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Research paper

Brachiopods of the northern North Atlantic and Arctic, with a focus on Norwegian fauna

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Ten species of Brachiopoda have been found living around Norway, including the Arctic Svalbard and Jan Mayen, while 26 are recorded here for the region extending from the Arctic Ocean in the North to the northernmost North Atlantic and Celtic Sea in the South. This paper provides an identification key and short descriptions for all species, including the new species *Xenobrochus islandicus* n. sp. from southwest of Iceland and the new East Atlantic species *Dallina lusitanica* n. sp. The distributions of all species have been reviewed and were generally found to follow the oceanic temperature, salinity and depth gradients of the region. Also organic enrichment had some influence on distribution. Some species have shown a possible ongoing northward shift of their biogeographic boundaries over the last two centuries, including the Arctic to subarctic species *Hemithiris psittacea*.

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INTRODUCTION

Brachiopoda is a small phylum exclusively comprising marine, shelled, filter-feeding and sedentary animals that includes just over 400 known extant species worldwide (Williams *et al.* 1997; Emig *et al.* 2021). A total of 24 species have been recorded from the northernmost region of the North Atlantic Ocean and up to the Arctic Ocean. Just 10 of these are known from the Norwegian region, including the Arctic Svalbard and Jan Mayen.

In general, the brachiopod fauna of the European, northeast American and Greenlandic shelves and upper slope environments are fairly well investigated. Some pre-eminent studies covering the Arctic and subarctic regions of Norwegian waters were conducted by Friele (1877a), Knipowitsch (1901, 1902), Hägg (1905), Arndt & Grieg (1933), Grieg (1933) and Gulliksen *et al.* (1999). Fewer - but still important - works have also been conducted on the fauna occurring around mainland Norway. These include studies by Lovén (1846), Wesenberg-Lund (1939), Thomsen (1990), and Thomsen & Brattegard (1997). Most relevant information is scattered, while a full and updated overview of the fauna, abundances and detailed maps of species distribution, as well as an identification key to all of the species within Norwegian and adjacent waters, remain missing. The closest overview containing descriptions, illustrations and an identification key was provided by Brunton & Curry (1979) on British fauna. Despite being an excellent work for the identification of British fauna, the key was not meant for undeveloped specimens or had a special focus on external features, and it is limited to British fauna. Not only has the lack of a full and updated overview made it challenging for non-specialists to work with the Norwegian fauna and identify them correctly during activities such as monitoring and environmental works, but the confusion of species has also made it more challenging to evaluate the sensitivity of species to environmental and climatic changes. This appears to be an increasing problem since non-verified data are being incorporated into national databases on species distribution.

Although its main focus is on the Norwegian brachiopod fauna, the present paper aims to provide a better overview of the number of species and revise their biogeographical distribution and ecological preferences within the region extending from the southern margin of the Celtic Sea across the northernmost North Atlantic Ocean to eastern Canada, and up to the Arctic Ocean, and to make that information more accessible. To achieve this aim, publications on brachiopods were reviewed and compared with updated data from the examination of most of the larger brachiopod collections housed at

Nordic museums and the Natural History Museum of London, as well as data extracted from novel sampling.

To assist with identification, a species key is provided containing all of the known species occurring in the region. This key focuses on external characters to avoid the need for opening shells whenever possible (Figure 1). It also facilitates the identification of the juvenile shells of most species. Short descriptions, illustrations and updated distribution maps for all species are provided after the key. The present paper aims to provide a baseline for future studies on the biogeographic changes of brachiopods in the region.

MATERIALS AND METHODS

Biogeographic maps are based on examined specimens in the collections housed at the University of Bergen (ZMBN), Natural History Museum of Copenhagen (NHMD), Natural History Museum in London (BMNH PI), Natural History Museum of Oslo (NHMO), Arctic University Museum of Norway (TSZ and TSZBr), NTNU University Museum (NTNU-VM) and new material collected by Akvaplan-niva AS (APN) as well as some material from the author's private comparative collection (JH) (the latter two have now transferred to the Arctic University Museum of Norway). Roughly half of the specimens housed at the visited museums have been checked by the author before inclusion in the study. Previously published data were also included after some validation of the information. Empty shells were excluded when not otherwise specified since they could be subfossils or fossils.

Though the maps show an accumulation of data points based on collections and earlier published works, they are not meant to show all existing published observations of species, which would be an almost impossible task. Instead, the maps are just meant to show the general biogeographic extent of each species. Since Norway has been the main focus of this study, this area includes the highest number of data points. The accumulated dataset is available upon reasonable request.

Maps were created using QGIS software with Esri Satellite (https://server.arcgisonline.com/ArcGIS/rest/services/World_Imagery/MapServer/tile/{z}/{y}/{x}) as the basic map while using IBCAO V3 500m RR (Jakobsson *et al.* 2012) to show the Arctic Ocean and TM_WORLD_BORDERS-0.1.ZIP (www.thematicmapping.org) to show country borders. A compilation of the borders between the oceanic surface water masses was added to provide a rough impression of the water masses influencing the shallower parts of the ocean.

The synonym lists are not meant as full overviews of which publications contain information about the species but present the oldest encountered occurrence of each synonym to give a chronological overview of the changes in synonyms. References to key publications are added in the environmental paragraphs and remarks for each species.

One month of continuous measurements of current, temperature, salinity and oxygen of bottom waters were in many cases executed by Akvaplan-niva at stations in the vicinity of grab samples. When

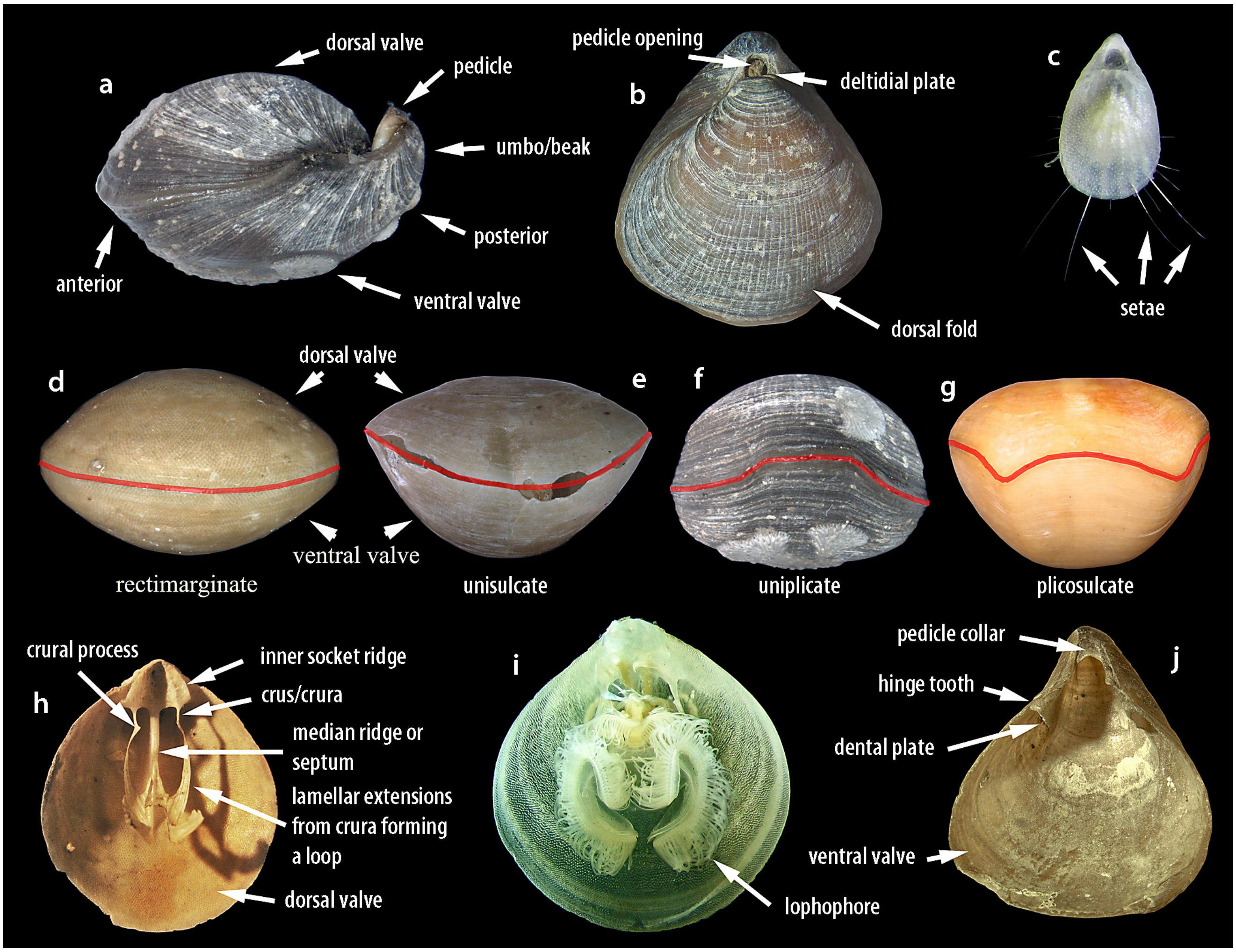
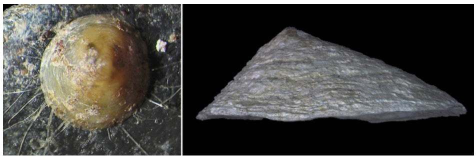


Figure 1. Terminology used in the paper. d–g show different shapes of the anterior commissure. Species shown: *Hemithiris psittacea* (a, b, f, j); juvenile *Terebratulina septentrionalis* (c); *Glaciarcula spitzbergensis* (d, h); *Dallina septigera* (e, g); *Macandrevia cranium* (i).

depth was comparable, this information was extracted to support the present study. In several cases, information about physical parameters from brachiopod stations not previously published together with the brachiopods has been obtained from non-brachiopod literature or collection labels for brachiopods housed at museums.

SPECIES KEY

1a An entire valve surface firmly attached to a substrate. Subconical. Inarticulate (no hinge) and with holoperipheral growth:



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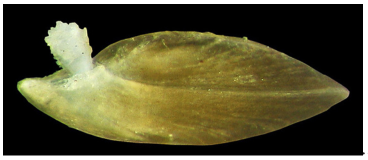
1b Shell articulated and with stalk (pedicle) posteriorly:



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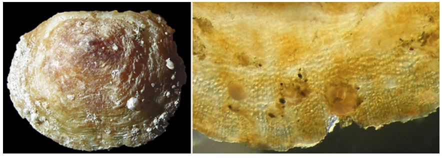
2a Small, non-punctate shell, up to 8 mm long, with long setae radiating out from valve margin. Subcircular outline. Rather thin, chitinophosphatic and whitish, yellow to brown or blackish-brown shell:

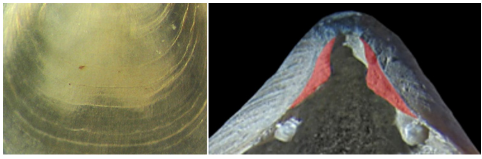
.... ***Pelagodiscus atlanticus*** (King, 1868)

2b Up to 25 mm wide, endopunctate shell, without setae. Transverse subangular outline. Calcium carbonate shell. Whitish to greyish or reddish brown:



.... ***Novocrania anomala*** (Müller, 1776)

3a Shell not punctate. Deltidial plates (red) not meeting:



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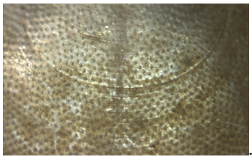
3b Shell endopunctate (fine pitting in shell):



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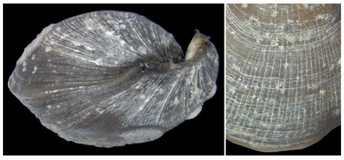
4a Slightly unisulcate anterior and gently S-shaped lateral commissure. No ornamentation and colourless or with a yellow tint. Small (6 mm). High internal dorsal median septum:

.... ***Cryptopora gnomon*** Jeffreys, 1869a

4b Moderate size (25–29 mm). Fine radiating striation from 1.2–4 mm valve length. No or rudimentary dorsal median ridge or septum:

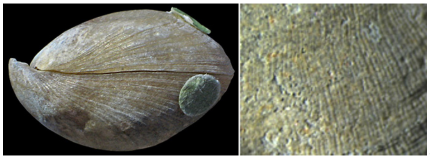
.... 5

5a Adults uniplicate and dark-coloured. Lateral commissure unevenly curved. Ventral umbo rather long. Weak internal dorsal ridge (lacking in juveniles). Width of interspace much wider than striae on shell surface. Pedicle opening V- to U-shaped:



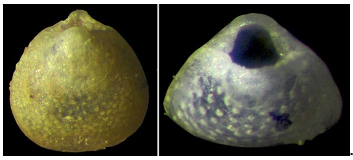
.... ***Hemithiris psittacea*** (Gmelin, 1791)

5b Rectimarginate anterior and straight lateral commissure. Shell brownish. Ventral umbo rather short. Short dorsal median septum or ridge. Very fine and dense striation. Pedicle opening typically partly enclosed by deltidial plates:



.... ***Hispanirhynchia cornea*** (Fischer, in Davidson 1887)

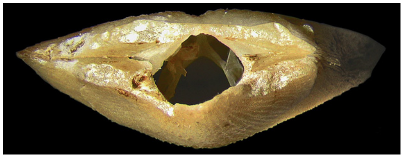
6a Up to 1.5 mm long, but usually less than 1 mm. Subcircular to elongate oval with small umbo and subequal valves. Rather inflated and lacking ornament. Pedicle opening large and partly extending into dorsal valve. Narrow but straight hinge line:



.... ***Gwynia capsula*** (Jeffreys, 1859)

6b Different 7

7a Pedicle opening large and partly extending into dorsal valve. Hinge line straight:



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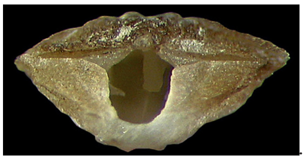
7b Pedicle opening restricted to ventral valve, or only very slightly notching dorsal valve. Dorsal umbo not raised above curved to nearly straight hinge line:

.... 14

8a Pedicle opening stretching far into the dorsal valve, typically forming a full half-circle on the upper surface. No radiate ornament. Dorsal umbo not raised above the hinge line. Short brachial loop:

.... 9

8b Pedicle opening not forming a half-circular hole on the upper surface of the dorsal valve, or, if so, then with some type of radiate ornament on ventral valve. Dorsal umbo usually slightly raised above the hinge line:



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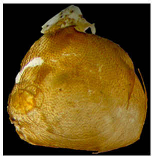
9a Only growth lines. Brachidial loop (=skeletal support of lophophore) with upper transverse band creating a triangular ring. Long setae (about 2/3 valve length) along valve margin. Subrectangular to transverse suboval:



.... **_Annuloplatidia annulata_** (Atkins, 1959)

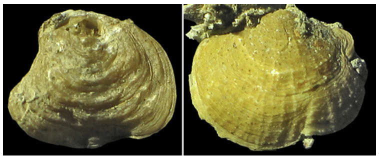
9b Only growth lines or with tuberculate ventral surface. No triangular brachial loop. Very short setae along valve margin. Subcircular to transverse suboval:

.... **_Platidia anomioides_** (Scacchi & Philippi, in Philippi, 1844)

10a Both valves with coarse costellate ribs lacking tubercles:

.... 11

10b Ornament of only growth lines, or with tubercles/spines and/or fine costellae:



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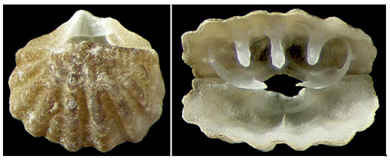
11a 8–16 coarse ribs. Up to 3 mm long. Brachial loop anteriorly just attached to median septum. Typically whitish with red between ribs:

.... **_Argyrotheca cuneata_** (Risso, 1826)

11b 7–18 broad ribs. Up to 6 mm long. Brachial loop attached to three to five septa including median septum. Light honey-coloured:



.... **_Megathiris detruncata_** (Gmelin, 1791)

12a At least ventral valve with ribs. Long brachial loop. Rectimarginate to unisulcate 13

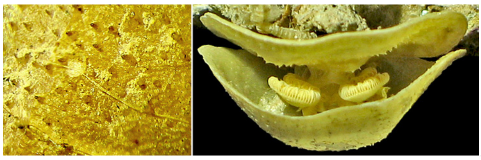
12b Ornamentation only composed of growth lines on both valves. Shell minute (3 mm) with median furrow in both valves (may be weak). Median septum in both valves:


.... ***Argyrotheca cistellula*** (Forbes & Hanley, 1849)

13a Both valves with dense, fine and tuberculate radiate ribs, though ventral valve usually has the stronger ornamentation. Shell biconvex and usually not markedly deformed from substrate


.... ***Megerlia truncata*** (Linnaeus, 1767)

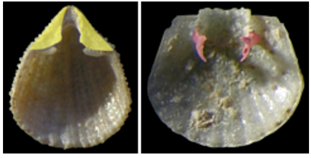
13b Ventral valve with radiate ribs as well as low tubercles and often minute alveolar spines or thorns scattered on surface. No or extremely weak and scattered radiating ribs on dorsal valve. Shell usually moulted after substrate, with nearly plane or even concave dorsal valve:


.... ***Megerlia echinata*** (Fischer & Œhlert, 1890)

14a Radiating ribs (may be absent on shells less than 1 mm long 15

14b Faint striation or no ornamentation except growth lines. Shell longer than wide 18

15a Ventral valve with interarea (yellow-marked plane triangular area bisected by pedicle opening). Nearly straight hinge line. Valve margins thickened and crenulate. Crura not extended to form a loop (red):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15b No interarea. Curved hinge line. Brachial loop (red). Valve margin not thickened and crenulate. Generally do not identify specimens less than 1.5 mm long to species level for the following:


.... 17

16a Up to about 44 beaded and rounded ribs distally. Middle dorsal rib and corresponding ventral interspace larger than other ribs. 5 mm long:


.... ***Eucalathis tuberata*** (Jeffreys, 1878)

16b Ornament of concentric bands and distally up to approximately 27 triangular ribs. Middle dorsal rib and corresponding ventral interspace not larger than other ribs. 7 mm long:

.... ***Eucalathis ergastica*** Fischer & Œhlert, 1890

17a Umbonal ribs on ventral valve of juvenile specimens normally separated by deep interspaces and consisting of tubercles, of which some along the shell crest are slightly overhanging rib interspaces. 9–14 (rarely 17) rather coarse ribs per 5 mm counted 10 mm anterior of ventral umbo. Generally pentagonal outline:

.... ***Terebratulina retusa*** (Linnaeus, 1758)

17b Tubercles lacking to dense, low and more like growth ridges on umbonal crest, and never overhanging interspaces. Stronger tubercles may occur laterally on umbo. 14–22 fine ribs per 5 mm counted 10 mm anterior of ventral umbo. Generally egg-shaped outline:

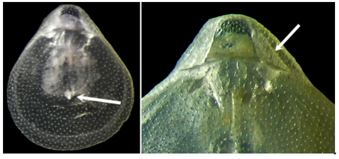
.... ***Terebratulina septentrionalis*** (Couthouy, 1838)

18a Some form of dorsal median septum or ridge present (visible as a line or point on the outside of wet shells):

.... 19

18b Dorsal median septum absent 26

19a Short dorsal pillar-like median septum (seen as a dot on wet shells) in shells between 2 and 6 mm in length. Umbo blunted and with moderately large pedicle opening. Rudimentary deltidial plates rectangular, never meeting and sharply defined by ridges:



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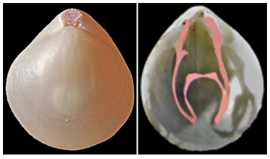
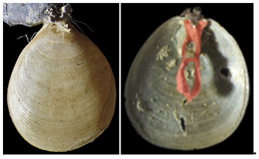
19b Dorsal median septum/ridge seen as a knife cut-formed scar on the outer side of shells larger than 2 mm long (can be dot-shaped or absent in smaller specimens) 21

20a Shell outline highly variable, from evenly rounded and very broad egg-shaped to nearly subpentagonal, elongate egg-shaped. Ventral umbo moderately developed. Moderately broad and broadly curved brachial loop (red):



.... ***Macandrevia cranium*** (Müller, 1776)

20b Shell outline usually elongate egg-shaped with poorly developed umbo and typically slightly truncated anterior margin. Fragile. Narrow loop with nearly subparallel sides (red):



.... *Macandrevia tenera* (Jeffreys, 1876a)

21a Short and poorly developed dorsal median ridge at umbo (~1/3 valve length):

.... 22

21b Long dorsal median septum or ridge (dot-shaped basis in specimens less than 2 mm long 23

22a Shell 10 mm long. Egg-shaped outline with clearly visible deltidial plates in dorsal view (red). Vascula media of mantle canal system faintly showing or invisible:

.... ***Xenobrochus islandicus* n. sp.**

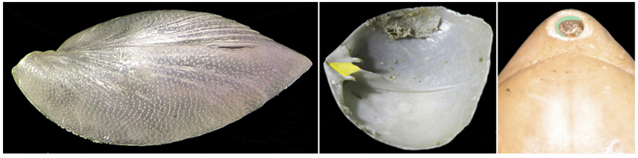
22b Shell 40 mm long. Typically with subpentagonal outline, and with short ventral umbo curved strongly in the dorsal direction, partly hiding the short deltidial plates (red). Imprints of vascula media of mantle canal system usually clearly visible on valve exterior as two straight, diverging, whitish lines on both dorsal and ventral valves (yellow):

.... ***Gryphus vitreus*** (Born, 1778)

23a Ventral umbo beak-shaped and curved in specimens >3.5 mm long. Pedicle opening egg-shaped. Teeth supported by dental plates (white arrow). Hinge plates not extended forward but connected to dorsal median septum at nearly right angles (yellow). Brachial loop always connected to median septum. Long pedicle collar (violet arrow):

.... 24

23b Ventral umbo blunt. No dental plates supporting teeth. Hinge plates extended forward to connect to dorsal median septum in a distinct V-shape (yellow). Brachial loop not connected to dorsal median septum on specimens larger than 13 mm. No or few spicules in soft tissue. Pedicle foramen subcircular or circular in adults (but deltidial plates disjunct in juveniles below 6 mm in length). Short pedicle collar (turquoise):



.... 25

24a Shell outline egg-shaped. Rectimarginate. Pedicle opening very elongate egg-shaped. 13 mm long:

.... ***Glaciarcula spitzbergensis*** (Davidson, 1852c)

24b Shell rather broad and truncated even at 7 mm in length. Abundant spicules in soft tissue. Pedicle opening is shorter egg-shaped and typically extends well up on the ventral side of umbo. 25 mm long:

.... ***Fallax dalliniformis*** Atkins, 1960a

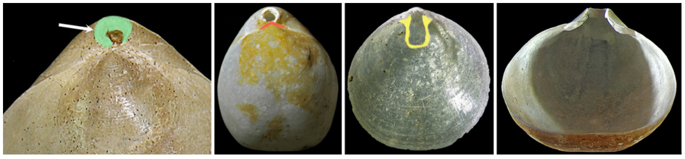
25a 45 mm long. Typically rounded pentagonal but can be subtriangular. Subtriangular to egg-shaped as juvenile. Usually only weakly truncate before reaching 20 mm in length (red line: growth stage). Lateral commissure usually straight to gently curved. Shell moderately robust:

.... ***Dallina septigera*** (Lovén, 1846)

25b 30 mm long. Adult shell subtriangular to strongly triangular with greatest width usually at anterolateral corners. Lateral commissure usually moderately curved. Relatively fragile shell:

.... ***Dallina lusitanica* n. sp.**

26a Shell whitish. Pedicle collar rather thick (green). Deltidial plates may be joined (red). Short loop (yellow). No dental plates supporting ventral hinge teeth:



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26b Pedicle collar rudimentary or absent (green). Deltidial plates never joined (red). Relatively long brachial loop (red):

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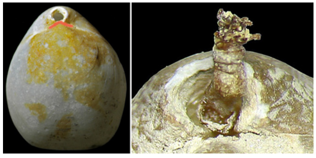
27a Broad egg-shaped to pentagonal outline. Low deltidial plates mostly not joined and partly hidden in the dorsal view due to curved beak (red). Stubby or no rootlets on pedicle. Shell surface typically dull:

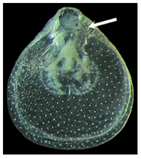


.... ***Arctosia arctica*** (Friele, 1877a)

27b Mostly elongate egg-shaped outline with dorsally clearly visible high and always joined deltidial plates (red). Distinct multiple rootlets on pedicle. Shell surface typically shiny and smooth:

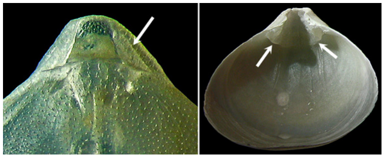
.... ***Xenobrochus islandicus*** **n. sp.**

28a Shell whitish. Less than 1.65 mm long. Deltidial plates not bordered by distinct ridges (at arrow). No dental plates supporting ventral hinge teeth:



.... Juvenile ***Dallina septigera*** (Lovén, 1846)

28b Shell of live specimens pale brownish (but empty shells become whitish). Deltidial plates of especially juvenile specimens bordered by ridges (arrow). Ventral hinge teeth supported by dental plates (arrows):



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29a Shell outline very variable, from evenly rounded and very broad egg-shaped to nearly subpentagonal elongate egg-shaped. 31 mm long. Ventral umbo comparatively large. Moderately broad and broadly curved brachial loop (red):

.... ***Macandrevia cranium*** (Müller, 1776)

29b Shell outline elongate egg-shaped with poorly developed umbo, with typically slightly truncated anterior margin. 13 mm long. Narrow loop with nearly subparallel sides (red):

.... ***Macandrevia tenera*** (Jeffreys, 1876a)

TAXONOMY

Phylum	Brachiopoda Duméril, 1805
Subphylum	Linguliformea Williams, Carlson, Brunton, Holmer & Popov, 1996
Class	Lingulata Gorjansky & Popov, 1985
Order	Lingulida Waagen, 1885
Superfamily	Discinoidea Gray, 1840
Family	DISCINIDAE Gray, 1840
Genus	*Pelagodiscus* Dall, 1908

Pelagodiscus atlanticus (King, 1868)

Figures 2–3

Discina atlantica King, 1868, p. 171–173, figs. 1–2.
Discina (*Discinisca*) (?) *atlantica*, Jeffreys – Dall (1873), p. 201.
Discinisca atlantica – Davidson (1888), p. 200–202, pl. 26, figs. 18–22.
Pelagodiscus atlanticus – Dall (1908), p. 440.

Description: Shell subcircular with semitransparent conical dorsal valve and flat ventral valve. Ventral valve very thin, attached to a hard substrate and markedly smaller than dorsal valve. Large subperipheral pedicle opening in ventral valve. Holoperipheral growth with apex slightly behind valve centre. Surface marked by dense concentric growth lines. Shell chitinophosphatic, impunctate and in most cases partly transparent. Juvenile shells nearly white or colourless, becoming yellow, reddish brown or even dark brown with increasing size. Dorsal valve margin with numerous radiating mantle setae, very long along anterior margin, shorter posteriorly. Ventral mantle margin lined with dense, short setae. No hinge. Maximum length 8 mm.

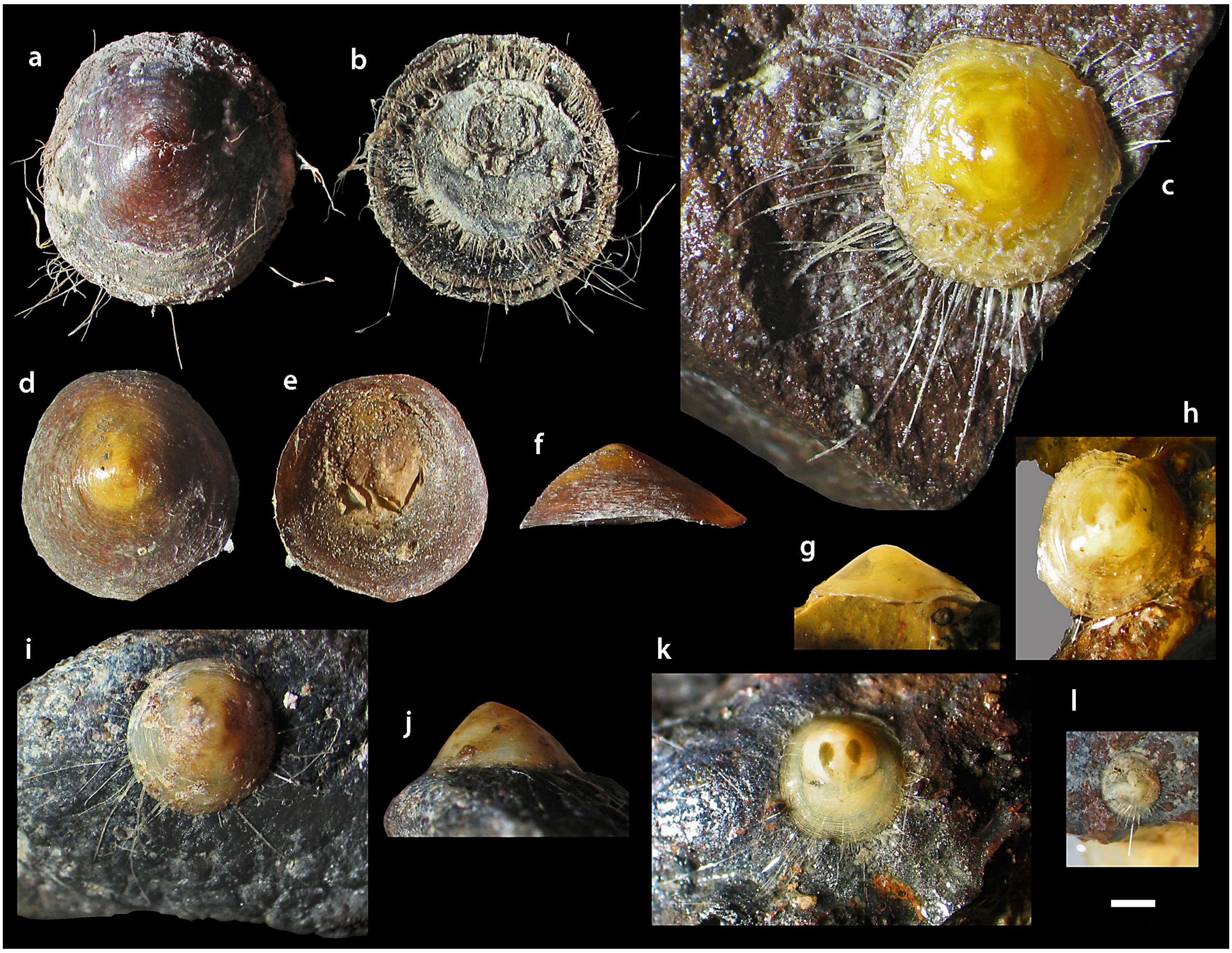

Figure 2. *Pelagodiscus atlanticus*. **a–b**: dorsal and ventral views of specimen, Davis Strait, W Greenland, 'Ingolf' expedition st. 36, 2702 m; **c**: dorsal view of attached specimen, W Iceland, 'Ingolf' expedition st. 10, 1484 m; **d–f**: dorsal, ventral and lateral views of the dorsal valve, W Iceland, 'Ingolf' expedition st. 10, 1484 m; **g–h**: lateral and dorsal views of specimen, W Africa, 'Galathea' expedition st. 99, 2690 m; **i–j**: dorsal and lateral views of specimen, W Africa, 'Galathea' expedition st. 99, 2690 m; **k**: dorsal view of specimen, South China Sea, 'Galathea' expedition st. 408, 4330 m; **l**: dorsal view of specimen, W Africa, 'Galathea' expedition st. 99, 2690 m. All specimens are housed at the Natural History Museum of Denmark, Zoological Museum of Copenhagen. Scalebar 1mm. Photos: Jesper Hansen.

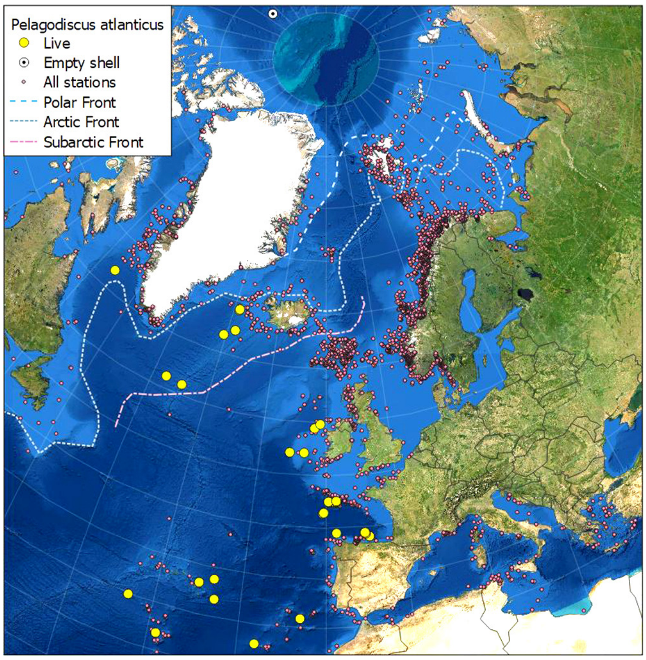

Figure 3. Distribution of *Pelagodiscus atlanticus*.

Depth range: Minimum range is 658–5530 m depth for live specimens (Davidson 1880; Zezina 2014). Although Dall (1920) reported two specimens from 294 fathoms (or possibly metres) off the coast of Florida, these should preferably be verified. Zezina (2010) also reported specimens from as shallow as 366–525 m depth near the Scandinavian Peninsula, in the South Ocean and the Malay Archipelago; however, more detailed information is missing and verification would thus be preferable.

