YOLDIELLA AND *PORTLANDIA* (BIVALVIA) FROM THE FAROE-SHETLAND CHANNEL AND ROCKALL TROUGH, NORTHEAST ATLANTIC

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Abstract *Benthic environmental assessments associated with oil and gas explorations along the UK Atlantic Margin have revealed deficiencies in the taxonomy of many deep-water taxa. Amongst the Bivalvia the protobranch genera* Yoldiella *and* Portlandia *are particularly complex. This study presents tabular keys, shell and gut loop descriptions for those taxa living on the continental slope and abyssal areas of the Atlantic Margin west and north of Scotland.*

The study is based primarily on samples collected in three surveys under the direction of the Atlantic Frontier Environmental Network (AFEN) between 1996 and 2000, with additional material from museum collections. Specimens were found at 239 stations from depths ranging from 98m on the outer continental shelf to 2046 m in Rockall Trough. One species of Portlandia *and eight species of* Yoldiella *were recognized in the AFEN material* P. intermedia, Y. annenkovae, Y. curta, Y. jeffreysi, Y. lucida, Y. nana, Y. philippiana, Y. propinqua *and* Y. valorousae *nom. nov.*

Yoldiella annenkovae *is recorded for the first time in British or Irish waters.*

Yoldiella valorousae *nom. nov. is a replacement name for* Y. lata *sensu Allen, Sanders & Hannah 1995).*

A further 8 species that occur in parts of the NE Atlantic adjacent to the AFEN study area are included. Y. biscayensis, Y. fabula, Y. frigida, Y. incala, Y. insculpta, Y. lenticula, Y. solidula, Y. thaerella *sp. nov.*

Y. thaerella *sp. nov. is* Y. inconspicua inconspicua *sensu Allen, Sanders & Hannah 1995 non* Y. inconspicua *Verrill & Bush, 1898.*

Y. incala *is a taxon raised to species rank from* Y. obesa incala *Allen, Sanders & Hannah 1995),*

Key words Yoldiella, Portlandia, *protobranch, taxonomy, Atlantic Margin, Atlantic Frontier Environmental Network*

INTRODUCTION

Following the expansion of oil and gas exploration in deep waters to the west of Shetland and into the Faroe-Shetland Channel (see Hartley, 2004 for a review), environmental surveys were carried out in 1996, 1998 and 2000. Collectively known as AFEN (Atlantic Frontier Environmental Network, see AFEN, 2000 for full details) surveys they attempted to provide an ecological framework for the area (Bett, 2001, Gage, 2001). It was quickly apparent that these surveys were hampered by a lack of identification guides for many of the benthic invertebrate groups and by many unresolved taxonomic problems, a view supported by Gage (2001). Material from these surveys was made available to taxonomists and descriptions of new taxa and taxonomic revisions have already been published for some Crustacea and Polychaeta (Chambers & Woodham, 2003; Bird, 2004; Shalla & Bishop, 2004).

This study is the first to examine the Bivalvia and initially aimed to provide a synthesis and identification guide to a diverse and prominent genus of protobranchiate genus, *Yoldiella*, which are frequent in samples from this region. However, because of taxonomic confusion the study now includes the related genus *Portlandia*. For completeness, species that occur in adjacent Scandinavian waters and the Rockall Trough, but which were not found in the AFEN material, have been included.

Bivalves of the genera *Yoldiella* Verrill & Bush, 1897 and *Portlandia* Mörch, 1857 are a major component of the molluscan fauna of the northern Atlantic and polar regions (Warén 1978, 1989a), and especially of the deep-sea (Allen, Sanders & Hannah 1995). Warén (1978) identified taxonomic problems with North Atlantic species of *Ledella* and *Yoldiella*, and subsequently he made an extensive review of the species of *Yoldiella* and allied genera from the NE Atlantic (Warén 1989a). This work made substantial progress towards elucidating the species present and refining the synonymy, in addition to facilitating identification. The subfamily Yoldiellinae was covered by Allen *et al.* (1995) as part of a series on the biology and ecology of the deep-sea protobranch bivalves of the Atlantic, based upon various research cruises

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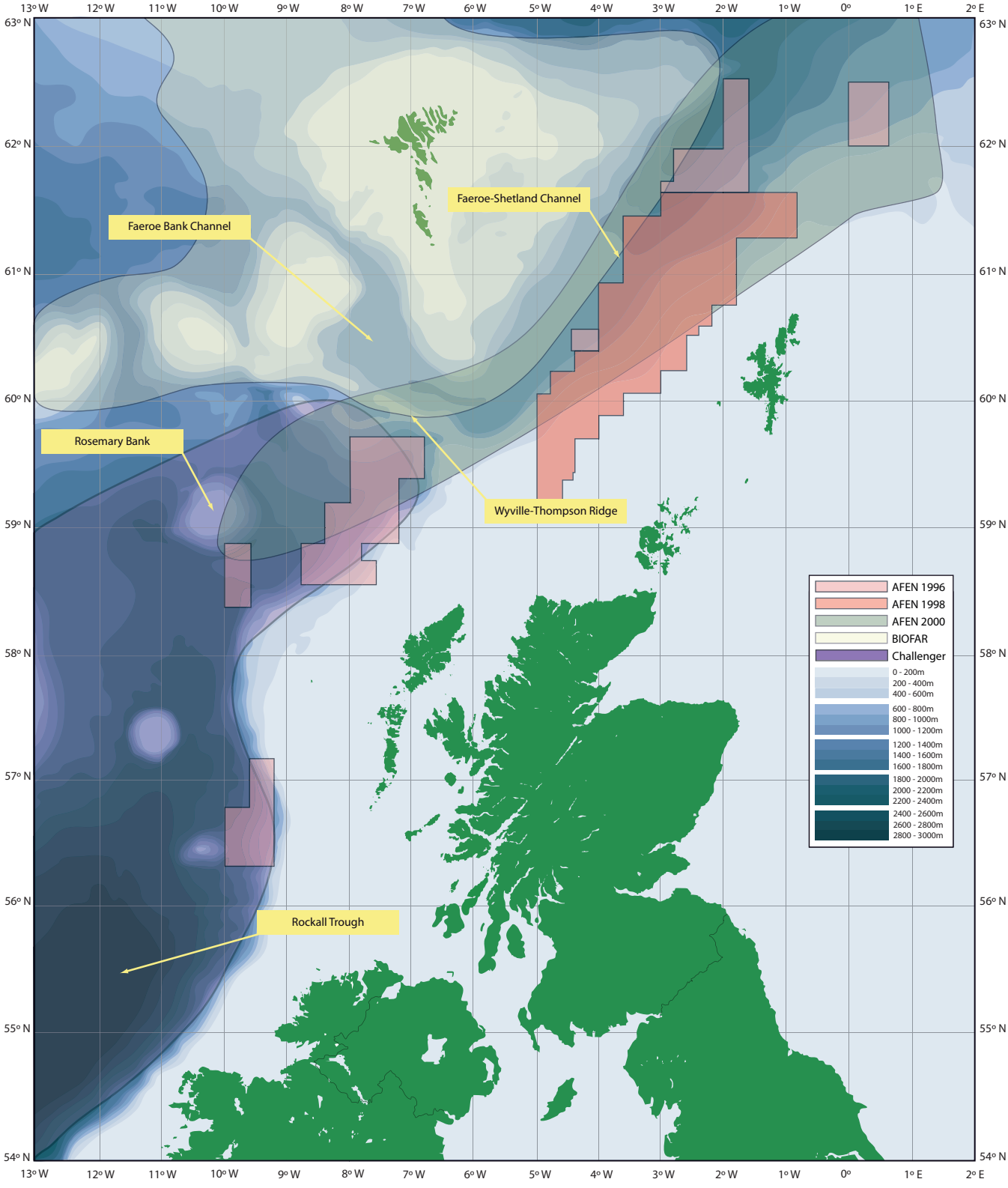

Figure 1 Study areas – *AFEN, Biofar, Challenger*

conducted between 1964 and 1976. Allen *et al.* (1995) describe 38 species and subspecies in the genera *Yoldiella* and *Portlandia*, including many for the first time. However, within this work they have omitted those species living from the outer shelf into bathyal depths, and those occurring at higher latitudes.

Seaward (1990) lists 15 species of Yoldiellinae from NW Europe, which includes the Norwegian coast to 61°50'N, and the Faroes to 62°50'N. The subsequent "British" checklist by Smith & Heppell (1991) lists 17 taxa of *Yoldiella*, but again, this list includes valid species and synonyms, as well as species of doubtful occurrence in the British and Irish sea areas, but does not include some deep-sea species subsequently listed by Allen *et al.* (1995).

A total of 31 valid species and subspecies are listed for the Mediterranean and North-east Atlantic (CLEMAM, 2008) and to illustrate the fluidity of the taxonomy some were described as recently as 2008 (La Perna, 2008).

THE *AFEN* SURVEYS

In 1996, 20,000 km^2 of seabed lying to the west of Shetland, north of the Wyville Thomson ridge were mapped and sampled in a survey commissioned by the Atlantic Frontier Environmental Network (AFEN). The 1996 survey included the UK Atlantic Margin, which had been licensed for oil & gas exploration before 1995. In 1998 a further 10,000 km^2 of seabed to the north and west of Scotland was surveyed. This survey included areas to the south of the Wyville Thomson ridge and on the slope of the Rockall Trough. In 2000 a third survey, as part of the DTI (now BERR) Strategic Environmental Assessment program, was made to the immediate north and west of the AFEN surveys. The bathymetric depths covered by the 3 surveys ranged from 98m on the outer continental shelf to 2046m in Rockall Trough. In the interest of brevity these three surveys will be collectively referred to as AFEN, distinguished by the year of survey. For a full outline of the surveys and data relating to the Atlantic Margin see the web sites for AFEN (http://www.ukooa.co.uk/issues/Afen) and AMES (Atlantic Margin Environmental Survey) (http://www.noc.soton.ac.uk/obe/PROJECTS/DEEPSEAS)

Most of the samples from these surveys were collected by use of a Bowers & Connelly Megacorer, deployed with 2-12 core tubes. This resulted in a sample collected from an area of seabed ranging from 0.016 to 0.071 m^2. Additional samples were collected by a Day grab or box core, each of which collected a sample from an area of 0.1 m^2. The material was passed over a 0.5mm sieve prior to preservation in formalin.

MATERIAL EXAMINED

AFEN

Specimens of *Yoldiella* were present in samples from 239 of the 439 stations containing molluscs. However, the number of individuals was low, only 775 specimens. Over 90% of the individuals were collected from depths >700m.

A significant proportion of the material, particularly from the 1996 survey, was found to be in a poor state of preservation. Many of the specimens had become partly or completely decalcified resulting from an overlong period of storage in formalin. Additionally, many specimens were crushed. The result of this was that much of the material had been damaged beyond recognition, and, therefore, only material that could be reliably identified has been used for this study. The bulk of this came from the 2000 survey, which yielded 471 *Yoldiella* individuals from 118 stations.

Details of the locations and depths for the stations from which material is illustrated is provided in the *Appendix*. Samples from the 1996 survey are prefixed 53, those from 1998 are prefixed 54, and those from the 2000 survey are prefixed 55.

ADDITIONAL MATERIAL

We have also examined the following:

All *Yoldiella* material present in the collections of the National Museum of Wales, Cardiff (NMW and NMGW). The *Yoldiella* material in the collections of the Swedish Museum of Natural History, Stockholm (SMNH). Material in the collections of the National Museums of Scotland from the research cruises of *RRS Challenger*, in deep waters to abyssal depths, between 1973 and 1991 under the direction of Dunstaffnage

Figure 2 *Portlandia arctica* (J E Gray, 1824). Melvill-Tomlin collection NMW.1955.158.16638

Marine Laboratory, Oban. The majority of the *Challenger* material was examined and identified by Shelagh Smith and Ian Killeen prior to its accession into the Edinburgh collections. All records of *Yoldiella* from this material have been extracted from a catalogue prepared by Shelagh Smith (unpublished).

Type material of *Y. inconspicua* and *Y. fraterna* were borrowed from the US National Museum of Natural History (USNM). Type material of *Y. solidula, Y. frigida, Y. nana, Y. lucida, Y. lenticula,* and *Y. propinqua* were borrowed from the Swedish Museum of Natural History (SMNH). The type of Y. *biscayensis* was borrowed from the Natural History Museum, London (BMNH).

A sample of *Y. insculpta*, collected in the West European Basin during the *Jean Charcot* cruise (Biogas IV), was borrowed from Professor John Allen, Millport.

We have also extracted records of *Yoldiella* species from the Biofar survey (Sneli, Schiøtte, Jensen, Wikander & Stokland 2005).

Details of all additional material illustrated is provided in the *Appendix*.

TAXONOMY

Family **Nuculanidae** H. & A. Adams, 1858

Genus ***Yoldiella*** Verrill & Bush 1897
Type species *Yoldiella lucida* (Lovén 1846)

Definition Shell small, fragile, subovate to deeply oval, usually slender though occasionally tumid and more solid; lunule and escutcheon not present, no carina, not gaping; smooth or with fine concentric sculpture and growth ridges, periostracum glossy or silky. Dorsal margins usually sloping gently posteriorly and anteriorly, usually slightly convex. Anterior margin usually rounded. Posterior margin may vary from subrostrate to rounded, often obliquely truncated. Umbo usually anterior to the mid-line, occasionally central or posterior to mid-line. Hinge teeth chevron in shape, occasionally less prominent and more lateral in appearance due to the lower arm of chevron being reduced. Ligament internal, amphidetic, inserted beneath the beaks or on a narrow hinge plate but resilifer not expanded into a chondrophore, may extend slightly anteriorly and/or posteriorly no chondrophore. Hindgut in various configurations, usually restricted to the right valve only, occasionally present in

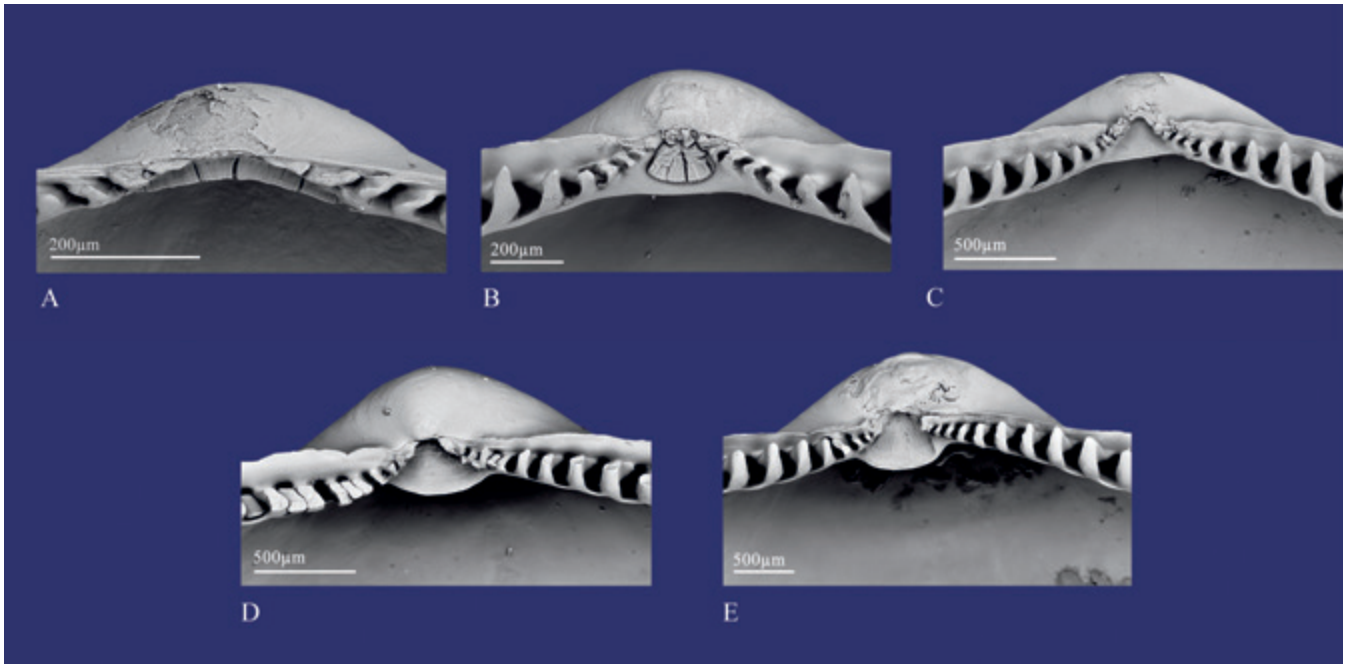

Figure 3 **A** *Yoldiella annenkovae* (Gorbunov, 1946) - Hinge plate that is not continuous and with the ligament attached internally to the underside of the beak (ligament type 1) **B** *Yoldiella propinqua* (Leche, 1878) - Broad hinge plate that is continuous with the ligament seated within a socket below the beak in a developed resilifer (ligament type 2) **C** *Yoldiella lenticula* (Møller, 1842) - Broad hinge plate that is continuous with the ligament seated within a socket below the beak in a developed resilifer **D** *Portlandia intermedia* (M. Sars, 1865) - Broad and continuous hinge plate with the ligament seated in a developed chondrophore (ligament type 3) **E** *Portlandia arctica* (J E Gray, 1824) – Broad and continuous hinge plate with the ligament seated in a well developed chondrophore

both valves, always located anteriorly, may consist of single loop or complex multiple coiling. Most species live in deep-water (>500m), but in high Arctic latitudes they may be found living in water as shallow as 10m.

