord cementstone, Mo-clay, chalk, peat and clay; and the Bælt Sea clayey bottoms.

Subfossil finds. The Bælt Sea, Limfjord, North Sea and Vendsyssel regions, Holocene. From the Bælt Sea region recorded from the Eemian and from the Vendsyssel region during the Late Weichselian (the Younger Yoldia Sea).

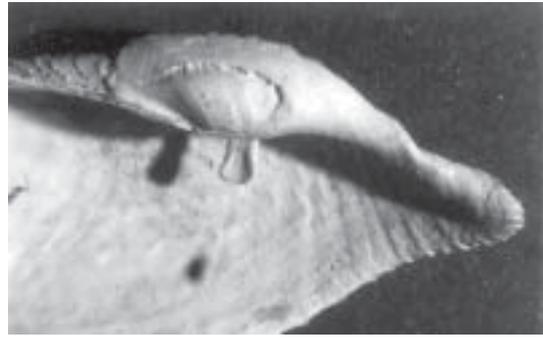


Fig. 88. **a:** *Pholas dactylus* Linnaeus 1758. Skagen 4, 20.0–20.5 m b.s., lab. no. 345,93. $\times 9.6$ Fragment with umbonal reflection with septa. MGUH 25399. **b:** *Pholas dactylus* Linnaeus 1758.

***Xylophaga dorsalis* Turton 1822**

Distribution. S and W Iceland, Norway from north of Lofoten, and south to the Mediterranean. Recorded from the Øresund region (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. According to Madsen (1949) the occurrences at Iceland have been from depths between 140–230 m found in sunken pieces of wood.

Subfossil finds. None.

***Teredo navalis* Linnaeus 1758**

Distribution. Norway off the Lofoten islands (Petersen 1968), and south to the Mediterranean (Madsen 1949). The species is found into the Bælt Sea (Jensen & Spärck 1934).

Occurrence. The Boreal and Lusitanian regions.

Habitat. Specialised wood-borers.

Subfossil finds. None.

***Nototeredo norvegica* (Spengler 1792)**

Distribution. S and W Iceland, Norway north of Lofoten, and south to the Mediterranean (Madsen 1949). The species extends from the North Sea (in driftwood) into the Bælt Sea as far as Kiel (Jensen & Spärck 1934), and was recorded from the Limfjord by Collin (1884).

Occurrence. The Boreal and Lusitanian regions.

Habitat. In driftwood.

Subfossil finds. None.

***Psiloteredo megotara* (Forbes & Hanley 1848)**

Distribution. W Greenland, Spitsbergen, around Iceland, Norway north of Lofoten, and south to the Mediterranean (Madsen 1949). In Danish waters common on the west coast of Jylland and recorded from the Kattegat, including Øresund (Jensen & Knudsen 1995).

Occurrence. The Arctic, Subarctic, Boreal and Lusitanian regions, although rare in the last region.

Habitat. Only in driftwood (Jensen & Knudsen 1995).

Subfossil finds. None.

**Subclass Anomalodesmata
Order Pholadomyoidea**

***Pandora glacialis* Leach 1819**

Distribution. W and E Greenland and Spitsbergen (Madsen 1949).

Occurrence. The Arctic and Subarctic regions.

Habitat. From 2 to 205 m deep on mixed bottoms (Ockelmann 1958).

Only subfossil finds. From the Vendsyssel region during Early/Middle and Late Weichselian (the Older *Yoldia* Sea and the Younger *Yoldia* Sea respectively).

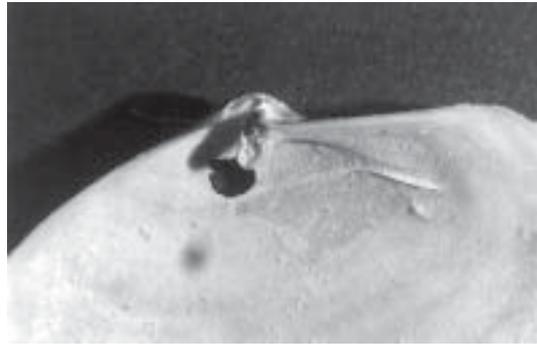
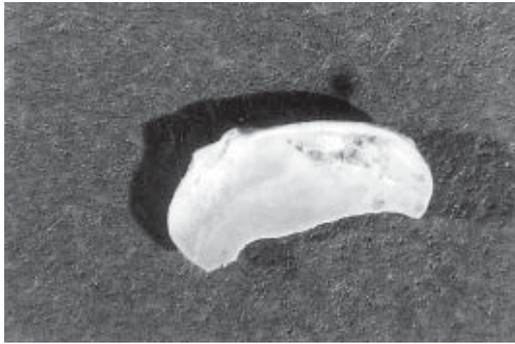


Fig. 89. **a:** *Cochloidesma praetenue* (Pulteney 1799). Skagen 3, 43.19–43.24, core sample-9. $\times 9.6$. View of the inside of a fragmented right valve. MGUH 25401. **b:** *Cochloidesma praetenue* (Pulteney 1799). GEUS collection. Læsø Rende, Denmark. $\times 4.8$. Detailed view of the inside of a right valve showing the resilifer. MGUH 25402.

***Lyonsia norwegica* (Gmelin 1791)**

Distribution. S and W Iceland, the Faeroes, Norway off the Lofoten islands, and south to the Mediterranean. In Danish waters recorded from the Kattegat.

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 20 to 250 m deep in sand, silty sand and mud bottoms.

Subfossil finds. Recorded from the Skagen region, Holocene. In the Skagen Well recorded from the Pre-boreal and Boreal.

***Lyonsia arenosa* (Möller 1842)**

Distribution. W and E Greenland, Spitsbergen, and Norway north of the Lofoten islands. Main distribution in the Arctic and Subarctic regions.

Habitat. From 3 to about 200 m on mixed bottoms (Ockelmann 1958).

Subfossil finds. Recorded from the Vendsyssel region during the Early/Middle Weichselian and the Late Weichselian (the Older *Yoldia* Sea and the Younger *Yoldia* Sea respectively).

***Cochloidesma praetenue* (Pulteney 1799)**

Fig. 89a, b

Distribution. S and W Iceland, the Faeroes, Norway off the Lofoten islands, and south to Gibraltar (Petersen 1968). The species is rare in Danish waters and has only once been taken live in the Kattegat (Jensen

& Spärck 1934), although shells are found in the Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the intertidal zone down to 110 m in sand, mud and gravel bottoms.

Subfossil finds. The North Sea and Skagen regions, Holocene. From the Skagen Well recorded from the Subatlantic. During the Eemian recorded from the Skagen region.

***Thracia convexa* (Wood 1815)**

Distribution. The Faeroes, Norway off the Lofoten islands, and south to the Mediterranean (Madsen 1949). In Danish waters recorded from the Kattegat (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian zones.

Habitat. Offshore down to over 800 m in mud and sand bottoms (Poppe & Goto 1993). In the Danish waters taken between 30–80 m (Jensen & Spärck 1934).

Subfossil finds. None.

***Thracia phaseolina* (Lamarck 1818)**

Fig. 90

Distribution. S and W Iceland, Norway off the Lofoten islands, and south to the Mediterranean (Madsen 1949). The species extends from the North Sea (Petersen 1977) into the Kattegat and Øresund, although with few records (Jensen & Knudsen 1995), and it has been re-

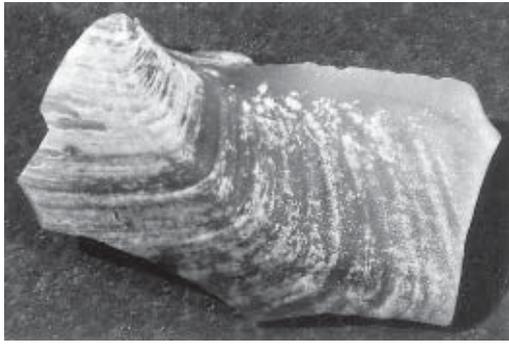


Fig. 90. *Thracia phaseolina* (Lamarck 1818). Skagen 4, 14.0–14.5 m b.s., lab. no. 339,93. × 9.6. Fragment of left valve. MGUH 25403.

corded from the Limfjord (Petersen 1986a).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From the low intertidal zone down to 50 m in fine sand, mud or gravel bottoms (Poppe & Goto 1993).

Subfossil finds. The Limfjord, North Sea, Vendsyssel and Skagen regions, Holocene. From the Skagen Well recorded from the Subatlantic. During the Eemian found in the Bælt Sea and North Sea regions.

***Thracia gracilis* (Jeffreys 1865)**

Distribution. Recorded from the Atlantic (Nordsieck 1969). From the Danish waters found in the northern Kattegat (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Subfossil finds. None.

***Thracia villosiuscula* (MacGillivray 1827)**

Distribution. S and W Iceland, the Faeroes, Norway off the Lofoten islands, and south to the British Isles

(Petersen 1968). According to Poppe & Goto (1993) also found in the Mediterranean.

Occurrence. The Boreal and Lusitanian regions.

Habitat. In the North Sea sampled at depths between 20 and 50 m on hard sand (Petersen 1977).

Subfossil finds. Recorded from the North Sea region during the Eemian.

***Cuspidaria cuspidata* (Olivi 1792)**

Distribution. Norway off the Lofoten islands, and south to the Mediterranean. In the Danish waters found in the Kattegat (Jensen & Spärck 1934) and Øresund (Jensen & Knudsen 1995).

Occurrence. The Boreal and Lusitanian regions.

Habitat. From 20 m to 250 m deep in muddy sand and gravel bottoms (Poppe & Goto 1993). In Danish waters at depths between 30 and 60 m (Jensen & Spärck 1934).

Subfossil finds. None.

***Cuspidaria obesa* (Lovén 1846)**

Distribution. E and W Greenland, Spitsbergen, around Iceland, Norway north of the Lofoten islands, and south to the Mediterranean; however, to the south only at depths greater than 400 m (Madsen 1949). In Danish waters recorded from the Skagerrak and Kattegat.

Occurrence. The Arctic, Subarctic and Boreal regions.

Habitat. At depths from 40 to 2500 m according to Madsen (1949), but in Danish waters fairly common in the deeper part of the Skagerrak.

Subfossil finds. None.

The Skagen Well

The Skagen Well – perspectives

The perspectives of the drilling of the Skagen Well can be seen by describing the sedimental changes observed in the succession of strata penetrated. However, for the first 30 m of Skagen Well III, only wash-samples were taken, in order to establish the well for further drilling down to the Prequaternary. Therefore, the first drilling segment, composed of sand and gravel, was later repeated elsewhere in order to obtain core samples also from the topmost part. This was done in a nearby position – the so-called Skagen IV Well – and consequently the full record of shell material and sediments can be given from the core samples obtained from the well, representing all the strata met with in the Skagen area from the Quaternary, the Skagen III Well DGU File No. 1.287.

The Skagen Wells III and IV are considered to represent one well and are therefore listed together. However, also the wash-samples obtained throughout the Quaternary are represented, but only as qualitative analyses with the first occurrences of macrofossils – especially the molluscs – indicated (Appendix 2).

Thirty metres below surface (+ 1 m a.s.), the sediment is well-sorted fine sand. For the following 10 m to 40 m b.s., the average grain size falls within the coarse silt fraction which is consistent down to 75 m b.s. as shown from 11 interjacent measurements, Appendix 3.

From the depth of 75 m b.s. the average diameter falls within that of medium silt, down to the level of 100 m b.s., still well sorted.

At the following levels to a depth of 133 m b.s., the material is fine silt and clay. At a depth of 135 m b.s., fine sand with poor sorting occurs, and at 136–137 m b.s., with very poor sorting and quartiles 40% / 90% of 54.099, which shows a diamict material with a content of stones and only allochthonous shell material, in contrast to the superjacent 130 m.

At a depth of 179 m, the well produced a fine-grained material of medium silt, moderately sorted, which is close to what was found above the diamict sequence.

With some rise in the average diameter to fine sand and a lowering of the sorting, the next remarkable shift happens at a depth of 187 m b.s., where a new diamict sequence is found down to 195 m b.s. Here

the boundary to the Prequaternary deposits is met with, most probably belonging to the Lower Cretaceous, according to Skagen II, DGU File No. 1, 43 (Sorgenfrei & Buch 1964).

From the above-mentioned strata in the cored sections, the well can be divided into two parts from the point of view of the present investigation on macrofossils. A sandy to gravelly, clayey to silty well-sorted material found in the upper 130 m of the well and in a smaller interval of almost 10 m at a depth of 179 to 187 m b.s. Between these two parts, diamict and well-sorted clayey layers without an *in situ* macrofauna are found.

As the main characteristic feature of the 140 m fine-grained and well-sorted material, its content of shell-bearing marine molluscs is considered. However, also other marine macrofossils have been recognised but not referred to species level, although recorded on a higher taxonomic level in Appendix 3, which represents the finds in the Skagen Well.

Also the sedimental data are all shown in Appendix 3, allowing a direct comparison between the finds of faunal elements and lithology *sensu lato*. The organic compound is shown with loss on ignition (550°C) and the occurrences of concretions such as pyrite and iron compounds. Also allochthonous shell materials are figured. In consequence of the quantitative analyses of molluscs, diversity and number of specimens are given for the marine strata throughout the whole sequence. It is shown that these figures are very greatly according to the different facies met with.

On the basis of the dating within the limits of the carbon-14 method (Heier-Nielsen *et al.* 1995), Appendix 4 and Fig. 3, it is seen that the 130 m thick upper sequence of the well is dated to the last 15 000 ¹⁴C years. This comprises the whole of the Holocene with its Boreal sea deposits and the Late Weichselian with the Arctic Younger *Yoldia* deposits.

But also from 140–150 m b.s., measurements on gas compounds of marine origin (T. Layer, personal communication 1999) and shell fragments have been dated, giving ages around 36 000 B.P. ¹⁴C years. This means that the diamictic sequence occurring between the two marine strata has taken up material which in age is equivalent to the younger part of the Older *Yoldia* Clay sediments. The deposition of the diamictic

sediments is referred to the time of the Late Weichselian ice advance to the Main Stationary Line in Jylland.

Molluscan shells (*Macoma calcarea*) from the younger part of the Older *Yoldia* Clay (the *Macoma calcarea* zone, *sensu* Petersen in Bahnson *et al.* (1974)), has recently been dated by the AMS method to be in ¹⁴C years around 32 000 – 33 000 B.P. (AAR-1410 and AAR-1411).

Consequently, it is likely that the older marine strata in the lower marine part of the Skagen Well can be correlated to part of the sequence demonstrated in the Skærumhede Well (Jessen *et al.* 1910; Bahnson *et al.* 1974) covering the Eemian and the main part of the Weichselian.

Regarding the 130 m thick upper sequence, this is from results of the ¹⁴C dates related to the time of the Younger *Yoldia* Sea and the Holocene, and as it appears from the dates of the sediments here is for the first time within the Danish area found in a continuous marine succession. This can be explained on the basis of the hitherto unsurpassed thickness of Late Weichselian–Holocene marine strata. Therefore, while most of the Danish area has a continental period in the time span 11 000 – 7500 B.P. in ¹⁴C years (Petersen 1985b), the Skagen area was so low-lying that it was continuously covered by the sea.

This is a reflection of a lesser glacial deposition and the glacio-isostatic down-pressing – the latter amounting to up to 200 m, as seen from the amount of isostatic rebound after the waning of the ice cap over northern Denmark (Petersen 1990). However, when only Holocene dates are used, the estimated rebound of 200 m seems to be greater than the present dates allow when also Late Weichselian dates are used (Petersen 1999). So the low stand of sea level during the latest part of the Weichselian and Early Holocene was not to be overtaken by the isostatic uplift at any time in this area. After the final large eustatic rise in the Early Atlantic, the marine sedimentation is a dominating factor in raising the levelled sea bottom, compared to a decreasing isostatic rebound up to the Subatlantic when the isostatic rebound in Denmark expired (Petersen 1990). Here the formation of the Skagen Spit takes over, so that the last event of changing depth depends on the large quantities of sand and gravel deposited as the Skagen Spit grows to the north.

The pre-Late Quaternary deposits

In the deeper part of the Skagen Well, the base of the Quaternary is found resting on pre-Quaternary deposits of Lower Cretaceous sand. In the following description, Appendix 3 should be consulted.

The pre-Quaternary strata consist of quartz sand and gravel. From a depth of 195.15–195.30 m b.s., which is the upper part of the pre-Quaternary stratum, a mean grain size of fine sand, poorly sorted, is found (lab. no. 789.93). At a depth of 194.35–194.48 m b.s., the sediment is poorly sorted and the mean grain size is within medium sand, and this sediment also contains much quartz, but has another component in the form of stones of granitic composition.

The cumulative curve shows an even distribution of all grain sizes, which refers this sediment to be a till (lab. no. 788.93). This is also true for the overlying strata up to around 189 m b.s. The mean grain size is here within fine sand; however, more fine-grained parts are found. The sediment contains siderite(?) concretions with pyrite, in which imprints of *Cyrena* sp. are found. This might show that Jurassic deposits have been eroded. Some traces in pyrite were found as well. The whole sequence can be regarded as till. The sediment analyses from 188.57 to 187.18 give a badly sorted sediment sustaining that this is a till. Also this level contains shell fragments, one of which can be shown to be a *Nuculana pernula*.

The Late Pleistocene

Eemian deposits

The granulometric composition is shown from sample lab. no. 800.93. At a depth of 185.37 m b.s. the sediment is very fine-grained but contains only fragmented bivalves. At 185.0 m b.s. the marine sediment can be demonstrated by the occurrences of *Dentalium vulgare* in many specimens and the bivalve *Kelliella miliaris* also in many specimens and with connected valves.

The granulometric composition can be seen from the two levels 182.65 and 180.57 m b.s., samples nos 784.93 and 797.93 respectively. It appears that the sediment is very fine-grained clay to fine silt and moderately sorted in the 180.57 m level. Accessory finds of spatangids and ophiroids occur at the 185.0 m level, and pyrite formed in former burrows in the clayey material.

Also finds of fish occur, as found at the 182 m level,

and under the name of other fossils also Crustacean remains have been listed. The third mollusc species found at this level is the Ophistobranch *Limacina retroversa*, which is found in large numbers (11 specimens in one sample) together with *Kelliella miliaris* (also of a number of 15 in one sample). The samples here referred to are all from the heavy weight separation of the Foraminifer samples.

The species diversity and number of specimens in the sediment appear from the sample at 182.24 m b.s. in which 25 specimens of *Kelliella miliaris* are found – most of them with connected valves and in some parts kept in pyrite.

Trace fossils in pyrite are found in great quantities recorded in the table from all levels.

An expression of the grade of fine-grained sediment occurring at this level can be seen from the fact that only a biogene residue occurs here including the pyritiferous biogene traces – Lebenspuren. The limpid *Delectopecten vitreus* also appears at this level. As mentioned in the chapter on the molluscan species, the two sedentary species which today are known from the deeper part of the Skagerrak are *Delectopecten vitreus* and *Kelliella miliaris*. The latter is also found in the *Turritella terebra* zone in the Skærumhede Well. From 183.4 m b.s. *Hiatella arctica* is found, which occurs also at the greater depths and furthermore is a species widely extended. The occurrence of *Entalina tetragonia* at 183.6 m b.s. goes together with the occurrence of *Delectopecten vitreus*, both of which are found in the deeper part of the Skagerrak today, where they are part of the *Amphilopsis norvegica/Delectopecten vitreus* community.

To this can be added *Cadulus jeffreysi* found at the 184.4 m level. This species is widely extended in the northern part of the Atlantic down to the Bay of Biscay and into the Mediterranean. However, a single find of *Siphonodentalium lobatum* at 184.6 m b.s. points to a more Arctic environment. Such shells are found in glaciation deposits according to Muus (1959). However, the species may extend into the Lusitanian region.

From the 182 m level and up to 180 m b.s. still with a fine-grained and well-sorted sediment, *Yoldiella frigida* appears, which is also known from the deeper part of the Skagerrak today.

This species can be referred to the same environment as has been mentioned above – the *Amphilopsis norvegica/Delectopecten vitreus* community. *Yoldiella frigida* is known from the *Turritella terebra* zone in the Skærumhede sequence and the *Portlandia arctica* zone according to Jensen & Spärck (1934). *Kelliella*

miliaris and *Limacina retroversa*, which have been very frequent in marine layers met with under 180 m b.s., are no longer found above 180 m b.s.

The Early/Middle Weichselian, marine and glaciogene deposits

Regarding the sediment which is to follow at the levels above, between 179.65 and 179.74, it appears that the mean grain size is somewhat bigger medium sand, moderately sorted. But the most significant is found in the cumulative curve showing two maxima on the frequency curve (Fig. 91). This points to the effects of two sedimentation agents which might be a drop till effect besides the general marine sedimentation. During the examination of the samples from this level, sand and fine gravel occur, in contrast to the levels below, where only biogene remains were found, including the pyritiferous biogene traces. The coarser minerogene elements are found higher up in the series to the level 175.30–175.50 m where a fine-grained sediment with a median grain size of 0.002 mm reveals Arctic marine molluscs.

This is the first appearance of *Portlandia arctica*, which as the name tells is the characteristic mollusc of the *Portlandia arctica* zone in the Skærumhede sequence. However, also the presence of *Yoldia hyperborea*, which is known today from the Arctic and down to the Lofoten area is characteristic. This species is also found in the *Portlandia arctica* zone together with *Nuculana pernula* and *Palliolium greenlandicum*.

The occurrence of *Macoma* sp. has been added from

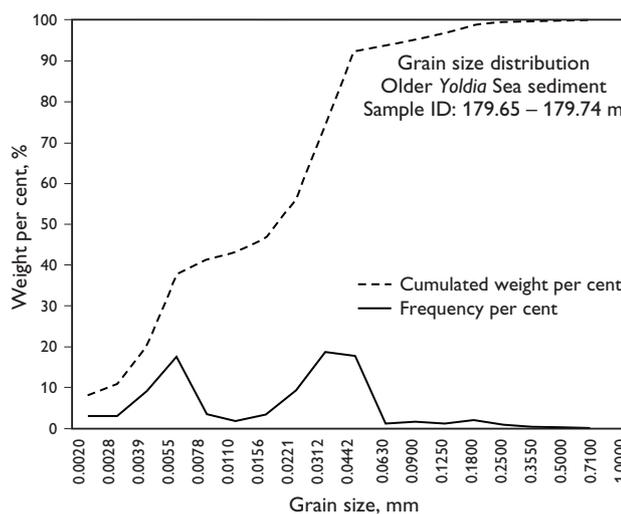


Fig. 91. The granulometric composition with two maxima on the frequency curve (lab. no. 483.93) at the 179.65–179.74 m level.

the 177.8 m level but not on species level because of the fragmentary state of the shell. Both spatangids and ophiurids are found and a fragment of cirriped at the 177.8 m level.

At 174.4 m b.s. a single find of *Yoldia hyperborea* occurs. The granulometric composition found at the 173.67–173.85 level (lab. no. 781.93) shows bad sorting in a clayey sediment with a median grain size within clay to fine silt. In this sediment fragments of *Arctica islandica* are found that can be regarded as being part of the redeposited material which can be found also higher up in the core. At a level of 166.5 m b.s. the sediment is well-sorted fine sand and regarded as fluvial. In the following 16 m up to 151.50 m b.s. the sediment is coarser, being a moderately sorted medium sand also regarded as fluvial sand. From here only some shell fragments are found and no record of *fossilia varia* (other fossils in Appendix 3).

In the next metres to the level of 143.83–144.00 m b.s. the mean grain size is within the medium silt grade. This is found to be a fine-grained fluvial material forming part of a glaciogene complex. Also here, fragmentary molluscs are found.

The Late Weichselian marine and glaciogene deposits

The first molluscs regarded as autochthonous above the glaciogene complex are found at the 130.2 m level, so this is regarded as the upper limit of the glaciogene sequence. In the interval from 141.00 and up to 130.2 m b.s. more shell fragments have been found – all showing signs of transport and wear. Finds of pyrite (137.8 m level), concretion (132.6 m level), and glacial stria on a stone (137.44 m level) all reflect typical features for a till deposit.

The marine shell material taken up by the glacier occurs in a fragmentary state, which is typical for redeposited material. However, it is from these strata that the absorption of gases from marine deposits has been dated. These dates form as mentioned a parallel to the age determination of the shells (*Macoma calcarea*) from the Skærumhede sequence where the Older *Yoldia* Clay fauna has been studied (Madsen *et al.* 1908; Bahnson *et al.* 1974). The ages found on *Macoma calcarea* shells from the Skærumhede II Well give for the first time, on the basis of molluscs, the absolute age of around 32 000 – 33 000 (¹⁴C years) of the younger part of the Older *Yoldia* Clay. Compared with the dating of the marine gases from the Skagen

Well, there is a good correlation to the stratigraphically now well-established Skærumhede sequence, so that the two cored sections found on Skagen and at Skærumhede can be regarded as deposited during the same time in the Weichselian. The Skagen sequence, however, has been strongly eroded by the ice sheet advancing during the Late Weichselian. However, the thick packet of up to 50 m glacial sediments consequently contains the traces (gases) of that marine environment, which has been eroded, but is hereby dated to give the maximum age of the glaciation. This age points to the glaciation event in the Late Weichselian around 20 000 – 18 000 B.P. (Petersen & Kronborg 1991). However, here the upper marine sequence found in the Skagen Well will be described.

From the 131.63–131.73 m level and up the core the sediment is extremely fine-grained with a medium grain size of fine silt which stays as such a size up to 100 m b.s. It should be noted that throughout the first 15 m of the core from the above-mentioned level finds of coarser material occur. This is seen at the 125.89–126.00 m level (lab. no. 526.93), where the granulometric composition reflects two maxima on the frequency curve (Fig. 92). This is taken as a typical sign of a supplementary sedimentation which might have been caused by the melting of floating ice with the coarser sediment imbedded – a drop till effect, as found deeper in the core (Fig. 91).

This suspected Arctic influence is sustained by the occurrences of Arctic molluscs up to the 114.0–115 m level, where both *Portlandia arctica* and *Bathyarca glacialis* are present.

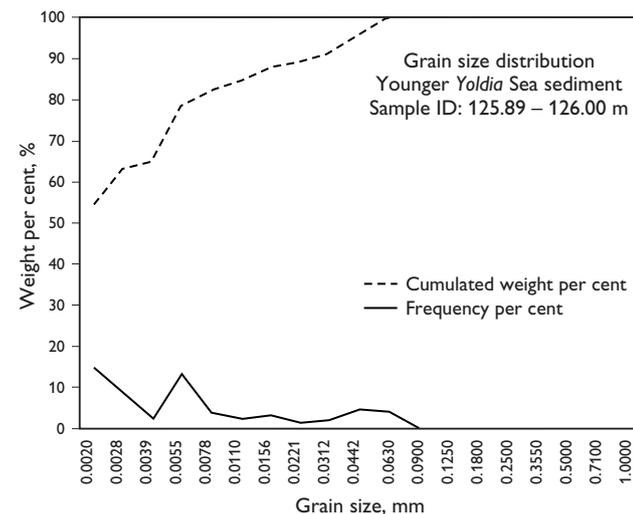


Fig. 92. The granulometric composition with two maxima on the frequency curve (lab. no. 526.93) at the 125.9–126.0 m level.

Furthermore, species such as *Nuculana pernula*, *Nuculana minuta* and *Yoldiella lenticula* occur, which are known from the Older *Yoldia* Clay in the Skærumhede sequence.

Yoldiella frigida is the first to occur at the 130.2 m level in the Skagen Well. From this level several finds of ophiuroids (fragments), cirripeds and remains of pisces. However, no finds of spatangoids have been demonstrated within the whole sequence referred to the Arctic marine deposits, but they are found all the way up in the Boreal sequence (Fig. 93E; fold-out, back cover).

In the upper part of the Arctic sequence *Siphonodentalium lobatum* occurs at the 116.0–114.6 m level and a single find of *Entalina tetragona*. Occurrences of *Nucula* sp. and *Macoma* sp. are also recorded in the Arctic part, but in such a fragmented state that the species cannot be given. From the recorded faunal composition it appears that it is a deeper-water fauna. This is also supported by the fact that forms reflecting an Arctic *Macoma calcarea* community are not present, and the fine-grained sediment points in the same direction.

As a comment to the sedimentary environment it should be mentioned that magnetic spherical concretions have been found all through the Arctic sequence. From five levels: 117.69–117.85, 124.34–124.50, 127.39–127.50, 128.13–128.33 and 132.69–132.77 m b.s. a high content of griegite (Fe_3S_4), which explains their magnetic quality, has been found by X-ray analysis together with quartz, calcite, feldspar and clay. Griegite has been reported as a constituent of reduced sediments. The occurrences in the Skagen Well are of interest in so far as the spherical magnetic concretions have been recorded only from the Arctic sequence.

This Arctic Sea deposit has been dated on material from the cores both foraminifers and macrofossils (Heier-Nielsen *et al.* 1995). From this it is seen that the actual time span ranges over 5000 ^{14}C years from 15 000 to 10 000 B.P.

The sudden change in the macrofauna, or better the abrupt stop of the occurrences of Arctic species, at the level of 114.2 to 114.00 m b.s. gives the Pleistocene–Holocene boundary.

The transition from the Pleistocene Younger *Yoldia* Sea to the Holocene marine deposits is here recorded for the first time within the Danish realm with a whole series of AMS datings supporting the chronostratigraphic position, see Appendix 4.

The dates are highly significant because the molluscan finds in the older part of the marine Holocene are

extremely poor. This, however, is not caused by the lack of samples from this core section, but is as will be shown dependent on the type of facies following the deposition of the youngest *Yoldia* Sea, which was a deeper-water deposit, followed by a Boreal deeper-water facies in the older part of the Holocene. The change from Arctic to Boreal conditions is regarded as influenced by a new current system from the Atlantic bringing in the new temperate fauna replacing the Arctic fauna of Late Weichselian age.

The change in fauna is, however, not reflected in the sedimentary record (Appendix 3, pp. 17, 21), which shows a very homogeneous clayey grain size distribution with nothing coarser than fine sand. Only in one sample (Appendix 3, p. 21, 115 m b.s.) at the sharp boundary between Late Weichselian and Holocene medium sand, coarse sand and gravel are observed. On this homogeneous sequence of clay to fine sand measurements of magnetic susceptibility and thermoluminescence sensitivity have been conducted.

It is worth noticing that in a diagram of magnetic susceptibility versus TL sensitivity the two samples forming the peak in the last part of the Late Weichselian also represent the more immature sediment (high susceptibility and high TL sensitivity). In contrast, the whole series of samples from the lower part of the Holocene seems more mature (low susceptibility and low TL sensitivity). So, in this way the peak can also be connected with the sudden break through of the water from the Baltic Ice Lake at Mt. Billingen, whereas the mature sediments from the Holocene may reflect the long-transported sediments introduced by the new current system from the Atlantic, bringing in the new temperate fauna in the early part of the Holocene and replacing the Arctic fauna of Late Weichselian age (unpublished data, K.L. Rasmussen and K.S. Petersen).

The Holocene

As mentioned earlier, the transition from the Arctic Younger *Yoldia* Sea to the oldest Holocene marine deposits is not to be seen from the sediment analyses except for the occurrences of griegite and some coarser material in the Arctic part. This appears when the cumulative curves from the 125.89–126.0 and 113.60–113.70 m levels from the Arctic and Boreal part (Figs 92, 94, lab. nos 526.93 and 522.93 respectively) are compared. The median grain size is for both samples fine silt, see Appendix 3, p. 21.

Considering the many samples analysed within the

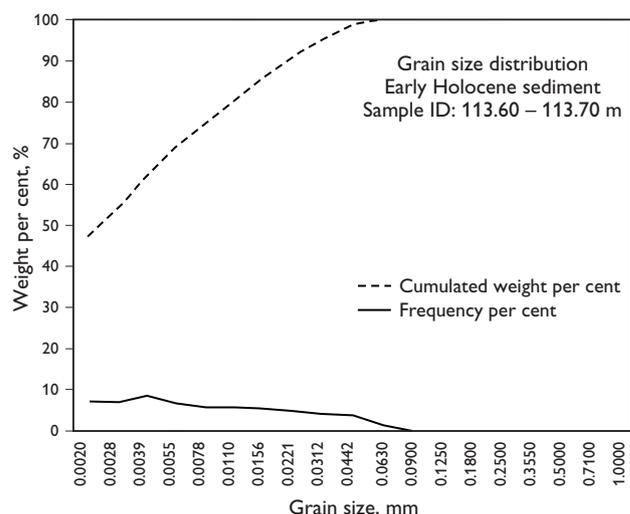


Fig. 94. The cumulative curve from the 113.60–113.70 m level, lab. no. 522.93.

lower part of the Holocene up to the 100 m level, which is dated to be around the Boreal–Atlantic boundary, only very few molluscan species have been found; also the number of specimens is low.

The Preboreal–Boreal 10 000 – 8000 ¹⁴C years B.P.

In the Preboreal–Boreal sequence only *Parvicardium minimum* has been found in more than a single find together with *Mysella bidentata*. However, three other genera are recorded: *Cardium*, *Abra* and *Lyonsia*.

Parvicardium minimum is known from the deeper part of the Skagerrak today and is found up to a depth of 30 m in the Kattegat. It is recorded also from the Eemian in the Skærumhede series. Compared with the occurrences of *Mysella bidentata* also in this core level at Skagen one can imagine a deeper-water environment, because *Mysella bidentata* is also found to great depth (600 m) today in the Skagerrak.

Spatangoids, apparently in great quantities – considering the many fragments – are found and in a lesser degree fragments of ophiuroids, which were also recorded from the Arctic part.

From the family Spatangidae, five genera are known in Nordic waters. From the Skagen Well at a depth of 108.34–108.56 m b.s. a well-preserved species of *Brissopsis lyrifera* (Forbes) has been collected (Fig. 95). This species lives only on pure muddy bottoms and totally embedded in the sediment.

As seen from the grain-size distribution from the



Fig. 95. The well-preserved *Brissopsis lyrifera* (Forbes) from the 108.34–108.56 m level. MGUH 25404.

level of 107.90–108.00 m b.s., this part is a fine-grained sediment. From the 109.39–109.50 m level the core section revealed a cut through the traces of a spatangoid similar to those that *Brissopsis lyrifera* could leave, with the typical backfilling (Bromley 1990, fig. 5.11; see Fig. 96).

Brissopsis lyrifera can be found in great quantities in the northern part of the Kattegat and Skagerrak, while it might be found in the Øresund but not in the Bælt Sea, the Baltic and the Limfjord region, according to Mortensen (1924).

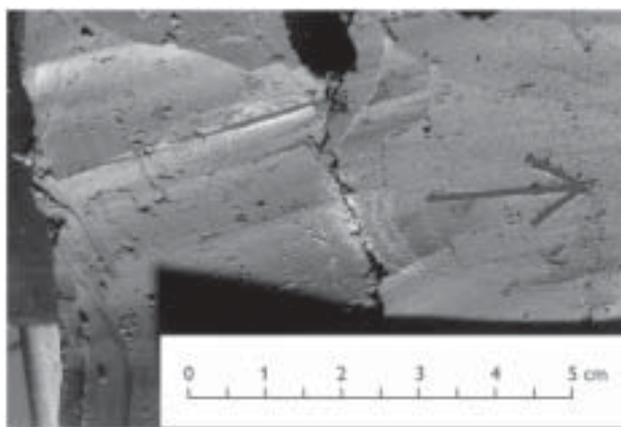


Fig. 96. Trace from the 109.39–109.50 m level. Might be similar to that of *Brissopsis lyrifera*.

Also other spatangoids might be found in the Skagen cores in the huge material of fragments. From the older strata the genus *Echinocardium* has been recorded earlier from the Skærumhede series by the author, and *Echinocardium cordatum* has been found in the *Cypripina* Clay from the Eemian (Madsen *et al.* 1908).

So poor in molluscan species this community from the Early Holocene appears to be, one may pay attention to the abundant remains of starfishes and echinoids which can be seen as a dominating element in this environment. In this way the sea bottom of those days was controlled by the echinoderms eating up most of the larvae of molluscs, as described by Thorson (1961). If one should be compared with a present-day community, it must be the *Maldane-Ophiura sarsi* community in which besides *Ophiura sarsi*, *Brissopsis lyrifera* is found as the only often found larger animal (Thorson 1968).

The *Maldane-Ophiura sarsi* community replaces the *Amphiura* community at depths of around 150 m and deeper in the Skagerrak.

A single find of Pisces (100.3–100.5 m) has been recorded and a few finds of plant remains and pyritified traces (chondrites?).

These rare finds of marine deeper-water facies from the very last part of the Pleistocene and the earliest Holocene will contribute to our knowledge of the land and sea configuration during the so-called Continental period (Petersen 1985b).

Considering the sedimentation rate during the first 2000 years of the Holocene, viz.: through the Preboreal and the Boreal from which there have been only a few records earlier within the Danish area, it is seen to be around 7.5 m per 1000 years. This is higher than the sedimentation rate for the Younger Yoldia Sea, as found also in the Skagen Well record of 3 m per 1000 years. When this is given in calendar years, the differences are even bigger, because then the sedimentation of 15 m in the Younger Yoldia Sea took about 6000 calendar years and still about 2000 calendar years in the Preboreal and Boreal seas within the Skagen area (Petersen & Rasmussen 1995a, b).

Regarding the sediment, 50% is found to be clay in the Younger Yoldia Sea – and in some parts at the level of 117.29–117.40 m b.s. around 63% – while during the Preboreal–Boreal the clay content has fallen from around 40% at the 113.60–113.70 m level to 20–30% at the 100 m level.

The Atlantic 8000–5000 ¹⁴C years B.P.

From the dates (Heier-Nielsen *et al.* 1995) the Atlantic covers the cored section from 100 to 80 m b.s. Here the sediment in the oldest part has 30–20% clay, falling to a content of 15% clay in the youngest part at the 80.60–80.70 m level (see Fig. 93A).

Throughout the Atlantic the echinoids still dominate the samples and among these the spatangoids, as in the Preboreal and Boreal. However, here small gastropods occur: *Melanella lubrica*, *Odostomia umbilicaris*, and *Eulimella scillae*.

Melanella lubrica is regarded as an ectoparasite on holothuroids, and *Odostomia umbilicaris* is often found together with *Mytilus adriaticus*. However, the latter bivalve has not been found in the Skagen Well material. It should be mentioned that the *Odostomia* species are difficult to determine (Fretter *et al.* 1986, p. 605) and no less so in subfossil material.

Furthermore, *Onoba vitrea* and *Aclis minor* are found in the younger part of the Atlantic, where the determination of *Onoba vitrea* is taken with some reservation because the three other species *Odostomia semicostata*, *Odostomia aculeus*, and *Odostomia proxima* are very much alike and difficult to tell apart on shell features alone.

Aclis minor belongs to a large group of predatory gastropods that mostly and perhaps always (cf. Fretter & Graham 1962) are associated with echinoderms.

From the Atlantic single finds of *Parvicardium minimum* from the 96 m level and *Spisula subtruncata* at the 86 m level occur. *Spisula subtruncata* is found next at the 73 m level in the Subboreal, but becomes the dominating bivalve at the 30 m level, which can be referred to the younger part of the Subatlantic. This depth is also within the range where this bivalve is found in large amount in the present-day Danish seas.

From the Atlantic the predatory gastropod *Lunatia alderi* occurs. This species is most probably the one which has bored into the many molluscs found in the overlying strata, but has not been recognised by its traces in the sparse material from the Atlantic.

Fragments of *Abra* sp. and *Macoma* sp. occur in the cored section from the Atlantic, and from the 80.60–80.70 m level also finds of Pisces and crustaceans have been recorded, as seen in Appendix 3.

It appears that also in the Atlantic the sampling reveals a deposit with low diversity and few specimens of molluscs, where the echinoderms dominate as in the Preboreal and the Boreal sequence. However, considering the older Holocene deposits which were ten-

tatively referred to the *Maldane-Ophiura sarsi* community, the one from the Atlantic can on the basis of the molluscs and the still dominating Echinoderms be regarded as another of the deeper-water communities found in the present-day deeper water in Skagerrak. Here it should be the *Amphiura* community, which as mentioned earlier is found above depths of 150 m.

The Subboreal 5000–2500 ¹⁴C years B.P.

