

Some bathyal and abyssal Thyasiridae from the Faroe-Shetland Channel and Rockall Trough: new species and new genera

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Abstract. Some bathyal Thyasiridae from the Faroe-Shetland Channel and Rockall Trough in the North-East Atlantic are described. Four new genera are introduced for species formerly included in *Thyasira* s.s. namely, *Rhombaxinus* gen. nov. with type species *Cryptodon equalis* A.E. Verrill & K.J. Bush, 1898, *Thyasirella* gen. nov. with type species *Cryptodon obsoletus* A.E. Verrill & K.J. Bush, 1898, *Cryothyas* gen. nov. with type species *Axinus flexuosa* var. *rotunda* Jeffreys, 1881, and *Odontothyas* gen. nov. with type species *Axinus succisa* Jeffreys, 1876. The generic status of *Mendicula* is discussed and *M. oblonga* (Monterosato, 1880) is transferred to *Adontorhina*. Comparisons with related taxa from across the entire North Atlantic and adjacent Arctic Ocean are made. Four new species are described: two from the Rockall Trough, *Rhombaxinus stellaris* sp. nov. and *Thyasirella rhampfos* sp. nov.; one from east Greenland, *Cryothyas milnelandensis* sp. nov.; one from the abyssal Norwegian Sea, *Mendicula atomus* sp. nov. *Cryothyas rotundus* (Jeffreys, 1881) comb. nov. is recognized from type material discovered in The Natural History Museum (London) and is widespread throughout the Faroe-Shetland Channel from 800–1100 m and ranges from Newfoundland, west and east Greenland, Iceland, Jan Mayen, Svalbard, northern Norway, and into the Barents Sea. It is the earliest available name for all previous records of *Thyasira dunbari* Lubinsky, 1976, except for the type material of that species from the Canadian High Arctic, which is a separate species and retains its original name. A form of *Thyasirella obsoleta* (A.E. Verrill & K.J. Bush, 1898) is present at depths below 500 m in the Faroe-Shetland Channel but rarely overlaps with the range of *Odontothyas succisa* (Jeffreys, 1876) comb. nov. that was found predominantly around the shelf edge at 200–300 m. *Mendicula pygmaea* (A.E. Verrill & K.J. Bush, 1898) was widespread in the Faroe-Shetland Channel at depths from 700 to 1200 m and was found to have a range that included the type locality of off Massachusetts north to Jan Mayen, Svalbard, northern Norway and the Barents Sea. Despite small variations, none are significant enough to warrant the recognition of new species. *Mendicula pygmaea* is compared with *M. ockelmanni* (Keuning & Schander, 2010), *M. ferruginosa* (Forbes, 1844), and two other small Arctic species, *Axinulus careyi* Bernard, 1979 and *Thyasira ottoschmidtii* Gorbunov, 1946. *Mendicula atomus* sp. nov. is described from abyssal depths in the Norwegian Sea. A short discussion on thyasirid systematics concludes the paper.

Key words. Taxonomy, shell morphology, North Atlantic Ocean, Arctic Ocean, Bivalvia

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INTRODUCTION

The Thyasiridae of the deep Atlantic were extensively reviewed by Payne & Allen (1991), who described 27 species or subspecies, of which 12 were new to science. Allen (2008) later indicated that there were a further 48 undescribed species present in the Atlantic Ocean. Oliver *et al.* (2016) listed and illustrated a number of species from bathyal and deeper depths from the U.K. and Irish Exclusive Economic Zones, namely: *Adontorhina keegani* Barry & McCormack, 2007; *Axinulus brevis* (A.E. Verrill & K.J.

Bush, 1898); *Axinulus croulinensis* (Jeffreys, 1847); *Axinus grandis* (A.E. Verrill & S. Smith, 1885); *Genaxinus eumyari* (M. Sars, 1870); *Leptaxinus incrassatus* (Jeffreys, 1876); *Mendicula ferruginosa* (Forbes, 1844); *Parathyasira subcircularis* (Payne & J.A. Allen 1991); *Thyasira scotiae* P.G. Oliver & Drewery, 2014; *Thyasira subovata* (Jeffreys, 1881); *Thyasira tortuosa* (Jeffreys, 1881). In addition, Olabarria (2005) listed from the Porcupine Sea Bight: *Thyasira equalis* (A.E. Verrill & K.J. Bush, 1898), *T. obsoleta* (A.E. Verrill & K.J. Bush, 1898), *Mendicula* (as *Thyasira*) *inflata* (Payne & J.A. Allen, 1991), *Mendicula* (as *Thyasira*) *ultima* (Payne

& J.A. Allen, 1991), *Thyasira succisa succisa* (Jeffreys, 1876), and *Mendicula* (as *Thyasira*) *pygmaea* (A.E. Verrill & K.J. Bush, 1898). An interesting feature is the very large bathymetric ranges cited by both Payne & Allen (1991) and Olabarria (2005). Some species, such as *A. croulinensis*, *T. obsoleta*, *T. equalis*, and *M. ferruginosa*, were apparently recorded from shelf to abyssal depths, a bathymetric range not seen in other bivalve families such as the Limopsidae and Arcidae (Oliver & Allen 1980a, b) or the Yoldiellidae (Killeen & Turner 2009). Payne & Allen (1991) observed variation within both *T. equalis* and *T. obsoleta* but concluded that this was insufficient to warrant species-level recognition. However, Allen (2008) later stated that there were some 48 undescribed species of Atlantic thyasirids, which perhaps indicates the problems when working with taxa that have relatively few morphological characters. It should, therefore, not be surprising to discover undescribed species from U.K. and adjacent bathyal waters.

In this paper, I attempt to identify a large set of specimens taken from the Faroe-Shetland Channel at depths between 150 m and 1600 m. Included are *T. succisa* (Jeffreys, 1881) from between 150 m and 250 m, *T. cf. obsoleta* from between 400 m and 600 m, *Mendicula cf. pygmaea* from 600 m to 1200 m, and a small *Thyasira* likened to *T. equalis* from 700 m to 1600 m. In addition, two new species from the adjacent Rockall Trough are described.

This paper describes the species from the Atlantic Frontier Environmental Network (AFEN) (Bett 2001) programme, but in doing so it considers related ampho-Atlantic and circumboreal species studied by Kurt Ockelmann (1924–2021) but never published. Following Kurt Ockelmann's death in 2021, the archive of his unpublished monograph was deposited in the Natural History Museum, Denmark. Ockelmann's archive and the extensive collection in the NHMD were made available to me with the aim of producing a retrospective of his work on thyasirids (Oliver 2025). This coincided with funding to visit the Smithsonian Institution to examine the type specimens of J.G. Jeffreys (1847, 1876, 1881) and Verrill & Bush (1898), which were pivotal to Ockelmann's conclusions and are also key to understanding the deepwater species from the AFEN samples. A similar paper on the AFEN and other material on the bivalve genera *Yoldiella* A.E. Verrill & K.J. Bush, 1897 and *Portlandia* Mörch, 1857 contains a useful discussion on distribution patterns (Killeen & Turner 2009). Killeen & Turner (2009) also gave a short review of the AFEN surveys and a map of the areas sampled, which are identical for the material reviewed here.

This paper is based on morphology alone, as very few samples of the species considered were suitably preserved for DNA extraction. I have introduced four new genera, based on morphology, that do not fit within the current concept of the genus *Thyasira* Lamarck, 1818. I have refrained from using subgenera as I have no molecular data to support the inferred relationships between subgenera and genera. While the introduction of new genera may be an inconvenience for many practitioners, retaining current, what one might call, “super-genera” such as *Thyasira s.l.* simply obscures the phylogenetics of the family. This paper is intended to provide a framework for future molecular studies, which can be expected to shed further light into the relationships within the Thyasiridae. At the species level, I have included descriptions of the many variations encountered, giving some nomenclatural status but taking a conservative approach with others. Again, I have done this to give a basis for future molecular studies, which I hope will resolve the phylogeny of those species that are variable and have wide geographical and bathymetric ranges.

Environmental setting of the Faroe-Shetland Channel

The Faroe-Shetland Channel (Fig. 1) separates the continental shelves of Shetland on the Scottish side and that of the Faroe Islands to the west. It is an important link between the warmer Atlantic waters and the Arctic waters of the Norwegian Sea (Wyville Thomson 1873; Narayanaswamy *et al.* 2010, 2011). A complex of currents flow through the channel. These currents in general are warmer Atlantic waters flowing north and colder Norwegian water flowing south. An excellent summary of the circulation was given by Berx (2012), from which the most pertinent data to this paper are the origins and temperature of the waters at various depths (Fig. 2). Most samples used here are from depths of 600–1000 m, and these sit in the influence of the south-flowing cold waters of the Norwegian Sea Intermediate Waters and the North Atlantic Deep Water. At these depths, the water temperature at these depths is 0–4 °C but mostly below 2 °C. The Wyville Thomson Ridge separates the Faroe-Shetland Channel from the Rockall Trough to the south and may also constitute a faunistic barrier between the two regions. A more detailed review of the influences of the hydrology on the benthos can be found in the works by Bett (2001, 2007).

The Rockall Trough (Fig. 1) was extensively studied by the Scottish Marine Biological Association in Oban and

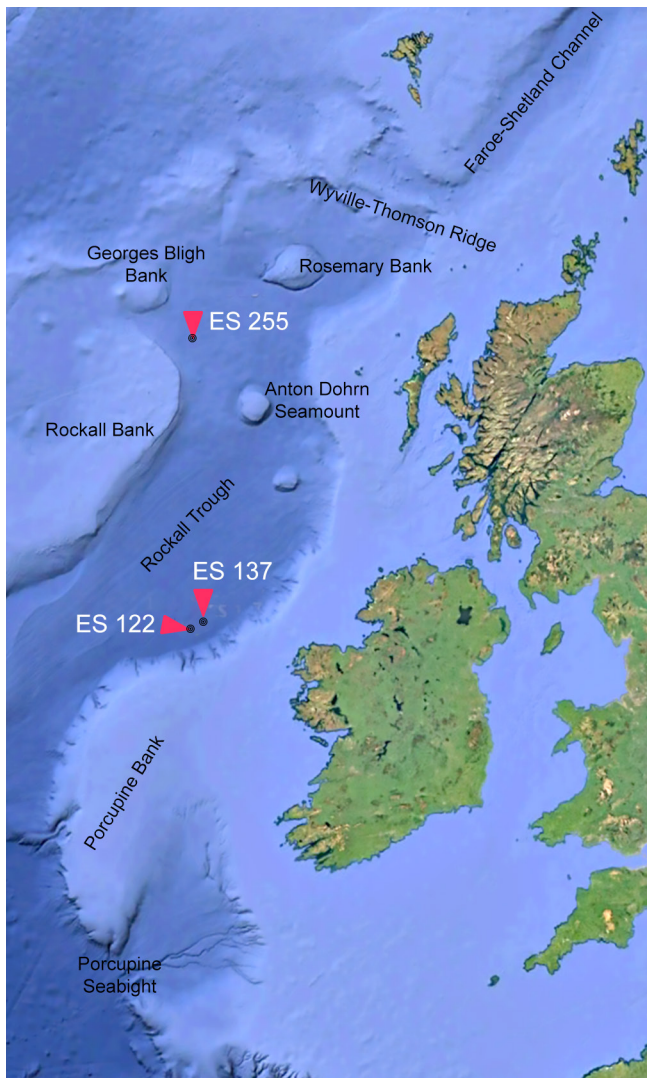


Figure 1. Map of the seabed features off the west coast of Britain and Ireland, with sampling stations in the Rockall Trough marked. Faroe-Shetland Channel lies to the north of the map.

papers by John Gage (1977, 1979, 1986) gave an overview of the environmental setting.

MATERIALS AND METHODS

The samples from the Rockall Trough originate from a series of benthic samples taken by the Scottish Marine Biological Association from 1973 onwards (Gage 1977, 1986). The specimens are part of a series of samples isolated by I.J. Killeen and donated to the National Museum of Wales in 2008.

The Faroe-Shetland Channel material was donated to the National Museum of Wales following a contract to identify the Mollusca collected by the RRS *Darwin* during

the AFEN programme. Comparative material comes from the collections of the National Museum of Wales, in particular a large series of samples from the North Sea oil-fields (Oliver & Killeen 2002) and material collected by the author from Northern Norway and the Barents Sea in 2012 and 2013 while participating in Mareano cruises aboard the RV *G.O. Sars*.

Type material was either borrowed or examined from high-resolution images on institutional collection sites, and some Western Atlantic material was borrowed from the National Museum of Natural History, Smithsonian Institution.

All photographs taken by the author were made using a Leica Z6 macroscope with subsequent frames modified using Helicon Focus image stacking software, unless otherwise stated. Anatomical preparations were made by removing the shell, either manually or by dissolution in 5% HCl and subsequently staining in methyl green. Scanning electron microscope images were made either after cleaning in hypochlorite for prodissococonch detail, or in water for periostracum structure. All micrographs were made with a Jeol JSM600 bench-top microscope, either under low vacuum and without coating, or after gold coating and at high vacuum.

Shell and anatomical characters of Thyasiridae

Shell. While the characters of the bivalve shell are well documented, the subtle distinctions found in thyasirid shells may not be so familiar to the general reader. The shell characters follow those used by Payne & Allen (1991) and modified by Oliver & Killeen (2002). The external features of the shell are shown in Figure 3. Of relevance are the characters of the submarginal sulcus (sms) and its associated auricle (au). The term sms was introduced by Payne & Allen (1991) and is essentially the escutcheon, which varies in expression of length and width as well as the sharpness of its margins. The ligament is generally sunken in the sms, but the shell margins can be raised into an auricle, which in profile can extend beyond the edge of the sms. When this happens, there is an associated indentation of the profile termed the submarginal sinus (smsn). On the posterior of the shell there is to some degree a radial furrow, termed the posterior sulcus (ps), which can be variably expressed from a distinct furrow to a mere flattening of the area to being absent. When the posterior sulcus is a distinct furrow, the profile of the shell is again indented and termed the posterior sinus (psn), but in shells with a weak posterior sulcus the posterior sinus may be expressed only as a straightening of the posterior margin. On the anterior margin there

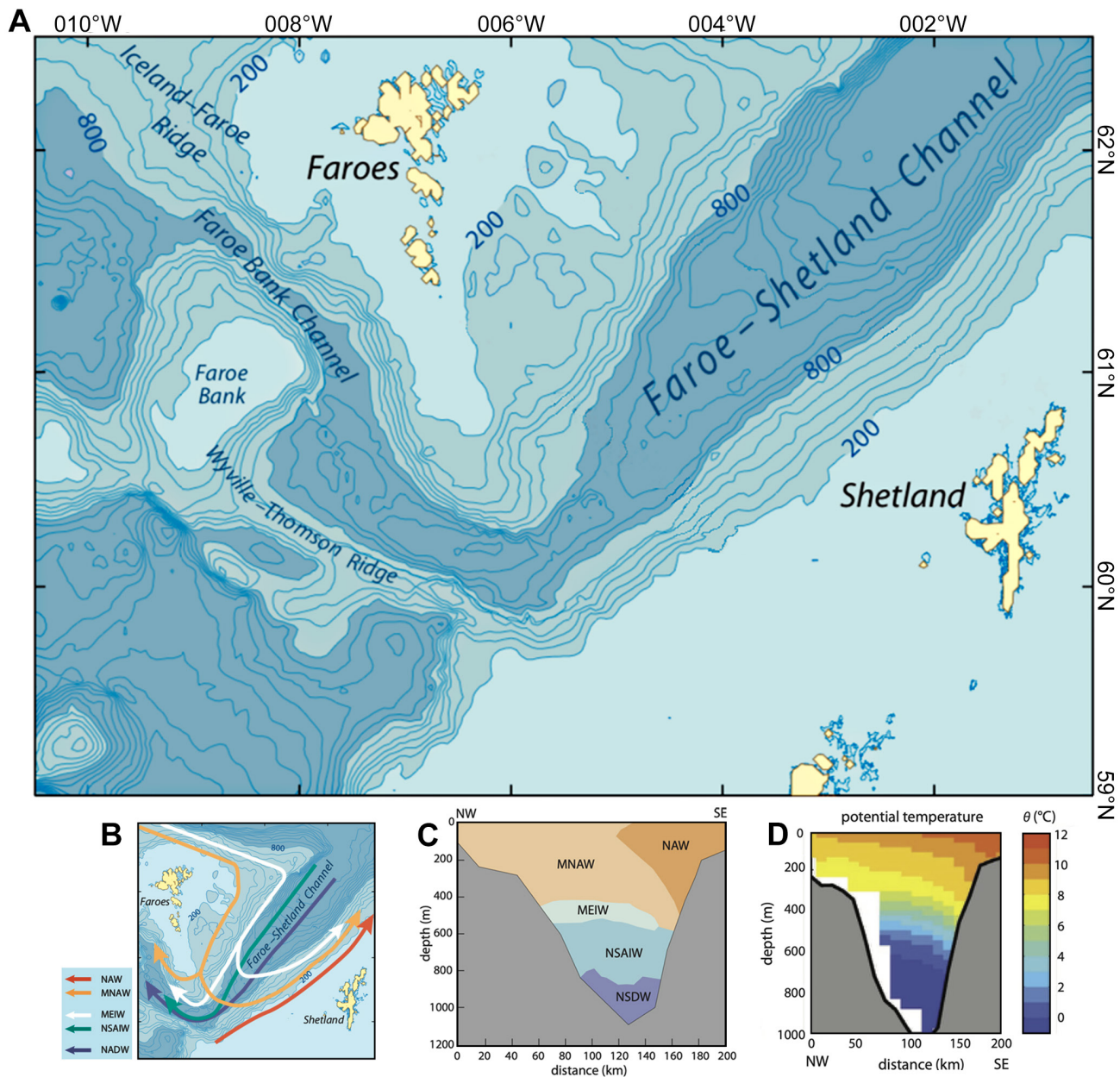


Figure 2. Bathymetry, currents, and water bodies in the Faroe-Shetland Channel (republished with permission from Berx 2012).

may be a short, straight edge below the lunule margin, and this marks the inhalant aperture and when expressed is termed the anterior inhalant margin (aim) or if indented then the inhalant aperture sinus (iasn).

Hinge. Characters of the hinge vary, but the absence of typical cardinal and lateral teeth make their description difficult. Most commonly there are no well-formed teeth as seen in typical bivalves, but beneath the beaks the hinge plate maybe variously thickened (Fig. 4A, B). Only in a few species is there a discreet pseudo-tooth (Fig. 4C) in a cardinal position. Particularly in *Mendicula*, there is an

elongate thickening of the anterior dorsal margin (Fig. 4D) which functions like a tooth but cannot be described as a lateral tooth. In *Adontorhina*, the dorsal anterior and dorsal posterior margins are thickened and bear irregular crenulations (Fig. 4E) that act as interlocking teeth.

Larval shell and prodissoconch. The size of the prodissoconch was extensively used by Ockelmann (see Oliver 2025), but the sculpture could not be discerned by light microscopy. Scanning electron microscopy reveals a variety of microstructures in those examined for this paper, but a wider ranging review may prove useful. Here six are

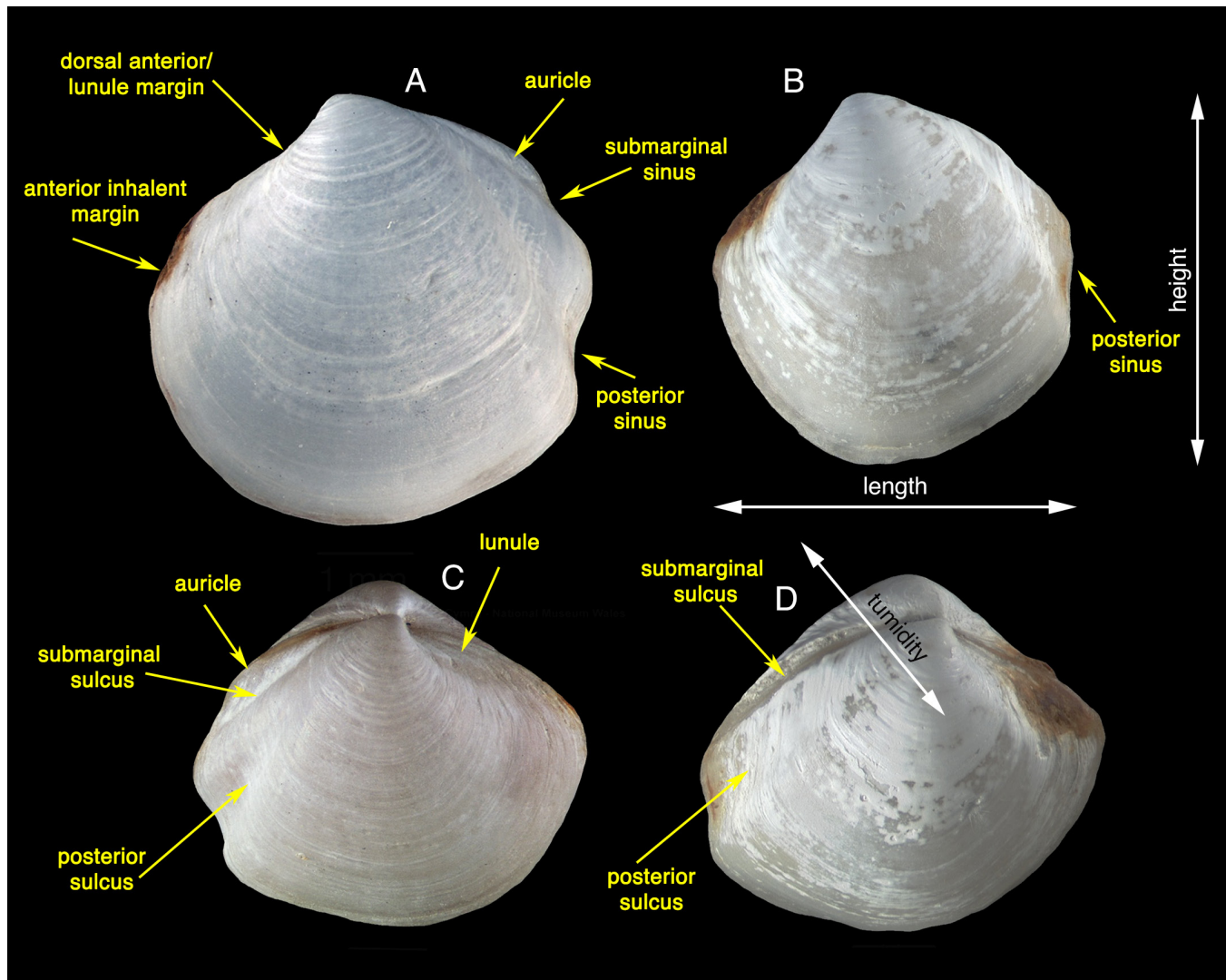


Figure 3. External structures of the thyasirid shell. **A**, polygonal outline. **B**, rhomboidal outline. **C**, dorsal oblique aspect of polygonal shell. **D**, dorsal oblique aspect of rhomboidal shell.

illustrated, the first being “vermiculate”, resembling dense, irregular wavy ridges like a mass of small worms. This sculpture may be prominent and over the whole of the prodissoconch (Fig. 5A) or less well developed and restricted to the apical area (Fig. 5B). In Figure 5C, D there is a small apical indentation (dimple) with a few irregular ridges within, while the remainder may be weakly commarginally ridged or smooth. Figure 5E shows a most striking pattern of ridges curving away from the apex and resembles the Jewish candlestick and thus termed here as “menorah-like sculpture”. Figure 5F shows a dense array of fine ridges radiating away from the apex.

Periostracum. The scanning electron microscope has also revealed interesting characters of the shell surface and periostracum and as with the prodissoconch sculptures

warrant a wider ranging review. It is important to distinguish the shell surface from the periostracum. In Figure 6A the cleaned surface shows a dense pitting, while Figures 6B–F shows periostracal features. The periostracum may be thin and show only commarginal thickening with some radial creases (Fig. 6B). In Figure 6C, the periostracum shows star-shaped creases. In Figures 6D and E, the periostracum displays secondary calcification, as spicules (Fig. 6D) and as polygonal thickening with calcareous centres (Fig. 6E).

Anatomy. Of relevance to the systematics of thyasirids are the gills (ctenidia). The range of gill types was first explored by Dufour (2005), building on the observations of Southward (1986), who was the first to record the bacterial symbiosis in some species. The typical gill is composed

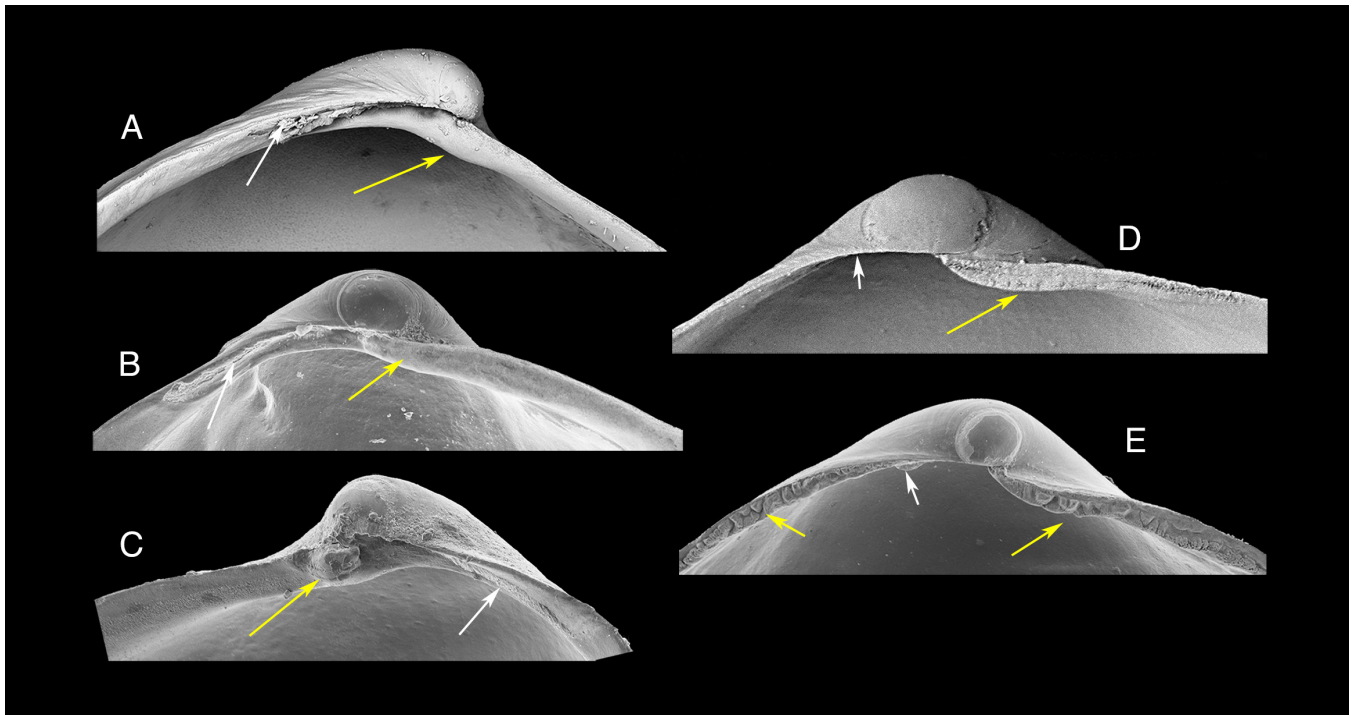


Figure 4. Some features of the thyasirid hinge. **A**, *Cryothyas rotundus* (Jeffreys, 1881). **B**, *Thyasirella obsoleta* (A.E. Verrill & K.J. Bush, 1898). **C**, *Odontothyas succisa* (Jeffreys, 1876). **D**, *Mendicula pygmaea* (A.E. Verrill & K.J. Bush, 1898). **E**, *Adontorhina similis* Barry & McCormack, 2007. White arrows point to ligament; yellow arrows point to hinge “teeth”.

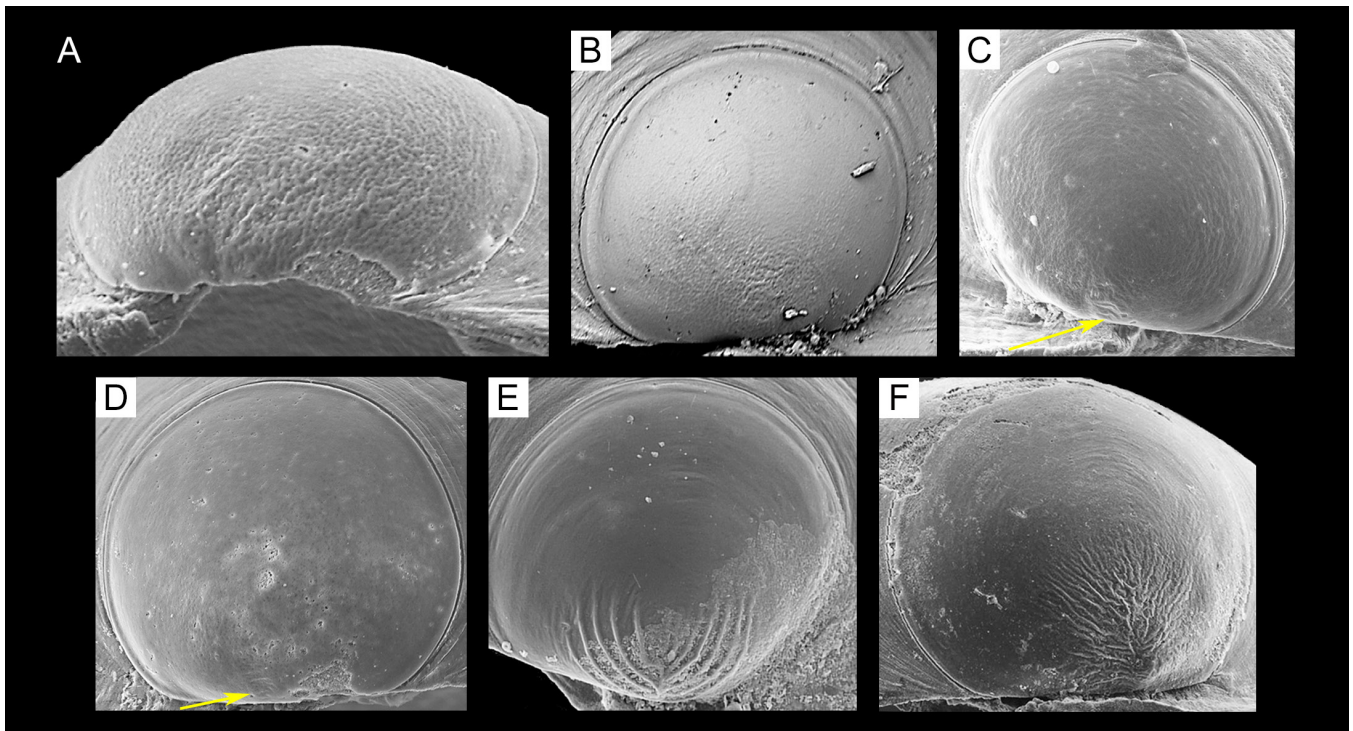


Figure 5. Microsculpture of the thyasirid prodissoconch. **A**, coarsely vermiculate (*Mendicula atomus* sp. nov.) **B**, fine apical vermiculation (*Cryothyas rotundus* Jeffreys, 1881). **C**, apical dimple (arrowed) and commarginal irregular ridges (*Thyasirella obsoleta* A.E. Verrill & K.J. Bush, 1898). **D**, apical dimple (arrowed) with remainder smooth (*Mendicula pygmaea* A.E. Verrill & K.J. Bush, 1898). **E**, menorah-like sculpture (*Rhombaxinus equalis* A.E. Verrill & K.J. Bush, 1898). **F**, irregular ridges radiating from apex (*Mendicula ferruginosa* Forbes, 1844).