Remarks As stated by La Perna (2004) the systematic arrangement of protobranchs is problematic and has been subject to much debate in recent times (Allen & Hannah, 1986; Maxwell, 1988; Ockelmann & Warén, 1998). This study follows the arrangement given by Ockelmann & Warén (1998), which is also followed by La Perna (2004), using the family Nuculanidae in its broadest sense and not adopting the Yoldiellidae as done by CLEMAM (2008).

Distinguishing between species and, to a certain extent the genera, of the Nuculanidae can be very difficult. Species from closely related genera share many common features, and this has lead to confusion as to the generic placement of certain species. Many species have at times been variously attributed to the genera *Yoldiella* and *Portlandia*.

According to Allen & Hannah (1986) *Yoldiella* and *Portlandia* may be differentiated by the following characteristics: *Portlandia* has a more robust shell, a lunule, escutcheon and moderate posterior carina are present; hinge long and continuous; ligament mostly internal, external part small; internal ligament seated within a variously-developed chondrophore projecting below the beaks. However, the illustrations and descriptions of *Portlandia* species within Allen *et al.* (1995) exhibit a large degree of variation in many of the characters that are used in their description of the genus. The development of the chondrophore is shown to be variable, with some species seeming to lack this feature completely. Variation seems also to be present in the formation of the lunule and escutcheon.

In the description of *Portlandia* given by Coan *et al.* (2000), the presence of a small, triangular, projecting resilifer and an inhalant siphon that is open ventrally are attributed to the genus. However, there is no mention of a lunule or escutcheon being present.

It seems that there is a certain degree of plasticity in the form of the hinge plate of *Yoldiella* and

Portlandia with subtle gradations in development. The hinge of *Yoldiella* in its strictest definition has a hinge plate that is not continuous and with the ligament attached internally to the underside of the beak and without a projecting chondrophore or resilifer (ligament type 1, Fig. 3A). This form can then be seen to grade into those with a broader hinge plate that is continuous, with the ligament seated within a socket below the beak in a triangular formed resilifer (ligament type 2, Fig. 3B). Further gradation continues to forms with a clearly defined projecting chondrophore (ligament type 3, Fig. 3D). Figure 3 illustrates the variation of the hinge from species with no resilifer or chondrophore through to species with a fully developed projecting chondrophore.

If one follows the generic description of *Portlandia* provided by Allen *et al.* (1995) and Coan *et al.* (2000), the taxa *propinqua*, *philippiana*, *lenticula* and *intermedia* with type 2 and type 3 ligaments could be placed within this genus. Indeed, Coan *et al.* (2000) follow Schileyko (1985) who placed both *lenticula* Møller, 1842 and *intermedia* M. Sars, 1865 into the genus *Portlandia* on the basis that they possess a subumbonal, rounded internal resilium and an inhalant siphon that is open ventrally. Allen *et al.* (1995) also place *lenticula* in *Portlandia*. Within their study, Allen *et al.* (1995) did not include *propinqua. philippiana* or *intermedia,* and, although there is mention of *P. propinqua* within the remarks of *lenticula*, Coan *et al.* (2000) did not include *philippiana*. Therefore, we assume that that they treat *propinqua* as a member of *Portlandia,* but we do not know where these authors would place *philippiana* generically.

Warén (1989a) treated *lenticula*, *intermedia*, *propinqua* and *philippiana* as *Yoldiella*, without reference to Schileyko (1985). The CLEMAM (2008) website lists these four species under the genus *Yoldiella*.

The variability and inconsistencies present in the written descriptions of the genera *Portlandia* and *Yoldiella* leads to much confusion when attempting to place species generically. One of the characters that Schileyko (1985) uses to place species within *Portlandia* is the presence of an inhalant siphon that is open ventrally. In their description of the Genus *Yoldiella*, it is clear that Coan *et al.* (2000) describe *Yoldiella* as having a siphon that is an entire, thick, closed tube. Allen *et al.* (1995) proclaim to base their descriptions for the genera and higher taxa on the study of Schileyko (1985), but then proceed to describe most species of *Yoldiella* covered in their study, including the type species *Y. lucida* (Lovén, 1846), as having an inhalant siphon that is open ventrally. The remaining species descriptions either omit the details of the inhalant siphon morphology or state that it is fused, or combined, with the exhalant siphon. Further more, although descriptions of some *Portlandia* species within their study contain reference to an inhalant siphon that is open ventrally, within other species of *Portlandia* there is no mention of a ventrally open inhalant siphon only reference to a combined inhalant and exhalant siphon.

When studied in comparison to the type species of *Portlandia* - *Portlandia arctica* (J. E. Grey) (Fig. 2; Fig. 3E) - the similarity in chondrophore development, robustness of shell, relatively large size, and the presence of an elongate and produced posterior end, leaves little doubt that *intermedia* be placed within the genus *Portlandia.* Therefore, we treat this species as a member of the *Portlandia.* We are less confident with regards to generic placement of *propinqua*, *philippiana* and *lenticula*, as these species all display characteristics that could place them within *Portlandia* or *Yoldiella* on equal merit. Indeed, these three species seem to form a group that is intermediate between *Yoldiella sensu stricto* and *Portlandia* in terms of shell morphology. However, for the purposes of this study we hereby follow the CLEMAM (2008) website placement for these taxa and treat the all three species as members of *Yoldiella.*

It is not the intention of this study to fully resolve the taxonomic issues regarding these closely related genera, although these clearly need to be addressed.

Other inconsistencies in the generic placement of nuculanids similar to *Yoldiella* are present in the recent literature. Sneli *et al.* (2005) record *Yoldiella messanensis* and *Yoldiella pustulosa* in their study area. However, these species should be correctly named as *Ledella messanensis* (Jeffreys, 1870) [= *Ledella acuminata* (Jeffreys, 1870) sensu Allen & Hannah 1989] (see Warén 1978 and 1989a) and *Ledella pustulosa* (Jeffreys, 1876). Both species were found in the AFEN and Challenger material and are illustrated (Fig. 4) but not covered in detail. *Ledella* differs from *Yoldiella* in that the former have more solid shells and are distinc-

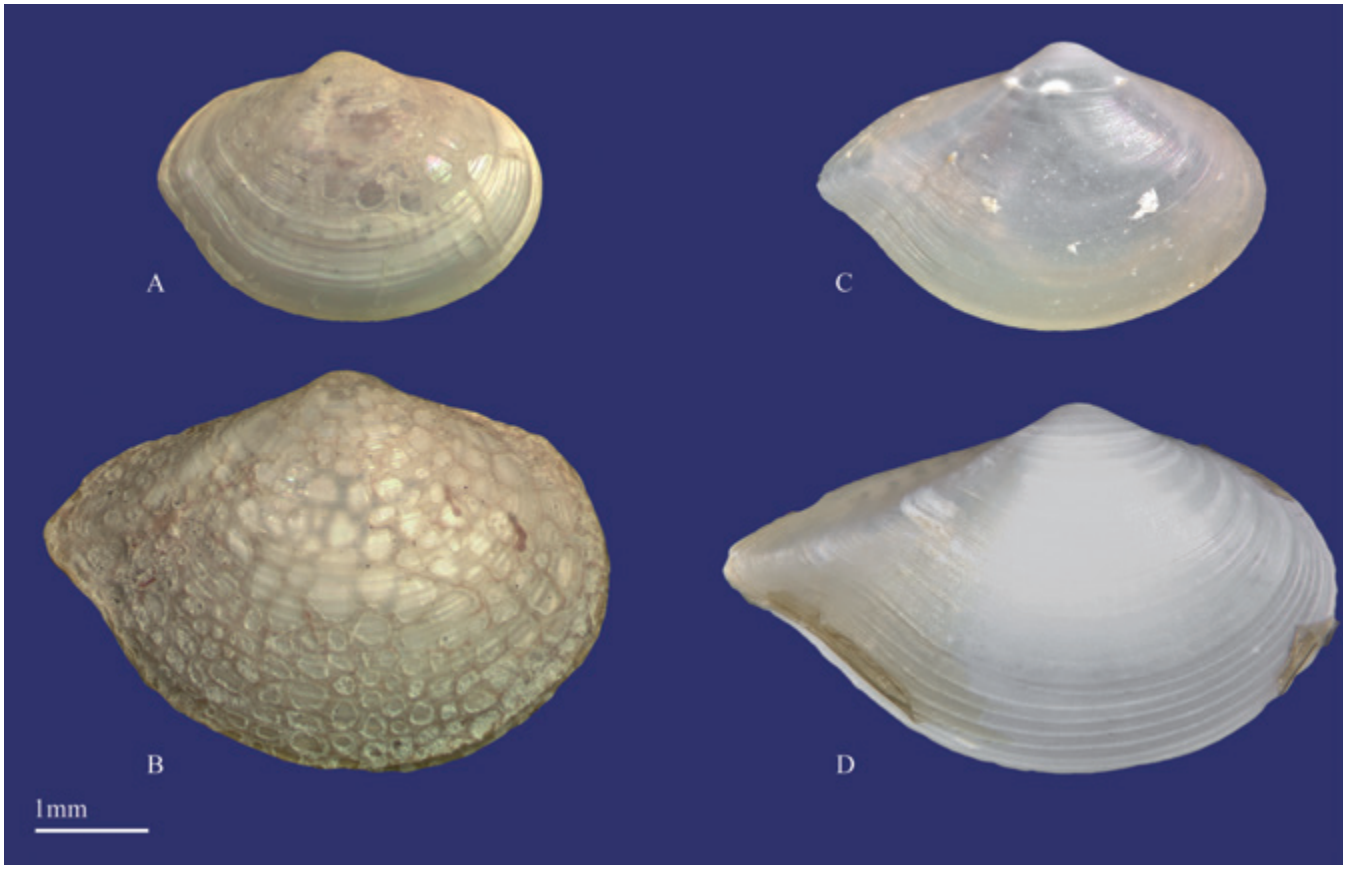

Figure 4 **A** *Ledella pustulosa* (Jeffreys, 1876), right valve, AFEN 54579 **B** *Ledella pustulosa* (Jeffreys, 1876), right valve, AFEN 54591 **C-D** *Ledella messanensis* (Jeffreys, 1870), right valve, Challenger ES250

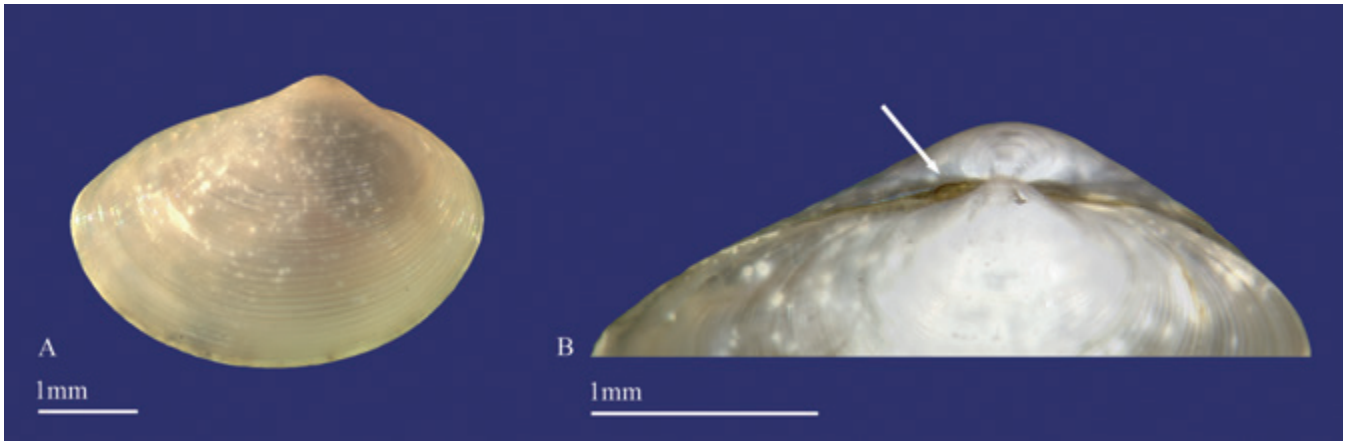

Figure 5 **A-B** *Pseudoneilonella latior* (Jeffreys, 1876), AFEN 55203#1,3 **A** right valve **B** Opisthodetic External ligament

tively rostrate posteriorly, often sinuously. The concentric sculpture of *Ledella* is variable and is often weak, or absent. However, *Ledella pustulosa* can be easily identified by the blistered appearance of the periostracum that can lead to a tortoiseshell patterning of the shell (La Perna, 2004). Although *Ledella pustulosa* is currently placed within the genus *Ledella*, La Perna *et al.* (2004)