The following 20 m of the Skagen Well cover the Subboreal, 80 to 60 m b.s. The sedimentation rate can be estimated to be 8 m per 1000 years, a slight rise from the 6.6 m per 1000 years found during the Atlantic.

The clay content falls in this part to below 10%, and the coarse silt and fine sand fractions become the dominating grain sizes. The material is well sorted. Fig. 93A, C.

In all the sampled cores within this section fragments of echinoderms occur – mostly spatangoids as found earlier – but the diversity of mollusc species is higher, up to 10 different species in one sample and several with five to seven species in each. However, the number of specimens is still low and most of the finds are of single specimens.

Only *Onoba vitrea* is found in a number of eight specimens in one sample (the 67.0 m level). Among the other species, only *Lunatia alderi* can be mentioned occurring in a number of eight within the whole section.

From the 73.0 m level *Turritella communis* occurs with boring of predatory gastropods – probably *Lunatia alderi*.

Furthermore, *Eulimella scillae* and *Retusa truncatula* are found from the 67 m level and *Mysella bidentata* together with *Corbula gibba* at the 65.6 m level. The latter will be more common in the above-lying strata belonging to the Subatlantic.

From the Subboreal sequence, one of the very few finds of Polyplacophora occurs sitting in the sediment, represented, however, only by one plate which does not allow further determination by the author.

Within the interval from 75.0 m to 72.0 m three finds of *Turritella communis* have been recorded. This is one of the characteristic species on the level muddy bottoms.

Nuculana minuta which has been found also in the Arctic Younger *Yoldia* Clay is here recorded for the first time in the Holocene in the Skagen Well. There are several finds of *Nuculana minuta* from the Subboreal, and it is found in the present-day Kattegat on

muddy bottoms at depths of more than 20 m. This fits very well with the occurrences of *Turritella communis*.

Acanthocardia echinata is also found for the first time and here recorded from 78.0 m. This species occurs on mixed bottoms and clay bottoms at depths of from 10 to 150 m.

Also *Phaxas pellucidus* occurs for the first time in the Skagen Well during the Subboreal. This mollusc occurs in general at depths of between 10 and 50 m, often together with *Abra alba*, also found in this section of the well.

The first occurrences of *Chamelea striatula* and *Corbula gibba* are in the Skagen Well during the Subboreal.

Chamelea striatula is one of the most common of the Danish marine bivalves but is connected to the sandy bottoms. According to Jensen & Spärck (1934), it is not found in the Kattegat at depths greater than 50 m, because the sandy bottom in this region goes no further out and the species is rarely taken on clayey bottoms. In this connection it should be noticed that just around the 75 m level, where *Chamelea striatula* occurs for the first time in the Skagen Well, the sediment changes to coarse silt with more than 50% fine sand.

Finally, at 61.09–61.14 m, is the first occurrence of *Tellimya ferruginosa*. This species will also be more common in the Subatlantic from the 30 m level. *Tellimya ferruginosa* is often connected with the occurrence of *Echinocardium cordatum* but can also be found free living (Jensen & Spärck 1934).

The many new species – new through time in the Skagen Well – introduced in the Subboreal point to water depths around 50 m with characteristic species from the present-day community such as *Turritella communis* and *Chamelea striatula* – the *Venus* community.

The changes to a more sandy sediment are perhaps the background for the occurrences of the new species. However, the echinoids have also decreased – and this may explain the more prolific mollusc faunas, for the toll of eaten molluscan larvae taken by the echinoderms is no longer so high (cf. Thorson 1961).

The Subatlantic 2500–¹⁴C years B.P.

The uppermost 60 m of the Skagen Well belongs to the Subatlantic. In general the 60 m cored section that falls within the Subatlantic can be divided into two parts of an equal length of 30 m: the lower 30 m with

a clay content of 30–40% of well-sorted sediment, and the upper 30 m mainly consisting of fine to medium sand with few intercalations of gravel.

Regarding the dated part of this upper sequence (Heier-Nielsen *et al.* 1995, table 1) – from 30.25 to 12.75 m b.s. the sedimentation is 17.50 m during 210 years from A.D. 950 to A.D. 1160. This gives a sedimentation rate of about 80 m per 1000 years. In this case showing a fine example of the building up of the Skagen spit, where the coarser material occurs as part of the long-shore transport, and deposited in foreset beds.

The older Subatlantic

The older part of the Subatlantic covers the interval from 60 to 30 m b.s. This section shows a slight coarsening upwards and a sedimentation rate of 30 m per 1000 years. The faunal composition can be analysed on the basis of 50 samples with a higher species diversity than found in the Subboreal. Some of the species are new to the record from the Skagen Well.

Hinia pygmaea appears for the first time at the 42 m level, as well as *Hinia reticulata*. They both belong to the sublittoral zone and are found on muddy bottoms. *Mangelia brachystoma*, which first occurred at the 58 m level, also belongs to the sublittoral fauna, but it occurs on sand and sandy muddy bottoms.

Polygireulima sinuosa is an ectoparasite on echinoderms which are still common and constitute a part of every one of the samples, but it has been found only within the level 38.19–38.24 m.

The first littoral species, *Mytilus edulis*, occurs at 49.14–49.24 m, and from this level it occurs regularly upwards, but only in small numbers until the 31 m level, where it is found in greater quantities. This species can be found out to 40 m depth, but must nevertheless be considered an eulittoral species where its occurrence is most abundant. The young specimens are often found on the vegetation.

Also *Chlamys varia* is common in the coastal zone and occurs at the 32.85–32.90 m level.

Heteranomia squamula is epifaunal on hard substrates but also on algae and crustaceans. It has a wide occurrence from the littoral zone out to a depth of 100 m. In the Skagen Well it is confined to the Subatlantic part.

Thyasira flexuosa is today a common bivalve on clayey bottoms from 20 m to 100 m, but it has been found only in two samples from the older Subatlantic. This is hard to explain, as it has a wide extension within the whole of the North Atlantic area (Jensen & Spärck

1934), and in numbers it is one of the most dominant species on the muddy bottoms which according to the sediment analysis have been prevalent for most of the Holocene in the Skagen area.

Turtonia minuta, belonging to the species from the coastal zone, is found in a single specimen at 39.85–40.02 m. It is not recorded from the recent Danish fauna, but lives off the Norwegian west coast and is found subfossil in the Limfjord region.

At 47.30–47.35 m is the youngest record of *Parvicardium minimum*, which was one of the few species occurring in the older Holocene reflecting deeper water.

A single find of *Angulus tenuis* is at 55.30–55.35 m. The common occurrence of this species starts at the 30 m level.

Also *Donax vittatus* occurs at 35.90–36.00 m level which must be seen as outside the general occurrence of this species, which is from littoral to around the 20 m depth *Donax vittatus* is found within the high energy zone.

A single find of *Abra prismatica* at 49.90–42.00 m is within the general depth interval for this species (20–60 m).

In connection with the depth indications given in the well in metres below surface and the common depth intervals indicated by various authors for the molluscan species, it is possible to use the actual depth recorded in the well as the living depth for the subfossil fauna found in the Skagen Well during the younger part of the Holocene. This because of the expiring isostatic movement and only little eustatic changes during the Late Holocene (Petersen 1991b).

Corbula gibba, which was also found during the Subboreal has in the Subatlantic an even occurrence through the older part.

Barnea candida, normally only found out to a depth of 30 m, occurs in the well already at the 51.54–51.59 m level, although only found in fragments.

Cochlodesma praetenue which was found in the Eemian at 183.77–184.00 m b.s. is also found in the Subatlantic at 43.19–43.24 m. This species is rare in Danish waters and has been taken alive only once north-east of the island of Læsø. However, shells have been found elsewhere in the Kattegat region, Jensen & Spärck (1934). It has a wide occurrence from the littoral zone and out to 110 m on different bottom types.

Finally *Thracia phaseolina* shall be mentioned. This species occurs to depths around 50 m on clayey bottoms.

As mentioned above, the echinoderms are also found

in the Subatlantic represented by the fragments of spatangoids. Also cirripeds occur in still higher quantities up towards the 30 m level (Appendix 3, p. 6). Furthermore, there are single finds of Pisces and other fossil remains such as crustaceans (other fossils in Appendix 3). However, also serpulæ are found and may have settled on the shells of the other animals as the crustacean carapax.

The younger Subatlantic

The increasing number of cirripeds in the upper 30 m should probably be regarded as allochthonous, since they occur together with the coarser material during the formation of the advancing Skagen Spit.

The change in the upper 30 m to coarser material also introduces new forms of molluscs that are characteristic of the littoral facies and high-energy coastal situation still prevailing in this area today.

The description of the upper 30 m is, as mentioned earlier, based on the Skagen IV Well 50 m away from the Skagen III Well and at the same level (+ 1 m). This was done because only washed samples were obtained from the upper 30 m of the Skagen III Well, and such samples could not form the best basis for a uniform description of the whole sequence – especially the necessary quantitative treatment of the molluscan faunas could not be fulfilled in that way. Furthermore, a total of 29 grain-size analyses have been made within this part of the column, showing two sequences of well-sorted sediment coarsening upwards, with a sorting coefficient lower than 2 (Fig. 97).

In order to control the degree of transported shell material, size analyses and counts on right and left valves have been considered relevant with such a high-energy near shore sedimentation (Fig. 98).

Especially the most prevalent bivalve within these uppermost 30 m, *Spisula subtruncata*, has been counted. Also observed borings have been figured in Appendix 3, to be seen in connection with the actual finds of the predatory gastropods. This is done in order to show the degree of mutual connection in the molluscan assemblages, between predatory elements and their prey.

The building-up of the upper 30 m took place within a very short period of time, and the sedimentation rate of this interval is estimated to be around 70 m per 1000 years. This high sedimentation rate has a serious effect on animal life.

The dates on the building-up of the Skagen Spit lead

to the conclusion that the extension of the coast line to the place where the wells have been sunk took place around A.D. 1400.

Taking into account that the final history of the coastal development takes place as a near-shore and littoral deposition history, the actual development on a west coast site similar to the Skagen area has been analysed. This has been done by way of several van Veen grab samples – altogether 61 outside the Agger Tange complex in the westernmost part of the Limfjord (Petersen 1994a). These investigations focused on the bivalves, evaluating their degree of being autochthonous from the preservation with both valves together, one valve but whole, a fragmented state or a rolled fragment. These observations have been summarised in Appendix 5.

The newcomers of molluscs from the Skagen Well will be mentioned. These also represent the species earlier known to live close to the recent Danish waters and species new compared to what is known to be part of the recent Danish fauna.

This part of the record has the highest diversity and number of specimens compared to other sections of the Skagen Well. The mean species diversity per sample shows a rise compared to the older part and reflects the new sedimentary facies. However, the near to shore situation also puts forward the question of whether part of the faunas, if not all, may have been reworked.

Eliminating the uppermost ten samples covering the 5 m which can be regarded as the medieval shore. First the species represented by only few finds that are commonly found in great quantities will be discussed.

Lacuna pallidula occurs only as a single find at 30.0–30.5 m level. This species occurs on *Fucus serratus* and in great quantities from the littoral and to a depth of 70 m. *Hydrobia ulvae* occurs normally in high numbers in shallow water. In the Skagen Well it has been recorded from only two levels (11.70–11.80 m and 25.0–25.5 m) and with few specimens. *Rissoa violacea* is connected with seaweeds and found from the tidal zone to a depth of 50 m. Here the only finds are from the 27.0–27.5 and 28.0–28.5 m levels. Also *Bittium reticulatum* appears not to be part of the environment, since this species has only one occurrence at the 22.0–22.5 m level. This species lives on *Zostera*, as do other of the above-mentioned species.

It can be concluded that the upper 30 m section of the well lacks the normal abundance of epifaunal elements connected with vegetation. This is also in good accordance with the high rate of sedimentation.

Histogram of 29 grain-size analyses from the upper 30 m of the Skagen Well 4

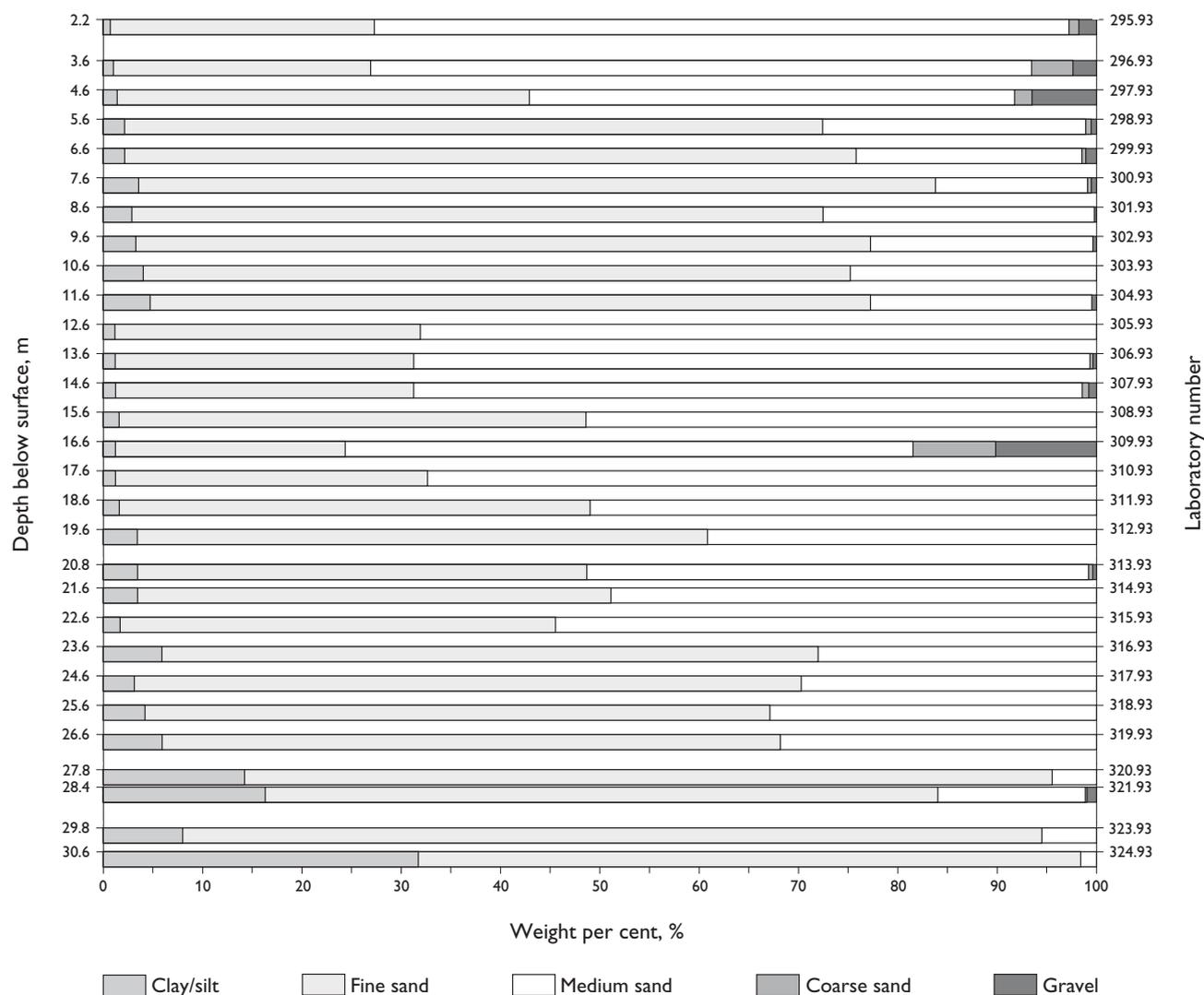


Fig. 97. Histogram of 29 grain-size analyses from the upper 30 m of the Skagen Well 4, showing two coarsening-upwards sequences.

Among the gastropods occurring in the upper part of the well, *Aporrhais pespelicani* occurs in the interval from 22.0–22.5 m to the 11.0–11.5 m level. This species is regarded as sublittoral from depths of 10–180 m on a sandy muddy bottom or muddy bottom. However, it has been found in large quantities as empty shells on the shore of the east coast of Skagen. This was rather puzzling until it was explained that the hermit crab might have been the actual agent bringing the shells on shore (G.H. Petersen, personal communication 1998).

The occurrence of *Lunatia montagui* is restricted to the 20.0–20.5 m level, while *Lunatia alderi* is rather frequent in the core samples. The impact of these predatory gastropods on the fauna – 15 species have been

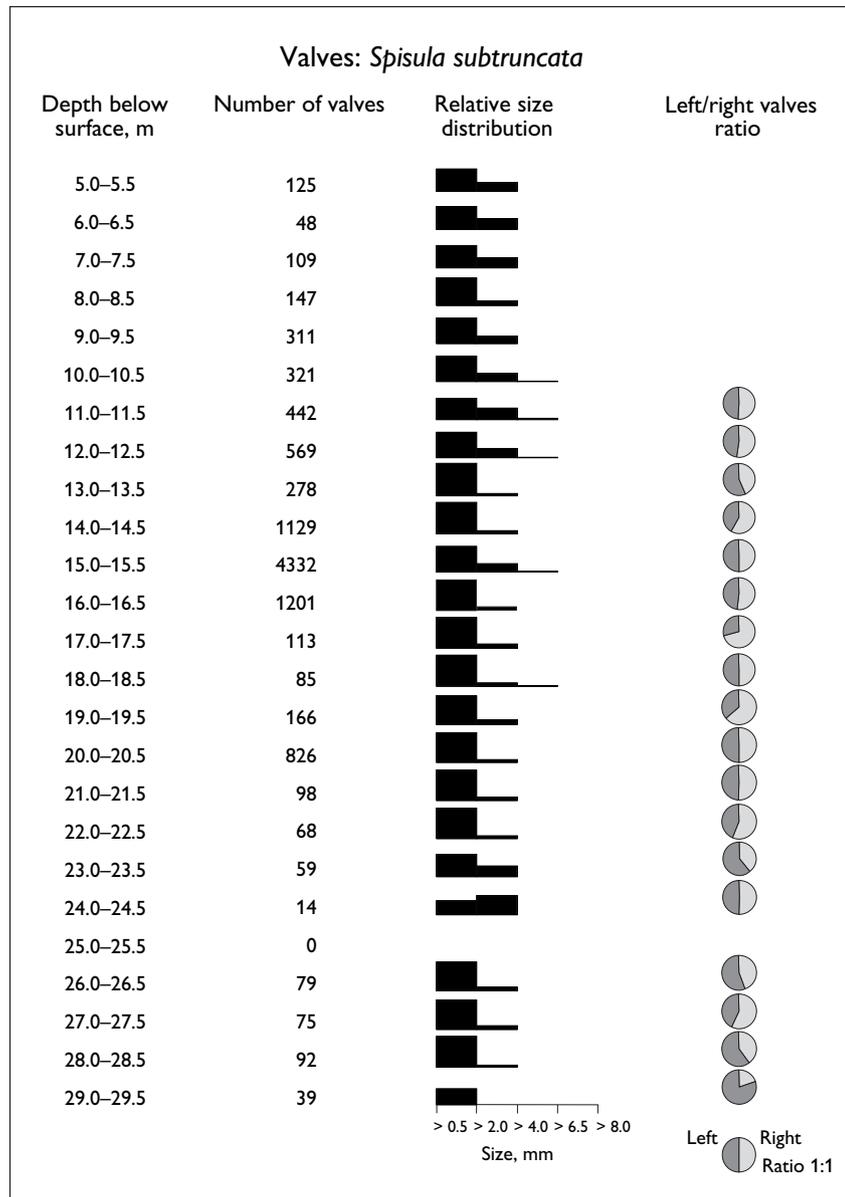
recorded with such borings, including some of the *Lunatia* species themselves – has been quantified in Appendix 3.

The high number of *Lunatia alderi* in the upper 30 m is in accordance with the preferred environment of clean sand of this species.

A new neogastropod to the fauna of the well is the *Buccinum undatum* from the 11.0–11.5 m level, while *Hinia pygmaea* now becomes common, occurring in most of the samples from the 28.0–28.5 m level to 6.0–6.5 m b.s. and represented in many specimens – some of them bored by predatory gastropods, as seen in Appendix 3.

The small gastropod *Oenopota turricula* has a wide depth range (20–200 m), so the single finds at the 23.5–

Fig. 98. Size histograms for *Spisula subtruncata* in the upper part of the Subatlantic sequence, the 29.0–29.5 m level to the 5.0–5.5 m level, with ratio on left and right valves from the 29.0–29.5 m level to the 11.0–11.5 m level.



21.0 m level most probably reflect that only in this part of the well does the clean sandy bottom occur which is preferred by *Oenopota turricula*.

Of the heterogastropod newcomers in the upper section, *Graphis albida* from the 25.0–25.5 m level can be mentioned. This species is not recorded among the recent Danish molluscs (Jensen & Knudsen 1995). It is found sublittorally out to a 30 m depth.

Hemiaclis ventrosa occurs at the 30.0–30.5 m and 11.0–11.5 m levels, but it is recorded in recent waters at a much deeper level: 100–200 m. Neither this nor the species mentioned above is recorded from Danish waters.

Vitreolina philippii, occurring within the interval from 29.5 to 7.0 m with seven specimens, is known

from the recent Danish fauna and is noted as sublittoral to a depth of 200 m. This gastropod is a parasite on echinoderms, as the other Eulimidae. Echinoderms are still present in the material as seen from Appendix 3.

From the 15.0–15.5 m level, finds of *Chrysallida decussata* occur, which is also recorded by Jensen & Knudsen (1995). This species occurs at the depth interval of 14–40 m.

Turboniella acuta has been recorded from Danish waters by Jensen & Knudsen (1995) although rare. The occurrence of this species in the Skagen Well is at the 21.0–21.5 m and 20.0–20.5 m levels with, two well-preserved specimens.

Among the ophistobranchs there are some fragmentary finds which have not been identified to species

level, but species such as *Retusa truncatula* and *Cylichna alba* are found also in the upper part of the well.

A fragmentary scaphopod from the 15.0–15.5 m level has not been referable to species level.

Among the bivalves, many are new to the already mentioned fauna from the well, and the number of specimens is for many of the species very high in comparison to what has been recorded from the older strata.

Of Palaeotaxodonta, *Nucula nitidosa* is found and represented all through the interval from 29.5 to 13.0 m b.s., occurring on sand bottom, which is the preferred substrate. Also *Nucula nucleus* is found within the interval from 30.5 to 8.0 m b.s. with many (13) specimens, part of them bored as the presiding species by the predatory gastropods.

In the Subclass Pteriomorpha, species from Mytiloidea and Pterioidea such as *Musculus discors* at the 28.0–28.5 level and *Mytilus edulis* in large quantities (113 specimens) are found, albeit most of the latter as juveniles. From the 28.0–29.5 m level individuals are found (with both valves). This latter species is typical in the littoral zone, but may occur at depths out to 40 m.

Pectinidae have been found, but all in fragments, in the interval 25.5–12.0 m b.s.

Ostrea edulis occurs in the interval 28.5–7.0 m b.s. – mostly as juveniles.

The Subclass Heterodonta, from where most of the found bivalves come also includes the species most often found and characteristic of the youngest part of the marine sequence.

Mysella bidentata is recorded from the entire Holocene, although only a few specimens are present in the Early Holocene. In the latest Holocene as the present 30 m, 125 specimens have been found. The closely related *Tellimya ferruginosa* occurs apart from a single find at the 61.09–61.14 m level, from the 29.5 m level where it is common up to 8.0 m b.s. Both of these species have specimens bored by the predatory gastropods. *Tellimya ferruginosa* is a commensal on *Echinocardium cordatum*, but can also be found on its own in the sediment.

Mactra stultorum has been found only in the upper part of the cored section and can be seen as connected with the clean sand that is the type of bottom preferred by this species. On a suitable bottom it may be found out to a depth of 60 m.

Spisula subtruncata, which has a wide distribution from the littoral zone and out to a depth of 200 m, can be found both on muddy and on sandy bottoms. It dominates the uppermost part of the sequence, with 11085 specimens! In recent waters on sandy bottoms

this species is one of the most common bivalves in the Kattegat at depths between 20 and 30 m (Jensen & Spärck 1934). On the cored material from the Skagen Well size histograms and counts on left and right valves have been made in order to ascertain from such measurements whether the shell material is autochthonous/parautochthonous. As seen from the figures in Fig. 98, it appears that there is an even representation of the left and right valves, and the size histograms reflect a life assemblage which also might appear from the well-preserved gracile valves.

The borings counted on valves of this species make it clear that *Spisula subtruncata* must have been the preferred victim of the predatory gastropods in this molluscan assemblage. At the 15.0–15.5 m level around 10% of the specimens are bored (2723 individuals out of which 268 have been bored). Individuals (with both valves) have been found up to the 21.0–21.5 m level, where also other bivalves have been found with closed valves. However, the most even occurrence of left–right valves also at the 15.0–15.5 m level (2147–2105 respectively) may speak in favour of an autochthonous state also at this depth. The size histogram from the same level points to the same conclusion (see Fig. 98). By way of the same kind of measurements it is possible to extend the possible life-assemblages up to a level of 10.0–10.5 m b.s., where the material still is present in such quantity that the measurements can be taken as bearing. Investigations performed on nearshore deposits off the west coast of Jylland in the Agger Tange area given in Appendix 4 support the view that life-assemblages can be found near to shore at depths of up to 6–7 m.

Almost all the AMS datings in the upper part of the well have been based on *Spisula subtruncata*, and these datings all fall within the right relative age according to their respective levels. This is not the case with the date on *Donax vittatus*, which has also been dated within the upper 30 m interval. As shown on the dating diagram (Heier-Nielsen *et al.* 1995; Appendix 3), the *Donax vittatus* age clearly appears as an older element in a younger part of the section. However, *Donax vittatus* will be commented upon later in the text.

Solenidae species often occur in the upper part of the sequence, but often in a fragmentary state. However, *Phaxas pellucidus* is common in the interval between the 30.5 and 20.0 m level, where it is found in several specimens in some of the samples. It lives on different bottom types from the sublittoral at a depth of 4 m out to a depth of 150 m. However, in the Skagen Well there is only a single occurrence at 73.39–73.44 m b.s.

One of the dominating bivalves is *Fabulina fabula*, which only occurs within the interval 28.5–4.0 m b.s. Some of the specimens have been the victims of the predatory gastropods. This species prefers a bottom type of fine sand, which might explain the interval of occurrence in the Skagen Well, where there are sandy layers only in the uppermost 30 m. On a suitable bottom this species goes out to a depth of 50 m.

Also *Tellina pygmaea* and *Angulus tenuis* occur in the upper part of the sequence and only there, with the exception of a single find of *Angulus tenuis* at the 55.30–55.35 m level. This is outside the general occurrence of this shallow-water species normally found from the intertidal zone out to a depth of 10 m.

Donax vittatus, which is found regularly in the interval from the 27.5–4.0 m level, but often in a fragmentary state, is a typical high-energy coastal form on a sandy bottom. As already mentioned in connection with the dates, *Donax vittatus* also occurs as an allochthonous element, which can be seen from the many rolled fragments of this sturdy shell. Its occurrence out to a depth of 20 m off high-energy shores characterises in the best way the situation by the building up of the Skagen Spit System. The species is not found in the Kattegat region and is absent from the inner part of the Limfjord.

Gari fervensis is found only in this upper part of the Skagen Well from the 27.5 to 23.0 m level. Accordingly, in Danish waters it is known from a depth of 15–40 m on mixed bottoms and sometimes on sandy bottoms.

Through most of the Holocene, fragments of the genus *Abra* have been found. *Abra nitida*, which has a wide depth distribution from the sublittoral zone out to a depth of 200 m, has been found through the last part of the Holocene from the 71.89–72.00 m level to the 10.70–10.80 m level mostly in single specimens. This species has its main distribution today in the deeper parts of the Skagerrak and the Kattegat on muddy bottoms.

A single find of a rolled fragment of *Arctica islandica* occurs at 14.70–14.80 m, which is the only find besides the fragment from the glacial series at the 173.67–173.85 m level. However, the washed samples have given another specimen also from the Subatlantic (Appendix 2).

Chamelea striatula is the characteristic animal of the *Venus* community on a sandy bottom in the North Sea and the Kattegat. At Skagen it occurred already at the 76.34–76.50 m level (late Subboreal). At this depth a change of weight per cent of clay takes place (from 13.7% to 7.8%), and the fine sand component becomes

the dominating grain size with a weight per cent of 54.9. From the 30 m level, *Chamelea striatula* is more common, and specimens with connected valves occur up to 21.0–21.5 m b.s., many of them bored by predatory gastropods, as shown in Appendix 3. From the point of view that also other bivalve species have been found as whole individuals up to the 20 m level, it can be regarded as the well-established limit for an autochthonous occurrence of the molluscs. However, as seen from the observations off the Agger Tange area given in Appendix 5, there will always be an element of allochthonous material in such a high-energy coastal environment which should be taken into account also for the Skagen area regarding the uppermost part of the sequence from the Skagen Well.

A single find of *Timoclea ovata* is also found in the upper part of the section at the 27.0–27.5 m level. This species is today found at a greater depth than *Chamelea striatula*, but is not very numerous.

Within the Order Myoida, *Corbula gibba* is also well represented in the upper section, with individuals found up to a level of 27.0–27.5 m b.s. This species also shows many specimens killed by predatory gastropods. *Corbula gibba* is found in the sublittoral zone out to a depth of 250 m. At Skagen its first occurrence is at 74.89–75.00 m, in the early Subboreal, but it becomes common in the Subatlantic and occurs in high numbers only in the last part of the Subatlantic from the 30 m level, often bored.

Finally, two single finds of *Saxicavella jeffreysi* and *Pholas dactylus* occurred at the 20.0–20.5 m level. *Saxicavella jeffreysi* is in recent Danish waters not very abundant at depths between 25 and 50 m, while *Pholas dactylus* would only be expected to be found at depths less than 10 m. *Pholas dactylus* is a boring form found in hard substrates, which is far from the actual sediment occurring at this level in the Skagen Well. The fragmentary *Pholas dactylus* can be regarded as one of the allochthonous elements that can be seen in connection with the accessory finds mentioned in Appendix 3 and commented upon below.

Among the accessory finds the barnacles and sea urchins dominate. Also fish remains are found, often in the form of vertebrae, but an otolith appears as well. Other fossil remains are serpulids, bryozoans, crustaceans, and plant and insect remains, which taken as a whole very well characterise the near-shore environment. On the other hand, no concretions are found like the ones from the Younger *Yoldia* Sea, or pyrite as found at the base of the Holocene and the Eemian. Although these accessory elements cannot be quanti-

fied, they offer some additional information when considered together with the sedimentological and mollusc records.

Conclusive remarks on the Skagen Well

In the description given above, the faunal record is the basis for understanding the climatic changes in the Skagen Well, supplemented by the observation on the changes in the sediments. However, the changes found during the Holocene are most likely to be connected with changes in facies, and here the changing depth is the most prominent agent, ending up with the last event represented by the depositional history of the Skagen Spit.

Based on the dating of the Holocene and the Late Weichselian, the descriptions have been given in terms of episodes. Especially the Holocene strata points to a development from deeper- to shallow-water facies from Preboreal to Subatlantic. In this development there appears to be a facies change that can be compared to

the bottom communities as known from the Skagerrak–Kattegat region when going from the deeper-water communities of the present day, the so-called *Maldane-Ophiura sarsi* community, to the *Venus* community of the more shallow seas.

The mollusc assemblages in the Skagen sequence indicate a deeper-water facies during the Eemian, the Weichselian and the older Holocene in contrast to what hitherto was known in other parts of the Danish area during the Late Quaternary.

The Skagen Well has a record of the changing seas during the Late Quaternary, from the Eemian through the Weichselian (although only in parts) and the Holocene. For the first time within the Danish area, the full record of the marine environmental transition from the Late Pleistocene to the Holocene can be demonstrated on the basis of molluscs. However, not all the episodes known from the Skagen Well can be found in marine facies of the other regions, but thanks to the new records from the North Sea around the Jydske Rev area, a near to full Holocene marine record is at hand, including part of the Preboreal (Petersen 1998).

The environmental changes through time in the seven sectors based on the molluscan records

The recorded mollusc species within each area are given in Appendix 6. Regarding the environmental changes through time within the Danish realm, the seven sectors will be considered from the Eemian, starting in the south within the classical area where Forchhammer named the deposits the *Cyprina* clay.

Eemian species sorted after climatic affinities

The Bælt Sea

Age: Eemian

Climatic regions: asbl

Class Bivalvia

Subclass Heterodonta

Order Myoida

Mya truncata Linnaeus 1758

Total for climatic regions asb. : 1 (1.7%)

Climatic regions: .sb.

Class Bivalvia

Subclass Heterodonta

Order Veneroida

Arctica islandica (Linnaeus 1767)

Order Myoida

Zirfaea crispata (Linnaeus 1758)

Total for climatic regions .sb. : 2 (3.4%)

Climatic regions: .sbl

Class Bivalvia

Subclass Pteriomorpha

Order Mytiloida

Mytilus edulis Linnaeus 1758

Order Pterioidea

Heteranomia squamula (Linnaeus 1758)
 Subclass Heterodonta
 Order Veneroida
Mysella bidentata (Montagu 1803)
Tellimya ferruginosa (Montagu 1803)
Spisula elliptica (Brown 1827)
Macoma balthica (Linnaeus 1758)
 Total for climatic regions .sbl: 6 (10.2%)

Climatic regions: ..bl

Class Gastropoda
 Subclass Prosobranchia
 Order Neotaenioglossa
Littorina littorea (Linnaeus 1758)
Hydrobia ulvae (Pennant 1777)
Rissoa inconspicua Alder 1844
Rissoa membranacea (J. Adams 1800)
Rissoa parva (da Costa 1779)
Caecum glabrum (Montagu 1803)
Bittium reticulatum (da Costa 1778)
Aporrhais pespelicani (Linnaeus 1758)
 Order Heterogastropoda
Triphora adversa (Montagu 1803)
Epitonium clathrus (Linnaeus 1758)
 Order Neogastropoda
Hinia pygmaea (Lamarck 1822)
Hinia reticulata (Linnaeus 1758)
 Subclass Heterobranchia
 Order Heterostropha
Odostomia scalaris MacGillivray 1843
Chrysallida obtusa (Brown 1827)
Chrysallida spiralis (Montagu 1803)
Ebala nitidissima (Montagu 1803)
Turbonilla crenata (Brown 1827)
Turbonilla lactea (Linné 1758)
 Subclass Opisthobranchia
 Order Bullomorpha
Philine aperta (Linnaeus 1767)
 Order Anaspidea
Retusa truncatula (Bruguière 1792)
Retusa umbilicata (Montagu 1803)
Akera bullata Müller 1776

Class Bivalvia

Subclass Palaeotaxodonta
 Order Nuculoida
Nucula nitidosa Winckworth 1930
Nucula sulcata (Bronn 1831)
 Subclass Pteriomorpha
 Order Mytiloida
Modiolula phaseolina (Philippi 1844)
 Order Pterioidea

Ostrea edulis Linnaeus 1758
 Subclass Heterodonta
 Order Veneroida
Lepton nitidum (Turton 1822)
Acanthocardia echinata (Linnaeus 1758)
Parvicardium exiguum (Gmelin 1791)
Cerastoderma edule (Linnaeus 1758)
Mactra stultorum (Linnaeus 1758)
Spisula subtruncata (da Costa 1778)
Ensis ensis (Linnaeus 1758)
Angulus tenuis (da Costa 1778)
Scrobicularia plana (da Costa 1778)
Abra alba (Wood 1802)
Abra prismatica (Montagu 1803)
Chamelea striatula (da Costa 1778)
Timoclea ovata (Pennant 1777)
Dosinia lincta (Montagu 1803)
 Order Myoida
Corbula gibba (Olivi 1792)
Barnea candida (Linnaeus 1758)
 Subclass Anomalodesmata
 Order Pholadomyoida
Thracia phaseolina (Lamarck 1818)
 Total for climatic regions ..bl: 43 (72.9%)

Climatic regions: ...l

Class Gastropoda
 Subclass Opisthobranchia
 Order Bullomorpha
Haminoea navicula (da Costa 1778)
 Class Bivalvia
 Subclass Pteriomorpha
 Order Mytiloida
Mytilaster solidus (Poli 1795)
 Subclass Heterodonta
 Order Veneroida
Lucinella divaricata (Linnaeus 1758)
Gastrana fragilis (Linnaeus 1758)
Abra segmentum (Récluz 1843)
Paphia senescens (Cocconi 1873)
Gouldia minima (Montagu 1803)
 Total for climatic regions ...l: 7 (11.9%)

Total for the Eemian Bælt Sea: 59 (23.9%)

Fifty-nine species have been found in the Bælt Sea region during the Eemian, seven of which are found or have been, as is the case with *Paphia aurea senescens*, in the Lusitanian region. All of the Lusitanian species are found only in the Eemian deposits and represent species living in the shallow-water environ-

ment. *Mytilaster solidus* is intertidal attached to rocks or algae, *Abra segmentum* is infralittoral on sandy mud, and *Haminoea navicula* found in *Zostera* beds in sheltered areas. The other three living species *Lucinella divaricata*, *Gastrana fragilis* and *Gouldia minima* are found from or just below the tidal zone and further out at different depths. *Paphia aurea senescens* may as well be regarded as a shallow-water species, considering the distribution of the other *Tapes* species. In this way the overall climatic characterising species of the Eemian in the Bælt Sea area are connected with the shallow-water environment.

All the Boreo-Lusitanian species are known from the recent Danish fauna. This is by far the largest group of molluscs, with 43 species forming 72.9% of the Eemian Bælt Sea fauna. 33 species can be found in the tidal to shallow-water environment, while 11 species – *Epitonium clathrus*, *Ebala nitidissima*, *Turbonilla crenata*, *Retusa umbilicata*, *Akera bullata*, *Nucula nitidosa*, *Nucula sulcata*, *Lepton nitidum*, *Acanthocardia echinata*, *Phaxas pellucidus* and *Timoclea ovata* – find their minimum depth, defined by *Acanthocardia echinata*, *Phaxas pellucidus* and *Timoclea ovata*, at 4 m, and *Epitonium clathrus* at 5 m. So rather considering the maximum depth indicated by some of the shallow-water species, there must be two faunas, of which one is shallow out to a depth of a few metres and another for deeper water.

There are six species with a rather broad range from the Subarctic to the Lusitanian regions. Five of these species can be found in shallow water, including the intertidal zone, except *Spisula elliptica*, which occurs only at greater depth.

The eulittoral species *Mytilus edulis* has given name to the *Mytilus* beds found in the lower part of the marine Eemian deposits in the Bælt Sea region, characterising the littoral deposits.

Only two species, *Arctica islandica* and *Zirfaea crispata* from the Bælt Sea region, have a Subarctic–Boreal distribution. The overall characteristic species for the Eemian Bælt Sea deposits – *Arctica islandica* – can be found from the intertidal zone to great depth, but in the inner recent Danish waters often at depths from 10 to 60 m. In the Eemian this species characterises the clay deposited during the deeper-water facies. The other mainly Boreal species *Zirfaea crispata* has been found only in the upper part of the *Tapes* sand at Stensigmosø (Madsen *et al.* 1908, p. 176) which fits well with the depth interval of this species from low tide to 7 m.

Finally *Mya truncata* covers the Arctic, Subarctic, Boreal and Lusitanian regions down to the Bay of Bis-

cay and can be found from the intertidal zone down to 75 m, in Danish waters often between 10 and 20 m.

Taken together, all the information from the above-mentioned climatic groups indicates that the Bælt Sea deposits are represented by two facies. One in littoral/infralittoral water not deeper than maximum 10 m, and one at depths of more than 5 m, and it is seen that all of the characteristic Eemian species within the Bælt Sea area are Lusitanian species connected with the shallow-water facies.