Temperature range: -1.2–3.5°C (Jackson 1912; this study).

Salinity range: 34.9–35.1 (4 measurements) (this study).

Substrate: Attached to rock, bones or shells, but typically on bottoms dominated by ooze (Davidson 1880; Wesenberg-Lund 1941; Brunton & Curry 1979; this study).

Geography: Panoceanic deep-water species mainly found along the mid-ocean ridges as well as along the bases of continental slopes. Presently not recorded from the Greenland Sea and the Norwegian Sea (Figure 3). Since the species is reported from both the North Atlantic and an empty shell from the Canadian Basin in the Arctic Ocean (e.g., Wesenberg-Lund 1941; Brunton & Curry 1979; Zezina 1997a, 2010), it is likely also living in the deep parts of the Norwegian and the Greenland Sea.

Subphylum	Craniiformea Popov, Basset, Holmer & Laurie, 1993
Class	Craniata Williams, Carlson, Brunton, Holmer & Popov, 1996
Order	Craniida Waagen, 1885
Superfamily	Cranioidea Menke, 1828
Family	CRANIIDAE Menke, 1828
Genus	*Novocrania* Lee & Brunton, 2001

Novocrania anomala (Müller, 1776)

Figures 4–6

Patella Kermes da Costa & Humphrey, in da Costa (1770).
Patella anomala Müller, 1776, p. 237.
Orbicula anomala – Cuvier (1798), p. 435–436.
Crania personata Lamarck, 1801, p. 138.
Orbicula norwegica Lamarck, 1801, p. 140.
Patella distorta Montagu, 1815, p. 195, pl. 13, fig. 5.
Orbicula norvegica – Schumacher (1817), p. 176–177, pl. 21, figs. 2a–c.
Crania personata Blainville [non Lamarck, 1801], 1818, p. 312.
Criopus anomalus – Fleming (1822a), p. 499.
Crania ringens Hoeninghaus, 1828, p. 4–5, figs. 2a–b.
Crania rostrata Hoeninghaus, 1828, p. 5, figs. 3a–b.
Crania anomala – Lovén (1846), p. 183.
Crania norvegica – Sowerby (1847), p. 368, pl. 73, figs. 15–17.
Criopus orcadensis Leach, 1852, p. 358, pl. 13, figs. 6–8.
Crania (? *anomala* var.) *Pourtalesii* Dall, 1871, p. 35, pl. 1, fig. 7.
Crania (*Crania*) *anomala* – Dall (1873) [partim], p. 198.
Crania Pourtalesii – Dall (1881), p. 104.
Neocrania anomala – Lee & Brunton (1986), p. 150–152.
Neocrania pourtalesi – Lee & Brunton (1986), p. 150.
Crania (*Neocrania*) *anomala* – Nielsen (1991).
Novocrania anomala – Lee & Brunton (2001), p. 5.
Novocrania pourtalesi – Lee & Brunton (2001), p. 5.

Description: Shell transverse oval or subangular with low conical dorsal valve and nearly straight and narrow posterior margin. Holoperipheral growth with apex slightly behind mid-valve length. Ventral valve cemented to hard substrate. Shell smooth, with fine radiating striation or reflecting surface of substrate. Shell matrix endopunctate. Dark brown or reddish outer layer, with light grey inner shell layer. No hinge. Dorsal interior with distinct muscle scars. Anterior adductor muscle scars not raised or slightly raised. Tiny dorsal ridge. Ventral interior rarely with calcified posterior adductor muscle scars. Anterior adductor muscles attached to organic rostellum. Outer margin poorly defined and relatively densely tuberculate. Maximum width 25 mm.

Depth range: 4–1805 m depth, though mostly 10–400 m depth (Zezina 2010; Robinson 2017; Toma *et al.* 2022; this study). Observations from visual surveys of the coastal waters of Norway indicate that dense populations are likely widespread on submarine cliff walls and rocky bottoms in these latitudes in a depth zone from the lower part of a belt of dense serpulid tubeworm populations and downwards (Figure 5). In the Vestfjord area of Nordland, this brachiopod zone seems to be mostly between 100 and 200 m in depth; however, it extends to shallower depths in many places. This compares well with visual surveys in the Mediterranean where dense populations were found especially frequent on cliff walls at 80–500 m depth, though with geographic variations (Toma *et al.* 2002).

Temperature range: 1.8–11.0˚C (Grieg 1924; this study). However, Brand *et al.* (2003) gave the temperature range 6–21˚C, indicating a much higher upper range than found in the present study.

Salinity range: 29–37 (Brand *et al.* 2003).

Oxygen range: 55–113% for oxygen saturation of bottom water (this study).

Current velocity: Mean current velocity between 1.1–9.5 cm/s, with daily maxima generally between 0–30 cm/s, with a maximum velocity of 4.4–42.5 cm/s over 1 month of measurements (this study).

Substrate: Attached to cliff faces, boulders, artificial substrates and the hard skeletons of other organisms (Brunton & Curry 1979; Toma *et al.* 2022; this study). Mostly collected on sea floors

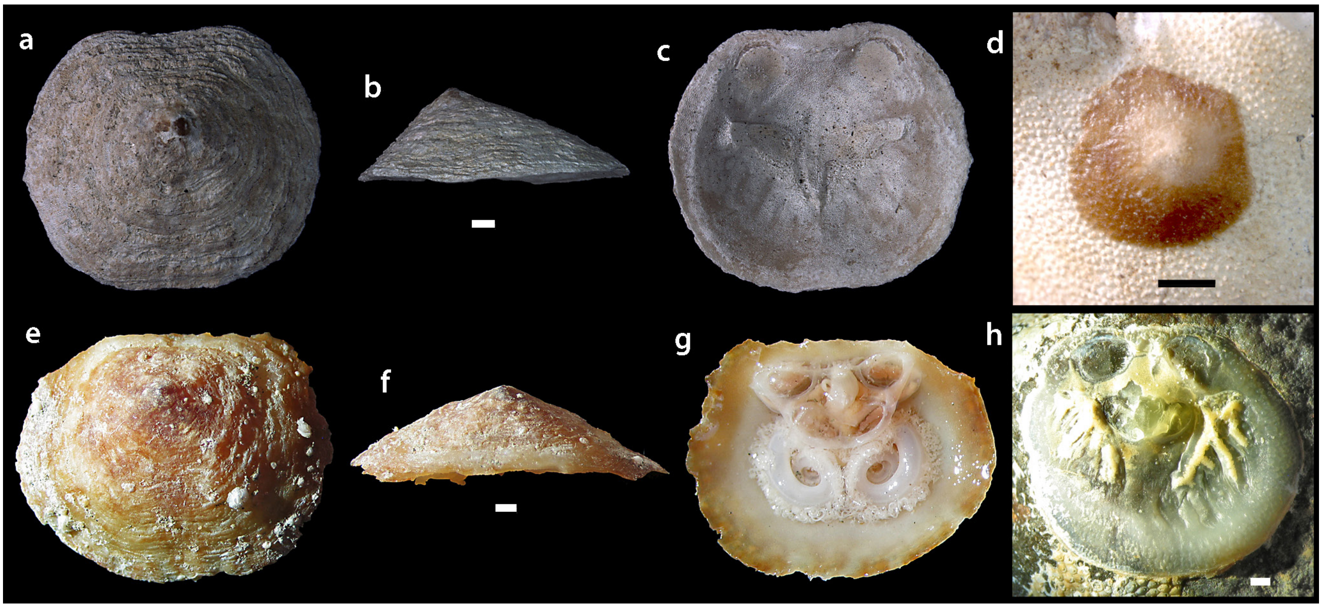

Figure 4. *Novocrania anomala*. **a–c**: dorsal, lateral and ventral views of dorsal valve, TSZBr 2396, Lødingen st. viii in Nordland, Norway, 70–80 m; **d**: specimen attached to coral with the ornament of the coral impressed on the shell, Brettingsneset in Trondheimsfjorden, Trøndelag, Norway, 100–400 m (JH); **e–g**: dorsal, posterior and ventral view of dorsal valve with soft tissue preserved, TSZ 3210 (APN), Øksfjord in Finnmark, Norway, 94 m; **h**: interior of ventral valve, Nordnes at Alta in Finnmark, Norway, 87 m (APN). Scalebar 1mm. Photos: Jesper Hansen.

Figure 5. Cliff face covered by both live and dead specimens of *Novocrania anomala*. 121 m depth in a Norwegian fjord. Photo: Akvaplan-niva.

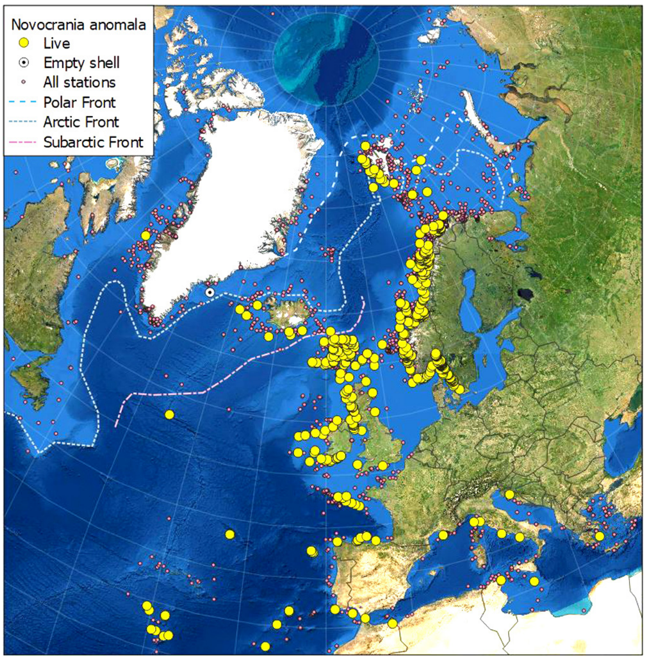

Figure 6. Distribution of *Novocrania anomala*.

dominated by sand, shell sand, gravel, cobbles and/or rock (Thomsen 2001), though visual surveys indicate this is a bias reflecting the sampling methods (Toma *et al.* 2022; this study).

Geography: Svalbard, Norway (but rare in NE Finnmark), Iceland, the Faroe Islands, Greenland (a live specimen collected on the west coast and one empty shell from the SE coast), SW Sweden, Great Britain, France, Spain, Portugal, the Mediterranean, Azores, Morocco, Cape Verde, Madeira, the Canary Islands, the Mexican Gulf and the Caribbean (Robinson 2017; this study) (Figure 6).

Remarks: No live specimens appear to have been collected around Svalbard before 1900; however, this is likely reflecting the sampling methods.

Subphylum	Rhynchonelliformea Williams, Carlson, Brunton, Holmer & Popov, 1996
Class	Rhynchonellata Williams, Carlson, Brunton, Holmer & Popov, 1996
Order	Rhynchonellida Kuhn, 1949
Superfamily	Dimerelloidea Buckman, 1918
Family	CRYPTOPORIDAE Muir-Wood, 1955
Genus	*Cryptopora* Jeffreys, 1869a

Cryptopora gnomon Jeffreys, 1869a

Figures 7, 8

Cryptopora gnomon Jeffreys, 1869a, p. 136.
Atretia gnomon – Jeffreys, in Carpenter *et al.* (1869), p. 421.
Dimerella gnomon – Dall (1873), p. 197.
Neatretia gnomon – Fischer & Œhlert (1891), p. 122–125, figs. 11a–c.

Description: Shell low to moderately biconvex. Outline subpentagonal to subtriangular with small, beak-shaped, acute umbo. Anterior valve commissure slightly unisulcate and lateral commissure gently S-shaped. Scattered short setae along valve margins. Dorsal sulcus broad, weak and restricted to the front. Ornamentation normally lacking, but weak striation from the growth tracks of setae attachments along valve margin can develop on larger specimens. Shell matrix impunctate. Shell thin, transparent and colourless or slightly yellowish. Pedicle opening triangular and deltidial plates rudimentary. Pedicle orange and varies from long and tread-like to short. Attachment end of pedicle with short rootlets. Dental plates extend to approximately 1/4 valve length. Dorsal median septum long, shark fin-like, high and thin, starting close to umbo and extending to between 1/2 and 2/3 valve length. Crura delicate, anteroventrally directed and moderately long, with lophophores extending to about mid-valve length. Maximum length 6 mm.

Depth range: 520–4390 m depth and mostly from deeper than

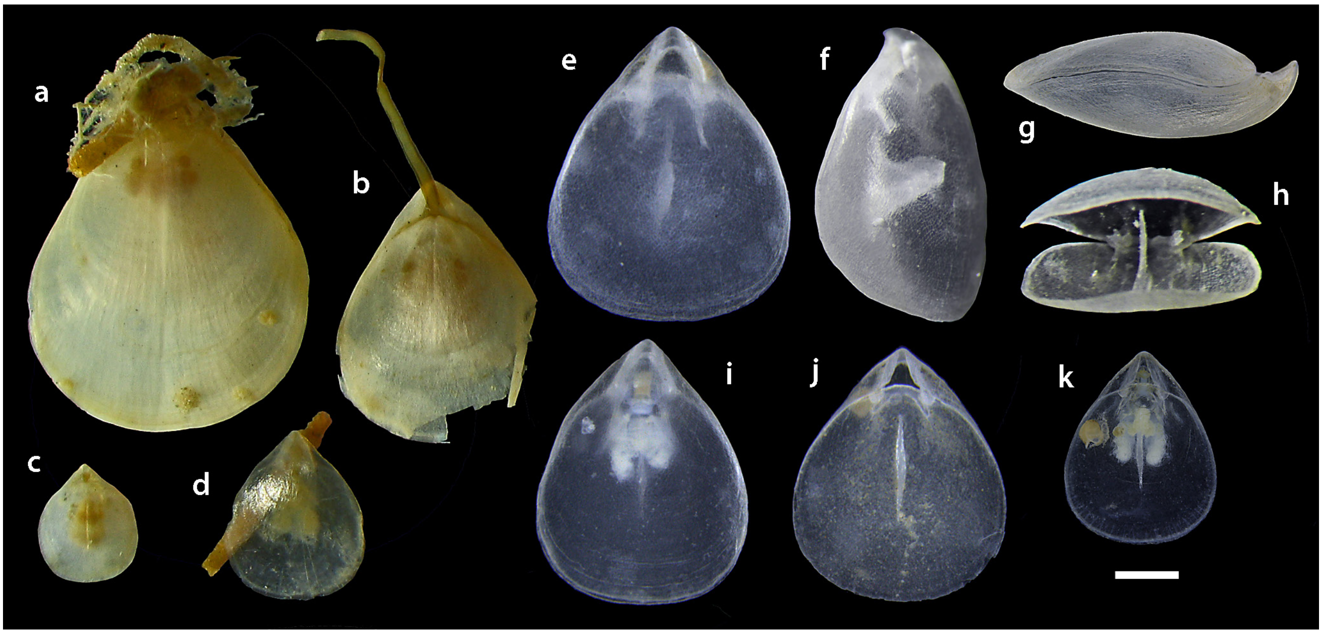

Figure 7. *Cryptopora gnomon*. **a–d**: four specimens, Davis Strait, W Greenland, 'Ingolf' expedition st. 36, 2702 m; **e–h**: dorsal, oblique ventral view with septum visible, lateral and anterior view of a shell, Eggagrunnen, Nordland, Mareano 2008 st. R297-347B, 808 m; **i–j**: ventral view of a specimen and dorsal view of an empty shell, Eggagrunnen, Nordland, Mareano 2008 st. R297-347B, 808 m; **k**: dorsal view of specimen, Eggagrunnen, Nordland, Mareano 2008 st. R297-346, 807 m. a–d: Natural History Museum of Denmark, Zoological Museum of Copenhagen. e–k: collected by the Institute of Marine Research and housed at the University Museum of Bergen. Photos e, i, j and k: Katrine Kongshavn. Scalebar 1mm. Photos a–d, f–h: Jesper Hansen.

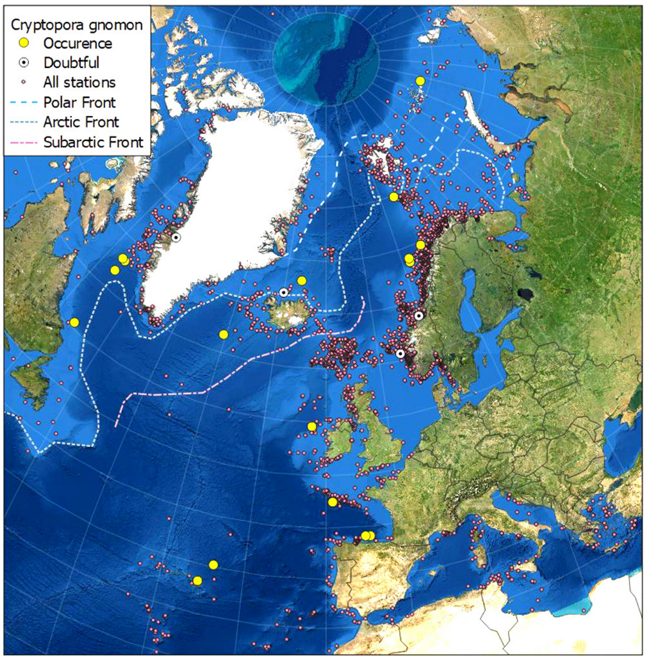

Figure 8. Distribution of *Cryptopora gnomon*. Doubtful observations in need of verification are marked as such.

1000 m (Posselt 1898; Zezina 2010). Specimens sampled at 35–450 m depth in Norway, Iceland, Greenland and the USA have also been referred to as this species (e.g., Dall 1920; Wesenberg-Lund 1938, 1939, 1940a, 1941). However, since one-third of these were located and examined at the visited museums and all turned out to be juvenile shells of *Macandrevia cranium* and *Hemithiris psittacea*, the rest are presently considered doubtful.

Temperature range: -1.2–3.4˚C (this study).

Salinity range: 32.3–35.1 (Wesenberg-Lund 1940a; Thomsen 2012; this study).

Substrate: Attached to sand grains, rocks, foraminiferan sand tubes and other hard surfaces on mud-dominated sea floors (Posselt 1898; Brunton & Curry 1979; this study).

Geography: Arctic Ocean off Graham Bell Island in the archipelago of Franz Josef Land, West of Bjørnøya, Norway (Nordland and Troms, and possibly also South to Vestland), Iceland, W Greenland, E Canada, Atlantic Ocean, Ireland, eastern USA, Azores, Morocco, Cuba, the Caribbean, and Panama (Fischer & Œhlert 1891; Posselt 1898; Dall 1920; Wesenberg-Lund 1939, 1940a; Cooper 1973a; Zezina 1997a, 2008, 2014; Thomsen 2012).

The species is also reported from the Falkland Islands in the SW Atlantic, off South Africa, and as empty shells from the Tasman Sea at Macquarie Island, S of New Zealand (Cooper 1973a; Zezina 2008, 2010, 2014). Although the shell morphology is very similar, these specimens require a rigorous examination since they are, as already pointed out by Cooper (1973a), very far outside the normal known distribution of the species.

Based on the available coordinates, this deep-water species appears to prefer the shelf edge, slope and abyssal marine environments.

Superfamily	Hemithiridoidea Rzhonsnitskaia, 1956
Family	HEMITHIRIDIDAE Rzhonsnitskaia, 1956
Genus	*Hemithiris* d'Orbigny, 1847a

Hemithiris psittacea **(Gmelin, 1791)**

Figures 1A, 1B, 1F, 1J, 9, 10

Anomia rostrum psittaci Chemnitz, 1785, p. 106, pl. 78, figs. 713a–b.
Anomia psittacea Gmelin, 1791, p. 3348.
Lampas psittacea – Calonne & Humphreys (1797), p. 45.
Terebratula psittacea – Lamarck (1819), p. 248.

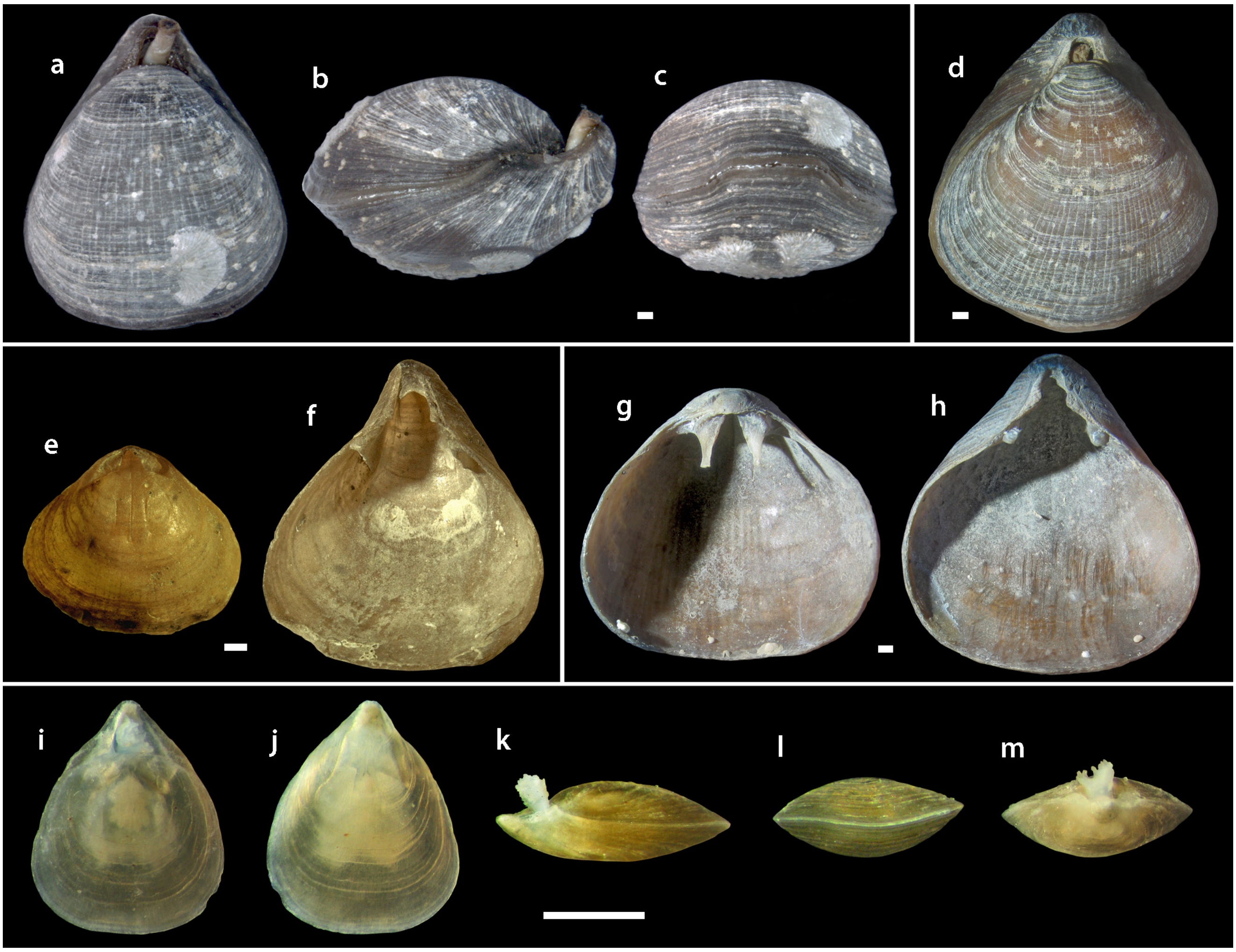

Figure 9. *Hemithiris psittacea*. **a–c**: dorsal, lateral and anterior views of specimen, Hinlopen Strait, Svalbard, 337 m (JH); **d**: dorsal view of specimen, Hinlopen Strait, Svalbard, 337 m (JH); **e–f**: inner sides of dorsal and ventral valves, Heleysund, Svalbard, 68 m (JH); **g–h**: inner sides of dorsal and ventral valves of an empty shell, Hinlopen Strait, Svalbard, 337 m (JH); **i–m**: dorsal, ventral, lateral, anterior and posterior views of juvenile specimen, TSZ 3012 (APN), Jernøya in Finnmark, Norway, 73 m. Scalebar 1mm. Photos: Jesper Hansen.

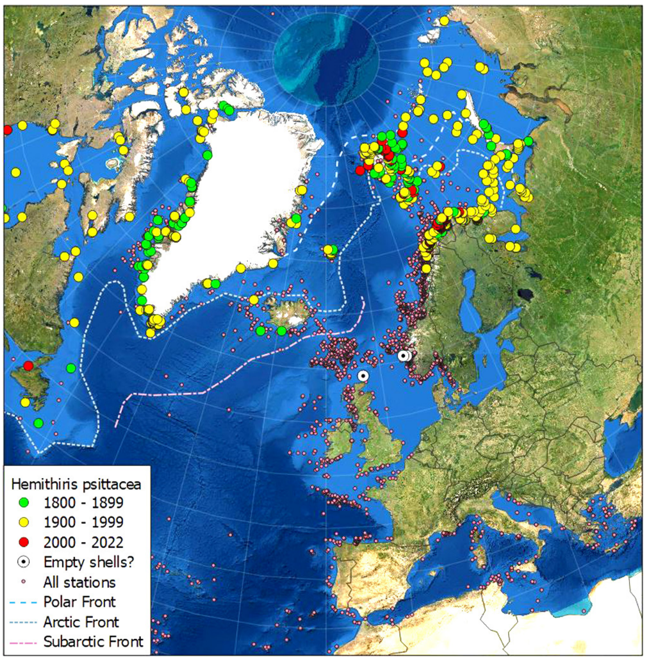

Figure 10. Distribution of *Hemithiris psittacea*. Colours mark which century the specimens were collected in. Possible fossil empty shells in need of verification are marked as such.

Gypidia psittacea – Menke (1830), p. 96.
Hypothyris psittacea – King (1846), p. 28.
Hemithiris psittacea – d'Orbigny (1847b), p. 246.
Rhynchonella psittacea – Davidson (1852a), p. 251–253, pl. xiii, figs. 1a–b.
Rhynchonella (*Hemithyris*) *psittacea* – Dall (1873), p. 196.

Description: Shell with subtriangular or subpentagonal outline and rather acutely pointed beak. Large specimens approximately as wide as long. Anterior commissure uniplicate on specimens larger than 16 mm, while gently unisulcate on specimens smaller than 4 mm. Lateral valve commissure unevenly curved. Ornament developing from 1.2–4 mm valve length and outwards as fine, broad and very flat radiating ribs or relatively well-separated striae. Shell matrix impunctate. Colour dark bluish, dark grey or brownish except in small specimens, which are light-coloured and transparent. Ventral umbo beak-shaped and rather long. Rudimentary triangular deltidial plates not joining but forming a roughly U-shaped pedicle opening. Distinct pedicle collar. Elongate, unbranched pedicel. Small specimens with setae protruding as prolongation of striae. Well-developed dental plates. Crura flattened. Weak and short dorsal median ridge. Maximum length 30.4 mm.

Depth range: 0–2078 m depth, though rarely found deeper than

400 m, and only two reports from deeper than 1000 m depth (Cooper 1973a; this study).

Temperature range: -2–12˚C (Knipowitsch 1901; Ullmann *et al.* 2017).

Salinity range: 26.2–35.5 (Zezina 2008; this study).

Oxygen range: Oxygen saturation 83–105% (this study).

Current velocity: Mean current velocity of 2.6–11.7 cm/s, with daily maxima of 4–30 cm/s and an absolute maximum velocity of 13.3–72.2 cm/s over 1 month of measurement (this study).

Substrate: Usually attached to small pebbles, shells or rocks, but can be attached to any kind of hard surface such as serpulid and *Nothria* tubes, bryozoans, Cirripedia fragments, rhodoliths or even Foraminifera and sand grains (this study). Found on mud- or sand-dominated sea floors mixed with shell sand, or on gravel, pebbles, stones, calcareous red algae, rock grounds or vertical cliffs (Leche 1878; Posselt 1898; Arndt & Grieg 1933; Wesenberg-Lund 1940a,b; Thomsen 2012; this study).

Geography: Arctic Ocean, E and W Canada, E and W Greenland, Svalbard, Jan Mayen, Kara Sea, Laptev Sea, the White Sea, Norway (from Folda in Nordland and north), S and W of Iceland, W USA, and Japan (e.g., Posselt 1898; Lamy 1913; Grieg 1933; Brunton & Curry 1979; Zezina 1997b, 2008; this study).

The species is also reported from the North Sea, Faroe Islands, at the Hebrides, Ireland, Orkney Isles and Shetland Isles (e.g., Lyell 1842; Dall 1920; Brunton & Curry 1979; Thomsen 2001). Following Jeffreys (1863, 1878) and based on specimens examined at the Natural History Museum of London, all certain observations around the British Isles are empty and likely of glacial age. The reported presence at the Faroe Islands by Lyell (1842) was based on the apparent glacial material (BMNH PI ZB 1667). Additionally, according to Thomsen (2001), there are no other possible recent specimens known from the area.

Jeffreys (1878) mentioned the species from Drontheim (=Trondheim) in Trøndelag, Norway, while Wesenberg-Lund (1939) reported it from Brettingsnes in the Trondheimsfjord. However, the latter are two empty shells most likely of glacial age. The first was a re-occurring mistake that Jeffreys (1869b: 164) admitted, using Trondheim instead of Tromsø.

Dall (1920) listed a specimen from Bergen in Vestland, Norway. According to the collection list, the University Museum of Bergen also houses a specimen from that area. However, the latter was missing, and both are most likely not recent shells.

In the collections housed at the Natural History Museum of London was a single specimen collected alive (BMNH PI B 24769) with no other information than ‘North Sea’. The label dates it to before the year 1900. However, it seems more likely that the information is incorrect rather than the specimen actually is originating from the North Sea.

Remarks: The species was first named, described and beautifully illustrated by Chemnitz (1785). However, since he used a trinomial name instead of the Linnean binominal system, Gmelin (1791) is accepted as having named the species.

Within Norwegian waters, it seems that this Arctic and subarctic species has been retreating northward within the last century since no live specimens appear to have been collected south of 69.2°N in Nordland and Troms after 1923, while it was collected from several localities south to 67.6°N before then.

Despite its wide depth range, *Hemithiris psittacea* is primarily associated with coastal environments.

Superfamily Norelloidea Ager, 1959
Family FRIELEIIDAE Cooper, 1959
Genus *Hispanirhynchia* Thomson, 1927

Hispanirhynchia cornea (Fischer, in Davidson 1887)
Figures 11, 12

Rhynchonella cornea Fischer, in Davidson (1887), p. 171–172, pl. 25, figs. 2–4.

Rhynchonella (*Hemithyris*) *cornea* – Fischer & Œhlert (1891), p. 13–18, pl. 1, figs. 2a–u.

Hemithyris cornea – Dall (1920), p. 288–289.

Hispanirhynchia cornea – Thomson (1927), p. 159–161, fig. 49.

Description: Shell low equibiconvex to inflated, but with flattened top in anterior profile. Outline elongate subtriangular. Ventral umbo rather short and incurved beak-shaped. Rectimarginate to faintly unisulcate anterior and straight lateral commissure. Triangular, disjunct deltidial plates more than halfway enclosing small to medium-sized pedicle opening. Short pedicle collar. Ornamentation of very fine, dense and radiating striation as well as concentric growth lines. Shell matrix impunctate. Colour light yellow to brownish. Teeth supported by dental plates. Subhorizontal inner hinge plates in dorsal valve connecting socket ridges with crural bases. Lophophore supported by short, thin crura. Sharp-edged short dorsal median septum. Maximum length 36 mm.

Depth range: 439–3645 m depth (Cooper 1981a; Zezina 2010). Davidson (1887) gave the extremely shallow depth of 105 m off Southern Portugal for the syntype specimen sampled during the Talisman Expedition in 1883. However, as concluded by Emig (2016) this location is wrong and should have been the Talisman station off Morocco at 1050 m depth reported by Fischer & Œhlert (1891).

Temperature range: 6–12˚C (Brand *et al.* 2003).

Salinity range: 35–36 (Brand *et al.* 2003).

Geography: English Channel, off SW Ireland, south to the Azores, the Canary Islands and Sudan (Fischer & Œhlert 1891; Brunton & Curry 1979; Cooper 1981a; Logan *et al.* 2007; Zezina 2014).

Remarks: Although the year of description is often given as 1886 since that is written on the first page of the paper, it was published in 1887.

No holotype was elected in the original description, but Emig (2016) has subsequently elected the Talisman station off Morocco at 1050 m depth as the type locality. Most type specimens from the Talisman expedition have lost their labelling according to Alvarez (2016), but based on the provided pictures it seems most likely that the bigger of the two specimens labelled ML-ZOO-MAL-00133 is identical with pl. 25, figure 2–2c of Davidson (1887) from the Talisman expedition. That would then be a candidate for election as a lectotype.