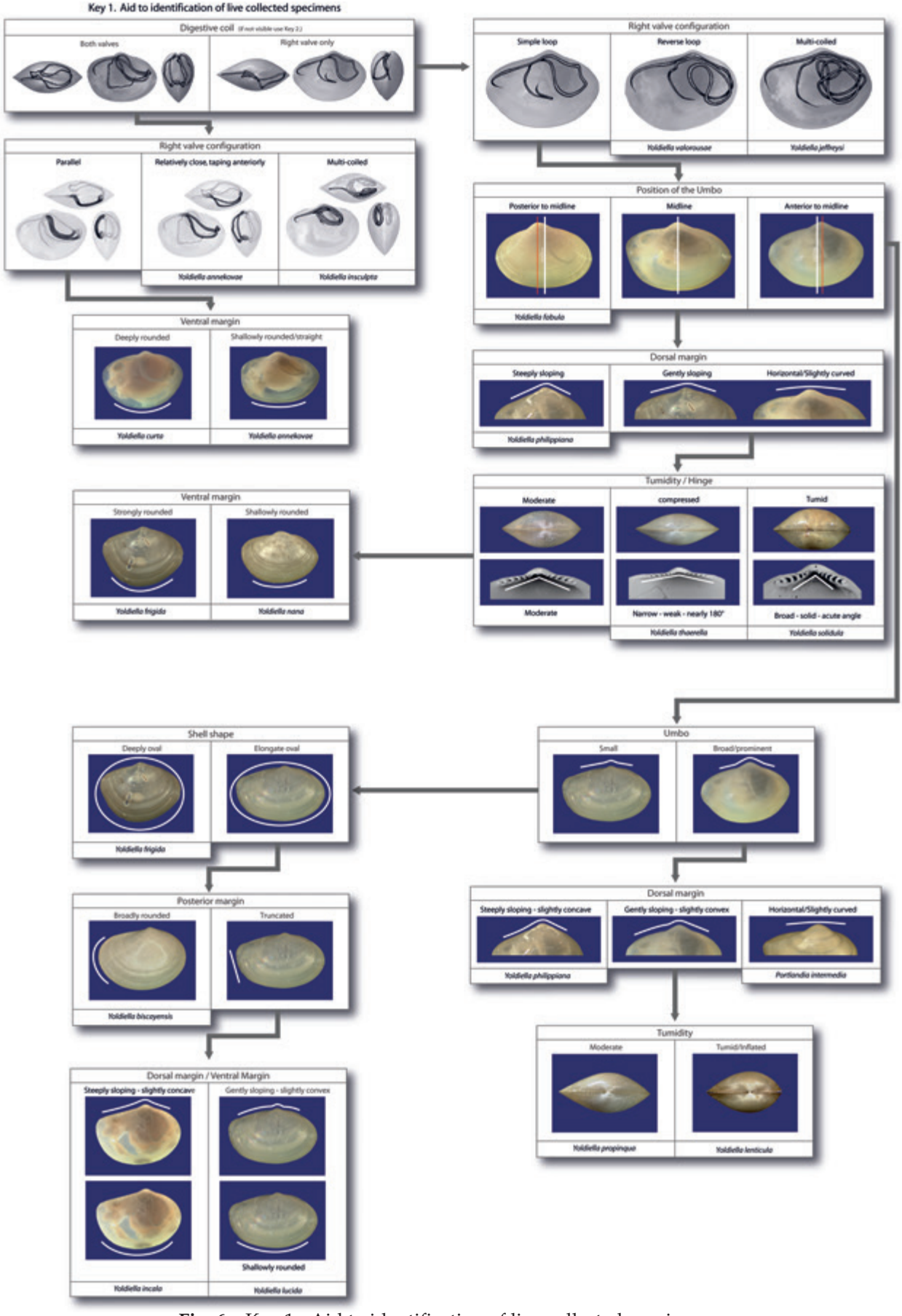

Fig. 6 Key 1 - Aid to identification of live collected specimens

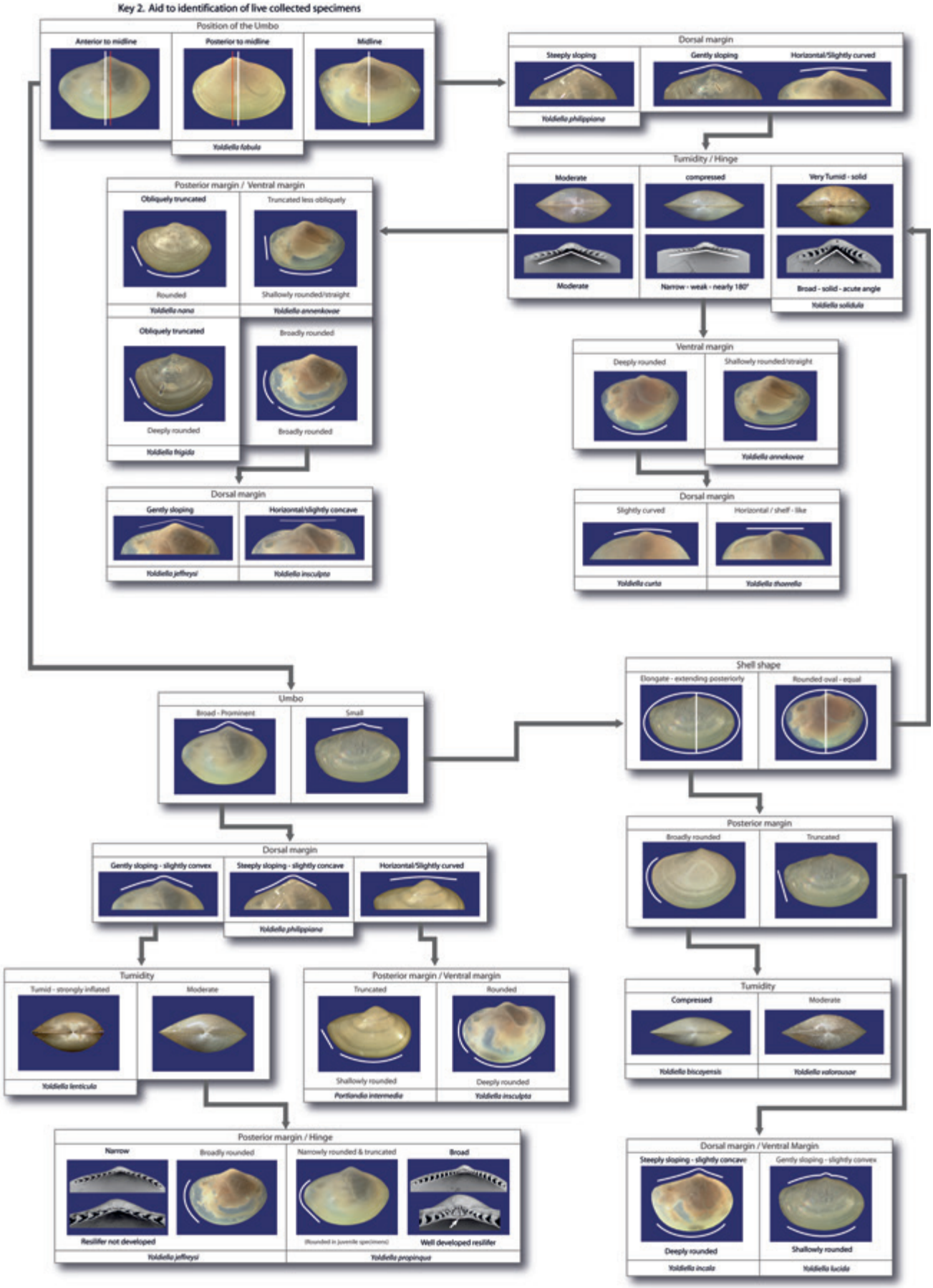

Fig. 7 Key 2 - Aid to identification of live collected specimens

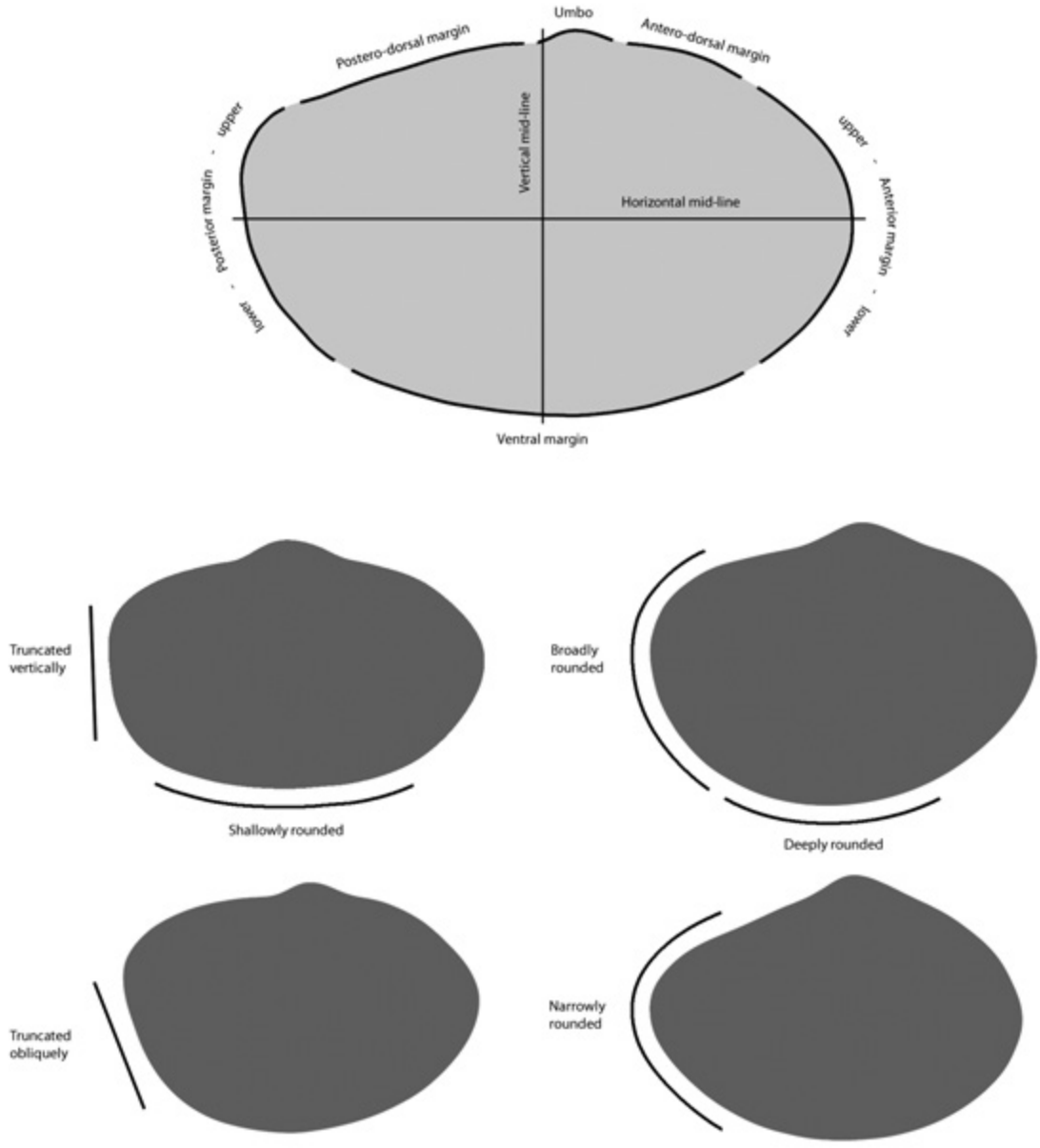

Figure 8 Illustrated examples of terminology used throughout the species accounts for the description of the shell.

propose, though not formally, that this species be assigned to the genus *Zealeda* Marwick, 1924, as the characteristics in the shell shape, sculpture and periostracum are more closely aligned to species within the genus *Zealeda* than *Ledella.*

Bivalves of the family Neilonellidae can also be very similar in appearance to *Yoldiella*. La Perna (2007) reviews the Neilonellidae, describing the characteristics that separate the genera *Neilonella*, *Pseudoneilonella* and *Austrotindaria*, which in turn can be used to distinguish them from *Yoldiella*. *Neilonella* species have prominent and uniform concentric sculpturing, and an umbo that leans towards the anterior. The ligament is amphidetic and external. *Pseudoneilonella* is morphologically similar to *Neilonella* but differs in possessing an opisthodetic external ligament (Fig. 5). *Austrotindaria* also possess an opisthodetic external ligament, but lacks the sculptural detail present in both *Pseudoneilonella* and *Neilonella*. In juvenile specimens of neilonellids the ligament is mostly internal.

Species of *Yoldiella* and *Portlandia* can be very difficult to identify reliably. Most species share

similar characteristics and to the untrained eye there is very little apparent difference in shell morphology. Subtle differences in the slope and angularity of the margins are important and the terminology associated is presented in Fig. 8. The coiling of the gut is also a useful character and can be seen through the shell of most species. The shell sculpture and sheen on the periostracum are also helpful. The keys focus primarily on characters visible in whole live collected specimens but in order to make a definitive identification of some species there may be the need to observe internal shell characters that are only visible once the valves has been separated.

The keys have been formulated using the characters found in adult specimens of the typical form of each species. Juvenile specimens often do not resemble the adults and therefore some characters may not be visible in juvenile specimens. Variation in shell morphology within a species is often common and this variation may not be accounted for in every species featured in the keys. Where possible growth series and variations of form have been included in the individual species plates as a further aid to identification.

The keys include the following taxa:

Portlandia intermedia; Yoldiella annenkovae, Y. curta, Y. jeffreysi, Y. lucida, Y. nana, Y. philippiana, Y. propinqua, *Y. valorousae* nom. nov., *Y. thaerella* sp. nov., *Y. biscayensis*, *Y. fabula*, *Y. frigida*, *Y. insculpta, Y. lenticula, Y. incala, Y. solidula*.

SPECIES ACCOUNTS

Yoldiella annenkovae (Gorbunov, 1946)

Portlandia annenkovae Gorbunov, 1946: 314, 320

Type locality Northeast of Franz Josef Land, 698m.

Type material Zoological Institute, Leningrad.

Key features

Shell To 2.5mm in length (Warén 1989a). Thin, fragile, laterally compressed, outline ovate. Antero-dorsal and postero-dorsal margins gently curved; anterior margin narrowly rounded; lower posterior margin obliquely, almost vertically, truncated;. ventral margin shallowly rounded, occasionally almost straight. Umbo central, narrow, prominent, projecting above the dorsal margin. External surface with virtually no sculpture; periostracum silky. Hinge plate very narrow, 5-6 blunt teeth in each set. Ligament, type 1, relatively long, resilifer very shallow. .

Gut loop The hind-gut forms a narrow loop on both sides of the body. It is curved with the dorsal and ventral sides relatively close together, tapering towards the anterior end, and is highly visible through the shell.

Figure 9 *Yoldiella annenkovae* (Gorbunov, 1946). Gut loop, AFEN 54522#1,2

Distribution Specimens of *Y. annenkovae* were identified from 11 of the AFEN stations from west of Shetland to northeast of Shetland. Depth range: 725 to 1623m, but in 900-1000m in the main cluster of stations northeast of Shetland.

Yoldiella annenkovae has been recorded on few occasions since the original discovery in 698m off Franz Josef Land (Gorbunov 1946). Warén (1989b) recorded specimens east of Svalbard in depths ranging from 995 to 3270m, and from west of the Lofoten Islands, Norway in 1000m. Richling (2000) found shells at an approximate depth of 200m in the Laptev Sea, Siberia. It was recorded at four of the Biofar stations southeast and northeast of the Faeroes at depths from 806-1032m (Sneli *et al.* 2005). Warén (1989a) also recognized *Y. annenkovae* in material in the National Museum of Canada and from an illustration in Clarke (1963) from the North Canadian Basin, and thus speculated that the species is widely distributed over the Polar Basin.

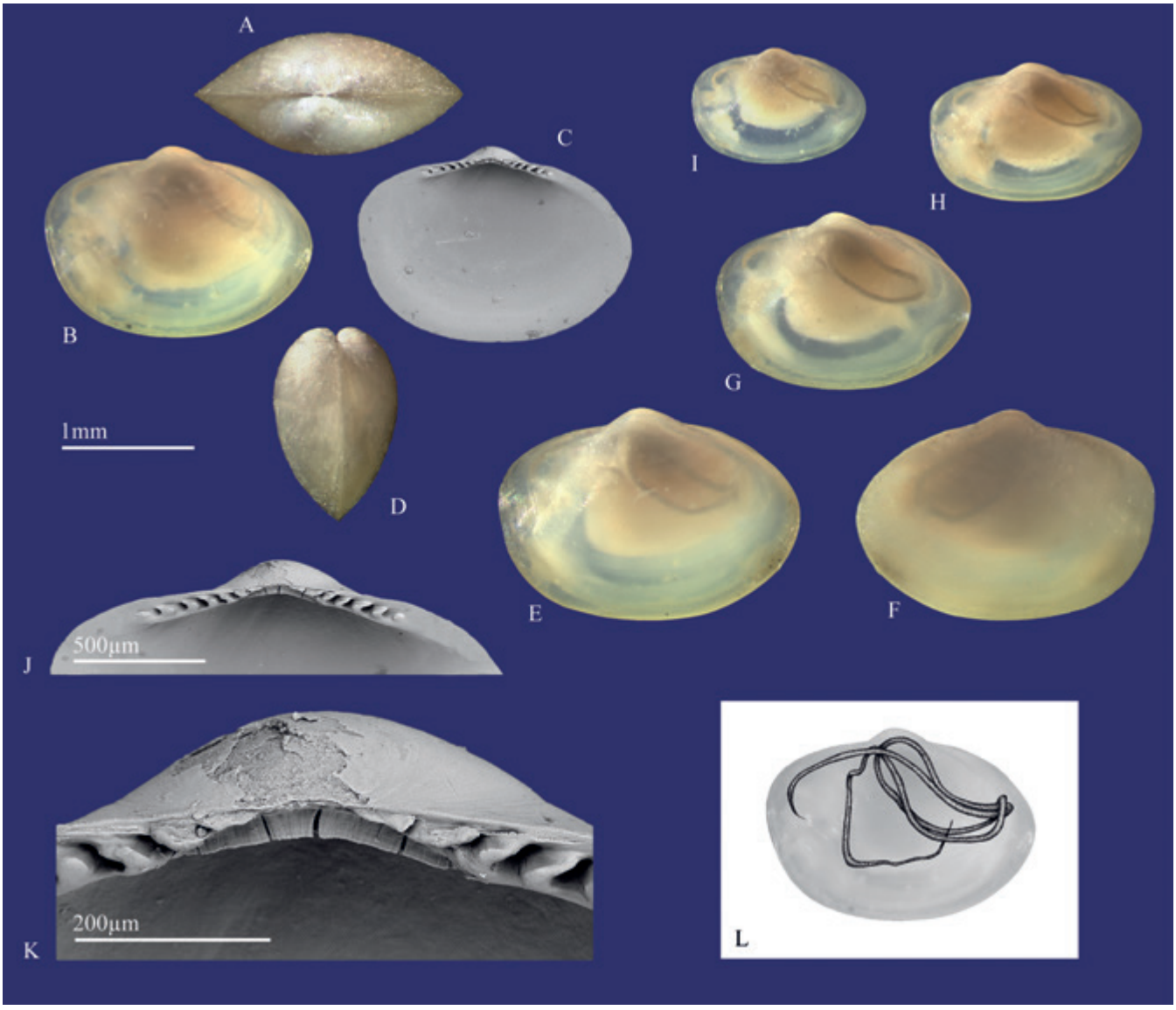

Figure 10 *Yoldiella annenkovae* (Gorbunov, 1946) **A-K** AFEN 55378#1 **A** Dorsal **B** Right valve **C** Left valve internal **D** Posterior **E** Right valve **F** Left valve **G-H, I** Right valve **J-K** Hinge detail **L** Gut loop, AFEN 54522#1,2

Specimens of *Y. annenkovae* collected during the AFEN surveys constitute the first records of the species from British and Irish waters.

Remarks This is the smallest *Yoldiella* species in the region. The largest AFEN specimen is 2.3mm in length. Within the study area, *Y. annenkovae* are only likely to be confused with *Y. nana* (which has a more obliquely truncated posterior end and a more rounded ventral margin) and *Y. thaerella* (which has a straighter dorsal margin and is rare at depths <1500m). However, *Y. annenkovae* is immediately separated from both by the presence of coils of the gut loop on both the right and left sides of the animal. Only three other species in the NE Atlantic and Arctic have this feature: *Y. curta* and *Y. insculpta* (see below) and *Y. tamara* (Gorbunov, 1946) (a high Arctic species), all of which have a different shell morphology from *Y. annenkovae*.

Yoldiella curta Verrill & Bush, 1898

Yoldiella minuscula Verrill & Bush, 1898: 870

Type locality North America Basin, off St Georges Bank, 40° 16.5'N, 67° 05.3'W. 1290 fathoms (2348m).