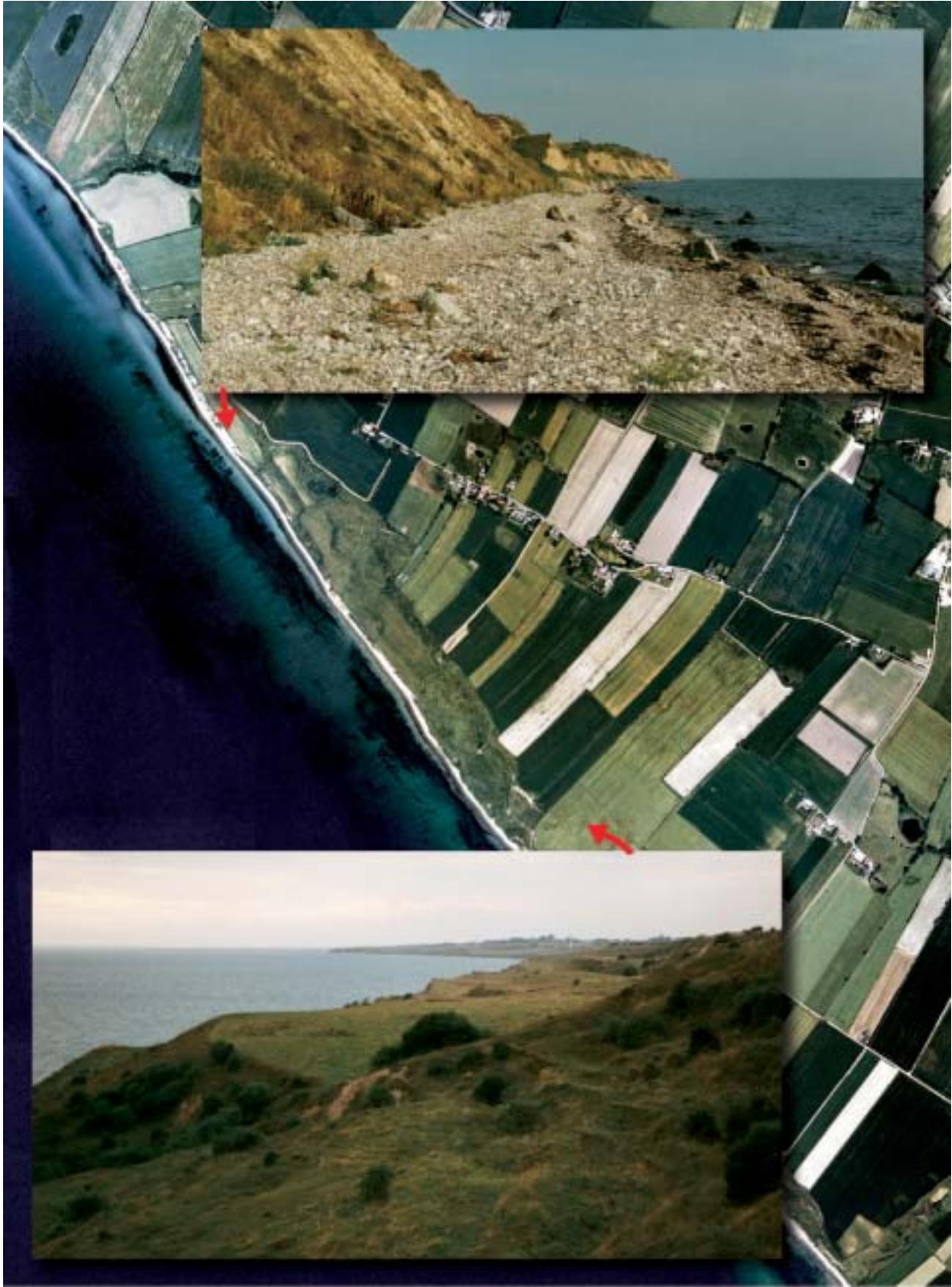
Fifteen mollusc species of the Eemian Bælt Sea fauna show by the region of lowest mean salinity they inhabit that the salinity of the Bælt Sea area must have been higher than present-day waters by up to 30–33‰ (Sorgenfrei 1958, table 11). Here listed as mentioned by Nordmann (1928, pp. 79–81): 33‰ *Circe minima* (*Gouldia minima*), 31‰ *Dosinia linctata*, 33‰ *Lepton nitidum*, 33‰ *Macra stultorum*, 30‰ *Montacuta ferruginosa* (*Tellimya ferruginosa*), 30‰ *Mytilus phaseolinus* (*Modiolula phaseolina*), 33‰ *Nucula sulcata*, 31‰ *Syndosmya prismatica* (*Abra prismatica*), 30‰ *Venus gallina* (*Chamelea striatula*), 30‰ *Parthenia interstincta* (*Chrysallida spiralis*), 32‰ *Rissoa parva*, 30‰ (*Epitonium clathrus*), 33‰ *Turbonilla lactea*, and 30‰ *Turbonilla rufa* (*Turbonilla crenata*).

In the recent bottom communities out in the Bælt Sea area, *Macoma balthica* is the overall characteristic mollusc occurring in all the samples from this region, in some cases being the only mollusc and in some cases together with others such as *Mytilus edulis*, *Cerastoderma edule* and *Scrobicularia plana* in shallow water and in places with a vegetation of gastropods like *Littorina littorea*, *Littorina tenebrosa*, *Rissoa membranacea* and *Rissoa inconspicua* (Petersen 1913). The littoral elements with *Mytilus edulis* are well documented in the Eemian deposits by the so-called *Mytilus* beds, together with the infaunal *Paphia aurea senescens* found *in situ* within the strata around the *Mytilus* beds or even down in the freshwater layers.

However, *Macoma balthica* is only found in the *Tapes* sands at Stensigmosø in southern Jutland (Fig. 1) and not at the many other Bælt Sea localities (Nordmann 1908, 1928).

In the deeper-water community of today the *Macoma* community is replaced by the *Abra alba* or *Astarte* communities (Petersen 1913). Here again the Eemian deposits differ on the leading species in that

Fig. 99. The Voderup Klint section on the island of Ærø with dislocated marine clays of Eemian age.



Abra alba is recorded only from Stensigmoose and the Astartidae *Tridonta borealis*, *Tridonta elliptica* and *Tridonta montagui* have not been found at all in the Bælt Sea region or further to the east within the Baltic.

The characteristic species of the Eemian deeper-water deposits, the *Cyprina* clay (with an abundant number of *Arctica islandica*), is also present in the recent deeper water of the Bælt Sea, but Petersen (1913, p. 4) avoided using this bivalve as one of his characterising species in his 'Evaluation of the Sea' because of its uneven distribution, which is certainly not the case considering the present outcrops of the *Cyprina* clay along the shores of the Bælt Sea region (Figs 99, 100).

The great difference between the Eemian Bælt Sea fauna and the recent one which has been outlined above can be considered together with the concluding remarks of Nordmann (1908, pp. 113 and 148) on *Cyprina islandica*, stating that this species cannot be regarded as a characterising fossil species of the Eemian deposits, but more probably should be seen as a relict in the inner part of the Eemian waters from the sea, of a more Arctic–Boreal nature, so to say forming a parallel to the occurrences of the *Astarte* species in the present Bælt Sea and Baltic regions.

The Baltic

Age: Eemian

Climatic regions: asb.

Class Bivalvia

Subclass Heterodonta

Order Veneroida

Macoma calcarea (Gmelin 1791)

Total for climatic regions asb. : 1 (5.3%)

Climatic regions: asbl

Class Bivalvia

Subclass Heterodonta

Order Myoida

Mya truncata Linnaeus 1758

Total for climatic regions asbl: 1 (5.3%)

Climatic regions: .sb.

Class Bivalvia

Subclass Heterodonta

Order Veneroida

Arctica islandica (Linnaeus 1767)

Total for climatic regions .sb. : 1 (5.3%)

Climatic regions: .sbl

Class Bivalvia

Subclass Pteriomorpha

Order Mytiloidea

Mytilus edulis Linnaeus 1758

Modiolus modiolus (Linnaeus 1758)

Subclass Heterodonta

Order Veneroida

Mysella bidentata (Montagu 1803)

Macoma balthica (Linnaeus 1758)

Total for climatic regions .sbl: 4 (21.1%)

Climatic regions: ..bl

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Littorina littorea (Linnaeus 1758)

Hydrobia ulvae (Pennant 1777)

Turritella communis Risso 1826

Aporrhais pespelicani (Linnaeus 1758)

Lunatia alderi (Forbes 1838)

Order Neogastropoda

Hinia reticulata (Linnaeus 1758)

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Nucula nitidosa Winckworth 1930

Nucula nucleus (Linnaeus 1767)

Subclass Heterodonta

Order Veneroida

Cerastoderma edule (Linnaeus 1758)

Spisula subtruncata (da Costa 1778)

Scrobicularia plana (da Costa 1778)

Order Myoida

Corbula gibba (Olivi 1792)

Total for climatic regions ..bl: 12 (63.2%)

Total for the Eemian Baltic: 19 (7.7%)

The Baltic Sea fauna comprises only 19 species. However, five are new here compared to the Eemian known from the Bælt Sea area: three from the Boreo-Lusitanian climatic region, i.e. *Turritella communis*, *Lunatia alderi* and *Nucula nucleus*; one from the Subarctic–Lusitanian region, i.e. *Modiolus modiolus*; and one with an Arctic–Boreal distribution, i.e. *Macoma calcarea*. According to the living depth of *Turritella communis*

Fig. 100. One of the *Cyprina* clay outcrops along the Voderup Klint profile on the island of Ærø.



and *Lunatia alderi*, this should be an indication of environment deeper than 10 m. But the eulittoral *Mytilus edulis* and *Cerastoderma edule* are nevertheless recorded from the Baltic Sea area, although these species do not come from layers in which they occur in great quantities in the Bælt Sea area (the *Mytilus* Beds).

From the climatic affinities of the molluscan finds in the Baltic Sea area, it appears that no pure Lusitanian species are found. This is the biggest contrast to the Bælt Sea region. It has also been the basis for keeping these finds apart, as done by Ødum (1933). However, considering the new element in this fauna, *Turritella communis*, compared to the Bælt Sea fauna, it has been argued by way of correlation on the basis of the Foraminifera that these deposits can be regarded as Eemian and that the facies belongs in deeper water than known from the Bælt Sea area (Petersen & Konradi 1974).

Such deposits occur, besides that at Strandegaard Dyrehave, also at some places on Møn characterised by the occurrences of *Turritella communis* (Berthelsen *et al.* 1977).

In the region of lowest mean salinity inhabited (Sorgenfrei 1958, table 11), for 5 species from the Baltic during the Eemian, i.e. *Modiolus modiolus*, *Turritella communis*, *Nucula nitidosa*, *Nucula nucleus*, and *Spisula subtruncata*, a salinity between 20‰ and 25‰ can be shown, which is above the present conditions in the Baltic. However, this might be caused by a higher tide in inner Danish waters during the Eemian, in this way giving the same situation as known during the Atlantic, when the salinity was higher.

Unlike the situation in the Bælt Sea, the present-day characterising species *Macoma balthica* is recorded from the localities on Sjælland, Strandegaards Dyrehave and Møn.

The drop in number of species among bivalves and gastropods from the Bælt Sea to the Baltic is from 45 to 11 species respectively in the present-day fauna (Sorgenfrei 1958), which is of the same order of magnitude as seen in the fossil fauna from the Bælt Sea to the Baltic during the Eemian. This means that in some way we have to do with the same basin structure/hydrographic situation, although the salinity was higher during the Eemian in the innermost Danish waters than at present.

The Kattegat

Age: Eemian

Climatic regions: asbl

Class Bivalvia

Subclass Heterodonta

Order Myoida

Hiatella arctica (Linnaeus 1758)

Total for climatic regions asbl: 1 (3.1%)

Climatic regions: .sbl

Class Gastropoda

Subclass Prosobranchia

Order Archaeogastropoda

Scissurella crispata Fleming 1828

Order Neogastropoda

Buccinum undatum Linnaeus 1758

Class Bivalvia

Subclass Pteriomorpha

Order Mytiloida

Mytilus edulis Linnaeus 1758

Total for climatic regions .sbl: 3 (9.4%)

Climatic regions: .bl

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Littorina littorea (Linnaeus 1758)

Hydrobia ulvae (Pennant 1777)

Rissoa inconspicua Alder 1844

Rissoa violacea Desmarest 1814

Bittium reticulatum (da Costa 1778)

Turritella communis Risso 1826

Lunatia alderi (Forbes 1838)

Order Neogastropoda

Hinia pygmaea (Lamarck 1822)

Hinia reticulata (Linnaeus 1758)

Subclass Heterobranchia

Order Heterostropha

Chrysallida spiralis (Montagu 1803)

Turbonilla lactea (Linné 1758)

Class Bivalvia

Subclass Pteriomorpha

Order Pterioda

Ostrea edulis Linnaeus 1758

Subclass Heterodonta

Order Veneroida

Acanthocardia echinata (Linnaeus 1758)

Parvicardium exiguum (Gmelin 1791)

Cerastoderma edule (Linnaeus 1758)

Laevicardium crassum (Gmelin 1791)
Spisula solida (Linnaeus 1758)
Spisula subtruncata (da Costa 1778)
Scrobicularia plana (da Costa 1778)
Abra prismatica (Montagu 1803)
Paphia aurea (Gmelin 1791)
Timoclea ovata (Pennant 1777)
 Order Myoida
Corbula gibba (Olivi 1792)
 Total for climatic regions ..bl: 23 (71.9%)

Climatic regions: ...l
 Class Gastropoda
 Subclass Opisthobranchia
 Order Bullomorpha
 Haminoea navicula (da Costa 1778)
 Class Bivalvia
 Subclass Pteriomorpha
 Order Mytiloida
 Mytilaster lineatus (Gmelin 1791)
 Subclass Heterodonta
 Order Veneroida
 Lucinella divaricata (Linnaeus 1758)
 Gastrana fragilis (Linnaeus 1758)
 Paphia senescens (Cocconi 1873)
 Total for climatic regions ...l: 5 (15.6%)

The Eemian Kattegat: 32 (13.0%)

From the region of the Kattegat *sensu lato* area, including the bordering landmasses with fjords, sounds and the northern part of the Lillebælt, Storebælt, and Øresund, three kinds of localities have been met with. As the information obtained from this area is based on a very different kind of material, the localities will be treated apart.

The first locality to be considered is Ejby Bro in northern Sjælland on the Isefjord. Here Erik Rasmussen (*in Madsen 1968*) described an *in situ* marine deposit.

Out of 15 mollusc species, two are Lusitanian, viz. *Lucinella divaricata* and *Paphia aurea senescens*, both of which are characteristic fossils of the Eemian.

Furthermore, out of ten Boreo-Lusitanian species, seven are not recorded from the recent Isefjord, viz. *Rissoa violacea*, *Lunatia alderi*, *Hinia reticulata* (the British form (Fretter & Graham 1984, p. 495)), *Ostrea edulis*, *Laevicardium crassum*, *Paphia aurea*, and *Spisula solida*. Among these are also the less tolerant species regarding the region of lowest mean salinity inhabited, which is five species between 28‰ and 33‰.

The present-day figure of salinity for the Isefjord is between 18 and 20‰. Although we have to do with a Saalien glacial topography, we may explain the higher salinity as a result of a higher tidal amplitude during the Eemian.

Only two species occurring in the Ejby Bro locality extend into the Subarctic: *Buccinum undatum* and *Mytilus edulis*, besides one – *Hiatella arctica* – having a wide range. All are present also in the recent Isefjord waters. This fauna points to a more oceanic environment than today and with a higher temperature; furthermore, the finds point to shallow-water or even beach deposits with some tidal influence (Rasmussen *in Madsen 1968*).

The second kind of locality includes redeposited sediments: either floes in the glacial deposits like the Stautrup locality at Aarhus or fluvioglacial deposits as at Høng in western Sjælland (Nordmann 1928, pp. 64–65; Ødum 1933; Sorgenfrei 1945). Both of these localities carried some of the characteristic molluscs of the Eemian deposits. From Høng the following have been recorded: *Lucinella divaricata* and *Paphia aurea senescens* together with 11 species known from the Boreo-Lusitanian zone and *Mytilus edulis* known from the Subarctic to the Lusitanian regions. Only four species were also found at the Ejby Bro locality, and the ‘new’ ones (nine species) point to deeper water with such species as *Acanthocardia echinata*, *Corbula gibba* and *Turritella communis*.

The Stautrup material records new species to the Kattegat region such as *Rissoa inconspicua*, *Mytilaster lineatus*, *Gastrana fragilis*, *Abra prismatica*, *Chrysalida spiralis*, and *Haminoea navicula*, all except *Mytilaster lineatus* and *Gastrana fragilis* being Boreo-Lusitanian, while the two bivalves are limited to the Lusitanian and characteristic of the Eemian – together with *Paphia aurea senescens*, which is also present in the Stautrup floe, as discussed by Sorgenfrei (1945).

From the material hitherto discussed it appears that the Eemian sea deposits were known from the Kattegat region both in a shallow-water facies (Ejby Bro) and a deeper-water facies (Høng), the latter only from redeposited material. Therefore, it is of great importance from a palaeogeographical point of view that information now has been obtained from borings in the central part of the Kattegat, on the island of Anholt (Lykke-Andersen *et al.* 1993). Foraminifera from this well (Seidenkrantz 1993) revealed a marine Upper Saalian and Eemian sequence. The macrofossils from the well were kindly placed at my disposal. It appears that a temperate fauna with species such as *Turritella*

communis, *Aclis minor*, *Hiatella arctica*, *Nuculana minuta*, and *Scissurella crispata* is resting on an Arctic deposit with *Portlandia arctica*. The information that we do have is that a *Turritella* facies within the Kattegat region in the Eemian found in an *in situ* position sustains the view of a continuation towards the north not only of the shallow-water deposits, but also of the deeper-water environment during the Eemian. Considering the bottom communities of the present-day Kattegat as revealed by Petersen (1913), *Turritella communis* is found in different associations at depths from 12–19 to 35 m on sand, fine sand and clay. The species from the Eemian of the Kattegat associated with *Turritella communis* in the Kattegat of today are *Hiatella arctica*, *Nuculana minuta*, *Acanthocardia echinata*, *Corbula gibba*, and *Hinia pygmaea*.

Considering the Eemian faunas demonstrated from the Kattegat region, it appears that here the lowest mean salinity inhabited by the species in question is within the present-day salinities reached for this area, at about 33‰, although the salinities for the present fjords bordering the Kattegat have a lower salinity, as mentioned in the case of the Isefjord with the Ejby Bro locality.

The North Sea

Age: Eemian

Climatic regions: asb.

Class Bivalvia

Subclass Heterodonta

Order Veneroida

Tridonta elliptica (Brown 1827)

Total for climatic regions asb. : 1 (1.1%)

Climatic regions: asbl

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Littorina saxatilis (Olivi 1792)

Class Bivalvia

Subclass Heterodonta

Order Veneroida

Thyasira flexuosa (Montagu 1803)

Tridonta montagui (Dillwyn 1817)

Order Myoida

Mya truncata Linnaeus 1758

Hiatella arctica (Linnaeus 1758)

Total for climatic regions asbl: 5 (5.5%)

Climatic regions: .sb.

Class Bivalvia

Subclass Heterodonta

Order Veneroida

Arctica islandica (Linnaeus 1767)

Total for climatic regions .sb. : 1 (1.1%)

Climatic regions: .sbl

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Littorina obtusata (Linnaeus 1758)

Lacuna vincta (Montagu 1803)

Order Neogastropoda

Buccinum undatum Linnaeus 1758

Class Bivalvia

Subclass Pteriomorpha

Order Mytiloida

Mytilus edulis Linnaeus 1758

Modiolus modiolus (Linnaeus 1758)

Order Pterioda

Heteranomia squamula (Linnaeus 1758)

Subclass Heterodonta

Order Veneroida

Mysella bidentata (Montagu 1803)

Tellimya ferruginosa (Montagu 1803)

Parvicardium ovale (Sowerby 1840)

Macoma balthica (Linnaeus 1758)

Total for climatic regions .sbl: 10 (11.0%)

Climatic regions: .bl

Class Gastropoda

Subclass Prosobranchia

Order Archaeogastropoda

Gibbula cineraria (Linnaeus 1758)

Order Neotaenioglossa

Littorina littorea (Linnaeus 1758)

Lacuna parva (Montagu 1803)

Hydrobia ulvae (Pennant 1777)

Onoba vitrea (Montagu 1803)

Rissoa albella Lovén 1846

Rissoa inconspicua Alder 1844

Rissoa membranacea (J. Adams 1800)

Rissoa parva (da Costa 1779)

Rissoa violacea Desmarest 1814

Caecum glabrum (Montagu 1803)

Bittium reticulatum (da Costa 1778)

Turritella communis Risso 1826

Aporrhais pespelicani (Linnaeus 1758)

Lunatia alderi (Forbes 1838)

Order Heterogastropoda

Triphora adversa (Montagu 1803)
Cerithiopsis tubercularis (Montagu 1803)
Epitonium clathrus (Linnaeus 1758)
 Order Neogastropoda
Hinia pygmaea (Lamarck 1822)
Hinia reticulata (Linnaeus 1758)
Cytherea coarctata (Forbes 1840)
 Subclass Heterobranchia
 Order Heterostropha
Brachystomia eulimoides Hanley 1844
Odostomia scalaris MacGillivray 1843
Chrysallida obtusa (Brown 1827)
Chrysallida spiralis (Montagu 1803)
Ebala nitidissima (Montagu 1803)
Odostomia albella Lovén 1846
Turbonilla crenata (Brown 1827)
Turbonilla lactea (Linné 1758)
 Subclass Opisthobranchia
 Order Bullomorpha
Acteon tornatilis (Linnaeus 1758)
Philine aperta (Linnaeus 1767)
 Order Anaspidea
Retusa truncatula (Bruguière 1792)
Akera bullata Müller 1776
 Class Bivalvia
 Subclass Palaeotaxodonta
 Order Nuculoida
Nucula nitidosa Winckworth 1930
Nucula sulcata (Bronn 1831)
 Subclass Pteriomorpha
 Order Mytiloida
Modiolula phaseolina (Philippi 1844)
Modiolaria tumida (Hanley 1843)
 Order Pterioida
Aequipecten opercularis (Linnaeus 1758)
Chlamys varia (Linnaeus 1758)
Ostrea edulis Linnaeus 1758
 Subclass Heterodonta
 Order Veneroida
Lepton nitidum (Turton 1822)
Acanthocardia echinata (Linnaeus 1758)
Parvicardium exiguum (Gmelin 1791)
Parvicardium scabrum (Philippi 1844)
Cerastoderma edule (Linnaeus 1758)
Spisula subtruncata (da Costa 1778)
Ensis ensis (Linnaeus 1758)
Phaxas pellucidus (Pennant 1777)
Angulus tenuis (da Costa 1778)
Tellina donacina Linnaeus 1758
Fabulina fabula (Gmelin 1791)
Donax vittatus (da Costa 1778)

Scrobicularia plana (da Costa 1778)
Abra alba (Wood 1802)
Abra prismatica (Montagu 1803)
Chamelea striatula (da Costa 1778)
Tapes decussatus (Linnaeus 1758)
Timoclea ovata (Pennant 1777)
Venerupis pullastra (Montagu 1803)
Dosinia linctata (Montagu 1803)
Mysia undata (Pennant 1777)
 Order Myoida
Corbula gibba (Olivi 1792)
Saxicavella jeffreysi Winckworth 1930
Barnea candida (Linnaeus 1758)
 Subclass Anomalodesmata
 Order Pholadomyoida
Thracia phaseolina (Lamarck 1818)
Thracia villosiuscula (MacGillivray 1827)
 Total for climatic regions ..bl: 66 (72.5%)
 Climatic regions: ...l
 Class Gastropoda
 Subclass Opisthobranchia
 Order Bullomorpha
Haminoea navicula (da Costa 1778)
 Class Bivalvia
 Subclass Pteriomorpha
 Order Mytiloida
Mytilaster lineatus (Gmelin 1791)
 Subclass Heterodonta
 Order Veneroida
Lucinella divaricata (Linnaeus 1758)
Plagiocardium papillosum Poli 1795
Gastrana fragilis (Linnaeus 1758)
Abra segmentum (Récluz 1843)
Paphia senescens (Cocconi 1873)
Gouldia minima (Montagu 1803)
 Total for climatic regions ...l: 8 (8.8%)

The Eemian North Sea: 91 (36.8%)

Regarding the Eemian deposits of south-western Jylland several localities are included: Tønder and surroundings, Forballum, Farup, Ydre Bjergum, Mandø Høllade (many places) and Inder Bjergum. Furthermore, also molluscs of Eemian age are recorded from the map sheet Blaavands Huk (Fig. 1). In all, 91 molluscan species have been recorded, 53 bivalves and 38 gastropods. This high number of species comprises 32 species new to the Eemian compared to the Bælt Sea deposits.

Considering the new elements from the climatic point of view, two are Lusitanian species, *Plagiocardium papillosum* and *Mytilaster lineatus*, which are regarded as part of the characteristic species of the Eemian fauna (Nordmann 1928).

By far the largest group of new species in the North Sea deposits are the Boreo-Lusitanian. Only one – *Tridonta elliptica* – does not extend into the Lusitanian region. This is close to the situation found in the Bælt Sea region, where only two species; *Arctica islandica* and *Zirfaea crispata*, do not reach the Lusitanian region.

Arctica islandica – so common in the Bælt Sea deposits – has been recorded only in a single find of a juvenile specimen at Mandø Høllade in south-western Jylland. The other species, *Zirfaea crispata*, has not been demonstrated at all in the Danish North Sea Eemian deposits.

The Boreo-Lusitanian species *Macra stultorum* has a high salinity requirement, occurring in the Bælt Sea region but not in the Danish North Sea region during the Eemian.

This has been used as an argument against uniting in time the deposits found on the western and eastern sides of southern Jylland. “On a voulu y voir une preuve que ces deux bassins de mer n’out en réalité rien eu à faire l’un avec l’autre, en sorte qu’ils pourraient très bien être d’âges fort différents” (Nordmann 1928, p. 63).

When the 15 mollusc species of the Eemian Bælt Sea fauna mentioned earlier with a salinity requirement between 30–33‰ are remembered, the former focus on *Macra stultorum* is of less significance.

While Nordmann states that the fauna on both sides of the Jylland peninsula can be regarded as one, he is right from the point of view of climatic conditions, as demonstrated above. However, he is also arguing for a connection between the North Sea and the Bælt Sea (Nordmann 1928, p. 63): “Les passes entre les parties orientale et occidentale de la mer eemienne, ce qui, autrement parlant, signifie les vallées et les plaines entre les collines insulaires qui sont aujourd’hui occupées par les plaines de landes du Slesvig et du Holstein, sont sans doute très étroites”. However, it is the author’s opinion that the difference between the southern Danish localities to the east (the Bælt Sea) and to the west (the North Sea) can be regarded as differences in facies that are also found in present-day Danish waters. Here the occurrences of *Donax vittatus* in the Eemian North Sea deposits, but not in the Bælt Sea deposits, should be considered. *Donax vittatus* is a characteristic species of the high-energy coastal envi-

ronment, where it is found all along the present-day west coast, but not in the inner Danish waters from the northernmost part of the east coast of Jylland.

However, many of the other molluscs might have made their way to the Bælt Sea and the Baltic region if there has been only the slightest passage over southern Jylland.

In the case of a passage, the situation can be looked upon as a parallel to the present-day marine colonisation of the Limfjord after the breaking through by the North Sea at the Spit at Agger in 1825. At the end of the 19th century a rich marine fauna could be recorded in the Limfjord (Collin 1884; Petersen 1888).

The question of connection between the North Sea and the Bælt Sea over the southern part of the peninsula of Jylland can be considered, based on the mollusc assemblages. It appears that the difference in faunal composition during the Eemian in both seas was very similar to the difference in faunas during the Holocene, although with Lusitanian shallow-water species occurring during the Eemian. Therefore it must be concluded that the land–sea configuration must be very much the same during the two periods so Jylland was also a peninsula during the Eemian.

Vendsyssel

Age: Eemian

Climatic regions: asb.

Class Gastropoda

Subclass Prosobranchia

Order Neogastropoda

Oenopota incisula (Verrill 1882)

Oenopota violacea (Mighels & Adams 1842)

Bela exarata G.O. Sars 1818

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Nuculana pernula (Müller 1776)

Yoldiella lenticula (Möller 1842)

Subclass Pteriomorpha

Order Mytiloida

Musculus niger (Gray 1824)

Subclass Heterodonta

Order Veneroida

Clinocardium ciliatum (Fabricius 1780)

Serripes groenlandicus (Bruguère 1798)

Macoma calcarea (Gmelin 1791)

Total for climatic regions asb. : 9 (16.4%)

Climatic regions: asbl
 Class Gastropoda
 Subclass Prosobranchia
 Order Neogastropoda
Oenopota trevelliiana (Turton 1834)
 Subclass Opisthobranchia
 Order Thecosomata
Limacina retroversa (Fleming 1823)
 Class Bivalvia
 Subclass Palaeotaxodonta
 Order Nuculoida
Nuculoma tenuis (Montagu 1808)
Yoldiella frigida (Torell 1859)
 Subclass Heterodonta
 Order Veneroida
Leptaxinus ferruginosus (Forbes 1844)
 Order Myoida
Mya truncata Linnaeus 1758
Hiatella arctica (Linnaeus 1758)
 Total for climatic regions asbl: 7 (12.7%)

Climatic regions: .sb.
 Class Bivalvia
 Subclass Palaeotaxodonta
 Order Nuculoida
Nuculana minuta (Müller 1776)
 Total for climatic regions .sb. : 1 (1.8%)

Climatic regions: .sbl
 Class Gastropoda
 Subclass Prosobranchia
 Order Neotaenioglossa
Lacuna vincta (Montagu 1803)
 Order Neogastropoda
Buccinum undatum Linnaeus 1758
 Class Bivalvia
 Subclass Palaeotaxodonta
 Order Nuculoida
Yoldiella lucida (Lovén 1846)
 Subclass Pteriomorpha
 Order Mytiloida
Mytilus edulis Linnaeus 1758
 Subclass Heterodonta
 Order Veneroida
Mysella bidentata (Montagu 1803)
Parvicardium ovale (Sowerby 1840)
 Total for climatic regions .sbl: 6 (10.9%)

Climatic regions: .b.
 Class Gastropoda
 Subclass Heterobranchia

Order Heterostropha
Chrysallida eximia (Jeffreys 1849)
 Total for climatic regions ..b. : 1 (1.8%)

Climatic regions: ..bl
 Class Gastropoda
 Subclass Prosobranchia
 Order Neotaenioglossa
Alvania abyssicola (Forbes 1850)
Rissoa parva (da Costa 1779)
Bittium reticulatum (da Costa 1778)
Turritella communis Risso 1826
Aporrbais pospelicani (Linnaeus 1758)
Lunatia alderi (Forbes 1838)
 Order Heterogastropoda
Vitreolina philippii (Rayneval & Ponzi 1854)
 Order Neogastropoda
Hinia incrassata (Ström 1768)
Hinia reticulata (Linnaeus 1758)
Mangelia brachystoma (Philippi 1844)
Raphitoma linearis (Montagu 1803)
 Subclass Heterobranchia
 Order Heterostropha
Eulimella scillae (Scacchi 1835)
Ondina divisa (J. Adams 1797)
Odostomia turrita Hanley 1844
 Subclass Opisthobranchia
 Order Bullomorpha
Acteon tornatilis (Linnaeus 1758)
 Order Anaspidea
Retusa umbilicata (Montagu 1803)
 Class Bivalvia
 Subclass Palaeotaxodonta
 Order Nuculoida
Nucula nucleus (Linnaeus 1767)
Nucula sulcata (Bronn 1831)
Yoldiella philippiana (Nyst 1845)
 Subclass Pteriomorpha
 Order Pterioda
Pseudamussium septemradiatum
 (Müller 1776)
Similipecten similis (Laskey 1811)
 Subclass Heterodonta
 Order Veneroida
Acanthocardia echinata (Linnaeus 1758)
Parvicardium minimum (Philippi 1836)
Ensis ensis (Linnaeus 1758)
Phaxas pellucidus (Pennant 1777)
Abra alba (Wood 1802)
Abra nitida (Müller 1776)
Abra prismatica (Montagu 1803)

Kelliella miliaris (Philippi 1844)
Chamelea striatula (da Costa 1778)
Order Myoida
Corbula gibba (Olivi 1792)
Total for climatic regions: 31 (56.4%)

The Eemian Vendsyssel: 55 (22.3%)

In Vendsyssel the mollusc faunas in the Skærumhede sequence have been studied by Nordmann (Jessen *et al.* 1910) and Petersen (Bahnsen *et al.* 1974). The conclusion reached in the latter study on molluscs points out that the difference between the Boreo-Lusitanian community – the *Turritella terebra* zone – in the boring and the typical Eemian community in southern Denmark is a difference in facies.

This statement will be discussed now on the basis of all the mollusc found and listed according to their climatic regions.

Among the 55 species of molluscs recorded from the Eemian in the Vendsyssel region, no Lusitanian species occur, but Boreo-Lusitanian species count for more than half of the assemblages (31 species, 56.4%). Of these, 25 are mentioned in the list for region of lowest mean salinity inhabited built on information from the Danish waters in the transition area between the North Sea (at Esbjerg) and the Baltic (Gulf of Bothnia) (Sorgenfrei 1958). Nearly 4/5 of this number have their region of lowest mean salinity between 24‰ and 34‰, which is the minimum, and mean salinities at the passage belt between the North Sea – Skagerrak and E and NW Kattegat. This situation for an Eemian assemblage indicates a high degree of similarity with the present-day environment in this area.

Within the Boreo-Lusitanian group of molluscs there is a clear dominance of species belonging to the deeper-water environment at around the 100 m depth. However, there are some few species which belong at a depth of less than 20–30 m. Such species are *Rissoa parva*, *Hinia reticulata* and *Retusa umbilicata*, which within their depth range live in great abundance, which is not the case in the Skærumhede sequences. Therefore they can be regarded as allochthonous or as stray finds outside their environment. Nordmann (*in* Jessen *et al.* 1910) mentioned that *Rissoa parva* and *Hinia reticulata* were redeposited. He also mentioned *Bittium reticulatum*, which according to the literature has some records from the deeper water (out to 250 m deep).

Taking the whole group of Boreo-Lusitanian species, there are many which occur in the tidal and shal-

low-water environments but have a wide range of depth. Rather few are those which are mainly connected with the deeper water – here depths of more than 10 m – viz.: *Turritella communis*, *Lunatia alderi*, *Mangelia brachystoma*, *Raphitoma linearis*, *Eulimella scillae*, *Nucula sulcata*, *Pseudamussium septemradiatum* and *Kelliella miliaris*. The last one strengthens the depth indications to be more than 100 m, since the species is recently known only from the deeper part of the Skagerrak.

Chrysallida eximia, which is found at depths from 20–1000 m is here regarded as a Boreal species, although it extends into the northernmost part of the Lusitanian zone, but there in deeper water.

Among the species known from the Subarctic to the Lusitanian regions, the finds of *Mytilus edulis* (Jessen *et al.* 1910; Bahnsen *et al.* 1974) can be regarded from the same point of view as mentioned in connection with *Rissoa parva* and *Hinia reticulata*. The few finds of *Mytilus* specimens clearly indicate that this normally gregariously living species is found outside its living zone and can be regarded also as stray finds.

The other finds of species occurring in the Subarctic to the Lusitanian zone do not oppose the view of a deeper-water environment.

Taking the species together which do not occur in the Lusitanian zone but extend into the Arctic or Subarctic (*Nuculana minuta*), there are two species *Clino-cardium ciliatum* and *Serripes groenlandicus*, which do pose a problem regarding their climatic indications within the Skærumhede sequence. These two species are found only in the High Boreal zone (Norway north of Lofoten). Nordmann (Jessen *et al.* 1910, pp. 127–128) mentioned the occurrences of these species off Iceland together with other species with which they occur in the Skærumhede sequence.

This picture has been to some degree changed by the publication of parts of the Zoology of Iceland, so it appears that *Turritella communis* is no longer regarded as being part of the Icelandic fauna, while *Eulimella scillae* (only empty shells) might be added. *Lunatia alderi* and *Raphitoma linearis* mentioned by Nordmann are confirmed (Thorson 1941), and so is *Acteon tornatilis* (Lemche 1938), in the new literature. However, in this way we still face the question of the climatic conditions indicated by the molluscan assemblage.

However, as seen from the latest Skærumhede boring (Bahnsen *et al.* 1974, fig. 7), there is a clear transition zone between the *Turritella communis* zone and the establishment of the *Turritella erosa* zone. In this zone, the so-called *Abra nitida* zone, we still find the

mixing of species with different climatic affinities, just as we do not have a sharp border zone to tell where we actually leave the Eemian and pass into the Weichselian. But we do have a well-defined bottom community for what we must call the Eemian from the Vendsyssel region, and that is the *Turritella communis* community. This community we find in deeper water, also in the recent Danish waters.

Oenopota incisula is one of the species also occurring in the transition zone between the two *Turritella* communities, the Boreal–Lusitanian with *T. communis*, and the Arctic with *T. erosa*. *Oenopota incisula* has been found in both borings (Jessen *et al.* 1910; Bahnson *et al.* 1974, fig. 7), but the species has still not been recorded from the European coast of the North Atlantic in recent time. In this way *Oenopota incisula* becomes one of the few species extinct in our part of the world since the Early/Middle Weichselian.

Finally the six species with a wide range within the climatic regions are all found in deeper water. However, here *Yoldiella frigida* occurs in deeper water in the southern part of its range. *Limacina retroversa* is a pelagic species and has been recorded in the present day to penetrate into the Kattegat – Bælt Sea regions.

Skagen

Age: Eemian

Climatic regions: asb.

Class Bivalvia
 Subclass Palaeotaxodonta
 Order Nuculoida
Nuculana pernula (Müller 1776)

Total for climatic regions asb. : 1 (7.1%)

Climatic regions: asbl

Class Gastropoda
 Subclass Opisthobranchia
 Order Thecosomata
Limacina retroversa (Fleming 1823)
 Class Scaphopoda
Siphonodentalium lobatum (Sowerby 1860)
 Class Bivalvia
 Subclass Palaeotaxodonta
 Order Nuculoida
Yoldiella frigida (Torell 1859)
 Subclass Heterodonta
 Order Myoida
Hiatella arctica (Linnaeus 1758)

Total for climatic regions asbl: 4 (28.6%)

Climatic regions: .sbl

Class Scaphopoda
Antalis entalis (Linnaeus 1758)
 Class Bivalvia
 Subclass Pteriomorpha
 Order Pterioida
Delectopecten vitreus (Gmelin 1791)

Total for climatic regions .sbl: 2 (14.3%)

Climatic regions: ..bl

Class Gastropoda
 Subclass Prosobranchia
 Order Neotaenioglossa
Lunatia alderi (Forbes 1838)
 Subclass Opisthobranchia
 Order Bullomorpha
Philine catena (Montagu 1803)

Class Scaphopoda
Cadulus subfusiforme (M. Sars 1865)
Entalina tetragona (Brocchi 1814)

Class Bivalvia
 Subclass Heterodonta
 Order Veneroida
Kelliella miliaris (Philippi 1844)
 Subclass Anomalodesmata
 Order Pholadomyoida
Cochlodesma praetenu (Pulteney 1799)

Total for climatic regions ..bl: 6 (42.9%)

Climatic regions: ...l

Class Scaphopoda
Dentalium vulgare da Costa 1778

Total for climatic regions ...l: 1 (7.1%)

The Eemian Skagen: 14 (5.7%)

In the Eemian part of the Skagen Well, one species, *Dentalium vulgare*, mainly occurs within the Lusitanian region and is not recorded from recent Danish waters, although it is found in the southern part of the North Sea.

Among the six Boreo-Lusitanian mollusc species, *Cochlodesma praetenu* is rare in Danish waters, while all the others as far as the information on habitats goes are connected with the deeper-water environment. This is also true for the species including the Subarctic region, viz.: *Antalis entalis* and *Delectopecten vitreus*, where the latter in general has a depth range from 30–600 m, but in Skagerrak is found between 400 and 600 m. Also *Antalis entalis* has a wide range of depth,

but within Danish water it is recorded only from 20–400 m.

The four species: *Siphonodentalium lobatum*, *Limacina retroversa*, *Yoldiella frigida* and *Hiatella arctica* with a wide geographical distribution from the Arctic to the Lusitanian also have a wide range of depth.

Also *Nuculana pernula*, here listed from the Arctic to the Boreal, could be considered to have a wide range like the other species mentioned above, however, in SW Europe it is found only at depths greater than 400 m. In recent Danish waters it occurs at depths from 20 to 200 m. Seen together with the other species in this region during the Eemian with a more southern affinity, *Nuculana pernula* shows accordance, considering that the species in the Arctic is mostly littoral.

