# Chapter 7
# Systematic Overview of the Pliocene Molluscs and Barnacles of the Barmur Group on Tjörnes, North Iceland

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**Abstract** Systematic overview of the molluscan and barnacle assemblages of the Pliocene Tjörnes sequence in North Iceland is primarily based on collections and fieldwork carried out during the last 50 years and collections of the Institute of Natural History in Reykjavík, the Geological Museum in Copenhagen, and the collection of the late farmer Jóhannes Björnsson in Ytri-Tunga on Tjörnes. We have identified 65 species of prosobranch gastropods, five opistobranch gastropod, 49 bivalve, one ammonite, and one barnacle species. Of the 119 molluscan species, 24 have not been recorded before from Tjörnes. About 25% of the mollusc species are extinct, and 25 of the recent molluscan species now live in southerly localities with higher sea temperatures. At least 32 of the species have their first appearance (FAD) in Tjörnes. The species are depicted on plates and variation in shape is demonstrated wherever possible. The distribution, recent or fossil, of species is shown, and ecological and biological features discussed. The larval development of the species is also summarized. The Tjörnes fauna is major record of trans-Arctic oceanic interchange that has been imperative in shaping the modern North Atlantic faunas. This review enables us to improve our understanding of the interchange.

**Keywords** Mollusc migration · Zoogeography · Pliocene paleoecology · Marine invertebrate systematics · Tjörnes · Iceland

## 7.1 Paleontology

The nomenclature used in this chapter mostly adheres to standard nomenclature used in, for example, Molluscabase, which is a taxonomically oriented database. Partly it follows that of "Treatise on Invertebrate Paleontology" (Moore, 1960, 1969a, 1969b), with additions from Lemche (1948), Ockelmann (1958), MacNeil

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(1965, 1967), Strauch (1972), Warén (1974, 1989, 1996a, 1996b), Bernard (1979), Lubinsky (1980), Høisæter (1986), Graham (1988), Bogdanov (1990), Golikov (1995), Sneli et al. (2005), Wesselingh and Pouwer (2011), Pouwer and Wesselingh (2012), and several other malacologists. The name of the *Balanus* is from Zullo (1968).

A few explanations are necessary about the terms used in the chapter. When dealing with conispiral gastropods the term "diameter" always means the maximal outer diameter of the shell. The following abbreviations are used: d = diameter, h = height, hlw = height of last whorl (body whorl), ha = height of aperture, h/d = height/diameter ratio, h/l = height/length ratio, and b/l = breath/length ratio. The terms length and breadth are used in the case of patellate gastropods (cf. Cox, 1960).

When dealing with bivalves the term "paired" always means that the valves were found articulated (united) in the sediment, whereas "single" means that they were disarticulated when collected. The following abbreviations are used: l = length, h = height (from the beak to the ventral margin), and b = breath (from the surface of the left valve to the surface of the right valve).

The stratigraphical terms are as far as possible adjusted to the traditional Pliocene/Pleistocene boundary in the Northern Hemisphere at 2.5–2.6 Ma (cf. Eiríksson, 2008; Gibbard et al., 1991; Símonarson et al., 1998; Zagwijn, 1992).

The distribution of the fossils in the Barmur Group is based on Bárðarson (1925), who divided the Tjörnes beds into 25 distinct shell bearing units, which he numbered 1–25, and 10 terrestrial or transitional horizons designated A–J (Fig. 7.1). He grouped the shell units into three biozones: the *Tapes* Zone (oldest), the *Mactra* Zone, and the *Cardium groenlandicum* or *Serripes* Zone (youngest).

The zoogeographical division of the North Atlantic is modified after Feyling-Hanssen (1955b), Dinter (2001), and Funder et al. (2002) based on the occurrence of indicator species (Fig. 7.2). The division of the Canadian Arctic and Northwest Atlantic follows Lubinsky (1980).

## 7.2 Gastropoda Prosobranchia

**Phylum Mollusca Linné, 1758**
**Class Gastropoda Cuvier, 1797**
**Subclass Prosobrancia Milne Edwards, 1848**
**Order Archaeogastropoda Thiele, 1925**
**Family Fissurellidae Fleming, 1822**
**Genus *Emarginula* Lamarck, 1801**

***Emarginula crassa* Sowerby, 1813**
Plate 7.1. Fig. 1

1813 *Emarginula crassa* – Sowerby: p. 73, Pl. 33, figs. 1–2.
1848 *Emarginula crassa*. J. Sow. – Wood: p. 165, Pl. 18, fig. 2a–e.
1878 *Emarginula crassa*, Sowb. – Sars: p. 125–126.

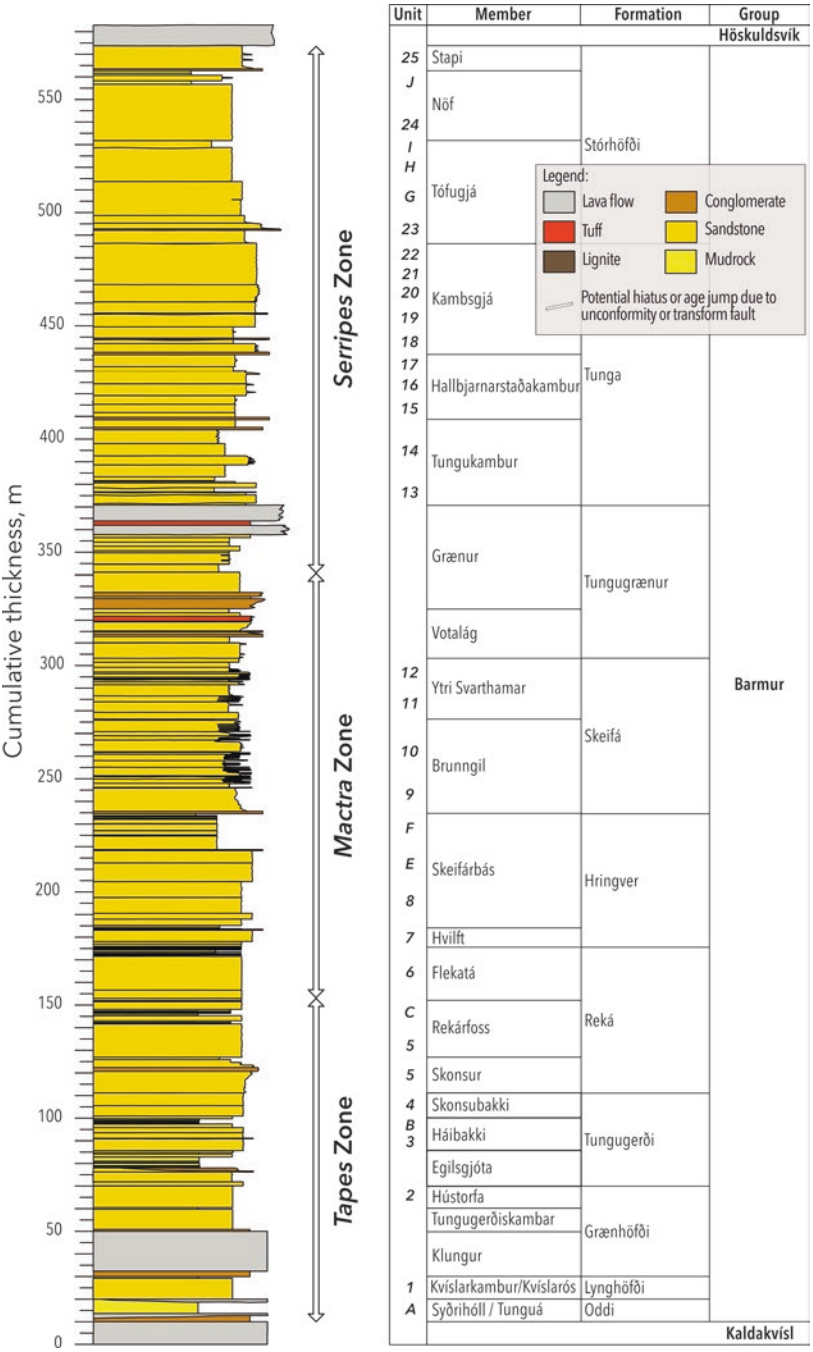

**Fig. 7.1** Stratigraphic column of the Barmur Group in the Tjörnes sequence (see also Eiríksson et al., 2020a). Unit numbers refer to the beds of (Bárðarson, 1925). The width of the column reflects grain-size changes from mudrocks and lignites (narrow) to conglomerates (wide)

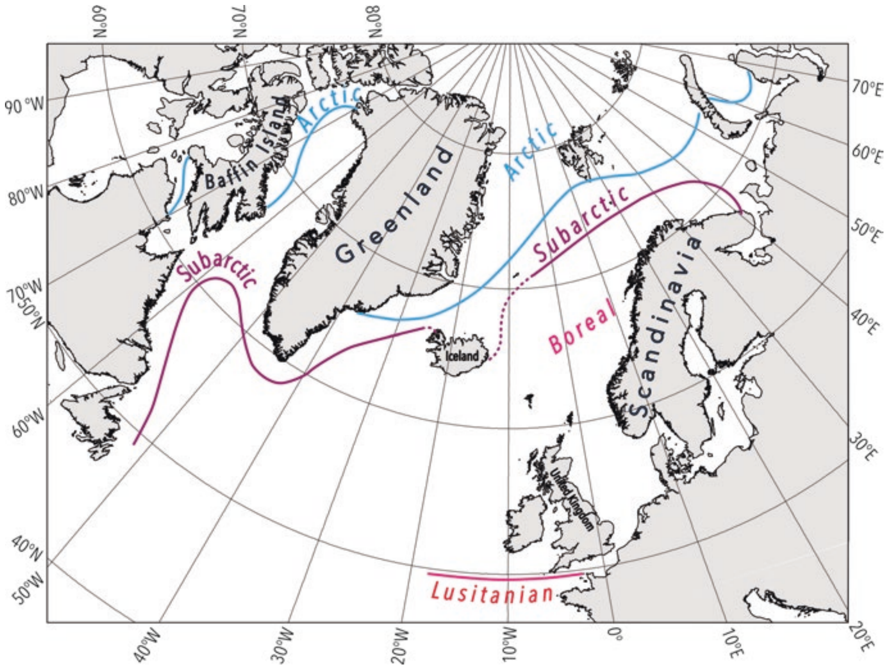

**Fig. 7.2** Zoogeographical division of the North Atlantic. The division is modified after Feyling-Hanssen (1955b), Dinter (2001), and Funder et al. (2002), and the division of Canadian Arctic and northwestern Atlantic follows Lubinsky (1980)

1923 *Emarginula crassa*, J. Sowerby – Harmer: p. 774–774, Pl. 62, figs. 1–3.
1924 ?*Emarginula crassa* Sowerby – Schlesch: p. 339 (from an unpublished manuscript, Poulsen, 1884).
1925 *Emarginula crassa*, Sow. – Bárðarson: p. 44, 74.

*Material:* Two shells from unit 10 in the *Mactra* Zone. Furthermore, Schlesch (1924) reported one specimen when he referred to unpublished manuscript by C. M. Poulsen (1884) kept in the Geological Institute of the University of Copenhagen. Bárðarson (1925) found few specimens in unit 11 and Norton (1975) also listed it as satisfactorily named without information about how many specimens he identified. With the exception of Bárðarson, these authors did not give any information about the stratigraphical distribution of the species in the Tjörnes beds.

*Remarks:* One of the shell is intact and measures (l × b × h): 17.8 × 12.8 × 8.6 mm. The anterior margin of the conical shell is marked by a short slit that continues up to the apex as a shallow groove. The shell is ornamented with numerous fine ridges, radiating from the apex, usually grouped in three or four ribs. They are decussated by fine concentric markings. The inner margin has crenulated edges (see Plate 7.1, Fig. 1). The ornamentation is on the whole finer than in typical *Emarginula fissura* Linné, 1758, and not as cancellated in appearance. Therefore, these specimens from the *Mactra* Zone are most comparable to *E. crassa*.

*Recent distribution, ecology, and biology: Emarginula crassa* is mainly a boreal species, but extends into the lusitanian region of the North Atlantic. From Iceland and western Norway (near 70°N) in the north, it extends to Spain and the Azores in the south (Høisæter, 1986; Óskarsson, 1982; Sneli et al., 2005). It has been recorded from Halland on the west coast of Sweden, but not from the Baltic or the Mediterranean (Sneli et al., 2005). In the Faroe Islands it prefers temperatures between 7.0 and 8.0 °C. Bathymetrical range: from the low water stand (the British Isles) to 600 m, but off the west coast of France it has been reported from depths of 748 to 1262 m (Sneli et al., 2005). The salinity tolerance is not well known, but most probably the species was living in polyhaline or euhaline water when the upper part of the *Mactra* Zone was deposited. There are no signs of reduced salinity or brackish water as preferred by some recent *Emarginula* species (cf. Graham, 1988). The larval development is not known.

*Emarginula crassa* is mostly a sublittoral species that lives on and under hard substrates (Poppe & Goto, 1991). In the Faroe Islands it seems to prefer soft bottom (Sneli et al., 2005). The species is algal-feeding (grazing) as other archaeogastropods, using the rasp-like tongue, with which it scrapes its food from the surface (Thorson, 1941; Thorson, 1944).

*Fossil occurrence:* Pliocene: Coralline Crag Formation in England (Harmer, 1923; Wood, 1848). Luchtbal Sand Member of the Lillo Formation in Belgium (Marquet & Landau, 2006). Pliocene/Lower Pleistocene: Red Crag Formation in England (Harmer, 1923), Walcheren, Ritthem, and Westerschelde beds in the Netherlands (van Regteren Altena et al., 1954). Various Netherlandish beaches (Wesselingh & Pouwer, 2011). Stratigraphical range: Pliocene to Recent.

### Family Patellidae Rafinesque, 1815
### Genus *Patella* Linné, 1758

### *Patella vulgata* Linné, 1758
Plate 7.1. Figs. 2–3

1758 *Patella vulgata* – Linné: p. 782.
1848 *Patella vulgata*. Linn. – Wood: p. 183, Pl. 20, fig. 8a–b.
1878 *Patella vulgata*, Lin. – Sars: p. 118–119.
1923 *Patella vulgata*, Linné – Harmer: p. 780–781, Pl. 62, fig. 11.
1980 *Patella vulgata* (Linné, 1758) – Gladenkov et al.: p. 62–63, Pl. 13, fig. 1–1a.

*Material:* One fragmented juvenile shell with apex and four plate fragments from unit 9 in the *Mactra* Zone, and two slightly damaged shells with apex in unit 11 in the same zone.

*Remarks:* The largest specimen measured by Gladenkov, Norton, and Spaink (1980) is (l × b × h): 40 × 34 × 15 mm. From the British Isles are recorded shells up to 60 × 50 × 30 mm (Fretter & Graham, 1976).

*Recent distribution, ecology, and biology: Patella vulgata* is a boreal-lusitanian species in the North Atlantic, extending from the north coast of Norway (at 70.5°N) and Southwest Iceland in the north to the Gibraltar Strait and the Mediterranean in the south (Høisæter, 1986; Óskarsson, 1962; Poppe & Goto, 1991). The species is absent from the east coast of the North Sea and the Baltic, but has been found as far south as Bohuslän on the west coast of Sweden (Fretter & Graham, 1976; Sneli et al., 2005). Bathymetrical range: *P. vulgata* is a littoral species living between mean high water neap (MHWN) and mean high water spring (MHWS), depending on local factors which may provide shelter (Fretter & Graham, 1976; Sneli et al., 2005). The species seems to be polyhaline-euhaline, and is not considered to live naturally in waters with salinity lower than 25‰, but it has been recorded from salinities down to 3‰ (Arnold, 1972). The larval development is with a pelagic stage, so it may occasionally be transported, for example, from the Faroe Islands, to the south coast of Iceland by northward going current (Thorson, 1941).

In the British Isles, *P. vulgata* occurs on any shore where the substratum is firm enough for attachment (Fretter & Graham, 1976). In the Faroe Islands it is very abundant on all rocky shores (Sneli et al., 2005).

*Fossil occurrence:* Pliocene: The *Mactra* Zone of the Tjörnes beds (Gladenkov et al., 1980). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1923; Wood, 1848). Upper Pleistocene: Selsey beds in England (Harmer, 1923), Netherlandish beaches (Wesselingh & Pouwer, 2011). Stratigraphical range: Pliocene to Recent.

### ***Patella* cf. *aspera* Röding, 1798**

Plate 7.1. Fig. 4

1798 *Patella Aspera* – Röding: p. 10.
1988 *Patella aspera* Röding, 1798 – Graham: p. 80–81, fig. 21.

*Material:* One shell with apex in unit 8 in the *Mactra* Zone. The species is new to the fossil fauna of Tjörnes.

*Remarks:* The specimen measures (l × b × h): 31.8 × 27.6 × 13.8 mm. A closer identification is difficult as the shell is slightly eroded and therefore some details of the surface structure are lost. However, what is left of that structure indicates that the ridges of the shell are finer than those of *Patella vulgata*. The shell is not as regularly oval as *P. vulgata* and not so conical, more comparable with *P. aspera*. The species identification within *Patella* has been a matter of dispute, and it is has been suggested that *P. aspera* is a more southern species, absent from north of the Mediterranean where *P. ulyssiponensis* Gmelin, 1791 is common (Delamotte & Vardala-Theodorou, 2001). Until the systematics of *Patella* is better clarified, we will follow (Fretter & Graham, 1976) and (Graham, 1988) and consider *P. aspera* living around the British Isles.

*Recent distribution, ecology, and biology: Patella aspera* is a boreal-lusitanian species (Fig. 7.3). It is distributed from western Norway (at 60.5°N) and the British Isles in the north to the Azores in the south (Fretter & Graham, 1976; Poppe & Goto, 1991). It is not known from the Baltic or the southern part of the North Sea but well known in the Mediterranean (Fretter & Graham, 1976). Bathymetrical range: It prefers the lower part of the intertidal zone, but it also extends into sublittoral habitats (Fretter & Graham, 1976; Poppe & Goto, 1991). The salinity tolerance and larval development are presumably the same as for *P. vulgata* (Fretter & Graham, 1976).

**Fig. 7.3** The recent known geographical distribution of *Patella aspera* Röding

The species prefers rocky shores, and in the British Isles it may constitute 90% of the limpet population on exposed shores heavily affected by waves (Fretter & Graham, 1976). At low tide it can be found in pools between the rocks (Poppe & Goto, 1991).

*Fossil occurrence:* Pliocene: *Mactra* Zone of the Tjörnes beds (this volume). Upper Pleistocene: Santa Maria Island, Azores (Ávila et al., 2008). The occurrence in the *Mactra* Zone seems to be the earliest known appearance of the species. Stratigraphical range: Pliocene to Recent.

***Patella pellucida* Linné, 1758**
Plate 7.1. Figs. 5–6

1758 *Patella pellucida* – Linné: p. 783.

1878 *Nacella pellucida*, Lin. – Sars: p. 119.
1923 *Helcion pellucidum* (Linné) – Harmer: p. 793–794, Pl. 62, fig. 31.
1924 *Nacella pellucida* (Linné) – Schlesch: p. 338–339, Pl. 10, figs. 18–19.
1925 *Nacella pellucida*, L. – Bárðarson: p. 55, 59, 70.
1980 *Helcion pellucidum* (Linné, 1758) – Gladenkov et al.: p. 63, Pl. 13, fig. 4.

*Material:* About 40 shells from units 6 and 9 in the *Mactra* Zone and units 13, 19, and 23 in the *Serripes* Zone. All the 25 shells from the bed unit 9 are juvenile.

*Remarks:* The largest specimen measures (l × b × h): 18.8 × 14.1 × 9.2 mm. However, Gladenkov et al. (1980) reported shells up to 25 mm in length. The thin and fragile shells are generally broken in the sediments.

*Recent distribution, ecology, and biology: Patella pellucida* is a boreal-lusitanian species extending in the North Atlantic from the Murman region in northern Russia and Iceland in the north to Portugal and Morocco in the south, and makes its way into the Mediterranean (Fretter & Graham, 1976; Sneli et al., 2005; Thorson, 1941). It occurs on the west coasts of Denmark and Sweden south to Øresund, but it is absent from the Baltic, east coast of Denmark and those of the Netherlands and Belgium (Fretter & Graham, 1976; Sneli et al., 2005). Bathymetrical range: from tide water mark (several places) to ?1521 m north of Scotland (Thorson, 1941). The recent distribution indicates that the species prefers polyhaline waters, and its salinity tolerance is probably well above 25‰ (cf. Funder et al., 2002). The larval development is with a short pelagic stage (Thorson, 1946).

In Norway it is invariably found on seaweeds, especially *Laminaria* and *Fucus serratus* (Vahl, 1971). Therefore, it is intertidal only close to the low water line, but prefers more sublittoral areas. The very deep records for this species are therefore doubtful. Normally, it is not found living where there is much sediment or freshwater inflow (Fretter & Graham, 1976).

*Fossil occurrence:* Pliocene: Estepona in southern Spain (Landau, Grigis, & Marquet, 2004). Lower Pleistocene: Threngingar Formation in Breiðavík (Vilhjálmsson, 1985). Middle Pleistocene: Bridlington Crag in England (Harmer, 1923). Upper Pleistocene: Selsey beds in England and beach finds in the Netherlands (Harmer, 1923; Wesselingh & Pouwer, 2011). Apparently, the specimens from the Pliocene *Mactra* Zone are among the earliest of the species. Stratigraphical range: Pliocene to Recent.

### Family Acmaeidae Carpenter, 1857
### Genus *Testudinalia* Moskalev, 1966
### Subgenus *Collisella* Dall, 1871

***Testudinalia (Collisella) testudinalis*** **(Müller, 1776)**
Plate 7.1. Figs. 7–8

1776 *Patella testudinalis* – Müller: p. 237.
1878 *Acmæa testudinalis*, Müll. – Sars; p. 120.
1941 *Acmaea testudinalis* (O. F. Müller) – Thorson: p. 8–9.
1962 *Acmaea testudinalis* (Müller) – Óskarsson: p. 40, fig. 9.

1980 ?*Acmaea scaldensis* Altena Van Regteren, 1954 – Gladenkov et al.: p. 64, Pl. 13, fig. 2.
1986 *Acmaea (Colisella) testudinalis* (Müller, 1776) – Malatesta & Zarlenga: p. 116–117, fig. 32.
1988 *Collisella tessulata* (Müller, 1776) – Graham: p. 74, fig, 19.
1995 *Testudinalia tesselata* (Mueller, 1776) – Golikov: p. 13, fig. 118A–B.

*Material:* Five juvenile shells from unit 9 in the *Mactra* Zone. Furthermore, Gladenkov et al. (1980) reported one shell from bed unit 19 in the *Serripes* Zone and named it *A. scaldensis* van Regteren Altena, 1954. They did not list this species in their table (between p. 8 and 9), where the species *A. scalaris* (Müller) was recorded from units 16 and 19 in the *Serripes* Zone. We cannot find this name in Müller's work (1776) and suggest it may be a misspelling.

*Remarks:* The largest shell kept in the collection of Bárðarson at the Icelandic Institute of Natural History is not well preserved, but it measures (l × b × h): 17.4 × 14.0 × 8.5 mm. The height is unusually high, but Graham (1988) has recorded shells with similar dimensions, up to 20 mm in length and 10 mm in height in British waters, and Macpherson (1971) found shells "of very variable height" in the Canadian arctic waters. Three of the juvenile specimens are rather fragmentary, but two are almost intact except for the apex, which is slightly eroded. The two largest specimens measure (l × b): 7.5 × 5.5 and 7.4 × 5.8 mm. We are not convinced that the shell referred to *Acmaea scaldensis* by Gladenkov et al. (1980) is correctly identified. Actually, the shell ratios of the Tjörnes shells are most similar to those of *Testudinalia (Collisella) testudinalis*. Icelandic recent specimens of *T. (C.) testudinalis* have b/l ratios 0.69–0.78 and h/l ratios 0.34–0.39, while the specimens of *A. scaldensis* that van Regteren Altena et al. measured in 1954 have b/l ratios about 0.90 and h/l ratios 0.40–0.44.

*Recent distribution, ecology, and biology: Testudinalia (Collisella) testudinalis* is a circumpolar, subarctic-boreal species with arctic to lusitanian distribution records as well. In the North Atlantic it extends from West Greenland south of Qaanaaq/Thule, and possibly East Greenland (close to 70°27′N), the Murman Coast, the White Sea, Novaya Zemlya, the Kara Sea, northern Alaska, Wellington Channel, and Baffin Island in the north to Azores and Connecticut in the south (Golikov, 1995; La Rocque, 1953; Macpherson, 1971; Posselt & Jensen, 1898; Thorson, 1941). The typical form has not been found living in the Pacific where a larger form, more rounded and almost smooth, has been separated as a subspecies *T. (C). testudinalis scutum* Eschscholtz. It is distributed from Alaska to the Gulf of California, but rarely found south of Oregon (La Rocque, 1953; Malatesta & Zarlenga, 1986). The species is distributed along the west coast of Norway and Sweden to Øresund, into the Danish fiords and to Kieler Bucht (Fretter & Graham, 1976; Ziegelmeier, 1966). Otherwise, it does not live in the Baltic nor at the eastern coast of the North Sea (Fretter & Graham, 1976), and we have not found any records from the Mediterranean. Bathymetrical range: from 0 m in Iceland (Óskarsson, 1962) to 850 m in Azores (Thorson, 1941). In Iceland it is very commonly found from the coast and down to a depth of 40 m, and in the British Isles it is abundant down to about 50 m (Fretter & Graham, 1976; Óskarsson, 1962). In the Arctic young animals are mainly living in sublittoral areas, whereas adults are mostly in the littoral zones (Matweeva, 1974). The species seems to be polyhaline, and in the Arctic it occurs almost exclusively at salinities above 24‰ (Golikov, 1995). The larval development is pelagic, and the time from fecundation and through the planktonic stage to formation of juvenile animals takes 13–15 days at 10°C (Golikov, 1995).

In Iceland the species prefers substrates of stones, gravel, and sand, but the shells are often devoured by fish and frequently found in the stomachs of cod and plaice (Thorson, 1941). In the British Isles it is typically found among small boulders and stones, and it prefers places where there is sufficient movement of water, perhaps to avoid silt or fine sand in the mantle cavity (Fretter & Graham, 1976).

*Fossil occurrence:* Pliocene: *Mactra* Zone of the Tjörnes beds (this volume). Lower Pleistocene: Emilian of the central Mediterranean (Malatesta & Zarlenga, 1986). Upper Pleistocene: Late Wisconsin deposits in the Hudson Bay area (Richards, 1962). Stratigraphical range: Pliocene to Recent. The occurrence in the Tjörnes beds is one of the oldest, if not the oldest of this species.

The genus *Testudinalia* (or *Acmaea*) is present in Oligocene deposits in the North Pacific, but in the North Atlantic it first occurs in Pliocene beds (Durham & MacNeil, 1967). *Testudinalia testudinalis* is by some authors referred to the subgenus *Collisella* Dall, 1871 (Malatesta & Zarlenga, 1986). At least one species of this subgenus is represented in the North Pacific Pliocene, and nine occur in Pleistocene beds (Grant, & Gale, 1931; Malatesta & Zarlenga, 1986). In the North Atlantic the only living species of *Collisella* is *T. (C.) testudinalis,* and it has not previously been found in European Pliocene deposits (Malatesta & Zarlenga, 1986). The occurrence of this species in North Atlantic Pliocene beds indicates that the species originated in the Pacific during migration through the Bering Strait into the Arctic Ocean and the North Atlantic while the Tjörnes beds were deposited. Most probably, it evolved from *Acmaea insessa/Discurria insessa/Lottia insessa* (Hinds), the only Pliocene North Pacific *Collisella.* As the species has not been found in Pliocene deposits in the British Isles or continental Europe, it is tempting to conclude that it first migrated southwards in the North Atlantic after the formation of the Tjörnes beds, presumably during the Lower Pleistocene.

### Family Lepetidae Gray, 1850
### Genus *Lepeta* Gray, 1847

**_Lepeta caeca_ (Müller, 1776)**
Plate 7.1. Figs. 9–10

1776 *Patella caeca* – Müller: p. 237.
1878 *Lepeta cæca*, Müll. – Sars: p. 123, Pl. 20, fig. 17a–b.
1925 *Lepeta caeca*. Müll. – Bárðarson: p. 59, 70.
1962 *Lepeta coeca* (Müller) – Óskarsson: p. 42, fig. 12.
1988 *Lepeta caeca* (Müller, 1776) – Graham: p. 84–85, fig. 23.

*Material:* One shell from unit 21 and two from unit 23 in the *Serripes* Zone. The two specimens from unit 23 were recorded by Bárðarson (1925).

*Remarks:* The intact specimen from bed unit 21 is not full grown and measures (l × b × h): 8.8 × 6.5 × 3.6 mm. The apex points upwards and not anteriorly as in *Acmaea,* and it is also located farther behind the anterior margin. The surface of the shell has several hundreds of low ridges and shallow furrows radiating from the apex and crossing a series of growth lines parallel to the aperture. Therefore, the surface has a more reticulate pattern than seen in any *Acmaea* species and the growth lines convert the ridges to lines of grains.

*Recent distribution, ecology, and biology: Lepeta caeca* is a circumpolar, arctic-subarctic-boreal species, extending from West and East Greenland, Franz Josef Land, Svalbard, Novaya Zemlya, the Kara Sea, the Siberian Arctic Sea, Parry Islands, and Ellesmere Island in the north to Shetland, West Scotland, Kattegat, and Cape Cod in the south (Fretter & Graham, 1976; Sneli et al., 2005; Thorson, 1941). In deeper water it is distributed in the North Atlantic southward to the Azores and the West Indies (Fretter & Graham, 1976). In the Pacific it extends south to the Sea of Okhotsk and Sea of Japan (Sneli et al., 2005). It is not known from the Baltic. Bathymetrical range: from 0 m in Iceland to about 1300 m near the Azores (Óskarsson, 1962; Thorson, 1941). The species is mesohaline rather than polyhaline or euhaline, with salinity tolerance down to 15‰ (Funder et al., 2002). The larval development is unknown, but Thorson (1946) concluded that the development is most probably direct as he did not find any prosobranch larvae in the East Greenland plankton, where this is a dominant species.

*Lepeta caeca* is sublittoral species and is generally found living on a hard bottom, but has also been collected from gravel and firm clays (Fretter & Graham, 1976). In Iceland it prefers rocky bottom and occurs mainly at depths below 30 m (Thorson, 1941).

*Fossil occurrence:* Pliocene: *Serripes* Zone of the Tjörnes beds (Bárðarson, 1925). Lower Pleistocene: Pattorfik beds in West Greenland (Símonarson, 1981b). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent. The occurrence in the Tjörnes beds seems to be the earliest of this species.

### Family Trochidae Rafinesque, 1815
### Genus *Gibbula* Risso, 1826

#### *Gibbula tumida* (Montagu, 1803)
Plate 7.1. Fig. 11

1803 *Trochus tumidus* – Montagu: p. 280, Pl. 10, fig. 4.
1848 *Trochus tumidus*. Mont. – Wood: p. 130–131, Pl. 14, fig. 2a–b.
1878 *Gibbula tumida*, Mont. – Sars: p. 141.
1923 *Trochus (Gibbula) tumidus* (Montagu) – Harmer: p. 733–734, Pl. 59, figs. 10–11.
1924 *Gibbula tumida* Montagu – Schlesch: p. 339, Pl. 10, figs. 20–21.
1925 *Gibbula tumida*, Mont. – Bárðarson: p. 53, 57–58.

*Material:* Two shells from unit 15 in the *Serripes* Zone. Schlesch (1924) has recorded two specimens from unit ?23 in the same zone, and Bárðarson (1925) mentioned several specimens from units 18, 21, and 22 in the *Serripes* Zone.

*Remarks:* The largest shell measures (h × d × ha): 18.3 × 16.6 × 11.1 mm. The protoconch is not preserved in the shells from unit 15 and the teleoconch is rather worn and somewhat fragmented. The outer layer of the shells is worn and therefore some structures of the surface are lost. However, the shape or form, pattern, and sculpture suggest that these shells represent *Gibbula tumida*. We are aware of the fact that it is somewhat variable species (cf. Poppe & Goto, 1991), but it seems very well comparable with some of the shells Harmer figured in 1923. We have not found the specimens Schlesch recorded in 1924, but his specimens of *G. tumida* are probably correctly identified.

*Recent distribution, ecology, and biology: Gibbula tumida* is a boreal-lusitanian species with subarctic outposts. It occurs from the Murman Coast and the west coast of Norway in the north to the Iberian coasts in the south (Fretter & Graham, 1977; Høisæter, 1986). This northern species lives in South and West Iceland, the Faroe Islands and the Swedish west coast and Øresund, but an occurrence in the Mediterranean is considered doubtful (Fretter & Graham, 1977; Sneli et al., 2005; Thorson, 1941). In the Faroe Islands it lives at temperatures from 0 to 9.1 °C (Sneli et al., 2005). Bathymetrical range: from 3–10 m to 601 m south west of the Faroe Islands, but it has been found down to about 1225 m (Sneli et al., 2005). The species seems polyhaline and can tolerate salinity as low as about 20‰ (Fretter & Graham, 1977). There is probably no pelagic larval stage as both the trochophor and veliger stages are passed within the egg mass (Thorson, 1941).

In the British Isles the species has been be found on both hard and soft bottom with small stones and shell gravel with *Laminaria* (Fretter & Graham, 1977).

*Fossil occurrence:* Pliocene: *Serripes* Zone of the Tjörnes beds (this volume). Lower Pleistocene: Waltonian Crag, Icenian, and Red Crag Formation at Sutton (Harmer, 1923), Ritthem, de Kaloot (van Regteren Altena et al., 1954). Stratigraphical range: Pliocene to Recent. Apparently, the specimens from the *Serripes* Zone represent the oldest occurrence of this species.

### ***Gibbula cineroides* (Wood, 1842)**

Plate 7.1. Fig. 12

1842 *Trochus cineroïdes* – Wood: p. 531.
1848 *Trochus cineroides.* S. Wood – Wood: p. 131–132, Pl. 14, fig. 8a–b.
1923 *Trochus (Gibbula) cineroides* (S. V. Wood) – Harmer: p. 730–731, Pl. 58, fig. 24.
1924 *?Trochus (Calliostoma) occidentalis* Mighels – Schlesch: p. 339, Pl. 10, figs. 22–24.
1980 *Gibbula* cf. *cineroides* S. Wood, 1842 – Gladenkov et al.: p. 65, Pl. 13, figs. 25–26.
1980 ?*Gibbula occidentalis* (Mighels, 1842) – Gladenkov et al.: p. 65, Pl. 13, fig. 7–7a.

*Material:* About 20 specimens from units 14–23 in the *Serripes* Zone.

*Remarks:* The shells occur in variable state of preservation, and generally, the material is rather fragmentary. Furthermore, some of the specimens are affected by dissolution. The largest shell measures (h × d): 8.9 × 10.5 mm. The d/h ratios average about 1.18 for the measurable specimens. The strong, subconical shell has fine crenulated spiral lines or ridges extending down to the base, which is rather characteristic for the species (see Plate 7.1, Fig. 12).

*Distribution, ecology, and biology: Gibbula cineroides* is extinct, but its distribution in sediments, where it is mainly found together with recent boreal species, indicates strongly that it preferred to live in environments similar to those in the boreal region today. In the Faroe Islands the recent *G. cineraria* (Linné, 1758) prefers temperatures around 7.6 °C, while *G. tumida* (Montagu, 1803) has been found at temperatures between 0 and 9.1 °C (Sneli et al., 2005). Generally, the recent species live from the coast and extends sublittorally to several hundreds of meters (Fretter & Graham, 1977). The Tjörnes sediments with *G. cineroides* were deposited in shallow sublittoral water close to the coast, which is also supported by the bathymetrical range of some of the co-occurring recent species. *G. cineroides* was probably polyhaline-mesohaline as most of the recent *Gibbula* species with salinity tolerance down to about 15‰. Generally, the recent *Gibbula* species have a very brief pelagic larval stage (cf. Fretter & Graham, 1977).

The recent *Gibbula* species prefer rocky coasts with stones, crannies, and pools, and can be found on and among weeds, especially laminarians (Fretter & Graham, 1977).

*Fossil occurrence:* Pliocene: Luchtbal Sand Member (Marquet & Landau, 2006). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1923). Stratigraphical range: Pliocene to Lower Pleistocene. Apparently, the species did not survive the first phases of major cooling at the beginning of the Pleistocene.

### Genus *Solariella* Wood, 1842

**_Solariella_ sp.**
Plate 7.2. Fig. 1

1924 *Solariella (Machaeroplax) bella* (Verkrüzen) – Schlesch: p. 339.
1975 *Solariella* cf. *bella* (Verkrüzen) – Norton: p. 109.

*Material:* We did not find this species in our collections, but Schlesch (1924) recorded one specimen from unit 19 in the *Serripes* Zone. Furthermore, Norton (1975) listed the species with no information about its stratigraphical distribution, or how many shells he found. He may have been referring to the single specimen found by Schlesch. Both Schlesch and Norton identified the species as *Solariella bella* which is considered as synonym of *S. obscura* (see the short list of synonyms).

*Remarks:* The specimen found by Schlesch is kept in the Geological Museum in Copenhagen (the stock room) and it measures (h × d): 4.3 × 5.1 mm. The outer lip of the aperture is slightly damaged, and the aperture and umbilicus are covered with sediments. We did not try to remove the sediments as the specimen is not in our possession.

The Tjörnes material seems to have higher spiral form than *Solariella obscura,* three spirals on the penultimate whorl, and stronger radial on the base. As these characters do not agree well with any of the known *Solariella* species, it may belong to another Pacific species or even a new one. *S. obscura* (Couthouy, 1838) and *S. varicosa* (Mighels & Adams, 1842) are now living in the Pacific, and Grant and Gale (1931) reported a number of *Solariella* species from the Eocene of California and Washington, but no species has been reported there from the Pliocene. Did *S. obscura* migrate from the Pacific while the specimens found in the Tjörnes beds reached the northern Iceland during the Pliocene, and did some of the *S. obscura* specimens evolve those characters found in the *Solariella* shells from Tjörnes?

Unfortunately, further identification of this very limited and somewhat damaged material from the Tjörnes beds seems hardly possible.

*Recent distribution, ecology, and biology: Solariella obscura* is an arctic-subarctic, circumpolar species with some boreal occurrences. It extends from West and East Greenland, Svalbard, Franz Josef Land, Novaya Zemlya, the Kara Sea, the Siberian Arctic Sea, and the Canadian Arctic in the north southward to the Faroe Islands, the Hebrides (in deep water), the New England area, and the Okhotsk Sea and Sea of Japan in the Pacific (Golikov, 1995; Sneli et al., 2005; Thorson, 1941). In the Faroe Islands it lives in waters with temperatures from –0.9 to 7.9 °C (Sneli et al., 2005). According to Golikov (1995), it has been recorded from sea temperatures up to 12.7°C. Bathymetrical range: from 3–4 m in the Kara Sea to 917 m off New England (Golikov, 1995; Thorson, 1941). According to Golikov (1995), the species is prefers euhaline salinity between 32 and 35‰. The biology is unknown, but the related and more southern species *Solariella amabilis* (Jeffreys) seems to have suppressed free-swimming larval stage or even no free larval stage at all (Graham, 1988).

*Solariella obscura* lives mainly on sandy or silty-sandy substrates and has also been found on gravel and even stones (Golikov, 1995; Sneli et al., 2005).

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Harmer 1923), Middle Pleistocene: Bridlington Crag (Harmer, 1923), Kotzebuan (Hopkins et al., 1972), Padymeiskii Suites (Merklin et al., 1979). Upper Pleistocene: Menzen Interglacial in the White Sea Region (Grøsfjeld et al., 2006). Stratigraphical range: Pliocene to Recent. The species is most probably of Pacific origin and migrated into the Arctic Ocean and the North Atlantic during the deposition of the *Serripes* Zone of the Tjörnes beds.

### Genus *Margarites* Gray, 1847

#### ***Margarites groenlandicus* (Gmelin, 1791)**

Plate 7.2. Figs. 2–3

1791 *Trochus groenlandicus* – Gmelin: p. 3574.
1872 *Margarita groenlandica*, Chemnitz – Wood: p. 83, Pl. 5, fig. 11a–b.
1878 *Margarita grönlandica*, Chemn. – Sars: p. 133–134.
1923 *Eumargarita grænlandica* (Chemnitz) – Harmer: p. 749–750, Pl. 60, fig. 9.
1924 *Margarites (Margarites) groenlandica* (Chemnitz) – Schlesch: p. 339 (from an unpublished manuscript of C. M. Poulsen, 1884).
1962 *Margarites groenlandicus* (Chemn.) – Óskarsson: p. 49–50, fig. 21.

*Material:* Nineteen shells from unit 9 in the *Mactra* Zone. Furthermore, Schlesch (1924) mentioned one specimen without any unit number referring to an unpublished manuscript by C. M. Poulsen (1884).

*Remarks:* All the shells from unit 9 are juvenile, and the largest measures (h × d): 2.3 × 2.6 mm. The d/h ratios are varying from 1.06 to 1.19.

*Recent distribution, ecology, and biology: Margarites groenlandicus* is an arctic-subarctic-boreal, circumpolar species distributed from West and East Greenland, Svalbard, Franz Josef Land, Novaya Zemlya, the Kara Sea, the Siberian Arctic Sea, and the Canadian Arctic in the north southward to Scotland, and Massachusetts Bay in the North Atlantic, and the Bering Sea and Kurile Islands in the Pacific (Fretter & Graham, 1977; Golikov, 1995; Thorson, 1941). It has not been found in Skagerrak, Kattegat, the Baltic, or the North Sea (Fretter & Graham, 1977). According to Golikov (1995), it has been found living at winter temperatures as low as −1.7°C and summer temperatures up to 18°C. Bathymetrical range: from 0 m in Iceland to 859 m off the Faroe Islands (Sneli et al., 2005; Thorson, 1941). The species is upper mesohaline to euhaline with salinity tolerance down to about 15‰ (Funder et al., 2002). Golikov (1995) recorded it from water with a salinity range of 24–35‰. The larval development is non-pelagic (Thorson, 1941).

In East Greenland the species is mainly attached to *Fucus, Laminaria,* and *Desmarestia,* as well as *Delessaria* and other red algae (Thorson, 1944). In Iceland it is also associated with the algal zone, and in the Faroe Islands it has been found living on algae, stones, sand, shell-gravel, and sponges (Sneli et al., 2005; Thorson, 1941).

*Fossil occurrence:* Pliocene: *Mactra* Zone of the Tjörnes beds (this volume) and most probably also the *Serripes* Zone (Schlesch, 1924). Lower Pleistocene: Pattorfik beds (Símonarson, 1981b). Middle Pleistocene: Bridlington Crag (Harmer, 1923). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent. The occurrences in the Tjörnes beds seem to represent the first appearance of the species. The species is most probably of Pacific origin (cf. Durham & MacNeil, 1967).

***Margarites costalis* (Gould, 1841)**
Plate 7.2. Fig. 4

1841 *Trochus costalis* – Gould: p. 252.
1878 *Margarita cinerea*, Couth. – Sars: p. 134–136, Pl. 9, fig. 1a–c.
1923 *Eumargarita cinerea* (Couthouy) – Harmer: p. 748, Pl. 60, fig. 7.
1924 *Margarites (Pupillaria) cinerea* (Couthouy) – Schlesch: p. 339.
1962 *Margarites cinereus* (Couth.) – Óskarsson: p. 50, fig. 22.

*Material:* Twelve shells from unit 9 in the *Mactra* Zone and one specimen recorded by Schlesch (1924) from the uppermost part of the *Serripes* Zone (without unit number).

*Remarks:* The shell from the *Serripes* Zone measures (h × d): 8.9 × 9.1 mm, while all the shells from the *Mactra* Zone are juvenile, the largest of them measures (h × d): 1.2 × 1.4 mm. The shell ratios d/h are 1.02–1.16. The aperture of all the specimens is rather fragmentary, and the umbilicus is usually filled with secondary calcite.

*Recent distribution, ecology, and biology: Margarites costalis* is an arctic-subarctic, circumpolar species with boreal outposts. It occurs from around Greenland, Svalbard, Franz Josef Land, Novaya Zemlya, the Kara Sea, the Siberian Arctic Sea, Alaska, and the Canadian Arctic in the north and southward to the west coast of Norway (at 61.5°N), Iceland, New England, and Cape Cod in the Atlantic and south to the Japan Sea in the Pacific (Golikov, 1995; Høisæter, 1986; Thorson, 1941). Bathymetrical range: from 3 m in East Greenland to 660 m west off Norway (Thorson, 1941). The species seems polyhaline living in salinity above 25‰ (Funder et al., 2002). According to Golikov (1995), it lives at salinity range of 26–34.5‰. The larval development is non-pelagic (Thorson, 1935).

In the Arctic, the species prefers silty substrates with stones and shell-debris where it can deposit the slimy egg lumps on algae (Golikov, 1995; Thorson, 1941).

*Fossil occurrence:* ?Miocene: Unalaska Formation (Grant & Gale, 1931). Pliocene: *Mactra* and *Serripes* Zones of the Tjörnes beds (Schlesch, 1924; this volume). Lower Pleistocene: Pattorfik beds (Símonarson, 1981b), Olkhov and Tusatuva-Yamsk Suites (Petrov, 1982). Middle Pleistocene: Bridlington Crag (Harmer, 1923), Mikulinsky horizon (Merklin et al., 1979), Karagin Suite (Petrov, 1982), Sicilian near Palermo (Malatesta & Zarlenga, 1986). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: ?Miocene to Recent.

Malatesta and Zarlenga (1986) discussed the reliability of the record by Grant and Gale (1931) from Miocene beds noting that there are no records from Pliocene deposits. However, after identification of the species in the Pliocene *Mactra* Zone we can verify a Pliocene occurrence. The fossil occurrence may indicate a Pacific origin and migration into the Arctic Ocean and the North Atlantic during the deposition of the *Mactra* Zone of the Tjörnes beds (cf. Durham & MacNeil, 1967).

### Order Mesogastropda Thiele, 1925
### Family Littorinidae Gray, 1840
### Genus *Littorina* Férussac, 1822

### *Littorina squalida* Broderip & Sowerby, 1829
Plate 7.2. Fig. 5

1829 *Littorina squalida* – Broderip & Sowerby: p. 370.
1924 *Littorina palliata* (Say) = *Littorina arctica* Möller – Schlesch: p. 336–337, Pl. 10, fig. 6.
1925 *Littorina* sp. – Bárðarson: p. 66, 70 (in part).
1980 *Littorina littorea* (Linné, 1758) – Gladenkov et al.: p. 65–66, Pl. 13, figs. 8–11.
1980 Littorina aff. saxatilis (Olivi, 1792) – Gladenkov et al. p. 66, Pl. 13, Fig. 12.

*Material:* About 150 specimens from units 9–11 in the upper part of the *Mactra* Zone and units 18–23 and 25 in the upper part of the *Serripes* Zone.

*Remarks:* The rather strong shell is generally well preserved and only a few are fragmentary. Generally, *Littorina squalida* has well-preserved spiral robs and zones, but some of the specimens from Tjörnes are almost smooth. Thus, the variability of the Tjörnes specimens can be considerable. The largest specimen measures (h × d): 22.8 × 19.3 mm with d/h ratio 0.85.

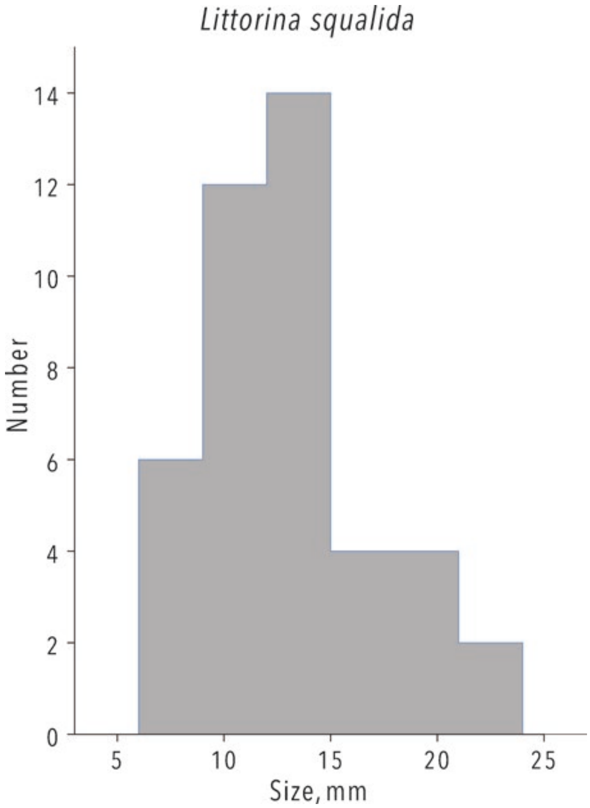

**Fig. 7.4** Size-frequency distribution of 42 measurable shells of *Littorina squalida* Broderip & Sowerby in a shelly lens in unit 10 in the *Mactra* Zone

In a shelly lens in bed unit 10 there were 42 measurable shells, and their size-frequency distribution is shows a considerably higher death rate among the younger individuals (Fig. 7.4), which indicates a little disturbed and residual life assemblage (biocoenosis). We interpret this as indication of a biocoenosis (life assemblage). Other samples contain transported assemblages (thanatocoenosis).

*Recent distribution, ecology, and biology: Littorina squalida* has a wide distribution in the North Pacific, but went extinct in the Atlantic after the Pliocene. From the Bering Strait in the north, it extends to the northern Japan Sea and Hokkaido, and the Aleutian Islands (Reid, 1996). Bathymetrical range: According to Reid (1996), all the occurrences of the species are on shores where it lives in intertidal and shallow subtidal areas. This littoral species is probably mesohaline as most of the *Littorina* species. It seems relatively tolerant to lowered salinity but the exact salinity tolerance is unknown, but several *Littorina* species tolerate large variations in salinity, mesohaline to polyhaline/euhaline. The species has a pelagic larval development, which is significant for its distribution (Reid, 1996).

The species lives on a range of substrates, mainly hard rocks, but also pebbles, gravel, sand, algae, and seagrasses (Reid, 1996). It is algal-feeding (grazing) as many other mesogastropods (Reid, 1996; Thorson, 1941).

*Fossil occurrence:* Miocene: Etolonian and Kekertian stage of Kamchatka (Reid, 1996). Pliocene: Tjörnes beds (Reid, 1996). Lower Pleistocene: Gubik Formation; Bigbendian and Fishcreekian transgressive beds (Reid, 1996). Middle Pleistocene: Anvilian (Hopkins et al., 1974), Karagin Suite (Petrov, 1982). Upper Pleistocene: Pelukian transgressive beds at Nome (MacNeil et al., 1943). Stratigraphical range: Miocene to Recent.

*Littorina squalida* is considered to be one of those North Pacific species that took part in the Pliocene migration into the Arctic Ocean and North Atlantic (Reid, 1996). It reached the Tjörnes area while the *Mactra* Zone was being deposited and has not been found in younger deposits in the North Atlantic. Probably, it did not survive in the Atlantic, but before it disappeared it became an ascendant to the well-known *L. littorea* (Linné, 1758). This indicates that the species separation took place during deposition of the uppermost *Serripes* Zone of Tjörnes, coinciding with a further migration of *L. squalida* southward to the North Sea area. The oldest fossil occurrence of *L. littorea* in Red Crag in England seems to be between 2.4 and 3.2 Ma (Reid, 1996).

### ***Littorina islandica* Reid, 1996**

Plate 7.2. Fig. 6

1996 *Littorina (Neritrema) islandica* – Reid: p. 246–248, fig. 89.
1924 *Littorina rudis* (Maton) – Schlesch: p. 336, Pl. 10, fig. 5.
1925 *Littorina* sp. – Bárðarson: p. 66, 70 (in part).
1980 *Littorina littorea* (Linné, 1758) – Gladenkov et al.: p. 65–66, Pl. 13, figs. 10–11.
1980 *Littorina* aff. *saxatilis* (Olivi, 1792) – Gladenkov et al. p. 66, Pl. 13, Fig. 12.

*Material:* About ?40 shells from units 17–25 in the *Serripes* Zone.

*Remarks:* The rather strong shell is generally well preserved, but in some specimens the outer lip (of the aperture) is slightly damaged and the protoconch is generally missing. The largest specimen measures (h × d): 18.5 × 14.6 mm, and the shell ratio d/h is close to 0.79.

*Distribution, ecology, and biology: Littorina islandica* is extinct, but it probably preferred boreal conditions as indicated by the distribution of recent species occurring together with it in the Tjörnes sediments. Apparently, it lived in similar way as *L. squalida*, in littoral and shallow sublittoral water. The species was apparently mesohaline as most of the *Littorina* species, but the exact salinity tolerance is not known. We do not know if the species had a pelagic larval development, which is generally the case with *Littorina* species.

The species is considered to have lived on rather coarse sand or gravel, but we cannot exclude hard rocks and algae. Probably, it was rather typical epifaunal species as most of *Littorina*.

*Fossil occurrence:* ?Pliocene: Only known from the Upper Pliocene *Serripes* Zone of the Tjörnes beds (Reid, 1996). According to Reid (1996), the species is related or even ancestral to the *Littorina saxatilis* group, but because it cannot be clearly connected to any of them, it was described as new (see Fig. 7.5).

### **Family Hydrobiidae Stimpson, 1865**

### **Genus *Hydrobia* Hartmann, 1821**

***Hydrobia ulvae*** **(Pennant, 1777)**
Plate 7.2. Fig. 7

1777 *Turbo ulvae* – Pennant: p. 132, Pl. 86, fig. 120.

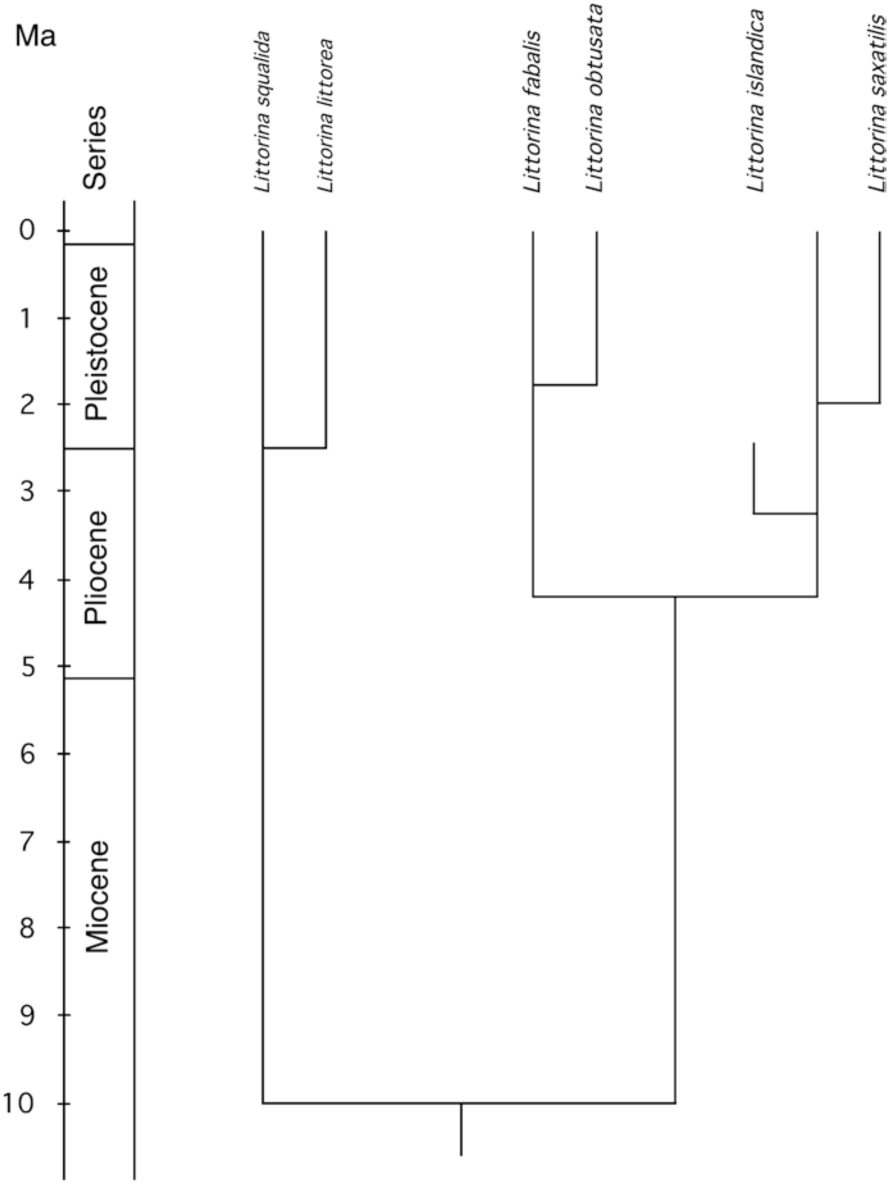

**Fig. 7.5** Phylogenetic tree of *Littorina* species found in Icelandic deposits. Slightly modified from Reid (1996)

1848 *Paludestrina ulvæ*. Penn. – Wood: p. 109.
1878 *Hydrobia ulvæ*, Penn. – Sars: p. 170, Pl. 22, fig. 2.
1925 *Peringia ulvæ* (Pennant) – Harmer: p. 873–874, Pl. 65, fig. 27.
1960 *Hydrobia ulvae* Pennant – Áskelsson: p. 22, Pl. 2, fig. 25.

*Material:* Five specimens from unit 9 in the *Mactra* Zone. The species is new to the fossil fauna of Tjörnes.

*Remarks:* We will follow most of the malacologist and refer this species to the genus *Hydrobia*, but *Peringia* of Paladilhe, 1874 is mostly considered a synonym of *Hydrobia.* One of the shells from the *Mactra* Zone is almost intact, while the outer lip (of the aperture) is damaged in the other specimens. The largest and the best preserved shell measures (h × d): 2.7 × 1.6 mm. The shell ratio d/h is 0.59.

*Recent distribution, ecology, and biology: Hydrobia ulvae* is a North Atlantic boreal-lusitanian species (Fig. 7.6). It extends from the west coast of Norway (at 69.5°N) along the Atlantic coasts of Europe and Africa to Senegal in the south (Graham, 1988; Høisæter, 1986). It is widely distributed in the Baltic, except the most eastern parts, and well known from the Mediterranean, but it has not been found in Iceland or the Faroe Islands (Graham, 1988; Óskarsson, 1962; Sneli et al., 2005). Bathymetrical range: The species prefers the upper parts of the intertidal zone, but it extends down to about 20 m (Poppe & Goto, 1991). The species is abundant in estuarine conditions and can live and breed at salinities 5–40‰ (Graham, 1988; Poppe & Goto, 1991). This is the only *Hydrobia* species which survives in water with salinity up to 33‰ (Poppe & Goto, 1991). The species has a pelagic larval development (Graham, 1988).

*Hydrobia ulvae* is common in the British Isles where it is often found in enormous numbers in estuarine areas on wet banks of mud and sand, and it also occurs on weeds and salt marshes (Graham, 1988). In Denmark it avoids black mud, but can be found in large numbers on soft, mixed or hard bottom (Muus, 1967).

*Fossil occurrence:* Pliocene: *Mactra* Zone of the Tjörnes beds (this volume). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1925). Lower Pleistocene: Icenian Crag at Bramerton in England (Harmer, 1925). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent. The occurrence in the Tjörnes beds is apparently the earliest known appearance of the species.

### Genus *Ecrobia* Stimpson, 1865

#### *Ecrobia* cf. *ventrosa* (Montagu, 1803)

Plate 7.2. Fig. 8

1803 *Turbo ventrosus* – Montagu: p. 317–318, Pl. 12, fig. 13.
1878 *Hydrobia minuta*, Totten – Sars: p. 171, Pl. 11a–b.
1991 *Hydrobia stagnalis* (Baster, 1765) – Poppe & Goto: p. 94, Pl. 10, figs. 20–21.

*Material:* Sixty-one specimens from unit 9 in the *Mactra* Zone. The species is new to the fossil fauna of Tjörnes.

Fig. 7.6 The recent known geographical distribution of *Hydrobia ulvae* (Pennant)

*Remarks:* Generally, the shell cavity is more or less filled up with secondary calcite, and the outer lip (of the aperture) is slightly damaged. The five largest and measurable shells were measured (h × d × ha) and the d/h ratio calculated: 2.1 × 1.1 × 0.7, 2.1 × 1.0 × 0.6, 1.5 × 0.9 × 0.6, 1.3 × 0.9 × 0.6, 1.3 × 0.8 × 0.5, and 1.2 × 0.8 × 0.5 mm. The shell ratios d/h are 0.47–0.67, and the smaller shells have the highest ratios. Actually the shell of *Ecrobia ventrosa* is like that of *H. ulvae*, but with a more slender spire and deeper sutures. Furthermore, the greatest diameter is apparently on the body whorl slightly above the aperture.

*Recent distribution, ecology, and biology: Ecrobia ventrosa* is a boreal-lusitanian species with a similar distribution in the North Atlantic as *H. ulvae.* It is distributed from Iceland and the west coast of Norway at Finnmark to the Mediterranean and the Black Sea in the south (Óskarsson, 1982; Poppe & Goto, 1991; Sars, 1878). In

Denmark the species is everywhere a shallow-water form living intertidally down to a depth of 2 m (Muus, 1967). In the British Isles it occurs mainly in drainage channels and lagoons with limited contact with the open sea (Graham, 1988). The species is mesohaline and prefers a lower salinity than *H. ulvae*, that is, 5–25‰ (Muus, 1967; Funder et al., 2002). The larval development is without a pelagic stage, and the young snails emerge at hatching (Graham, 1988).

*Ecrobia ventrosa* seems to prefer sheltered localities, almost free from tidal movements where it lives on soft substrates and vegetation (Graham, 1988). In Denmark it can be found in large numbers on soft, mixed or hard bottom, but avoids black mud as the other hydrobiid species (Muus, 1967).

*Fossil occurrence:* Pliocene: *Mactra* Zone of the Tjörnes beds (this volume). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent. The occurrence in the Tjörnes beds appears to represent the earliest known appearance of the species.

### Family Rissoidae Gray, 1847
### Genus *Rissoa* Fréminville, 1814

#### *Rissoa obsoleta* (Wood, 1848)
Plate 7.2. Fig. 9

1848 *Rissoa obsoleta*. S. Wood – Wood: p. 105, Pl. 11, fig. 11a–b.
1954 *Rissoa (Turboella) obsoleta* S.V. Wood, 1848 – van Regteren Altena et al.: p. 63, fig. 40.

*Material:* A total of 132 specimens from unit 9 in the *Mactra* Zone. The species is new to the fossil fauna of Tjörnes.

*Remarks:* The five largest shells were measured (h × d × ha): 3.7 × 2.0 × 1.7, 3.5 × 1.9 × 1.6, 3.4 × 1.7 × 1.6, 3.4 × 1.7 × 1.5, and 3.0 × 1.6 × 1.4 mm. The d/h ratios are 0.50–0.54.

The shell of *Rissoa obsoleta* looks like that of *Cingula substriata* (Philippi, 1844). However, in *R. obsoleta* the outer lip is distinctly thickened with varix as generally seen in *Rissoa*, and the ornamentation is far from as reticulate as in *C. substriata* because the longitudinal striae are almost invisible. The size-frequency distribution of the found shells shows especially high death rate among the young individuals (Fig. 7.7), strongly indicating a residual life assemblage (biocoenosis). However, it is probably of an accumulated type where the shells are not reworked by currents, but have accumulated from sediments where currents have removed the sedimentary grains, while the larger and heavier shells were left to form lenticular lag deposits.

*Distribution, ecology, and biology: Rissoa obsoleta* is extinct, but apparently it preferred conditions comparable to the boreal region of the North Atlantic. This can be concluded from its fossil distribution such as in Pliocene sediments and also from its co-occurrence with recent species as, for example, in the *Mactra* Zone of the Tjörnes beds. Bathymetrical range: The species presumably lived mainly in the foreshore-tidal zone as most of the recent *Rissoa* species. It was most probably a mesohaline species, but its salinity tolerance is not known. Neither do we know its larval development.

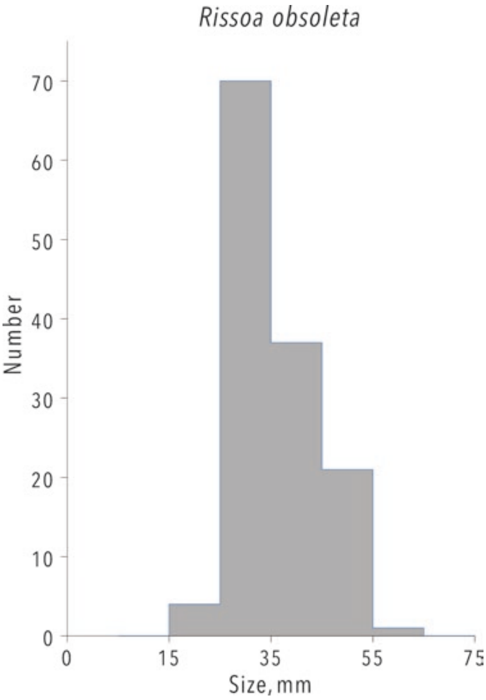

**Fig. 7.7** Size-frequency distribution of all measurable shells of *Rissoa obsoleta* (Wood) in a shelly lens in unit 9 in the *Mactra* Zone

In the British Isles the *Rissoa* species are generally found living on rocky shores or gravel amongst weeds, especially *Zostera* (Graham, 1988).