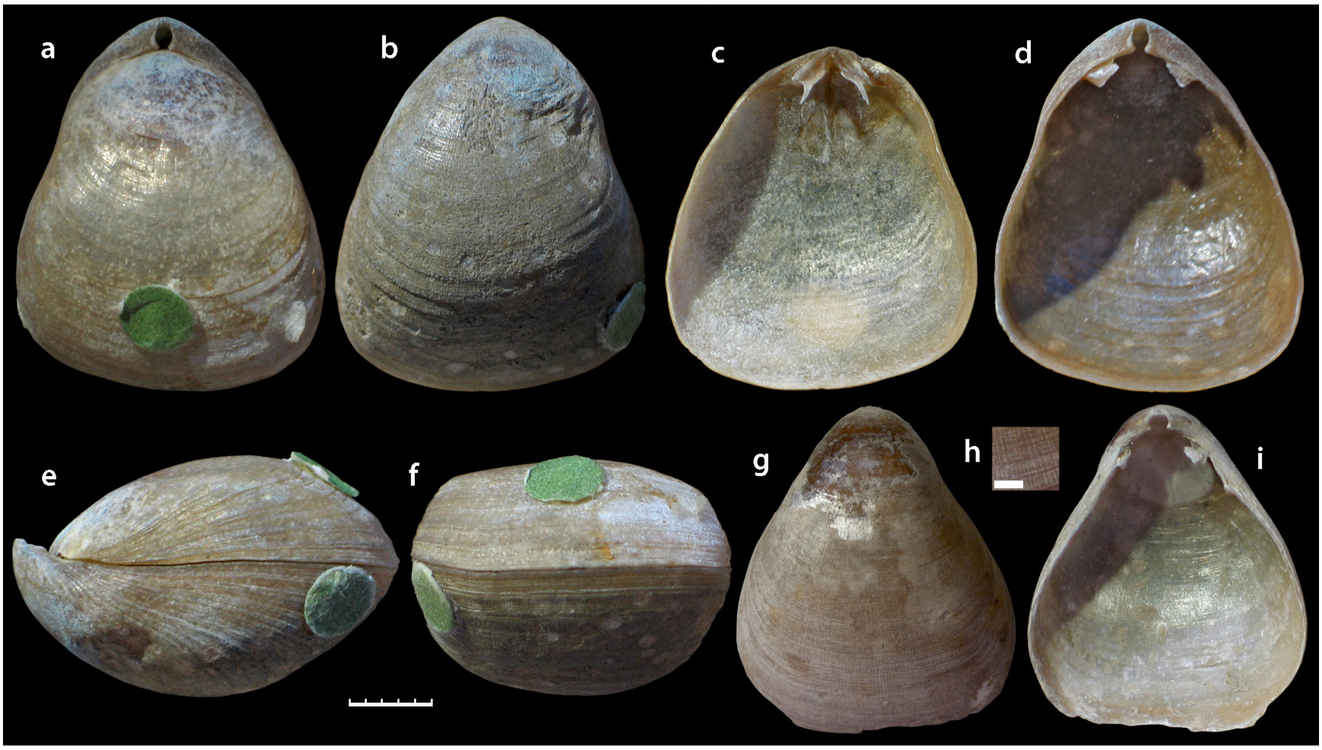

Figure 11. *Hispanirhynchia cornea*. **a–f**: dorsal, ventral, dorsal inner, ventral inner, lateral and anterior views of syntype BMNH PI ZB 281, English Channel, 1262 m; **g–i:** outer side, detail of ornamentation and inner side of the ventral valve of syntype BMNH PI ZB 4954, English Channel, 1262 m. Solid scalebar 1mm and segmented calebar 5mm. Photos: Jesper Hansen.

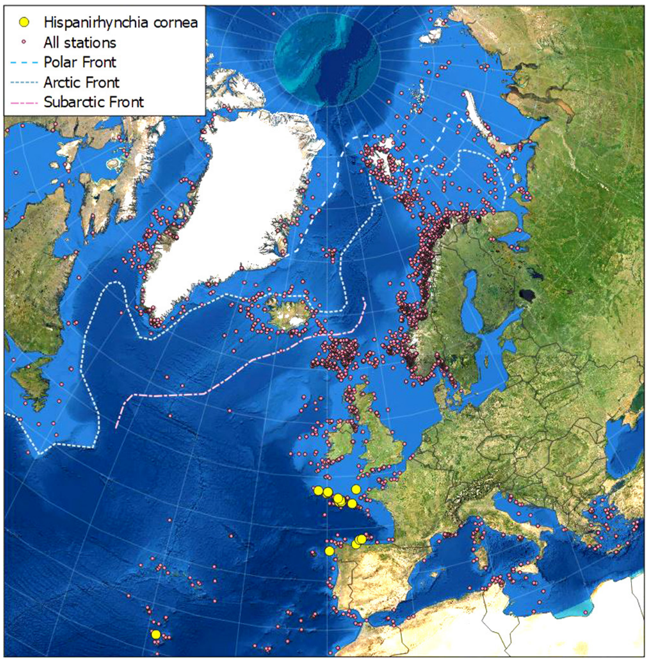

Figure 12. Distribution of *Hispanirhynchia cornea*.

Order	Terebratulida Waagen, 1883
Superfamily	Terebratuloidea Gray, 1840
Family	TEREBRATULIDAE Gray, 1840
Subfamily	Gryphinae Sahni, 1929
Genus	*Gryphus* Megerle von Mühlfeld, 1811

Gryphus vitreus (Born, 1778)

Figures 13, 14

Anomia vitrea Born, 1778, p. 104.
non *Anomia vitrea* – Chemnitz (1785), pl. 78, figs. 707 and 709 [=*Dallina septigera*].
Terebratula vitrea – Lamarck (1801), p. 139.
Gryphus vitreus – Megerle von Mühlfeld (1811), p. 64.
Liothyris vitrea – Douvillé (1879), p. 265, fig. 6.
Terebratula (*Liothyris*) *vitrea* – Deslongchamps (1884), p. 190–195, pl. 5, figs. 8–12.
Terebratula (*Liothyrina*) *vitrea* – Œhlert (1887), p. 1316, fig. 1104.

Description: Shell moderately to strongly inflated ventribiconvex. Outline elongate egg-shaped to subpentagonal. Rectimarginate to broadly uniplicate anterior commissure; shiny and smooth without ornamentation. Shell matrix densely endopunctate, greatly thickened and heavy posteriorly. Colour white to light grey or yellowish. Ventral umbo short and curled greatly towards dorsal valve. Deltidial plates unite and partly fuse together, forming a symphytium and confining an egg-shaped, variably-sized foramen. Pedicle collar thick. Hinge teeth without dental plates. Vascula media of mantle canal system strongly impressed on valve floor and usually visible on valve exterior as two straight, diverging, whitish lines on both dorsal and ventral valves. Cardinal process small and transverse. Short, poorly developed dorsal median ridge reaching slightly anterior of 1/3 valve length and forked at the very front (usually visible through the shell). Short brachial loop about 1/4 valve length. Dorsal muscle scars reaching to about 1/5–2/7 valve length. Maximum length 40 mm.

Depth range: 73–2663 m depth (Jeffreys 1878; Dall 1920).

Temperature range: 4.6–13.6˚C (Jeffreys 1878; Allmen *et al.* 2010).

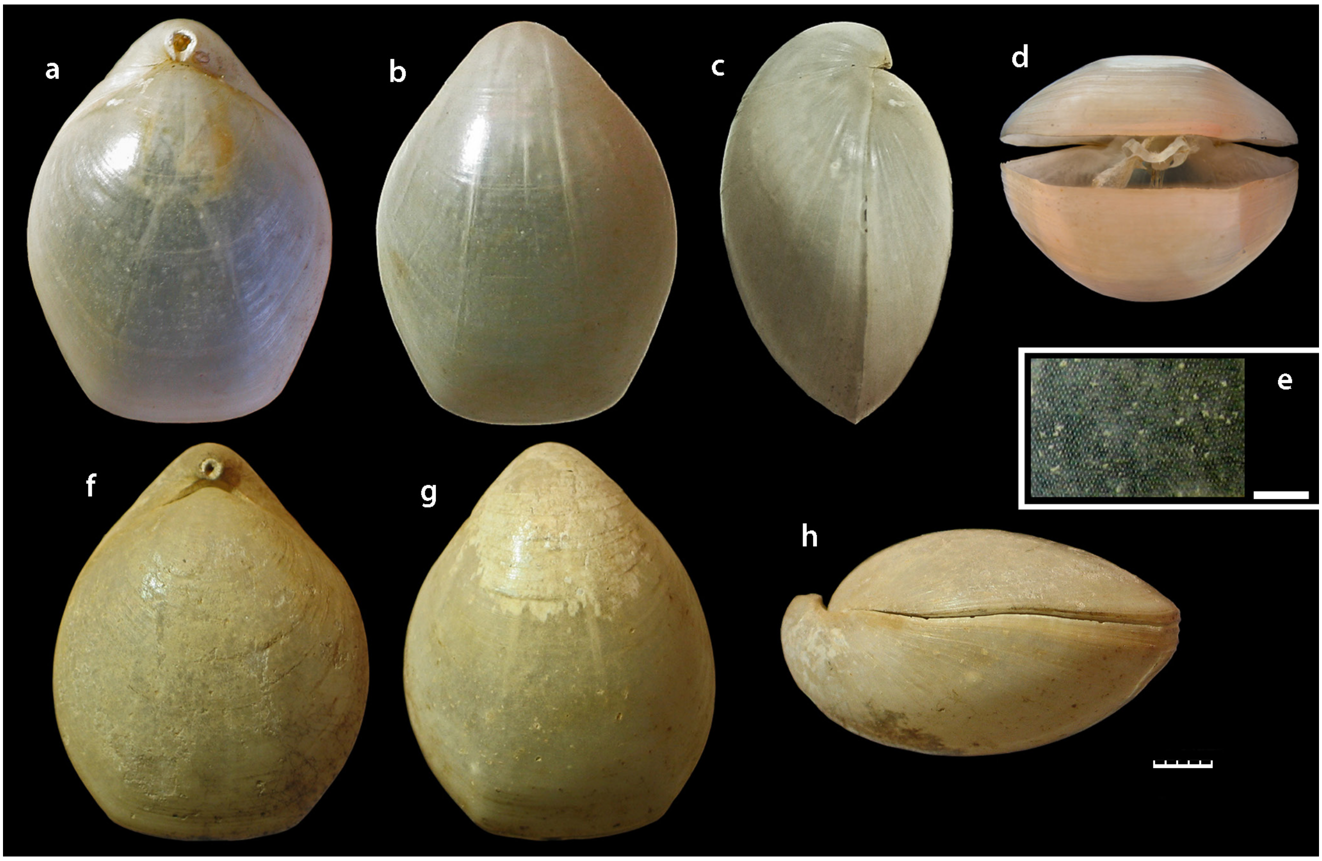

Figure 13. *Gryphus vitreus*. **a–e**: dorsal, ventral, lateral and anterior views of shell and close-up image of endopunctae (JH); **f–h**: dorsal, ventral and lateral views of shell (JH). Both from near Alboran, Spain, 300 m. Solid scalebar 1mm and segmented scalebar 5mm. Photos: Jesper Hansen.

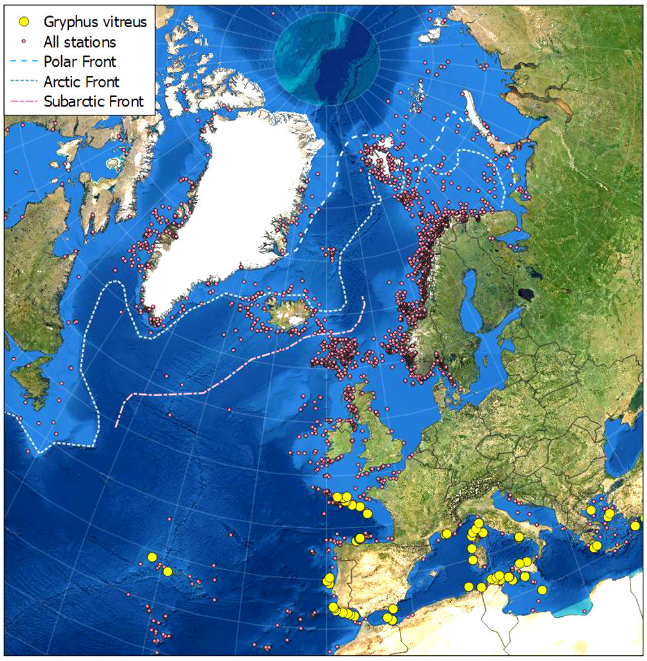

Figure 14. Distribution of *Gryphus vitreus*.

Salinity range: 38.1–38.5 (Allmen *et al.* 2010).

Current velocity: 25–100 cm/s (Emig 1987; Emig & García-Carrascosa 1991).

Substrate: Rock, gravel, artificial substrates and shells (Fischer & Œhlert 1891; Logan 1979; Allmen *et al.* 2010; Toma *et al.* 2022).

Geography: Southern margin of the Celtic Sea, Bay of Biscay, Portugal, the Mediterranean, off North Africa, Cape Verde (Fischer & Œhlert 1891; Logan 1979; Brunton & Curry 1979; Zezina 2014).

Subfamily Tichosininae Cooper, 1983
Genus *Arctosia* Cooper, 1983

Arctosia arctica **(Friele, 1877a)**

Figures 15, 16

Terebratula arctica n. s. Friele, 1877a, p. 221, fig. 1, 1a–c.
Liothyris arctica – Davidson (1886), p. 10, pl. 1, figs. 17–18.
Liothyris (*Terebratula*) *arctica* – Grieg (1907), p. 540.
Gryphus arcticus – Dall (1920), p. 317.
Liothyrella arctica – Thomson (1927), p. 198.
Arctosia arctica – Cooper (1983), p. 250–251, pl. 58, figs. 1–8, pl. 60, fig. 9, pl. 65, figs. 7–8.

Description: Shell moderately to strongly equi- to ventribiconvex. Outline subtriangular in smaller specimens, changing to broadly subpentagonal and somewhat truncated. Posterior margins form an angle of 75–80°. Dorsal valve without median fold or depression. Valves rarely with shallow sulcus. Anterior commissure rectimarginate. Relatively dull and thin-shelled, semitransparent to opaque, and endopunctate. Ornamentation generally lacking except for faint growth lines, but faint, dense, radiating striation can occur. Colour whitish. Beak short and rounded in lateral profile, slightly incurved, and often with short triangular deltidial plates narrowly conjoining in larger specimens. Foramen moderately large. Deltidial plates are bordered by ridges, especially in smaller specimens. Pedicle collar thick. Pedicle typically with short rootlets distally. Brachial loop very small and short, with a nearly straight, thin transverse band. Crural process just anterior to mid-loop and loop reaches to 1/4 to 1/3 valve

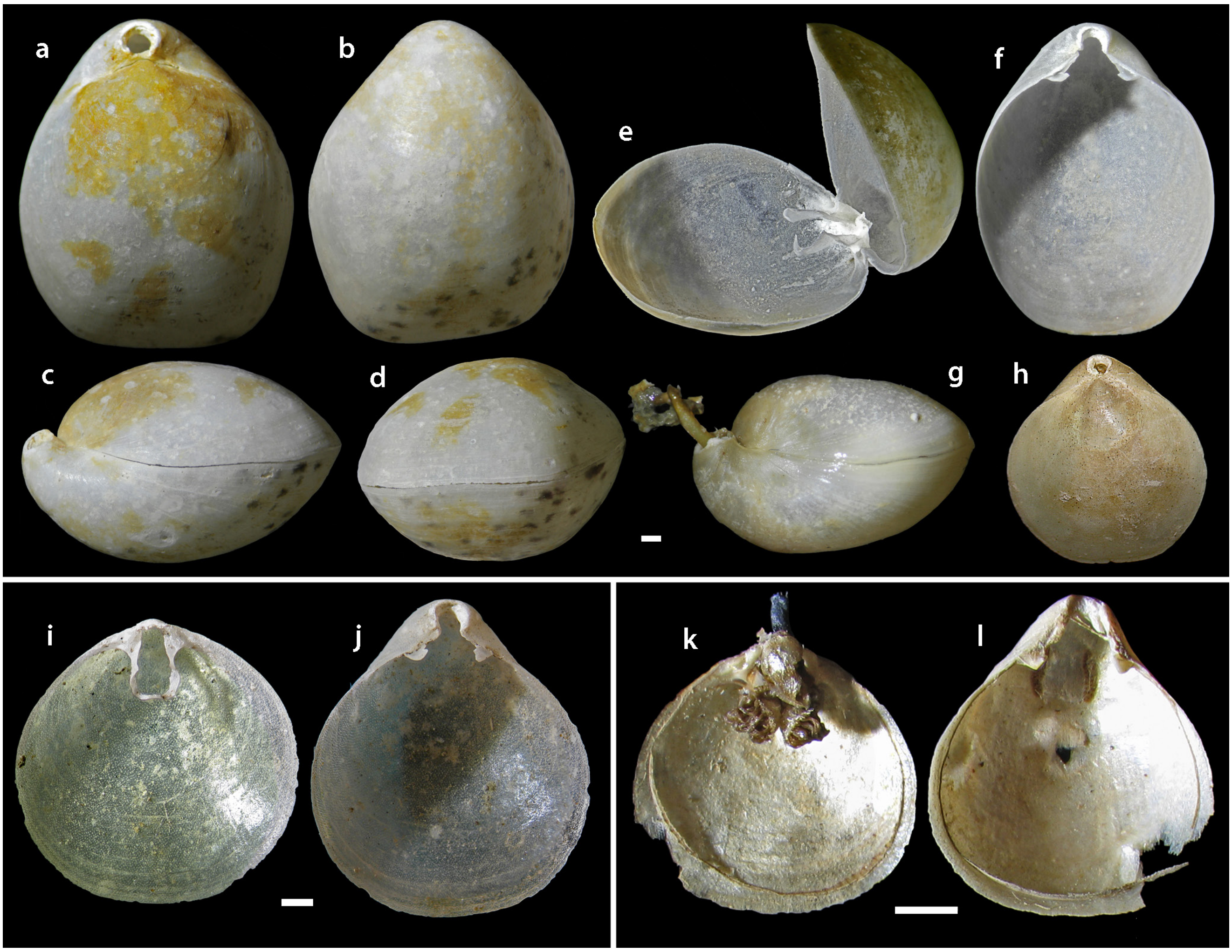

Figure 15. *Arctosia arctica*. **a–d**: dorsal, ventral, lateral and anterior views of specimen from batch TSZBr-2480, Kap Petersen, E Greenland, 200 m; **e**: dorsal interior of shell from batch TSZBr-2480, Kap Petersen, E Greenland, 200 m; **f**: ventral valve interior from batch TSZBr-2480, Kap Petersen, E Greenland, 200 m; **g**: lateral view of specimen from batch TSZBr-2480, Kap Petersen, E Greenland, 200 m; **h**: dorsal view of specimen NHMD-1201199, Forsblad Fjord, E Greenland, 35 m; **i–j**: dorsal and ventral interior views of empty shell NHMO H93, type locality SW of Jan Mayen, the Norwegian North Atlantic expedition 1877 st. 237, 481 m; **k–l**: dorsal and ventral interior views of juvenile specimen, Jan Mayen, the Danish East Greenland Expedition 1891, 301 m, the Zoological Museum of Copenhagen. Scalebar 1mm. Photos: Jesper Hansen.

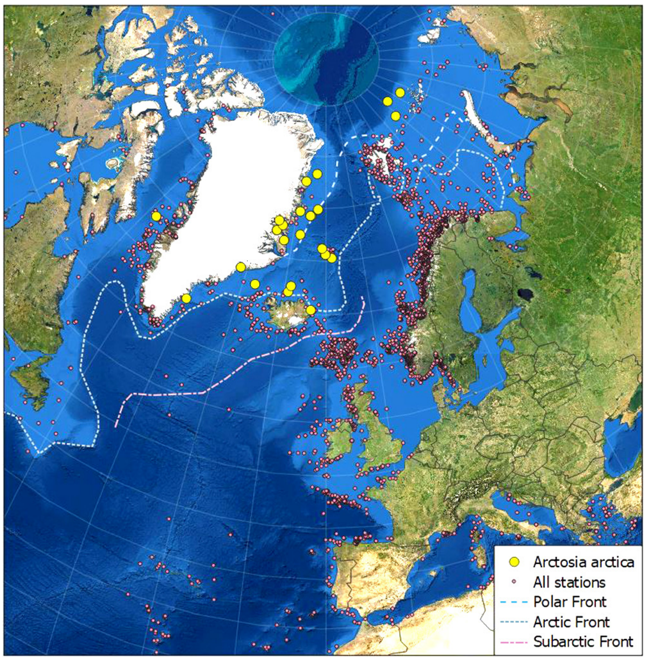

Figure 16. Distribution of *Arctosia arctica*.

length. No median ridge in dorsal valve. Dorsal muscle scars reaching 1/4 to 2/5 (typically 1/3) valve length. Dental plates absent. Shell up to 16.4 mm long, 13.5 mm wide and 9.2 mm deep.

Depth range: 35–481 m depth (Friele 1877a; this study). Wesenberg-Lund (1941) reported it occurring down to 1500 m depth; however, this was based on misidentified material.

Temperature range: -1.8–1.5˚C (this study).

Salinity range: 33.7–34.9 (this study).

Substrate: Clay or sand with stones, fine mud, or on coarse gravel and small stones (Friele 1877a; Posselt 1898; Hägg 1905; this study). Specimens were found attached to gravel, bryozoan branches, tubes of serpulid worms and to other specimens of *Arctosia* (this study).

Geography: Greenland, Jan Mayen and N and NE Iceland (Friele 1877a; Grieg 1933; Zezina 1997b). Zezina (1997b) reported the species from just north of Franz Josef Land, bordering the Barents Sea to the North. Reports from off West Spitsbergen and NE Barents Sea by Grieg (1924), latter referred to by Gulliksen *et al.* (1999) were, as stated by Grieg (1933), misidentifications of young specimens of *Hemithiris psittacea*. The same is true for reports from SW of Iceland, which proved to be a new species of *Xenobrochus* following re-examination.

Comment: In many new publications, the year of publication is given as 1878 or even 1879. However, the publication year is specified as 1877 in the original preprint, which, according to the International Code of Zoological Nomenclature (Chapter 5, Article 21.8), is the date of publication.

This species is easily confused with *Macandrevia cranium* but is externally most easily distinguished by the shape of the pedicle opening and thick pedicle collar.

The rather few verified occurrences of this species are from 1973 or earlier. It has thus not been possible to evaluate whether there have been any changes in the abundance and distribution of this species. Since this is a truly Arctic species, its geographical range is likely shrinking due to increasing oceanic temperatures.

Superfamily	Dyscolioidea Fischer & Œhlert, 1891
Family	DYSCOLIIDAE Fischer & Œhlert, 1891
Subfamily	Aenigmathyridinae Cooper, 1983
Genus	*Xenobrochus* Cooper, 1981b

***Xenobrochus islandicus* n. sp.**

Figures 17, 18

Liothyris arctica – Wesenberg-Lund (1941) [partim], p. 9–10.

Waldheimiathyris cranium – Wesenberg-Lund (1941) [partim], p. 10–12.

Liothyrella arctica – Zezina (1997b) [partim], p. 72.

LSID: zoobank.org:act:14CCB184-6D1B-4FA6-88CF-E13D04668E72

Type locality: Off W Iceland, The Danish 'Ingolf' expedition 1896 st. 84, 62°58'N, 25°24'W, 1192 m depth.

Etymology: From the geographical name 'Island' (Iceland), around which the species was found.

Diagnosis: *Xenobrochus* species with elongate, pointy, egg-shaped outline and evenly rounded to slightly flattened anterior margin; beak erect with visible symphytium; permesothyrid medium large foramen; transverse cardinal process; angular brachial loop reaching about 1/3 valve length, with broad transverse band with a weak median fold.

Material: Holotype: Reykjanes Ridge, off SW Iceland, the Danish 'Ingolf' expedition 1896 st. 84, 62°58'N, 25°24'W, 1192 m depth, one specimen (NHMD-1201208 (holotype). Paratypes: Irminger Sea, off W Iceland, the Danish 'Ingolf' expedition 1896 st. 10, 64°24'N, 28°50'W, 1484 m depth, one specimen NHMD-1186285; Reykjanes Ridge, Iceland Basin, the Danish 'Ingolf' expedition 1896 st. 78, 60°37'N, 27°52'W, 1505 m depth, three specimens and two empty ventral valves (NHMD-1186283, NHMD-1186284); Reykjanes Ridge, off SW Iceland, the Danish 'Ingolf' expedition 1896 st. 84, 62°58'N, 25°24'W, 1192 m depth, two specimens and one empty shell (NHMD-1201194); Irminger Sea, off W Iceland, the Danish 'Ingolf' expedition 1896 st. 90, 64°45'N, 29°06'W, 1070 m depth, two empty shells (NHMD-1201179); Denmark Strait, W Iceland, the Danish 'Ingolf' expedition 1896 st. 98, 65°38'N, 26°27'W, 260 m depth, two specimens (NHMD-1201193).

Description: Holotype 8.2 mm long and 5.9 mm wide. L/W ratio of 1.16–1.50 and generally increasing with shell size. Shell moderately to rather strongly equi- to ventribiconvex. Outline pointy and egg-shaped with evenly rounded to slightly flattened anterior margin. No median folds or depressions developed on valves. Anterior commissure rectimarginate to slightly sulcate. Lateral commissure slightly S-curved. Fragile, transparent to semitransparent and endopunctate. Typically shiny and smooth except for faint growth lines and occasionally very weak radiating striation, as seen on the holotype (Figure 17 a–b). Colour whitish. Beak pointy and only slightly curved in dorsal direction. Comparatively high deltidial plates conjoined and fused to form a visible symphytium, often depressed along midline. Ridges bordering deltidial plates poorly developed or absent. Pedicle foramen moderately large permesothyrid (=beak ridges bisecting foramen in lower half) and circular to subtriangular. Pedicle short and branched in multiple rootlets. Pedicle collar short. Teeth form moderately high transverse plates. Dental plates absent. Cardinal process in dorsal valve a transverse semi-elliptical ridge on top of the inner socket ridges (Figure 17k, ae). Outer hinge plate connecting inner socket ridges with crural bases narrow, triangular and poorly developed. Inner hinge plates absent. Brachial loop short and narrow, with subparallel sides and a broad, angular transverse band with anterolateral angles. Transverse band gently convex in anterodorsal direction, though a small indention can occur at the suture line at front edge. Crural processes barely anterior of mid-loop length, blunt and bending towards each other. Brachial loop reaches approximately 30% of valve length. No true dorsal median ridge, though imprints of the two main trunks of the vascular system may create a thickening on the valve floor extending to 30% of valve length. Dorsal muscle scars clearly visible and reaching slightly anterior of 1/4 valve length. Largest specimen 12.4 mm long and 8.3 mm wide.

Depth range: 260–1505 m depth.

Temperature range: 3.5–5.9°C.

Salinity range: 34.9–35.4.

Substrate: Attached to Porifera spicules or bryozoan branches.

Geography: North Atlantic Ocean off E and SE Iceland.

Remarks: The specimens are assigned to the genus *Xenobrochus* Cooper, 1981b based on the presence of the diagnostic characters, such as a visible symphytium, small shell size with basically rectimarginate anterior commissure, transverse cardinal process, and a short loop with subparallel sides and an anteriorly convex transverse band. This makes this species the second of that genus to be recorded from the Atlantic Ocean and outside the W Pacific and Indian Ocean when following the opinion of Bitner & Molodtsova (2020) and including *Abyssothyris*? *parva* Cooper, 1977 in the genus (see Bitner 2011; Bitner & Molodtsova 2020).

To date, 10 species have been included in the genus. These are *Xenobrochus africanus* (Cooper, 1973b), *X. agulhasensis* (Helmcke, 1938), *X. anomalus* Cooper, 1981b, *X. australis* Cooper, 1981b, *X. indianensis* (Cooper, 1973b), *X. naudei* Hiller, 1994, *X. norfolkensis* Bitner, 2011, *X. parvus* (Cooper, 1977), *X. rotundus* Bitner, 2008 and *X. translucidus* (Dall, 1920).

Most of these species have a distinctly subtriangular or pentagonal outline with a somewhat truncated front, or a subcircular outline distinguishing them from the present species. This includes the subtriangular to subcircular *Xenobrochus parvus*, which according to descriptions and illustrations of Cooper (1977) and Bitner & Molodtsova (2020) is more equidimensional, is distinctly ventribiconvex, lacks anterolateral angles on the transverse band of the brachial loop, and seems to have a dull shell surface.

Among the remaining four, the shallow-water species *X. indianensis* (from the Indian Ocean and SW Pacific) appears morphologically very close, except for a distinctly more incurved beak and a narrower cardinal process.

The equally close *X. agulhasensis* from approximately 275 m depth off South Africa differs by a very small brachial loop reaching to about 1/4 valve length, and a generally lower L/W ratio of approximately 1.2.

X. africanus, from the Indian Ocean and SW Pacific with the

Figure 17. *Xenobrochus islandicus* n. sp. **a–d**: dorsal, ventral and lateral views of specimen, and close-up image of deltidial plates fused to form symphytium, holotype NHMD-1201208, Reykjanes Ridge, 1192 m; **e–g**: dorsal, ventral and lateral views of paratype from batch NHMD-1201193, Denmark Strait, 260 m; **h**: ventral interior of paratype from batch NHMD-1186284, Reykjanes Ridge, 1505 m; **i**: dorsal view of paratype from batch NHMD-1201194, Reykjanes Ridge, 1192 m; **j–l**: dorsal interior view with close-up image of hinge region and brachial loop, and ventral interior view of paratype NHMD-1186285, Irminger Sea, 1484 m; **m–p**: exterior and interior views of dorsal and of ventral valve, paratype NHMD-1186283, Reykjanes Ridge, 1505 m; **q**: dorsal view of ventral valve of paratype from batch NHMD-1201194, Reykjanes Ridge, 1192 m; **r, ad**: dorsal and lateral views of paratype NHMD-1186284 with lophophore visible, Reykjanes Ridge, 1505 m; **s**: dorsal interior view showing vascular ridges of paratype from batch NHMD-1201194, Reykjanes Ridge, 1192 m; **t**: dorsal view of paratype from batch NHMD-1186284, Reykjanes Ridge, 1505 m; **u**: ventral interior view of paratype from batch NHMD-1186284, Reykjanes Ridge, 1505 m; **v**: ventral interior and **ae**: enlarged dorsal interior views of paratype from batch NHMD-1201194, Reykjanes Ridge, 1192 m; **w–y**: dorsal, ventral and lateral views of paratype from batch NHMD-1201193, Denmark Strait, 206 m; **z–aa**: dorsal and ventral views of paratype from batch NHMD-1201179, Irminger Sea, 1070 m; **ab–ac**: dorsal and ventral views of paratype from batch NHMD-1201179, Irminger Sea, 1070 m. Scalebar 1mm. Photos: Jesper Hansen.

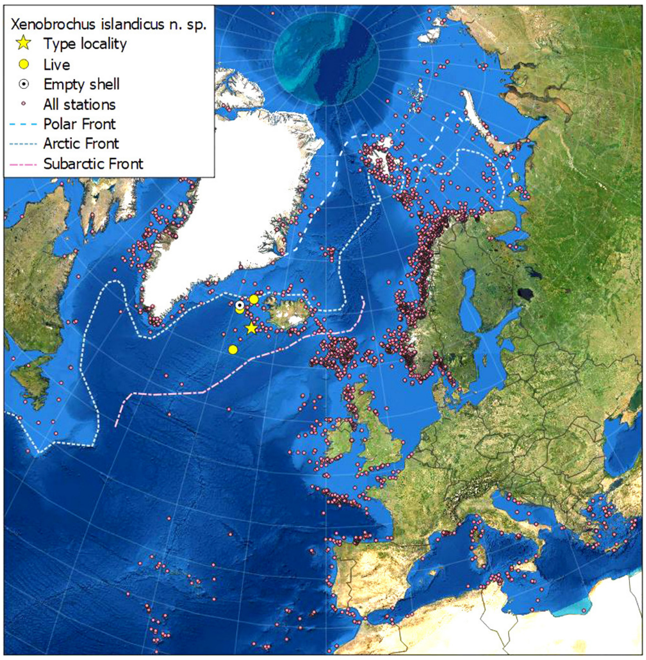

Figure 18. Distribution of *Xenobrochus islandicus* n. sp.

holotype taken at 366 m depth, has a much more robust shell, slightly truncated front and a distinctly narrower and broadly V-shaped transverse band in the brachial loop.

X. australis, from 790 m depth in the South Indian Ocean, has a larger foramen with a longer pedicle collar, while the anterior end of the brachial loop does not bend in the dorsal direction and the L/W ratio of the shell is approximately 1.5.

Superfamily Cancellothyridoidea Thomson, 1926
Family CANCELLOTHYRIDIDAE Thomson, 1926
Subfamily Cancellothyridinae Thomson, 1926
Genus *Terebratulina* d'Orbigny, 1847a

Terebratulina retusa (Linnaeus, 1758)

Figures 19, 20

?*Anomia aurita* Linnaeus, 1758, p. 701.
Anomia retusa Linnaeus, 1758, p. 701.
Anomia pubescens Linnè, 1767, p. 1153.
Terebratula pubescens – Müller (1776), p. 249.
Anomia Caput serpentis – Born (1780), p. 119, pl. 6, fig. 13 – non Linnaeus (1758), p. 703 (see discussion in Hanley (1855) and Dall (1920)).
Terebratula caput serpentis – Retzius (1788), p. 13.
Terebratula retusa – Retzius (1788), p. 14.
Criopoderma caput serpentis – Poli (1795), p. 192 and 261, pl. 30, fig. 15y.
Terebratula aurita – Fleming (1822a,b), p. 498–499, pl. 4, fig. 5.
Terebratula costata Lowe, 1825, p. 105–107, pl. 5, figs. 8, 9, 9b.
Terebratula emarginata Risso, 1826, p. 388, pl. 12, fig. 175.
Terebratula quadrata Risso, 1826, p. 389, pl. 12, fig. 176.
Delthyris spatula Menke, 1830. p. 96.
Terebratulina caput serpentis – d'Orbigny (1847b), p. 248–249, pl. 7, figs. 7, 8, 17.
Terebratula striata Leach, 1852, p. 359, pl. 14, figs. 1–2.
Terebratula (*Terebratulina*) *caput-serpentis* – Lovell (1861), p. 172.
Terebratula caput-serpentis mediterranea Jeffreys, 1878, p. 401.
Terebratulina retusa – Dall (1920), p. 294.
Terebratulina retusa emarginata – Dall (1920), p. 296.