Comparing the assemblages from the faunal elements from Skærumhede, it appears that the Skagen Well depicts a deeper-water community without any influence from more shallow-water facies.

The occurrence of three of the four Scaphopoda *Cadulus subfusiforme*, *Entalina tetragona* and *Antalis entalis* speaks in favour of an environment which is likely to be found in the deeper Skagerrak, such as the *Amphilepis norvegica*/*Pecten vitreus* community with *Entalina tetragona* and of which one of the other molluscs, *Delectopecten vitreus*, is considered a characteristic species.

The demonstrated Eemian assemblages in most of the Danish regions show differences in climatic affinities – more Lusitanian in the southern part – which, however, can be explained through an analysis of the faunas in their relation to depth – shallow-water Lusitanian species in the south – and in some parts in relation to the community.

The community concept which was developed for the recent Danish waters does not find its equivalent in the Eemian Bælt Sea and Baltic regions, only partly in the Kattegat region, but has a good correlation with the occurrences of the faunal assemblages in the regions to the north in Jylland – the Vendsyssel and Skagen regions – only in these two regions does the succession of strata allow us to follow the development into the Weichselian cooler/Arctic molluscan fauna, although we find some deposits from the Kattegat region (Holmstrup and Holbæk sites) which can be correlated to the Early/Middle Weichselian in the Vendsyssel and Skagen region.

Early/Middle Weichselian species sorted after climatic affinities

The Kattegat

Age: Early/Middle Weichselian

Climatic regions: a...

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Portlandia arctica (Gray 1824)

Total for climatic regions a... : 1 (14.3%)

Climatic regions: as..

Class Gastropoda

Subclass Opisthobranchia

Order Bullomorpha

Cylichna occulta (Mighels 1841)

Total for climatic regions as.. : 1 (14.3%)

Climatic regions: asb.

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Nuculana pernula (Müller 1776)

Subclass Heterodonta

Order Veneroida

Macoma calcarea (Gmelin 1791)

Total for climatic regions asb. : 2 (28.6%)

Climatic regions: asbl

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Nuculoma tenuis (Montagu 1808)

Subclass Heterodonta

Order Myoida

Mya truncata Linnaeus 1758

Hiatella arctica (Linnaeus 1758)

Total for climatic regions asbl: 3 (42.9%)

The Early/Middle Weichselian Kattegat: 7 (2.8%)

In the Kattegat region, two localities (Holbæk and Holmstrup, Fig. 1) have mollusc faunas of Early/Middle Weichselian age, which could be correlated to the Older *Yoldia* Clay deposits found in the Vendsyssel and Skagen regions.

Nordmann (Ødum 1933) described the mollusc fauna in the borings at Holbæk to represent part of the *Port-*

landia arctica zone in the Skærumhede sequence (Jessen *et al.* 1910). Later, Petersen & Buch (1974) referred the outcrops at Holmstrup with marine clay, characterised by *Macoma calcarea*, to the Weichselian part of the sequence close to the *Macoma calcarea* zone (Bahnson *et al.* 1974) in the new well at Skærumhede in the Vendsyssel region.

The later correlation was mainly based on the foraminiferal studies (Buch *in* Petersen & Buch 1974). Also aminostratigraphic investigations have to some extent sustained this correlation (Miller & Mangerud 1985, p. 261). The mollusc faunas from these two localities point to an Arctic environment as seen from the climatic indications, in that all seven species are found in the Arctic and only three of them with a wide range: *Hiatella arctica*, *Mya truncata* and *Nuculoma tenuis*.

Taken into account that these deposits show an Arctic affinity, the interpretation of depth ranges of the species found point to the more shallow-water environment. This is also true for species such as *Nuculoma tenuis*, which is recorded from offshore down to 300 m deep, but in the Arctic is more littoral.

Macoma calcarea is found intertidal to several hundred metres, but only in deeper water in the southern part of the range for this species. In the Arctic it is the characterising mollusc in shallow water: the Arctic *Macoma calcarea* community. Furthermore, *Nuculana pernula*, as mentioned earlier, is littoral in the Arctic.

The conclusion to draw from these finds in the Kattegat region is that we have a part – the more shallow water – of the Arctic zones recorded from the Vendsyssel region represented within the Kattegat region – southern part.

Vendsyssel

Age: Early/Middle Weichselian

Climatic regions: a...

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Portlandia arctica (Gray 1824)

Total for climatic regions a... : 1 (2.8%)

Climatic regions: as..

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Alvania cruenta Odhner 1915

Turritella erosa Couthouy 1838

Subclass Opisthobranchia

Order Bullomorpha

Cylichna occulta (Mighels 1841)

Class Bivalvia

Subclass Pteriomorpha

Order Arcoida

Bathyarca glacialis (Gray 1824)

Subclass Anomalodesmata

Order Pholadomyoida

Pandora glacialis Leach 1819

Lyonsia arenosa (Möller 1842)

Total for climatic regions as.. : 6 (16.7%)

Climatic regions: asb.

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Alvania scrobiculata (Möller 1842)

Alvania jan mayeni (Friele 1886)

Lunatia pallida (Broderip & Sowerby 1829)

Order Neogastropoda

Oenopota incisula (Verrill 1882)

Admete viridula (Fabricius 1780)

Subclass Opisthobranchia

Order Anaspidea

Retusa obtusa (Montagu 1803)

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Nuculana pernula (Müller 1776)

Yoldia hyperborea Lovén 1859

Yoldiella lenticula (Möller 1842)

Subclass Pteriomorpha

Order Mytiloida

Musculus laevigatus (Gray 1824)

Musculus niger (Gray 1824)

Crenella decussata (Montagu 1803)

Order Pterioidea

Palliolium greenlandicum (Sowerby 1842)

Subclass Heterodonta

Order Veneroida

Axinopsida orbiculata (G.O. Sars 1878)

Tridonta borealis Schumacher 1817

Tridonta elliptica (Brown 1827)

Clinocardium ciliatum (Fabricius 1780)

Serripes groenlandicus (Bruguière 1798)

Macoma calcarea (Gmelin 1791)

Total for climatic regions asb. : 19 (52.8%)

Climatic regions: asbl
 Class Gastropoda
 Subclass Prosobranchia
 Order Neotaenioglossa
Natica affinis (Gmelin 1790)
 Subclass Opisthobranchia
 Order Bullomorpha
Cylichna alba (Brown 1827)
 Class Bivalvia
 Subclass Palaeotaxodonta
 Order Nuculoida
Nuculoma tenuis (Montagu 1808)
Yoldiella frigida (Torell 1859)
 Subclass Heterodonta
 Order Veneroida
Tridonta montagui (Dillwyn 1817)
 Order Myoida
Mya truncata Linnaeus 1758
Hiatella arctica (Linnaeus 1758)
 Total for climatic regions asbl: 7 (19.4%)

Climatic regions: .sb.
 Class Bivalvia
 Subclass Pteriomorpha
 Order Pterioda
Chlamys islandica (O.F. Müller 1776)
 Subclass Heterodonta
 Order Myoida
Panomya arctica (Lamarck 1818)
 Total for climatic regions .sb. : 2 (5.6%)

Climatic regions: .sbl
 Class Gastropoda
 Subclass Prosobranchia
 Order Neotaenioglossa
Lacuna vincta (Montagu 1803)
 Total for climatic regions .sbl: 1 (2.8%)

The Early/Middle Weichselian Vendsyssel: 36 (14.6%)

The mollusc fauna from the Vendsyssel region during the Early/Middle Weichselian amounts to 36 species, which would have been even more if not reduced to this number by excluding species regarded as redeposited by V. Nordmann (Jessen *et al.* 1910). Almost all the recorded species have been found in the Skærumhede borings I and II (Jessen *et al.* 1910; Bahnson *et al.* 1974 respectively), except *Lunatia pallida*, *Bathyarca glacialis*, *Musculus laevigatus* and *Tridonta borealis*, which have been recorded from the Older *Yoldia* Clay elsewhere in Vendsyssel.

Taken together, the two borings form a most excellent base for evaluating the mollusc faunal development in the Early/Middle Weichselian represented by the Arctic sea deposits characterised by *Portlandia arctica*. However, on the basis of the material from Skærumhede (Bahnson *et al.* 1974), the *Portlandia arctica* zone is divided into three parts each characterised by other macrofossils from the older to the younger beds: the *Turritella erosa*, *Balanus crenata* and *Macoma calcarea* zones. By doing so, it is emphasised that the development in the Arctic part of the marine sequence goes from a deeper-water facies into a shallow-water facies, where in the latter the *Macoma calcarea* species is the dominant bivalve, as it is in the present-day Arctic *Macoma* community of East Greenland (Thorson 1933).

From a climatic point of view, nearly all the molluscan species can be found in the High Arctic, except *Lacuna vincta*, *Panomya arctica* and *Chlamys islandica*, which are recorded only from the Subarctic. However, two of them occur in the *Turritella erosa* zone, which at the same time has the most abundant representation of the other species with northern/Arctic affinities, including the purely Arctic species *Portlandia arctica*. Therefore, no rise in temperature can be suggested on the basis of the molluscan record, only changes in facies through time.

Together with the dominant molluscan species *Portlandia arctica* and *Macoma calcarea* in the upper part of the Arctic sequence – the *Balanus crenata* and the *Macoma calcarea* zones (as seen on fig. 7 in Bahnson *et al.* 1974) – the following mollusc species have been recorded only from these zones: *Natica affinis*, *Musculus niger*, *Palliolium greenlandicum*, and *Axinopsida orbiculata*. All of them can be found in shallow water in the Arctic. Considering the change of facies from deeper water to shallow water and the lack of climatic changes as seen in the molluscan fauna the question arises of what length of time this development covers.

This question has been answered by the two AMS dates of the topmost part of the marine Skærumhede sequence 33 m b.s., which give the age of around 32 000 ¹⁴C years before present (AAR-1410: 32 400 ± 520 and AAR-1411: 32 050 ± 420 – both reservoir corrected ¹⁴C age (B.P.)). This shows that the marine Arctic deposits in this part of the Danish area represent nearly the whole part of the Early and Middle Weichselian, because there is an unbroken marine sequence below the level for these AMS dates and back into the Eemian.

On the basis of the correlation of the Holmstrup sequence of clay with *Macoma calcarea*, there are rea-

sons to think that also the southern part of the Kattegat region was part of the Older *Yoldia* Clay Sea far into the Weichselian, even though two AMS datings from the Holmstrup site were infinite (AAR-1408: > 38 000 ¹⁴C age (B.P.) and AAR-1409: > 42 000 ¹⁴C age (B.P.)).

Skagen

Age: Early/Middle Weichselian

Climatic regions: a...

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Portlandia arctica (Gray 1824)

Total for climatic regions a... : 1 (25.0%)

Climatic regions: asb.

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Nuculana pernula (Müller 1776)

Yoldia hyperborea Lovén 1859

Subclass Pteriomorpha

Order Pterioida

Palliolium greenlandicum (Sowerby 1842)

Total for climatic regions asb. : 3 (75.0%)

The Early/Middle Weichselian Skagen: 4 (1.6%)

In the Skagen region, where all the information coming from the well has been described in more detail earlier, the macrofossil fauna can be presented on the basis of quantitative analyses and sedimentological data (Appendix 3). Therefore, the material can be seen on the background of a certain bottom community. Such a relation was already seen realised in the discussion of the Eemian strata in the Skagen region, which pointed out that these strata could be correlated with an environment of the deeper part of the present Skagerrak. However, the change found in the Arctic section of the Skagen Well on the basis of the mollusc record occurs rather abruptly, turning the scenario into an Arctic environment with ice-rafted minerogene material.

Such a palaeoenvironment is far from the communities demonstrated in recent Danish waters, but is well known from East Greenland. Regarding the finds from

the Arctic part of the Skagen sequence following the tempered Eemian strata, it appears that there are no finds of bias from nearshore or indications of other climatic conditions than from the Arctic. The four molluscan species found are recorded either only in the High-Arctic, viz. *Portlandia arctica*, or in the three zones from the Arctic to the Boreal, viz. *Nuculana pernula*, *Yoldia hyperborea*, and *Palliolium greenlandicum*.

This is a different situation than found in the Vendssysel region, where the two Skærumhede Wells revealed a clear transition zone – the so-called *Abra nitida* zone – and within the Arctic part, with occurrence of molluscs which have been regarded as redeposited (Nordmann in Jessen *et al.* 1910), such as: *Mytilus edulis*, *Pseudamussium septemradiatum*, *Zirfaea crispata*, and *Bittium reticulatum*.

It has been argued in the present paper in connection with the Holocene strata from Skagen that, due to the expired isostatic uplift since the Weichselian glaciation, the actual depth below present sea level of the Holocene beds can be regarded as representing the palaeodepth – taken into account the eustatic movements through time. If this is true, the older strata – the Eemian and Early Weichselian – may also be in a position below present sea level, which could reflect their palaeodepth, here also taking into consideration the older eustatic situation and the question of consolidation. Neotectonic movements might be the black horse together with the higher level of the sea during the Eemian, max. 7–8 m above the present level. This shows that the transition zone – the *Abra nitida* zone – in the Skærumhede II Well is found at a present depth below sea level of between 78 and 88 m (Bahnsen *et al.* 1974, fig. 7), while the sharp boundary between the temperate and the Arctic zone in the Skagen Well is at a depth of 180 m b.s.

The sea level must have been the same for the two stations at this time, so the difference in depth must be around 100 m. Therefore the difference in development of the mollusc fauna within the two sequences depends on depths. This might also explain the occurrences of redeposited molluscs from shallow water in the Skærumhede sequence and not in the Skagen sequence by a closer coastal environment.

The further development of the marine Arctic in the Skagen region has been truncated by the glaciation within the area. However, as demonstrated earlier, the overlying glacial deposits have indeed accumulated the ‘missing’ younger marine strata up to an age of around 32 000 before present, as shown by dating of the marine gases.

Late Weichselian species sorted after climatic affinities

Vendsyssell

Age: Late Weichselian

Climatic regions: a...

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Portlandia arctica (Gray 1824)

Subclass Heterodonta

Order Veneroida

Macoma torelli Jensen 1904

Total for climatic regions a... : 2 (5.7%)

Climatic regions: as..

Class Gastropoda

Subclass Opisthobranchia

Order Bullomorpha

Cylichna occulta (Mighels 1841)

Class Bivalvia

Subclass Heterodonta

Order Veneroida

Macoma loveni Jensen 1904

Subclass Anomalodesmata

Order Pholadomyoidea

Pandora glacialis Leach 1819

Lyonsia arenosa (Möller 1842)

Total for climatic regions as.. : 4 (11.4%)

Climatic regions: asb.

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Lunatia pallida (Broderip & Sowerby 1829)

Order Neogastropoda

Boreotrophon clathratus (Linnaeus 1767)

Buccinum cyaneum Bruguière 1792

Neptunea despecta (Linnaeus 1758)

Oenopota turricola (Montagu 1803)

Subclass Opisthobranchia

Order Anaspidea

Retusa obtusa (Montagu 1803)

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Nuculana pernula (Müller 1776)

Yoldiella lenticula (Möller 1842)

Subclass Pteriomorpha

Order Mytiloida

Musculus laevigatus (Gray 1824)

Musculus niger (Gray 1824)

Subclass Heterodonta

Order Veneroida

Axinopsida orbiculata (G.O. Sars 1878)

Tridonta borealis Schumacher 1817

Macoma calcarea (Gmelin 1791)

total for Climatic regions asb. : 13 (37.1%)

Climatic regions: asbl

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Littorina saxatilis (Olivi 1792)

Natica affinis (Gmelin 1790)

Subclass Opisthobranchia

Order Bullomorpha

Cylichna alba (Brown 1827)

Order Thecosomata

Limacina retroversa (Fleming 1823)

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Nuculoma tenuis (Montagu 1808)

Subclass Heterodonta

Order Veneroida

Thyasira flexuosa (Montagu 1803)

Order Myoidea

Mya truncata Linnaeus 1758

Hiatella arctica (Linnaeus 1758)

Total for climatic regions asbl: 8 (22.9%)

Climatic regions: .sb.

Class Bivalvia

Subclass Pteriomorpha

Order Pterioidea

Chlamys islandica (O.F. Müller 1776)

Subclass Heterodonta

Order Veneroida

Arctica islandica (Linnaeus 1767)

Order Myoidea

Zirfaea crispata (Linnaeus 1758)

Total for climatic regions .sb. : 3 (8.6%)

Climatic regions: .sbl

Class Polyplacophora

Order Neoloricata

Tonicella marmorea (Fabricius 1780)
 Class Gastropoda
 Subclass Prosobranchia
 Order Neotaenioglossa
Lacuna vincta (Montagu 1803)
 Order Neogastropoda
Buccinum undatum Linnaeus 1758
 Class Bivalvia
 Subclass Pteriomorpha
 Order Mytiloidea
Mytilus edulis Linnaeus 1758
 Subclass Heterodonta
 Order Veneroidea
Macoma balthica (Linnaeus 1758)
 Total for climatic regions .sbl: 5 (14.3%)

The Late Weichselian Vendsyssel: 35 (14.2%)

Marine molluscs from the time after the main glaciation of Denmark have been recorded only from Vendsyssel and Skagen, but new studies are increasing our knowledge from the Kattegat region, but are not included in this work.

The marine mollusc assemblages in Vendsyssel have been mainly based on open profiles. The recorded mollusc species amount to 35. However, there are some problems in classifying the whole fauna in communities.

Three climatic groups can be demonstrated: a purely Arctic and Subarctic with six species, an Arctic, Subarctic and Boreal consisting of 13 species, and a group of species which does not enter the Arctic but might be found extending into the Lusitanian. A fourth group with a wide range can be differentiated according to depth ranges. *Littorina saxatilis* is intertidal, while *Natica affinis*, *Cylichna alba*, and *Thyasira flexuosa* are species found from infratidal to great depths. *Nuculoma tenuis* is found offshore to 300 m, and *Limacina retroversa* is pelagic.

So the species with a climatically wide range show the existence of two facies: a littoral and a deeper-water facies.

Considering the five species with a representation within the Subarctic, Boreal and Lusitanian regions, *Macoma balthica* is a shallow-water species, *Mytilus edulis* is eulittoral and here the species occurs in great quantities, *Lacuna vincta* is intertidal to depths of 60 m, *Tonicella marmorea* from 0 to 183 m but more common at depths of less than 20 m, and finally *Buccinum undatum* which is found sublittorally to great depths (1200 m).

The characteristic depth for the dominating part of

these molluscs is seen to be the shallow water.

Two of the species from the Subarctic–Boreal group, *Arctica islandica* and *Zirfaea crispata*, have very different characteristics as to depth of living. The depth range for *Arctica islandica* is in general intertidal to 480 m, but Jensen (1902, pp. 38–39) writes that *Arctica* is a genuine Boreal species and bases this on the fact that in the White Sea area, which is in the northernmost part of its distribution, it is found in more shallow water than elsewhere. A relatively high temperature is reached only in the shallow water in this region.

This means that *Arctica islandica* in the present setting among other molluscs of purely Arctic and Subarctic relations must be an indicator of Boreal waters in the shallow-water environment. *Zirfaea crispata* is on the other hand a clear indicator of shallow water, having its range of depth between the low tide line and out to a depth of about 7 m.

The third member of the Subarctic–Boreal climatic region, *Chlamys islandica*, is known from the tidal zone and down to depths of 300 m.

Of the 13 species represented within the climatic regions of the Arctic, Subarctic and Boreal, half of the members are infralittoral from 6–10 m to great depths: *Lunatia pallida*, *Boreotrophon clathratus*, *Neptunea despecta*, *Oenopota turricola*, *Nuculana pernula*, *Yoldiella lenticula*, and *Musculus niger*. The other half can be found in the tidal zone but also at greater depths. Among these, *Macoma calcarea* and *Tridonta borealis* are the characteristic bivalves in the Arctic shallow-water *Macoma calcarea* community with the *Astarte borealis* zone in the most shallow parts from 3 to about 12–14 m in East Greenland (Thorson 1933, pp. 8–18). According to Thorson (1933), the *Astarte borealis* zone is no tide-water community such as for instance the *Macoma balthica* community in some Boreal seas. This is discussed in further detail by Madsen (1936, p. 71), who concludes: “The littoral fauna [north of c. 66–67°N lat. East Greenland] is especially characterised by the absence of littoral molluscs and Balanidea, notably *Mytilus edulis*, *Littorina saxatilis* var. *groenlandica*, and *Balanus balanoides*, all of which occur south of the above-mentioned limit”.

The Arctic–Subarctic species in Vendsyssel, represented by four species, can be found at water depths from 2 to 5 m and out to around 200 m, except *Cylichna occulta*, which has a depth range of from 20 m to nearly 400 m.

The purely Arctic species *Portlandia arctica* and *Macoma torelli* are recorded from 2 and 5 m out to

around 340 m and 90 m respectively. This shows that the Arctic–Subarctic part of the recorded species from the Vendsyssel region have a wide range of occurrence restricted not by a single species to the shallow-water environment as is the case among the more temperate mollusca and the species with a wide climatic range: *Arctica islandica*, *Zirfaea crispata*, *Macoma balthica*, *Mytilus edulis*, and *Littorina saxatilis*.

It can therefore be stated that all the Arctic species could be together in deeper water and some also in the more shallow water. However, some of the more temperate species are restricted to shallow water, and *Arctica islandica* is a distinctly shallow-water species in the northern part of its range. So, within the time span of deposition for the Late Weichselian Younger Yoldia Sea deposits, an amelioration of the shallow-water environment including the tidal zone must have happened.

Nordmann (1910) noticed that certain marine strata in the Vendsyssel region had a distinct littoral fauna, and he suggested that these beds were of a more recent origin than the Younger Yoldia Clay, introducing the so-called *Zirphaea* transgression named after one of the characteristic bivalves from the shallow-water environment discussed above. However, Petersen (1984), on the basis of molluscan studies combined with the many ¹⁴C dates, could conclude that the deposition of Yoldia Clay containing a cold marine fauna from deeper water is seen to continue into Bølling, but with a contemporaneous temperate fauna in the shallow-water deposits – the *Zirphaea* Beds. The evaluation of the marine history from Vendsyssel is highly influenced by experiences obtained from work on Holocene raised marine deposits and recent bottom samples in East Greenland, as seen in Petersen (1986b, figs 2, 3), where beds from the *Astarte borealis* zone with *Mytilus edulis* are overlying the *Ophiocten* zone (deeper part of the Arctic *Macoma calcarea* community (Thorson 1933, pp. 18–27)) with *Portlandia arctica*. These observations may also explain the occurrences of redeposited material mentioned within the discussion of the Older Yoldia Clay at Skærumhede in the Vendsyssel region. Still, it must be regarded as redeposited, but not necessarily differing so much in time, as long as the above-mentioned observations show that a more temperate zone can be found in the shallow-water environment contemporaneous with an Arctic fauna in deeper water.

Skagen

Age: Late Weichselian

Climatic regions: a...

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Portlandia arctica (Gray 1824)

Total for climatic regions a... : 1 (11.1%)

Climatic regions: as..

Class Bivalvia

Subclass Pteriomorpha

Order Arcoida

Bathyarca glacialis (Gray 1824)

Total for climatic regions as.. : 1 (11.1%)

Climatic regions: asb.

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Nuculana pernula (Müller 1776)

Yoldia hyperborea Lovén 1859

Yoldiella lenticula (Möller 1842)

Total for climatic regions asb. : 3 (33.3%)

Climatic regions: asbl

Class Gastropoda

Subclass Opisthobranchia

Order Gymnosomata

Clione limacina (Phipps 1774)

Class Scaphopoda

Siphonodentalium lobatum (Sowerby 1860)

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Yoldiella frigida (Torell 1859)

Total for climatic regions asbl: 3 (33.3%)

Climatic regions: .sb.

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Nuculana minuta (Müller 1776)

Total for climatic regions .sb. : 1 (11.1%)

The Late Weichselian Skagen: 9 (3.6%)

The Skagen region has contributed with only nine species, out of which the *Clione limacina* species must be taken with some reservation, being based on an

imprint only. All the recorded species have been taken from the Skagen Well core superjacent to the older Eemian and Weichselian deposits discussed above. Therefore the fauna represents an assemblage from a certain depth – through time – and can be seen in relation to the sedimentological information (Appendix 3). The granulometric composition in the Older *Yoldia* Sea sequence reflects two maxima on the frequency curve, which tells that part of the material, other than the extremely fine-grained, can be taken as ice-rafted material. However, no such redeposited material was found in the fauna. The whole mollusc assemblage resembles the *Arca-Astarte crenata* community as described by Thorson (1934) from Hurry Inlet, East Greenland.

First of all the *Arca glacialis* (*Bathyarca glacialis*) is represented among the molluscs recorded from the Skagen Well. This species is one of the characteristic species from this community. Furthermore, the following species are mentioned (Thorson 1934, p. 48): *Siphonodentalium vitreum* (*S. lobatum*), *Leda pernula* (*Nuculana p.*), *Portlandia arctica*, *Portlandia lenticula* (*Yoldiella l.*), *Portlandia frigida* (*Yoldiella f.*), and *Saxicava arctica* (*Hiatella a.*) which have all been recorded from the Skagen Well. Only *Nuculana minuta*, a Subarctic–Boreal species, and *Yoldia hyperborea* are not recorded from Hurry Inlet. Ockelmann (1958, pp. 19–22) mentioned that *Nuculana minuta* is “lacking in the most high-Arctic seas” and that according to Thorson (1934) *Yoldia hyperborea* is associated with calm, sheltered places, and besides *Yoldia hyperborea* is otherwise known from only a few places in East Greenland.

These records from Greenland demonstrate a good agreement with the Danish Late Weichselian finds from the Skagen Well and permit further comparison with the *Arca-Astarte crenata* community. According to Thorson (1933, p. 67), this community inhabits depths from ca. 45 to ca. 200 m. Furthermore, it is poor in species, and the temperature is negative and constant all the year round.

The well-dated strata of Late Weichselian age, from 15 000 – 10 000 before present in ¹⁴C years, around 17 000 – 11 000 in calibrated age B.P. (see Appendix 4) in the Skagen Well have no influence from the shallow-water Boreo-Arctic assemblage as found in the Vendsyssel region around 13 000 before present (Petersen 1984, p. 65), but reveal with their Arctic deeper-water mollusc fauna a sharp boundary to the Holocene Boreo-Lusitanian faunas.

Holocene species sorted after climatic affinities

The boundary between the Pleistocene and the Holocene marine strata as seen in the Skagen Well is unique within the Danish realm. Furthermore, the approximately 115 m of Holocene marine beds as described earlier represent a well-dated sequence to be compared to the other Holocene marine finds recorded in the six regions, many of which offer dated strata as well. The following description will proceed in the same way as taken for the marine Pleistocene strata, and it will present the entire molluscan fauna from each region from the point of view of climatic affinities for each species, with subsequent comments upon certain aspects for selected species.

Within each region, reference to well-dated strata and their molluscan assemblages will be given and worked out to facilitate the correlation in time to assemblages in other regions.

Finally, the juncture of occurrence during the Holocene of some of the molluscan species in all regions can be estimated, as presented in Appendix 6.

The Bælt Sea

Climatic regions: asb.

Class Gastropoda

Subclass Opisthobranchia

Order Anaspidea

Retusa obtusa (Montagu 1803)

Class Bivalvia

Subclass Heterodonta

Order Veneroida

Tridonta borealis Schumacher 1817

Total for climatic regions asb. : 2 (4.3%)

Climatic regions: asbl

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Littorina saxatilis (Olivi 1792)

Lacuna pallidula (da Costa 1778)

Class Bivalvia

Subclass Pteriomorpha

Order Mytiloida

Musculus discors (Linnaeus 1767)

Subclass Heterodonta

Order Myoida

Mya truncata Linnaeus 1758

Hiatella arctica (Linnaeus 1758)

Total for climatic regions asbl: 5 (10.6%)

Climatic regions: .sb.

Class Bivalvia

Subclass Heterodonta

Order Veneroida

Arctica islandica (Linnaeus 1767)

Order Myoida

Zirfaea crispata (Linnaeus 1758)

Total for climatic regions .sb. : 2 (4.3%)

Climatic regions: .sbl

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Littorina obtusata (Linnaeus 1758)

Lacuna vincta (Montagu 1803)

Onoba semicostata (Montagu 1803)

Subclass Heterobranchia

Order Heterostropha

Omalogyra atomus (Phillippi 1841)

Class Bivalvia

Subclass Pteriomorpha

Order Mytiloida

Mytilus edulis Linnaeus 1758

Modiolus modiolus (Linnaeus 1758)

Subclass Heterodonta

Order Veneroida

Mysella bidentata (Montagu 1803)

Parvicardium ovale (Sowerby 1840)

Macoma balthica (Linnaeus 1758)

Total for climatic regions .sbl: 9 (19.1%)

Climatic regions: ..b.

Class Bivalvia

Subclass Heterodonta

Order Myoida

Mya arenaria Linnaeus 1758

Total for climatic regions ..b. : 1 (2.1%)

Climatic regions: ..bl

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Littorina littorea (Linnaeus 1758)

Littorina tenebrosa (Montagu 1803)

Hydrobia ulvae (Pennant 1777)

Hydrobia ventrosa (Montagu 1803)

Rissoa albella Lovén 1846

Rissoa inconspicua Alder 1844

Rissoa membranacea (J. Adams 1800)

Bittium reticulatum (da Costa 1778)

Order Heterogastropoda

Triphora adversa (Montagu 1803)

Order Neogastropoda

Hinia reticulata (Linnaeus 1758)

Subclass Heterobranchia

Order Heterostropha

Odostomia conoidea Winckworth 1932

Subclass Opisthobranchia

Order Anaspidea

Retusa truncatula (Bruguière 1792)

Akera bullata Müller 1776

Subclass Pulmonata

Order Basommatophora

Lymnaea peregra (Müller 1774)

Class Bivalvia

Subclass Pteriomorpha

Order Mytiloida

Modiolula phaseolina (Phillippi 1844)

Order Pterioda

Subclass Heterodonta

Order Veneroida

Parvicardium exiguum (Gmelin 1791)

Parvicardium scabrum (Phillippi 1844)

Cerastoderma edule (Linnaeus 1758)

Spisula subtruncata (da Costa 1778)

Angulus tenuis (da Costa 1778)

Scrobicularia plana (da Costa 1778)

Abra alba (Wood 1802)

Paphia aurea (Gmelin 1791)

Tapes decussatus (Linnaeus 1758)

Venerupis pullastra (Montagu 1803)

Order Myoida

Corbula gibba (Olivi 1792)

Barnea candida (Linnaeus 1758)

Total for climatic regions ..bl: 28 (59.6%)

The Holocene Bælt Sea: 47 (19.0%)

The Holocene molluscs in the Bælt Sea region amount to 47 mainly Boreo-Lusitanian species. There are no purely Lusitanian species, only two Arctic-Subarctic and Boreal species, and five species with a wide range of distribution. This is a clear difference compared to the Eemian molluscan fauna from the same region with no less than seven purely Lusitanian species.

This is not connected with differences in depth ranges. All of the subfossil species from the Holocene could be found within the intertidal zone except: *Odostomia conoidea* and *Parvicardium ovale* occur-

ring below 5–10 m, or infratidal species such as *Tridonta borealis*, *Modiolus modiolus* and *Abra alba*. *Abra alba* characterises the Bælt Sea deeper-water community and *Tridonta borealis* the community in the Baltic, the so-called *Abra alba* and *Astarte* communities *sensu* Petersen (1913, p. 16).

The overall dominating part of the species could be associated with the *Macoma* community *sensu* Petersen (1913, p. 14) which nowadays is recorded from the fjords and the more sheltered coasts from the shore and out to a depth of 10–12 m. This community is named after *Macoma balthica*, also present in the Bælt Sea subfossil molluscan fauna. The great similarity between the subfossil Holocene fauna and the recent, as seen from the above-mentioned dates on the communities met with, is also revealed in the present distribution of the species in question. Almost all the species occur in the present-day Bælt Sea or even further into the Baltic region – east of Darss. The few species no longer found in the Bælt Sea region are: *Littorina saxatilis*, *Odostomia conoidea*, *Modiolula phaseolina*, *Ostrea edulis*, *Parvicardium scabrum*, *Angulus tenuis* and *Venerupis pullastra* which only extend into the Kattegat region today, while *Paphia aurea*, *Tapes decussatus*, and *Omalogyra atomus* are no longer recorded in the Danish mollusc fauna.

The absence of certain species is most likely an effect of the salinity reached in the Bælt Sea at present. However, as mentioned by Rasmussen (1973, p. 303) in the case of *Venerupis pullastra*, the distribution might be connected with the bottom conditions (see the chapter on molluscan species). Most of the species now absent from the Bælt Sea were present during the Atlantic, and, in all, 31 molluscan species have their first appearance in this period (Appendix 6).

Among the 31 species with dated appearances in the Atlantic, *Littorina saxatilis* and *Mya truncata* have a wide climatic range. *Arctica islandica* is found in the Boreal region, and *Lacuna vincta*, *Onoba semicostata*, *Mytilus edulis*, *Mysella bidentata*, and *Macoma balthica* are Subarctic–Boreal–Lusitanian. The rest of the species appearing in the Atlantic amount to 23 species with dated appearances during the Atlantic within the Bælt Sea area.

The 31 species constitute 12.6% of the known subfossil molluscan finds from the Late Quaternary, while the total finds of molluscs from the Holocene Bælt Sea represent 19.0% (47 species out of the 247 subfossil species).

This might indicate that the more prolific fauna in the Bælt Sea was connected with a time interval when

the inner Danish waters were still affected by a higher tidal impact which expired at the beginning of the Subboreal (Petersen 1993).

However, *Paphia aurea* and *Ostrea edulis* are still met with as food elements, although rather rare, in the Iron Age ‘køkkenmøddinger’ (kitchen middens) in the western part of the Bælt Sea (Petersen 1985c, fig. 5, p. 22). *Mya arenaria* has been found in the Bælt Sea embedded in strata from the Atlantic. The appearance of this species within the Atlantic strata is explained by the deep-burrowing habit of this infauna species. However, the first appearance of the species must be referred to the Subatlantic after new dates in the Bælt Sea region following the study of the immigration of *Mya arenaria* to Danish waters (Petersen *et al.* 1992b).

The Baltic

Climatic regions: .sbl

Class Bivalvia

Subclass Pteriomorpha

Order Mytiloida

Mytilus edulis Linnaeus 1758

Subclass Heterodonta

Order Veneroida

Macoma balthica (Linnaeus 1758)

Total for climatic regions .sbl: 2 (10.5%)

Climatic regions: ..bl

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Littorina littorea (Linnaeus 1758)

Littorina tenebrosa (Montagu 1803)

Hydrobia ulvae (Pennant 1777)

Hydrobia ventrosa (Montagu 1803)

Rissoa albella Lovén 1846

Rissoa inconspicua Alder 1844

Rissoa membranacea (J. Adams 1800)

Bittium reticulatum (da Costa 1778)

Aporrhais pespelicani (Linnaeus 1758)

Order Neogastropoda

Hinia reticulata (Linnaeus 1758)

Subclass Opisthobranchia

Order Anaspidea

Retusa truncatula (Bruguière 1792)

Subclass Pulmonata

Order Basommatophora

Lymnaea peregra (Müller 1774)

Class Bivalvia

Subclass Heterodonta
 Order Veneroida
Parvicardium exiguum (Gmelin 1791)
Cerastoderma edule (Linnaeus 1758)
Cerastoderma glaucum (Poiret 1798)
Scrobicularia plana (da Costa 1778)
 Order Myoida
Corbula gibba (Olivi 1792)
 Total for climatic regions .:bl: 17 (89.5%)

The Holocene Baltic: 19 (7.7%)

Among the 19 species recorded from the Holocene of the Baltic, there is relatively many, which do not occur in the recent Baltic fauna, viz.: *Rissoa albella*, *Rissoa inconspicua*, *Bittium reticulatum*, *Hinia reticulata*, *Retusa truncatula*, and *Scrobicularia plana*, but they are present in the neighbouring recent Bælt Sea fauna. Furthermore, *Aporrbais pespelicani* can be added which today extends into the Kattegat region, while only empty shells have been recorded from the Bælt Sea region off Kiel (Arntz *et al.* 1976).

So, although the spectacular oyster and *Tapes* species did not occur as in the Bælt Sea, the subfossil Baltic fauna has quite a few species that no longer live in the Baltic. The geological mapping from this region (Milthers 1908) does not provide further information on the chronostratigraphic position of these mollusc species, and is also rather poor, since they are based on samples from near present-day sea level.

This is also corroborated by Munthe (1894, p. 9): “in the south part of the Baltic region we possess but comparatively little knowledge of the fauna which results partly from the circumstances that the Litorina strata are here to be sought only to a small extent above the sea level”. This has obviously hampered the study within the Danish region, so that Holocene marine deposits in the Baltic are little known up to the present. However, recent activities by marine geologists have given new material from the westernmost part of the Baltic – Fakse Bugt (Jensen 1995). As far as the mollusc studies have been submitted (Petersen 1994b) but not published in detail, the following comments will be given to Fig. 101.

The 4 m of sampling from vibrocore 225B comes from the cored section 17.5–13.5 m b.s.l. and has been dated within a time span of 4000 ¹⁴C years covering the early part of the Holocene from the Preboreal to the Atlantic, through time represented by freshwater,

brackish and marine deposits as deduced from the occurrences of mollusc.

The loss on ignition shows that the lower third of the sequence has around 25 weight per cent of organic material, while the upper two-thirds of the sequence has less than 5 weight per cent loss on ignition (Fig. 101).

Considering the mollusc species, it appears that the high amount of organic material is not connected solely with the freshwater deposits, but continues into the brackish-water layers.

The first rise of sea level is demonstrated by the occurrences of *Cerastoderma* and *Mytilus* and the disappearance of the freshwater molluscs such as *Valvata macrostoma* and the *Sphaeriidae*. The persistent occurrence of the *Bithynia tentaculata* operculae in the oldest part of the brackish-water deposits shows that salinity was lower than 12‰.

Within this interval, seven mollusc species occur (see Fig. 101), viz.: two *Hydrobia* and one *Rissoa* species and the bivalves *Mytilus*, *Macoma* and *Cerastoderma*. The *Cerastoderma* species are rather difficult to identify in all the samples because of their poor state of preservation.

At a level of about 15.5 m b.s.l., the change to higher diversity of marine molluscs occurs with such new species as *Aporrbais pespelicani*, *Nassarius reticulatus* and *Scrobicularia plana* besides the steady occurrence of *Littorina littorea*, *Retusa truncatula* and *Corbula gibba*. Even *Bittium reticulatum* has been found in one sample. This species tolerates only water with a salinity above 25‰ (Sorgenfrei 1958). In all circumstances the more prolific marine fauna is well demonstrated in this part of the sequence, and furthermore, single occurrences of species such as *Rissoa membranacea*, *Lacuna vincta*, and *Parvicardium exiguum* sustain this view. The occurrence of freshwater gastropods is a product of transport from the nearby land, where freshwater streams run into the bay or may be eroded from older deposits by currents. In the topmost part of the core especially fishbones occur up to the present sea bottom at 13.5 m b.s.l.