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Wood, 1848), *Nassarius reticosus* and *Chlamys opercularis* Subzone in the Netherlands (Spaink, 1975), Luchtbal Sand Member (Marquet & Landau, 2006). Pliocene/Lower Pleistocene: Westerchelde (van Regteren Altena et al., 1954). Stratigraphical range: Pliocene to Lower Pleistocene. As we could not find any fossil records younger than those from Westerschelde, it is supposed that the species became extinct in the beginning of the Pleistocene.

### Genus *Pusillina* Monterosato, 1884

### *Pusillina* cf. *sarsi* (Lovén, 1846)

Plate 7.3. Fig. 1

1846 *Rissoa sarsii* – Lovén: p. 155.
1978 *Rissoa albella* Lovén, 1846 – Fretter & Graham: p. 200–203, fig. 172.
1996 *Pusillina sarsi* (Lovén, 1846) – Warén: p. 1041–1048, figs. 19–23.

*Material:* Two specimens from unit 9 in the *Mactra* Zone. The species is new to the fossil fauna of Tjörnes.

*Remarks:* The thin and fragile shells are well preserved and measure (h × d): 2.4 × 1.9 and 1.8 × 1.5 mm. The shell ratios d/h are 0.79 and 0.83, slightly higher than those of *Hydrobia ventrosa*. The protoconch has about two whorls, smooth and rather flat. The teleoconch is void of ribbing (forma *sarsii*). The oval aperture is slightly angulated. No colored spots or lines (e.g. brownish) were observed in the fossil shells, but they may have disappeared during burial or pre-depositional transport in the sediments.

*Recent distribution, ecology, and biology: Pusillina sarsi* is a boreal species with lusitanian outposts extending in the North Atlantic from the Norwegian west coast (at 68°N) in the north and south to the Mediterranean (Graham, 1988; Warén, 1996a). It is found living in the Baltic, but has not been recorded from Iceland or the Faroe Islands and is rare on British coasts (Graham, 1988; Warén, 1996a). Bathymetrical range: The species prefers to live in the tidal zone and foreshore areas and has rarely been found at depths exceeding 10 m (Funder et al., 2002; Warén, 1996a). The species seems to live in a range of salinities down to 6.5–7.0‰ (Warén, 1996a). It is not quite clear if the species has a pelagic larval stage, but it is considered more likely since the eggs develop into free veliger larvae (Graham, 1988).

In the British Isles the species lives among weeds on rocky shores with *Zostera* and *Codium* (Fretter & Graham, 1978). Warén (1996a) found the species almost always together with *Rissoa membranacea* (Adams) on algae and *Zostera*, but never on open coasts in exposed environments.

*Fossil occurrence:* Pliocene: *Mactra* Zone of the Tjörnes beds (this volume). Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent. The occurrence in the Tjörnes beds seems to be the earliest of the species. We have not found any Lower or Middle Pleistocene records, for example, in the crag formations in the British Isles or elsewhere in the North Atlantic area. Possibly, specimens from these sediments have been misidentified as the taxonomy of the *Rissoa* groups is not always easy to deal with.

### Genus *Obtusella* Cossmann, 1921

#### *Obtusella tumidula* (Sars, 1878)

Plate 7.3. Fig. 2

1878 *Cingula tumidula* n. sp. – Sars: p. 174–175, Pl. 10, fig. 2a–b.
1995 *Punctulum minutum* Golikov & Fedjakov, 1987 – Golikov: p. 25, fig. 26 (cf. Warén, 1996b).
1996 *Obtusella tumidula* (G.O. Sars, 1878) – Warén: p. 215, fig. 12d.

*Material:* Seventeen specimens from unit 9 in the *Mactra* Zone. The species is new to the fossil fauna of Tjörnes.

*Remarks:* The five largest shells measured (h × d × ha): 2.2 × 1.1 × 0.9, 1.9 × 1.2 × 0.8, 1.8 × 1.1 × 0.8, 1.8 × 0.9 × 0.8, 1.6 × 0.9 × 0.8 mm. The d/h ratios are 0.5–0.6. The shells all have fine sculpture of numerous spiral lines, much finer than in *Cingula aculeus* (Gould, 1841). Furthermore, the aperture is slightly square, but unfortunately the outer lip is slightly damaged in all the found specimens. This makes identification somewhat hard.

*Recent distribution, ecology, and biology: Obtusella tumidula* is nowadays an arctic-subarctic-high boreal species extending from Svalbard, Barents Sea, the

White Sea, and the Kara Sea southward to great depths near the Faroe Islands (Golikov, 1995; Sneli et al., 2005; Warén, 1996b). It has been found north of Iceland (Tjörnes) and in the Okhotsk Sea (Golikov, 1995; Warén, 1996a). Bathymetrical range: from 5 m in the White Sea to 850 m near the Faroe Islands (Golikov, 1995; Sneli et al., 2005). According to Golikov (1995), it prefers salinity from 27.2 to 33.5‰. The larval development is unknown to the authors.

The species lives mainly on silty or sandy substrates, as well as on gravels (Golikov, 1995; Sneli et al., 2005).

*Fossil occurrence:* Pliocene: *Mactra* Zone of the Tjörnes beds (this volume), otherwise unknown. Stratigraphical range: Pliocene to Recent. The specimens from the *Mactra Zone* apparently represent the earliest appearance of this species.

### Genus *Alvania* Risso, 1826

#### *Alvania* cf. *punctura* (Montagu, 1803)

Plate 7.3. Fig. 7.3

1803 *Turbo puncturus* – Montagu: p. 320, Pl. 12, fig. 5.
1920 *Alvania punctura* (Montagu) – Harmer: p. 615–616, Pl. 51, fig. 32.
1978 *Alvania punctura* (Montagu, 1803) – Fretter & Graham: p. 184–186, figs. 158–159.
1996 *Alvania punctura* (Montagu, 1803) – Warén: p. 225, fig. 17e–f.

*Material:* A total of 59 specimens from unit 9 in the *Mactra* Zone. The species is new to the fossil fauna of Tjörnes.

*Remarks:* The five largest shells measure (h × d × ha): 3.0 × 1.8 × 1.1, 2.6 × 1.8 × 1.3, 2.6 × 1.6 × 1.0, 2.5 × 1.5 × 1.1, and 2.2 × 1.5 × 1.0 mm. The d/h ratios are 0.60–0.69.

Most of the found shells are not fully mature, which is also characteristic for other species found in this lens in unit 9. The apex is rather eroded, but apparently it is not particularly pointed and rather flat, and the protoconch seems to be 2.2–2.5 whorls, hardly 2.5–3.0 as recorded by Warén (1996b). The teleoconch has deep sutures, longitudinal ribs, and spiral ridges. The longitudinal ribs are considerably higher than the spiral ridges, although they form a delicate cancellation. The longitudinal ribs reach the uppermost part of the base. The aperture is oval and slightly angulated above with a thickened outer lip. The shell can best be compared with *Alvania punctura*, but the protoconch is slightly smaller and the longitudinal ribs seem higher in the Tjörnes specimens than generally figured (cf. Warén, 1996b). It can also be compared in form and sculpture with *A. abyssicola* (Forbes) or *A. subsoluta* (Aradas), but these species are now living at a considerably greater depth than estimated for the depositional environments, when the aforementioned lens was formed. The Tjörnes specimens seem to be wider than typical *A. punctura*, with somewhat more prominent axial ribbing and wider interspace than the typical form. However, in spite of the differences mentioned above, we refer these shells from the *Mactra* Zone to *Alvania punctura* with some reservations.

*Recent distribution, ecology, and biology: Alvania punctura* is a boreal-lusitanian species (Fig. 7.8). It extends in the North Atlantic region from the Kola Peninsula, western Norway (at about 70°N), and the Faroe Islands in the north to the Mediterranean in the south (Fretter & Graham, 1978; Nekhaev, 2014; Warén, 1996b). It is present at the Swedish west coast and the western part of Øresund, but not in the Baltic, the east shores of the North Sea nor the eastern basin of the English Channel (Fretter & Graham, 1978; Jensen & Knudsen, 1995). It is not known from Iceland. Bathymetrical range: from 0 m or intertidal (several localities) to about 100 m (Fretter & Graham, 1978; Warén, 1996b) or 2–120 m (Sneli et al., 2005). The species is probably mesohaline, but we have no records of its salinity tolerance. The larval development is with a pelagic stage, and in the Plymouth plankton the larvae are common throughout summer and autumn (Lebour, 1934).

The species prefers sandy bottom even silty, but it also lives on algae and among intertidal rocks (Warén, 1996b).

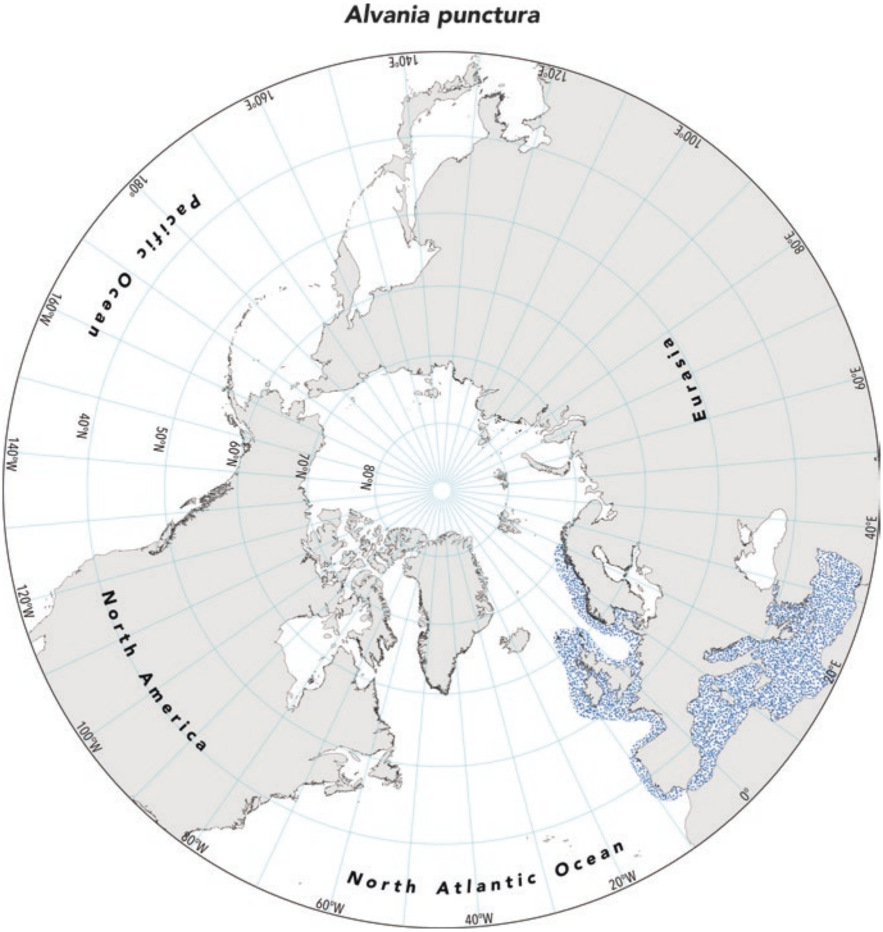

**Fig. 7.8** The recent known geographical distribution of *Alvania punctura* (Montagu)

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Harmer, 1920), Estepona in southern Spain (Landau et al., 2004). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1920). ?Lower Pleistocene: Palosco beds in the Po Basin (Gianolla et al., 2010). Middle Pleistocene: Trezzo beds in the Po Basin (Gianolla et al., 2010). Upper Pleistocene: Selsey beds (Harmer, 1920). Stratigraphical range: Pliocene to Recent.

### Genus *Onoba* H. & A. Adams, 1854

#### *Onoba aculeus* (Gould, 1841)

Plate 7.3. Fig. 4

1841 *Cíngula acúleus* – Gould: p. 266, fig. 172.
1878 *Onoba aculeus*, Gould – Sars: p. 172–173, Pl. 9, fig. 12a–b.
1920 *Onoba aculeus* (Gould) – Harmer: p. 643, Pl. 51, fig. 43.
1996 *Onoba aculeus* (Gould, 1841) – Warén: p. 228, figs. 20e–h, 21d–e.

*Material:* One shell from unit 9 in the *Mactra* Zone. The species is new to the fossil fauna of Tjörnes.

*Remarks:* The found specimen is fairly well preserved and measures (h × d × ha): 2.8 × 1.3 × 1.0 mm. The ratio d/h is 0.46.

The shell is covered with slight spiral striae, but there are no longitudinal ribs as found in *Onoba semicostata* (Montagu). It is quite similar to the shell of *O. proxima* (Forbes & Hanley), which has a thinner outer lip, more whitish and less sculptured shell with more oblique sutures. According to Warén (1974), all the records of *O. proxima* from Scandinavia and Iceland are based on misidentifications.

*Recent distribution, ecology, and biology: Onoba aculeus* is an arctic-subarctic-boreal species in the North Atlantic distributed from West and East Greenland, Svalbard, the Murman Coast, the whole Norwegian west coast, and Nova Scotia southward to northwestern Spain and New Jersey (Sneli et al., 2005). The species is common in Iceland, the Faroe Islands, Skagerrak, Kattegat, and the southernmost parts of the Baltic (Warén, 1996b). Bathymetrical range: from 0 m in Iceland to about 200 m in East Greenland (Thorson, 1941). In Iceland the species lives preferably in the tidal zone, and only very few specimens have been found at greater depths than 4 m (Thorson, 1941). The species is a marine species with salinity tolerance down to 5‰ (Funder et al. 2002). Thorson (1941, 1946) stressed that apparently the species has not a pelagic larval development.

The species prefers sheltered rocky shores and is often found in very large numbers under stones or on algae, avoiding silty areas (Fretter & Graham, 1978; Warén, 1996b).

*Fossil occurrence:* Pliocene: *Mactra* Zone of the Tjörnes beds (this volume). Lower Pleistocene: Svarthamar Member in Breiðavík (Vilhjálmsson, 1985). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent. As we have not found any older records of fossil *Onoba aculeus,* than those from Upper Pleistocene, the occurrence in the *Mactra* Zone appears to be the earliest known so far.

### *Onoba semicostata* (Montagu, 1803)

Plate 7.3. Fig. 5

1803 *Turbo semicostatus* – Montagu: p. 326–327.
1848 *Rissoa striata*. Mont. – Wood: p. 100–101, Pl. 11, fig. 1a–b.
1878 *Onoba striata*, Mont.– Sars: p. 172, Pl. 22, fig. 3.
1920 *Onoba striata* (J. Adams) – Harmer: p. 641–643, Pl. 51, fig. 42.
1980 *Cingula* cf. *semicostata* (Montagu, 1803) – Gladenkov et al.; p. 66–67.
1996 *Onoba semicostata* (Montagu, 1803) – Warén: p. 226–228, figs. 20a–d, 21a–c.

*Material:* Twenty-one shells from units 2–4 in the *Tapes* Zone and units 7 and 9 in the *Mactra* Zone. Ten specimens were found in a shelly lens in unit 9.

*Remarks:* The shell is covered with slight spiral striae, but generally longitudinal ribs are in the adapical parts of the whorls, but they die out before reaching the sutures. The shells are rather fragmentary as many of them lack the protoconch, and also the outer lip of the aperture is generally damaged. Two measureable specimens measure (h × d × ha): 3.4 × 1.7 × 1.1 and 2.3 × 1.0 × 0.9 mm. The d/h ratios are 0.50 and 0.43.

*Recent distribution, ecology, and biology: Onoba semicostata* is a boreal-lusitanian species extending in the North Atlantic from the west coast of Norway (at about 70°N) and Iceland southward to the Mediterranean and possibly farther south to Morocco (Warén, 1996b). It is distributed in Skagerrak and Kattegat, but has neither been found living in inner Danish waters nor the Baltic, and it is absent from the Danish and German North Sea coasts (Fretter & Graham, 1978; Warén, 1996b). Bathymetrical range: from 0 m in several localities to about 1000 m in the Faroe Islands (Sneli et al., 2005). In the British Isles it is common on the shores from near the low water mark to about 100 m (Fretter & Graham, 1978). The species is apparently polyhaline with salinity tolerance above 25‰, and in Skagerrak and Kattegat it avoids the uppermost 1–5 m because of salinity variations (Funder et al., 2002; Warén, 1996b). The embryos hatch in the crawling stage and the larval development is without a pelagic stage (Thorson, 1941).

The species is common, even abundant, on rocky and stony shores, as well as sandy bottoms with algae (Fretter & Graham, 1978; Warén, 1996b). It seems to avoid more open areas close to the coasts.

*Fossil occurrence:* Miocene: Borehole Lullingen 1 (depth 57 m), Niederrhein (Wienrich, 2001). Pliocene: Coralline Crag Formation (Harmer, 1920), Kallo and Doel sections in Belgium (Marquet, 1997a). Pliocene/Lower Pleistocene: Westerschelde (van Regteren Altena et al., 1954). Lower Pleistocene: Icenian Crag at Aldeby (Harmer, 1920). Middle Pleistocene: Bridlington Crag (Harmer, 1920). Upper Pleistocene: Selsey beds (Harmer, 1920), Baltic Eemian (Funder et al., 2002). Stratigraphical range: Miocene to Recent.

## Family Omalogyridae Sars, 1878

### Genus *Omalogyra* Jeffreys, 1860

**_Omalogyra atomus_ (Philippi, 1841)**
Plate 7.3. Fig. 6

1841 *Truncatella atomus* – Philippi: p. 54, Pl. 5, fig. 4.
1878 *Homalogyra atomus*, Phil. – Sars: p. 215–216, Pl. 22, fig. 21a–c.
1923 *Homalogyra atomus* (Philippi) – Harmer: p. 849–850, Pl. 64, fig. 34.
1941 *Homalogyra atomus* (Philippi) – Thorson: p. 44.
1995 *Omalogyra atomus* (Philippi, 1841) – Golikov: p. 57, fig. 59.

*Material:* Six specimens from unit 9 in the *Mactra* Zone. The species is new to the fossil fauna of Tjörnes.

*Remarks:* The shell is minute, with up to about three whorls lying in one plane and form a biconcave, almost smooth disk. The largest measureable shell is 0.5 mm in height (h) and the diameter (d) is 1.3 mm. The d/h ratio is 1.53. The minute and fragile shell is generally fragmentary in the sediment.

*Recent distribution, ecology, and biology: Omalogyra atomus* is a boreal-lusitanian species with subarctic occurrences. It is distributed in the North Atlantic from the White Sea, the Norwegian coast and West Iceland in the north to the Mediterranean and Madeira in the south (Golikov, 1995; Thorson, 1941). It has been found living along the Swedish west coast to Øresund, but has not been reported from the Baltic (Sneli et al., 2005). It occurs in West Greenland and from Maine to Road Island off the American east coast (Graham, 1988; Thorson, 1941). Bathymetrical range: from 0 m in Iceland to 38 m in West Greenland (Thorson, 1941) or from the littoral zone to 40 m (Golikov, 1995). The species seems polyhaline with salinity tolerance 26–34.5‰ (Golikov, 1995). The larval development is non-pelagic (Thorson, 1941).

The species is widespread on British coasts, except those of the southern North Sea, and there it is often found in large numbers on fine weeds growing on rocks and in rock pools on the lower parts of the shore (Graham, 1988).

*Fossil occurrence:* Miocene: Korytnica clay in Poland (Bałuk, 1975). Pliocene: Coralline Crag Formation (Harmer, 1923), Rodes Formation in Greece (Koskeridou et al., 2009). Upper Pleistocene: Selsey beds (Harmer, 1923), Kapp Wijk beds in Svalbard (Feyling-Hanssen, 1955a). Stratigraphical range: Miocene to Recent.

There are rather few records of this species in sediments, probably due to its minute size.

### Family Skeneopsidae Iredal, 1915
### Genus *Skeneopsis* Iredal, 1915

**_Skeneopsis planorbis_ (Fabricius, 1780)**
Plate 7.3. Fig. 7

1780 *Turbo planorbis* – Fabricius: p. 399.
1878 *Skenea planorbis*, Fabr. – Sars: p. 184–185.
1941 *Skeneopsis planorbis* (Fabricius) – Thorson: p. 42–44.
1995 *Skeneopsis planorbis* (Fabricius, 1780) – Golikov: p. 29, fig. 39, 121c–d.

*Material:* A total of 81 shells from unit 9 in the *Mactra* Zone. The species is new to the fossil fauna of Tjörnes.

*Remarks:* The five largest specimens were measured (h × d): 0.8 × 1.6, 0.8 × 1.5, 0.8 × 1.4, 0.6 × 1.2, and 0.6 × 1.1 mm. The d/h ratios are 1.8–2.0 or considerably higher than in the biconcave *Omalogyra atomus.*

*Recent distribution, ecology, and biology: Skeneopsis planorbis* is an arctic-boreal-lusitanian species extending in the North Atlantic region from southwestern Greenland, Svalbard, and the White Sea southward to the Mediterranean and Madeira or the Azores (Fretter & Graham, 1978; Golikov, 1995; Sneli et al., 2005; Thorson, 1941). It has neither been recorded from the eastern coasts of the North Sea nor the Baltic (Fretter & Graham, 1978). From Arctic Canada it reaches south to Florida (Fretter & Graham, 1978). Bathymetrical range: from 0 m in Iceland to 75 m off Norway (Thorson, 1941). The species seems mainly polyhaline, but has been recorded from euhaline, as well as mesohaline areas, and Golikov (1995) found its salinity tolerance to be 22–34‰. According to Thorson (1941), the species has a direct larval development and no pelagic stage.

In the British Isles the species is mainly found on the lower parts of rocky shores in pools and on weeds where it can be extremely abundant (Graham, 1988). In Iceland it is a typical inhabitant of the tidal zone along the whole coast on stones, gravel, sand, mud, and *Zostera* (Thorson, 1941).

*Fossil occurrence:* Pliocene: Kallo and Doel sections (Marquet, 1997a). Upper Pleistocene: Eemian in Borehole M in the Netherlands (Meijer, 1993), Lateglacial beds on Seltjarnarnes, Southwest Iceland (Eiríksson et al., 2004), Santa Maria Island, Azores (Ávila et al., 2009). Stratigraphical range: Pliocene to Recent.

There are surprisingly few records from Pleistocene sediments of this species which is so extremely abundant in British and Icelandic waters today. Perhaps it has been overlooked due to its minute size, although it is slightly larger than *Omalogyra atomus.*

### Family Capulidae Fleming, 1822
### Genus *Capulus* Montfort, 1810

#### *Capulus* cf. *unguis* (Sowerby, 1816)
Plate 7.3. Fig. 8

1816 *Patella unguis* – Sowerby: p. 88, Pl. 139, fig. 7.
1848 *Capulus ungaricus*. Linn. var. *unguis* J. Sow. – Wood: p. 155, Pl. 17, fig. 2a–g.
1923 *Capulus unguis* (J. Sowerby) – Harmer: p. 765–766, Pl. 61, fig. 7.
1955 *Capulus unguis* (J. Sowerby, 1816) – van Regteren Altena et al.: p. 33, Pl. 8, fig. 81–81a.

*Material:* One specimen from unit 9 in the *Mactra* Zone. The species is new to the fossil fauna of Tjörnes.

*Remarks:* The left margin of the aperture is damaged, but the diameter appears to have been 3.2–3.3 mm and the height 3.9 mm. There are no signs of ridges radiating from the apex so characteristic for *Capulus ungaricus* (Linné, 1758). The surface is smooth, but as the outer layer of the shell is somewhat eroded some details of the surface structure may be lost. The shell is not as inequilateral and oblique as *C. obliquus* (Wood, 1848) and has a distinctly narrower base than *C. ungaricus*. Therefore, our specimen can best be compared with *C. unguis*.

According to van Regteren Altena et al., (1955; 1957), *Capulus obliquus* and *C. fallax*, both described by Wood, 1848, should be treated as synonyms of *C. unguis*.

*Distribution, ecology, and biology: Capulus unguis* is extinct, but, as it apparently preferred conditions today in the boreal-lusitanian regions of the North Atlantic, it had probably similar distribution as *C. ungaricus*. That species extends from Hammerfest in northern Norway and western Iceland in the north to the Mediterranean and the Azores or even Gulf of Guinea in the south (Sneli et al., 2005). It is known from Skagerrak and Kattegat, but seems absent from the Baltic (Thorson, 1941). The bathymetrical range is recorded by Thorson (1941) from 0 m in Iceland to 190 m in Norway, whereas Graham (1988) stressed a sublittoral living. Sneli et al. (2005) record the world bathymetrical range 10–2500 m. The salinity tolerance is unknown, but *C. ungaricus* has a long pelagic larval stage (Thorson, 1941).

In the British Isles *Capulus ungaricus* can be found on stones, but is mainly found attached to shells of living bivalves (Graham, 1988). In Iceland it has also been found on substrates of clay and sand (Thorson, 1941).

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Harmer, 1923), Luchtbal Sand Member (Marquet & Landau, 2006). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1923), Walcheren, Ritthem, and Westerschelde (van Regteren Altena et al., 1955). Stratigraphical range: Pliocene to Lower Pleistocene.

Apparently, the species did not survive the first phases of major cooling at the beginning of the Pleistocene, consistently with the inferred boreal-lusitanian preference of the species.

### Family Calyptraeidae Blainville, 1824
### Genus *Calyptraea* Lamarck, 1799

### *Calyptraea* cf. *chinensis* (Linné, 1758)
Plate 7.4. Fig. 1

1758 *Patella chinensis* – Linné: p. 781.
1848 *Calyptræa chinensis*. Linn. – Wood: p. 159, Pl. 18, fig. 1a–e.
1923 *Calyptraea chinensis* (Linné) – Harmer: p. 772–774, Pl. 61, figs. 19–20.
1924 *Calyptraea chinensis* (Linné) – Schlesch: p. 337, Pl. 10, fig. 7.
1955 *Calyptraea chinensis* (L.) – van Regteren Altena: p. 34, Pl. 8, fig. 83–83a.
1980 *Calyptraea chinensis* (Linné, 1766) – Gladenkov et al.: p. 68.

*Material:* Six specimens from units ?19, 20–21, and 23 in the *Serripes* Zone. We do not have the exact unit number for the two specimens recorded by Schlesch (1924).

*Remarks:* The shells are rather well preserved and the largest one measures about 25 mm in diameter. Generally, the protoconch is eroded in the found specimens.

*Recent distribution, ecology, and biology: Calyptraea chinensis* is mainly lusitanian in the North Atlantic, but has also been met with in the southernmost part of the boreal region (Fig. 7.9). It is distributed from the British Isles, where it has been found in the Firth of Clyde, off Isle of Man, and in the western part of the Channel

Fig. 7.9 The recent known geographical distribution of *Calyptraea chinensis* (Linné)

southward to Zaire in western Africa (Graham, 1988; Poppe & Goto, 1991). It is common in the Mediterranean, as well as the Black Sea (Poppe & Goto, 1991). Bathymetrical range: from intertidal shores down to 70 m (Poppe & Goto, 1991). The salinity tolerance is unknown, but the larval development seems to be without a pelagic stage (cf. Lebour, 1936).

The species is most commonly found on substrates of sand or mud, but may also be found on shells or under stones (Graham, 1988; Poppe & Goto, 1991).

*Fossil occurrence:* Miocene: Arnum Formation in Denmark (Sorgenfrei, 1958). Pliocene: Coralline Crag (Harmer, 1923), Luchtbal Sand Member (Marquet & Landau, 2006). Pliocene/Lower Pleistocene: Red Crag (Harmer, 1923), Walcheren, Ritthem, and Westerschelde (van Regteren Altena et al., 1955). Lower Pleistocene: Bramerton Crag (Harmer, 1923), ?Palosco beds in the Po Basin (Gianolla et al., 2010). Middle Pleistocene: Trezzo beds in the Po Basin (Gianolla et al., 2010). Stratigraphical range: Miocene to Recent.

### Family Lamellariidae d'Orbigny, 1841
### Genus *Velutina* Fleming, 1822

#### *Velutina velutina* (Müller, 1776)

Plate 7.4. Fig. 2

1776 *Bulla velutina* – Müller: p. 242.
1848 *Velutina lævigata*. Linn. – Wood: p. 152, Pl. 19, fig. 8a–b.
1878 *Velutina lævigata*, Penn. – Sars: p. 146.
1923 *Velutina lævigata* (Pennant) – Harmer: p. 760–761, Pl. 60, fig. 26.
1924 *Velutina velutina* (Müller) – Schlesch: p. 338, Pl. 10, fig. 25.
1988 *Velutina velutina* (Müller, 1776) – Graham: p 322, fig. 130.

*Material:* One specimen recorded by Schlesch (1924) from unit 22 or 23 in the *Serripes* Zone.

*Remarks:* The shell is kept in the Geological Museum of the University of Copenhagen (the stock room) and it measures (h × d): 9.0 × 7.7 mm. The specimen is rather eroded, but faint spiral lines characteristic for *Velutina velutina* are visible near the apex. The shell cavity is filled with sediment, and because of the poor state of preservation and its fragility, it is impossible to clean it further. In fact the shell is kept together with the sediment.

*Recent distribution, ecology, and biology: Velutina velutina* is a circumpolar form distributed from the Arctic and southward into the lusitanian region. From West and East Greenland, Svalbard, Franz Josef Land, Novaya Zemlya, the Kara Sea, the Siberian Arctic Sea, Arctic Canada, and Ellesmere Island it extends southward to the Mediterranean and Cape Hatteras in the North Atlantic and to Monterey Bay, the Okhotsk Sea, and Japan Sea in the Pacific (Sneli et al., 2005; Thorson, 1941). The species is found living in Skagerrak and Kattegat, but not known from the Baltic (Sneli et al., 2005). Bathymetrical range: 0 m in Norway to 1098 m off the Faroe Islands (Sneli et al., 2005; Thorson, 1941). Off northern Kurile Islands it has been found down to a depth of 2440 m (Golikov, 1995). In the British Isles it is sometimes found at extreme low water on the shores, but generally it lives sublittorally (Graham, 1988). The species seems polyhaline with salinity tolerance above 25‰ (Funder et al., 2002; Golikov, 1995). The larvae have a long pelagic stage (Thorson, 1941).

In Iceland the species has been found living on mud, sand, and stones, and in the British Isles it also inhabits rocky shores (Graham, 1988; Thorson, 1941). It is one of the carnivore mesogastropods (Thorson, 1944).

*Fossil occurrence:* Pliocene: *Serripes* Zone of the Tjörnes beds (this volume). Pliocene/Lower Pleistocene: San Joaquin Formation (Durham & MacNeil, 1967). Lower Pleistocene: Icenian Crag (Harmer, 1923). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

The occurrence of *Velutina velutina* in Pliocene sediments in northern Pacific is apparently of similar age as the occurrence in the *Serripes* Zone. The specimen in the Tjörnes beds is probably the oldest record from the North Atlantic area, which may indicate a migration from the Pacific to the Atlantic while the *Serripes* Zone was deposited. The long-lasting pelagic larval stage might have facilitated the migration of the species.

### Family Naticidae Forbes, 1838
### Genus *Cryptonatica* Dall, 1892

**_Cryptonatica affinis_ (Gmelin, 1791)**
Plate 7.4. Fig. 3

1791 *Nerita affinis* – Gmelin: p. 3675.
1848 *Natica clausa.* Broderip and Sowerby – Wood: p. 147, Pl. 16, fig. 2a–b.
1863 *Natica clausa,* Brodery u. Sowerby – Winkler; p. 209.
1878 *Natica clausa*, Brod. & Sow. – Sars: p. 159–160, Pl. 21, figs. 12a–b, 13.
1923 *Natica clausa*, Broderip and Sowerby – Harmer: p. 672–674, Pl. 61, figs. 1–5.
1923 *Natica affinis* (Gmelin) – Harmer: p. 674–675, Pl. 61, figs. 6–7.
1924 *Natica (Cryptonatica) clausa* (Broderip et Sowerby) – Schlesch: p. 337, Pl. 10, fig. 25.
1924 *Natica (Cryptonatica) affinis* (Gmelin) – Schlesch: p. 337.
1960 *Natica clausa* Broderip & Sowerby – Áskelsson: p. 22.
1980 *Natica clausa* Broderip et Sowerby, 1829 – Gladenkov et al.: p. 68–69, Pl. 13, figs. 13–15.

*Material:* About 350 shells from units 10–12 in the uppermost part of the *Mactra* Zone and units 14–22 and ?25 in the *Serripes* Zone.

*Remarks:* The largest specimen measures (h × d): 22.4 × 20.6 mm and the d/h ratios are 0.91–1.00. Ten shells measured by Gladenkov et al. (1980) are included in these numbers. The thin and rather fragile shells are often fragmentary, and the distribution in the sediments strongly indicates these specimens were part of a death assemblage (thanatocoenosis).

*Recent distribution, ecology, and biology: Cryptonatica affinis* is circumpolar, being distributed from the Arctic and south into the lusitanian region. It occurs from West and East Greenland, Svalbard, Franz Josef Land, Novaya Zemlya, the Kara Sea, the Siberian Arctic Sea, Alaska (off Point Barrow), and Ellesmere Island southward to the Mediterranean and Cape Hatteras in the North Atlantic and to Vancouver and Japan in the Pacific (MacGinitie, 1959; Macpherson, 1971; Thorson, 1944). It has not been recorded from the Baltic and only a few specimens have been found in the British Isles, especially in northern British waters (Funder et al., 2002; Graham, 1988). Bathymetrical range: from 0 m in Norway to 2660 m in Algeria (Thorson, 1944). The habitat of the species deepens south in the North Atlantic with increasing depths (Graham, 1988). The lower salinity tolerance is 15‰ (Funder et al., 2002), and Golikov (1995) reported salinity ranges between 23 and 35‰. The larval development is non-pelagic (Thorson, 1935).

The species belongs to the infauna, and in Iceland it is commonly found in the Arctic *Macoma* community in shallow water on mud or silt bottom, as well as in the *Yoldia hyperborea* community at depths of 45–162 m (Spärck, 1937). *Cryptonatica* *affinis* is carnivorous, which is a very common feeding habit among the boring Naticidae species (Thorson, 1941, 1944).

*Fossil occurrence:* Oligocene/Miocene: Narrow Cape Formation (Grant & Gale, 1931), Yakataka Formation, Alaska (Addicott et al., 1971). Miocene: Arnum Formation (Sorgenfrei, 1958). Pliocene: Oosterhout Formation, *Nassarius propinquus* and *Lentidium complantum* Zone in the Netherlands (Spaink, 1975). Pliocene/Pleistocene: Red Crag Formation (Harmer, 1921; Wood, 1848). Lower Pleistocene: Pattorfik beds (Símonarson, 1981b), Olkov and Tusatuva-Yamsk Suites (Petrov, 1982), Santernian in Calabria (Malatesta & Zarlenga, 1986). Middle Pleistocene: Kresta, Kolvin, and Padymeiskii Suites (Petrov, 1966, 1982; Merklin et al., 1979), Kotzebuan (Hopkins et al., 1972), Anvilian (Hopkins et al., 1974). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Miocene to Recent.

Durham and MacNeil (1967) referred to *Cryptonatica affinis* (*C. clausa*) as a Pliocene immigrant from the Pacific to the North Atlantic. The occurrence in the Arnum Formation in Denmark indicates earlier migration.

***Cryptonatica smithii* (Brown, 1839)**
Plate 7.4. Fig. 4

1839 *Globulus Smithii* – Brown: p. 104, Pl. 1, fig. 18.
1857 *Natica Smithii*, Brown – Wood: p. 321.
1878 *Ampullina Smithii* (Brown) – Sars: p. 155–156, Pl. 12, fig. 2a–b, Pl. 21, fig. 18.
1921 *Acrybia Smithii* (Brown) – Harmer: p. 699–700, Pl. 55, fig. 9.
1924 *Bulbus smithii* (Brown) – Schlesch: p. 338, Pl. 10, figs. 16–17.
1925 *Acrybia flava*, Gould – Bárðarson: p. 47, 55, 72–73.
1941 *Acrybia flava* (Gould) – Thorson: p. 57–58.
1980 *Natica smithii* (Brown, 1839*)* – Gladenkov et al.: p. 70, Pl. 13, fig. 20–20b.

*Material:* Sixteen specimens from unit 11 in the *Mactra* Zone and units 14 and 19 in the *Serripes* Zone.

*Remarks:* The three largest shells measure (h × d): 28.0 × 24.1, 24.4 × 18.6, and 23.1 × 19.2 mm. The d/h ratios were calculated for four measureable shells, and they are slightly lower than those of *Cryptonatica affinis* or 0.80–0.90. Shells of *C. smithii* are fragile and were found mostly as fragments.

*Recent distribution, ecology, and biology: Cryptonatica smithii* is an arctic-boreal species, but is very rarely found living. It extends in the North Atlantic from Svalbard and the Barents Sea southward to Lofoten at the Norwegian west coast and at considerable depths to the Faroe Islands (Sneli et al., 2005). It is known from Iceland and the American east coast from Gulf of St. Lawrence to George Bank in Massachusetts (Sneli et al., 2005; Thorson, 1941). In the Pacific it is known from the Bering Sea, Sea of Okhotsk, and off northern Kurile Islands (Golikov, 1995; Thorson, 1941). Bathymetrical range: from 28 m in Norway to 725 m near the Faroe Islands (Sneli et al., 2005; Thorson, 1941). According to Golikov (1995), it lives at depths from 30 to ?6000 m. It is probably euhaline living at salinity 32.4–35‰ (Golikov, 1995). The larval development is unknown.

The species seems to prefer substrate of sand, sand mixed with shells, and gravel (Sneli et al., 2005).

*Cryptonatica smithii* had a more proximal, shallow distribution during the Pliocene given the general shallow nature of the Tjörnes beds. Some species belonging to *Cryptonatica* or *Euspira* have a thin and fragile shell, and very few of them live in or close to the littoral zone, while many of them having been found living at considerable depths (cf. Sneli et al., 2005; Thorson, 1941). Therefore, it is tempting to explain these apparent changes in the bathymetry of some of the Naticidae as a result of migration from shallow (coastal) water out to greater depths during the first Cainozoic glaciations when the inland ice approached the coasts, as was the case in the Tjörnes area 2.5–2.6 Ma ago.

*Fossil occurrence:* Pliocene: *Mactra* and *Serripes* Zones of the Tjörnes beds (Gladenkov et al., 1980). ?Upper Pleistocene beds of Ardincaple, Tayport (Harmer, 1921; Wood, 1857). Stratigraphical range: Pliocene to Recent. The specimens from Tjörnes seem to represent the earliest appearance of the species and the only Pliocene occurrence known so far.

***Cryptonatica occlusa* (Wood, 1848)**
Plate 7.4. Fig. 5

1848 *Natica occlusa* – Wood: p. 146, Pl. 12, fig. 4a–b.
1863 *Natica occlusa,* Wood – Winkler: p. 209.
1921 *Natica occlusa*, S.V. Wood – Harmer: p. 676–677, Pl. 56, fig. 14.
1924 *Natica (Cryptonatica) occlusa* (J. Sowerby*)* – Schlesch: p. 337.
1980 *Natica occlusa* S. Wood, 1848 – Gladenkov et al.: p. 69–70, Pl. 13, fig. 16.

*Material:* Thirty-nine shells from unit 11 in the *Mactra* Zone and units 15–16 and 18–19 in the *Serripes* Zone.

*Remarks:* The largest specimen measures (h × d): 21.5 × 19.4 mm. The d/h ratios are 0.86–0.93, compared to 0.90–1.00 in *Cryptonatica affinis* and 0.80–0.90 in *C. smithii*. The thin and fragile valves are rather fragmentary in the sediments.

The shell is rather globose, the body whorl being by far the largest. The sutures are distinct and rather deep, but the whorls are not flattened below the sutures as in *C. affinis.* The aperture is less expanded than in *C. smithii,* but higher than in *C. affinis*, and the outer lip curves not as sharply to meet the body whorl as in *C. affinis.* The umbilicus is entirely closed by callus of the inner lip.

*Distribution, ecology, and biology:* Harmer (1921) recorded living *Cryptonatica occlusa* as recent from Finnmark and the Swedish coast without any further information. He considered it as a form of *C. affinis,* named *elatior* by von Middendorf (1849). However, Harmer (1921) also referred to the expression of E. A. Smith that it should be regarded as specifically distinct. As we have not found any records of living *C. occlusa,* we are inclined to regard it as extinct. From its distribution in sediments and also considering its co-occurrences with recent species, it probably preferred conditions as in the boreal region in the North Atlantic today. The bathymetrical range is not known, but apparently it lived sublittorally not far from coast. In the Tjörnes beds it is frequently found together with *C. affinis*, with salinity tolerance down to 15‰. *C. occlusa* does not have a pelagic larval stage (Thorson, 1941), otherwise the larval development is unknown.

In the Tjörnes environments the species obviously preferred substrates of sand and gravel.

*Fossil occurrence:* Pliocene: *Mactra* and *Serripes* Zones of the Tjörnes beds (Gladenkov et al., 1980). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1921). Middle Pleistocene: Bridlington Crag (Harmer, 1921). Stratigraphical range: Pliocene to Middle Pleistocene. The specimens in the Tjörnes beds seem to be the earliest representatives of this species.

### Genus *Euspira* Agassiz, 1837

***Euspira pallida* (Broderip & Sowerby, 1829)**
Plate 7.4. Fig. 6

1829 *Natica pallida* – Broderip & Sowerby: p. 372.
1848 *Natica Grænlandica*. Beck – Wood: p. 146–147, Pl. 12, fig. 5a–b.
1878 *Lunatia grönlandica*, Beck – Sars: p. 158, Pl. 21, fig. 15.
1921 *Natica (Lunatia) pallida*, Broderip and Sowerby – Harmer: p. 693–695, Pl. 56, figs. 8–11.
1924 *Natica (Euspira) pallida* (Broderip et Sowerby) = *N. groenlandica* Beck – Schlesch: p. 338.
1980 *Polinices* aff. *pallidus* (Broderip et Sowerby) – Gladenkov et al.: p. 72, Pl. 22, fig. 22–22a.

*Material:* About 30 specimens from unit 11 in the *Mactra* Zone and units 14–23 in the *Serripes* Zone.

*Remarks:* The largest specimen measures (h × d): 24.0 × 20.8 mm. The d/h ratios are 0.75–0.88. The shells are thin and often damaged or fragmented in the sediment.

*Recent distribution, ecology, and biology: Euspira pallida* is a circumpolar species extending from the Arctic and south into the temperate regions of Atlantic and Pacific oceans. It is distributed from West and East Greenland, Svalbard, Franz Josef Land, Novaya Zemlya, the Barents Sea, the Kara Sea, the Siberian Arctic Sea, Arctic Canada, and Ellesmere Island southward to Skagerrak, the Swedish west coast, the North Sea, Isles of Man, Durham on the British east coast, and North Carolina in the North Atlantic and in the Pacific to Monterey, the Sea of Okhotsk, and Japan (Sneli et al., 2005; Thorson, 1941). It has been found in Øresund, but not farther east into the Baltic (Sneli et al., 2005; Thorson, 1941). Bathymetrical range: from 0 m in Norway to 2430 m off Cape Hatteras (Thorson, 1941). It is by no means a littoral species, and in the Faroe Islands it has been found from a depth of 65 m down to 1319 m (Sneli et al., 2005). Salinity ranges have been reported as 23–34.5‰, with salinity tolerance down to about 15‰ (Funder et al., 2002; Golikov, 1995). The larval development is non-pelagic (Thorson, 1941).

The species belongs to the infauna, and in Iceland it is commonly found in the Arctic *Macoma* community in shallow sublittoral water on mud, silt, or sand bottom, as well as in the *Yoldia hyperborea* community at depths of 45–162 m (Spärck, 1937).

*Fossil occurrence:* Pliocene/Lower Pleistocene: San Joaquin Formation (Durham & MacNeil, 1967), Red Crag Formation (Harmer, 1921). Lower Pleistocene: Baventian (West et al., 1980), Pattorfik beds (Símonarson, 1981b), Olkov Suite (Petrov, 1982). Middle Pleistocene: Kresta, Kolvin, and Padymeiskii Suites (Merklin et al., 1979; Petrov, 1966, 1982), Kotzebuan (Hopkins et al., 1972), Anvilian (Hopkins et al., 1974). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

The species probably has its origin in the Pacific having migrated to the North Atlantic during Upper Pliocene while the *Mactra* Zone was deposited in the Tjörnes area (Durham & MacNeil, 1967; Malatesta & Zarlenga, 1986).

***Euspira montagui*** **(Forbes, 1838)**
Plate 7.4. Fig. 7

1838 *Natica Montagui* – Forbes: p. 32–33, Pl. 2, figs. 3–4.
1863 ?*Natica catena,* Da Costa – Winkler: p. 208.
1872 *Natica Montacuti*, Forbes – Wood: p. 78, Pl. 4, fig. 10.
1878 *Lunatia Montagui*, Forb. – Sars: p. 157.
1921 *Natica (Lunatia) Montagui*, Forbes – Harmer; p. 690–691, Pl. 55, fig. 10.
1924 ?*Natica (Euspira) catena* (Da Costa) – Schlesch: p. 338.
1980 *Natica helicina* (Brocchi, 1814) – Gladenkov et al.: p. 69, Pl. 13, fig. 19–19a.

*Material:* About 45 specimens from units 8 and 11–12 in the *Mactra* Zone and units 15 and 18–23 in the *Serripes* Zone. This distribution in the Tjörnes beds is based on the assumption that all specimens recorded by Gladenkov et al. (1980) as *Lunatia helicina* (Brocchi) belong to *Euspira montagui.* The species has not been recorded before from the Tjörnes beds.

*Remarks:* The largest specimen measures (h × d): 30.0 × 24.9 mm. The d/h ratios are 0.83–0.90 or slightly higher than in *Euspira pallida*. The thin and fragile shell is rather fragmentary in the sediments, and in particular the outer lip of the aperture is often damaged.

The shell is similar to that of *Euspira pallida,* but the body whorl is not so flattened below the suture, and the outer lip arises not at right angles to the body whorl as is does in *E. catena* (da Costa). The body whorl is not quite as big as in *E. alderi* (Forbes) and the spire is more prominent. The inner lip forms a callus which does not cover the umbilicus entirely as in *E. pallida,* and the umbilicus seems most comparable to that of *E. montagui* (cf. Fretter & Graham, 1981). Therefore, attribute these specimens from the Tjörnes beds to *E. montagui.*

*Recent distribution, ecology, and biology: Euspira montagui* is a boreal-lusitanian species in the North Atlantic, extending from the northernmost parts of the Norwegian west coast and West and South Iceland in the north to northwestern Morocco in the south (Sneli et al., 2005). It has been found living in Skagerrak and Kattegat, but not in the Baltic whereas it is well known from the Mediterranean (Fretter & Graham, 1981; Thorson, 1941). Bathymetrical range: from 2 m in Norway to about 1520 m off Iceland (Thorson, 1941). The species prefers offshore areas, and in the Faroe Islands it has been found at depths between 90 and 1078 m

(Sneli et al., 2005). It has a salinity tolerance down to 15‰ (Funder et al., 2002). The larval development is planktotrophic (Malatesta & Zarlenga, 1986).

The species lives on substrates of mud, silt, sand, sand mixed with shells, and gravel, and in the British Isles it prefers finer sediments than *E. catena* and *E. alderi* (cf. Fretter & Graham, 1981; Sneli et al., 2005).

*Fossil occurrence:* Pliocene: *Mactra* and *Serripes* Zones of the Tjörnes beds (Gladenkov et al., 1980). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1921). Lower Pleistocene: Emilian and Sicilian units in Sicily (Malatesta & Zarlenga, 1986). Middle Pleistocene: Bridlington Crag (Harmer, 1921). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent. The specimens in the Tjörnes beds seem to be the earliest representatives of the species in the North Atlantic area.

Durham and MacNeil (1967) stated that the genus *Lunatia* (=*Euspira*) migrated from the Pacific to the North Atlantic during the Pliocene and Pleistocene. This obviously took place while the Tjörnes beds were deposited.

***Euspira catenoides* (Wood, 1842)**
Plate 7.4. Fig. 8

1842 *Natica catenoides* – Wood: p. 529.
1848 *Natica catenoides*. S. Wood – Wood: p. 141–142, Pl. 16, fig. 10a–c.
1921 *Natica (Lunatia) catenoides* (S.V. Wood) – Harmer: p. 686–687, Pl. 55, fig. 1.
1924 *Natica (Euspira) catenoides* (S.V. Wood) = *N. heros* Say – Schlesch: p. 338, Pl. 10, fig. 15.
1925 *Natica* sp. – Bárðarson: p. 26, 28, 35, 39, 41, 44, 45, 76–77 (in part).
1980 *Polinices catenoides* (S. Wood, 1842) – Gladenkov et al.: p. 71, Pl. 13, figs. 17–18.

*Material:* About 60 specimens from unit 5 in the *Tapes* Zone and units 8–12 in the *Mactra* Zone.

*Remarks:* The largest shell measures (h × d): 38.1 × 37.5 mm and the d/h ratios are 0.91–0.99 (for 10 specimens). This species is much larger than any other Naticidae found in the Tjörnes beds, and has distinctly higher d/h ratio than the other *Euspira* species. Furthermore, its umbilicus is considerably larger.

*Distribution, ecology, and biology: Euspira catenoides* is extinct, but apparently it preferred conditions similar to those in the boreal region of the North Atlantic today. This can be concluded from its distribution as fossil in Pliocene sediments and also from its co-occurrence with recent species in, for example, in the *Mactra* Zone of Tjörnes. Bathymetrical range: The species preferred offshore areas and has not been found in any of the littoral sediments in the Tjörnes beds. The salinity tolerance is not known. Neither do we know its larval development, but most of the Naticidae lack pelagic larval stage.

When the species lived in the Tjörnes area it obviously lived on substratum of sand and rather fine gravel.

*Fossil occurrence:* ?Upper Miocene: *Tapes* Zone of the Tjörnes beds (Gladenkov et al., 1980). Pliocene: Coralline Crag Formation (Harmer, 1921), Krusschans

Member, Lillo Formation at Kallo (Marquet, 1997b). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1921). Stratigraphical range: Pliocene to Lower Pleistocene.

### Order Neogastropoda Wenz, 1838
### Family Muricidae, Fleming, 1828
### Genus *Boreotrophon* Fischer, 1884

#### *Boreotrophon clathratus* (Linné, 1767)

Plate 7.5. Fig. 1

1767 *Murex clathratus* – Linné: p. 1223.
1848 *Trophon scalariforme*. Gould – Wood: p. 48, Pl. 6, fig. 7a–c.
1878 *Trophon clathratus*, Lin. – Sars: p. 247–248, Pl. 15, fig. 10.
1918 *Trophon (Boreotrophon) clathratus* (Linné) – Harmer: p. 350–352, Pl. 12, fig. 25, Pl. 36, figs. 3–6.
1924 *Trophon (Boreotrophon) clathratus* (Linné) = *B. scalariforme* Gould – Schlesch: p. 335.
1980 *Trophon clathratus* (Linné, 1767) – Gladenkov et al.: p. 73.
2005 *Boreotrophon clathratus* (Linnaeus) – Sneli et al.: p. 64, fig. 21.

*Material:* Two specimens from unit 18 in the *Serripes* Zone. Furthermore, Schlesch (1924) recorded two shells from Hallbjarnarstaðakambur in accordance with Poulsen's unpublished manuscript (Poulsen, 1884). Most likely these specimens were found in unit 16 in the *Serripes* Zone. Norton (1975) also mentioned the species without further stratigraphical information or number of specimens. We have not found the shells mentioned by Schlesch or Norton.

*Remarks:* The larger specimen from unit 18 is very well preserved and measures (h × d): 19.1 × 10.5 mm with d/h ratio 0.55. The other shell is damaged.

*Recent distribution, ecology, and biology: Boreotrophon clathratus* is an arctic-subarctic-boreal species with circumpolar distribution. It extends from West and East Greenland, Svalbard, Franz Josef Land, Novaya Zemlya, the Siberian Arctic Sea, and northern Alaska to the west coast of Sweden (Bohuslän), North England, the Hebrides, and Cape Cod (Sneli et al., 2005; Thorson, 1941). In the Pacific it is distributed southward to Puget Sound and Japan (Thorson, 1941). The species is not known from the Baltic. Bathymetrical range: from 8 m in Svalbard to 1033 m off the Hebrides (Thorson, 1941) or 1–1060 m (Poppe & Goto, 1991). In the Faroe Islands it prefers depths from 50 to 260 m (Sneli et al., 2005). The species is polyhaline with salinity tolerance above 25‰ (Funder et al., 2002). The larval development is non-pelagic (Thorson, 1941).

In Iceland the species lives on a substrate of boulders, gravel, sand, mud, and algae. It has also been found in the stomach of a cod (Thorson, 1941).

*Fossil occurrence:* Pliocene: *Serripes* Zone of the Tjörnes beds (Gladenkov et al., 1980). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1848). Lower Pleistocene: Pattorfik beds (Símonarson, 1981b), Tusatuva-Yamsk Suites (Petrov, 1982). Middle Pleistocene: Ragov Suite and Mikulin horizon (Merklin et al., 1979). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent. The occurrence in the Tjörnes beds seems to be the oldest stratigraphic record of the species.

Grant and Gale (1931) mentioned at least ten species of *Boreotrophon* from the Pacific area, the oldest from Miocene sediments, and Durham and MacNeil (1967) mentioned the genus among Pacific Pliocene immigrants. Probably, *Boreotrophon clathratus* evolved from one of these Pacific groups during migration to the North Atlantic while the *Serripes* Zone of the Tjörnes beds were deposited.

### Family Buccinidae Latreille, 1825
### Genus *Buccinum* Linné, 1758

#### *Buccinum undatum* Linné, 1758
Plate 7.5. Fig. 2

1758 *Buccinum undatum* – Linné: p. 740.
1848 *Buccinum undatum.* Linn. – Wood: p. 35–36, Pl.3, fig. 12a–b.
1863 *Buccinum undatum*, Linn. – Winkler: p. 210.
1878 *Buccinum undatum*, Lin. – Sars: p. 254–256, Pl. 13, fig. 12, Pl. 24, figs. 2–4.
1914 *Buccinum undatum*, Linné, 1758 – Harmer: p. 90–97, Pl. 6, figs. 1–10, Pl. 7, figs. 1–6, Pl. 8, figs. 1–2, Pl. 10. fig. 13.
1924 *Buccinum undatum* (Linné) – Schlesch: p. 333–334.
1925 *Buccinum undatum,* L. – Bárðarson: p. 48, 53, 55, 72–73.
1980 *Buccinum undatum* Linné, 1758 – Gladenkov et al.: p. 73–74, Pl. 14, figs. 1–5.

*Material:* About 60 specimens from units 14–20 and 25 in the *Serripes* Zone. The species is especially common in units 14–15 in the lowermost part of the *Serripes* Zone.

*Remarks:* The largest shell (measured by Gladenkov et al. (1980)) is (h × d): 38 × 26 mm. The d/h ratios are 0.54–0.62. The specimens from the Tjörnes beds are small compared to recent Icelandic shells, which are up to 150 mm high. The larger specimens are usually damaged, whereas the smaller ones are generally entire. Their distribution in the sediments indicates reworking and death assemblages (thanatocoenosis), as the death rate seems rather low among young animals.

*Recent distribution, ecology, and biology: Buccinum undatum* is a subarctic-boreal species in the North Atlantic, with arctic, as well as lusitanian outposts (Fig. 7.10). It extends from Jones Sound, West Greenland (between Disko Island and Nuuk), Svalbard, Novaya Zemlya, the White Sea, and the Barents Sea in the north to the Bay of Biscay and New Jersey in the south (Sneli et al., 2005; Thorson, 1941, 1951). It does not occur off northern Alaska or in the Pacific (Macpherson, 1971), and Thorson (1944) has excluded it from the East Greenland fauna. According to Golikov (Golikov, 1995), it is not living in the Kara Sea, Laptev Sea, or the Siberian Arctic Sea. The species has been found in Wadden Sea, Skagerrak and Kattegat south to Øresund, but is not known from the Baltic (cf. Thorson, 1941). Bathymetrical range: from 0 m in Iceland to 1319 m in the Faroe Islands (Óskarsson, 1962; Sneli et al., 2005) or 0–2000 m (Nordsieck, 1968). The species lives in shallower water in more northern localities. It is mesohaline with salinity tolerance

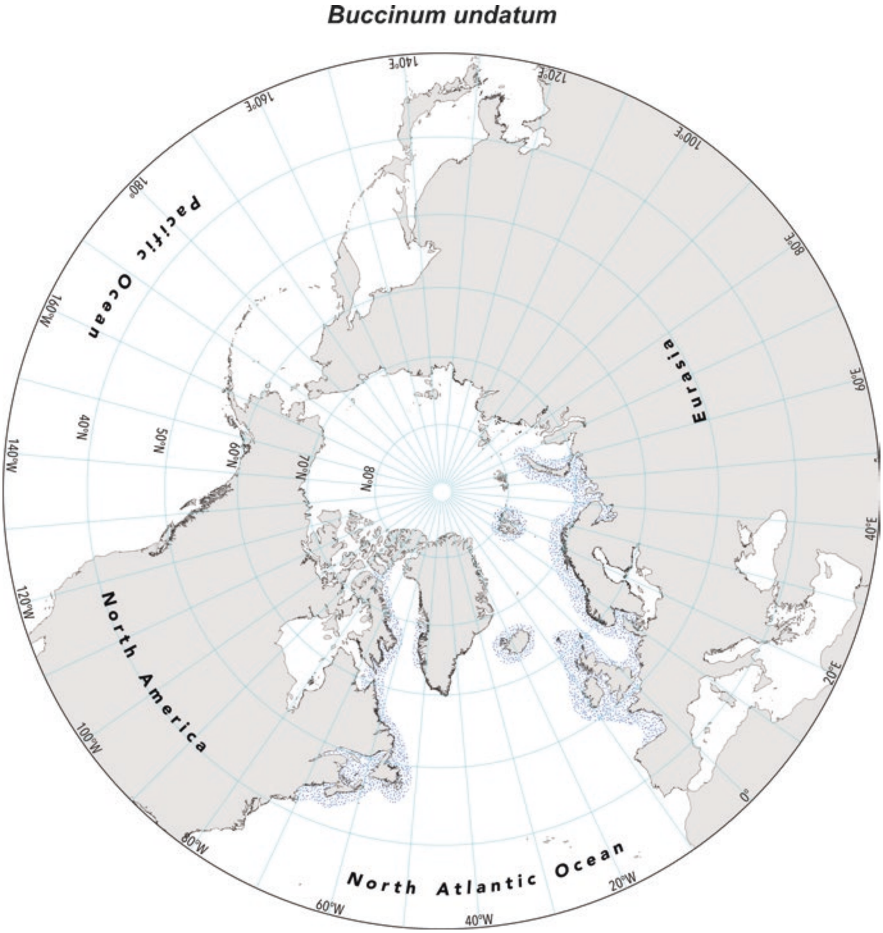

**Fig. 7.10** The recent known geographical distribution of *Buccinum undatum* Linné

down to 15‰ (Funder et al., 2002). The larval development is non-pelagic (Thorson, 1941).

In the Faroe Islands it lives at the northern, as well as the southern islands, equally frequent in the fiords and off the islands, on a substrate of sandy mud, gravel, and stones (Sneli et al., 2005).

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Wood, 1848), Luchtbal Sand Member, Lillo Formation (Marquet & Landau, 2006). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1914; Wood, 1848). Lower Pleistocene: Pattorfik beds (Símonarson, 1981b), Emilian and Sicilian (Malatesta & Zarlenga, 1986). Middle Pleistocene: Padymeiskii Suite (Merklin et al., 1979; Petrov, 1982). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

Durham and MacNeil (1967) mentioned *Buccinum undatum* among Pacific Pliocene immigrant species. The genus *Buccinum* first appeared in the late Oligocene of the Pacific, and Grant and Gale (1931) recorded at least three species from the Miocene of Alaska and the state of Washington. Presumably, *Buccinum undatum* evolved from one of these Pacific groups, especially from the *Buccinum plectrum* stock, during migration to the North Atlantic while the Tjörnes beds were deposited.

***Buccinum cyaneum*** **Bruguière, 1792**
Plate 7.5. Fig. 3

1792 *Buccinum cyaneum* – Bruguière: p. 266.
1878 *Buccinum grönlandicum,* Chemn. – Sars: p. 259–261, Pl. 13, fig. 9a–b, Pl. 25, figs. 1–2.
1914 *Buccinum grœnlandicum,* Chemnitz – Harmer: p. 97–99, Pl. 8, figs. 4–6, Pl. 9, figs. 10.
1924 *Buccinum groenlandicum* Chemnitz? – Schlesch: p. 334, Pl. 8, figs. 18–23.
1925 *Buccinum groenlandicum*, Chemn. – Bárðarson: p. 48, 50, 52–53, 57, 72–73.
1980 *Buccinum groenlandicum* Chemnitz, 1788 – Gladenkov et al.: p. 74, Pl. 14, figs. 7–8.
1995 *Buccinum cyaneum* Bruguière, 1789–1792 – Golikov: p. 46, figs. 100, 135C.

*Material:* Thirteen specimens from units 14–16, 18, 20–21, and 25 in the *Serripes* Zone. About half of the shells were found in unit 15.

*Remarks:* The largest shell measures (h × d): 52.4 × 32.4 mm, and the d/h ratios are 0.62–0.68. The thin shells are often damaged, especially the larger specimens.

We agree with Sneli et al. (2005) that the name Chemnitz gave this species in 1788 is not in accordance with the binominal nomenclature and therefore unacceptable, and it should therefore be referred to as *Buccinum cyaneum*. Some authors obviously regard both *B. cyaneum* and *B. glaciale* Linné, 1761 as synonyms of *B. groenlandicum.* However, we follow the opinions of Macpherson (1971) and Golikov (1995) that we are dealing with two different species. The difference is especially visible when regarding the spiral ridges on the body whorl. In *B. cyaneum* those spiral ribs are rather low, almost equal, and progressively more widely separated, while *B. glaciale* has up to eight spiral carinae on the last whorl, usually forming knobs where they meet the axial folds (cf. Macpherson, 1971: Pl. 6, figs. 2 and 9).

*Recent distribution, ecology, and biology: Buccinum cyaneum* is an arctic-subarctic-boreal species with circumpolar distribution. It extends from West and Southeast Greenland, Svalbard, Franz Josef Land, Novaya Zemlya, and the Siberian Arctic Sea in the north to Lofoten at the Norwegian west coast and the Faroe Islands in the south (Sneli et al., 2005; Thorson, 1941). Along the western Atlantic coasts it is distributed from Ellesmere Island southward to Cape Cod and in the Pacific from Alaska to British Columbia (Golikov, 1995; Sneli et al., 2005). Bathymetrical range: from the littoral zone in several localities to 992 m in the Russian Arctic (Golikov, 1995). In the Faroe Islands it lives at depths from 99 to 728 m (Sneli et al., 2005). The species is polyhaline with salinity tolerance above 25‰ (Funder et al., 2002) or

29–35‰ (Golikov, 1995). The larval development lacks a pelagic stage (Thorson, 1941).

The species prefers coarse sand, gravel or stony and rocky substrates (Golikov, 1995; Sneli et al., 2005).

*Fossil occurrence:* ?Miocene: Quyllayute Formation of Washington (Grant & Gale, 1931). Pliocene: *Serripes* Zone of the Tjörnes beds (this volume). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1914). Lower Pleistocene: Pattorfik beds (Símonarson, 1981b), Sicilian of Monte Pellegrino (Malatesta & Zarlenga, 1986). Middle Pleistocene: Kotzebuan (Hopkins et al., 1972). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: ?Miocene to Recent.

The species seems of Pacific origin and probably to be migrated into the North Atlantic while the deposition of sediments of the *Serripes* Zone.

### ***Buccinum finmarkianum*** **Verkrüzen, 1875**

Plate 7.5. Fig. 4

1875 *Buccinum Finmarkianum* – Verkrüzen: p. 237, Pl. 8, figs. 1–5.
1878 *Buccinum finmarchianum*, Verkrüzen – Sars: p. 262–263, Pl. 13, fig. 10, Pl. 25, figs. 3–4.
1914 *Buccinum finmarchianum*, Verkrüzen – Harmer: p. 161–162, Pl. 8, fig. 3.
1914 *Buccinum inexhaustum*, Verkrüzen – Harmer: p. 109–110, p. 10, figs. 1–3.
1924 *Buccinum inexhaustum* Verkrüzen – Schlesch: p. 334, Pl. 9, figs. 2–4.
1980 *Buccinum* ex. gr. *inexhaustum* Verkrüzen, 1881 – Gladenkov et al.: p. 75, Pl. 14, fig. 6–6b.
1995 *Buccinum finmarchianum* Verkrüzen, 1875 – Golikov: p. 46, figs. 99, 133G-H.