Description: Shell outline subpentagonal to nearly egg-shaped, and fully grown specimens generally with narrowly truncated or even incurved front. Anterior commissure gently to moderately uniplicate or, more rarely, rectimarginate. Ornamentation of 9–14 radiating, rather coarse costellate ribs per 5 mm counted 10 mm anterior of ventral umbo (occasionally up to 17 ribs). Ribs lacking on specimens less than 1 mm long, but rapidly become high and subangular, then weaken again with increased shell size. Ribs beaded with coarse tubercles on umbonal part, especially the ventral valve. In young specimens, these tubercles tend to partly overhang deep rib-interspaces along valve crest. Umbonal tip of ventral valve continuously becomes resorbed with growth, making umbo less pointed. Pedicle often strongly branched. Deltidial plates lacking or small and separate. Pedicle opening 11–13% as wide as valve. Shell matrix endopunctate. Colour white or yellowish-grey. Short brachial loop often, but far from always, with crural processes joining. Joined crural processes seem to be more common in larger specimens. Brachial loop not pointy in front. Median ridge absent or very rudimentary and restricted to posterior part of valve floor. Long setae radiating out from where ribs meet anterior valve margin. Soft tissue dense with spicules, especially in lophophores. Largest encountered was 26 mm long.

Depth range: 12–1492 m depth, though most common at 15–600 m depth (Jeffreys 1878; this study). By mistake, the maximum depth was given as 1180 ft (~2157 m) by Jeffreys (1878), which was then quoted by others; however, in Jeffreys' station table, the correct depth (1492 m) is given. However, since Jeffreys (1878) did not distinguish *Terebratulina septentrionalis* from *T. retusa*, the maximum depth could be for the other species. The maximum depth given Wesenberg-Lund (1938) distinguishing the two species is 1302 m.

Temperature range: 0.0–13.0˚C (Curry 1982; Thomsen 2001). Jeffreys (1878) reported the species from several British samples, which, according to Carpenter *et al.* (1869), were taken at sub-zero temperatures down to -1.2˚C; however, Jeffreys did not distinguish the colder-water species *Terebratulina septentrionalis* from *T. retusa*.

Salinity range: 33.1–35.3 (Nordgaard 1905; Thomsen 2001; this study).

Oxygen range: 77–105% saturation (this study).

Current velocity: Mean velocity measured at one locality was 9.5 cm/s, with daily maxima mostly 12–25 cm/s and 30 cm/s as the absolute maximum measured over 1 month (this study).

Substrate: Attached to bryozoans, hydroids, shells, sand, stones, Porifera, seaweeds, etc. (Jeffreys 1863; Brunton & Curry 1979; Thomsen 2001; this study). Sea floor typically dominated by sand, shell sand, gravel, cobbles or stones (Thomsen 2001).

Geography: Bjørnøya, Norway, Iceland, the Faroe Islands, SW Sweden, Great Britain, France, Spain, Portugal, the Mediterranean, the Canary Islands and the Cape Verde Islands (Fischer & Œhlert 1892; Brunton & Curry 1979; Cohen *et al.* 1993; Thomsen 2001; Logan *et al.* 2007; this study). Neither the northernmost (Bjørnøya), easternmost two (Finnmark), nor all the records from the NW side of Iceland have been verified in the present study or in molecular studies.

Remarks: A comparison with the next and closely related *Terebratulina septentrionalis* is provided in the comments on that species.

The shells are often overgrown by a Demospongia of the genus

Figure 19. *Terebratulina retusa*. **a–d**: dorsal, ventral, lateral and anterior views of specimen showing the brachidium, Brettingsnes, Trøndelag, Norway (JH); **e–g**: shell interior showing brachial lope with fully joined crural processes, and examples of spicules from same specimen, TSZ 3204 (APN), Norwegian Sea at Nordland, Norway, 348 m; **h**: dorsal view of empty shell, NW of Tjärnö, Sweden, >50 m (JH); **i–k**: dorsal interior with crural processes not joined, ventral interior and ventral exterior of shell, Tjärnö, Sweden, 60 m (JH); **l–m**: dorsal and ventral views of juvenile specimen, TSZ 3013 (APN), Haltenbanken, Norwegian Sea, Norway, 318 m; **n–o**: dorsal and ventral views of juvenile specimen, TSZ 3016 (APN), Flyndretind, Haltenbanken, Norwegian Sea, Norway, 242 m; **p–q**: dorsal and ventral views of juvenile specimen, TSZ 3014 (APN), Nona/Tussen, Haltenbanken, Norwegian Sea, Norway, 245 m. Scalebar 1mm. Photos: Jesper Hansen.

Hymedesmia (Tendal & Thomsen 2005).

Plotting specimens according to the century of sampling did not reveal any changes in distribution within Norwegian waters. Despite the impression of the map, this species is only sporadically encountered along northern Norway.

Terebratulina septentrionalis (Couthouy, 1838)

Figures 21, 22

Terebratula septentrionalis Couthouy, 1838, p. 65–66.
Terebratulina septentrionalis – (Davidson 1852b), p. 366.
Terebratulina caput-serpensis var. *septentrionalis* – Davidson (1880), p. 33–36, pl. 1, figs. 3–9.

Description: This species is very similar to *Terebratulina retusa* and has overlapping ranges of almost all diagnostic characters. As noted by Sars (1878) and Wesenberg-Lund (1941), *T. septentrionalis* tends to have the following characters: more egg-shaped outline; rectimarginate or weakly uniplicate anterior commissure; thinner shell-wall; weaker growth lines; denser ribs with 14–22 usually low subtriangular or rounded radiating ribs per 5 mm counted 10 mm anterior of ventral umbo; tubercles on umbonal crest missing or less strongly developed; stronger tubercles usually scattered laterally on umbone; ribs lower and tend to be nearly absent distally on larger specimens; often slightly wider pedicle opening (11–15% as wide as valve). In the present study, the most stable difference from *T. retusa* was found to be the absence of or denser, lower and more transverse tubercles never overhanging deep interspaces between the ribs on the ventral umbonal crest. The largest measured specimen was 27.5 mm long.

Depth range: 0–3614 m depth (Dall 1920; Brunton & Curry 1979), but mostly occurring at 10–550 m depth, with the second-deepest recorded occurrence at approximately 1325 m (Thomsen 2012).

Temperature range: -1.7–10.6˚C (Allmen *et al.* 2010; this study).

Salinity range: 28–35.4 (Brand *et al.* 2003; this study).

Oxygen range: 55–104% saturation (this study).

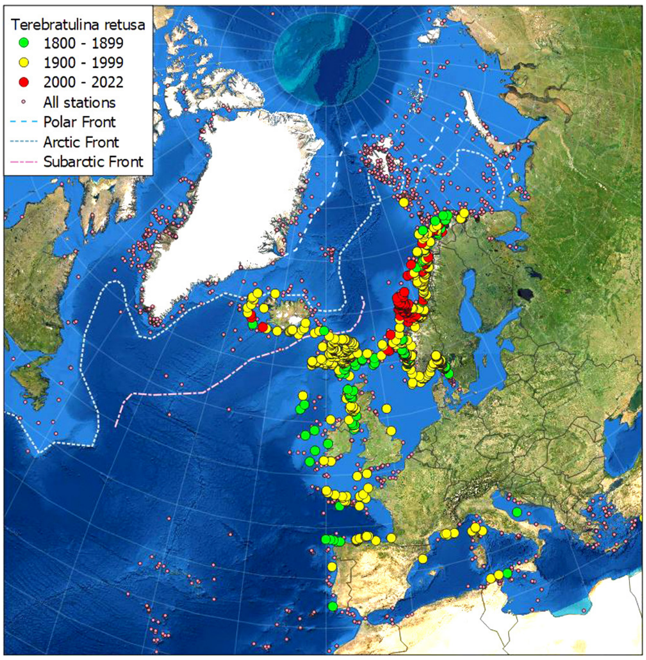

Figure 20. Distribution of *Terebratulina retusa*. Colours mark which century the specimens were collected in.

Current velocity: Mean current velocity at four locations measured at 2.7–6.9 cm/s, with a normal daily maximum of 2–18 cm/s and 10.8–24.8 cm/s as the absolute maximum over 1 month of measurement (this study).

Substrate: Commonly attached to serpulid tubes, but also to shells, shell sand, branched bryozoans, the coral *Desmophyllum*, Porifera, other polychaete tubes, or gravel (this study).

Geography: S, W and E Greenland, Svalbard (Bjørnøya, Spitsbergen, and verified from off northern Nordaustlandet in 2009, and from the Hinlopen Strait), Murmansk, the White Sea, Norway (Hordaland and North), Baffin Bay, East Canada, Jan Mayen, Iceland, Scotland, Ireland and E USA (Grieg 1933; Wesenberg-Lund 1941; Brunton & Curry 1979; Curry & Endo 1991; Thomsen 2001; Allmen *et al.* 2010; Thomsen 2012; this study).

Remarks: *Terebratulina septentrionalis* has been synonymised with the species *Terebratulina retusa* several times (e.g., Jeffreys 1878; Davidson 1880; Posselt 1898; Knipowitsch 1901; Hägg 1905; Zezina 1997a,c) since the species are very similar and intermediate morphotypes are found to occur in places where both species are present (e.g., Wesenberg-Lund 1941; Lüter *et al.* 2017). Cohen *et al.* (1991) addressed this question through a molecular study on specimens from British and Icelandic waters. They concluded that there were two distinct species and found no evidence of hybridisation. Recently, in their follow-up study, Lüter *et al.* (2017) found hybrids in places where both species co-occur in Iceland. Hybridisation could explain some observed morphological trends along Norway, where *T. retusa* tends to show finer costellae, thinner shells and weaker tubercles in northern regions dominated by *T. septentrionalis.*

Sars (1878) found that the crural processes in *T. septentrionalis* were not connected, in contrast to those of *T. retusa*. This difference was not supported by the examined material in the present study, which included both specimens with disconnected and connected processes for both species. Logan (1979) found there to be an ontogenetic trend with the connection generally developing latter in *T. septentrionalis* than in *T. retusa*. Blochmann (1908) used the spicules in the tissue to distinguish the two species. However, Wesenberg-Lund (1941) questioned the usefulness of this method. In the present study, I also failed to separate the two species based on spicules.

The variability and usefulness of all the expected diagnostic features of the two species were rigorously examined based on a large

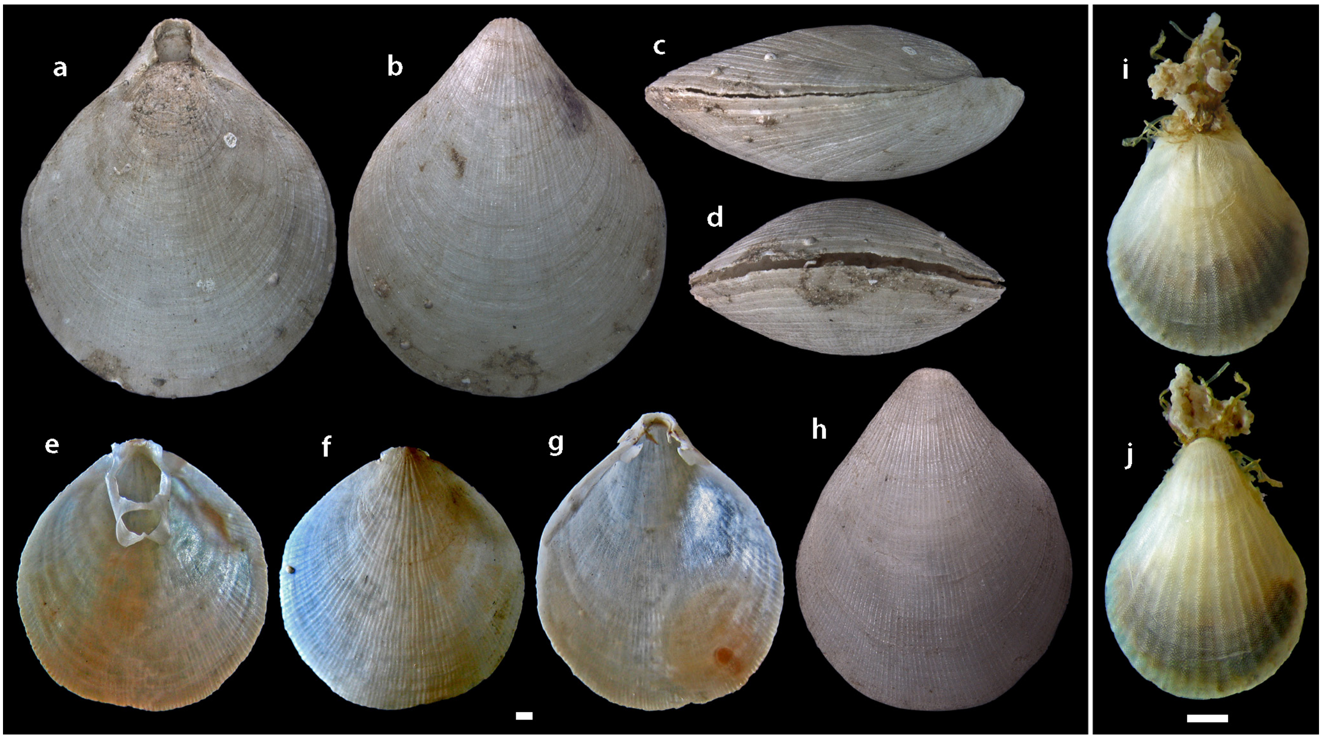

Figure 21. *Terebratulina septentrionalis*. **a–d**: dorsal, ventral, anterior and lateral views of specimen, Ullsfjord in Troms, the Arctic University Museum of Norway; **e–g**: dorsal interior and exterior and ventral interior views of shell NHMO H2899, Øksfjord in Finnmark, Norway; **h**: ventral exterior view of specimen from batch TSZBr-2095, Vardø in Finnmark, Norway, 188 m; **i–j**: dorsal and ventral views of juvenile specimen, N of Rossøya, Spitsbergen (JH). Scalebar 1mm. Photos: Jesper Hansen.

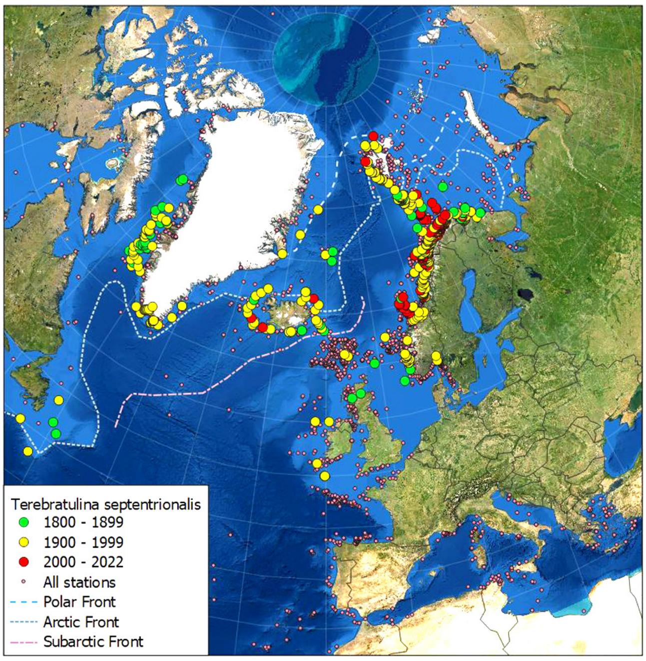

Figure 22. Distribution of *Terebratulina septentrionalis*. Colours mark which century the specimens were collected in.

collection containing a wide range of shell sizes, population samples and geographically separated material of both species. As expected, the shell shape and ornamentation of both species show strong variability between specimens within the same population, but also along different growth stages of single specimens, with most features varying independently of each other. It can be concluded that the range of variation within each single feature shows a considerable overlap between the two species. The most stable differences surprisingly turned out to be the ornamentation on the umbonal part, especially in specimens 2–10 mm in length.

Due to the past synonymisation and confusion of the two species, the published geographic distribution—especially in the Arctic region—may be based on a mix of the species in many cases. Therefore, in the present study, the more uncertain observations were excluded. Some of the earlier identifications made in the present study are also erroneous since a greater understanding of the value of various diagnostic features evolved along the way. This latter problem has been addressed to some extent by re-examining the specimens from many of the border occurrences.

Material collected from southern Norway during the present century was not available for the present study. Therefore, no conclusions can be drawn from the absence of data from this area.

Like the previous species, this species is often overgrown by sponges, most likely of the genus *Hymedesmia* (belonging to Demospongia) (Tendal & Thomsen 2005; Thomsen 2012).

Family CHLIDONOPHORIDAE Muir-Wood, 1959
Subfamily Eucalathinae Muir-Wood, 1965
Genus *Eucalathis* Fischer & Œhlert, 1890

Eucalathis ergastica Fischer & Œhlert, 1890

Figures 23, 24

Eucalathis ergastica Fischer & Œhlert, 1890, p. 73.

Description: Shell low to moderately ventribiconvex and slightly longer than wide. Outline subtriangular to subpentagonal and widest close to front. Ventral umbo pointed and with moderately high interarea bisected by elongate subtriangular pedicle opening. Pedicle divided into many rootlets. Anterior commissure rectimarginate. Dorsal valve often with slight sulcus. Ornamentation of 14–27 costellate ribs, as well as abundant and strong lamellar growth breaks. Ribs triangular in cross section. Middle dorsal rib not larger than the others. Shell matrix endopunctate with very tiny punctae. Colour porcelain white to slightly yellowish. Broad hinge teeth not supported by dental plates. Short and anteriorly directed loop. Crural processes not meeting. Dorsal median septum lacking. Maximum shell size 7 mm.

Depth range: 280–2736 m depth (Logan 2007).

Temperature range: 9.5–12˚C (this study).

Substrate: Mud, sand, stones and rock, and often associated with corals (Fischer & Œhlert 1891; Logan 1983; Anadón 1994; Anadón *et al.* 2022). Can also be attached to Porifera as in the illustrated examples.

Geography: Celtic Sea, Bay of Biscay, W Spain, Azores, Morocco, the Canary Islands and Western Sahara (Fischer & Œhlert 1890; Cooper 1981a; Logan *et al.* 2007).

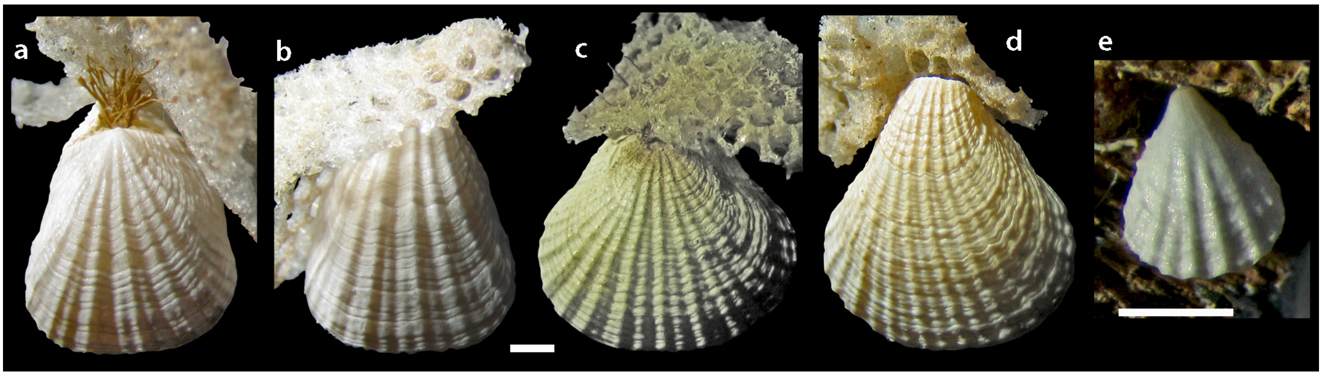

Figure 23. *Eucalathis ergastica*. **a–b**: dorsal and ventral views of specimen from batch BMNH PI. ZB 4975, Bay of Biscay, 950–1005 m; **c–d**: dorsal and ventral views of another specimen from the same batch; **e**: ventral exterior view of juvenile specimen from the same batch. Scalebar 1mm. Photos: Jesper Hansen.

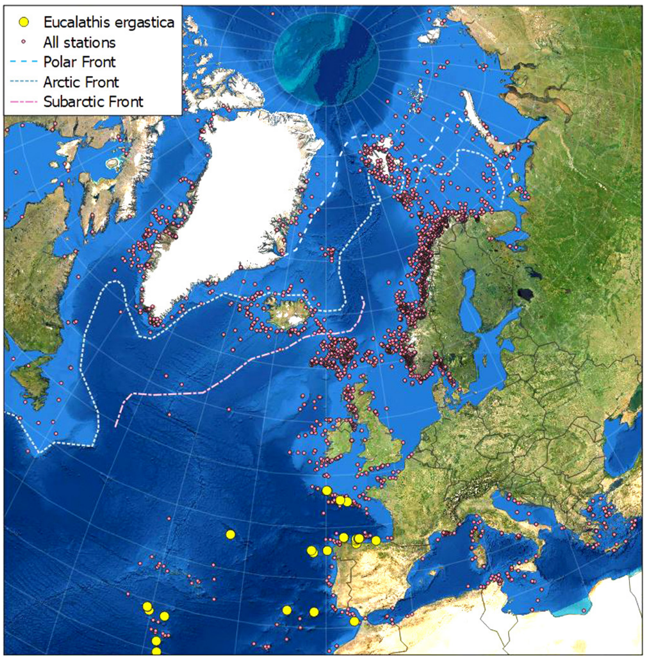

Figure 24. Distribution of *Eucalathis ergastica*.

Eucalathis tuberata (Jeffreys, 1878)

Figures 25, 26

Terebratula tuberata Jeffreys, 1878, p. 401–402, pl. 22, fig. 2.
Terebratulina tuberata – Davidson (1880), p. 13.
Eucalathis tuberata – Fischer & Œhlert (1890), p. 72.

Description: Shell moderately ventribiconvex. Outline subtriangular to subpentagonal with rounded front and greatest width anteriorly. Shell usually not much longer than wide. Hinge line nearly straight. Ventral umbo pointed and with high interarea bisected by long V- or U-shaped pedicle opening. Deltidial plates small and triangular. Pedicle collar distinct and strongly raised. Pedicle divided into rootlets. Anterior commissure rectimarginate. Ornamentation of 14–44 costellate ribs, typically strongly beaded by tubercles—especially on ventral valve. Middle dorsal rib stronger or higher than the others and corresponded by an intercosta or two smaller and lower median costellae on ventral valve. Shell matrix endopunctate with very small punctae. Colour greyish to yellowish white. Crenulate valve margin. Strong and very wide hinge teeth not supported by dental plates. Dorsal valve with short but highly raised crura with a short, fragile loop extension usually not preserved. Median septum lacking, but weak median thickening of valve floor often presents in both valves. Shell up to 5 mm long.

Depth range: 549–2995 m depth (Brunton & Curry 1979; Logan 2007).

Geography: Celtic Sea, Bay of Biscay, Mauritania, ? Mediterranean, the Azores, the Mediterranean and south to the Canary Islands (Brunton & Curry 1979; Logan *et al.* 2007; Zezina 2014).

Superfamily Gwynioidea MacKinnon, 2006
Genus *Gwynia* King, 1859

Gwynia capsula (Jeffreys, 1859)

Figures 27, 28

Terebratula capsula Jeffreys, 1859, p. 43, pl. 2, figs. 7a–b.
Gwynia capsula – King (1859), p. 258, figs. 1–5.
Terebratula (*Gwynia*?) *capsula* – Lovell (1861), p. 183.
Argiope capsula – Jeffreys (1863), p. 21.
Gwynia (Terebratula) capsula – Davidson (1880), p. 14.

Description: Minute, thin-walled shell, moderately to inflated biconvex with ventral valve usually slightly shorter but higher than dorsal. Outline egg-shaped oval to subtriangular. Rectimarginate anterior commissure. Hinge line narrow but straight. Ornamentation lacking except for growth lines. Shell matrix semitransparent and densely endopunctate. Colour white or yellowish. Pedicle opening relatively large and V- or U-shaped, extending into the dorsal

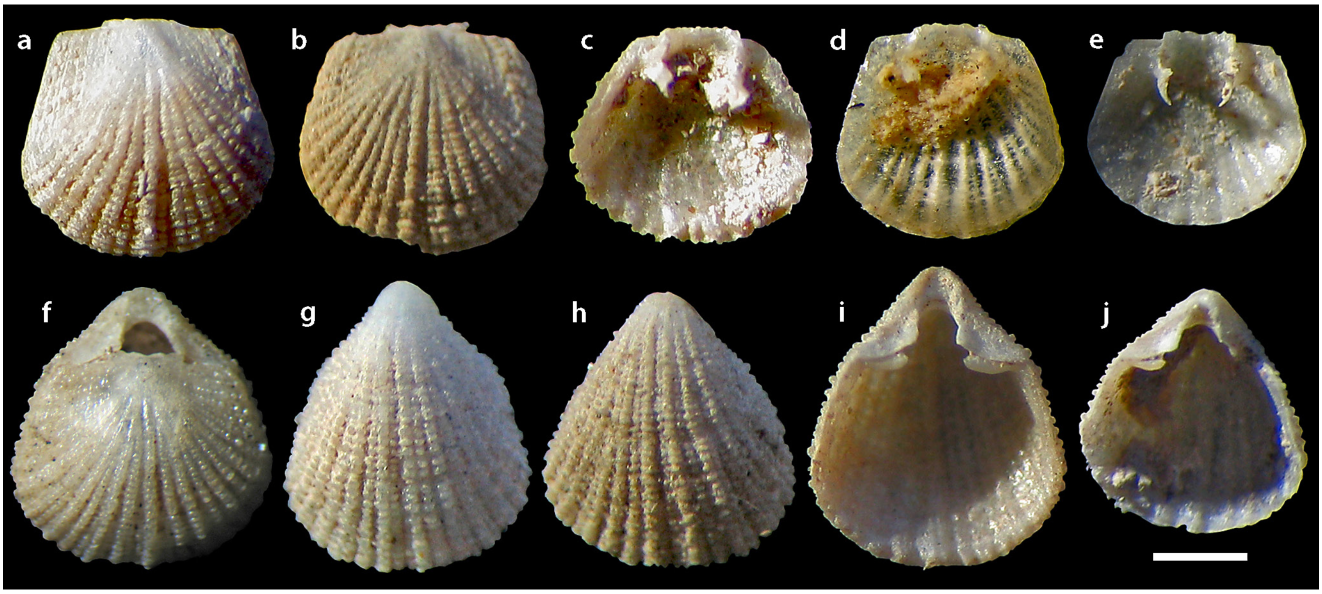

Figure 25. *Eucalathis tuberata*. **a–e**: dorsal exteriors and interior views of shell batch BMNH PI. ZB 423–427, NE Atlantic; **f**: dorsal view of specimen BMNH PI. ZB 3049, Margins de Jolin, France; **g–j**: ventral exterior and interior views of shells from batch BMNH PI. ZB 423–427, NE Atlantic. Scalebar 1mm. Photos: Jesper Hansen.

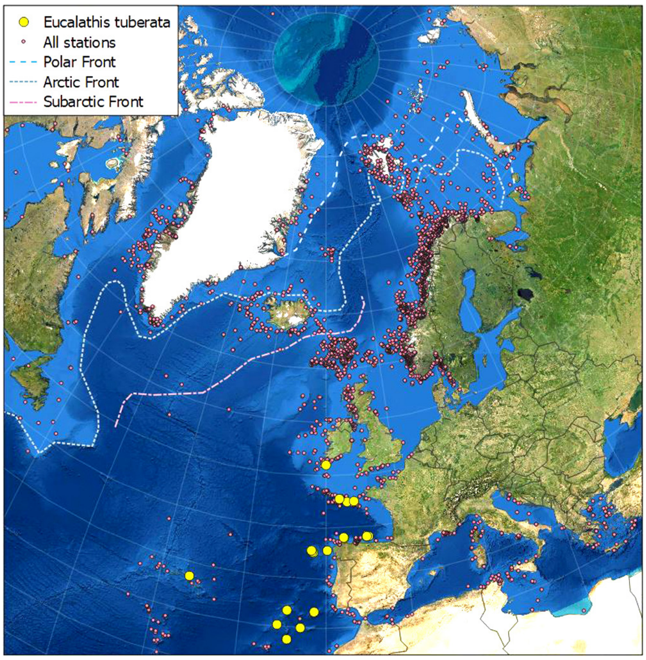

Figure 26. Distribution of *Eucalathis tuberata*.

valve. Ventral umbo short and, in some cases, shorter than dorsal umbo. Deltidial plates rudimentary and not joined. Hinge teeth not supported by dental plates. No visible muscle scars. Dorsal valve with prominent inner and outer socket ridges, the inner of which continues as submarginal ridges on valve floor. Notothyrium (raised platform) bisected by a simple, weak, ridge-like cardinal process. Dorsal median ridge usually present, though rudimentary and restricted to the posterior-most part of the valve floor. Short, broad, but incomplete brachial loop supported by submarginal ridges on valve floor. Lophophores reaching approximately 4/5 valve length. Maximum shell length 1.5 mm.

Depth range: Intertidal to 46 m depth (Jeffreys 1859; Logan *et al.* 1997), but empty shells have been collected down to 100 m depth (Harper *et al.* 1996).

Temperature: 11–13°C (Simon & Willems 1999).

Substrate: Found attached to rocks, gravel, in shells and serpulid tubes, and on shell sand and sand (Jeffreys 1859; Davidson 1887; Harper *et al.* 1996; Logan *et al.* 1997; Francis *et al.* 2011).

Geography: Coastal waters of Scotland, Wales, England, Ireland, the southernmost North Sea off the Netherlands and Belgium, the coast of France in the English Channel, off SE France, the Spanish Bay of Biscay, Portugal, the Adriatic Sea at Croatia, Greece, and

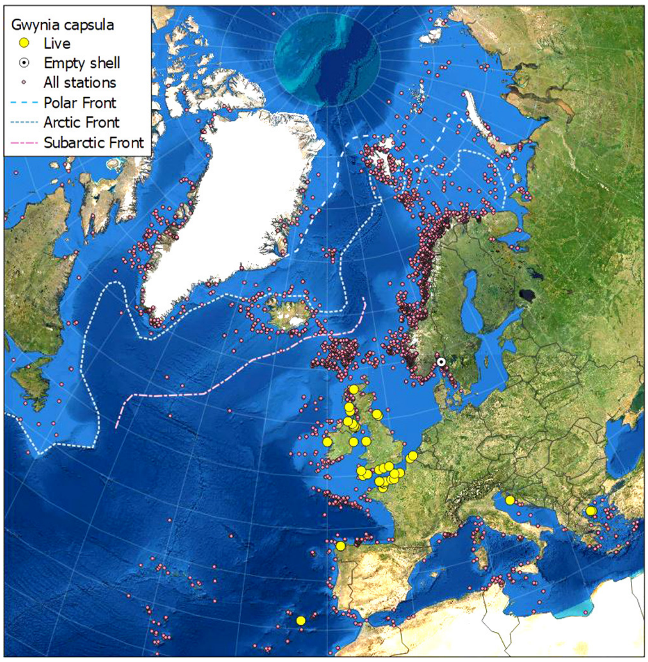

Figure 28. Distribution of *Gwynia capsula*.

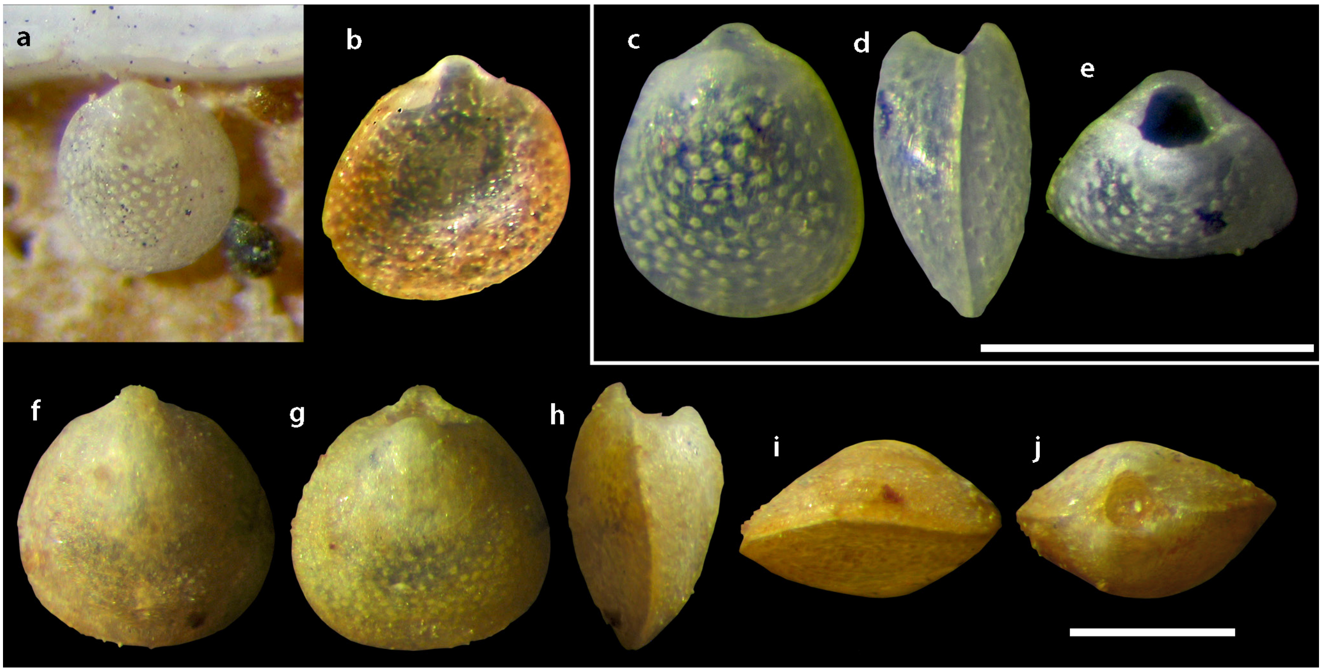

Figure 27. *Gwynia capsula*. **a**: dorsal view of specimen in batch BMNH PI. ZB 4245–4247, Belfast Bay, Ireland; **b**: interior view of ventral valve BMNH PI. B 12433, near Jersey; English Channel; **c–e**: ventral, lateral view with dorsal valve right, and posterior view of small empty shell in batch BMNH PI. ZB 4203–4207, Dog Strand, Connemara, Ireland; **f–j**: dorsal, ventral, lateral (with dorsal valve left), anterior and posterior views of iron oxide-coated specimen BMNH PI. ZB 3009, Jersey, English Channel. Scalebar c, d and e 0.5mm, otherwise 1mm. Photos: Jesper Hansen.

on a seamount in the North Atlantic at approximately 30°N and 13°W (Davidson 1887; Brunton & Curry 1979; Besteiro & Urgorri 1986; Logan *et al.* 1997; Simon & Willems 1999; Antoniadou & Chintiroglou 2005; Logan *et al.* 2007; Francis *et al.* 2011). A Holocene subfossil of the species has also been reported and illustrated from an isostatic raised shell banks located approximately 50 m above present-day sea level near Korshavn on the island Kirkøya at the Oslofjord, Norway (Sars 1865).