The faunal development in the 4 m core reflects as the oldest element a small lake dated to the time span 9370 ± 135 (K-5649) up to 7900 ± 115 (K-5652) in ¹⁴C years B.P. Around 7900 B.P. the marine influence is found at the present level of 16.5 m b.s.l. with the establishment of a brackish-water fauna. At a level of 15.30 m b.s.l., which has been dated to 6520 ± 135 ¹⁴C years B.P. (AAR-633), the change to the more prolific *Littorina* Sea fauna has taken place. But, the samples

The occurrences of molluscan species in the Fakse Bugt Well

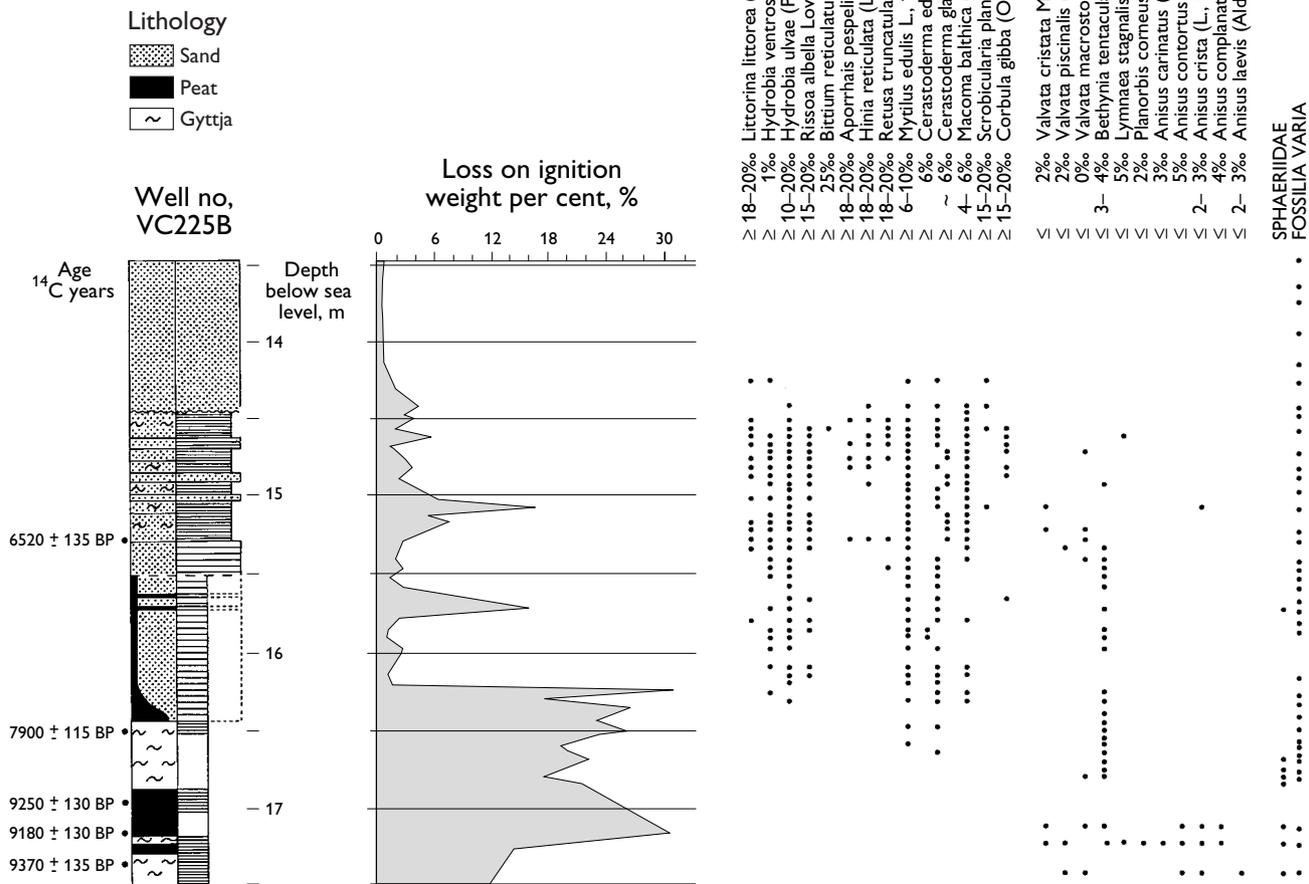


Fig. 101. The occurrences of molluscan species in the Fakse Bugt Well no. VC225B with indication of loss on ignition and sedimentary log with datings (¹⁴C years) based on Jensen (1995).

from higher up in the core do not show any development into the present-day molluscan fauna, first of all because of the absence of *Mya arenaria* that characterises the present-day Baltic Sea.

In conclusion, the *Littorina* Sea fauna from the Fakse Bugt as demonstrated from this core is from the Atlantic and shows the molluscs of the transgression around 8000 B.P. (¹⁴C years) and the established marine fauna of the Atlantic.

The fauna from this core contains most of the above-mentioned species no longer found in the Baltic, and it is shown that this fauna was most probably established during the Atlantic. Therefore, the marine molluscs from the cored section immigrated to the Baltic

during the Atlantic (Appendix 6).

Among the 15 species with dated appearances in the Atlantic only *Mytilus edulis* and *Macoma balthica* have their climatic range within the Subarctic–Boreal–Lusitanian regions, while the rest belong to the Boreal–Lusitanian group as in the Bælt Sea area. However, the number of mollusc species from this region is very low with the 19 species found forming only 7.7% of the subfossil fauna.

As in the case of the Bælt Sea, the more prolific fauna can be connected with the Atlantic, and this could be caused by the higher tidal amplitude during this time span giving a higher salt content.

In the introduction it was mentioned that there is

no record of mollusc species from the geological mapping of the island of Bornholm (Grönwall & Milthers 1916). Several bottom samples have been analysed from east of Bornholm by the author, showing large amounts of *Tridonta elliptica* and *Tridonta borealis*, but the material was never dated, so they could be subrecent specimens. They have therefore not been included in the present list of subfossil Holocene molluscs from the Baltic.

The Kattegat

Climatic regions: asb.

Class Gastropoda

Subclass Opisthobranchia

Order Anaspidea

Retusa obtusa (Montagu 1803)

Total for climatic regions asb. : 1 (2.2%)

Climatic regions: asbl

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Littorina saxatilis (Olivi 1792)

Class Bivalvia

Subclass Pteriomorpha

Order Mytiloidea

Musculus discors (Linnaeus 1767)

Subclass Heterodonta

Order Myoidea

Mya truncata Linnaeus 1758

Hiatella rugosa (Linnaeus 1758)

Total for climatic regions asbl: 4 (8.9%)

Climatic regions: .sb.

Class Bivalvia

Subclass Heterodonta

Order Veneroidea

Arctica islandica (Linnaeus 1767)

Total for climatic regions .sb. : 1 (2.2%)

Climatic regions: .sbl

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Littorina obtusata (Linnaeus 1758)

Lacuna vincta (Montagu 1803)

Skeneopsis planorbis (Fabricius 1780)

Onoba semicostata (Montagu 1803)

Order Neogastropoda

Buccinum undatum Linnaeus 1758

Subclass Heterobranchia

Order Heterostropha

Omalogyra atomus (Phillippi 1841)

Class Bivalvia

Subclass Pteriomorpha

Order Mytiloidea

Mytilus edulis Linnaeus 1758

Order Pterioidea

Heteranomia squamula (Linnaeus 1758)

Subclass Heterodonta

Order Veneroidea

Mysella bidentata (Montagu 1803)

Macoma balthica (Linnaeus 1758)

Total for climatic regions .sbl: 10 (22.2%)

Climatic regions: ..b.

Class Bivalvia

Subclass Heterodonta

Order Myoidea

Mya arenaria Linnaeus 1758

Total for climatic regions ..b. : 1 (2.2%)

Climatic regions: ..bl

Class Gastropoda

Subclass Prosobranchia

Order Archaeogastropoda

Theodoxus fluviatilis (Linnaeus 1758)

Order Neotaenioglossa

Littorina littorea (Linnaeus 1758)

Littorina tenebrosa (Montagu 1803)

Hydrobia ulvae (Pennant 1777)

Hydrobia ventrosa (Montagu 1803)

Onoba vitrea (Montagu 1803)

Rissoa albella Lovén 1846

Rissoa inconspicua Alder 1844

Rissoa membranacea (J. Adams 1800)

Bittium reticulatum (da Costa 1778)

Order Heterogastropoda

Triphora adversa (Montagu 1803)

Order Neogastropoda

Hinia reticulata (Linnaeus 1758)

Subclass Heterobranchia

Order Heterostropha

Brachystomia eulimoides Hanley 1844

Chrysallida spiralis (Montagu 1803)

Subclass Opisthobranchia

Order Anaspidea

Retusa truncatula (Bruguière 1792)

Akera bullata Müller 1776

Class Bivalvia

Subclass Pteriomorpha

Order Pterioidea

Ostrea edulis Linnaeus 1758

Subclass Heterodonta

Order Veneroidea

Acanthocardia ecbinata (Linnaeus 1758)

Parvicardium exiguum (Gmelin 1791)

Parvicardium scabrum (Philippi 1844)

Cerastoderma edule (Linnaeus 1758)

Cerastoderma glaucum (Poiret 1798)

Scrobicularia plana (da Costa 1778)

Abra alba (Wood 1802)

Paphia aurea (Gmelin 1791)

Tapes decussatus (Linnaeus 1758)

Venerupis pullastra (Montagu 1803)

Order Myoidea

Corbula gibba (Olivi 1792)

Total for climatic regions ..bl: 28 (62.2%)

The Holocene Kattegat: 45 (18.2%)

The molluscs from the Kattegat region have to a great extent been collected in the raised marine forelands to the Kattegat itself during the geological mapping in contrast to some of the sampling localities referred to in the preceding two regions. So, although part of the information from Djursland comes from borings to a depth of about 10 m b.s.l., it does not present deeper-water deposits as met with in the Kattegat proper (Petersen 1993). This is also true of the maximum palaeodepth reached, when it is taken into account that the present area is within the isostatic uplift zone with the highest marine shoreline – up to about 10 m – within this region (Mertz 1924).

Forty-five mollusc species have been recorded from the Kattegat region. There are no purely Lusitanian species, but Boreo-Lusitanian species. Reflecting the above-mentioned facts on maximum palaeodepth, all the species can be found within the tidal/shallow-water zone, viz.: *Littorina saxatilis*, *Littorina obtusata*, *Littorina tenebrosa*, *Hydrobia ulvae*, *Theodoxus fluviatilis*, *Mytilus edulis*, *Cerastoderma edule*, and *Tapes decussatus*. *Tapes decussatus* and *Paphia aurea* are no longer found in Danish waters, but occur off western and southern Norway in the immediate neighbourhood. Rørdam (1891) discussed at some length the different mollusc assemblages in north-eastern Sjælland and related these faunas to their relative positions from the open sea and into the innermost part of the fjords. Petersen (*in* Rørdam 1891, pp. 106–111), who deter-

mined most of the molluscan species in Rørdam's thesis (Rørdam 1891, p. 106), stated that: "The deposition of the *Tapes* layers has happened in a period where the Danish waters from a hydrographical point of view have been more like the North Sea or the open sea than now".

This was clearly demonstrated by the large oyster banks present far into the Roskilde Fjord in north-eastern Sjælland, and it has also been recorded from other mapped areas on Fyn and in Jylland. The innermost part of the former fjords always carried a rich subfossil mollusc fauna compared to the recent fjord complexes. Recent studies from Jylland of the faunal changes through time have shown that the rich faunas in the innermost part of such fjord regions developed during the Atlantic. This situation is most probably connected with a higher tidal amplitude in the inner Danish waters during the Atlantic than in the following Subboreal period, as argued in Petersen (1993).

The absence of purely Lusitanian species in the mid-Holocene fauna from the Kattegat region shows, as mentioned above, that climatic changes have not been of major significance. The most characteristic species for the Holocene subfossil fauna in this region – the *Tapes* species – is still to be found within the Boreal region.

Of the 25 dated molluscan species from Djursland, 23 species have immigrated during the Atlantic along with the transgression (Petersen 1993, table 1). Only two species, *Littorina tenebrosa* and *Onoba semicostata*, immigrate after the change to more brackish-water conditions that prevailed in the Subboreal. Among the species with a dated appearance in the Atlantic, which form nearly half of the mollusc species known from this region, the dominating climatic group is the Boreo-Lusitanian, with 18 species.

The whole fauna of 45 species from the Kattegat region constitutes 18.2% of the subfossil molluscs. This is close to the percentage for the Bælt Sea area but much less than could be expected regarding the number of species from the recent Kattegat region. This recalls the above-mentioned fact that the sampling of the molluscan material has been from raised marine forelands and therefore does not include the deeper-water fauna from the vast area of the Kattegat proper. However, as mentioned earlier in connection with the Late Weichselian marine deposits, new studies are progressing recording the deeper-water fauna with, *inter alia*, *Turritella communis* from the Kattegat during the Holocene.

The Limfjord

Climatic regions: asb.

Class Gastropoda

Subclass Prosobranchia

Order Archaeogastropoda

Margarites belicinus (Phipps 1774)

Order Neogastropoda

Oenopota turricola (Montagu 1803)

Subclass Opisthobranchia

Order Anaspidea

Retusa obtusa (Montagu 1803)

Class Bivalvia

Subclass Heterodonta

Order Veneroida

Tridonta borealis Schumacher 1817

Total for climatic regions asb. : 4 (2.7%)

Climatic regions: asbl

Class Gastropoda

Subclass Prosobranchia

Order Archaeogastropoda

Acmaea tessulata (Müller 1776)

Order Neotaenioglossa

Littorina saxatilis (Olivi 1792)

Lacuna pallidula (da Costa 1778)

Subclass Opisthobranchia

Order Bullomorpha

Cylichna alba (Brown 1827)

Order Anaspidea

Diaphana minuta Brown 1827

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Nuculoma tenuis (Montagu 1808)

Subclass Pteriomorpha

Order Mytiloida

Musculus discors (Linnaeus 1767)

Subclass Heterodonta

Order Veneroida

Thyasira flexuosa (Montagu 1803)

Order Myoida

Mya truncata Linnaeus 1758

Hiatella arctica (Linnaeus 1758)

Total for climatic regions asbl: 10 (6.8%)

Climatic regions: .sb.

Class Bivalvia

Subclass Heterodonta

Order Veneroida

Arctica islandica (Linnaeus 1767)

Order Myoida

Zirfaea crispata (Linnaeus 1758)

Total for climatic regions .sb. : 2 (1.4%)

Climatic regions: .sbl

Class Gastropoda

Subclass Prosobranchia

Order Archaeogastropoda

Acmaea virginea (Müller 1776)

Order Neotaenioglossa

Littorina obtusata (Linnaeus 1758)

Lacuna vincta (Montagu 1803)

Skeneopsis planorbis (Fabricius 1780)

Onoba semicostata (Montagu 1803)

Order Neogastropoda

Nucella lapillus (Linnaeus 1758)

Buccinum undatum Linnaeus 1758

Subclass Heterobranchia

Order Heterostropha

Omalogyra atomus (Phillippi 1841)

Class Bivalvia

Subclass Pteriomorpha

Order Mytiloida

Mytilus edulis Linnaeus 1758

Modiolus modiolus (Linnaeus 1758)

Order Pterioda

Delectopecten vitreus (Gmelin 1791)

Heteranomia squamula (Linnaeus 1758)

Subclass Heterodonta

Order Veneroida

Mysella bidentata (Montagu 1803)

Tellimya ferruginosa (Montagu 1803)

Turtonia minuta (Fabricius 1780)

Parvicardium ovale (Sowerby 1840)

Spisula elliptica (Brown 1827)

Macoma balthica (Linnaeus 1758)

Gari fervensis (Gmelin 1791)

Total for climatic regions .sbl: 19 (12.9%)

Climatic regions: ..b.

Class Gastropoda

Subclass Heterobranchia

Order Heterostropha

Chrysallida eximia (Jeffreys 1849)

Total for climatic regions ..b. : 1 (0.7%)

Climatic regions: ..bl

Class Gastropoda

Subclass Prosobranchia

Order Archaeogastropoda

Patella vulgata Linnaeus 1758

Helcion pellucidum (Linnaeus 1758)

- Iotbia fulva* (Müller 1776)
Gibbula cineraria (Linnaeus 1758)
Gibbula tumida (Montagu 1803)
Skenea basistriata (Jeffreys 1877)
- Order Neotaenioglossa
Littorina littorea (Linnaeus 1758)
Littorina tenebrosa (Montagu 1803)
Lacuna parva (Montagu 1803)
Hydrobia ulvae (Pennant 1777)
Hydrobia ventrosa (Montagu 1803)
Alvania punctura (Montagu 1803)
Cingula semistriata (Montagu 1808)
Onoba vitrea (Montagu 1803)
Rissoa albella Lovén 1846
Rissoa inconspicua Alder 1844
Rissoa membranacea (J. Adams 1800)
Rissoa parva (da Costa 1779)
Rissoa violacea Desmarest 1814
Caecum glabrum (Montagu 1803)
Bittium reticulatum (da Costa 1778)
Turritella communis Risso 1826
Aporrhais pespelicani (Linnaeus 1758)
Lunatia alderi (Forbes 1838)
Lunatia catena (da Costa 1778)
- Order Heterogastropoda
Triphora adversa (Montagu 1803)
Cerithiopsis barleei Jeffreys 1867
Cerithiopsis tubercularis (Montagu 1803)
Epitonium clathrus (Linnaeus 1758)
Epitonium turtonis (Turton 1819)
Acis minor (Brown 1827)
Vitreolinaphilippii (Rayneval & Ponzi 1854)
- Order Neogastropoda
Hinia incrassata (Ström 1768)
Hinia pygmaea (Lamarck 1822)
Hinia reticulata (Linnaeus 1758)
Raphitoma purpurea (Montagu 1803)
Raphitoma linearis (Montagu 1803)
- Subclass Heterobranchia
Order Heterostropha
Brachystomia eulimoides Hanley 1844
Odostomia scalaris MacGillivray 1843
Chrysallida decussata (Montagu 1803)
Chrysallida indistincta (Montagu 1808)
Chrysallida obtusa (Brown 1827)
Chrysallida spiralis (Montagu 1803)
Ebala nitidissima (Montagu 1803)
Eulimella laevis (Brown 1827)
Eulimella scillae (Scacchi 1835)
Ondina divisa (J. Adams 1797)
Ondina diaphana (Jeffreys 1848)
- Odostomia acuta* Jeffreys 1848
Odostomia conoidea Winckworth 1932
Odostomia turrita Hanley 1844
Odostomia albella Lovén 1846
Odostomia plicata (Montagu 1803)
Turbonilla crenata (Brown 1827)
Turbonilla delicata (Monterosato 1874)
Turbonilla lactea (Linné 1758)
- Subclass Opisthobranchia
Order Bullomorpha
Acteon tornatilis (Linnaeus 1758)
Cylichna cylindracea (Pennant 1777)
Philine aperta (Linnaeus 1767)
Philine punctata (Adams 1800)
- Order Anaspidea
Retusa truncatula (Bruguière 1792)
Retusa umbilicata (Montagu 1803)
Akera bullata Müller 1776
- Class Bivalvia
Subclass Palaeotaxodonta
Order Nuculoida
Nucula nitidosa Winckworth 1930
Nucula nucleus (Linnaeus 1767)
- Subclass Pteriomorpha
Order Mytiloida
Modiolula phaseolina (Philippi 1844)
Modiolus adriaticus (Lamarck 1819)
Modiolaria tumida (Hanley 1843)
- Order Pterioidea
Aequipecten opercularis (Linnaeus 1758)
Chlamys varia (Linnaeus 1758)
Palliolum striatum (Müller 1776)
Palliolum tigerinum (Müller 1776)
Pododesmus patelliformis (Linnaeus 1761)
Ostrea edulis Linnaeus 1758
- Subclass Heterodonta
Order Veneroida
Lucinoma borealis (Linnaeus 1758)
Lepton nitidum (Turton 1822)
Acanthocardia echinata (Linnaeus 1758)
Parvicardium exiguum (Gmelin 1791)
Parvicardium scabrum (Philippi 1844)
Cerastoderma edule (Linnaeus 1758)
Cerastoderma glaucum (Poiret 1798)
Mactra stultorum (Linnaeus 1758)
Lutraria lutraria (Linnaeus 1758)
Spisula solida (Linnaeus 1758)
Spisula subtruncata (da Costa 1778)
Ensis ensis (Linnaeus 1758)
Phaxas pellucidus (Pennant 1777)
Angulus tenuis (da Costa 1778)

Fabulina fabula (Gmelin 1791)
Donax vittatus (da Costa 1778)
Scrobicularia plana (da Costa 1778)
Abra alba (Wood 1802)
Abra nitida (Müller 1776)
Abra prismatica (Montagu 1803)
Chamelea striatula (da Costa 1778)
Clausinella fasciata (da Costa 1778)
Paphia aurea (Gmelin 1791)
Tapes decussatus (Linnaeus 1758)
Timoclea ovata (Pennant 1777)
Venerupis rhomboides (Pennant 1777)
Venerupis pullastra (Montagu 1803)
Mysia undata (Pennant 1777)
 Order Myoida
Corbula gibba (Olivi 1792)
Saxicavella jeffreysi Winckworth 1930
Barnea candida (Linnaeus 1758)
Pholas dactylus Linnaeus 1758
 Subclass Anomalodesmata
 Order Pholadomyoida
Thracia phaseolina (Lamarck 1818)
 Total for climatic regions ..bl: 107 (72.8%)

 Climatic regions: ...l
 Class Gastropoda
 Subclass Prosobranchia
 Order Archaeogastropoda
Skenea serpuloides (Montagu 1808)
 Order Neotaenioglossa
Alvania lactea (Michaud 1830)
Onoba proxima (Forbes & Hanley 1850)
 Class Bivalvia
 Subclass Pteriomorpha
 Order Pterioidea
Anomia ephippium Linnaeus 1758
 Total for climatic regions ...l: 4 (2.7%)

The Holocene Limfjord: 147 (59.5%)

The mollusc species in the Limfjord region amount to 147, and within this relatively high number only four purely Lusitanian species are found. *Skenea serpuloides* is known from recent waters in the British Isles and southward, *Alvania lactea* and *Onoba proxima* from the western coast of Britain and to the south, and *Anomia ephippium* also from the British Isles, although including the Orkney Islands and south to the Mediterranean. According to Jensen & Spärck (1934), *Anomia ephippium* has often not been separated from *Heteranomia squamula*.

On the occurrences of *Anomia ephippium* and the three Lusitanian gastropods, which are all tiny and difficult species to work with in the subfossil state, the question may then arise whether much reliance should be put in these circumstances indicating that the subfossil Holocene fauna of the Limfjord region had a more Lusitanian affinity than is the case at present.

The next climatic group is the Boreo-Lusitanian, which is by far the largest, with 107 species, 72.8% of all the species recorded from this region. In the Limfjord region it is possible to distinguish between the recent fauna that arrived after the breakthrough at the Agger Tange in 1825, when the Limfjord again was established as a saltwater basin, and the older long stage before the Middle Ages and back to the transgression in the early Holocene.

The faunal record of the recent mollusc species from the Limfjord is an illustration of how fast a population can be established, although not studied from the very beginning (Spärck 1943, p. 78). The 85 species established there during the period of about 100 years picture recent immigration (Petersen 1986a, p. 223).

Already the early studies by Collin (1884) and Petersen (1888) demonstrated that within the subfossil Holocene fauna there was a certain number of mollusc species no longer known from the present fauna in the Limfjord or within the Danish waters at all. These deposits were called the *Tapes* beds by Petersen (1888, p. 56).

The *Tapes* species *sensu* Petersen (1888) include: *Paphia aurea*, *Tapes decussatus*, and *Venerupis rhomboides*, the last one has lately been recorded as part of the recent Danish fauna (Jensen & Knudsen 1995).

The way to have a firmer basis for discriminating between the recent and the Holocene fauna in the Limfjord region would be to split the Boreal climatic region into the three zones: The High-Boreal, the Mid-Boreal and the Low-Boreal following the indications on distribution given in the chapter on the molluscan species, following Feyling-Hanssen (1955) in Fig. 4.

In this way it turns out that the recent Boreo-Lusitanian group, with a number of 51, has 45% reaching to the north into the High-Boreal, 47% the Mid-Boreal, and 9% the Low-Boreal zone. While the subfossil Boreo-Lusitanian group of 107 species shows 41% reaching into the High-Boreal, 45% the Mid-Boreal, and 14% the Low-Boreal zone. There is, so to say, only a slightly higher affinity to more temperate southern waters for the subfossil molluscan fauna, meaning that a hypsothermal period is not clearly demonstrated in the ma-

rine environment from the Limfjord.

In the case of the Limfjord region, it should be emphasised that we do have a special situation in connection with the living depths of certain species. Taking into consideration again the largest group of molluscs recorded from the Holocene Limfjord deposits – the Boreo-Lusitanian group – 12 species have their main occurrence below the tidal zone, and 26 species out of the 107 species encountered occur at a deeper level. When this is seen from the fact that the collection of molluscs during the geological mapping has been done mostly in outcrops, and that the highest marine limit goes up to only about 5 m a.s.l. in this area (Mertz 1924), the palaeodepth reached cannot be as deep as figured on the basis of the general depth range of the recent molluscs in Danish waters. This was a point stressed by Nordmann (Jessen 1905, pp. 151–152) and clearly indicates a smaller living depth, found for the molluscs from the Limfjord region than from other regions in Denmark during the Holocene.

Such a difference in the habitat can still be observed on the beaches of the Limfjord, where *inter alia* the deeper-living mytilid *Modiolus modiolus* is found washed ashore quite commonly in quantities not seen elsewhere along the shores of Denmark.

The remaining climatic groups are the ones with a distribution extending into the Arctic or the Subarctic, some with a wide range reaching the Lusitanian or the Boreal zones to the south.

Here it should be pointed out that all of the species with their southern limit in the Boreal zone have been recorded also from the Low-Boreal sector, although *Tridonta borealis* is said to be rare in the North Sea, but is common in the Bælt Sea and Baltic regions.

From this it can be concluded that all the species recorded from the Holocene/recent Limfjord region could have coexisted in various habitats – except for the three purely Lusitanian species.

Several ¹⁴C dates from the Limfjord region on molluscs from the Holocene reveal the immigration time of a few species (Petersen & Rasmussen 1995a, table 1), although the actual number of dated shells of certain species are low. From the Atlantic: *Mytilus edulis*, *Cerastoderma edule*, *Ostrea edulis*, *Arctica islandica*, *Spisula subtruncata*, *Corbula gibba*, *Scrobicularia plana*, *Acanthocardia echinata*, and *Venerupis pullastra*. From the Subboreal: *Lucinoma borealis*, *Tapes decussatus*, and *Paphia aurea*. From the Subatlantic: *Donax vittatus*.

This is a function of the same species being used in many more datings, because specimens of these spe-

cies have been present in a sufficient number or weight to allow a conventional ¹⁴C dating of the whole assemblage or bed of molluscs. Therefore, also the other species present in the samples or stratum shall be considered dated, just as dating of certain levels in borings are taken into account (Petersen 1976, 1981, 1985b, 1986c; Rasmussen & Petersen 1980).

In this way a far higher number of first occurrence of species can be demonstrated, still on the basis of absolute dates, as presented in Appendix 6.

For as many as 114 species out of the total number of recorded species (147) from the Holocene mollusc faunas in the Limfjord area first occurrence has been dated: 77 species dated to the Atlantic, 36 species to the Subboreal and one species to the Subatlantic.

In the Atlantic and the Subboreal the dominating climatic groups are the Boreal–Lusitanian species with 55 and 28 species, forming 71.4% and 77.8% respectively.

Two of the purely Lusitanian species which have been dated, *Alvania lactea* and *Onoba proxima*, appeared in the Subboreal.

The total number of species recorded from the Limfjord (147) constitutes 59.5% of the subfossil Late Quaternary molluscs, which is much higher than seen in the inner Danish waters.

The North Sea

Climatic regions: asb.

Class Gastropoda

Subclass Opisthobranchia

Order Anaspidea

Retusa obtusa (Montagu 1803)

Total for climatic regions asb. : 1 (1.1%)

Climatic regions: asbl

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Littorina saxatilis (Olivi 1792)

Lacuna pallidula (da Costa 1778)

Subclass Opisthobranchia

Order Bullomorpha

Cylichna alba (Brown 1827)

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Nuculoma tenuis (Montagu 1808)

Subclass Pteriomorpha

Order Mytiloida
Musculus discors (Linnaeus 1767)
Subclass Heterodonta
Order Veneroida
Thyasira flexuosa (Montagu 1803)
Order Myoida
Mya truncata Linnaeus 1758
Hiatella arctica (Linnaeus 1758)
Total for climatic regions asbl: 8 (8.4%)

Climatic regions: .sb.
Class Bivalvia
Subclass Heterodonta
Order Veneroida
Arctica islandica (Linnaeus 1767)
Order Myoida
Zirfaea crispata (Linnaeus 1758)
Total for climatic regions .sb. : 2 (2.1%)

Climatic regions: .sbl
Class Gastropoda
Subclass Prosobranchia
Order Neotaenioglossa
Littorina obtusata (Linnaeus 1758)
Lacuna vincta (Montagu 1803)
Order Neogastropoda
Nucella lapillus (Linnaeus 1758)
Buccinum undatum Linnaeus 1758
Class Bivalvia
Subclass Pteriomorpha
Order Mytiloida
Mytilus edulis Linnaeus 1758
Order Pterioidea
Heteranomia squamula (Linnaeus 1758)
Subclass Heterodonta
Order Veneroida
Mysella bidentata (Montagu 1803)
Tellimya ferruginosa (Montagu 1803)
Parvicardium ovale (Sowerby 1840)
Spisula elliptica (Brown 1827)
Macoma balthica (Linnaeus 1758)
Total for climatic regions .sbl: 11 (11.6%)

Climatic regions: ..b.
Class Gastropoda
Subclass Prosobranchia
Order Neotaenioglossa
Cingula turgida (Jeffreys 1870)
Total for climatic regions ..b. : 1 (1.1%)
Climatic regions: ..bl
Class Gastropoda

Subclass Prosobranchia
Order Archaeogastropoda
Gibbula cineraria (Linnaeus 1758)
Theodoxus fluviatilis (Linnaeus 1758)
Order Neotaenioglossa
Littorina littorea (Linnaeus 1758)
Lacuna parva (Montagu 1803)
Hydrobia ulvae (Pennant 1777)
Hydrobia ventrosa (Montagu 1803)
Onoba vitrea (Montagu 1803)
Rissoa albella Lovén 1846
Rissoa inconspicua Alder 1844
Rissoa membranacea (J. Adams 1800)
Rissoa violacea Desmarest 1814
Caecum glabrum (Montagu 1803)
Bittium reticulatum (da Costa 1778)
Turritella communis Risso 1826
Aporrhais pespelicani (Linnaeus 1758)
Lunatia alderi (Forbes 1838)
Lunatia catena (da Costa 1778)
Order Heterogastropoda
Tripbora adversa (Montagu 1803)
Epitonium clathrus (Linnaeus 1758)
Aclis ascaris (Turton 1819)
Aclis minor (Brown 1827)
Aclis walleri Jeffreys 1867
Order Neogastropoda
Hinia pygmaea (Lamarck 1822)
Hinia reticulata (Linnaeus 1758)
Subclass Heterobranchia
Order Heterostropha
Brachystomia eulimoides Hanley 1844
Chrysallida indistincta (Montagu 1808)
Chrysallida spiralis (Montagu 1803)
Eulimella laevis (Brown 1827)
Ondina diaphana (Jeffreys 1848)
Odostomia conoidea Winckworth 1932
Odostomia albella Lovén 1846
Turbonilla crenata (Brown 1827)
Turbonilla delicata (Monterosato 1874)
Turbonilla lactea (Linné 1758)
Subclass Opisthobranchia
Order Bullomorpha
Acteon tornatilis (Linnaeus 1758)
Order Anaspidea
Retusa truncatula (Bruguière 1792)
Retusa umbilicata (Montagu 1803)
Class Bivalvia
Subclass Palaeotaxodonta
Order Nuculoida
Nucula nitidosa Winckworth 1930

Nucula nucleus (Linnaeus 1767)
Nucula sulcata (Bronn 1831)
 Subclass Pteriomorpha
 Order Pterioida
 Chlamys varia (Linnaeus 1758)
 Ostrea edulis Linnaeus 1758
 Subclass Heterodonta
 Order Veneroidea
 Lepton nitidum (Turton 1822)
 Acanthocardia echinata (Linnaeus 1758)
 Parvicardium exiguum (Gmelin 1791)
 Parvicardium scabrum (Philippi 1844)
 Parvicardium minimum (Philippi 1836)
 Cerastoderma edule (Linnaeus 1758)
 Mactra stultorum (Linnaeus 1758)
 Spisula solida (Linnaeus 1758)
 Spisula subtruncata (da Costa 1778)
 Ensis ensis (Linnaeus 1758)
 Phaxas pellucidus (Pennant 1777)
 Angulus tenuis (da Costa 1778)
 Fabulina fabula (Gmelin 1791)
 Donax vittatus (da Costa 1778)
 Scrobicularia plana (da Costa 1778)
 Abra alba (Wood 1802)
 Abra nitida (Müller 1776)
 Chamelea striatula (da Costa 1778)
 Clausinella fasciata (da Costa 1778)
 Paphia aurea (Gmelin 1791)
 Tapes decussatus (Linnaeus 1758)
 Timoclea ovata (Pennant 1777)
 Venerupis pullastra (Montagu 1803)
 Dosinia exoleta (Linnaeus 1758)
 Dosinia lincta (Montagu 1803)
 Order Myoidea
 Corbula gibba (Olivi 1792)
 Saxicavella jeffreysi Winckworth 1930
 Barnea candida (Linnaeus 1758)
 Subclass Anomalodesmata
 Order Pholadomyoidea
 Cochlodesma praetenue (Pulteney 1799)
 Thracia phaseolina (Lamarck 1818)
 Total for climatic regions .:bl: 72 (75.8%)

The Holocene North Sea: 95 (38.5%)

From the North Sea region, 95 species have been recorded, and here no purely Lusitanian mollusc species has been found. Almost all the North Sea finds are recorded also from the Limfjord.

The Boreo-Lusitanian group in the North Sea region is also, compared to the Limfjord, by far the largest

group, with 72 species.

In this group, only five species can be pointed out as not occurring in the Holocene of the Limfjord, viz.: *Parvicardium minimum*, *Clausinella fasciata*, *Dosinia exoleta*, *Dosinia lincta*, and *Cochlodesma praetenue*. Furthermore, *Donax vittatus*, as remarked earlier in the chapter on the mollusc species, this species does not belong to the Limfjord proper, but is recorded from old (Subatlantic) beach ridges once facing the Skagerrak. Today, this bivalve is bound to the exposed coast of Denmark, not penetrating into the inner Danish waters. The dated occurrences of this species in the North Sea area fall in the Subatlantic, when the present coastline of Jylland was developed (Petersen 1994a).

Donax vittatus has a distribution to the north up into the Mid-Boreal sector between Trondheim Fjord and Lofoten. The other Boreo-Lusitanian species in the North Sea region which are not in the Limfjord go as far north as the High-Boreal sector north of Lofoten. It is seen that the species not found in the Limfjord but in the Holocene North Sea are to be regarded not as newcomers showing any amelioration, but more probably as representing other conditions prevailing in the North Sea area than in the Limfjord, as seen in the case of *Donax vittatus*.

Parvicardium minimum is common only at depths of more than 30 m. *Clausinella fasciata* is far from common in the inner Danish waters and, when occurring, is so only at depths of between 15 and 30 m.

Dosinia exoleta and *Dosinia lincta* can be found from the intertidal zone and out to depths of 70 and 200 m respectively; these species have been recorded from the northern Kattegat, although the latter extends into the Øresund (Jensen & Knudsen 1995).

The great similarity and the few differences found when the Holocene North Sea fauna is compared with the Limfjord record are explained in the recent study on the Agger Tange complex (Petersen 1994a, 1998). This study, being based on material from several vibrocores west of the Agger Tange complex, revealed that the Jydske Rev forms a continuation of the Limfjord complex 75 km further towards the west.

AMS dates of molluscs from this part of the North Sea and the oldest cored sections in the Agger Tange complex show that the marine record can be established from the Preboreal and up into the Subatlantic (Petersen 1985a).

The fauna dated from the older part of the Holocene is very similar to the Limfjord fauna and the younger fauna, containing only a few differences to

Table 1. Boreo-Lusitanian group

Time interval	Species	%
The Preboreal-Boreal	20	76.9
The Atlantic	23	85.2
The Subboreal	12	63.2
The Subatlantic	5	62.5

the Limfjord fauna, as indicated by the *Dosinia* species.

During the older stages of the Holocene, the Jydske Rev complex formed a landscape much the same as that of the present Limfjord, while in the younger part of the Holocene erosion has taken place and the present coastline of western Jylland developed.

The appearance of such molluscs as the *Dosinia* and *Donax* species must be connected with the new facies in the exposed coastal areas rather than indicating climatic changes.

The well-dated molluscs from the vibrocores in the North Sea and borings in the Agger Tange complex allow the fixing of a first appearance of most of the 95 species recorded from the North Sea region as seen in Appendix 6 (Petersen 1985a, 1994a).

The total number of recorded species from the Holocene North Sea is 95, forming 38.5% of the subfossil molluscs from the Late Quaternary, which is less than recorded from the Limfjord, but out of this number 80 species have been dated with their first appearance. What is of special interest from this area is that the record also covers 26 dated species from the Preboreal-Boreal and furthermore 27 species from the Atlantic, 19 species from the Subboreal and eight species from the Subatlantic.

In all time intervals, the Boreo-Lusitanian group is by far the dominating part as shown in Table 1.

As the Boreo-Lusitanian group in the North Sea constitutes the most temperate species, the Atlantic can be pointed out as having a slightly higher proportion of

Table 2. The climatic trend for the Holocene

Climatic regions	Holocene subfossil spp.	Recent spp.
asb.	5 (0.7%)	5 (5.4%)
asbl	11 (6.0%)	9 (9.6%)
.sb.	3 (1.6%)	0
.sbl	19 (10.4%)	7 (7.4%)
.b.	3 (1.6%)	7 (7.4%)
.bl	136 (74.3%)	64 (68.1%)
...l	6 (3.3%)	2 (2.1%)

warmer mollusc faunal element than the other periods.

In order to find the climatic trend for the Holocene, the climatic affinity of the recent species not found in the subfossil deposits is compared with that of the subfossil Holocene species (Table 2).

When the affinities to the climatic regions for the 183 Holocene subfossil species are compared with those of the 94 recent species that do not occur in the Holocene subfossil fauna, a slightly higher affinity to the more temperate regions for the subfossil species appears.

From the North Sea material it was concluded that the Atlantic has a slightly higher proportion of warmer elements than the other periods. So within the Danish realm the indication of amelioration, as seen from the molluscan material, points to the Atlantic.

Vendsyssel

Climatic regions: asb.