*Material:* Twenty specimens from units 10–11 in the *Mactra* Zone and units 15, 18–19, and 25 in the *Serripes* Zone.

*Remarks:* The three largest shells in our collection measure (h × d): 37.5 × 22.0, 34.6 × 19.8, and 25.8 × 14.0 mm. The d/h ratios are 0.54–0.59, slightly lower than found by Gladenkov et al. (1980). The d/h ratios are somewhat lower in *Buccinum finmarkianum* than *B. cyaneum* and longitudinal ribs or plicatures are entirely missing. Some of the shells are extensively bored, probably by sponges (?*Cliona*).

We consider *B. finmarkianum* and *B. inexhaustum*, both species described by Verkrüzen (1875, 1881), as a single species. Taken into consideration how variable the species of *Buccinum* can be, we are not able to verify the differences between these two species given different names by Verkrüzen.

*Recent distribution, ecology, and biology: Buccinum finmarkianum* is mainly subarctic in the North Atlantic. It extends from Baffin Island, West Greenland, Southeast Greenland, Svalbard, and Franz Josef Land in the north to Cape Cod, Iceland, and the west coast of Norway (at 69.5°N) in the south (Golikov, 1995; Høisæter, 1986; Thorson, 1941). The bathymetrical range is from the lowermost part of the littoral zone to a depth of 992 m (Golikov, 1995). It seems to be polyhaline, almost euhaline, with salinity tolerance above 29‰ (Golikov, 1995). The larval development is non-pelagic as generally found in *Buccinum* species (Thorson, 1941).

According to Golikov (1995), the species lives mainly on stony and rocky substrates, but also on silty sand with gravel and shell debris. The same is the case nowadays in Iceland.

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Harmer, 1914). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1914). Stratigraphical range: Pliocene to Recent.

According to Durham and MacNeil (1967), the species migrated from the Pacific to the North Atlantic while the Tjörnes beds were deposited during the late Pliocene.

### Genus *Liomesus* Stimpson, 1865

***Liomesus dalei* (Sowerby, 1825)**
Plate 7.5. Fig. 5

1825 *Buccinum Dalei* – Sowerby: p. 139, Pl. 486, figs. 1–2.
1872 *Trophon elegans,* Charlesworth – Wood: p. 22, Pl. 2, fig. 6a–b.
1920 *Liomesus Dalei* (J. Sowerby) – Harmer: p. 520–521, Pl. 45, figs. 4–6.
1924 *Liomesus dalei* (J. Sowerby) = *Buccinopsis crassa* Nyst = *B. eburnea* M. Sars – Schlesch: p. 330.
1924 *Liomesus canaliculatus* (Dall) – Schlesch: p. 329, Pl. 7, figs. 3–6.
1980 *Liomesus dalei* (J. et G. Sowerby) – Gladenkov et al.: p. 75, Pl. 15, fig. 35.

*Material:* Eleven specimens from units 11–12 in the *Mactra* Zone and 14–18, and 21 in the *Serripes* Zone.

*Remarks:* The two largest specimens measure (h × d): 38.8 × 20.0 and 34.3 × 19.3 mm. The d/h ratios are 0.52–0.56.

Some authors consider *Liomesus dalei* as a synonym of *L. ovum* (Turton). Graham (1988) described *Buccinum ovum* as "smooth to the naked eye." The majority of shells from the Tjörnes beds are ornamented by rather coarse spiral striation. Furthermore, Poppe and Goto (1991) stated that the name *L. dalei* is sometimes used for *L. ovum*, but "in fact this is a fossil species, slightly different from the recent *L. ovum.*" Therefore, we will use the name *L. dalei* for these specimens from Tjörnes.

*Distribution, ecology, and biology: Liomesus dalei* is apparently extinct, but has often been confused with the closely related *L. ovum*. Therefore, it is not easy to get a clear picture of its distribution. Probably, it lived similar to *L. ovum.* The latter lives now from West Iceland and western Norway (at ?62° N) in the north and southward to Brittany in France (Høisæter, 1986; Óskarsson, 1982; Poppe & Goto, 1991). In Iceland it has mainly be found in haddock stomachs (Óskarsson, 1982). The bathymetrical range of *L. ovum* is from 20 to about 400 m (Óskarsson, 1982; Poppe & Goto, 1991). The species is probably polyhaline, but the salinity tolerance, as well as the larval development, is unknown.

In the British Isles *L. ovum* lives on soft bottom at depths between 70 and 400 m (Graham, 1988). As *L. dalei* has been found in the Tjörnes beds in sediments deposited in nearshore environments, it cannot be excluded that it was brought to shallower depths by fish.

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Harmer, 1920), Luchtbal Sand Member (Marquet & Landau, 2006). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1920). Stratigraphical range: Pliocene to Lower Pleistocene.

Glibert (1952) did not record it from the Miocene of Belgium, and it has not been identified with safety elsewhere in Miocene sediments in the North Sea Basin (Harmer, 1920; Rasmussen, 1968; Sorgenfrei, 1958).

### Genus *Colus* Röding, 1798

#### *Colus olavii* (Mörch, 1871)

Plate 7.5. Fig. 6

1871 *Fusus (Sipho) Olavii,* Beck – Mörch: p. 396.
1872 ?*Trophon propinquus*, Alder var. *contortus* – Wood: p. 24, Pl. 2, fig. 15b.
1914 *Sipho Olavii* (Beck), Mörch – Harmer: p. 193–195, Pl. 23, figs. 5–6, 7–9, 14.
1924 *Sipho olavii* (Beck, Mörch) – Schlesch: p. 331, Pl. 7, figs. 16–17.
1925 *Sipho Olavii*, Mörch – Bárðarson: p. 48, 50, 52, 72–73.
1980 *Sipho (Sipho) olavii* Mörch, 1871 – Gladenkov et al.: p. 76, Pl. 15, figs. 1–3.

*Material:* About 80 specimens from units 8–12 in the *Mactra* Zone and units 13–22 and 25 in the *Serripes* Zone. Bárðarson (1925) considered the species “one of the most conspicuous forms” in unit 15.

*Remarks:* The three largest specimens in our collection measure (h × d): 49.1 × 21.2, 37.8 × 17.9, and 34.2 × 16.7 mm. The d/h ratios in our material are 0.43–0.49, while Gladenkov et al. (1980) reported ratios of 0.43–0.51.

The most striking character of the species is the long, semi-tubular and sometimes twisted canal, which turns to the left (cf. Harmer, 1914).

*Distribution, ecology, and biology: Colus olavii* is extinct, but considered to be closely related to *Colus tortuosus* (Reeve), now regarded as synonym of *C. holboelli* (Møller). When considering the recent species occurring together with *C. olavii* in the Tjörnes beds, it seems evident that the species preferred more boreal conditions than *C. holboelli*, which is mostly arctic-subarctic in its distribution. The bathymetrical range is unknown, but in the Tjörnes area it lived certainly in nearshore sublittoral environments during the Pliocene. The bathymetrical range for *C. holboelli* is 10–1500 m (Sneli et al., 2005). The salinity tolerance is unknown, as well as the larval development type, which probably was without a pelagic stage similar to most *Colus* species today.

In the Faroe Islands, *Colus holboelli* lives on a substrate of fine sand and gravel (Sneli et al., 2005), and *C. olavii* probably preferred similar substrate as it obviously lived on sandy bottom while it inhabited the Tjörnes area.

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Wood, 1872), *Mactra* and *Serripes* Zones of the Tjörnes beds (Gladenkov et al., 1980; this volume). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1914). Stratigraphical range: Pliocene to Lower Pleistocene.

Most probably *Colus olavii,* frequently found in several units of the Tjörnes beds, became extinct in Lower Pleistocene because it could not cope any longer with increasing cooling.

### ***Colus* cf. *imperspicuus* (Wood, 1848)**

Plate 7.5. Fig. 7

1848 *Trophon imperspicuum* – Wood: p. 50, Pl. 6, fig. 12.
1918 *Fusus imperspicuus,* S.V. Wood – Harmer: p. 360–361, Pl. 38, figs. 17–18.

*Material:* One damaged specimen from unit 18 in the *Serripes* Zone. The species is new to the fossil fauna of Tjörnes.

*Remarks:* The fragmentary shell is 27.5 mm high and the diameter is 14.7 mm. These measurements are by no means accurate as the body whorl is incomplete. The shell is obviously elongated and fusiform, turreted and rather slender. The whorls are ornamented by numerous longitudinal ribs or costae that are fading on the upper part of the body whorl. Fine spiral ridges or costae cross the longitudinal ribs with slight granulation at the crossing points. This is in rather good agreement with the description of Wood (1848), as well as Harmer (1918). Further identification is hardly possible because of the fragmentary state of the shell.

*Distribution, ecology, and biology: Colus imperspicuus* is extinct. It probably preferred more or less boreal conditions as we know them in the North Atlantic today. It mainly occurs in sediments with boreal species both in Iceland and the English Crag formations. The bathymetrical range is unknown, but probably it could live in nearshore environments. The salinity tolerance and larval development is unknown.

While the species lived in the Tjörnes area, as well as the British Crag area, it probably preferred substrate of sand or gravel, but it is rather difficult to estimate its ecological demands from one single specimen.

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Harmer, 1918; Wood, 1848). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1918). Stratigraphical range: Pliocene to Lower Pleistocene. Perhaps *Colus imperspicuus* became extinct together with *C. olavii* during a harsh glaciation in Lower Pleistocene.

### ***Colus elegans* (Harmer, 1914)**

Plate 7.5. Fig. 8

1914 *Sipho elegans*, sp. nov. – Harmer; p. 199–200, Pl. 24, figs. 7–8.
1924 *Sipho elegans* F.W. Harmer – Schlesch: p. 331, Pl. 8, figs. 2–3.

*Material:* Four specimens from units 15 and 23 in the *Serripes* Zone.

*Remarks:* The only shell in our collection (the others identified by Schlesch) measures (h × d): 40.7 × 19.6 mm.

*Colus elegans* is ornamented by numerous fine spiral ridges crossed by even finer longitudinal ribs, forming a delicate reticulate pattern. The siphonal canal is considerably shorter than in *Colus olavii*.

*Distribution, ecology, and biology: Colus elegans* is extinct, but it probably lived in similar way as *C. olavii*, preferring boreal conditions in nearshore environments. Salinity tolerance and larval development are unknown.

The rather short siphonal canal may indicate shorter siphon than in many other *Colus* species. It is therefore possible that it did not burrow as deep as many other species of this genus.

*Fossil occurrence:* Pliocene: *Serripes* Zone of the Tjörnes beds (this volume). Lower Pleistocene: Butleyan Crag (Harmer, 1914). Stratigraphical range: Pliocene to Lower Pleistocene. The occurrence in the Tjörnes beds seems to be the earliest of this species. Apparently, it disappeared earlier than *Colus olavii* and *C. imperspicuus* because it could not resist the first Pleistocene glaciations.

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

1778 *Buccinum gracile* – da Costa: p. 124, Pl. 6, fig. 5.
1848 *Trophon gracile.* Da Costa – Wood: p. 46–48, Pl. 4, fig. 10a–c.
1914 *Sipho gracilis* (Da Costa) – Harmer: p. 175–178, Pl. 20, figs. 3–7, Pl. 25, figs. 6–7.
1914 *Sipho curtus* (Jeffreys) – Harmer: p. 178–180, Pl. 21, figs. 1–8.
1980 *Sipho (Sipho)* aff. *gracilis* (Da Costa, 1778) – Gladenkov et al.: p. 77, Pl. 14, fig. 4 (in part).
1988 *Colus gracilis* (da Costa) – Graham: p. 386, fig. 158.

*Material:* Four specimens from unit 15 in the *Serripes* Zone. The best preserved shell in our collection is shown in Plate 7.6, Fig. 1.

*Remarks:* The largest shell in our collection measures (h × d): 41.0 × 19.4 mm. The d/h ratio is 0.47, a little higher than in the closely related *Colus olavii* that has a slightly lower shell. The shell of *C. gracilis* is ornamented with fine spiral striae crossed by fine longitudinal striae forming a fine reticulated pattern. The inner lip generally forms a rather thick glaze on the columella, and the siphonal canal varies considerably in length, usually turning sharply to the left.

*Recent distribution, ecology, and biology: Colus gracilis* is mainly a boreal species in the North Atlantic with subarctic, as well as lusitanian outposts. It is distributed from Southeast Greenland, Svalbard, and the Murman Coast in the north to Portugal in the south (Sneli et al., 2005). It extends to the southern part of Kattegat, but is unknown from the Baltic, and in Iceland only empty shells have been found (Óskarsson, 1962; Sneli et al., 2005). Thorson (1941) stressed that some of the Icelandic shells have so well-preserved periostracum that they can hardly be subfossil, and therefore it is very likely that living population exist off the Icelandic coast. Bathymetrical range: from 10 m in the Faroe Islands (Thorson, 1941) to a depth of about 1500 m (Sneli et al., 2005). The Icelandic shells were found at 27–164 m depths (Óskarsson, 1962). The species is apparently euhaline living in salinities above 30‰. The larval development is unknown.

The species seem to prefer muddy to sandy substrates where it lives as scavenger or carnivore (Graham, 1988).

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Harmer, 1914). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1914). Middle Pleistocene: Bridlington Crag (Harmer, 1914), Nordre Laksebugt beds in West Greenland

(Bennike et al., 1994). Upper Pleistocene: Estuarian clay of Belfast (Harmer, 1914). Stratigraphical range: Pliocene to Recent.

***Colus glaber*** **(Kobelt, 1876)**
Plate 7.6. Fig. 2

1876 *Sipho glaber* – Verkrüzen (MS) in Kobelt: p. 174, Pl. 3, fig. 3.
1878 *Sipho glaber,* Verkrüzen – Sars: p. 271–272, Pl. 15, fig. 7.
1914 *Sipho glaber* (Verkrüzen), Kobelt – Harmer: p. 188, p. 24, figs. 1–2.
1924 *Sipho glaber* (Verkrüzen) Kobelt – Schlesch: p. 331 (from Poulsen's manuscript).
1995 *Colus (Colus) glaber* (Verkruzen in Kobelt, 1876) – Golikov: p. 39, figs. 90, 130D0.

*Material:* We only have one specimen in our collection from unit 15 in the *Serripes* Zone. According to Schlesch (1924), the species is also mentioned in Poulsen's manuscript (1884), without further stratigraphical information or how many shells he found.

*Remarks:* The single specimens in our collection measures (h × d): 40.9 × 20.5 mm. The d/h ratio is 0.50, similar to *Colus gracilis.*

The shell is smooth and there are no signs of spiral striae, ridges or longitudinal ridges. The aperture is very similar to that of *C. gracilis*, but the protoconch is missing. On the whole, the shell is similar to the shell of *C. gracilis*, except that there are no striae on the smooth surface. Some researchers consider *C. gracilis* and *C. glaber* conspecific (i.e., Graham, 1988; Sneli et al., 2005), and several others refer to *C. glaber* as a northern form of *C. gracilis* (i.e., Poppe & Goto, 1991). Here, we follow Sars (1878), Harmer (1914), Thorson (1941), Óskarsson (1962), Nordsieck (1968), Høisæter (1986), and Golikov (1995) in regarding *C. glaber* as a distinct species.

*Recent distribution, ecology, and biology: Colus glaber* is a subarctic-boreal species extending in the North Atlantic from the Barents Sea in the north to the Faroe Islands and Shetland Islands in the south (Golikov, 1995; Thorson, 1941). In the Pacific it has also been recorded from the Bering Sea (Thorson, 1941). Bathymetrical range: from 57 m in Norway and down to 326 m in Iceland (Thorson, 1941) or 0–848 m in northern Norway (Nordsieck, 1968). In Skutilsfjörður, northwestern Iceland, there are three finds from the shore, possibly brought there in fish stomachs (Thorson, 1941). The species seems to be euhaline living at salinity between 33.5 and 35‰ (Golikov, 1995). The larval development is unknown.

The species prefers sandy substrates with shell debris, silt, and stones (Golikov, 1995).

*Fossil occurrence:* Pliocene: *Serripes* Zone of the Tjörnes beds (? Schlesch, 1924; this volume). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1914). ?Upper Pleistocene: Surtsey xenoliths (Símonarson, 1974). Stratigraphical range: Pliocene to Recent. The species is only rarely found in Pleistocene sediments and the occurrence in the *Serripes* Zone of the Tjörnes beds seems to be the earliest appearance of *Colus glaber.*

**_Colus altus_ (Wood, 1848)**
Plate 7.6. Fig. 3

1848 *Trophon altus* – Wood: p. 47, Pl. 6, fig. 13.
1914 *Anomalosipho Verkrüzeni* (Kobelt) var. *plicifera,* Brögger – Harmer: p. 149–150, Pl. 15, fig. 10.
1924 *Anomalosipho verkrüzeni plicifera* Brögger – Schlesch: p. 330, Pl. 7, fig. 12.
1925 *Anomalosipho Verkrüzeni*, Kobelt. var. *plicifera,* Brögger – Bárðarson: p. 55, 70.
1975 *Anomalosipho verkrüzeni* var. *plicifera* (Dall) – Norton: p. 109.
1980 *Sipho (Animalosipho) verkrüzeni plicifera* Brogger, 1901 – Gladenkov et al.: p. 77–78, Pl. 15, fig. 6–6a.

*Material:* Seven specimens from units 18–22 in the *Serripes* Zone.

*Remarks:* The largest shell measures (h × d): 43.1 × 19.0 mm, and the d/h ratio is close to 0.44.

According to Brøgger (1900–1901) and Harmer (1914), the subspecies *plicifera* differs from the typical *Colus verkruzeni* in having a longer aperture and shorter spire and a number of inconspicuous plications dying out toward the base of the shell.

Harmer (1914) emphasized that the form *plicifera* may be an evolutionary intermediate, connecting link with *Colus altus* (Wood, 1848) known from the English Crag. Furthermore, Golikov (1995) included *Sipho verkruzeni* in the synonym list of *Colus (Anomalosipho) altus* (Wood, 1848) and considered these species conspecific. We cannot see any specific differences between the shells from Tjörnes and the species *C. altus* and will therefore refer the shells from the *Serripes* Zone to that species. Furthermore, Thorson (1944) in his paper on the East Greenland prosobranc fauna referred the forma *plicifera* to *C. altus*.

*Recent distribution, ecology, and biology: Colus altus* is an arctic-boreal species in the North Atlantic. It extends from East Greenland, Svalbard, the Barents Sea, the Kara Sea, and the Laptev Seas in the north to northern Iceland and western Norway (Nordlandet) in the south (Thorson, 1941, 1944; Golikov, 1995). In the Pacific it is known from Kamchatka and northern Kurile Islands (Golikov, 1995). Nowadays the species mainly lives at temperatures from subzero to 6°C (Golikov, 1995). We cannot exclude that the species has changed its distribution from boreal conditions to more arctic during the Pleistocene. Bathymetrical range: from 22 m in the Laptev Sea to 640 m in the Norwegian Sea (Golikov, 1995; Thorson, 1944). The species seems euhaline with salinity tolerance down to 32‰ (Golikov, 1995). The larval development is unknown.

In the Arctic, the species has been found on substrates of silt and sand, gravels, pebbles, and stones (Golikov, 1995).

*Fossil occurrence:* Pliocene: *Serripes* Zone of the Tjörnes beds (this volume). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1914). Upper Pleistocene: Older *Yoldia* Clay in the Oslo Region (Brøgger, 1900). Stratigraphical range: Pliocene to Recent. If our identification is correct, the occurrence in the *Serripes* Zone seems to be the earliest for this species.

### Genus *Neptunea* Bolten, 1798

**_Neptunea lyratodespecta_ Strauch, 1972**
Plate 7.6. Fig. 4

1972 *Neptunea lyratodespecta* – Strauch: p. 42–44, Pl. 1, figs. 1–16, Pl. 2, figs. 1–4.
1848 *Trophon antiquum*. Mull. var. *carinatum* Lam. – Wood: p. 44–45, Pl. 5, fig. 1b.
1863 *Trophon antiquum*, Müller – Winkler: p. 210.
1914 *Neptunea despecta* (Linné) var. *carinata,* Pennant – Harmer: p. 162–163, p.17, fig. 5a–b.
1924 *Neptunea despecta carinata* Lamarck = var. *fornicata* Fabricius – Schlesch: p. 335, Pl. 10, fig. 1.
1980 *Neptunea carinata* (Pennant, 1777) – Gladenkov et al.: p. 78, Pl. 14, figs. 9–11.
1980 *Neptunea decemcostata* (Say, 1825) – Gladenkov et al.: p. 78–79, Pl. 14, figs. 12–14.
1980 *Neptunea* cf. *subantiquata* Maton et Rackett, 1807 – Gladenkov et al.: p. 79, Pl. 14, fig. 15.

*Material:* About 65 specimens from units 13, 15, 17–18, 21, 23, and 25 in the *Serripes* Zone.

*Remarks:* The largest measureable specimen is 55.1 mm high and the diameter is 36.0 mm. The d/h ratios are 0.47–0.67. The recent species *Neptunea despecta* (Linné, 1758) is the largest marine gastropod now living in Icelandic waters, measuring up to 200 mm in height.

*Neptunea lyratodespecta* is a very variable species, and in our opinion all the *Neptunea* specimens we have seen from the Tjörnes beds can be referred to this species (cf. Strauch, 1972). The variation within the *Neptunea* material from Tjörnes is not as striking as the variation within the recent *Neptunea despecta* in Iceland.

*Distribution, ecology, and biology: Neptunea lyratodespecta* has not been found living today. It was probably a boreal-lusitanian species, when its distribution in sediments is compared to the recent faunal region of the North Atlantic (Strauch, 1972). It has been found in sediments from Iceland in the north to the British Isles and Belgium in the south. We have no references from northern Alaska or Greenland, for example, the Kap København Formation in Northeast Greenland, which is slightly younger than the *Serripes* Zone. Bathymetrical range is not known exactly, but most probably it lived in shoreface environments in the Tjörnes area while the *Serripes* Zone was deposited, which fits well with the southern North Sea Basin records. Probably, the species was polyhaline with salinity tolerance higher than 25‰ as in the case of the recent *N. despecta.* The larval development is unknown, but the only *Neptunea* species now living along the Icelandic coasts has non-pelagic larval stage (Thorson, 1941).

When compared to recent species of *Neptunea* and taking into consideration the sediments with *N. lyratodespectea* in the Tjörnes beds, it seems most likely that it lived on substrates of sand, gravel, stones, shells, and algae (cf. Thorson, 1941).

*Fossil occurrence:* Pliocene: Kallo and Doel sections (Marquet, 1998). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1914). Stratigraphical range:

Pliocene to Lower Pleistocene. The species has never been found in Lower Pleistocene sediments in Iceland, and it probably disappeared during the cooling in uppermost Pliocene before the first extensive glaciation reached the coast in the Tjörnes area at 2.5–2.6 Ma.

According to Strauch (1972), *Neptunea lyratodespecta* evolved from the Pacific stock of *N. lyrata* (Martyn, 1784) during a migration into the North Atlantic in Pliocene time when the *Serripes* Zone was deposited.

### Genus *Searlesia* Harmer, 1914

#### *Searlesia costifera* (Wood, 1848)

Plate 7.6. Fig. 5

1848 *Trophon costiferum* – Wood: p. 48–49, Pl. 6, fig. 9a–b.
1914 *Searlesia costifer* (S.V. Wood) – Harmer: p. 136–140, Pl. 13, figs. 1, 3–12.
1924 *Searlesia costifer islandica* F.W. Harmer – Schlesch: p. 332, Pl. 8, figs. 4–6.
1924 ?*Searlesia björnssoni* (Mörch) F.W. Harmer – Schlesch: p. 332, Pl. 8, figs. 9–10.
1925 *Searlesia costifer,* Wood – Bárðarson: p. 57, 70.
1980 *Searlesia costifera* S. Wood, 1848 – Gladenkov et al.: p. 79–80, p. 15, fig. 7–7a.

*Material:* Eight specimens from unit 11 in the *Mactra* Zone, and units 15 and 21 in the *Serripes* Zone.

*Remarks:* The two largest specimens measure (h × d): 32.2 × 15.8 and 26.8 × 13.3 mm. The d/h ratios are 0.49–0.50. The shell of *Searlesia costifera* is considerably larger than in *S. lundgrenii*, and it is slightly higher and the longitudinal ribs extend farther down to the base. They are not tuberculate at the point of intersections with the spiral lines. *S. bjoernsoni* (Harmer, 1914) is very similar to small specimens of *S. costifera,* and it cannot be excluded that we are dealing with juvenile specimens of *S. costifera*. We need to find considerably more material to clarify if *S. bjoernsoni* is a distinct species.

*Distribution, ecology, and biology: Searlesia costifera* is apparently extinct as most of the few specimens that were dredged in the Atlantic during the Porcupine Expedition are in "semi-fossil condition" (Harmer, 1914). The species was probably boreal-lusitanian, when its distribution in sediments is compared to the recent faunal regions of the North Atlantic. It has been found in sediments from Iceland in the north to the British Isles and the Netherlands in the south together with boreal-lusitanian species. Bathymetrical range is not known, but most probably it lived in shoreface environments while it inhabited the Tjörnes area. Probably, the species was polyhaline, but the salinity tolerance, as well as the larval development is unknown.

While the species lived in the Tjörnes area it obviously preferred sandy substrates.

*Fossil occurrence:* Pliocene: Coralline Crag (Harmer, 1914; Wood, 1848). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1914; Wood, 1848). Stratigraphical range: Pliocene to Lower Pleistocene. Apparently, it could not survive some of the severe glaciations of Middle Pleistocene.

Durham and MacNeil (1967) considered the species of Pacific affinity, and it may have migrated to the Tjörnes area while the *Mactra* Zone was deposited.

***Searlesia lundgrenii* Harmer, 1914**
Plate 7.6. Fig. 6

1914 *Searlesia Lundgrenii* (Mörch and Poulsen, MS) – Harmer: p. 143–144, Pl. 14, figs. 10–14.
1924 *Searlesia lundgreni* (Mörch) F.W. Harmer – Schlesch: p. 332, Pl. 8, figs. 4–6.
1925 *Searlesia Lundgreni,* Mörch – Báròarson: p. 50, 72.
1980 *Searlesia lundgrenii* (Mörch et Poulsen, 1887) – Gladenkov et al.: p. 79–80, p. 15, fig. 7–7a.

*Material:* Seven specimens from units 11–12 in the *Mactra* Zone, and units 15–16, 18 in the *Serripes* Zone.

*Remarks:* The largest specimen in our collection measures (h × d): 17.0 × 8.8 mm. The d/h ratios are close to 0.52, slightly higher than in the larger *Searlesia costifera*. The longitudinal ribs extend farther down to the base, and they are tuberculate at the points of intersection with the spiral lines. Harmer (1914) recorded dimensions (h × d) up to 30 × 16 mm for the Crag material, and Gladenkov et al. (1980) found a shell with a height of 25 mm in the Tjörnes samples. Thus, the shells in our collections are relatively small.

Mörch and Poulsen were the first to describe and name this species (*Urosalpinx Lundgrenii*) in their manuscript from 1887, which was never published. The first published record was in the extensive monograph of Harmer in 1914, printed for the Palæontographical Society in London.

*Distribution, ecology, and biology: Searlesia lundgrenii* is extinct, but the species was probably boreal-lusitanian, when its distribution in sediments is compared to recent faunal regions. It occurs in sedimentary deposits together with boreal-lusitanian species from Iceland in the north and southward to the British Isles. Bathymetrical range is unknown, but it seems to have preferred shoreface environments while it lived in the Tjörnes area. Most probably the species was polyhaline, although its salinity tolerance is not known. It is not known if there was a pelagic larval stage.

While the species inhabited the Tjörnes area it obviously preferred sandy substrates similar to *Searlesia costifera*.

*Fossil occurrence:* Pliocene: *Mactra* and *Serripes* Zones of the Tjörnes beds (this volume). Pliocene/Lower Pleistocene: Red Crag (Harmer, 1914). Middle Pleistocene: Little Oakley (Harmer, 1914). Stratigraphical range: Pliocene to Middle Pleistocene. The occurrence in the *Mactra* Zone of the Tjörnes beds seems to be the earliest of this species. This species could obviously not survive one of the harsh glaciation in Middle Pleistocene.

**Family Nassaridae Linné, 1758**
**Genus *Nassarius* Duméril, 1806**

### *Nassarius tjoernesensis* Spaink, 1980

Plate 7.6. Fig. 7

1980 *Nassarius (Hinia) tjörnesensis* – Gladenkov et al. : p. 87–88, Pl. 16, figs. 1–7.
1924 *Nassa lamellilabra* Nyst – Schlesch: p. 332.
1924 *Nassa lamellilabra elegantula* (S.V. Wood Mss) – Schlesch: p. 333.
1925 *Nassa lamellilabra*, Nyst – Báráarson: p. 44, 52, 55, 59, 74–75.
1975 *Nassarius* sp., '*tjörnesensis*' – Norton: p. 109.
1980 *Nassa lamellilabra* (Nyst, 1835) – Gladenkov et al.: p. 81, Pl. 15, figs. 10–11, 13–14.

*Material:* Fifty-six specimens from units 11–12 in the *Mactra* Zone and 13–15, as well as units 17–20 in the *Serripes* Zone.

*Remarks:* The largest specimen in our collection measures (h × d): 11.0 × 5.9 mm, whereas Gladenkov et al. (1980) recorded a shell measuring up to 16 × 8 mm. The d/h ratios are 0.47–0.56. The ratios between the height of the body whorl and the shell height (hbw/h) are 0.60–0.65 or slightly higher than in *Nassarius reticosus* (Sowerby, 1818).

Norton listed *Nassarius* sp., "*tjörnesensis*" in 1975 in a paper on the paleoecology of the Tjörnes sequence and stated that it is perhaps a new species close to *N. lamellilabrus* (Nyst, 1835). He did not describe it any further, but five years later, Spaink described it as a distinct species and compared it to *N. lamellilabrus* (cf. Gladenkov et al., 1980). The most striking differences seems to be broader and higher longitudinal ribs on the spire, as well as coarse spiral ribs on the lower part of the body whorl of *N. tjoernesensis*. Furthermore, the apex is more obtuse, it has more convex first whorls on the spire, and lamellae are always absent on the inner side of the outer lip, where *N. lamellilabrus* has generally 14 lamellas (cf. its species name).

Norton (1975) and Spaink (Gladenkov et al., 1980) refer this species to the genus *Nassarius* Duméril, 1806, and we will follow them, also with the other species of Nassaridae found in the Tjörnes beds (see furthermore Rijken and Pouwer (2014)).

*Distribution, ecology, and biology: Nassarius tjoernesensis* is extinct and has only been recorded from the Pliocene Tjörnes beds. The species preferred boreal ecological conditions, as we know them in the North Atlantic today. This is strongly indicated by the recent species occurring together with it in the Tjörnes beds. However, it was probably more northern in its distribution than *Nassarius lamellilabrus*, which has not been found fossil outside the North Sea Basin (Spaink, in Gladenkov et al. (1980)). Bathymetrical range is not known, but most likely it lived in shoreface environments. The species was probably polyhaline, but the salinity tolerance and the larval development are unknown. However, all recent species of *Nassarius* found in the British Isles and Iceland seem to have pelagic larval development (Graham, 1988; Thorson, 1941).

While the species lived in the Tjörnes area it obviously preferred silty and sandy substrates.

*Fossil occurrence:* The species was only recorded from the uppermost part of the *Mactra* Zone and the *Serripes* Zone of the Tjörnes beds. However, in the Museum of Natural History in Reykjavík there is one well-preserved specimen, probably collected by Gladenkov et al. (1980). The shell is reported from the Breiðavík beds apparently from bed 14 in the Svarthamar Member. However, the shell seems to be in a sediment which is more similar to that in unit 14 in the Pliocene Tjörnes deposits. Apparently, it was not correctly reported? Stratigraphical range: ?Pliocene.

***Nassarius reticosus* (Sowerby, 1815)**
Plate 7.6. Fig. 8

1815 *Buccinum reticosum* – Sowerby: p. 17, Pl. 110, fig. 2.
1848 *Nassa reticosa*. J. Sow. – Wood: p. 33–34, Pl. 3, fig. 10a–h.
1914 *Nassa reticosa* (J. Sowerby) – Harmer: p. 61–64, Pl. 3, figs. 4, 14–19.
1957 *Nassarius (?Hinia) reticosus* (J. Sowerby, 1815) – van Regteren Altena et al.: p. 68, Pl. 14, fig. 135.
1980 ?*Nassa lamellilabra* (Nyst, 1835) – Gladenkov et al.: p. 81, Pl. 15, fig. 12.
1980 *Nassa* aff. *reticosa* (Sowerby, 1818*)* – Gladenkov et al.: p. 81, Pl. 15, figs. 15–16.

*Material:* Forty-two specimens from units 10–11 in the *Mactra* Zone and 13, 18–23 in the *Serripes* Zone.

*Remarks:* The four largest specimens measure (h × d): 17.4 × 9.7, 15.5 × 7.8, 13.3 × 6.6, and 13.2 × 6.7 mm. The d/h ratios are 0.50–0.56. The ratios between the height of the body whorl and the shell height (hbw/h) are close to 0.54.

The shell of *Nassarius reticosus* is more elongated than *N. tjoernesensis* and the aperture is slightly lower. The longitudinal ribs on the surface of the shell are of similar height as the spiral striations intersecting the ribs, forming more reticulate pattern than in *N. tjoernesensis* (cf. the species name). There is no difference between the *N. reticosus* figured by Gladenkov et al. (1980: Pl. 15, fig. 16) and our specimens from Tjörnes.

*Distribution, ecology, and biology: Nassarius reticosus* is extinct, but apparently the species preferred boreal conditions, as we know them in the North Atlantic today. This is strongly indicated by its distribution in sediments from Iceland in the north to the British Isles and Belgium in the south. Bathymetrical range is not known, but most probably it lived in shoreface environments while it inhabited the Tjörnes area. The species was probably polyhaline, but the salinity tolerance and the larval development are unknown. However, all recent species of *Nassarius* found in the British Isles and Iceland seem to have pelagic larval development (Graham, 1988; Thorson, 1941).

In the Tjörnes sediments it is found in sandy and gravelly substrates as *Nassarius tjoernesensis.*

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Harmer, 1914), *Nassarius reticosus* and *Chlamys opercularis* Subzone (Spaink, 1975), Luchtbal Sand Member (Marquet & Landau, 2006). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1914). Stratigraphical range: Pliocene to Lower Pleistocene.

**_Nassarius_ cf. _consociatus_ (Wood, 1848)**
Plate 7.7. Fig. 1

1848 *Nassa consociata* – Wood: p. 31, Pl. 3, fig. 7.
1914 *Nassa consociata*, S.V. Wood – Harmer: p. 75–76, Pl., figs. 17–18, Pl. 13, fig. 19.
1957 *Nassarius (Hinia) consociatus* (S.V. Wood, 1848) – van Regteren Altena et al.: p. 69, Pl. 15, fig. 138.

*Material:* Two specimens from unit 9 in the *Mactra* Zone. Norton (1975) listed *Nassarius consociatus* among species from the Tjörnes beds, but without further stratigraphical information or how many shells he found. Otherwise, it has not been recorded from the Tjörnes beds until now.

*Remarks:* The shells are rather fragmentary, but they measure (h × d): 12.1 × 5.4 and 2.5 × 1.3 mm. The d/h ratios are 0.45–0.52. The larger shell is more slender with an elongate spire indicating an allometric growth of the species, which is rather common within marine gastropods.

There are considerable variation within the *Nassarius* species and our Tjörnes specimens have few and strong axial ribs and rather strong teeth in the aperture.

*Distribution, ecology, and biology: Nassarius consociatus* is almost certainly extinct, although Jeffreys, in Prestwich (1871) stated that it is living in the mid-Atlantic and West European seas (Harmer, 1914). Its occurrence in the Tjörnes deposits in Iceland and the North Sea Basin in warm temperate faunas implies a boreal paleodistribution. The species preferred boreal ecological conditions, as we know them in the North Atlantic today. This is strongly indicated by its occurrence in sediments from Iceland in the north and southward to Belgium. Bathymetrical range is not known, but most likely it preferred shoreface environments while living in the Tjörnes area. The salinity tolerance is not known, but probably the species was polyhaline. The larval development is unknown, but as mentioned before, all recent species of *Nassarius* found in the British Isles and Iceland seem to have pelagic larval development (Graham, 1988; Thorson, 1941).

It is difficult to estimate the preferred type of substrate from only two recorded specimens, but they were found in silty and sandy substrates.

*Fossil occurrence:* Pliocene: Coralline Crag (Harmer, 1914; Wood, 1848), Oosterhout Formation (Spaink, 1975), Luchtbal Sand Member (Marquet & Landau, 2006). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1914; Wood, 1848). Stratigraphical range: Pliocene to Lower Pleistocene. Apparently, the species became extinct during one of the severe glaciation in Lower Pleistocene, as also happened to the two aforementioned *Nassarius* species found in the Tjörnes beds.

**Family Cancellariidae Gray, 1853**
**Genus _Admete_ Kröyer, 1842**

**_Admete viridula_ (Fabricius, 1780)**
Plate 7.7. Fig. 2

1780 *Tritonium viridulum* – Fabricius: p. 402.

1848 *Cancellaria costellifera*. J. Sow. – Wood: p. 66, Pl. 7, fig. 21.
1878 *Admete viridula*, Fabr. – Sars: p. 216–217, Pl. 13, fig. 1a.
1918 *Admete viridula* (Fabricius) – Harmer: p. 406–407, Pl. 39. figs. 42–47.
1924 *Admete viridula* (Fabricius) – Schlesch: p. 326, Pl. 6, figs. 8–9.
1925 *Admete viridula*, Fabr. var. *costellifera*, Sow. – Bárðarson: p. 51, 70.
1980 *Admete viridula* (Fabricius, 1780) – Gladenkov et al.: p. 83, Pl. 15, fig. 21.

*Material:* Eleven specimens from units 14–16 in the *Serripes* Zone.

*Remarks:* The three largest specimens measure (h × d): 14.5 × 8.0, 11.9 × 6.3, and 11.6 × 5.9 mm. The d/h ratios range from 0.51 to 0.57. All the shell ratios are similar to those of *Admete couthouy* (Jay, 1839), except the ratios between height of aperture and the shell height (ha/h), which are 0.53–0.55 for *A. viridula* and 0.59–0.63 for *A. couthouy*. Therefore, the aperture is slightly lower in *A. viridula.*

We are aware that Dall (1887) examined the type of Fabricius' species and stated that it was "a *Bela*, like *B. exarata* and not an *Admete* at all." *Bela exarata* (*Propebela exarata* (Møller, 1842)) is quite different from *Admete viridula* as we know these species from Iceland, where they are rather commonly found living off the coasts. It is not likely that a competent malacologist as Dall did not realize the differences. Possibly, some mix-up with Fabricius specimens had taken place? There are significant differences between the two groups of *Admete* found in the *Serripes* Zone, and therefore we will follow authors like Harmer (1918), Schlesch (1924), Nordsieck (1968), Gladenkov et al. (1980), and Petrov (1982) in separating these two forms.

*Recent distribution, ecology, and biology: Admete viridula* is an arctic-subarctic-boreal, circumpolar species extending from West and East Greenland, Svalbard, the Barents Sea, Novaya Zemlya, the Kara Sea, the Siberian Arctic Sea, northern Alaska, and Baffin Land in the north to the northern borders of the North Sea and Massachusetts in the North Atlantic and to California and northern Japan in the Pacific in the south (Golikov, 1995; Graham, 1988; Thorson, 1941). Bathymetrical range: from 3 m in Novaya Zemlya to 1319 m off the Faroe Islands (Golikov, 1995; Sneli et al., 2005). In Iceland it lives from 9 to 170 m (Óskarsson, 1962). The species is polyhaline with a lower salinity limit of 25‰ (Funder et al., 2002) and has a range reported 26 and 35‰ (Golikov, 1995). The larval development is direct, without a pelagic stage (Golikov, 1995; Graham, 1988; Thorson, 1944).

The species prefers soft substrates, and in the Faroe Islands it has been found on silt, sand, gravel, and sponge spicules (Sneli et al., 2005).

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Harmer, 1918; Wood, 1848), Kallo and Doel sections (Marquet, 1998), Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1918; Wood, 1848). Lower Pleistocene: Sicilian of Ficarazzi (Malatesta & Zarlenga, 1986). Middle Pleistocene: Bridlington Crag (Harmer, 1918), ?Kotzebuan (Hopkins et al., 1972), Karagin Suite (Petrov, 1982). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

*Admete* species first occurred in the North Pacific Miocene and later in the North Atlantic Pliocene. The earliest known fossil occurrence of *A. viridula* in the Pacific area is the record of Petrov (1982) from the Middle Pleistocene Karagin Suite (cf.

Malatesta & Zarlenga, 1986). However, Durham and MacNeil (1967) considered it of Pacific affinity, and it may have migrated to the Tjörnes area together with *A. couthouyi* while the *Serripes* Zone was deposited.

***Admete couthouyi*** **(Jay, 1839)**
Plate 7.7. Fig. 3

1839 *Cancellaria Couthouyi* – Jay: p.77.
1872 ?*Cancellaria viridula,* Fab. var. *Couthouy* – Wood: p. 97–98, Pl. 6, fig. 12.
1918 *Admete viridula* (Fabricius) var. *Couthouy* (Jay) – Harmer: p. 407–408, Pl. 39. figs. 48–49.
1924 *Admete viridula couthouy* (Jay) – Schlesch: p. 326, Pl. 6, figs. 10–11.
1925 *Admete viridula*, Fabr. var. *Couthouy*, Jay – Bárðarson: p. 53, 55, 57, 59.
1980 *Admete couthouyi* (Jay, 1839) – Gladenkov et al.: p. 82, Pl. 15, figs. 17–20.

*Material:* About 70 specimens from units 13, 15–16, 18–21, and 23 in the *Serripes* Zone.

*Remarks:* The three largest specimens measure (h × d): 19.1 × 10.5, 18.2 × 10.3, and 15.3 × 7.8 mm. The d/h ratios are 0.51–0.57. All the shell ratios are very similar to those of *Admete viridula*, except the ratios between height of aperture and the shell height (ha/h) which are 0.59–0.63. The aperture is slightly higher than in *A. viridula.* The sculpture in *A. couthouyi* (Jay, 1839) is finer than in *A. viridula,* the longitudinal ribs are shorter and mostly limited to the uppermost part of the whorls close to the sutures (cf. Plate 7.7, Fig. 3).

According to Nordsieck (1968), *A. couthouyi* is a "stammform," and therefore it is tempting to suggest that a part of the migrating stock evolved into *A. viridula* during the Pliocene migration.

*Recent distribution, ecology, and biology: Admete couthouyi* is an arctic-subarctic-boreal, circumpolar species. Many authors have considered the species as a variety of *A. viridula* and not made a distinction between them when recording the geographical distribution of the species. The distribution of *A. couthouyi* was probably similar to that of *A. viridula* (cf. Macpherson, 1971). If that is correct, the species extends from West and East Greenland, Svalbard, the Barents Sea, Novaya Zemlya, the Kara Sea, the Siberian Arctic Sea, northern Alaska, and Prince Regent Inlet in the north southward to the northern borders of the North Sea and Massachusetts in the North Atlantic and to California and northern Japan in the Pacific (Golikov, 1995; Graham, 1988; MacGinitie, 1959; Macpherson, 1971; Thorson, 1941). Bathymetrical range: from 3 m off Novaya Zemlya to 1010 m in the English Channel (Golikov, 1995; Macpherson, 1971; Sneli et al., 2005). The species is probably polyhaline with salinity tolerance above 25‰ (Funder et al., 2002) or living at salinity between 26 and 35‰ (Golikov, 1995). The larval development is not with a pelagic stage (Golikov, 1995; Graham, 1988; Thorson, 1941).

The species apparently prefers soft bottom as does *Admete viridula,* which lives in the Faroe Islands on substrates of silt, sand, gravel, and sponge spicules (Sneli et al., 2005).

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Harmer, 1918), Bathhouse Beach, Santa Barbara (Grant & Gale, 1931). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1918). Lower Pleistocene: Lower San Pedro Series (Grant & Gale, 1931), Kap København Formation (Símonarson et al., 1998). Middle Pleistocene: Kotzebuan (Hopkins et al., 1972), Karagin, Kolvin, and Padymeskii Suites (Merklin et al., 1979; Petrov, 1982). Upper Pleistocene: ?Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

Durham and MacNeil (1967) included the species among immigrants from the Pacific to the North Atlantic while the Pliocene *Serripes* Zone was deposited in the Tjörnes area.

**Family Mangeliidae Fischer, 1883**
**Genus *Oenopota* Mörch, 1852**

***Oenopota pyramidalis* (Strøm, 1788)**
Plate 7.7. Fig. 4

1788 *Buccinum pyramidale* – Strøm: p. 296–297, fig. 22.
1872 *Pleurotoma pyramidalis,* Ström – Wood: p. 43, Pl. 3, fig. 9a–b, Pl. 7, fig. 22.
1878 *Bela pyramidalis,* Ström – Sars: p. 222–223, Pl. 16, figs. 3–4.
1915 *Bela pyramidalis* (Ström) – Harmer: p. 295–298, Pl. 28, figs. 1, Pl. 29, fig. 34–35, Pl. 32, figs. 1–6.
1924 *Lora pyramidalis* (Ström) = *L. pleurotomaria* (Couthouy) – Schlesch: p. 327, Pl. 11, figs. 9–10.
1925 *Bela* sp. – Bárðarson: p. 47, 50–53, 55, 57–59, 74–75 (in part).
1980 *Lora pyramidalis* (Ström), 1788 – Gladenkov et al.: p. 84, Pl. 15, figs. 22–23.
1995 *Oenopota (Oenopota) pyramidalis* (Stroem) – Golikov: p. 50, fig. 137V.

*Material:* Nine specimens from units 14–16, 20–21, and 23 in the *Serripes* Zone.

*Remarks:* The three largest shells measure (h × d): 21.1 × ?8.1, 21.1 × 9.0, and 19.9 × 9.1 mm. The d/h ratios range from ?0.38 to 0.46.

The species has an elongated and fusiform shell with 7–8 convex whorls ornamented with 12–16 flexuous and oblique longitudinal costae and fine spiral ridges. The upper part of the pyriform aperture is slightly angulated, and the outer lip is gently curved and passing into a short and open siphonal canal. These characteristics are very similar to those in *Oenopota conoidea (Curtitoma conoidea),* described by Sars (1878), which may be conspecific with *O. pyramidalis* (cf. Sneli et al., 2005).

*Recent distribution, ecology, and biology: Oenopota pyramidalis* is an arctic-boreal, circumpolar species extending from West and East Greenland, Svalbard, the Barents Sea, Novaya Zemlya, the Kara Sea, the Siberian Arctic Sea, northern Alaska, and the North Canadian Basin in the north and southward to western Norway (at 68°N), north of the Hebrides, Hudson Bay, Ungava Bay, and Martha's Vineyard in the North Atlantic and to Puget Sound in the Pacific (Golikov, 1995; Macpherson, 1971; Sneli et al., 2005; Thorson, 1941). Bathymetrical range: from 0 m in Iceland to ?2010 m in Arctic Canada (Clarke, 1963; Óskarsson, 1962). Today, it is mainly living in shoreface environments, but is lives off the Icelandic coasts down to a depth of about 150 m (Óskarsson, 1962). The species is polyhaline with lower salinity limit around 25‰ (Funder et al., 2002; Golikov, 1995). The larval development is without a pelagic stage (Thorson, 1941).

*Oenopota pyramidalis* seems to prefer soft substrates, mud or sand, but has also been found on cobbles, stones, and algae (Macpherson, 1971; Thorson, 1941).

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Harmer, 1915). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1915). Middle Pleistocene: Kotzebuan (Hopkins et al., 1972). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

Durham and MacNeil (1967) listed *Oenopota pyramidalis* among species whose direction of migration is uncertain.

***Oenopota borealis* (Reeve, 1845)**
Plate 7.7. Fig. 5

1845 *Pleurotoma borealis* – Reeve: p. [179], pl. 31, fig. 277.
1915 *Bela borealis* (Reeve) – Harmer: p. 298, Pl. 32, figs. 12–13.
1924 *Lora borealis* (Reeve) = *L. viridula* (Möller) – Schlesch: p. 327, Pl. 7, figs. 1–2.
1924 *Lora borealis cossmanni* n. subsp. – Schlesch: p. 327, Pl. 11, fig. 11.
1925 *Bela* sp, – Bárðarson: p. ?44, 47, 50–53, 55, 57–59, 74–75 (in part).
1980 *Lora borealis* (Reeve, 1845) – Gladenkov et al.: p. 83–84, Pl. 15, figs. 24–28.

*Material:* About 250 specimens from units 15–23 in the *Serripes* Zone. This is the most common species of Mangeliidae found in the Tjörnes beds.

*Remarks:* The two largest shells measure (h × d): 16.0 × 6.7 and 14.5 × 6.9 mm. The d/h ratios are 0.42–0.48, but 0.48–0.53 in *Oenopota decussata* (Couthouy, 1839), which is slightly shorter. The ratios between the height of the body whorl and the shell height (hbw/h) are 0.68–0.79 in *Oenopota borealis*, but 0.65–0.67 in *O. pyramidalis* in accordance with a higher body whorl in *O. borealis.*

The elongate and fusiform shell is ornamented with inconspicuous spiral lines and longitudinal costae, which die out on the body whorl. The longitudinal costae are not as flexuous and oblique as in *O. pyramidalis* or *O. decussata.* The radial striae (spiral lines) on the body whorl are much more unclear than in *O. decussata*. The aperture is oval, but slightly angulated adapically and ending in a rather short siphonal canal. The outer lip is regularly curved.

At first, Reeve (1843–1846) described and figured the species under the name of *Pleurotoma scalaris* (p. 179), but in a corrective note (fig. 277), in the same paper, he changed the name to *P. borealis.* It was only recorded as living in Greenland.

*Distribution, ecology, and biology: Oenopota borealis* seems to be extinct, although Reeve (1843–1846), as well as Harmer (1915) reported it as living today in Greenland. Thorson (1944, 1951) did not record the species neither from West or East Greenland, and no one has investigated the marine gastropod fauna of Greenland, as well as he did. Therefore, we consider the species to be extinct. In the Tjörnes beds, *O. borealis* occurs along with recent species of *Oenopota* and *Propebela*, and this may indicate that it lived in boreal conditions (cf. the species name). Bathymetrical range is unknown, but most probably it lived in shoreface environments. Probably, the species was polyhaline, but the salinity tolerance and the larval development are unknown. The larval development is not very well known within recent species of *Oenopota* and *Propebela,* but where this is known it is exclusively non-pelagic (Thorson, 1944; Thorson, 1951).

While the species lived in the Tjörnes area it clearly preferred silty and sandy substrates.

*Fossil occurrence:* Pliocene: *Serripes* Zone of the Tjörnes beds (Gladenkov et al., 1980). Lower Pleistocene: Norwich Crag Formation at Aldeby (Harmer, 1915). The occurrence in the Pliocene *Serripes* Zone seems to be the earliest of this rare species. Stratigraphical range: Pliocene to ?Lower Pleistocene.

Durham and MacNeil (1967) included the species among immigrants from the Pacific to the North Atlantic while the Pliocene *Serripes* Zone was deposited in the Tjörnes area.

***Oenopota pingeli* (Møller, 1842)**
Plate 7.7. Fig. 6

1842 *Defrancia pingeli* – Møller: p. 86.
1878 *Bela Pingelii,* Beck – Sars: p. 223–224, Pl. 16, fig. 5.
1924 *Lora pingeli* (Beck) – Schlesch: p. 328 (from Poulsen's manuscript).
1941 *Bela pingeli* (Beck) – Thorson: p. 98.
1962 *Bela pingelii* (Beck) – Óskarsson: p. 279, fig. 128.
1995 *Oenopota (Oenopota) pyngelii* (Moeller) – Golikov: p. 50, fig. 137M-N.

*Material:* Seven specimens from units 15 in the *Serripes* Zone. The record of Mörch (cf. Schlesch, 1924) is without further stratigraphical information nor did he mention how many shells he found.

*Remarks:* The four largest shells measure (h × d): 11.0 × 4.5, 10.4 × 3.9, 9.8 × 4.0, and 8.8 × 4.5 mm. The d/h ratios are 0.36–0.41. The specimens figured by Sars (1878) and Schiøtte and Warén (1992) have these ratios 0.36–0.38. The ratios between the height of the body whorl and shell height (hbw/h) are 0.59–0.69 compared to 0.60–0.64 in the shells figured by Sars (1878) and Schiøtte and Warén (1992). Their shells have slightly lower ratios between the height of aperture and shell height (ha/h) or 0.40–0.41 compared to 0.44–0.52 in the Tjörnes material.

The shell has seven whorls ornamented by inconspicuous longitudinal costae crossed by oblique spiral ridges forming a reticulate pattern on the surface. The outer lip of the aperture is regularly curved, but slightly angulated adapically. The aperture is ending in a rather short and straight siphonal canal. Unfortunately, all the specimens from Tjörnes are somewhat worn.

*Recent distribution, ecology, and biology: Oenopota pingeli* is a subarctic-boreal species with arctic outposts. It extends from West Greenland, Southeast Greenland, Svalbard, the Barents Sea, the Kara Sea, and the Laptev Sea in the north to western Norway at Lofoten, Iceland, and Cape Cod in the south (Golikov, 1995; La Rocque, 1953; Thorson, 1941). It has also been recorded from the Okhotsk Sea in the Pacific (Golikov, 1995). Bathymetrical range: from 3 m in Iceland to 774 m off the American east coast (Thorson, 1941). The species is apparently polyhaline, almost euhaline, as Golikov (1995) has reported it living at salinity of 28–34.5‰. The larval development is unknown.

The species seems to prefer silty substrates mixed up with gravel (Golikov, 1995).

*Fossil occurrence:* We have not found any records of this species from sediments in the North Atlantic area or the Pacific. It seems to be very rare, and if our identification is correct the Pliocene Tjörnes deposits is the only finding place for the species as a fossil. Stratigraphical range: Pliocene to Recent.

### Genus *Curtitoma* Bartsch, 1941

***Curtitoma decussata tjoernesensis* (Schlesch, 1924)**
Plate 7.7. Fig. 7

1924 *Lora decussata tjörnesensis* – Schlesch: p. 328, Pl. 11, fig. 15.
1975 *Bela decussata tjörnesensis* Mörch – Norton: p. 109.
1980 *Lora decussata tjörnesensis* Schlesch, 1924 – Gladenkov et al.: p. 85, Pl. 15, figs. 30–31a.

*Material:* Five specimens from units 18–19 and 21 in the *Serripes* Zone.

*Remarks:* The two largest shells measure (h × d): 17.6 × 9.3 and 15.3 × 7.3 mm, respectively. The d/h ratios are 0.48–0.53 compared to 0.49–0.52 for the five largest specimens of *Curtitoma decussata* (Couthouy, 1839) from the Lower Pleistocene Pattorfik beds, West Greenland (cf. Símonarson, 1981b).

The subspecies *tjoernesensis* differs from the typical species in having more prominent spiral costae on the lower part of the body whorl where the longitudinal ribs are fading.

*Distribution, ecology, and biology: Curtitoma decussata tjoernesensis* is not known living today, whereas typical *C. decussata* has been found in the arctic, subarctic, and boreal regions of the North Atlantic and Pacific. It extends from West and East Greenland, Svalbard, the Barents Sea, Novaya Zemlya, the Kara Sea, the Laptev Sea, the Siberian Arctic Sea, northern Alaska (Point Barrow), the Foxe Basin, and Baffin Island in the north to New England and north of Scotland in the south in the North Atlantic and to the Okhotsk Sea and Japan in the Pacific (Golikov, 1995; MacGinitie, 1959; Macpherson, 1971; Thorson, 1941). The species is not known from the Baltic. In Iceland it is mainly found in the northern and eastern parts of the island where it occurs at depths between 15 and 139 m (Óskarsson, 1962). Bathymetrical range: from 3 m in Novaya Zemlya to 2582 m in the North Atlantic (?north of Scotland) (Golikov, 1995; Thorson, 1944). The species is mainly polyhaline with salinity tolerance above 24.8‰ (Golikov, 1995). The larval development is unknown.

In Iceland, *Curtitoma decussata* prefers silty or muddy substrates of the Arctic *Macoma* community (Thorson, 1941). Golikov (1995) recorded the species mainly from silty bottom.

*Fossil occurrence: Curtitoma decussata tjoernesensis* is only known in the Pliocene sediments of the *Serripes* Zone. Otherwise we have no knowledge of its stratigraphical range. Durham and MacNeil (1967) recorded the subspecies among Icelandic fossil molluscs with Pacific affinity.

The fossil occurrence of *C. decussata:* Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1915). Lower Pleistocene: Pattorfik beds (Símonarson, 1981b), Kap København Formation, Member B (Símonarson et al., 1998). Middle Pleistocene: Bridlington Crag (Harmer, 1915). Stratigraphical range: Pliocene to Recent.

***Curtitoma trevelliana*** **(Turton, 1834)**
Plate 7.7. Fig. 8

1834 *Pleurotoma Trevellianum* – Turton: p. 351.
1848 *Clavatula Trevelliana*. Turt. – Wood: p. 63, Pl. 7, fig. 14.
1878 *Bela Trevelyana*, Turt. – Sars: p. 235, Pl. 16, fig. 13.
1915 *Bela Trevelyana* (Turton) – Harmer: p. 294–295, Pl. 32, figs. 30–33.
1924 *Lora trevelyana* (Turton) = *L. concinnata* (Wood) – Schlesch: p. 327.
1980 *Lora trevelyana* (Turton, 1834) – Gladenkov et al.: p. 84–85, Pl. 15, fig. 29.
1988 *Oenopota trevelliana* (Turton, 1834) – Graham: p. 430, fig. 178.
1995 *Curtitoma trevelliana* (Turton, 1834*)* – Golikov: p. 49, fig. 137A–B.

*Material:* Twelve specimens from units 15, 18–21, and 23 in the *Serripes* Zone.

*Remarks:* The three largest specimens measure (h × d): 14.8 × 6.9, 11.3 × 5.2, and 10.1 × 4.6 mm. The d/h ratios are 0.46–0.51.

The fusiform shell has six slightly keeled whorls. They are ornamented by more than 20 inconspicuous longitudinal ribs crossed by fine spiral striae. The longitudinal ribs fade on the middle of the body whorl. The outer lip of the ovate and oblong aperture is slightly angulated adapically by a keel. The siphonal canal is rather short and open.

The species is often referred to as *Pleurotoma trevelliana* of Turton (1834), but some authors consider it identical with *Bela* or *Lora reticulata* (Brown). As the species name *reticulata* is older, it should have priority to *trevelliana* and may therefore be considered the strictly proper species name (cf. Harmer, 1915; Macpherson, 1971). However, we will here follow Harmer (1915) when he stated that the latter name has been so widely and universally adopted for more than a century (today actually two centuries) that it seems "inexpedient" to alter it. Jeffreys (1867) considered Brown's name as "obsolete."

*Recent distribution, ecology, and biology: Curtitoma trevelliana* is an arctic-boreal, circumpolar species with some lusitanian outposts. It extends from West and East Greenland, the Barents Sea, the Kara Sea, the Laptev Sea, and the Siberian Arctic Sea in the north to the British Isles and Maine in the south (Golikov, 1995; Graham, 1988; Sneli et al., 2005; Thorson, 1941). In Scandinavia it has been recorded from Kattegat, Bohuslän, and southeast to Øresund (Thorson, 1941). Furthermore, it is distributed from northern Alaska to California in the eastern Pacific (Graham, 1988; Sneli et al., 2005). Bathymetrical range: from 5 m in the White Sea to 1447 m in Svalbard (Golikov, 1995). In the British Isles it is commonly recorded from depths of 25–30 m, and in the Faroe Islands it seems to prefer depths below 65 m (Graham, 1988; Sneli et al., 2005). The species is probably mesohaline with salinity tolerance down to about 15‰ (Funder et al., 2002). In the

Arctic Golikov (1995) found it living at salinities between 23.4 and 34.5‰. The larval development seems to be non-pelagic (cf. Graham, 1988).

In the British Isles the species is mainly recorded from sandy bottoms where it feeds on small annelid worms (Graham, 1988). In the Faroe Islands it is most frequently found on muddy and sandy substrates (Sneli et al., 2005), and in the Arctic, Golikov (1995) found it especially on silty bottom mixed with sand, gravel, and pebbles.

*Fossil occurrence:* Pliocene: *Serripes* Zone of the Tjörnes beds (Gladenkov et al., 1980). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1915; Wood, 1848). Lower Pleistocene: Pattorfik beds (Símonarson, 1981b). Middle Pleistocene: Padymeiskii Suite (Merklin et al., 1979). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

Durham and MacNeil (1967) considered the species of Pacific origin, but referred to it as "*L. reticulata* (Brown) [*trevelliana*]." The species migrated from the Pacific to the North Atlantic while the *Serripes* Zone was deposited on Tjörnes.

### Genus *Propebela* Iredal, 1918

### *Propebela harpularia* (Couthouy, 1838)

Plate 7.8. Fig. 1

1838 *Fusus harpularius* – Couthouy: p. 106, Pl. 1, fig. 10.
1878 *Bela harpularia*, Couth. – Sars: p. 234–235, Pl. 16, fig. 17, Pl. 23, fig. 20.
1915 *Bela harpularia* (Couthouy) – Harmer: p. 287–288, Pl. 32, figs. 14–17.
1924 *Lora woodiana* (Möller) – Schlesch: p. 326, Pl. 11, figs. 2–3.
1924 *Lora* cf. *harpularia* (Couthouy) – Schlesch: p. 328, Pl. 11, fig. 12.
1941 *Bela harpularia* (Couthouy) – Thorson: p. 104–105.
1982 *Oenopota harpularia* (Couthouy), 1838 – Petrov: p. 60, Pl. 9, fig. 2.
1995 *Propebela (Propebela) harpularia* (Couthouy, 1838) – Golikov: p. 54, fig. 138O.

*Material:* One almost complete specimen from each of the units 15 and 23 in the *Serripes* Zone. Furthermore, Schlesch (1924) has recorded one specimen from unit ?19 and four from unit 23 in this zone. The latter he referred to *Lora woodiana* (Møller, 1842).

*Remarks:* The largest shell measures (h × d): 17.1 and 8.2 mm which corresponds to d/h ratios of 0.47–0.51.

The whorls are ornamented by 16–18 longitudinal ribs, slightly nodulous on the keel, intersected by rather fine spiral ridges. The longitudinal ribs are extending down to the upper half of the body whorl and more prominent there than in *Curtitoma trevelliana*. The aperture is ovate and distinctly more angulated by the keel than *C. trevelliana.* The form is actually intermediary between *C. trevelliana* and *Propebela nobilis*.

Thorson (1951) did not distinguish between *Propebela harpularia* and *P. woodiana* and obviously considered *P. woodiana* as a junior synonym.

*Recent distribution, ecology, and biology: Propebela harpularia* is an apparently discontinuously circumpolar, boreal species with subarctic and even arctic outposts.

From West Greenland (south of Uummannaq), Svalbard, the Barents Sea, Novaya Zemlya, the Kara Sea, the Laptev Sea, the Siberian Arctic Sea, northern Alaska, and Grinnell Land in the north, it extends southward to the west coast of Norway south to 63°N, Iceland, ?the Faroe Islands, and Cape Cod in the North Atlantic and Puget Sound, Monterey (California), and Japan in the Pacific (Golikov, 1995; Høisæter, 1986; MacGinitie, 1959; Macpherson, 1971; Óskarsson, 1962; Sneli et al., 2005; Thorson, 1941, 1951). Neither Posselt and Jensen (1898) nor Thorson (Thorson, 1944, 1951) did record it from East Greenland. Bathymetrical range: from 11 m in Iceland to 693 m off the North American east coast (Óskarsson, 1962; Thorson, 1941) or living at depths from 5 to 693 m (Golikov, 1995). The species is polyhaline with salinity tolerance above 25‰ (Funder et al., 2002) or living at salinity 27.1–35‰ (Golikov, 1995). The larval development is unknown, but most probably it is without a pelagic stage.

In the Arctic the species is mainly found on silty substrates (Golikov, 1995), but apparently it preferred more sandy bottom while it lived in the Tjörnes area during the deposition of the *Serripes* Zone.