Remarks: Due to its minute size, *Gwynia capsula* is extremely easy to miss—even when knowing that it is present. This small size also easily leads to confusion with juvenile specimens of other brachiopod species. Combining this with how many findings have been made around the entire British Isles, it seems very likely that the species is still living along some parts of southern Norway despite no records other than the one subfossil specimen from deposits containing a shelly faunal assemblage pointing towards the Holocene climatic optimum.

Superfamily Zeillerioidea Allan, 1940
Family ZEILLERIIDAE Allan, 1940
Subfamily Macandreviinae Cooper, 1973a
Genus *Macandrevia* King, 1859

Macandrevia cranium (Müller, 1776)

Figures 1I, 29–31

Terebratula cranium Müller, 1776, p. 249.
Anomia cranium – Gmelin (1791), p. 3347.
Terebratula euthyra Philippi, 1844, p. 68, pl. 18, figs. 8a–d.
Terebratula glabra Leach, 1852, p. 359, pl. 14, figs. 3–5.
Waldheimia cranium – Gray (1853), p. 58.
Macandrevia cranium – King (1859), p. 261.
Terebratula (*Waldheimia*) *cranium* – Lovell (1861), p. 175.
Waldheimia (*Waldheimia*) *cranium* – Dall (1870), p. 110.
Waldheimia (*Macandrevia*) *cranium* – Davidson (1886), p. 61–66, pl. 12, figs. 11–23, pl. 13, figs. 1–2.
Magellania (*Macandrewia*) *cranium* – Fischer & Œhlert (1891), p. 72–79, pl. 5, figs. 10a–s.
Macandrevia cranium, new var. *novangliae* Dall, 1920, p. 355–356.
Waldheimiathyris cranium – Helmcke (1940), p. 275.
Macandrevia novangliae – Cooper (1977), p. 127, pl. 26, figs. 1–11.

Description: Highly variable. Shell equi-biconvex to ventribiconvex. Outline egg-shaped oval to pentagonal with truncated anterior valve margin in large specimens, and typically with dorsal valve about as wide as long. Ventral umbo blunt and short. Hinge line narrow and curved. Anterior commissure generally rectimarginate but can be slightly unisulcate. Small specimens with numerous long and very thin setae along anterior margin, easily falling off during handling. Rudimentary rectangular deltidial plates not joining. Deltidial plates separated from rest of valve by distinct ridges, especially in juveniles. Pedicle short and with a simple attachment base or very rudimentary rootlets. Ornamentation lacking in grown specimens except for very weak and sporadic growth lines. Small specimens often show very fine radiating ridges from which the setae protrude. Shell matrix endopunctate. Colour usually pale brownish, but especially old or empty shells can become grey or whitish. Dental plates supporting hinge teeth in ventral valve. Hinge teeth usually rather small and approximately twice as long as high. Cardinal process in the middle of dorsal hinge area often not developed, but otherwise typically rather broad, triangular and widest posteriorly. Socket ridges (ridges defining sockets for ventral teeth) well developed. Long

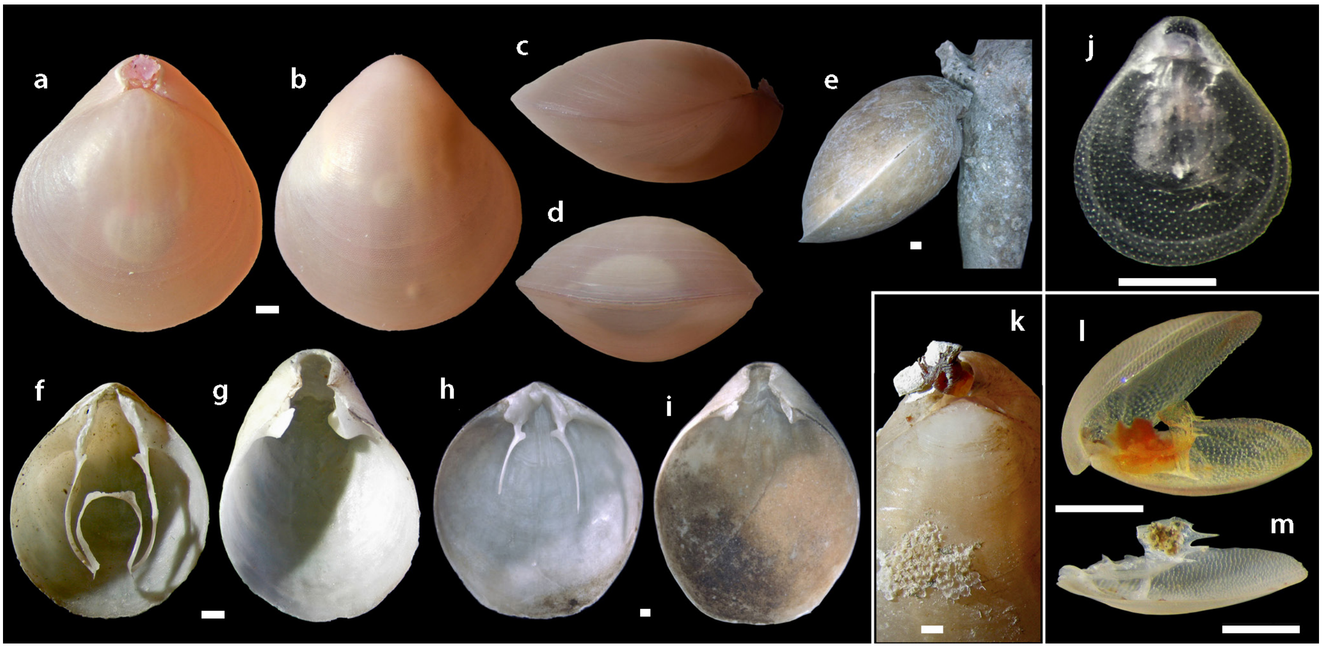

Figure 29. *Macandrevia cranium*. **a–d**: dorsal, ventral, lateral and anterior views of specimen, Rossmola in Finnmark, Norway, 60 m (APN); **e**: lateral view of specimen attached to coral, Brettingsneset in Trondheimsfjord, Trøndelag, Norway, 100–400 m (JH); **f–g**: interior view of dorsal valve with brachial loop preserved, and of unusually large-toothed ventral valve of empty shell, TSZ 3214 (APN), Melkøya in Finnmark, Norway, 64 m; **h–i**: interior view of dorsal valve with damaged brachial loop, and of ventral valve of empty shell, Norway (JH); **j**: dorsal view of small specimen with septum visible as a whitish spot, TSZ 3212 (APN), Norwegian Sea at Trøndelag, Norway, 239 m; **k**: detail of specimen with well-developed rootlets on pedicle, TSZ 3197 (APN), Tortenneset in Nordland, Norway, 135 m; **l–m**: two small shells with developed dorsal septum, TSZ 3008 (APN) and unnumbered APN-specimen, Norwegian Sea at Trøndelag, Norway, 305 and 300 m. Scalebar 1mm. Photos: Jesper Hansen.

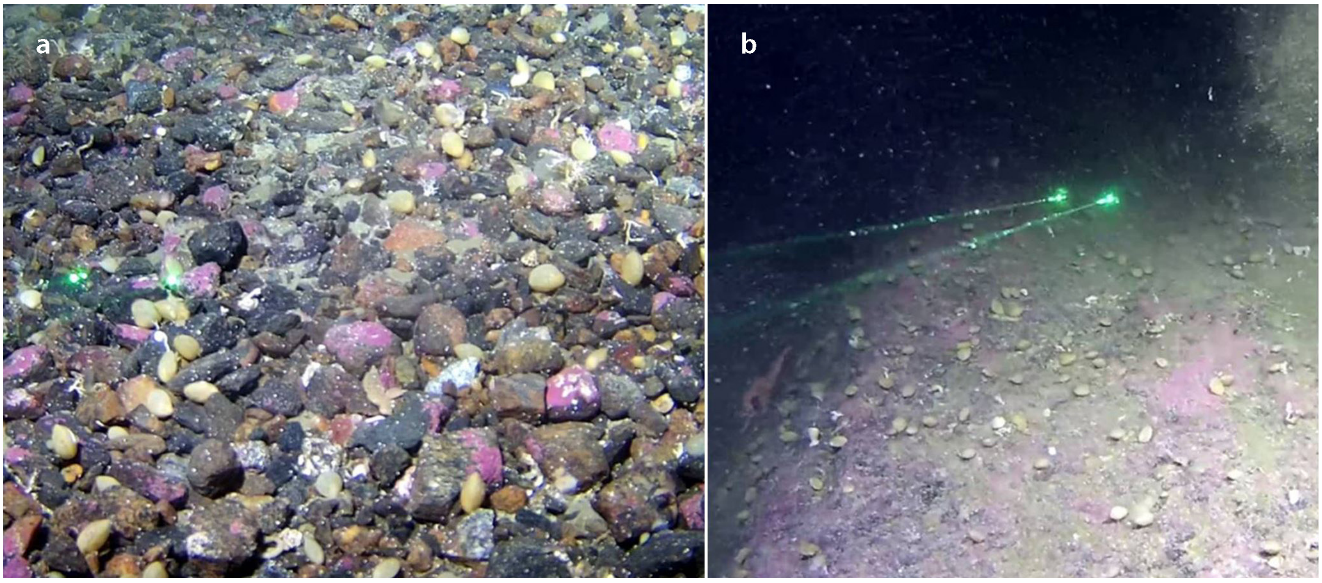

Figure 30. **a**: Pebble bottom with *Macandrevia cranium* (light brown shells) at 68 m depth; **b**: Exposed bedrock with a colony of *M. cranium* at 64 m depth. Photos: Akvaplan-niva.

brachial loop reaching to 2/3 to 4/5 valve length, with triangular crural processes situated close to base, and with small and few anteriorly directed spines in front. Specimens up to 2 mm long lack median ridge or septum. Specimens between 2 and 5–6 mm long develop a high, pillar-like septum highly elevating lophophores. Septum visible on the shell surface as a lighter spot or node around mid-valve length, sometimes extending partway back to umbo. Dorsal septum lost in specimens exceeding 6 mm in length. A study of septal development in this species was conducted by Friele (1877b). Maximum shell length 31 mm.

Depth range: 2–4700 m depth (Dall 1920; Anadón *et al.* 2022), but with the overwhelming majority occurring at 40–400 m and only one observation from deeper than 3000 m.

Temperature range: -1.1–12.0°C (Jeffreys 1878; this study).

Salinity range: 31.9–36.0 (this study).

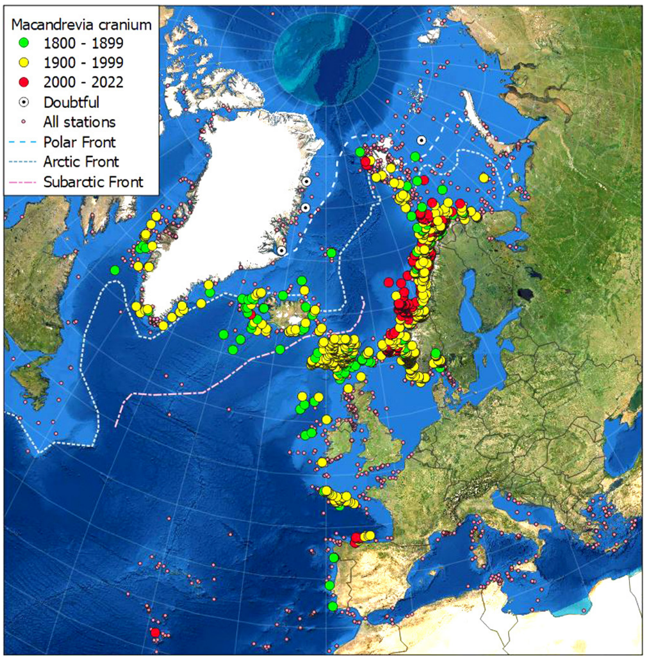

Figure 31. Distribution of *Macandrevia cranium*. Colours mark which century the specimens were collected in.

Oxygen range: 55–113% saturation (this study).

Current velocity: Mean current velocity was 1.1–12.0 cm/s, with daily maxima of approximately 0.2–31 cm/s and a maximum velocity of 16.2–42.7 cm/s measured over 1 month (this study).

Substrate: Attached to sand grains, gravel, stones, exposed bedrock, calcareous algae, corals, bryozoans, cirripeds, serpulid tubes, shells, etc. (Thomsen 1990, 2001; this study) (Figure 30). Mostly on sea floor dominated by sand, shell sand, gravel, cobbles or stones (Thomsen 2001), but can occur on silt-/clay-dominated bottoms.

Geography: Greenland, NE America to Rhode Island in the USA, Svalbard, Barents Sea, Novaya Zemlya, Norway, NW Russia, SW Sweden, Iceland, the Faroe Islands, N and W portions of the British Isles, France, Spain, Portugal, W Sahara and the Canary Islands (Jeffreys 1878; Posselt 1898; Derjugin 1915; Grieg 1933; Brunton & Curry 1979; Thomsen 1990, 2001; Gulliksen *et al.* 1999; Zezina 2014).

Remarks: See under *Dallina septigera* for distinguishing characters from that species.

This is undoubtedly by far the most common species in Norwegian waters. Despite a wide depth range, this species prefers coastal and inner shelf environments.

Relatively few specimens are found as far north as Svalbard. However, there is no strong evidence of a continuation of the northern expansion of its geographical range that Thomsen (1990) found in association with the strengthening of the warm Atlantic current up along the Norwegian coast during the Holocene warming after the last ice age.

Macandrevia cranium has previously been recorded along the mid and northeastern coast of Greenland (Posselt 1898; Arndt & Grieg 1933; Wesenberg-Lund 1940b; Thomsen 2012). However, four of the seven samples with specimens were located and examined during the present study and solely contained *Arctosia arctica*. Therefore, it appears likely that the remaining specimens from the area, influenced by the polar water masses of the East Greenlandic Current, also are *Arctosia arctica*. The presence of *Macandrevia cranium* along W Greenland is related to the slightly warmed West Greenlandic Current flowing north along the coast.

Macandrevia tenera (Jeffreys, 1876a)

Figures 32, 33

Terebratula tenera Jeffreys, 1876a, p. 250.
Terebratula (*Waldheimia*) *tenera* – Jeffreys (1878), p. 405, pl. 22, fig. 7.
Waldheimia (*Macandrevia*) *tenera* – Davidson (1886), p. 66, pl. 12, figs. 6–10.
Macandrevia tenera – Beecher (1893), p. 396, pl. 1, fig. H2.

Description: Compressed equi- to ventribiconvex shell with L/W ratio 1.06–1.43. Outline typically slightly truncated, elongate and egg-shaped, but smaller specimens and occasionally larger specimens are broad and egg-shaped. Dorsal valve usually longer than wide. Shell fragile and rather dull. Ventral umbo small, less prominent and more delicate than that of *Macandrevia cranium*. Anterior commissure rectimarginate. Deltidial plates rudimentary, bordering moderately sized and elongate pedicle opening. Ridges bordering deltidial plates hardly developed. Ornamentation lacking except for weak growth lines, which are more distinct than those of *M. cranium*. Shell matrix densely endopunctate. Colour light yellowish-brown. Hinge teeth in ventral valve high, but delicate and supported by short dental plates. Brachial loop in dorsal valve narrow and horseshoe-shaped. Cardinal process is a short ridge between socket ridges and attached directly to valve floor. Small specimens with a short but high septum centred at approximately 2/5 valve length. Largest specimen 13 mm long and 10 mm wide.

Depth range: 207–2652 m (Jeffreys 1876a,b; Cooper 1973a).

Temperature range: Based on four stations, the range is 1.6–4.5°C (this study).

Salinity range: Based on three stations, the range is 34.96–35.33 (this study).

Substrate: *Globigerina* ooze with stones (Jeffreys 1876a). Specimens are found attached to gravel.

Geography: NW North Atlantic, Labrador in Canada, and

Figure 32. *Macandrevia tenera*. **a–d**: dorsal, ventral, lateral and anterior views of specimen attached to gravel, Denmark Strait, E Greenland, the 'Ingolf' 1895 expedition st. 91, 2328 m, Zoological Museum of Copenhagen; **e–f**: interior view of dorsal and ventral valve of specimen, Denmark Strait, E Greenland, the 'Ingolf' 1895 expedition st. 91, 2328 m, Zoological Museum of Copenhagen; **g**: lateral view of specimen from batch NHMD-1201197, Irminger Sea, 2448 m; **h–i**: dorsal and anterolateral views of shell from batch NHMD-1201197, Irminger Sea, 2448 m; **j**: Dorsal view of specimen NHMD-1201195, W Greenland, mouth of Ameralik Fjord; **k–l**: dorsal views of two shells from batch NHMD-1201197, Irminger Sea, 2448 m; **m**: interior view of ventral valve from batch NHMD-1201197, Irminger Sea, 2448 m. Scalebar 1mm. Photos: Jesper Hansen.

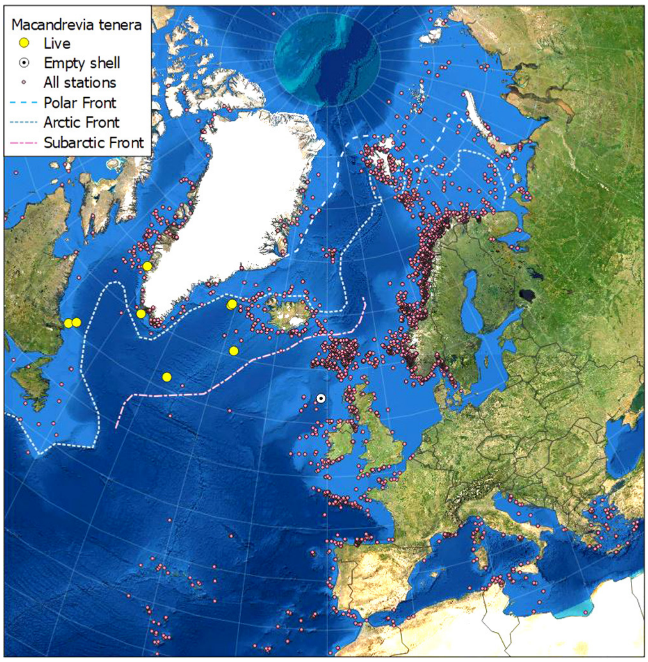

Figure 33. Distribution of *Macandrevia tenera*.

S Greenland (Jeffreys 1876a; Cooper 1973a). A 'recently dead' specimen collected NW of Ireland was also assigned to this species by Brand *et al.* (2003).

Superfamily Laqueoidea Thomson, 1927
Family LAQUEIDAE Thomson, 1927
Subfamily Glaciarculinae MacKinnon & Lee in MacKinnon et al. (2006)
Genus *Glaciarcula* Elliott, 1956

Glaciarcula spitzbergensis (Davidson, 1852c)
Figures 1D, 1H, 34, 35

Terebratella spitzbergensis Davidson, 1852c, p. 78–79.
Terebratula (*Terebratella*) *spitzbergensis* – Lovell (1861), p. 178.
Magasella spitzbergensis – Dall (1870), p. 137.
Terebratalia spitzbergensis – Dall (1920), p. 347.
Diestothyris(?) *spitzbergensis* – Thomson (1927), p. 244.
Diestothyris spitzbergensis – Helmcke (1938), p. 252.
Glaciarcula spitzbergensis – Elliott (1956).

Description: Shell egg-shaped. Rectimarginate anterior commissure. No ornamentation except irregular growth lines. Shell

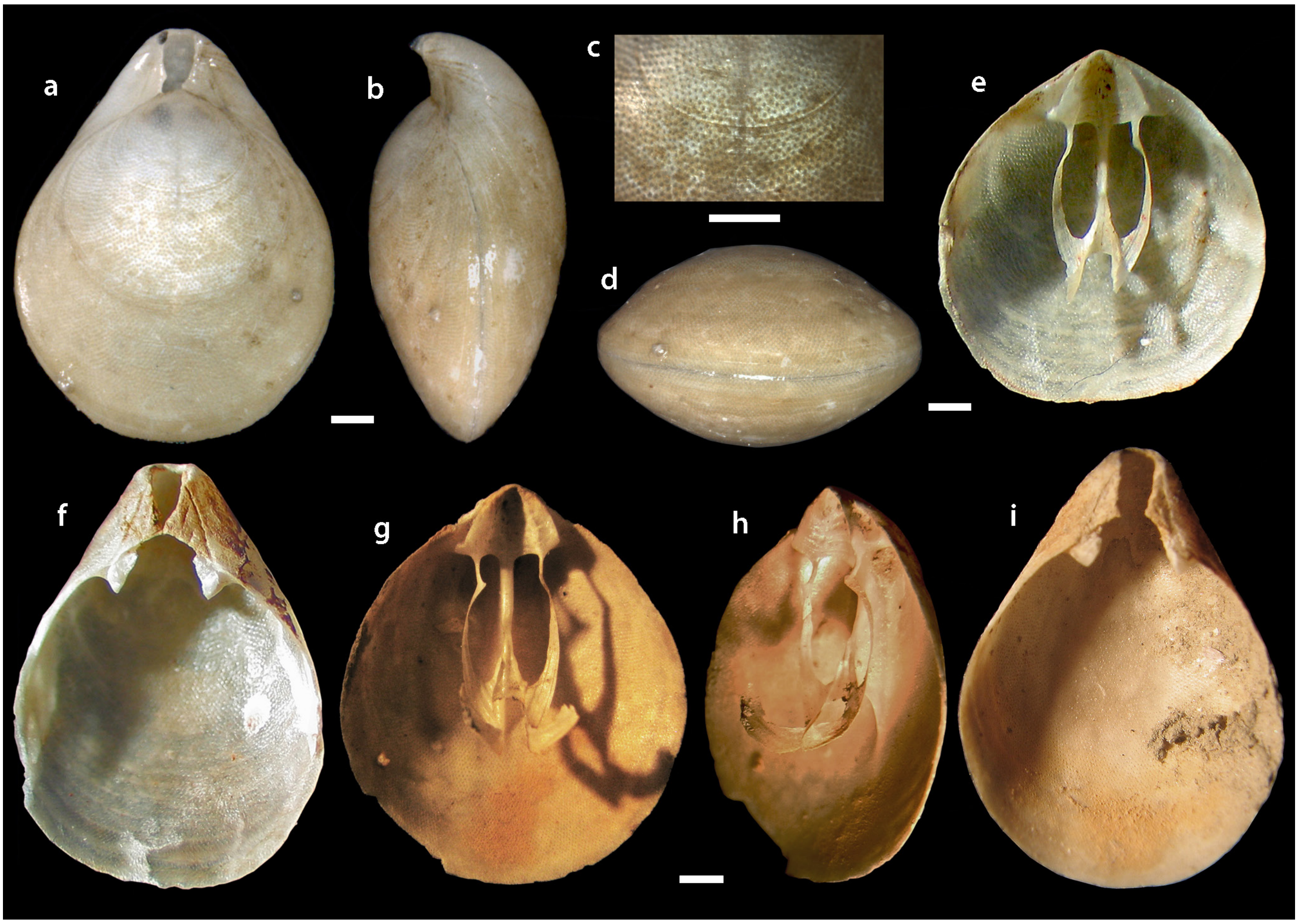

Figure 34. *Glaciarcula spitzbergensis*. **a–d**: dorsal, lateral, (close-up) surface and anterior views of specimen, Rijpfjorden, Spitsbergen, RV 'Jan Mayen' 2009 st. 67, 168 m (JH); **e–f**: dorsal and ventral interior views of glacial shell BMNH PI ZB 2763, from raised beach at Uddevalla, Bohuslän, Sweden; **g–i**: interior and oblique internal views of dorsal valve, and ventral valve interior of shell TSZBr-2409, Jarfjord, Finnmark, Norway, 110 m. Scalebar 1mm. Photos: Jesper Hansen.

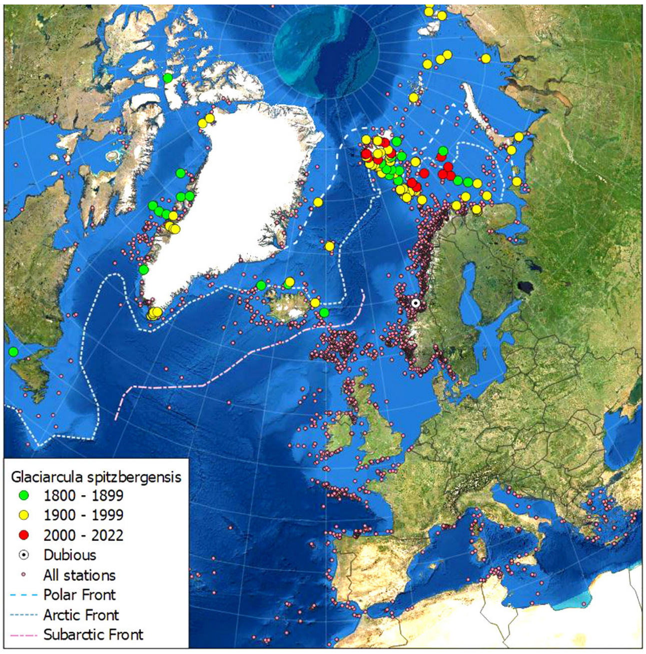

Figure 35. Distribution of *Glaciarcula spitzbergensis*. Colours mark which century the specimens were collected in, as well as the dubious observation.

matrix endopunctate. Colour yellowish white. Umbo long, curved and beak-shaped, except in specimens below 3.5 mm long. Pedicle opening very elongate. Deltidial plates usually not joined and rudimentary in small specimens. Pedicle commonly strongly branched. Ventral teeth supported by dental plates. Long pedicle collar (thickening of valve floor) extending to front of dental plates. Dorsal median septum in subadult and adult shells triangular and reaching from umbo to approximately 3/5 to 2/3 valve length and terminating gradually. Juveniles below 3 mm long with a short, more pedestal-like septum. Brachial loop long. Maximum shell length 13.3 mm.

Depth range: 26–547 m depth (Friele & Grieg 1901; this study), mostly from the shelf seas at 40–400 m depth. This species was described by Wesenberg (1940a, 1941) from several samples collected deeper than 1000 m. However, a re-examination of the specimens revealed them to be *Cryptopora gnomon* or juvenile *Macandrevia cranium*.

Temperature range: -2–3.8˚C (Knipowitsch 1901; Grieg 1933; Ullmann *et al.* 2017).

Salinity range: 32.5–35.1 (Wesenberg-Lund 1940a; this study).

Substrate: Attached to sand grains, gravel, Sessilia shells, polychaete tubes or bryozoan branches (this study). Found on muddy or sandy bottoms with annelid tubes or gravel (Posselt 1898; Knipowitsch 1901, 1902; Grieg 1933).

Geography: Arctic Ocean, N Canada, Greenland, Beaufort Sea, Chukchi Sea, Laptev Sea, Kara Sea, Svalbard, Barents Sea, Norway (Finnmark), N and E Iceland, and Japan (e.g., Jeffreys 1878; Posselt 1898; Derjugin 1915; Grieg 1933; Zezina 1997a,b; Thomsen 2001; Ullmann *et al.* 2017).

The species is also found in glacial deposits from SW Sweden, the Shetland Islands and the Oslofjord (Lyell 1835 (as *Terebratula*); Jeffreys 1869b; Davidson 1887).

Three specimens collected by Jeffreys and reported by Davidson (1887) from three stations on the slope at the Western Approaches and from just SW of Portugal have been assigned to this species. The bottom-water temperatures at these stations were 9, 10 and 11.5˚C, respectively (Jeffreys 1878), and thus far higher than where the species otherwise occurs. However, Jeffreys (1878) noted that he did not find any individuals of that species, but had initially misidentified a juvenile *Dallina* from one of the two northern stations. In fact, the specimen (BMNH PI ZB 790) was a *Fallax dalliniformis*, which, as a juvenile, is easily confused with *Glaciarcula spitzbergensis*. The other northern specimen (BMNH PI ZB 4946) was an empty valve of a new species, *Dallina lusitanica*. Moreover, Brunton & Curry (1979) misread Davidson (1887) and assumed that these two stations were at the Scilla Isles.

Glaciarcula spitzbergensis was reported from two places at Trondheim by Wesenberg-Lund (1939); however, both of these finds turned out to be juvenile *Macandrevia cranium*. The same occurred for the specimens from the Faroe Islands and most of those from Iceland reported by Wesenberg-Lund (1938, 1940a,c, 1941).

Three specimens, which, according to their label are from the Haltenbank off western Norway, are housed at the University Museum of Bergen. However, since there are some information disagreements between labels and information published by Grieg (1933) (he had assigned finds from that locality to the species *Hemithiris psittacea*), it is likely that the label does not belong to the specimens.

Remarks: When comparing new and old observations of this Arctic species, it cannot be excluded that the southern limit of the species is shifting further north, away from Norway.

Superfamily Megathyridoidea Dall, 1870
Family MEGATHYRIDIDAE Dall, 1870
Genus *Megathiris* d'Orbigny, 1847a

Megathiris detruncata (Gmelin, 1791)

Figures 36, 37

Anomia decollata Chemnitz, 1785, p. 96, pl. 78, fig. 705.
Terebratula ungula Philipsson in Retzius (1788), p. 15.
Terebratula detruncata – Bruguière (1789), pl. 213, fig. 10.
Anomia detruncata Gmelin, 1791, p. 3347
Terebratula urna antiqua Risso, 1826, p. 388, pl. 12, fig. 177.
Terebratula cardita Risso, 1826, p. 389, pl. 12, fig. 180.
Terebratula aperta Blainville, 1828, p. 144.
Terebratula decollata – Deshayes (1832), p. 1029.
Terebratula dimidiata Scacchi, (1833), p. 17.
Argiope detruncata – Deslongchamps (1842), p. ix.
Orthis detruncata – Philippi (1844), p. 69.
Megathiris detruncata – d'Orbigny (1847b), p. 253, pl. 7, figs. 26–27.
Terebratula pectiniformis Costa, 1844, p. 39–40, pl. 1, fig. 6.
Argiope decollata – Gray (1853), p. 113.
Megathyris (*Megathyris*) *decollata* – Dall (1870), p. 145.
Megathyris detruncata – Dall (1920), p. 330–331.