Class Gastropoda

Subclass Prosobranchia

Order Neogastropoda

Oenopota turricola (Montagu 1803)

Subclass Opisthobranchia

Order Anaspidea

Retusa obtusa (Montagu 1803)

Class Bivalvia

Subclass Heterodonta

Order Veneroida

Macoma calcarea (Gmelin 1791)

Total for climatic regions asb. : 3 (2.3%)

Climatic regions: asbl

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Littorina saxatilis (Olivi 1792)

Lacuna pallidula (da Costa 1778)

Subclass Opisthobranchia

Order Anaspidea

Diaphana minuta Brown 1827

Class Bivalvia

Subclass Pteriomorpha

Order Mytiloida

Musculus discors (Linnaeus 1767)

Subclass Heterodonta

Order Veneroida

Thyasira flexuosa (Montagu 1803)

Order Myoida
Mya truncata Linnaeus 1758
Hiatella arctica (Linnaeus 1758)
Hiatella rugosa (Linnaeus 1758)
Total for climatic regions asbl: 8 (6.0%)

Climatic regions: .sb.
Class Bivalvia
Subclass Heterodonta
Order Veneroida
Arctica islandica (Linnaeus 1767)
Order Myoida
Zirfaea crispata (Linnaeus 1758)
Total for climatic regions .sb. : 2 (1.5%)

Climatic regions: .sbl
Class Gastropoda
Subclass Prosobranchia
Order Archaeogastropoda
Acmaea virginea (Müller 1776)
Order Neotaenioglossa
Littorina obtusata (Linnaeus 1758)
Lacuna vincta (Montagu 1803)
Skeneopsis planorbis (Fabricius 1780)
Onoba semicostata (Montagu 1803)
Order Neogastropoda
Nucella lapillus (Linnaeus 1758)
Buccinum undatum Linnaeus 1758
Subclass Heterobranchia
Order Heterostropha
Omalogyra atomus (Phillippi 1841)
Class Bivalvia
Subclass Pteriomorpha
Order Mytiloida
Mytilus edulis Linnaeus 1758
Modiolus modiolus (Linnaeus 1758)
Order Pterioidea
Heteranomia squamula (Linnaeus 1758)
Subclass Heterodonta
Order Veneroida
Mysella bidentata (Montagu 1803)
Tellimya ferruginosa (Montagu 1803)
Turtonia minuta (Fabricius 1780)
Parvicardium ovale (Sowerby 1840)
Spisula elliptica (Brown 1827)
Macoma balthica (Linnaeus 1758)
Gari fervensis (Gmelin 1791)
Total for climatic regions .sbl: 18 (13.5%)
Climatic regions: .b.
Class Bivalvia
Subclass Heterodonta

Order Myoida
Mya arenaria Linnaeus 1758
Total for climatic regions .b. : 1 (0.8%)

Climatic regions: .b1
Class Gastropoda
Subclass Prosobranchia
Order Archaeogastropoda
Helcion pellucidum (Linnaeus 1758)
Gibbula cineraria (Linnaeus 1758)
Gibbula tumida (Montagu 1803)
Order Neotaenioglossa
Littorina littorea (Linnaeus 1758)
Littorina tenebrosa (Montagu 1803)
Lacuna parva (Montagu 1803)
Hydrobia ulvae (Pennant 1777)
Alvania cimicoides (Forbes 1844)
Alvania punctura (Montagu 1803)
Cingula semistriata (Montagu 1808)
Onoba vitrea (Montagu 1803)
Rissoa albella Lovén 1846
Rissoa inconspicua Alder 1844
Rissoa membranacea (J. Adams 1800)
Rissoa parva (da Costa 1779)
Rissoa violacea Desmarest 1814
Caecum glabrum (Montagu 1803)
Bittium reticulatum (da Costa 1778)
Turritella communis Risso 1826
Aporrhais pespelicani (Linnaeus 1758)
Lunatia alderi (Forbes 1838)
Lunatia catena (da Costa 1778)
Order Heterogastropoda
Triphora adversa (Montagu 1803)
Epitonium clathrus (Linnaeus 1758)
Epitonium turtonis (Turton 1819)
Vitreolina philippii (Rayneval & Ponzi 1854)
Order Neogastropoda
Neptunea antiqua (Linnaeus 1758)
Hinia incrassata (Ström 1768)
Hinia pygmaea (Lamarck 1822)
Hinia reticulata (Linnaeus 1758)
Cytherea coarctata (Forbes 1840)
Raphitoma linearis (Montagu 1803)
Subclass Heterobranchia
Order Heterostropha
Brachystomia eulimoides Hanley 1844
Odostomia scalaris MacGillivray 1843
Chrysallida indistincta (Montagu 1808)
Chrysallida obtusa (Brown 1827)
Chrysallida spiralis (Montagu 1803)
Ebala nitidissima (Montagu 1803)

Eulimella laevis (Brown 1827)
Odostomia conoidea Winckworth 1932
Odostomia turrata Hanley 1844
Odostomia albella Lovén 1846
Odostomia plicata (Montagu 1803)
Turbonilla lactea (Linné 1758)
 Subclass Opisthobranchia
 Order Bullomorpha
Acteon tornatilis (Linnaeus 1758)
Cylicbna cylindracea (Pennant 1777)
Philine aperta (Linnaeus 1767)
Philine punctata (Adams 1800)
 Order Anaspidea
Retusa truncatula (Bruguière 1792)
Retusa umbilicata (Montagu 1803)
Akera bullata Müller 1776
 Class Bivalvia
 Subclass Palaeotaxodonta
 Order Nuculoida
Nucula nitidosa Winckworth 1930
Nucula nucleus (Linnaeus 1767)
 Subclass Pteriomorpha
 Order Mytiloida
Modiolula phaseolina (Philippi 1844)
Modiolus adriaticus (Lamarck 1819)
Modiolaria tumida (Hanley 1843)
 Order Pterioda
Aequipecten opercularis (Linnaeus 1758)
Chlamys varia (Linnaeus 1758)
Pecten maximus (Linnaeus 1758)
Pododesmus patelliformis (Linnaeus 1761)
Ostrea edulis Linnaeus 1758
 Subclass Heterodonta
 Order Veneroida
Lucinoma borealis (Linnaeus 1758)
Lepton nitidum (Turton 1822)
Kellia suborbicularis (Montagu 1803)
Acanthocardia echinata (Linnaeus 1758)
Parvicardium exiguum (Gmelin 1791)
Parvicardium scabrum (Philippi 1844)
Cerastoderma edule (Linnaeus 1758)
Laevicardium crassum (Gmelin 1791)
Macra stultorum (Linnaeus 1758)
Lutraria lutraria (Linnaeus 1758)
Spisula solida (Linnaeus 1758)
Spisula subtruncata (da Costa 1778)
Ensis ensis (Linnaeus 1758)
Phaxas pellucidus (Pennant 1777)
Angulus tenuis (da Costa 1778)
Fabulina fabula (Gmelin 1791)
Donax vittatus (da Costa 1778)

Gari depressa (Pennant 1777)
Scrobicularia plana (da Costa 1778)
Abra alba (Wood 1802)
Abra nitida (Müller 1776)
Abra prismatica (Montagu 1803)
Chamelea striatula (da Costa 1778)
Clausinella fasciata (da Costa 1778)
Paphia aurea (Gmelin 1791)
Tapes decussatus (Linnaeus 1758)
Timoclea ovata (Pennant 1777)
Venerupis rhomboides (Pennant 1777)
Venerupis pullastra (Montagu 1803)
Dosinia exoleta (Linnaeus 1758)
Dosinia lincta (Montagu 1803)
Mysia undata (Pennant 1777)
 Order Myoida
Corbula gibba (Olivi 1792)
Saxicavella jeffreysi Winckworth 1930
Barnea candida (Linnaeus 1758)
Pholas dactylus Linnaeus 1758
 Subclass Anomalodesmata
 Order Pholadomyoida
Thracia phaseolina (Lamarck 1818)
 Total for climatic regions ..bl: 98 (73.7%)
 Climatic regions: ...l
 Class Gastropoda
 Subclass Prosobranchia
 Order Neotaenioglossa
Alvania lactea (Michaud 1830)
Trivia monacha (da Costa 1778)
 Class Bivalvia
 Subclass Pteriomorpha
 Order Pterioda
Anomia ephippium Linnaeus 1758
 Total for climatic regions ...l: 3 (2.3%)

The Holocene Vendsysse: 133 (53.8%)

In the Vendsysse region the mollusc species amount to 133, nearly the same as recorded from the Limfjord region (147). However, some other species occur, although the grouping of species according to the climatic regions to which they belong is almost the same.

This is a very important fact considering the large number of species recorded from both regions and according to the conclusions drawn from the Limfjord material when compared to the recent fauna in the Limfjord, with only a slight difference between the climatic affinities of the subfossil and the recent mol-

lucos, including the recent species which have invaded the Limfjord since 1825, but not recorded in the subfossil material.

The Vendsyssel fauna counts three purely Lusitanian elements, but they are far from common, and *Alvania lactea* and *Trivia monacha* are not typical for the former Vendsyssel palaeoenvironment.

Within the Boreo-Lusitanian group, only ten molluscs are new in the fauna compared to the Holocene of the Limfjord: *Alvania cimicoides*, *Neptunea antiqua*, *Cythereella coarctata*, *Pecten maximus*, *Kellia suborbicularis*, *Laevicardium crassum*, *Gari depressa*, *Clausinella fasciata*, *Dosinia exoleta*, and *Dosinia lincta*.

Nordmann (1904) states that the mollusc fauna recorded from the sites north of Frederikshavn have a distinct Lusitanian affinity. However, as seen above, only ten species are new to the Vendsyssel region compared to the Limfjord, and here four species reach into the High-Boreal sector (north of Lofoten), five species into the Mid-Boreal (between Lofoten and Trondheim), and only one, *Neptunea antiqua*, has its northern limit within the Low-Boreal sector (south of Trondheim and to the Channel). Therefore, the designation of the *Dosinia* fauna cannot be one of the special southern appearances. However, Nordmann also states that the same species in the *Dosinia* fauna are new compared to the *Tapes* fauna. This is true only for four species, viz. *Laevicardium crassum*, *Neptunea antiqua*, *Trivia monacha*, and *Kellia suborbicularis*, while *Venerupis rhomboides*, *Lutraria lutraria*, *Gari fervensis* and *Hinia incrustata* also occur to the south of Frederikshavn and in the Limfjord region. Furthermore, the characterising species of these beds – *Dosinia exoleta* – is now also recorded from the Subatlantic beds at a depth of 32.5 m in the North Sea, occurring together with, among others, *Dosinia lincta*.

Nordmann (1904, pp. 30–31) also argued for the *Dosinia* fauna to be a shallow-water assemblage and discussed in greater detail *Dosinia exoleta*, *Venerupis rhomboides*, *Lutraria lutraria*, *Laevicardium crassum*, *Lucinoma borealis*, *Arctica islandica*, and *Neptunea antiqua*. From the general information at hand on depth relations of these species (chapter on molluscan species), it appears that all except *Neptunea antiqua* can be found from the intertidal zone and out to various depths in deeper water, while *Neptunea antiqua* has a minimum depth of 15 m.

Taking into account all the recorded molluscan finds from the Vendsyssel region, it appears that 84 species (63%) can be found in the tidal-intertidal zone and 48 species (36%) in water deeper than that. Therefore it

cannot be characteristic of the *Dosinia* fauna that it is a shallow-water assemblage.

The new dates which have been used in the discussion of the *Dosinia* fauna date its appearance by the oldest date for the *Dosinia exoleta*, at 4240 B.P. (K-5318; in Petersen 1991b).

Skagen

Climatic regions: asb.

Class Gastropoda

Subclass Prosobranchia

Order Neogastropoda

Oenopota turricola (Montagu 1803)

Total for climatic regions asb. : 1 (1.4%)

Climatic regions: asbl

Class Gastropoda

Subclass Prosobranchia

Order Neotaenioglossa

Lacuna pallidula (da Costa 1778)

Subclass Opisthobranchia

Order Bullomorpha

Cylichna alba (Brown 1827)

Class Bivalvia

Subclass Pteriomorpha

Order Mytiloida

Musculus discors (Linnaeus 1767)

Subclass Heterodonta

Order Veneroida

Thyasira flexuosa (Montagu 1803)

Order Myoida

Hiatella arctica (Linnaeus 1758)

Total for climatic regions asbl: 5 (7.0%)

Climatic regions: .sb.

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Nuculana minuta (Müller 1776)

Subclass Heterodonta

Order Veneroida

Arctica islandica (Linnaeus 1767)

Total for climatic regions .sb. : 2 (2.8%)

Climatic regions: .sbl

Class Gastropoda

Subclass Prosobranchia

Order Neogastropoda

Buccinum undatum Linnaeus 1758

Class Bivalvia
 Subclass Pteriomorpha
 Order Mytiloida
Mytilus edulis Linnaeus 1758
 Order Pterioidea
Heteranomia squamula (Linnaeus 1758)
 Subclass Heterodonta
 Order Veneroidea
Mysella bidentata (Montagu 1803)
Tellimya ferruginosa (Montagu 1803)
Turtonia minuta (Fabricius 1780)
Gari fervensis (Gmelin 1791)
 Total for climatic regions .sbl: 7 (9.9%)

Climatic regions: ..b.

Class Bivalvia
 Subclass Heterodonta
 Order Myoidea
Mya arenaria Linnaeus 1758
 Total for climatic regions ..b. : 1 (1.4%)

Climatic regions: ..bl

Class Gastropoda
 Subclass Prosobranchia
 Order Neotaenioglossa
Hydrobia ulvae (Pennant 1777)
Barleeia unifasciata (Montagu 1803)
Onoba vitrea (Montagu 1803)
Rissoa albella Lovén 1846
Rissoa violacea Desmarest 1814
Bittium reticulatum (da Costa 1778)
Turritella communis Risso 1826
Aporrhais pespelicani (Linnaeus 1758)
Lunatia alderi (Forbes 1838)
Lunatia montagui (Forbes 1838)
 Order Heterogastropoda
Epitonium trevelyanum (Johnston 1841)
Aclis minor (Brown 1827)
Polygireulima sinuosa (Sacco 1836)
Vitreolina philippii (Rayneval & Ponzi 1854)
Graphis albida (Kanmacher 1798)
Melanella lubrica (Monterosato 1891)
Melanella alba (da Costa 1778)
Hemiaclis ventrosa (Jeffreys MS Fricle 1874)
 Order Neogastropoda
Hinia pygmaea (Lamarck 1822)
Hinia reticulata (Linnaeus 1758)
Mangelia brachystoma (Philippi 1844)
 Subclass Heterobranchia
 Order Heterostropha
Chrysallida decussata (Montagu 1803)

Eulimella scillae (Scacchi 1835)
Odostomia conoidea Winckworth 1932
Odostomia umbilicaris (Malm 1863)
Turbonilla delicata (Monterosato 1874)
Turbonilla sinuosa (Jeffreys 1884)

Subclass Opisthobranchia
 Order Anaspidea
Retusa truncatula (Bruguière 1792)
Retusa umbilicata (Montagu 1803)

Class Bivalvia
 Subclass Palaeotaxodonta
 Order Nuculoida
Nucula nitidosa Winckworth 1930
Nucula nucleus (Linnaeus 1767)

Subclass Pteriomorpha
 Order Pterioidea
Chlamys varia (Linnaeus 1758)
Ostrea edulis Linnaeus 1758

Subclass Heterodonta
 Order Veneroidea
Acanthocardia echinata (Linnaeus 1758)
Parvicardium minimum (Philippi 1836)
Macra stultorum (Linnaeus 1758)
Spisula subtruncata (da Costa 1778)
Phaxas pellucidus (Pennant 1777)
Angulus tenuis (da Costa 1778)
Fabulina fabula (Gmelin 1791)
Tellina pygmaea (Lovén 1846)
Donax vittatus (da Costa 1778)
Abra alba (Wood 1802)
Abra nitida (Müller 1776)
Abra prismatica (Montagu 1803)
Chamelea striatula (da Costa 1778)
Timoclea ovata (Pennant 1777)

Order Myoidea
Corbula gibba (Olivi 1792)
Saxicavella jeffreysi Winckworth 1930
Barnea candida (Linnaeus 1758)
Pholas dactylus Linnaeus 1758

Subclass Anomalodesmata
 Order Pholadomyoidea
Lyonsia norvegica (Gmelin 1791)
Cochlodesma praetenu (Pulteney 1799)
Thracia phaseolina (Lamarck 1818)

Total for climatic regions ..bl: 54 (76.1%)

Climatic regions: ...l

Class Gastropoda
 Subclass Prosobranchia
 Order Heterogastropoda
Vitreolina collensi (Sykes 1903)

Total for climatic regions ...: 1 (1.4%)

The Holocene Skagen: 71 (28.7%)

From the Skagen boring, 71 Holocene species have been recorded.

The Boreo-Lusitanian group dominates with 54 species (76.1%) of the Holocene mollusc species from the Skagen Well.

One purely Lusitanian species, *Vitreolina collensi*, has been found, while all the other species occur in the Boreal and to some extent the Arctic. In this way the Skagen Well material resembles that of other regions like the Vendsyssel, Limfjord and North Sea during the Holocene.

The Skagen Well material has all been recorded to certain stratigraphical levels, as seen in Appendix 6, so the climatic indications through time appear, but the number of molluscan species is very low. In the Pre-

boreal/Boreal, only three species have been recorded. This has been explained as a result of a deeper water where the echinoids dominate.

Higher up in the sequence, the number of molluscs increases – 23 species in the Subboreal and 68 species in the Subatlantic.

Through the chronostratigraphical levels, the climatic regions of the Boreo-Lusitanian from the dominating one, and the purely Lusitanian *Vitreolina collensi* as mentioned above occurs in the Subboreal and Subatlantic. However, as already stated, the development of the facies in the Skagen Well during the Holocene does change the environment from the deeper-water facies with few molluscs through the bottom community with *Turritella communis* into the prolific shallow-water community. In this way the youngest part covering the Subboreal–Subatlantic is also by far the part with the highest species diversity.

The environmental changes within the seven regions through the Late Quaternary evaluated by the molluscan communities met with in the seven stages

The seven chronological stages which have been described according to their climatic affinities are seen in Fig. 102 and Fig. 103 covering the Eemian, the Early/Middle Weichselian, the Late Weichselian, the Preboreal/Boreal, the Atlantic, the Subboreal, and the Subatlantic.

In this way the climatic cycle during the Late Quaternary is demonstrated on the basis of marine mollusc species which indicate that the Eemian has by far the highest amount of the more temperate species, while the Holocene reached its maximum during the Atlantic, although only slightly more than the other stages within the Holocene, as already commented upon in the previous chapter.

It is generally accepted that the Eemian summer temperatures were higher – about 2°C above the present. With glaciers smaller than the present day, this means that the sea level was 4–6 m higher than today (Andersen & Borns 1994, pp. 44–49). And as pointed out by Donner (1995, p. 39): “the submergence was clearly greater after the Saalian glaciation than after the Weichselian and possibly after the older glaciations”.

Donner sees this in northern Europe as “a result of a comparatively great downwarping of the earth’s crust during the extensive Saalian glaciation”. The rebound since the last glaciation has come to an end within the Danish area (Petersen 1985c, 1991b). This means that the Eemian deposits, when found in Denmark in non-glacio-dislocated state, can be regarded as being in the original position related to sea level, although there might be some movements in relation to neo-tectonic activities, as mentioned earlier. In the light of the observations mentioned above, the seven regions will be discussed according to the environmental characteristics such as the climatic affinities for the molluscs recorded in Appendix 6 for each region, as appearing in Fig. 103. However, for the Holocene still as many as 130 species including the recent ones (95) not found as subfossil have not been dated to give their first appearance, see Fig. 102: Unknown arrival in Holocene. At the end of each of the seven stages the molluscan communities *sensu* C.G.J. Petersen will be presented in Tables 3–9.

Eemian stage 130 000 – 115 000 B.P.

The Bælt Sea, region 1

Appendix 6 and Fig. 103

Already Forchhammer (1842, p. 64) designated *Cyprina (Arctica) islandica* to be the characteristic bivalve of the Bælt Sea Eemian, as known to the present-day geologists. Furthermore, Forchhammer points out that the characteristic bivalve, *Cyprina islandica*, occurs every where in large quantities, but always in crust specimens. However, all the shell fragments occurring together show that the specimen has been broken after deposition in the clay, most probably by the cataclysms which have given the beds their tilt.

Johnstrup (1882a, p. 55) points to the indications of the molluscs as being a deposition of a shallow-water sea and also mentioned the *Mytilus* beds.

Johnstrup points out (1882a, p. 56) that the dislocated floes – as already noticed by Forchhammer – have the original succession within each floe, saying that the *Cyprina* clay and the *Mytilus* beds have not been disconnected during the dislocations.

Later investigations by Nordmann (Harder 1900; Nordmann 1908, 1913) demonstrated that the *Venus aurea* as observed by Johnstrup (1882a, p. 66) could be regarded in parts as the no longer living *Tapes aureus* Gm. var. *eemiensis* Nordmann or *Tapes senescens* Doederlein; in this book *Paphia aurea senescens*. The *Tapes* species do represent shallow-water environments (see the chapter on the molluscan species), and therefore the whole of the Bælt Sea region can be characterised by the three bivalves mentioned above, from the eulittoral to the infralittoral shallow-water zones: *Mytilus*, *Tapes* and *Cyprina*. Among the three species mentioned, the *Tapes* species (*Paphia aurea senescens*) also remains as the only subfossil bivalve from Denmark which can be regarded as an index fossil from the marine Eemian. The stratigraphical position of the marine Eemian is according to Jessen & Milthers (1928, p. 179) contemporaneous with the mixed oak forest zone and the *Carpinus* zone in the interglacial bogs; furthermore, Jessen & Milthers conclude (1928, p. 341) that the climate of Jylland and NW Germany in that part of the interglacial period which answers to zone f [culmination of the curves for mixed oak forest] was no less Atlantic in character than

Climatic affinity	Time: The seven Stages Frequency: Number of Molluscs Column per cent, %								Total number of species		
	Pleistocene			Holocene							
	Eemian	Early/Middle Weichselian	Late Weichselian	Unknown arrival in Holocene	Preboreal/Boreal	Atlantic	Subboreal	Subatlantic			
Arctic	-	1 (3%)	2 (5%)	35 subfossil species	95 recent species	-	-	-	-	3	
Arctic, Subarctic	-	6 (17%)	5 (12%)			-	-	-	-	-	11
Arctic, Subarctic, Boreal	10 (7%)	19 (53%)	14 (34%)			1 (4%)	1 (1%)	2 (3%)	1 (1%)	48	
Arctic, Subarctic, Boreal, Lusitanian	11 (8%)	7 (19%)	11 (27%)			2 (7%)	6 (6%)	5 (6%)	6 (8%)	48	
Subarctic, Boreal	3 (2%)	2 (6%)	4 (10%)			-	2 (2%)	3 (4%)	2 (3%)	16	
Subarctic, Boreal, Lusitanian	15 (11%)	1 (3%)	5 (12%)			3 (11%)	14 (15%)	7 (9%)	8 (11%)	53	
Boreal	1 (1%)	-	-			-	-	1 (1%)	1 (1%)	3	
Boreal, Lusitanian	90 (64%)	-	-			21 (78%)	70 (75%)	56 (73%)	53 (74%)	290	
Lusitanian	10 (7%)	-	-			-	-	3 (4%)	1 (1%)	14	
Total number of species Column per cent, %	140 (100%)	36 (100%)	41 (100%)				27 (100%)	93 (100%)	77 (100%)	72 (100%)	486

Fig. 102. The seven stages from the Eemian through the Weichselian – comprising the Early/Middle Weichselian and Late Weichselian – to the end of the Holocene. Preboreal–Boreal, Atlantic, Subboreal, and Subatlantic are here shown according to their climatic affinities based on the molluscan record.

Epoch	Age	Region	Climatic Affinity								Total of species: in number Row per cent, % Column per cent, %		
			A: Arctic, S: Subarctic, B: Boreal, L: Lusitanian										
			Arctic	A, S	A, S, B	A, S, B, L	S, B	S, B, L	Boreal	B, L		Lusitanian	
Pleistocene	Eemian	1. Bælt Sea	-	-	-	1 (2%)	2 (3%)	6 (10%)	-	43 (73%)	7 (12%)	59 (100%)	
		2. Baltic Sea	-	-	1 (5%)	1 (2%)	1 (5%)	4 (5%)	-	12 (63%)	-	19 (100%)	
		3. Kattegat	-	-	-	1 (3%)	-	3 (9%)	-	23 (72%)	5 (16%)	32 (100%)	
		5. North Sea	-	-	1 (2%)	5 (8%)	1 (5%)	10 (12%)	-	66 (73%)	8 (9%)	91 (100%)	
		6. Vendsyssel	-	-	9 (16%)	7 (11%)	1 (2%)	6 (5%)	1 (2%)	31 (56%)	-	55 (100%)	
		7. Skagen	-	-	1 (7%)	4 (29%)	-	2 (6%)	-	6 (43%)	1 (7%)	14 (100%)	
		3. Kattegat	1 (14%)	1 (14%)	2 (8%)	3 (4%)	-	-	-	-	-	-	7 (100%)
	6. Vendsyssel	1 (3%)	6 (17%)	19 (53%)	7 (19%)	2 (6%)	1 (3%)	-	-	-	-	36 (100%)	
	7. Skagen	1 (25%)	-	3 (75%)	-	-	-	-	-	-	-	4 (100%)	
	Late Weichselian	6. Vendsyssel	2 (6%)	4 (11%)	13 (33%)	8 (23%)	3 (15%)	5 (9%)	-	-	-	35 (100%)	
	7. Skagen	1 (11%)	1 (8%)	3 (5%)	3 (5%)	1 (5%)	-	-	-	-	-	9 (100%)	
	Holocene	Preboreal/ Boreal	5. North Sea	-	-	1 (4%)	2 (8%)	-	3 (12%)	-	20 (77%)	-	26 (100%)
			7. Skagen	-	-	-	-	-	1 (33%)	-	2 (67%)	-	3 (100%)
Atlantic		1. Bælt Sea	-	-	-	2 (6%)	1 (3%)	5 (16%)	-	23 (74%)	-	31 (100%)	
		2. Baltic Sea	-	-	-	-	-	2 (13%)	-	13 (87%)	-	15 (100%)	
		3. Kattegat	-	-	-	-	-	5 (22%)	-	18 (78%)	-	23 (100%)	
		4. Limfjorden	-	-	1 (1%)	6 (8%)	2 (3%)	13 (17%)	-	55 (71%)	-	77 (100%)	
		5. North Sea	-	-	-	2 (7%)	-	2 (3%)	-	23 (85%)	-	27 (100%)	
		6. Vendsyssel	-	-	-	-	1 (50%)	-	-	1 (50%)	-	2 (100%)	
		7. Skagen	-	-	-	-	-	-	-	8 (100%)	-	8 (100%)	
Subboreal		3. Kattegat	-	-	-	-	-	1 (50%)	-	1 (50%)	-	2 (100%)	
		4. Limfjorden	-	-	2 (6%)	2 (3%)	-	2 (6%)	-	28 (78%)	2 (6%)	36 (100%)	
		5. North Sea	-	-	-	3 (16%)	2 (11%)	1 (5%)	1 (5%)	12 (63%)	-	19 (100%)	
		6. Vendsyssel	-	-	-	-	-	1 (33%)	-	2 (67%)	-	3 (100%)	
		7. Skagen	-	-	-	1 (4%)	1 (4%)	2 (9%)	-	18 (78%)	1 (4%)	23 (100%)	
		4. Limfjorden	-	-	-	-	-	-	-	1 (100%)	-	1 (100%)	
		5. North Sea	-	-	-	1 (13%)	-	2 (25%)	-	5 (63%)	-	8 (100%)	
Subatlantic		7. Skagen	-	-	1 (1%)	5 (7%)	2 (3%)	7 (10%)	1 (1%)	51 (75%)	1 (1%)	68 (100%)	
	Total of species in number	6	12	57	64	20	84	3	462	25	733		
	Row per cent, %	(100%)	(100%)	(100%)	(100%)	(100%)	(100%)	(100%)	(100%)	(100%)	(100%)		

Fig. 103. Climatic characterisation (affinity) of mollusk assemblages for each region over the seven stages (ages) since the Eemian.

the climate of the Litorina period in postglacial time.

Also S.T. Andersen (1965, pp. 499–500) points to the Eemian as having an oceanic and warm climate. In his diagram from Hollerup, zone 5 represents the climax forest.

Jessen & Milthers (1928, p. 179) bring forth the view of Nordmann saying that the Lusitanian mollusc fauna was moving into the Baltic basin by way of the sounds that cut diagonally through the southern portion of the Cimbrian peninsula. However, this idea is, as discussed earlier, not accepted by the present author, where a connection to the west is advocated to be over the Kattegat–Vendsyssel–Skagen regions.

An eastern open connection to the White Sea over Finland and Russia will be discussed in connection with the Baltic region.

The Baltic, region 2

Appendix 6 and Fig. 103

In the Baltic Sea part of Denmark the number of recorded marine molluscs from the Eemian has fallen to 19 species compared to the Bælt Sea region, and no purely Lusitanian species occur. However, as pointed out earlier, this change in the climatic situation regarding the Baltic fauna can be seen as a consequence of the fact that here only the deeper-water assemblage characterised by *Turritella communis* occurs, although one of the species known from the characteristic part of the Bælt Sea fauna is recorded, i.e. *Arctica islandica*. However, the *Tapes* species are not met with in this region.

The deeper-water environment is therefore well characterised by the *Turritella* community.

Although the decline in number of species very much resembles the present-day situation between the Bælt Sea and the Baltic as mentioned earlier, five species in the Eemian fauna, including *Turritella communis*, show a salinity above the present conditions in the Baltic.

From the study of diatoms at Ollala in eastern Fennoscandia, Forsström *et al.* (1988, p. 322) write: “This mixture of warm and cold indicators probably means that the Eemian sea in the Baltic Basin had a connection both to the North Sea in the west and to the Arctic Ocean via the White Sea Basin in the northeast”.

Only a few works from eastern Fennoscandia have been based on molluscan studies. However, among the papers by Zans (1936), Sokolova *et al.* (1972), and Gross (1967), Gross mentions the following molluscs:

Portlandia arctica, *Clinocardium ciliatum*, *Heteranomia squamula*, *Macoma calcarea*, *Littorina littorea*, and *Cerastoderma edule*. Here the three last mentioned species occur in the Eemian from the Danish Baltic and *Clinocardium ciliatum* from the Vendsyssel region, although here in the upper *Turritella terebra* zone correlated to the Early Weichselian, as discussed later.

Portlandia arctica has not been recorded from the Danish Eemian, although it occurs in the beds below the Eemian in the Anholt boring (the Kattegat region), where Seidenkrantz (1993, p. 284) also has demonstrated foraminiferal zones A–D with Arctic species.

Gross (1967, p. 118) regards the Arctic and Arctic–Boreal molluscs in the Eemian clay as: “Relikte aus der *Portlandia*-Transgression des Dnepr II-Spätglazials, die nach dem Pollen-Profil und -Diagramm der Eem-Transgression voranging”.

The older correlation of the so-called Weissmeer transgression by Zans (1936, table 1) contains further details on the molluscs upon which the correlation has been based, and it also includes the Danish area, mentioning ‘Dänische Inseln’ after Ødum (1933) and ‘Skaerumhede’ after Jessen *et al.* (1910). However, the occurrence of the High-Arctic *Portlandia arctica* should be placed in the Late Saalian, as seen in the Kattegat region mentioned above, while the Arctic–Boreal species *Clinocardium ciliatum* could be taken as a relict in the Skærumhede sequence from the Late Saalian environment within the Danish area or introduced by the cooling in the Early Weichselian.

The faunal development has been worked out in more detail between the eastern Fennoscandia and the Danish area (Funder *et al.* 2002). The connection to the Arctic over the White Sea during the Eemian seems to be well established, but only for a shorter time, 1000–2000 years of the more than 10 000 years that the Eemian Sea existed in the Baltic region (Funder 2000, p. 68).

The Kattegat, region 3

Appendix 6 and Fig. 103

From the Kattegat region, 32 species have been recorded, with a high amount of Boreo-Lusitanian species (72%). Five species are Lusitanian, among which are found the characteristic Eemian species of the shallow-water environment, including the *Tapes* species. However, also the deeper-water environment is represented by the *Turritella* community in this region.

On Anholt, the *Turritella* community occurs at a depth of around 70 m b.s.l., and the *Tapes* fauna in the Isefjord area at Ejby at a depth of around 10 m a.s.l. The latter is considered to be *in situ* (Madsen 1968). It is tempting to regard the two localities as being at about their original elevation in relation to an Eemian sea level some what higher than the recent one, since the glacio-isostatic rebound had expired (Petersen 1991b).

On the basis of the scattered Eemian localities of which some are floes in the Weichselian glacial deposits, the maximum extent of the Eemian sea cannot be given. However, both the shallow-water environment characterised by the *Tapes* species and the deeper water by the *Turritella* species have been demonstrated. In this way both of the characteristic marine environments from the Bælt Sea and the Baltic respectively are represented in the Kattegat region.

The North Sea, region 5

Appendix 6 and Fig. 103

The largest amount of mollusc species within the Eemian have been recorded from the North Sea region, or to be more precise from the coastal region of the North Sea. In the Danish part of the North Sea, many studies on microfossils from the oil and gas fields have demonstrated Eemian deposits in the central North Sea, but their macrofossils have not been studied (Knudsen 1985a, 1986). However, the large amount (91) of molluscs from the coastal region fall into different facies, as seen in the previous regions when a much lower number was looked at.

Gripp (1964) uses the 'Senescens Sand' and 'Turritella Ton' to give his idea of the marine order of the strata. However, in this context, working with regions and not with localities, it should be emphasised that the development of different facies most probably happened in parallel. Gripp (1964, p 223) expresses this himself in saying: "Tapes-Sand und Turritellen-Ton sind die beiden Facies, die während des Ansteigs des Meeresspiegels entstanden".

As seen from the species found in the Danish North Sea coastal region, we do find the *Turritella* species and *Tapes* species, but also the occurrences of *Donax vittatus* should be mentioned as a facies indicator, characterising the high-energy coastal environment from this area facing the Eemian North Sea.

From recent studies on Foraminifera in northern

Germany at the Kiel Canal, Knudsen (1986) shows that the marine transgression took place in the warm part of the Eemian, and Hinsch (1985) in his mollusc study from the same area revealed three mollusc communities characterising the shallow-water environment, with such genera as *Mytilus-Cerastoderma*, *Acanthocardia-Venerupis* and *Bittium-Varicorbula*. However, the old material from many localities in the Danish North Sea region cannot be worked out to such detail, although all the marine mollusc species mentioned by Hinsch (1985) have been recorded from the Danish Eemian North Sea region.

When the molluscan fauna in the Danish Eemian North Sea region is compared with the Eemian on the west coast of Norway as described by Mangerud *et al.* (1981), 20 molluscan species out of the 35 species recorded from the Fjøsangerian are known from the North Sea region and 7 species from other Eemian regions in Denmark. Here *Macoma calcarea* and *Nuculana pernula* belonging to the Arctic-Boreal group occur in the Vendsyssel and Skagen regions, and in the Baltic region *Macoma calcarea* representing deeper water during the Eemian, while *Chlamys islandicus*, which does not occur in the Danish Eemian deposits, is found in the Weichselian recorded from the Vendsyssel region. This means that the Fjøsangerian can be regarded as slightly cooler than the Danish North Sea Eemian deposits.

Another marine Eemian deposit in Norway described by Andersen *et al.* (1983) at Bø on Karmøy (SW Norway) revealed 25 molluscan species from the Avaldsnes Interglacial described in detail by Sejrup (1987). Here as many as 20 species are in common with those in the Danish North Sea region, and one, *Hinia incrassata*, has been recorded from the Eemian in the Vendsyssel region.

Four species have not been found in the Danish Eemian. These are the Arctic-Lusitanian and Arctic-Boreal species *Puncturella noachina* and *Boreotrophon clatbratus* respectively, the latter occurring in the Late Weichselian deposits in the Vendsyssel region. This is much in line with the observations from the Fjøsangerian deposits. The four non-occurrences in the Danish Eemian among the Boreo-Lusitanian species *Pecten maximum* and *Lucinoma borealis*, the latter being common at both Norwegian localities, are difficult to explain. Among the 8 purely Lusitanian species recorded from the North Sea region, only *Plagiocardium papillosum* occurs in the Norwegian Eemian at Fjøsanger, which again points to a slightly cooler position for the Norwegian localities.

The Vendsyssel region, region 6

Appendix 6 and Fig. 103

The Eemian mollusc fauna from Vendsyssel comprises 55 species with no purely Lusitanian climatic affinity, while quite a few (nine species ~ 16%) are found in the Arctic and the Boreal zones. The stratigraphical position has been well elucidated through foraminiferal investigations (Knudsen & Lykke-Andersen 1982; Knudsen 1984, 1985b, 1992; Lykke-Andersen 1987).

The study by Lykke-Andersen (1987, fig. 5) also involves the molluscs, and references are made to the zones established on the basis of macrofossils. According to the foraminiferal studies, the transition to the Early Weichselian takes place around 120 m b.s.l. in the Skærumhede I sequence (Jessen *et al.* 1910), which is about 140 m b.s. This means that the upper part of the *Turritella terebra* zone falls within the Early Weichselian.

The two Arctic to High Boreal species *Serripes groenlandicus* and *Clinocardium ciliatum* at depths of 132 m and 127 m b.s. respectively are discussed by Nordmann (Jessen *et al.* 1910, pp. 124–128), and the climatic indications from *Turritella communis* mean that the assemblage existed at the transition between the High and Middle Boreal.

In the paper by Knudsen (1992), it is said that an abrupt faunal change at the Eemian–Weichselian boundary reflects a drop in water depth of at least 50 m and a subsequent drop in temperature of several degrees.

The drop in temperature might well be reflected in the mollusc fauna by the occurrences of the two bivalves mentioned above, and for the drop in sea level it is tempting to recall the observed occurrence of the eulittoral *Mytilus edulis* at a depth of 135 m b.s.l. in the Skærumhede I boring and up to the *Abram nitida* zone, which forms the transition to the Arctic *Turritella erosa* community as mentioned earlier. Therefore, within the Vendsyssel area the Eemian (isotopic stage 5e) is represented by a *Turritella* community that continues into the beds representing the isotopic stages 5d–a (Knudsen 1992, fig. 4). The Hordalandian stage in western Norway contains *Serripes groenlandicus* and *Clinocardium ciliatum* species and is referred to the Early Weichselian (Mangerud *et al.* 1981). Arctic conditions first occurred in the macrofossil zones *Turritella erosa*, *Balanus crenatus* and *Macoma calcarea* (Bahnsen *et al.* 1974), which cover the *Portlandia arctica* zone *sensu* Nordmann (Jessen *et al.* 1910, fig. 8).

The Skagen region, region 7

Appendix 6 and Fig. 103

The 14 Eemian molluscs found in the Skagen boring are the lowest number recorded within the Eemian sites. However, the finds are a clear omen of the deeper-water environment not encountered earlier in Denmark on the basis of molluscs. The recorded molluscs point to an environment like the deeper part of the Skagerrak today, with a community such as the *Amphilepis norvegica*/*Pecten vitreus*, where the latter (*Delectopecten vitreus*) occurs in the Skagen Well, as mentioned earlier.

The boundary to the overlying Arctic deposits characterised by the occurrences of *Portlandia arctica* is sharp and coincides with a sedimentological change to a diamicton with dropstones in the Arctic part, as found in the Skærumhede sequence within the *Turritella erosa* zone (Bahnsen *et al.* 1974). Therefore, in the Skagen Well no transition zone from substage 5e to 5d–a can be demonstrated in the molluscan faunas.

The recorded Eemian communities and/or characteristic molluscan species for six regions with Eemian marine deposits are given in Table 3.

Table 3. Eemian communities and/or characteristic molluscan species

Region	Community	Species	Depth
1. Bælt Sea		<i>Mytilus edulis</i>	littoral shallow deeper
		<i>Tapes</i> spp.	
		<i>Arctica islandica</i>	
2. Baltic			littoral shallow deeper
	<i>Turritella</i>	<i>T. communis</i>	
3. Kattegat		<i>Mytilus edulis</i>	littoral shallow deeper
	<i>Turritella</i>	<i>T. communis</i>	
5. North Sea		<i>Donax vittatus</i>	littoral shallow deeper
	<i>Turritella</i>	<i>T. communis</i>	
6. Vendsyssel	<i>Turritella</i>	<i>T. communis</i>	littoral shallow ~ 100 m
7. Skagen		<i>Amphilepis/Pecten</i> <i>Delectopecten vitreus</i>	littoral shallow > 100 m

Early/Middle Weichselian stage 115 000 – 25 000 B.P.

The Kattegat, region 3

Appendix 6 and Fig. 103

Although the number of mollusc species recorded from the Kattegat region during the Early/Middle Weichselian is low – seven species – the climatic indications for the Arctic environment are clear, considering that all species can be found in the High Arctic, and that one species, *Portlandia arctica*, is High Arctic *par excellence*, and *Macoma calcarea* indicates shallow water.

The stratigraphical position of the Arctic *Macoma* community found in the Kattegat region – Holmstrup on Sjælland – has been determined by foraminiferal correlation and aminostratigraphical investigations, as mentioned earlier (Petersen & Buch 1974; Miller & Mangerud 1985). Recently, the foraminiferal studies of the Quaternary sequence in the Anholt boring have demonstrated a Middle Weichselian deposit at a depth of about 50 m b.s.l. (Seidenkrantz 1993). Considering the information given by Knudsen (1992) on a drop of sea level of around 50 m during the transition from the Eemian to the Weichselian, the Middle Weichselian beds in the cored section on Anholt may represent rather shallow-water deposits. This is in accordance with the occurrence of the Arctic *Macoma* community.

The Vendsyssel region, region 6

Appendix 6 and Fig. 103

Foraminiferal studies by Lykke-Andersen (1987) indicate that the Early Weichselian beds are represented by the upper *Turritella terebra* zone, and that the deeper-water temperate *Turritella* community continued into the first part of the Weichselian with the following *Abra nitida* zone as a transition to the Arctic deeper-water *Turritella* community (*Turritella erosa*).