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Harmer, 1915), *Serripes* Zone of the Tjörnes beds (Schlesch, 1924; this volume)). Lower Pleistocene: Olkhov Suite (Petrov, 1982). Middle Pleistocene: Bridlington Crag (Harmer, 1915). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

***Propebela nobilis*** **(Møller, 1842)**
Plate 7.8. Fig. 2

1842 *Defrancia nobilis* – Møller: p. 12.
1848 *Clavatula turricula.* Mont. – Wood: p. 62, Pl. 7, fig. 13a–b.
1863 *Clavatula turricula*, Mont. – Winkler: p. 211.
1878 *Bela nobilis*, Møller – Sars: p. 228, Pl. 16, figs. 19–20.
1915 *Bela nobilis* (Møller) – Harmer: p. 281–282, Pl. 31, figs. 17–21.
1924 *Lora nobilis* (Møller) – Schlesch: p. 327, Pl. 6, figs. 13–14, Pl. 11, fig. 14.
1924 *Lora rugulata* (Troschel) = *L. turricula* (Gould) – Schlesch: p. 326.
1924 *Lora rugulata scalaroides* (G.O. Sars) – Schlesch: p. 326, Pl. 11, fig. 4.
1962 *Lora nobilis* (Möller) – Óskarsson: p. 288–289, fig. 141.
1980 *Lora rugulata* (Troschel, 1866) – Gladenkov et al.: p. 84.
1980 *Mangelia (Bela)* aff. *scalaris* (Möller, 1842) – Gladenkov et al.: p. 86, Pl. 15, figs. 32–33a.
1995 *Propebela (Propebela) nobilis* (Moeller) – Golikov: p. 53, fig. 138J.
2005 *Oenopota nobilis* (Møller, 1842) – Sneli et al.: p. 85, fig. 31.

*Material:* Eleven specimens from units 14–15 and 17–19 in the *Serripes* Zone.

*Remarks:* The three largest shells measure (h × d): 15.7 × 7.4, 14.1 × 6.5, and 10.7 × 4.7 mm. The d/h ratios are 0.44–0.54, similar to those of *Curtitoma trevelliana.*

The fusiform shell consists of up to eight whorls with a flattened subsutural shelf. The whorls are ornamented by 16–20 longitudinal ribs that form nodes on the intersection with the keel, intersected by rather fine spiral ridges. The ribs are extending further down on the body whorl than in *P. harpularia*. The aperture is ovate and distinctly more angular by the keel than in *Curtitoma trevelliana* and *Propebela harpularia.*

*Recent distribution, ecology, and biology: Propebela nobilis* is a circumpolar, arctic-subarctic-boreal species. From West and East Greenland, Svalbard, the Barents Sea, the Kara Sea, the Laptev Sea, the Siberian Arctic Sea, northern Alaska, and northern Baffin Island in the north, it extends southward to Oslo Fjord, the Faroe Islands, and Cape Cod in the North Atlantic (Macpherson, 1971; Sneli et al., 2005; Thorson, 1941). It is distributed in the Pacific from the Bering Strait and southward to northern Japan, the Bering Sea, and the Okhotsk Sea (Golikov, 1995). It is not known from the Baltic, but *Oenopota turricula* (Montagu, 1803), recorded from the British Isles, may be conspecific with *P. nobilis* (cf. Graham, 1988). Bathymetrical range: from 5 m in Svalbard to 990 m off the Faroe Islands (Sneli et al., 2005; Thorson, 1941) or living at depths from 7 to 1710 m (Golikov, 1995). The species is polyhaline with salinity tolerance above 25‰ (Funder et al., 2002; Golikov, 1995). The larval development lacks a pelagic stage (Thorson, 1941).

In the Arctic the species prefers silty and sandy bottoms, but in the Faroe Islands it has also been found living on a substrate of gravel (Golikov, 1995; Sneli et al., 2005).

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Harmer, 1915). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1915; Wood, 1848). Lower Pleistocene: Pattorfik beds (Símonarson, 1981b). Middle Pleistocene: Padymeiskii and Rakov Suites (Merklin et al., 1979), Karagin Suite (Petrov, 1982). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

The species is considered to have originated in the Pacific and immigrated to the North Atlantic while the *Serripes* Zone was deposited (Durham & MacNeil, 1967).

### Genus *Cytharella* Monterosato, 1875

**_Cytharella_ sp.**
Plate 7.8. Fig. 3

*Material:* One specimen from unit 9 in the *Mactra* Zone. The genus and the species are new to the fossil fauna of Tjörnes.

*Remarks:* The single shell measures (h × d): 8.9 × ?4.6 mm. The d/h ratio is 0.52, and all shell ratios are very similar to those of *Cytharella costata* (Donovan). Unfortunately, the outer lip of the aperture is damaged except the very lowermost part close to the lower end of the siphonal canal. There, we can see two large teeth on the inner side of the lip, which indicate a row of teeth on the entire inner side of the lip. The shell has a cyrtoconoid spire with blunt tip, and the whorls are ornamented with ribs or costae, the intervening spaces with almost invisible spiral striae. The shell is more or less chocolate brown, especially the costae. The aperture is long and narrow and hardly distinguishable from the siphonal canal.

The shell is most similar to that of *Cytharella costata*, but apparently had a row of teeth on the inner side of the outer lip, which we have not seen in any specimens we have investigated of *C. costata.* Further identification is therefore difficult, and it is not possible to refer to it as a new species based only on one fragmentary specimen.

*Recent distribution, ecology, and biology:* The recent species of *Cytharella,* as well as *Mangelia*, is almost exclusively boreal-lusitanian, best known from the Mediterranean area (Poppe & Goto, 1991). Some of them extend northwards to the British Isles and western Norway at 61°N (Graham, 1988; Høisæter, 1986). According to Sneli et al. (2005) three species of *Mangelia* have been found around the Faroe Islands and one of them seems to be *C. costata* (cf. Forbes, 1840: as *Mangelia coarctata*). Bathymetrical range: In the British Isles *C. costata* has been found living from the low water stand and down to a depth of 250 m (Graham, 1988). It cannot be excluded that the species living in the Tjörnes area during the Pliocene had a similar depth range. We have only few information on the salinity tolerance of *Cytharella* or *Mangelia* species, but *Mangelia brachystoma* (Philippi) living in the Arkhangelsk region seems to be polyhaline with salinity tolerance above 25‰ (Funder et al., 2002). The larval development is not known, but related recent species seem to have a free veliger larval stage (Richter & Thorson, 1975).

The recent species of *Cytharella* and *Mangelia* prefer soft substrates, sand or fine shelly sand (Graham, 1988; Sneli et al., 2005).

*Fossil occurrence: Cytharella costata* has been found in Pliocene deposits, as the Coralline Crag Formation in England (Harmer, 1915). The species has also been found in Pleistocene sediments in the Mediterranean area, as well as in the British Isles (Harmer, 1915). The geological history of the genus *Mangelia*, and possibly also *Cytharella*, goes back to the Eocene (Grant & Gale, 1931)

### Order Heterogastropoda Fretter & Graham, 1982
### Family Cerithiopsidae H. & A. Adams, 1853
### Genus *Metaxia* Monterosato, 1884

#### *Metaxia metaxa* (delle Chiaje, 1828)
Plate 7.8. Fig. 4

1828 *Murex metaxa* – delle Chiaje: p. 222, Pl. 49, figs. 29–31.
1848 *Cerithium metaxa* (?). Delle Chiaje – Wood: p. 71, Pl. 8, fig. 6.
1918 *Cerithiopsis Metaxæ* (Delle Chiaje) – Harmer: p. 422–423, Pl. 41, figs. 16–19.
1988 *Cerithiopsis metaxa* (delle Chiaje, 1828*)* – Graham: p. 470, fig. 198.

*Material:* Five damaged specimens from unit 9 in the *Mactra* Zone. The species is new to the fossil fauna of Tjörnes.

*Remarks:* The largest shell consists of seven whorls and its height is about 3.4 mm. The tubercles on the surface of the whorls are not quite as large or square as in *Cerithiopsis tubercularis* (Montagu, 1803), and one fragment has an intact aperture with basal notch, resembling the aperture of *Metaxia metaxa* (cf. Graham, 1988: fig. 198). The protoconch seems intact and has not as many whorls as *C. tubercularis.* The first whorl of the protoconch is smooth, but the others (?two) have faint spiral lines. In our opinion, the specimens from the Tjörnes bed can best be attributed to *M. metaxa*, which indeed is not properly defined (cf. Graham, 1988).

*Recent distribution, ecology, and biology: Metaxia metaxa* is mostly a lusitanian species with boreal outposts. It ranges from Shetland, Southwest England, and the Channel Islands south to the Mediterranean (Graham, 1988). Apparently, it has not been found living in the British Isles for more than a century, and possibly all British records are of fossil specimens (cf. Fretter & Graham, 1982). The bathymetrical range is not well known, but the species seems restricted to sublittoral areas (?4–366 m), whereas *C. barleei* (Jeffreys, 1867) and *C. tubercularis* live in the foreshore/tidal zone (Funder et al., 2002; Graham, 1988; Rosenberg, 2009). While *C. tubercularis* is euhaline with salinity tolerance above 30‰, *C. barleei* is mesohaline with salinity tolerance down to about 15‰ (Funder et al., 2002). The species has probably pelagic larval development (Richter & Thorson, 1975).

According to Graham (1988), the species seems to have lived on sponges in the British Isles, but no remains of sponges have been found together with the specimens in the Tjörnes beds.

*Fossil occurrence:* Miocene: Korytnica Formation, Poland (Bałuk, 1975). Pliocene: Coralline Crag Formation (Harmer, 1918; Wood, 1848), Kattendijk Formation at Kallo, Belgium (Marquet, 1996). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1918). Lower Pleistocene: Calabrian at Ficarazzi, Italy (Harmer, 1918). Upper Pleistocene: Selsey beds (Harmer, 1918). Stratigraphical range: Miocene to Recent.

### Family Eulimidae H. & A. Adams, 1853
### Genus *Melanella* Bowdich, 1822

#### *Melanella* cf. *frielei* (Jordan, 1895)
Plate 7.8. Fig. 5

1895 *Eulima Frielei* – Jordan: p. 266–267, Pl. 16, fig. 6.
1848 *Eulima polita*. Linn. – Wood: p. 96–97, Pl. 19, fig. 1a–b.
1878 *Eulima intermedia,* Cantr. – Sars: p. 210, Pl. 11, fig. 20.
1920 *Eulima (Acicularia) intermedia* (Cantraine) – Harmer: p. 592–593, Pl. 50, figs. 21–22.
1988 *Melanella frielei* (Jordan, 1895) – Graham: p. 530, fig. 226.

*Material:* One damaged specimen from unit 9 in the *Mactra* Zone. The species is new to the fossil fauna of Tjörnes.

*Remarks:* The fragmentary shell is 1.3 mm in height and seems more slender than *Melanella lubrica* (Monterosato) or 0.6 mm in diameter. It is without spiral lines on the whorls, and the outer lip seems to turn forward to join the last whorl (cf. Graham, 1988: fig. 220, 8). However, as the aperture is somewhat damaged a close species identification is not possible.

*Recent distribution, ecology, and biology: Melanella frilei* is a boreal-lusitanian species extending from northern Norway (at 62°N), ?southern Iceland and the Faroe Islands south to the Mediterranean and the Canary Islands (Høisæter, 1986; Óskarsson, 1962; Sneli et al., 2005). It has been found in Skagerrak and Kattegat, but is unknown from the Baltic (Sneli et al., 2005; Thorson, 1941). Bathymetrical range: from 19 m in Denmark to 565 m in Norway (Thorson, 1941) or 30–1300 m (Sneli et al., 2005). In the British Isles it has been found living at 20–100 m depths (Graham, 1988). The species is apparently sublittoral and may now live at even greater depths than probably occurred in the Tjörnes area when the Pliocene sediments were deposited. The salinity tolerance is not known, but most of the *Melanella* species are polyhaline. *Melanella alba* (da Costa, 1778) has free veliger larvae, which may indicate pelagic larval development (Graham, 1988).

In the Faroe Islands the species has been found on substrate of fine sand, sand mixed with shell, and gravel (Sneli et al., 2005). In the British Isles it lives on muddy and sandy bottom as ectoparasites of holothurians (Graham, 1988).

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Harmer, 1920). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1920). Stratigraphical range: Pliocene to Recent.

### Family Epitoniidae Berry, 1910
### Genus *Boreoscala* Kobelt, 1902

***Boreoscala greenlandica* (Perry, 1811)**
Plate 7.8. Fig. 6

1811 *Scalaria greenlandica* – Perry: pl. 28, fig. 8.
1848 *Scalaria Grænlandica*. Chemn. – Wood: p. 90, Pl. 8, fig. 11a–b.
1878 *Scalaria grønlandica*, Chemn. – Sars: p. 194, Pl. 10, figs. 15–16, Pl. 23, fig. 1.
1920 *Scala (Boreoscala) grænlandica* (Chemnitz) – Harmer: p. 547–549, Pl. 47, figs. 13–16.
1924 *Scala (Boreoscala) groenlandica crebricostata* G.O. Sars – Schlesch: p. 336 Pl. 10, figs. 2–3, Pl. 11, fig. 22.
1995 *Boreoscala groenlandica* (Moeller, 1842) – Golikov: p. 55, fig. 138R.
2005 *Epitonium greenlandicum* (Perry, 1811) – Sneli et al.: p. 44–45, fig. 12.

*Material:* During an excursion to Tjörnes several years ago, two of our students found a specimen in unit 8 in the *Mactra* Zone. Two specimens were found by Schlesch (1924), most probably in unit 23 in the *Serripes* Zone. Furthermore, Norton (1975) listed the species as satisfactorily named, without any further stratigraphical information and he did not mention how many shells he found.

*Remarks:* The largest shell measures (h × d): 23.2 × 10.9 mm. The shells are rather worn, but clearly ornamented by obtuse longitudinal ribs with lower spiral ridges in between.

*Recent distribution, ecology, and biology: Boreoscala greenlandica* is an arctic-subarctic-boreal, almost circumpolar species. It extends from West and East Greenland, Svalbard, the Barents Sea, Novaya Zemlya, and the Kara Sea in the north to Oslofjord (South Norway), the Faroe Islands, and Massachusetts in the south (Golikov, 1995; Sneli et al., 2005; Thorson, 1941). From Wrangell Island and Point Barrow in northern Alaska it has been found in the Pacific south to northern Japan and British Columbia (Golikov, 1995; MacGinitie, 1959; Sneli et al., 2005). Macpherson (1971) did not record it from Arctic Canada. Bathymetrical range: The species prefers offshore areas from 19 m in Norway to a depth of 650 m in the southernmost part of its area of distribution (Poppe & Goto, 1991; Thorson, 1941). The species is polyhaline with salinity tolerance down to 25‰ (Funder et al., 2002) or 29‰ (Golikov, 1995). The larval development is unknown.

In Iceland it seems to prefer silty and sandy substrates, but has also been found on shell debris, as well as algae, especially *Laminaria* (Thorson, 1941).

*Fossil occurrence:* Pliocene: *Serripes* Zone of the Tjörnes beds (Norton, 1975; Schlesch, 1924). Pliocene/Pleistocene: Red Crag (Harmer, 1920; Wood, 1848), Walcheren, de Kaloot, and Westerschelde (van Regteren Altena et al., 1955). Lower Pleistocene: Olkov Suite (Petrov, 1982). Middle Pleistocene: Bridlington Crag (Harmer, 1920), Mikulin horizon (Merklin et al., 1979). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

According to Durham and MacNeil (1967) the species is most probably of Pacific origin and among the immigrants that reached the Tjörnes area while the *Serripes* Zone was deposited.

### Family Janthinidae Leach, 1823
### Genus *Janthina* Röding, 1798

#### *Janthina* cf. *exigua* Lamarck, 1816
Plate 7.8. Fig. 7

1816 *Janthina exigua* – Lamarck: p. 12, Pl. 456, fig. 2a–b.
1988 *Janthina exigua* Lamarck, 1816 – Graham: p. 500, fig. 211.
1991 *Janthina exigua* Lamarck, 1816 – Poppe & Goto: p. 184, Pl. 34, fig. 28.

*Material:* One damaged specimen from unit 9 in the *Mactra* Zone. The genus and the species are new to the fossil fauna of Tjörnes.

*Remarks:* The shell is 1.1 mm high and the diameter is about 0.9 mm, but it cannot be measured exactly as the outer lip is damaged. Therefore, it is not possible to see if there is/was a V-shaped notch on the outer lip. The d/h ratio seems close to 0.92 which is considerably lower than in *Janthina janthina* (Linné, 1758) with this ratio close to 1.35. This indicates a relatively taller spire than in the other *Janthina* species. The species has prosocline delicate ridges crossing the whorls of the spire and the upper half of the body whorl, but they change direction and are opisthocline on the base where they are rather faintly seen in our shell. The shell is most similar to *Janthina exigua*, but as we have only found a single fragmentary shell with a damaged aperture a closer identification is not possible.

*Recent distribution, ecology, and biology:* Apparently, *Janthina exigua* has the same distribution as the better known *J. janthina.* It is probably cosmopolitan, floating in the oceans between 50°N and 40°S, but occasionally it drifts beyond these boundaries (Graham, 1988; Poppe & Goto, 1991). In the North Atlantic it has been found living from the British Isles and southward to the Canary Islands, but it is rare in the Mediterranean (Poppe & Goto, 1991). All the janthinids seems holopelagic, but occasionally they drift ashore (Poppe & Goto, 1991). They are probably euhaline or polyhaline, but the salinity tolerance is not known. The species is ovoviviparous, the eggs developing within the female, but later they are shed as veliger larvae (Graham, 1988).

As the *Janthina* species are holopelagic they do not depend on a special type of substrate, but in the *Mactra* Zone the specimen was found in a lenticular shelly unit within a sand bed.

*Fossil occurrence:* The fossil history of *Janthina exigua* seems unknown. It may have been overlooked though hardly because of its size as it can be up to 17 mm high (cf. Graham, 1988). The record from the Pliocene *Mactra* Zone is apparently the earliest known occurrence of the species. Stratigraphical range: Pliocene to Recent.

### Family Aclididae Sars, 1878
### Genus *Aclis* Lovén, 1846

### *Aclis* cf. *minor* (Brown, 1827)

Plate 7.8. Fig. 8

1827 *Turritella minor* – Brown: pl. 51, figs. 57–58.
1842 *Aclis supranitida* – Wood: p. 534.
1925 *Aclis supranitida* (Wood) – Harmer: p. 868–869, Pl. 65, fig. 24.
1982 *Aclis minor* (Brown, 1827) – Fretter & Graham: p. 398–399, figs. 282–283.

*Material:* Eighteen specimens from unit 9 in the *Mactra* Zone. The genus and the species are new to the fossil fauna of Tjörnes.

*Remarks:* The shells are all more or less fragmentary, but the three most intact specimens measure (h × d): 2.0 × 0.9, 1.9 × 0.8, and 1.8 × 0.8 mm. The d/h ratio seems to be close to 0.43.

Originally, Brown (1827) named the species *Turritella minor*, but in 1842 Wood changed it to *Aclis minor*.

The shells from Tjörnes have 26–27 costae and three more prominent spiral ridges on the body whorl. The whorls are more tumid and the apical angle is wider in the specimens from Tjörnes, however, they seem best comparable to *Aclis minor.*

*Recent distribution, ecology, and biology: Aclis minor* is mainly a lusitanian species but extends northward into the southernmost part of the boreal region (Fig. 7.11). It seems to range from the southern Scandinavia into the Mediterranean, with wide scatters of records from places around the British Isles (Graham, 1988). Its distribution, bathymetrical range, and biology are not well known, and probably it is hard to find because of the small size (cf. Graham, 1988). In the British Isles it seems to live from about 15 m down to 150 m (Graham, 1988). Most probably the species is mesohaline with salinity tolerance down to 15‰, but the larval development is unknown.

In the British Isles, *Aclis minor* has been found alive on sandy and shelly substrates and seems to have lived in or on a sandy bottom when unit 9 was deposited in the Tjörnes area.

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Harmer, 1920; Wood, 1848), *Mactra* Zone of the Tjörnes beds (this volume). Lower Pleistocene: Calabrian

**Fig. 7.11** The recent known geographical distribution of *Aclis minor* (Brown)

on Sicily (Harmer, 1920). Stratigraphical range: Pliocene to Recent. The species is rarely found in fossil state.

### Genus *Ondina* de Folin, 1870

### *Ondina divisa* (Adams, 1797)

Plate 7.9. Fig. 1

1797 *Turbo divisus* – Adams: p. 254.
1872 *Odostomia insculpta*, Montagu – Wood: p. 62, Pl. 4, fig. 18.
1878 *Auriculina insculpta*, Mont. – Sars: p. 204–205, Pl. 11 figs. 11–12.
1923 *Odostomia (Ondina) insculpta* (Montagu) – Harmer: p. 839–840, Pl. 64, fig. 20.
1962 *Menestho insculpta* (Mont.) – Óskarsson: p. 211–212, fig. 62.

1988 *Evalea divisa* (J. Adams, 1797) – Graham: p. 566–567, fig. 244.
2005 *Ondina divisa* (J. Adams, 1797) – Sneli et al.: p. 94.

*Material:* Two almost intact specimens and one damaged shell from unit 9 in the *Mactra* Zone. The genus and the species are new to the fossil fauna of Tjörnes.

*Remarks:* The two almost intact shells measure (h × d): 11.9 × 4.7 and 8.0 × 4.4 mm. The d/h ratios are ?0.40 and 0.55.

The shell has a moderately tall spire, rather narrow and with a blunt apex. Low spiral ridges are present on the surface of the whorls, especially on the basal part of each of them. The outer lip of the aperture is slightly damaged, but on the columella there is a tooth as a low bulge. The tooth is less prominent than in *Odostomia* species.

*Recent distribution, ecology, and biology: Ondina divisa* is a boreal species with lusitanian outposts. It is distributed from northern Norway and western Iceland in the north to the Bay of Biscay in the south (Graham, 1988; Sneli et al., 2005). It has been found living off the Swedish west coast to Øresund, but not any further into the Baltic and not in the Mediterranean (Sars, 1878; Sneli et al., 2005). The species lives sublittorally and the bathymetrical range of 10–350 m has been reported (Sneli et al., 2005). In Iceland it is only known from depths below 28 m, and in the British Isles it has been found in depths between 18 m and 200 m (Graham, 1988; Óskarsson, 1962). The salinity tolerance and the larval development are unknown.

In the British Isles the species has been found on mud mixed with sand and gravel, but most records are of dead (empty) shells, and the species is never common in the British Isles or elsewhere (Graham, 1988)

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Harmer, 1923), Kallo and Doel sections (Marquet, 1998). Upper Pleistocene: Eemian in Denmark (Petersen, 2004). Stratigraphical range: Pliocene to Recent. The species is rarely found in Caenozoic sediments.

## 7.3 Gastropoda Opisthobranchia

**Phylum Mollusca Linné, 1758**
**Class Gastropoda Cuvier, 1797**
**Subclass Opisthobranchia Milne Edwards, 1848**
**Family Acteonidae d'Orbigny, 1835**
**Genus *Acteon* Montfort, 1810**

***Acteon tornatilis* (Linné, 1758)**
Plate 7.9. Fig. 2

1758 *Voluta tornatilis* – Linné: p. 1187.
1848 *Actæon tornatilis.* Linn. – Wood: p. 170, Pl. 19, fig. 5a–b.
1878 *Actæon tornatilis*, Lin. – Sars: p. 280–281, Pl. 17, fig. 11.
1923 *Actæon tornatilis* (Linné) – Harmer: p. 782–783, Pl. 62, figs. 13–14.

1938 *Actaeon tornatilis* (Linné) – Lemche: p. 3.
1976 *Acteon tornatilis* (L., 1758) – Thompson & Brown: p. 17, fig. 2.
1960 *Acteon tornatilis* Linné – Áskelsson: p. 21.
1980 *Actaeon tornatils* (Linné, 1758) – Gladenkov et al.: p. 86–87, Pl. 15, figs. 34–34a (in part).

*Material:* Five specimens from units 15–16 in the *Serripes* Zone.

*Remarks:* The two largest shells measure (h × d): 24.0 × 12.4 and 20. 4 × 11.0 mm. The d/h ratios of the Tjörnes material are 0.51–0.53.

According to Fretter and Graham (1954), *Acteon* is actually a gastropod with an admixture of prosobranch and opisthobranch characters. The external appearance is chiefly prosobranch while the gill is of an opisthobranch organization. Several tens of species have been described, both recent and fossil, but frequently the stated differences are questionable. Thus, *Acteon tornatilis* is indeed very similar to *A. noae* Sowerby, 1822; however, it is more slender with a larger fold (?tooth) on the inner lip of the aperture. The lower part of the aperture in *A. tornatilis* is less projecting than in *A. noae.* Possibly, these differences are not consistent enough to keep them separate as two distinct species. However, until taxonomic revision has taken place, based on better material than we have from the Tjörnes deposits, we will keep them separate. Both species are ornamented with bifurcated costae extending to the base. Unfortunately, the apex is eroded in all the found specimens, so we are not able to observe any differences in the apex in this report.

Norton (1975) listed both species from the Tjörnes beds and Áskelsson (1960) recorded them both from sedimentary xenoliths in the palagonite formation in Skammidalur, South Iceland. He considered the xenoliths, with the *Acteon* species, of similar or same age as the *Serripes* Zone on Tjörnes.

*Recent distribution, ecology, and biology: Acteon tornatilis* is a boreal-lusitanian species. It is distributed from western Norway at 70°N and West and South Iceland in the north to the Mediterranean as far as the Aegean Sea in the south (Bárðarson, 1920; Høisæter, 1986; Sneli et al., 2005). It has not been recorded from the Baltic, but from the Wadden Sea west of Denmark (Funder et al., 2002). Bathymetrical range: from the intertidal zone (several localities) to 250 m off the British Isles (Lemche, 1938; Poppe & Goto, 1991). In the Faroe Islands it has been found in depths between 40 and 160 m (Sneli et al., 2005). The species seems to be with salinity tolerance down to 15‰ (Funder et al., 2002). In most opisthobranch species, the eggs hatch as swimming shelled veliger larvae spending a relatively short time in the plankton (Thompson & Brown, 1976).

In the British Isles, *Acteon tornatilis* generally occurs burrowing in sandy substrates, mainly in sheltered bays where it feeds on infaunal polychaetes (Fretter & Graham, 1954; Thompson & Brown, 1976). In the Faroe Islands it prefers bottom of shelly gravel, gravel, and stones (Sneli et al., 2005).

*Fossil occurrence:* Miocene: Arnum Formation in Denmark, Grund and Steinabrunn in the Vienna Basin (Sorgenfrei, 1958). Pliocene: Coralline Crag Formation (Harmer, 1923; Wood, 1848), Luchtbal Sand Member (Marquet & Landau, 2006). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1923;

Wood, 1848). Upper Pleistocene: Belfast estuarian clays (Harmer, 1923), Baltic Eemian (Funder et al., 2002). Stratigraphical range: Miocene to Recent.

***Acteon noae* (Sowerby, 1822)**
Plate 7.9. Fig. 3

1822 *Acteon Noœ* – Sowerby: p. 101–102, Pl. 374.
1848 *Actœon Noœ*. J. Sow. – Wood: p.169, Pl. 19, fig. 6a–b.
1923 *Actœon Noœ,* J. Sowerby – Harmer: p. 781–782, Pl. 62, fig. 15.
1924 *Actaeon noae* J. Sowerby – Schlesch: p. 325, Pl. 6, fig. 7.
1925 *Actœon Noœ*, Sow. – Bárðarson: p. 48, 57.
1960 *Acteon noae* J. Sowerby – Áskelsson: p. 21, Pl. 3, figs. 20–21.
1980 *Actaeon tornatilis* (Linné, 1758) – Gladenkov et al.: p. 86–87, Pl. 15, figs. 34–34a (in part).

*Material:* Thirty-seven specimens from units 15–16 and 21 in the *Serripes* Zone.

*Remarks:* The two largest shells measure (h × d): 20.1 × 11.7 and 17.0 × 10.1 mm. The d/h ratios are 0.58–0.59 or somewhat higher than in *Acteon tornatilis,* which is more slender. It has also a shorter spire than *A. tornatilis.* Unfortunately, the shells are all fragmented, especially the outer lip of the aperture is damaged, as well as the protoconch.

*Distribution, ecology, and biology: Acteon noae* is extinct, but it probably had similar distribution as *A. tornatilis.* This is supported by the presence of recent boreal-lusitanian species together with *A. noae* in Pliocene sediments. Apparently, bathymetrical range and salinity tolerance were comparable to those of *A. tornatilis.* The larval development is not known.

The species seems to have preferred substrate of sand and gravel in the Tjörnes area while the *Serripes* Zone was deposited.

*Fossil occurrence:* Pliocene: Luchtbal Sand Member (Marquet & Landau, 2006). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1923; Wood, 1848). Stratigraphical range: Pliocene to ?Lower Pleistocene. Apparently, the species could not survive one of the severe Lower Pleistocene glaciations.

### Family Scaphandridae Sars, 1878
### Genus *Cylichna* Lovén, 1846

***Cylichna alba* (Brown, 1827)**
Plate 7.9. Figs 4–5

1827 *Volvaria alba* – Brown: [p. 38], Pl. 38, figs. 43–44.
1874 *Bulla alba*, Brown – Wood: p. 211.
1878 *Cylichna alba*, Brown – Sars: p. 283–284, Pl. 17, figs. 15, 16a–b.
1923 *Cylichna alba* (Brown) – Harmer: p. 801–802, Pl. 63, fig. 12.
1924 *Cylichna (Cylichna) alba* (Brown) – Schlesch: p. 325, Pl. 11, figs. 21–22.
1938 *Cylichna alba* (Brown) – Lemche: p. 8–9.
1962 *Cylichna alba* – Óskarsson: p. 294, fig. 154.

*Material:* Two specimens from unit 17 in the *Serripes* Zone. Furthermore, Norton (1975) listed the species from the Tjörnes beds without any stratigraphical information or mentioning how many shells he found.

*Remarks:* The larger specimen from bed unit 17 measures (h × d): 4.2 × 2.0 mm, and the d/h ratio are 0.48. The other shell is too damaged to be measured.

The shell is short and oblong with wider mouth (aperture) than in *Cylichna cylindracea* (Pennant). The outer lip is relatively higher than the apex, and generally there are no visible spiral striae on the surface of the shell.

*Recent distribution, ecology, and biology: Cylichna alba* is a circumpolar species with an arctic-boreal range. It is distributed from West and East Greenland, Svalbard, the Barents Sea, the Laptev and Kara Seas, the Siberian Arctic Sea, northern Alaska, and the Canadian Arctic in the north to Cape Cod in the south in the North Atlantic (Golikov, 1995; Lemche, 1938; Sneli et al., 2005). In the Pacific it is known as far south as northern Japan and California (Golikov, 1995; Sneli et al., 2005). It is not known living in the Baltic, but occurs in the Wadden Sea west of Denmark and is known from the Mediterranean (Funder et al., 2002; Sneli et al., 2005). Bathymetrical range: The species has been reported from 2 m depth in the White Sea to 2222 m in the Norwegian Sea (Golikov, 1995) and even down to 2700 m (Lemche, 1938). The species seems to be polyhaline-euhaline with salinity tolerance down to about 15‰ (Funder et al., 2002; Golikov, 1995). The larval development is not well known, but it may undergo a short pelagic stage (Malatesta & Zarlenga, 1986).

In the Faroe Islands the species has been found on almost all combination of clay, silt, sand, gravel, stones, and sponge spicules (Sneli et al., 2005), and Golikov (1995) recorded it from the Arctic on substrates of silt, sand, and pebbles.

*Fossil occurrence:* Pliocene: San Joaquin beds (Durham & MacNeil, 1967). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1923). Lower Pleistocene: Emilian (Malatesta & Zarlenga, 1986), Kap København Formation (Símonarson et al., 1998). Middle Pleistocene: Bridlington Crag (Harmer, 1923), Padymeiskii Suite (Merklin et al., 1979; Petrov, 1982). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

The species is considered to have originated in the Pacific and immigrated to the North Atlantic while the *Serripes* Zone was deposited (Durham & MacNeil, 1967; Malatesta & Zarlenga, 1986).

### ***Cylichna cylindracea*** **(Pennant, 1777)**

Plate 7.9. Figs 6–7

1777 *Bulla cylindracea* – Pennant: p. 117, Pl. 70, fig. 85.
1848 *Bulla cylindracea*. Penn. – Wood: p. 175, Pl. 21, fig. 1a–b.
1878 *Cylichna cylindracea*, Penn. – Sars: p. 283, Pl. 17, figs. 12.
1923 *Cylichna cylindracea* (Pennant) – Harmer: p. 803–805, Pl. 63, fig. 12.
1938 *Cylichna cylindracea* (Pennant) – Lemche: p. 8.
1962 *Cylichna cylindracea* – Óskarsson: p. 294, fig. 155.
1976 *Cylichna cylindracea* (Pennant, 1777) – Thompson & Brown: p. 26, fig. 9a–b.

*Material:* Two specimens from unit 15 in the *Serripes* Zone. Furthermore, Bárðarson (1925) found one shell in unit 19, and Norton (1975) listed the species from the Tjörnes beds without any stratigraphical information and he did not mention how many shells he found.

*Remarks:* The specimens from bed unit 15 measure (h × d): 7.6 × 3.2, ?6.9 × 3.0 mm, and the d/h ratios are 0.42–?0.43. The shells are rather fragmentary, especially the outer lip is badly damaged.

*Cylichna cylindracea* is distinctly more cylindrical than *C. alba* and ornamented with delicate spiral striae, almost never seen in *C. alba* (cf. Harmer, 1923; Óskarsson, 1962). The outer lip is not higher than the apex as generally seen in *C. alba.*

*Recent distribution, ecology, and biology: Cylichna cylindracea* is a boreal-lusitanian species extending from Iceland and western Norway at 68°N in the north to the Canary Islands and Azores in the south (Høisæter, 1986; Lemche, 1938; Thompson & Brown, 1976). It is not known living in the Baltic or the Faroe Islands, but all around the British Isles and is well known from the Mediterranean (Lemche, 1938; Poppe & Goto, 1991; Thompson & Brown, 1976). Bathymetrical range: It seems to prefer sublittoral environments, but ranges from the tidal zone down to a depth of 1500 m (Funder et al., 2002; Thompson & Brown, 1976). The species seems to have salinity tolerance down to about 15‰ (Funder et al., 2002). The larval development is not known; possibly it has a short pelagic stage similar to *C. alba.*

In the British Iles the species prefers sublittoral fine sand and is rarely found (Thompson & Brown, 1976). Generally, it lives buried into sand where it feeds on protozoans (Poppe & Goto, 1991).

*Fossil occurrence:* Miocene: Grund and Steinabrunn beds in the Vienna Basin (cf. Sorgenfrei, 1958). Pliocene: Coralline Crag Formation (Harmer, 1923; Wood, 1848), Luchtbal Sand Member (Marquet & Landau, 2006). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1848; Harmer, 1923). Upper Pleistocene: Belfast estuarian clays (Harmer, 1923), Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

### Genus *Cylichnoides* Mighels & Adams, 1842

#### *Cylichnoides occultus* (Mighels, 1841)

Plate 7.9. Figs. 8–9

1841 *Bulla occulta* – Mighels & Adams: p. 50.
1878 *Cylichna propinqva*, M. Sars – Sars: p. 284–285, Pl. 18, fig. 5a–d.
1923 *Cylichna scalpta* (Reeve) – Harmer: p. 803, Pl. 63, fig. 11.
1924 *Cylichna (Cylichna) reinhardti* (Holböll) Mörch = *C. propinqua* M. Sars – Schlesch: p. 325 (from Poulsen's manuscript 1884).
1938 *Cylichna insculpta* (Totten) – Lemche: p. 9–10.
1948 *Cylichna occulta* (Mighels, 1841) – Lemche: p. 78–79.
1995 *Cylichna occulta* (Mighels, 1841) – Golikov: p. 58, fig. 139c.

*Material:* Fifty-five specimens from unit 5 in the uppermost *Tapes* Zone and one shell from unit 9 in the *Mactra* Zone. Schlesch (1924) recorded the species from the

?*Serripes* Zone, actually from Poulsen's manuscript 1884, but neither with any further stratigraphical information nor did he mention how many shells were found.

*Remarks:* In the paper of Mighels and Adams (1841), it was pointed out that Mighels was the only author of the name of this species, although they were both authors of the paper (Lemche, 1948).

The five largest specimens measure (h × d): 8.9 × 5.7, 8.8 × 5.9, 7.3 × 4.8, 7.0 × 4.8, and 6.8 × 4.8 mm. The d/h ratios are 0.63–0.71, considerably higher than in *Cylichna alba* and *C. cylindracea*. Unfortunately, the shell material is generally dissolved, especially in unit 5 where the shells were found in sandy sediments overlain by a thick layer of lignite. The dissolution was probably caused by acidic water percolating from the lignite and through the marine sediments. Therefore, the specimens from unit 5 are almost exclusively preserved as casts (inner cores) and the measurements reflect minimum values.

The bell-shaped size-frequency distribution of all measureable specimens (53) from unit 5 strongly show an assemblage where the death rate is higher among the younger animals, which indicates residual life assemblage (Fig. 7.12).

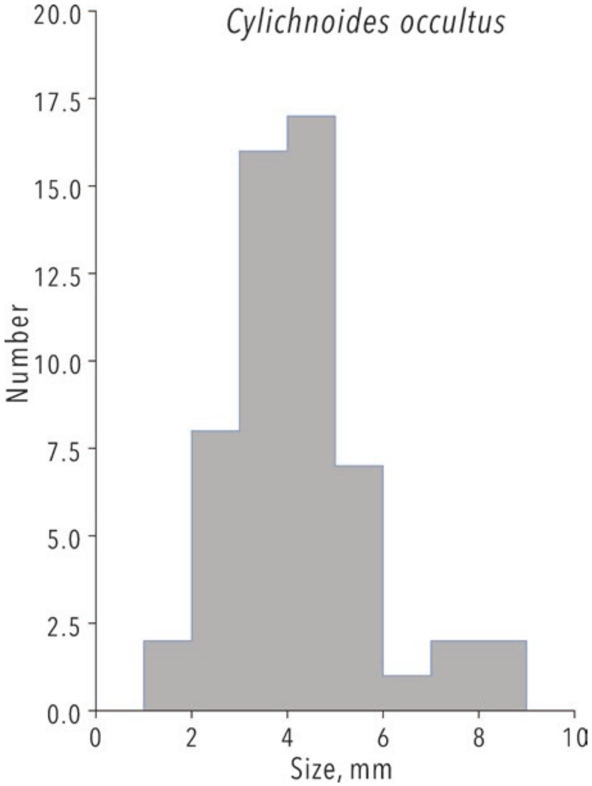

**Fig. 7.12** Size-frequency distribution of all measurable shells of *Cylichnoides occultus* (Mighels) in unit 5 in the *Tapes* Zone

*Recent distribution, ecology, and biology: Cylichnoides occultus* is an arctic-high boreal species with circumpolar distribution. It extends from West and East Greenland, Svalbard, Franz Josef Land, Novaya Zemlya, the Kara Sea, the Siberian Arctic Sea, northern Alaska and the northeast coast of North America in the north and southward to Scotland and Cape Cod in the North Atlantic (Golikov, 1995; Lemche, 1938; Lemche, 1941a; Lemche, 1941b; MacGinitie, 1959). In the Pacific it has been found living to the southern part of the Bering Sea (Golikov, 1995). It has not been recorded from the Baltic nor the Faroe Islands where the closely related *C. magna* Lemche, 1941 has been found (Funder et al., 2002; Sneli et al., 2005). Bathymetrical range: Recorded from 2 m depth in Franz Josef Land to 329 m in the Norwegian Sea (Golikov, 1995). Empty shells have been found at Greenland down to a depth of 900 m (Lemche, 1938). The species seems to euhaline-polyhaline with salinity tolerance down to about 23‰ (Golikov, 1995). The larval development is unknown.

The species seems to prefer silty and sandy substrates, and in Iceland it is commonly found in the Arctic *Macoma* bottom infaunal community, often in great numbers (Lemche, 1938).

When comparing the occurrences of this species in Pliocene and Pleistocene sediments to the recent distribution it cannot be excluded that it has changed its distribution from boreal areas toward more subarctic and arctic. Perhaps increased frequency of the broader and more striated *scalpta* form or variety is associated with such a change in habitat. This form was originally described by Reeve (1843–1846), and many authors have considered it as a distinct species (Lemche, 1948).

*Fossil occurrence:* ?Upper Miocene: *Tapes* Zone of the Tjörnes beds (this volume). Pliocene: *Mactra* Zone of the Tjörnes beds (this volume). Lower Pleistocene: Pattorfik beds (Símonarson, 1981b), Olkov Suite (Petrov, 1982), Kap København Formation (Símonarson et al., 1998). Middle Pleistocene: Bridlington Crag (Harmer, 1923), Kotzebuan (Hopkins et al., 1972). Upper Pleistocene: *Portlandia arctica* Zone in the Skærumhede sequence in Denmark (Nordmann, in Jessen et al., 1910). Stratigraphical range: Pliocene to Recent.

## 7.4 Bivalvia

**Phylum Mollusca Linné, 1758**
**Class Bivalvia Linné, 1758**
**Subclass Palaeotaxodonta Korobkov, 1954**
**Order Nuculoidea Dall, 1889**
**Family Nuculidae Gray, 1824**
**Genus *Nucula* Lamarck, 1799**

***Nucula* cf. *nucleus* (Linné, 1758)**
Plate 7.10. Figs. 1–2

1758 *Arca nucleus* – Linné: p. 695.
1851 *Nucula nucleus*, Linnæus – Wood: p. 85–86, Pl. 10, fig. 6a–b.

1878 *Nucula nucleus*, Lin. – Sars: p. 32.
1924 ?*Nucula tenuis* Montagu – Schlesch: p. 318 (from an unpublished manuscript of Poulsen, 1884).
1925 *Nucula* sp. – Bárðarson: p. 31, 44, 51.
1934 *Núcula núcleus* L. – Jensen & Spärck: p. 24–25, fig. 11.
1950 *Nucula nucleus* (Linné, 1758) – Heering: p. 15–16, Pl. 9, figs. 23–26.
1980 *Nucula nucleus* (Linné, 1758) – Gladenkov et al.: p. 26, Pl. 1, figs. 1–2.

*Material:* We found 24 specimens with articulated valves and 36 disarticulated valves from units 6–7, and 8 in the *Mactra* Zone and unit 14 in the *Serripes* Zone. Schlesch (1924) mentioned three valves from Poulsen's manuscript (Poulsen, 1884).

*Remarks:* The specimens are generally rather badly preserved due to dissolution, especially of the nacreous inner layer (mother-of-pearl/perlmütter) of the shell. Some of the specimens are reworked, fragmented, and scattered in the sediments, but the high number of paired specimens may indicate a lot of in situ material. The largest specimen with united valves measures (l × h): 13.5 × 10.1 mm, but most of the specimens are smaller.

*Recent distribution, ecology, and biology: Nucula nucleus* is a subarctic, boreal, and lusitanian species in the eastern part of the modern North Atlantic (Fig. 7.13). In the north, it is known from the Norwegian west coast at 68°N and the Faroe Islands south to South Africa (Høisæter, 1986; Petersen, 1968; Posselt & Jensen, 1898; Sars, 1878; Sneli et al., 2005). It is well known in the Mediterranean, but rarely found or even absent from the Baltic (Funder et al., 2002; Jensen & Spärck, 1934; Tebble, 1966). The species is not known from Iceland or East Greenland today, but in West Greenland there is apparently an isolated outpost in the Aasiaat/Egedesminde area (Posselt & Jensen, 1898). It is tempting to regard this occurrence as a relic from a milder period (Símonarson et al., 1998). Bathymetrical range: from 1 to ?219 m in West Greenland (Posselt & Jensen, 1898). It is a euhaline species with a lower salinity limit of 30‰ (Funder et al., 2002). This might explain its absence from the Baltic. The larval development is with a pelagic stage, as frequently found in boreal and lusitanian species (Jørgensen, 1946).

In the British Isles it lives offshore on rather coarse bottom of muddy gravel and sand (Tebble, 1966). The species is a deposit feeder as all other species of this family (Ockelmann, 1958).

*Fossil occurrence:* Oligocene: North Sea Basin (Heering, 1950). Miocene: Arnum Formation, Aquitanian, Burdigalian, Anversian, and Hemmoor Stage (Sorgenfrei, 1958). Pliocene: Coralline Crag (Wood, 1851), Vreeburg-Utrecht Well and Goes Well in the Netherlands (Heering, 1950), Luchtbal Sand Member (Marquet, 2002). Lower Pleistocene: Kap København Formation, Member B (Símonarson et al., 1998), Île de France glaciomarine sediments, East Greenland (Bennike et al., 2002). Stratigraphical range: Oligocene to Recent.

### Family Nuculanidae Adams & Adams, 1858

### Genus *Nuculana* Link, 1807

**Fig. 7.13** The recent known geographical distribution of *Nucula nucleus* (Linné)

### ***Nuculana minuta*** **(Müller, 1776)**

Plate 7.10. Fig. 3

1776 *Arca minuta* – Müller: p. 247.
1851 *Leda caudata,* Donovan – Wood: p. 92–93, Pl. 10, fig. 12a–b.
1878 *Leda minuta,* Müll. – Sars: p. 36, Pl. 5, fig. 2a–b.
1924 *Leda minuta* (Müller) – Schlesch: p. 318 (from an unpublished manuscript of Poulsen, 1884).
1950 *Leda (L.) minuta* (Müller, 1776) – Heering: p. 19–20, Pl. 9, figs. 5–6.
1980 *Nuculana minuta* (Müller, 1776) – Gladenkov et al.: p. 27, Pl. 1, fig. 7–7a.
2005 *Jupiteria minuta* (O.F. Müller, 1779) – Sneli et al.: p. 118, fig. 42.

*Material:* Two specimens with paired valves and six single valves from unit 14 in the *Serripes* Zone. Schlesch (1924) mentioned one valve from Poulsen's manuscript (Poulsen, 1884).

*Remarks:* The shells are rather well preserved, generally unbroken, and up to 14 mm in length. This species has more prominent ribs on the surface of the shell than *Nuculana pernula* (Müller, 1779) and fewer teeth. While the valve of *N. pernula* in Iceland has about 42 teeth in the taxodont hinge, *N. minuta* has only about 33. However, the species distinction is not always straightforward.

The species identification is not always easy, and the valves from Tjörnes seem to be more truncate toward the back instead of toward the front. They have somewhat wider rostrum and umbo pointing up or to the front instead of backwards as in more typical specimens. Thus, considerable variation is known in the form of these valves.

*Recent distribution, ecology, and biology: Nuculana minuta* is distributed in the eastern North Atlantic in the arctic, subarctic, and boreal regions. It is discontinuously circumpolar, lacking in the most arctic seas. The species extends from West and Southeast Greenland, Svalbard, the White Sea, the Beaufort Sea, Grinnell Land, and Baffinland south to the British Isles, Ireland, Maine, and North Japan (Bernard, 1979; Ockelmann, 1958; Sneli et al., 2005). It has been found along the west coast of Sweden south to Øresund (Sneli et al., 2005). Bathymetrical range: 4–1900 m (Madsen, 1949; Ockelmann, 1958). It seems to prefer depths between 10 and 190 m (Poppe & Goto, 1993; Tebble, 1966). The species has salinity tolerance down to 15‰ (Funder et al., 2002). The pelagic larval stage is probably very short or entirely lacking (Jørgensen, 1946).

In the British Isles the species prefers substrates of muddy sand and gravel (Tebble, 1966). In Iceland it mainly lives as an infaunal deposit feeder in the Arctic *Macoma* community together with *N. pernula* (Spärck, 1937).

*Fossil occurrence:* Pliocene: *Serripes* Zone of the Tjörnes beds (Gladenkov et al., 1980). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1851). Lower Pleistocene: Maassluis Formation (Heering, 1950), Olkov Suite (Petrov, 1982). Middle Pleistocene: Karagin Suite (Petrov, 1982). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). The specimens in the *Serripes* Zone seem to be among the oldest occurrence of this species. Stratigraphical range: Pliocene to Recent.

***Nuculana pernula* (Müller, 1779)**
Plate 7.10. Fig. 4

1779 *Arca Pernula* – Müller: p. 57.
1851 *Leda pernula,* Müller – Wood: p. 93, Pl. 10, fig. 13a–c.
1878 *Leda pernula,* Müll. – Sars: p. 35, Pl. 5, fig. 1a–d.
1924 *Leda pernula* (Müller) – Schlesch: p. 318 (from an unpublished manuscript of Poulsen, 1884).
1950 *Leda (L.) pernula* (Müller, 1779) – Heering: p. 20–21, Pl. 9, figs. 3–4.
1958 *Leda pernula costigera* Leche – Ockelmann: p. 15–18, Pl. 1, fig. 9.
1980 *Nuculana pernula* (Müller, 1779) – Gladenkov et al.: p. 28, Pl. 1, figs. 5–6a.

*Material:* Two pairs and four valves are known from the units 17–19 in the *Serripes* Zone. Schlesch (1924) mentioned only one fragment from Poulsen's manuscript (1884).

*Remarks:* The largest specimen measures (l × h): 21.1 × 11.2 mm. The surface of the valves is not quite smooth, but has regular, fine commarginal lines or ribs (see Plate 7.10, Fig. 4). The specimens are not particularly fragmented, although the material seems somewhat reworked.

*Recent distribution, ecology, and biology: Nuculana pernula* is widely distributed in the arctic, subarctic, and boreal regions in the North Atlantic. This circumpolar species extends from West and East Greenland, Svalbard, Franz Josef Land, Novaya Zemlya, the Kara Sea, the Siberian Arctic Sea, Ellesmere Island, Beaufort Sea, and the Bering Strait southward to the Sea of Okhotsk, Queen Charlotte Islands, northern Japan, Cape Cod, the English Channel, and Denmark (Bernard, 1979; Ockelmann, 1958; Sneli et al., 2005). In the Baltic it lives in the Belt Sea and along the Swedish west coast to Øresund (Sneli et al., 2005). Only empty valves have been found in the Bay of Biscay (Ockelmann, 1958). Bathymetrical range: 3–9 m in East Greenland or 4 m in Svalbard to 1275 m near Jan Mayen (Ockelmann, 1958) or 1400 m in North Japan (Bernard, 1979). In Kattegat (Denmark) it seems to prefer offshore areas with depths exceeding 20 m (Jensen & Spärck, 1934). The species has salinity tolerance down to 15‰ (Funder et al., 2002). The pelagic larval stage is probably very short or entirely lacking (Ockelmann, 1958).

In East Greenland, *N. pernula* lives mainly infaunally as a deposit feeder in mud or clay bottom, often mixed with sand or gravel (Ockelmann, 1958). It attains greatest abundance in the Arctic *Macoma* community (Thorson, 1934, 1936).

*Fossil occurrence:* Pliocene: The *Serripes* Zone of the Tjörnes beds (Gladenkov et al., 1980), Diemerbrug Well in the Netherlands (Heering, 1950). Lower Pleistocene: Maassluis Formation (Heering, 1950), Chukotka Peninsula (Petrov, 1966), Olkov Suite (Petrov, 1967, 1982), Pattorfik beds (Símonarson, 1981b). Middle Pleistocene: Karagin and Padymeiskii Suites (Merklin et al., 1979) (Petrov, 1982). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

### Genus *Yoldia* Möller, 1842

#### *Yoldia myalis* (Couthouy, 1838)

Plate 7.10. Figs. 5–6

1838 *Nucula myalis* – Couthouy: p. 62–63, Pl. 3, fig. 7.
1851 *Leda myalis*, Couthouy – Wood: p. 90, Pl. 10, fig. 17 & 17c.
1924 ?*Yoldia hyperborea* Lovén – Schlesch: p. 318 (from an unpublished manuscript of Poulsen, 1884).
1950 *Yoldia (Y.) myalis* (Couthouy, 1838) – Heering: p. 24–25, Pl. 9, figs. 9–12.
1954 *Yoldia myalis* (Couthouy) – Ockelmann: p. 18–20, Pl. 1, fig. 5, Pl. 2, figs. 5, 10.
1980 *Yoldia myalis* (Couthouy, 1838) – Gladenkov et al.: p. 29, Pl. 1, figs. 8–11.

*Material:* Twelve specimens with paired valves and 27 single valves from units 13–14 in the lowermost part of the *Serripes* Zone.

*Remarks:* The largest specimen measures (l × h): 22.6 × 12.2 mm. The material is somewhat reworked, but not very fragmented. Valves of taxodont bivalve species are more frequently found united in the Tjörnes sediments than valves belonging to species with other hinge types.

*Recent distribution, ecology, and biology: Yoldia myalis* is apparently a subarctic-boreal species. It is not found living in the northeastern Atlantic, but has been found in the Northwest Atlantic from the Hudson Strait southward to Maine (Bernard, 1979). It is not known from Iceland, Greenland, or the Canadian Arctic (Bernard, 1979; Lubinsky, 1980). It has been met with sporadically in the Beaufort Sea, along the coast of Alaska to Point Barrow and the Siberian Arctic Sea in the north, and it extends to the Chuckchi Sea and the Washington State in the south in the Pacific (Bernard, 1979; Lubinsky, 1980). Apparently, the distribution is discontinuous, there are consistent differences between the Atlantic and Pacific forms, and the arctic specimens seem more related to the Atlantic form (Bernard, 1979; Ockelmann, 1954). Bernard (1979) pointed out that the arctic specimens could be relicts from an earlier circumpolar distribution. Bathymetrical range: 13–150 m at the east coast of North America (Johnson, 1934) or 20–165 m in the Sea of Okhotsk (Scarlato, 1981). Bernard (1983) reported depths down to 360 m. The closely related *Yoldia hyperborea* Torell has salinity tolerance down to 15‰ (Funder et al., 2002). The larval development is unknown.

In the Tjörnes deposits the species is mostly found in sediments representing a bottom of muddy sand. The species is most probably a deposit feeder as many other taxodont bivalves.

*Fossil occurrence:* Pliocene: The Diemerbrug Well in the Netherlands (Heering, 1950). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1851). Middle Pleistocene: Kotzebuan (Hopkins et al., 1972). Upper Pleistocene: Maine in Northeast America (Richards, 1962). Stratigraphical range: Pliocene to Recent.

### Subclass Pteriomorphia Beurlen, 1944
### Order Arcoida Stoliczka, 1871
### Family Glycymerididae Newton, 1916
### Genus *Glycymeris* da Costa, 1778

### *Glycymeris glycymeris* (Linné, 1758)
Plate 7.10. Figs. 7–8

1758 *Arca glycimeris* – Linné: p. 695.
1851 *Petunculus glycimeris*, Linnæus – Wood: p. 66–69, Pl. 9, fig. 1a–i.
1925 *Petunculus glycimeris* L. – Bárðarson: p. 44, 74–75.
1950 *Glycimeris glycimeris glycimeris* (Linné, 1758) – Heering: p. 32–33, Pl. 8, figs. 7–8.
1980 *Glycymeris glycymeris* (Linné, 1758) – Gladenkov et al.: p. 31–32, Pl. 1, figs. 26–26a, 27–27a.
2005 *Glycymeris glycymeris* (Linnaeus, 1758) – Sneli et al.: p. 127.

*Material:* One specimen with articulated valves and seven single valves from units 10 and 11 in the upper part of the *Mactra* Zone.

*Remarks:* The material is clearly reworked, even though the specimen with the united valves is intact. The single valves are scattered in the sediments and generally fragmented, but most of them with the umbonal part undamaged. Therefore species identification is possible. The largest specimen measures (l × h × b): 67.2 × 64.6 × 38.8 mm.

*Recent distribution, ecology, and biology: Glycymeris glycymeris* occurs in the eastern parts of the North Atlantic from the mid-boreal area and well into the lusitanian region (Fig. 7.14). It extends from the Faroe Islands and about 62.5°N on the Norwegian west coast southward to the Canary Islands, Madeira, and Morocco (Høisæter, 1986; Tebble, 1966). It has been reported from the Baltic, but apparently it does not live there today and in Danish waters the only records are from the west coast of Jutland (Jensen & Spärck, 1934; Tebble, 1966). It is rarely found in the Mediterranean, eastward into the Ionian Sea (Delamotte & Vardala-Theodorou,

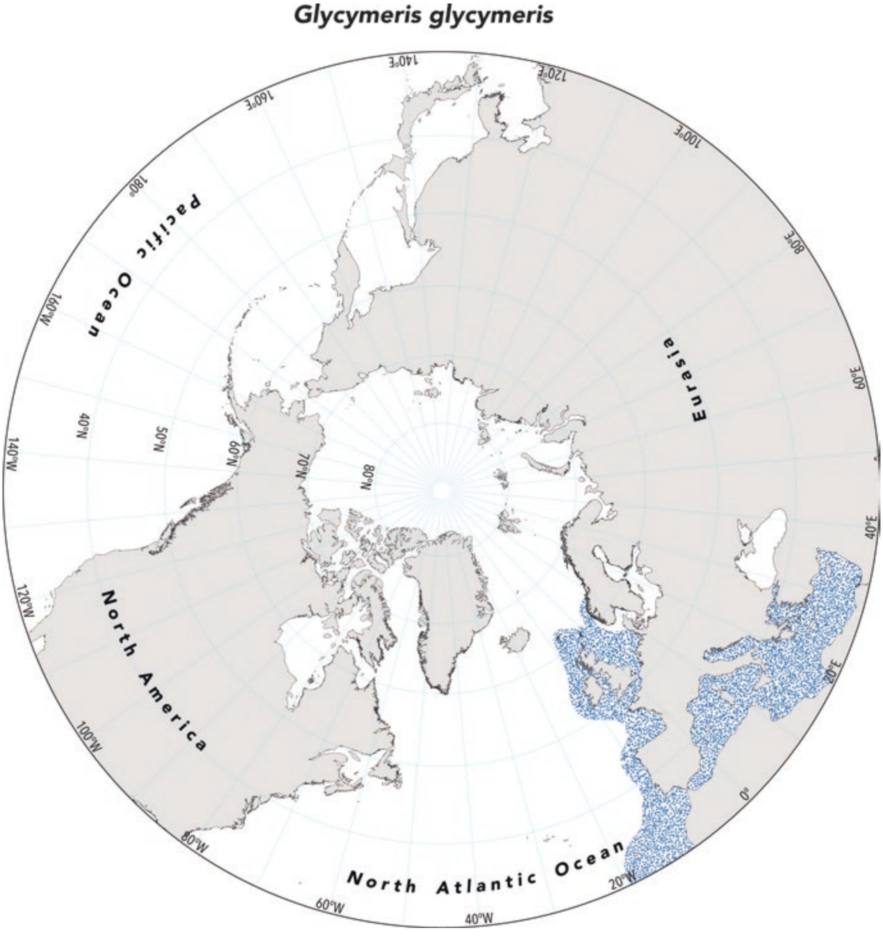

**Fig. 7.14** The recent known geographical distribution of *Glycymeris glycymeris* (Linné)

2001; Tebble, 1966). Bathymetrical range: The species inhabits mainly the foreshore/tidal zone, and in the Faroe Islands it has been found off-shore down to 99 m (Sneli et al., 2005). There is a doubtful record in the literature down to 1200 m (cf. Poppe & Goto, 1993). It is a euhaline species with salinity range above 30‰ (Funder et al., 2002). This might explain its absence from the Baltic. The larval development within the glycymerids is mainly pelagic, and the availability of suitable phytoplankton is particularly critical for the veligers (cf. Thomas, 1975).

The species is very common around the British Isles on bottom of muddy, sandy, or shelly gravel into which it can burrow (Tebble, 1966).

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Wood, 1851), Vreeburg-Utrecht Well in the Netherlands (Heering, 1950). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1851). ?Lower Pleistocene: Norwich Crag (Wood, 1851). Upper Pleistocene: Baltic Eemian (Funder et al., 2002) and likely Eem Formation in the Netherlands (cf. Moerdijk et al., 2010). Stratigraphical range: Pliocene to Recent.

### Order Mytiloidea Férussac, 1822
### Family Mytilidae Rafinesque, 1815
### Genus *Mytilus* Linné, 1758

### *Mytilus edulis* Linné, 1758
Plate 7.10. Figs. 9–10

1758 *Mytilus edulis* – Linné: p. 705.
1851 *Mytilus edulis,* Linnæus – Wood: p. 52–54, Pl. 8, fig. 9a–e.
1878 *Mytilus edulis* – Sars: p.27.
1924 *Mytilus edulis* Linné – Schlesch: p. 318.
1924 *Mytilus hesperianus* Lamarck – Schlesch: p. 318–319.
1924 *Mytilus incurvatus* Montagu – Schlesch: p. 319.
1950 *Mytilus (M.) edulis* Linné, 1758 – Heering: p. 38–40.
1960 *Mytilus edulis* Linné – Áskelsson: p. 16–17.
1980 *Mytilus edulis* Linné, 1758 – Gladenkov et al.: p. 32–33, Pl. 3, figs. 10–13.
2005 *Mytilus edulis* Linnaeus, 1758 – Sneli et al.: p. 131.

*Material:* About 100 specimens in almost all shell-bearing units of the three biozones. It is among the few species found in the oldest and youngest part of the Tjörnes sequence, but it is especially abundant in the lowermost part of the *Tapes* Zone (unit 1).

*Remarks:* The two largest specimens measure (l × h × b): 68.6 × 30.5 × 24.7 and 66.2 × 31.4 × 25.2 mm, respectively. The specimens from the *Tapes* Zone are generally badly preserved as percolating water has led to extensive dissolution of the calcite shell, especially in sediments close to the lignite layers. These specimens are generally preserved as internal or external casts. Most of them had intact and united valves, which indicates a low degree of reworking or pre-burial transport (Fig. 7.15). The size-frequency distribution of 71 measureable specimens (mainly casts) from unit 1 in the lowermost part of the *Tapes* Zone shows skewness, implying removal of a significant amount of younger animals and a slightly reworked residual life

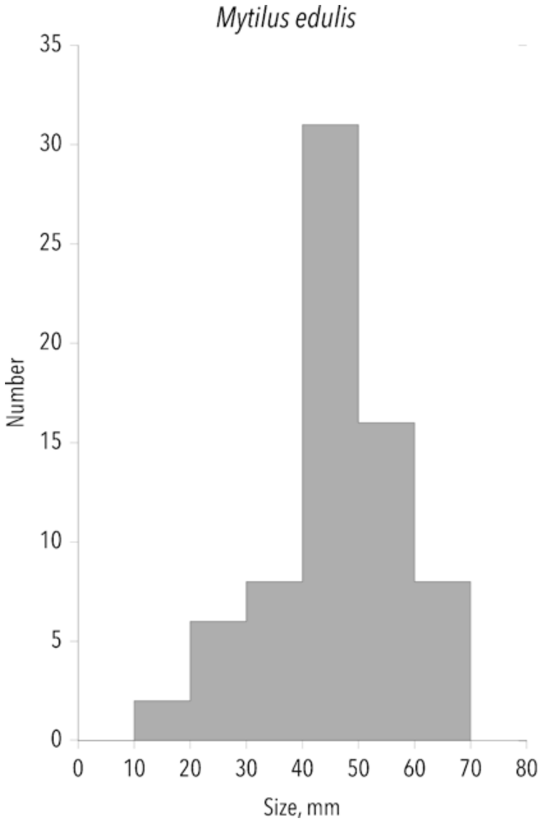

**Fig. 7.15** Size-frequency distribution of all measurable shells of *Mytilus edulis* Linné in unit 1 in the *Tapes* Zone

assemblage (cf. Fagerstrom, 1964). In the *Mactra* and *Serripes* Zones the valves are generally disarticulated and fragmented which may indicate a still higher degree of reworking.

We follow the older geologists and paleontologists that referred all mytilids they found in the Tjörnes beds to *Mytilys edulis* of Linné, 1758. The species is of Pacific origin and one of the first molluscan species to migrate into the North Atlantic across the Arctic Ocean during Caenozoic time (Durham & MacNeil, 1967). The *Mytilus* saga in the Pacific is really difficult as several of the *Mytilus* species do hybridize. Therefore, *Mytilus galloprovincialis* Lamarck and *Mytilus trossulus* Gould have often been referred to as synonym of *M. edulis*. However, *M. galloprovincialis* was first introduced in the Pacific after AD 1900, and these species cannot be distinguished with certainty only on shell characters (Coan, Scott, & Bernard, 2000).