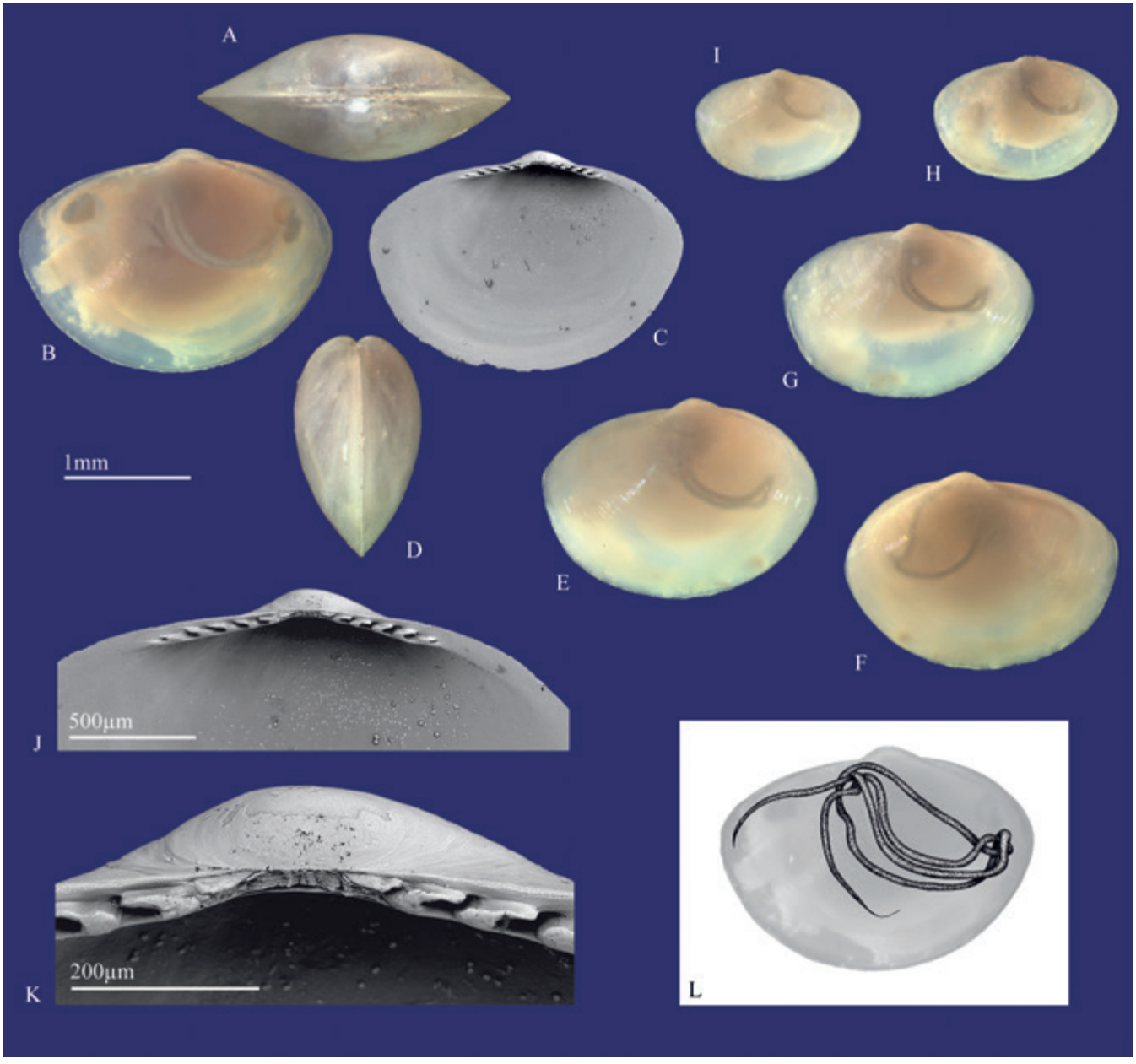

Figure 11 *Yoldiella curta* Verrill & Bush 1898 **A-D, J-K** Challenger ES250 **A** Dorsal **B** Right valve **C** Left valve internal **D** Posterior **E-F, I** AFEN 54625#1 **E** Right valve **F** Left valve **G** Right valve, AFEN 54598#1 **H** Right valve, AFEN 54587#1 **I** Right valve **J-K** Hinge Detail **L** Gut loop, AFEN 54586#2

Type material Holotype USNM 38457.

Key features

Shell To 5mm in length (frequently <4mm). Thin, fragile, laterally compressed. Outline ovate; antero-dorsal margin short, gently sloping; postero-dorsal margin slightly rounded; anterior and posterior margins slightly pointed; lower posterior margin slightly obliquely truncated; ventral margin deeply rounded. Umbo small, not prominent, situated just anterior of mid-line. Sculpture obsolete, periostracum glossy. Hinge plate short, very narrow with 5-6 chevron-shaped teeth on either side of the umbo. Ligament, type 1, relatively long.

Gut loop The hind-gut forms a narrow loop on both sides of the body that is highly visible through the semi-transparent shell. On the right side of the body the loop is curved with the two

Figure 12 *Yoldiella curta* Verrill & Bush 1898. Gut loop, AFEN 54586#2

sides running parallel along the same course towards the anterior adductor muscle. The coil then crosses to the left side of the body where it forms a simple rounded loop

Distribution *Yoldiella curta* was recorded from 11 AFEN stations on the slopes of Rockall Trough to the west of the Outer Hebrides, and to the south and east of Rosemary Bank, at depths of 1364-2046m.

It was common amongst the *Challenger* material occurring at a number of stations, mostly on the slopes of Rockall Trough in depths ranging from 1270 to 2275m, but only rarely in deeper water at 2900m. Allen *et al.* (1995) considered *Y. curta* to be the most widely distributed of the deep-water *Yoldiella* species, occurring in most of the Atlantic basins and recording it from numerous stations in the West European Basin, including several from the Bay of Biscay (44 °N) to Rockall Trough (58 °N), in depths of 1537 to 2634m.

Remarks This was the commonest *Yoldiella* species in the deeper water stations (>1500m) of the AFEN surveys. It is also one of the most easily identified species due to the highly distinctive gut loop which makes live collected specimens of *Y. curta* unmistakable. However, when attempting to identify this species using the shell characteristics alone it can be more difficult, as it can be easily confused with *Y. thaerella* and *Y. frigida*. *Yoldiella thaerella* has a shelf-like dorsal margin, and *Y. frigida* has greater shell tumidity, a thicker shell and hinge, and greater shell height relative to length.

Yoldiella jeffreysi (Hidalgo, 1877)

Leda lata Jeffreys, 1876: 431
Leda jeffreysi Hidalgo, 1877: 396 (replacement name for *L. lata* Jeffreys, 1876)

Type locality H.M.S Valorous Sta. 16, Iceland Basin, west of Rockall Plateau, south Maury Channel, 55°10′N, 25°58′E, 1785 fm.

Type material Lectotype USNM 199696, selected by Allen *et al.* (1995).

Key features
Shell To 3.7mm in length. Thin, tumid. Outline oval; postero-dorsal and antero-dorsal margins gently sloping; posterior and anterior margins broadly rounded; ventral margin deeply rounded with the lowest point slightly posterior to the mid-line. Umbo prominent, moderately broad, projecting just above the dorsal margin, and lies anterior of the mid-line. Posterior adductor muscle scar elongate-rounded. Surface smooth; periostracum silky. Hinge long, narrow, with 8-10 posterior and 7-9 anterior, chevron-shaped teeth on either side of the type 1 ligament.

Gut loop The hind-gut lies on the right side of the body a forms a complex series of clockwise and anticlockwise coils.

Figure 13 *Yoldiella jeffreysi* (Hidalgo, 1877). Gut loop, *Challenger ES399*

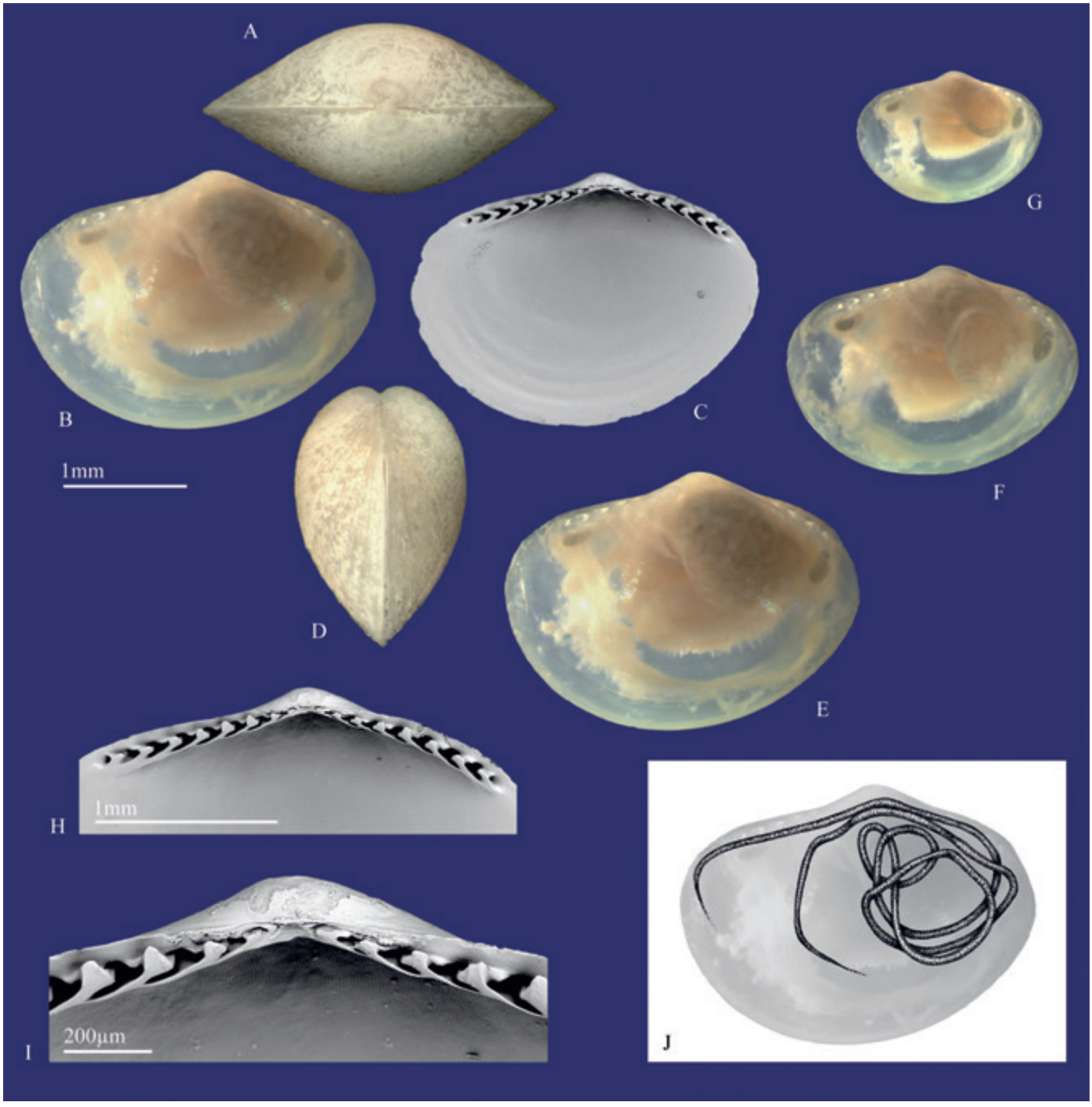

Figure 14 *Yoldiella jeffreysi* **(**Hidalgo, 1877). **A-J** Challenger ES399 **A** Dorsal **B** Right valve **C** Left valve internal **D** Posterior **E-G** Right valve **H-I** Hinge detail **J** Gut loop

Distribution *Yoldiella jeffreysi* was recorded from 1 AFEN station northeast of Rosemary bank (59º41'N, 08º42'W) in a depth of 1291m.

Y. jeffreysi is probably the most widespread member of the genus (Allen *et al.* 1995). It was the most frequently occurring *Yoldiella* species amongst the *Challenger* material occurring at a number of stations, from the southern part of Rockall Trough to the Wyville Thomson Ridge, in depths ranging from 862 to 2900m. Allen *et al.* (1995) record the species from most of the Atlantic deep-sea basins, including many locations in the Western European Basin, especially Rockall Trough from latitudes of 44ºN to 58ºN, and at depths of 2040-4862m. Allen *et al.* (1995) also state that the species has been recorded from

western Greenland, the Gulf of Mexico and the Mediterranean off Palermo.

Nomenclature The nomenclatural history of this taxon is complex. Comments are to be found in Warén (1980), Allen *et al.* (1995), and in the CLEMAM website.

As stated by Allen *et al.* (1995), Jeffreys original 'Valorous' specimens collected from the North Atlantic (Valorous stations 9, 12, 13 & 16) were described as his species *Leda lata* Jeffreys 1876. Hidalgo (1877) suggested that the name *Leda lata* Jeffreys 1876 was preoccupied by *L. lata* (Hinds, 1843), following the placement and illustration of *Nucula lata* Hinds 1843 under the genus *Leda* by Reeve (1871), and thus proposed the replacement name *Leda jeffreysi* Hidalgo, 1877. Jeffreys (1879) accepted this change.

Recent examination of Jeffreys' material by Allen *et al.* (1995) found that the material from the 'Valorous' stations actually contained two distinct species, which are very similar in form. The original description given by Jeffreys (1876) for his species *Leda lata* (= *jeffreysi* Hidalgo 1877) is too general to ascertain which of the two species Jeffreys was describing at the time. Allen *et al.* (1995) accept *Leda jeffresyi* Hidalgo (1877) as the first unequivocal specific designation. Allen *et al.* (1995) described and illustrated the two species, retaining the replacement name *Yoldiella jeffreysi* (Hidalgo, 1877) for the species originally believed to have been described as *Leda lata* Jeffreys, and described and illustrated the second species under the name *Yoldiella lata* (Jeffreys, 1876). Allen *et al.* (1995) selected and designated lectotypes for each of these species from the syntype series of *Leda lata* Jeffreys (= *jeffreysi* Hidalgo 1877).

Allen *et al.* (1995) can be considered to be the first revisers of the genus *Yoldiella* and given that the two species concerned are clearly defined by them it is appropriate to follow their work as close as possible. However, the nomenclature used by Allen *et al.* (1995) must be revisited as they can now be seen to be in error in describing two different species under the names *Y. lata* (Jeffreys, 1876) and *Y. jeffreysi* (Hidalgo, 1877) as *Y. jeffreysi* (Hidalgo, 1877) is a replacement name and thus an objective synonym of *Y. lata* (Jeffreys, 1876) (CLEMAM 2008).

Consequently, this paper adopts their concept of *Y. jeffreysi* (Hidalgo, 1877) and the lectotype designation from *Valorous* station 16. This paper also adopts their concept of the species named by Allen *et al.* (1995) as *Y. lata* (Jeffreys, 1876) but cannot adopt that name for the reasons given above. The species *Yoldiella lata* (Jeffreys, 1876) *sensu* Allen, Sanders & Hannah 1995 is therefore given the new replacement name *Yoldiella valorousae*. Since the use of the name *Yoldiella lata* (Jeffreys, 1876) by Allen *et al.* (1995) was invalid, the lectotype designation given for *Yoldiella lata* (Jeffreys, 1876) *sensu* Allen, Sanders & Hannah 1995 is also deemed invalid. However, this specimen can be selected as the name bearing type for *Y. valorousae*. In doing so this retains all of the taxonomic conclusions of the first revisers (Allen *et al.* 1995) with only a simple name replacement.

Remarks *Y. jeffreysi* is very similar in shape to *Y. valorousae* and *Y. biscayensis*, but is more tumid than both species. Young individuals of *Y. jeffreysi* are also similar to young specimens of *Y. propinqua*. However, *Y. jeffreysi* is easily differentiated from these similar shaped species by the complex, multiple coiling of the gut loop present in *Y. jeffreysi*.

Yoldiella lucida (Lovén, 1846)

Yoldia lucida Lovén, 1846: 35
Leda obesa Stimpson, 1851a: 113
Leda lucida var. declivis Jeffreys, 1879: 578
Leda lucida var. truncata Jeffreys, 1879: 578
Yoldiella iris Verrill & Bush, 1898: 863
Yoldiella subangulata Verrill & Bush, 1898: 865

Type locality Hammerfest, northern Norway.

Type material Lectotype SMNH 1533, selected by Warén (1989a).