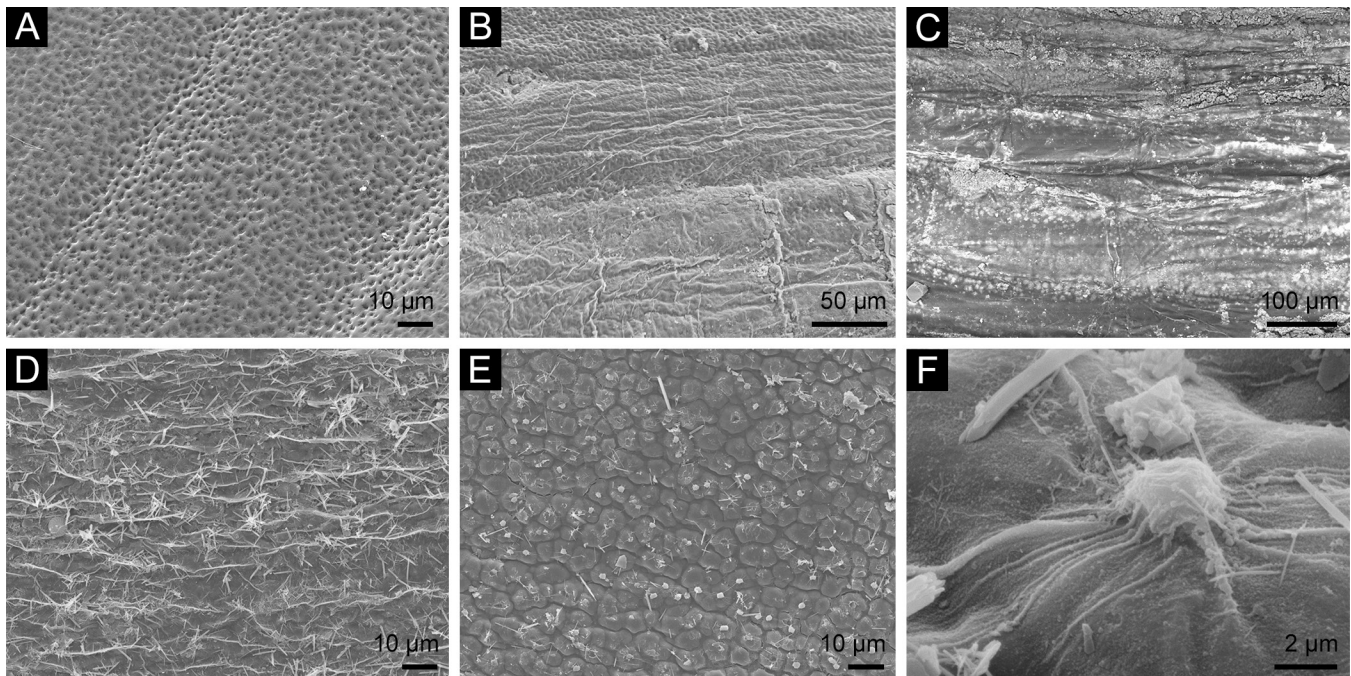


Figure 6. Microsculpture of the thyasirid shell surface and periostracum. **A**, cleaned shell surface showing dense pitting (*Cryothyas rotundus* Jeffreys, 1881). **B**, periostracum with commarginal thickening (*Rhombaxinus equalis* A.E. Verrill & K.J. Bush, 1898). **C**, periostracum with star-shaped creases (*Cryothyas dunbari* Lubinsky, 1976). **D–F**, periostracum with secondary calcification. **D**, spicules (*Rhombaxinus stellaris* sp. nov.). **E, F**, polygonal thickening with calcareous centres (*Thyasira flexuosa* Montagu, 1803).

of two demibranchs (like an inverted W in cross section), with reflected filaments that are rod-shaped. In small species, the gills can be reduced to a single demibranch in which the filaments are not reflected (like an inverted V in cross section). In species hosting chemosymbiotic bacteria, the abfrontal part of each filament becomes extended, giving the filaments a laminar form. In gross appearance these ctenidia appear rather thick and fleshy, often tinged pink or dull grey. The ctenidium is so thick in some species that the filaments are not apparent, and rather the surface has a netted appearance arising from the cross-linking of the filaments. In section these gills are seen to be complex of tubules lined by bacteria-hosting cells (Oliver 2014). With the discovery of more complex tubular gills, Oliver (2014) modified Dufour's (2005) classification (Table 1) and additional genera have been included here. In describing genera, the gill type is cited as set out in Table 1.

The lateral body pouches, which are unique to thyasirids, exhibit a range of form from a simple lobe to a complex series of tubules and small lobes. While the gross differences between unlobed or few to many small lobes have been cited for different genera (Payne & Allen 1991; Oliver & Killeen 2002), not enough work has been done to ascertain if the degree of lobulation can be used to distinguish species. This is because there has been no study

charting the growth of the lateral body pouch within a species or between populations of the same species. The shape of the lobules may differ from pointed to cuboid, but again we cannot be sure if this is a constant feature or can be affected by the method of preservation.

The mantle openings of thyasirids (Figs 8, 12) have not been used in systematics, probably because the various openings are formed by ciliary rather than muscle connections and are not consistently preserved in fixed specimens. Only the posterior exhalant aperture is defined by mantle fusion. Other mantle openings are the anterior inhalant, ventral pedal, and posterior ventral pseudofaecal apertures, the latter previously referred to as the “aperture ventral to the exhalant aperture” (Payne & Allen 1991) and the “sa2” aperture of Zelaya (2009). Associated with the mantle apertures are areas of glandular tissue that are best seen after staining (methyl green was used here), but their significance to taxonomy is uncertain, although the extent of the anterior glandular area was used by Oliver & Killeen (2002).

Abbreviations (shell). **aa** anterior adductor scar; **au** auricle; **aim** anterior inhalant margin; **H** height, **hg** hind gut, **l** lunule, **L** length, **pa** posterior adductor scar, **ps** posterior sulcus, **psn** posterior sinus, **pt** pseudo-tooth, **res** resiliifer,

Table 1. Classification of gill types found in the Thyasiroidea, modified from Dufour (2005) and Oliver (2014).

Revised type	Dufour type	Demi-branches	Reflec-tion	Abfrontal extension	Frontal ciliation	Filament form	Genera
Type 1R	Type 1	2	+	Absent	Complete	Rod-like	<i>Axinopsida</i>
Type 2aR	Type 2	2	+	Absent	Complete	Rod-like	<i>Parathyasira</i> , <i>Thyasirella</i> , <i>Cryothyas</i> , <i>Odontothyas</i>
Type 2aR	Type 2	2	+	Absent/slight in some	Complete	Rod-like	<i>Rhombaxinus</i>
Type 2bR	Type 2	1	–	Absent/slight in some	Complete	Rod-like	<i>Axinulus</i>
Type 2bR	Type 2	1	–	Absent	Complete	Rod-like	<i>Adontorhina</i> , <i>Mendicula</i> , <i>Leptaxinus</i> , <i>Genaxinus</i>
Type 3L	Type 3	2	+	Extensive	Complete	Laminar	<i>Thyasira s.s.</i> , <i>Maorithyas</i> , <i>Axinus</i> , <i>Spinaxinus</i> , <i>Channelaxinus</i> , <i>Ascetoaxinus</i>
Type 4T/L		2	+	Extensive	Absent?	Tubular/ laminar	<i>Conchocele</i>
Type 5T		2	+	Most of filament	Reduced	Tubular	<i>Ochetoctena</i>
Type 6 symbionts intracellular		2	+	extensive	Complete	Laminar	<i>Tartarothyasira</i>

SEM scanning electron micrograph, **sms** submarginal sulcus, **smsn** submarginal sinus, **T** tumidity.

Abbreviations (anatomy). **aa** anterior adductor muscle, **a. gl** anterior glandular tissue, **apr** anterior pedal retractor muscle, **ex.a** exhalant aperture, **f** foot, **gl** glandular tissue, **hg** hind gut, **id** inner demibranch, **in.a** inhalant aperture, **iasn** inhalant aperture sinus, **lbp** lateral body pouch, **lp** labial palp, **me** mantle edge, **of** oral fold, **od** outer demibranch, **pa** posterior adductor muscle, **p.gl** posterior glandular tissue, **pd.a** pedal aperture, **pf.a** pseudofaecal aperture, **ppr** posterior pedal retractor muscle, **sk** stalk of lateral body pouch, **t(f)** toe of foot.

Institutional abbreviations. **AMS**, Australian Museum, Sydney; **CMN**, Canadian Museum of Nature, Gatineau; **EXEMS**, Royal Albert Memorial Museum, Exeter; **LACM**, Los Angeles County Museum; **NHMD**, Natural History Museum Denmark, Copenhagen; **NHMUK**, The Natural History Museum, London; **NMW**, **NMW. Z**, National Museum of Wales, Cardiff; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington D.C.; **ZMZI**, Zoological Museum of the Zoological Institute, Russian Academy of Sciences, Saint Petersburg.

Other abbreviations. **sh.** shell(s), **spec.** specimen(s), **v** valve(s).

SYSTEMATICS

The generic systematics of the Thyasiridae remains unresolved, and as already noted, the definition of *Thyasira s.s.* does not apply to many of the species included by MolluscaBase (2026) and Huber (2015), and subgenera, such as *Parathyasira*, have been variously applied mainly to small asymbiotic taxa (Payne & Allen 1991; Oliver 2015; Kamenev 2020, 2023a, b). This paper deals with small species that do not fit the definition of *Thyasira s.s.* Rather than prolong this discrepancy, four new genera are introduced. Such revisions would ideally be accompanied by genetic sequence data, but most of the samples available for study have not been suitably preserved and, thus, the new genera are defined on morphology alone. I am fully aware that morphology-based systematics may be considerably altered by the addition of DNA sequence data, but I hope that the genera proposed here will form the basis for a future sequence-based phylogeny by highlighting the diversity of forms that should be included in such a study.

The new genera described here were previously associated with *Thyasira*, *Parathyasira*, and *Mendicula*, as used by Payne & Allen (1991) and Oliver & Killeen (2002). Consequently, I have included revised definitions of these genera to allow comparison with the new genera introduced here. I list the species that currently can be included in each genus, but I recognise that there are many other species attributed *Thyasira* (e.g. MolluscaBase Eds. 2026) that cannot be definitively placed at this time. Most of the unassigned species are known from shells only and I would not wish conjecture on their correct affinities without supporting anatomical data. I accept that there are many generic placements to be resolved and that a wide-ranging revision of the Thyasiridae remains far from complete. So, for the time being, we will continue to use *Thyasira s.l.* as a taxonomic container for unresolved species.

Genus *Thyasira* Lamarck, 1818

Figure 7A, B

Type species. *Tellina flexuosa* Montagu, 1803 (syntypes, 1 sh. + 8 v., EXEMS Moll3894-9, Montagu collection; type locality: England; Falmouth Harbour, Cornwall).

Species included. *Thyasira flexuosa* (Montagu, 1803); *T. biplicata* (R.A. Philippi, 1836); *T. gouldii* (R.A. Philippi, 1845); *T. trisinuata* (A. d'Orbigny, 1853); *T. polygona* (Jeffreys, 1864); *T. obesa* (A.E. Verrill, 1872); *T. barbarensis* (Dall, 1890); *T. tokunagai* Kuroda & Habe, 1951; *T. inadai* Amano & Haga, 2023.

Revised definition. Shell to 15 mm, thin, equivalve, equilateral. Outline ovate, mostly higher than long, trisinuate, posterior sulcus well developed, posterior sinus prominent; submarginal sulcus developed, auricle raised giving a submarginal sinus; anterior slope variable in length, reflecting size of poorly defined flattened lunule. Sculpture of commarginal growth stops and fine lines. Periostracum may have complex secondary calcification patterns. Muscle scars unequal; anterior muscle scar elongate, much larger than posterior one. Ligament deeply sunken within auricle. Hinge weak, with small cardinal peg in right valve, corresponding to depression in left valve. Prodissoconch with a well-defined rim; microsculpture vermiculate.

Gill type 3L. Foot vermiform. Lateral body pouches with numerous small lobes.

Remarks. The genus *Prothyasira* Iredale, 1930 contains three species from Australia and New Zealand (*P. peregrina* Iredale, 1930; *P. peroniana* Iredale, 1930; *P. waikanae* C.A. Fleming, 1950) that on shell shape alone have similarity to the polygonal *T. polygona* and *T. trisinuata*. However, I have no supporting anatomical data for these species that

would allow me to place them in *Thyasira s.s.* and therefore, the status of the genus *Prothyasira* remains unresolved.

Genus of larger *Thyasira* (Kokarev & Dufour in press)

Name and type species in press (Suzanne Dufour pers. comm.)

Species included (estimated here on morphology alone). *T. sarsii* (R.A. Philippi, 1845); *T. insignis* (A.E. Verrill & K.J. Bush, 1898); *T. oleophila* A.H. Clarke, 1989; *T. methanophila* P.G. Oliver & Sellanes, 2005; *T. southwardae* P.G. Oliver & Holmes, 2006; *T. vulcolutre* Rodrigues & P.G. Oliver, 2008; *T. scotiae* P.G. Oliver & Drewery, 2014. Possibly *Thyasira capitanea* Åström & P.G. Oliver, 2017 but data on anatomy are lacking.

Definition. Shell 20–40 mm in maximum dimension, equivalve, more or less equilateral. Outline subcircular to ovate; posterior sulcus shallow; posterior sinus weak; submarginal sulcus long; auricle narrow, low. Teeth lacking or a with a poorly defined cardinal protuberance. Ctenidia of both demibranchs, filaments thick, fleshy. Gill type 3L.

Remarks. The recognition that this group was separated from *Thyasira s.l.* by Taylor *et al.* (2007) in their molecular study of thyasirids. They showed that *T. methanophila* and *T. sarsii* were not in the same clade as *T. flexuosa*, *T. polygona*, or *T. gouldii*. A more detailed study of this group is in press where a full description and species compliment will be presented including a discussion on the genus *Maorithyas* C.A. Fleming, 1950 (Suzanne Dufour pers. comm.).

Genus *Parathyasira* Iredale, 1930

Figure 7C

Type species. *Parathyasira resupina* Iredale, 1930 (holotype, AMS C.57834; type locality: Australia; Port Kembla, New South Wales (34° 30' 22" S 151° 00' 54" E); in mud and pebbles).

Species included. *P. resupina* Iredale, 1930; *P. granulatus* (Monterosato, 1874); *P. neozelanica* Iredale, 1930; *P. subcircularis* (Payne & J.A. Allen, 1991); *P. bamberi* P.G. Oliver, 2015; undescribed species from the Caribbean Sea.

Revised definition. Shell small, 8–19 mm in largest dimension. Outline rhomboidal to subcircular; posterior margin long sloping steeply; posterior sulcus shallow or a simple, flattened region; posterior sinus slightly indented or marked as a distinct straightening of posterior margin. Submarginal sulcus well defined; auricle absent. Hinge lacking developed teeth; ligament deeply sunken. External sculpture of fine, dense, radially arranged rows of microscopic tubercles, often condensed into raised ridges. Pro-

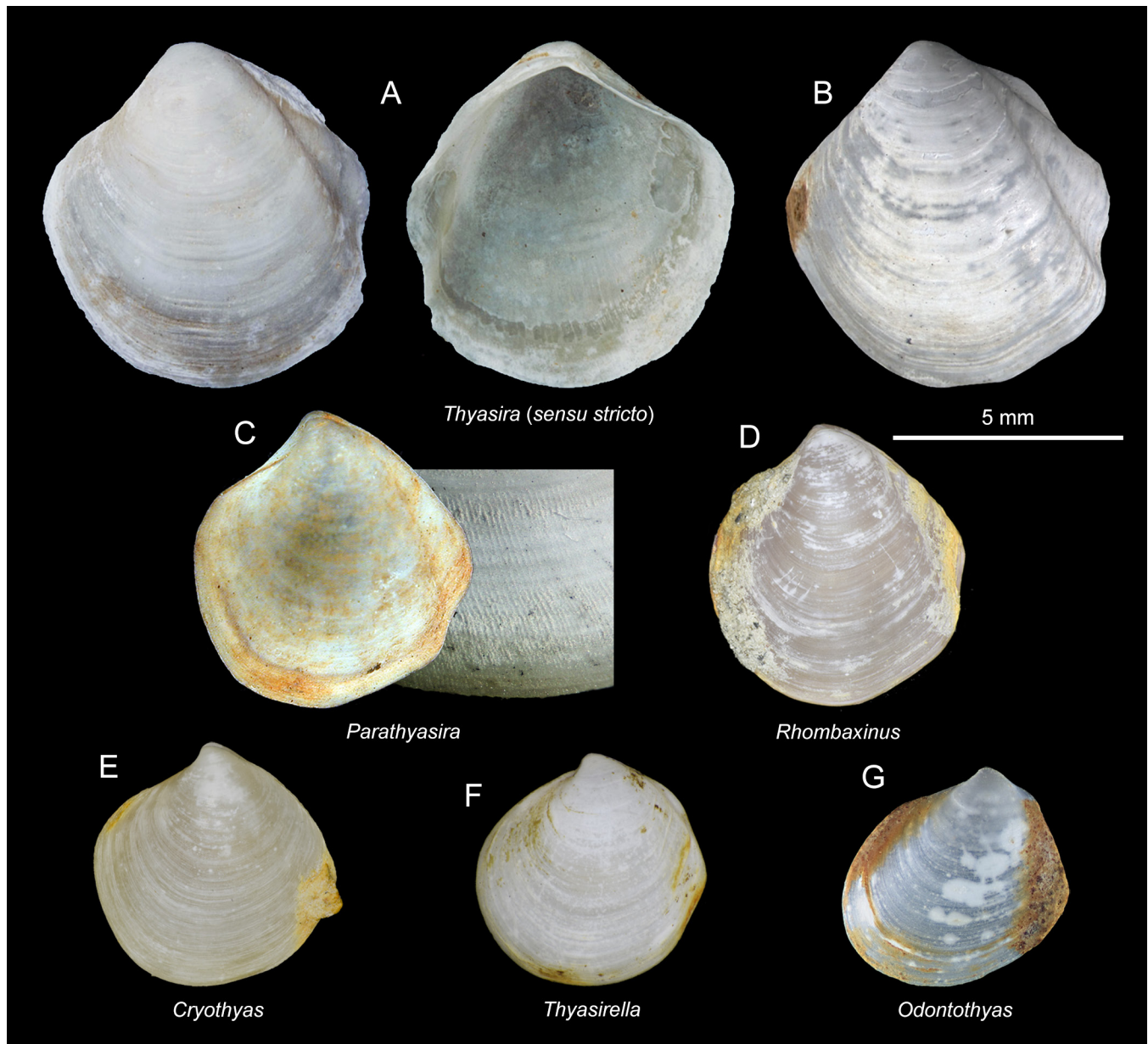


Figure 7. Comparisons of the shells of the genera discussed. **A**, *Thyasira flexuosa* (Montagu, 1803), syntype, EXEMS Moll3894. **B**, *T. polygona* (Jeffreys, 1864). **C**, *Parathyasira resupina* Iredale, 1930, holotype, AMS C57834. **D**, *Rhombaxinus equalis* (A.E. Verrill & K.J. Bush, 1898). **E**, *Cryothyas rotundus* (Jeffreys, 1881). **F**, *Thyasirella obsoleta* (A.E. Verrill & K.J. Bush, 1898). **G**, *Odontothyas succisa* (Jeffreys, 1876).

dissoconch with scattered tubercles or smooth with weak, radiating lines on the apex. Gill type 2aR. Mantle apertures 2 or 3.

Remarks. The genus *Parathyasira* originally only included the type species, but two other austral species, namely *P. neozelanica* Iredale, 1930 and *P. verconis* Cotton & Godfrey, 1938, were later described within *Parathyasira*. The primary difference from *Thyasira* inferred from Iredale's (1930) description, was the weak posterior folds and fine

radial sculpture. Payne & Allen (1991) recognised *Parathyasira* as a subgenus of *Thyasira* and gave a revised definition with a wider set of characters that did not include the radial sculpture. Payne & Allen (1991) described seven additional species of *Parathyasira*, of which only one, *T. (P.) subcircularis* Payne & J.A. Allen, 1991, has a radial sculpture. Two other species originally assigned to *Parathyasira* by Payne & Allen (1991) have since been reassigned to *Thyasira*, namely *T. subovata* (Jeffreys, 1881) and *T. tortu-*

osa (Jeffreys, 1881) (MolluscaBase Eds 2026). Neither of these latter species belong to *Thyasira* s.s. and both differ widely in shape from any of the new genera listed below. Huber (2015) placed *T. subovata* in his T4 group and *T. tortuosa* in his T5 group. Both species may warrant separate generic distinction, but I have not included them here due to lack of data. Given the varied application of *Parathyasira*, I have chosen to restrict the genus to include those species with radial sculpture of microscopic tubercles.

Genus *Rhombaxinus* gen. nov.

Figures 7D, 8–12

ZooBank. urn:lsid:zoobank.org:act:62C58137-6E2D-4A A1-9508-A0EBC3E93CCC

Type species. *Cryptodon equalis* A.E. Verrill & K.J. Bush, 1898 (Fig. 8) (lectotype, USNM 74302 (Fig. 8D); type locality: USA; Casco Bay, Maine, 46.30° N 070.05° W, 172 m, 26 Aug. 1873).

Species included. With menorah-like prodissoconch: *R. equalis* (A.E. Verrill & K.J. Bush, 1898); *R. magellanica* (Dall, 1901); *R. dearborni* (Nicol, 1965); *R. patagonica* (Zelaya, 2010); *R. coani* (Kamenev, 2023); *R. pauli* (Kamenev, 2023); *R. kharkovenesis* (Kamenev, 2023); *R. stellaris* sp. nov. With prodissoconch sculpture unknown: *R. biscayensis* (Payne & J.A. Allen, 1991).

Etymology. *Rhombaxinus*, from the Latin *rhombus*, referring to the lozenge-shaped shell outline, and *Axinus*, an early synonym of *Thyasira*. Masculine.

Definition. Shell small, to 10 mm. Outline rhomboidal-oval to rhomboidal-pyriform; posterior sulcus shallow

but well defined; submarginal sulcus well defined; auricle absent or shell margins within submarginal sulcus slightly raised. Hinge lacking developed teeth but some species with cardinal thickenings; ligament deeply sunken. External sculpture weak of commarginal ridges and growth lines, microscopically punctate (Fig. 6A). Prodissoconch with menorah-like sculpture (Fig. 5E). Gill type 2aR. Mantle with 3 or 4 apertures (Fig. 8B, C).

Remarks. I had initially thought that the menorah-like sculpture of the prodissoconch may have been an apomorphy for *Rhombaxinus*, but it is present in *Axinulus oliveri* Kamenev, 2020 but not all species of *Axinulus* A.E. Verrill & K.J. Bush, 1898. It is also present in some *Adontorhina* (s.s.) S.S. Berry, 1947 (Kamenev & Lisitsyna 2024) and in the much differently shaped *T. tortuosa*. Given that menorah-like sculpture is not apomorphic, I initially thought that all small, rhomboidal species lacking a raised auricle should be included in *Rhombaxinus*. However, I have been informed (Suzanne Dufour pers. comm) that the small, rhomboidal boreal/arctic species with a vermiculate prodissoconch belong to a distinct clade, which is described here as *Cryothyas* gen. nov.

Rhombaxinus stellaris sp. nov.

Figures 9–12, Table 2

ZooBank. urn:lsid:zoobank.org:act:29104FA5-D7DC-4 BA4-92BC-66FFD86D5D49

Type locality. NE Atlantic, between George Bligh and Rosemary Banks, North Rockall Trough, RRS *Challenger* Sta. ES 255, 1977, 58° 26' N 012° 042' W, 1595 m.

Type specimens. **Holotype**, a complete dry spec., NMW.

Table 2. Measurements of *Rhombaxinus stellaris* sp. nov.

	Height (mm)	Length (mm)	Tumidity (mm)	L/H	H/T
Holotype (dry, sh)	4.50	4.20	2.90	0.93	1.55
Paratype 1 (wet)	4.15	3.95	2.55	0.95	1.63
Paratype 2 (wet)	3.55	3.45	2.05	0.97	1.73
Paratype 3 (wet)	3.35	3.10	2.05	0.93	1.63
Paratype 4 (wet)	2.95	2.85	1.70	0.97	1.74
Paratype 5 (wet)	2.90	2.85	1.75	0.98	1.66
Paratype 6a (dry, disarticulated sh)	4.20	3.80	—	0.91	—
Paratype 6b (dry, disarticulated sh)	3.20	3.00	—	0.94	—
Paratype 6c (dry, disarticulated sh)	2.10	2.00	—	0.95	—
Non-type specimen	3.25	3.15	2.05	0.97	1.58
Non-type specimen	2.95	2.85	1.75	0.97	1.69
Non-type specimen	3.40	3.10	2.00	0.91	1.70
Non-type specimen	3.10	2.95	1.95	0.95	1.59
Non-type specimen	2.65	2.50	1.50	0.94	1.77

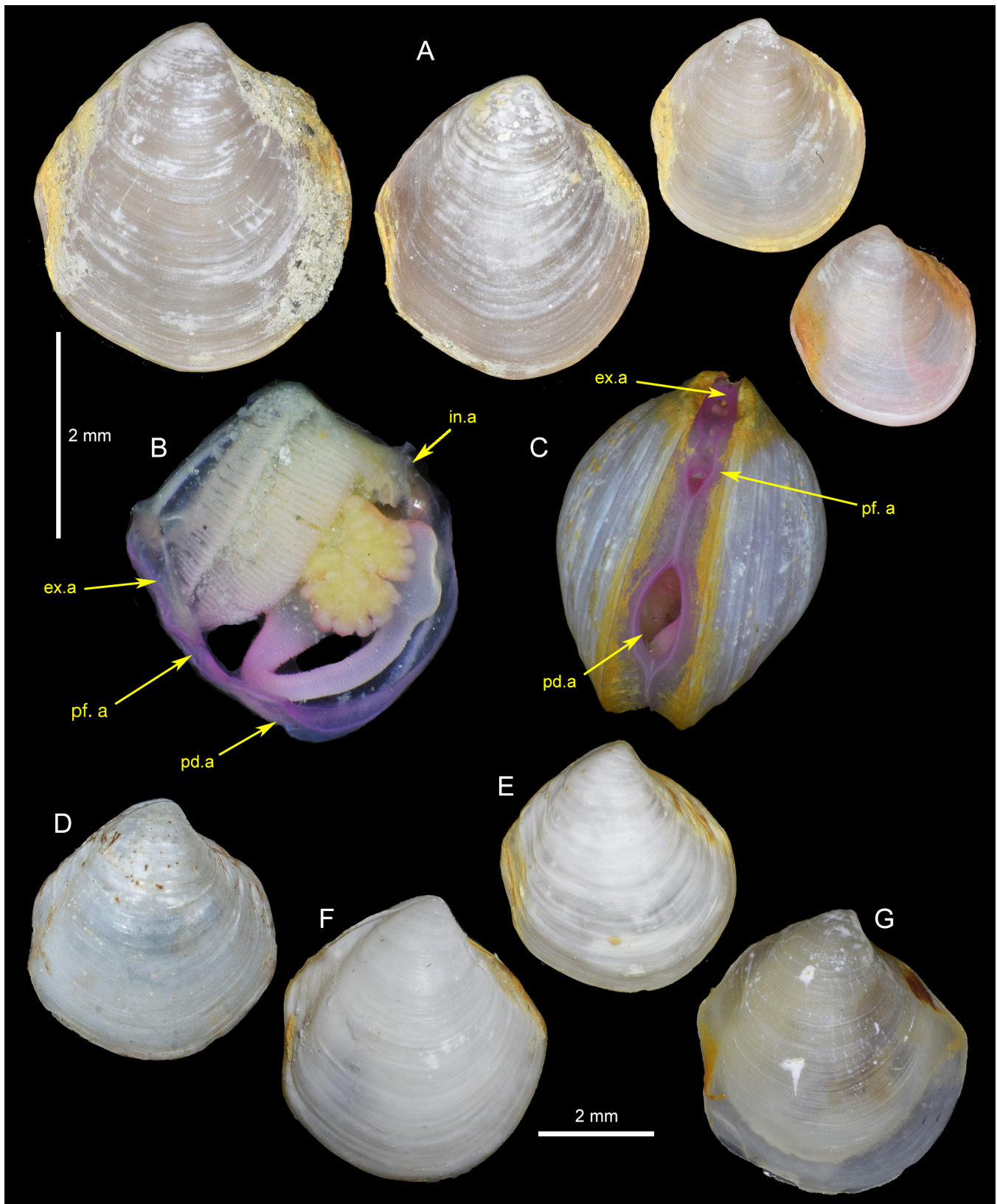


Figure 8. *Rhombaxinus equalis* (A.E. Verrill & K.J. Bush, 1898). A–C, from off Cape Hatteras, USNM 14828838. A, growth series. B, gross anatomy. C, mantle edge apertures. D, lectotype, from off New England USNM74302; E, from Skagerrak, North Sea; F, from West Greenland; G, from Barents Sea.