*Recent distribution, ecology, and biology: Mytilus edulis* is at present, widely distributed in the subarctic, boreal, and lusitanian regions of the North Atlantic and in the Pacific from Alaska in the north to California and Japan in the south (Fig. 7.16). In the eastern North Atlantic it extends from Svalbard, Novaya Zemlya, and the western Kara Sea and Chuckchi Sea (where it is rare) to the Bay of Biscay (Filatova,

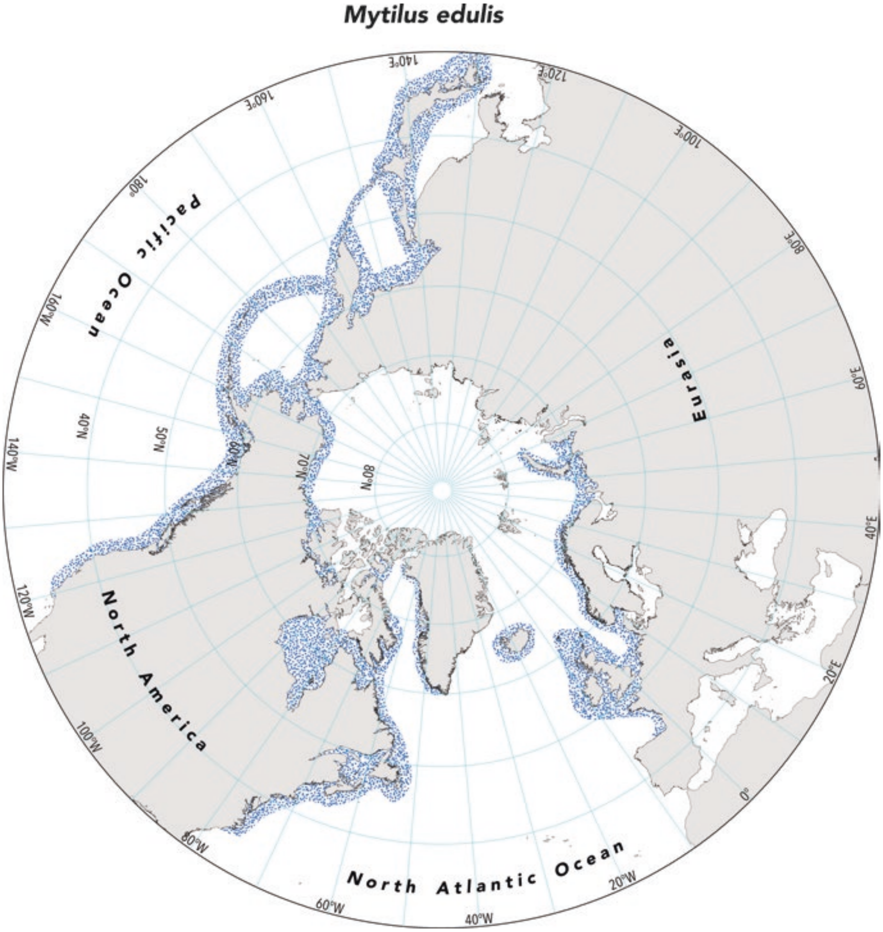

Fig. 7.16 The recent known geographical distribution of *Mytilus edulis* Linné

1957; Malatesta & Zarlenga, 1986; Mangerud & Svendsen, 2017; Scarlato, 1981). It is not known living in Franz Josef Land and the Siberian Arctic Sea, but it returned to Svalbard in 2004 after almost 4000 years of absence, excluding a short re-appearance during the Medieval Warm Period 900 years ago (Mangerud & Svendsen, 2017; Símonarson et al., 1998). In North America it lives in the Beaufort Sea, Victoria Island, Hudson Bay, Baffin Bay, and Padloping Island south to Cape Hatteras, California and Japan in the Pacific (Ellis, 1960; La Rocque, 1953; Lubinsky, 1980; Sneli et al., 2005). In West Greenland it is known from Dundas and Siorapaluk in the north (Theisen, 1973) to Qaqortoq/Julianehåb in the south (Hjort & Funder, 1974; Madsen, 1940). In East Greenland it is known from the Ammassalik district and further south near 61°N (Ockelmann, 1958). Bathymetrical range: 0 m (several localities) to 180 m in Jan Mayen (Ockelmann, 1958). The species is mainly littoral-intertidal and most frequently found at depths less than 10 m. The species is apparently with salinity tolerance down to 5‰ (Funder et al., 2002). Its reproduction is by a rather long pelagic larval stage which explains the widespread distribution (Thorson, 1936).

In Iceland and East Greenland the young animals most probably belong to the algal epifauna while the adults belong to the epifauna associated with gravel, stones, and rocks (Madsen, 1949; Ockelmann, 1958). It is attached to the substratum with byssus-threads (Jensen & Spärck, 1934), but belongs to the suspension feeders (Ockelmann, 1958).

*Fossil occurrence:* ?Miocene: Blakeley Formation (Grant & Gale, 1931). Pliocene: Diemerbrug Well, Vreeburg-Utrecht Well, and Goes Well in the Netherlands (Heering, 1950), *Nassarius reticosus* and *Chlamys opercularis* Subzone of the Netherlands (Spaink, 1975), Kallo and Doel sections (Marquet, 2002). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1851). Lower Pleistocene: Ludhamnian (Norton, 1967), Baventian (West et al., 1980), Emilian and Sicilian (Malatesta & Zarlenga, 1986), Pattorfik beds (Símonarson, 1981b), Kap København Formation (Símonarson et al., 1998), Olkov Suite (Petrov, 1967, 1982). Middle Pleistocene: Anvilian (Hopkins et al., 1974), Karagin, Kolvin, and Padymeiskii Suites (Merklin et al., 1979; Petrov, 1982). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Miocene to Recent.

*Mytilus edulis* is considered to have originated in the Pacific and migrated to the North Atlantic through the Bering Sea and Bering Strait more than 4 Ma ago, before the lowermost part of the *Tapes* Zone was deposited (Durham & MacNeil, 1967; Grant & Gale, 1931; Símonarson & Eiríksson, 2008).

### Genus *Musculus* Röding, 1798

### ***Musculus niger*** **(Gray, 1824)**

Plate 7.11. Figs. 1–2

1824 *Modiola nigra* – Gray: p. 244.
1878 *Modiolaria nigra*, Gray – Sars: p. 31.
1924 *Musculus niger* Gray – Schlesch: p. 319.
1925 *Modiolaria nigra*, Gray – Bárðarson: p. 47, 49, 52, 56, 72–73.
1934 *Modiolária nígra* Gray – Jensen & Spärck: p. 80–81, fig. 62.
1980 *Musculus niger* (Gray, 1824) – Gladenkov et al.: p. 33–34, Pl. 4, figs. 1–2.
2005 *Musculus niger* (J.E. Gray, 1824) – Sneli et al.: p. 130.

*Material:* Three paired specimens and two single valves from unit 9 in the *Mactra* Zone and three specimens with paired valves and 17 single valves from units 14–23 in the *Serripes* Zone.

*Remarks:* The largest valve from the *Serripes* Zone measures (l × h): 54.1 × 25.9 mm, but most of the valves from the *Mactra* Zone are juvenile and well preserved.

*Recent distribution, ecology, and biology: Musculus niger* has been found living in the arctic, subarctic, and the boreal regions in the North Atlantic. The species extends from Northeast Greenland, Svalbard, Franz Josef Land, the Barents Sea, Novaya Zemlya, the Kara Sea, and the Siberian Arctic Sea, the Beaufort Sea, the

Canadian Arctic Archipelago, Baffin Bay, and Labrador south to the western Baltic, the North Sea, Cape Hatteras, California, and Japan (Bernard, 1979; Lubinsky, 1980; Ockelmann, 1958). In West Greenland it has been found here and there north to about 71°N (Thorson, 1951). Bathymetrical range: from 3 m in Novaya Zemlya to 376 m in West Greenland (Ockelmann, 1958). It was found scattered in Jørgen Brønlunds Fjord in North Greenland between 9 and 19 m (Schiøtte, 1989). In East Greenland it is rarely found at depths below 40 m (Ockelmann, 1958). The *Musculus* species seems to have salinity tolerance down to 15‰ (Funder et al., 2002). The species has no pelagic larval stage (Ockelmann, 1958; Thorson, 1936).

It concerns an epifaunal species, and in East Greenland it mainly occurs on mud, sand, and gravel where the vegetation is scarce (Ockelmann, 1958). It is most probably a suspension feeder (Thorson, 1935, 1936).

*Fossil occurrence:* Pliocene: *Mactra* and *Serripes* Zones of the Tjörnes beds (Gladenkov et al., 1980; this volume). Lower Pleistocene: Olkhov and Tusatuva-Yamsk Suites (Petrov, 1982), Kap København Formation, Member A (Símonarson et al., 1998), Middle Pleistocene: Pinakul, Karagin, Kolvin, and Padymeiskii Suites (Merklin et al., 1979; Petrov, 1982). Upper Pleistocene: *Turritella terebra* and *Portlandia arctica* Zones in Denmark (Jessen et al., 1910). Stratigraphical range: Lower Pleistocene to Recent.

*Musculus niger* is considered to have originated in the Pacific (Durham & MacNeil, 1967). However, the oldest occurrence (FAD) seems to be in the *Mactra* Zone up to 1.5 Ma older than its appearance in the Kap København Formation. The species might signify the earliest penetration of cold water south to mid-latitudes (Símonarson et al., 1998).

### Genus *Modiolus* Lamarck, 1799

***Modiolus modiolus* (Linné, 1758)**
Plate 7.11. Figs. 3–4

1758 *Mytilus modiolus* – Linné: p. 706.
1851 *Modiola modiolus*, Linnæus – Wood: p. 57–58, Pl. 8, fig. 1a–d.
1878 *Mytilus modiolus*, Lin. – Sars: p. 23.
1924 *Modiolus modiolus* (Linné) = *M. umbilicatus* Pennant – Schlesch: p. 319 (from an unpublished manuscript of Poulsen, 1884).
1966 *Modiolus modiolus* (Linnaeus) – Tebble: p. 43, Pl. 3, figs. c, g.
2005 *Modiolus modiolus* (Linnaeus, 1758) – Sneli et al.: p. 129.

*Material:* One specimen with paired valves from unit 7, eight single valves, mainly juvenile, from unit 9, and one valve from unit 10. Thus, all the specimens were found in the *Mactra* Zone. Schlesch (1924) only mentioned one rather doubtful fragment from Poulsen's manuscript (1884).

*Remarks:* The length of the valve from unit 10 is about 11 cm, but it is fragmentary and the outer layer is more or less dissolved. However, the juvenile valves from unit 9 are better preserved. They are inequilateral with the beak a short distance from the anterior end (see Plate 7.11, Fig. 3).

*Recent distribution, ecology, and biology: Modiolus modiolus* is widespread in the Atlantic boreal region with occurrences in the subarctic and lusitanian regions. From the Gulf of Onega and Iceland in the north, it extends to the Bay of Biscay in the south (Sneli et al., 2005; Tebble, 1966). In East America it has been found living along the coasts from Labrador and southward to North Carolina or even Florida and in the Pacific from the Bering Strait to Japan and California (San Pedro) in the south (Malatesta & Zarlenga, 1986; Tebble, 1966). It has not been found living in Greenland or Svalbard, but is among the most common bivalve species along the Icelandic coasts. Bathymetrical range: 0–500 m (Madsen, 1949; Sneli et al., 2005). In the British Isles and Iceland the species lives mainly on the lower shore, especially adult animals (Madsen, 1949; Tebble, 1966). The species seems to have a salinity tolerance down to about 15‰ (Funder et al., 2002). The larval development is pelagic (Malatesta & Zarlenga, 1986).

The species belongs to the epifauna on rocky bottoms or it lives attached to laminarians and may form very large communities (Tebble, 1966).

*Fossil occurrence:* Pliocene: ?Coralline Crag Formation (Wood, 1851), Lillo Formation, Kallo and Doel sections (Marquet, 2002). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1851). Lower Pleistocene: Santernian (Malatesta & Zarlenga, 1986). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent (see below).

Apparently, *Modiolus modiolus* evolved in the Pacific during the ?late Miocene most probably from *M. capax* (Soot-Ryen, in Malatesta and Zarlenga (1986). Durham and MacNeil (1967) mentioned the species as being of Pacific origin, but did not report it from the Pacific Pliocene.

### Order Pterioida Newell, 1965
### Family Pectinidae Rafinesque, 1815
### Genus *Aequipecten* Fisher, 1886

#### *Aequipecten opercularis* (Linné, 1758)
Plate 7.11. Fig. 5

1758 *Ostrea opercularis* – Linné: p. 698.
1851 *Pecten opercularis*, Linnæus – Wood: p. 35–37, Pl. 6, fig. 2a–d.
1878 *Pecten opercularis*, Lin. – Sars: p. 16.
1950 *Pecten (Chlamys) opercularis* (Linné, 1758) – Heering: p. 46–49, Pl.14, figs. 3–9 & 25.
1966 *Chlamys (Aequipecten) opercularis* (Linnaeus) – Tebble: p. 60–61, Pl. 5, figs. b, d.
2005 *Aequipecten opercularis* (Linnaeus, 1758) – Sneli et al.: 131–132.

*Material:* One left valve from unit 8 in the *Mactra* Zone. The species is new to the fossil fauna of Tjörnes.

*Remarks:* The valve measures (l × h): 15.3 × 16.9 mm, and it seems to be of a young animal hardly halfgrown. The species is very variable, which has caused it to be separated into many different species (synonyms), and therefore Wood (1851) stated that scarcely any description could be given of its structure. The only name referred to the occurrence in Iceland is *Aequipecten opercularis*, and the two most closely related species or varieties, *A. radians* (Nyst & Westendorp) and *A. wagenari* Marquet and Dijkastra, seem to be considerably smaller species, from more southern localities (in the North Sea Basin). Therefore, we have referred this only valve from the *Mactra* Zone to *A. opercularis.*

*Recent distribution, ecology, and biology: Aequipecten opercularis* is distributed in the boreal and lusitanian regions of the North Atlantic. From southeastern Iceland, northern Norway, and the Faroe Islands it extends to the Mediterranean, Azores, and the Canary Islands (Dijkastra et al., 2009; Sneli et al., 2005; Tebble, 1966). In the Baltic it is known south to Øresund (Sneli et al., 2005). Bathymetrical range: 0–2664 m (Sneli et al., 2005). In the Faroe Islands it has been found at depths from 21 m down to 450 m, where the temperature range is 6.2–8.7 °C (Sneli et al., 2005). The species seems to have a salinity tolerance down to 15‰ (Funder et al., 2002). The larval development most probably has a pelagic larval stage as almost all boreal species of pectinids.

The species belongs to the epifauna, and in the British Isles it has been found in great abundance on firm sandy gravel and mud or shelly bottom (Tebble, 1966). In early life *A. opercularis* lives attached by a byssus becoming free and active swimmer able to clap the valves together and move off from the bottom (Tebble, 1966).

*Fossil occurrence:* Miocene: Vienna Basin and Touraine in France (Heering, 1950). Pliocene: Coralline Crag Formation (Wood, 1851), Diemerbrug Well, Vreeburg-Utrect Well, and Goes Well in the Netherlands (Heering, 1950), *Nassarius reticosus* and *Chlamys opercularis* Subzone of the Netherlands (Spaink, 1975), Kallo and Doel sections (Marquet, 2002), Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1851). Lower Pleistocene: Icenian (Heering, 1950), Lower Emilian (Sami & Taviani, 1997). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

### Genus *Chlamys* Bolten in Röding, 1798

#### *Chlamys tjoernesensis* MacNeil, 1967

1967 *Chlamys tjornesensis* – MacNeil: p. 16–17, Pl. 25, figs. 1–3.
1924 *Pecten (Chlamys) islandicus* (Müller) – Schlesch: p. 318.
1925 *Pecten (islandicus* Müll.?*)* – Bárðarson: p. 43, 59, 74–75.
1980 *Chlamys (Chlamys) tjörnesensis* MacNeil, 1967– Gladenkov et al.: p. 35, Pl. 2, figs. 1–2, 3–6.

*Material:* Twelve single valves from units 9–10, and 11 in the *Mactra* Zone and unit 23 in the *Serripes* Zone.

*Remarks:* The thin valves are very damaged and therefore difficult to measure. They are generally large and some of them with height exceeding 10 cm. The length of the found valves is up to 3 cm shorter than the height.

In his study of Pectinidae from North Atlantic, MacNeil (1967) described a new species from the Tjörnes beds and named it after Tjörnes. Before that, the only pectinid reported from the layers had been referred to the recent *Chlamys islandica* (Müller, 1776) (=*Pecten islandica* Müller, 1776). *C. tjoernesensis* is similar in size to *C. islandica,* up to about 12 cm long and the height slightly exceeds the length.

The anterior ear of the right valve is shorter but slightly broader in *C. tjoernesensis.* The posterior ear in the left valve is also broader in *C. tjoernesensis* with coarser and more unequal ribs. The byssal notch is rather blunt and not as sharp as in *C. islandica.* The dysodont teeth seen in the latter are not visible in our specimens of *C. tjoernesensis* (Plate 7.11, Figs. 7–8). The numerous ribs on the surface of the valve of *C. tjoernesensis* are similar to those of *C. islandica*. However, the ribs of *C. tjoernesensis* have more numerous and larger scales on the crest, and also in the space between the ribs. Therefore, the surface pattern is finer in *C. islandica,* and we have not seen the reticulate rasp-like structure so often found in *C. islandica* (Plate 7.11, Figs. 9 and 10).

The ribs of *Chlamys tjoernesensis* are varying somewhat as shown by Gladenkov et al. (1980), in their Pl. 2, figs. 1–2. The number of ribs and their structure in fig. 2 in the paper of Gladenkov et al. are very similar to the ribs in the umbonal part of our largest specimen. Therefore, it is tempting to follow MacNeil (1967) and Gladenkov et al. (1980) and refer all the *Chlamys* specimens found in the older Tjörnes layers to *C. tjoernesensis.*

*Distribution, ecology, and biology: Chlamys tjoernesensis* is extinct and has not been reported from elsewhere. According to MacNeil (1967), it seems most related to *C. wainwrightensis* MacNeil, 1967, known from Arctic Alaska. Probably it evolved as a boreal form during the Pliocene while the Tjörnes beds were being deposited and became extinct at the onset of the Pleistocene when the first tillites were formed on Tjörnes. The bathymetrical range is not known, but most probably the species lived offshore associated with the algal epifauna on a bottom of silt, sand, and shells as *C. islandica* does today in Iceland (see Madsen, 1949). When compared to the salinity profile for the Tjörnes beds, it is tempting to conclude that this was euhaline-mesohaline species. It is not possible to exclude a pelagic larval stage.

*Fossil occurrence:* Pliocene: Tjörnes beds (Gladenkov et al., 1980; MacNeil, 1967). The species is only met with in the *Mactra* and *Serripes* biozones deposited in Upper Pliocene. Obviously, it did not survive into the Pleistocene, and in Iceland it is not known from the Pleistocene Breiðavík deposits resting directly on the Tjörnes beds (MacNeil, 1967). Stratigraphical range: Pliocene.

The exact relationship between *Chlamys tjoernesensis* and *C. wainwrightensis* is not known, nor if the former originated in the Pacific or North Atlantic (MacNeil, 1967).

### Family Anomiidae Rafinesque, 1815
### Genus *Heteranomia* Winckworth, 1922

***Heteranomia squamula* (Linné, 1758)**
Plate 7.12. Fig. 1

1758 *Anomia squamula* – Linné: p. 701.
1851 *Anomia ephipium*, Linnæus – Wood: p. 8–9, Pl. 1, fig. 3a–d.
1878 *Anomia ephippium*, Lin. var. *squamata* – Sars: p. 14.
1934 *Anómia (Heteranomia) squámula* L. – Jensen & Spärck: p. 51–52, fig. 32.

1950 *Anomia (Heteranomia) squamula* (Linné, 1758) – Heering: p. 54–55.
2005 *Heteranomia squamula* (Linnaeus, 1758) – Sneli et al.: p. 137.

*Material:* Three disarticulated valves from unit 5 in the *Tapes* Zone, seven valves from unit 9 in the *Mactra* Zone, one valve from unit 13, and two from unit 15 in the *Serripes* Zone. The species is new to the fossil fauna of Tjörnes.

*Remarks:* No specimen with paired valves was found, only rather well-preserved disarticulated valves. The largest valves measure (l × h × b): 12.1 × 11.7 × 2.5, and 11.5 × 11.9 × 2.4 mm.

The specimens referred to *Heteranomia squamula* have the beaks almost at the shell margin but not central, and we have not observed any "tooth" above the ligament pit. The valves found in the Tjörnes beds occurred together with valves of *Heteranomia squamula aculeata* (Müller), and therefore it is still more tempting to refer them to *Heteranomia.*

*Recent distribution, ecology, and biology: Heteranomia squamula* is a boreal species that extends into lusitanian and possibly subarctic regions. It has been found in the North Atlantic from the White Sea and Iceland south along the European coasts to the Bay of Biscay and the Mediterranean (Sneli et al., 2005; Tebble, 1966). In East North America it extends from Labrador in the north to North Carolina in the south (Madsen, 1949). In the Baltic it extends south to ?Øresund (Jensen & Spärck, 1934). Bathymetrical range: 0 m in several places to almost 2000 m south of Vestmannaeyjar in South Iceland (Madsen, 1949). In the Faroe Islands it has been found at depths from 66 m to 1006 m where the temperatures range from 6.0° to 8.6°C (Sneli et al., 2005). The species has salinity tolerance down to about 15‰ (Funder et al., 2002). The larval development includes a pelagic stage (Jørgensen, 1946).

The species is epifaunal, and in the British Isles it is widely distributed on stones, shells, and seaweeds and in the Faroe Islands it has been found on sand, gravel, and shells (Sneli et al., 2005; Tebble, 1966).

*Fossil occurrence:* Miocene: Gram Formation in Denmark (Schnetler, 2005). Pliocene: Coralline Crag Formation (Wood, 1851), Oosterhout Formation and Maassluis Formation (Heering, 1950), Kattendijk and Lillo Formations (Marquet, 2002), Middle Pleistocene: Mikulin horizon (Merklin et al., 1979). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Miocene to Recent.

***Heteranomia squamula aculeata* (Müller, 1776)**
Plate 7.12. Fig. 2

1776 *Anomia aculeata* – Müller; p. 249.
1851 *Anomia aculeata*, Müller – Wood: p. 9–10, Pl. 1, fig. 2a–b.
1878 *Anomia aculeata*, Lin. – Sars: p. 15, Pl. 19, fig. 1a–d.

*Material:* Two single valves from unit 9 in the *Mactra* Zone. This subspecies is new to the fossil fauna of Tjörnes.

*Remarks:* The two found valves measure (l × h × b): 3.9 × 4.7 × ?0.8 and 2.7 × 3.1 × ?0.6 mm.

Most authors today do not regard the *aculeata*-form as a distinct species or even subspecies. Usually, it is only regarded as a variety belonging to *Heteranomia squamula*. However, there have been authors like Wood (1851) and Sars (1878) regarding it as a distinct species. When comparing the two forms, typical *H. squamula* and the *aculeata*-form, the differences in the left valves clearly exceed those often used to separate two species within the same genus. Further studies might eventually reveal the relationship of these two forms. Here, the *aculeata*-form is treated as a subspecies of *H. squamula*.

*Recent distribution, ecology, and biology:* As *Heteranomia squamula aculeata* has almost always been treated as a form belonging to *H. squamula* we are not having separate information on the distribution, ecology, and biology of this subspecies. However, it seems mainly boreal in its distribution, but in Iceland it has more frequently been found off the northern part of the island (Óskarsson, 1952).

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Wood, 1851), *Mactra* Zone of the Tjörnes beds (this volume). Stratigraphical range: Pliocene to Recent.

**Subclass Heterodonta Neumayr, 1884**
**Order Veneroida Adams & Adams, 1856**
**Family Astartidae d'Orbigny, 1844**
**Genus *Astarte* Sowerby, 1816**

***Astarte crenata* (Gray, 1824)**
Plate 7.12. Fig. 3

1824 *Nicania crenata* – Gray: p. 242.
1878 *Astarte crebricostata*, Forb. – Sars: p. 54, Pl. 5, fig. 7a–b.
1863 ?*Astarte Hjaltalini* Winkl. – Winkler: p. 204–205.
1924 *Astarte crebricostata* Forbes = *A. crenata* Gray = *A. hjaltalini* Winkler – Schlesch: p. 319, Pl. 5, figs. 1–2.
1950 ? *Astarte crebricostata* Forbes 1847 – Heering: p. 80–81, Pl. 5, figs. 14–15.
1958 *Astarte crenata* (Gray) – Ockelmann: p. 89–98.
1980 *Astarte crenata* (Gray, 1824) – Gladenkov et al. : p. 38–39, Pl. 4, figs. 3–9a.
2005 *Astarte acuticostata* Friele, 1877 – Sneli et al.: p. 144.

*Material:* Seven specimens with paired valves and 24 single valves from units 17–23 in the *Serripes* Zone.

*Remarks:* The largest valve measures (l × h): 35 × 29 mm. The h/l ratios are close to 0.80, which is lower than with *A. basterotii* De la Jonkaire, 1923, with h/l ratios about 0.90.

*Recent distribution, ecology, and biology: Astarte crenata* (incl. subspecies) is distributed in the arctic to boreal regions in the North Atlantic. It extends from Franz Josef Land, Svalbard, East Greenland, the Barents Sea, Novaya Zemlya, the Kara Sea, the Siberian Arctic Sea, and the Canadian Arctic south to the Hebrides, West Norway (north of Lofoten), and Maine (Lubinsky, 1980; Ockelmann, 1958). In Iceland it has been found scattered along the northwestern, northern, and eastern coasts, but only empty valves have been found in West Iceland (Madsen, 1949; Ockelmann, 1958). Bathymetrical range: from 4 m in Svalbard to 1275 m near Jan

Mayen (Ockelmann, 1958). In the colder regions of the eastern Canadian Arctic it prefers depths of 20–700 m (Lubinsky, 1980). The salinity tolerance is not known, but most likely it is a euhaline species as indicated by its occurrence within the Polar water in East Greenland where the salinity is about 32–34.5‰ (Ockelmann, 1958). The larva appears to have a very short or no pelagic stage (Ockelmann, 1958).

In East Greenland this suspension feeder characterizes the *Astarte crenata* community, an infaunal community especially found at depths between 40 and 200 m on muddy substratum with gravel and stones (Ockelmann, 1958).

*Fossil occurrence:* Pliocene: *Serripes* Zone of the Tjörnes beds (this volume). Middle Pleistocene: Padymeiskii Suite (Merklin et al., 1979). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

The occurrence of *Astarte crenata* in the Pliocene Tjörnes beds seems to be the earliest for the species.

***Astarte* cf. *basterotii* de la Jonkaire, 1823**

Plate 7.12. Fig. 4

1823 *Astarte Basterotii* – De la Jonkaire: p. 129, Pl. 6, fig. 3a–c.
1853 *Astarte Basterotii*, Lajonkaire – Wood: p. 177–178, Pl. 17, fig. 2a–d.
1950 *Astarte basterotii* De la Jonkaire, 1823 – Heering: p. 68–70, Pl. 3, figs. 1–10.
1980 *Astarte basterotii* De La Jonkaire, 1823 – Gladenkov et al.: p. 39, Pl. 4, figs. 10–12a.

*Material:* Eight disarticulated valves from units 14 and 18–23 in the *Serripes* Zone. The valves are generally well preserved, but they are clearly reworked in the sediments. Steinn Emilsson (1929) reported *Astarte* sp. 2 as the most frequent species found in the Eyvík Formation (cf. Eiríksson et al., 2020a). *Astarte* or *Tridonta* species have never been found in the Tjörnes deposits older than the *Serripes* Zone. Therefore, the fauna of the Eyvík Formation seems best correlated with the fauna in the lower part of *Serripes* Zone.

*Remarks:* The largest valve measures (l × h × b): 34.5 × 31.1 × 7.6 mm. The h/l ratio is about 0.90 while the same ratio for *Astarte crenata* is closer to 0.80 or even lower (cf. Ockelmann, 1958). Gladenkov et al. (1980) reported height/length ratios for seven valves from the Tjörnes beds as 0.90–0.92. The five figured specimens from the Netherlands Heering (1950) have almost the same ratios or 0.87–0.90.

Pouwer (2010) pointed out that the specimens shown by Gladenkov et al. (1980) are too triangular in form and have more pronounced ribs on the ventral side of the valve to be identified as *A. basterotii*. Furthermore, he considered the species to be restricted to the North Sea Basin. We agree with him that the specimen figured by Gladenkov et al. in Pl. 4, fig. 10 is somewhat doubtful, but hardly those in figs. 11 and 12. Having studied the variation in shell form and ornamentation of the *Astarte* and *Tridonta* species now living in Iceland we are tempted to consider the characteristic features Pouwer mentioned within the variation of *A. basterotii* (cf. Heering, 1950). Therefore, until further evidence is available, we will use that name although with reservation. There are several recent molluscan species in the Tjörnes beds that are not living in Iceland today but commonly found fossil, as well as recent in the North Sea Basin area.

Pouwer (2010) also pointed out that *A. basterotii* is a *Laevastarte* species, a genus characterized by the disappearance of the ribs toward the ventral margin. However, WoRMS (World Register of Marine Species – Bivalvia) is very conservative in the subdivision of Astartidae, and *Laevastarte,* as well as *Tridonta* are not recognized as valid genera. We do not agree with that, especially not when dealing with *Tridonta* where we follow the names in Treatise on Invertebrate Paleontology (Moore, 1969a).

*Distribution and ecology:* The distribution of the extinct *Astarte basterotii* in Pliocene sediments indicates strongly that it preferred conditions as prevailing in the boreal region today. Further support is the presence of several recent boreal species occurring together with *A. basterotii* in the *Serripes* Zone of Tjörnes. It was probably a suspension feeder as *Tridonta elliptica*, mainly living on a bottom of silt and sand. It probably lived offshore in mesohaline water. The larval development is unknown.

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Wood, 1853), Vreeburg-Utrecht Well and Goes Well in the Netherlands (Heering, 1950), Luchtbal Sand Member (Pouwer, 2010). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1853). Stratigraphical range: Pliocene to Lower Pleistocene.

***Astarte galeotti* Nyst, 1835**
Plate 7.12. Fig. 5

1835 *Astarte Galeotti* – Nyst: p. 8, Pl. 1, fig. 30.
1853 *Astarte gracilis,* Münster – Wood: p. 185–186, Pl. 17, fig. 3a–e.
1924 *Astarte incerta* Wood=*Astarte galeottii* Nyst – Schlesch, p. 319 (from an unpublished manuscript of Poulsen, 1884).
1925 ?*Astarte incerta*, Wood – Bárðarson: p. 53, 70.
1950 *Astarte galeotti* Nyst, 1835 – Heering: p. 62–63, Pl. 5, figs. 11–12, 16–17 & 19, Pl. 6, fig. 6.
1975 ?*Astarte* aff. *incerta* Wood – Norton: p. 110.

*Material:* One right valve from unit 14 and one left valve from unit 15 in the *Serripes* Zone. Schlesch (1924) mentioned four valves from Poulsen's manuscript (1884).

*Remarks:* The right valve has a slightly damaged but crenulated shell margin and measures (l × h × b): 14.3 × 13.3 × 3.5 mm. The left valve is slightly larger and measures: 16.7 × 15.0 × 5.0 mm. Bárðarson (1925) recorded two valves of *Astarte incerta* Wood, 1853 from unit 18 in the *Serripes* Zone, and most probably they should be referred to *A. galeotti.* The same was probably the case when Norton (1975) mentioned *A.* aff. *incerta* Wood, without further stratigraphical information or how many valves (or specimens) he found.

*Distribution and ecology: Astarte galeotti* is extinct, but was mainly a boreal species as indicated by the fact that several recent boreal species have been found together with *A. galeotti* in the Tjörnes sediments. The distribution in Cainozoic sediments is a further support. It seems to have lived offshore on a rather sandy bottom.

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Wood, 1853), Diemerbrug Well, Vreeburg-Utrecht Well, Gorkum Well, and Goes well in the Netherlands (Heering, 1950), Kallo and Doel sections (Marquet, 2002). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1853). Stratigraphical range: Pliocene to Lower Pleistocene.

### Genus *Tridonta* Schumacher, 1817

#### *Tridonta borealis* Schumacher, 1817

Plate 7.12. Fig. 6

1817 *Tridonta borealis* – Schumacher: p. 147, Pl. 17, fig. 1.
1853 *Astarte borealis,* Chemnitz – Wood: p. 175–177, Pl. 16, fig. 3a–b.
1878 *Tridonta borealis,* Chemn. – Sars: p. 50, Pl. 5, fig. 8.
1924 *Tridonta borealis* (Chemnitz) = *T. semisulcata* Leach – Schlesch: p. 320 (from an unpublished manuscript of Poulsen 1884.
1925 *Astarte* (*borealis*, Chemn.?) – Bárðarson: p. 53, 70.
1934 *Astárte (Tridónta) boreális* (Chemnitz) – Jensen & Spärck: p. 83–84, fig. 63.
1950 ?*Astarte semisulcata* (Leach 1819) – Heering: p. 76–77, Pl. 2, figs. 3–8.
1958 *Astarte borealis* (Chemnitz) – Ockelmann: p. 74–79.
1980 *Tridonta borealis* (Schumacher), 1817 – Gladenkov et al.: p. 40, Pl. 4, figs. 24–27.

*Material:* Four specimens with united valves and 26 single valves from units 17–19 in the *Serripes* Zone. Schlesch (1924) only mentioned one fragment from Poulsen's manuscript (1884).

*Remarks:* The largest valve measures (l × h): 38.1 × 26.9 mm. The h/l ratios range between 0.72–0.87 which is slightly higher than the ratios 0.69–0.76 found for the largest valves in the Kap København Formation (see Símonarson et al., 1998). We will use the name *T. borealis* in this publication. The section *Tridonta* of Schumacher, 1817, with the type *T. borealis* is like *Astarte*, but the inner margins are always smooth (Petersen, 2001). The valves of *T. borealis* are rather thick and strong and generally well preserved in the Tjörnes sediments. The high number of disarticulated valves indicates post-mortal transport and somewhat reworked material.

Petersen (2001) described and redescribed some species of Arctic and Baltic Astartidae and gave name to several new species, and he came to the conclusion that the *Tridonta borealis* complex in Iceland contains at least two species, viz. *T. borealis* and *T. jenseni* sp. nov. The latter was regarded more triangular in shape than the former and having larger muscle scars. Minor differences were also seen in the hinges. Petersen (2001) recorded 22 samples from 12 to 30 m depth off southwestern Iceland. There is a considerable variation within the species of Astartidae, and we are not convinced that the stated differences between *T. borealis* and *T. jenseni* are consistent to that degree that species separation is possible.

*Recent distribution, ecology, and biology: Tridonta borealis* is widespread in the arctic, subarctic, and the boreal regions of the North Atlantic. It is distributed from

Franz Josef Land, Novaya Zemlya, the Kara Sea, the Siberian Arctic Sea, the Beaufort Sea, the Bering Strait, Parry Islands, and Ellesmere Island southward to the Baltic, Massachusetts, the Gulf of Alaska, and northern Japan (Ockelmann, 1958). It is very common in Iceland, but not known living from the Faroe Islands or the British Isles (Madsen, 1949; Sneli et al., 2005). In Norway it has been found to Bergen in the south, and the occurrence in the Baltic seems therefore isolated and may be a relic from colder times (Jensen & Spärck, 1934; Madsen, 1949). Bathymetrical range: from 0 m in East Finnmark to 463 m north of Svalbard, but empty shells have been found in the North Atlantic down to a depth of 2710 m (Ockelmann, 1958). In North Greenland it was common in Jørgen Brønlunds Fjord at depths between 6 and 16 m (Schiøtte, 1989). The salinity tolerance of the species goes down to about 5‰ (Funder et al., 2002). This explains how frequently it has been found in the Baltic. The larval development is with a very short or lacking pelagic stage (Thorson, 1936).

*Tridonta borealis* is a suspension feeder living on a bottom varying from mud to rocks in the Arctic *Macoma* community, the *Gomphina fluctuosa* community or even the *Astarte crenata* community in East Greenland (Ockelmann, 1958; Thorson, 1933, 1934). In Iceland, where it also belongs to the infauna, it has been recorded on a bottom of clay, sand, gravel, shells, or mixed substrates (Madsen, 1949).

*Fossil occurrence:* Pliocene: *Serripes* Zone of the Tjörnes beds (Gladenkov et al., 1980). Lower Pleistocene: Maassluis Formation (Heering, 1950), Norwich Crag Formation (Funnell et al., 1979), Pattorfik beds (Símonarson, 1981b), Lodin Elv Formation, East Greenland (Feyling-Hanssen et al., 1983), Olkov and Tusatuva-Yamsk Suites (Petrov, 1982, 1986), Gubik Formation, Fishcreekian (Repenning et al., 1987). Middle Pleistocene: Pinakul, Kresta, Karagin, Kolvin, and Padymeiskii Suites (Merklin et al., 1962, 1979; Petrov, 1982), Kotzebuan (Hopkins et al., 1972), Anvilian (Hopkins et al., 1974). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

The occurrence of *Tridonta borealis* in the *Serripes* Zone of the Tjörnes beds is among the oldest, if not the oldest. The species is considered to have originated in the Atlantic as most of the Astartidae (Bernard, 1979; Durham & MacNeil, 1967). The records from the northern Pacific, especially the Fishcreekian, may indicate an early migration into the North Pacific (Símonarson et al., 1998).

***Tridonta montagui* (Dillwyn, 1817)**
Plate 7.12. Fig. 7

1817 *Venus montagui* – Dillwyn: p. 167.
1853 *Astarte compressa*, Montague – Wood: p. 183–184, Pl. 16, fig. 8a–c.
1878 *Nicania Banksii*, Leach – Sars: p. 51–52, Pl. 6, fig. 1a–b.
1924 *Nicania banksi* (Leach) = *N. montagui* Dillwyn = *N. compressa* Montagu – Schlesch: p. 319.
1950 *Astarte montagui* (Dillwyn, 1817) – Heering: p. 77–79, Pl. 2, figs. 9–10, Pl. 6, figs. 19–20.
1958 *Astarte montagui* (Dillwyn) – Ockelmann: p. 80–85.
1980 *Astarte montagui* (Dillwyn, 1817) – Gladenkov et al.: p. 37–38, Pl. 4, figs. 18–23.

*Material:* Three specimens with paired valves and 29 single valves from units 14–23 in the *Serripes* Zone.

*Remarks:* The largest valve measures (l × h × b): 18.1 × 16.5 × 2.6 mm. The h/l ratios were calculated for nine valves from the *Serripes* Zone and compared to the ratios for the six largest specimens found in the Kap København Formation in North Greenland. While the ratios from the *Serripes* Zone are 0.84–0.93, or 0.91 on the average, the ratios from the Kap København Formation are 0.74–0.97 and 0.89 on the average. Therefore, the specimens from Tjörnes, as well as those from the Kap København Formation, are referred to the typical form and not the subspecies *striata* (Leach, 1819) or *warhami* (Hancock, 1846) in accordance with Ockelmann (1958).

*Recent distribution, ecology, and biology: Tridonta montagui* is a circumpolar species distributed in the arctic, subarctic, and boreal regions of the North Atlantic. It occurs from Franz Josef Land, Novaya Zemlya, the Kara Sea, the Siberian Arctic Sea, the Beaufort Sea, and Ellesmere Island southward to the British Isles, Denmark, the western Baltic, Massachusetts, the Aleutians, and northern Japan (Bernard, 1979; Ockelmann, 1958). Bathymetrical range: The species prefers shoreface areas and has been found from 0 m in the western Baltic (Ockelmann, 1958) to 455 m in the Beaufort Sea (Bernard, 1979). In North Greenland it is rather common in the Jørgen Brønlund Fjord at depths between 6 and 16 m (Schiøtte, 1989). It is a marine species with a salinity tolerance down to 15‰ (Funder et al., 2002). The larval development includes either a very short pelagic stage or it is entirely lacking (Thorson, 1936).

The species is a suspension feeder, and in East Greenland it lives on a bottom varying from mud to gravel and rocks in the Arctic *Macoma* community, as well as in the *Gomphina fluctuosa* and *Astarte crenata* communities (Ockelmann, 1958; Thorson, 1933, 1934).

*Fossil occurrence:* Pliocene: *Serripes* Zone of the Tjörnes beds (Gladenkov et al., 1980). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1853), Tugidak Formation (Allison, 1978). Lower Pleistocene: Maassluis Formation (Heering, 1950), Yakataga Formation (Allison, 1978), Norwich Crag Formation (Funnell et al., 1979), Norwch Crag Formation (West et al., 1980), Pattorfik beds (Símonarson, 1981b), Olkov and Tusatuva-Yamsk Suites (Petrov, 1982), Middle Pleistocene: Pinakul, Kresta, Karagin, Kolvin, and Padymeiskii Suites (Merklin et al., 1962, 1979; Petrov, 1982), Kotzebuan (Hopkins et al., 1972). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

The specimens of *Tridonta montagui* in the *Serripes* Zone on Tjörnes are therefore among the oldest occurrences of the species.

***Tridonta* cf. *elliptica* (Brown, 1827)**
Plate 7.12. Fig. 8

1827 *Crassina elliptica* – Brown: Pl. 18, fig. 3.
1853 *Astarte elliptica,* Brown – Wood: p. 181–182, Pl. 16, fig. 7.
1878 *Astarte compressa*, Lin. – Sars: p. 53–54.
1924 ?*Astarte compressa* (Linné) – Schlesch: p. 319.

1950 *Astarte sulcata* (da Costa) var. *elliptica* (Brown, 1827) – Heering: p. 71–72, Pl. 4, figs. 11–13, Pl. 5, fig. 1.
1958 *Astarte elliptica* (Brown) – Ockelmann: p. 86–89.
1980 *Tridonta* cf. *elliptica* (Brown, 1827) – Gladenkov et al.: p. 41, Pl. 12, fig. 26.
1980 ?*Astarte* aff. *sulcata* (da Costa, 1778) – Gladenkov et al.: p. 39–40, Pl. 4, figs. 13–17a.

*Material:* Two single valves from units 14–15, and ?11 valves from units 16–23 in the *Serripes* Zone (cf. Gladenkov et al., 1980).

*Remarks:* The two valves from units 14 and 15 measure (l × h × b): 18.4 × 17.2 × 3.9 and 18.2 × 15.9 × 3.8 mm. The h/l ratios are rather high 0.87 and 0.93, respectively. Gladenkov et al. (1980) found similar ratios of 0.84–0.91 for *Astarte sulcata* from the *Serripes* Zone, while Símonarson (1981a, 1981b) reported ratios between 0.75 and 0.88 for the 10 largest specimens of *A. elliptica* with paired valves from the Pattorfik beds in West Greenland.

All seven valves referred to *A. sulcata* by Gladenkov et al. (1980) from the *Serripes* Zone lack the crenulated inner shell margin. Several authors have stressed that *A. sulcata* has “almost always” crenulated shell margin, but specimens without crenulation can certainly be found. A sample from a depth of 242 m off Southwest Iceland (Reykjanes Ridge) contained 30 disarticulated valves of *A. sulcata,* all with crenulated shell margin except four of them. Why is not a single valve from the *Serripes* Zone with this crenulation if it is the more common type? Are we perhaps here dealing with two closely connected species with and without crenulation? Further studies might reveal that.

*Astarte sulcata* lives offshore, and in Iceland it has exclusively been found living at greater depths than 104 m (Madsen, 1949; Óskarsson, 1952). In the Faroe Islands its bathymetrical range is 100–803 m (Sneli et al., 2005), and almost everywhere it seems to prefer much deeper water than prevailing in the Tjörnes area when the *Serripes* Zone was deposited. Considering these facts and having no further evidence we can hardly agree with Gladenkov et al. (1980) that these valves from the *Serripes* Zone belong to *A. sulcata*. They are referred to *A.* cf. *elliptica* in this publication.

*Recent distribution, ecology, and biology: Tridonta elliptica* is distributed in the arctic to lower/mid boreal regions of the North Atlantic. It extends from Franz Josef Land, Svalbard, Novaya Zemlya, the Kara Sea, the Smith Sund, and Baffin Bay southward to the British Isles and Massachusetts Bay (Lubinsky, 1980; Ockelmann, 1958; Sneli et al., 2005). It is known from Kattegat and Øresund and the western Baltic southward to Bornholm (Jensen & Spärck, 1934; Sneli et al., 2005). It is very common all around Iceland (Madsen, 1949; Óskarsson, 1952). Bathymetrical range: The species lives offshore from 2 m in East Greenland to 442 m in West Greenland (Ockelmann, 1958). It is a marine species with salinity tolerance down to about 15‰ (Funder et al., 2002). The pelagic larval stage is very short or lacking (Thorson, 1936).

In East Greenland *T. elliptica* belongs to the infaunal Arctic *Macoma* community where it lives as suspension feeder on a substratum of mud, silt, and sand

(Ockelmann, 1958). In Iceland it is also common on a bottom of mixed substrates (Madsen, 1949).

*Fossil occurrence:* Pliocene: *Serripes* Zone of the Tjörnes beds (this volume). Pliocene/Lower Pleistocene: Tugidak Formation (Allison, 1978). Lower Pleistocene: Norwich Crag Formation (Funnell et al., 1979), Pattorfik beds (Símonarson, 1981b), Yakataga Formation, Middelton Island (Allison, 1978). Middle Pleistocene: Kolvin and Padymeiskii Suites (Merklin et al., 1979; Petrov, 1982), Pre-Cape Christian beds (Andrews et al., 1981). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Holocene.

*Tridonta elliptica* has been reported from Pliocene deposits in the Netherlands, Belgium, Italy, and ?France by Heering (1950) as *Astarte sulcata* var. *elliptica.* This was contested by Glibert (1957) who referred these specimens to the extinct *A. basterotii,* also found in the *Serripes* Zone. Closely related species *A. alaskensis* Dall, 1903 has been found in the Lower Pleistocene Tusatuva-Yamsk Suit in the Bering Sea region (Petrov, 1982). The occurrence in the *Serripes* Zone is therefore among the earliest, if not the oldest. Apparently, *A. elliptica* originated in the Atlantic and migrated to the North Pacific close to the boundary between the Pliocene and the Pleistocene (Durham & MacNeil, 1967).

### Family Arcticidae Newton, 1891
### Genus *Arctica* Schumacher, 1817

#### *Arctica islandica* (Linné, 1767)

Plate 7.13. Figs. 1–3

1767 *Venus islandica* – Linné: p. 1131.
1853 *Cyprina Islandica.* Linn. – Wood: p. 196–197, Pl. 18, fig. 2a–e.
1863 *Cyprina islandica* Linn. – Winkler: p. 200–201.
1878 *Cyprina islandica*, Lin. – Sars: p. 50.
1924 *Cyprina islandica* (Linné) – Schlesch: p. 320.
1924 *Cyprina islandica pumilis* Wood – Schlesch: p. 320, Pl. 5, fig. 7.
1934 *Cyprína isländica* (L.) – Jensen & Spärck: p. 111–113, fig. 94.
1950 *Cyprina islandica* (Linné, 1767) – Heering: p. 91–93, Pl. 11, figs. 23–26.
1960 *Cyprina islandica* Linné – Áskelsson: p. 17, Pl. 1, fig. 6.
1980 *Arctica islandica* (Linné, 1767) – Gladenkov et al.: p. 52, Pl. 6, figs. 1–10.

*Material:* Several thousands of specimens in almost all shell-bearing units of the three biozones. It is among the few species found in the oldest, as well as youngest part of the Tjörnes sequence, but it is especially abundant in the *Mactra* Zone. Only very few paired specimens were found.

*Remarks:* The specimens from the *Tapes* Zone and the lower part of the *Mactra* Zone are generally badly preserved due to extensive dissolution or recrystallization of the aragonite shell, especially in sediments close to the lignite layers. These specimens are generally preserved as internal or external casts. Most of them were paired, which indicates a low degree of reworking or pre-burial transport. In the upper part of the *Mactra* Zone, as well as in the *Serripes* Zone, the valves are generally disarticulated and damaged, and here and there they form shell beds of variable thickness. These beds are formed by accumulation and transport of rather fragmented shell material by currents that removed the sediment grains but left the heavier shells and shell fragments to accumulate on the bottom (see Eiríksson et al., 2020a: fig. 5.8). Occasionally, the inner cavity is more or less filled up with calcite crystals (sugar stone), mainly in specimens from the *Mactra* Zone (see Eiríksson et al., 2020a: fig. 5.12).

A number of juvenile and half-grown specimens of *A. islandica* have been found, whereas the largest one measured 82.0 mm in length and 64.1 mm in height. The species is one of the most common bivalve in Iceland and has been found along all the coasts. The largest recent Icelandic specimens are about 120 mm in length and as they are rather convex the shell cavity contains considerable entrails. Up to last century, Icelandic fishermen used it as bait and left here and there considerable heaps of empty shells along the coast in some places still visible today. It was also popular in children games where it almost always symbolized the cow, as strongly indicated by the literal meaning of the old Icelandic name “cow shell.”

Annual growth increments of living specimen of *Arctica islandica,* found close to the North Atlantic Polar Front, were used to construct multicentennial and absolutely dated chronology for the marine environment of the North Icelandic shelf. The maximum age was determined as 507 years, hence the animal seems to be the longest-lived solitary animal known so far (Wanamaker et al., 2012). Remarkable longevities have been found in several specimens of the species.

*Recent distribution, ecology, and biology: Arctica islandica* ranges from subarctic to lusitanian regions of the North Atlantic (Fig. 7.17). It is amphiatlantic extending from Newfoundland, the southeastern Barents Sea and the Spitsbergen Bank in the north to North Carolina and the Gulf of Cádiz in the south (Funder & Weidick, 1991; Madsen, 1949; Zenkevitsch, 1963). The warm North Atlantic Current seems to control its occurrence on the Spitsbergen Bank and in the Barents Sea; the species inhabits areas with summer temperatures above 6 °C (Funder & Weidick, 1991; Zenkevitsch, 1963). The species is absent from Greenland waters today, but has lived in West Greenland during milder Holocene time from c. 7500 to slightly after 5000 BP (Funder, 1989; Kelly, 1986). Bathymetrical range: from 0 m in the British Isles (Tebble, 1966) to 2000 m west of Ireland (Madsen, 1949). It prefers foreshore areas, and in Iceland it is most abundant at depths between 10 and 90 m (Eiríksson, 1988). It is a marine species with salinity tolerance down to about 5‰ (Funder et al., 2002). The planktotrophic larvae have a rather long pelagic stage of great significance for its distribution (Jørgensen, 1946).

In the British Isles the species lives on a rather firm bottom of sand and muddy sand from the lower parts of the intertidal zone to considerable depths (Tebble, 1966). In Iceland it lives mainly on a sandy bottom from a depth of 3–5 m to about 100 m within the *Spisula elliptica* community (Madsen, 1949; Spärck, 1937). In Iceland this suspension feeder also prefers depths just below the low water mark, in the winter it burrows shallow in the bottom, but in the summer it is lying in abundance on the surface of the bottom (Eiríksson, 1988; Madsen, 1949).

*Fossil occurrence:* ?Oligocene: Borszony in Hungary (Malatesta & Zarlenga, 1986). Miocene: Lenham beds (Harmer, 1900), Edegem, Kiel, Atwerpen, Zonderschot, and Breda Formation (Herman & Marquet, 2007). Miocene/Pliocene:

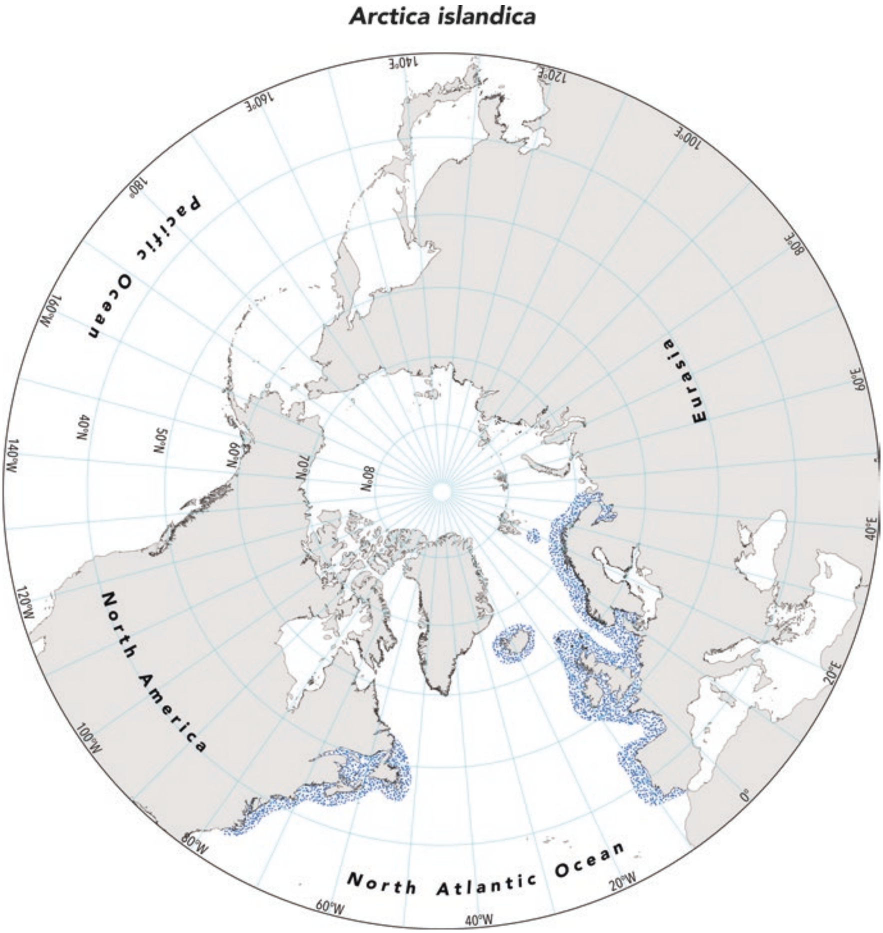

**Fig. 7.17** The recent known geographical distribution of *Arctica islandica* (Linné)

*Acroperna sericea* and *Chlamys tigerinus* Zone of the Netherlands (Spaink, 1975). Pliocene: Coralline Crag Formation (Herman & Marquet, 2007; Wood, 1853), Kallo and Doel sections (Marquet, 2002). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1853). Lower Pleistocene: Ludhamnian (Norton, 1967), *Serripes groenlandicus* and *Yoldia lanceolata* Zone of the Netherlands (Spaink, 1975), Yagataga Formation on Middelton Island (Allison, 1978), Baventian (West et al., 1980), Santernian, Emilian, and Sicilian (Malatesta & Zarlenga, 1986), Kap København Formation (Símonarson et al., 1998), Île de France Formation (Bennike et al., 2002). Middle Pleistocene: Kolvin and Padymeiskii Suites (Merklin et al., 1979; Petrov, 1982). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: ?Oligocene to Recent.

*Arctica islandica* is considered to have originated in the Atlantic, possibly during the Oligocene. At the transition from the Pliocene to the Pleistocene, the species was distributed in the North Atlantic from Northeast Greenland in the north and southward to the Mediterranean. Obviously, it never became as widespread again and even did not reach former southward propagation.

### Genus *Pygocardia* Fischer, 1887

**Pygocardia rustica* (Sowerby, 1818)**
Plate 7.13. Fig. 4

1818 *Venus rustica* – Sowerby: p. 217, Pl. 196.
1853 *Cyprina rustica*, J. Sowerby – Wood: p. 197–198, Pl. 18, fig. 1a–c.
1863 *Cyprina rustica* Sow. – Winkler: p. 201–202.
1924 *Cyprina rustica gaimardi* (E. Robert) – Schlesch: p. 320, Pl. 5, fig. 6.
1950 *Cyprina rustica* (J. Sowerby, 1818) – Heering: p. 94–95, Pl. 11, figs. 19–22 (*Cyprina rustica* (J. Sowerby, 1818) var. *defranchii* van Beneden 1835).
1960 Cf. *Cyprina rustica* J. Sowerby – Áskelsson: p. 17–18, Pl. 1, fig. 7, Pl. 2, figs. 8–9.
1980 *Pygocardia rustica* (Sowerby, 1818) – Gladenkov et al.: p. 51, Pl. 5, figs. 7–11.

*Material:* About 120 specimens with paired valves and 220 single valves from units 11–12 in the *Mactra* Zone and units 14–23 and ?25 in the *Serripes* Zone.

*Remarks:* The largest valve measures (l × h × b): 69.1 × 49.7 × 22.8 mm. Several valves are articulated, and even though most of the specimens are reworked they have not been subject to heavy post-mortal transport as indicated by the many unbroken thin valves.

Schlesch (1924) reported the typical form of *Pygocardia rustica* from the *Serripes* Zone and also three subspecies: *Cyprina rustica gaimardi* (E. Robert), *C. rustica tumida* Nyst, and *C. rustica elongata* Wood. However, Gladenkov et al. (1980) did not mention any other form than the typical one, and we prefer to follow them because we are not convinced of the differences.

*Distribution and ecology:* The distribution of the extinct *Pygocardia rustica* in Pliocene and Lower Pleistocene sediments indicates that it preferred conditions as found today in the boreal region of the North Atlantic. Further support is the presence of several recent boreal species occurring together with *P. rustica* in Cainozoic sediments in Iceland and the British Isles, as well as in continental sites. It probably lived offshore in marine water on a rather firm substrate of sand and muddy sand from the lower parts of the intertidal zone to considerable depths just like *Arctica islandica* today. It occurs frequently together with that species in Cainozoic sediments, and it is tempting to conclude that it lived in a similar way.

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Wood, 1853), Kattendijk and Lillo Formations (Marquet, 2002). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1853). Stratigraphical range: Pliocene to Lower Pleistocene.

*Pygocardia rustica* is probably of Atlantic origin as it seems unknown in Pacific areas.

### Family Carditidae Lamarck, 1809

### Genus *Cyclocardia* Conrad, 1867

***Cyclocardia chamaeformis*** **(Sowerby, 1825)**
Plate 7.13. Fig. 5

1825 *Venericardia chamaeformis* – Sowerby: p. 145, Pl. 490, fig. 1.
1853 *Cardita chamœformis,* Leathes'MSS – Wood: p. 167–168, Pl. 15, fig. 3a–b.
1924 ?*Venericardia borealis* (Conrad) = *V. scalaris* Leathes? – Schlesch: p. 320, Pl. 5, fig. 3.
1924 *Venericardia chamaeformis* (Leathes) – Schlesch: p. 320, Pl. 5, fig. 5.
1925 ?*Venericardia borealis*, Conrad – Bárðarson: p. 54, 56, 59, 70.
1950 *Cardita chamaeformis* (Leathes M.S., J. Sowerby, 1825) – Heering: p. 86–87, Pl. 13, figs. 5–6, 10–11 & 15–16.
1980 ?*Venericardia* aff. *scalaris* (Sowerby, 1825). – Gladenkov et al.: p. 37, Pl. 5, figs. 5–6.
1980 ?*Venericardia borealis* (Conrad, 1831) – Gladenkov et al.: p. 36–37, Pl. 5, figs. 1–4.

*Material:* Seventeen disarticulated valves from units 18–23 in the *Serripes* Zone. Furthermore, Schlesch (1924) mentioned ?two specimens from the lowermost part of the *Serripes* Zone.

*Remarks:* The largest valve measures (l × h): 19.0 × 19.1 mm. The h/l ratios are close to 1.0 or varying from 0.92 to 1.08. The rather thick valves are generally well preserved, and even though they are reworked in the sediments they are not crushed.

Schlesch (1924) reported *Venericardia borealis* (Conrad, 1831) from the *Serripes* Zone and considered it as identical with *V. scalaris*. Bárðarson (1925) also recorded *V. borealis* from the zone as did Gladenkov et al. (1980). We are not convinced that *Cyclocardia borealis* (*Venericardia borealis*) and *C. scalaris* are identical. *C. borealis* has been recorded living in the North Atlantic, but seems restricted to the east coast of North America from Hudson Strait in the north and south to Cape Hatteras (La Rocque, 1953). It apparently prefers rather cold water. If the specimens of *C. borealis* from Tjörnes are correctly identified (cf. Gladenkov et al., 1980), they are probably the only occurrence in North Atlantic sediments east of Greenland. However, it should be borne in mind that Wood (1874) mentioned a shell, *Cardita borealis* ?Conrad, from the Upper Glacial sediments at Bridlington, but "with a doubt, as I am not altogether satisfied on the point." Therefore, we are not convinced that *Cyclocardia borealis* (*V. borealis*) has been found in the Tjörnes sediments or ever lived in the eastern parts of the North Atlantic.

*Cyclocardia chamaeformis* has a lower number of ribs than *C. scalaris,* or 14–16, and wider space between them.

*Distribution and ecology: Cyclocardia chamaeformis* is extinct, but seems to have preferred conditions similar to those in the boreal region in the North Atlantic today. Several recent boreal species have been found together with it in the Tjörnes sediments, and the species was probably considerably more thermophilic than the recent *C. borealis. C. corbis* (Philippi) and *C. senilis* (Lamarck) are obviously part of the recent mollusc fauna in the Mediterranean (Heering, 1950). Apparently, the species lived offshore near the coasts on a sandy bottom.

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Heering, 1950; Wood, 1853), Kallo and Doel sections (Marquet, 2002). Pliocene/Lower Pleistocene: Red Crag Formation (Heering, 1950; Wood, 1853). Lower Pleistocene: Icenian, Chillesford bed (Wood, 1874). Stratigraphical range: Pliocene to Lower Pleistocene.

### Family Cardiidae Lamarck, 1809

### Genus *Parvicardium* Monterosato, 1884

**Parvicardium pinnulatum** **(Conrad, 1831)**
Plate 7.13. Fig. 6

1831 *Cardium pinnulatum* – Conrad: p. 260, Pl. 11, fig. 8.
1853 *Cardium nodosum*, Montague – Wood: p. 153, Pl. 13, fig. 4a–c.
1874 *Cardium pinnatulum*, Conrad – Wood: p. 134.
1874 *Cardium fasciatum*, Mont. – Wood: p. 133.
1934 *Cárdium fasciátum* Montagu – Jensen & Spärck: p. 106–107, fig. 87.
1950 *Cardium fasciatum* Montagu 1808 – Heering: p. 114–115, Pl. 11, figs. 5–6.
1980 *Parvicardium ovale* (Sowerby, 1840) – Gladenkov et al.: p. 41–42, Pl. 7, fig. 10.

*Material:* Six valves from units 13–14 in the lower part of the *Serripes* Zone.

*Remarks:* The valves are fairly well preserved and only few of them are damaged. The largest valve measures (l × h): 6.5 × 6.5 mm (cf. Gladenkov et al., 1980), and the h/l ratio is close to 1.0 for all the found valves.

The equilateral valve has generally 26 ribs with cusp-like spines and very narrow intercostal space (Jensen & Spärck, 1934).

*Recent distribution, ecology, and biology: Parvicardium pinnulatum* is widely distributed in the boreal region of the North Atlantic and extends well into the lusitanian region. From the White Sea, northern Iceland, and Labrador in the north it extends southward to Morocco, Canary Islands, and North Carolina (Sneli et al., 2005; Tebble, 1966). It goes into the Baltic south to Øresund and is well known in the Mediterranean (Sneli et al., 2005). Bathymetrical range: 4–350 m (Sneli et al., 2005). It lives offshore around the British Isles at depths from about 4 m down to 110 m (Tebble, 1966). In the Faroe Islands it is very common in fiords from shallow depths water to a depth of more than 200 m (Petersen, 1968). It is a marine species with salinity tolerance down to about 15‰ (Funder et al., 2002). The larval development is not known.

In the British Isles it prefers bottom of muddy sand and gravel, and in the Faroe Islands it is commonly found on shelly sand as well (Sneli et al., 2005; Tebble, 1966). In North Iceland (Eyjafjörður) it belongs to the infaunal Arctic *Macoma* community on a muddy bottom (Spärck, 1937).

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Wood, 1874). Pliocene/Pleistocene: Red Crag Formation (Wood, 1874). Lower Pleistocene: Icenian, Chillesford bed (Wood, 1874). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

### Genus *Acanthocardia* Gray, 1851

**_Acanthocardia echinata_ (Linné, 1758)**
Plate 7.14. Fig. 1

1758 *Cardium echinatum* – Linné: p. 679.
1853 *Cardium echinatum,* Linnæus – Wood: p. 152, Pl. 14, fig. 3a–b.
1863 *Cardium echinatum* Linn. – Winkler: p. 202.
1878 *Cardium echinatum*, Lin. – Sars: p. 46.
1924 ?*Cardium echinatum* (Linné)? – Schlesch: p. 322.
1925 Cardium echinatum L. – Bárðarson: p. 22, 26, 35, 39, 41, 44, 46, 49, 76–77.
1934 *Cárdium echinátum* L. – Jensen & Spärck: p. 104, fig. 83.
1950 *Cardium echinatum* Linné, 1758 – Heering: p. 117–118, Pl. 10, figs. 23–26.
1980 *Acanthocardia echinata* (Linné), 1767 – Gladenkov et al.: p. 42–43, Pl. 7, figs. 5–9.

*Material:* Almost 100 valves from the three biozones, from unit 1 in the oldest *Tapes* Zone to unit 14 in the lowermost part of the *Serripes* Zone. Generally, the valves are disarticulated, but paired specimens occur especially in the *Tapes* Zone.

*Remarks:* The largest valve measures (l × h): 70.0 × 63.6 mm, but there are many juvenile specimens, especially in the lower part of the *Tapes* Zone. The valves are rather badly preserved in the *Tapes* Zone and the lower part of the *Mactra* Zone and mostly preserved as internal or external casts as the shell material is dissolved, especially in sediments close to the lignite layers. They are much better preserved in the upper part of the *Mactra* Zone and in the lower part of the *Serripes* Zone. The specimens from the upper part of the *Mactra* Zone and the *Serripes* Zone seem more reworked than the specimens from the older beds where paired valves are more frequently found.

*Recent distribution, ecology, and biology: Acanthocardia echinata* is widely distributed in the boreal and lusitanian regions in the North Atlantic. From West Iceland and western Finnmark in North Norway it extends southward to Morocco and the Canary Islands (Madsen, 1949; Sneli et al., 2005). It is well known from the Mediterranean (Tebble, 1966) and living in the Baltic south to Øresund (Sneli et al., 2005). In Iceland it seems confined to the south and west coasts, and only empty valves have been found on the northwest coast (Madsen, 1949; Óskarsson, 1952). Bathymetrical range: from 4 m in the British Isles to a depth of about 350 m (Sneli et al., 2005; Tebble, 1966). In the Faroe Islands it has been found at depths between 21 and 283 m (Sneli et al., 2005). *A. echinata* is a marine species with salinity tolerance down to 15‰ (Funder et al., 2002). The larval development is with a pelagic stage (Jørgensen, 1946).