Description: Shell highly ventribiconvex. Outline subtriangular to semicircular. Ventral umbo high or long. Straight hinge line. Anterior commissure rectimarginate. Ventral umbo high or long and with high apsacline to almost catacline interarea (plane area between hinge line and umbo) bisected by long V- or U-shaped pedicle opening also extending slightly into dorsal valve. Deltidial plates narrow and triangular. Pedicle collar strongly raised but relatively short. Ornamentation of 7–18 broad, radiating ribs, and shell surface marked

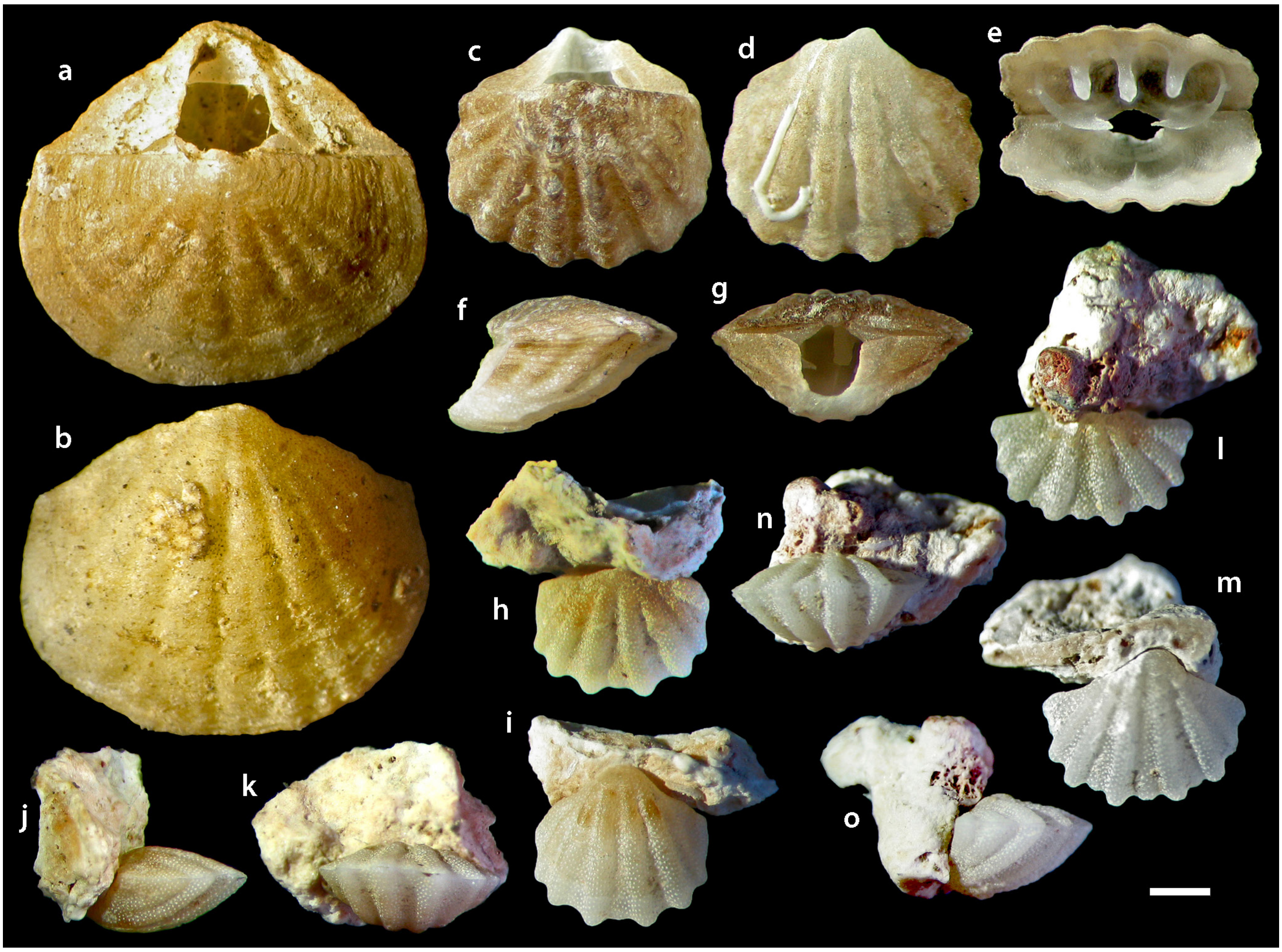

Figure 36. *Megathiris detruncata*. **a–b**: dorsal and ventral views of a 6-mm-long specimen, Zoological Museum of Copenhagen; **c–g**: dorsal, ventral, anterior, lateral, and posterior views of shell, Saronic Gulf, Greece, 80 m (JH); **h–k**: dorsal, ventral, lateral and anterior views of specimen attached to stone, Saronic Gulf, Greece, 55 m (JH); **l–o**: dorsal, ventral, anterior and lateral views of specimen attached to stone, Saronic Gulf, Greece, 55 m (JH). Scalebar 1mm. Photos: Jesper Hansen.

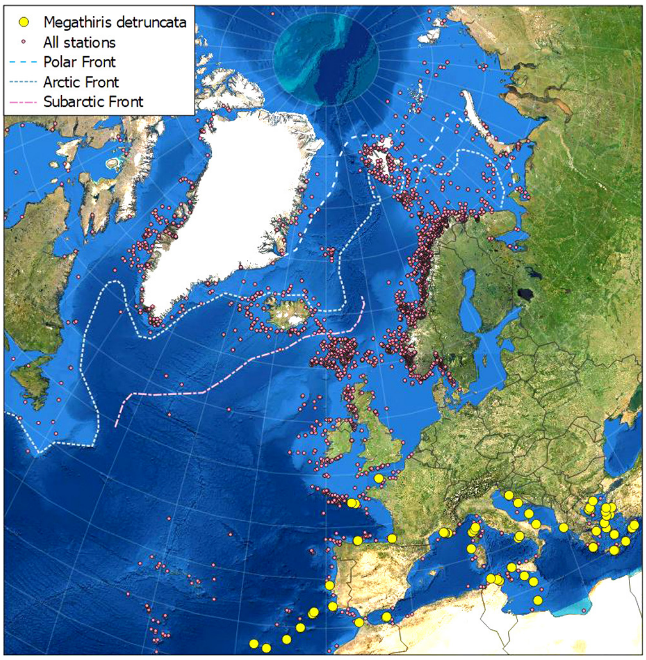

Figure 37. Distribution of *Megathiris detruncata*.

by growth lines. Ribs fading away distally on largest specimens. Shell matrix endopunctate. Colour light honey or greyish. Dental plates lacking. Ventral valve floor with narrow and low median septum or ridge. Long brachial loop reaching 2/3 valve length and attached to median and two or (rarely) four lateral ridges or septa. Dorsal median septum or ridge reaching close to valve front. Maximum shell size 6.7 mm long.

Depth range: Minimum range is 5–1940 m depth (Gaspard 2003; Logan 2007). The species is rarely found deeper than 500 m.

Temperature range: 11.5–25°C (Jeffreys 1878; Brand *et al.* 2003).

Salinity range: 37–38 (Brand *et al.* 2003).

Geography: English Channel, Southernmost Celtic Sea, Bay of Biscay, Portugal, the Mediterranean, Madeira, the Canary Islands and the Cape Verde Islands (Jeffreys 1878; Logan 1979; Logan *et al.* 2007; Evangelisti *et al.* 2011).

Remarks: Bruguière (1789) did not provide a description with the name, which is why the authorship of the name was transferred to Gmelin (1791). The year of authorship is 1791, not 1790 as often cited in the literature.

Genus *Argyrotheca* Dall, 1900

***Argyrotheca cistellula* (Forbes & Hanley, 1849)**
Figures 38, 39

Terebratula cistellula Wood, 1840, p. 253.
Megathyris cistellula – Forbes & Hanley (1849), p. 361–363, pl. 57, fig. 9.
Argiope cistellula – Davidson (1852b), p. 373.
Argiope (*Cistella*) *cistellula* – Gray (1853), p. 114.
Terebratula (Argiope) cistellula – Lovell (1861), p. 186.
Megathyris (*Cistella*) *cistellula* – Dall (1870), p. 146.
Cistella cistellula – Davidson (1887), p. 139–140, pl. 22, figs. 1–4.
Argyrotheca cistellula – Dall (1900), p. 44.
Argyrotheca lunifera Philippi – Helmcke (1938), p. 245.

Description: Shell with transverse subangular outline and can have weakly indented front. Both dorsal and ventral valves with weak median furrow. Hinge line wide and straight. No ornamentation except for growth stops. Colour white, yellow or grey. Pedicle opening large and extending into dorsal valve. Deltidial plates not meeting. Shell matrix endopunctate. Brachial loop in dorsal valve long, simple, bilobed and anteromedially fixed. Triangular dorsal median septum sometimes with pillar-like anterior thickening. Median septum also developed in ventral valve, though smaller. Maximum shell length 3 mm.

Depth range: 2–255 m depth (Logan *et al.* 1997; Gaspard 2003). However, this species is rarely found deeper than 100 m.

Temperature range: 11–13˚C (Simon & Willems 1999).

Substrate: On bedrock, stones, sand or shells (Jeffreys 1863; this study).

Geography: Norway (Vestland, Møre and Romsdal, Trøndelag), East Shetland, Scotland, the Hebrides, Ireland, the English Channel, SE France, Spanish Bay of Biscay, Portugal, Sardinia, Aegean Sea, Sicily, Adriatic Sea, Greece, and the Azores (Jeffreys 1863; Friele 1873; Davidson 1887; Logan 1979; Brunton & Curry 1979; Besteiro & Urgorri 1986; Logan *et al.* 1997; Thomsen & Brattegard 1997; Simon & Willems 1999; Logan *et al.* 2007; Bitner & Gerovasileiou 2021; this study). From Norway, it has also been reported from Østfold, Nordland and Troms by Thomsen & Brattegard (1997), but despite searching, no specimens were encountered in the present study to support this. One empty shell was taken from Rogaland in SW Norway during the present study, suggesting its presence there.

Comment: This species was first named by Wood (1840); however, as pointed out by Jeffreys (1863), neither a description nor an illustration was provided with the name. Due to the lack of a description, the naming is not a true one in the sense of the International Code of Zoological Nomenclature (Article 12); therefore, it is here assigned to Forbes & Hanley (1849), who provided the first description.

Argyrotheca cistellula is uncommon in samples from Norway but seems to prefer shallow waters. Although the species is undoubtedly uncommon, its small shell size additionally makes it easy to overlook.

***Argyrotheca cuneata* (Risso, 1826)**
Figures 40, 41

Terebratula cuneata Risso, 1826, p. 388, pl. 12, fig. 179.
Terebratula soldaniana Risso, 1826, p. 389, pl. 12, fig. 178.
Anomia pera Megerle von Mühlfeld, 1829, p. 205, pl. 1, fig. 1a–b.
Terebratula pera – Küster (1843), p. 30, pl. 2b, figs. 14–17.
Orthis pera – Philippi (1844), p. 69.
Argiope cuneata – Davidson (1852b), p. 373.

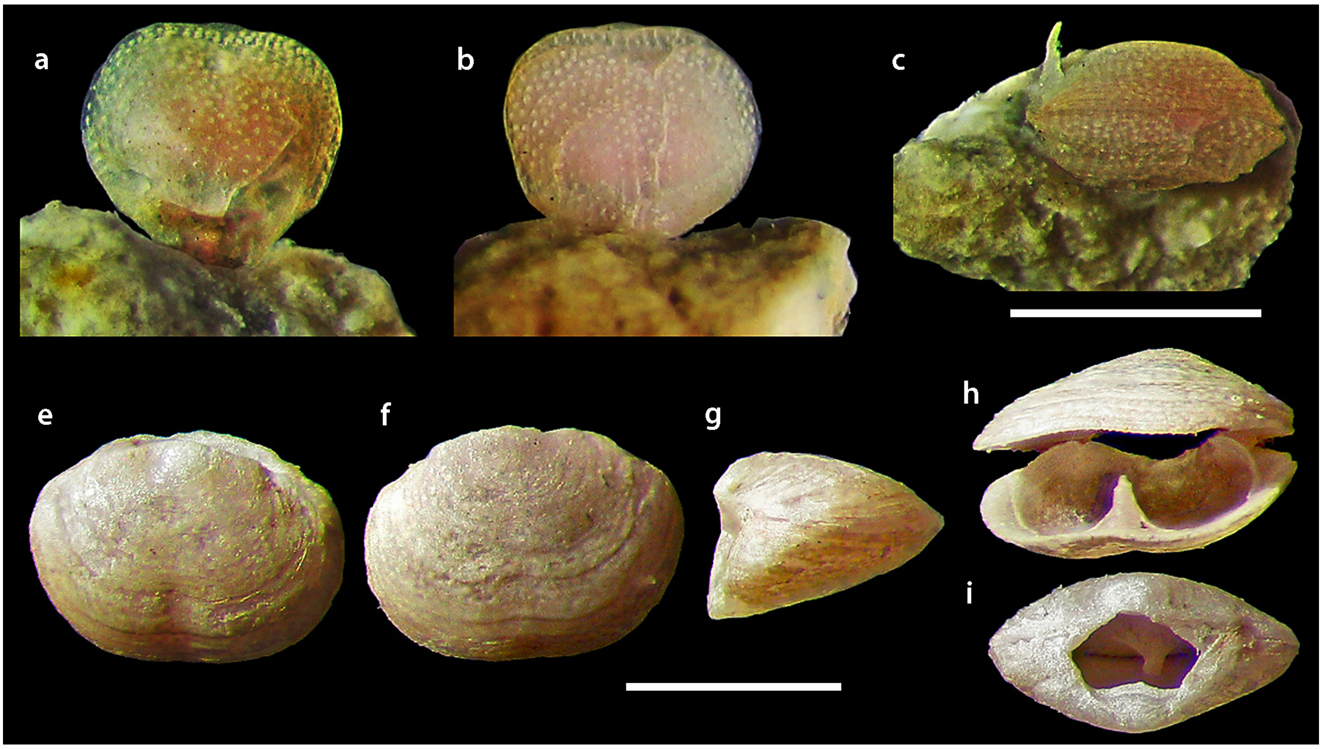

Figure 38. *Argyrotheca cistellula*. **a–c**: dorsal, ventral and anterior views of specimen with anteriorly situated pillar-like dorsal septum visible through the shell of the dorsal valve, TSZ 3011 (APN), Tennøya in Trøndelag, Norway, 83 m; **e–i**: dorsal, ventral, lateral, anterior and posterior views of empty shell, Årdalsfjorden in Rogaland, Norway, 69 m (APN). Scalebar 1mm. Photos: Jesper Hansen.

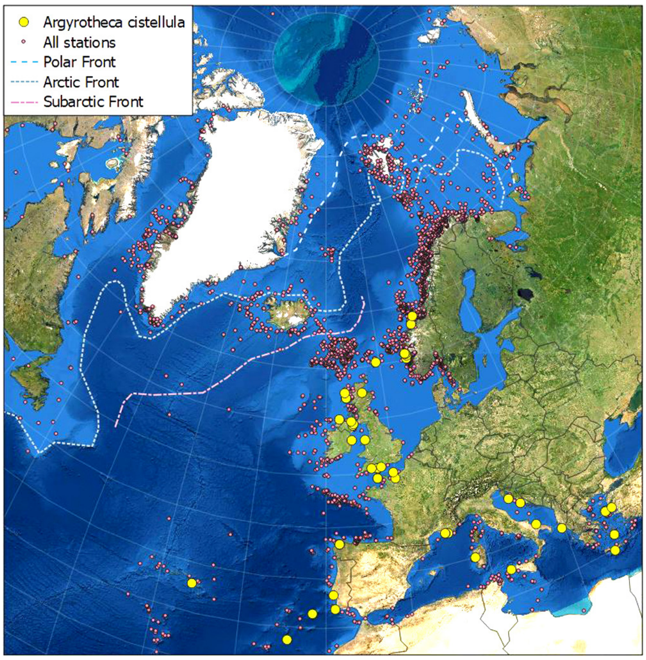

Figure 39. Distribution of *Argyrotheca cistellula*.

Argiope (*Cistella*) *cuneata* – Gray (1853), p. 114.
Terebratula (Argiope) cuneata – Lovell (1861), p. 185.
Argiope pera – Brusina (1866), p. 47.
Megathyris (*Cistella*) *cuneata* – Dall (1870), p. 146.
Argiope barroisi Schulgin, 1885, p. 122, pl. 8, fig. 4.
Argyrotheca cuneata – Dall (1900), p. 44.

Description: Shell gently to moderately ventribiconvex. Outline transverse and semicircular with acuminate cardinal extremities to equidimensional subangular, occasionally with weakly indented front. Both dorsal and ventral valves with weak median furrow. Hinge line wide and straight. Ventral umbo typically high and straight. Anterior commissure rectimarginate to unisulcate. Ornament of approximately 8–16 coarse, radiating, broadly rounded ribs. Shell white, red or grey, and typically red between ribs. Large round to triangular pedicle opening extending into dorsal valve. Deltidial plates rudimentary. Shell matrix endopunctate. Brachial loop in dorsal valve long, simple, bilobed and anteriorly attached to median septum. Triangular dorsal median septum reaching 4/5 valve length with a peak at 2/3 valve length. Ventral valve with a distinct median ridge extending to 4/5 valve length. Maximum shell length 3 mm.

Depth range: 2–645 m depth (Logan 1979; Logan 2007). However, from the available data, it seems that this species is mostly found shallower than 60 m.

Temperature range: 12–20°C (Brand *et al.* 2003).

Salinity range: 37–38 (Brand *et al.* 2003).

Geography: Southernmost Celtic Sea, the Mediterranean, Madeira, the Canary Islands and the Cape Verde Islands (Logan 1979; Brunton & Curry 1979; Simon & Willems 1999; Logan *et al.* 2007).

Superfamily	Platidioidea Dall, 1870
Family	PLATIDIIDAE Dall, 1870
Subfamily	Platidiinae Dall, 1870
Genus	*Platidia* Costa, 1852

Platidia anomioides (Scacchi & Philippi, in Philippi, 1844)

Figures 42, 43

Orthis anomioides Scacchi & Philippi in Philippi (1844), p. 69–70, pl. 18, fig. 9.
Terebratula appressa Forbes, 1844, p. 193.
Platidia anomioides – Costa (1852), p. 48, pl. 3, figs. 4 and 6.
Morrisia anomioides – Davidson (1852c), p. 79–80, pl. 14, fig. 29.
Morrisia davidsoni Deslongchamps, 1855, p. 443, pl. 10, figs. 20a–d.
Terebratula (*Morrisia*) *anomioides* – Lovell (1861), p. 184.
Terebratula (*Morrisia*) *anomioides* – Reeve (1861), pl. 10, fig. 40.
Terebratula (*Morrisia*) *davidsoni* – Reeve (1861), pl. 10, fig. 42.
Argiope (*Zellania*) *davidsoni* – Weinkauff (1867), p. 290.

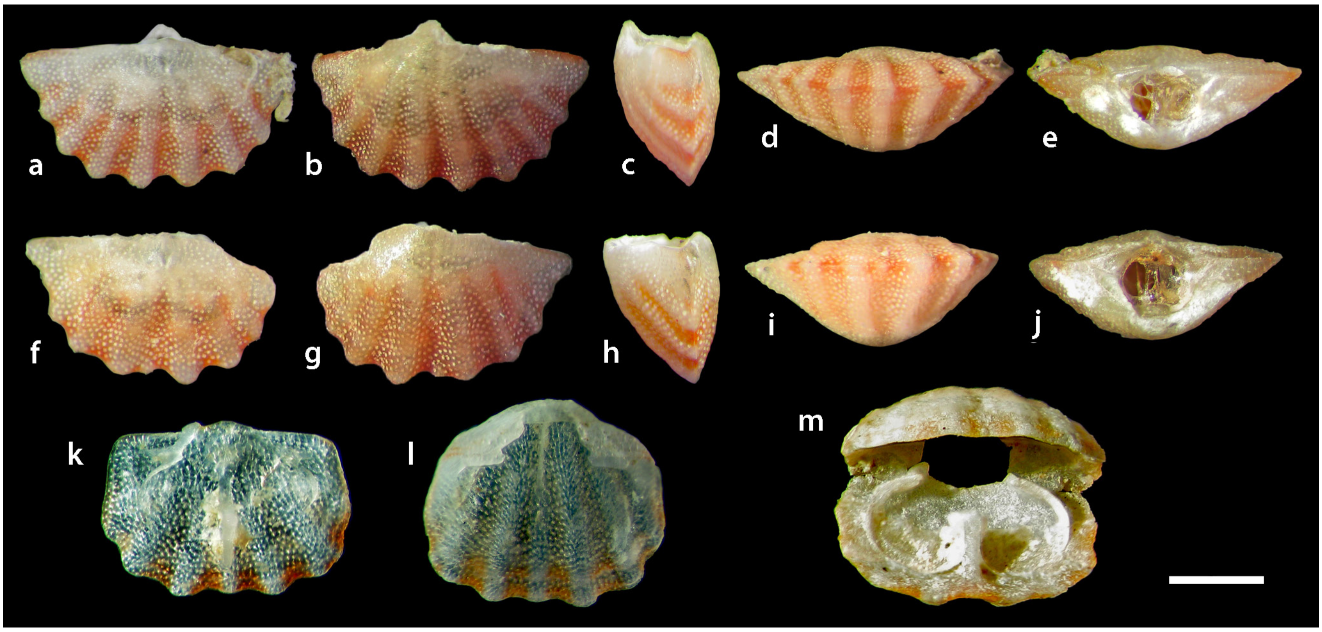

Figure 40. *Argyrotheca cuneata*. **a–e**: dorsal, ventral, lateral, anterior and posterior views of specimen, 55 m (JH); **f–j**: dorsal, ventral, lateral, anterior and posterior views of specimen, 55 m (JH); **k–l**: dorsal and ventral interior views of empty shell, 80 m (JH); **m**: frontal view of dorsal valve interior of empty shell, 80 m (JH). All from the Saronic Gulf, Greece. Scalebar 1mm. Photos: Jesper Hansen.

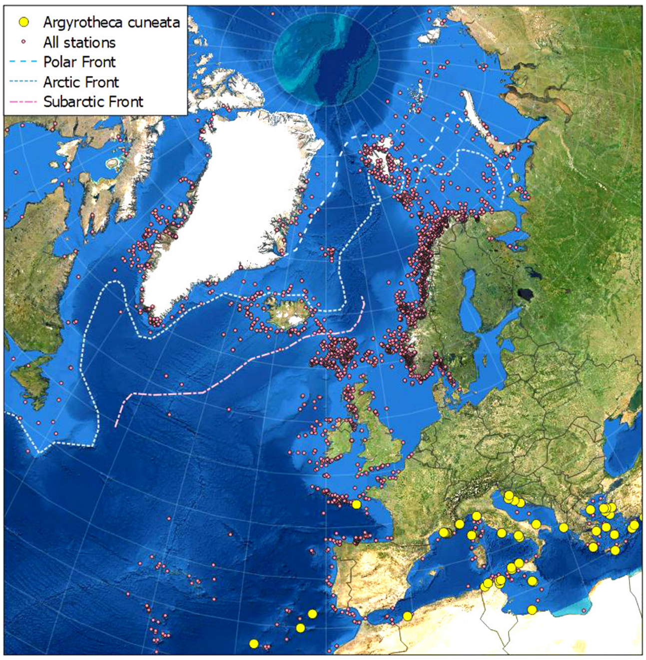

Figure 41. Distribution of *Argyrotheca cuneata*.

Platidia davidsoni – Dall (1870), p. 143.
Platydia anomioïdes – Jeffreys (1878), p. 411.
Platydia davidsoni – Davidson (1880), p. 21.
Platidia seminula Philippi – Dall (1920) [partim], p. 332.

Description: Shell typically very uneven, concavoconvex to ventribiconvex, shaping itself after the substratum. Outline circular to transversely oval, but juveniles can be more egg-shaped. Hinge line straight and shorter than greatest shell width. Ornamentation of concentric growth lines, with randomly distributed pustules (tubercles) on ventral valve. Pustules missing on juvenile shells. Shell matrix endopunctate. Colour yellowish-brown or white. Pedicle foramen large and extending well into posterior part of dorsal valve. Deltidial plates narrow. Short brachidium (=lophophoral support) when fully developed, forming a brachial loop supported by short median septum. Median septum very high triangular and can reach slightly anterior of mid-valve length. Very short setae along valve margin. Maximum shell length 8 mm.

Depth range: 8–2190 m depth (Logan 2007).

Temperature range: -1.2–12.0°C (Carpenter *et al.* 1869; this study).

Salinity range: 35.2–35.3 (Thomsen 2001).

Substrate: Attached to pebbles, shells and corals (Davidson 1887; Brunton & Curry 1979; Logan 1979; Thomsen 2001). Found on all from mud- to stone-dominated bottoms (Thomsen 2001).

Geography: SW of Faroe Islands, Florida, North of Shetland, the Hebrides, Western Approaches, Bay of Biscay, Portugal, Mediterranean, Azores, Morocco, Canary Islands, Cuba, the West Indies, Red Sea, Argentina, South Africa, southernmost S America, Prince Edward Islands, and Antarctica (Fischer & Œhlert 1891, 1892; Cooper 1973a; Brunton & Curry 1979; Thomsen 2001; Logan *et al.* 2007, 2008; Zezina 2008).

Genus *Annuloplatidia* Zezina, 1981

Annuloplatidia annulata (Atkins, 1959)

Figures 44, 45

Platidia annulata Atkins, 1959, p. 133–142.
Platidia anomioides var. *annulata* – Brunton & Curry (1979), p. 48.
Annuloplatidia annulata – Zezina (1981).

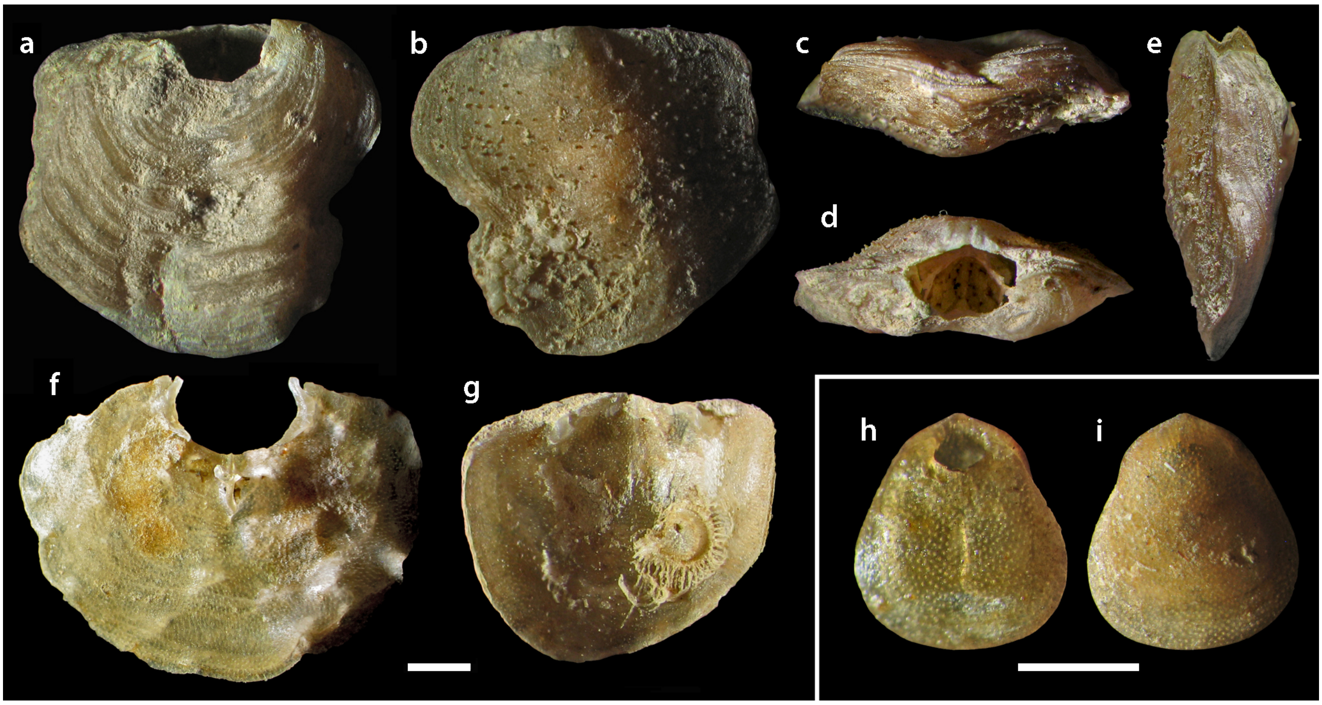

Figure 42. *Platidia anomioides*. **a–e**: dorsal, ventral, anterior, posterior and lateral views of specimen; **f**: interior view of a dorsal valve; **g**: interior view of a ventral valve; **h–i**: dorsal and ventral views of juvenile specimen. All specimens are housed at the Zoological Museum of Copenhagen, Natural History Museum of Denmark. The shells all belong to the old collection of Chr. viii. Scalebar 1mm. Photos: Jesper Hansen.

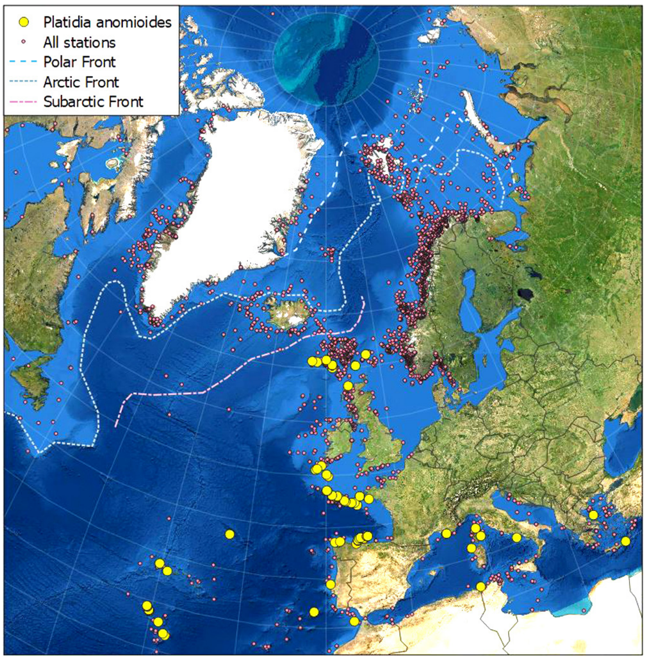

Figure 43. Distribution of *Platidia anomioides*.

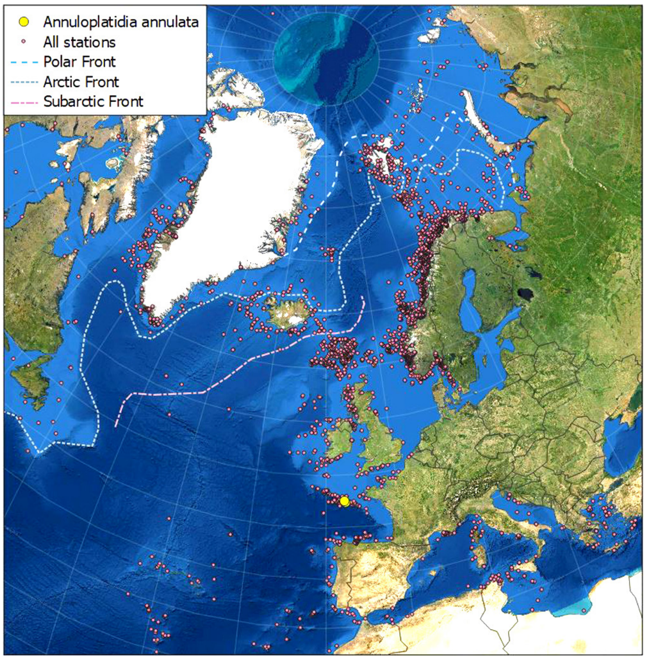

Figure 45. Distribution of *Annuloplatidia annulata*.

Description: Shell planoconvex to concavoconvex with dorsal valve almost flat and ventral valve gently convex. Outline subrectangular to transverse oval with very short but pointed beak. Shell surface marked by concentric growth lines. Colour yellowish-white. Shell matrix endopunctate. Pedicle short. Pedicle foramen large and extending well into posterior part of dorsal valve. Deltidial plates narrow. Short brachidium with an upper transverse band creating a triangular brachial ring supported by and just above median septum. Median septum pillar-like in juveniles, but extending from hinge region to mid-valve length in adults. Setae dense along valve margin and approximately 2/3 of the length of the shell. Maximum shell length 5 mm.

Figure 44. *Annuloplatidia annulata*. Ventral exterior view of syntype BMNH PI. ZB 2910, Celtic Sea. OBS: only peristracum and soft tissue are preserved, as is the case for the rest of the type specimens. Scalebar 1mm. Photo: Jesper Hansen.

Depth range: Minimum depth range is 1260–2197 m (Lüter 2007).

Substrate: Attached to the coral *Enallopsammia rostrata* (Atkins 1959).

Geography: Celtic Sea and the English Channel (Atkins 1959). The species is also reported from the E Pacific (Lüter 2007), but the great distance and oceanographic separation of the populations make it more likely they are two different—though morphologically very similar—species.

Remarks: The shells of all type specimens are dissolved, with only periostracum and soft tissue remaining.

Superfamily Kraussinoidea Dall, 1870
Family KRAUSSINIDAE Dall, 1870
Genus *Megerlia* King, 1850

Remarks: The validity of the three species *Megerlia truncata*, *M. monstruosa* and *M. echinata* has been a matter of debate for the last nearly 200 years, with many of the greatest brachiopodologists in history taking opposite views. As the issue is still not settled, I feel it is necessary to give an overview of the history of these species. Already, when erecting *M. monstruosa*, Scacchi (1833) admitted doubt, whether the specimen of his new species in reality was the species *M. truncata*, which just had shaped itself after the substrate. This opinion of synonymy was shared among others by Costa, Monterosato and Jeffreys based on the internal features, though Jeffreys kept the species as a variety of *M. truncata* (see: Costa 1838; Monterosato 1872; Jeffreys 1878). Davidson (1887) followed the lead of the others but observed that all specimens he had encountered of *M. monstruosa* differed in a uniform way from *M. truncata*, why he chose to keep it as a variety. Subsequently, Fischer & Œhlert (1890) erected a very similar species, *M. echinata*, mainly differing by having minute spines on the surface. They then followed up by restoring *M. monstruosa* to species level arguing that while *M. truncata* often showed deformation due to confinement of substrate, the degree of deformation in shells of *M. monstruosa* was so extreme and consistent, like the mode of convexity; ornamental characteristics; narrower shell; pedicle opening moved into dorsal valve; the smaller interarea; and the cardinal area on the inside, that they were species-specific (Fischer & Œhlert 1891). Dall (1919 and 1920) found the shared feature of the pedicle opening allocated to the dorsal valve warranted, that *M. echinata* and *M. monstrousa* with *M. monstruosa* as type species were moved into a new genus *Pantellaria*. Based on observed variability within *Megerlia truncata*, Thomson (1927) questioned the validity of the suggested generic differences as more than species-level differences. Atkins (1961a) followed up with a study on *M. echinata*. There she did not find support for separating this species, but lacking specimens for the study of *M. monstruosa*, did not suggest transferring that back as well. Most accepted the transfer, though some maintained *Pantellaria* for *M. monstruosa* long after (e.g.: Cooper 1981a, 1982; Zezina 2010, 2014). While noting *M. monstruosa* externally closely resembled species of the genus *Platidia*, Logan (1979) again put *M. monstruosa* into synonymy with *M. truncata*, though not providing a discussion on why. Comparing the specimens of *M. echinata* from Atkins (1961a) with those of *M. monstruosa* used by Davidson (1887), Brunton (1988) disagreed on this synonymy and argued that *M. monstruosa* and *M. echinata* were synonymous though distinct from *M. truncata*. He thus placed them under the senior name *M. monstruosa*, an opinion which was followed by Anadon (1994). His study seems to be rather unique in that it directly compared the two species and did not just give a discussion on how each of them differed from *M. truncata*.