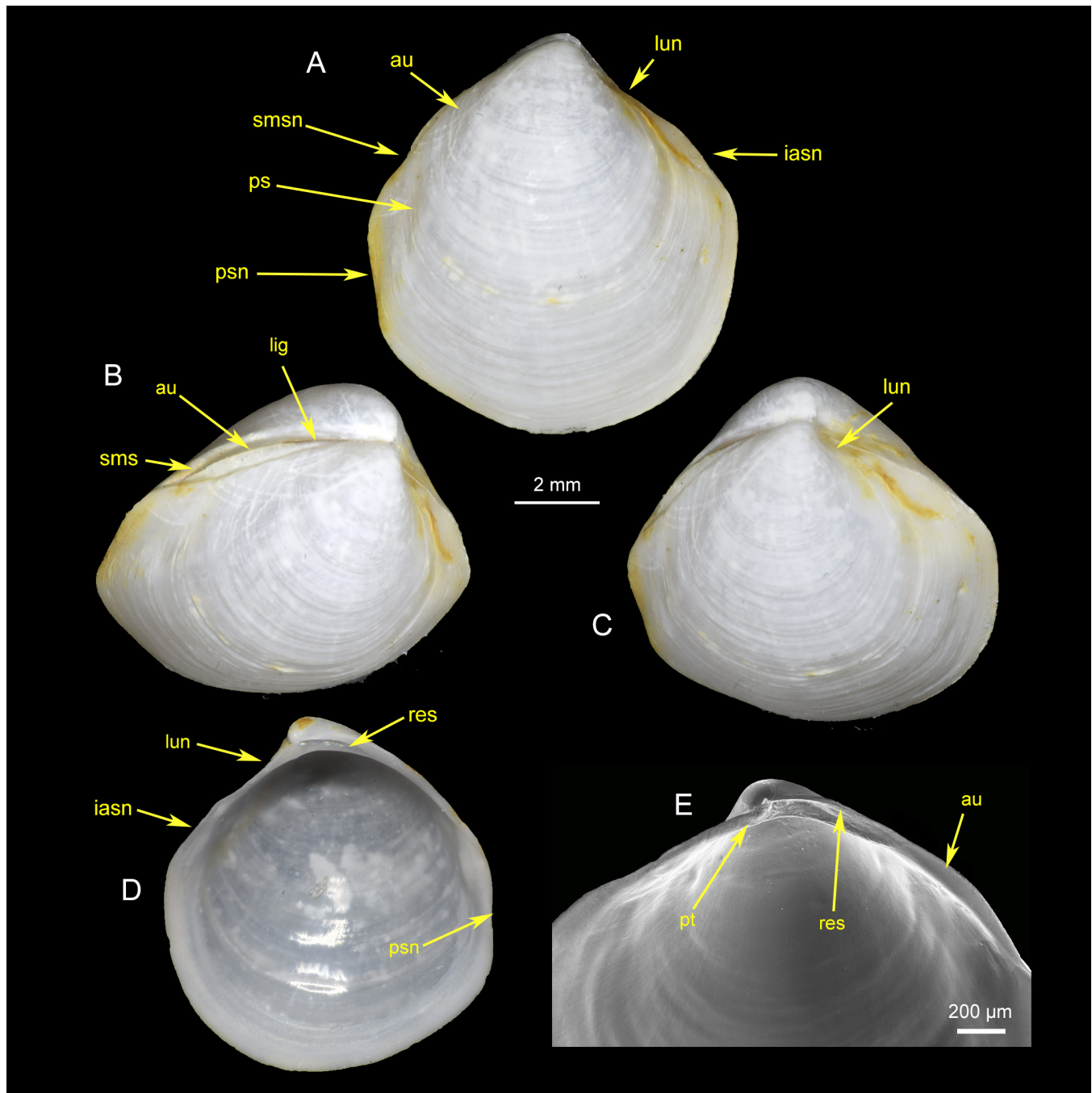


Figure 9. *Rhombaxinus stellaris* sp. nov., from Sta. ES255, Rockall Trough. **A–C**, holotype, NMW.Z.2009.036.03472. **D, E**, paratypes, NMW.Z.2009.036.03474: (**D**) interior of right valve; (**E**) SEM of hinge of right valve.

Z. 2009.036.03472 (Fig. 9). **Paratypes**, all from type locality: 5 spec. in 70% ethanol, NMW. Z. 2009.036.03473 • 3 dry disarticulated sh., NMW. Z. 2009.036.03474 • 3 sh. disarticulated, gold-coated, on SEM mount & 1 broken v., gold-coated, on SEM mount, NMW. Z. 2009.036.03475.

Other material. 15 spec. & 3 bodies in 70% ethanol, NMW. Z. 2009.036.03476, from type locality.

Etymology. *Stellaris*, Latin, meaning “starry”, referring to the scattered placement, like stars in the night sky, of microscopic periostracal calcified spicules.

Diagnosis. Shell to 4.5 mm, a little higher than long, rhomboidal, with posterior outline weakly bisinuate; sub-marginal sulcus with a low auricle; prodissoconch with menorah-like sculpture of 9 or 10 ridges; periostracum

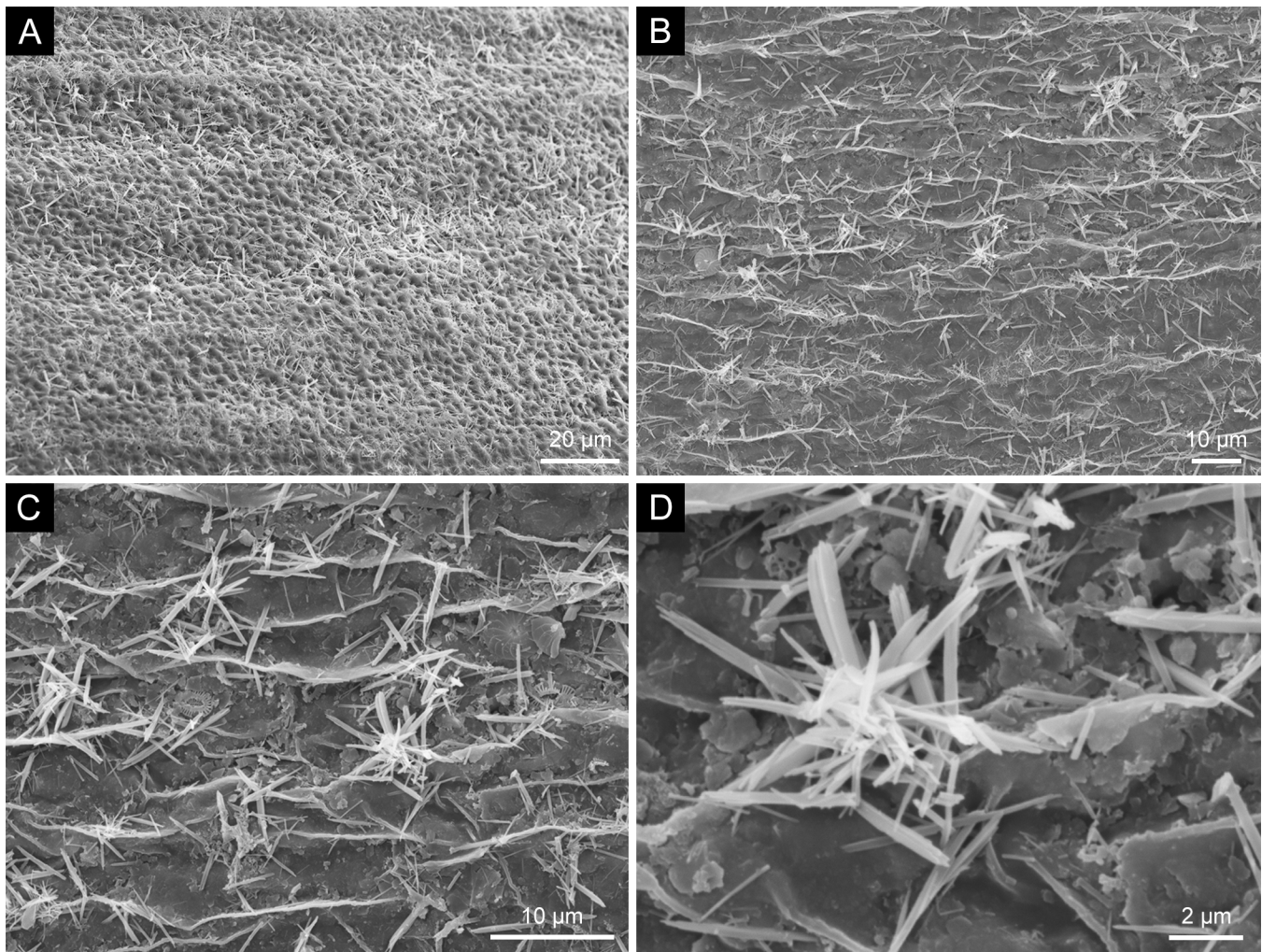


Figure 10. *Rhombaxinus stellaris* sp. nov., from Sta. ES255, Rockall Trough, NMW. Z. 2009.036.03475. SEM of periostracum at various magnifications.

with stellate calcareous clusters.

Description. Shell (Fig. 9) to 4.5 mm high (holotype 4.5 mm; Table 2), a little higher than long (H/L ratio 1:0.95), moderately inflated (H/T ratio 1:1.7), fragile, equivalve, equilateral. Outline rhomboidal; lunule margin short; lunule small, a little depressed; anterior inhalant margin (iasn) short, distinct, straight; ventral margin a little narrowed; posterior weakly bisinuate; posterior sinus (psn) almost straight, scarcely indented; submarginal sinus weak; dorsal margin sloping, marking edge of submarginal sulcus; submarginal sulcus with a low auricle scarcely extending above margin of submarginal sulcus. Hinge edentulous, except for very indistinct swelling (pseudo-tooth) beneath beaks (Fig. 9D, E). Ligament deeply sunken, *c.* $\frac{1}{2}$ length of submarginal sulcus. Sculpture of weak growth stops and fine commarginal lines. Microsculpture (Fig. 10) of dense, irregular reticulations most visible on umbonal

region, elsewhere obscured by a thin periostracum with broken, commarginal lirae: these bearing clusters of thin, needle-shaped calcareous growths reminiscent of a cactus. Muscle scars indistinct. Prodissoconch (Fig. 11) with a marginal rim, 165–170 μ m in diameter; apex sculpture menorah-like, of 9 or 10 crescentic ridges radiating from either side of a median ridge.

Anatomy (Fig. 12). Anterior adductor muscle elongate, diverging from mantle edge; posterior adductor oval, $\frac{1}{2}$ size of anterior adductor muscle. Mantle edge with 3 openings; anterior opening to outside of anterior adductor muscle, highly glandular, and marking inhalant aperture; ventral opening or pedal probing aperture; exhalant aperture immediately ventral of posterior adductor and adjacent to attachment of ctenidium. Fusion between exhalant and pedal apertures muscular or ciliary uncertain; anterior inhalant and pedal apertures not always fused. Ctenidium

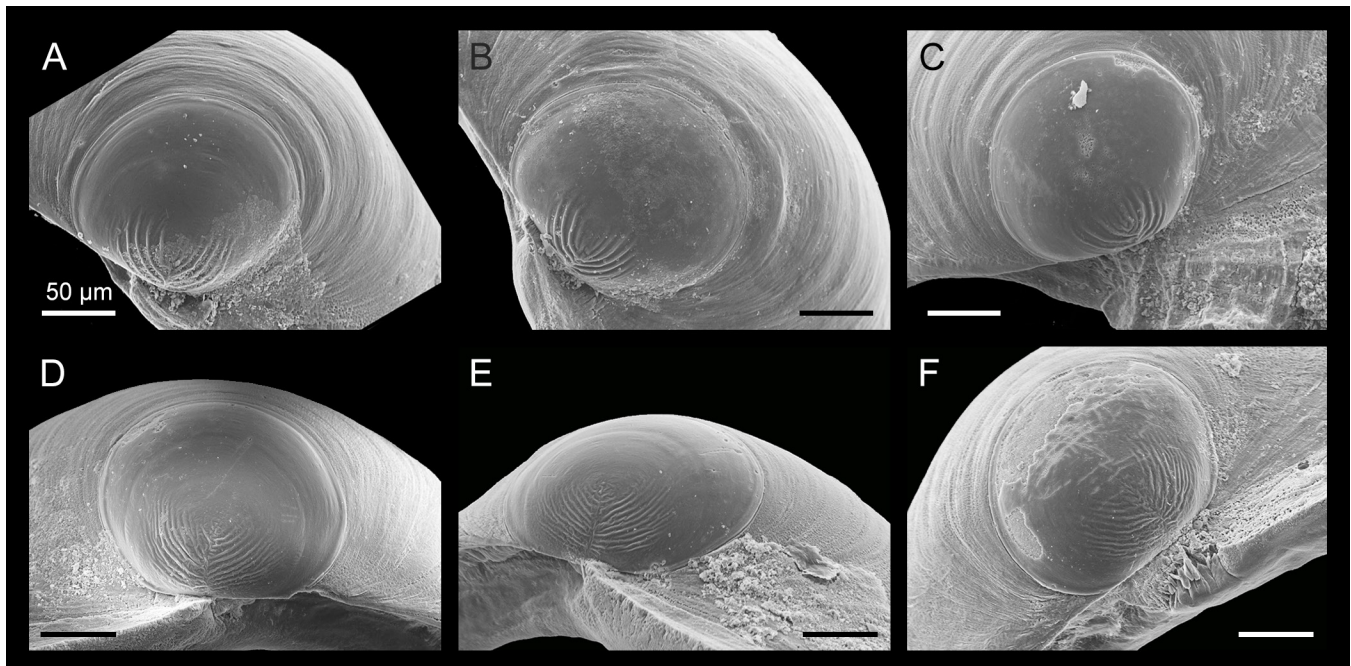


Figure 11. Prodissoconch sculpture in *Rhombaxinus*. **A–C**, *R. equalis*, **A**, off Cape Hatteras, USNM 1482838. **B**, North Sea, NMW.Z.2001.113 **C**, Barents Sea, coll. P.G. Oliver. **D–F**, *R. stellaris* sp. nov. from Sta. ES255, Rockall Trough, NMW. Z. 2009.036.03475.

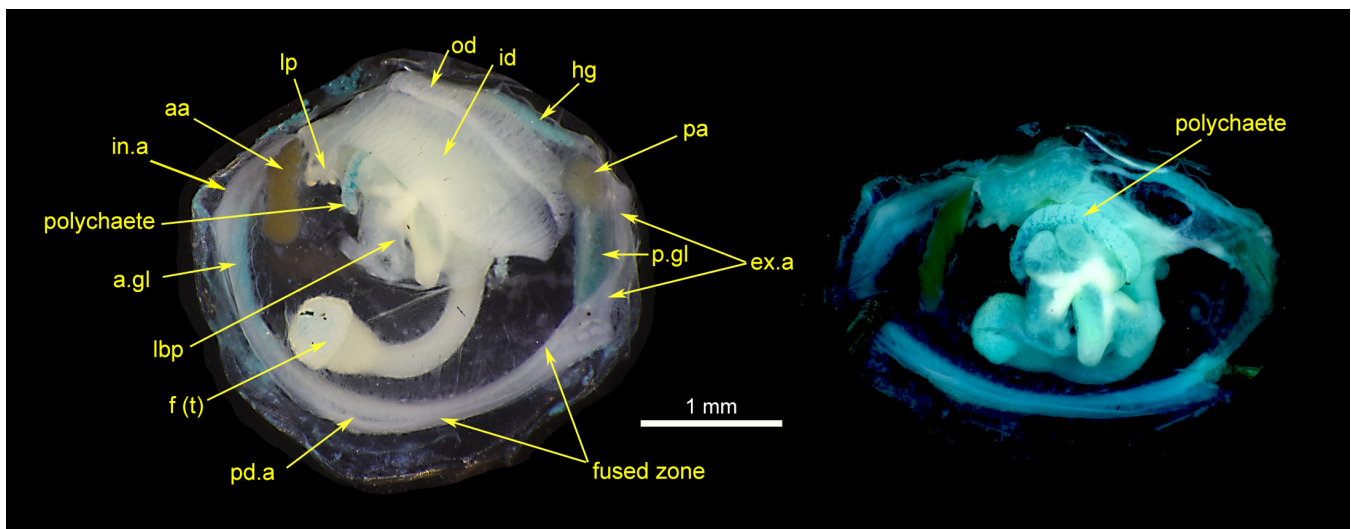


Figure 12. Anatomy of *Rhombaxinus stellaris* sp. nov., from Sta. ES255, Rockall Trough, NMW. Z. 2009.036.03476. Lower image, specimen stained in methyl green showing commensal polychaete wrapped around the lateral body pouch.

of 2 demibranchs; outer demibranch *c.* $\frac{1}{3}$ depth of inner one, both with fully reflected filaments; tips with lamellar junctions; bacteriocytes not confirmed. Labial palps distinct, with small distinctly ridged sorting areas. Lateral body pouches with 2 or 3 major processes, carrying few, smaller swellings. Foot vermiform with a swollen tip; heel indistinct.

Commensal polychaete. While dissecting the soft part to prepare the anatomical description, a commensal polychaete was observed entangled in the branches of the lateral body pouches (Fig. 12).

Distribution. Known only from the type locality in the Rockall Trough from the abyssal rise at a depth of 1595 m.

Remarks. *Rhombaxinus stellaris* has features in common with other small North Atlantic species; notably, the prodissoconch sculpture is shared with *R. equalis* (Fig. 11A). Payne & Allen (1991) recorded *R. equalis* as amphi-Atlantic and having a bathymetric range of 37–4734 m. They also considered *R. equalis* to be highly variable but gave no detailed descriptions, but it is possible that *R. stellaris* is present in their samples. Payne & Allen (1991) may have overlooked critical features due to the techniques they used or rather did not use. The use of scanning electron microscopy here and by Kamenev (2020, 2024) have revealed subtle but significant differences in adult shell and prodissoconch sculpture. A review of the Payne & Allen's samples using SEM may be instructive but beyond the scope of the present study. Consequently, I focus only with comparisons of nominal taxa already described.

Rhombaxinus equalis was described from off New England and Ockelmann thought it to be amphi-Atlantic, although he never published any comparative descriptions. Here I illustrate shells (Fig. 8), including prodissoconchs (Fig. 11), from both the Eastern and Western Atlantic along with scanning electron micrographs. Morphologically there are no substantive differences between populations from throughout the species' entire range.

Although the general pattern of the prodissoconch sculpture is shared with *R. equalis*, the number of crescentic ridges is about twice that present in *R. equalis* and the diameter is larger (170 μ m compared to 155 μ m). The absence of an auricle in *R. equalis* is confirmed from the shells illustrated in Figure 8. The calcified periostracal spicules have been looked for in *R. equalis* samples but have not been found. The underlying micro-punctate sculpture seen on the umbonal region of *R. stellaris* is also seen in *R. equalis*, but the marginal periostracum in the latter consists of thin, irregular, sub-commarginal lamellae, and calcareous structures have not been seen. Intricate patterns of calcification of the periostracum are not unique to *R. stellaris* but have been observed in *Thyasira flexuosa* (Fig. 6E, F).

Comparative material, *R. equalis* (A.E. Verrill & K.J. Bush, 1898). Lectotype, Casco Bay, off Maine, USNM 74302 • 15 spec., off Cape Lookout, North Carolina, 34° 16' 18" N 075° 45' 36" W, 599 m, USNM 1484494 • 42 spec., off Cape Hatteras, North Carolina, 35° 26' 26" N 074° 41' 18" W, 1985 m, USNM 1482831 • 95 spec., off Cape Hatteras, North Carolina, 35° 26' 20" N 074° 41' 34" W, 1985 m, USNM 1482838 • 46 spec., off Cape Hatteras, North Carolina, 35° 26' 16" N 074° 41' 26" W, 2003 m, USNM 1482829 • 50+ shells, Skagerrak, NMHD-1175731 • 20+ spec., West Greenland, Ingolf Sta. 25, 63° 51' N 053° 03' W,

249 m, NHMD1175734 • 20+ spec., West Greenland, Ingolf Sta. 28, 65° 14' N 055° 42' W, 791 m, NHMD1175917 • 6 spec., West Greenland, Pisigsarfik Fjord, 260 m, NHMD-1175908 • 5 spec., Barents Sea, RV *Sarsia*, Mareano Sta. 1200-BT, 70° 51.55' N 032° 31.01' E, 252 m, P. Oliver coll. • 20+ spec., Skagerrak, Dana Sta. 13351, 58° 17' N, 010° 58' E, 120 m, NHMD1175745 • 1 spec., Skagerrak, Dana Sta. 13353, 58° 16' N 009° 37' E, 700 m • 3 spec., Dana Sta. 2608, Seydisfjord, Iceland, 75 m, NHMD-1175743 • 7 spec., Iceland, Dana Sta. 3063, NHMD-1175741 • All material in NMW from the North Sea listed by Oliver & Killeen (2002).

Genus *Cryothyas* gen. nov.

Figures 7E, 13–15

ZooBank. urn:lsid:zoobank.org:act:923DE6A5-C333-4490-9DE7-B5EB119C484F

Type species. *Axinus flexuosa* var. *rotunda* Jeffreys, 1881 (lectotype, NHMUK 1885.11.5.886 (Fig. 13); type locality: Faroe-Shetland Channel, *Porcupine* Sta. 78).

Species included. *C. rotundus* (Jeffreys, 1881); *C. dunbari* (Lubinsky, 1976); *C. milnelandensis* sp. nov.

Derivation. *Cryo*, derived from Greek *kryos*, meaning “icy cold”, and *thyas*, a contraction of *Thyasira*. The name is in reference to the cold-water environments inhabited by species of this genus. Feminine.

Definition. Shell small, to 9 mm, equivalve, equilateral, not inflated. Outline rhomboidal; posterior sinus very shallow; posterior sulcus weak; submarginal sulcus well defined, lacking a raised auricle. Hinge lacking developed teeth but some species with a cardinal thickening; ligament deeply sunken. External sculpture weak, of commarginal ridges and growth lines, microscopically punctate. Prodissoconch sculpture vermiculate. Gill type 2aR. Mantle with 3 apertures. Assumed asymbiotic.

Remarks. See under *Rhombaxinus*.

Cryothyas rotundus (Jeffreys, 1881) comb. nov.

Figures 13–15, Table 3

Type locality. North-east Atlantic, Faroe-Shetland Channel, 60° 14' N 04° 30' W, 290 fms (530 m), HMS *Porcupine* cruise, summer 1869, station 78.

Type material. Lectotype (Fig. 14): 1 complete dry disarticulated sh., NHMUK 1885.11.5.886, leg. J.G. Jeffreys.

Paralectotype: 1 complete sh., valves joined, data as for holotype, NHMUK 1885.11.5.887.

Other material examined. The following material came

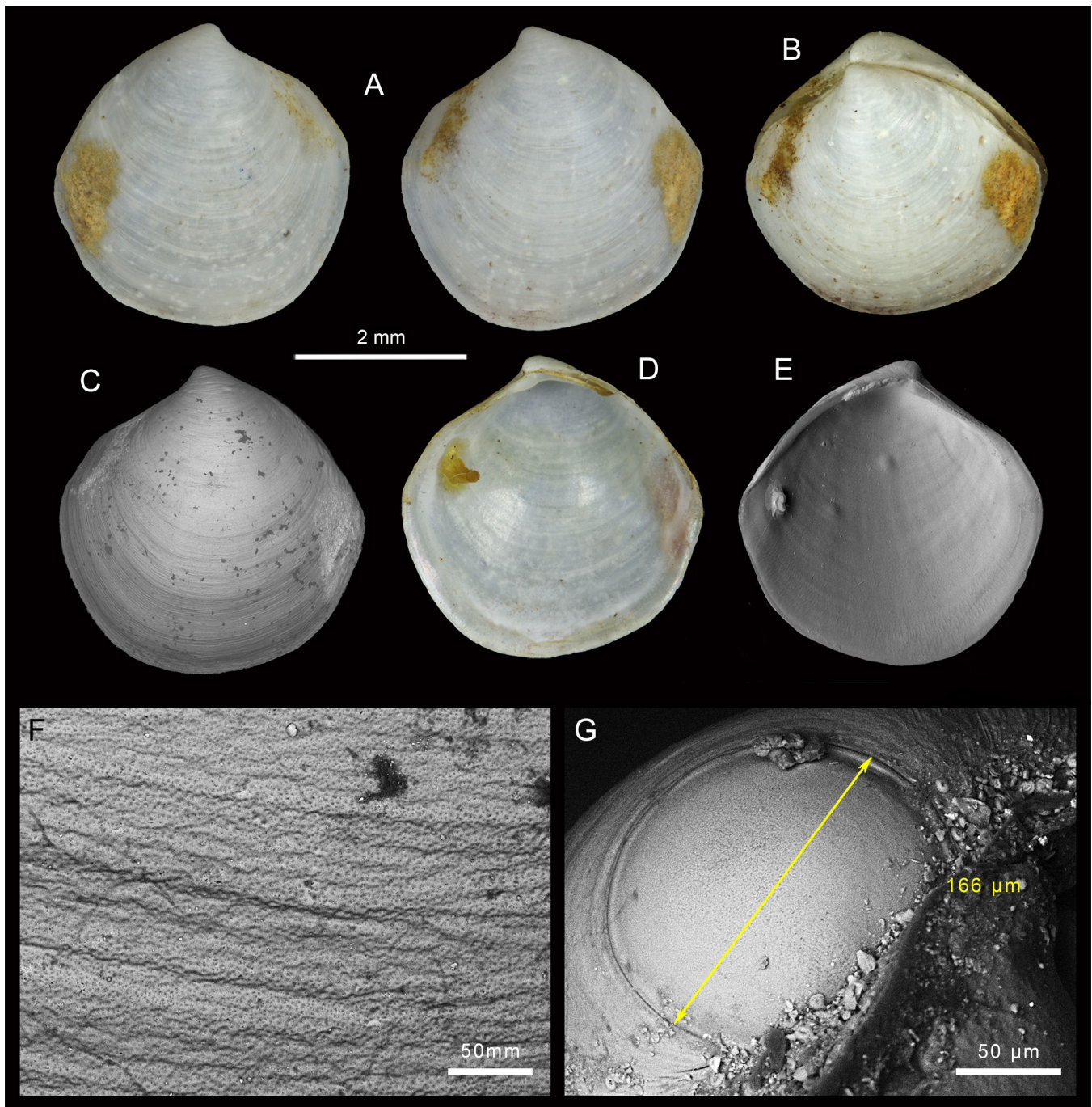


Figure 13. *Axinus flexuosus* var. *rotunda*, lectotype of *Cryothyas rotundus* (Jeffreys, 1881), NHMUK 1885.11.5.886. **A**, exterior of right and left valves. **B**, oblique view from left side. **C**, SEM of exterior of left valve. **D**, interior of right valve. **E**, SEM of interior of left valve. **F**, SEM of detail of exterior. **G**, SEM of prodissoconch.

from the North-east Atlantic, Faroe-Shetland Channel collected during RRS *Charles Darwin* Cruise 123C3-4 in 2000 (Figs 15, 16). Some additional material came from an earlier cruise of the RRS *Challenger* to the same region in 1976, all are deposited in NMW.

RRS *Charles Darwin* material: 3 sh., 4 apices on SEM

stub, 1 sh. on SEM stub, 5 spec. figured and measured, 4 spec. measured, 2 soft parts only, 25 spec. in 70% ethanol, 60°00.30'N 006°13.68'W, 1157 m, Sta. 55265#1/2, WTS4, 01 Aug. 2000, NMW. Z. 2026.001.01 • 13 spec. in 70% ethanol, 3 figured, 60°01.74'N 006°18.3'W, 998 m, Sta. 55263#1, Site J, 01 Aug. 2000, NMW. Z. 2026.001.02

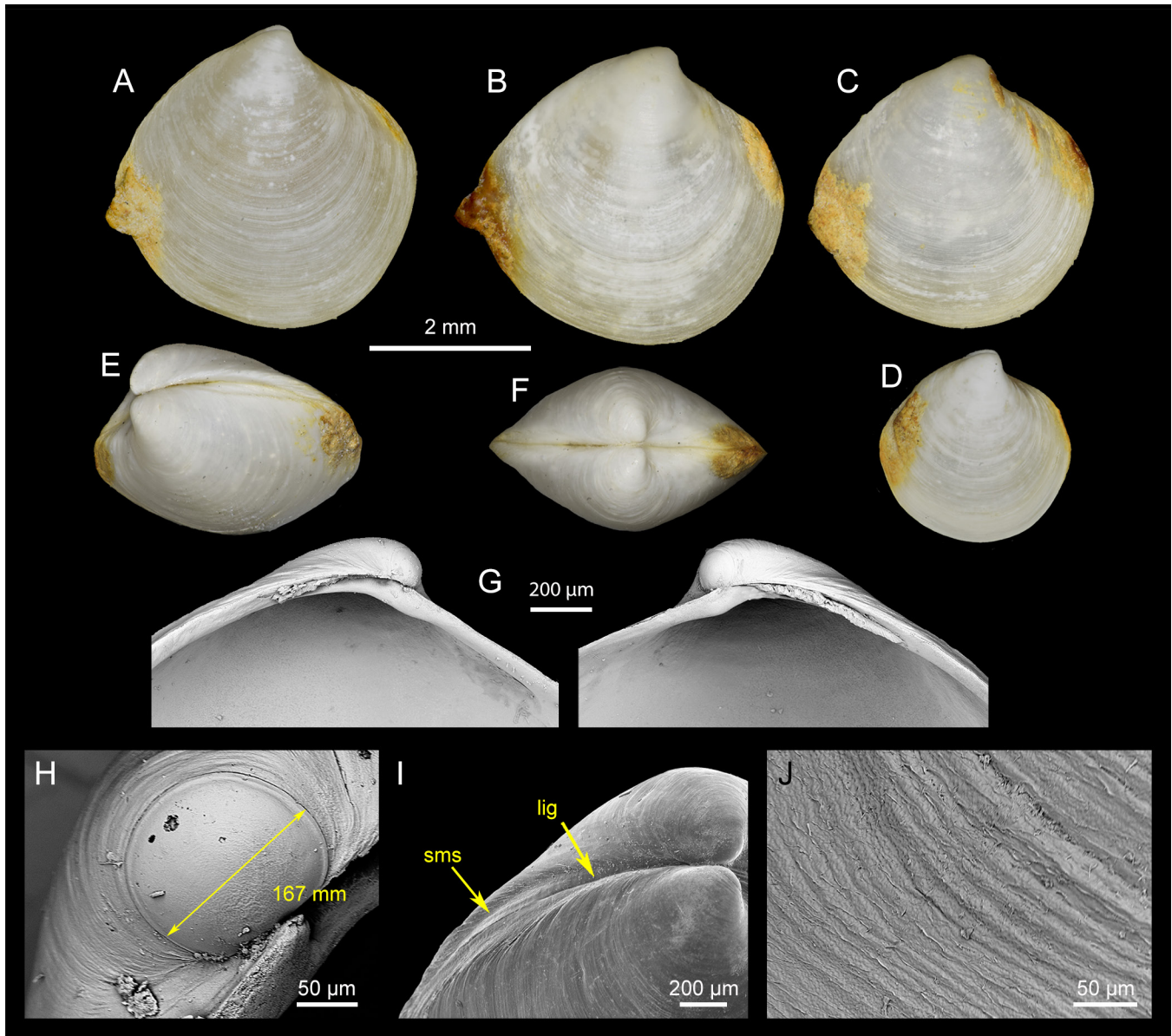


Figure 14. *Cryothyas rotundus*, from RRS *Charles Darwin* Cruise 123C3-4, Sta. WTS4, Faroe-Shetland Channel, 1157 m, NMW.Z.2026.001.01. **A–D**, size series. **E**, dorsal view. **F, G**, SEM of hinge of right and left valves. **H**, prodissoconch. **I**, submarginal sulcus and sunken ligament. **J**, SEM detail of periostracum.