Key features

Shell To 7mm in length. Thin, laterally compressed. Outline elongate-oval; antero-dorsal margin short, gently sloping; anterior rounded; postero-dorsal margin long, gently sloping, with a slight dorsal margin - posterior margin junction; lower posterior margin obliquely truncated and may be weakly rostrate in larger specimens. Dorsal margin crimped either side of the umbo and also dipping down to give a small notch. Ventral margin long, shallowly rounded, occasionally more deeply rounded in smaller specimens. Umbo small, narrow, not prominent, projecting just

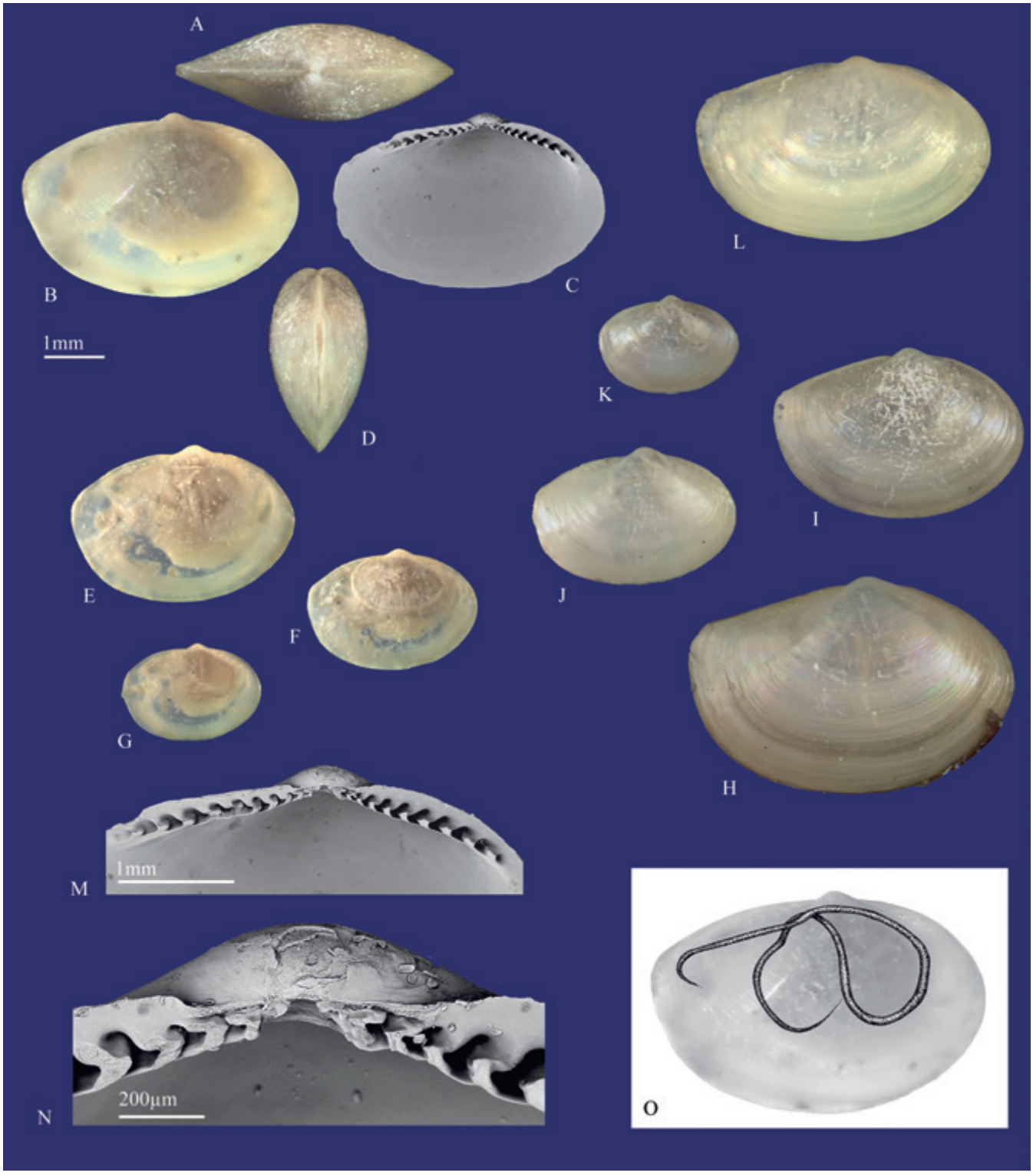

Figure 15 *Yoldiella lucida* (Lovén, 1846) **A-D, M-N** *AFEN 55268#1* **A** Dorsal **B** Right valve **C** Left valve internal **D** Posterior **E-G** Right valve, *AFEN 55207#2,3* **H-K** Right valve, *SMNH 38782* **L** Right valve, *Lectotype SMNH 1533* **M-N** Hinge detail **O** Gut loop, *AFEN 53757#1*

above the dorsal margin, and lies anterior of midline. Sculpture of weak striations; periostracum silky. Hinge long, curved, with at least 10 chevron-shaped teeth on either side of the type 1 ligament

Figure 16 *Yoldiella lucida* (Lovén, 1846). Gut loop, *AFEN 53757#1*

Gut loop The hind-gut forms a simple, rounded loop on the right side of the body.

Distribution The species was identified from 7 AFEN stations to the west of Shetland, at depths of 543-1158m.

Y. lucida is found on both sides of the Atlantic and into the Arctic, most commonly in depths from 100-1000m. It occurs all along the Norwegian coast (Bratteggard & Holthe, 1997). It is also known from the Mediterranean (Warén 1989a). It was recorded at many of the Biofar stations around the Faeroes at depths from 200-1096m (Sneli *et al.* 2005). The species was not found amongst the amongst the *Challenger* material although Allen *et al.* (1995) recorded it at two stations on the slopes of Rockall Trough at depths of 609-619m.

Remarks There are several previous records of *Y. lucida* off the coasts of western Ireland, and northern and western Scotland, but very few of these refer to living animals (Seaward 1990).

Yoldiella nana (M. Sars, 1865)

Yoldia nana M. Sars, 1865: 99
Yoldiella fraterna Verrill & Bush, 1898: 867
Yoldiella inconspicua Verrill & Bush, 1898: 869

Type locality *Y. nana*, Lofoten, northern Norway, 146-218m. *Y. fraterna* and *Y. inconspicua*, off Martha's Vineyard, 581m.

Type material *Y. nana* lectotype and several paralectotypes SMNH 3686, selected by Warén (1989a). *Y. fraterna* holotype USNM 159714. *Y. inconspicua* USNM 48867.

Key features

Shell To 3mm in length. Thin, moderately tumid. Outline ovate; antero- and postero-dorsal margins short, almost horizontal and slightly convex; anterior margin narrowly rounded, upper part very slightly obliquely truncated; lower posterior margin obliquely truncated; ventral margin shallowly rounded. Umbo central, moderately broad, prominent, projecting above the dorsal margin. Sculpture virtually absent, although growth rings may be present in larger specimens; periostracum silky. Hinge plate moderately broad with 5-6 blunt teeth on either side of the umbo, and with a relatively long type 1ligament.

Gut loop The hind-gut forms a simple, rounded loop on the right side of the body.

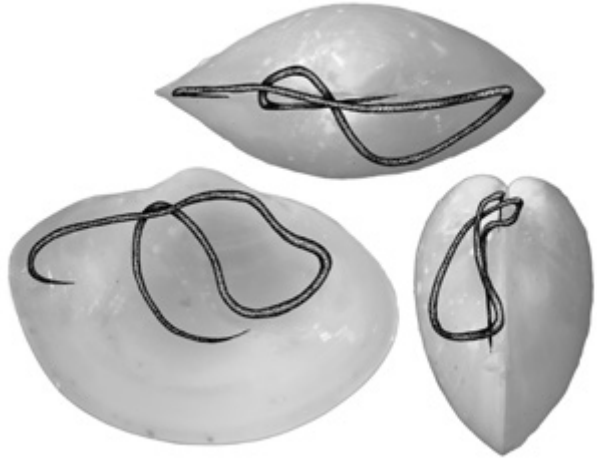

Figure 17 *Yoldiella nana* (M. Sars, 1865). Gut loop, *AFEN 53903#1*

Distribution *Y. nana* was identified from 15 AFEN stations to the west of Shetland, with a depth range of 450-1200m

Yoldiella nana is found over a large area of the North Atlantic from Martha's Vineyard in the west to Lofoten, northern Iceland and the entire Norwegian coast in the east and south to include the Mediterranean. Warén (1989a) notes its presence in the Scandinavian Fjords and the adjacent continental shelf and the upper slope. Richling

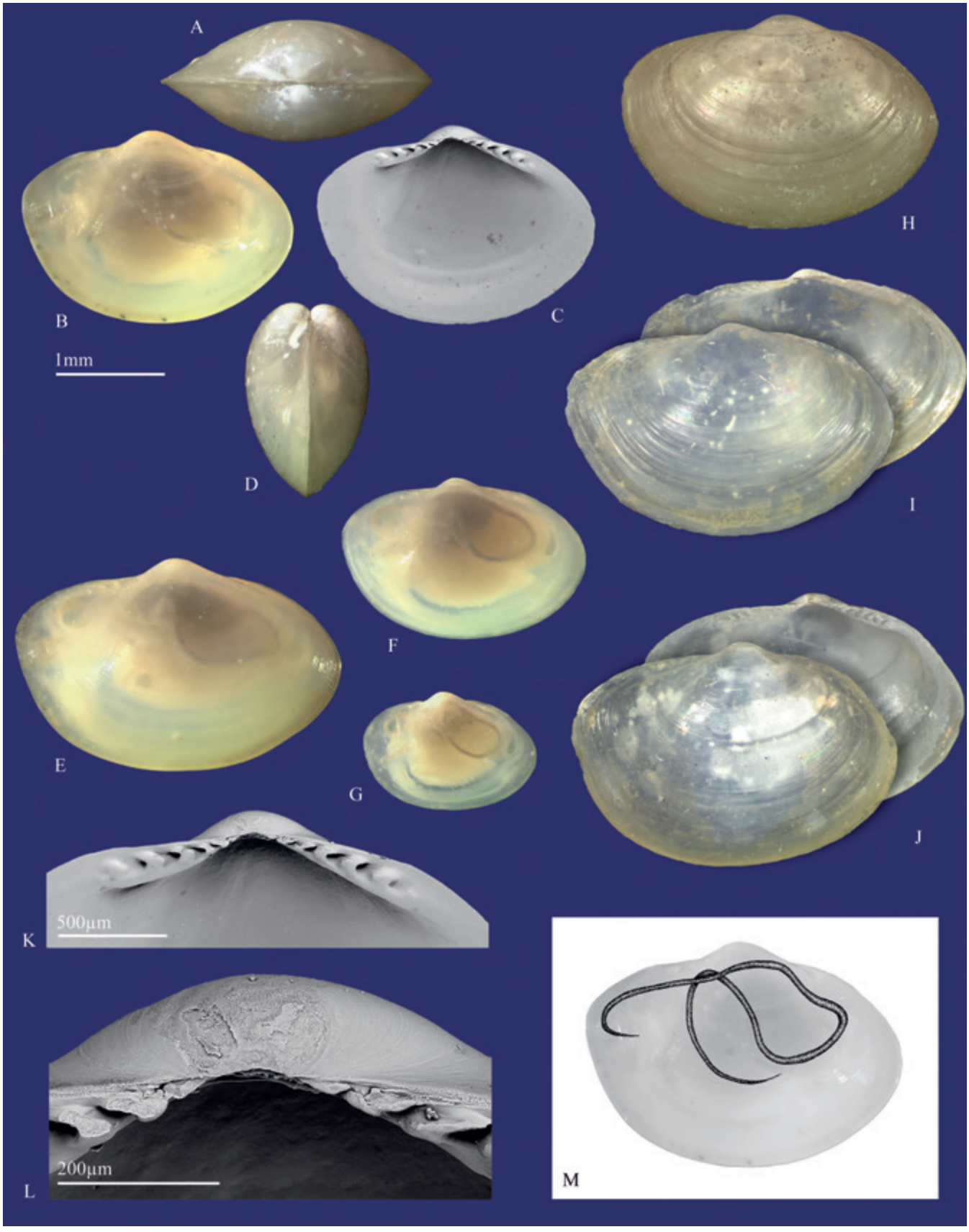

Figure 18 *Yoldiella nana* (M. Sars, 1865) **A-D, I-J** AFEN 55237#1 **A** Dorsal **B** Right valve **C** Left valve internal **D** Posterior **E** Right valve, AFEN 55301#1 **F** Right valve, AFEN 55363#2 **G** Right valve, AFEN 55452#1 **H** Right valve, Paratype SMNH 3686 **I** *Yoldiella inconspicua* Verrill & Bush 1898 (= *nana* M. Sars, 1865) Holotype USNM 48867 **J** *Yoldiella fraterna* Verrill & Bush, 1898 (= *nana* M. Sars, 1865) Holotype USNM 159714 **K-L** Hinge Detail **M** Gut loop, AFEN 53903#1

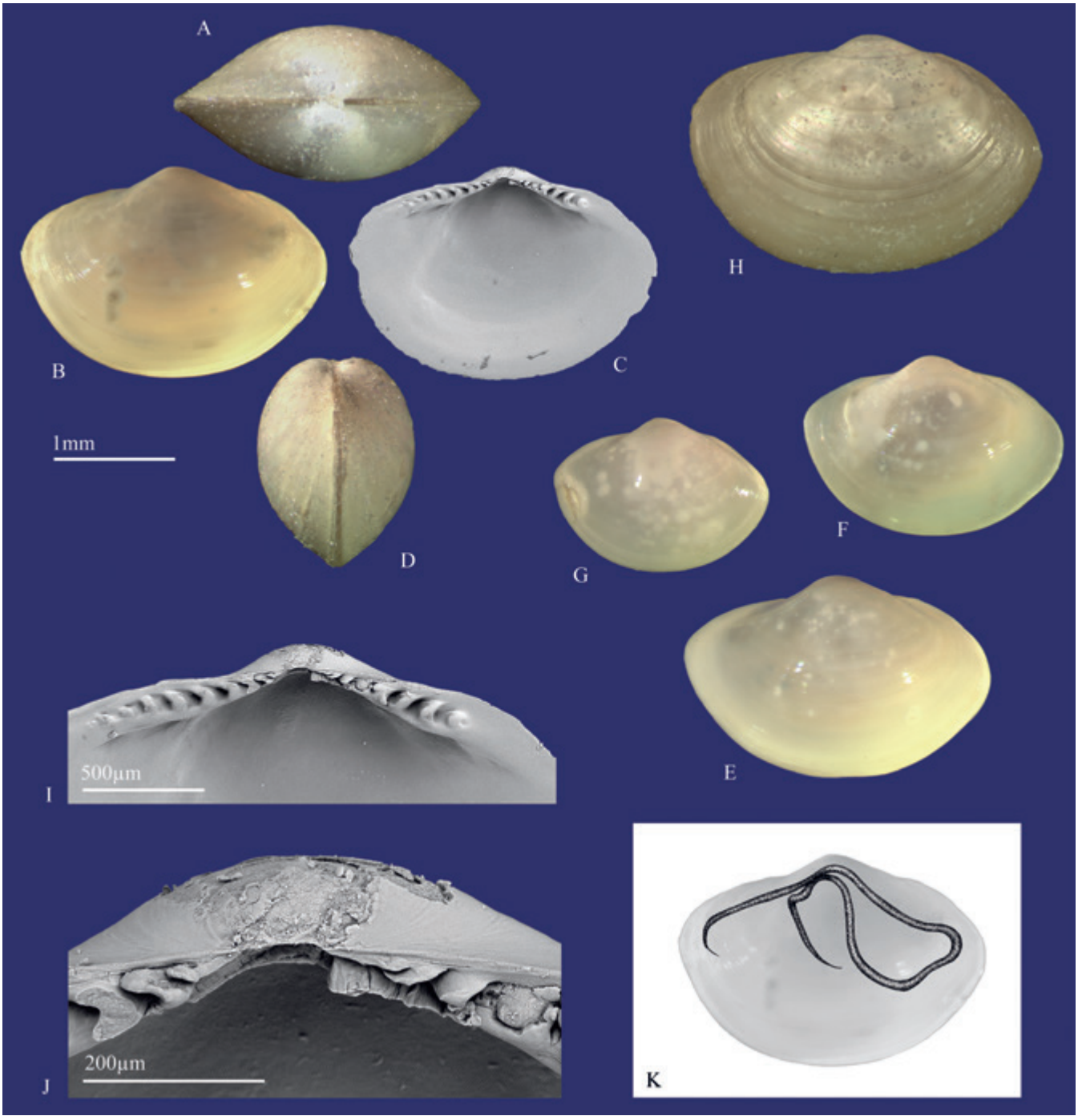

Figure 19 *Yoldiella nana* form A **A-E, I-J** AFEN 55387#1 **A** Dorsal **B** Right valve **C** Left valve internal **D** Posterior **E** Right valve **F** Right valve, AFEN 55337#1 **G** Right valve, AFEN 55237#1 **H** Right valve, Paratype SMNH 3686 **I-J** Hinge detail **K** Gut loop, AFEN 54503#1

(2000) also has records of *Y. nana* from the Laptev Sea, Siberia, giving a depth range of 96-670m. It was recorded at many of the Biofar stations around the Faeroes at depths from 170-1200m (Sneli *et al.* 2005).

Remarks This species is most likely to be confused with *Y. annenkovae* and *Y. solidula*. In live collected material it can be easily distinguished from the former by the configuration of the gut loop. Using shell morphology alone, separation is more difficult. However, *Y. nana* is generally larger in size, has a more rounded ventral margin, and a more obliquely truncated posterior margin. The hinge of *Y. nana* is slightly more robust than in *Y. annenkovae*.

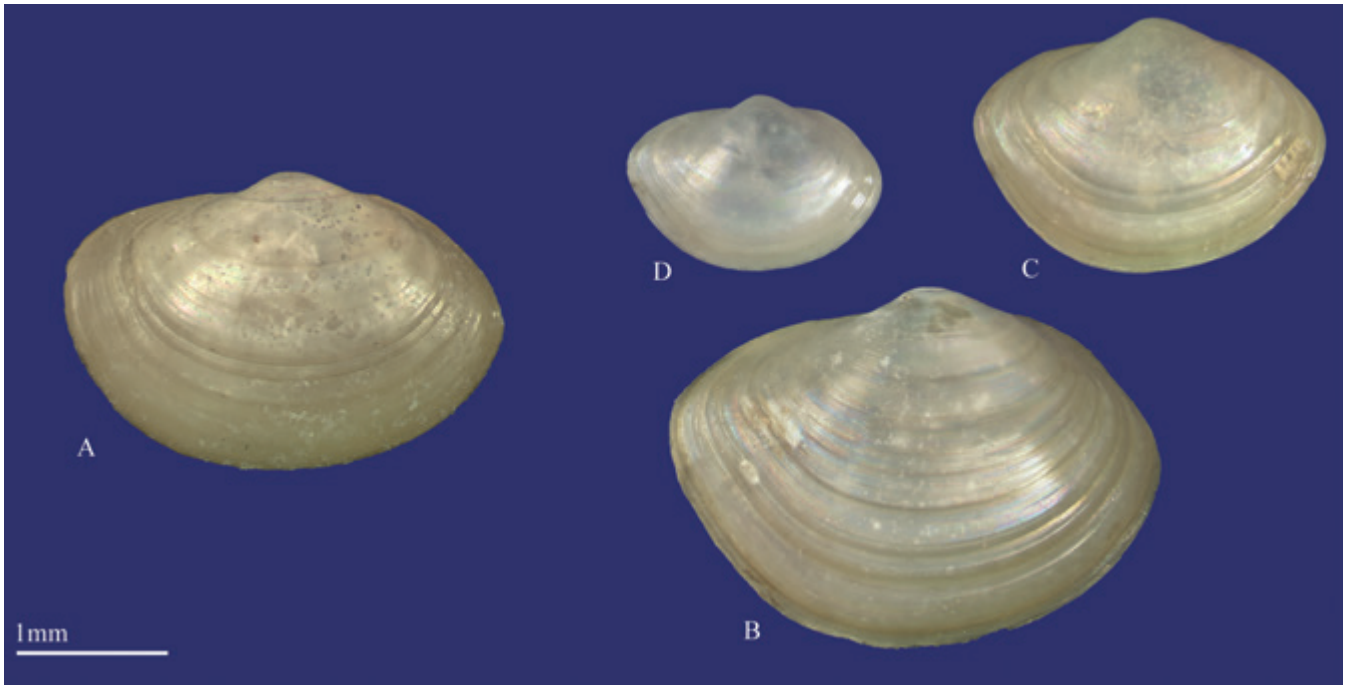

Figure 20 *Yoldiella nana* form B **A** Right valve, Paratype SMNH 3686 **B-D** Right valve, SMNH 60872

Yoldiella nana may be distinguished from *Y. solidula* due to the latter being much more solid and tumid, with a broader umbo and a more deeply rounded ventral margin. The hinge of *Y. solidula* is very solid, broad and with the lower margins forming a more acute angle than found in *Y. nana*.