In the British Isles it prefers bottom of mud, muddy sand, fine sand, and gravel (Tebble, 1966). Also in Iceland it is mainly found on sandy or muddy substrates within the infaunal Arctic *Macoma* community (Madsen, 1949; Spärck, 1937). The species is most probably a suspension feeder.

*Fossil occurrence:* ?Upper Miocene: *Tapes* Zone of the Tjörnes beds (this volume). Pliocene: Gorkum Well in the Netherlands (Heering, 1950). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1853). Lower Pleistocene: Emilian and

Sicilian (Malatesta & Zarlenga, 1986). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: ?Upper Miocene to Recent.

**Genus *Ciliatocardium* Kafanov, 1974**

***Ciliatocardium ciliatum* (Fabricius, 1780)**
Plate 7.14. Fig. 2

1780 *Cardium ciliatum* – Fabricius: p. 410.
1878 *Cardium ciliatum*, Fabr. – Sars: p. 46, Pl. 5, fig. 4a–b.
1924 *Cardium (Cerastoderma) ciliatum* (Fabricius) = *C. islandicum* Chemn. = *C. pubescens* Couthouy – Schlesch: p. 321, Pl. 5, fig. 9.
1925 *Cardium (ciliatum* Fabr.?) – Bárðarson: p. 39, 51, 74–75.
1958 *Cardium (Clinocardium) ciliatum* Fabricius – Ockelmann: p. 118–121.
1980 *Clinocardium ciliatum* (Fabricius, 1780) – Lubinsky: p. 38–39, Pl. 8, fig. 1.
1980 *Clinocardium ciliatum* (Fabricius, 1780*)* – Gladenkov et al.: p. 43, Pl. 8, figs. 1–3.

*Material:* Thirty-six valves mainly disarticulated from unit 13 to ?23 in the *Serripes* Zone.

*Remarks:* The largest valve measures (l × h × b): 42.1 × 38.8 × 13.1 mm.

The shell ratios h/l are 0.76–0.92 and the b/l ratios are 0.26–0.32. Generally, the thin valves are rather fragmented.

*Recent distribution, ecology, and biology: Ciliatocardium ciliatum* is probably circumpolar, living in the arctic and subarctic regions of the North Atlantic and Pacific and extends into the northern part of the boreal region. From Northeast Greenland, Svalbard, Franz Josef Land, the Barents Sea, Novaya Zemlya, the Kara Sea, and the Siberian Arctic Sea it is distributed southward to South Iceland, East Finnmark, and northern Japan (Ockelmann, 1958). In North America it is known from the Beaufort Sea, the Canadian Arctic Archipelago, and Baffin Bay south to Cape Cod and the Gulf of Alaska (Bernard, 1979; Lubinsky, 1980). Bathymetrical range: from 0 m in Iceland (Óskarsson, 1952) to 677 m in West Greenland (Ockelmann, 1958). In Iceland, where it attains largest size at the north and east coast, it is distributed all around the country at moderate depths (Madsen, 1949). The marine species has a lower salinity tolerance of about 15‰ (Funder et al., 2002). The larval development is with a very short or lacking pelagic stage (Thorson, 1936).

In Iceland *C. ciliatum* is mainly found on muddy bottom in the infaunal *Yoldia hyperborea* community in the fiords of East Iceland at depths between 45 and 160 m (Spärck, 1937). The species is a suspension feeder, and in East Greenland it prefers more clayey bottom than *Serripes groenlandicus* (Ockelmann, 1958).

*Fossil occurrence:* Pliocene: *Serripes* Zone of the Tjörnes beds (Gladenkov et al., 1980). Lower Pleistocene: Pattorfik beds (Símonarson, 1981b), Lodin Elv Formation (Feyling-Hanssen et al., 1983), Olkov and Tusatuva-Yamsk Suites (Petrov, 1982), Gubik Formation, Fishcreekian (Repenning et al., 1987). Middle Pleistocene: Pinakul, Kolvin, Kresta, Karagin, and Padymeiskii Suites (Merklin et al., 1962, 1979; Petrov, 1982), Kotzebuan (Hopkins et al., 1972), Pre-Cape

Christian beds (Andrews et al., 1981). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

The specimens of *Ciliatocardium ciliatum* in the *Serripes* Zone on Tjörnes are among the earliest of the species, if not the oldest. However, it is considered to have migrated from the Pacific into the North Atlantic while the sediments of the *Serripes* Zone were deposited (Durham & MacNeil, 1967).

### Genus *Serripes* Gould, 1841

#### *Serripes groenlandicus* (Mohr, 1786)

Plate 7.14. Figs. 3–4

1786 *Cardium Grönlandicum* – Mohr: p. 129.
1853 *Cardium Groenlandicum,* Chemnitz – Wood: p. 160–161, Pl. 13, fig. 1a–d.
1863 *Cardium groenlandicum* Chemnitz – Winkler: p. 202–203.
1878 *Aphrodite grønlandica,* Chemn. – Sars: p. 49, Pl. 5, fig. 3a–b.
1924 *Serripes groenlandica* (Chemnitz) Gmelin = *S. islandica* Fabricius – Schlesch: p. 322.
1925 *Cardium groenlandicum* Chemn. – Bárðarson: p. 47, 49, 51–52, 54, 56, 59, 64, 66.
1950 *Serripes groenlandicus* (Bruguière 1758) – Heering: p. 108–109, Pl. 11, figs. 13–16.
1958 *Serripes groenlandicus* (Bruguière) – Ockelmann: p. 113–118.
1980 *Serripes groenlandicus* (Bruguiere, 1789) – Gladenkov et al.: p. 44–45, Pl. 8, figs. 4–8.

*Material:* Several hundreds of valves in almost all units (13–25) of the *Serripes* Zone. *Serripes groenlandicus* is the index fossil for the zone and has given name to this biozone, as well as to different *Serripes* biozones in Britain and the Netherlands. Some of the valves are paired in the sediments, but most of them are disarticulated.

*Remarks:* The largest valve measures (l × h × b): 70.5 × 53.6 × 17.7 mm. The shell ratios h/l are 0.78–0.86 and the b/l ratios are 0.25–0.34. The species has thin valves and the material is rather fragmented and more or less reworked.

*Recent distribution, ecology, and biology:* Apparently, *Serripes groenlandicus* is circumpolar and well known in the arctic and subarctic regions of the North Atlantic and Pacific and extends into the northern part of the boreal region slightly farther to the south than *Ciliatocardium ciliatum*. It is widespread from Northeast Greenland, Svalbard, Franz Josef Land, the Barents Sea, Novaya Zemlya, the Kara Sea, and the Siberian Arctic Sea southward to South Iceland, Finnmark, and Japan (Ockelmann, 1958). In North America it is known from the Beaufort Sea, the Canadian Arctic Archipelago, and Baffin Bay south to Cape Cod and Oregon (Bernard, 1979; Lubinsky, 1980). Bathymetrical range: from 0 m in Iceland (Madsen, 1949) to 303 m in West Greenland (Ockelmann, 1958). In Iceland it is mainly found living in West, North and East Iceland at depths from 0 to about 120 m (Madsen, 1949). The species is marine with salinity tolerance down to about 15‰ (Funder et al., 2002). The larval development is supposed to be planktotrophic with a pelagic stage (Ockelmann, 1958; Thorson, 1936).

In Iceland this suspension feeder has been found on a bottom of mud, sand, and gravel in the infaunal Arctic *Macoma* community (Madsen, 1949; Spärck, 1937). In East Greenland it prefers more sandy and less clayey substrates than *Ciliatocardium ciliatum* (Ockelmann, 1958).

*Fossil occurrence:* Pliocene: Diemerbrug Well, Vreeburg-Utrecht Well, and Goes Well in the Netherlands (Heering, 1950). Pliocene/Lower Pleistocene: Red Crag Formation (Harmer, 1925; Wood, 1853), Omma-Manganji Fauna (Chinzei, 1978). Lower Pleistocene: Maassluis Formation of the Netherlands (Spaink, 1975), Baventian (West et al., 1980), Pattorfik beds (Símonarson, 1981b), Olkov and Tusatuva-Yamsk Suites (Petrov, 1982), Gubik Formation, Fishcreekian (Repenning et al., 1987). Middle Pleistocene: Pinakul, Kolvin, Kresta, Karagin, and Padymeiskii Suites (Merklin et al., 1962, 1979; Petrov, 1982), Kotzebuan (Hopkins et al., 1972), Anvilian (Hopkins et al., 1974), Pre-Cape Christian beds (Andrews et al., 1981). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

The specimens of *Serripes groenlandicus* in the *Serripes* Zone on Tjörnes are obviously among the oldest of the species. It is considered to have originated in the Pacific and migrated into the North Atlantic while the sediments of the *Serripes* Zone were deposited (Durham & MacNeil, 1967).

### Genus *Cerastoderma* Poli, 1795

#### ***Cerastoderma decorticata*** **(Wood, 1840)**

Plate 7.14. Figs. 5–6

1840 *Cardium decorticatum* – Wood: p. 251.
1853 *Cardium decorticatum*, S. Wood – Wood: p. 159, Pl. 14, fig. 1a–d.
1924 ?*Cardium edulinum* Sowerby? – Schlesch: p. 322.
1950 *Laevicardium decorticatum* (S. Wood, 1840*)* – Heering: p. 106–107.
1980 *"Cardium"* aff. *decorticatum* Wood, 1840 – Gladenkov et al.: p. 44. Pl. 7, figs. 1–4.

*Material:* About 100 valves, both paired and disarticulated, from unit 1 in the *Tapes* Zone to unit 9 in the *Mactra* Zone. There are several juvenile valves, especially in a lens in unit nine where shell material has accumulated.

*Remarks:* The largest valve we found measures (l × h × b): 38.0 × 34.5 × 14.4 mm, but Gladenkov et al. (1980) reported specimen about 54 mm in length. The shell ratios h/l are 0.75–0.90 and the b/l ratios are 0.29–0.38. The specimens from the *Tapes* Zone are generally poorly preserved and consist mainly of internal or external casts as the valves are dissolved. On the other hand, the juvenile specimens from unit 9 are very well preserved and show no signs of dissolution.

*Cerastoderma decorticata* is sculptured with radiating ribs, generally 34–36, with numerous fine transverse lists like in *Cerastoderma edule* (Linné). The valve of *C. decorticata* is generally slightly longer than the valves of *C. edule.* While the h/l ratios for the former are 0.75–0.89, they are 0.80–0.99 for the latter. This can best be observed when comparing juvenile specimens.

*Distribution and ecology:* The distribution of *Cerastoderma decorticata* in Pliocene sediments indicate that this extinct species preferred conditions as found today in the boreal region of the North Atlantic. It might have lived in a similar way as the recent *C. edule.* In the Tjörnes beds *C. decorticata* is mainly found in sandy sediments deposited in nearshore environments. It was probably living close to the coast in polyhaline waters. In the British Isles *C. edule* lives from mid-tide level to just below low water mark, where it is a common suspension feeder in sandy bays and estuaries (Tebble, 1966).

The first living specimens of *C. edule* were found in Iceland during the summer of 1948 (Óskarsson, 1953). However, a few specimens have been reported from the Pliocene Skammidalur Formation in South Iceland, being considered of same age as the *Serripes* Zone on Tjörnes (Áskelsson, 1960; Símonarson, 1981a). Subsequently, the species became extinct in Iceland in Upper Pliocene or early in the Pleistocene. When taken into the consideration that *C. edule* was first found living in Iceland in the mid-twentieth century and close to Gufunes near Reykjavík, a busy anchorage during the Second World War, it has been suggested that it was carried to the country by ship (Óskarsson, 1953). The fact that the species can live and reproduce in Iceland today supports the idea that the absence was not due to environmental factors, but rather migration difficulties posed by water depth and currents (Símonarson, 1981a). It is now living along the Icelandic coasts where it has been found down to a depth of only 3 m (Óskarsson, 1982).

*Fossil occurrence:* ?Upper Miocene: *Tapes* Zone of the Tjörnes beds (this volume). Pliocene: Coralline Crag Formation (Wood, 1853), Vreeburg-Utrecht Well in the Netherlands (Heering, 1950). Stratigraphical range: ?Upper Miocene-Pliocene.

### Family Veneridae Rafinesque, 1815
### Genus *Paphia* Röding, 1798

**_Paphia aurea_ (Gmelin, 1791)**
Plate 7.14. Fig. 7

1791 *Venus aureus* – Gmelin in Linné: p. 3288.
1853 *Tapes aurea*, Gmelin – Wood: p. 202–203, Pl. 20, fig. 2a–b.
1924 *Tapes aureus* (Gmelin)? – Schlesch: p. 321 (from an unpublished manuscript of Poulsen, 1884).
1925 *Tapes aureus* Gmel. – Bárðarson: p. ?21, ?24, 27, 76–78.
1934 *Tápes aureus* (Gmelin) – Jensen & Spärck: p. 120, fig. 101.
1950 *Venerupis (P.) aurea* (Gmelin 1790) – Heering: p. 136–137, Pl. 12, figs. 17–18.
1980 *Venerupis* aff. *aurea* (Gmelin, 1790) – Gladenkov et al.: p. 53, Pl. 8, figs. 18–19.

*Material:* About 30 valves from units 2–5 in the *Tapes* Zone. The majority of valves are articulated in the sediments. This species has never been found in the *Mactra* or the *Serripes* Zone.

*Remarks:* The largest specimen with paired valves measures (l × h): 40.1 × 33.6 mm, which is slightly shorter than the maximal length of 45 mm recorded by Poppe and Goto (1993). The shell ratios h/l are 0.72–0.84 for all the measurable valves. The aragonite shells are generally poorly preserved, the shell material being dissolved, and most of the specimens are preserved as casts (internal or external cores). Generally, the valves have more oval outline than those of *Paphia rhomboides* (Pennant) (see Jensen & Spärck, 1934: fig. 101). However, the shells are not damaged and probably they have only slightly been subject to preburial transport.

*Recent distribution, ecology, and biology: Paphia aurea* is now living in the boreal and lusitanian regions of the North Atlantic. It extends from the Norwegian Sea (from 63.5°N) and southward to Morocco and Rio de Oro (Tebble, 1966). It is known from the Baltic south to the Belt Sea and reach through the Mediterranean into the Black Sea (Jensen & Spärck, 1934; Poppe & Goto, 1993). Bathymetrical range: The species prefers shoreface conditions, and in the British Isles it has been found down to a depth of about 37 m (Tebble, 1966). It is a euhaline species with salinity tolerance above 30‰ (Funder et al., 2002). The larval development is probably with a pelagic stage.

In the British Isles it burrows in a bottom of soft black mud, muddy gravel, and gravel (Tebble, 1966). Apparently, the specimens in the *Tapes* Zone preferred more sandy sediments than those living today in British waters.

*Fossil occurrence:* ?Upper Miocene: *Tapes* Zone of the Tjörnes beds (Gladenkov et al., 1980). Pliocene: St. Erth beds in southern England (Heering, 1950). Lower Pleistocene: Bramerton Crag (Wood, 1853). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

***Paphia aurea senescens* (Cocconi, 1873)**
Plate 7.14. Fig. 8

1873 *Tapes senescens* – Cocconi: p. 695–696, Pl. 9, figs. 1–2.
1913 *Tapes senescens* Doederlein – Nordmann: p. 287–299, Pl. 5, figs. 1–6 & Pl. 6, figs. 1–4.
1913 *Tapes aureus* Gm. var. *eemiensis* Nordm. – Nordmann: p. 287–299, Pl. 5, figs. 1–6, pl. 6, figs. 1–4.
1950 *Venerupis aurea senescens* (Doederlein M.S., Cocconi, 1873) – Heering: p. 137–139, Pl. 13, figs. 1–4.
1980 *Venerupis perovalis* (S. Wood, 1840) – Gladenkov et al.: p. 53, Pl. 8, fig. 9.
1993 *Paphia aurea senescens* (Cocconi) – Poppe & Goto: p. 123.
1998 *Venerupis rhomboides* (Pennant, 1777) – Símonarson & Eiríksson: p. 32–33, fig. 1d.

*Material:* One intact right valve from unit 5 in the *Tapes* Zone.

*Remarks:* The valve measures (l × h): 56.3 × 42.8 mm and the shell ratio h/l is therefore 0.76. This is similar to the ratio recorded for *Paphia aurea.* Eight valves from Denmark showed on the average 0.75, four from Holland had 0.74, whereas six from Italy showed h/l ratio 0.81 on the average (Nordmann, 1913). However, the valve is considerably larger than the maximal length of 45 mm recorded for *P. aureus* by Poppe and Goto (1993). Apparently, it has also slightly more wavy concentric lines and finer radial lines on the posterior side of the valve than *P. aureus*, but actually the ornamentation of the species is rather variable. However, we have decided to refer this one valve to the subspecies *senescens* (cf. Heering, 1950).

In 1908, Nordmann described large specimens of *Tapes* from Eemian interglacial deposits in Denmark, North Germany, and the Netherlands (Nordmann et al., 1908). He referred to them as a new variety of *Tapes aureus* and named them *eemiensis,* and he considered the species as an index fossil for the Eemian. Later, he came to the conclusion that this variety is identical with the species *T. senescens* described from Italy by Cocconi in 1873 (cf. Nordmann, 1913). Actually, Doederlein had given the name to a specimen kept in the Parma Museum, but he did neither describe it nor publish the name. In this volume, we refer to it as a subspecies, but further studies might reveal if it is a distinct species that became extinct as late as in the Upper Pleistocene.

*Distribution and ecology:* The youngest specimens of the extinct *Paphia aurea senescens* have been found in Eemian deposits in northern Europe. Its distribution in Pliocene and Pleistocene sediments indicates strongly that it preferred environmental conditions as now prevail in the lusitanian and boreal regions in the North Atlantic. From Iceland in the north it was at least distributed southward to the Mediterranean (Italy). The bathymetrical range is not known, but it might have lived close to the coast like *P. aurea.* In Tjörnes the valve was found in sandy sediment deposited in nearshore environment shortly before a thick lignite layer was accumulated during a considerable regression. In Italy (i.e., Malagrotta) it has been found in gravelly sand considered to have deposited in a lagoon (Nordmann, 1913). We do not know if it was mesohaline rather than euhaline, and we have no information about its salinity tolerance, even though it may have lived in a lagoon. The larval development is unknown, but was probably with a pelagic stage.

*Fossil occurrence:* ?Upper Miocene: *Tapes* Zone of the Tjörnes beds (Gladenkov et al., 1980). Lower Pleistocene: Lower Emilian (Sami & Taviani, 1997). ?Middle Pleistocene: Sandy fossiliferous sediments at Malagrotta in Italy (Heering, 1950; Nordmann, 1913). Upper Pleistocene: Eemian deposits in Denmark, northern Germany, and the Netherlands (Jensen & Spärck, 1934; Nordmann, 1913). Stratigraphical range: Pliocene to Upper Pleistocene (Eemian).

If the age of the Italian deposits is correct, the record of *Paphia aurea senescens* in the *Tapes* Zone on Tjörnes is the first appearance data (FAD).

***Paphia rhomboides*** **(Pennant, 1777)**
Plate 7.15. Fig. 1

1777 *Venus rhomboides* – Pennant: p. 97, Pl. 55.
1853 *Tapes virginea*, – Wood: p. 201–202, Pl. 20, fig. 1a–e.
1863 ?*Tapes virginea* Forbes – Winkler: p. 203–204.
1878 *Tapes edulis*, Lin. – Sars: p. 354.
1925 *Tapes aureus* Gmel. – Bárðarson: p. ?21, ?24, 27, 76–78 (in part).
1934 *Tápes edúlis* (Chemnitz) – Jensen & Spärck: p. 121–122, fig. 104.
1950 *Paphia rhomboides* (Pennant, 1777) – Heering: p. 139–140.
1980 *Venerupis rhomboides* (Pennant, 1777) – Gladenkov et al.: p. 52–53, Pl. 8, figs. 10–17a.

*Material:* About 400 valves from units 1–5 in the *Tapes* Zone and units 6 and 10 in the *Mactra* Zone. Generally, the valves are paired in the sediments, especially those found in the *Tapes* Zone.

*Remarks:* The largest specimen with paired valves measures (l × h × b): 48.0 × 33.1 × 10.6 mm. The shell ratios h/l are 0.65–0.72 and b/l ratios 0.17–0.22 for about 100 measurable valves from the *Tapes* Zone. The aragonite valve is somewhat broadly oval in outline, with a line from the beaks backwards broken by a smooth curve before descending to the posterior margin (see Tebble, 1966). They are generally badly preserved, and the shell material is dissolved and most of the specimens are preserved as casts. However, the shells are not damaged and probably they have only been subject to slight preburial transportation, especially those found in the *Tapes* Zone.

*Recent distribution, ecology, and biology: Paphia rhomboides* is a boreal–lusitanian species (Fig. 7.18). It lives in the North Atlantic from western Norway (at 67.5°N) and the Faroe Islands south to the Atlantic coast of Morocco (Høisæter, 1986; Tebble, 1966). It has been found in Skagerrak eastward to Bohuslän on the


**Paphia rhomboides**

**Fig. 7.18** The recent known geographical distribution of *Paphia rhomboides* (Pennant) west coast of Sweden and in the Mediterranean (Jensen & Spärck, 1934; Poppe & Goto, 1993). Bathymetrical range: 0 m (several places) to 183 m in the British Isles (Tebble, 1966). The occurrence close to a river channel in the British Isles (cf. Holme, 1961) may indicate a mesohaline habit, but otherwise the salinity tolerance is unknown. The species probably has pelagic larval development.

In the British Isles it burrows in gravel, sandy and muddy gravel, shell gravel, and rather coarse sand from the low tide-mark to a depth of about 183 m (Tebble, 1966).

*Fossil occurrence:* Upper Miocene – Pliocene: *Tapes* Zone of the Tjörnes beds (Gladenkov et al., 1980; Símonarson & Eiríksson, 1998). Pliocene: Coralline Crag Formation (Wood, 1853), Lillo Formation (Heering, 1950). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1853). Lower Pleistocene: Norwich Crag (Wood, 1853), *Nassarius reticulatus* and *Lentidium complantum* Zone of the Netherlands (Spaink, 1975). Holocene: *Dosinia* beds in Denmark (Jensen & Spärck, 1934). Stratigraphical range: Pliocene to Recent.

### Genus *Venerupis* Lamarck, 1818

**_Venerupis corrugata_ (Gmelin, 1791)**
Plate 7.15. Figs. 2–3

1791 *Venus corrugata* – Gmelin in Linné: p. 3280.
1853 *Tapes perovalis,* S. Wood – Wood: p. 203–204, Pl. 19, fig. 7a–d.
1878 *Tapes pullastra*, Lin. – Sars: p. 56.
1934 *Tápes pullástra* (Montagu) – Jensen & Spärck: p. 120–121, figs. 102–103.
1950 *Venerupis pullastra* (Montagu, 1803) – Heering: p. 134–135, Pl. 12, figs. 15–16.
1998 *Venerupis pullastra* (Montagu, 1803) – Símonarson & Eiríksson: p. 32–33, fig. 2e–g.
2005 *Phapia pullastra* (Montagu, 1803) – Sneli et al.: p. 153.

*Material:* Three specimens with united valves and one internal cast from unit 5 in the *Tapes* Zone. The cast shows clearly the pallial sinus while the shell material is dissolved.

*Remarks:* The largest specimen measures (l × h): 44.3 × 30.7 mm and the h/l ratio are 0.69. About 30 valves from mid-Holocene sediments (*Tapes* beds) in Denmark showed this ratio to vary from 0.59 to 0.69. The valves of *Venerupis corrugata* are therefore slightly shorter than those of *Paphia rhomboides*, but they are indeed quite similar in shape. The sculpture of both species consists of numerous concentric ridges and grooves, but generally *V. corrugata* also has fine radiating ribs sometimes becoming a little coarse posteriorly. The internal cast (Plate 7.15, Fig. 3) shows the pallial sinus which is rather deep and wide and most comparable to that of *V. corrugata* (cf. Holme, 1961: text-fig. 9).

*Recent distribution, ecology, and biology: Venerupis corrugata* is a boreal-lusitanian species extending in the North Atlantic from Tromsø in northern Norway (about 70°N) and the Faroe Islands southward to the Atlantic coast of Morocco (Sneli et al., 2005; Tebble, 1966). In Scandinavian waters it is distributed in Kattegat and Øresund and it goes far into the Mediterranean (Sneli et al., 2005). Bathymetrical range: 0 m in several places to ?58 m in the Faroe Islands (Petersen, 1968). In the British Isles it lives from mid-tide level down to a depth of about 37 m (Tebble, 1966). The species seems euhaline-mesohaline with salinity tolerance down to about 15‰ (Funder et al., 2002). It has most probably pelagic larval development.

In the British Isles *V. corrugata* burrows a few cm in the bottom of stony sand, hard or muddy sand, and muddy gravel near rocks or empty shells, generally attached by byssus threads to a solid object (Tebble, 1966).

*Fossil occurrence:* ?Upper Miocene: *Tapes* Zone of the Tjörnes beds (this volume). Pliocene: Coralline Crag Formation (Wood, 1853). Lower Pleistocene: Icenian of the British Isles and the Netherlands (Heering, 1950). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

### Family Mactridae Lamarck, 1809
### Genus *Spisula* Gray, 1837

***Spisula arcuata* (Sowerby, 1817)**
Plate 7.15. Figs. 4–6

1817 *Mactra arcuata* – Sowerby: p. 135, Pl. 160, figs. 1 and 6.
1857 *Mactra arcuata*, J. Sowerby – Wood: p. 243–244, Pl. 23, fig. 5a–c.
1924 *Mactra arcuata* Sowerby – Schlesch: p. 321.
1924 ?*Mactra solidissima* (Chemnitz) = *M. procrassa* Wood = *M. ponderosa* Phil. – Schlesch: p. 321.
1924 ?*Mactra stultorum* (Linné) = *M. subtruncata* (da Costa) – Schlesch: p. 321 (from an unpublished manuscript of Poulsen, 1884).
1924 ?*Mactra deaurata* Turton – Schlesch: p. 321.
1950 *Spisula arcuata* (J. Sowerby, 1817) – Heering: 143–144, Pl. 16, fig. 28.
1980 *Spisula arcuata* (Sowerby, 1817) – Gladenkov et al.: p. 45–46, Pl. 10, figs. 5–10.

*Material:* About 600 valves, both paired and disarticulated, from all the units 1–5 in the *Tapes* Zone, all units 6–12 in the *Mactra* Zone, and units 13–21 in the *Serripes* Zone. The species is most frequently found in the *Mactra* Zone, and therefore Bárðarson (1925) used it as an index fossil for this biozone. It disappeared in the middle part of the *Serripes* Zone, and apparently it did not survive in Iceland to the end of Pliocene.

*Remarks:* The largest specimen measures (l × h × b): 56.1 × 46.5 × 25.2 mm. The h/l ratios and the b/l ratios were calculated for 18 specimens with paired valves from units 7 and 9 in the *Mactra* Zone. The h/l ratios seem to be 0.77–0.89 and the b/l ratios are 0.41–0.52. There are many well-preserved juvenile specimens with paired valves in a lens in unit 9. However, the valves of *Spisula arcuata* are rather thin and fragile, and larger single valves are generally fragmented, especially in the *Mactra* and *Serripes* Zones if they have been subject to post-mortal transport before they became buried in the sediments. A lot of fish and bird predation does fragmenting without seriously transporting shells. The specimens from the *Tapes* Zone are generally with paired valves, but they are usually preserved as casts because the valves have dissolved, especially close to the lignite layers.

*Distribution, ecology, and biology: Spisula arcuata* is extinct, but it probably lived under marine conditions similar to those prevailing in the recent boreal region of the North Atlantic. It was widely distributed around the British Isles, especially when the Red Crag Formation was deposited, and apparently it extended from North Iceland to the northwestern European continent. There are no signs of lusitanian or subarctic outposts. In the Tjörnes beds it occurs frequently together with *Arctica islandica,* and it is therefore possible that its bathymetry was similar and it might have preferred to live close to the coast in foreshore areas. The species has never been found recent in Iceland, where the closely related species *Spisula solida* (Linné, 1758) is living with the variety *elliptica.* This variety is even more common from a depth about 20 m down to 207 m (Madsen, 1949; Óskarsson, 1952). The majority of the recent species of *Spisula* is mesohaline, but the salinity tolerance of *S. arcuata* is unknown. Probably the species had a planktonic stage during its development (cf. Malatesta & Zarlenga, 1986).

The Tjörnes sediments with *Spisula arcuata* indicate strongly that the species preferred sandy substrates.

*Fossil occurrence:* ?Upper Miocene: *Tapes* Zone of the Tjörnes beds (this volume). Pliocene: Coralline Crag Formation (Wood, 1857), Lillo Formation and Oosterhout Formation (Heering, 1950; Spaink, 1975). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1857). Lower Pleistocene: Norwich Crag Formation (Spaink, 1975; Wood, 1874). Stratigraphical range: Pliocene to Lower Pleistocene.

### Family Semelidae Stoliczka, 1870
### Genus *Abra* Lamarck, 1818

#### *Abra alba* (Wood, 1802)
Plate 7.15. Figs. 7–10

1802 *Mactra alba* – Wood: p. 174, Pl. 16, figs. 9–12.
1857 *Abra alba,* W. Wood – Wood: p. 237–238, Pl. 22, fig. 10a–b.
1878 *Abra alba,* Wood – Sars: p. 73–74, Pl. 20, fig. 3a–c.
1924 ?*Syndosmia prismatica* (Montagu) – Schlesch: p. 323.
1934 *Syndosmýa álba* (Wood) – Jensen & Spärck: p. 143–144, figs. 130–131.
1950 *Abra alba* (W. Wood, 1802) – Heering: 159–160, Pl. 16, fig. 1.
1980 *Abra alba* (W. Wood, 1802) – Gladenkov et al.: p. 50, Pl. 9, figs. 23–26a.
1980 *Abra fabalis* (S. Wood, 1853) – Gladenkov et al.: p. 50, Pl. 9, figs. 27–29a.

*Material:* About 50 valves, both paired and disarticulated, from units 5 in the *Tapes* Zone and units 6–8 in the *Mactra* Zone, as well as units 14 or ?17–19 in the *Serripes* Zone.

*Remarks:* The largest valve measures (l × h × b): 22.2 × 14.9 × 10.1 mm.

The thin and fragile valves are not very well preserved and many of them are damaged. The h/l ratios are 0.62–0.71. Gladenkov et al. (1980) recorded three valves of *Abra fabalis* from unit 14 in the *Serripes* Zone (in their table 1 the species is recorded from units 17–19). Their measurements of *A. fabalis* are somewhat doubtful (see their p. 50), but the specimens they figured Pl. 9, figs. 27–29a have h/l ratios between 0.63 and 0.68. According to Wood (1853), *Abra fabalis* is more elongated and slender than *A. alba* and has a more pointed posterior end. As we cannot see those differences in the specimens from Tjörnes, we refer them all to *A. alba.*

*Recent distribution, ecology, and biology: Abra alba* is widely distributed in the boreal and lusitanian regions of the North Atlantic. From the Norwegian west coast at 67.5°N (Lofoten) and the Faroe Islands it extends southward to Senegal on the west coast of Africa (Høisæter, 1986; Sneli et al., 2005; Tebble, 1966). In the Baltic it has been found in Øresund and south to Neustadt, and it is well known from the Mediterranean and the Black Sea (Jensen & Spärck, 1934; Tebble, 1966). Bathymetrical range: from the infralittoral zone it goes down to a depth of 1257 m (Poppe & Goto, 1993), the range is also recorded as 2–1000 m (Sneli et al., 2005). In the British Isles it has been found from the extreme low water-mark to about 66 m and is especially abundant down to about 18 m (Tebble, 1966). It is a marine species with salinity tolerance down to 15‰ (Funder et al., 2002). Most probably the species has a pelagic larval development.

In the British Isles *Abra alba* belongs to the infauna in a bottom of mud, silty sand, and muddy gravel (Tebble, 1966). The specimens from the Tjörnes beds were all found in more sandy sediments. The two recent species known from Iceland, *A. prismatica* (Montagu, 1808) and *A. nitida* (Müller, 1776), are frequently found in the stomachs of haddock (cf. the Icelandic name "ýsuskeljar"). In Iceland as elsewhere *Abra* species are important food for fish.

*Fossil occurrence:* Miocene: Vienna Basin (Heering, 1950). Pliocene: Coralline Crag Formation (Wood, 1857), Lillo Formation (Heering, 1950). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1857). Lower Pleistocene: Maassluis Formation, Norwich Crag Formation (Heering, 1950; Wood, 1857). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Miocene to Recent.

### Family Tellinidae de Blainville, 1814
### Genus *Macoma* Leach, 1819

#### *Macoma calcarea* (Gmelin, 1791)
Plate 7.16. Fig. 1

1791 *Tellina calcarea* – Gmelin in Linné: p. 3236.
1857 *Tellina lata*, Gmelin – Wood: p. 228–229, Pl. 21, fig. 6a–d.
1878 *Macoma calcaria*, Chemn. – Sars: p. 76, Pl. 6, fig. 2a–b.
1924 *Macoma calcarea* (Chemnitz) – Schlesch: p. 322.
1925 *Macoma calcaria,* Chemn. – Bárðarson: p. ?51, 53–54, 57, 59, 70.
1934 *Macóma calcáría* (Chemnitz) – Jensen & Spärck: p. 130–131, fig. 113.
1950 *Macoma (M.) calcarea* (Gmelin 1790) – Heering: p. 170–171, Pl. 15, figs. 15–16.
1958 *Macoma calcaria* (Chemnitz) – Ockelmann: p. 125–128, Pl. 2, fig. 10.
1980 *Macoma calcarea* (Gmelin, 1790) – Gladenkov et al.: p. 47–48, Pl. 9, figs. 1–2 & 5–10.

*Material:* About 40 pairs and valves from units 14–21 and 25 in the *Serripes* Zone.

*Remarks:* The largest valve measures (l × h × b): 46.1 × 33.2 × 6.9 mm. The shell ratios h/l and b/l were calculated for 32 measurable valves and they are 0.67–0.75 and 0.13–0.17, respectively. The thin valves are rather well preserved and show very few signs of dissolution, but many of them are fragmented. All the *Macoma* bivalve in the Tjörnes beds have a deep pallial sinus, two small cardinal teeth, but no laterals (see Plate 7.16, Figs. 1–3).

*Recent distribution, ecology, and biology: Macoma calcarea* is circumpolar and widely distributed in the arctic, subarctic, and boreal regions of the North Atlantic and also well known from the North Pacific. It extends from Northeast Greenland, Svalbard, Franz Josef Land, the Barents Sea, Novaya Zemlya, the Kara Sea, and the Siberian Arctic Sea southward to the Faroe Islands, New York, Oregon, and ?northern Japan (Heering, 1950; Madsen, 1949; Ockelmann, 1958; Petersen, 1968). The occurrence in the Oslofjord, Kattegat, and the Baltic is probably isolated and has been considered a relic by Petersen (1888) and Jensen (1905). In North America it is known living in the Beaufort Sea, the Canadian Arctic Archipelago, Baffin Bay, Hudson Bay, and the Labrador Sea to New York or even Washington in the south (Bernard, 1979; Lubinsky, 1980). In West Greenland it has been found living to Iita in the north (Thorson, 1951), and in North Greenland it is common in Jørgen Brønlund Fjord at depths between 2 and 16 m (Schiøtte, 1989). Bathymetrical range: from 0 m in Iceland (Madsen, 1949) to 677 m in West Greenland (Ockelmann, 1958). *M. calcarea* is a marine species with salinity tolerance down to 5‰ (Funder et al., 2002). The larval development is with a pelagic stage (Ockelmann, 1958; Thorson, 1936).

The species is one of the most characteristic animals of the infaunal Arctic *Macoma* community (Thorson, 1957). In Iceland and East Greenland this deposit feeder lives mainly in the fiords in rather shallow water on a bottom of mud and fine sand sometimes mixed up with gravel and stones (Ockelmann, 1958; Spärck, 1937).

*Fossil occurrence:* Pliocene: Sagavannirktok Formation, Middle Nuwok beds, and Gubik Formation (MacNeil, 1957). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1857), Merksem Member, Lillo Formation (Moerdijk et al., 2010). Lower Pleistocene: Norwich Crag Formation (Norton, 1967), Maassluis Formation (Spaink, 1975), Norwich Crag Formation (West et al., 1980), Pattorfik beds (Símonarson, 1981b), Olkhov and Tusatuva-Yamsk Suites (Petrov, 1982). Middle Pleistocene: Kotzebuan (Hopkins et al., 1972), Pinakul, Karagin, Kolvin, Kresta, and Padymeiskii Suites (Merklin et al., 1979; Petrov, 1982), Pre-Cape Christian beds (Andrews et al., 1981). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). It has also been collected in a beach material in the Netherlands where only Late Pleistocene occurrences are found (pers. comm. R. Pouwer and F. Wesselingh). Stratigraphical range: Pliocene to Recent.

*Macoma calcarea* is considered a Pacific species that migrated into the North Atlantic while the *Serripes* Zone was deposited in the Tjörnes area (Durham & MacNeil, 1967).

### ***Macoma praetenuis* (Woodward, 1830)**

Plate 7.16. Fig. 2

1830 *Tellina prætenuis* –Woodward: p. 11.
1857 *Tellina prætenuis,* Leathes´MSS – Wood: p. 230–231, Pl. 21, fig. 5a–c.
1924 *Macoma praetenuis* (Leathes) – Schlesch: p. 323.

1924 ?*Macoma balthica* (Linné) – Schlesch: p. 322.
1925 *Macoma* sp. – Bárðarson: p. 50, 72–73 (in part).
1924 ?*Macoma fusca* (Say) – Schlesch: p. 322.
1950 *Tellina praetenuis* Leathes M.S.S. 1830 – Heering: p. 176–178, Pl. 15, figs. 11–14.
1980 *Macoma praetenuis* (Woodward, 1933) – Gladenkov et al.: p. 49, Pl. 9, figs. 3–4 & 16–22.

*Material:* About 800 valves, both paired and disarticulated, from unit 12 in the *Mactra* Zone, and units 13–23 and ?25 in the *Serripes* Zone.

*Remarks:* The largest valve measures (l × h × b): 40.2 × 34.1 × 9.2 mm. The shell ratios h/l and b/l were calculated for 70 valves and they are 0.72–0.87 and 0.11–0.23, respectively. When compared to *Macoma calcarea* it is evident that *M. praetenuis* is generally shorter with more variable height and thicker valves. This may explain why they are more often undamaged and less damaged in the *Serripes* Zone than *M. calcarea.*

*Distribution, ecology, and biology:* The distribution of *Macoma praetenuis* in sediments and its general occurrence with recent boreal species indicates that this extinct species preferred conditions similar to those in the boreal region of the North Atlantic today. It is far the most common *Macoma* species in the *Serripes* Zone, and possibly it preferred fiords with shallow water and sandy bottom where it lived together with *M. calcarea* and many other shallow-water species. Many recent *Macoma* species are mostly polyhaline, but can extend into euhaline, as well as mesohaline settings (cf. *M. balthica* (Linné, 1758)), but the salinity tolerance is not known for this extinct species. It is likely that it had pelagic larval development since the more arctic *M. calcarea* has a pelagic stage.

*Fossil occurrence:* Pliocene: Lillo Formation and the Vreeburg-Utrecht Well in the Netherlands (Heering, 1950). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1857). Lower Pleistocene: Icenian, Chillesford bed (Wood, 1857). Middle to ?Upper Pleistocene units, A5/009 and F8/006, in the central part of the North Sea (Meijer, 1993). Therefore, the species probably may have lived during the Eemian (Meijer, 1993). Stratigraphical range: Pliocene to possibly Late Pleistocene.

***Macoma obliqua* (Sowerby, 1817)**
Plate 7.16. Fig. 3

1817 *Tellina obliqua* – Sowerby: 137, Pl. 161, fig. 1.
1857 *Tellina obliqua,* J. Sowerby – Wood: p. 228, Pl. 21, fig. 7a–d.
1924 *Macoma obliqua* (J. Sowerby) – Schlesch: p. 323.
1960 *Tellina obliqua* J. Sowerby – Áskelsson: p. 19–20, Pl. 3. figs. 14–16.
1950 *Macoma obliqua* (J. Sowerby, 1817) – Heering: p. 168–169, Pl. 15, figs. 3–6.
1971 *Macoma (Macoma) obliqua* (Sowerby, 1817) – Coan: p. 26, Pl. 6, fig. 31, Pl. 7, fig. 33, text-fig. 4.
1980 *Macoma obliqua* (Sowerby, 1817) – Gladenkov et al.: p. 48–49, Pl. 9, figs. 11–15a.

*Material:* About 80 valves, both paired and disarticulated, from units 14–23 in the *Serripes* Zone. At least 15 specimens were found with united valves and about 50 single valves.

*Remarks:* The largest valve measures (l × h × b): 35.1 × 29.8 × 8.6 mm. The h/l and b/l ratios were calculated for 30 valves and they are 0.81–0.89 and 0.19–0.27, respectively. Compared to the other *Macoma* species found in the *Serripes* Zone, *M. obliqua* is the shortest and most ovate.

The species was considered to be extinct until 1969 when Coan pointed out its conspecific with the extant Pacific species *Macoma incongrua* (Martens, 1865) of authors, but according to Coan (1971) it is not of Martens 1865.

*Recent distribution, ecology, and biology: Macoma obliqua* is distributed from Point Barrow and along the western coast of Alaska southward to Washington and the Japan Sea (Bernard, 1983; Coan, 1971). It is not living any more in the North Atlantic. The recent and fossil distributions indicate that the species prefers conditions as now prevailing in the boreal region of the North Atlantic. Furthermore, Bernard (1983) recorded it living at water temperatures between –2° and 16°C. Bathymetrical range: from the intertidal zone down to 183 m (Bernard, 1983; Coan, 1971). It probably preferred fiords with rather shallow water and sandy or gravelly bottom, where it lived together with other shallow-water species, as it certainly did when the *Serripes* Zone was deposited. Many recent *Macoma* species are living in full marine assemblages, but the salinity tolerance is not known for this species. It is likely that it had pelagic larval development since the more arctic *M. calcarea* has a pelagic stage (cf. Ockelmann, 1958).

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Wood, 1857), uppermost Kattendijk Formation, Lillo Formation and the Oosterhout Formation (Heering, 1950; Moerdijk et al., 2010). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1857). Lower Pleistocene: Norwich Crag Formation (Wood, 1857), Maassluis Formation and Middle and Upper Pleistocene assemblages in Dutch offshore boreholes (Meijer, 1993). Stratigraphical range: Pliocene to Recent.

*Macoma obliqua* (Sowerby) was probably among the first group of boreal Pacific *Macoma* to reach the North Atlantic during the trans-Arctic migration (cf. Coan, 1971). Apparently, it migrated into the North Atlantic while the *Serripes* Zone was deposited in the Tjörnes area.

*Macoma obliqua* extended in range episodically into the Mediterranean (Malatesta & Zarlenga, 1986). The occurrence in Italy indicates that this took place during the Late Emilian and the latest Sicilian, but it has not been found in Italian sediments after the Sicilian (Bellomo & Raffi, 1991; Sami & Taviani, 1997). Possibly, the species disappeared from the North Atlantic in the Late Pleistocene, but kept on living in the North Pacific.

### Family Solenidae Lamarck, 1809

### Genus *Ensis* Schumacher, 1817

***Ensis* cf. *ensis* (Linné, 1758)**
Plate 7.16. Fig. 4

1758 *Solen ensis* – Linné: p. 672.
1857 *Solen ensis,* Linnæus – Wood: p. 256, Pl. 25, fig. 6a–f.
1878 *Solen ensis,* Lin. – Sars: p. 80.
1924 *Solen ensis* Linné – Schlesch: p. 323, Pl, 5, fig. 10.
1925 *Solen ensis*, L. – Bárðarson: p. 47, 72–73.
1934 *Énsis énsis* (L.) – Jensen & Spärck: p. 153, fig. 140.
1950 *Ensis ensis* (Linné, 1758) – Heering: p. 180–181.
1980 *Ensis* cf. *ensis* (Linné, 1758) – Gladenkov et al.: p. 46, Pl. 10, figs. 1–4.

*Material:* Thirty-three valves, mainly disarticulated, from unit 8 in the *Mactra* Zone and units 13–19 and ?25 in the *Serripes* Zone. They were most frequently found in the lower part of the *Serripes* Zone (from units 13–14 and 17). Furthermore, Emilsson (1929) has reported a few badly preserved specimens from the Eyvík Formation (cf. Eiríksson et al., 2020a).

*Remarks:* The largest valve measures (l × h): 78.1 × 12.9 mm. The long and brittle valves are with slightly curved dorsal and ventral margins and both ends are rounded and gaping. We will follow Schlesch (1924), Bárðarson (1925), and Gladenkov et al. (1980) and refer this species from the Tjörnes beds to *Ensis ensis*, however with some hesitation. It should be mentioned that the Pliocene species *Ensis waltoniensis* of van Urk, 1971 is shorter than *E. ensis* and has even more distinguishing characters (Moerdijk et al., 2010).

The valves are generally somewhat damaged even though they are articulated in the sediments, and the majority is reworked, although they have not been subjected to heavy transport. In a fine-grained sand lens in unit 15 there is a small concentration of specimens, both articulated and disarticulated, but occasionally with left and right valves lying side by side. This indicates a restricted post-mortal transport and reworking and a death assemblage, however, of the parautochtonous type. Burrowing species such as *Enis ensis* and *Cyrtodaria angusta* (see later) are more often found with articulated valves and occasionally in life position.

*Distribution, ecology, and biology: Ensis ensis* is a boreal-lusitanian species. It extends from the Faroe Islands and northern Norway (Nord Møre) southward to the coasts of Morocco (Sneli et al., 2005; Tebble, 1966). In Scandinavia it is known from Skagerrak and Kattegat, as well as the western part of the Danish Limfjord (Jensen & Spärck, 1934). It has been found scattered in the Mediterranean eastward to the coasts of Greece (Delamotte & Vardala-Theodorou, 2001). Bathymetrical range: from the intertidal zone down to at least 80 m (Nordsieck, 1969; Poppe & Goto, 1993). The species is polyhaline with salinity tolerance above 25‰ (Funder et al., 2002). The larval development is with a pelagic stage lasting for around a month (Fish & Fish, 1996).

In Denmark and the British Isles this suspension feeder prefers a bottom of sand and mixed substrates where it remains close to the surface of the sediments, but when disturbed it descends to half a meter below the surface of the bottom (Fish & Fish, 1996; Jensen & Spärck, 1934; Tebble, 1966).

*Fossil occurrence:* Miocene: Vienna Basin, ?Breda Formation in Dorst I (Heering, 1950). Pliocene: Coralline Crag Formation (Wood, 1857), Lillo Formation in Belgium, the Vreeburg-Utrecht Well, Gorkum Well, and the Goes Well in the Netherlands (Heering, 1950). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1857, #53941}). Lower Pleistocene: Icenian, Chillesford bed (Wood, 1857). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Miocene to Recent.

### Order Myoida Stoliczka, 1870
### Family Myidae Lamarck, 1809
### Genus *Mya* Linné, 1758

Two species of *Mya* are now living in Iceland; *Mya truncata* Linné, 1758 and *Mya arenaria* Linné, 1758. Additionally, one extinct species, *Mya schwarzbachi* Strauch, 1972, has been recorded from the *Serripes* Zone of the Tjörnes beds. Three subspecies of *Mya truncata* have been recorded from Iceland, *M. truncata uddevalensis* Forbes, 1846 and *M. truncata pseudoarenaria* Schlesch, 1931 have been found both living and fossil, and the third *M. truncata gudmunduri* Strauch, 1972 has only been found fossil in the *Serripes* Zone (Fig. 7.19).

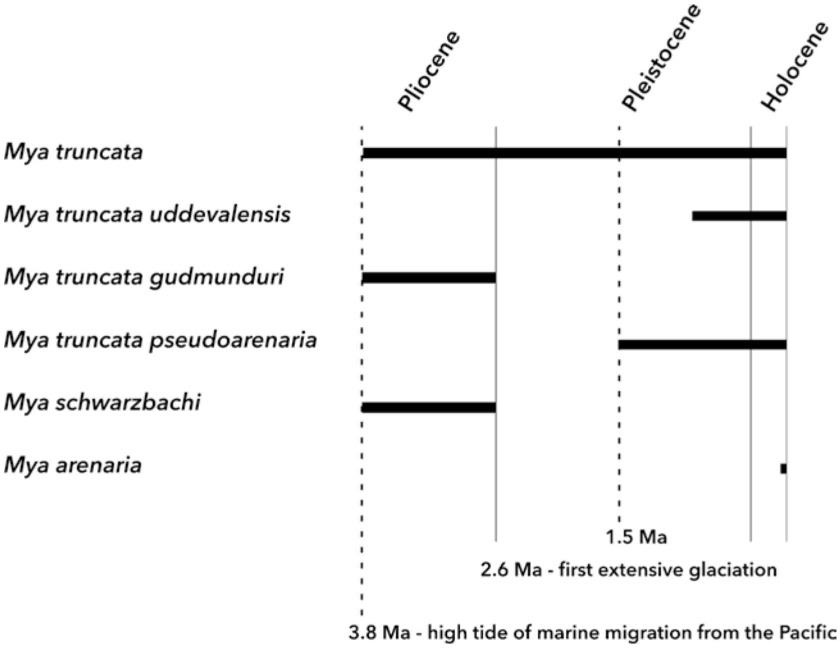

**Fig. 7.19** The stratigraphical range of the genus *Mya* in Iceland. The tide of the marine migration from the Pacific at 3.8 Ma is shown and the first extensive glaciation at 2.6–2.7 Ma

***Mya truncata*** **Linné, 1758**
Plate 7.16. Fig. 5

1758 *Mya truncata* – Linné: p. 670.
1857 *Mya truncata*, Linnæus – Wood: p. 277–279, Pl. 28, fig. 1a–f.
1878 *Mya truncata*, Lin. – Sars: p. 92.
1924 ?*Mya truncata* Linné – Schlesch: p. 323.
1934 *Mýa truncáta* (L.) – Jensen & Spärck: p. 169–171, fig. 155.
1950 *Mya (M.) truncata* Linné, 1758 – Heering: p. 196–197.
1958 *Mya truncata* Linné – Ockelmann: p. 144–149.
1965 *Mya (Mya) truncata* Linné – MacNeil: p. G38-G40, Pl. 8, figs. 1–12, Pl. 9, figs. 1–3, 5–20.
1972 *Mya (Mya) truncata truncata* Linné, 1758 – Strauch: p. 140–141, Pl. 10, figs. 5, 7–8, Pl. 11, fig. 7.
1979 *Mya (Mya) truncata* Linné, 1758 – Bernard: p. 53–54, fig. 88.
1980 *Mya truncata* Linné, 1758 – Gladenkov et al. : p. 54, Pl. 11, figs. 10–11.

*Material:* One left valve has been reported from unit 15 in the *Serripes* Zone. We have not found this species in the Tjörnes beds and according to MacNeil (1965), as well as Strauch (1972) it first arrived in the Tjörnes area in the Lower Pleistocene when the Breiðavík Group was deposited. They also suggested that the oldest European occurrences post-date the Pliocene (see further fossil occurrence). The single valve from unit 15 was found in the collection of Bárðarson at the Icelandic Institute of Natural History. Bárðarson (1925) recorded *Mya truncata*, f. *ovata*, Jensen, but not *Mya truncata* in sensu stricto. Norton (1975) mentioned *Mya truncata* L. incl. var. *ovata* Jensen, and apparently he had found the specimen in Bárðarson's collection. He left a hand-written note in the collection suggesting the valve belongs to *Mya truncata*, but reported in 1975 that it required some confirmation or further investigation.

*Remarks:* The single valve with the characteristic truncate posterior end is intact and measures (l × h): 50.6 × 36.5 mm. The desmodont hinge is well preserved with the spoon more symmetrical than in the subspecies and the posterior furrow not extended as in *Mya schwarzbachi* (cf. MacNeil, 1965; Strauch, 1972). No juvenile specimens have been found in the Tjörnes beds, but these have an ovate posterior end similar to fully grown *Mya arenaria* Linné (referred to the subgenus *Arenomya* by some authors, e.g., Strauch (1972)). Only after initiation of burrowing the posterior end become truncate. Generally, this development starts when the shell has reached a length of about 20 mm.

Petersen (1999) considered *Mya truncata* Linné as boreal in the North Atlantic and concluded that specimens from Thule in Northwest Greenland and down along the West Greenland coast to the East Greenland fiords and hitherto referred to that species actually belong to another species, *M. eideri* sp. nov. He based his diagnosis especially on the form of the pallial sinus and the pallial line in each type and concluded that there is more space for the siphons in *M. truncata* than *M. eideri.* Taken into the consideration the great variation in these characters in Icelandic modern specimens of *M. truncata,* we are not able to separate *M. eideri* from the typical form in Icelandic material.

*Recent distribution, ecology, and biology: Mya truncata* is the most widespread living species of *Mya.* It is a well-known circumpolar species occurring in the arctic, subarctic, and boreal regions of the North Atlantic and Pacific, and extends well southwards. It extends from West and East Greenland, Svalbard, Franz Josef Land, Novaya Zemlya, the Barents Sea, the Kara Sea, the Laptev Sea, the Siberian Arctic Sea, the Beaufort Sea and the Canadian Arctic Archipelago in the north to the western Baltic (to Øresund), the English Channel, the Bay of Biscay, Massachusetts, Hakodadi in Japan, and Port Orchard in Washington in the south (Bernard, 1979; Lubinsky, 1980; Ockelmann, 1958; Sneli et al., 2005). In North Greenland it has been found living in Jørgen Brønlund Fjord at depths between 2 and 40 m (Schiøtte, 1989). Bathymetrical range: It prefers shoreface areas, but ranges from 0 m at several localities down to 625 m in West Greenland (Ockelmann, 1958). It is marine species with salinity tolerance down to 5‰ (Funder et al., 2002). The larval development is planktotrophic with a long-lasting pelagic stage (Jørgensen, 1946; Thorson, 1936).

The species is a suspension feeder, and in East Greenland the young animals are found attached to the algal epifauna in large numbers, while the adults burrow in the sediments in the infaunal Arctic *Macoma* community (Ockelmann, 1958). In the British Isles it prefers substrates of clay, muddy sand, or sand (Tebble, 1966).

*Fossil occurrence:* Miocene: Takinoue Formation, Yakataga Formation (MacNeil, 1965). Pliocene: Coos Conglomerate, Towsley Formation, Quillayute Formation (MacNeil, 1965), Beaufort Formation, Meighen Island (Fyles et al., 1991), *Serripes* Zone of the Tjörnes beds (this volume). Lower Pleistocene: Baventian (West et al., 1980), Emilian and Sicilian (Malatesta & Zarlenga, 1986), Pico Formation (MacNeil, 1965), Gubik Formation, Fishcreekian (Repenning et al., 1987), Pattorfik beds (Símonarson, 1981b), Kap København Formation (Símonarson et al., 1998), Lodin Elv Formation (Feyling-Hanssen et al., 1983), Île de France Formation (Bennike et al., 2002), Breiðavík beds (Eiríksson, 1981), Olkov and Tusatuva-Yamsk Suites (Petrov, 1982). Middle Pleistocene: Kotzebuan (Hopkins et al., 1972), Anvilian (Hopkins et al., 1974), Karagin, Pinakul, Kresta, Kolvin, and Padymeiskii Suites (Merklin et al., 1979; Petrov, 1982). Upper Pleistocene: Baltic Eemian (Funder et al., 2002), *Portlandia arctica* Zone in the Skærumhede sequence in Vendsyssel, Denmark (Nordmann, in Jessen et al., 1910). Stratigraphical range: Miocene to Recent.

*Mya truncata* is considered a Pacific species that migrated into the Arctic Ocean and the North Atlantic while the Tjörnes beds were deposited (Durham & MacNeil, 1967; Strauch, 1972). The earliest appearance of *Mya truncata* in Iceland and probably in Europe as well is in the *Serripes* Zone of the Tjörnes beds. There, the species is extremely rare, and it is first in the Lower Pleistocene Breiðavík Group that it is commonly found. While we have found about 100 valves of *Mya schwarzbachi* in the Tjörnes beds, we have only this single valve of *Mya truncata* and several valves of *Mya truncata gudmunduri* reported by Strauch (1972). We do not know about any other Pliocene deposits east of Arctic Canada where the species occurs, and several authors (cf. MacNeil, 1965; Strauch, 1972) have indeed regarded it as characteristic for Pleistocene deposits in the North Atlantic area, and it may still be so with this one exception?

*Mya truncata* is widespread and well known in the Icelandic Breiðavík beds, as well as in Lower Pleistocene Greenlandic localities. It reached Meighen Island during the Pliocene and shortly after that, it appeared in the Tjörnes area, but apparently it did not arrive in the British Isles and continental Europe until in Lower Pleistocene.

***Mya truncata gudmunduri* Strauch, 1972**
Plate 7.17. Figs. 1–2

1972 *Mya truncata gudmunduri* – Strauch: p. 138–140, Pl. 10, fig. 6, Pl. 11, figs. 8–9.

*Material:* Strauch (1972) reported several valves from units 14, 17, and 19 in the S*erripes* Zone, but did not mention how many shells he found. Unfortunately, we have not found this subspecies in our collection, and Gladenkov et al. (1980) did not mention it.

*Remarks:* The valve shown by Strauch (1972: pl. 10, fig. 9) is 51 mm in length and 32 mm high. He found the average h/l ratio for the specimens from the *Serripes* Zone to be 0. 628.

The typical *Mya truncata* with straight truncate posterior end has only been found in one specimen in the Tjörnes beds, whereas Strauch (1972) has reported this subspecies named after the Icelandic naturalist Guðmundur G. Bárðarson (1880–1933). The first biostratigraphic description and division of the Tjörnes beds was given by him in 1925, and it has been retained since then. This subspecies has an oblique instead of a straight posterior margin resulting in a ventral margin that is longer than the dorsal margin. Apparently, juvenile specimens had an ovate posterior end characteristic for the typical *Mya truncata* until it begins to bury into the bottom sediments. At that stage the posterior end became truncate. In some southerly populations of *Mya truncata* there is a tendency to this form which has been regarded as adaption to higher sea temperatures (see Strauch, 1972: p. 139). This form is opposite to the form of *Mya truncata uddevalensis,* regarded as adapted to colder sea water (Fig. 7.20).

Strauch (1972) also recorded this subspecies from the Coralline Crag Formation and selected a specimen from Ramsholt in East Anglia reported by Wood in 1857 (pl. 28, fig. 196) as the holotype.

*Distribution, ecology, and biology: Mya truncata gudmunduri* is extinct, but seems to have preferred somewhat higher sea-water temperatures than the typical form. It was probably a boreal species when comparing its distribution and occurrences with boreal recent species found in sediments. It is more likely that it had lusitanian rather than subarctic or arctic outposts. Bathymetrical range was apparently similar to that of *Mya truncata,* from the coast and down to several hundreds of meters. The juveniles were probably living closer to the coast than the burrowing adults. The salinity tolerance is unknown, but the subspecies was probably a suspension feeder with a planktotropic larval development (cf. Símonarson et al., 1998).

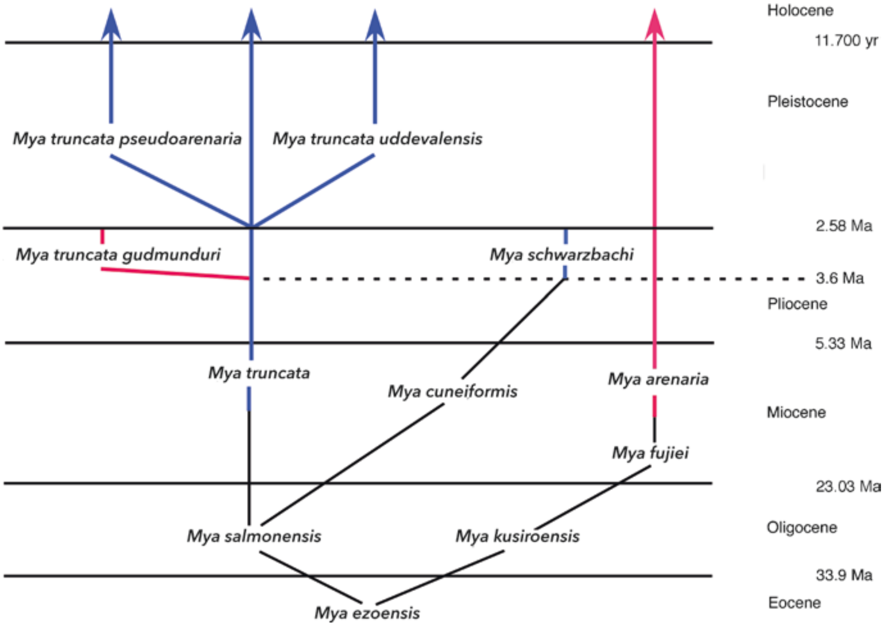

**Fig. 7.20** Phylogeny of myarian species and subspecies found in Iceland. Species and subspecies marked with red arrows are more thermophilic than those marked with the blue ones. The time scale is not proportional. Slightly modified from MacNeil (1965) and Strauch (1972)

*Mya truncata gudmunduri* seems to have preferred sandy bottom where the adults could burrow in the bottom eventually in offshore areas.

*Fossil occurrence:* Pliocene: Coralline Crag (Wood, 1857), revised by Strauch (1972), *Serripes* Zone in the Tjörnes beds (Strauch, 1972), Oorderen Sand Member and Kruisschans Sand Member in Belgium (Marquet, 2005). Stratigraphical range: Pliocene.

As this subspecies reached Iceland at the same time as *Mya truncata,* it most probably evolved from that species when it migrated into the North Atlantic during the Pliocene while the *Serripes* Zone was deposited in the Tjörnes area.

### *Mya schwarzbachi* Strauch, 1972

Plate 7.17. Fig. 3

1972 *Mya schwarzbachi* – Strauch: p. 143–147, Pl. 10, figs. 1–4, Pl. 11, figs. 1–4.
1857 ?*Mya pullus* J. Sow. – Wood: p. 278.
1863 *Mya arenaria* Linn. – Winkler: p. 205–206.
1924 *Mya truncata ovata* Ad. Jensen – Schlesch: p. 323, Pl. 6, fig. 1.
1925 *Mya truncata*, L. f. *ovata* Jensen – Bárðarson: p. 47, 50–53, 55, 57, 72–73.
1980 *Mya* cf. *ovata* Jensen, 1900 – Gladenkov et al.: p. 55.

1980 *Mya pseudoarenaria* Schlesch, 1931 – Gladenkov et al.: p. 55–56, Pl. 11, figs. 6–9 (in part).

*Material:* About 100 valves and a few paired specimens from units 13–23 and 25 in the *Serripes* Zone, where it is most abundant in the lower part of the zone (units 13–14).

*Remarks:* Some of the found specimens are paired in the sediment, but generally they are disarticulated and the thin shells are often damaged, especially the larger shells. Only a few were found in the position of life. The largest specimen measures (l × h × b): 86.3 × 52.3 × 33.8 mm.

Strauch (1972) described this species from the *Serripes* Zone and compared it to the *Mya truncata*-group, and he pointed out that the posterior end is ovate and not truncate as in typical *Mya truncata*, and distantly more tapering than in *M. truncata pseudoarenaria* (see Plate 7.17, Fig. 3). The chondrophore in the left valve of *Mya schwarzbachi* is much more tapering toward the posterior end than in *Mya truncata* and distinctly less spoon-shaped, and it is not at all projecting as in *Mya arenaria* (Fig. 7.21). Furthermore, Strauch (1972) emphasized that the h/l ratios are close to 0.578 in *M. schwarzbachi* while they are about 0.664 in *M. truncata pseudoarenaria*. We share the opinion of Strauch (1972) that these specimens from the Tjörnes beds differ significantly from other species of *Mya,* and therefore it seems justifiable to describe *M. schwarzbachi* as a separate species.