• 7 spec. in 70% ethanol, 62° 19.50'N 000° 09.51'E, 940 m, Sta. 55375#2, 22 Aug. 2000, NMW. Z. 2026.001.03 • 4 spec in 70% ethanol, 61° 12.83'N 002° 25.92'W, 777 m, Sta. 55438#1, 31 Aug. 2000, NMW. Z. 2026.001.04 • 1 spec. in 70% ethanol, 61° 16.01'N 002° 31.32'W, 1029 m, Sta. 55441 #1, 31 Aug. 2000, NMW. Z. 2026.001.05 • 8 spec. in 70% ethanol, 62° 19.4'N 000° 12.03'E, 920 m, Sta. 55388#1, 24 Aug. 2000, NMW. Z. 2026.001.06 • 9 spec. in 70% ethanol, 60° 10.22'N 006° 32.88'W, 1183 m, Sta. 55237#1, 27 Aug. 2000, NMW. Z. 2026.001.07 • 3 spec. in 70% ethanol, 61° 08.07'N 002° 41.70'W, 792 m, Sta. 55402#1, 27

Aug. 2000, NMW. Z. 2026.001.08 • 62 spec. in 70% ethanol, 60° 04.24'N 006° 16.97'W, 1048 m, Sta. 55264#1-3, 01 Aug. 2000, NMW. Z. 2026.001.09 • 10 spec. in 70% ethanol, 62° 19.39'N 000° 12.02'E, 919 m, Sta. 55380#1, 24 Aug. 2000, NMW. Z. 2026.001.10 • 12 spec. in 70% ethanol, 62° 21.3"N 000° 32.18"E, 766 m, Sta. 55387#1, 2, NR6, 24 Aug. 2000, NMW. Z. 2026.001.11 • 1 spec. in 70% ethanol, 62° 14.3"N 000° 20.84"E, 676 m, Sta. 55331 #1–3, NR4, 17 Aug. 2000, NMW. Z. 2026.001.12 • 1 spec. in 70% ethanol, 61° 54.89'N 002° 48.24'W, 1623 m, Stat. 55447#3, 02 Sep. 2000, NMW. Z. 2026.001.13 • 5 spec. in

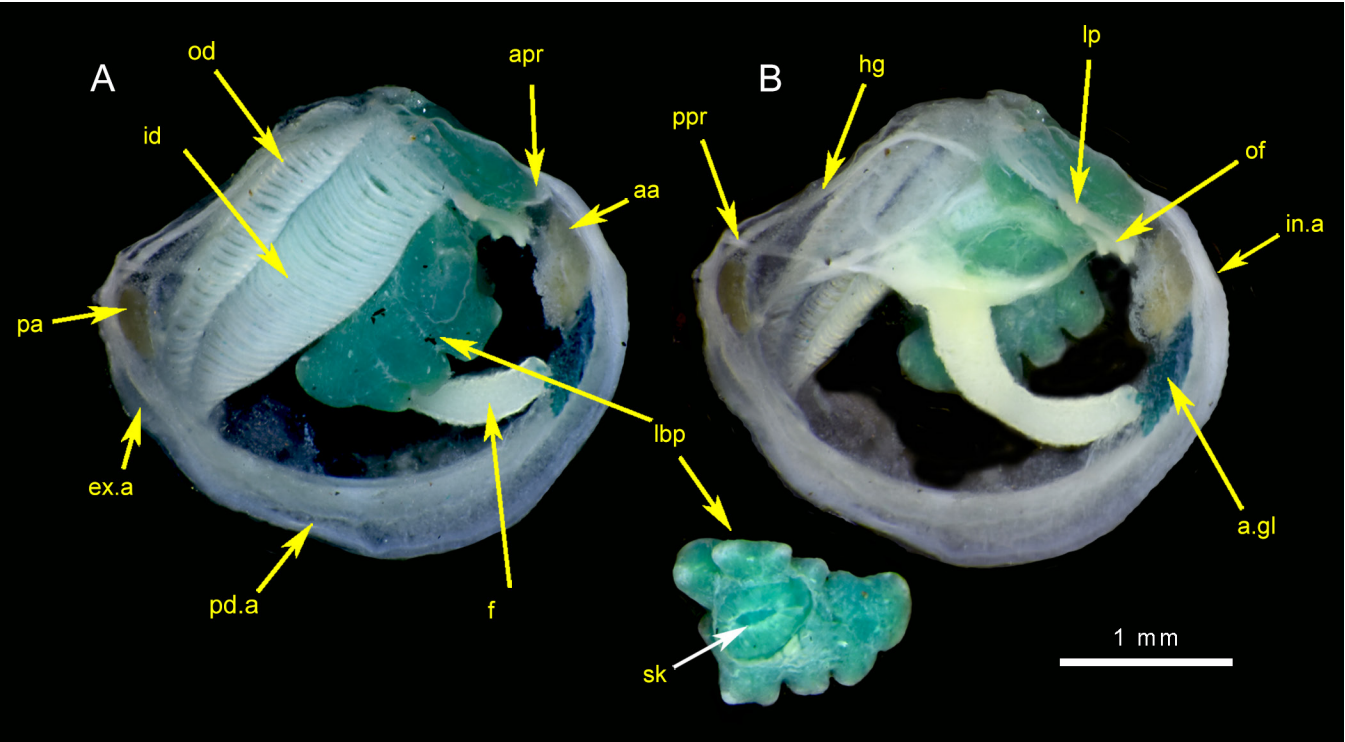


Figure 15. Anatomy of *Cryothyas rotundus* (Jeffreys, 1881) from RRS *Charles Darwin* Cruise 123C3-4, Sta. WTS4, Faroe-Shetland Channel, 1157 m, NMW.Z.2026.001.01. **A**, right side with mantle removed. **B**, right side with mantle and ctenidium removed.

70% ethanol, 60° 4.43'N 005° 56.22'W, 1067 m, Sta. 55249 #1, WTS9, 30 Jul. 2000, NMW. Z. 2026.001.14 • 41 additional lots, all NMW. Z. 2026.001 in 70% ethanol all from North-east Atlantic, Faroe-Shetland Channel collected during RRS *Charles Darwin* Cruise 123C3-4.

RRS *Challenger* cruise 10/76, 30 June–13 July 1976:

Table 3. Measurements of selected specimens of *Cryothyas rotundus* (Jeffreys, 1881) from the Faroe-Shetland Channel.

	Height (mm)	Length (mm)	Tumidity (mm)	L/H	L/T
Lectotype, dry	3.5	3.5	—*	1.00	—
WTS4 dry	3.7	3.65	2.2	0.99	1.66
Site J	3.55	3.6	2.1	1.01	1.71
Site J	3.2	3.2	2.0	1.0	1.60
Site J	3.05	3.0	1.9	0.98	1.57
Site J	3.15	3.05	1.9	0.97	1.61
WTS4	3.0	3.15	1.9	1.05	1.66
WTS4	3.15	3.2	1.9	1.02	1.68
WTS4	3.5	3.5	2.1	1.0	1.67
WTS4	2.85	2.9	1.75	1.02	1.66
WTS4	3.45	3.65	2.0	1.05	1.82

*Shell too delicate to manipulate and measure.

Challenger 10/76 Sta. SMG83, 60° 05.6'N 005° 55.4'W, 1100 m, NMW. Z. 2026.001.15 • *Challenger* 10/76 Sta. SMG85, 60° 05.1'N 005° 55.8'W, 1100 m, NMW. Z. 2026.001.16.

Description of lectotype and other specimens from the Faroe-Shetland Channel. Shell small, to 3.7 mm high (lectotype 3.5 mm; Table 3), fragile. Height and length approximately equal (H/L ratio 1:1.01), moderately inflated (L/T ratio 1.66:1), equivalve, equilateral. Beaks prosogyrate. Outline subcircular; anterior dorsal (lunule) margin short; lunule small, a little depressed, poorly defined; anterior inhalant margin short, not well defined; ventral evenly curved, a little narrowed in some; posterior sulcus weak, often indistinct; posterior sinus scarcely indented; submarginal sinus absent; postero-dorsal margin almost straight, slightly angled where ligament ends, sloping to a marked angular junction with ventral margin at just over ½ height; submarginal sulcus shallow, well defined; shell edges very slightly raised (auricle) posterior to sunken ligament. Hinge edentulous, except for very indistinct cardinal swelling. Ligament deeply sunken, about ½ length of submarginal sulcus, only anterior part visible in joined valves. Sculpture weak, of growth stops and fine commarginal lines, a little rugose over anteri-

or-dorsal slope and edges of submarginal sulcus. Microsculpture densely punctate, obscured by a thin periostracum with broken commarginal lirae. Muscle scars indistinct. Prodissoconch (Fig. 14H) with a marginal rim, 160–166 μm in diameter (166 μm in lectotype), with vermiculate microsculpture on apex.

Anatomy (Fig. 15, specimens from station WTS4). Anterior adductor muscle oval, diverging slightly from mantle edge for $c. \frac{1}{3}$ length; posterior adductor oval, $\frac{1}{2}$ size of anterior one. Mantle edge with 3 openings: anterior inhalant aperture to outside of anterior adductor muscle, with adjacent highly glandular area; ventral opening or pedal aperture; exhalant aperture immediately ventral of posterior adductor and adjacent to attachment of ctenidium. Fusion between exhalant and pedal apertures long, whether muscular or ciliary uncertain; fusion between anterior inhalant and pedal apertures not always present. Ctenidium of 2 demibranchs; outer demibranch $c. \frac{1}{3}$ depth of inner demibranch; both with fully reflected filaments; tips with lamellar junctions; bacteriocytes not confirmed. Labial palps small; ridged sorting areas indistinct; oral flaps prominent. Lateral body pouches with 7 large, smooth lobes. Foot vermiform with a long toe; heel indistinct.

Lectotype designation. *Axinus flexuosus* var. *rotunda* was very briefly described by Jeffreys (1881: 701) as “more circular and symmetrical, and not so globose, having the fold or groove very slight and only perceptible on the inside; perhaps a distinct species”. There is no exact type locality, although the first two stations he mentioned were from

the 1868 *Lightning* Expedition south of the Faroes. Jeffreys listed all stations from where he recorded this species (Table 4), and these ranged from 62°N to 38°N at depths of 173–2003 m. Verifiable material is scarce, with only two lots now available, one in NHMUK and the other in USNM.

The USNM material consists of two shells, USNM 16942 and USNM 16942a (Fig. 16A–D), which were selected as the “lectotype” and “paralectotype”, respectively, by Kurt Ockelmann but never formally published as such. Scanning electron microscopy reveals that these shells bear radially arranged spicules (Fig. 16C, D) and, therefore, have affinity to the genus *Parathyasira*. From labels in the USNM collection one can interpret that Ockelmann assumed these to be juveniles of *P. granulosa* (Monterosato, 1874). The USNM shells were taken in 1870 from *Porcupine* Sta. 22 off Portugal, adjacent to Sta. 23 where Jeffreys recorded *Axinus orbiculatus* Seguenza, 1876 *sensu* Jeffreys, 1881, which is now regarded as a synonym of *P. granulosa* (MolluscaBase Eds 2026). The figure by Jeffreys (1881: fig. 5) of his *A. orbiculatus* shows a shell with three radial ridges that are not seen in shells from the Gulf of Cadiz (Fig. 16E). Therefore, it seems improbable *Axinus orbiculatus* and *P. granulosa* are conspecific. The prodissoconch of the USNM lectotype (Fig. 16C) appears to have scattered granules over the surface a feature not seen in the prodissoconch of *P. granulosa* (Fig. 16F) from the Troll Oilfield in the northern North Sea. It is possible that the granules on the lectotype are artefacts but, regardless of this, the shape difference suggests that

Table 4. List of stations from which Jeffreys recorded *Axinus flexuosus* var. *rotunda*. L and P in the map correspond to the *Lightning* and *Porcupine* expeditions, respectively.

Station number	Geographic coordinates	Depth (fathoms) (equivalent m)	Equivalent depth (m)	
<i>Lightning</i> Expedition, 1868				
Sta. L1	59° 20' N 007° 05' W	500	914	
Sta. L3,	60° 31' N 009° 10' W	229	419	
<i>Porcupine</i> Expedition, 1869				
Sta. 35	49° 07' N 010° 57' W	96	176	
Sta. 39	49° 01' N 011° 56' W	557	1,019	
Sta. 62	61° 59' N 004° 38' W	125	229	
Sta. 78	60° 14' N 004° 30' W	290	530	
<i>Porcupine</i> Expedition, 1870				
Sta. 3	48° 31' N 010° 03' W	690	1,272	
Sta. 16	39° 55' N 009° 56' W	994	1,818	
Sta. 17	39° 42' N 009° 43' W	1,095	2,003	
Sta. 17a	39° 39' N 009° 39' W	740	1,353	
Sta. 22	38° 15' N 009° 33' W	718	1,313	

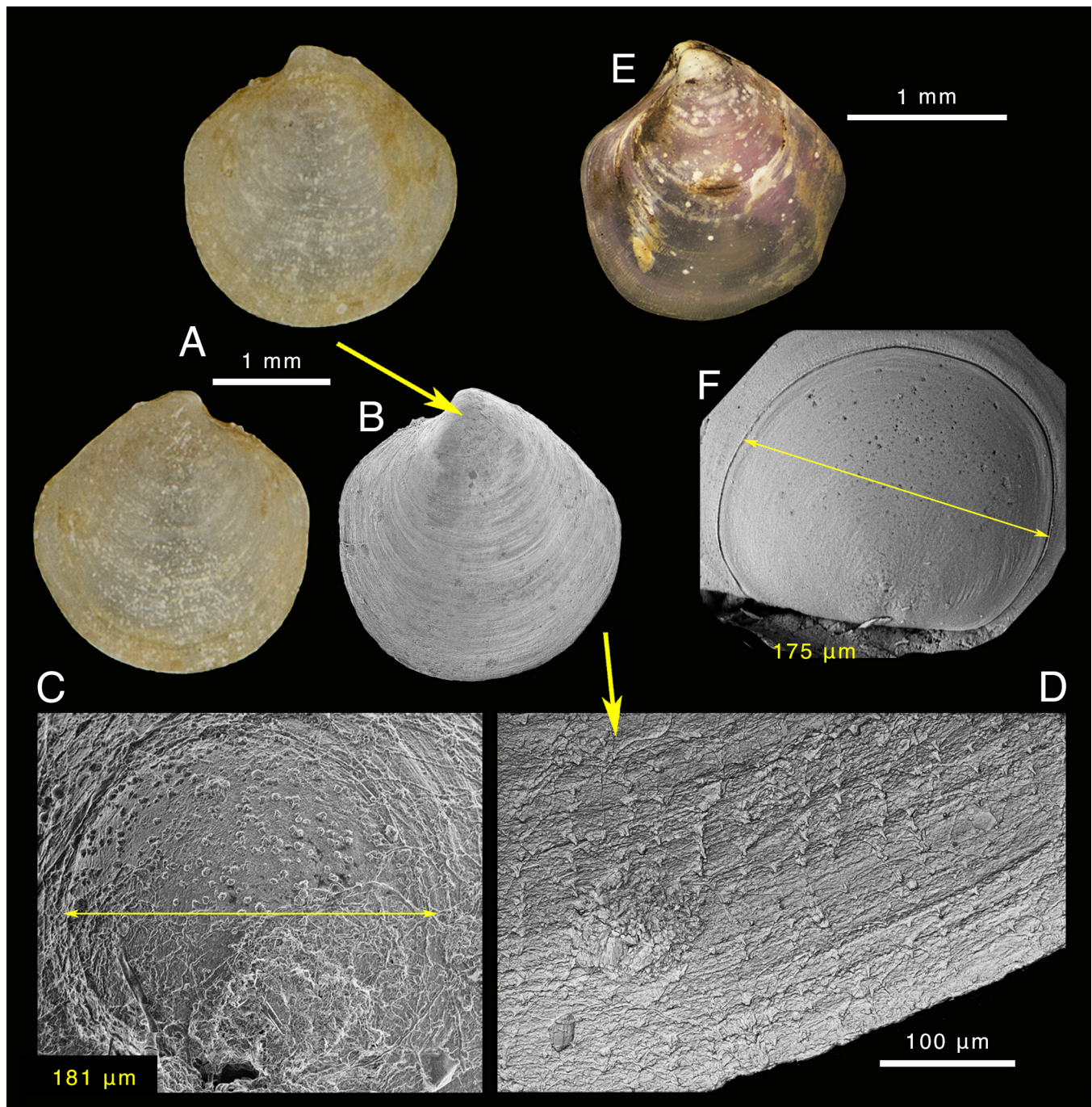


Figure 16. *Axinus flexuosus* var. *rotundus* Jeffreys, 1881 and *Parathyasira granulosa*. **A–D**, *A. flexuosus* var. *rotundus*, unpublished “lectotype” selected by K. Ockelmann, USNM 61942. **A**, exterior of left and right valves. **B**, SEM of exterior of left valve. **C**, SEM of prodissocoach. **D**, SEM detail of marginal sculpture. **E, F**, *Parathyasira granulosa* from Troll oilfield, North Sea: (**E**) exterior of right valve; (**F**) prodissocoach.

this shell is not *P. granulosa*. As Ockelmann’s lectotype designation was never published, and the identity of the Ockelmann’s “lectotype” is uncertain, a syntype from the NHMUK is selected here.

The NHMUK lot is listed in their register as consisting

of three shells donated by J.G. Jeffreys and coming from 61° 59'N 004° 38'W, which equates to *Porcupine* Sta. 62. The labelling with the contents is at variance to this; three shells and one larger valve are present with *Porcupine* Sta. 39, 62, and 78 given with a depth of 229 fathoms. This

depth equates to station 78. Originally the shells were attached to a rectangle of black, shiny paper but only three scars are visible, so it appears that the single larger valve has been added to the lot later. Of the three complete shells, only two are type material of *Axinus flexuosus* var. *rotunda*; the third is identified here as *T. obsoleta*.

As the earliest materials listed by Jeffreys are from the *Lightning* Expedition of 1868 and *Porcupine* Expedition of 1870 and fit best with Jeffreys' description, I have chosen a lectotype from the NHMUK material.

Comparisons. It is likely that *C. rotundus* has been misidentified and confused with *R. equalis* and *Thyasirella obsoleta* comb. nov. The microsculpture of the prodissococonch is very different from *R. equalis* in being vermiculate rather than menorah-like and the posterior margin is not vertically truncated.

Thyasirella obsoleta differs in having a developed auricle resulting in the presence of a submarginal sulcus seen in profile, in the posterior sulcus more developed, and in the microsculpture of the prodissococonch, which consists of an apical indentation (dimple) with weak commarginal puckered ridges over most of the disc (Fig. 9E). Payne & Allen (1991: fig. 23) postulated that *C. rotundus* was a variant of *T. obsoleta*, but the auricle is present in their figure of *C. rotundatus*, suggesting affinity with *T. obsoleta*.

From the collection in NHMD and from Kurt Ockelmann's archive (Oliver, 2025) it can be seen that Ockelmann recorded a widespread Atlantic/Arctic species under the manuscript name "*Thyasira frigida*". Despite making illustrations of this species, Ockelmann never published a description. This is the species he erroneously identified and figured as *P. equalis* (Ockelmann 1959: 108, fig. 7). At some time, he received a specimen collected from Isachsen, Arctic Canada in 1954 that he labelled "*Thyasira* n. sp.", which was later described by Lubinsky as *T. dunbari* Lubinsky, 1976. After the introduction of *T. dunbari*, Ockelmann adopted that name for his *T. frigida*. Since then, *T. dunbari* has been recorded from throughout the Arctic Ocean and in boreal and the temperate North Atlantic. It has been recorded from Arctic Canada at 83°N, south along the east coast of Greenland to Newfoundland at 49°N, north into the Labrador Sea and Baffin Bay, across the North Atlantic from Jan Mayen, Iceland, and Svalbard into the Barents Sea, and south along the coast of Norway to 60°N. Ockelmann's data give a bathymetric range of 6–536 m, with most records from within the 200 m contour, but it has more recently been recorded from the Haa-kon Mosby mud volcano at 1250 m (Aström *et al.* 2018).

From an examination of the extensive collections made

by Ockelmann, now in the NHMD, I believe that Ockelmann's *T. frigida* and *Cryothyas rotundus* are conspecific but not with *T. dunbari*, as described by Lubinsky (1976). However, I remain uncertain whether the entire spectrum of forms included in Ockelmann's *T. frigida* can be considered conspecific with *C. rotundus*. Very few shallow-water Arctic/East Greenland bivalves range into boreal waters of Western Europe (Ockelmann 1959). Most of the East Greenland bivalve biomass is concentrated around 100 m, and here it is influenced by the polar cold-water current from the north. In shallow fjords the fauna is subjected to the summer meltwater, which raises temperatures and lowers salinity. In the Faroe-Shetland Channel, most samples of *C. rotundus* come from 600–1000 m and reside in the cold-water area influenced by Norwegian Cold Deep Water, where the temperature ranges from 0 to 4 °C. At shallower depths on the slope, warm north-flowing Atlantic waters mix and increase the temperatures variably up to 9 °C, depending on the seasonal instability. The warm Atlantic current influences the entire coast of Norway and runs into the Barents Sea. Norwegian records of *C. rotundus*, originally identified as *C. dunbari*, show a pattern where most have been found in waters less than 500 m in depth and have become increasingly found in warmer coastal areas to the north following the warmer Atlantic current (Thomas Hansen pers. comm.) Such variations in habitat and bathymetric range suggest that the bathyal *C. rotundus* may well not be conspecific with the mostly shallower samples from the Arctic, East Greenland, and northern Norway.

However, if both shallow water and bathyal populations are conspecific then *C. rotundus* becomes the earliest available name for that wide-ranging species. For comparison I illustrate here the variety of forms from across the North Atlantic and Arctic previously identified as *T. frigida* and *T. dunbari* by Ockelmann in his collection in the NHMD.

Samples from Iceland and Ockelmann's unpublished "T. frigida" (Fig. 17)

Material examined. All North Atlantic Ocean, north of Iceland, Danish *Ingolf* Expedition: 1 sh. selected as "holotype" by Kurt Ockelmann, Sta. 126, 67° 19' N 015° 52' W, 293 fms (536 m), NHMD-1175760 • 84 spec. in 70%, Sta. 126, 67° 19' N 015° 52' W, 293 fms (536 m), NHMD-1175753 • 48 spec in 70% ethanol & 50+ dry sh., v. & 1 sh., 6 v. gold-coated for SEM, Sta. 128, 66° 50' N 020° 02' W, 194 fms (355 m), NHMD-1175737 (wet) NHMD-1175758 (dry).

Description. Shell to 5 mm high, equivalve, equilateral. Beaks prosogyrate. Outline rhomboidal; height equal to or

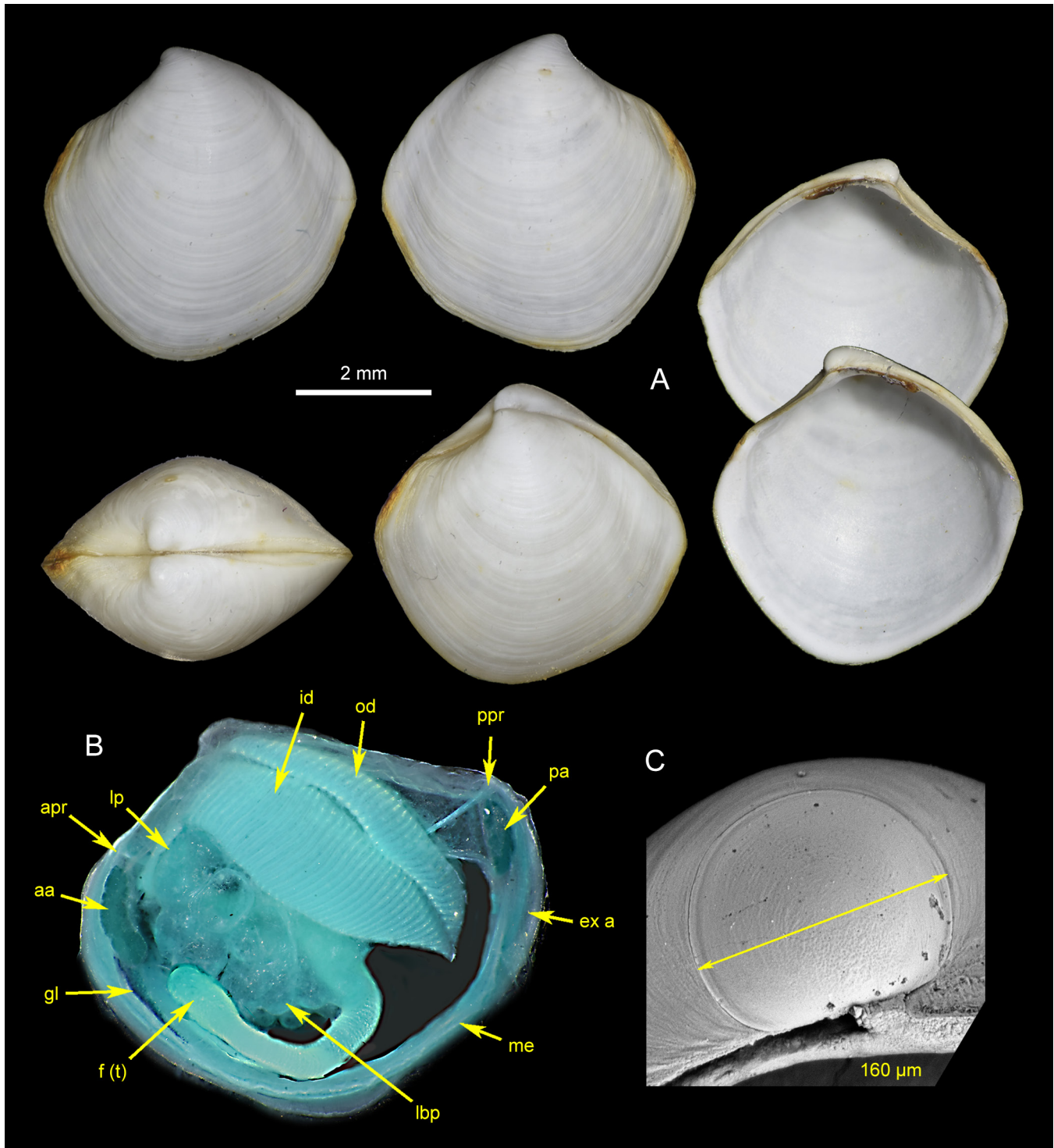


Figure 17. *Cryothyas cf. rotundus* (Jeffreys, 1881), all from Ingolf Sta. 126. A, “holotype” of *Thyasira frigida* Ockelmann MS chosen by Ockelmann, NHMD-1175760. B, anatomy. C, prodissoconch. NHMD-1175753.

slightly greater than length; posterior sulcus shallow; posterior sinus as a slight straightening; ventral margin slightly attenuated; anterior inhalant margin distinctly angled. Lunule slightly sunken; submarginal sulcus sharply de-

fined; auricle absent or midline slightly raised. Sculpture of fine commarginal lines and growth stops. Hinge weak, with a single, poorly developed pseudo-tooth; ligament $\frac{1}{2}$ length of submarginal sulcus, deeply sunken. Prodisso-

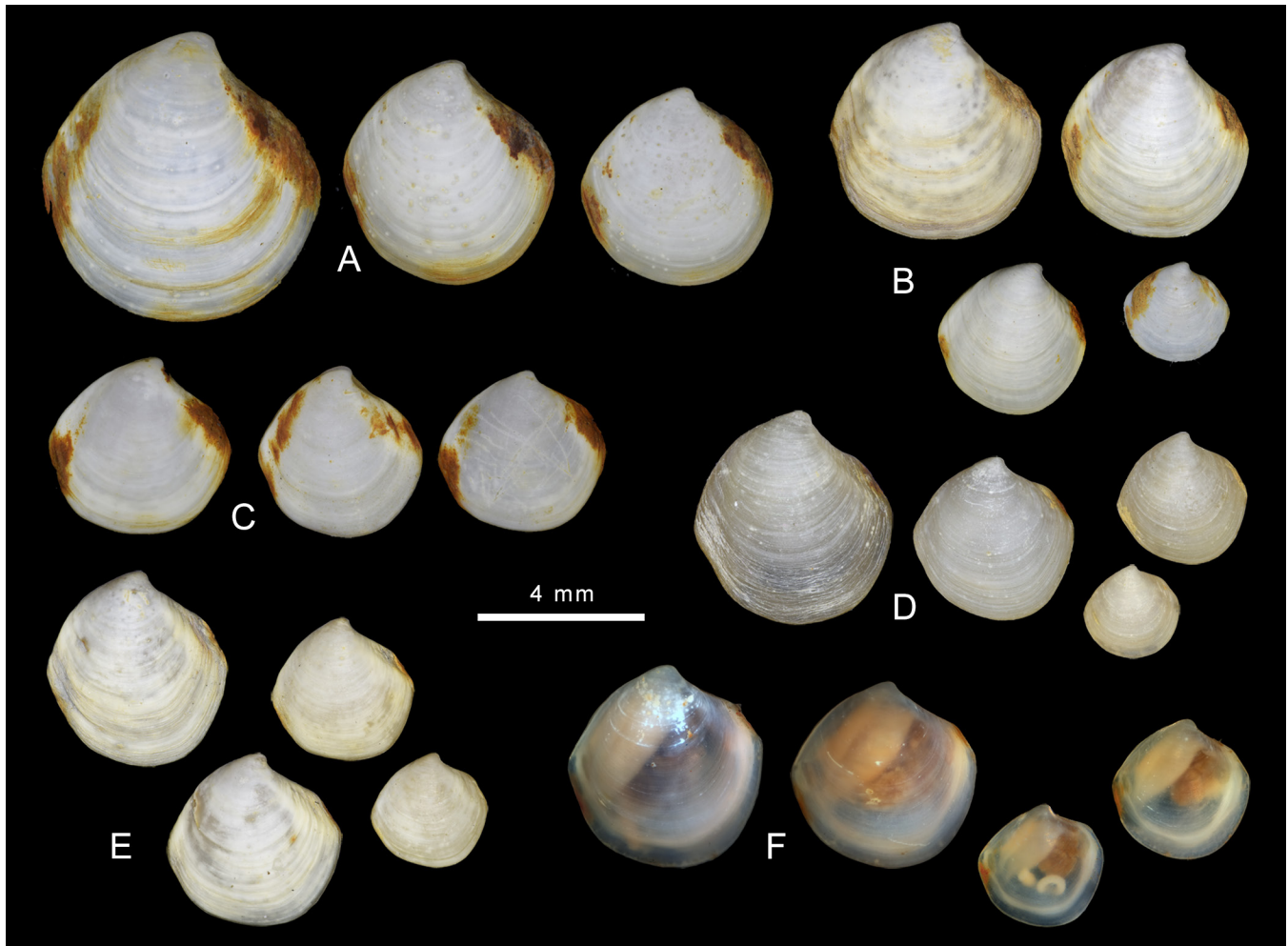


Figure 18. *Cryothyas* cf. *rotundus* (Jeffreys, 1881) from Newfoundland to Scoresby Land, East Greenland, and Jan Mayen. **A**, from Nordbugten Bay, NHMD-1175798. **B**, from Hurry Inlet, NHMD-1175799. **C**, west coast of Jameson Land, NHMD-1175804. **D**, Jan Mayen, NHMD-1175733. **E**, from Lindenow Fjord, NHMD-1175906. **F**, Bonne Bay, photos courtesy of Suzanne Dufour.

conch 160 mm, with vermiculate apex. Periostracum with weak commarginal threads; underlying shell microsculpture deeply, densely punctate.