Yoldiella nana forms

Having examined the AFEN material and SMNH loan material it is clear that there is variation within the species *Y. nana*, resulting in what we consider to be three distinct forms, including the typical form.

The species description provided for *Y. nana* is based on what we consider to be the typical form of *Y. nana*, corresponding to the paralectotype of *Y. nana* and the holotypes of *Y. fraterna* and *Y. inconspicua*. Warén (1989a Fig. 5. E, F) and Richling (2000 fig. 30-31.) figure non-type material that we consider to be of the typical form of *Y. nana*.

Within the AFEN material and SMNH loan material there are a small number of specimens closely resembling *Y. nana*, which consistently exhibit a number of differences in shell morphology.

Yoldiella nana form A is much more tumid than the typical form of *Y. nana*, and the shell is slightly more solid. The umbo is broader and more prominent in relation to the size of the shell. This form is also more angular at the postero-dorsal and antero-dorsal regions. The ventral margin is shallowly rounded as found in the typical *Y. nana*. Warén (1989a fig. 5. G, H) figures specimens of *Y. nana* that we consider to closely resemble this form.

Yoldiella nana form B is also more tumid than the typical form of *Y. nana*, and the shell is slightly more solid. The umbo is broader and more prominent in relation to the size of the shell. The postero-dorsal and antero-dorsal regions more closely resemble that of typical *Y. nana*, but the ventral margin is much more strongly rounded and is more similar to ventral margin found in *Y. solidula*. Warén (1989a fig. 5. C, D) figures specimens of *Y. nana* that we consider to closely resemble this form.

The characteristics that differentiate these forms from typical *Y. nana* may also be seen in *Y. solidula*. However, in *Y. solidula* the shell is much more tumid and solid. The hinge is also unmistakably more solid and acutely angled in *Y. solidula* than either of the two forms of *Y. nana*, of which the hinges are more closely aligned to that of typical *Y. nana*. Richling (2000) also suggested that some forms of

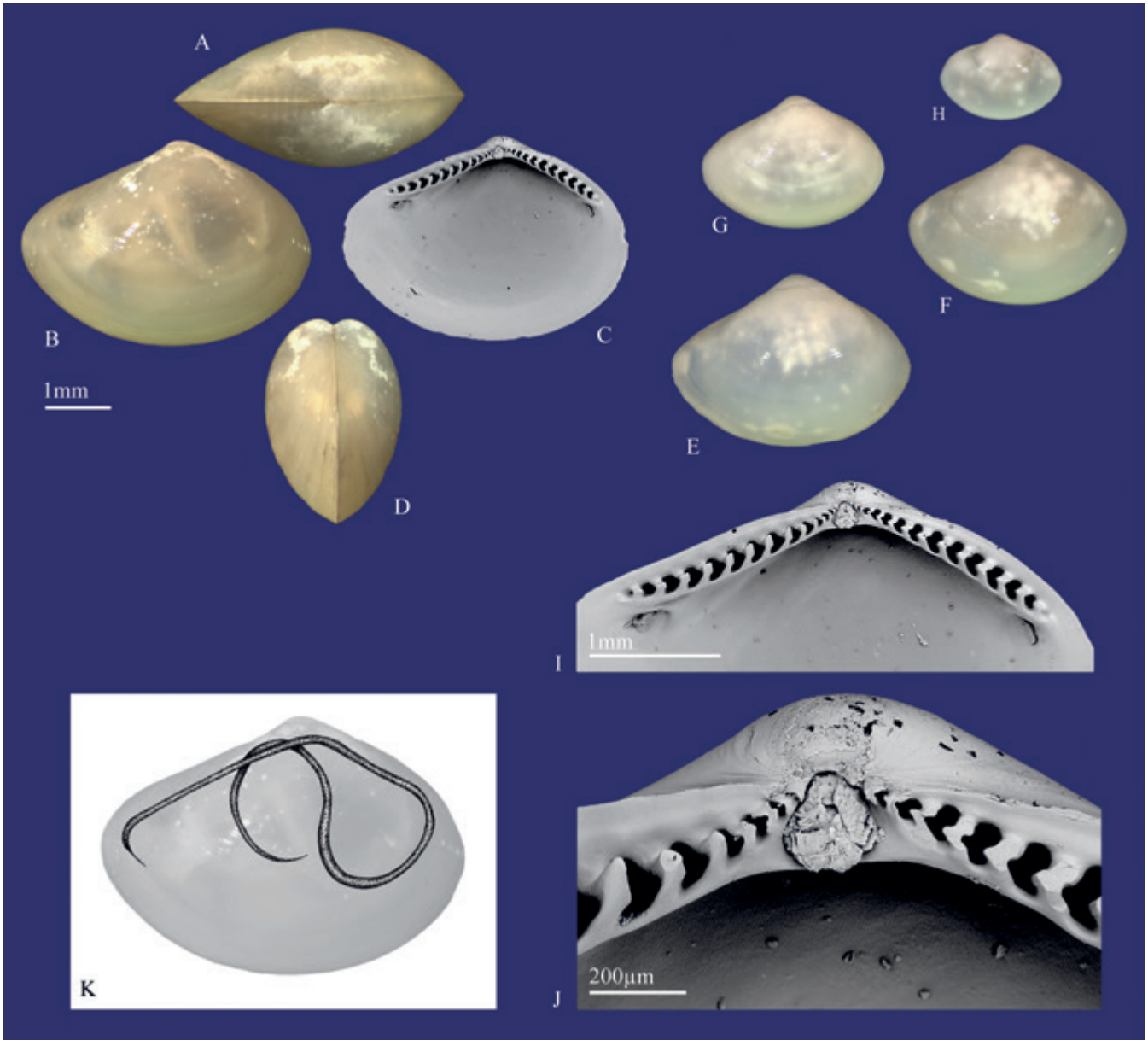

Figure 21 *Yoldiella philippiana* (Nyst, 1845) **A-D, I-J** AFEN 55217#2 **A** Dorsal **B** Right valve **C** Left valve internal **D** Posterior **E-H** Right valve, 53815#4,5 **I-J** Hinge detail **K** Gut loop, AFEN 53796#5

Y. solidula more closely resembled *Y. nana*.

Although it is apparent that these forms exist within *Y. nana*, at present we have insufficient material with which to resolve the taxonomic issues. In the AFEN material, these forms of *Y. nana* were recorded only from a cluster of stations around 00 º30′E, 62º30′N in depths of 725-919m.

Yoldiella philippiana (Nyst, 1845)

Nucula tenuis Philippi, 1836: 65
Nucula philippiana Nyst, 1845: 224 (replacement name for *N. tenuis* Philippi, 1836, non Montagu, 1803)
Leda pygmaea Münster 1835: sensu Philippi, 1844: 46
Yoldiella lenticula tomlini Winckworth, 1932: 239, 251
Yoldiella frigida mediterranea Nordsieck, 1974: 14

Type locality *Y. philippiana*, Sicily, Pleistocene fossil. *Y. tomlini*, northern Scotland, 30-156m.

Type material Lectotype SMNH 1533, selected by Warén (1989a).

Key features

Shell To 4.5mm in length (rarely 5mm). Solid, tumid. Outline roundly triangular; antero-dorsal margin curved, steeply sloping down to broadly

rounded anterior margin; postero-dorsal margin straight or slightly concave, steeply sloping to a narrowly rounded posterior; ventral margin deeply rounded. Umbo broad, rounded, and lies on the mid-line. Surface smooth; periostracum glossy. Hinge plate broad, continuous, resilifer present, ligament type 2. 12-13 chevron shaped teeth, which are drawn up into points, on either side of the ligament.

Gut loop The hind-gut forms a simple, rounded loop on the right side of the body.

Figure 22 *Yoldiella philippiana* (Nyst, 1845). Gut loop, *AFEN 53796#5*

Distribution Specimens of *Y. philippiana* were identified from 11 of the AFEN stations from northeast of Rosemary Bank (59º49'N, 08º22'W) to north of Shetland (61º26'N, 00º49'W). Depth range: 152 to 536m.

This is a common species of the outer continental shelf and upper slope within the study area. Elsewhere, *Y. philippiana* is widespread in the NE Atlantic from NW Africa to northern Norway, usually in depths of 100-300m, although in Scandinavia it is found as shallow as 25m (Warén 1989a). It is also known from the Mediterranean (Philippi, 1844, Nordsieck, 1974).

Remarks The hinge of *Y. philippiana* is very similar to that of *Y. propinqua* but the teeth of *Y. philippiana* are not drawn into to such a long point. Also, the hinge is much more robust in *Y. philippiana*. Large specimens of *Y. philippiana*, which are more elongate posteriorly, resemble *Y. lenticula*, but the latter has a more gently sloping, slightly convex dorsal margin. *Yoldiella lenticula* is also an Arctic species but there is no evidence for its modern occurrence within the study area.

Yoldiella propinqua (Leche, 1878)

Yoldia propinqua Leche, 1878 : 26
Yoldia pygmaea var. symmetrica Friele, 1878: 222
Portlandia persei Messjatsev, 1931: 42

Type locality Kara Sea, 74º34'N, 57º36'E, 100m.

Type material Lectotype SMNH 1570, selected by Warén (1989a)

Key features

Shell To 5.5mm in length. Moderately tumid. Outline oval, occasionally sub-rostrate in larger specimens; antero-dorsal margin short, gently sloping; anterior margin rounded to narrowly rounded; postero-dorsal margin long, slightly curved, gently sloping; lower posterior margin obliquely truncated and slightly indented (rostrate in larger specimens); ventral margin deeply rounded. Umbo relatively prominent, broad, rounded, projecting well above the dorsal margin, and lies anterior of mid-line. Shell surface relatively smooth; periostracum glossy. Hinge plate broad, continuous; resilifer developed, ligament type 2. 12-13 chevron shaped teeth, which are drawn up into points, on either side of the ligament.

Gut loop The hind-gut forms a simple, rounded loop on the right side of the body.

Figure 23 *Yoldiella propinqua* (Leche 1878). Gut loop, AFEN 53874#1

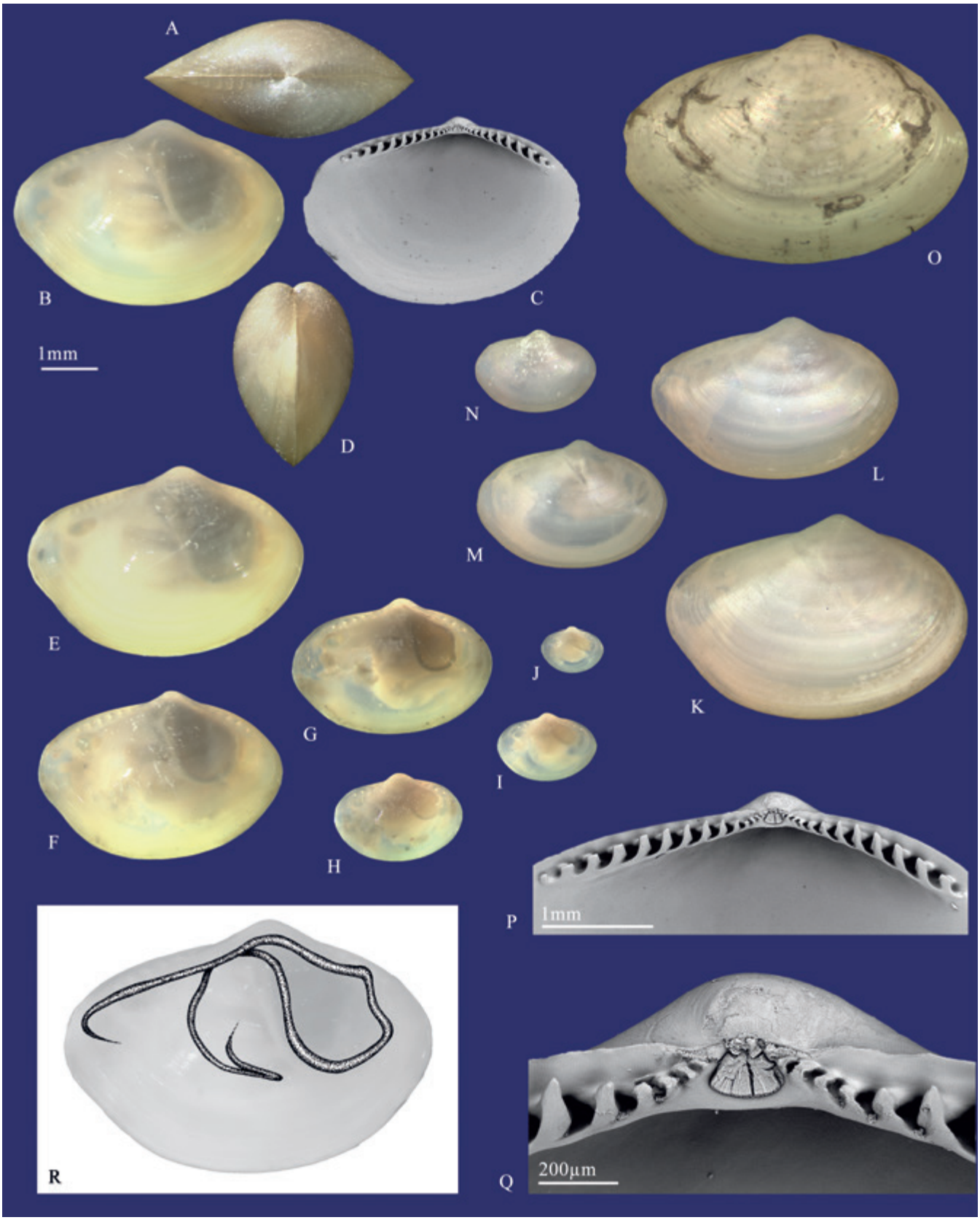

Figure 24 *Yoldiella propinqua* (Leche 1878) **A-D, P-Q** AFEN 55450#1 **A** Dorsal **B** Right valve **C** Left valve internal **D** Posterior **E-G** Right valve, AFEN 55292#1,2 **H-J** Right valve, AFEN 55378#1 **K-N** Right valve, SMNH 53404 **O** Right valve, Lectotype SMNH 1570 **P-Q** Hinge detail **R** Gut loop, AFEN 53874#1

Distribution Specimens of *Y. propinqua* were identified from 66 of the AFEN stations from northeast of Rosemary Bank (59°49'N, 08°22'W) to northeast of Shetland (62°29'N, 00°26'W). Depth range: 417 to 1624m, but most common in 800-1200m.

Yoldiella propinqua is widespread in the north Atlantic and Arctic (possibly circumpolar) occurring from west Greenland to Norway and the Kara Sea (Warén 1989a) and east to the Laptev Sea (Richling 2000). It is considered to be a northern species within the Norwegian fauna (Anon 1997). It was recorded at many of the Biofar stations around the Faroes at depths from 402-1098m (Sneli *et al.* 2005) but not recorded in the *Challenger* material or by Allen *et al.* (1995) from the Atlantic deep-sea basins.

Remarks *Y. propinqua* was by far the commonest species recorded in the AFEN samples both in frequency of occurrence and abundance.

Yoldiella valorousae nom. nov.

New replacement name for *Yoldiella lata* (Jeffreys 1876) *sensu* Allen, Sanders & Hannah, 1995

Type locality Off southern Greenland, *Valorous* Station 9, 59°10'N, 50°25'W, 1750fms.

Type material USNM 199695, selected by Allen *et al.* (1995).

Derivation of name *"valorousae"* after the survey ship HMS Valorous that collected the samples from which Jeffreys original specimens were selected.

Key features

Shell To 4.4mm in length. Thin, slightly tumid. Outline elongate-oval; postero-dorsal margin long, gently sloping; antero-dorsal margin sloping more steeply; posterior margin broadly rounded; anterior margin rounded with the extremity situated above the horizontal mid-line; ventral margin deeply rounded, lowest point posterior of mid-line. Umbo small, not prominent, projecting just above the dorsal margin, and lies anterior of mid-line. Posterior adductor muscle scar rounded. Sculpture of very weak concentric striations; periostracum silky. Hinge long, narrow with 8-10 posterior and 7-9 anterior, chevron-shaped, teeth on either side of the type 1 ligament.