Together with the Arctic and Arctic-subarctic species (seven in number, forming nearly 20% of the mollusc species), the sedimentological data show the occurrences of ice-rafted material recorded both from the Skærumhede I and the Skærumhede II borings (Jessen *et al.* 1910, p. 76; Bahnson *et al.* 1974, figs 3, 4, 7) reflecting Arctic conditions.

It has been argued by Nordmann (Jessen *et al.* 1910) that species within the genera *Mytilus*, *Cyprina*,

Zirpbaea, *Nassa*, and *Bittium* must be regarded as allochthonous and older elements. However, they could also be regarded as stray finds from contemporary shallow-water to littoral deposits occurring within times of higher temperatures in the near-shore areas, similar to the near-shore fauna of Middle Weichselian age – the Bø Interstadial (40–64 ka) with *Gibbula cineraria* and *Mytilus edulis*, the latter occurring frequently (Sejrup 1987).

During the younger part of the marine Middle Weichselian – around 32 000 B.P. – when the shallow-water Arctic *Macoma* community was established, no *Mytilus edulis* or *Bittium reticulatum* have been recorded.

The development of the bottom communities within the Older Weichselian sequence is therefore given by the transition from the *Turritella* communities in deeper water to the Arctic *Macoma* community in shallow water.

The Skagen region, region 7

Appendix 6 and Fig. 103

Very few molluscs have been found in the Skagen boring of Older Weichselian age. The four species are all Arctic, and the occurrence of *Portlandia arctica* shows that High Arctic conditions have prevailed and ice-rafted material occurs. There is no indication of near-shore fauna as recorded from the Vendsyssel region. From this, it might be concluded that the deposition of these beds took place in the first part of the Middle Weichselian, contemporaneous with the deposition of the *Turritella erosa* beds of the Skærumhede sequence, but at a water depth of more than 100 m, as demonstrated earlier.

From the few finds, it is not safe to point to a certain community on the basis of molluscs. However, the community in deeper Arctic waters is described by other animals than molluscs, i.e. the Ascidia–Spongia epifauna, and at depths exceeding 200 m by *Gorgonocephalus* species. From the estimate on water depth taken in comparison with the early part of the Arctic sequence in the Vendsyssel region, the palaeodepth must have been well above 100 m.

The recorded Early/Middle Weichselian communities and/or characteristic molluscan species are given in Table 4.

Table 4. Early/Middle Weichselian communities and/or characteristic molluscan species

Region	Community	Species	Depth
3. Kattegat	Arctic <i>Macoma</i>	<i>M. calcarea</i>	littoral shallow deeper
6. Vendsyssel	Arctic <i>Macoma</i> Arctic <i>Turritella</i> <i>Turritella</i>	<i>M. calcarea</i> <i>T. erosa</i> <i>T. communis</i>	littoral shallow ~ 90 m ~ 90 m
7. Skagen	Ascidia-Spongia		littoral shallow 100–200 m

Late Weichselian stage 25 000 – 10 000 B.P.

The Vendsyssel region, region 6

Appendix 6 and Fig. 103

The 35 mollusc species found in the Vendsyssel region are in number very close to the number of species encountered in the Vendsyssel region during the Early/Middle Weichselian (36 species). However, as seen in Fig. 103, the percent of molluscs with a wide range and only connected to the Subarctic and southwards is higher in the Late Weichselian (46%) compared to the Early/Middle Weichselian (28%). This can be explained by the way the development in the two seas before and after the Main Glaciation, the Older and Younger *Yoldia* Sea respectively took place.

The deposits from the Older *Yoldia* Sea reflect the transition from deeper Arctic to shallow-water Arctic communities, the *Turritella* and *Macoma* communities respectively. The Late Weichselian beds within the shallow-water environment show a development from the Arctic *Macoma* community to the Boreo-Arctic *Mytilus-Zirphaea* community after 13 000 B.P., with a deeper-water community characterised by the *Portlandia arctica* species, as outlined by Petersen (1984), which could be part of the deeper *Macoma* community – the so-called *Ophioceten* zone.

These observations form the background for the earlier given explanation of the occurrences of Boreal shallow-water species such as *Mytilus edulis* in the deeper-water Arctic community in the Older Weichselian deposits from the Vendsyssel region.

The occurrences of the *Mytilus edulis* species in the Late Weichselian deposits in large quantities are described by Jessen (1899). The dates of the earliest occurrences of *Zirphaea* and *Mytilus* go back to 12 770 and 12 520 B.P. ¹⁴C years respectively.

All the 30 ¹⁴C dates forming the base for the evaluation of the Late Weichselian sea levels and occurrences of fauna communities as figured in Petersen (1984, fig. 1) have been listed by Petersen & Rasmussen (1995a, table 1). It appears that the dates older than 13 000 B.P. ¹⁴C years all come from *Hiatella arctica* and *Macoma calcarea* (only one date) going as far back as 14 650 ± 190 B.P. ¹⁴C age. Considering the mollusc species inhabiting the waters “of the Swedish west coast shortly after deglaciation” (Fredén 1986, p. 55), one finds also *Chlamys islandica* and *Mytilus edulis* shortly after 13 000. The latter within the time span of its first dated occurrence in the Younger *Yoldia* Sea deposits in Denmark.

As to the deeper-water deposits also around 13 000, one can take the sample from the Dybvad clay pit (Fig. 1) dated to 13 010 ± 190 B.P. ¹⁴C which contained the following molluscs: *Hiatella arctica*, *Mya truncata*, *Macoma torelli*, *Portlandia arctica*, *Buccinum groenlandicum* and *Cylichna occulta* (Petersen 1984). It is seen that still after the immigration of Boreo-Arctic fauna to the shallow-water environment, showing an amelioration in climate, the Arctic community persisted in the deeper water as shown by the dating from the Bindslev clay pit giving 12 650 ± 180 ¹⁴C age B.P., with species such as *Macoma calcarea* and *Portlandia arctica*.

The same situation can be estimated from the investigation of the Pleistocene/Holocene Boundary in south-western Sweden (the Moltemyr core) where “zone Z comprising the samples from 560 cm to 650 cm, is characterised by *Portlandia arctica* and *Nucula tenuis* (*Nuculoma tenuis*, here taken as a species with a wide climatic range), and by the absence of many of the species of the overlaying zone (such as *Mytilus edulis*) ... The water depth during deposition of zone Z was greater than during any of the other zones (above) probably more than 20 m” (Feyling-Hanssen 1982, p. 128).

Regarding the climatic indication of *Portlandia arctica*, Feyling-Hanssen (1982, p. 131) quotes Andersen (1975, p. 54) saying: “Evidently, *Portlandia arctica* lived near the ice fronts [in southern Norway] also during older, glacial phases, but it seems to have disappeared from our coasts shortly after the Ra event, probably due to a warming of the sea”.

According to Sørensen (1979), the disappearance of *Portlandia arctica* from the Oslo Fjord area occurred somewhat before 10 000 B.P.

The Younger Dryas marine deposits have not been demonstrated in the Vendsyssel region but are recorded from the Skagen region, which will be discussed next.

The Skagen region, region 7

Appendix 6 and Fig. 103

The nine species recorded from the Skagen Well indicate an Arctic deeper-water community very much like the *Arca-Astarte crenata* community (Ockelmann 1958). There are no finds of species which could be referred to the more shallow-water environment as seen in the case of the Vendsyssel region to the south both during the Early/Middle Weichselian and the Late Weichselian.

Through most of the history of the cored section of Pleistocene age, the Skagen Well has revealed mollusc assemblages from a deeper-water environment. Also the transition to the Holocene takes place in deeper water.

The purely Arctic species *Portlandia arctica* together with *Bathyarca glacialis* is found right up to the strata dated to around 10 000 B.P. forming the Pleistocene–Holocene boundary in the Skagen Well. However, in the description of the shell fauna of the marine clays in the Oslo Fjord region, Brögger (1900, p. 685) states: “*Portlandia arctica* is never found in the *Arca* Clay”. Later datings of the ‘Middle *Arca* Clay’ and the ‘Younger *Arca* Clay’ given by B.G. Andersen (1965, p. 118) yielded early Preboreal ages. In the Younger *Arca* Clay from Norway, species such as *Mytilus edulis*, *Zirfaea crispata*, and *Macoma balthica* (B.G. Andersen 1965, table 2) are also found, which characterise the shallow-

water deposits in Vendsyssel after 13 000 B.P. ¹⁴C age. The recorded recent occurrence of *Bathyarca glacialis* from southern Iceland implicates extension into the High-Boreal region, although the main extension is in the Arctic. The Norwegian records of *Bathyarca glacialis* come from a more shallow-water environment, as seen from the occurrences of the three shallow-water species mentioned above.

The recorded Late Weichselian communities and/or characteristic molluscan species are given in Table 5.

The Preboreal–Boreal stage 10 000 – 8000 ¹⁴C years B.P.

The North Sea, region 5

Appendix 6 and Fig. 103

Mollusc faunas from the Late Weichselian have here been recorded only from the Vendsyssel and Skagen regions. As seen in Fig. 103, the early part of the Holocene, the Preboreal and Boreal, have a record of 26 species, with as many as 77% (20 species) Boreo-Lusitanian. This is in contrast to the records from the Late Weichselian, when the Arctic–Boreal elements dominated, with 54% in the Vendsyssel region and 55% in the Skagen Well, the latter with only a few species and representing a deeper-water environment. The Preboreal–Boreal North Sea faunas contain eulittoral as well as shallow-water species.

Mytilus edulis, *Littorina littorea* and *Cerastoderma edule* characterise the littoral zone and *Macoma balthica* the shallow-water zone. Using the characteristic species from the C.G.J. Petersen community concept, the oldest recorded faunal communities from the North Sea might be the *Mytilus* epifauna community with *Littorina littorea*, and the *Macoma* infauna community with *Cerastoderma edule*. Also the *Abra* community on mixed bottoms with *Phaxas pellucidus*, *Corbula gibba* and *Mya truncata* might be reflected in the recorded species.

Table 5. Late Weichselian communities and/or characteristic molluscan species

Region	Community	Species	Depth
6. Vendsyssel	<i>Mytilus/Zirphaea</i>	<i>Z. crispata</i>	littoral
	Arctic <i>Macoma</i>	<i>M. calcarea</i>	shallow
	Ophioceten zone	<i>Portlandia arctica</i>	deeper
7. Skagen			littoral
	<i>Arca-Astarte</i>	<i>Bathyarca glacialis</i>	shallow deeper

The Skagen region, region 7

Appendix 6 and Fig. 103

As discussed earlier, the environment of the earliest Holocene, the Preboreal and Boreal, can be referred to the *Maldane-Ophiura sarsi* community. This deep-

Table 6. Preboreal–Boreal communities and/or characteristic molluscan species

Region	Community	Species	Depth
5. North Sea	<i>Mytilus</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i>	shallow
	<i>Abra</i>	<i>A. alba</i>	deeper
7. Skagen			littoral
	Maldana/Ophiura		shallow > 150 m

water community observed in the Skagen region compared to the shallow-water communities recorded from the North Sea coastal region once more demonstrates the unique position of the deeper-water communities observed in the Skagen Well material compared to the other regions in Denmark through the Late Quaternary.

The recorded Preboreal–Boreal communities and/or characteristic molluscan species are given in Table 6.

The Atlantic stage 8000–5000 ¹⁴C years B.P.

The Bælt Sea, region 1

Appendix 6 and Fig. 103

Out of the 47 species known from the Bælt Sea region, 31 have been recorded from the Atlantic (Fig. 103).

The littoral zone with *Mytilus edulis*, *Littorina littorea*, *Littorina saxatilis*, *Cerastoderma edule*, and *Macoma balthica* from the shallow-water zone, is recorded; furthermore, the *Abra alba* community together with *Corbula gibba*.

These faunal elements reveal the *Mytilus* epifauna community with *Ostrea edulis*, which no longer occurs in this area. In the infralittoral zone is the *Macoma* infauna community where such species as *Paphia aurea*, *Tapes decussatus*, and *Venerupis pullastra* have been found, and finally the *Abra* community with *Corbula gibba*.

Also the epifauna on the vegetation is reflected in *Rissoa albella*, *R. membranacea*, and *R. inconspicua* and other gastropods. Also the bivalve *Parvicardium exiguum* is associated with the vegetation.

The communities mentioned are still to be found in the Bælt Sea region, whereas *Paphia*, *Tapes*, *Venerupis* and *Ostrea* are no longer found in this region.

The Baltic, region 2

Appendix 6 and Fig. 103

Fifteen mollusc species out of the 19 recorded from the Baltic region during the Holocene can be referred to the Atlantic (Fig. 103).

The occurrences of *Mytilus edulis* and *Littorina littorea* are referred to the *Mytilus* epifauna community in the littoral zone, while species, as *Macoma balthica*, *Cerastoderma edule*, and *Scrobicularia plana* represent the *Macoma* infauna community in shallow water.

The occurrences of both *Littorina littorea* and *Scrobicularia plana* are characteristic for the Atlantic in the Baltic and are now absent. Spärck (1950) points to the wider extent of *Scrobicularia plana* in the Stone Age as a consequence of warmer water in those days; however, in the present work the higher salinity is preferred as an explanation, as mentioned earlier. This is supported by the occurrences of gastropods like *Bittium reticulatum*, *Rissoa albella*, and *Aporrhais pes-pellicani*, species recorded from other regions today with higher salinity.

It should be noticed that *Scrobicularia plana* and *Littorina* species have been demonstrated as far north in the Baltic as Estonia (Kessel & Raukas 1979, fig. 9), although only with a low percentage but persisting into the Subboreal. The unexpected find of *Ostrea edulis* from Estonia has later been re-evaluated as transported there by some seamen and thrown then overboard (in a letter from Prof. A. Raukas, May 1995).

According to Nordmann (1903b, 1906), Madsen (1944), and Spärck (1942, fig. 21), the southernmost finds of subfossil oysters are the Bælt Sea and Øresund off Landskrona.

The Kattegat, region 3

Appendix 6 and Fig. 103

From the Kattegat region, only half of the recorded species have been dated so as to give a first appearance date. This amounts to 23 species from the Atlantic (Fig. 103).

All of the dated species come from geologically mapped areas and not from the Kattegat proper. Therefore the observed species all come from shallow-water environments, excluding the deeper-water environment recorded from foraminifera (Christiansen *et al.* 1993; Seidenkrantz & Knudsen 1993).

From the listed species dated to the Atlantic the *Mytilus* epifauna community with *Littorina littorea* and the *Macoma* infauna community with *Cerastoderma edule* and *Tapes decussatus* can be pointed out. Furthermore, the *Abra* community with *Corbula gibba*, which is common in present-day inner Danish waters (Thorson 1950), is present.

The Limfjord, region 4

Appendix 6 and Fig. 103

This region has the highest number of recorded mollusc species from the Holocene, viz. 147 species, and 77 have been dated to the Atlantic (Fig. 103).

Petersen (1918, pp. 22–36) described the communities in the Limfjord region covering the *Macoma balthica*, the *Venus* and the *Abra* communities. Also an area with *Mya truncata* is mentioned, forming a transition zone between the *Macoma* and the *Abra* communities. In patches the epifauna elements such as *Mytilus edulis* and *Modiola modiolus* are found.

From the *Zostera* vegetation, the *Rissoa* and *Bittium* species are mentioned.

All of the characterising species from these communities have been recorded from the Atlantic. *Paphia aurea*, *Tapes decussatus*, *Venerupis rhomboides* and *Venerupis pullastra* were represented during the Atlantic, where as only *Venerupis pullastra* is present in the Limfjord today. *Ostrea edulis* was well established during the Atlantic, as seen from the species composition of the 'køkkenmødding' (kitchen midden) (Petersen 1986a, figs 3, 4). The above-mentioned species and *Cerastoderma edule* occurred in the infralittoral zone in large quantities most probably in the tidal zone which was the best collecting grounds for the Stone Age people. In a multi-lobed body of water such as the Limfjord, many habitats have existed during the Atlantic. However, also the development through time has been considered, as seen in the case of the marine stages in Tastum Sø – once the southernmost part of Skive Fjord (Rasmussen & Petersen 1980).

In the northern part of the former Limfjord during the Atlantic, the deeper-water fauna with *Abra alba* and *Corbula gibba* can be demonstrated at the Vust locality (Petersen 1981, p. 502). The recorded Atlantic communities have very much in common with the recent communities.

The North Sea, region 5

Appendix 6 and Fig. 103

Twenty-seven species immigrated during the Atlantic in the North Sea coastal region (Fig. 103), and *Chamelea striatula* and *Spisula subtruncata* characterise the *Venus* community and are very common in the recent North Sea region.

Also *Paphia aurea* and *Tapes decussatus* make their appearance in the North Sea region during the Atlantic.

According to Hessland (1943), *Tapes decussatus* should immigrate to the west coast of Sweden already in the Boreal, while *Paphia aurea*, *Venerupis rhomboides* and *Venerupis pullastra* followed in the Atlantic. This is a close parallel to the recorded immigration to the Limfjord region, although here following the transgression and not superjacent to older marine deposits as in the North Sea.

The Vendsyssel region, region 6

Appendix 6 and Fig. 103

The dates from the Vendsyssel region during the Holocene are made on only a few species. However, the faunal assemblages *sensu* Nordmann (Jessen 1905) can be commented upon in the light of immigration dates observed in the neighbouring Limfjord region.

Nordmann (Jessen 1905, p. 145) operates with five assemblages (from a to e) with the following headings:

- a) Beach deposits
- b) Oyster banks
- c) Deposits in coves and sounds
- d) Deposits in fjords and sounds with muddy bottoms and no current
- e) Lagoonal deposits

- a) Beach deposits

The first type – the beach deposits – cannot be considered in any relation to the community concept *sensu* C.G.J. Petersen, since the dominating part of the shell material has been redeposited. However, as a geological unit, it points to a former sea level stand, albeit difficult to date, because of the allochthonous character of these deposits.

Among the 90 species listed from this region (south-

ern part of Vendsyssel), Nordmann (Jessen 1905, table a) points to *Spisula subtruncata* and *Fabulina fabula* as being conspicuous, but other species may dominate at some localities, as seen from the table. Both species pointed out by Nordmann are recorded from the Limfjord during the Atlantic.

b) Oyster banks

As pointed out by Petersen (1918, p. 52), the so-called oyster banks in the recent Limfjord have 1 or 2 specimens per m². However, the places recorded by Nordmann are located on former narrow channels where the oysters occurred in large quantities together with *Chlamys varia*, *Hiatella arctica*, *Retusa truncatula*, *Mysella bidentata*, *Parvicardium exiguum*, *Paphia aurea*, *Venerupis pullastra*, *Bittium reticulatum*, *Rissoa inconspicua*, *Rissoa parva*, *Buccinum undatum*, *Nucula nitidosa*, *Triphora adversa*, *Cerastoderma edule*, and *Hydrobia ulvae*, all of which are recorded from the Limfjord during the Atlantic. Only two species mentioned by Nordmann (Jessen 1905, p. 147) as being characteristic from some of the oyster banks, *Caecum glabrum* and *Acmaea virginea*, have their earliest record from the Limfjord in the Subboreal. Therefore the oyster banks *sensu* Nordmann seem to be well established in the Vendsyssel region already during the Atlantic, considering the dates obtained from the Limfjord region.

The oyster banks from the Atlantic appear to be characteristic features with their high diversity of species and huge quantities of *Ostrea edulis* not met with in present-day Danish waters. This could be seen as a parallel to the fluctuation in the population of oysters observed during the last hundred years in Danish waters, but should rather be connected with changes in the tidal currents which changed to a minimum during the following stage – the Subboreal (Petersen 1993), and put an end to the large oyster banks.

c) Deposits in coves and sounds

From these deposits Nordmann points to species such as *Spisula subtruncata*, *Modiolus modiolus*, *Thracia phaseolina*, and *Corbula gibba* as being characteristic of coves and sounds. They have all been recorded from the Limfjord during the Atlantic, and they represent species known from the deeper-water deposits both as epifaunal elements (*Modiolus modiolus*) and infaunal elements as found in the C.G.J. Petersen communities, the *Modiola* and *Abra* communities respectively.

This is further demonstrated by the following spe-

cies mentioned by Nordmann (Jessen 1905, p. 148): *Cerastoderma edule*, *Parvicardium scabrum*, *Nucula nitidosa*, *Hiatella arctica*, *Chamelea striatula*, *Timoclea ovata*, *Venerupis pullastra*, *Fabulina fabula*, *Tellimya ferruginosa*, *Lunatia alderi*, and *Retusa truncatulus*. Also these species have been dated back to the Atlantic in the Limfjord region. *Ostrea edulis* occurs, but as stray finds among the infauna elements dominating in the above-mentioned assemblage that includes *Abra alba*, which occurs in most of the samples, although not frequently (Jessen 1905, table c).

d) Deposits in fjords and sounds with muddy bottoms and no current

From such deposits Nordmann mentioned the finds of *Zostera*, which was a well established vegetational element in the recent Limfjord, according to Petersen & Jensen (1911, map 1).

The dominating species in this assemblage, which resembles the present-day fauna in such environments, are *Hydrobia ulvae*, *Littorina littorea*, *Littorina obtusata*, *Rissoa membranacea*, *Cerastoderma edule*, *Mytilus edulis*, *Scrobicularia plana*, *Paphia aurea*, *Bittium reticulatum*, *Hinia reticulata*, *Onoba semicostata*, *Parvicardium exiguum*, *Macoma balthica*, and *Ostrea edulis*, the last two species only with a few specimens. All the above-mentioned species occurred in the Limfjord region during the Atlantic.

The *Littorina*, *Rissoa*, and *Parvicardium* species might often be found on the *Zostera* vegetation.

Among the dominating species also mentioned by Nordmann, some have not been dated back to the Atlantic (in the Limfjord region) but occur in the Subboreal, viz. *Littorina tenebrosa*, *Akera bullata*, and *Retusa obtusa*. However, already the species recorded from the Atlantic point to the so-called *Echinocyamus* community (Spärck & Lieberkind 1921), although the echinoids have not been recorded by Nordmann (Jessen 1905).

e) Lagoonal deposits

These deposits represent two assemblages, according to Nordmann (Jessen 1905, p. 150), viz. an older more open-water environment with species such as *Macra stultorum*, *Tellimya ferruginosa*, *Chamelea striatula*, *Fabulina fabula*, *Ensis ensis*, *Lunatia catena*, *Lunatia alderi*, and *Aporrhais pespelicani*, which are mixed with faunal elements from the lagoon itself, such as *Hydrobia ulvae*, *Scrobicularia plana*, and *Mytilus edulis*. In connection with a *Zostera* vegetation, *Rissoa membranacea* and *Lacuna vincta* may occur in huge quantities.

Such a deposit cannot be compared to any of the Petersen communities, although they play an important role in the geological setting, as was the case also with the beach deposits.

In the northern and eastern part of Vendsyssel, further comments will be added to the shallow-water and beach deposits with the finds of the *Dosinia* and *Mya arenaria* species. They have been dated to the Subboreal and Subatlantic respectively and are therefore commented upon later.

The Skagen region, region 7

Appendix 6 and Fig. 103

Nearly all of the eight recovered species from the Atlantic (Fig. 103) show a deep-water fauna, which on the basis of the dominating role of the echinoids is tentatively referred to the *Amphiura* community known from the present-day Skagerrak.

The final large eustatic rise took place during the Late Boreal – Early Atlantic, and the difference in

isostatic rebound from 8000 B.P. between the Skagen and Limfjord regions is around 31 m, with the highest amount in the north (Skagen). It appears that the water depth in the Skagen region must have been up to 100 m during the Atlantic (Petersen 1981, 1991b). Therefore, the occurrence of a single *Spisula subtruncata* shell must be taken as far outside its habitat, considering that the modern depth range of this species is 0–36 m (Petersen 1986c, table 2).

The recorded Atlantic communities and/or characteristic molluscan species are given in Table 7.

The Subboreal stage 5000–2500 ¹⁴C years B.P.

The Bælt Sea, region 1

Appendix 6 and Fig. 103

There are no dated mollusc finds from the Subboreal in the Bælt Sea region. As stated for the Atlantic in this region, the bottom communities known from the present day were already established, but they included some species such as *Tapes* and *Ostrea* which are no longer extant in this area. However, as *Paphia aurea* and *Ostrea edulis* still occurred in the Iron Age sites – from the Subatlantic – it is most probable that these species persisted there, while *Tapes decussatus* and *Venerupis pullastra* expired during the Subboreal in the Bælt Sea region (Petersen 1985c, fig. 5).

The Baltic, region 2

Appendix 6 and Fig. 103

There is no dated record of molluscs from the Subboreal in the Danish part of the Baltic. Therefore the change in the Atlantic *Littorina* fauna, into the *Lymnaea* Sea fauna, which occurred during the Subboreal around 4000 B.P. (Fredén 1980, p. 70), must be taken from observations outside Denmark. The mollusc fauna from Estonia shows that *Littorina littorea*, *Rissoa membranacea*, and *Scrobicularia plana* persisted there until about the end of the Subboreal (Kessel & Raukas 1979, fig. 9). The implications of this should be that these species must have been present in the Danish area throughout the Subboreal.

In the central part of the Baltic, around Gotland, *Lymnaea peregra* f. *baltica* re-immigrates after the

Table 7. Atlantic communities and/or characteristic molluscan species

Region	Community	Species	Depth
1. Bælt Sea	<i>Mytilus</i>	<i>M. edulis/Ostrea edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica/Tapes</i> spp.	shallow
	<i>Abra</i>	<i>A. alba</i>	deeper
2. Baltic	<i>Mytilus</i>	<i>M. edulis/Littorina littorea</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i>	shallow deeper
3. Kattegat	<i>Mytilus</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica/Tapes</i> spp.	shallow
	<i>Abra</i>	<i>A. alba</i>	deeper
4. Limfjord	<i>Mytilus/Modiola</i>	<i>M. edulis/Tapes</i> spp.	littoral
	<i>Macoma</i>	<i>M. balthica</i>	shallow
	<i>Abra/Venus</i>	<i>A. alba</i>	deeper
5. North Sea			littoral
	<i>Venus</i>	<i>Chamelea striatula</i>	shallow deeper
6. Vendsyssel	<i>Modiola</i>	<i>M. modiolus</i>	littoral
	<i>Abra</i>	<i>A. alba</i>	shallow deeper
7. Skagen			littoral
	<i>Amphiura</i>	<i>Parvicardium minimum</i>	shallow ~ 100 m

maximum of the *Littorina* transgression (Munthe 1940, p. 124). This gastropod was also present in the early, more brackish part of the *Littorina* Sea deposits in Fakse Bugt.

In Estonia (Kessel & Raukas 1979, fig. 9), the reappearance of *Lymnaea* took place around 4000 B.P., implying that the salt-demanding species (*Littorina*, *Rissoa*, and *Scrobicularia*) occurred together with the brackish *Lymnaea* species throughout the later part of the Subboreal!

The Kattegat, region 3

Appendix 6 and Fig. 103

The mollusc faunas recorded from the Kattegat region represent only part of the total faunal complex within this large region, and have been dated only on Djursland. However, this demonstrates the expiring tidal amplitude in the early part of the Subboreal.

The only dated immigrants to the fauna from the central part of Djursland during the Subboreal are *Onoba semicostata* and *Littorina tenebrosa*. Both extended into the Baltic today and tolerate brackish water. In this way they are typical for the environmental changes recorded in the marine faunas from Djursland.

The fauna during the Atlantic was characterised by *Ostrea edulis*, *Tapes decussatus*, *Macoma balthica*, and *Corbula gibba*. *Bittium reticulatum* was present in large quantities, but disappeared in the Subboreal. Also the decline in numbers of *Hydrobia ulvae* and its replacement in equal numbers by *Hydrobia ventrosa* speak in favour of a more brackish-water influence. The implications of the study of mollusc species on a quantitative basis in connection with ¹⁴C dates and pollen analyses confirm that the fauna during the *Tapes* Sea period was more prolific than nowadays. However, it also demonstrates as a new point of view that this applies only for the Atlantic. In Petersen (1993, p. 368) it is argued that the change in sedimentation rate from the Atlantic to the Subboreal, which has been calculated for the Korup Sø area on Djursland, points to a lowering of the tidal range in Danish waters since the Atlantic. This is explained in that way that sedimentation will stay low as far as the tidal current reaches and allows halophilous species to live far up in the fjords according to the observations on the faunal record. Furthermore, an older record from the mapping of the area of flaser bedding seen as a tidal bedding supports such an explanation.

It was tempting to see the change from the *Littorina* Sea to the *Lymnaea* Sea in the Baltic on the background of such a lowering of the tidal impact in the inner Danish waters. However, as shown in the preceding section on the Baltic, the change occurred around 4000 B.P.

Recalling the statement by C.G.J. Petersen that the deposition of the *Tapes* layers has happened in a period when the Danish waters from a hydrographical point of view have been more like the North Sea or the open sea than now, it is clear that a tidal impact could make the difference and explain the large oyster banks far into the Roskilde Fjord in north-eastern Sjælland and other former fjord regions facing the Kattegat region.

The well-dated Ertebølle coastal sites ('køkkenmøddinger' – kitchen middens) from all over Denmark also present a large amount of *Ostrea edulis* from the Atlantic and demonstrate that the molluscan diet later in the Subboreal was based on the *Cardium* species (Andersen 1991, 1995). This situation has lasted into the Iron Age, as seen in the shell middens from the Bælt Sea area (Petersen 1985c, fig. 5).

However, this change mostly affected the fjord complex. Consequently the Kattegat region still has the communities listed for the Atlantic.

The Limfjord, region 4

Appendix 6 and Fig. 103

The 36 species which immigrated into the Limfjord during the Subboreal (Appendix 6) can be considered according to their way of life, presented from the list below.

Age: Subboreal

Climatic regions: asb.

Class Gastropoda

Subclass Prosobranchia

Order Archaeogastropoda

Margarites helicinus (Phipps 1774)

Subclass Opisthobranchia

Order Anaspidea

Retusa obtusa (Montagu 1803)

Total for climatic regions asb. : 2 (5.6%)

Climatic regions: asbl

Class Gastropoda

Subclass Prosobranchia
 Order Archaeogastropoda
Acmaea tessulata (Müller 1776)
 Order Neotaenioglossa
Lacuna pallidula (da Costa 1778)
 Total for climatic regions asbl: 2 (5.6%)

Climatic regions: .sbl
 Class Gastropoda
 Subclass Prosobranchia
 Order Archaeogastropoda
Acmaea virginea (Müller 1776)
 Class Bivalvia
 Subclass Pteriomorpha
 Order Pterioidea
Delectopecten vitreus (Gmelin 1791)
 Total for climatic regions .sbl: 2 (5.6%)

Climatic regions: ..bl
 Class Gastropoda
 Subclass Prosobranchia
 Order Archaeogastropoda
Helcion pellucidum (Linnaeus 1758)
Gibbula tumida (Montagu 1803)
Skenea basistriata (Jeffreys 1877)
 Order Neotaenioglossa
Littorina tenebrosa (Montagu 1803)
Lacuna parva (Montagu 1803)
Cingula semistriata (Montagu 1808)
Rissoa violacea Desmarest 1814
Caecum glabrum (Montagu 1803)
Aporrhais pespelicani (Linnaeus 1758)
 Order Heterogastropoda
Epitonium turtonis (Turton 1819)
Vitreolina philippii (Rayneval & Ponzi 1854)
 Order Neogastropoda
Hinia incrassata (Ström 1768)
Raphitoma purpurea (Montagu 1803)
Raphitoma linearis (Montagu 1803)
 Subclass Heterobranchia
 Order Heterostropha
Chrysallida decussata (Montagu 1803)
Chrysallida indistincta (Montagu 1808)
Ebala nitidissima (Montagu 1803)
Eulimella laevis (Brown 1827)
Ondina divisa (J. Adams 1797)
Ondina diaphana (Jeffreys 1848)
 Subclass Opisthobranchia
 Order Anaspidea
Akera bullata Müller 1776
 Class Bivalvia

Subclass Palaeotaxodonta
 Order Nuculoida
Nucula nucleus (Linnaeus 1767)
 Subclass Pteriomorpha
 Order Pterioidea
Palliolum striatum (Müller 1776)
Palliolum tigerinum (Müller 1776)
 Subclass Heterodonta
 Order Veneroida
Mactra stultorum (Linnaeus 1758)
Lutraria lutraria (Linnaeus 1758)
Ensis ensis (Linnaeus 1758)
 Order Myoida
Pholas dactylus Linnaeus 1758
 Total for climatic regions ..bl: 28 (77.8%)

Climatic regions: ...l
 Class Gastropoda
 Subclass Prosobranchia
 Order Neotaenioglossa
Alvania lactea (Michaud 1830)
Onoba proxima (Forbes & Hanley 1850)
 Total for climatic regions ...l: 2 (5.6%)

Total for age Subboreal: 36 (14.6%)

The Archaeogastropoda are all (six) epifauna on seaweeds or on hard substrates.

The Neotaenioglossa have seven epifaunal elements mostly on seaweeds and two infauna species, of which *Aporrhais pespelicani* is a shallow infauna animal.

The Heterogastropoda with *Epitonium turtonis* and *Vitreolina philippii* are associated with other animals, the former feeding on anemone or preying on other species and the latter being an intermittent parasite of echinoderms (Fretter & Graham 1982, p. 387).

The Heterostropha with six species are predators or external parasites.

The Anaspida with two species, *Akera bullata* and *Retusa obtusa*, are epifauna and infauna species respectively, the former on *Zostera* in shallow water and the latter in mud or fine sand connected with the *Macomma* community.

The only Nuculoida found, *Nucula nucleus*, belongs to the shallow infauna.

The Pterioidea with three species are referred to the epifauna, since the *Delectopecten vitreus* is found attached with its byssus on hard substrates.

The Veneroida have three species which are all referred to the infauna. *Lutraria lutraria* and *Ensis ensis* are deep-borrowing.

The Myoida with *Pholas dactylus* bores in different substrates.

When taking the above-mentioned groups of species associated with other animals, carnivores, predators, and boring species as a whole, we have three categories: the epifauna with 47.2%, the infauna with 19.4%, and other elements with 33.4% of the species immigrated during the Subboreal. When the same procedure is followed for the 77 species which have been dated to the Atlantic in the Limfjord region, we find that the percentages for the epifauna, the infauna and other elements are 31%, 46.8% and 22% respectively, which shows that the epifauna element becomes the dominating one in the Subboreal among the newcomers. This might tentatively be connected with a denser vegetation in the Subboreal of sea-weed.

The North Sea, region 5

Appendix 6 and Fig. 103

Nineteen species make their first appearance in the Danish North Sea during the Subboreal.

When considering their way of living and their grouping into epifauna, infauna and other elements, it appears that the groups are of equal size, i.e. five, six and eight species respectively. However, the number is too low to be used for any comparison with other regions. In the North Sea region the dates of first appearance go back to the Preboreal–Boreal stage, showing that the initial stages were dominated by the infauna species; the Preboreal–Boreal: seven epifauna, 16 infauna, and four other elements; the Atlantic: six epifauna, 17 infauna, and four other elements.

The development of the bottom communities in the North Sea region seems in this way to corroborate the changes observed in the Limfjord region from the Atlantic to the Subboreal.

These changes are in facies rather than climatic. A slightly more temperate fauna was met with during the Atlantic, as mentioned earlier, and it has consequently no bearing on the observed changes. But the expiring tidal influence in the Danish waters taking place in the early Subboreal might have been of some importance for the environmental changes reflected through the bottom communities.

The Vendsyssel region, region 6

Appendix 6 and Fig. 103

The Vendsyssel region does not give much information on the immigration of species during the Holocene. However, the *Dosinia* beds were described from this area and have been dated quite recently in the type area around Strandby north of Frederikshavn (Nordmann 1904; Petersen 1991b). The oldest date for the *Dosinia exoleta*, which is the characteristic species for the *Dosinia* beds, is 4240 ± 85 B.P. in ^{14}C years (K-5318). This earliest dated occurrence of *Dosinia exoleta* corresponds to a hydrographical change in the Kattegat region described by Nordberg & Bergsten (1988) and Nordberg (1989). The demonstrated lowering of the tidal influence in the inner Danish waters took place also in the early part of the Subboreal.

Petersen (1976) pointed out that seven mollusc species hitherto known only from the *Dosinia* beds also occur in the raised marine deposits from the western part of the Limfjord, i.e. *Lucinoma borealis*, *Hinia incrassata*, *Venerupis rhomboides*, *Abra prismatica*, *Lutraria lutraria*, *Pholas dactylus*, and *Helcion pellucidum*.

Furthermore, not only ten species from the *Dosinia* beds are also in the deposits from the Limfjord but five of them occurred already during the Atlantic: *Gari fervensis*, *Turritella communis*, *Lucinoma borealis*, *Abra prismatica*, and *Venerupis rhomboides*. These species, representing an infauna assemblage very much like the *Dosinia* species, were also characteristic of the early Holocene dominating infauna mollusc assemblage.

Mörner (1969, pp. 384–386, and table 1) points out that some species in the *Dosinia* fauna occur in older layers along the Swedish west coast, referring to the works by Hessland (1943) and Antevs (1917). However, this is not the case with the characterising *Dosinia* species, in as much as *Dosinia exoleta* has not been demonstrated in the studies by Hessland and Antevs and *Dosinia lincta* occurs only in the younger deposits referred to the Subboreal.

Among the 15 species listed, eight have been recorded from the Limfjord, out of which *Epitonium turtonis*, *Oenopota turricola*, *Acteon tornatilis*, and *Cylichna cylindracea* have their first appearance in the Atlantic, and *Lutraria lutraria*, *Pholas dactylus*, and *Alvania lactea* appeared in the Subboreal, whereas the occurrence of *Modiolus adriaticus* in the Limfjord has not been dated. In this way, we are left with only six species which have not been found in other re-

gions outside Vendsyssel older than the Subboreal: *Pecten maximus*, *Dosinia exoleta*, *Dosinia lincta*, *Gari depressa*, *Alvania cimicoides*, and *Trivia monacha*.

Only the characterising species *Dosinia exoleta* has been dated as mentioned above, and recently *Donax vittatus* from Vr. Holmen in the northern part of Vendsyssel, west of Strandby, with the oldest date of this bivalve hitherto obtained in the Danish deposits, 4240 ± 75 ^{14}C age B.P. (AAR-1481).

This date shows that *Donax* characterising the high-energy shore deposits occurred in Danish waters since the Subboreal.

The further revision of the *Dosinia* fauna shows that only very few species are limited to the Vendsyssel region both in time and space. Therefore, it cannot be sustained for the Danish material as mentioned by Mörner (1969, p. 384) that: "The *Dosinia* layers contains a great number of new boreo-lusitanic immigrants" of the molluscs entirely belonging to the *Dosinia* layers according to Nordmann (1904), only three species, out of the 26 species mentioned, do not occur in Danish waters today, according to Jensen & Knudsen (1995), viz. *Trivia monacha*, *Gari depressa*, and *Alvania cimicoides*.

Only *Trivia monacha* seems to be purely Lusitanian, since a recent distribution to the North Sea is questioned by Fretter & Graham (1981, p. 329), and there is no record from Scandinavia. The other two species have a Boreo-Lusitanian distribution.

The Skagen region, region 7

Appendix 6 and Fig. 103

The 23 species, out of which only *Vitreolina collensi* is purely Lusitanian, can be evaluated according to their way of life.

Vitreolina collensi belongs together with *Aclis minor* and *Melanella alba* to the Eulimacea, which are probably associated with echinoderms (Fretter & Graham 1982, p. 397). The Eulimacea, together with the Epitoniacea, usually prey on anthozoans. The Heterostropha, including the Family Pyramidellidae which lives ectoparasitically on other marine organisms (Jensen & Knudsen 1995), are here represented by *Eulimella scillae*. Finally within the Veneroidae, *Mysella bidentata* and *Tellimya ferruginosa* are commensals on echinoids, but can also be found free-living.