Anatomy (Fig. 17B). Anterior adductor muscle elongate, twice size of posterior adductor muscle. Mantle edge posteriorly fused to form a small exhalant aperture; elsewhere open, with glandular tissue adjacent to inhalant aperture. Ctenidium of 2 demibranchs, with outer demibranch $\frac{1}{2}$ depth of inner one; filaments reflected. Labial palps with small, ridged sorting area. Lateral body pouches with few large lobes. Foot vermiform; toe often bulbous.

Remarks. The rhomboidal shape of the shell is shared with many other samples previously labelled as *T. dunbari*, and this form is widely distributed in the Arctic, East Greenland, and south to Newfoundland. Typical *C. rotundus* is

less rhomboidal, the lunule is not sunken, and the anterior inhalant margin is less developed.

I have not given Ockelmann's *T. frigida* manuscript name nomenclatural status, although it represents well the samples from the Arctic and cold waters of East Greenland and the Labrador Sea. As *T. frigida* has never been formally published, it can be used, if the *frigida* form is later shown to be distinct from *C. rotundus*.

Samples from Newfoundland (48°N) to Scoresby Sound (70°N) (Fig. 18)

Material examined. All the following material was labelled as *T. flexuosa* then changed to *T. frigida* or *T. dunbari* by Kurt Ockelmann: 5 spec. in 70% ethanol, Nordbugten Bay in Nordvestfjord, Godthab Sta. 208, 71°35'N 026°27.2'W, 28 m, 21 Jul. 1933, NHMD-1175798 • 5 spec. in 70% ethanol, Vestkysten af Jamesonland opposite Bjør-

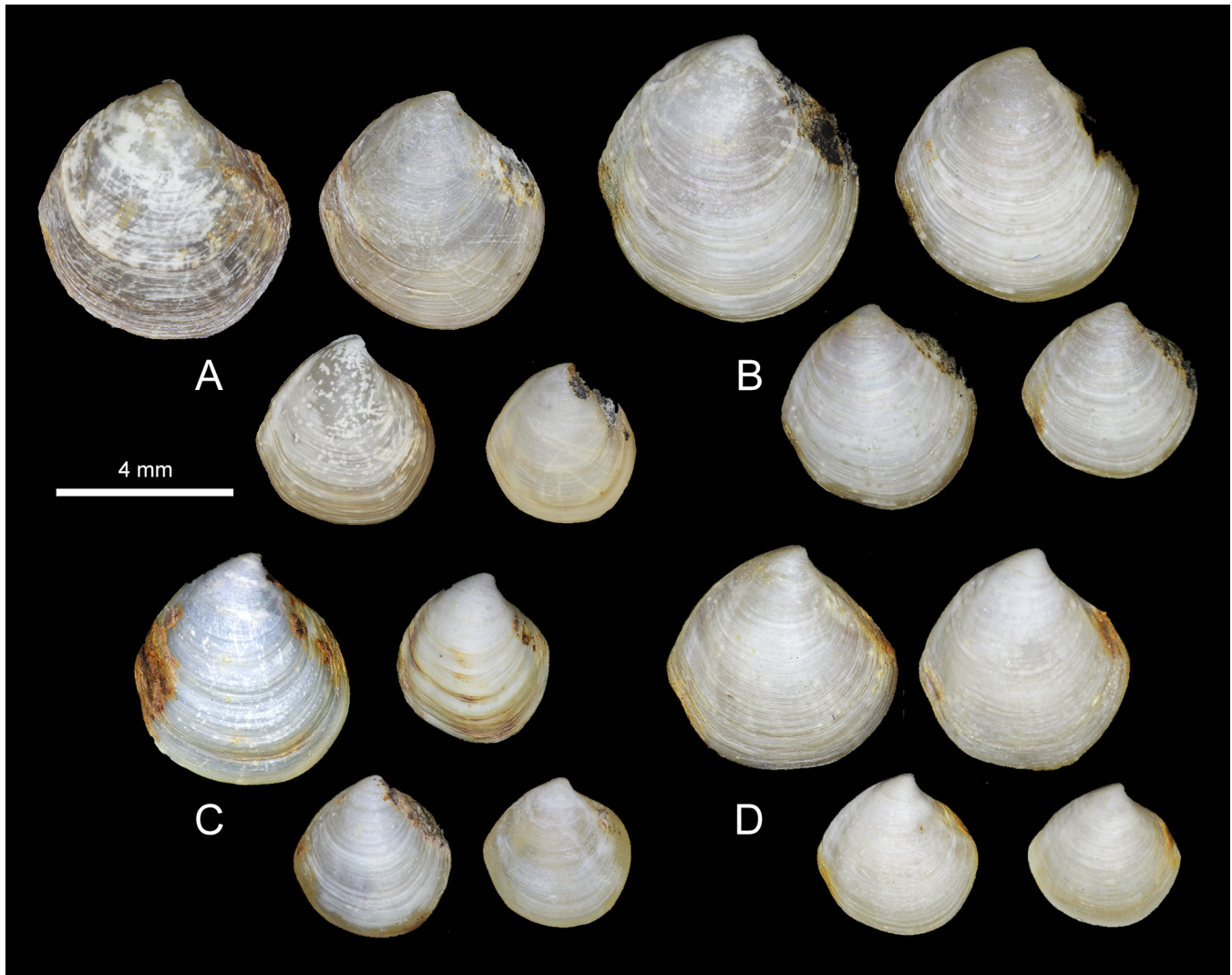


Figure 19. *Cryothyas cf. rotundus* (Jeffreys, 1881) from the Greenland Sea, Franz Joseph Fjord (c. 73°N) to Jørgen Brønlund Fjord (c. 82°N), **A**, Jørgen Brønlund Fjord NHMD-1175792–1175795. **B**, Moskusse Fjord, 45m, NHMD-117800. **C**, Moskusse Fjord, 200m, NHMD-1175803. **D**, Zoologdalen NHMD-1175801.

neøerne, Godthab Sta. 261, c. 71°09'N 025°0'W, 78 m, NHMD-1175804 • 11 spec., in 70% ethanol, Udfor Mundingen, Hurry Inlet, Godthab Sta. 56, c. 70°36.0'N 022°31.0'W, 153 m, NHMD-1175799 • 20+ spec. in 70% ethanol, Lindenow Inner Fjord, E. Berthelsen Sta. 14³, c. 60°31'N 043°40'W, 100–150 m, 22 Jul. 1935, NHMD-1175906 • 20+ spec. in 70% ethanol. Lindenow Inner Fjord, E. Berthelsen Sta. 16⁴, c. 60°31'N 043°40'W, 125–150 m, 24 Jul. 1935, NHMD-1175907 • 20+ spec. in 70% ethanol, Jan Mayen, *Ingolf* Sta. 115, 70°50'N 008°29'W, 157 m, NHMD-1175733.

Remarks. Specimens from Newfoundland, identified as *Thyasira dunbari* Lubinsky, 1976 but considered here to be *Cryothyas cf. rotundus*, are included for comparison.

This determination is based on photographs supplied by Suzanne Dufour.

Most of these samples contain shells with a rhomboidal outline and agree with Ockelmann's *T. frigida*. An exception may be the shells up to 7 mm long from a depth of 28 m in Nordbugten Bay, which may represent small examples of those from Milne Land.

The prodissoconch slightly varies in size, 170–176 µm, in specimens from between 60°N and 71°N, and these are substantially larger than in specimens from Bonne Bay, Newfoundland at 48°N (147 µm).

Samples from Franz Joseph Fjord (73°N) to Jørgen Brønlund Fjord (82°N) (Fig. 19)

Material examined. Jørgen Brønlund Fjord off Pileodden,

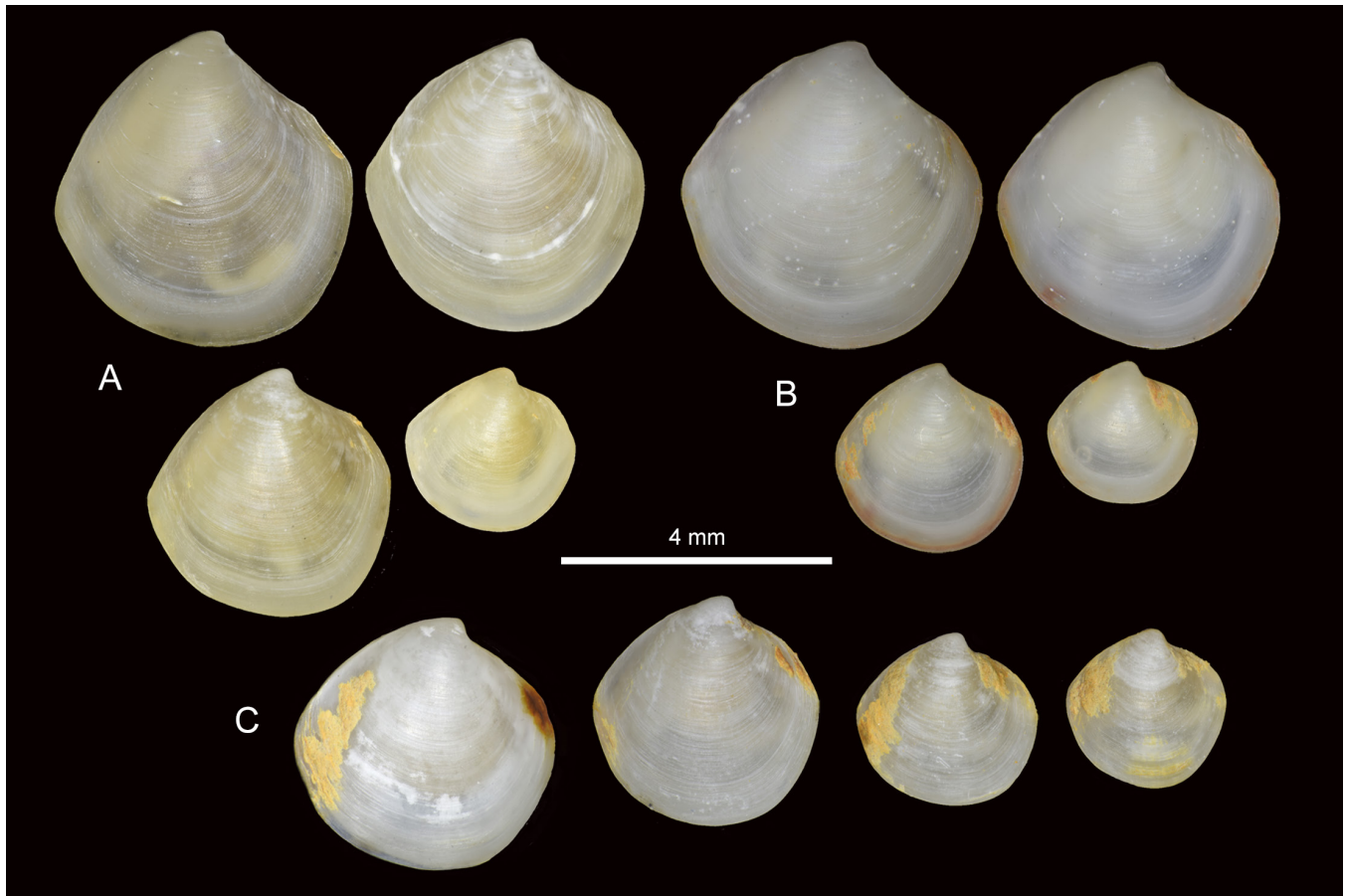


Figure 20. *Cryothyas cf. rotundus* (Jeffreys, 1881) from eastern Arctic seas and Svalbard, all coll. P.G. Oliver. **A**, from Barents Sea. **B**, Inner Kongsfjord, Svalbard **C**, north of Svalbard at 80.5°N. All specimens in P.G. Oliver coll.

82° 11.2'N 030° 32'W, 47.5 m, Just & Andersen Sta. 3, 4, 5 & 15, 19 May & 21 May 1966, cited by Schiøtte (1989): 2 spec. in 70% ethanol & 1 disarticulated on SEM stub plus 1 apex, Sta. 4, NHMD-1175795 • 1 good spec. in 70% ethanol, 5 poorly preserved & 1 apex on SEM stub, Sta. 3, NHMD-1175792.

14 spec. in 70% ethanol & 1 v. on SEM stub, Moskusoksefjord, adjacent to Mt Anker Dalen, Godthab Sta. 20, 45 m, NHMD-1175800 • 5 spec., 3 v. in 70% ethanol & 2 v. & 3 apices on SEM stubs, Moskusoksefjord, adjacent to Mt Høgborn, Thorson 1982, Godthab Sta. 22, 200 m, NHMD-1175803 • 9 spec. in 70% ethanol, Zoologdalen, off Ymer Ø, Godthab Sta. 68, 160 m, NHMD-1175801 • 6 spec. in 70% ethanol, S. of Kap Franklin Godthab Sta. 115, 160 m, NHMD-1175796.

Remarks. The shells from shallow water in Jørgen Brønlund Fjord and Moskusoksefjord are distinctly higher than long and with long lunule margins. The shells from deep water at Zoologdalen and Moskusoksefjord are more rounded and ventrally less attenuated.

Samples from Svalbard and Barents Sea (Fig. 20)

Material examined. 5 spec., Barents Sea RV G.O. Sars, Mareano Sta. 1137RP, 72° 20.885'N 032° 13.842'E, 272 m, P.G. Oliver coll. • 5 spec., Barents Sea RV G.O. Sars, Mareano Sta. 1200BT, 70° 30.93'N 032° 18.606'E, 251 m, P.G. Oliver coll. • 4 spec. Svalbard, NW Spitsbergen, Inner Kongsfjord, 78° 55.486'N 012° 21.061'E, 43.88 m, leg. J. Steger, P.G. Oliver coll. • 4 spec. Svalbard, N of Spitsbergen, 80° 49.407'N 014° 14.690'E, 1008 m, leg. J. Steger, P.G. Oliver coll.

Remarks. The shells from the Barents Sea (Fig. 20A) and Kongsfjord (Fig. 20B) in Svalbard are distinctly rhomboidal but the shells from the deep water north of Svalbard (Fig. 20C) are more rounded or less attenuated with height and length roughly equal.

Thorson's and Rass's rules propose that egg size and larval size increase with latitude (Laptikhovsky, 2006). The prodissoconch in the Jørgen Brønlund Fjord sample is large at 180 µm but smaller than that of *C. dunbari* at 193 µm although living at a higher latitude 82°N as opposed

to 78°N. The Svalbard samples come from roughly similar high latitudes at 78°N to 80°N but the prodissoconch size is significantly smaller at around 170 mm. Similar anomalies are seen in Svalbard shells that regardless of bathymetry have prodissoconchs of the same size at 170 mm. Despite coming from a similar latitude in the Barents Sea the prodissoconch is only 157 mm. Such observations suggest that Thorson's and Rass's rules are not as strict as first proposed or perhaps there is a genetic basis to the differences in prodissoconch sizes observed here.

Combined distribution. Assuming that the above are all one species, the combined range of *C. rotundus* is: North Atlantic from Newfoundland into the Labrador Sea, Greenland Sea (including the entire coast of East Greenland, Iceland, Jan Mayen, Svalbard, Faroe-Shetland Channel), Norwegian Sea (including the northern coast of Norway), and Barents Sea.

Combined bathymetric range. Typically, at depths between 40 and 250 m, but shallower in Greenland fjords and deeper, to 1250 m, in the Norwegian Sea and Faroe-Shetland Channel.

Samples from Lydonia Canyon, off Massachusetts (Fig. 21)

Material examined. 8 spec., Lydonia Canyon, off Massachusetts, 40°27'32"N 067°40'20"W, 560 m, USNM 1482392 • 6 spec., Lydonia Canyon, off Massachusetts, 40°27'30"N 067°40'16"W, 560 m, USNM 1482732 • 7 spec., Lydonia Canyon, off Massachusetts, 40°29'32"N 67°40'13"W, 560 m, USNM 1482734

Remarks. Although identified as *Thyasira rotunda* in the USNM collections, the outline of the shells is almost circular and the largest shell has a distinct posterior sinus. The largest shell (part of USNM 1482734) is more similar to *Thyasira plana* A.E. Verrill & K.J. Bush, 1898 which was described from off Massachusetts.

Cryothyas dunbari (Lubinsky, 1976)

Figure 22

Type material. Holotype: sh., Hole in Fog Bay, Isachsen, Eilef Rignes Island, 78°47'N 103°32'W, 12.5 m, 14 June 1954, CMN 75803.

Other material examined. 1 sh. + 1 v., as *Thyasira* sp. nov., Isachsen, Sta. 14, 14 July 1954, CMN, leg. Ockelmann, NHMD-1175909.

Description. Dimensions: H 8.5 mm, L 7.1 mm, W 5.0 mm (from type description: H/L ratio 1.16–1.30, W/L ratio 0.70–0.84; Lubinsky 1976).

Shell thin, inflated, equivalve. Beaks distinctly prosogyrate. Outline pyriform, much higher than long; dor-

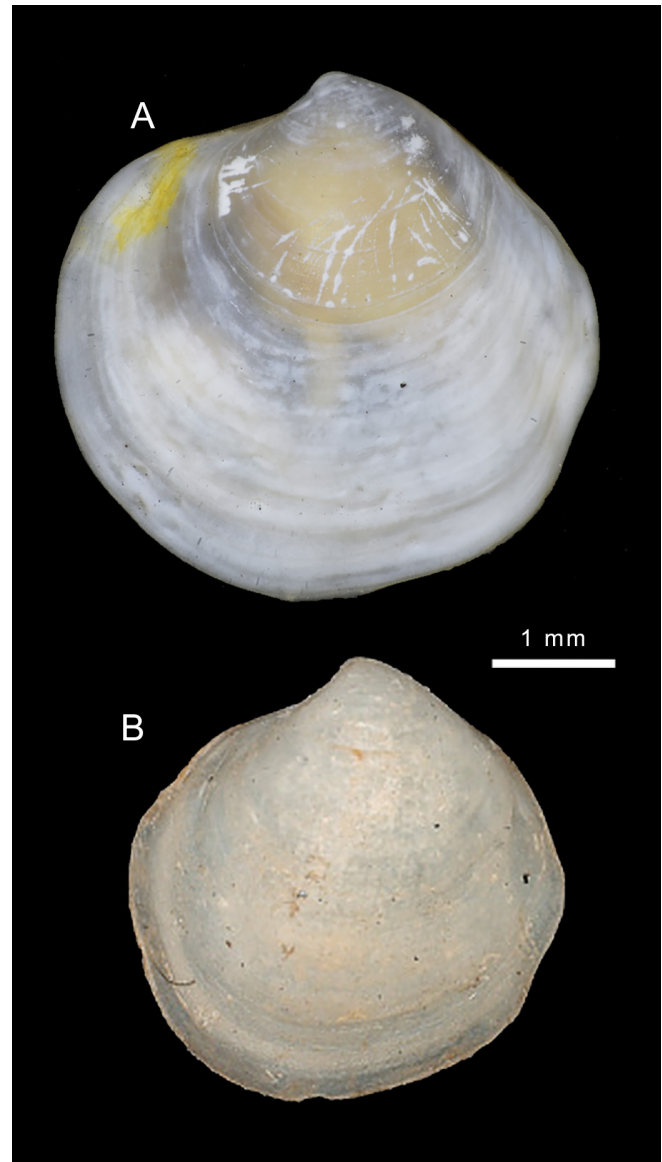


Figure 21. **A**, *Thyasira* from Lydonia Canyon identified as *C. rotundus* (Jeffreys, 1881) but probably *T. plana* (A.E. Verrill and Bush, 1898), USNM 1482734. **B**, syntype of *Cryptodon planus* (A.E. Verrill & K.J. Bush, 1898), USNM 159893.

sal anterior slope (lunule margin) long, slightly concave; dorsal posterior slope (submarginal sulcus margin) long, slightly curved; ventral margin attenuated; submarginal sulcus narrow, defined by sharp edge, auricle absent, ligament deeply sunken. Posterior sulcus scarcely developed. Lunule large, sunken, defined by a weak, rounded ridge. Hinge with prominent, bulging pseudo-tooth and accompanying socket in each valve; hinge plate thickened below ligament (Fig. 22E, F). Sculpture of distinct commarginal, raised threads, ventrally increasing in density. Periostracum persistent, adherent, thin, but developed into star-like

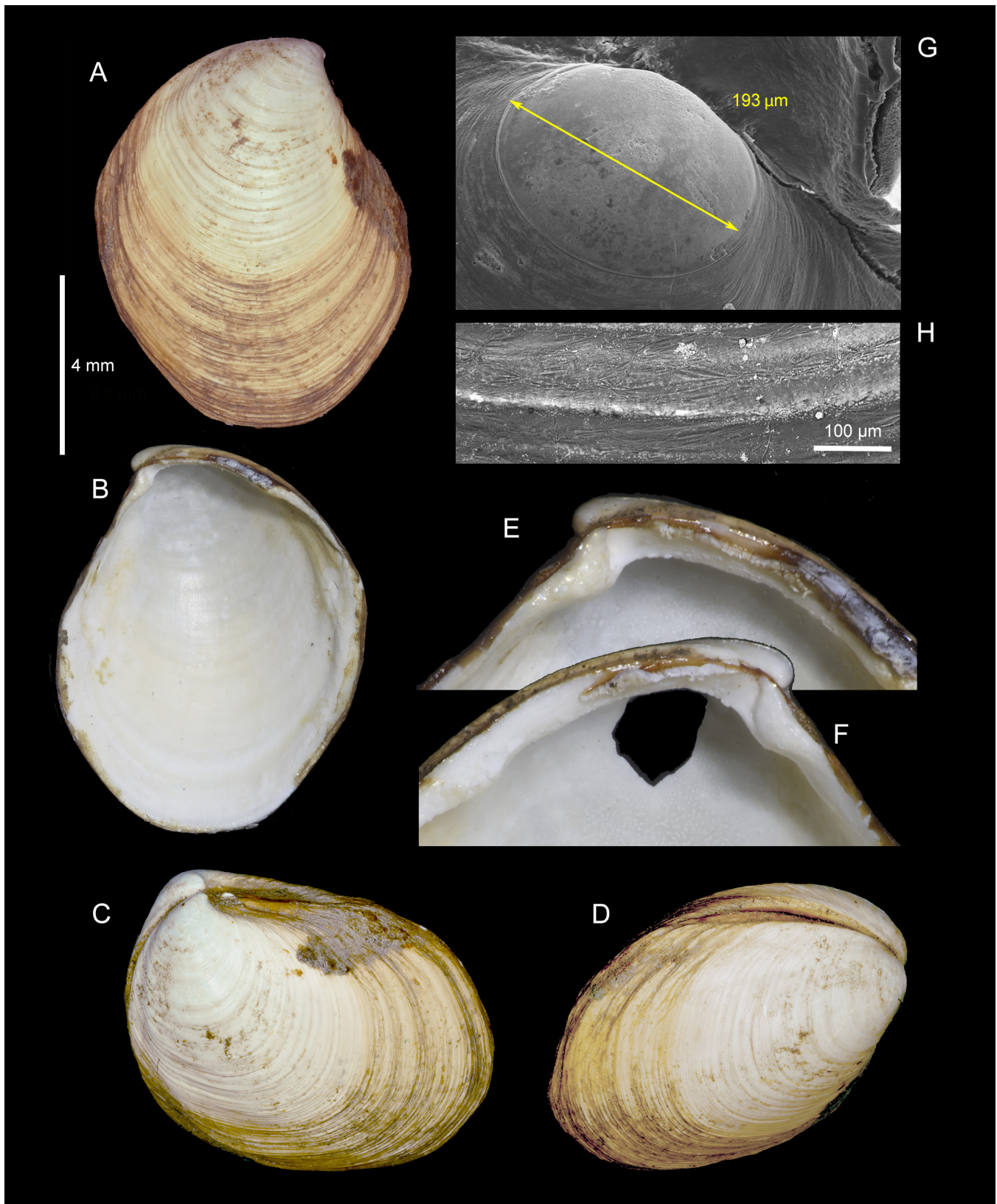


Figure 22. *Cryothyas dunbari* Lubinsky, 1976, paratype, NHMD-1175909. **A, B**, external and internal of right valve. **C**, anterior oblique view to show lunule. **D**, posterior oblique view to show submarginal sulcus. **E, F**, hinge of right valve and left valve (not to scale). **G**, prodissoconch. **H**, SEM detail of the periostracum.

shapes (Fig. 22H); microsculpture under periostracum finely punctate. Prodissoconch with a weak rim, oval, 193 μm wide, with minutely vermiculate apex (Fig. 22G).

Remarks. The oblique pyriform outline, prominent pseudo-teeth, periostracal structure, and very large prodissoconch separate *C. dunbari* from all other materials in Ockelmann's samples. Both the type material of *C. dunbari* and the large specimens from Milne Land were taken from shallow water, less than 20 m, and will have been subjected to summer melt waters with temperatures much greater than 0°C. These forms have not been found elsewhere in the entire given range previously assigned to *C. dunbari*.

***Cryothyas milnelandensis* sp. nov.**

Figure 23

ZooBank. urn:lsid:zoobank.org:act:93CAF41D-95AE-41E8-9CC9-6B0A7BB02A5C

Type locality. Off Milneland, East Greenland.

Type material. Holotype: sh., East Greenland, NOA Veg på Milne Land, Thorson Sta. 340, 10–15 m, 26 August 1933, NHMD-1175905/1. **Paratypes:** 3 v., data as for holotype, NHMD-1175905/2 • 3 spec., shells fragmented, in 80% ethanol, NHMD-1175905/3 • 2 apices and 1 fragment on SEM stubs, data as holotype, NHMD-1175905/4.

All of the above material was originally labelled *Thyasira flexuosa*, then *T. dunbari*, by Kurt Ockelmann.

Etymology. The name is in reference to the type locality, Milneland.

Diagnosis. Shell to 10 mm high; outline pyriform; anterior and posterior margins steeply sloping; posterior sulcus prominent; submarginal sulcus narrow; auricle absent; lunule wide, flat; hinge with weak cardinal thickenings.

Description. Shell of holotype 9.8 mm high, thin, equivalve, inflated. Beaks prosogyrate. Outline pyriform, much higher than long; dorsal anterior slope (lunule margin) long, more or less straight, slightly concave; dorsal poster slope (submarginal sulcus margin) long, slightly curved, with a small shallow sinus at junction with ventral margin; ventral margin evenly curved; submarginal sulcus narrow, defined by sharp edge; auricle absent; posterior sulcus distinct, shallow, narrow, close to posterior edge. Lunule large, sunken, defined by a weak, rounded ridge (Fig. 23C). Hinge thickened below beaks but without discernible tooth or bulge (Fig. 23D, E); ligament just under $\frac{1}{2}$ length of submarginal sulcus. Sculpture of numerous narrow, commarginal lirae, ventrally increasing in density. Periostracum thin, scarcely visible (Fig. 23G). Black surface deposits over anterior siph-

onal margin only. Prodissoconch with a weak rim, oval, 173 μm wide; apex densely vermiculate (Fig. 23F).

Anatomy. Adductor muscles relatively small; anterior adductor muscle elongate-oval; posterior adductor muscle oval, $\frac{1}{2}$ size of anterior one. Mantle edge not fused, except for small posterior exhalant aperture (Fig. 23H ex.a) ventral to posterior adductor; anterior inhalant aperture adjacent to anterior adductor marked by associated glandular tissue (Fig. 23H, a.gl); ventral opening or pedal aperture not distinguished. Ctenidium (Fig. 23H, H¹) of two demi-branches: outer one c. $\frac{1}{3}$ depth of inner one; both with fully reflected filaments; filament tips with lamellar junctions; bacteriocytes not confirmed. Labial palps small; ridged sorting areas indistinct. Lateral body pouches very large, with numerous smooth lobes. Foot vermiform, very long; heel indistinct; tip slightly swollen (Fig. 23H, f(t)).

Distribution. Known only from Scoresby Sund, East Greenland, in shallow water to 20 m.

Remarks. This species is much larger than any of the varieties of *C. rotundus* and has a much more tumid, symmetrically pyriform outline with a distinct posterior sulcus. In size it is most similar to *C. dunbari*, but that shell has strong pseudo-teeth, a distinctly angled posterior margin, and a much larger prodissoconch.

Cryothyas milnelandensis lives in relatively very shallow water in the mouth of a creek where one assumes it is subjected to considerably lower salinity in summer with freshwater meltwater.

Genus *Thyasirella* gen. nov.

Figures 7F, 24

ZooBank. urn:lsid:zoobank.org:act:8CBF62CF-E585-403D-B652-A558960BF5C4

Type species. *Cryptodon obsoletus* A.E. Verrill & K.J. Bush, 1898 (lectotype, USNM 159886; type locality: USA: Martha's Vinyard, Massachusetts, 40.05°N 070.5167°W, 183 m, 23 August 1881).

Species included. *Cryptodon obsoletus* A.E. Verrill & K.J. Bush, 1898; *Axinopsis debilis* Thiele, 1912; *Thyasira succisa atlantica* Payne & J.A. Allen, 1991; *Thyasira fernandezensis* Zelaya, Güller & Bieler, 2024; 1; *Thyasirella rhamphos* sp. nov.

Etymology. Name formed by the genus *Thyasira* and the Latin diminutive suffix *-ella*. Feminine.