Gut loop The hind-gut lies on the right side of the body. It runs along the antero-dorsal margin then clockwise up towards the umbo then turning anticlockwise and then back on itself.

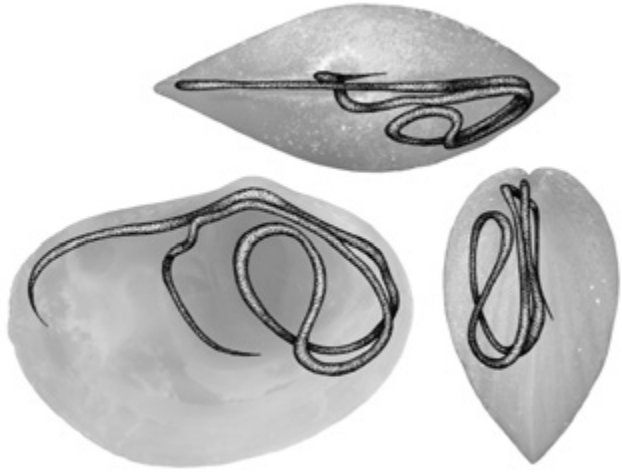

Figure 25 *Yoldiella valorousae* nom. nov. Gut loop, AFEN 54585#2a/b

Distribution *Yoldiella valorousae* was recorded at 4 AFEN stations on the slopes of Rockall Trough, west of the Outer Hebrides. Depth range: 1612 to 1886m.

The species was frequent amongst the *Challenger* material occurring at a number of stations, mostly on the slopes of Rockall Trough in depths ranging from 1050 to 2200m. It was not found at the stations in the deeper (c. 2900 m) parts of Rockall Trough. Allen *et al.* (1995) record the species from many locations in the Western European Basin from latitudes of 43°N to 58°N, and at depths of 1491-3220 m, and at single locations in the Canaries and Sierra Leone Basins.

Nomenclature See *Y. jeffreysi* (Hidalgo 1877) p.746.

Remarks In terms of shell morphology, this species is very similar in appearance to *Y. biscayensis* and *Y. jeffreysi*. *Yoldiella valorousae* is slightly less tumid than *Y. jeffresyi, but* more tumid than the distinctly laterally compressed *Y. biscayensis.* These species are more readily separated by the configuration of their gut loops. *Y. jeffreysi* has

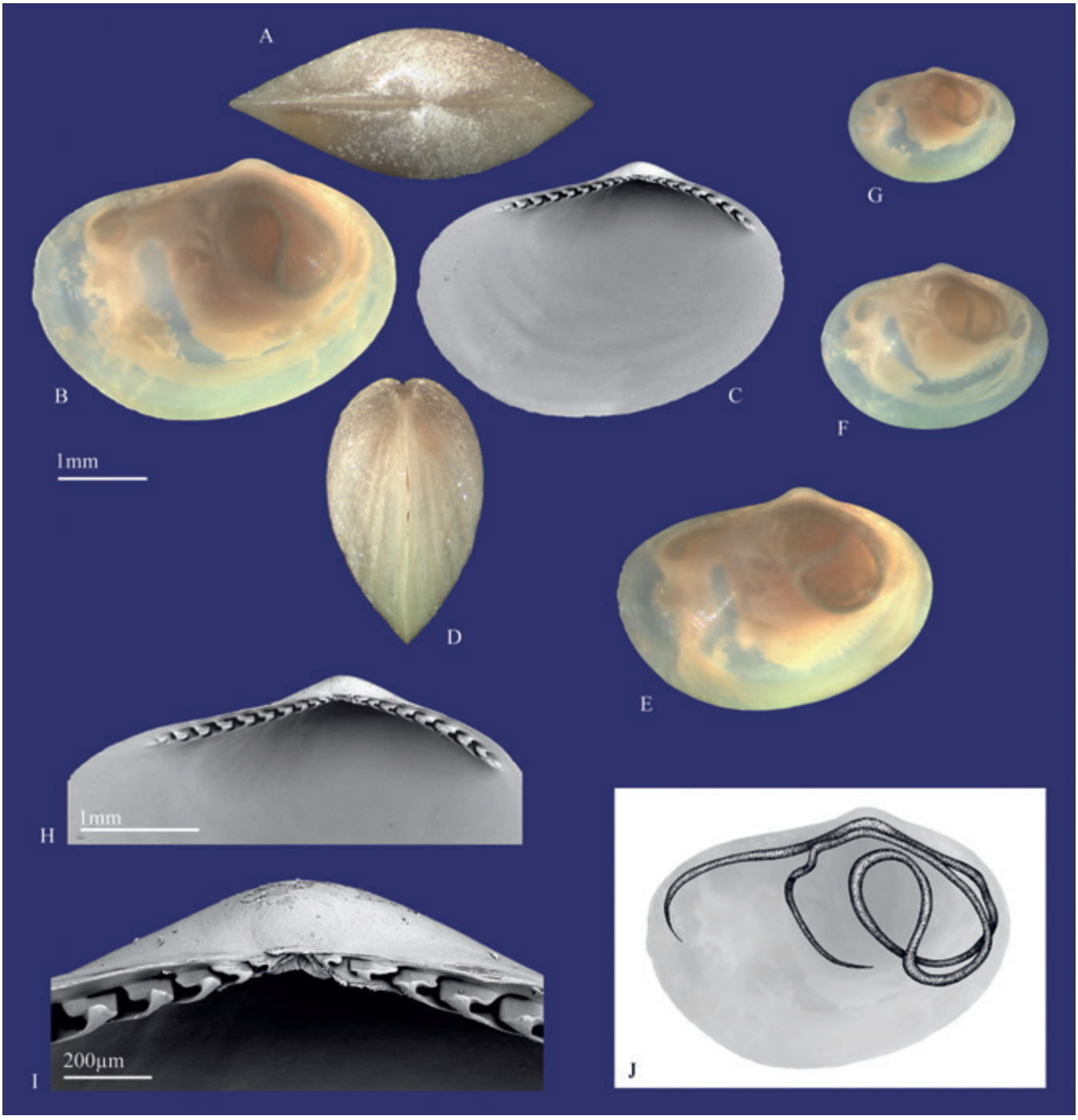

Figure 26 *Yoldiella valorousae* nom. nov. **A-I** Challenger ES261 **A** Dorsal **B** Right valve **C** Left valve internal **D** Posterior **E-G** Right valve **H-I** Hinge detail **J** Gut loop, AFEN 54585#2a/b

a much more complex series of coils whereas *Y. biscayensis* has a simple single gut loop.

Genus ***Portlandia*** Mörch, 1857

Type species *Nucula arctica* J. E. Gray, 1824

Definition Shell small, fragile. Inequilateral, umbo usually anterior to the mid-line. Outline roundly oblong; posterior pointed to subrostrate; postero-dorsal margin rather long, almost straight. Posterior area weakly, to distinctly, carinate. Lunule and escutcheon variably developed. Smooth or with fine concentric sculpture and growth ridges; periostracum glossy or silky. Hinge teeth chevron in shape, occasionally less prominent and more lateral in appearance due

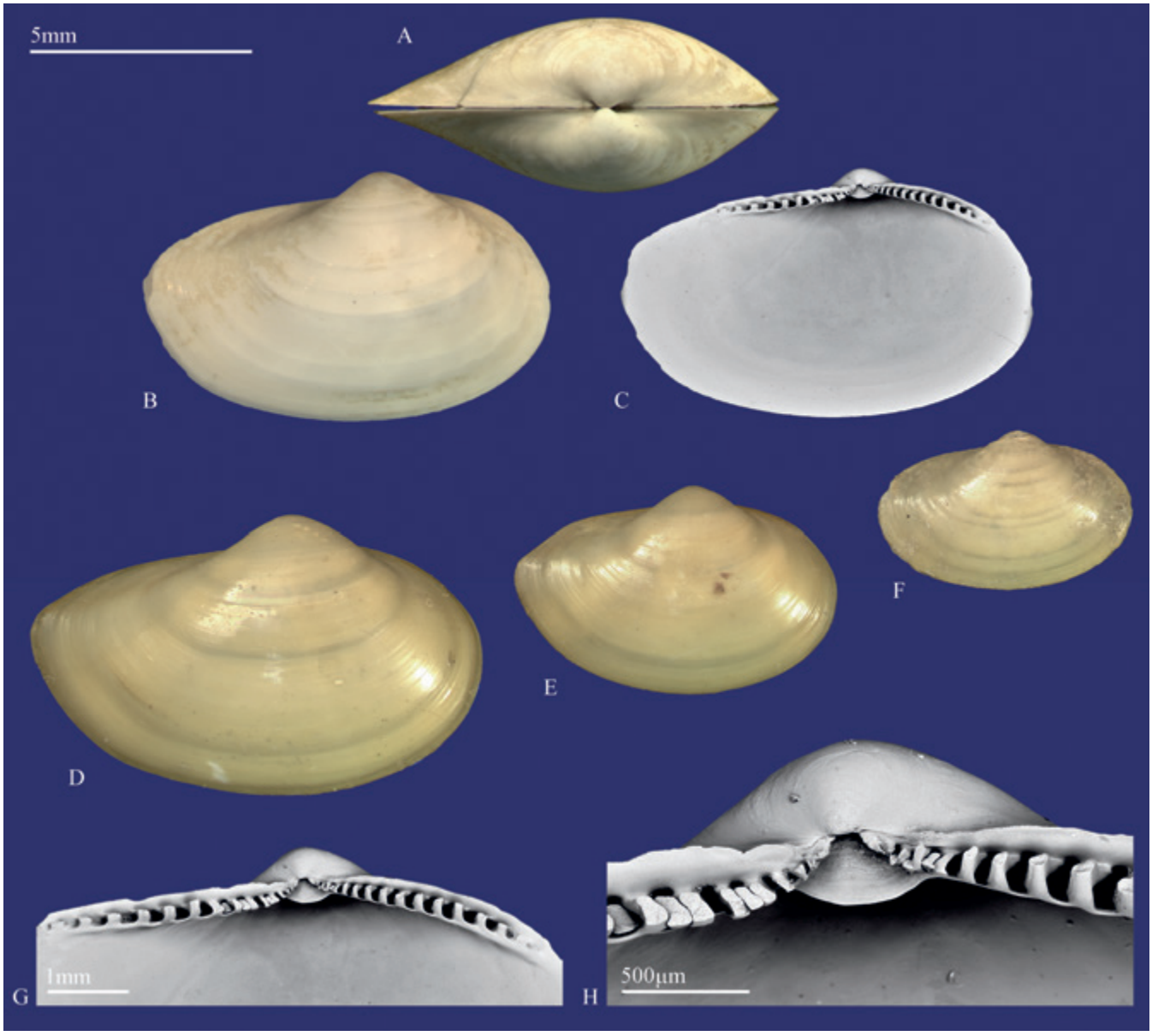

Figure 27 *Portlandia intermedia* (M. Sars, 1865) A-C, G-H. AFEN 55217#2 **A** Dorsal **B** Right Valve **C** Left valve internal **D-F** Right valve, Melvill-Tomlin collection NMW 1955.158, 'Varanger' **G-H** Hinge detail

to the lower arm of chevron being reduced. Ligament internal, amphidetic, inserted beneath the beaks on a chondrophore that projects ventrally, Most species live in deep-water (>500m), but in high Arctic latitudes they may be found living in water as shallow as 10m.

Remarks See under *Yoldiella* p. 737.

Portlandia intermedia (M. Sars, 1865)

Yoldia intermedia M. Sars, 1865: 38

Yoldia intermedia var. major Leche 1878: 24

Type locality Northern Norway, Vadsö.

Type material None in Oslo (Warén 1989a), syntypes of *intermedia* var. *major* in Stockholm (SMNH 4082, 4083).

Key features

Shell To 13mm in length. Solid, moderately tumid. Outline elongate-oval; antero-dorsal margin short, slightly curved; postero-dorsal margin long, almost horizontal with a dorsal margin

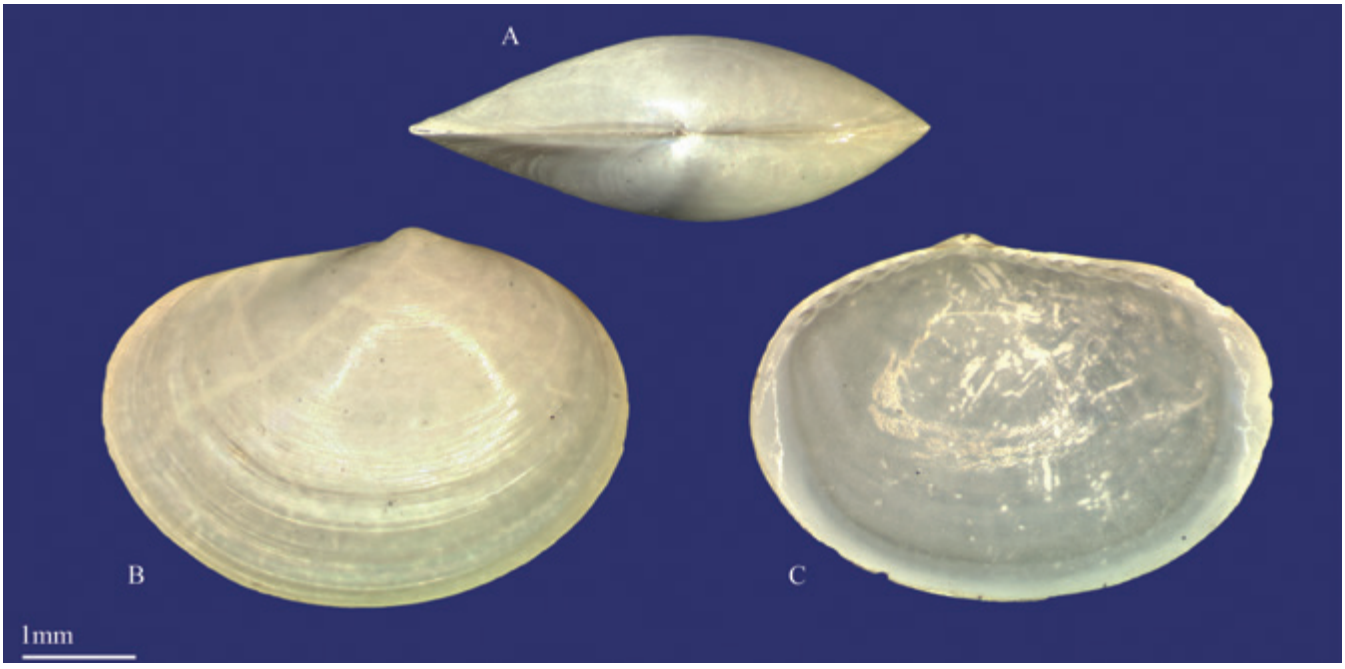

Figure 28 *Yoldiella biscayensis* Allen, Sanders & Hannah, 1995 **A-C** Holotype BMNH 1992024 **A** Dorsal **B** Right valve **C** Left valve internal

– posterior margin junction; lower posterior margin obliquely truncated; to a lesser extent the upper posterior margin may also be obliquely truncated, creating a pointed or weakly rostrate posterior margin; anterior margin rounded; ventral margin shallowly curved. Dorsal margin crimped either side of the umbo. Umbo broad, swollen and prominent above the dorsal margin, well to the anterior of mid-line. Surface virtually lacking sculpture; periostracum glossy. Hinge plate relatively narrow with 5-6 blunt teeth on either side of umbo; chondrophore well developed, ligament type 3.

Gut loop The hind-gut forms a simple, rounded loop on the right side of the body (see Richling 2000, figure 28).

Distribution No living specimens of *P. intermedia* were found in the AFEN material, but dead shells (not fossil) were found at two stations: 59°55'N, 08°07'W, 536m (articulated pair), and 62°03'N, 00°12'E, 428m (single valve).

According to Warén (1989a), *P. intermedia* is an Arctic, circumpolar species, living mostly in depths of 20-300m. Richling (2000) gives a depth range of 7-520m. There is only one previous record for the study area, off Shetland in a depth of 1150m (Ockelmann 1959) but this was later regarded as a fossil (Seaward 1990).

Remarks *P. intermedia* is relatively easy to identify due to its large size, solid shell, distinct oblong shape and broad, prominent umbo. Internally, it may be recognized by the presence of a well-developed chondrophore.

SPECIES NOT RECORDED IN AFEN MATERIAL BUT OCCURRING WITHIN THE STUDY AREA AND ADJACENT REGIONS

Yoldiella biscayensis Allen, Sanders & Hannah, 1995

Yoldiella biscayensis Allen, Sanders & Hannah, 1995: 30

Type locality R. V. Chain, Cruise 106, Sta. 326, Bay of Biscay, 50°04.9'N, 14°23.8'W, 3859m.

Type material Holotype BMNH 1992024.