For the rest of the 23 species found during the Subboreal in the Skagen Well, it applies that 16 species

Table 8. Subboreal communities and/or characteristic molluscan species

Region	Community	Species	Depth
1. Bælt Sea	<i>Mytilus</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i> / <i>Ostrea/Paphia</i>	shallow
	<i>Abra</i>	<i>A. alba</i>	deeper
2. Baltic	<i>Mytilus</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i>	shallow deeper
3. Kattegat	<i>Mytilus</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i>	shallow
	<i>Abra</i>	<i>A. alba</i>	deeper
4. Limfjord	<i>Mytilus/Modiola</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i>	shallow
	<i>Venus/Abra</i>	<i>A. alba</i>	deeper
5. North Sea			littoral
	<i>Venus</i>	<i>Chamelea striatula</i>	shallow deeper
6. Vendsyssel	<i>Donax</i>	<i>D. vittatus</i>	littoral
	<i>Dosinia</i>	<i>D. exoleta</i>	shallow deeper
7. Skagen			littoral
	<i>Venus/Turritella</i>	<i>T. communis</i>	shallow deeper

belong to the infauna, including *Onoba vitrea* which tends "to live in muddy places, often so muddy that one wonders how the animals keep the mantle cavity clear" (Fretter & Graham 1978b, p. 170).

It appears from the above-mentioned dates based on type of bottom-dwelling animals that the fauna belongs to the deep-level sea bottoms which goes well together with the *Turritella-Venus* communities.

The recorded Subboreal communities and/or characteristic molluscan species are given in Table 8.

The Subatlantic stage 2500– ^{14}C years B.P.

The configuration of land and sea in the Danish realm was very close to that of today. The isostatic movements during this time span have been so small that they did not affect the general outline (Petersen 1991b). However, the coastal development, in the formation of simplified coastline and spits especially in the west towards the North Sea and in the north facing the Skagerrak and the Kattegat respectively, still affected the contour of the land.

For the main part of the Danish waters, the recent marine bottom communities were established, some of them already since the Atlantic, although the few characterising *Tapes* and *Ostrea* species are no longer extant in great numbers or have totally vanished from the Danish seas. Therefore, the actual map of the Petersen (1914, 1918) bottom communities as seen today will be commented upon in relation to the few, but important changes observed during the Subatlantic, region by region.

The Bælt Sea, region 1

Appendix 6 and Fig. 103

The bottom communities mapped from the Bælt Sea region comprise the *Macoma balthica* community in the shallow-water area and the *Abra alba* community in deeper water (Petersen 1918), the latter community with *Tridonta borealis* and *Macoma calcarea*. The former has been recorded from the subfossil finds but not dated, while the latter has a dated occurrence back in the Atlantic and is considered part of the *Abra alba* community as a deep infauna element.

Considering the present distribution of the *Astarte* species, it is most probable that *Tridonta borealis* invaded the Bælt Sea and the Baltic already in the early Holocene along with the transgression in the Early Atlantic.

The gregarious occurrences of *Ostrea edulis* recorded from the Atlantic in the Bælt Sea region vanished in the Iron Age (Petersen 1985c). This species is no longer found in the Bælt Sea region, nor is *Paphia aurea*, which also occurred at the Iron Age sites too (Petersen 1985c, fig. 5). The steady occurrence of *Ostrea edulis* since the Atlantic, although in reduced numbers, might have led to an experiment in cultivating oysters south of Lolland in the Fehmern Bælt (Winther 1876, p. 114), although an unsuccessful one.

The distribution of oysters within the Danish waters seems to have changed very much right up to the present day, with many records from the 19th century of oyster banks from places where no records are found today (Krøyer 1837; Seaman & Ruth 1997).

The Baltic, region 2

Appendix 6 and Fig. 103

The *Macoma balthica* community covers the whole area of the Baltic, implying that in this area the otherwise shallow-water bivalve extends into greater depths – more than 50 m (Petersen 1918).

Also in this area, *Tridonta borealis* and *Tridonta elliptica* have been found in great quantities east of Bornholm but not dated. However, according to Johansen (1916, fig. 5), *Tridonta borealis* and *Tridonta elliptica* are recorded only from areas with a salinity of more than 10‰, but Zenkevitch (1963, p. 338, fig. 167) points to many finds further to the north in the Baltic, where the salinity is lower.

As stated earlier, the change from the *Littorina* Sea stage to the *Lymnaea* Sea stage took place during the Subboreal. The present situation with a *Mya* Sea stage – a term established by Munthe (1894) – took place at a very late date. Munthe (1894, p. 14) said: “Since *Mya arenaria* is an easily identified and characteristic species in the present Baltic it seems suitable to call the present time the ‘*Mya-time*’ or ‘*Mya arenaria-time*’ in opposition to ‘*Littorina-time*’ etc.”

The Kattegat, region 3

Appendix 6 and Fig. 103

Among the subfossil species both, dated and undated, no records of *Chlamys striatula* and *Turritella communis* are found. These characterising species for the *Venus* and deeper *Venus* communities respectively have a wide extension on the map by Petersen (1918) in the Kattegat region. Also the deeper-water epifaunal elements – characterised by *Modiolus modiolus* – are missing in our subfossil record. Only the *Macoma balthica* and *Abra alba* communities are recognised in the subfossil material. However, the development in the Skagen Well sequence to the north in the Kattegat region of mollusc species reveals the *Venus-Turritella* communities and can be taken as part of the development in the central Kattegat region not sampled at the time of this study on molluscs.

In the present day northern Kattegat, stray specimens of *Ostrea edulis* have been recorded (Jensen & Knudsen 1995, p. 40). Otherwise among the more spectacular *Tapes* Sea species, *Tapes decussatus*, dated from the Atlantic, and *Paphia aurea*, not dated but occur-

ring in the subfossil fauna, have disappeared from the Danish waters.

The Limfjord, region 4

Appendix 6 and Fig. 103

This region has been studied in more detail, regarding the recent fauna, than the other regions, and references can be made also to Jensen (1919).

The *Abra* community is here divided into three associations, i.e. *Nucula-Corbula*, *Abra-Solen*, and *Abra-Solen-Mya* associations. In more shallow water the *Abra* community is replaced by the *Macoma balthica* community. All of these communities are recorded by their mollusc species in the subfossil fauna, here including the *Mya arenaria* in the subfossil assemblage. However, the only dated subfossil immigrating species from the Subatlantic is *Donax vittatus*, which appeared around 2000 years B.P. in the northernmost part of the Limfjord region in the beach ridges, around 1000 years before the closing of the western and northern entrance to the Limfjord.

The closing of the entrances from the North Sea and Skagerrak changed the Limfjord region into a freshwater basin between A.D. 1200 and 1825, however, with periods of saltwater influence (Kristensen *et al.* 1995).

A comparison between the subfossil fauna before the freshwater stage and the recent one after the North Sea broke through in the western part of the Limfjord in 1825 shows that the subfossil fauna had only a slightly higher affinity to more temperate water than the recent one. Also in this place the *Tapes*, *Venerupis* and *Paphia* species make the difference, in the way that only *Venerupis pullastra* finds its way back to the region after 1825.

Paphia aurea, however, has a dated occurrence from the same deposits as *Donax vittatus* to 1910 ± 100 ^{14}C years B.P. (Petersen 1976). It is seen that *Paphia aurea* in this region, as in the Bælt Sea, has a record up into the Iron Age before it became extinct in the Danish waters.

Ostrea edulis repopulated the Limfjord region after 1825 and reached a wide extension in this region already in the second half of the 19th century (Collin 1871). However, the population has suffered from strong fluctuations not only in the Limfjord but also in other Danish waters, as shown on the map by Krøyer (1837).

Spärck in several papers on the biology of oysters (*Ostrea edulis*), published in Reports of the Danish Biological Station, also discussed the fluctuations in the NW European population of oysters (Spärck 1950, pp. 43–45). Spärck reached the conclusion that the summer temperature of the water was crucial, both being too low and too high, which affected the oyster in its reproduction and in food supply respectively. Furthermore, severe winters might affect the population, although less than the summer temperatures. However, these changes did not mean a total disappearance of the oyster, but only a reduction to such a level that the industrial exploitation had to stop.

When taking into account the many studies on the population of oysters, one could use the results in a general conclusion on the variations found in the whole population of molluscan species, especially for the group having their northern limit within the Boreal region: even small variations in the climate may influence the size of the population.

Also the environmental changes as shown within the Danish area during the Holocene, such as the lowering of the tidal amplitude in the early part of the Subboreal, had a severe influence on the populations in the inner Danish waters. Here again, oysters can be taken as an example by the termination of the huge oyster banks known from the Atlantic. Spärck (1950, p. 44) draws attention to the oyster banks in Holland and the British Isles, where the density of the population is far greater because of the tidal movements. However, not only the hydrographical changes through time, in the tide, but also the coastal evolution, such as the formation of simplified coastline and spits, play an important role in the distribution and new finds of molluscan species.

The North Sea, region 5

Appendix 6 and Fig. 103

Only eight species have been recorded as immigrants during the Subatlantic. However, two of them, *Donax vittatus* and *Dosinia lincta*, deserve special attention.

Only *Parvicardium ovale* and *Dosinia lincta* have their first dated appearance. The other species, except *Donax vittatus* with occurrence in the Subboreal, have been recorded from the Atlantic at various places listed in Appendix 6.

In referring to the C.G.J. Petersen bottom community map covering also the North Sea, the *Macoma*

balthica and the *Venus* communities are found in the Danish North Sea coastal region, the former in bays and off the southern part of the west coast (Petersen 1914), the latter around the westernmost part of the Limfjord and the Jydske Rev WNW of the Bovbjerg coastal cliff (Petersen 1994a).

A landscape like the Limfjord of today was found 75 km towards WNW in the area of the Jydske Rev. Following the transgression in the early part of the Holocene, the glacial landscape in an area of the present Jydske Rev was eroded and the high-energy coast approached the appearance of the present one. In the northern part forming an erosion coast and in the southern part at Blåvands Huk an aggradation coast, both characterised by the presence of *Donax vittatus*.

In the southern part the aggradation started around 800 BC some 2000 m east of the present coastline (Petersen 1994a, p. 24) as seen from the dating of *Donax vittatus* to 2620 ± 75 B.P. ^{14}C years (AAR-1480) off the inland cliff at Grærup (Fig. 1).

At Bovbjerg, the strata with *Donax vittatus* in the Agger spit are dated to 410 ± 65 B.P. (Petersen 1985a). The formation of the spits closing the former bays on the Jylland west coast is a consequence of the formation of a simplified coast. Further to the north, *Donax vittatus* from Kovad Bro in the northernmost part of the Limfjord, 6 km inland, gave a date of 1910 ± 100 B.P. (Petersen 1976), showing that the beach progressed 6 km during approximately 2000 years (Petersen & Andreasen 1989, fig. 1).

It is tempting to introduce the idea that the enormous change in the land–sea configuration in the eastern part of the North Sea affected the tidal currents in the inner Danish waters. This could possibly have occurred when most of the Jydske Rev Formation was eroded to such a level that the tidal current from the south was no longer braked and consequently the present-day interference with the tidal current came into existence. It is the interference between the two tidal currents in the Skagerrak today that makes the tidal amplitude small in the inner Danish waters (Nielsen 1939; Kuenen 1950).

Dosinia linctia has been dated (870 ± 110 B.P. ^{14}C years) in the Jydske Revsand Formation in the vibrocore 562001 around 75 km off the coast of Jylland at a depth of 32 m (Petersen 1994a, p. 18, fig. 3).

The assemblage from these strata comprises *Spisula subtruncata*, *Phaxas pellucidus*, *Fabulina fabula*, *Chamelea striatula*, *Dosinia exoleta*, *Corbula gibba*, *Cochlodesma praetenua* and *Thracia phaseolina*, most of them characterising the Jydske Revsand Formation.

The Vendsyssel region, region 6

Appendix 6 and Fig. 103

The coastal development in the eastern part of the region facing the Kattegat takes place in the form of migrating bars (Schou 1949, fig. 17b), the so-called Rimmer and Doppe system *sensu* Jessen (1905).

The *Venus* and the *Macoma balthica* communities are found in the coastal zone, the former dominating in the northern part, whereas the latter forms a small area between shore and the *Venus* community to the south towards the entrance to the Limfjord at Hals (Petersen 1918).

In the north at Strandby, *locus typicus* of the *Dosinia* beds, the layers with *Dosinia exoleta* are superposed by a layer characterised by *Spisula subtruncata*. These beds with *Spisula* in great quantities were dated to 2640 ± 75 (Petersen 1991b), the end of the Subboreal, and at a level of 4.2 m a.s.l. This corresponds to a stage in the development of the Skagen spit up to 4 km south of Højen, where the beach ridges have an elevation of 5 m a.s.l.

In the southern part of the Vendsyssel region around Hals another of the faunal elements of the *Dosinia* beds – *Lutraria lutraria* – has for long been regarded as extinct (Petersen 1992). However, “from 1990 onwards live specimens have been collected regularly near Frederikshavn and on the Skagerrak-coast” (Jensen & Knudsen 1995, p. 43).

Also many shells of *Lutraria lutraria* were found along the shore south of Jerup halfway between Frederikshavn and Aalbæk.

The immigration of *Mya arenaria* cannot be taken as an indication of changes in climate, as this species mainly belongs to the Boreal region and has been transferred by man from North America. What made the find so important has a more historical than geological bearing, namely that the dates obtained from the sampling at Jerup demonstrated that the American soft-shell clam (*Mya arenaria*) predated Columbus' voyage in 1492, having an age of A.D. 1245–1295 at ± 1 s.d. This led to the conclusion that the Vikings were better candidates than Columbus to be the first to find North America (Petersen *et al.* 1992b).

The significance of changes in facies is clearly demonstrated in the next and final section describing the Subatlantic faunal development in the Skagen region.

The Skagen region, region 7

Appendix 6 and Fig. 103

The Subatlantic molluscan fauna from the Skagen Well comprises 68 species with 75% belonging to the Boreo-Lusitanian region and only one Lusitanian species, *Vitreolina collensi*. However, the more interesting fact from the younger part of the Skagen sequence is the total lack of *Macoma balthica*. In this way it presents the finest resemblance with the recent bottom community map (Petersen 1918), and shows that the *Macoma balthica* community disappears in the northern part of the east coast of Jylland. This means that during the last stage of the spit formation at the site of the present Skagen animals, from the *Venus* community dominated along shore. This is also documented by the high amount of infauna elements, with 35 out of the 68 species recorded.

Furthermore, some of the 11 epifauna gregarious species usually connected with the vegetation can be excluded, since they occur only as stray finds, viz. *Lacuna pallidula*, *Rissoa violacea*, and *Bittium reticulatum*, as discussed earlier.

The rest of the molluscs (22 species) are carnivores, predators, external parasites, and commensals.

Turning these figures into percentages, the epifauna species amount to 16.2% and the infauna to 51.5%.

Comparing this with the Limfjord region where an equal number of species have been found during the Atlantic and the Subboreal, it appears that the number of infauna species from the Atlantic to the Subboreal falls from 46.8% to 19.4% and the epifauna elements rise from 31.2% to 47.2% in the Limfjord.

Counting the Limfjord region as an inner Danish water today, it is worth noticing that during the Atlantic the situation was much more like the 'open' waters as seen in the Skagen figures.

Table 9. Subatlantic communities according to the bottom community maps* with characteristic molluscan species

Region	Community	Species	Depth
1. Bælt Sea	<i>Mytilus</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i> ± <i>Ostrea/Paphia</i>	shallow
	<i>Abra</i>	<i>A. alba</i>	deeper
2. Baltic	<i>Mytilus</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i> + <i>Mya arenaria</i>	shallow
	<i>Macoma</i>	<i>M. balthica</i>	deeper
3. Kattegat	<i>Mytilus</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i>	shallow
	<i>Abra/Venus</i>	<i>A. alba</i>	deeper
4. Limfjord	<i>Mytilus/Modiola</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i> ± <i>Paphia aurea</i>	shallow
	<i>Abra</i>	<i>A. alba</i>	deeper
5. North Sea	<i>Donax</i>	<i>D. vittatus</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i>	shallow
	<i>Venus</i>	<i>Chamelea striatula</i>	deeper
6. Vendsyssel	<i>Macoma</i>	<i>M. balthica</i>	littoral
	<i>Venus</i>	<i>Chamelea striatula</i>	shallow
			deeper
7. Skagen	<i>Donax</i>	<i>D. vittatus</i>	littoral
	<i>Spisula</i>	<i>S. subtruncata</i>	shallow
	<i>Venus</i>	<i>Chamelea striatula</i>	deeper

*Petersen (1914, 1918).

Considering that the tidal amplitude really was lowered in the early part of the Subboreal, this would to some extent explain the observed changes in the Limfjord from the Atlantic to the Subboreal.

The recorded Subatlantic communities according to the maps by Petersen (1914, 1918) with characteristic molluscan species are shown in Table 9.

Concluding remarks

In the last section on the environmental changes within the seven regions through the Late Quaternary, it has been demonstrated how the Skagen sequence 'moved' into the present-day faunal community known from this area, 'coming' from older deposits in many ways, according to the molluscs, different from what hitherto was known in other parts of the Danish area during the Late Quaternary. The development is graphically shown in Fig. 93 (fold-out, back cover).

Regarding the climatic changes, recalling Figs 102 and 103, the molluscs have given a clear record as far as the main trends are concerned – the interglacial–glacial cycle. However, the climatic changes during the Holocene, if they were ever more than small, were overshadowed by the facies changes affecting the Danish area. From the Eemian as well, it must be concluded that differences in facies made the difference between the regions, and that the well-established more temperate Eemian marine fauna was connected only with the shallow-water environment.

Among the 140 species recorded from the Eemian, 118 or 84.3% occur in the Holocene subfossil material and/or recent fauna. However, it should be noticed that among the 22 species only found in the Eemian, ten species or 45.5% are purely Lusitanian forms, which include the no longer extant species *Paphia senescens*. The Lusitanian forms are: one gastropod – *Haminoea navicula*; one Scaphopod – *Dentalium vulgare*; and seven bivalves – *Mytilaster lineatus*, *Mytilaster solidus*, *Lucinella divaricata*, *Plagiocardium papillosum*, *Gastrana fragilis*, *Abra segmentum* and *Gouldia minima*.

Along with the high percentage of purely Lusitanian forms – compared with and not found in the Holocene – it is shown that among the 90 Boreo-Lusitanian species from the Eemian, by far the dominating group covering 64.3% of the fauna, 87 species occur also in the Holocene.

The Weichselian marine fauna known from the Older *Yoldia* and Younger *Yoldia* Sea deposits also has a characteristic of its own, with about one third of the fauna restricted to the *Yoldia* seas. Nearly half of them are either purely Arctic, such as the two bivalves *Portlandia arctica* and *Macoma torelli*, or with Arctic–Subarctic affinities, such as the three gastropods *Alvania cruenta*, *Turritella erosa* and *Cylichna occulta*, and the four bivalves *Bathyarca glacialis*, *Macoma loveni*, *Pandora glacialis*, and *Lyonsia arenosa*. One third of

the Weichselian fauna is found both among the Eemian and the Holocene species (subfossil and/or recent). For the last third, the majority (11 out of 17) are also recorded only from the Holocene.

When the Weichselian marine fauna itself is looked at, comparing the Older and Younger *Yoldia* Sea faunas, 23 out of the 54 species are common to both, while one third is only found in the Younger *Yoldia* Sea deposits from where the Subarctic–Boreal species among the bivalves are: *Nuculana minuta*, *Arctica islandica*, and *Zirfaea crispata*. The Subarctic–Boreal–Lusitanian species count one polyplacophor: *Tonicella marmorea*; one gastropod: *Buccinum undatum*; and two bivalves: *Mytilus edulis* and *Macoma balthica*. This demonstrates in the best way the Boreo-Arctic impact around 13 000 B.P. (¹⁴C years) in the shallow-water environment characterised by *Zirfaea crispata* and *Mytilus edulis* – the former giving name to the deposits of that time in Vendsyssel.

However, the main result of this investigation was the comparison between the fossil faunas and the molluscan faunas now living before our eyes – as C.G.J. Petersen expressed it in 1910 – using the C.G.J. Petersen bottom community concept step by step in the seven stages from the Eemian to the Subatlantic within the seven regions in the Danish realm.

Acknowledgements

This study was supported by a one-year grant from the Carlsberg Foundation. During that year – and the following years – the Geological Survey of Denmark and Greenland (GEUS) has supplied me with all the facilities needed for the research. The support of both these institutions is greatly appreciated.

Among the many helpful colleagues at the Survey, I would like to thank Lasse Gudmundsson for keeping order in the many samples that were analysed, and Frants von Platen-Hallermund for making the compilations seen in the figures and appendix listing the molluscan species and other data.

State Geologist at that time Johnny Fredericia, who caused me to take up the challenge and continued to support me is thanked, as is Richard Bradshaw, State Geologist of my new department at the Survey, the Department of Environmental History and Climate

Change. J. Heinemeier contributed with Appendix 4 on the ^{14}C dates on shell macrofossils from the Skagen cores. Kaare L. Rasmussen read an early draft of the work and the referees H.G. Petersen and S. Funder contributed to make the work better – all are thanked.

With great experience in writing for me, Birgit Jørgensen did the typing and commented upon the

English. Susanne Veng Christensen has made the final copy.

Peter John Crabb revised the English in the most thorough way.

To the former curator of the Vertebrate Collection at the Geological Museum, University of Copenhagen, now happily at the Gram Museum, Ella Hoch, this book is dedicated.

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List of synonyms

- Abra alba* (Wood 1802)
Syndesmya alba
- Abra nitida* (Müller 1776)
- Abra prismatica* (Montagu 1803)
Syndesmya prismatica
- Abra segmentum* (Récluz 1843)
Syndesmya ovata
- Acanthocardia echinata* (Linnaeus 1758)
Cardium echinatum
- Acar nodulosa* (Müller 1766)
- Aclis ascaris* (Turton 1819)
- Aclis minor* (Brown 1827)
- Aclis walleri* Jeffreys 1867
- Acmaea tessulata* (Müller 1776)
- Acmaea virginea* (Müller 1776)
Tectura virginea
- Acteon tornatilis* (Linnaeus 1758)
- Adipicola simpsoni* (Marshall 1900)
- Admete viridula* (Fabricius 1780)
- Aequipecten opercularis* (Linnaeus 1758)
Pecten opercularis
- Akera bullata* Müller 1776
- Alvania abyssicola* (Forbes 1850)
Rissoa abyssicola
- Alvania cimicoides* (Forbes 1844)
Rissoa cimicoides
- Alvania cruenta* Odhner 1915
- Alvania jan mayeni* (Friele 1886)
Rissoa jan mayeni
- Alvania jeffreysi* (Waller 1864)
- Alvania lactea* (Michaud 1830)
Rissoa lactea
- Alvania punctura* (Montagu 1803)
Rissoa punctura
- Alvania scrobiculata* (Möller 1842)
Rissoa scrobiculata
- Amauropsis islandicus* (Gmelin 1791)
- Angulus fabulus* → *Fabulina fabula*
- Angulus tenuis* (da Costa 1778)
Tellina tenuis
- Anomia aculeata* → *Heteranomia squamula*
- Anomia ephippium* Linnaeus 1758
- Anomia patelliformis* → *Pododesmus patelliformis*
- Anomia squamula* → *Heteranomia squamula*
- Antalis agile* G.O. Sars 1878
- Antalis entalis* (Linnaeus 1758)
Dentalium entalis
- Aporrhais pespelicani* (Linnaeus 1758)
- Aporrhais serresianus* (Michaud 1828)
- Arca glacialis* → *Bathyarca glacialis*
- Arcinella plicata* → *Saxicavella jeffreysi*
- Arcopagia crassa* (Pennant 1778)
- Arctica islandica* (Linnaeus 1767)
Cyprina islandica

Assiminea grayana Fleming 1828
Astarte banksie → *Tridonta montagui*
Astarte borealis → *Tridonta borealis*
Astarte compressa → *Tridonta elliptica*
Astarte sulcata (da Costa 1778)
Axinopsida orbiculata (G.O.Sars 1878)
 Axinopsis orbiculata
Axinopsis orbiculata → *Axinopsida orbiculata*
Axinus ferruginosus → *Leptaxinus ferruginosus*
Axinus flexuosus → *Thyasira flexuosa*
Balcis devians → *Vitreolina philippii*
Barleeia unifasciata (Montagu 1803)
Barnea candida (Linnaeus 1758)
 Pholas candida
Bathyarca glacialis (Gray 1824)
 Arca glacialis
Bathyarca pectunculoides (Scacchi 1834)
Bela exarata G.O.Sars 1818
Bela incisula → *Oenopota incisula*
Bela nobilis → *Oenopota turricola*
Bela trevelliana → *Oenopota trevelliana*
Bela turricola → *Oenopota turricola*
Bela violacea → *Oenopota violacea*
Bittium reticulatum (da Costa 1778)
 Cerithium reticulatum
Boreotrophon clathratus (Linnaeus 1767)
 Trophon clathratus
Boreotrophon truncatus (Ström 1768)
Brachystomia carozzai van Aartsen 1987
Brachystomia eulimoides Hanley 1844
 Odostomia eulimoides
 Odostomia pallida
Buccinum cyaneum Bruguière 1792
 Buccinum groenlandicum
Buccinum groenlandicum → *Buccinum cyaneum*
Buccinum undatum Linnaeus 1758
Cadulus jeffreysi → *Cadulus subfusiforme*
Cadulus subfusiforme (M. Sars 1865)
 Cadulus jeffreysi
Caecum glabrum (Montagu 1803)
Calliostoma formosa (Mighels 1842)
Calliostoma zizyphinum (Linnaeus 1758)
Callochiton septemvalvis (Montagu 1803)
Capulus ungaricus (Linnaeus 1758)
Cardium ciliatum → *Clinocardium ciliatum*
Cardium echinatum → *Acanthocardia echinata*
Cardium edule → *Cerastoderma edule*
Cardium edule → *Cerastoderma glaucum*
Cardium exiguum → *Parvicardium exiguum*
Cardium fasciatum → *Parvicardium ovale*
Cardium groenlandicum → *Serripes groenlandicus*

Cardium minimum → *Parvicardium minimum*
Cardium nodosum → *Parvicardium scabrum*
Cardium norvegicum → *Laevicardium crassum*
Cardium papillosum → *Plagiocardium papillosum*
Cerastoderma edule (Linnaeus 1758)
 Cardium edule
Cerastoderma glaucum (Poiret 1789)
 Cardium edule var. *balticum*
Cerithiella metula (Lovén 1846)
Cerithiopsis barleei Jeffreys 1867
Cerithiopsis tubercularis (Montagu 1803)
Cerithium reticulatum → *Bittium reticulatum*
Chamelea striatula (da Costa 1778)
 Venus gallina
Chemnitzia lactea → *Turbonilla lactea*
Chlamys islandica (O.F.Müller 1776)
 Pecten islandicus
Chlamys varia (Linnaeus 1758)
 Pecten varius
Chrysallida eximia (Jeffreys 1849)
 Parthenina eximia
Chrysallida decussata (Montagu 1803)
Chrysallida indistincta (Montagu 1808)
 Parthenia indistincta
Chrysallida obtusa (Brown 1827)
 Parthenia interstincta
Chrysallida spiralis (Montagu 1803)
 Parthenia spiralis
Cingula proxima → *Onoba proxima*
Cingula semistriata (Montagu 1808)
 Putilla semistriata
 Rissoa semistriata
Cingula striata → *Onoba semicostata*
Cingula turgida (Jeffreys 1870)
Cingula vitrea → *Onoba vitrea*
Circe minima → *Gouldia minima*
Claturella linearis → *Raphitoma linearis*
Clausinella fasciata (da Costa 1778)
 Venus fasciata
Clinocardium ciliatum (Fabricius 1780)
 Cardium ciliatum
Clione limacina (Phipps 1774)
Cochlodesma praetenuae (Pulteney 1799)
Colus gracilis (da Costa 1778)
Colus jeffreysianus (Fischer 1868)
Colus sabini (Gray 1824)
Corbula gibba (Olivi 1792)
Crenella decussata (Montagu 1803)
Crepidula fornicata (Linnaeus 1758)
Cultellus pellucidus → *Phaxas pellucidus*
Cupidaria cuspidata (Olivi 1792)

Cyamium minutum → *Turtonia minuta*
Cylicbna alba (Brown 1827)
Cylicbna cylindracea (Pennant 1777)
Cylicbna occulta (Mighels 1841)
 Cylicbna scalpta
 Cylicbna propinqua
Cylicbna propinqua → *Cylicbna occulta*
Cylicbna scalpta → *Cylicbna occulta*
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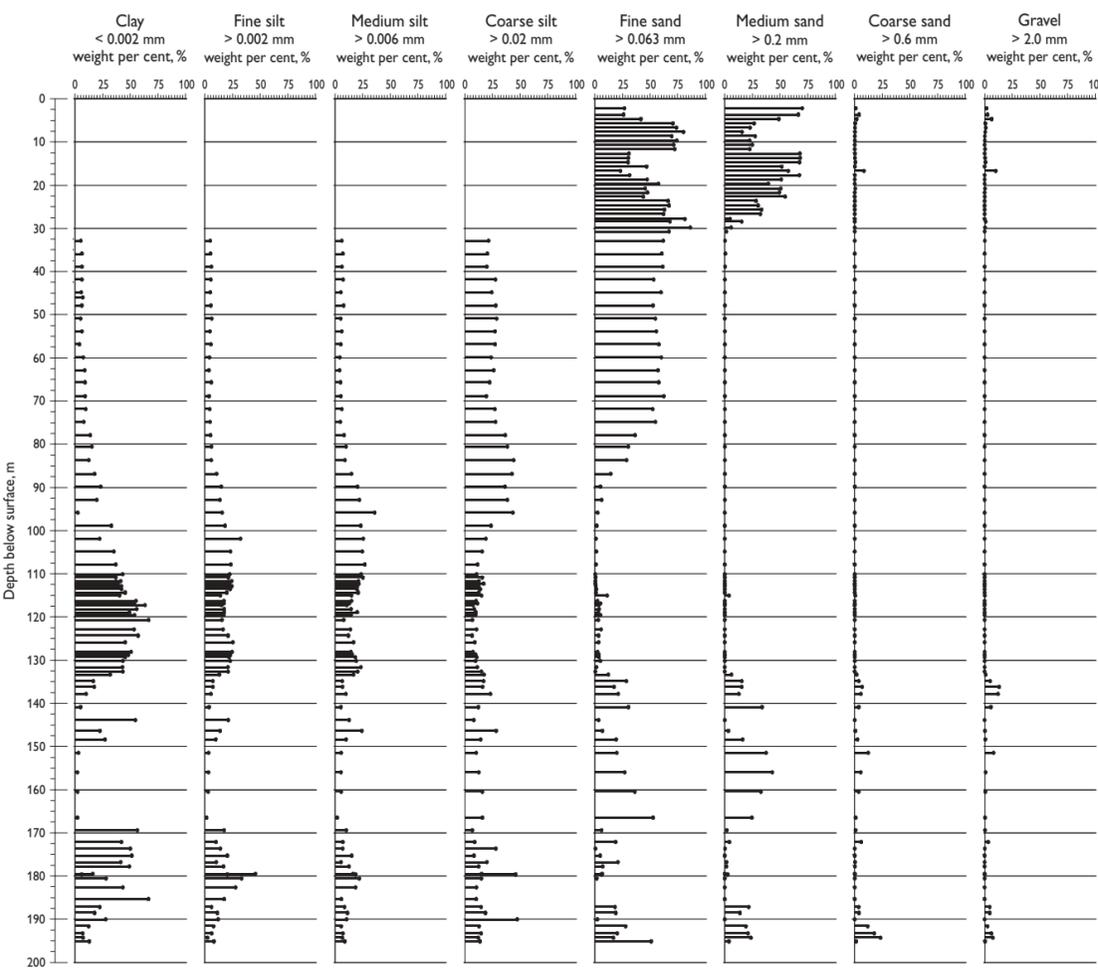
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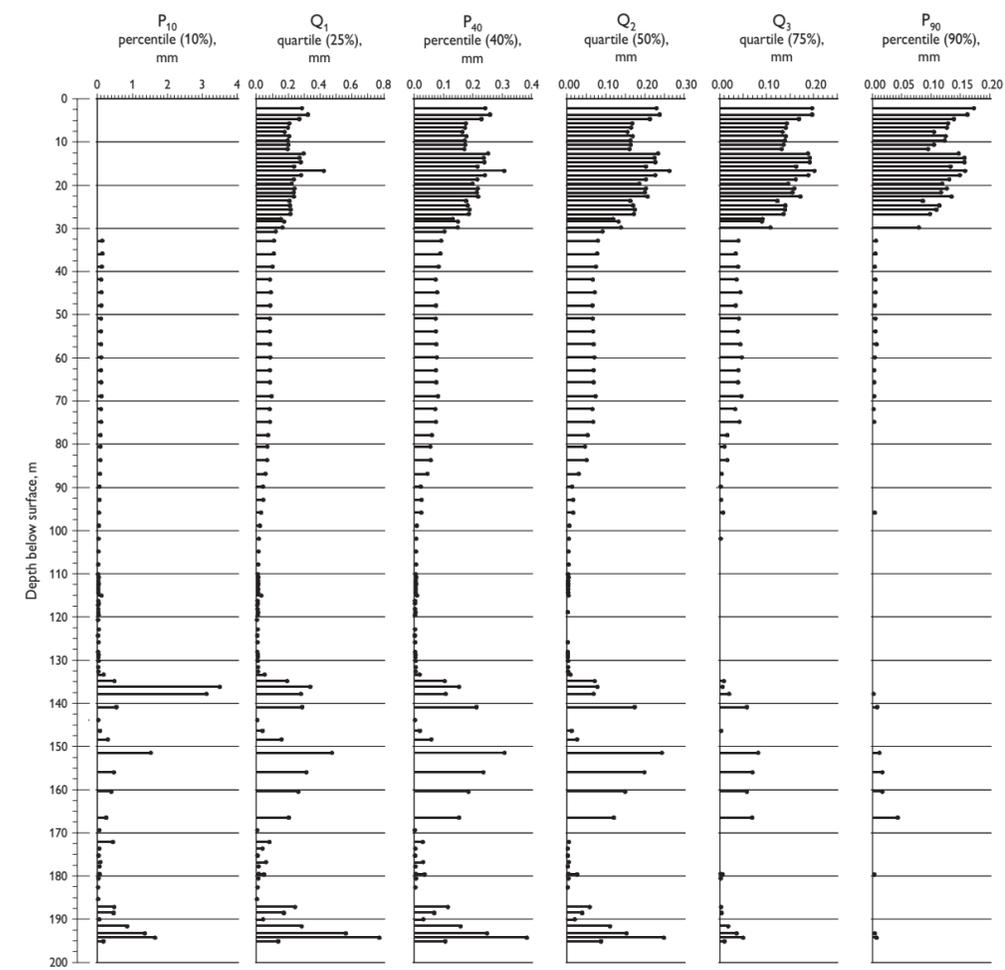
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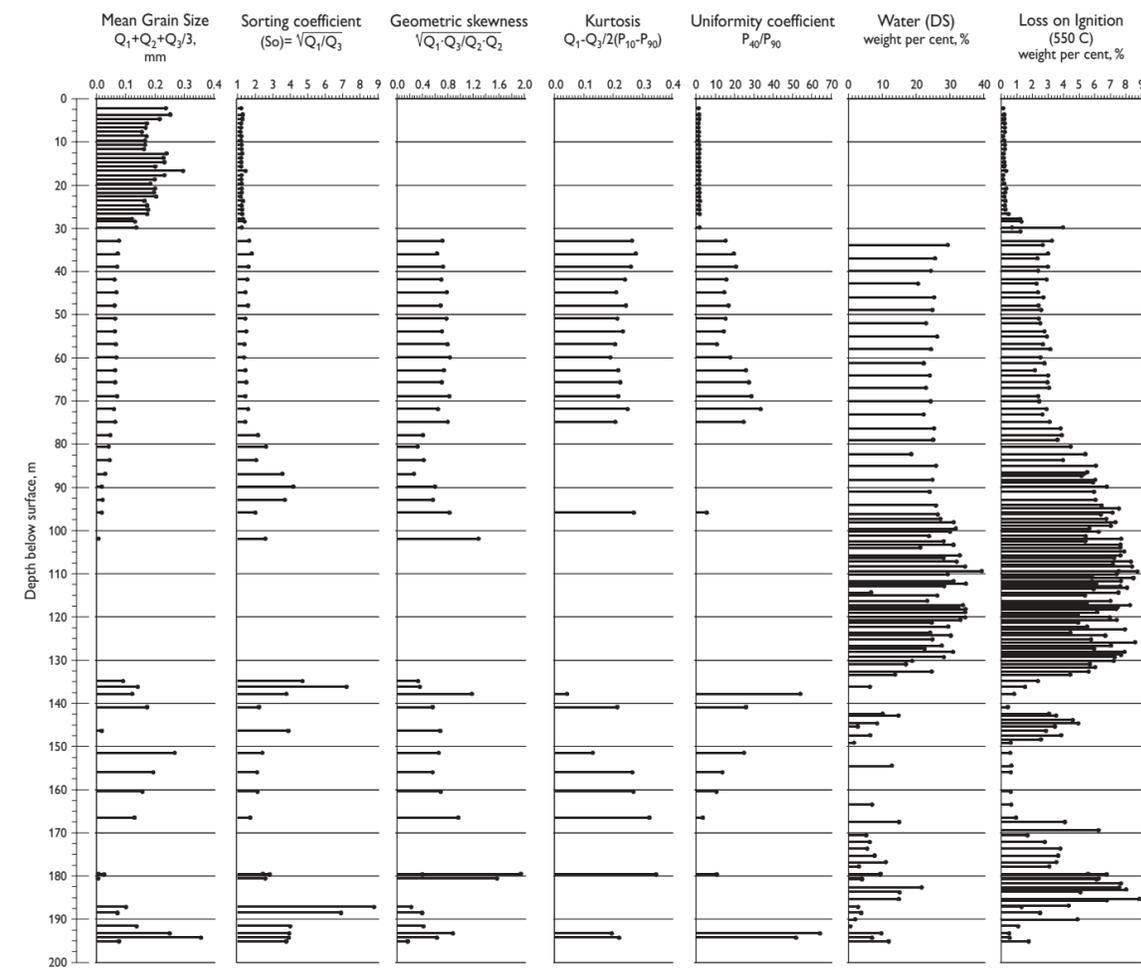
A: Grain size distribution



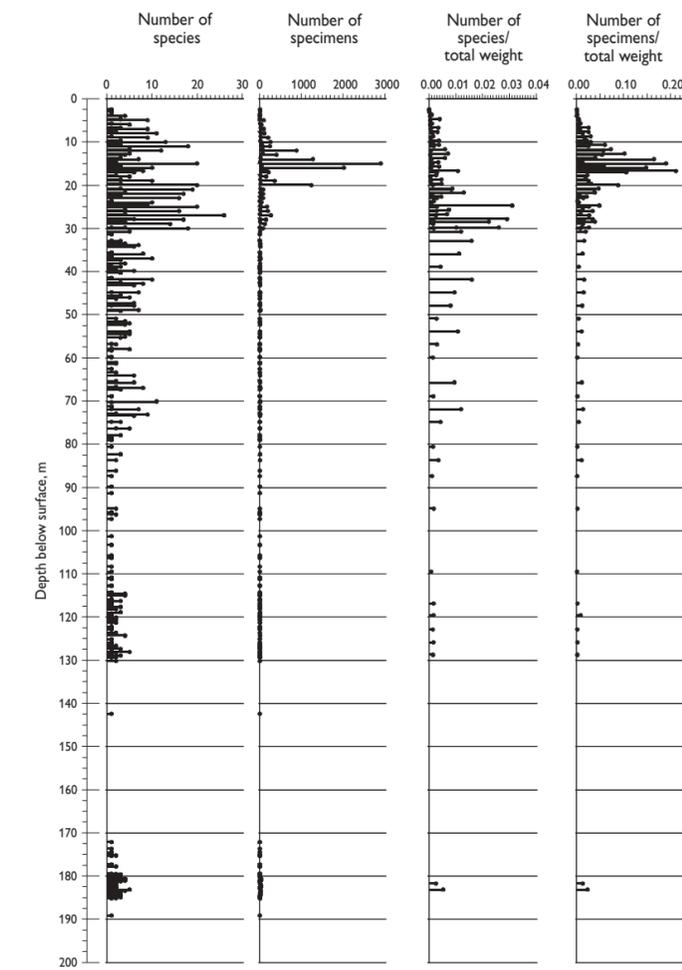
B: Quartiles and percentiles



C: Classification of fragmental deposits



D: Species and specimens diversity



E: Occurrences of minerals, fossils and reworked molluscs