Definition. Shell small, to 10 mm. Outline ovate to rhomboidal to pyriform; posterior sulcus shallow; submarginal sulcus with an auricle. Sculpture of commarginal lines and growth stops. Hinge lacking obvious teeth or with a sub-

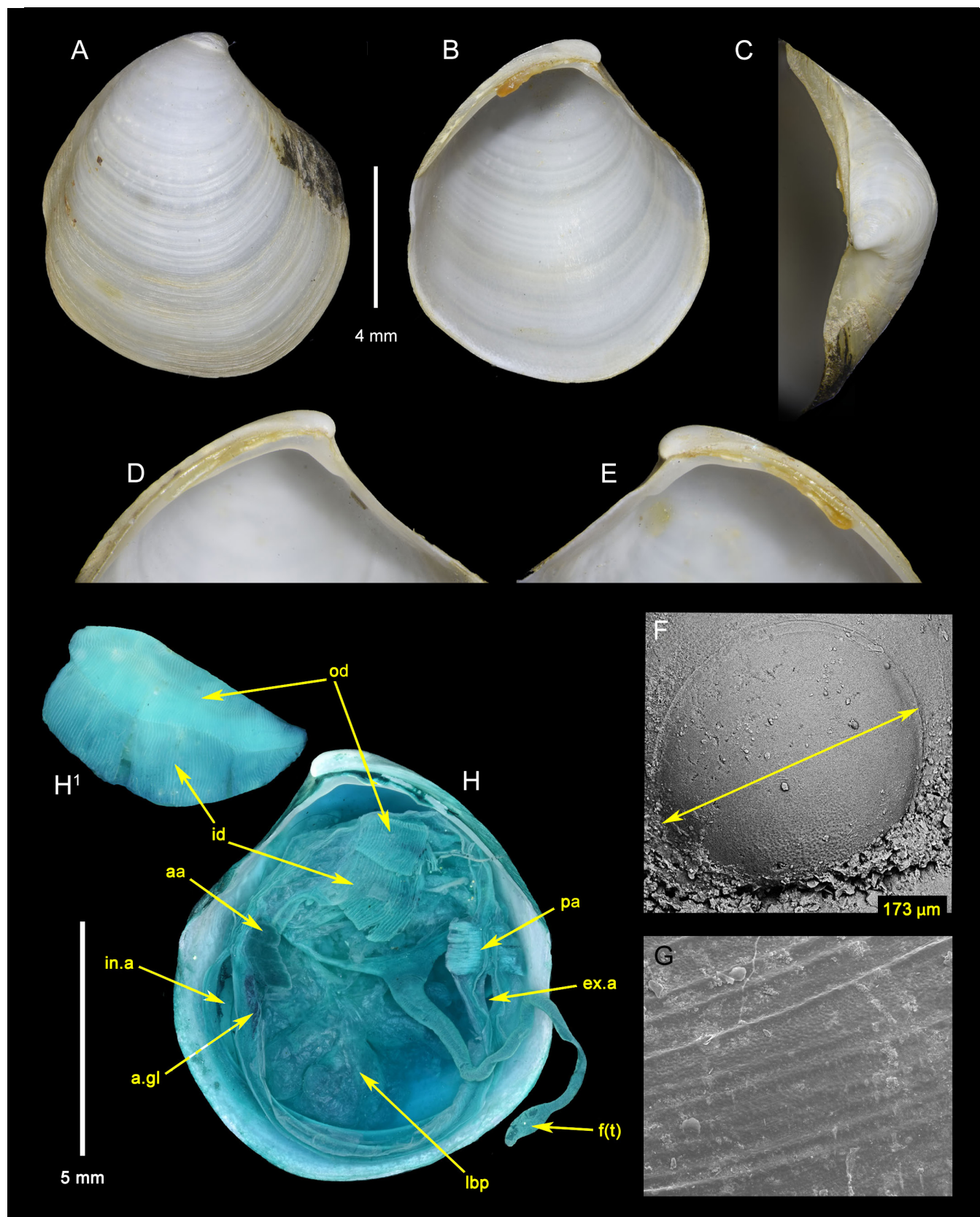


Figure 23. *Cryothyas milnelandensis* sp. nov. Milne Land, East Greenland. A–E, holotype NHMD-1175905/1; C–E not to scale F, prodissoconch of paratype. G, anatomy of paratype after removal of left valve. H, excised intact ctenidium from a different specimen.

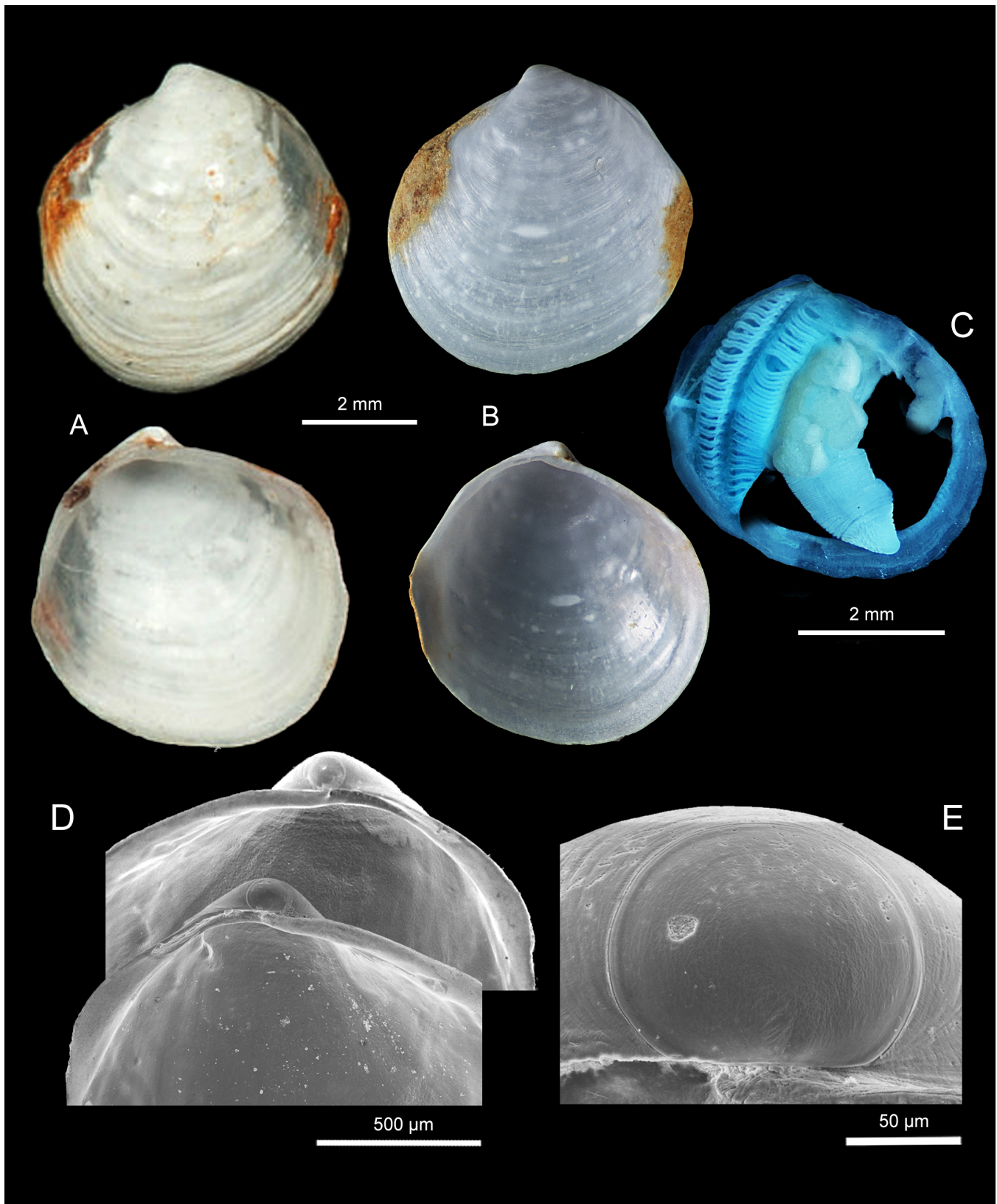


Figure 24. *Thyasirella obsoleta* (Verrill & Bush, 1898). **A**, lectotype, USNM 159886, from off Massachusetts, 183 m. **B**, from Thistle Oilfield, North Sea, 165 m, NMW.Z.1996.110. **C**, gross anatomy, from Thistle Oilfield, 165 m. **D**, SEM of hinge of right and left valves, from Brent Oilfield, North Sea, 140 m, NMW.Z.2001.107. **E**, SEM prodissococonch, from Brent Oilfield, North Sea, 140 m.

umbonal protuberance. Prodissoconch vermiculate, some species with an apical dimple. Gill type 2aR. Asymbiotic.

Remarks. I have included small species having a distinct auricle but weak flexures and an edentulous hinge. Consequently, I have proposed a separate genus, *Odontothyas* gen. nov., for similarly shaped shells but having a prominent cardinal tooth.

In the original figures of *Thyasira succisa atlantica* by Payne & Allen (1991: figs 29, 30), there is no prominent cardinal tooth, and this subspecies is probably a species in its own right. MolluscaBase Eds (2026) list *Thyasira succisa atlantica* Payne & J.A. Allen, 1991 as a synonym of *T. tortuosa* (Jeffreys, 1881), which is an error that can be clearly seen by comparing the illustrations in Payne & Allen (1991). I suggest that it is closer to *T. obsoleta* and should be placed within *Thyasirella*, not as a synonym of *Odontothyas succisa* comb. nov. as done by Payne & Allen (1991). The availability of the species name *atlantica* is questionable, as Payne & Allen (1991) also described *Thyasira* (*Parathyasira*) *atlantica* (Payne & Allen 1991: 509–510, fig. 43), which is similar to *T. tortuosa* but doubtfully conspecific. A reworking of the material described by Payne & Allen (1991) is needed to resolve this issue and is beyond the scope of this study.

Thyasirella obsoleta has often been confused with *Axinulus croulinensis* (Payne & J.A. Allen 1991), but the latter does not possess a raised auricle and the ctenidium consists of a single demibranch.

***Thyasirella* cf. *obsoleta* (A.E. Verrill & K.J. Bush, 1898)**
Figure 25

Material examined. All RRS *Charles Darwin* cruise 123C3-4, 19 July–15 Sept 2000: 4 sh., Sta. 55452#1, 61° 16.11'N 002° 19.99'W, 829 m, NMW. Z. 2026.001.17 • 4 spec., Sta. 55406#1, 2, 61° 0.98'N 002° 31.80'E, 543 m, NMW. Z. 2026.001.18 • 3 sh., Sta. 55359#1, 62° 09.31'N 000° 30.85'W, 543 m, NMW. Z. 2026.001.19 • 6 spec., Sta. 55328#1, 2, 62° 14.48'N 000° 11.07'E, 725 m, NMW. Z. 2026.001.20 • 4 spec., Sta. 55444#3, 4, 61° 10.87'N 002° 23.94'W, 699 m, NMW. Z. 2026.001.21 • 1 spec., Sta. 55303#1, 2, 61° 37.87'N 001° 42.38'W, 927 m, NMW. Z. 2026.001.22 • 1 spec., Sta. 55443#1, 2, 61° 11.81'N 002° 25.38'W, 740 m, NMW. Z. 2026.001.23 • 3 spec., Sta. 55244#4, 59° 52.70'N 007° 4.69'W, 967 m, NMW. Z. 2026.001.24 • 2 spec., Sta. 55238#1, 60° 06.79'N 006° 50.52'W, 991 m, NMW. Z. 2026.001.25 • 1 spec., Sta. 55290#1, 61° 38.80'N 001° 48.24'W, 1148 m, NMW. Z. 2026.001.26 • 5 spec., Sta. 55247#2, 3, 60° 00.05'N 005° 31.33'W, 790 m, NMW. Z. 2026.001.27 • 1 spec., Sta. 55358#2, 62° 09.91'N 000° 24.13'E, 573 m, NMW. Z. 2026.

001.28 • 5 spec., Sta. 55403#1, 2, 61° 05.65'N 002° 40.86'W, 700 m, NMW. Z. 2026.001.29 • 1 spec., Sta. 55354#1, 62° 17.49'N 000° 6.71'E, 863 m, NMW. Z. 2026.001.30 • 7 spec. + 2 sh., Sta. 55386#1, 62° 24.06'N 000° 35.18'E, 776 m, NMW. Z. 2026.001.31 • 1 spec., Sta. 55438#1, 3, 61° 12.80'N 002° 27.36'W, 795 m, NMW. Z. 2026.001.32 • 1 spec., Sta. 55443#1, 2, 61° 14.25'N 002° 28.80'W, 886 m, NMW. Z. 2026.001.33 • 1 spec., Sta. 55273#1, 60° 11.52'N 005° 02.74'W, 779 m, NMW. Z. 2026.001.34 • 1 spec., Sta. 55310#3, 60° 39.80'N 004° 24.12'W, 1074 m, NMW. Z. 2026.001.35 • 1 spec., Sta. 55336#1, 62° 18.10'N 000° 10.80'E, 870 m, NMW. Z. 2026.001.36 • 1 spec., Sta. 55304#1, 61° 36.71'N 001° 46.01'W, 1007 m, NMW. Z. 2026.001.37 • 1 spec., Sta. 55332#1, 2, 62° 12.42'N 000° 22.87'W, 630 m, NMW. Z. 2026.001.38 • 6 spec., Sta. 55330#1, 2, 62° 14.72'N 000° 17.05'E, 712 m, NMW. Z. 2026.001.39 • 4 spec., Sta. 55207#2, 3, 59° 48.97'N 008° 22.14'W, 1004 m, NMW. Z. 2026.001.40 • 2 spec., Sta. 55331#1, 3, 62° 14.31'N 000° 20.84'W, 686 m, NMW. Z. 2026.001.41 • 2 spec., Sta. 55445#1, 2, 61° 11.77'N 002° 46.80'W, 1042 m, NMW. Z. 2026.001.42 • 1 spec., Sta. 55223#2, 59° 52.53'N 008° 50.70'W, 1298 m, NMW. Z. 2026.001.43 • 1 spec., Sta. 55264#1-3, 60° 04.24'N 006° 16.97'W, 1048 m, NMW. Z. 2026.001.44 • 10 sh., *Challenger* 10/76 Sta. SMG85, 60° 05.1'N 005° 55.8'W, 1100 m, NMW. Z. 2026.001.45.

Description. Shell rarely exceeding 4 mm high, moderately inflated, oval, and a little oblique; relative height increasing in larger shells. Posterior sulcus distinct but shallow, producing a weak posterior ventral sinus. Posterior margin long, steeply sloping, with a well-defined submarginal sulcus and with a distinct auricle rising beyond margins of submarginal sulcus in most specimens. Lunule margin not sunken. Hinge with a weak anterior marginal thickening in both valves. Prodissoconch poorly preserved but c. 145 mm in diameter.

Anatomy. Ctenidium with 2 demibranchs; lateral body pouches weakly divided.

Remarks. The Faroe-Shetland Channel specimens are very similar to those from the shelf in the North Sea (Fig. 26) and the type specimen (Fig. 24A), but the larger shells are distinctly more attenuated. I can find no substantive differences in the hinge, or size and sculpture of the prodissoconchs, which in both are c. 145 mm in diameter. While there seems little to separate the two forms on shell morphology, the distribution pattern suggests they differ. While the North Sea samples occur at shelf depths above 200 m, the Faroe-Shetland Channel samples are only found below 500 m, with most below 700 m and ranging to over 1200

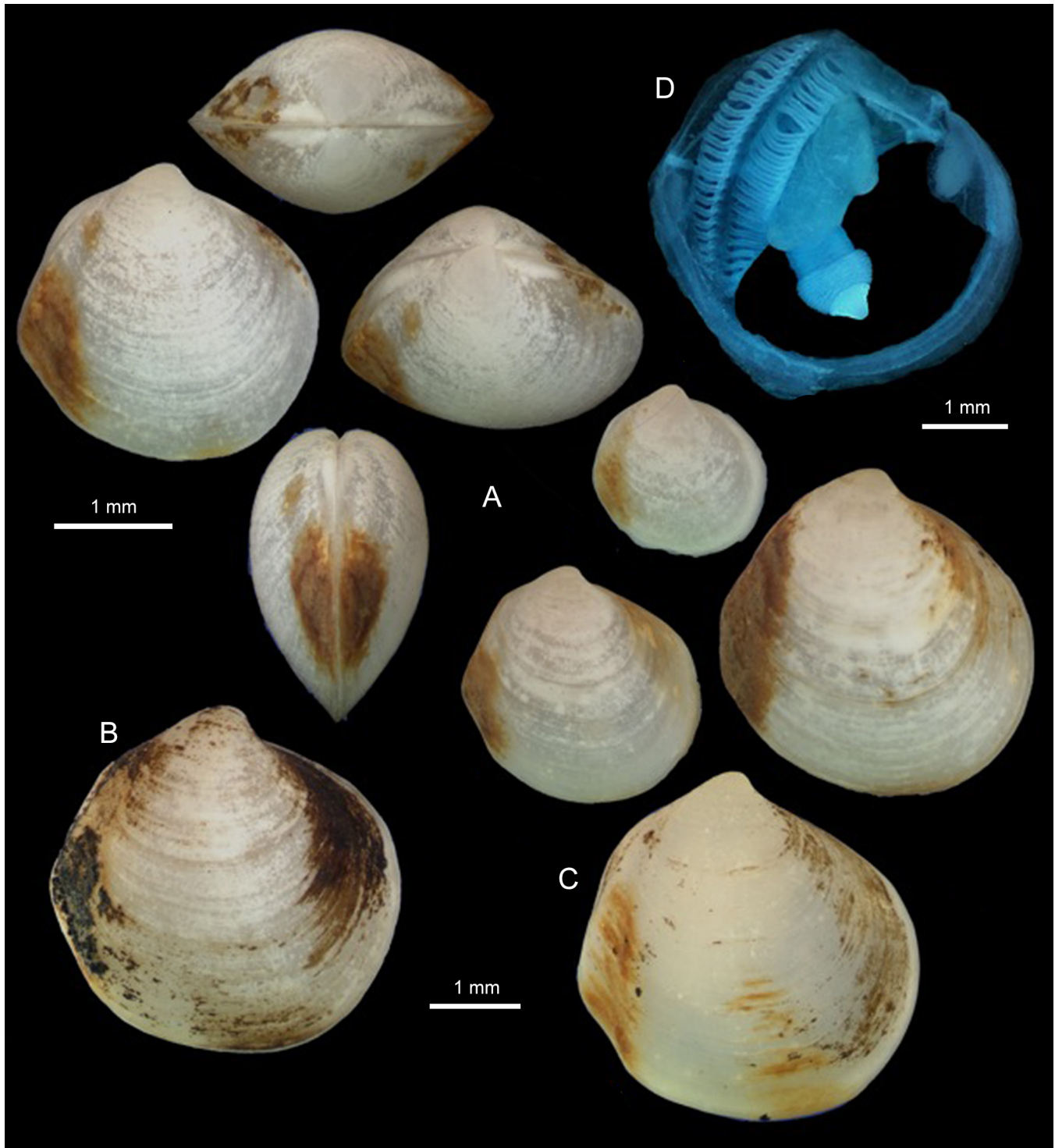


Figure 25. *Thyasirella* cf. *obsoleta* from Faroe-Shetland Channel. **A**, size series from AFEN Sta. 55207, 1004 m. **B**, AFEN St 55304, 1007 m. **C**, AFEN Sta. 53823, 735 m. **D**, Gross anatomy, AFEN Sta. 53823, 735 m. (Reproduced from Oliver *et al.* 2016.)

m. No *T. obsoleta* were found in samples containing *Odonotothyas succisa* from along the margins of the Faroe-Shetland Channel while *T. obsoleta* and *O. succisa* co-occur in the North Sea Oilfields. However, *T. obsoleta* has a broader

depth range in Norwegian waters, mainly between 50 m and 400 m, but very few samples are from greater depths, although the number of samples from such depths are few (Thomas Hansen pers. comm) For now, the Faroe-Shet-

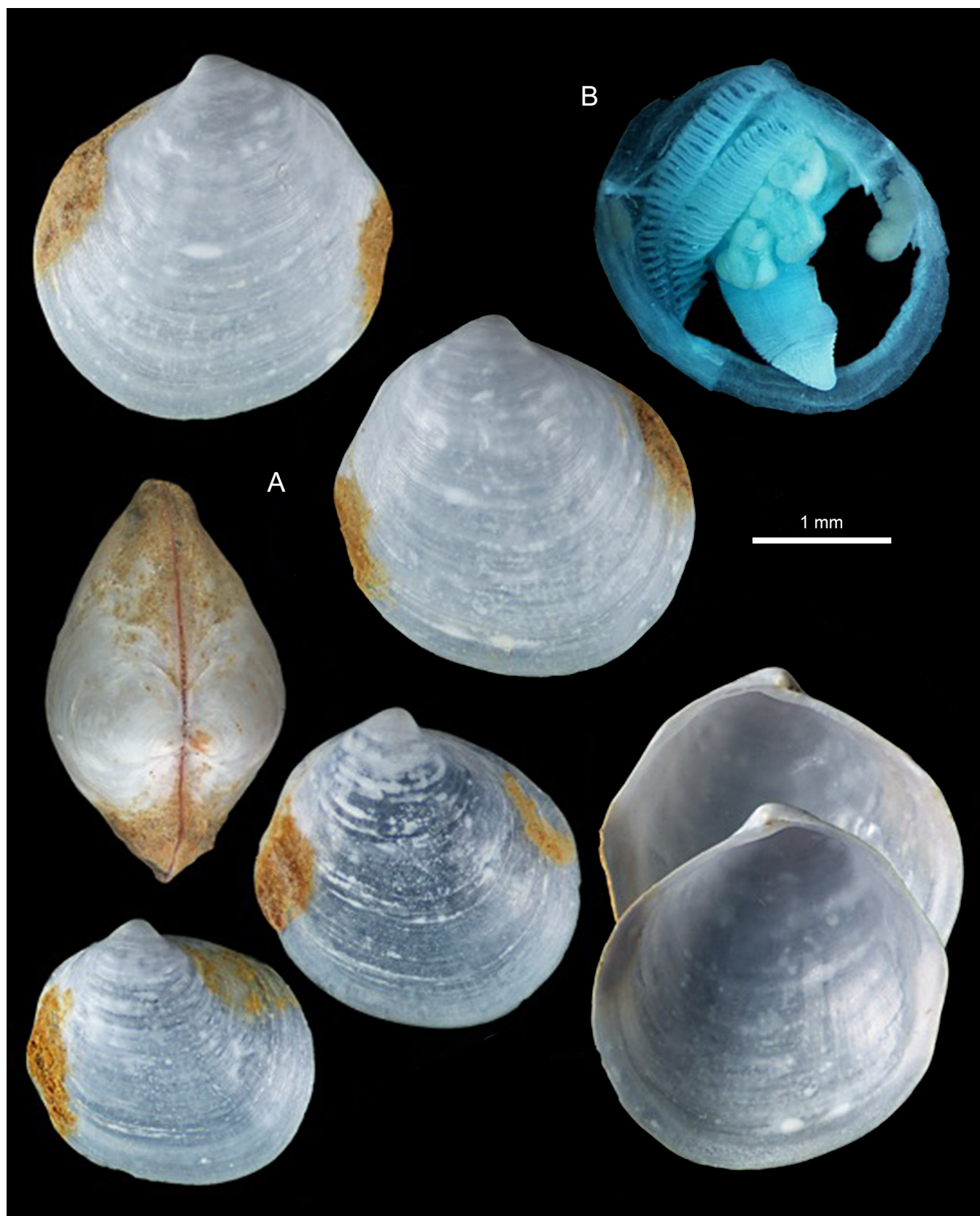


Figure 26. *Thyasirella obsoleta* from Thistle Oilfield, North Sea, 165 m. **A**, shells. **B**, gross anatomy. (Reproduced with modification from Oliver *et al.* 2016.)

land material is provisionally identified here as *Thyasirella* cf. *obsoleta*. DNA sequencing could be informative.

***Thyasirella rhamphos* sp. nov.**

Figure 27

ZooBank. urn:lsid:zoobank.org:act:7BFA434C-EA08-4643-AC07-FE80A5A6B74A

Type locality. NE Atlantic, Rockall Trough, RRS *Challenger* Sta. ES 122, 54° 31' N 012° 31' W, 2951 m, 29 January 1977.

Type material. Holotype: dry sh., NMW. Z. 2009.036.03477. **Paratypes:** 4 spec.+ 3 broken in 70% ethanol, same data as holotype, NMW. Z. 2009.036.03478.

Other material. 1 spec. in 70% ethanol, NE Atlantic, Rockall Trough, RRS *Challenger* Sta. ES 137, 54° 34' N 012° 19' W, NMW. Z. 2009.036.03479.

Etymology. From the Greek *rhamphos*, a beak or bill, pertaining to the beaked appearance of the anterior shell. Noun in apposition.

Diagnosis. Shell small to 4.8 mm in height, outline rhomboidal, anterior markedly pronounced, submarginal sulcus shallow, auricle prominent, posterior sulcus shallow, hinge edentulous.

Description. Shell fragile, to 4.8 mm high (Table 5 for measurements of all specimens examined), higher than long, moderately inflated, equivalve, equilateral. Outline rhomboidal; anterior dorsal (lunule) margin long, sloping, almost straight; anterior margin asymmetric, extremity well above midline, giving a beaked appearance; ventral margin narrowly rounded; posterior dorsal slope long, accompanying shallow submarginal sulcus; auricle prominent, rising well above edge of submarginal sulcus; posterior sulcus shallow; posterior margin weakly sinuous.

Table 5. Measurements of *Thyasirella rhamphos* sp. nov.

	H (mm)	L (mm)	T (mm)
ES122			
Holotype	4.1	3.8	2.3
Paratype	3.95	3.5	2.0
Paratype	3.5	3.3	2.0
Paratype	4.8	4.4	2.8
Paratype	2.2	2.1	1.3
Broken shell	4.1	—	—
Broken shell	3.0	—	—
Broken shell	4.5	—	—
ES 137	3.5	3.3	2.2

Ligament sunken, extending c. 1/3 length of submarginal sulcus. Hinge edentulous. Sculpture of weakly undulating with growth stops, fine commarginal lines, and surface wrinkles (Fig. 27H). Prodissoconch (Fig. 27G) 180 mm in diameter, with a narrow rim; sculpture weak, apical area weakly vermiculate. Muscle scars indistinct.

Anatomy. Ctenidium with two demibranchs, outer demibranch c. 1/3 depth of inner one, both with fully reflected filaments (Fig. 27F, od, id) and not fleshy, so presumed not to harbour symbionts. Lateral body pouches swollen, with 4 or 5 digitate processes (Fig. 27F, lbp). Foot vermiform, with swollen tip (Fig. 27F, f(t)); heel indistinct. Anterior adductor adjacent to anterior dorsal junction and approximately twice the size of posterior adductor situated on upper area of posterior sulcus.

Distribution. Known only from the Rockall Trough on the abyssal plain at 2900 m.

Remarks. The shape of the shell of *T. rhamphos* is so distinctive that the designation of a new species is justifiable even though so few specimens are available. There are no similar forms described by Jeffreys from the *Lightning* and *Porcupine* Expeditions (Jeffreys 1881), or by Verrill & Bush (1898), or by Payne & Allen (1991).

Genus *Odontothyas* gen. nov.

Figures 7G, 28

ZooBank. urn:lsid:zoobank.org:act:4978E95C-A985-452B-8E5C-0EB0E0120E97

Type species. *Axinus succisa* Jeffreys, 1881 (lectotype, USNM 61973; type locality: Mediterranean, Adventure Bank between Sicily and Tunisia, *Porcupine* Sta. 55/56).

Species included. Monotypic.

Etymology. From the Greek *odontodos*, meaning “with teeth”, and *thyas*, a contraction of *Thyasira*. The name refers to the presence of the prominent cardinal tooth. Feminine.

Definition. Shell small, to 5 mm (Table 5), equivalve, inequilateral. Outline oblique, antero-ventrally extended; posterior sinus very shallow, posterior sulcus weak; submarginal sulcus well defined, with a raised auricle. Hinge bearing a strong cardinal tooth in right valve (Fig. 31E, F). Gill type 2aR. Asymbiotic.

Remarks. This genus differs from *Thyasirella* in being more oblique and possessing a hinge with a prominent cardinal tooth. It may be argued that *Odontothyas* should not be distinguished from *Thyasirella* given that *O. succisa* comb. nov. is often confused with *Thyasirella obsoleta* comb. nov. However, I regard the presence of the cardinal tooth sufficiently significant.

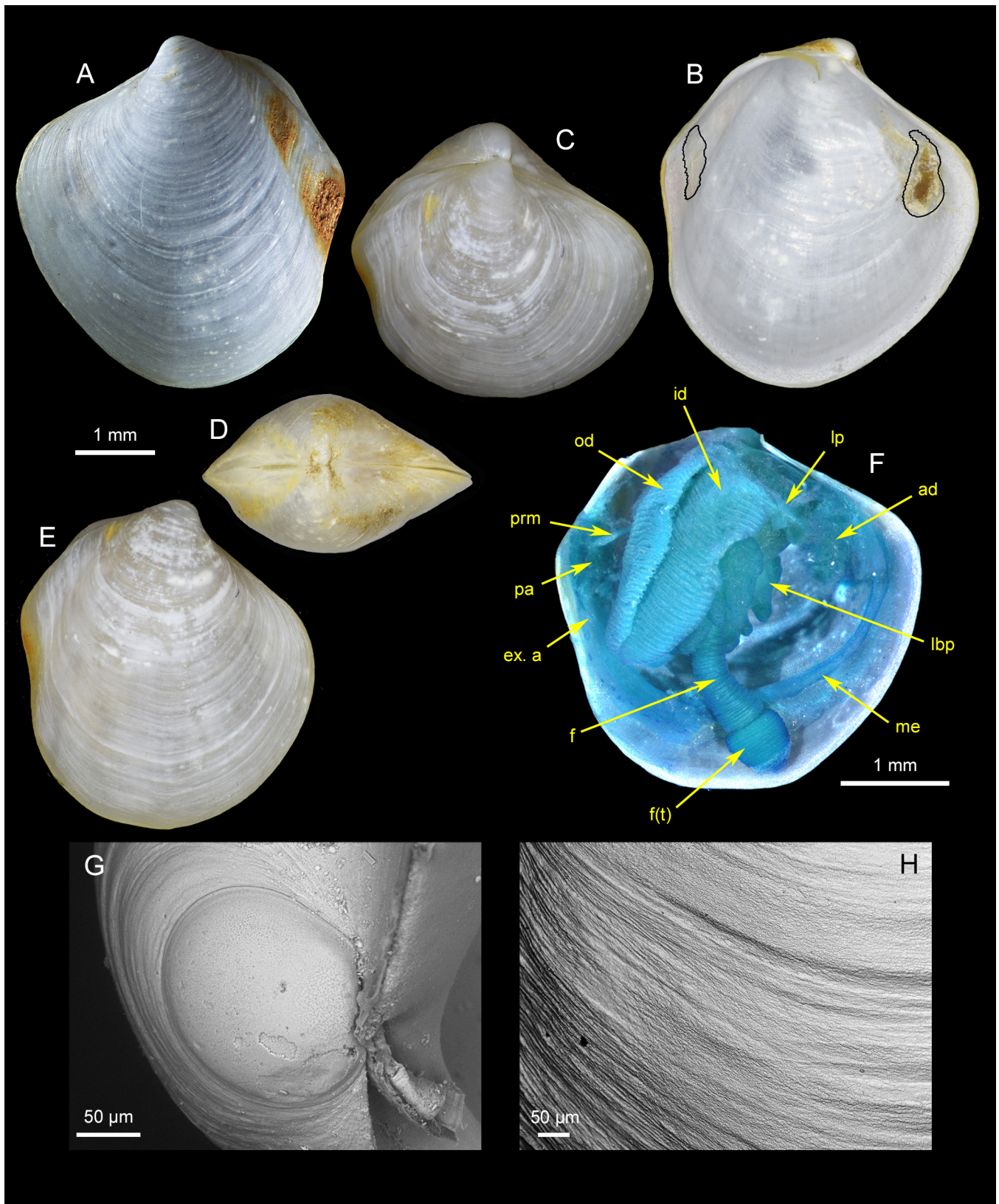


Figure 27. *Thyasirella rhampfos* sp. nov. **A, B**, holotype, exterior and interior of left valve, NMW.Z.2009.036.03477. **C–F**, paratypes NMW.Z.2009.036.03478. **C**, oblique view showing lunule and submarginal sulcus with auricle. **D**, dorsal view. **E**, exterior of right valve. **F**, anatomy, right side. **G**, SEM of prodissoconch. **H**, detail of external sculpture.