Just two years later, Bitner (1990) published a study on 13–16 million-year-old Middle Miocene Polish fossils. Though she did not find specimens fully resembling *M. echinata* and *M. monstruosa* among her more than 2500 specimens, she did have intermediate specimens and thus concluded, that all three species were one and the same. In general, I hesitate to put too much weight on using the shell morphology of so old specimens as a proof of species synonymy of living brachiopods. This is because 15 million years is a very long time for a species, and both the morphology, and the degree of morphological variability, can change significantly over such a time span, as well as that species can split up in a shorter time (e.g.: Sheldon 1987; Wei & Kennett 1988). Nonetheless, this publication became an important basis for changing the major opinion towards the existence of only one species. Interestingly, in a simultaneous study on nearly 1000 specimens from the same Polish deposits, Barczyk & Barczyk (1990) came to the opposite conclusion, that they had two distinct species, *M. truncata* and *M. monstruosa*. Barczyk & Barczyk (1990) found the differences so distinct and ontogenetic stable, that they preferred to follow the opinion of generic division of the two species.

With supporting observations of recent morphologically intermediate specimens, Logan *et al.* (2004) agreed with Bitner (1990) that evidence points to *M. monstruosa* being conspecific with *M. truncata*, though they recognized it as a variety and accepted *M. echinata* as a valid species. This opinion on synonymy was followed by Anadon *et al.* (2022), Logan (2007), and Logan *et al.* (2007, 2008). Others, like Alvarez & Emig (2005), Hiller *et al.* (2008), Alvarez (2016) and Emig (2016), were more inclined to agree with Bitner (1990) in that all three species are synonymous. Trying to give a better basis for comparison, Simon *et al.* (2016) provided SEM pictures of the holotype of *M. echinata* together with a discussion. They found the nature of the micro-ornament differed from that of *M. truncata*, why they concluded *M. echinata* is a valid species distinct from *M. truncata*.

At present, it seems that the greater majority consider both *M. monstruosa* and *M. echinata* synonymous with *M. truncata*, while a large minority consider *M. echinata* a valid species.

The division in the present work is based on the following reasoning. On a general basis when assuming two species are synonymous, it would be expected that the various features show more intermediate forms as of the type form of the least common form group. Similarly, it would seem unlikely to encounter a relatively consistent combination of seemingly uncorrelated features differentiating two subgroups within the species if no external barriers keep populations separate over an extended time.

Going through the available material of the genus, there turned out to be two distinct form groups for which I did not manage to find intermediates among the probable nearly 1000 specimens I have seen. The biggest group contained specimens rather conservatively biconvex and unisulcate, with the major part of the pedicle opening in the ventral valve, and with both valves exhibiting dense, finely costellate ribs as well as low tubercles. Deformation in these specimens appeared only to occur in cases where the specimens had been cramped by substratum or damaged during life. This form group has the typical shape of *M. truncata*.

The smallest group contained the specimens with dorsal valve typically nearly plane to concave, shaping itself after the substratum and rarely showing any hint of ornament other than growth lines; a convex ventral valve with sparse and uneven, weak costellae with scattered tubercles, as well as variably developed minute and alveolate thorns and spines; and a pedicle opening moved almost entirely into the dorsal valve in mature specimens. Specimens still attached to their substrate, showed that the odd shape was not due to confined space or shell damage during life. The shape and the minute spines place this form group as *M. echinata*. I was unable to find any evidence of external reasons for the general shape of the specimens of *M. echinata*. I thus find myself in support of the opinion, that *M. echinata* is not synonymous with *M. truncata*, and therefore chose to keep them separate in this publication.

Another observation from this study was how unevenly distributed the minute thorns and spines were developed on the ventral valve of many of the examined specimens in the form group of *M. echinata*. These spines were evenly and densely distributed on some valves, while only present on parts of valves or nearly lacking on others. Specimens lacking these spines fit in both shape and ornamentation the description of *M. monstruosa* and I therefore feel inclined to think that Brunton (1988) and Anadon (1994) were right in that the two species are synonymous rather than *M. monstruosa* with *M. truncata*. However, I here realise there are strong opinions to the contrary, and as I have not seen the type specimen of *M. monstruosa*, I leave this question for others to clarify. If, however, the two species turn out to be synonymous, the name *M. monstruosa* is the senior synonym.

Megerlia echinata (Fischer & Œhlert, 1890)

Figures 46, 47

?*Terebratula monstruosa* Scacchi, 1833, p. 17.

?*Megerlia truncata* var. *monstruosa* – Davidson (1887), p. 108, pl. 9, figs. 21–22.

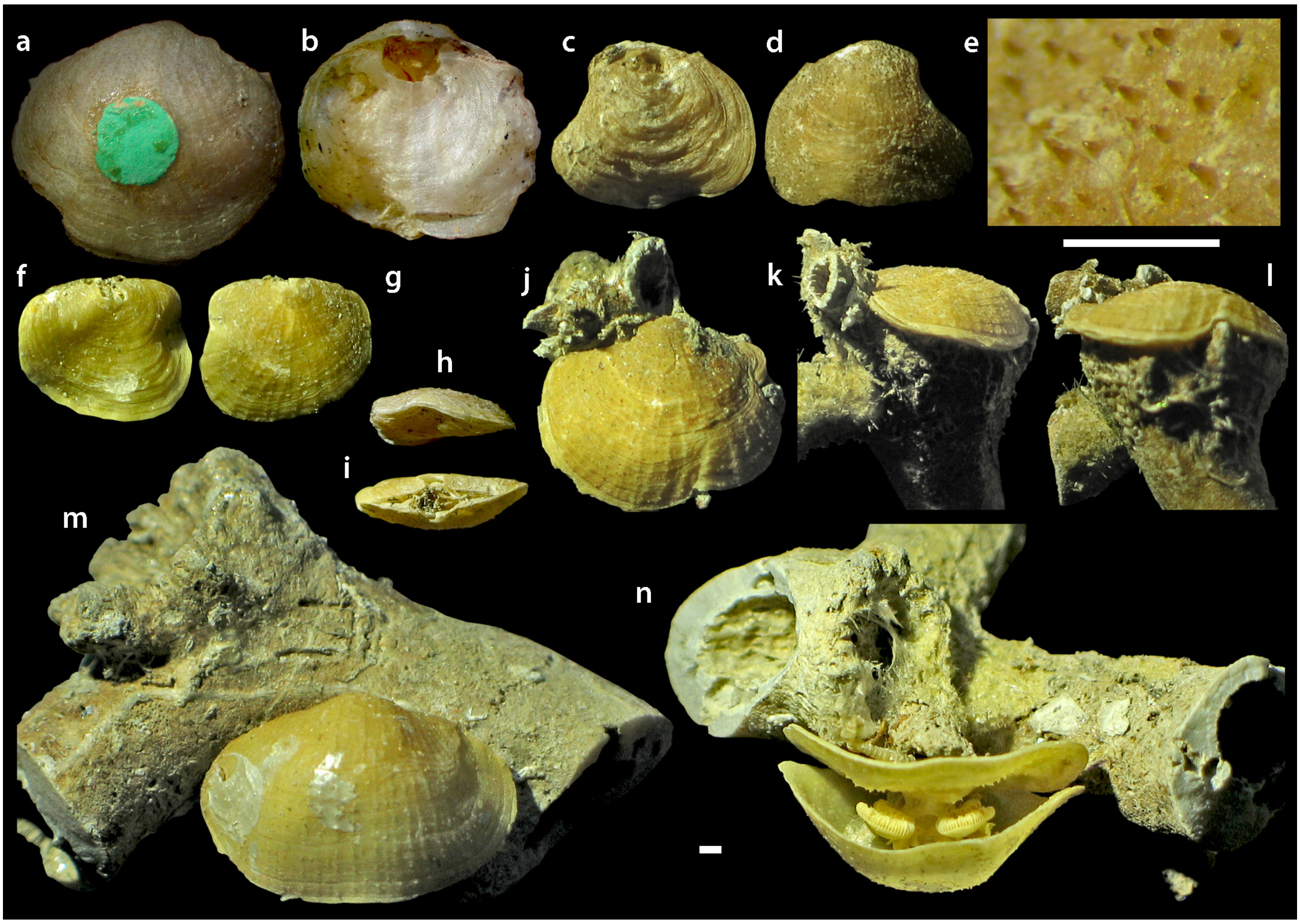

Figure 46. *Megerlia echinata*. **a**: ventral view of specimen in batch BMNH PI ZB 4258–4259, near Tunis, Tunisia, Mediterranean; **b**: dorsal view of specimen in batch BMNH PI ZB 4258–4259, near Tunis, Tunisia; **c–e**: dorsal and ventral views, as well as close-up details of spiny ornamentation on ventral valve of specimen in batch BMNH PI ZB 2721–2723, Sardinia, Italy; **f–i**: dorsal, ventral, lateral (with ventral side up) and posterior views of specimen from batch BMNH PI ZB 4975, southern Celtic Sea, 585–896 m; **j–l**: ventral, lateral (with ventral side up) and anterior views of specimen from batch BMNH PI ZB 4975, southern Celtic Sea, 585–896 m; **m–n**: ventral and anterior views of large specimen from batch BMNH PI ZB 4975, southern Celtic Sea, 585–896 m. Scalebar 1mm. Photos: Jesper Hansen.

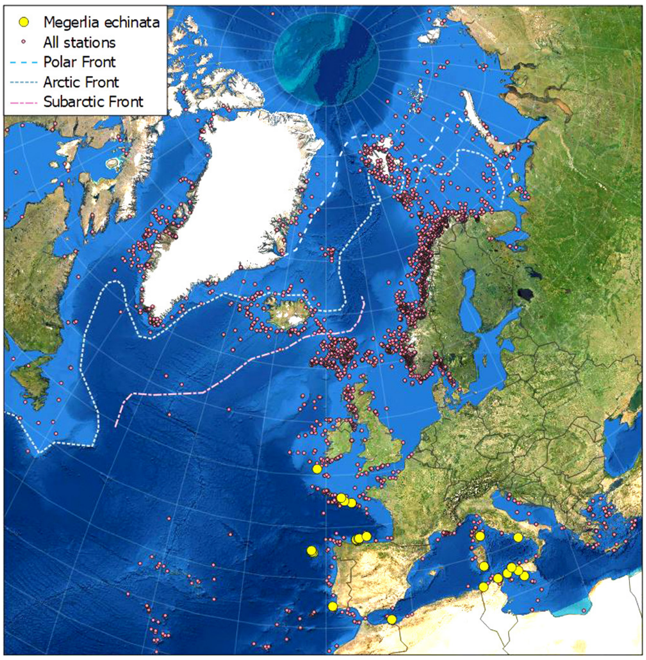

Figure 47. Distribution of *Megerlia echinata*.

Mühlfeldtia echinata Fischer & Œhlert, 1890, p. 73–74.
?*Mühlfeldtia monstruosa* – Fischer & Œhlert (1891), p. 87–90, pl. 7, figs. 12a–c.
Pantellaria echinata – Dall (1919), p. 251.
?*Pantellaria monstruosa* – Dall (1919), p. 251.
Megerlia echinata – Atkins (1961b), p. 89–94.
?*Megerlia monstruosa* – Brunton (1988).

Description: Shell low, ventribiconvex to concavoconvex and typically taking shape after the substrate that the dorsal valve is lying on. Adult specimens transverse oval to subrectangular. Umbo blunt and very broad. Narrow and slightly unisulcate anterior commissure in less deformed adults, but rectimarginate in juveniles. Hinge line straight. Narrow deltidial plates not joined. Very large and subcircular pedicle opening almost entirely located in dorsal valve. Ornamentation on ventral valve of generally widely spaced, unequal, uneven, fine and rather poorly defined costellae with scattered tubercles. Minute alveolate thorns or spines usually on and between costellae, though often unevenly distributed and may be lacking entirely. Surface of dorsal valve usually just marked by coarse growth lines, but very weak and sporadic costellae may occur. Shell matrix endopunctate. Colour yellow or white. Dorsal interior with long brachial loop reaching 2/3 valve length and supported by median septum. Lophophoral filaments approximately as long as or longer than 1/2 shell length. Dorsal septum extending to approximately mid-valve length of shell. Inner surface of valves with radiating lines of tubercles, especially strongly developed in a broad submarginal rim. Maximum shell size 13.5 mm long and 18.5 mm wide.

Depth range: 10–2780 m depth (Koskeridou 2007; Logan 2007). However, after excluding geographically isolated reports and certain misidentifications of the species, the depth range narrows to 128–2780 m, making it a moderately deep- to deep-water species (Koskeridou 2007; Simon *et al.* 2016; Anadón *et al.* 2022).

Temperature range: 9.5–13.6˚C (this study).

Substrate: Attached to corals (*Dendrophyllia ramea* and *Desmophyllum pertusum*) or shells (Costa 1838; Fischer & Œhlert 1891; Massy 1916; Atkins 1961c). This species usually seems to be associated with corals.

Geography: Along the shelf edge of the Celtic Sea and the Bay of Biscay, off Portugal and West Sahara, as well as in the Mediterranean Sea (Jeffreys 1878; Fischer & Œhlert 1890; Massy 1916; Dall 1920; Atkins 1961c; Gaspard 2003). Observations were also reported from Florida, the Caribbean, the Cape of Good Hope, the Red Sea and SE Australia (Dall 1920; Cooper 1981b; Logan *et al.* 2008); however, those from the Red Sea were later recognised as a new species within another genus by Simon *et al.* (2016), while the remainder are more likely representatives of other species.

Remarks: See the above remarks for the genus concerning synonymy for the species. The present study was based mostly on the collection housed at the Natural History Museum of London, including numerous specimens of *M. truncata* and many specimens and even populations assigned to both *M. echinata* and *M. monstruosa.*

Megerlia truncata (Linnaeus, 1767)
Figures 48, 49

Anomia scobinata Linnaeus, 1758, p. 701.
Anomia disculus Pallas, 1766, p. 184, pl. 14, figs. 1a–g.
Anomia truncata Linnaeus, 1767, p. 1152.
Terebratula scobinata – Retzius (1788), p. 14.
Terebratula truncata – Retzius (1788), p. 14.
Criopoderma truncatum – Poli (1795), p. 191–192, 261, pl. 30, figs. 15, 15b.
Terebratula decustata Blainville, 1828, p. 142.
Terebratula disculus – Blainville (1828), p. 140.
Terebratula irregularis Blainville, 1828, p. 140.
Terebratula oblita Michelotti, 1839, p. 22.
Delthyris (*Orthis*) *truncata* – Anton (1839), p. 22.
Orthis oblita – Sismonda (1842), p. 11.
Orthis truncata – Philippi (1844), p. 69.
Terebratella truncata – d'Orbigny (1847b), p. 248, pl. 7, figs. 11, 12, 16.
Megerlia truncata – King (1850), p. 145.
Megathiris oblita – d'Orbigny (1852), p. 94.
Terebratula (*Megerlia*) *truncata* – Lovell (1861), p. 180.
Megerlea truncata – Brusina (1866), p. 47.
Muhlfeldtia truncata – Bayle (1880), p. 240.
Mühlfeldtia truncata –Œhlert (1887), p. 1322.
Mühlfeldtia disculus – Dall (1920), p. 333–334.

Description: Shell resembling *Megerlia echinata* but differs in the following features. Shell low and biconvex with rather sharp dorsal sulcus and corresponding fold in ventral valve. Adult shells

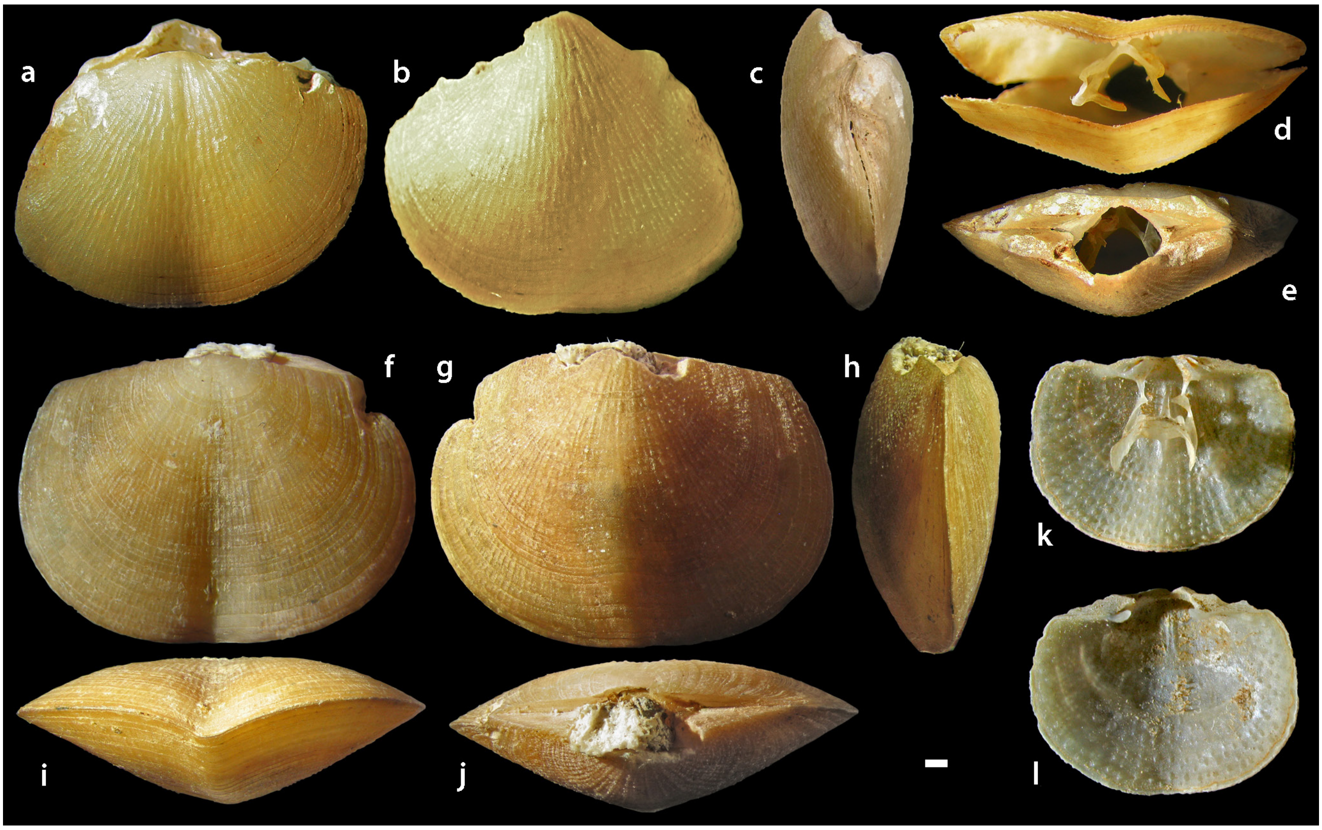

Figure 48. *Megerlia truncata*. **a–e**: dorsal, ventral, lateral, anterior and posterior views of shell, Arenys de Mar, Barcelona, Spain, 30–60 m (JH); **f–j**: dorsal, ventral, lateral, anterior, and posterior views of specimen, Samothraki Island, Greece, 240 m (JH); **k–l**: dorsal and ventral interior views of specimen ZMBN 42048, Penmarch, Brittany, France. Scalebar 1mm. Photos: Jesper Hansen.

with sharply sulcate anterior commissure. Ornamentation of dense, subequal and fine costellate ribs on both valves, typically with low tubercles along rib crests and with growth lines and stops. Higher tubercles can develop posterolaterally on ventral valve. The radiating ornamentation and tubercles are strongest on ventral valve. Tubercles always situated on rib crests. Shell less often markedly deformed from attachment to substrate. Longest filaments in lophophore shorter than half shell length. Maximum shell length 20 mm.

Depth range: 8–1086 m depth (Logan 2007), but since *Megerlia echinata* is broadly synonymised with the species, the range is somewhat uncertain. When restricting to confirmed specimens from the Mediterranean and NE Atlantic region, the range is 16–586 m depth (Fischer & Œhlert 1891; Anadón *et al.* 2022).

Temperature range: 11.5–19°C (Jeffreys 1878; Brand *et al.* 2003).

Salinity range: 37–39 (Brand *et al.* 2003).

Substrate: Attached to corals (*Dendrophyllia corniger*), shells, artificial substrates or rocky substrates (Gray 1853; Atkins 1961c; Koskeridou 2007; Toma *et al.* 2022).

Geography: Coast of Brittany in W France, Bay of Biscay, Portugal, Azores, the Mediterranean, the Canary Islands, and Cap Blanc in Mauritania (Jeffreys 1878; Fischer & Œhlert 1891). The specimen collected by Turton and identified as *Megerlia truncata* from off Torquay/Torbay in S England was, according to Jeffreys (1878), needing verification. However, Dall (1920) maintained the identification. No other specimens appear to have been collected since. Zezina (2014) listed it from the mid-Atlantic ridge Reykjanes Ridge at 58°23'N south of Iceland, which requires verification.

Remarks: When synonymising the two species *Anomia truncata* Linnaeus, 1767 and *Anomia scobinata* Linnaeus, 1758, the name *Anomia scobinata* was mistakenly attributed to Gmelin (1791) (e.g., Dall 1870, 1873). Thus, *Anomia truncata* was given seniority. According to the International Code of Zoological Nomenclature (Article 23) the senior name should normally be given precedence. However, Article 29.3 states that prevailing usage must be followed when the senior synonym has not been used as a valid name after 1899, and the junior synonym has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years. In the present case, the demands for the exception are fulfilled, while the name *A. truncata* Linnaeus, 1767 is given precedence over *A. scobinata* Linnaeus, 1767.

In their study on Kraussinid brachiopods, Simon *et al.* (2016) questioned the worldwide distribution previously attributed to the species and argued that true *M. truncata* are restricted to the Mediterranean and the Lusitanian Province of the Eastern Atlantic.

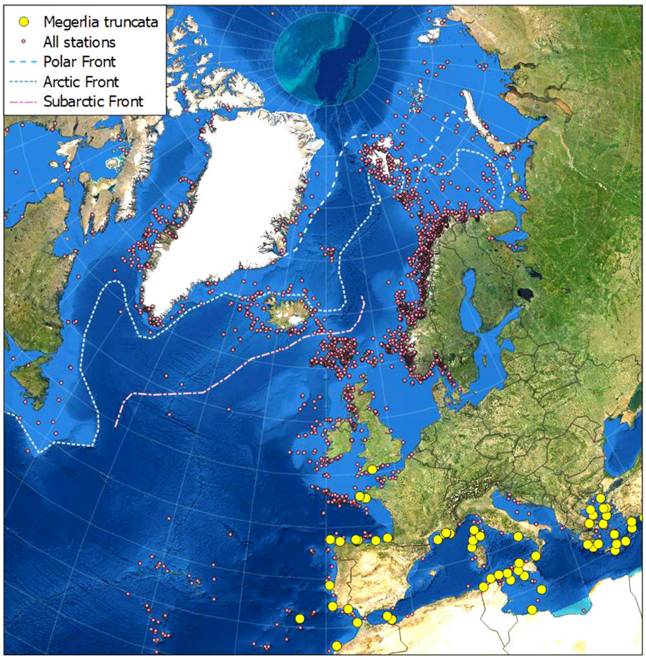

Figure 49. Distribution of *Megerlia truncata*.

Superfamily Terebratelloidea King, 1850
Family DALLINIDAE Beecher, 1893
Subfamily Dallininae Beecher, 1893
Genus *Dallina* Beecher, 1893

Dallina septigera (Lovén, 1846)
Figures 1E, 1G, 50, 51

Terebratula septigera Lovén, 1846, p. 183.
Waldheimia septigera – Gray (1853), p. 59.
Terebratula (*Waldheimia*) *septigera* – Lovell (1861), p. 176.
Waldheimia (*Waldheimia*) *septigera* – Dall (1870), p. 112.
Terebratula (*Waldheimia*) *septata* (Philippi) – Jeffreys (1878) [partim], p. 407–409, pl. 23, figs. 1–1c.
Magellania septigera – Fischer & Œhlert (1891) [partim], p. 64–71.
Dallina septigera – Beecher (1893), p. 382.
Waldheimia (*Macandrevia*) *septigera* – Wesenberg-Lund (1939), p. 203.

Description: Shell longer than wide (L/W ratio: 1.06–1.56; mean: 1.20), and moderately to strongly biconvex. Adult shells with pentagonal to subtriangular outline and widest in anterior portion of shell. Juvenile specimens with egg-shaped outline, though typically with weakly truncated front. Umbo short and stubby in adults, but somewhat narrow in juveniles. Anterior commissure changing from rectimarginate in juveniles, over broadly unisulcate, to distinctly parasulcate in adult specimens. Lateral commissure is straight to gently curved. Shell surface as a rule smooth except for sporadic growth lines, but large specimens can show sporadic radiating weak striation resembling that of *Hemithiris*. Shell white or straw-coloured. Shell matrix endopunctate. Circular, rather large and usually slightly transverse pedicle foramen developed in specimens over 6 mm long, but subtriangular to triangular deltidial plates disjunct in smaller specimens. Deltidial plates not separated from rest of shell by distinct beak ridges, but typically forms a raised ridge along midline when conjoined. Pedicle collar (thickening in pedicle tube) very short and lacking in juveniles. Ventral teeth never supported by dental plates. Hinge plates extended forward to join dorsal median septum in a V-shape. Brachial loop long and with wide transverse band. Brachial loop not attached to median septum on specimens longer than 13 mm. Long and low dorsal median septum reaches 60–84% of valve length, except in juvenile specimens, and visible as a whitish knife-cut line on dorsal valve exterior. Juvenile specimens below 1.65 mm long lack dorsal median septum. A short septum with dot-shaped basis later evolves, which very soon becomes knife-cut shaped. Spicules in tissue mostly absent. Maximum shell length 45 mm.

Depth range: 37–1800 m depth (Fischer & Œhlert 1892; this study), but common between 180–800 m.

Figure 50. *Dallina septigera*. **a–d**: dorsal, ventral, lateral and anterior views of large specimen TSZBr 2410, Trondheimsfjord in Trøndelag, Norway; **e**: dorsal view of specimen, Norwegian Sea at Nordland, Norway, Mareano 2012106 st. R821-16, 553–559 m, the Arctic University Museum of Norway; **f–i**: dorsal, ventral, lateral and anterior views of specimen TSZ 3004 (APN), Norwegian Sea at Trøndelag, Norway, 298 m; **j**: ventral exterior view of shell NHMD-656590; **k–m**: dorsal interior and oblique views of the same, and hinge region view of ventral valve of empty shell TSZ 3181, Norwegian Sea at Nordland, Norway, Mareano 2012106 st. R821-16, 553–559 m; **n–o**: lateral and dorsal interior views of small shell with preserved brachidium still attached to median septum, TSZ 3209 (APN), Haltenbanken in Norwegian Sea at Trøndelag, Norway, 347 m; **p–t**: dorsal, ventral, lateral, posterior and anterior views of juvenile specimen TSZ 3207 (APN), Norwegian Sea at Vestland, Norway, 307 m. Solid scalebar 1mm and segmented scalebar 5mm. Photos: Jesper Hansen.

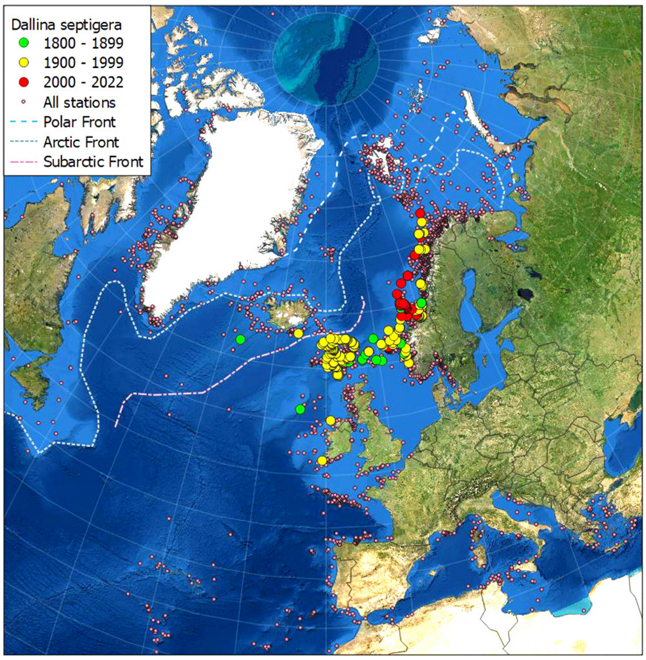

Figure 51. Distribution of *Dallina septigera*. Colours mark which century the specimens were collected in. Irish specimens require verification.

Temperature range: -1.1–10.2˚C (Carpenter *et al.* 1869; Jeffreys 1878).

Salinity range: 34.9–36 (Thomsen 2001; Brand *et al.* 2003).

Substrate: Attached to sand, gravel, corals, shells, bryozoans, serpulid tubes or Foraminifera (Atkins 1960a; Thomsen 2001; this study). Sea bottom varies from silt- and sand-dominated to stony (Thomsen 2001).

Geography: Southwestern-most Barents Sea and south along the Norwegian coastline to Hordaland, northernmost North Sea, NE Atlantic S of Iceland, and along the W part of the British Isles (Lovén 1846; Fischer & Œhlert 1891, 1892; Wesenberg-Lund 1939, 1941; Atkins 1960a; Thomsen 2001; this study). The southern border of the species is uncertain since the southernmost verified specimen is from Scotland. However, *Dallina septigera* seems to be absent from the southern margin of the Celtic Sea.

Remarks: In his original description of *Dallina septigera*, Lovén (1846) did not provide illustrations. Likely for this reason, subsequent researchers simply assumed French and Spanish specimens belonged to the same species and adjusted the species description accordingly. In contrast to the strongly triangular outline of the following species, the true *D. septigera* is normally subpentagonal in outline. The geographical boundary between the two species appears to be on the W side of Great Britain. In her redescription of *D. septigera*, Atkins (1960b) did not realise that the genus included two European species, and thus based her redescription almost solely on the material of *Dallina lusitanica* n. sp., assuming the differences between the single available Norwegian specimen and the remaining material were intraspecific differences. In his study on material from France, Cooper (1981a) stated that the species could usually be distinguished from the morphologically close species *Fallax dalliniformis* by its triangular shape with its greatest width at the front when compared to the typically more subpentagonal outline with its greatest width a bit further back on the other species, thus showing that the specimens from France were representatives of the new species and not *D. septigera*.

A comparison with *Fallax dalliniformis* is provided in the discussion of that species.

Subadult and juvenile specimens are often mistaken for *Macandrevia cranium* but are distinguished by the earlier development of the dorsal median septum (which rapidly becomes long) and by the absence of bordering ridges along the deltidial plates.

There are presently no indications that this species is negatively influenced by ongoing ecological changes within the Norwegian region.

Dallina lusitanica n. sp.

Figures 52, 53

Terebratula septata – Jeffreys (1878) [partim], p. 407–409.
Magellania septigera – Fischer & Œhlert (1891) [partim], p. 64–71, pl. 4, figs. 9a–9ab; pl. 5, figs. 9ac–9ah.
Magellania septigera – Joubin (1907), p. 7–8.
Dallina septigera – Atkins (1960a) [partim], p. 91–99, 1a–d, 3a–d.
Dallina septigera – Brunton & Curry (1979) [partim], p. 55, fig. 28.
Dallina septigera – Cooper (1981a), p. 23–24, pl. 2, figs. 41–43.
Dallina septigera – Anadón (1994), p. 74, pl. 3, figs. 3–5.
Dallina septigera – Logan (1998), p. 558, figs. 4h–n.
Dallina septigera – Gaspard (2003), p. 297–299, figs. 5(10), 6(1–10).
Dallina septigera – Anadón *et al.* (2022), p. 7–8, figs. 3d–e.

LSID: zoobank.org:act:0AB0E914-2A5A-4E48-B671-979AF4B0EC92

Type locality: Southernmost Celtic Sea, off France, 47°11'–47°14'N, 6°11'–6°13'W, 1143 m depth.

Etymology: After the Lusitanian marine region of the temperate Northern Atlantic realm, in which the species mostly occurs.

Diagnosis: Moderately large *Dallina* species. Mature specimens characterised by their typically strongly subtriangular outline with greatest width close to anterolateral corners. Lateral commissure distinctly curved and anterior commissure gently to moderately parasulcate. Dorsal septum extended to approximately 80–90% of valve length.

Material: Holotype: Celtic Sea, 47°11' – 47°14'N, 06°11' – 06°13'W, 1143 m depth, one specimen, BMNH PI ZB 4948. Paratypes: Celtic Sea, 47°37'N, 07°27'W, 722 m depth, eight specimens, BMNH PI ZB 4955–4962; Celtic Sea, 48°06' – 48°26'N, 09°18' – 09°44'W, 977 m depth, one juvenile ventral valve, BMNH PI ZB 4946; Celtic Sea, 48°32' – 48°33'N, 10°09' – 10°10'W, 686–896 m depth, 14 specimens BMNH PI ZB 4944–4945, 4951–4953, 4963, 4967–4969, 4972, 4973, 4977; Celtic Sea, 48°38' – 48°39'N, 09°45' – 09°50'W, 933–1061 m depth, one specimen, BMNH PI ZB 4970; ?Celtic Sea (from study material of D. Atkins), seven specimens, BMNH PI ZB 4953, 4964–4966, 4971, 4976; Celtic Sea, 47°11' – 47°14'N, 06°11' – 06°13'W, 1143 m depth, one damaged ventral valve kept together with holotype.