*Distribution, ecology, and biology: Mya schwarzbachi* has not been found living today. It seems to have preferred conditions comparable to the boreal region of the North Atlantic. It was probably a boreal species when comparing its distribution and occurrences with boreal recent species in the sediments. It is more likely that it had lusitanian rather than subarctic or arctic outposts. Bathymetrical range was apparently similar to that of *Mya truncata,* from the coast and down to several hundreds

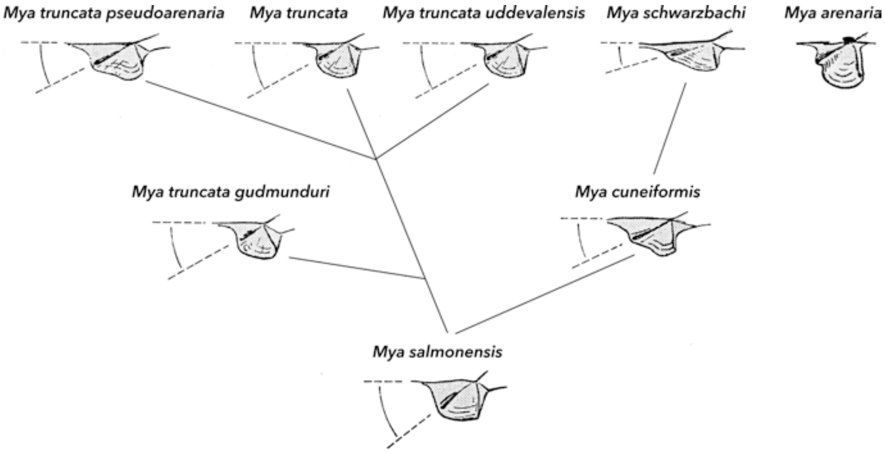

**Fig. 7.21** Phylogeny of the chondrophors in myarian species and subspecies found in Iceland. Slightly modified from Strauch (1972)

of meters. The juvenile were probably living closer to the coast than the burrowing adults. The salinity tolerance is unknown but the species was probably a suspension feeder with a planktotropic larval development (cf. Símonarson et al., 1998).

*Mya schwarzbachi* seems to have preferred sandy bottom where the adults could burrow in the bottom.

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Wood, 1857), revised by Strauch (1972), *Serripes* Zone in the Tjörnes beds (Gladenkov et al., 1980; Strauch, 1972). Stratigraphical range: Pliocene.

Strauch (1972) regarded *Mya schwarzbachi* as evolved from *M. cuneiformis* (Böhm, 1915) during the Pliocene, when it migrated from the Pacific into the Arctic Ocean, but apparently *M. cuneiforms* did never reach the North Atlantic or the Tjörnes area.

### Family Corbulidae Lamarck, 1818

### Genus *Lentidium* Christofori & Jan, 1832

***Lentidium complanatum* (Sowerby, 1822)**
Plate 7.17. Figs. 4–8

1822 *Corbula complanata* – Sowerby: p. 86, Pl. 362, figs. 7–8.
1857 *Corbula complanata*, J. Sowerby – Wood: p. 275–276, Pl. 30, fig. 2a–d.
1863 *Corbulomya complanata* Sow. – Winkler: p. 206–207.
1924 *Corbulomya complanata* J. Sowerby – Schlesch: p. 325, Pl. 6, fig. 6.
1925 *Corbulomya complanata* (Sow.) – Bárðarson: p. 35, ?41, 74–75.
1925 *Corbulomya Winkleri*, Mörch – Bárðarson: p. 45, 59, 72–73.
1950 *Aloidis (L.) complanata* (J. Sowerby, 1822) – Heering: p. 190–191, Pl.17, figs. 23–24, 27–28.
1980 *Lentidium complanatum* (Sowerby, 1822) – Gladenkov et al.: p. 56, Pl. 12, figs. 1–11.

*Material:* Numerous valves, both paired and disarticulated, from almost all units in the three biozones; however, the species is most common in the *Mactra* Zone. In unit 12 in the *Mactra* Zone there is a layer up to 50 cm in thickness consisting almost entirely of this species. There most adult specimens consist of disarticulated valves, but the smaller (juvenile) specimens are frequently paired. Furthermore, Emilsson (1929) has reported a few badly preserved specimens from the Eyvík Formation (cf. Eiríksson et al., 2020a).

At last but not least, Jóhannes Björnsson, a farmer in Ytri-Tunga on Tjörnes, found 527 specimens belonging to this species in a shelly lens in unit 9 in the *Mactra* Zone. The majority (about 90%) of the specimens in the lens are juvenile and with paired valves.

*Remarks:* The largest valve measures (l × h): 34.6 × 20.1 mm. The ratios h/l and b/l were calculated for about 70 valves and the h/l ratios vary from 0.52 to 0.65 and the b/l ratios are 0.16–0.22. The valves are rather thick and usually entire.

The size-frequency distribution of *Lentidium complanatum* from the lens in unit 9 is right-skewed and therefore the death rate seems especially high among the young animals (Fig. 7.22). This indicates strongly biocoenosis from different layers

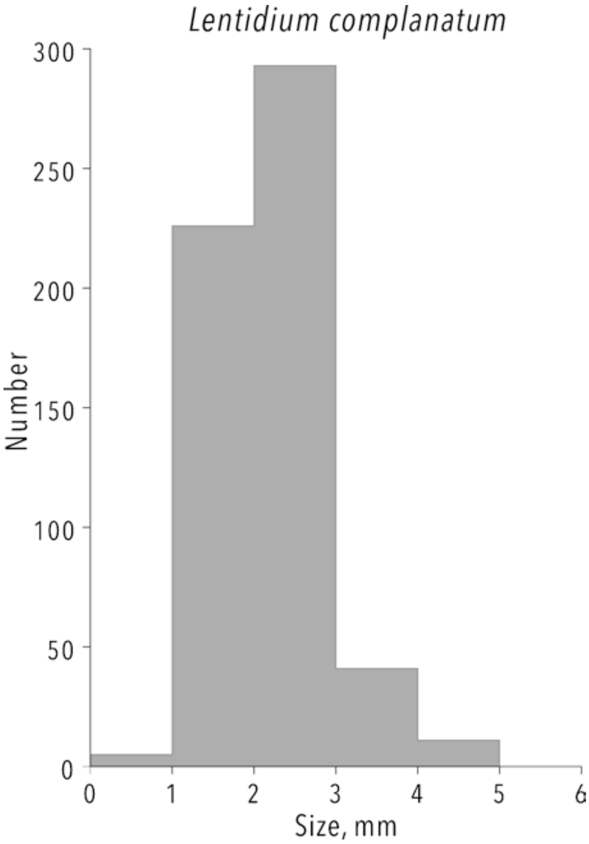

**Fig. 7.22** Size-frequency distribution of all measurable shells of *Lentidium complanatum* (Sowerby) in a shelly lens in unit 9 in the *Mactra* Zone

where currents size-sorted the sediment, but left the heavier shells to accumulate as a lenticular lag deposit.

*Distribution, ecology, and biology:* The distribution of the extinct *Lentidium complanatum* indicates strongly that the species lived in boreal settings. The bathymetrical range is not known, but almost everywhere it has been found in sediments deposited close to the coast in rather shallow water. In the Tjörnes beds it occasionally forms layers of various thickness almost entirely consisting of this one species in very great numbers. This distributional pattern indicates that the species had salinity tolerance down to about 5‰. Furthermore, Wood (1857) pointed out that this was probably an estuary shell. Apparently, the larval development had a pelagic stage as frequently found with boral-lusitanian bivalves.

The species lived mainly on sandy substrates, but in the Tjörnes beds the occurrence is usually in layers consisting almost exclusively of shell material of *Lentidium complanatum.*

*Fossil occurrence:* Miocene: Touraine in France (Heering, 1950). Pliocene: Lillo Formation (Heering, 1950), *Nassarius propinquus-Lentidium complanatum* Zone in the Netherlands (Spaink, 1975). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1857). Stratigraphical range: Miocene to Lower Pleistocene.

### Family Hiatellidae Gray, 1824
### Genus *Hiatella* Bosc, 1801

***Hiatella arctica* (Linné, 1767)**
Plate 7.17. Figs. 9–10

1767 *Mya arctica* – Linné: p. 113.
1857 *Saxicava arctica*, Linnæus – Wood: p. 287–288, Pl. 29, fig. 4a–b.
1878 *Saxicava arctica*, Lin. – Sars: p. 95–96, Pl. 20, fig. 8a–c.
1924 *Saxicava rugosa* Pennant = *S. arctica* (Linné) – Schlesch: p. 324.
1925 *Saxicava* sp.? – Bárðarson: p. 66, 70.
1934 *Saxicáva árctíca* (L.) – Jensen & Spärck: p. 165–166, fig. 150.
1950 *Saxicava (S.) arctica* (Linné, 1767) – Heering: p. 184–185.
1980 *Hiatella arctica* (Linné, 1767) – Gladenkov et al.: p. 57, Pl. 12, figs. 14–16.
2005 *Hiatella arctica* (Linnaeus, 1767) – Sneli et al.: p. 153–154.

*Material:* Two single valves from unit 9 in the *Mactra* Zone, and 27 valves, mostly disarticulated, from units 13–19 in the *Serripes* Zone. Furthermore, Bárðarson (1925) reported *Saxicava* sp.? which we attribute to *Hiatella arctica* from unit 25 in the *Serripes* Zone.

*Remarks:* The largest valve measures (l × h × b): 23.4 × 13.2 × 6.6 mm. The valves from the Tjörnes beds are small, especially when compared to the rounded type as the only *Hiatella* larva in the East Greenland plankton, and Sullivan (1948) found it also as the only *Hiatella* type in Malpeque Bay, East Canada. Regarding the existence of these different larval forms as evidence of different species of *Hiatella,* their distribution indicates strongly that *H. arctica* is a more southerly form in spite of the specific name (cf. Thorson, 1951).

Some authors have pointed out that only *H. rugosa* is a borer, whereas *H. arctica* never bores. Hunter (1949) has stressed the improbability of this after studying the two *Hiatella* larvae in the Clyde area. He concluded that larvae attributed to *H. rugosa* do not necessarily become borers, those to *H. arctica* may settle and begin to bore. The character of the larva does not determine the boring or non-boring habit of the adult, which instead is determined by the nature of the substratum upon which settlement takes place. Some malacologists (cf. Poppe & Goto, 1993) have pointed out that *H. arctica,* especially as juvenile, is attached by byssal threads to all kinds of substrates, while *H. rugosa* has no byssus at all. Furthermore, shell of *H. arctica* is more equivalve, thinner and less chalky, and generally smaller than the shell of *H. rugosa,* but the spines on the surface of the juvenile shell seem to disappear when they burrow into the substrates. However, it is difficult to separate the two species when they become mature because of an extreme convergence in form, and it is not possible to discern the larval forms in fossil material (cf. Fig. 7.23).

Specimens of *Hiatella* from Greenland were referred to *H. byssifera* by Petersen (1978). However, as he based his arguments on different parasites and life strategy, it is hardly possible to use his methods on a fossil material.

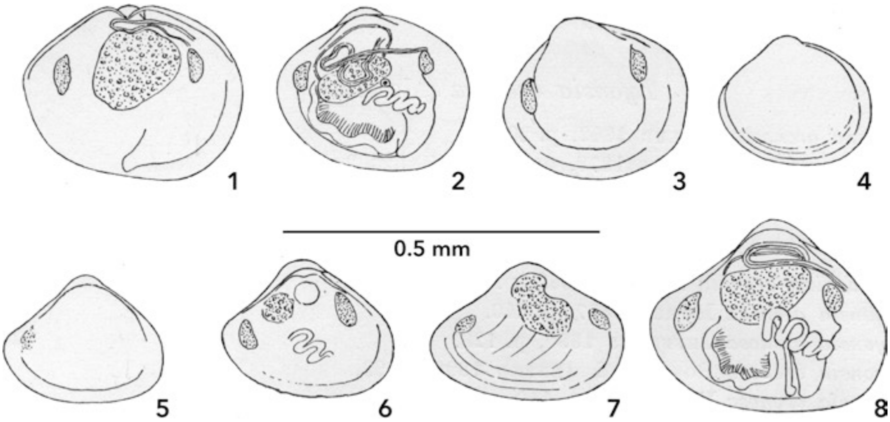

**Fig. 7.23** Pelagic larvae of *Hiatella* from the North Atlantic and Mediterranean. The rounded larvae 1–4 were identified as *H. rugosa* (Linné), while the more triangular form, 5–8, was referred to *H. arctica* (Linné). From Thorson (1951)

*Recent distribution, ecology, and biology:* The two *Hiatella* species have different distribution in the North Atlantic, but *Hiatella arctica* seems to have its northern limit in Southwest Greenland, North Iceland, northern Norway, and ?northern Alaska (MacGinitie, 1959; Símonarson, 2004; Thorson, 1951). *H. arctica* is distributed farther south in the Atlantic to North Angola and the West Indies and in the Pacific to northern Japan, Panama, and Hawaii, whereas *H. rugosa* reaches Morocco, but the southern limit on the east coast of North America is unknown, and apparently *H. rugosa* is not living in the Pacific (Bernard, 1979; Poppe & Goto, 1993; Strauch, 1968). *H. arctica* occurs in the Mediterranean (Poppe & Goto, 1993) and it goes into the Baltic southward to Øresund and the Kiel area (Jensen & Spärck, 1934). The geographical distribution indicates strongly that *H. rugosa* is circumpolar, but the occurrences of *H. arctica* seem too discontinuous for a circumpolar species. However, it must be pointed out that it is difficult to give the exact geographical distribution, as well as bathymetrical range for each species because they are treated together as one species in most papers.

The geographical distribution indicates that *Hiatella arctica* generally prefers higher sea temperature than *H. rugosa*. In the Faroe Islands *H. arctica* prefers water temperatures above 7.0°C, whereas *H. rugosa* has been found living at 6.8°C (Sneli et al., 2005). However, Strauch (1968) has pointed out that there is a close relationship between sea temperatures and the shell length of *H. arctica* and suggested that it can be used to estimate palaeotemperatures. According to Strauch (1968) there is only one species of *Hiatella* in the Atlantic, as well as the Pacific and he did not accept that we are dealing with two species with different geographical distribution and preferring different sea temperatures. His method has been discussed by Rowland and Hopkins (1971) who stressed that in the Pacific the length is governed by mode of life of each population and not only the sea temperature. Therefore, this method should be used with care as an exact paleothermometer, although it is often a good indicator (Símonarson, 2004).

The bathymetrical range for *Hiatella arctica* is from the littoral zone or 0 m in several localities down to 2190 m west of Ireland, ?alive (Ockelmann, 1958). In the British Isles it is very common from the lower shore to considerable depths, and in the Faroe Islands it is common in the fiords, as well as offshore in shallow water to a depth of about 300 m (Sneli et al., 2005; Tebble, 1966). The marine species has a lower salinity tolerance of 5‰ (Funder et al., 2002). The larval development has a prolonged pelagic stage as described by Thorson (1936, 1951). That explains the almost cosmopolitan distribution of the species (Barash & Danin, 1987; Poppe & Goto, 1993).

In the British Isles *Hiatella arctica* is living as a nestler, attached by its byssus in holes or rock crevices, or it is living as a borer in rather soft sediments or rocks (Tebble, 1966). Some authors have stated that *H. rugosa* is a borer, but *H. arctica* never bores. As mentioned before, this is most probably not the case.

*Fossil occurrence:* Oligocene: North Sea Basin in Denmark, Germany, and the Netherlands (Sorgenfrei, 1958). Oligocene/Miocene: Narrow Cape and Yakataga Formations (Allison, 1978; MacNeil, 1965). Miocene: Arnum, Ribe, and Gram Formations in Denmark, Aquitanian, Elveziano, and Tortoniano (Schnetler, 2005; Sorgenfrei, 1958). Pliocene: Coralline Crag Formation (Wood, 1857), Oosterhout Formation (Heering, 1950), Kallo and Doel sections (Marquet, 2005). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1857). Lower Pleistocene: Norwich Crag Formation (West et al., 1980), Pattorfik beds (Símonarson, 1981b), Olkov and Tusatuva-Yamsk Suites (Petrov, 1982), Gubik Formation, Fishcreekian (Repenning et al., 1987). Middle Pleistocene: Kotzebuan (Hopkins et al., 1972), Anvilian (Hopkins et al., 1974), Rogov Suite and the Mikulin and Molovo-Seknyn horizons (Merklin et al., 1979), Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Oligocene to Recent. However, it is difficult to give the exact fossil occurrence for *Hiatella arctica,* as well as *H. rugosa* as they are treated as one species in most papers.

Durham and MacNeil (1967) considered *Hiatella arctica* to have originated in the Atlantic before it migrated to the Pacific. On the other hand, Bernard (1979) and Gordillo (2001), however, regarded it as a Pacific species that migrated into the Arctic Ocean and the North Atlantic and suggested it evolved from *H. sahalinensis* (Takeda, 1953). These three authors supposed the species migrated through the Bering Strait after its opening before 4.8 Ma ago, but after 5.5 or even 7.4 Ma ago (Marincovich, 2000; Marincovich & Gladenkov, 1999). If the Oligocene specimens are correctly identified as *H. arctica,* then the species was already distributed in the North Sea Basin long before the opening of the Bering Strait (see Gordillo, 2001; Sorgenfrei, 1958). It is therefore tempting to follow Durham and MacNeil (1967) and consider it as an Atlantic form as *H. arctica* has distinctly an earlier appearance in the Atlantic than in the Pacific. If it migrated into the Pacific before the opening of the Bering Strait, another route in the form of the Central American Seaway was available before it became closed at least 3.6 Ma ago (Marincovich, 2000).

### Genus *Panomya* Gray, 1857

### ***Panomya trapezoidis*** **Strauch, 1972**
Plate 7.17. Fig. 11

1972 *Panomya trapezoidis* – Strauch: p. 70–74, Pl. 4, figs. 3–14.
1857 *Panopea norvegica,* Spengler – Wood: p. 281–283, Pl. 29, fig. 1a–e.
1863 ?*Panopaea norwegica* Spengler – Winkler: p. 208.
1924 *Panomya norvegica* (Spengler) = *P. turgida* Dall = *P. arctica* Lamarck – Schlesch: p. 324.
1950 *Panomya arctica* (Lamarck, 1818) – Heering: p. 187–188.
1972 ?*Panomya ampla* Dall, 1898 – Strauch: p. 61, Pl. 4, fig. 13.
1980 *Panopea (Panomya)* cf. *trapezoides* Strauch, 1972 – Gladenkov et al.: p. 60, Pl. 10, figs. 11–14.
1986 *Panopea (Panomya) norvegica* Spengler, 1793 – Malatesta & Zarlenga: p. 111–112, fig. 24.

*Material:* Twenty-six valves, mostly disarticulated, from unit 12 in the *Mactra* Zone and units 13–19 and 23 in the *Serripes* Zone.

*Remarks:* The largest valve measures (l × h): 56.1 × 37.0 mm, and the average h/l ratio is around 0.69.

Strauch (1972) described two new species of *Panomya* from the *Serripes* Zone on Tjörnes, viz. *Panomya trapezoidis* and *P. obliquelongata.* Furthermore, he came to the conclusion that *P. trapezoidis* is still living as several recent, as well as fossil specimens in the Pacific area are identical with Strauch's fossil forms. Earlier, they were generally referred to as *P. ampla* (see Grant & Gale, 1931). Strauch based his species identifications almost entirely on differences in shell forms or outlines. His conclusions have been discussed, and it has been emphasized that Strauch's new species are based on subtleties in shape, characters that are hardly usable in this genus consisting of species very variable in intraspecific forms (Coan et al., 2000). We are aware of these difficulties, but are tempted to follow Strauch's identifications at least concerning the Tjörnes specimens. Having compared them with recent, as well as fossil specimens, especially from the North Atlantic area, it seems justifiable to treat *P. trapezoidis* and *P. obliquelongata* as separate species as their form or shape is rather constant and obviously different from other known species. This is predominantly the case when dealing with *P. trapezoidis.*

*Recent distribution, ecology, and biology:* The distribution of fossil *Panomya trapezoidis* in the North Atlantic basins and faunas implies boreal preferences. Strauch (1972) reported the species from the Bering Sea southward to Puget Sound and considered this boreal "westamerikanische" species that generally had been referred to *P. ampla*, as identical with his new fossil form. Furthermore, he recorded it living in the Point Barrow area in North Alaska (from MacGinitie, 1959: as *P. arctica*). The bathymetrical range is not well known, but in the Tjörnes beds it has been found in sandy sediments deposits. The closely related *P. norvegica* is polyhaline with salinity tolerance above 25‰ (Funder et al., 2002), and it is tempting to suppose somewhat similar for *P. trapezoidis* when considering the paleoenvironments it preferred. The long migration route from the Pacific into the North Atlantic during the Pliocene indicates pelagic larval development.

*Fossil occurrence:* ?Oligocene: Poul Formation in South Alaska (Clarke, 1932: as *Panomya* n. sp.?). Pliocene: Lillo Formation (Heering, 1950: as *Panomya arctica*), Empire Formation in Oregon (Grant & Gale, 1931: as *Panope (Panomya) ampla*). Pliocene/Lower Pleistocene: Red Crag Formation and ?the Chillesford beds of Icenian (Wood, 1857: as *Panopea norvegica*). Lower Pleistocene: Santernian, Sicilian (Malatesta & Zarlenga, 1986: as *Panopea (Panomya) norvegica*). Upper Pleistocene: ?Eemian/Sangamonian at Sankaty Head, Nantucket (MacClintock & Richards, 1936 as *Panomya arctica*). Stratigraphical range: ?Oligocene to Recent.

The revision of the fossil material mentioned above was made by Strauch (1972) and according to him, *Panomya trapezoidis* originated in the Pacific and migrated into the Arctic Ocean and the North Atlantic during the Pliocene. Then, it evolved into *P. obliquelongata* which has been found together with *P. trapezoidis* in the *Serripes* Zone, and, furthermore, it evolved via *P. bivonae* into the recent *P. norvegica* during the Lower or Middle Pleistocene. According to Durham and MacNeil (1967), *P. norvegica* also has Pacific affinities.

***Panomya obliquelongata* (Strauch, 1972)**
Plate 7.18. Fig. 1

1972 *Panomya obliquelongata* – Strauch: p. 77–76, Pl. 6, figs. 1–11.
1924 *Panomya norvegica* (Spengler) – Schlesch: p. 324 (in part).
1980 *Panopea (Panomya) obliquelongata* Strauch, 1972 – Gladenkov et al.: p. 59–60, Pl. 10, figs. 15–16.

*Material:* Eleven valves mainly disarticulated from units 14–18 in the *Serripes* Zone.

*Remarks:* The largest valve measures (l × h): 58.2 × 36.7 mm and the h/l ratio is close to 0.63. The species is therefore more elongated than *P. trapezoidis*.

The valves we refer to as *Panomya obliquelongata* have all a more rounded anterior margin than *P. trapezoidis* while the posterior end is less obliquely truncated than that of *P. trapezoidis* (cf. Gladenkov et al., 1980: pl. 10, fig. 15). The dorsal shell margin is distinctly more sloping from umbo both posterior and anterior when compared to *P. norvegica*, a species with clearly more parallel dorsal and ventral margins (see Jensen & Spärck, 1934; Óskarsson, 1952; Tebble, 1966: fig. 92). However, it should be born in mind that the *Panomya* species are rather irregular in outline.

*Distribution, ecology, and biology:* The distribution of *Panomya obliquelongata* in the Tjörnes sediments together with several boreal species indicates that this extinct species preferred conditions prevailing in the boreal region today. The bathymetrical range is not well known, but in the Tjörnes beds it has been found in sandy sediments deposited not far from the coast, and apparently it lived closer to the coast than the recent *P. norvegica*. The closely related *P. norvegica* has a salinity tolerance above 25‰, and it is tempting to suppose a somewhat similar tolerance for *P. obliquelongata*. The larval development is unknown, but if it migrated from the

North Atlantic to the Pacific area as Strauch (1972) postulated, the long migration route might indicate pelagic larval development.

*Fossil occurrence:* Pliocene: The *Serripes* Zone of Tjörnes (Gladenkov et al., 1980; Strauch, 1972). ?Lower Pleistocene: Second beach at Nome, Alaska (MacNeil et al., 1943: as *P. ampla*, according to Strauch's revision). Stratigraphical range: Pliocene to ?Lower Pleistocene.

### Genus *Cyrtodaria* Reuss, 1801

**_Cyrtodaria angusta_ (Nyst & Westendorp, 1839)**
Plate 7.18. Figs. 2–4

1839 *Glycimeris angusta* – Nyst & Westendorp: p. 396, Pl. 1, fig. 1.
1857 *Glycimeris angusta*, Nyst & Westendorp – Wood: p. 291, Pl. 29, fig. 2a–d.
1863 *Cyrtodaria siliqua* Spengler – Winkler: p. 207–208.
1863 *Cyrtodaria Heeri*. Winkler – Winkler: p. 208.
1924 *Cyrtodaria angusta* Nyst = *C. heeri* Winkler – Schlesch: p. 324, Pl. 6, figs. 3–4.
1924 *Cyrtodaria siliqua* Spengler – Schlesch: p. 324, Pl. 6, fig. 2.
1950 *Cyrtodaria angusta* (Nyst et Westendorp 1839) – Heering: p. 189–190.
1960 *Cyrtodaria* (?) *angusta* Nyst & Westendorph – Áskelsson: p. 20–21, Pl. 2, fig. 19a, Pl. 3, fig. 19.
1972 *Cyrtodaria angusta* (Nyst & Westerndorp 1839) – Strauch: p. 93–95, Pl. 8, figs. 1–20.
1972 *Cyrtodaria jenisseae* Sachs 1953 – Strauch: p: 92–93, Pl. 7, fig. 9.
1980 *Cyrtodaria angusta* (Nyst et Westendorp, 1839) – Gladenkov et al.: p. 58, Pl. 10, figs. 17–21, Pl. 21, figs. 1–5.

*Material:* About 500 valves from almost all units in the Tjörnes beds, from unit 1 in the *Tapes* Zone, through the *Mactra* Zone, and up to the uppermost part of the *Serripes* Zone. The species is one of the most common bivalve in the Tjörnes beds. Furthermore, Emilsson (1929) has reported a few badly preserved specimens from the Eyvík Formation (cf. Eiríksson et al., 2020a).

*Remarks:* The largest valve measures (l × h × b): 83.1 × 38.2 × 17.5 mm with the h/l ratios 0.41–0.50 and the b/l ratios 0.18–0.21.

Some valves are paired or articulated in the sediment, but the majority is disarticulated and reworked indicating death assemblages (thanatocoenosis). However, in some units there are several articulated valves, even in life position, or the left and the right valves are lying side by side after disarticulation. This indicates a restricted post-mortal transport and reworking before sedimentation and parautochtonous type of a death assemblage rather than biocoenosis. Burrowing species as *Cyrtodaria angusta* are more often found with articulated valves and occasionally in life position.

*Distribution, ecology, and biology: Cyrtodaria angusta* occurred in boreal fauna assemblages in the Northeast Atlantic, in Iceland and the North Sea Basin. The distribution of sediments with the extinct *Cyrtodaria angusta* indicates strongly that the species preferred conditions as now prevailing in the boreal region of the North Atlantic. It was apparently distributed from Iceland in the north to South England in the south. The bathymetrical range is not known, but almost everywhere it has been found in sediments deposited in rather shallow water close to the coasts. The occurrence together with *Lentidium complanatum* here and there in the Tjörnes beds indicates a marine species, but the salinity tolerance is unknown, possibly it was down to 15‰. Apparently, the larval development had a pelagic stage as frequently found in boreal bivalves today.

The species was most probably a suspension feeder that lived infaunally in sandy bottom. The burrowing depth of *C. angusta* is unknown, whereas the recent and closely related infaunal species *C. siliqua* (Spengler, 1793) prefers a bottom of fine-grained sand, but its burrowing depth is only a few centimeters as the siphons are rather short (Nesis, 1965). Perhaps it could descend several tens of centimeters from the bottom surface if disturbed as has been observed in the sword razor (*Ensis ensis*) of similar elongated form.

*Fossil occurrence:* Miocene: Edegem, Kiel, Antwerpen, Zonderschot, and Deume in Belgium (Herman & Marquet, 2007). Pliocene: Coralline Crag Formation (Wood, 1857), ?Breda Formation, Oosterhout Formation (Heering, 1950). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1857). Lower Pleistocene: Svarthamar Member in Breiðavík (Eiríksson, 1981; Vilhjálmsson, 1985). Middle Pleistocene: Russian Arctic, from Kolgujew Island to Khatanga River (Nesis, 1965). Stratigraphical range: Miocene to Middle Pleistocene.

Strauch (1972) considered *Cyrtodaria angusta* evolved from *C. rutupiensis* (Morris, 1852) via *C. parva* (Speyer, 1866), and *C. neuvillei* Cossmann & Peyrot, 1909. *C. rutupiensis* was originally described from Lower Paleocene sediments in the London Basin (near Kent) and according to Strauch (1972), it evolved along a thermophilic line to the recent *C. siliqua* and a colder one to the recent *C. kurriana* Dunker, 1862. These two species are the only living representatives of the genus.

### Family Pholadidae Lamarck, 1809
### Genus *Zirfaea* Gray, 1842

**_Zirfaea crispata_ (Linné, 1758)**
Plate 7.18. Figs. 5–6

1758 *Mya crispata* – Linné: p. 1111.
1857 *Pholas crispata,* Linnæus – Wood: p. 296–297, Pl. 30, fig. 9a–c.
1878 *Zirphæa crispata,* Lin. – Sars: p. 97.
1924 *Zirphaea crispata* (Linné) – Schlesch: p. 325.
1925 *Zirphæa crispata*, L. – Bárðarson: p. 35, 59, 74–75.
1934 *Zirphæa crispáta* (L.) – Jensen & Spärck: p. 174–175, fig. 157.
1950 *Zirfaea crispata* (Linné, 1758) – Heering: p. 200.
1980 *Zirfaea crispata* Linné, 1758 – Gladenkov et al.: p. 60–61.

*Material:* One valve from units 8 and 10 in the *Mactra* Zone and 15 valves from units 17, 20, 23, and 25 in the *Serripes* Zone.

*Remarks:* The valves are mainly disarticulated and rather damaged. The single valve from the *Mactra* Zone is juvenile and measures (l × h × b): 15.0 × 10.2 × 0.56 mm. The largest measurable valve from the *Serripes* Zone measures 44.4 × 31.0 × 15.4 mm.

*Recent distribution, ecology, and biology: Zirfaea crispata* is mostly a boreal species with lusitanian, as well as subarctic outposts, extending from the northernmost parts of the Norwegian coasts and Iceland southward to the Bay of Biscay (Høisæter, 1986; Tebble, 1966). Feyling-Hanssen (1955b) reported the species from Svalbard in deposits from the Postglacial Warm Period and Mangerud and Svendsen (2017) recorded it in deposits from early Holocene at around 10.2–9.2 cal. ka BP. Then it reached Svalbard during a short warm period, but is not living today close to Svalbard. The species was living in northern Iceland in mid-Holocene, but then it disappeared and returned in the beginning of last century when the climate ameliorated and the sea temperatures rose around 1920 (Áskelsson, 1935). In the Baltic it has been reported from the Belt Sea to the northern part of Øresund and south to Kiel (Jensen & Spärck, 1934). It is not known from the Mediterranean. In northeastern America it is known living from Labrador and south to New Jersey (La Rocque, 1953; Tebble, 1966). It has been recorded from the North Pacific (Nordsieck, 1969), but Coan et al. (2000) did not mention it from western coasts of North America and considered it as an Atlantic species. Bathymetrical range: It is a shoreface species living down to the depth of 7 m (Poppe & Goto, 1993). In Iceland it has been found living down to 5 m (Madsen, 1949; Óskarsson, 1952). The marine species has a lower salinity tolerance of 5‰ (Funder et al., 2002). The larval development is with a pelagic stage as frequently found in thermophilic bivalves today (Jørgensen, 1946).

The species is an active burrower that bores into peat, siltstone, sandstone, and rarely in wood (Tebble, 1966). In Iceland it is named “bergbúi” which means simply “living in rock.”

*Fossil occurrence:* Pliocene: Coralline Crag Formation (Wood, 1857), Middle-Pliocene sediments of the Peel district in the Netherlands (Heering, 1950), Oorderen Sand Member and Kruisschans Sand Member in Belgium (Marquet, 2005). Pliocene/Lower Pleistocene: Red Crag Formation (Wood, 1857). Lower Pleistocene: Butleyan, Newbornian, and Waltonian (Wood, 1857). Middle Pleistocene: Mikulin horizon (Merklin et al., 1979). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Pliocene to Recent.

Durham and MacNeil (1967) listed *Zirfaea crispata* (Linné) as Icelandic fossil with Pacific affinities, even though it is not known to live in the Pacific area. On the other hand, Bernard (1983) reported it as introduced from the Atlantic. This shallow-water species reached the Tjörnes area during the deposition of the *Mactra* Zone, but it cannot be excluded that it developed from a Pacific *Zirfaea* (e.g., *Z. pilsbryi* Lowe) during the migration through the Arctic Ocean in Pliocene time.

### Family Teredinidae Rafinesque, 1815
### Genus *Teredo* Linné, 1758

***Teredo* sp.**
Plate 7.18. Figs. 7–8

*Material:* Several hundreds of tubes in a petrified piece of wood from unit 9 in the *Mactra* Zone. Unfortunately, no valves were found at the anterior end of the tubes or pallets at the posterior end, and therefore further species identification is not possible.

Paijkull (1867) reported *Teredo* sp. from the Tjörnes beds without further stratigraphical information, and Bárðarson (1925) mentioned a small piece of petrified woodbored by *Teredo* and suggested it derived from unit 8 in the *Mactra* Zone.

*Remarks:* The tubes are wider in the anterior end than in the posterior, up to 32.4 mm in length and having 3.8 mm as the largest diameter. They are very closely spaced in the wood, almost side by side (Plate 7.18, Figs. 7–8). They are filled with fine-grained gravel or coarse sand. The inner sides of the tubes were obviously coated by a thin calcareous layer secreted from the mantle (see Plate 7.18, Fig. 8). The sizes of the tubes, the calcareous coating, and the shallow-water sediments in this part of the *Mactra* Zone suggest a species belonging to *Teredo* rather than *Xylophaga*, but they occur both in Iceland today. In England, as well as Iceland, *Xylophaga* is mainly found in submerged woodwork (McMillan, 1968; Óskarsson, 1982). However, until either valves or pallets are found, further identification is not possible.

*Teredo navalis* Linné, 1758 has been shown to ingest wood in the night, whereas plankton is collected from inhalant water during the day (Morton, 1979). Apparently, the tubes are not entirely of the domichnia type.

*Fossil occurrence:* Wood (1857) reported *Teredo norvagica* Spengler, 1792 from the Pliocene Coralline Crag in England, as well as the Pliocene/Lower Pleistocene Red Crag deposits. The genus is known at least from the Eocene (Coan et al., 2000).

### Subclass Anomalodesmata Dall, 1889
### Order Pholadomyoida Newell, 1965
### Family Thracidae Stoliczka, 1870
### Genus *Thracia* Sowerby, 1823

#### *Thracia convexa* (Wood, 1815)
Plate 7.19. Fig. 1

1815 *Mya convexa* – Wood: p. 92, Pl. 18, fig. 1.
1857 *Thracia ventricosa*, Philippi – Wood: p. 262, Pl. 26, fig. 5a–c.
1934 *Thrácia convéxa* Wood – Jensen & Spärck: p. 188–189, fig. 172.
1950 *Thracia ventricosa* Philippi 1844 – Heering: p. 204.
1966 *Thracia convexa* (Wood) – Tebble: p. 197–198.
2005 *Thracia convexa* (Wood, 1815) – Sneli et al.: p. 155.

*Material:* Two specimens with paired valves from unit 5 in the uppermost *Tapes* Zone. The species is new to the fossil fauna of the Tjörnes beds.

*Remarks:* The larger specimen measures (l × h × b): 52.6 × 43.9 × 19.8 mm.

*Thracia convexa* is probably closely related to *T. inflata* Sowerby, 1845. However, the shell of the former is granulated, whereas the valves of *T. inflata* are very smooth (cf. Poppe & Goto, 1993; Tebble, 1966; Wood, 1857). Unfortunately, our valves from Tjörnes are rather badly preserved, the thin shells are somewhat dissolved, but they were far from smooth and apparently finely granulated. When the large size is also taken into consideration, it is most likely to refer the specimens from Tjörnes to *T. convexa*.

*Recent distribution, ecology, and biology: Thracia convexa* is a boreal-lusitanian species extending from Trondheimsfjord at the Norwegian west coast and South Iceland, where it was first found living in 1960, southward to the Mediterranean (Óskarsson, 1962; Sneli et al., 2005; Tebble, 1966). In the Baltic it has been found living in the Belt Sea south to Øresund (Jensen & Spärck, 1934; Sneli et al., 2005). Bathymetrical range: The species lives offshore from 10 to 824 m (Madsen, 1949; Nordsieck, 1969). It is polyhaline and its salinity tolerance is above 25‰ (Funder et al., 2002). The larval development is probably with a reduced or absent pelagic stage (cf. Thorson, 1936).

*Thracia convexa* prefers to live in sand or muddy bottom and is widely distributed around the British Isles except off the east coast of Scotland (Tebble, 1966).

*Fossil occurrence:* Miocene: Medina section, northern Italy (Beransconi & Robba, 1993). Pliocene: Coralline Crag Formation (Wood, 1857), Vreeburg-Utrecht Well in the Netherlands (Heering, 1950). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). The species is rarely found as fossil, but the stratigraphical range seems to be Miocene to Recent. *Thracia convexa* is considered an Atlantic species.

***Thracia phaseolina* (Lamarck, 1818)**
Plate 7.19. Fig. 2

1818 *Amphidesma phaseolina* – Lamarck: p. 492.
1857 *Thracia phaseolina*, Lamarck – Wood: p. 260–261, Pl. 26, fig. 2a–c.
1878 *Thracia papyracea*, Poli – Sars: p. 83–84.
1924 *Thracia truncata* (Brown) – Schlesch: p. 319 (from an unpublished manuscript of Poulsen, 1884).
1925 ?*Thracia* (*truncata*, Brown?) – Bárðarson: p. 51–52, 70.
1934 *Thrácia papyrácea* Poli – Jensen & Spärck: p. 188, fig. 171.
1950 *Thracia phaseolina* (Lamarck, 1818) – Heering: p. 203–204, Pl. 16, figs. 11–12.
1980 *Thracia* sp. – Gladenkov et al.: p. 62, Pl. 12, figs. 17–19.

*Material:* Eleven disarticulated valves from units 16–19 in the *Serripes* Zone.

*Remarks:* The largest valve measures (l × h × b): 14.3 × 11.1 × 3.4 mm. The h/l ratios for the specimens from Tjörnes are: 0.74–0.81. Heering (1950) recorded h/l ratios for *Thracia pubescens* (Pulteney, 1799) close to 0.67, and therefore *T. phaseolina* seems slightly more elongated. *Thracia truncata* (Sars, 1878) recorded by Bárðarson (1925) should probably be referred to *T. phaseolina* rather than *T. myopsis* (Møller, 1842).

The specimens in the Tjörnes beds are obviously reworked and subjected to postmortal transport before sedimentation representing a death assemblage (thanatocoenosis).

*Recent distribution, ecology, and biology: Thracia phaseolina* has been found living in the North Atlantic in the boreal, as well as the lusitanian region. It is distributed from the west coast of Norway at 68°N and southward to Morocco and Madeira (Soot-Ryen, 1941; Tebble, 1966), or even farther south to Angola (Poppe

& Goto, 1993). It has been recorded from the Belt Sea in the Baltic and in the Mediterranean, as well as the Black Sea (Jensen & Spärck, 1934; Tebble, 1966). Bathymetrical range: from the intertidal zone down to 55 m (Tebble, 1966). In Iceland it has been recorded at depths down to 143 m (Madsen, 1949). It is a polyhaline species with salinity tolerance down to 25‰ (Funder et al., 2002). The larval development is unknown.

In the British Isles the species prefers sand, muddy, or gravelly bottom (Tebble, 1966).

*Fossil occurrence:* Miocene: Vienna Basin (Heering, 1950). Pliocene: Coralline Crag Formation (Wood, 1857), Oosterhout Formation in the Netherlands (Heering, 1950). Upper Pleistocene: Baltic Eemian (Funder et al., 2002). Stratigraphical range: Miocene to Recent.

**Order Pholadomyoida Newell, 1965**
**Family Lyonsiidae Fischer, 1887**
**Genus *Lyonsia* Turton, 1822**

***Lyonsia* sp.**
Plate 7.19. Fig. 3

1980 *Lyonsia* sp. – Gladenkov et al.: p. 61, Pl. 12, figs. 12–13.

*Material:* Gladenkov et al. (1980) recorded three disarticulated valves, preserved as casts with only fragmentary remains of the shell material, in unit 14 in the *Serripes* Zone. The largest valve measures (l × h): 31.3 × 16.1 mm. Unfortunately, we have not found more specimens of this genus in the Tjörnes beds.

*Remarks:* The valves from Tjörnes can best be compared with *Lyonsia norwegica* (Gmelin, 1791). However, they differ in outline as the posterior end of *Lyonsia* sp. is much more oval and not so abruptly truncated as in *L. norwegica.* Furthermore, the dorsal margin of the posterior end is not bent upwards as is the case in *L. norwegia* (cf. Tebble, 1966: fig. 105). Actually, the Tjörnes valves can hardly be compared with any recent or fossil species of *Lyonsia,* but it is not possible to describe a new species based on such a few and rather badly preserved valves.

## 7.5 Cephalopoda

**Phylum Mollusca Linné, 1758**
**Class Cephalopoda Cuvier, 1797**
**Subclass Ammonoidea Zittel, 1884**
**Order Ammonitida Hyatt, 1889**
**Family Baculitidae Gill, 1871**
**Genus *Baculites* Lamarck, 1799**

***Baculites* sp.**
Plate 7.19. Figs. 4–6

Strauch (2006) reported fragments of *Baculites* sp. in a phosphoritic concretion found isolated on the shore north of Reká. Therefore, the exact stratigraphic position is not known, but as concretions like this are most frequently found in unit 6 in the lowermost *Mactra* Zone it is the most probable source.

The largest fragment is of a body chamber 28 mm long and a smaller fragment is a slightly elliptic cross section with a diameter up to 7 mm. The cross section is clearly along one of the sutures (Plate 7.19, Figs. 5–6). The shell material is almost entirely lost so the outer side of the shell is not preserved, but instead the sutures are visible. They are rather simple with slightly bifurcated saddles and small extra saddle in the lobes. Therefore, the sutures seem of lytoceratoid type and rather characteristic for *Baculites.*

*Baculites* became extinct close to the boundary between the Cretaceous and Palaeogene, long before the deposition of the Tjörnes sediments. Therefore, Strauch (2006) suggested that these shell remains were erratic and transported to the Tjörnes area by currents along a Pliocene land bridge that connected Iceland and Greenland. Among his arguments were remains of land-living mammals found in sediments of Pliocene age in eastern Iceland (cf. Símonarson, 1990). He assumed they represent animals which lived in Iceland, having been able to pass the bridge. Several plants and land-living animals are known to have become isolated in Iceland when it became an island already in Middle Miocene. They lived and evolved in Proto-Iceland or Iceland of that time for millions of years, but many of them disappeared during the earliest glaciations during the Lower Pleistocene.

Several possibilities for this erratic occurrence of *Baculites* in the Tjörnes beds may be suggested. It is conceivable fact that sea ice or icebergs may have carried them, but as we have not found any ice-rafted material within the sediments, it is not very likely. It is even more probable that it has been transported to the Tjörnes area by marine animals, that is, walrus, but remains of whales, walruses, and seals have been found in the sediments (Field et al., 2017). Even birds or fishes cannot be excluded as the fragments are rather small.

## 7.6 Arthropoda

**Phylum Arthropoda von Siebold, 1848**
**Class Crustacea Pennant, 1777**
**Subclass Cirripedia Burmeister, 1834**
**Order Thoracica Darwin, 1854**
**Family Balanidae Leach, 1817**
**Genus *Balanus* da Costa, 1778**

***Balanus hopkinsi*** **Zullo, 1968**
Plate 7.19. Figs. 6–11

1968 *Balanus hopkinsi* – Zullo: p. 4–6, figs. 3–10.
1925 Balanus sp. – Bárðarson: p. 21, 24, 31, 39.
1980 *Balanus hopkins* Zullo – Gladenkov et al.: table p. 8–9, table 1, p. 15.

*Material:* Several tens of wall rings (shells) and a few scuta and terga from all biozones, but it is most abundant in unit 1 in the *Tapes* Zone and unit 7 in the *Mactra* Zone (cf. Gladenkov et al., 1980; Zullo, 1968). Fragmentary parietal plates found in units 24–25 in the *Serripes* Zone are probably the youngest occurrence of the species in the Tjörnes area.

*Remarks:* The holotype and paratypes are kept in the U.S. National Museum, Washington, D.C. The paratypes have rostral height up to 31 mm, lateral diameter up to 17 mm, and carinorostral diameter up to 19.4 mm (Zullo, 1968).

The wall ring or shell is high conical to tulipform, bent towards short, acutely concave carina. The orifice is toothed, as broad or broader than the base. The parietal plates are almost smooth, only ornamented by fine longitudinal striae, much finer than the ribs in *Balanus balanus* (Linné, 1758). They reflect longitudinal tubes in the parietal plates, crossed by closely spaced transverse septa. The species has a calcareous basal plate. The scutum is strongly arched, with external longitudinal striae, and tergum is trident shaped with long and narrow pointed spur (cf. Zullo, 1968).

*Distribution, ecology, and biology: Balanus hopkinsi* is extinct and has not been recorded from other sites than the Tjörnes beds. Most probably the species preferred boreal condition as we know them today in the North Atlantic. Its occurrence in the littoral unit 1 and elsewhere in the *Tapes* Zone strongly indicates littoral habits, but it is also found in more sublittoral units in the *Serripes* Zone. Apparently, the species preferred marine environments as many of the molluscs occurring together with it in the lower parts of the Tjörnes beds. Its biology is not very well known, but generally the cirripeds have internal fertilization and do not shed sperm or eggs into the water for subsequent fertilization (Schäfer, 1972). Subsequently, the larvae have a pelagic stage lasting up to about one month before settlement, which generally takes place near the adults (Kaestner, 1967). It is rather likely that the larval development of *B. hopkinsi* was similar to what we find in recent species of cirripeds.

The species belonged to the epifauna living on shells, stones, and other subjects on the bottom. There are shells, especially in unit 7, almost entirely covered by *B. hopkinsi*, and they were actually sitting on each other in the struggle for suitable substrates.

*Fossil occurrence: Balanus hopkinsi* has not yet been recorded from any other sediments than the Tjörnes beds, where it has also been found in the lowermost units of the *Tapes* Zone, which may be of Upper Miocene age. We have never found it in the Pleistocene Breiðavík sediments resting on the Tjörnes beds, where *Balanus balanus* frequently occurs. *B. hopkinsi* was probably of Atlantic origin and became extinct by the cooling preceding glaciation in the Tjörnes area early in the Lower Pleistocene (Zullo, 1968). Stratigraphical range: ?Upper Miocene to Pliocene.

*Balanus hopkinsi* is similar and seems closely related to the western North Atlantic species *B. eburneus* Gould, 1841, which range today from Massachusetts in the north to Rio de Janeiro in the south (Zullo, 1968).

## 7.7 Correlation with Other Cainozoic Faunas

The molluscs and barnacle assemblages of the Barmur Group of Tjörnes is unique among Cainozoic marine faunas in the North Atlantic area. It contains the only marine Pliocene mollusc and barnacle assemblages north of the North Sea Basin. The only exception seems to be the xenolith fauna in the Skammidalur Formation in South Iceland. These faunal assemblages lived in sedimentary basins off the north and south coasts of Iceland, and the Tjörnes Basin was presumably the first stepping stone for some invertebrate species that migrated from the Pacific into the North Atlantic in Pliocene time.

In the present survey, 119 species of marine molluscs from the Tjörnes Beds Group have been treated, that is, 65 species of prosobranch gastropods, five opisthobranch gastropod species, 49 species of bivalves, and one ammonite species (reworked). Furthermore, one barnacle species is dealt with in this publication. Other groups such as foraminifera, dinoflagellates, sponges, annelids, ostracods, decapods, bryozoans, brachiopods, echinoderms, trace fossils, fishes, birds, and marine mammals (seals, walruses, and whales) are not included in this chapter. However, it should be mentioned that Cronin (1991) has dealt with the ostracods from the Tjörnes deposits, Verhoeven et al., (2011) studied the dinoflagellates, and Knudsen et al., (2020a) described the foraminifera from the Tjörnes beds. Their results are discussed and compared with the mollusc data, as well as lithological data by Símonarson et al., (2020).

At least 24 of the molluscan species have not been recorded before from the Tjörnes deposits, 19 gastropod species and five species of bivalves:

*Patella* cf. *aspera* Röding
*Hydrobia ulvae* (Pennant)
*Ecrobia* cf. *ventrosa* (Montagu)
*Rissoa obsoleta* (Wood)
*Pusillina* cf. *sarsi* (Lovén)
*Obtusella tumidula* (Sars)
*Alvania* cf. *punctura* (Montagu)
*Onoba aculeus* (Gould)
*Omalogyra atomus* (Philippi)
*Skeneopsis planorbis* (Fabricius)
*Capulus* cf. *unguis* (Sowerby)
*Colus* cf. *imperspicuus* (Wood)
*Nassarius* cf. *consociatus* (Wood)
*Cytharella* sp.

*Metaxia metaxa* (delle Chiaje)
*Melanella* cf. *frielei* (Jordan)
*Janthina* cf. *exigua* Lamarck
*Aclis* cf. *minor* (Brown)
*Ondina divisa* (Adams)
*Aequipecten opercularis* (Linné)
*Heteranomia squamula* (Linné)
*H. squamula aculeata* (Müller)
*Mya truncata* Linné
*Thracia convexa* (Wood)

About 25% of the mollusc species are extinct: 18 gastropod species and 14 species of bivalves. The only barnacle species found in the Tjörnes sediments, *Balanus hopkinsi* Zullo, has not been found living (Zullo, 1968). Recent molluscan species found in the Tjörnes beds, but not living in Iceland anymore, seems to be 25 species. At present, these species now live in more southerly localities with higher sea temperature than now prevailing in Iceland. About 62 of the mollusc species dealt with in this survey are still living in Icelandic waters; 37 gastropod species and 25 species of bivalves. At least 32 species dealt with in this publication have their first appearance (FAD) in the Pliocene Tjörnes beds.

There are two distinct faunal changes in the molluscan assemblages in the Tjörnes sequence (Símonarson & Eiríksson, 2008). One in the middle part of the *Mactra* Zone is clearly connected to environmental changes reflecting changes from intertidal or tidal flat environments to more sublittoral. *Paphia* and *Cerastoderma* species almost disappeared while *Arctica islandica* (Linné) and *Spisula arcuata* (Sowerby) became more common. The other faunal change, mainly visible in the lowermost part of the *Serripes* Zone, is of quite different character and not connected to environmental changes in the Tjörnes area. At that time, about 3.8 Ma ago, several species of North Pacific origin migrated into the North Atlantic and have since been among dominants in arctic, subarctic, and even boreal assemblages within marine faunas in the northern part of the Atlantic (Durham & MacNeil, 1967; Símonarson & Eiríksson, 2008). They include *Neptunea* species, *Buccinum undatum* Linné, *Serripes groenlandicus* (Mohr), *Ciliatocardium ciliatum* (Fabricius), *Macoma* species, and species belonging to the genus *Mya*. The younger faunal changes will be further discussed in a separate paper by Símonarson and Eiríksson (2020a) on the migration of the Pacific species into the North Atlantic in Pliocene time. At least 36 species of molluscs seem to be of Pacific origin, but 10 species are apparently of uncertain origin. The rest is probably species that originated in the Atlantic area.

The oldest species found in the Barmur Group sediments on Tjörnes are recorded from Oligocene formations, including well-known species as *Nucula nucleus* (Linné), *Hiatella arctica* Linné, and most probably *Arctica islandica* (Linné). They all live today in Icelandic waters, except for *Nucula nucleus* which is now very common around the British Isles (Tebble, 1966). Almost 20 species have their first appearance in Miocene sediments, that is, species such as *Littorina squalida*

(Broderip & Sowerby)*,* *Boreoscala greenlandica* (Perry), *Acteon tornatilis* (Linné), *Heteranomia squamula* (Linné), *Macoma calcarea* (Gmelin), *Ensis ensis* (Linné), *Mya truncata* Linné, and most probably *Mytilus edulis* Linné. They have all been recorded from post-Miocene deposits. The majority of the molluscan species found in the Tjörnes beds have their first appearance in Pliocene deposits and have not been recorded from younger sediments. They include prosobranch gastropods such as *Littorina islandica* Reid*,* *Nassarius tjoernesensis* Spaink*,* and *Curtitoma decussata tjoernesensis* (Schlesch), as well as the bivalves *Cerastoderma decorticata* (Wood)*, Mya truncata gudmunduri* (Strauch*),* and *Mya schwarzbachi* (Strauch). Furthermore, the barnacle *Balanus hopkinsi* has most probably not been found in post-Pliocene deposits (Zullo, 1968). At least 32 species of molluscs have their first appearance (FAD) in the Tjörnes beds. They include several well-known species such as the prosobranch gastropods *Patella pellucida* (Linné), *Lepeta caeca* (Müller), *Margarites groenlandicus* (Gmelin), *Hydrobia ulvae* (Pennant), *Onoba aculeus (*Gould*), Cryptonatica smithii* (Brown), and *Curtitoma trevelliana* (Turton), the opisthobranch gastropod *Cylichnoides occultus* (Mighels & Adams), as well as the bivalves *Nuculana minuta* (Müller)*,* *Musculus niger* (Gray), *Tridonta borealis* (Schumacher) and *T. elliptica* (Brown), and *Ciliatocardium ciliatum* (Fabricius).

Several mollusc species became extinct during the first cold episodes of Lower Pleistocene. Some of them have been frequently found in the Tjörnes beds, including bivalve species such as *Spisula arcuata* (Sowerby), the index fossil for the *Mactra* Zone, and *Lentidium complanatum* (Sowerby) the frequently used indicator for low salinity conditions. The prosobranch gastropods *Gibbula cineroides* (Wood), *Rissoa obsoluta* (Wood), and *Euspira catenoides* (Wood) also disappeared during the Lower Pleistocene. Even more molluscan species became extinct during the severe glaciations of Middle Pleistocene. This includes species such as the gastropods *Colus olavii* (Mörch*)*, ?*Neptunea lyratodespecta* Strauch*, Searlesia costifera* (Wood) and *S. lundgrenii* Harmer, *Nassarius reticosus* (Sowerby), and *Acteon noae* (Sowerby), together with the frequently found bivalve *Cyrtodaria angusta* Nyst & Westendorp, recorded from almost all units of the Tjörnes beds.

### *7.7.1 Other Icelandic Sites*

In the central part of South Iceland (Fig. 7.24) sedimentary xenoliths with marine molluscs have been found several places in the Skammidalur Formation (Áskelsson, 1960; Einarsson, 1962, 1968). The xenoliths have been carried up with hot magma during subglacial or submarine eruptions, most probably in Upper Pleistocene. The sediments were deposited in a sedimentary basin that evolved in the south end of the volcanic zone, with the Tjörnes basin in the north. This sedimentary basin in South Iceland is underlying the central part of the south coast and extends at least to Vestmannaeyjar in the south, where fossiliferous xenoliths have also been found in several places (Símonarson, 1974, 1982). The sedimentary xenoliths in Skammidalur contain marine fauna very similar to the faunal assemblages in the *Serripes* Zone of

**Fig. 7.24** The most important localities with faunal assemblages compared with Barmur Group (Tjörnes) fauna. They are mostly older than Lower Pleistocene. (TJ Barmur Group, Tjörnes, SK Skammidalur, South Iceland, EA East Anglia, NO North Sea Basin, LE Lodin Elv, East Greenland, SK Store Koldewey, East Greenland, IF Île de France, East Greenland, KK Kap København, North Greenland, PA Pattorfik, West Greenland, HL Hvitland, North Canada, MI Meighen Island, North Canada, AP Gubik Formation, Alaska, YF Yakataga Formation, Alaska, CH Chukotka, East Siberia, KA Kamchatka)

Tjörnes. Coastal proximity strongly indicated by plant remains in the sediments and the fauna was considerably more thermophilic than the recent fauna along the south and southwest coasts and contains no arctic taxa. Among extinct molluscan species found in the xenoliths are the opisthobranch gastropod *Acteon noae* (Sowerby*)*, and the bivalves *Pygocardia rustica* (Sowerby), *Macoma obliqua* (Sowerby), and *Cyrtodaria angusta* Nyst & Westendorp (Áskelsson 1960). They all occur in the *Serripes* Zone, and therefore those xenoliths are considered of similar Pliocene age. They were probably embedded in the oldest sediments in the southern basin, which was gradually filled up with sediments, lavas, and glacial pyroclastic products from the north or northeast so that the sediments became younger upwards and toward the south. The fossiliferous xenoliths found in Vestmannaeyjar support strongly this consideration, as well as data from the 1565 m deep drillhole on Heimaey (Pálmason et al., 1965; Símonarson, 1974, 1982).

Áskelsson (1960) came to the conclusion that the marine fauna in the Skammidalur xenoliths from South Iceland belong to "one animal society," which corresponds to the molluscan assemblages in the *Serripes* Zone of Tjörnes. He suggested that the zone is correlative with the Norwich-Red Crag beds and the Calabrian age of the European continent and considered it of Lower Pleistocene age. He based his suggestion on the occurrence of the opisthobranch gastropod *Acteon noae* (Sowerby) and the bivalves *Macoma obliqua* (Sowerby) and *M. calcarea* (Gmelin), but also concluded that recent species with subarctic and even arctic outposts in their distribution are more frequently found in the *Serripes* Zone than in the older zones of the Tjörnes beds. As mentioned before, it is not likely that the higher frequency of boreal species with subarctic or even arctic outpost in the *Serripes* Zone is due to significant changes in sea temperature in the Tjörnes area while this biozone was deposited. It is more probably result of immigration of North Pacific species into the deposits. The migration fauna is therefore not supposed to reflect changes in sea temperature in the Tjörnes area while the *Serripes* Zone was deposited, but in fact the temperature conditions farther north in the Arctic Ocean during the migration (see also Símonarson et al. (2020)).

The sediments of the Breiðavík Group on northern Tjörnes (see Símonarson & Eiríksson, 2020b) are younger than the Tjörnes beds and considered of Lower Pleistocene age, younger than 2.6–2.5 Ma (Eiríksson, 2008; Eiríksson et al,, 1992). The molluscan and the barnacles faunal assemblages in the Breiðavík sequence are quite different from those in the Tjörnes beds, arctic taxa are frequently found, and the more thermophilic species in the Tjörnes beds have disappeared (cf. Eiríksson et al., 2020b). About 2.1 Ma ago arctic marine fauna with *Portlandia arctica* (Gray) lived in the Breiðavík area while the Hörgi Formation was deposited. It has also been found higher up in the Breiðavík sediments. The disappearance of most of the thermophilic species found in the Tjörnes beds and glacial sediments in the Breiðavík beds is a further indication of a Lower Pleistocene age (Eiríksson, 1981, 2008).

### 7.7.2 North Sea Sites

The molluscan and barnacles faunal assemblages found in the sediments of the Barmur Group show the strongest faunal correlation with the marine faunal assemblages in the Pliocene sediments of the Crag basin of the North Sea area (Fig. 7.24). Although the lowermost units of the *Tapes* Zone most probably are of Upper Miocene age, none of the most characteristic Miocene species recorded from the North Sea Basin have been found in this part of the sequence (Glibert, 1952; Rasmussen, 1968; Sorgenfrei, 1958). The Tjörnes assemblages pre-date the Lower Pleistocene Pre-Pastonian/Baventian cold marine episodes recorded from Covehite in Suffolk (Gibbard et al., 1991; West et al., 1980). Distinctly arctic species such as *Portlandia arctica* (Gray), *Yoldiella frigida* (Torell), *Cyrtodaria kurriana* Dunker, or *Pandora glacialis* Leach have never been found in the Tjörnes beds. Arctic species are first met with in Iceland in the younger Lower Pleistocene deposits in Breiðavík, resting on the Barmur Group sediments and younger than 2.5–2.6 Ma.

The molluscan assemblages in the Tjörnes beds show the strongest correlation with the Pliocene assemblages in the Crag basin of the North Sea. There are even species that seem restricted to Pliocene deposits in the North Sea area. They include *Cerastoderma decorticata* (Wood), known from the *Tapes* and *Mactra* Zones and the Coralline Crag in England (Wood, 1874) and the Vreeburg-Utrect Well in the Netherlands (Heering, 1950), and *Mya truncata gudmunduri* Strauch, known from the *Serripes* Zone, has also been recorded from Coralline Crag sediments in England (Wood, 1851), revised by Strauch (1972), and Oorderen Sand Member and Kruisschans Sand Member in Belgium (Marquet, 2005). Furthermore, *Mya schwarzbachi* Strauch is only known with certainty outside the *Serripes* Zone in the English Coralline Crag deposits (Wood, 1851), revised by Strauch (1972). These species seem to be actually restricted to Pliocene deposits. Several molluscs, well known and frequently found in the Tjörnes beds, as well as the Pliocene deposits in the North Sea area, disappeared and became extinct at the beginning of the Pleistocene. Apparently, they could not withstand the cooling during the first glacials. Among these species are the prosobranch gastropods *Euspira catenoides* (Wood) and *Oenopota borealis* (Reeve), and the bivalves *Astarte* cf. *basterotii* de la Jonkaire, *Pygocardia rustica* (Sowerby), *Spisula arcuata* (Sowerby), *Macoma praetenuis* (Woodward), and *Lentidium complanatum* (Sowerby).

### 7.7.3 Greenlandic Sites

The mollusc and barnacle fauna in the Pattorfik beds, as well as the Kap København Formation and the late Cainozoic formations at Lodin Elv, Store Koldewey, and Île de France (Fig. 7.24) correlate better with the Lower Pleistocene Breiðavík fauna than the Pliocene Tjörnes fauna (Bennike et al., 2002, 2010; Feyling-Hanssen et al., 1983; Símonarson, 1981b; Símonarson et al., 1998). In all those formations, the well-known bivalve *Mya truncata* Linné has been frequently found, which strongly indicates a Pleistocene age. The arctic bivalve *Portlandia arctica* (Gray) is most probably of Lower Pleistocene origin (Símonarson et al., 1998) and has been found in the aforementioned Greenlandic sites, except in the Pattorfik beds and at Lodin Elv, and in Iceland it first occurred in the Breiðavík deposits. However, the Lodin Elv mollusc fauna is poor in species, but they are all living today and of arctic provenance, as emphasized by the occurrence of the arctic bivalve *Yoldiella frigida* (Torell) and *Similipecten greenlandicus* (Sowerby). Feyling-Hanssen et al. (1983) considered the Lodin Elv Formation to be of Pliocene age after comparison with foraminiferal assemblages in deep borings in the central North Sea. While a Pliocene age cannot be excluded for Member A of the Lodin Elv Formation, the fauna, as well as the age determination indicate strongly that the Member B is of Lower Pleistocene age (cf. Bennike et al., 2010). Therefore, the molluscan assemblages can best be correlated with the oldest faunal assemblages of the Breidavík Group, but no molluscs have been reported from Member B at Lodin Elv. Lower Pleistocene age is now considered more likely as indicated by amino acid analysis indicating an age either shortly after 2.4 Ma or about 2.6 Ma (Penney, 1993), further supported by the absence of the more thermophilic species found in the Kap København Formation.

The Pattorfik beds are considered deposited after the major Caenozoic climatic deterioration in the Northern Hemisphere as strongly indicated by the occurrence of the extinct prosobranch gastropod *Alvania patorfikensis* Laursen, described from the Pattorfik beds and found in Store Koldewey and in the Breiðavík beds, but not in the Tjörnes beds (Bennike et al., 2002, 2010; Símonarson, 1981b). Furthermore, there is higher frequency of species with subarctic or even arctic outpost in the Pattorfik beds than has been found in the Tjörnes beds. They include the prosobranch gastropod *Tachyrhynchus erosus* (Couthouy), and the bivalves *Similipecten greenlandicus* (Sowerby) and *Mya pseudoarenaria* Schlesch (Símonarson, 1981b). These are further indications for stronger faunistic correlation between these late Cainozoic Greenland sites and the Breiðavík beds than the Tjörnes beds (see Knudsen et al., 2020b). Thus, we are not aware of any marine deposits in Greenland contemporaneous with the Tjörnes beds.

### *7.7.4 North American Sites*

The Yakataga Formation is a late Miocene to Pleistocene record of temperate glacial marine sediments in the Gulf of Alaska (Fig. 7.24) at least 5 km in thickness. There are some faunal similarities with the Pliocene and Lower Pleistocene parts of the succession and the Tjörnes beds, but the formation has considerably more molluscs of Pacific origin as may be expected (Addicott et al., 1971; Allison, 1978). The common species include the prosobranch gastropod *Cryptonatica affinis* (Gmelin) and the bivalves *Tridonta elliptica* (Brown) and *Arctica islandica* (Linné), all known especially from the *Serripes* Zone of the Tjörnes beds.