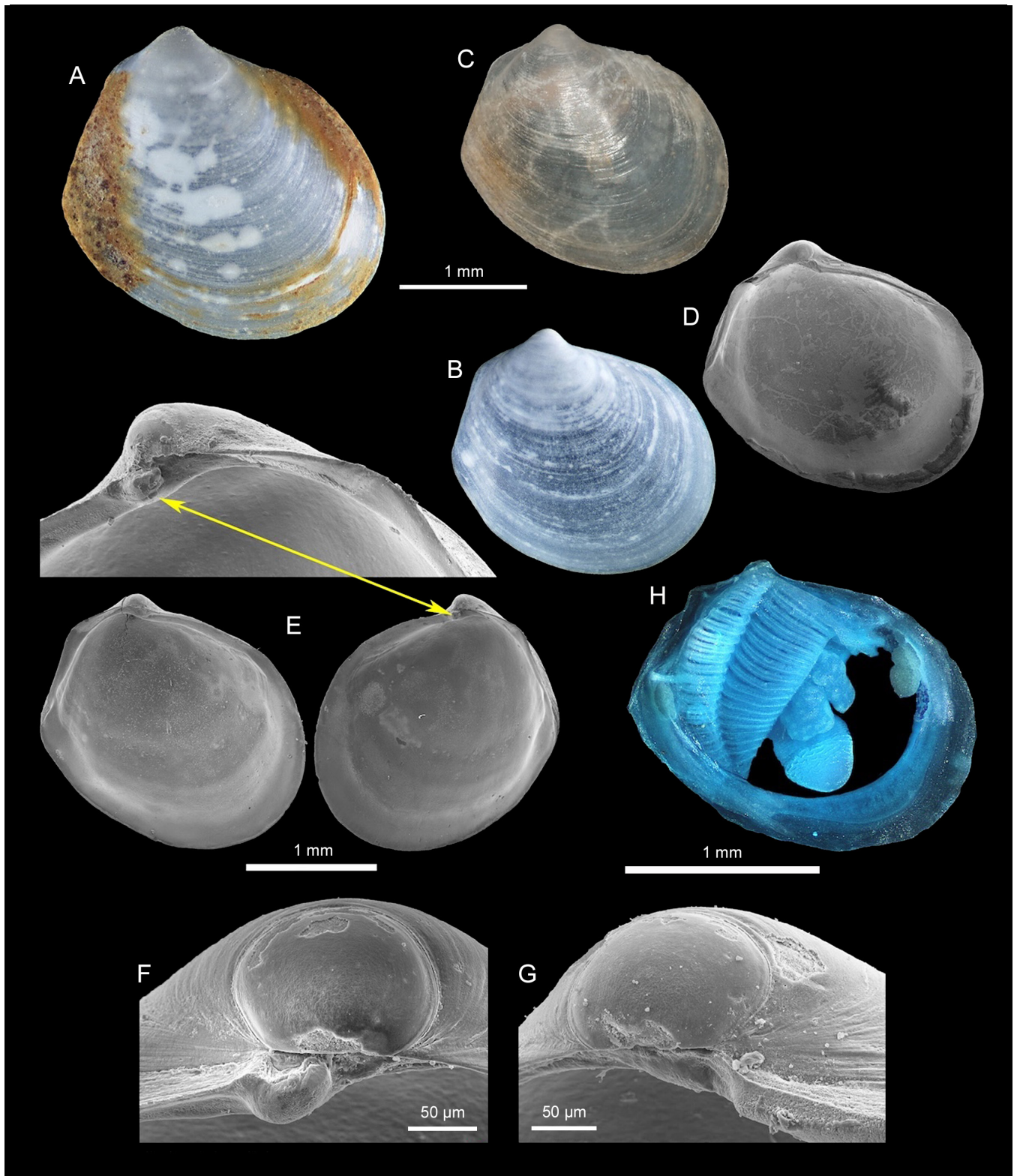


Figure 28. *Odontothyas succisa* (Jeffreys, 1876). **A**, from Gulfaks, northern North Sea, NMW.Z.1996.065. **B**, from Magnus oilfields, northern North Sea, NMW.Z.1996.080. **C**, **D**, lectotype, USNM 61973, from Adventure Bank, Mediterranean Sea. **E–G**, from Faroe-Shetland Channel, Sta. 53816#4, 232 m, NMW.Z.2026.001.48. **E**, SEM of interiors of left and right valves and detail (not to scale) of hinge in right valve. **F**, **G**, from Faroe-Shetland Channel, SEMs of hinge and prodissoconchs in right and left valves. **H**, gross anatomy, NMW.Z.1996.080, from Magnus oilfield.

***Odontothyas succisa* (Jeffreys, 1876)**

Figure 28

Axinus incrassatus succisa Jeffreys 1876.**Type specimen.** Lectotype USNM 61973**Type locality.** Mediterranean Sea, Adventure Bank, between Sicily and Tunisia; *Porcupine* Expedition, 1870, Sta. 55/56, 160 m.**Material examined.** Faroe-Shetland Channel, all AMES 96 Survey by RRS *Charles Darwin* (see Bett 2000): 1 spec., Sta. 53738, 60° 51.10'N 002° 52.80'W, 465 m, NMW. Z. 2026.001.46 • 4 spec., Sta. 53933#1, 60° 23.01'N 004° 00.85'W, 410 m, NMW. Z. 2026.001.47 • 1 spec., Sta. 53816#4, 61° 29.54'N 001° 06.88'W, 232 m, NMW. Z. 2026.001.48 • 5 spec., 1 on SEM stub, Sta. 53813#2, 61° 34.24'N 001° 10.27'W, 347 m, NMW. Z. 2026.001.49 • 2 spec., Sta. 53864# 60° 14.42'N 004° 08.77'W, 235 m, NMW. Z. 2026.001.50 • 4 spec., Sta. 53808#3, 61° 34.25'N 1° 10.21'W, 344 m, NMW. Z. 2026.001.51 • 1 spec., Sta. 53796, 61° 10.45'N 1° 38.14'W, 247 m, NMW. Z. 2026.001.52 • 2 spec., Sta. 53750, 60° 55.59'N 2 24.19'W, 343 m, NMW. Z. 2026.001.53 • 4 spec., Sta. 53875#5, 60° 15.74'N 004° 16.59'W, 369 m, NMW. Z. 2026.001.54 • 4 spec., Sta. 53932#1, 60° 28.21'N 003° 39.89'W, 396 m, NMW. Z. 2026.001.55 • 4 spec., Sta. 53729#2, 60° 32.47'N 003° 19.95'W, 333 m, NMW. Z. 2026.001.56 • 5 spec., Sta. 53797#7 61° 18.20'N 001° 32.21'W 326 m, NMW. Z. 2026.001.57 • 1 spec., Sta. 53882, 60° 26.56'N 003° 23.10'W, 237 m, NMW. Z. 2026.001.58 • 5 spec., Sta. 53728, 60° 32.93'N 003° 23.33'W, 376 m, NMW. Z. 2026.001.59 • 2 spec., Sta. 53815, 61° 26.12'N 000° 49.91'W, 180 m, NMW. Z. 2026.001.60 • 1 spec., Sta. 53740, 60° 54.24'N 002° 42.72'W, 455 m, NMW. Z. 2026.001.61.**Remarks.** This species is represented by a series of samples from along the upper margins of the Faroe-Shetland Channel at depths of 180–450 m but with most samples from less than 350 m deep. These samples have the same morphology (Fig. 28C–G) as those taken from the northern North Sea (Fig. 28A, B). *Odontothyas succisa* is most likely to be confused with *Thyasirella obsoleta*, but the latter has no prominent tooth, is not distinctly oblique, and has a much less prominent auricle.**Genus *Mendicula* Iredale, 1924****Type species.** *Lucina induta* Hedley, 1907, accepted as *Mendicula memorata* Iredale, 1924.**Species included.** *Mendicula memorata* Iredale, 1924; *M. ferruginosa* (Forbes, 1844); *M. ovata* (A.E. Verrill &K.J. Bush, 1898); *M. pygmaea* (A.E. Verrill & K.J. Bush, 1898); *M. bushae* (Payne & J.A. Allen, 1991); *M. carrozae* (Payne & J.A. Allen, 1991); *M. inflata* (Payne & J.A. Allen, 1991); *M. verrilli* (Payne & J.A. Allen, 1991); *M. ockelmanni* (Keuning & Schander, 2010); *M. sudamericana* Zelaya, 2010; *M. ultima* (Payne & J.A. Allen, 1991).Although listed as a species of *Mendicula* in MolluscaBase (MolluscaBase Eds 2026), *Axinus oblongus* Monterosato, 1880 cannot be included in this genus. Scanning electron microscopy of one of the syntypes reveals minutely crenulated dorsal margins, which is the defining character of *Adontorhina* s.s. S.S. Berry, 1947. Thus, this species should be referred to as *Adontorhina oblonga* (Monterosato, 1880) comb. nov.**Revised definition.** Shell small, to 4.5 mm, equivalve, thin, equilateral to slightly inequilateral with beaks just behind mid-line. Outline subcircular, ovate, oblong, or pyriform, generally anteriorly expanded; posterior with slight sulcus in some, posteriorly sinuate. Hinge lacking teeth or thickened with a single pseudo-tooth in left valve, with a single lateral flange in some. Some with myophoric ridges. Gill type 2bR. Asymbiotic. Lateral body pouches scarcely divided.**Remarks.** The original description of *Mendicula* was based only on the type species (Iredale 1924) but has since been modified by Payne & Allen (1991: 534) as follows:

The subgenus *Mendicula* is used here to include small species in which the shell is longer than high and in which there is a strong posterior marginal angle. The hinge plate usually bears cardinal tubercles and sometimes lateral teeth. Internally the anatomy is characterized by a gill with a single demibranch. Lateral body pouches sometimes bear small lobes and exceptionally may be divided. A heel to the foot is usually present.

Although Payne & Allen (1991) gave the general outline as longer than high, they contradicted this in describing *M. ultima*, which is higher than long. The single, non-reflected demibranch and simple lateral body pouch are shared across all species, but these features are also present in *Axinulus* A.E. Verrill & K.J. Bush, 1898 and *Leptaxinus* A.E. Verrill & K.J. Bush, 1898. In some species, there is a pseudo-tooth, while in others there is an anterior marginal thickening. These variances suggest that a more precise definition of *Mendicula* is needed, but any attempt results in the inclusion of characters that are not shared by all species, suggesting that the group may be polyphyletic. Splitting the current compliment of species into further genera is cur-

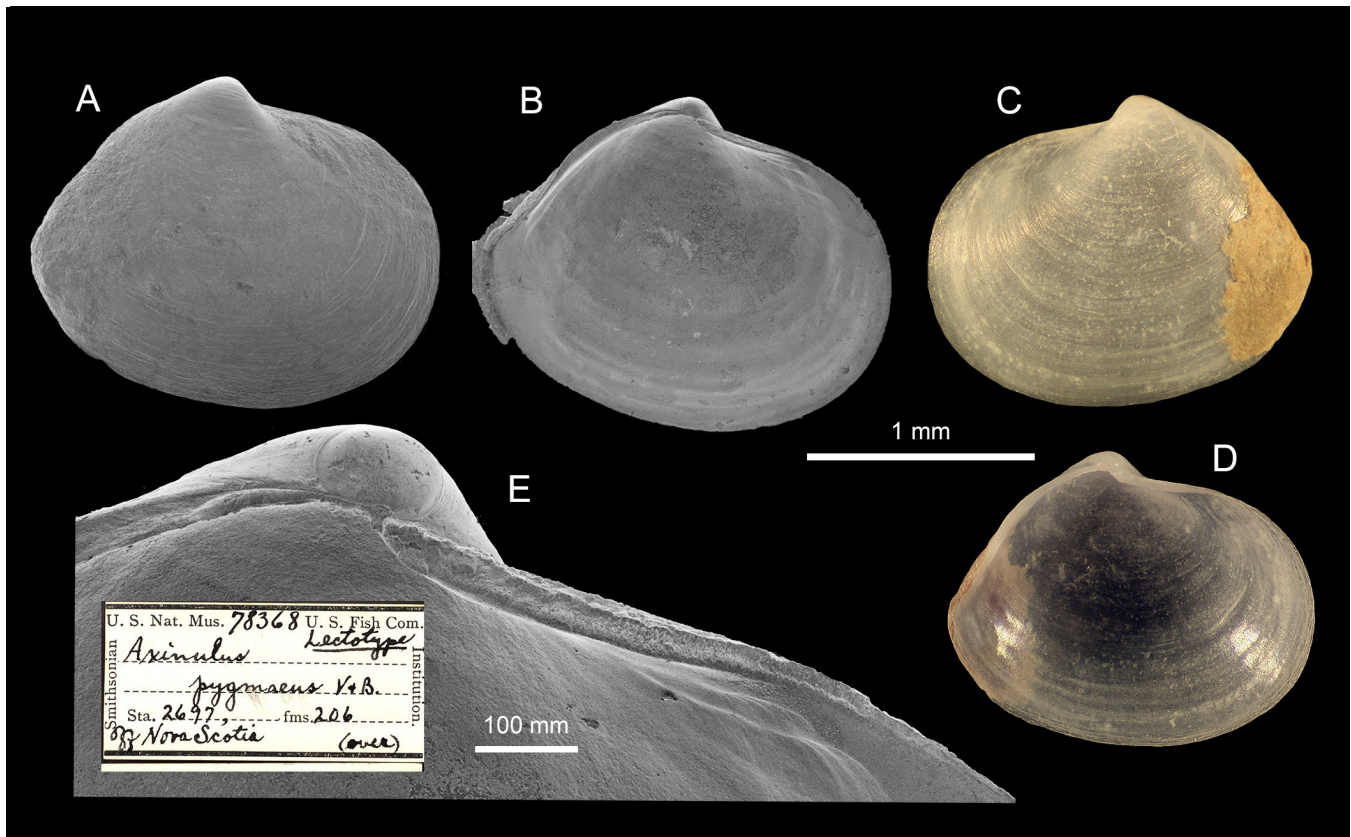


Figure 29. *Mendicula pygmaea* A.E. Verrill & K.J. Bush, syntype USNM 78368. **A, B**, SEM of exterior of right valve and interior of left valve. **C, D**, *ibid.*, but under normal light. **E**, SEM of hinge and prodissococonch in left valve, prodissococonch 126 μ m in diameter. Inset: label (not to scale).

rently not warranted due to uncertainties over the defining characters. Perhaps the presence of the myophoric ridges in *Mendicula verrilli* Payne & J.A. Allen, 1991 and *M. ultima* are significant as might be the radically different outline of *Mendicula carrozzae* Payne & J.A. Allen, 1991.

***Mendicula pygmaea* (Verrill & Bush, 1898)**

Cryptodon (*Axinulus*) *pygmaeus* A.E. Verrill & K.J. Bush, 1898

Type material. Lectotype, *Cryptodon pygmaea* A.E. Verrill & K.J. Bush, 1898. USNM 78368 (Fig. 29). Selected by Kurt Ockelmann but never published, formally adopted by Payne & Allen, 1991.

Type locality. As given by Verrill & Bush (1898), “between 47° 40’ N 47° 35’ 30” W and 39° 54’ 30” N 70° 20’ W, 206 to 499 fms” (377–913 m). Lectotype locality: Grand Banks Newfoundland, Canada, 47° 50.00’ N 057° 35.30’ W, 377 m.

Material examined. **Faroe-Shetland Channel:** all from RRS *Charles Darwin* Cruise 123C3-4 material: 9 spec. in 70% ethanol, 8 sh. dry, SEM mount; 61° 08.07’ N 002° 41.70’ W; Sta. 55402#1, 2, TR800, 792 m, NMW. Z. 2026.

001.62 • 5 spec. in 70% ethanol, Sta. 55339#1, 62° 22.21’ N 000° 06.85’ E, 991 m, NMW. Z. 2026.001.63 • 13 spec. in 70% ethanol, Sta. 55387#1, 2, NR6, 62° 21.28’ N 000° 32.13’ E, 767 m, NMW. Z. 2026.001.64 • 17 spec. in 70% ethanol, Sta. 55380#1, SBD3, 62° 19.39’ N 000° 12.02’ E, 919 m, NMW. Z. 2026.001.65 • 6 spec. in 70% ethanol, Sta. 55403#1, 2 S2, 61° 05.65’ N 002° 40.86’ W, 711 m, NMW. Z. 2026.001.66 • 10 spec. in 70% ethanol, Sta. 55430#1, TR800, 61° 08.01’ N 002° 41.64’ W, 785 m, NMW. Z. 2026.001.67 • 5 spec. in 70% ethanol, Sta. 55434#1, 2 CS4, 61° 16.00’ N 002° 20.16’ W, 826 m, NMW. Z. 2026.001.68 • 20 spec. in 70% ethanol, Sta. 55402#1, 2 TR800, 61° 08.07’ N 002° 41.70’ W, 792 m, NMW. Z. 2026.001.69 • 6 spec. in 70% ethanol, Sta. 55444#3, 4 CS11, 61° 10.87’ N 002° 23.94’ W, 699 m, NMW. Z. 2026.001.70 • 7 spec. in 70% ethanol, Sta. 55347#1, SBB2, 62° 18.56’ N 000° 15.00’ E, 864 m, NMW. Z. 2026.001.71. **North-west Atlantic:** lectotype, Grand Banks, off Newfoundland, USNM 78368 • 93 spec., off Massachusetts, 39° 54’ 15” N 079° 55’ 02” W, 563 m, USNM 1482700 • 67 spec., off Cape Hatteras, North Carolina, 35° 26’ 02” N

074° 41' 34" W, 1988 m, USNM 1482721. **Greenland Sea:** 30+ spec. in 70% ethanol, off Jan Mayen, *Ingolf* Sta. 115, 70° 50' N 008° 29' W, 86 fms (157 m), NHMD 1175732. **Nordland, Norway, Mareano Cruise 2012106:** 10+ spec. in 70% ethanol, Sta. 818, 67.35918° N 009.186367° E, 918 m, beam trawl and RP sledge combined, P.G. Oliver collection • 10+ spec. in 70% ethanol, Stn. 882, 67.1706° N 008.0798° E, 117 m, beam trawl and RP sledge combined, P.G. Oliver collection. **Nordland, Norway:** leg. Thomas Hansen, Akvaplan-Niva • 10+ spec. in 70% ethanol. Salt-dasfjorden, 67° 08.515' N 015° 24.902' E, 245 m, P.G. Oliver collection • 10+ spec. in 70% ethanol, Salt-dasfjorden, 67° 08.723' N 015° 25.310' E, 260 m, P.G. Oliver collection. **Svalbard, CAGE 15-2 cruise:** 10+ spec. now dry, Sta. 922, 76° 06.3637' N 016° 02.0845' W, 383 m, gas hydrate pingo area, P.G. Oliver collection • 10+ spec. now dry, Sta. 925, 75° 50.4941' N 016° 37.5577' E 350 m, Storfjordrenna, P.G. Oliver collection • 10+ spec. now dry, Sta. 946, 74° 54.0753' N 027° 33.4143' E, 334 m, Crater area, Bjørnyrenna, P.G. Oliver collection. **Barents Sea Mareano cruise 2013110 RS G.O. Sars:** 20+ sh. + 15 spec. fixed in formalin, Sta. 1137 72.3483° N 032.2302° E, 271 m, beam trawl and RP sledge combined, P.G. Oliver collection • 20+ sh., 20+ spec. in 70% ethanol & 12 v. on SEM stubs, Sta. 1139 72.1845° N 032.2056° E, 314 m, beam trawl and RP sledge combined, P.G. Oliver collection • 12 sh., Sta. 1150 72.0595° N 033.4210° E, 251 m, beam trawl and RP sledge combined, P.G. Oliver collection • 15 spec. in 70% ethanol, 10 fixed in formalin & 20+ sh., Sta. 1165, 71.4661° N 033.3242° E, 332 m, beam trawl and RP sledge combined, P.G. Oliver collection • 20+ sh, 20+ spec. in 70% ethanol, 10 fixed in formalin & 9 v. on SEM stub, Sta. 1174, 71.3720° N 032.1363° E, 298 m, beam trawl and RP sledge combined, P.G. Oliver collection • 50+ spec. in 70% ethanol & 15 fixed in formalin, Sta. 1180, 71.3685° N 033.0025° E, 305 m, beam trawl and RP sledge combined, P.G. Oliver collection • 20+ spec. in 70% ethanol & 22 v. on 3 SEM stubs, Sta. 1196, 71.1151° N 032.1470° E, 228 m, beam trawl and RP sledge combined, P.G. Oliver collection.

Description of lectotype (Fig. 29) **and specimens from off the east coast of the USA** (Fig. 30). Shell small, to 2 mm long (lectotype 1.65 mm), thin, white to semitransparent, slightly inflated, slightly inequilateral; beaks rounded, immediately posterior to midline. Outline longitudinally ovate, with a posterior angulation; L/H ratio c. 1.23:1; antero-dorsal margin horizontal for short distance before merging into broadly curved anterior margin; ventral margin gently curved; postero-dorsal margin evenly sloping to posterior angulation. Submarginal sulcus very

narrow; margins weakly flared to form a weak auricle; primary sulcus defined by faint postero-ventral flattening of shell margin; lunule distinct. Hinge plate narrow, with a narrow, projecting ridge anterior to beak of right valve fitting over similar ridge on left valve. Ligament in short groove on ventral margin of hinge plate. Sculpture of very fine, concentric growth lines and distinct radial striations most visible over anterior median area; small patches of ferruginous deposit adhere to anterior and posterior shell margins. Muscle scars indistinct. Prodissoconch with a weak rim and an apical dimple, 126 µm in diameter in lectotype and in discrepant in other specimens: c. 127 µm in left valve and 138 µm in right valve.

Differential description of Faroe-Shetland Channel material (Fig. 31). Shell reaching 2 mm long. Outline posteriorly less angulate and more rounded, with a smaller L/H ratio of 1.11:1. Auricle less flared. Radial sculpture weak. Coating of thick black deposits over dorsal and apical areas. Prodissoconchs mostly eroded but c. 118 µm in right valve.

Anatomy. Gill of a single demibranch with few filaments, c. 20. Lateral body pouch with few lobes.

Differential description of Nordland and Barents Sea material (Figs 32, 33). Shell outline very similar to Faroe-Shetland Channel material, but with strong radial sculpture (Fig. 32A). Extensive black mineralisation over dorsal areas (Figs 32D, 33A). Prodissoconch discrepant, c. 115 µm in right valve, 130 µm in left valve (Figs 33 D, E).

Anatomy. As in Faroe-Shetland Channel specimens.

Differential description of Jan Mayen material (Fig. 32F). Similar in outline to Faroe-Shetland Channel shells, but prodissoconch c. 128 µm.

Conclusion. From shell morphology alone, no pattern can be seen from the slight variations in shell outline and strength of the radial sculpture. One can only conclude that this form of *Mendicula* comprises a single variable species that ranges from the North-west Atlantic, across the boreal Atlantic, and into the Arctic. The bathymetric range is 200–1100 m. This distribution pattern is similar to that seen for *Cryothyas rotundus*.

Species comparisons. Consideration must be given to *Thyasira ockelmanni* Keuning & Schander, 2010 (Fig. 34), which was described from abyssal depths of the Norwegian Sea (Keuning & Schander 2010). It belongs in the genus *Mendicula*. In the original description this species was not compared with *M. pygmaea* and unfortunately is only represented by the type specimen held in the Trondheim Museum. The figure of this shell, reproduced here as

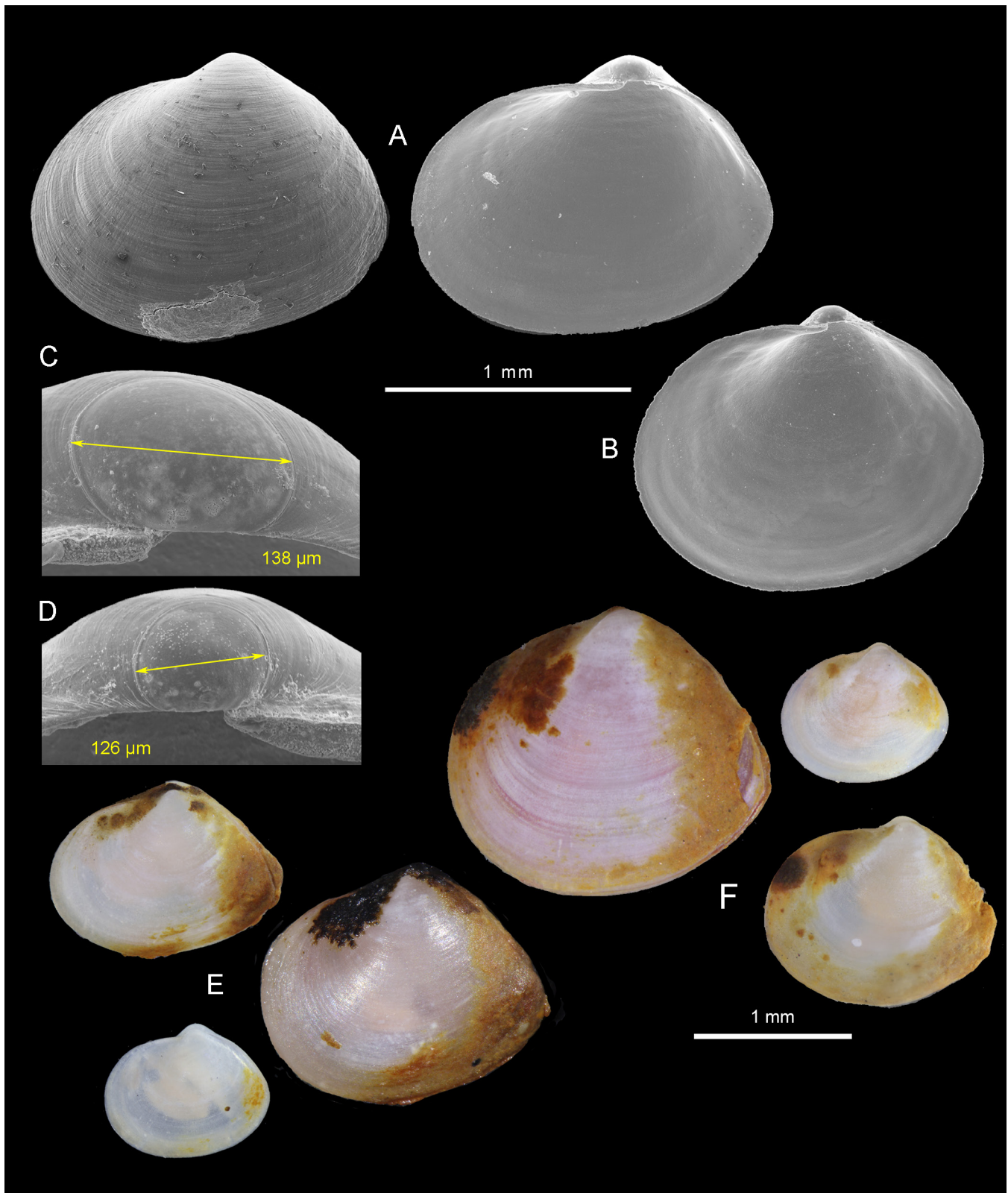


Figure 30. *Mendicula pygmaea* from the North-west Atlantic. From off Massachusetts at **563 m** depth, USNM 1482700 or from off Cape Hatteras at 1988 m depth, USNM 1482721. **A**, SEM of external and interior of right valve from 563 m. **B**, SEM interior of right valve, from 1988 m. **C**, SEM of prodissoconch of right valve from 563 m. **D**, SEM of prodissoconch of left valve from 573 m. **E**, growth series, from 563 m. **F**, growth series from 1988 m.