Description: Shell moderately to strongly biconvex. Outline variable, but adult shell normally with subtriangular to strongly triangular outline, and widest typically at or very close behind anterolateral corners. L/W ratio 0.94–1.37 with mean of 1.15. Juvenile specimens with more egg-shaped outline. Umbo short and stubby. Anterior commissure changing from rectimarginate in juveniles, over broadly unisulcate, to strongly parasulcate. Lateral commissure usually moderately curved in adults. Anterior part of dorsal valve typically with two very pronounced folds along the flanges. No

Figure 52. *Dallina lusitanica* n. sp. **a–e**: dorsal, ventral, lateral, anterior, and posterior views of holotype BMNH PI ZB 4948, southernmost Celtic Sea, France, 1143 m; **f–k**: dorsal, ventral, lateral and anterior views, and interior views of dorsal and ventral valves of specimen BMNH PI ZB 4953; **l–q**: dorsal, ventral, lateral and anterior views, and interior views of dorsal and ventral valves of specimen BMNH PI ZB 4970, Celtic Margin, Celtic Sea, 933–1061 m; **r–w**: dorsal, ventral and lateral views, and interior views of dorsal and ventral valves of specimen BMNH PI ZB 4971; **v–ab**: dorsal and ventral views, dorsal and ventral valve interior, and lateral and anterior views of specimen BMNH PI ZB 4966; **ac**: dorsal interior view of specimen in batch BMNH PI ZB 4953; **ad**: dorsal interior view of specimen in batch BMNH PI ZB 4967–4968, Celtic Sea, 686–896 m; **ae**: dorsal interior view of specimen in batch BMNH PI ZB 4945, Celtic Sea, 686–896 m. Segmented scalebar 5mm. Photos: Jesper Hansen.

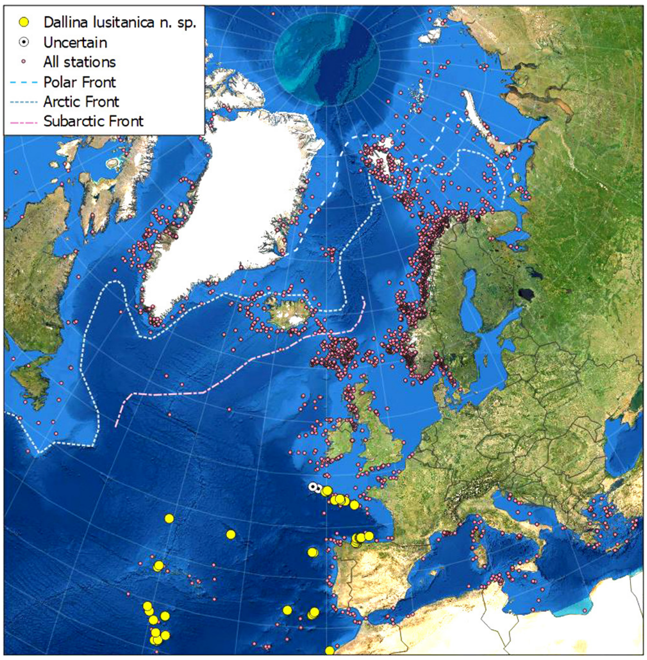

Figure 53. Distribution of *Dallina lusitanica* n. sp. ‘Uncertain’ are unverified *Dallina* specimens that likely belong to this species.

ornamentation besides growth lines. Shell somewhat translucent, fragile and white with a thin yellowish periostracum often peeling in stored specimens. Shell matrix endopunctate. Egg-shaped subcircular and rather large pedicle foramen. Deltidial plates fused to form a symphytium, often with a raised longitudinal ridge. Deltidial plates well-defined, but not separated from rest of valve by ridges. Pedicle collar (thickening in pedicle tube) very short. No dental plates supporting ventral teeth. Descending lamellae of brachial support thin and gently diverging and joined by broad transverse band to form a long loop. Brachial loop not attached to median septum at least on specimens longer than 17 mm. Long and low dorsal median septum usually extends to 80–91% of valve length (a few dorsal valves below 21 mm length with septum down to 51% of valve length), and always visible as a whitish knife-cut line on dorsal valve exterior. Spicules in tissue mostly absent. Maximum shell length 30 mm.

Depth range: 460–3000 m depth (Logan 1998; Anadón *et al.* 2022), but mostly between 600–1500 m.

Temperature range: Based on three stations 7.0–9.5˚C (this study).

Substrate: Typically found on mud- or fine sand-dominated bottoms, very often in connection with hard corals and coral debris, where it is found attached to corals, shells, gravel and stones (Joubin 1907; Anadón 1994; Anadón *et al.* 2022; this study).

Geography: Celtic Sea, Bay of Biscay, NE Atlantic, Portugal, Azores and Canary Islands. This species most likely has its northern border at the Celtic Sea, but a systematic examination of the Irish *Dallina* specimens is required to clarify this.

Remarks: *Dallina lusitanica* n. sp. is smaller and more fragile, subtriangular to strongly triangular with the greatest width typically at or close to the anteroventral corners, and with distinctly curved lateral commissure in contrast to *Dallina septigera*, which is more solid, pentagonal to subtriangular with the greatest width mostly located well behind the anterolateral corners, and with the main part of the lateral commissure nearly straight.

Among the 10 species included in the genus, this new species most closely resembles *Dallina floridana* (Pourtalès, 1868) and *Dallina triangularis* Yabe & Hatai, 1934. However, the approximately 28 mm long species *Dallina floridana* (known from Florida, the Gulf of Mexico and the West Indies) is generally as wide or wider than long, with the dorsal septum reaching 64–76% of valve length, anterior commissure more strongly parasulcate and a ventral umbo that is more strongly curved. Based on descriptions and five new shells from the Philippines’ Balut Island housed at the Arctic University Museum of Norway, the up to 32.5 mm long *Dallina triangularis* known from Japan, the South China Sea and Fiji differs by having a shorter dorsal septum reaching 70–80% of valve length, typically being much more strongly parasulcate, with a shell matrix markedly thinner around the foramen, dorsal umbo markedly more acute and lateral ridges on ventral valve diverging increasingly at the front on adult shells, giving the valve a bell-shaped outline (Yabe & Hatai 1934; Hatai 1940; Bitner 2008, 2019; this study).

Atkins (1960b) redescribed *Dallina septigera* largely based on the material of the present species whilst assuming the observed variations were intraspecific. Also, Cooper (1981a) and Anadón *et al.* (2022) used the diagnostic external features of the new species to distinguish what they thought were *D. septigera* from the morphologically close species *Fallax dalliniformis*, suggesting *D. septigera* is at least nearly absent from France and N Spain. To date, there appears to be very little, if any, overlap in the geographical ranges of these two species.

Superfamily Kingenoidea Elliot, 1948
Family AULACOTHYROPSIDAE Dagys, 1972
Subfamily Babukellinae MacKinnon, Smirnova & Lee, 2006
Genus *Fallax* Atkins, 1960a

Fallax dalliniformis Atkins, 1960a

Figures 54, 55

Fallax dalliniformis Atkins, 1960a, p. 71–89, pl. 1, figs. 1–5.

Description: Shell inflated biconvex. Outline of adult shells triangular to distinctly truncated subpentagonal and widest close to front. Small specimens with more egg-shaped outline. Ventral umbo beak-shaped, curved and acute in profile. Anterior commissure normally parasulcate. Shell surface marked by growth lines. Shell matrix endopunctate. Colour whitish to slightly brownish, but older shells often with brownish secondary colour. Deltidial plates disjunct in specimens below 10 mm long, but then joining and restricting pedicle opening to a relatively small and egg-shaped foramen. Long pedicle collar (raised shell matrix in umbo). Short dental plates supporting strong hinge teeth. Hinge plates not extended forward to form a V-shape at connection with dorsal median septum but meet it in a right angle or with median indention. Long brachial loop with wide transverse band and supported by median septum. Long, low dorsal median septum reaching to 2/3–15/16 valve length and always visible as whitish knife-cut line on dorsal valve exterior. Abundant spicules in soft tissue (can disappear when stored too long in ethanol). Maximum shell length 29.7 mm.

Depth range: 702–2100 m depth (Anadón 1994; Anadón *et al.* 2022). Although Brunton & Curry (1979) gave a depth range starting

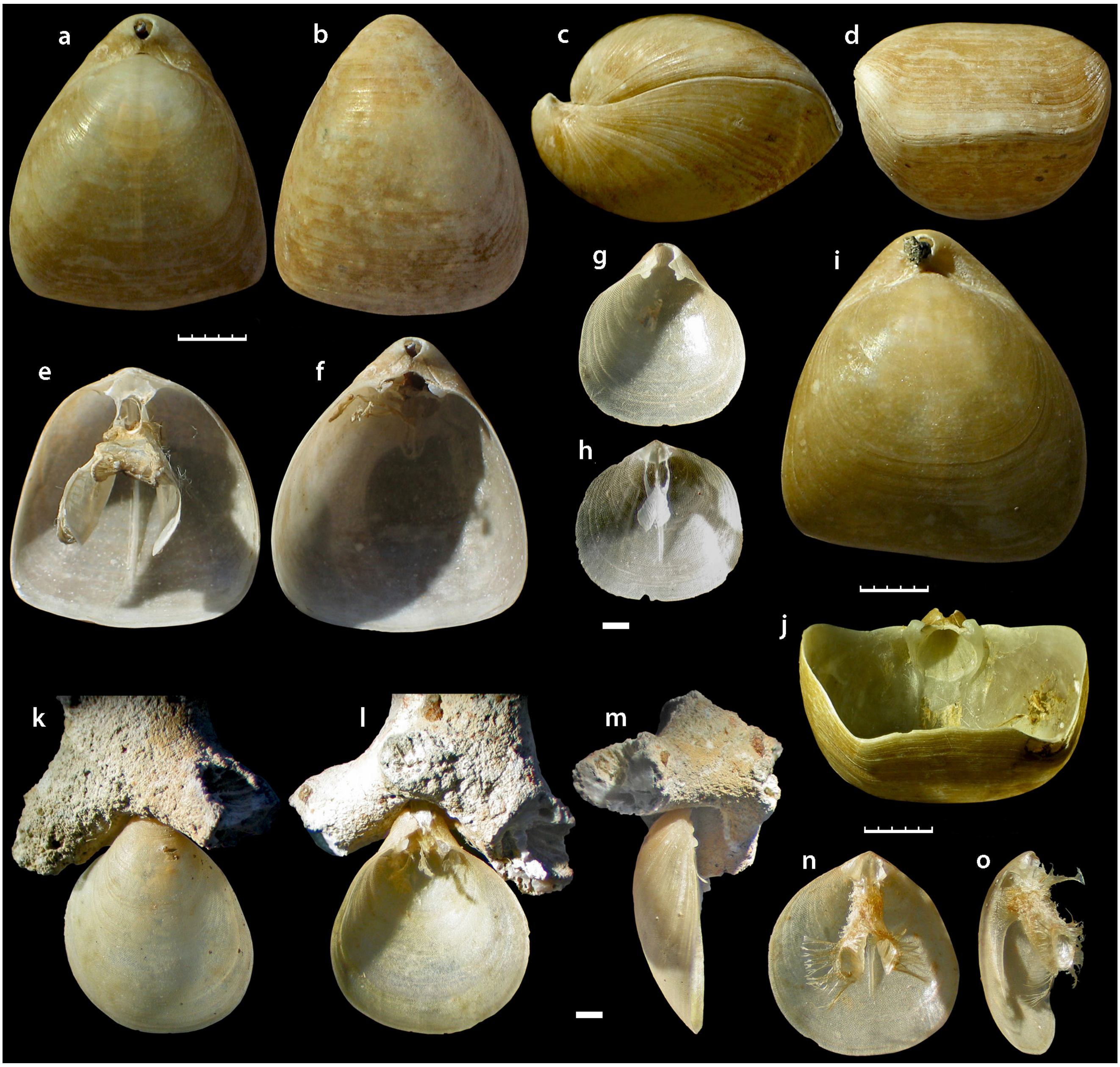

Figure 54. *Fallax dalliniformis*. **a–f**: dorsal, ventral, lateral and anterior views, and dorsal and ventral interior views of holotype BMNH PI ZB 2988, Celtic Sea, Great Britain, 1060–1245 m; **g–h**: ventral and dorsal interior views of small specimen BMNH PI ZB 2987, Celtic Sea, Great Britain, 933–1006 m; **i**: dorsal view of specimen BMNH PI ZB 2990, Celtic Sea, France, 722 m; **j**: oblique view of dental plates and pedicle collar of specimen BMNH PI ZB 2991, Celtic Sea, Great Britain, 990–1190 m; **k–o**: inner, outer and lateral views of ventral valve, and inner and oblique lateral views of dorsal valve of small specimen BMNH PI ZB 790, Celtic Sea, Great Britain, 977 m. Solid scalebar 1mm and segmented scalebar 5mm. Photos: Jesper Hansen.

from 210 m, the origin of that figure is uncertain.

Substrate: Attached to rocks, shells or corals (Atkins 1960a).

Geography: Celtic Sea and Bay of Biscay (Atkins 1960a).

Remarks: This species is externally very similar to the two *Dallina* species. However, the ventral umbo is curved and beak-shaped with an egg-shaped foramen, the pedicle collar is long, the ventral hinge teeth are supported by dental plates and the brachial loop is always supported by the median septum.

Juvenile specimens may easily be confused with the species *Glaciarcula spitzbergensis*, which has previously led to the assumption that this subarctic and Arctic species was present in waters around Spain and the Scilly Isles (see discussion for *Glaciarcula spitzbergensis*). However, juveniles of *Fallax dalliniformis* can be externally distinguished by a less elongated pedicle opening, broader outline with the early development of anterior truncation, and thinner shell wall.

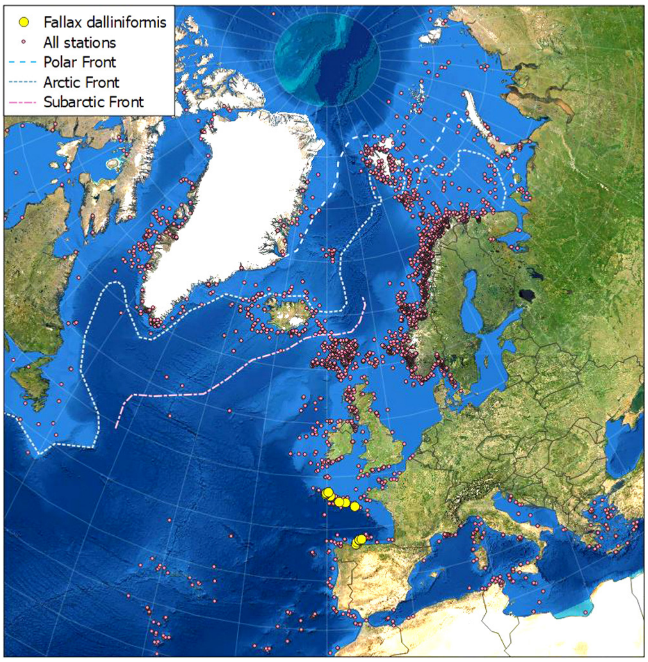

Figure 55. Distribution of *Fallax dalliniformis*.

DISCUSSION

Diversity and abundance in Norwegian waters

To date, 10 brachiopod species have been collected live in Norway, Svalbard and Jan Mayen. Of these, nine live along the Norwegian coast while *Arctosia arctica* is restricted to Jan Mayen. The five most common species; *Macandrevia cranium* (55%), *Terebratulina retusa* (17%), *Hemithiris psittacea* (11%), *Terebratulina septentrionalis* (8%) and *Novocrania anomala* (5%), make up 95% of the specimens examined and/or reported in published studies. Of the remaining five species, *Dallina septigera* was the most common (4%), followed by *Glaciarcula spitzbergensis* (1%), *Argyrotheca cistellula* (0.2%), and *Cryptopora gnomon* and *Arctosia arctica* (both with < 0.1%). However, there is little doubt that the relative frequencies are biased by sampling methods since most samples were taken from areas dominated by soft-bottom substrates in coastal regions such as fjords. The species *Novocrania anomala* typically lives cemented to bedrock (Figure 5) and is thus less likely to appear in benthic samples than most of the other species. Based on unpublished visual surveys, there seems to be a bathymetric zone at approximately 100–200 m depth with very high densities of *Novocrania anomala* along the Norwegian coastline, suggesting that this species is strongly underrepresented in the above figures.

The relative abundances of the different species show a distinct warmer- to colder-water gradient, which is visualised here through pooled specimen numbers from Norway, Svalbard and Jan Mayen (Figure 56). Although *Macandrevia cranium* is the most abundant species overall, *Terebratulina retusa* is becoming an increasingly more important part of the fauna southward and the more abundant species along the warmer and generally more terrestrially influenced coastline of SW and SE Norway. This trend continues south to the British Isles, where Brunton & Curry (1979) found that *Terebratulina retusa* and *Novocrania anomala* were the two most abundant species. As illustrated and discussed by Thomsen (1990), in the northward direction, *Hemithiris psittacea* takes over completely as the most abundant species when entering areas influenced by Arctic water masses, represented here by the regions around Svalbard and Jan Mayen.

In addition to the above species, the minute shallow-water species *Gwynia capsula* has been found as a subfossil in deposits of the Holocene warm optimum at the Oslofjord in southern Norway (Sars 1865) and is presently known to have its northern boundary along the coasts of Great Britain, Belgium and the Netherlands (Logan *et al.* 1997; Francis *et al.* 2011). The species is typically overlooked in classical surveys due to its small size (maximum length 1.5 mm) and restriction to shallow water. Combined with its known distribution, this fact makes it likely that a living population still may occur along southern Norway.

Another species that has not been found in Norway thus far but is very likely present is the deep-water species *Pelagodiscus atlanticus*. Living on the continental slope or deeper, this species was collected live from just south of Iceland and also represented by an empty shell from the Arctic Ocean (Wesenberg-Lund 1941; Zezina 1997a, 2014).

Platidia anomioides is another species that, if not already present offshore along southern Norway, is expected to be found in the near future since it lives close to the Faroe and Shetland islands (Carpenter *et al.* 1869; Thomsen 2001; Figure 43).

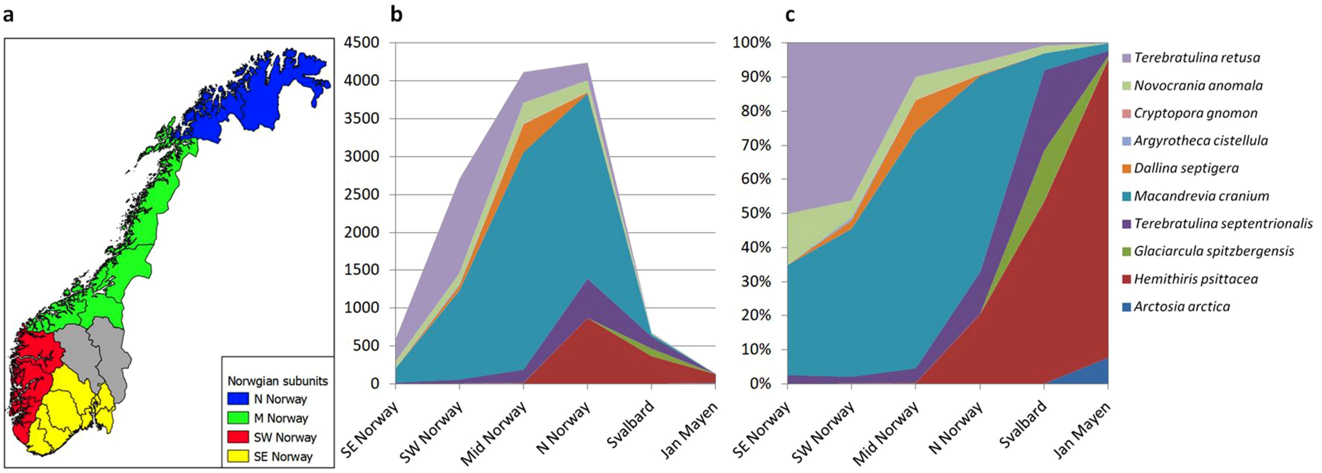

Figure 56. **a**: subdivision of Norway for an overview of abundance trends along the Norwegian coastline; **b**: actual numbers of specimens on which the study is based from along Norway, Svalbard and Jan Mayen; **c**: pooled relative abundances of the brachiopod species from Norway, Svalbard and Jan Mayen.

Main trends in the biogeography of Norwegian and adjacent brachiopods

Part of the present study aimed to provide a better overview of brachiopod species distributions by revisiting museum collections combined with examinations of new material. Many specimens on which previously published studies are based are now lost or located at other institutions than those visited. Still, the examination of those available did result in distributional adjustments and clearer borders for several species.

Water masses and temperature:

As also noted by Thomsen (2001), the 'shallow-water' species generally show a good correlation with water masses; however, it is worth noting that species seemingly associated with the Atlantic water masses often also seem to thrive in coastal environments with markedly different water chemistry. Most of the species are either directly or indirectly linked to temperature variations, as illustrated by comparing the species distributions with the roughly drawn borderlines (or oceanic fronts) between the various surface water masses, with the flow of warmer water coming up along the Norwegian coastline and the cold water masses flowing southwards along the eastern coastline of Greenland. This link to water temperatures was previously highlighted by authors such as Wesenberg-Lund (1941) and Thomsen (2012) for the transatlantic and Arctic species, and very recently by Ye *et al.* (2021) in their study on the global biogeographic patterns of brachiopods. Ye *et al.* (2021) concluded water temperature in combination with the North Atlantic gyre were major contributors to the modern biogeography of the North Atlantic brachiopods, bringing the species north along the European coastline and then across to Greenland and southward along North America. Due to the high level of shared taxa, their global analysis did not manage to subdivide the Mediterranean and NE Atlantic to Arctic brachiopod fauna into distinct units despite massive temperature differences within the region. Nonetheless, by comparing the distribution maps of the present study, there is a strong faunal boundary just south of the British Isles, where at least 11 species have their northern border and two have their southern border.

The two deep-water species *Pelagodiscus atlanticus* and *Cryptopora gnomon*, for which there exist moderately good distribution data, are influenced by the deep bottom-water masses and have much broader distributions that are disconnected from the distributions of the surface water masses. The newly discovered species *Xenobrochus islandicus* occupies both abyssal and shelf environments influenced by the warm Irminger Current. Therefore, this species is likely to have a much wider distribution than that mapped thus far. Other better-known semi-deep-water species such as *Macandrevia tenera*, *Hispanirhynchia cornea*, *Eucalathis ergastica*, *Eucalathis tuberata*, *Platidia anomioides*, *Dallina lusitanica*, *Dallina septigera* and *Fallax dalliniformis* show distributions more strongly resembling those of the surface water masses.

Substrate:

When it comes to the substrate as a factor governing the distribution of brachiopod species, it appears that all the temperate and cold-water species living in the Nordic and Arctic seas are generalists since none of them showed strong preferences for any specific type or size of the substrate as long as it had a hard surface to settle on (e.g., Figure 57). For each species, the dominant choices of substrate for settlement were found to be locality dependent, which more likely illustrates the dominant type of hard substrate at a given site rather than active selection by the brachiopods. This point is congruent with observations of generalist species by Richardson (1997a). In a study on substrate relationships for brachiopods around the Faroe Islands WSW of Norway, most specimens were found to have settled on stones (Thomsen 2005). This result most likely reflects the composition of available hard substrates around these islands.

Figure 57. Example of substrate choice, with juvenile *Terebratulina* sp. TSZ 3205 (APN) attached to Foraminifera that is attached to the periostracal bristle of the bivalve *Modiolula phaseolina*. Scalebar 1mm. Photo: Jesper Hansen.

Salinity:

In general, there is little available knowledge about the tolerance of brachiopod species to various salinity regimes since salinity data seldom are collected with brachiopods (Richardson 1997a). As far as possible, this information has been added for the species treated here, both based on literature research and new material. However, since most of the data are from northern Norway, the upper salinity limit is likely significantly higher for many of the species. Indirect information on relative tolerance to low salinity can also be extracted from studies on the geographic distribution of species. For the Norwegian brachiopods, the seaway confined by Norway and Sweden

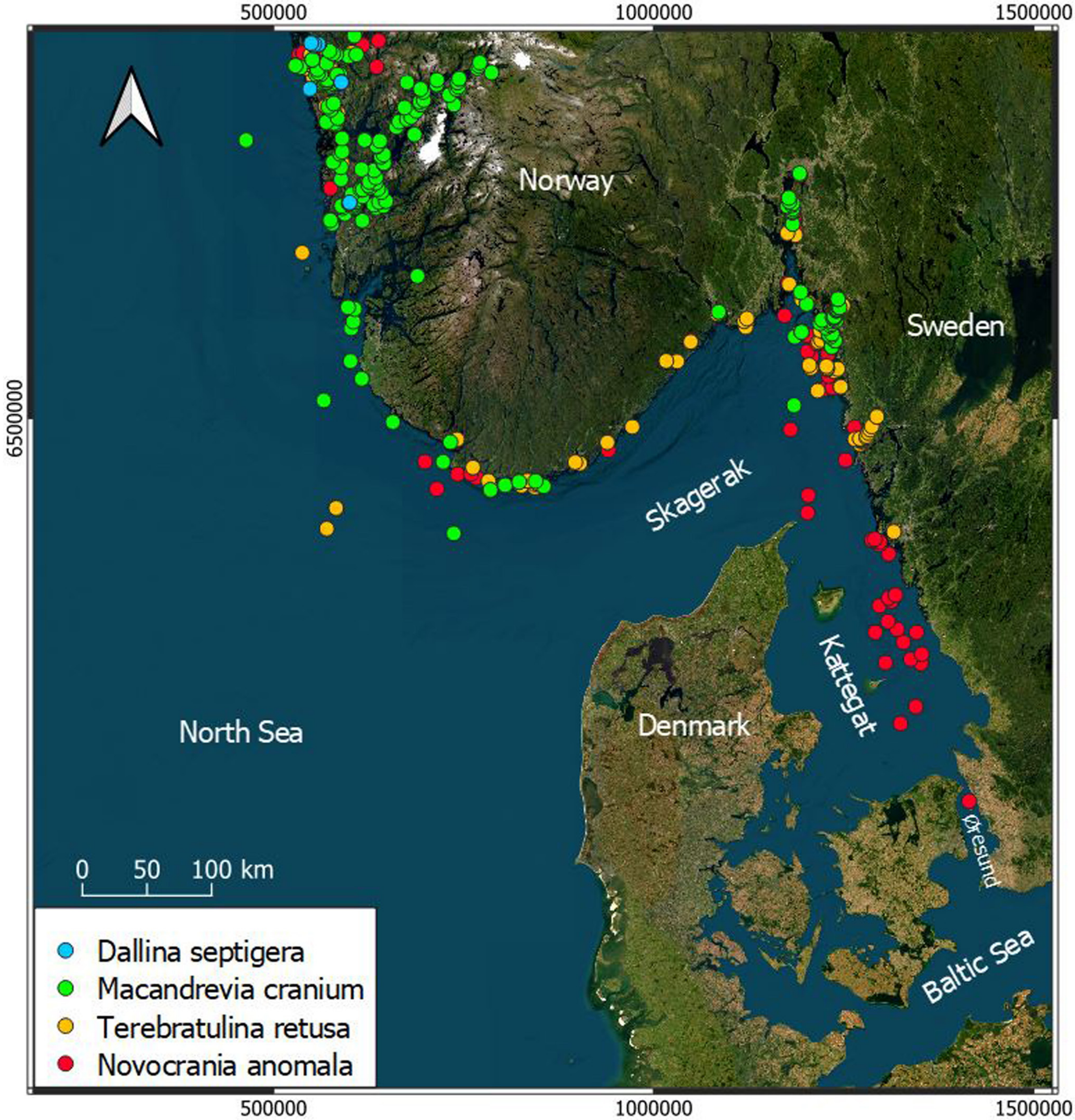

Figure 58. Distribution of four brachiopod species in the North Sea, Skagerak, Kattegat and Øresund.

on one side and Denmark on the other, which connects the low-salinity Baltic Sea with the North Sea, is a good place for such a study (Figure 58). There, *Novocrania anomala* extends into Øresund, the innermost part of the seaway before the Baltic Sea, while *Terebratulina retusa* reaches just into the outer part of the more saline Kattegat, and *Macandrevia cranium* is found no further in than the outermost part of the seaway, at Skagerrak and the Oslofjord. In comparison, *Dallina septigera* seems to be entirely restricted to normal saline environments with its lower salinity limit at 34.9. The Arctic species *Hemithiris psittacea* is also tolerant to low salinity, being encountered in water with only 26.2 salinity.

Response to organic enrichment:

Like most sedentary, filter-feeding organisms, most brachiopod species are sensitive to sedimentation and the influx of organic matter since they are unable to escape and their filtering system cannot handle high particles loads (e.g., Zezina 2008). Based on the available dataset, it was possible to observe the impact of organic enrichment on the distribution of the brachiopods. Pooling all the species provided 677 data points with information on the impact of organic enrichment. Approximately 90% of live specimens were collected from environments with normal background levels or very slightly raised levels of organic enrichment, while approximately 10% of the samples (or 8% of 1767 specimens) were from environments with lightly increased organic enrichment. Only four (0.2%) live specimens were taken from environments with moderate organic enrichment. For comparison, the mean division of impact levels for the sampled localities involved approximately 70% of samples being classified as showing no or very low organic impact, 17% showing lightly heightened impact and 14% showing a moderate or higher impact on the marine benthic fauna. This suggests that brachiopods do not survive long in environments that are experiencing significant organic enrichment. Rhynchonelliformean brachiopods, and thus most of the Norwegian brachiopod species, only have a very short free-swimming larval stage of a few hours or up to two days before settlement, thus limiting their spreading ability (Richardson 1997b). Therefore, it cannot be excluded that increased densities of organic waste sources from human activities in marine environments may have a long-term negative impact on the rarer or patchily distributed species. On the other hand, brachiopods typically have a short generation time of approximately 3–4 years (Rickwood 1977; Curry 1982; Buening & Carlson 1992). Therefore, it is to be expected that most species will resettle fairly quickly after organic enrichment lowers to normal background levels, as long as populations exist nearby and suitable substrate is available.

Responses to climate changes

Studies by Thomsen (1990) and Curry & Endo (1991) have shown that at least some brachiopod species, like *Macandrevia cranium* and *Terebratulina retusa*, responded to climatic changes at the end of the last ice age by rapidly migrating north as the warm Northeast Atlantic current started flowing up along Norway.

These studies certainly open the question of whether this northward migration continues. Dividing the dataset of each of the more abundant species according to what century they were collected in does not reveal any undisputable large-scale biogeographic changes. Uneven sampling across space and time conceals smaller-scale changes to a great extent. However, three species show some possible ongoing shifts.

Despite a number of prominent scientific cruises at Svalbard in the late 19th century, all 15 samples and records of *Novocrania anomala* encountered during this study are from more recent years, thus opening the possibility that the species has spread further northward over the last century. However, their absence in older samples can just as likely be due to insufficient sampling methods.

The subarctic to Arctic species *Hemithiris psittacea* appears to have been retreating slightly northward along the Norwegian coastline over the last century since no live specimens appear to have been collected south of 69.2°N in Troms after 1923 despite many sampling stations, while it was collected from several more southern localities south to 67.6°N in Nordland before that.

Glaciarcula spitzbergensis is also possibly retreating northward, and it cannot be excluded that it no longer lives in the north Norwegian fjords.

CONCLUSIONS

Overall, 26 brachiopod species are recorded in the region from the Arctic Ocean and south to the North Atlantic from E Canada in the west and to the Celtic Sea in the East. Two of these, *Dallina lusitanica* n. sp. and *Xenobrochus islandicus* n. sp., are new to science. The NE Atlantic *D. lusitanica* has been confused with *D. septigera* but differs by its triangular outline and curved lateral commissure, among other features. The NW Atlantic species *Xenobrochus islandicus* n. sp. has so far only been found at five stations within and at the margin of the Irminger Sea SW of Iceland. The genus *Xenobrochus* includes 10 previously described species and is essentially restricted to the southern hemisphere, with the mid-western Atlantic having the closest record.

Of the above transatlantic to Arctic species, 10 were found living around Norway, including the Arctic Svalbard and Jan Mayen, while *Gwynia capsula*, *Pelagodiscus atlanticus* and *Platidia anomioides* are likely to also be present. *Macandrevia cranium* was the species most commonly encountered in samples along Norway, though with *Terebratulina retusa* being more common in the south, and *Hemithiris psittacea* replacing it in the Arctic. *Novocrania anomala* was more rarely encountered in samples, likely because it typically lives attached to vertical cliffs, making it difficult to sample.

Despite being named as Arctic species, *Hemithiris psittacea* and *Glaciarcula spitzbergensis* have been broadly reported from the mid-Norwegian Trondheim, SW Norwegian Bergen, the Faroe Islands, Scotland, Ireland and the Celtic Sea. However, a review of the literature combined with the examination of material stored at Nordic and London natural history museums does not support reports of their occurrences in more southern areas.

In general, the distributions of the shelf and coastal species strongly match the temperature gradients of the surface water masses, overriding the differing water chemistries of the water masses. However, the distributions were also found to correspond to variations in salinity and depth. A strong biogeographic border is observed just south of the British Isles, separating a highly diverse southeastern brachiopod fauna from a significantly less diverse boreal to Arctic fauna in the north and west.

On local scales, the studied brachiopods are associated with environments that have low organic enrichment.

The three species *Glaciarcula spitzbergensis*, *Hemithiris psittacea* and *Novocrania anomala* may have shown ongoing northward shifts in their biogeographic boundaries over the last two centuries. However, more systematic sampling is required to verify these possible changes.

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