Although there is stronger faunal correlation with the Pliocene-Pleistocene Colvillian, Bigbendian, and Fischcreekian faunas of the Gubik Formation in northern Alaska (Fig. 7.24), they include considerably more Pacific molluscs than the Tjörnes beds (Durham & MacNeil, 1967; Gladenkov, 1981). The age of the oldest part of the Gubik Formation, the Nulavik unit of the Colvillian transgression, is supposed to be 2.7–2.48 Ma, the Killi Creek unit of the Bigbendian transgression about 2.48 Ma, and the Tuapaktushak unit of the Fischreekian 2.48–2.14 Ma (Brigham-Grette & Carter, 1992). All these faunas include taxa of Pacific origin and must post-date the tide of the migration which occurred while the Tjörnes beds were deposited. There are no arctic elements in these units, and a considerably higher sea-water temperature than at present is indicated, with absence of sea ice, preceding the major Cainozoic climatic deterioration in the Northern Hemisphere with successive glaciations. These faunas include taxa as the prosobranch gastropod *Littorina squalida* Broderip & Sowerby and the bivalve species *Serripes groenlandicus* (Mohr), *Macoma calcarea* (Gmelin), *Mya truncata* Linné, and *Hiatella arctica* (Linné) (Brigham-Grette & Carter, 1992; MacNeil, 1957). They all occur in the *Serripes* Zone of the Tjörnes beds. In Meighen Island, one of the Queen Elisabeth Islands in Arctic Canada (Fig. 7.24), sediments belonging to the Beaufort Formation with the marine bivalves, *Arctica islandica* (Linné), *Mya truncata,* and *H. arctica* have been found (Fyles et al., 1991). The age of the sediments is apparently 2.8–5.1 Ma (Kaufman, Farmer, Miller, Carter, & Brigham-Grette, 1990). Therefore, the sediments seem contemporaneous with the Tjörnes beds. The occurrence of *M. truncata* is interesting because the species had arrived at Meighen Island when the Tjörnes beds were formed, while it had hardly reached the Tjörnes area where *Mya schwarzbachi* Strauch became the dominating Pliocene *Mya* species. In Hvitland beds on the west coast of Ellesmere Island (Fig. 7.24), a molluscan fauna has been found with *H. arctica, Similipecten greenlandicus* (Sowerby), *Yoldiella* cf. *lenticula* (Møller), *Astarte* sp., *Dentalium* sp., and *Arctica* sp., most probably *A. islandica*. The faunal assemblages lived most probably at depth of about 25–30 m and the age is probably no younger than 2.4 Ma and correlation with the Bigbendian unit of the Gubik Formation is suggested (Fyles et al., 1998). The fauna may be contemporaneous with the Tjörnes fauna, but correlation with the Lower Pleistocene Breiðavík deposits is more appropriate, especially the Hörgi Formation.

### *7.7.5 Siberian and Russian Sites*

Comparison with late Neogene Siberian deposits shows certain faunal similarities between the Tjörnes faunal assemblages and the fauna in the Lower Pleistocene Olkov-Tusatuva Yamsk Suites (Fig. 7.24) in eastern Kamchatka (Petrov, 1982). These are about 2 Ma old, with the first appearance of *Cyrtodaria kurriana* Dunker in arctic assemblages, which indicates Lower Pleistocene age rather than Pliocene, even though the suites have nearly 20% extinct species (Gladenkov, 1981; Petrov, 1982, 1986). In the coastal plain area of Chukotka (Fig. 7.24), the extant arctic marine assemblages with *Portlandia arctica* (Gray) in the Pinakul Suite is even younger and considered to date from Middle Pleistocene (Petrov, 1967, 1982, 1986). The Pinakul Suite rests on the eroded preglacial sediments of the Koynatkhun Suite both in the northern and southern parts of Chukotka (Petrov, 1967). These deposits are possibly of Pliocene age and seem contemporaneous with the Tjörnes beds, but we have no knowledge about marine shells in the sediments (Hopkins et al., 1965). They seem to be lacustrine and alluvial with numerous plant remains, mainly derived from conifers, spruce, and pine. The spore-pollen spectra indicate a coniferous forest, possibly with some broad-leaved trees. The annual rings of the wood remains up to more than one meter in diameter and with 3–4 mm large radius of curvature indicate climate with annual mean temperature above freezing (Petrov, 1967). The base of the Koynatkhun Suite is below sea level along the Kresta Bay, which indicates a much lower position of the sea level when these sediments were deposited (Petrov, 1967).

Cainozoic shelf deposits are known from the European part of Russia (see Símonarson & Eiríksson, 2020b: fig. 11.5) in the Barents Sea (Zarkhidze & Samoilovich, 1989). The mollusc fauna in these deposits contains more or less arctic species such as *Portlandia arctica* (Gray), *Yoldiella lenticula* (Møller), *Tridonta borealis* (Schumacher), *Ciliatocardium ciliatum* (Fabricius), and *Serripes groenlandicus* (Mohr), and Bennike et al. (2010) consider the fauna to be comparable to the Lower Pleistocene mollusc fauna on Store Koldewey, East Greenland.

## 7.8 Concluding Remarks

The mollusc and barnacle assemblages found in the Barmur Group sediments consist of infaunal, as well as epifaunal species. Generally, they died at the place where they lived or they only suffered a limited post-mortal transport (reworking). The only remarkable exception is *Baculites* sp., the only ammonite found in the deposits. It was collected in the *Mactra* biozone, but the genus became extinct at the end of the Cretaceous, long before the deposition of the Pliocene Tjörnes beds. The species is considered erratic in these layers and most probably it was transported to the Tjörnes area by marine animals long after its death. However, transport by ocean currents cannot be excluded.

We have identified 65 species of prosobranch gastropod and five opistobranch gastropod species, 49 species of bivalves, and one barnacle species that lived in the Tjörnes area in Pliocene time. About 25% of the mollusc species are extinct and the molluscan assemblages compare best with Pliocene marine assemblages. At least 32 species dealt with in this publication have their first appearance (FAD) in the Pliocene Barmur Group sediments. About 25 of the recent molluscan species found in the Pliocene Tjörnes beds are not living in Iceland any more. The majority is now living in more southerly localities with higher sea temperatures. Thus, the Pliocene faunal assemblages found in the Tjörnes beds indicate stronger boreal conditions in the area during the deposition of the beds than now prevailing in North Iceland. The fact that species with lusitanian outposts are even more frequently found in the sediments than those with subarctic or arctic outposts is further indication of the mild climatic character.

Generally, the molluscs, as well as the *Balanus* species were living close to the coast at limited depths and littoral facies with many juvenile forms are frequently found. Regressive facies are mainly found close to the lignite beds in the lower, as well as the uppermost part of the Tjörnes beds and the salinity decreased upwards to these terrestrial facies and increased again during the following transgressive phase. Most reported species have pelagic larval development, which is important for their ability to migrate.

There are two distinct faunal changes in the Tjörnes beds. The older one in the middle part of the *Mactra* Zone is clearly connected to environmental changes reflecting a change from intertidal or tidal flat environments to more sublittoral conditions. The younger faunal change is of quite another character when an abrupt appearance of mollusc species of Pacific ancestry took place in the lowermost part of the *Serripes* Zone. These species are almost exclusively with pelagic larval development and some of them have since been among the dominants in North Atlantic marine faunas.

The Tjörnes fauna plays a very important role in our understanding of the Pliocene Pacific immigration wave that has made impact on the evolution of modern Atlantic faunas.

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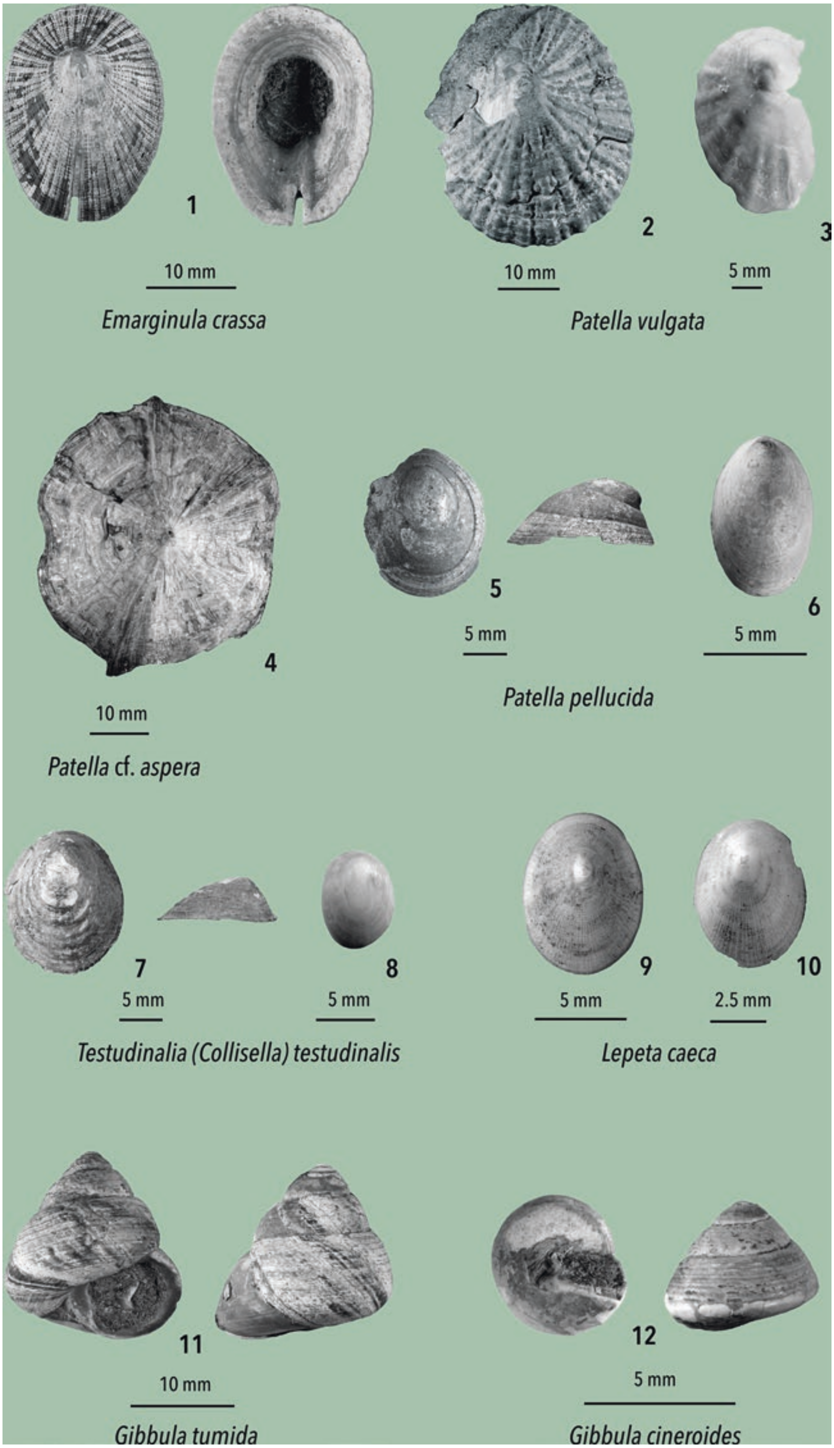
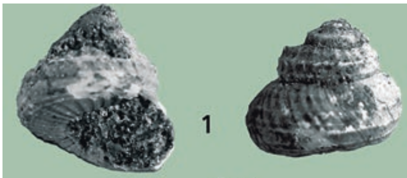
→

**Plate 7.1** **1**. *Emarginula crassa* Sowerby, specimen from unit 10 in the *Mactra* Zone. **2**. *Patella vulgata* Linné, shell from unit 9 in the *Mactra* Zone. **3**. *Patella vulgata* Linné, juvenile shell from unit 11 in the *Mactra* Zone. **4**. *Patella* cf. *aspera* Röding, specimen from unit 8 in the *Mactra* Zone. **5**. *Patella pellucida* Linné, shell from unit 23 in the *Serripes* Zone. **6**. *Patella pellucida* Linné, specimen from unit 9 in the *Mactra* Zone. **7**. *Testudinalia (Collisella) testudinalis* (Müller), half-grown specimen from unit 9 in the *Mactra* Zone. **8**. *Testudinalia (Collisella) testudinalis* (Müller), specimen from unit 9 in the *Mactra* Zone. **9**. *Lepeta caeca* (Müller), shell from unit 21 in the *Serripes* Zone. **10**. *Lepeta caeca* (Müller), juvenile specimen from unit 23 in the *Serripes* Zone. **11**. *Gibbula tumida* (Montagu), shell from unit 15 in the *Serripes* Zone. **12**. *Gibbula cineroides* (Wood), specimen from unit 14 in the *Serripes* Zone

## Plates

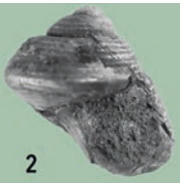

1
10 mm
Emarginula crassa
2
3
10 mm
5 mm
Patella vulgata
4
10 mm
Patella cf. aspera
5
6
5 mm
5 mm
Patella pellucida
7
8
5 mm
5 mm
Testudinalia (Collisella) testudinalis
9
10
5 mm
2.5 mm
Lepeta caeca
11
10 mm
Gibbula tumida
12
5 mm
Gibbula cineroides



1

5 mm

*Solariella* sp.



2

10 mm

3

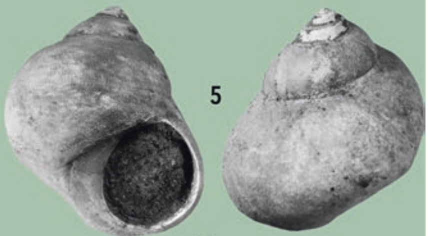
3 mm

*Margarites groenlandicus*

4

1.5 mm

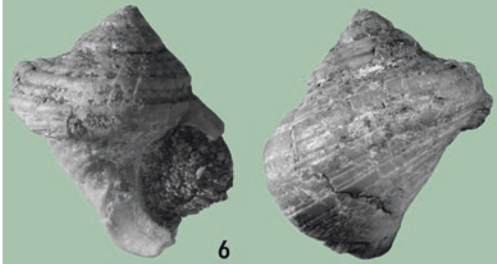
*Margarites costalis*



5

20 mm

*Littorina squalida*



6

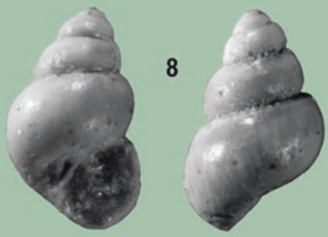
15 mm

*Littorina islandica*

7

2 mm

*Hydrobia ulvae*



8

1.5 mm

*Ecrobia* cf. *ventrosa*

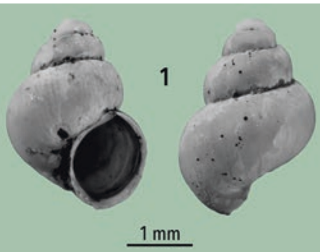
9

2 mm

*Rissoa obsoleta*

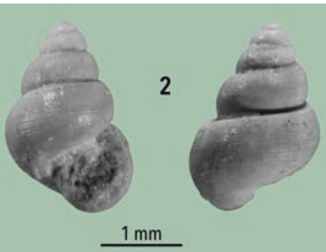
**Plate 7.2** **1**. *Solariella* sp., shell from unit 19 in the *Serripes* Zone. **2**. *Margarites groenlandicus* (Gmelin), specimen from an unknown unit in the *Serripes* Zone (from Schlesch 1924). **3**. *Margarites groenlandicus* (Gmelin), juvenile shell from unit 9 in the *Mactra* Zone. **4**. *Margarites costalis* (Gould), juvenile specimen from unit 9 in the *Mactra* Zone. **5**. *Littorina squalida* Broderip & Sowerby, shell from unit 11 in the *Mactra* Zone. **6**. *Littorina islandica* Reid, specimen from unit 25 in the *Serripes* Zone. The shell is somewhat deformed. **7**. *Hydrobia ulvae* (Pennant), shell from unit 9 in the *Mactra* Zone. **8**. *Ecrobia* cf. *ventrosa* (Montagu), specimen from unit 9 in the *Mactra* Zone. **9**. *Rissoa obsoleta* (Wood), shell from unit 9 in the *Mactra* Zone

1



*Pusillina* cf. *sarsi*

2



*Obtusella tumidula*

3

*Alvania* cf. *punctura*

4

*Onoba aculeus*

5

*Onoba semicostata*

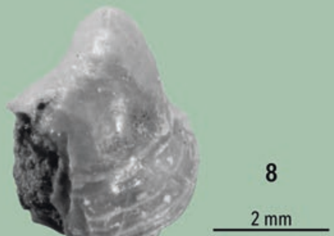
6

*Omalogyra atomus*

7

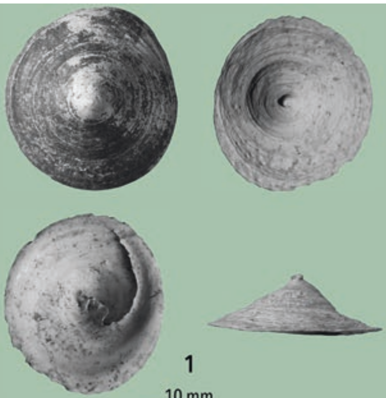
*Skeneopsis planorbis*

8



*Capulus* cf. *unguis*

**Plate 7.3** **1**. *Pusillina* cf. *sarsi* (Lovén), specimen from unit 9 in the *Mactra* Zone. **2**. *Obtusella tumidula* (Sars), shell from unit 9 in the *Mactra* Zone. **3**. *Alvania* cf. *punctura* (Montagu), specimen from unit 9 in the *Mactra* Zone. **4**. *Onoba aculeus* (Gould), shell from unit 9 in the *Mactra* Zone. **5**. *Onoba semicostata* (Montagu), specimen from unit 9 in the *Mactra* Zone. **6**. *Omalogyra atomus* (Philippi), shell from unit 9 in the *Mactra* Zone. **7**. *Skeneopsis planorbis* (Fabricius), specimen from unit 9 in the *Mactra* Zone. **8**. *Capulus* cf. *unguis* (Sowerby), juvenile shell from unit 9 in the *Mactra* Zone. The shell is somewhat damaged

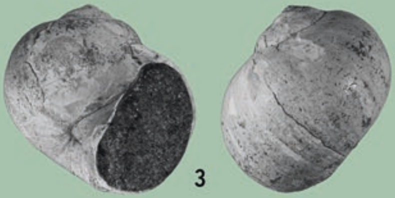


1

*Calyptraea* cf. *chinensis*

2

*Velutina velutina*



3

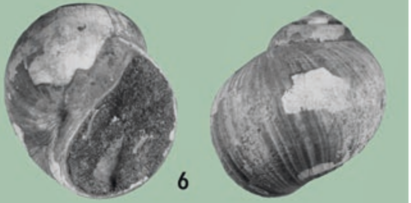
*Cryptonatica affinis*

4

*Cryptonatica smithii*

5

*Cryptonatica occlusa*



6

*Euspira pallida*

7

*Euspira montagui*

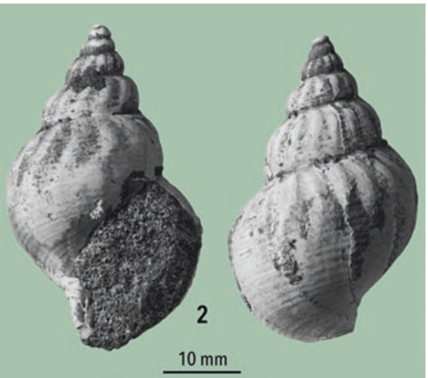
8

*Euspira catenoides*

**Plate 7.4** **1**. *Calyptraea* cf. *chinensis* (Linné), specimen from unit 23 in the *Serripes* Zone. **2**. *Velutina velutina* (Müller), shell from unit 22 (or 23) in the *Serripes* Zone. It is rather eroded but faint spiral lines are visible near the apex. **3**. *Cryptonatica affinis* (Gmelin), specimen from unit 19 in the *Serripes* Zone. **4**. *Cryptonatica smithii* (Brown), shell from unit 19 in the *Serripes* Zone. **5**. *Cryptonatica occlusa* (Wood), specimen from unit 19 in the *Serripes* Zone. **6**. *Euspira pallida* (Broderip & Sowerby), shell from unit 19 in the *Serripes* Zone. **7**. *Euspira montagui* (Forbes), specimen from unit 19 in the *Serripes* Zone. **8**. *Euspira catenoides* (Wood), the shell is from unit 14 in the *Mactra* Zone and is the largest Naticidae found in the Tjörnes beds


1

*Boreotrophon clathratus*


2

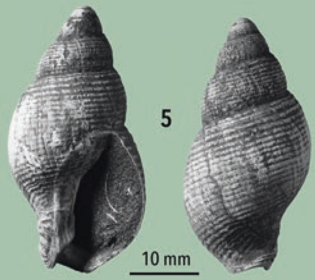
*Buccinum undatum*


3

*Buccinum cyaneum*


4

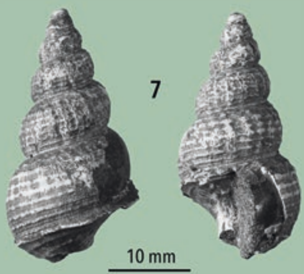
*Buccinum finmarkianum*


5

*Liomesus dalei*


6

*Colus olavii*

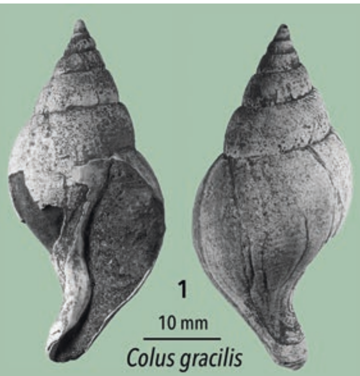

7

*Colus* cf. *imperspicuus*


8

*Colus elegans*

**Plate 7.5** **1**. *Boreotrophon clathratus* (Linné), specimen from unit 18 in the *Serripes* Zone. **2**. *Buccinum undatum* Linné, shell from unit 15 in the *Serripes* Zone. **3**. *Buccinum cyaneum* Bruguière, specimen from unit 15 in the *Serripes* Zone. **4**. *Buccinum finmarkianum* Verkrüzen, shell from unit 15 in the *Serripes* Zone. **5**. *Liomesus dalei* (Sowerby), specimen from unit 15 in the *Serripes* Zone. **6**. *Colus olavii* (Mörch), shell from unit 15 in the *Serripes* Zone. **7**. *Colus* cf. *imperspicuus* (Wood), damaged and broken specimen from unit 18 in the *Serripes* Zone. **8**. *Colus elegans* (Harmer), shell from unit 18 i the *Serripes* Zone


1

*Colus gracilis*


2

*Colus glaber*


3

*Colus altus*


4

*Neptunea lyratodespecta*


5

*Searlesia costifera*


6

*Searlesia lundgrenii*

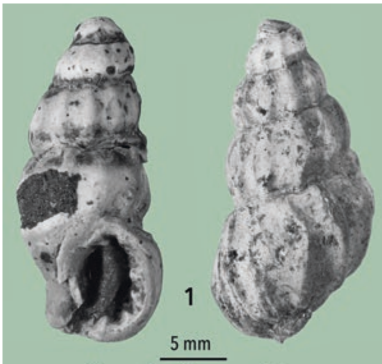

7

*Nassarius tjoernesensis*


8

*Nassarius reticosus*

**Plate 7.6** **1**. *Colus gracilis* (da Costa), shell from unit 15 in the *Serripes* Zone. **2**. *Colus glaber* (Kobelt), specimen from unit 15 in the *Serripes* Zone. **3**. *Colus altus* (Wood), shell from unit 19 in the *Serripes* Zone. **4**. *Neptunea lyratodespecta* Strauch, specimen from unit 19 in the *Serripes* Zone. **5**. *Searlesia costifera* (Wood), shell from unit 21 in the *Serripes* Zone. **6**. *Searlesia lundgrenii* Harmer, specimen from unit 15 in the *Serripes* Zone. **7**. *Nassarius tjoernesensis* Spaink, shell from unit 19 in the *Serripes* Zone. **8**. *Nassarius reticosus* (Sowerby), specimen from unit 23 in the *Serripes* Zone



1

*Nassarius* cf. *consociatus*

2

*Admete viridula*

3

*Admete couthouyi*

4

*Oenopota pyramidalis*

5

*Oenopota borealis*

6

*Oenopota pingeli*

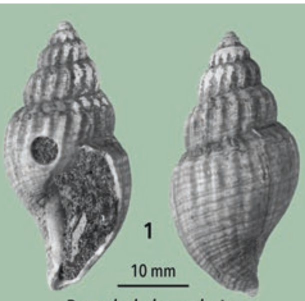
7

*Curtitoma decussata tjoernesensis*

8

*Curtitoma trevelliana*

**Plate 7.7** **1.** *Nassarius* cf. *consociatus* (Wood), rather badly preserved shell from unit 9 in the *Mactra* Zone. **2.** *Admete viridula* (Fabricius), specimen from unit 16 in the *Serripes* Zone. **3.** *Admete couthouyi* (Jay), shell from unit 18 in the *Serripes* Zone. **4.** *Oenopota pyramidalis* (Ström), specimen from unit 21 in the *Serripes* Zone. **5.** *Oenopota borealis* (Reeve), shell from unit 21 in the *Serripes* Zone. **6.** *Oenopota pingeli* (Møller), specimen from unit 15 in the *Serripes* Zone. **7.** *Curtitoma decussata tjoernesensis* (Schlesch), shell from unit 19 in the *Serripes* Zone. **8.** *Curtitoma trevelliana* (Turton), specimen from unit 21 in the *Serripes* Zone


1

*Propebela harpularia*


2

*Propebela nobilis*


3

*Cytharella* sp.


4

*Metaxia metaxa*


5

*Melanella* cf. *frielei*


6

*Boreoscala greenlandica*

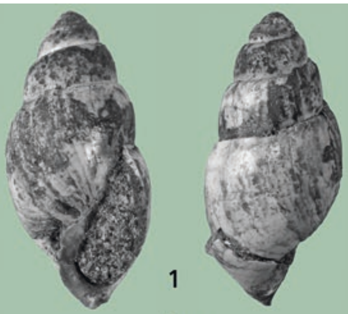

7

*Janthina* cf. *exigua*


8

*Aclis* cf. *minor*

**Plate 7.8** **1**. *Propebela harpularia* (Couthouy), shell from unit 23 in the *Serripes* Zone. The shell is bored by a gastropod probably belonging to a Naticidae. **2**. *Propebela nobilis* (Møller), specimen from unit 19 in the *Serripes* Zone. **3**. *Cytharella* sp. Rather badly preserved shell from unit 9 in the *Mactra* Zone. It is more or less chocolate brown, especially the costae. **4**. *Metaxia metaxa* (delle Chiaje). The shell is broken in all the five specimens from unit 9 in the *Mactra* Zone. **5**. *Melanella* cf. *frielei* (Jordan). The only specimen from unit 9 in the *Mactra* Zone is broken, the oldest whorls are missing. **6**. *Boreoscala greenlandica* (Perry), shell from unit 23 i the *Serripes* Zone. **7**. *Janthina* cf. *exigua* Lamarck. The small specimen (1 mm high) from unit 9 in the *Mactra* Zone is probably full-grown. **8**. *Aclis* cf. *minor* (Brown), shell from unit 9 in the *Mactra* Zone



1

5 mm

*Ondina divisa*

2

10 mm

*Acteon tornatilis*

3

10 mm

*Acteon noae*

4

1 mm

*Cylichna alba*

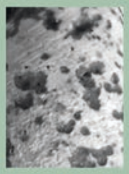
5

2 mm

*Cylichna alba*

6

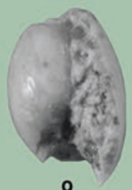
*Cylichna cylindracea*



7

*Cylichna cylindracea*

8



9

5 mm

*Cylichnoides occultus*

**Plate 7.9** **1.** *Ondina divisa* (Adams), almost intact specimen from unit 9 in the *Mactra* Zone**.** **2.** *Acteon tornatilis* (Linné), shell from unit 16 in the *Serripes* Zone. **3.** *Acteon noae* (Sowerby), specimen from unit 16 in the *Serripes* Zone. **4–5.** *Cylichna alba* (Brown), shells from unit 17 in the *Serripes* Zone. **6.** *Cylichna cylindracea* (Pennant), specimen from unit 15 in the *Serripes* Zone. **7.** *Cylichna cylindracea* (Pennant), with enlarged part of the surface showing spiral striae in the shell in Plate 7.9, fig. 7. **8–9.** *Cylichnoides occultus* (Mighels), shells from unit 5 in the *Tapes* Zone

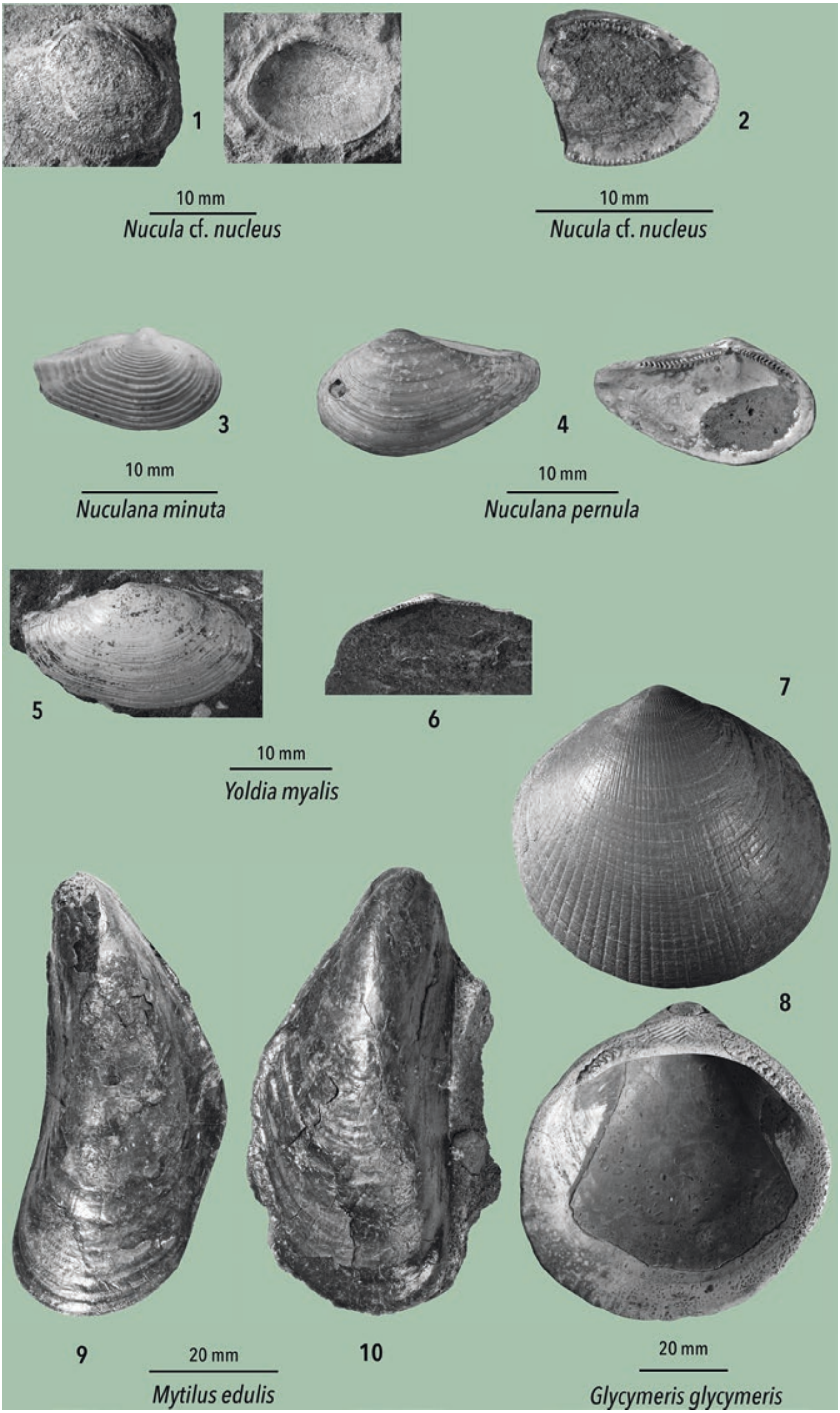

1
2
10 mm
Nucula cf. nucleus
10 mm
Nucula cf. nucleus
3
4
10 mm
Nuculana minuta
10 mm
Nuculana pernula
5
6
7
10 mm
Yoldia myalis
8
9
20 mm
10
Mytilus edulis
20 mm
Glycymeris glycymeris

**Plate 7.10** **1.** *Nucula* cf. *nucleus* (Linné), internal mold and cast showing the internal form of the inner side of a right valve from unit 8 in the *Mactra* Zone. The taxodont hinge and the crenulation of the shell margin of the shell is visible. **2.** *Nucula* cf. *nucleus* (Linné), the taxodont hinge and the crenulation of the inner side of the left valve from unit 7 in the *Mactra* Zone. **3.** *Nuculana minuta* (Müller), right valve from unit 14 in the *Serripes* Zone. **4**. *Nuculana pernula* (Müller), left valve with taxodont hinge from unit 19 in the *Serripes* Zone. **5.** *Yoldia myalis* (Couthouy), right valve from unit 14 in the *Serripes* Zone. **6.** *Yoldia myalis* (Couthouy), valve with taxodont hinge from unit 14 in the *Serripes* Zone. **7–8.** *Glycymeris glycymeris* (Linné), the surface of a left valve and interior side of a left valve with taxodont hinge from unit 11 in the *Mactra* Zone. **9–10.** *Mytilus edulis* Linné, left and right valve from unit 1 in the *Tapes* Zone. This is the first Pacific species to reach the Tjörnes area before the end of the Miocene

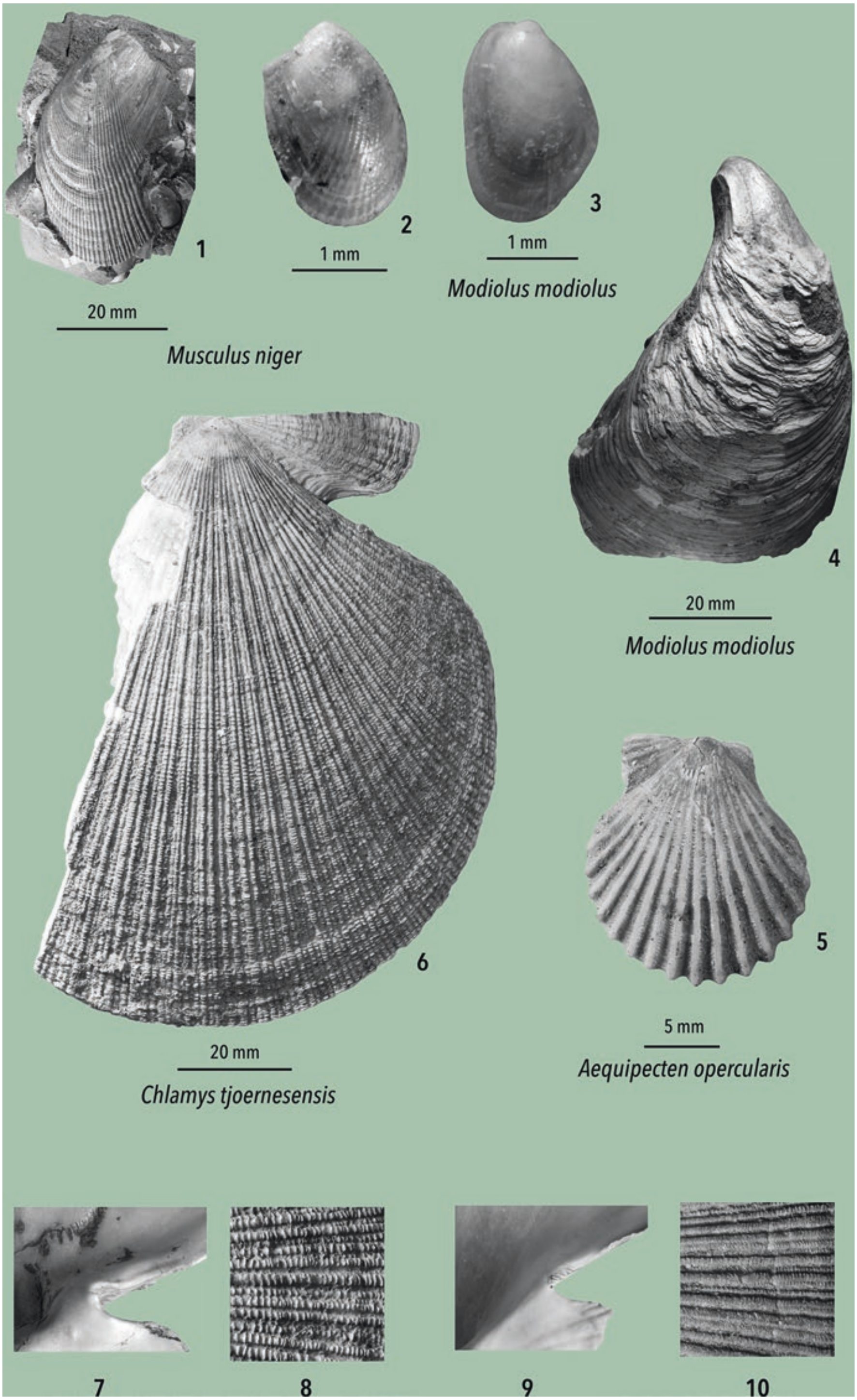
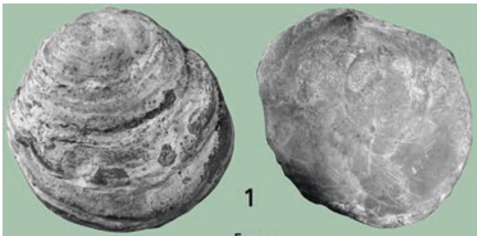

1
20 mm
Musculus niger
2
1 mm
3
1 mm
Modiolus modiolus
4
20 mm
Modiolus modiolus
6
20 mm
Chlamys tjoernesensis
5
5 mm
Aequipecten opercularis
7
8
9
10

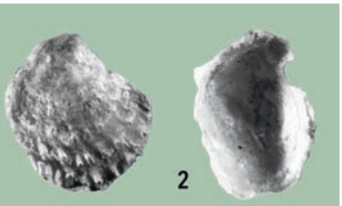
**Plate 7.11** **1.** *Musculus niger* (Gray), rather damaged valve from unit 20 in the *Serripes* Zone. **2.** *Musculus niger* (Gray), juvenile left valve from unit 9 in the *Mactra* Zone. **3.** *Modiolus modiolus* (Linné), juvenile left valve from unit 9 in the *Mactra* Zone. **4.** *Modiolus modiolus* (Linné), rather badly preserved valve from unit 10 in the *Mactra* Zone. **5.** *Aequipecten opercularis* (Linné), single left valve from unit 8 in the *Mactra* Zone. **6.** *Chlamys tjoernesensis* MacNeil, rather damaged right valve from unit 10 in the *Mactra* Zone. **7–8.** *Chlamys tjoernesensis* MacNeil, with no dysodont teeth and coarser and more unequal ribs than *Chlamys islandica* (Müller). **9–10.** *Chlamys islandica* (Müller), with small dysodont teeth and finer and more equal ribs than *C. tjoernesensis*



1

5 mm

*Heteranomia squamula*



2

2 mm

*Heteranomia squamula aculeata*

3

20 mm

*Astarte crenata*

4

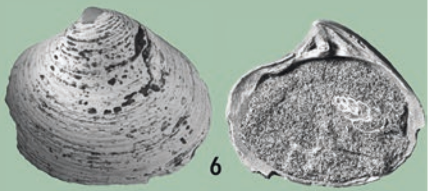
20 mm

*Astarte* cf. *basterotii*

5

10 mm

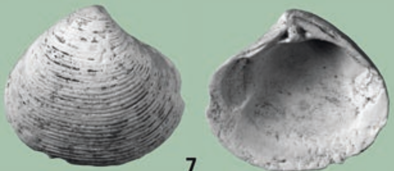
*Astarte* galeotti



6

20 mm

*Tridonta borealis*



7

10 mm

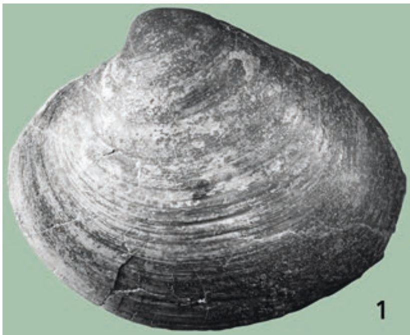
*Tridonta montagui*

8

10 mm

*Tridonta* cf. *elliptica*

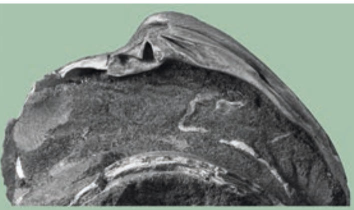
**Plate 7.12** **1.** *Heteranomia squamula* (Linné), left valve from unit 9 in the *Mactra* Zone. **2.** *Heteranomia squamula aculeata* (Müller), left valve from unit 9 in the *Mactra* Zone. **3.** *Astarte crenata* (Gray), left valve from unit 20 in the *Serripes* Zone. **4.** *Astarte* cf. *basterotii* de la Jonkaire, left valve from unit 23 in the *Serripes* Zone. **5.** *Astarte galeotti* Nyst, left valve from unit 14 in the *Serripes* Zone. **6.** *Tridonta borealis* Schumacher, left valve from unit 19 in the *Serripes* Zone. **7.** *Tridonta montagui* (Dillwyn), right valve from unit 18 in the *Serripes* Zone. **8.** *Tridonta* cf. *elliptica* (Brown), right valve from unit 15 in the *Serripes* Zone



1

20 mm

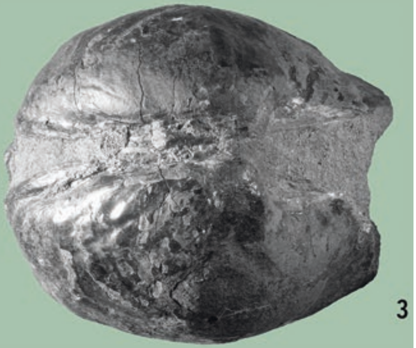
*Arctica islandica*



2

20 mm

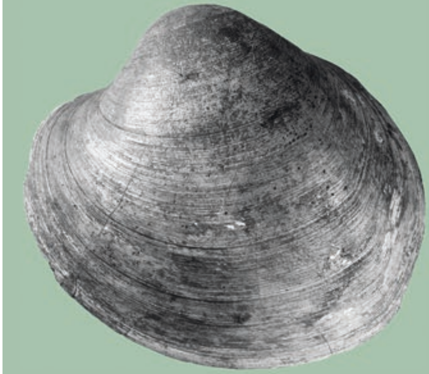
*Arctica islandica*



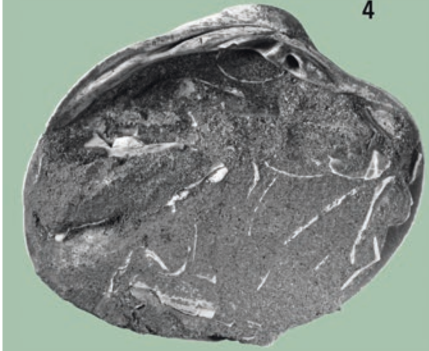
3

20 mm

*Arctica islandica*



4



20 mm

*Pygocardia rustica*

5

10 mm

*Cyclocardia chamaeformis*

6

1 mm

*Parvicardium pinnulatum*

**Plate 7.13** **1.** *Arctica islandica* (Linné), left valve from unit 10 in the *Mactra* Zone. **2.** *Arctica islandica* (Linné), the heterodont hinge in the right valve from unit 15 in the *Serripes* Zone. **3.** *Arctica islandica* (Linné), sedimentary core of united shells in unit 1 in the *Tapes* Zone. The shell material (aragonite) is generally dissolved close to lignite layers. **4.** *Pygocardia rustica* (Sowerby), left valve from unit 23 in the *Serripes* Zone. **5.** *Cyclocardia chamaeformis* (Sowerby), right valve from unit 20 in the *Serripes* Zone. **6.** *Parvicardium pinnulatum* (Conrad), right valve from unit 14 in the *Serripes* Zone

1

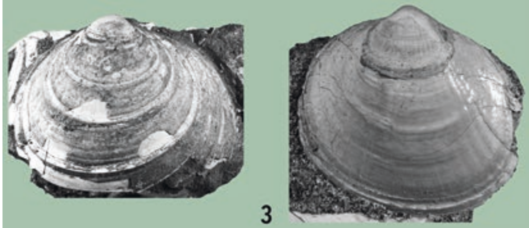
30 mm

*Acanthocardia echinata*

2

10 mm

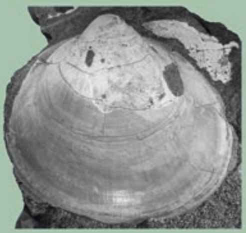
*Ciliatocardium ciliatum*



3

10 mm

*Serripes groenlandicus*



4

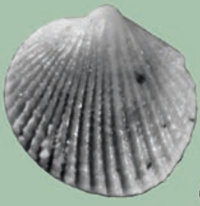
10 mm

*Serripes groenlandicus*

5

20 mm

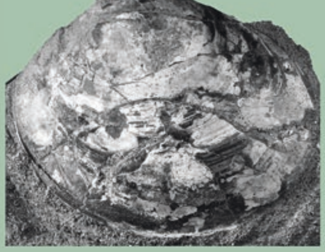
*Cerastoderma decorticata*



6

1 mm

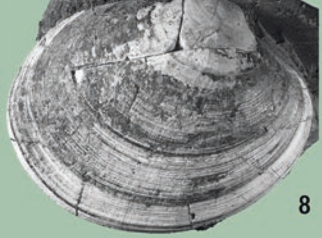
*Cerastoderma decorticata*



7

20 mm

*Paphia aurea*

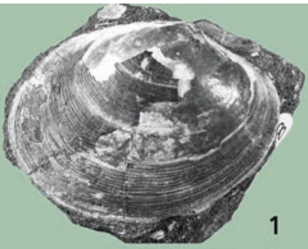


8

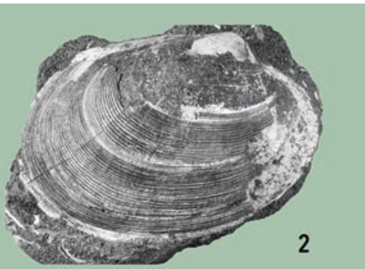
20 mm

*Paphia aurea senescens*

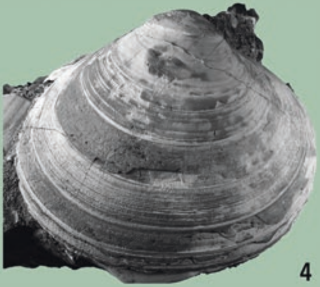
**Plate 7.14** **1.** *Acanthocardia echinata* (Linné), right valve from unit 5 in the *Tapes* Zone. **2.** *Ciliatocardium ciliatum* (Fabricius), right valve from unit 14 in the *Serripes* Zone. **3.** *Serripes groenlandicus* (Mohr), two left valves from unit 14 in the *Serripes* Zone. **4.** *Serripes groenlandicus* (Mohr), left valve from unit 19 in the *Serripes* Zone. **5.** *Cerastoderma decorticata* (Wood), left valve from unit 5 in the *Tapes* Zone. **6.** *Cerastoderma decorticata* (Wood), juvenile left valve from unit 9 in the *Mactra* Zone. **7.** *Paphia aurea* (Gmelin), rather badly preserved left valve from unit 5 in the *Tapes* Zone. **8.** *Paphia aurea senescens* (Cocconi), right valve from unit 5 in the *Tapes* Zone


1

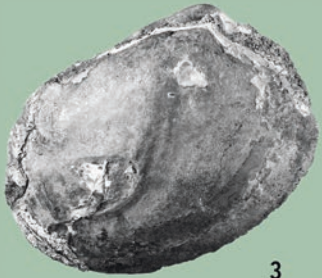
*Paphia rhomboides*


2

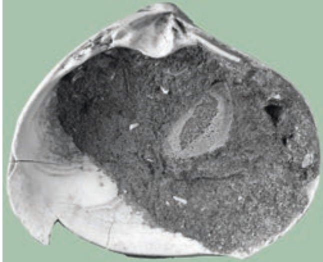
*Venerupis corrugata*


4

*Spisula arcuata*

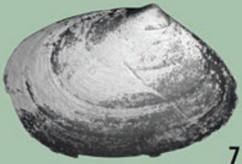

3

*Venerupis corrugata*

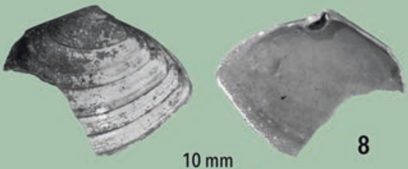

5


6

*Spisula arcuata*


7

*Abra alba*


8

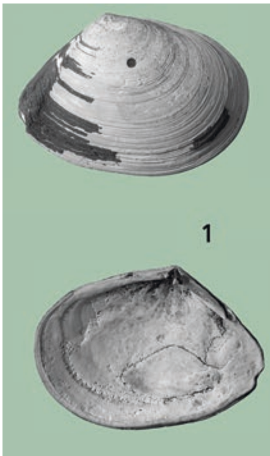
*Abra alba*


9


10

*Abra alba*

**Plate 7.15** **1.** *Paphia rhomboides* (Pennant), right valve from unit 5 in the *Tapes* Zone. **2.** *Venerupis corrugata* (Gmelin), right valve from unit 5 in the *Tapes* Zone. **3.** *Venerupis corrugata* (Gmelin), right valve rather badly preserved from unit 5 in the *Tapes* Zone. However, the cast shows clearly the pallial sinus while the shell material is mostly dissolved. **4.** *Spisula arcuata* (Sowerby), left valve from unit 8 in the *Mactra* Zone. **5.** *Spisula arcuata* (Sowerby), left valve from unit 8 in the *Mactra* Zone showing the heterodont hinge. **6.** *Spisula arcuata* (Sowerby), juvenile valve from unit 9 in the *Mactra* Zone. **7.** *Abra alba* (Wood), left valve from unit 8 in the *Mactra* Zone. **8.** *Abra alba* (Wood), left valve from unit 8 in the *Mactra* Zone showing the hinge. **9–10.** *Abra alba* (Wood), two right valves from unit 7 in the *Mactra* Zone, in Fig. 9 the hinge is visible



1

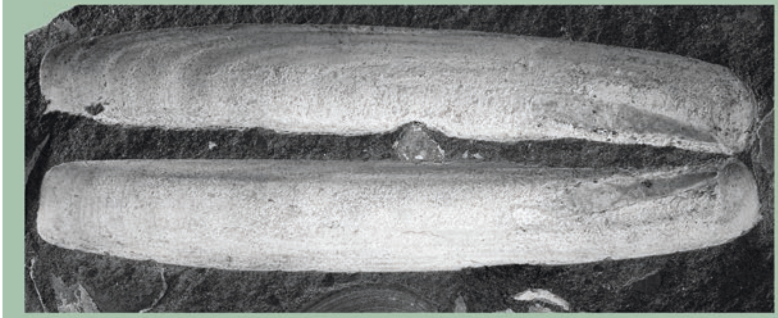
*Macoma calcarea*

2

*Macoma praetenuis*

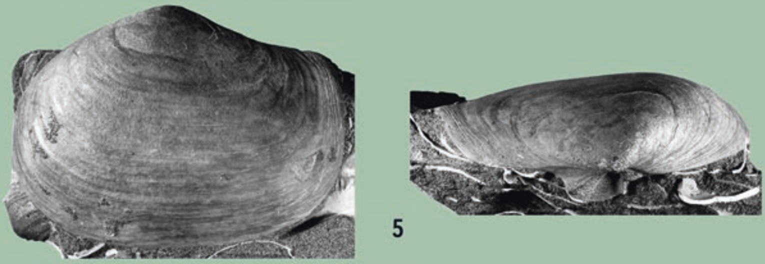
3

*Macoma obliqua*



4

*Ensis cf. ensis*



5

*Mya truncata*

**Plate 7.16** **1.** *Macoma calcarea* (Gmelin), right valve from unit 15 in the *Serripes* Zone. The rather deep pallial sinus is visible in the inner side of the shell. **2.** *Macoma praetenuis* (Woodward), right valve from unit 15 in the *Serripes* Zone. **3.** *Macoma obliqua* (Sowerby), left valve from unit 17 in the *Serripes* Zone. All the *Macoma* species in the Tjörnes beds have two cardinal teeth, but no laterals. **4.** *Ensis* cf. *ensis* (Linné), the inner side of pared valves from unit 17 in the *Serripes* Zone. The valves are slightly moved, but not separated. **5.** *Mya truncata* Linné, left valve from unit 15 in the *Serripes* Zone

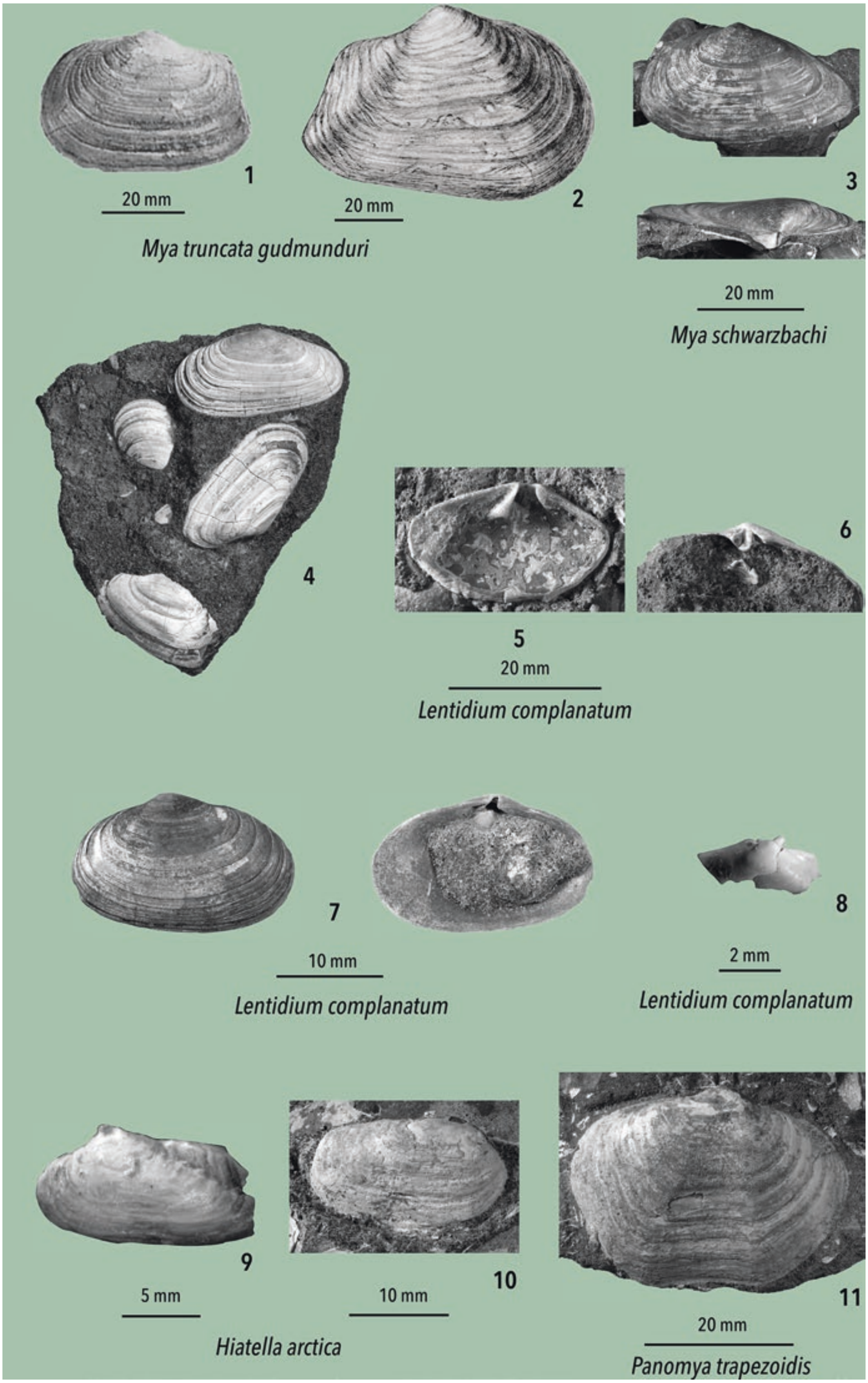
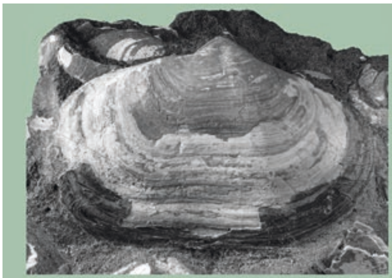

1
20 mm
20 mm
2
Mya truncata gudmunduri
3
20 mm
Mya schwarzbachi
4
6
5
20 mm
Lentidium complanatum
7
10 mm
Lentidium complanatum
8
2 mm
Lentidium complanatum
9
5 mm
10
10 mm
Hiatella arctica
11
20 mm
Panomya trapezoidis

**Plate 7.17** **1.** *Mya truncata gudmunduri* Strauch, left valve from unit 17 in the *Serripes* Zone (from Strauch, 1972). **2.** *Mya truncata gudmunduri* Strauch, right valve from the Upper Pliocene Coralline Crag at Ramsholt England (from Wood, 1857). **3.** *Mya schwarzbachi* Strauch, left valve from unit 15 in the *Serripes* Zone. **4–8.** *Lentidium complanatum* (Sowerby), left and right valves showing the surface, as well as the inner side with the hinge from different units in all the biozones. **9.** *Hiatella arctica* (Linné), left valve from unit 9 in the *Mactra* Zone. **10.** *Hiatella arctica* (Linné), right valve from unit 15 in the *Serripes* Zone. **11.** *Panomya trapezoidis* Strauch, left valve from unit 14 in the *Serripes* Zone



1

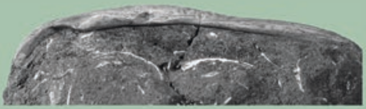
*Panomya obliquelongata*

2

*Cyrtodaria angusta*

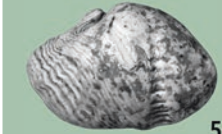
3

*Cyrtodaria angusta*



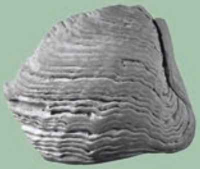
4

*Cyrtodaria angusta*



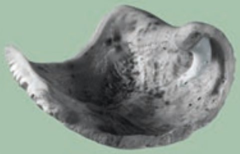
5

*Zirfaea crispata*

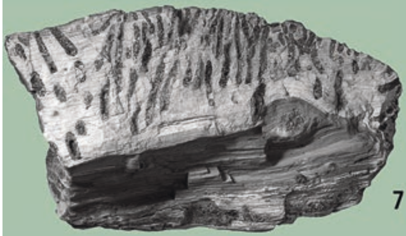


*Zirfaea crispata*

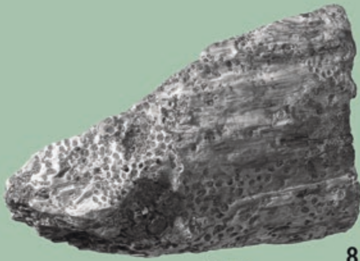
6



*Zirfaea crispata*



7

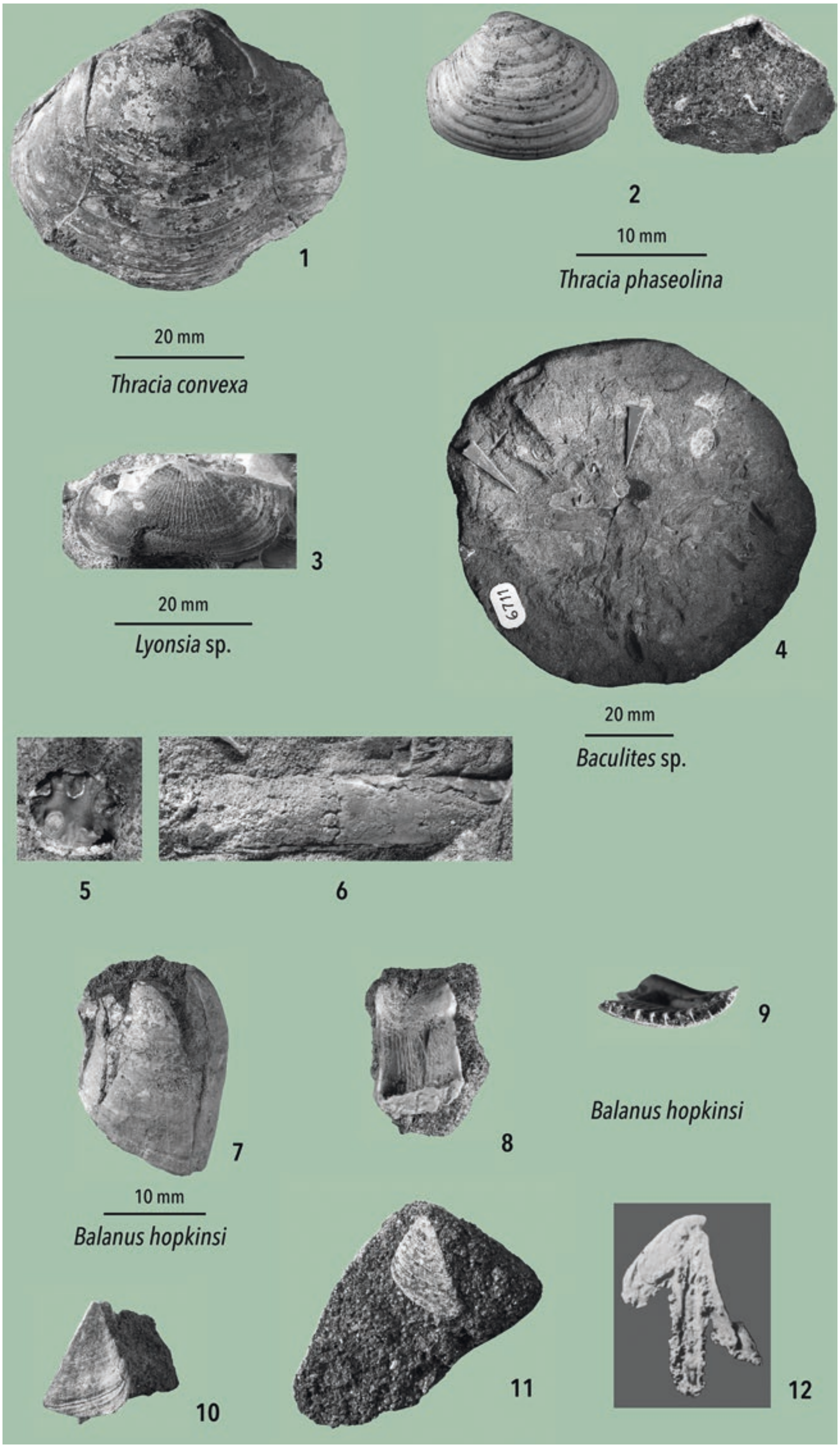


8

*Teredo* sp.

◄

**Plate 7.18** **1.** *Panomya obliquelongata* (Strauch), right valve from unit 15 in the *Serripes* Zone. **2.** *Cyrtodaria angusta* (Nyst & Westendorp), right valve from unit 14 in the *Serripes* Zone. **3.** *Cyrtodaria angusta* (Nyst & Westendorp), left valve from unit 18 in the *Serripes* Zone. **4.** *Cyrtodaria angusta* (Nyst & Westendorp), left valve from unit 18 in the *Serripes* Zone, showing the degenerate weak hinge. **5.** *Zirfaea crispata* (Linné), left valve from unit 8 in the *Mactra* Zone. **6.** *Zirfaea crispata* (Linné), right valve from unit 8 in the *Mactra* Zone, showing the apophysis from the umbo inside the shell. **7–8.** *Teredo* sp. from unit 9 in the *Mactra* Zone. Apparently, the tubes were coated by a thin calcareous layer secreted from the mantle


1
20 mm
*Thracia convexa*
2
10 mm
*Thracia phaseolina*
3
20 mm
*Lyonsia* sp.
6711
4
20 mm
*Baculites* sp.
5
6
7
10 mm
*Balanus hopkinsi*
8
9
*Balanus hopkinsi*
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11
12

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**Plate 7.19** **1.** *Thraca convexa* (Wood), left valve from unit 5 in the *Tapes* Zone. **2.** *Thracia phaseolina* (Lamarck), right valve from unit 17 in the *Serripes* Zone. **3.** *Lyonsia* sp. Badly preserved valve from unit 14 in the *Serripes* Zone. The shell material is mostly dissolved. **4–6.** *Baculites* sp. Strauch (2006) reported fragments of *Baculites* sp. in a phosphoritic concretion found isolated on the shore north of Reká. Therefore, the exact stratigraphic position is not known, but as concretions like this are most frequently found in unit 6 in the lowermost *Mactra* Zone it is the most probable source. The phragmocone is about 7 mm in diameter and 28 mm long. **7.** *Balanus hopkinsi* Zullo, conic shell from unit 1 in the *Tapes* Zone. **8–9.** Parietal plates from the shell ring, and in Fig. 8, a part of the basal plate is visible. **10–12.** *Balanus hopkinsi* Zullo, in full-grown specimens the height of scutum is generally 8.2–9.5 mm (Figs. 10–11), and tergum 8.2–8.5 mm (Fig. 12)