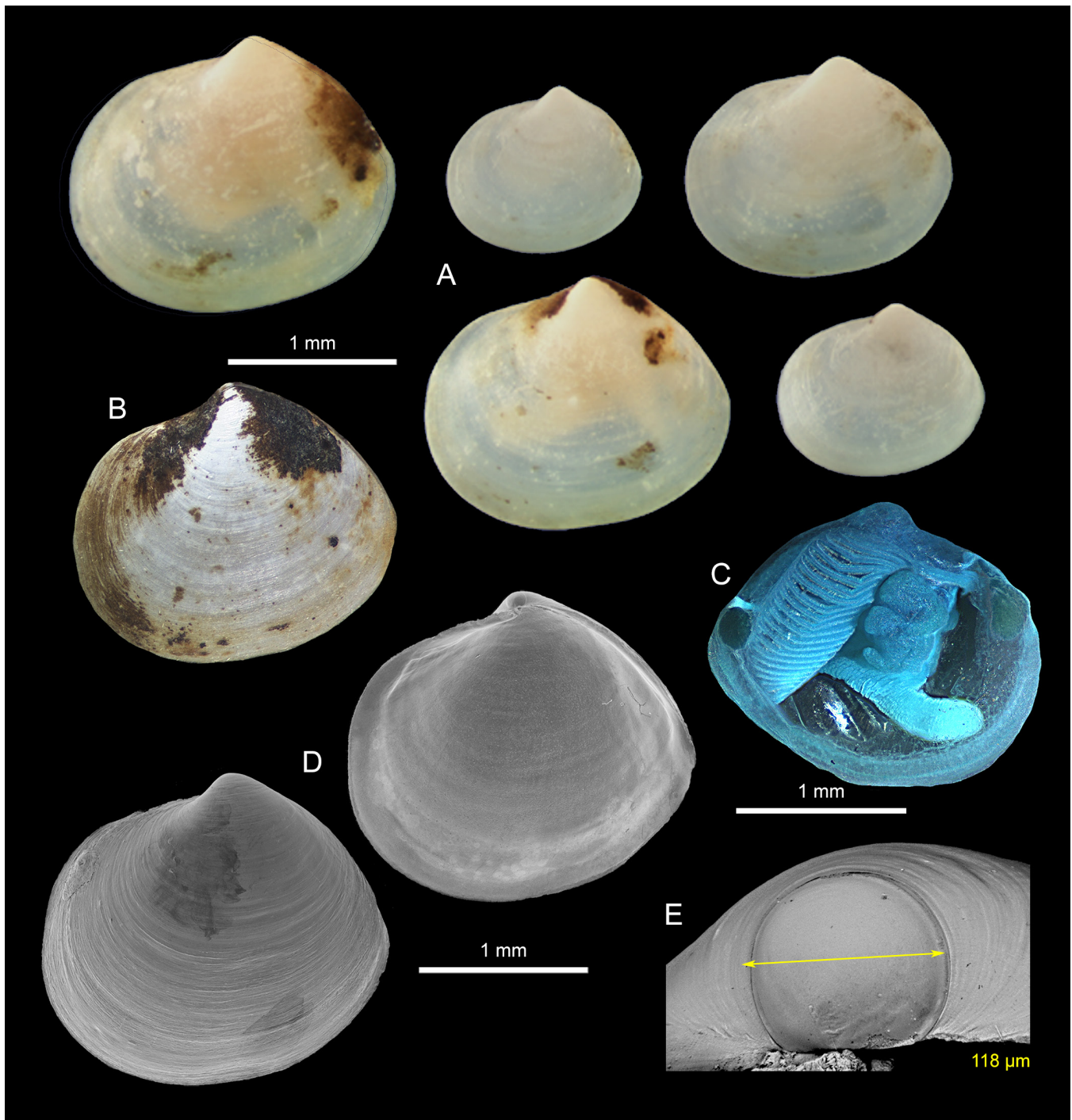


Figure 31. *Mendicula pygmaea* from Faroe-Shetland Channel. **A**, growth series from Sta. 55339#1, 1010 m, NMW.Z.2026.001.63. **B**, typical dry shell from Sta. 55434#1, 2 CS4, 826 m, NMW.Z.2026.001.67. **C**, gross anatomy from Sta. 55434#1, 2 CS4, 828 m, NMW.Z.2026.001.67. **D**, SEM of whole shells, from Sta. 55402#1, 2, TR800, 807 m, NMW.Z.2026.001.68. **E**, SEM of prodissoco-nch, from Sta. 55402#1, 2, TR800, 807 m, NMW.Z.2026.001.68.

Figure 34, shows that it is very similar in outline to shells from the Faroe-Shetland Channel but with a more pronounced flange-shaped tooth and a prominent prodissoco-nch of 134 μ m diameter. I have been unable to examine

a range of specimens from the abyssal Norwegian Sea, and therefore I am unable to conclude if *M. ockelmanni* is distinct from *M. pygmaea*.

The most encountered *Mendicula* is *M. ferruginosa*

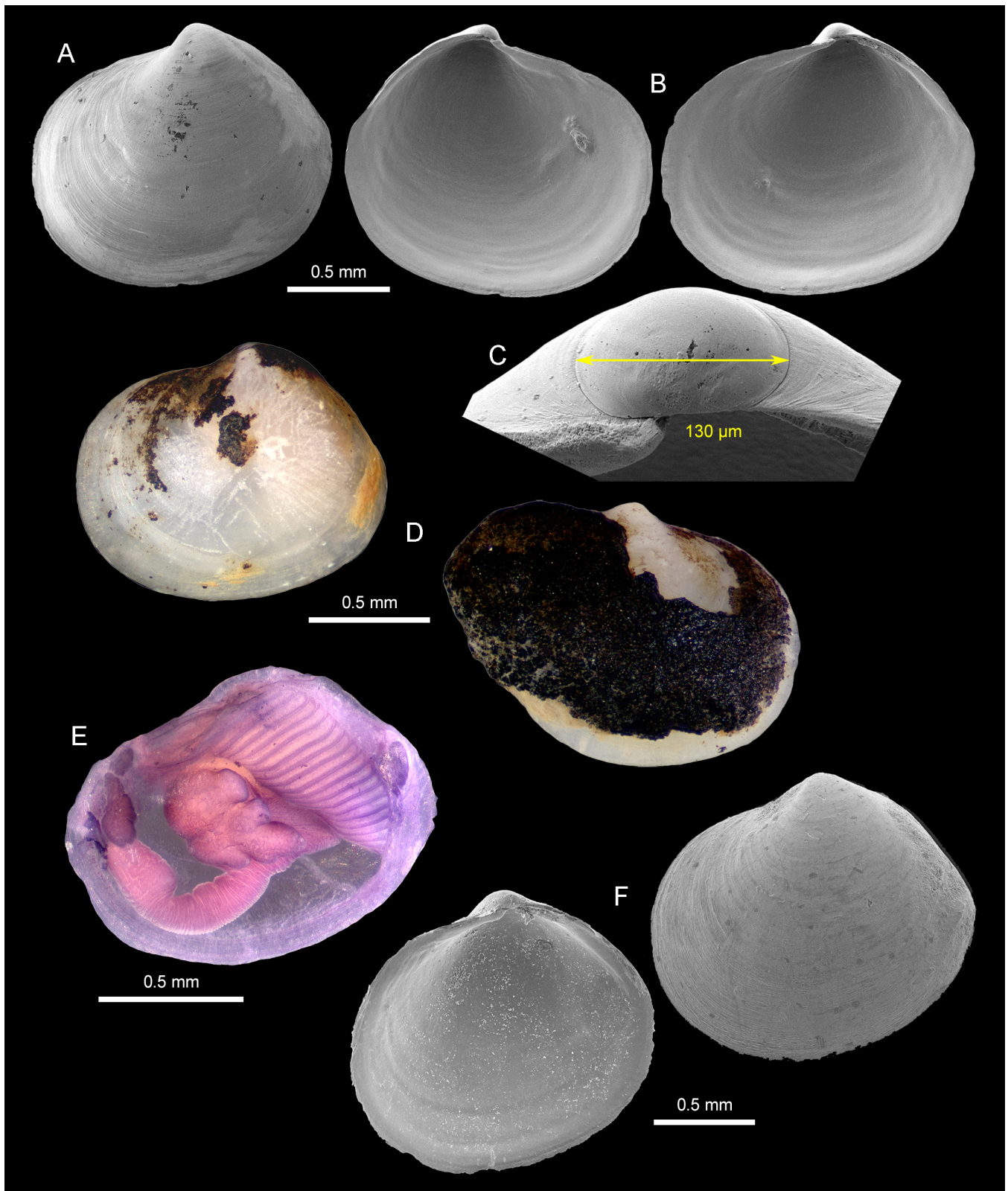


Figure 32. *Mendicula pygmaea*. **A–E**, from off Nordland, Norway, Mareano Sta. 818, 897 m, coll. P.G. Oliver. **A**, SEM of exterior of left valve. **B**, SEM on internal of right and left valves. **C**, SEM of prodissoconch **D**, shells with varying degrees of black ferrous/manganese coating. **E**, gross anatomy. **F**, SEM of exterior of left valve and interior of right valve, from Jan Mayen, *Ingolf* Sta. 115, 157 m, NHMD-1175732.

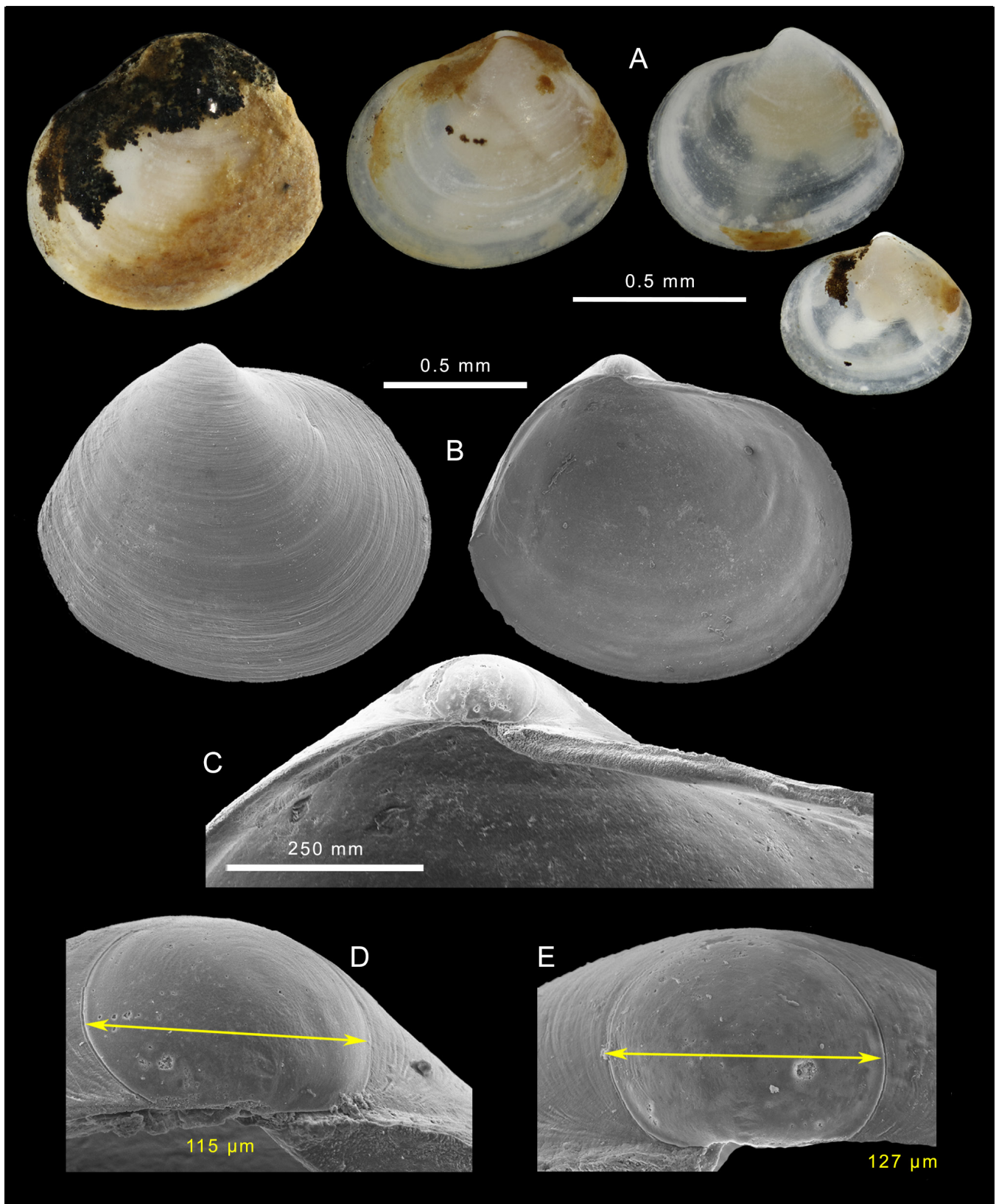


Figure 33. *Mendicula pygmaea* from Barents Sea, Mareano Sta. 1196, coll. P.G. Oliver. **A**, growth series. **B**, SEM of exterior of right valve and interior of left valve. **C**, SEM of hinge in left valve. **D**, SEM of prodissoconch in left valve. **E**, SEM of prodissoconch in right valve

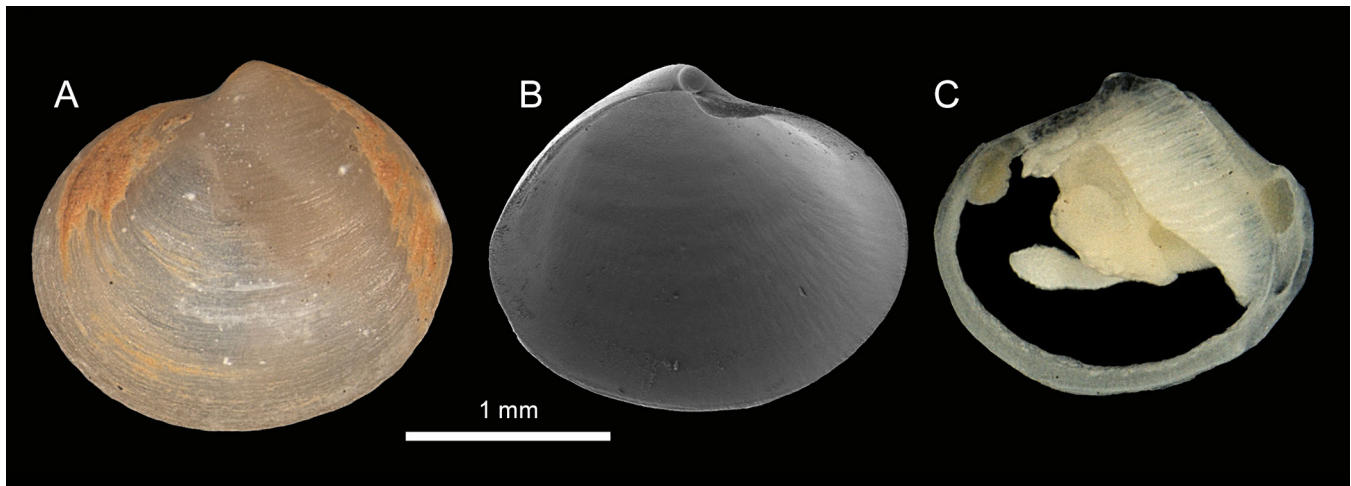


Figure 34. A–C, *Thyasira* (*Mendicula*) *ockelmanni* Keuning & Schander, 2010. Original figures (reproduced from Keuning & Schander 2010: fig. 2a, d, e).

(Forbes, 1844) (Fig. 35), which has been recorded from depths as shallow as 20 m in Scottish sea-lochs and to abyssal depths across the entire Atlantic and into the Arctic Ocean (Oliver *et al.* 2016). Typically, it attains a larger size, to 4.5 mm, and is entirely coated with a thick, ferruginous coating that obscures the underlying shell. In some *M. ferruginosa* from deeper water, and in juveniles in general, the coating may be thin and partial, and such shells are not dissimilar to *M. pygmaea*. *Mendicula ferruginosa* is more circular in outline and has a distinct protruding cardinal process in the right valve, but this process is less obvious in juveniles. The prodissococonch sculpture is also distinct, consisting of a medial ridge with striations radiating from it (Fig. 38B).

Adontorhina similis P.J. Barry & McCormack, 2007 was originally confused with *M. pygmaea* by Oliver & Killeen (2002), despite their observation of the distinctive crenulated dorsal margins typical of all *Adontorhina* species. *Adontorhina similis* is now thought to be restricted to shelf depths in the North Sea, Skagerrak, and southern Norway.

A species said to be similar to *M. pygmaea* from the abyssal zone of the Norwegian Sea was noted by Bouchet and Waren (1979). Kurt Ockelmann intended to describe this species but never did, and for the sake of completeness, it is described here as *Mendicula atomus* sp. nov.

Other high-Arctic species with similarity to *Mendicula* species are *Axinulus careyi* F.R. Bernard, 1964 (Fig. 36A) and *Thyasira otoschmidtii* Gorbunov, 1946 (Fig. 36B). Photographs of the holotype of *A. careyi* show an ovate shell with a deep escutcheon and anterior-lateral tooth-like structures suggesting closer affinity to *Leptaxinus* than *Mendicula*. *Thyasira otoschmidtii* (Gorbunov 1946: pl. 1,

fig. 2a–c) and the syntype in ZMZI (collected by the ice-breaker *G. Sedov* at Sta. 101, 82° 10' N 137° 23' E, 3,700–3,800 m) has an inflated shell, with the posterior margin truncated, and it is altogether unlike *M. pygmaea*.

***Mendicula atomus* sp. nov.**

Figure 37

Thyasira sp. n.—Bouchet & Warén 1979: 216, fig. 4.

ZooBank. urn:lsid:zoobank.org:act:5EAFDBA0-EEA6-4EDC-BBE1-0CCB7897CB4B

Type locality. Greenland Sea, between Jan Mayen and Svalbard, 074° 42' N–074° 43' N 003° 03' W–003° 30' W, NORBI Station 8, CP 14, 3595–3617 m; summer 1975.

Type material. Holotype: an entire specimen in 70% ethanol, NHMD-117586/1. **Paratypes:** 20+ spec., same locality and depth as holotype; SEM mounts, NHMD-117586/2–4.

Other material examined. 20+ spec. & sh., same locality and depth as holotype, NHMD-117586/5 • 50+ shells dry, Greenland Sea, between Jan Mayen and Svalbard, 76° 01'–76° 02' N 01° 49'–01° 41' W, NORBI Station 7, DS 14, 3709 m, summer 1975, NHMD-117587

Etymology. From Greek, *atomos*, a small particle, atom. A noun in apposition.

Diagnosis. Shell minute, not exceeding 1.3 mm long; outline subovate, with anterior rounded, posterior subacute, lunule and submarginal sulcus weak. Anterior dorsal margin of hinge slightly thickened. Prodissococonch prominent, with vermiculate sculpture.

Description. Shell minute, to 1.3 mm long, equivalve, inequilateral, with beaks just behind midline. Outline

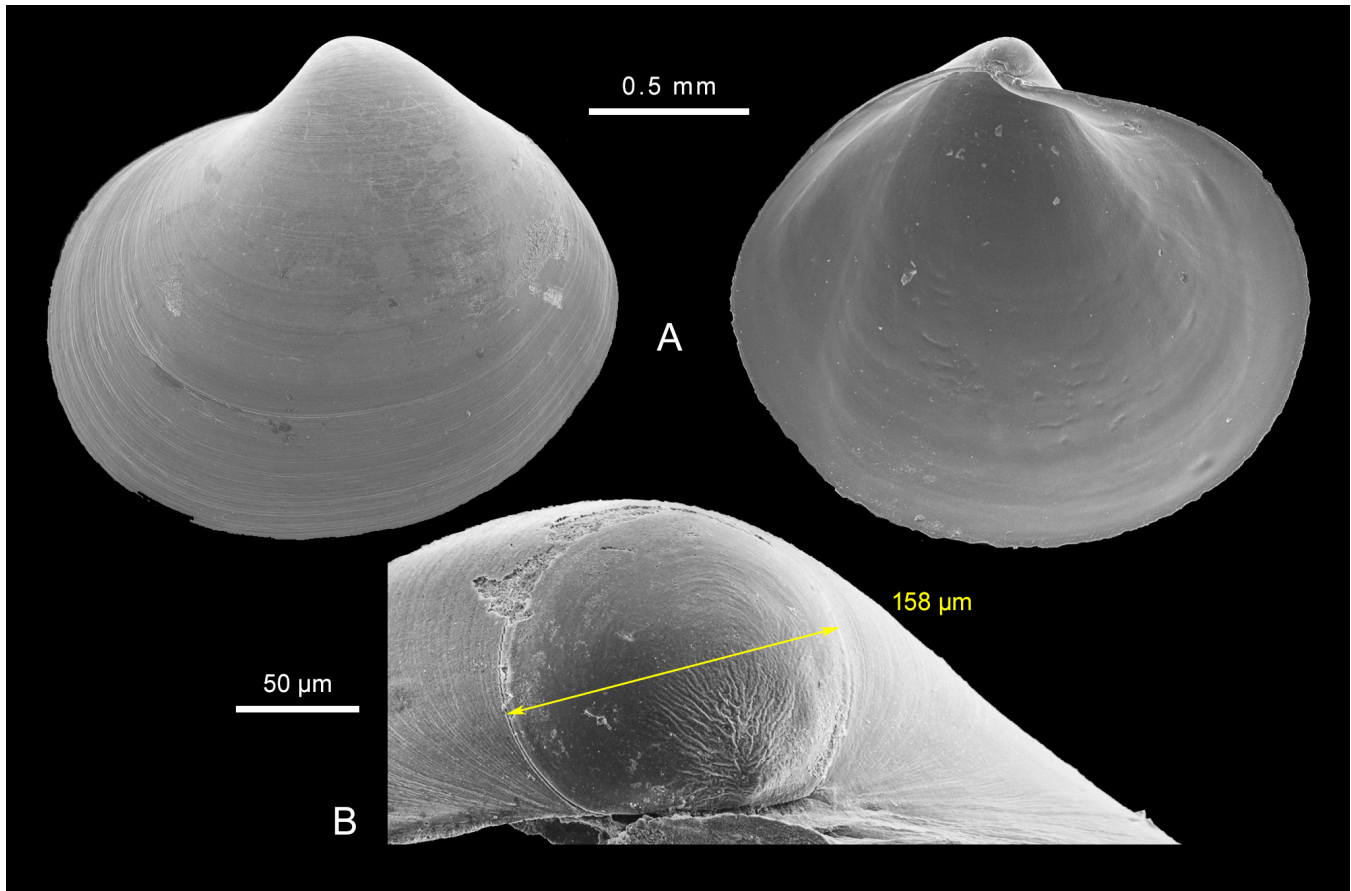


Figure 35. *Mendicula ferruginosa* (Forbes, 1844) from Rockall Trough, RRS *Challenger* Sta. ES 255, 1595 m, NMW.Z.2009.036. 03480. **A**, SEM of juvenile lacking ferruginous coating. **B**, SEM of prodissoconch.

subovate; anterior broadly rounded; posterior subacute; postero-dorsal margin gently sloping but some specimens with a slight hump towards beak. Posterior slope a little flattened but not sulcate. Lunule not demarcated, not sunken. Submarginal sulcus scarcely discernible. Sculpture faint, under SEM consisting of dense commarginal threads and weak, irregular radial markings on umbonal area. Hinge weak; anterior dorsal margin slightly thickened anterior of beaks. Ligament very small, deeply sunken. Muscle scars not apparent. Prodissoconch prominent, *c.* 138 µm in diameter, densely vermiculate all over.

Anatomy. Visceral mass contained within umbonal cavity. Mantle edge simple. Adductor muscles small, oval; anterior adductor muscle with an accessory dorsal portion. Foot vermiform, with a swollen toe and small heel. Ctenidium greatly reduced, of no more than 6 simple filaments. Lateral body pouches simple, spherical, not divided.

Distribution. Greenland Sea between Jan Mayen and Svalbard at abyssal depths below 3500 m.

Comparisons. Bouchet & Warén (1979) noted a similar-

ity to *M. pygmaea*, but that species reaches a larger size, has a more prominent submarginal sulcus, has distinct radial striations, and has much weaker sculpture on the prodissoconch consisting of an apical dimple surrounded by weak vermiculation.

Mendicula ockelmanni was described from abyssal depths in the Norwegian Sea, but comparison here is limited to the figure of the holotype by Keuning & Schander (2010: fig. 2a–e, reproduced here as Fig. 37). *Mendicula ockelmanni* is slightly larger, to 2 mm long, and with a very prominent anterior hinge thickening. The shell is more pointed anteriorly and is partially coated with a ferruginous deposit that is not present in *M. atomus*. The number of gill filaments in *M. ockelmanni* is about twice that of *M. atomus*, and the lateral body pouch is partially lobed.

DISCUSSION

The systematics in this paper are entirely based on morphological characters, and it is recognised that this may not



Figure 36. **A**, holotype of *Axinulus careyi* Bernard, 1979, LACM 1900 (photos courtesy of Paul Valentich-Scott). **B**, syntype of *Thyasira ottoschmidtii* Gorbunov, 1946, ZMZI, with label (not to scale).

adequately reflect the phylogeny within the Thyasiridae (Taylor *et al.* 2007; Fukasawa *et al.* 2017). DNA sequencing is an obvious technique to further our understanding of thyasirid phylogeny, but suitable specimens for genetic material are mostly unavailable or not easy to collect. Thyasirids are predominantly found in deeper, colder seas where collecting samples can be expensive and require the use of specialised survey or research vessels. The large series of samples studied by Payne & Allen (1991), collected before the advent of molecular sequencing, were unfortunately fixed in formalin prior to storage in 70 or 80% ethanol and are unsuitable for extracting DNA. The same applies to the many samples taken for environmental impact surveys, such as those from the oilfields of the North Sea. Most of the samples used by Payne & Allen, including the 48 undescribed taxa cited by Allen (2008), came from the oligotrophic basins of the deep Atlantic where there is now little research emphasis. This contrasts with the charismatic vent and seep settings from where most recently described species have originated, the latest being that from a seep

in the Hatton-Rockall Basin (Oliver & Drewery 2014) and sites off Svalbard (Åström *et al.* 2017).

With the present study, I hope that I have shown that modern microscopy can make advances on the earlier work by Payne & Allen (1991) and the unpublished study by Ockelmann (Oliver 2025). Scanning electron microscopy has not been used until recently, but it can reveal characters of the prodissoconch, periostracum and sculpture unknown to past researchers. Consequently, there is value in revisiting Payne & Allen's (1991) samples to identify and describe their 48 undescribed species. I doubt that *Rhombaxinus stellaris* sp. nov. would have been recognised without the use of SEM. I also believe that describing the entire range of morphologies is a prerequisite to any detailed phylogeny, so that the entire family is surveyed. Some advances in the North-west Pacific are being made by Kamenev and co-workers, who have described several new deep-sea thyasirids (Kamenev 2020, 2023a, b; Kamenev & Lisitsyna 2024; Kamenev & Sigwart 2025), but they established no new genera.

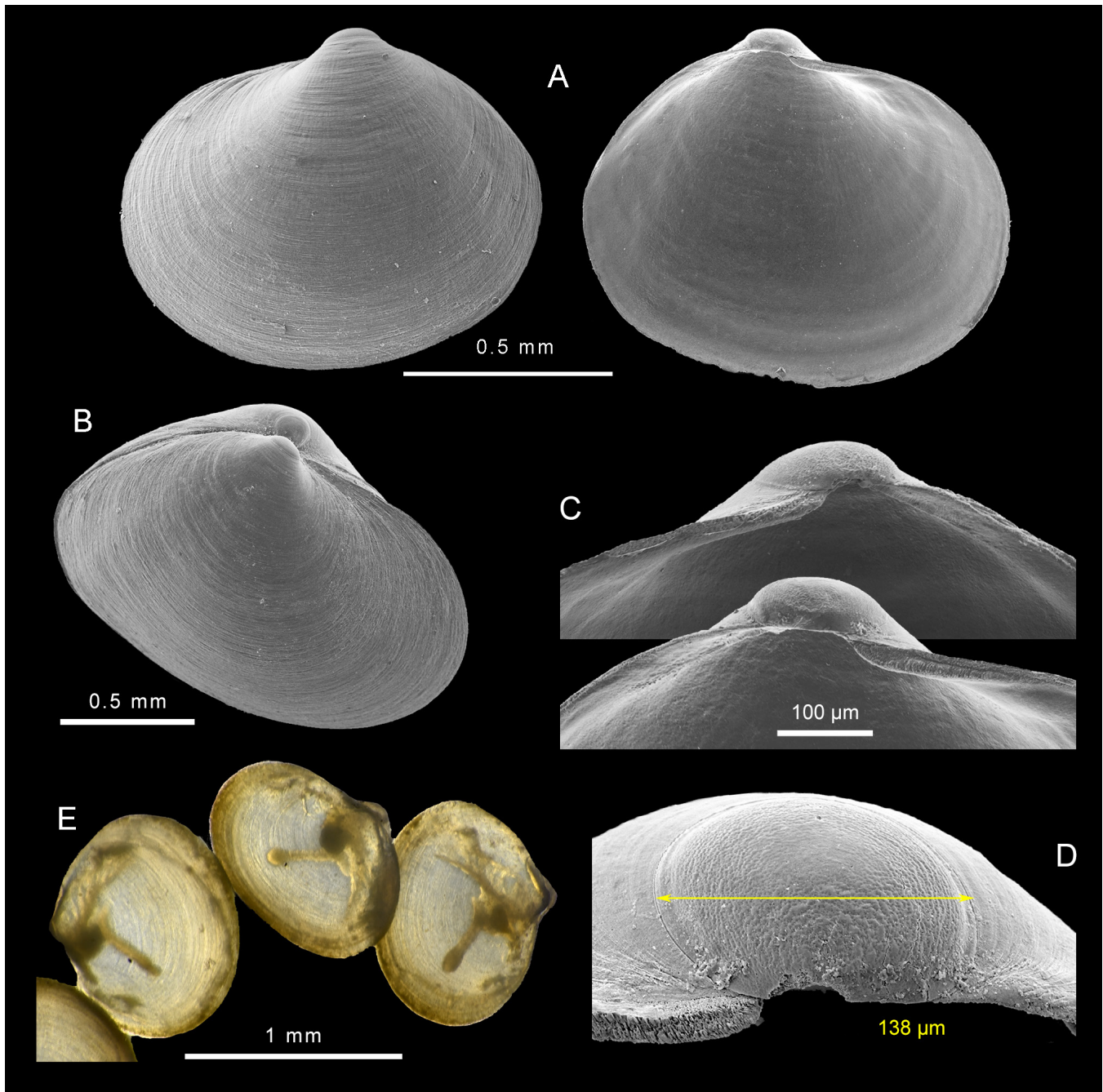


Figure 37. *Mendicula atomus* sp. nov. **A–D**, SEM of paratypes, from NorBI Sta. 8, CP14, NHMD-117586/2–4. **A**, exterior and interior of left valve. **B**, in oblique view. **C**, hinge in right and left valves. **D**, prodissoconch. **E**, three specimens under transmitted light showing gross anatomy.

Why we have persisted in using so few genera within the Thyasiridae compared to other bivalve families is unclear, but this may be due to the relatively small number of species within the family (c. 150); new genera would likely contain few species or be monospecific. It may also be that there has been a general lack of taxonomic interest in these mostly small, white, unattractive bivalves. Handling and

observing adult specimens of *Mendicula* species, which are less than 2 mm, certainly can be challenging.

However, the distribution and ecology of many thyasirid species are of interest. The amphi-Atlantic and apparent cosmopolitan range of some species is unusual and unconfirmed, as is the extreme bathymetric range of some species. The possibility of cryptic species cannot be excluded,

and the exclusively bathyal population of *Thyasirella* cf. *obsoleta*, as discussed above, is an example. Although we have come to accept amphi-Atlantic species in the Thyasiridae, it is relatively uncommon in other bivalve families, but in these this may have been overlooked. One substantiated amphi-Atlantic species, belonging to the family Cardiidae, is *Parvicardium pinnulatum* (Conrad, 1831) (ter Poorten 2024). Are there other amphi-Atlantic species in other families?

The relationship of thyasirids with chemosymbiotic bacteria is well known, but the symbiosis is not obligatory in all species and appears completely absent in others (Dufour 2005). Asymbiotic species are found at seep sites along with chemosymbiotic species (Åström *et al.* 2017; Oliver & Rodrigues 2017). It is unknown if, in such occurrences, the seep environment plays a role in the ecology of asymbiotic species. Southward (1986) illustrated and discussed the role of large mitochondrial structures in the gills of some asymbiotic species and suggested there may be an analogous function, but this has never been followed up.

In conclusion, I believe that additional genera and species within the Thyasiridae warrant description, based initially on morphology. Later, once suitable samples have been amassed, molecular data can be used to refine the phylogeny and investigate the unusual geographical and bathymetric ranges.

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