Key features

Shell To 5.8mm in length. Thin, laterally compressed. Outline oval; antero-dorsal margin short, gently sloping. postero-dorsal margin long, gently sloping; junction between the umbo and postero-dorsal margin distinctly angled or notched; at the. anterior and posterior margins broadly rounded; ventral margin is deeply curved. Umbo relatively narrow, not

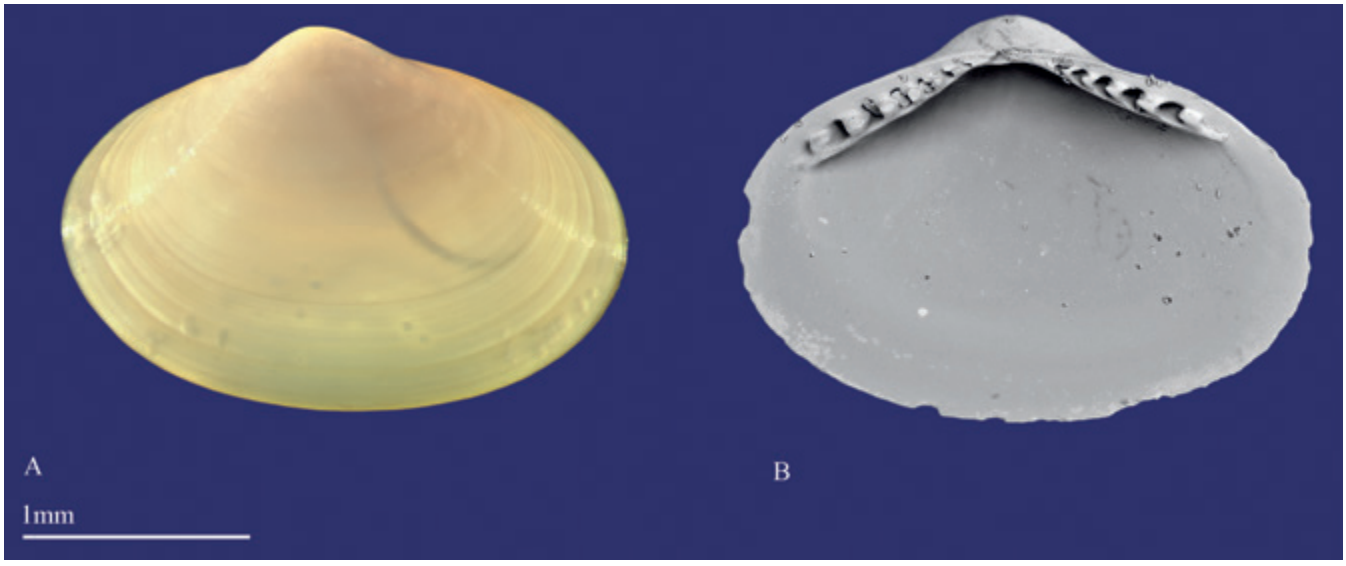

Figure 29 *Yoldiella fabula* Allen, Sanders & Hannah, 1995 **A** Right valve, Challenger ES137 **B** Left valve internal, *Challenger ES252*

prominent, projecting only just above the dorsal margin, situated well to the anterior of mid-line. Sculpture of very weak and irregular striations; periostracum silky, pale yellow in colour. Hinge plate relatively long, slightly curved posteriorly; 8-10 well-developed chevron-shaped teeth on either side of the ligament

Gut loop The hind-gut forms a simple, rounded loop on the right side of the body (Allen *et al*. 1995).

Distribution At present the species appears to be known only from material described by Allen *et al.* (1995) from the Bay of Biscay where it was common between 44ºN and 50ºN in depths of 2150-4829m.

Yoldiella fabula Allen, Sanders & Hannah, 1995

Yoldiella fabula Allen, Sanders & Hannah, 1995: 72

Type locality R. V. Chain, Cruise 50, Sta. 85, North America Basin, 37º59.2'N, 69 º26.2'W, 3834m.

Type material Holotype BMNH 1992037

Key features

Shell To 3.1mm in length. Thin, moderately tumid. Outline elongate-oval; dorsal margins gently curved and slightly crimped; anterior and posterior margins rounded; ventral margin long, shallowly rounded. Umbo relatively broad, prominent, projecting above the dorsal margin, situated posterior of mid-line. Sculpture of fine regular striations, coarser towards the ventral margin, periostracum silky, yellowish in colour. Hinge, long, curved, relatively strong, v-shaped; 7-8 posterior and 8-9 anterior, chevron-shaped teeth on either side of the ligament.

Gut loop The hind-gut forms a simple, rounded loop on the right side of the body.

Distribution Allen *et al.* (1995) record *Y. fabula* from most of the Atlantic deep-sea basins in depths ranging from 2503-5223m, including 2 stations in Rockall Trough. They note that low numbers of individuals was a feature of all sites. *Y. fabula* occurred frequently in the *Challenger* material from Rockall Trough in depths ranging from 1510-2900m, but was present in low numbers.

Remarks *Yoldiella fabula* is a distinctive species easily recognized by the 'bean' shape, the posteriorly located umbo and the yellowish periostracum. According to La Perna (2004) *Y. fabula* is very similar to, and could possibly be a junior synonym of, *Y. dissimilis* Verrill & Bush, 1898, a species not recorded by Allen *et al.* (1995).

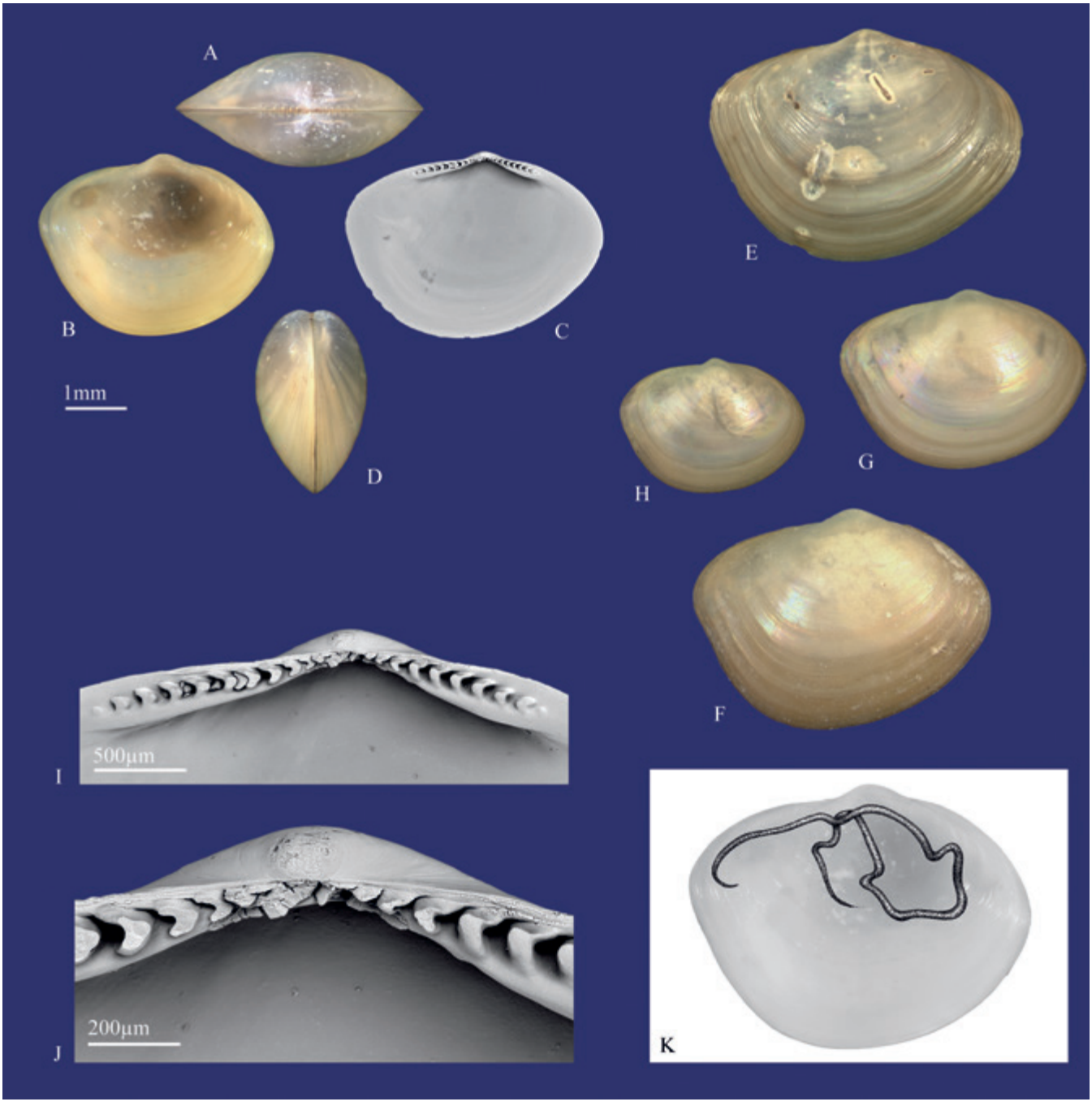

Figure 30 *Yoldiella frigida* **(Torell, 1859) A-D, K** SMNH 68062 **A** Dorsal **B** Right valve **C** Left valve internal **D** Posterior **E** Right valve, Lectotype SMNH 1986 **F-J** SMNH 35639 **F-G** Right valve **I-J** Hinge detail **K** Gut loop

Yoldiella frigida (Torell, 1859)

Yoldia frigida Torell, 1859: 148

Type locality Ice Sound, Svalbard.

Type material Lectotype SMNH 1986, selected by Warén (1989a)

Key features

Shell To 5mm in length. Thin, slightly tumid. Outline deeply-oval, height of shell approximately 75-80% of length; antero-dorsal and postero-dorsal margins gently sloping; postero-dorsal margin slightly the longer; anterior margin narrowly rounded; lower posterior margin obliquely truncated and weakly rostrate (flexured) in larger specimens; posterior extremity lies well above the horizontal mid-line; ventral margin very deeply

rounded, lowest point posterior of the mid-line. Umbo small, relatively narrow, slightly pointed, projecting just above the dorsal margin, situated at, or slightly anterior of mid-line. Sculpture of very weak striations, growth ridges and colour bands; periostracum silky. Hinge moderately strong, up to 8 chevron-shaped teeth on either side of the type 1ligament

Gut loop The hind-gut forms a rounded loop on the right side of the body.

Figure 31 *Yoldiella frigida* (Torell, 1859). Gut loop, *SMNH 68062*

Distribution North Atlantic and high Arctic in 10-100m (Warén 1989a). This species was originally considered to be Arctic-circumpolar, but the actual distribution is uncertain due to past confusion with other species (see Warén 1989a, Allen *et al.* 1995). Recorded by Allen *et al.* (1995) from 2 stations in Rockall Trough, west of the Outer Hebrides in 609-619m. Other records from UK and Irish waters (Seaward 1990) may refer to *Y. frigida* or *Y. solidula* (see below).

Yoldiella incala Allen, Sanders & Hannah, 1995

Yoldiella obesa incala Allen, Sanders & Hannah, 1995: 19

Type locality R. V. Jean Charcot, Cruise INCAL, Sta. DS01, East of Rockall Island, 57º59'N, 10 º 40'W, 2091m depth.

Type material Holotype, MNHN Paris.

Key features

Shell To 5mm in length. Thin, laterally compressed. Outline elongate-oval; dorsal margin crimped either side of the umbo, dipping down to give a small notch; postero-dorsal margin long, straight (or slightly concave), gently sloping with a dorsal margin – posterior margin junction; antero-dorsal margin shorter and gently sloping; lower posterior margin obliquely truncated, weakly rostrate in larger specimens; anterior margin broadly rounded; ventral margin long, deeply rounded. Umbo relatively narrow, but prominent, projecting just above the dorsal margin, situated anterior of mid-line. Sculpture of weak striations, periostracum silky. Hinge long, v-shaped with up to 8 well-developed chevron-shaped teeth on either side of the ligament

Gut loop The hind-gut forms a simple, rounded loop on the right side of the body.

Figure 32 *Yoldiella incala* Allen, Sanders & Hannah, 1995. Gut loop, Challenger ES399

Distribution The species was frequent amongst the *Challenger* material occurring at a number of stations, from the southern part of Rockall Trough to northwest of Rosemary Bank in depths ranging from 1270 to 2900m. Allen *et al.* (1995) record *Y. incala* (as *Y. obesa incala* n.ssp) from locations in the Western European Basin (including Rockall Trough) from latitudes of 44ºN to 58ºN, and at depths of 1913-2170m.

Nomenclature Warén (1989a) and CLEMAM

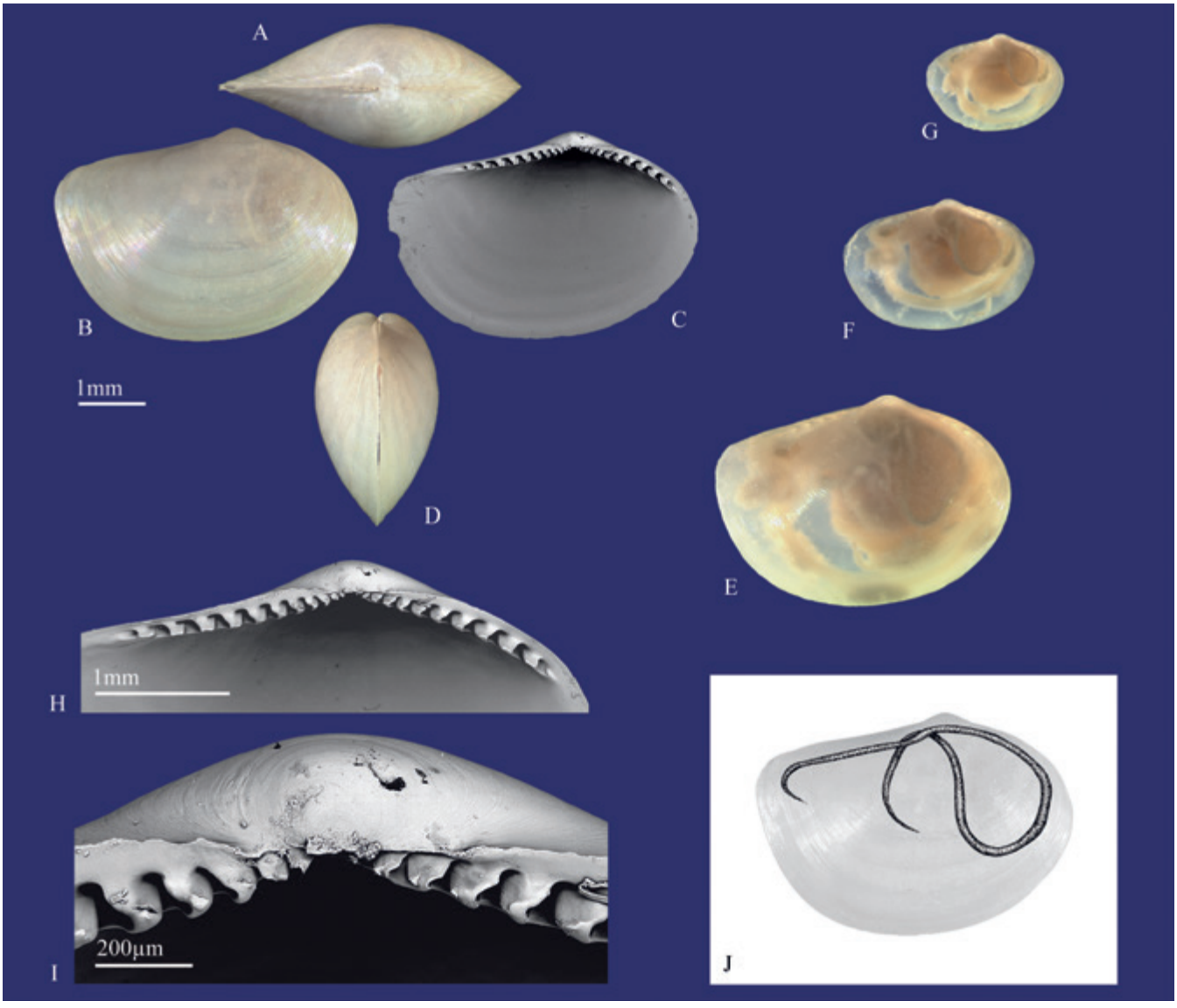

Figure 33 *Yoldiella incala* Allen, Sanders & Hannah, 1995 **A-D, H-I** Challenger ES289 **E-G, J** Challenger ES399 **A** Dorsal **B** Right valve **C** Left valve internal **D** Posterior **E-G** Right valve **H-I** Hinge detail **J** Gut loop

(2000) consider *Y.* (as *Leda*) *obesa* Stimpson, 1851a to be a junior synonym of *Y. lucida* (Lovén, 1846). Given the original illustration (Stimpson, 1851b) and the shallow water (80m) type locality we concur with their opinion. Allen *et al.* (1995), by implication, do not agree with this synonymy, treating *Y. obesa s.l.* separately from *Y. lucida.* We consider *Y. obesa obesa sensu* Allen et al. (1995), which was recorded in from the North American Basin at depths ranging between 1254m-2886m, to be distinct from *Leda obesa* Stimpson 1851a. Therefore, the use by Allen *et al.* (1995) of the name *Y. obesa obesa* (Stimpson, 1851a) and neotype designation for *Y. obesa obesa* (Stimpson, 1851a) *sensu* Allen *et al.* (1995) is deemed incorrect and will need revising.

Allen *et al*. (1995) under the name of *Y. obesa* (Stimpson, 1851a) describe two subspecies: *Y. o. obesa* and *Y. o. incala* Allen, Sanders & Hannah, 1995. The differences between these are, in our opinion, equivalent to species rank differences used to distinguish many other closely related *Yoldiella* species. Consequently, we raise these subspecies to species rank, and recognize the taxon recorded from the deep-water locations of the Western European Basin as *Y. incala* Allen, Sanders & Hannah, 1995. The name bearing type specimen and type locality given in Allen *et al.* (1995) for the subspecies *Y. o. incala* remain as the name bearing type specimen and type locality for the species *Y. incala*

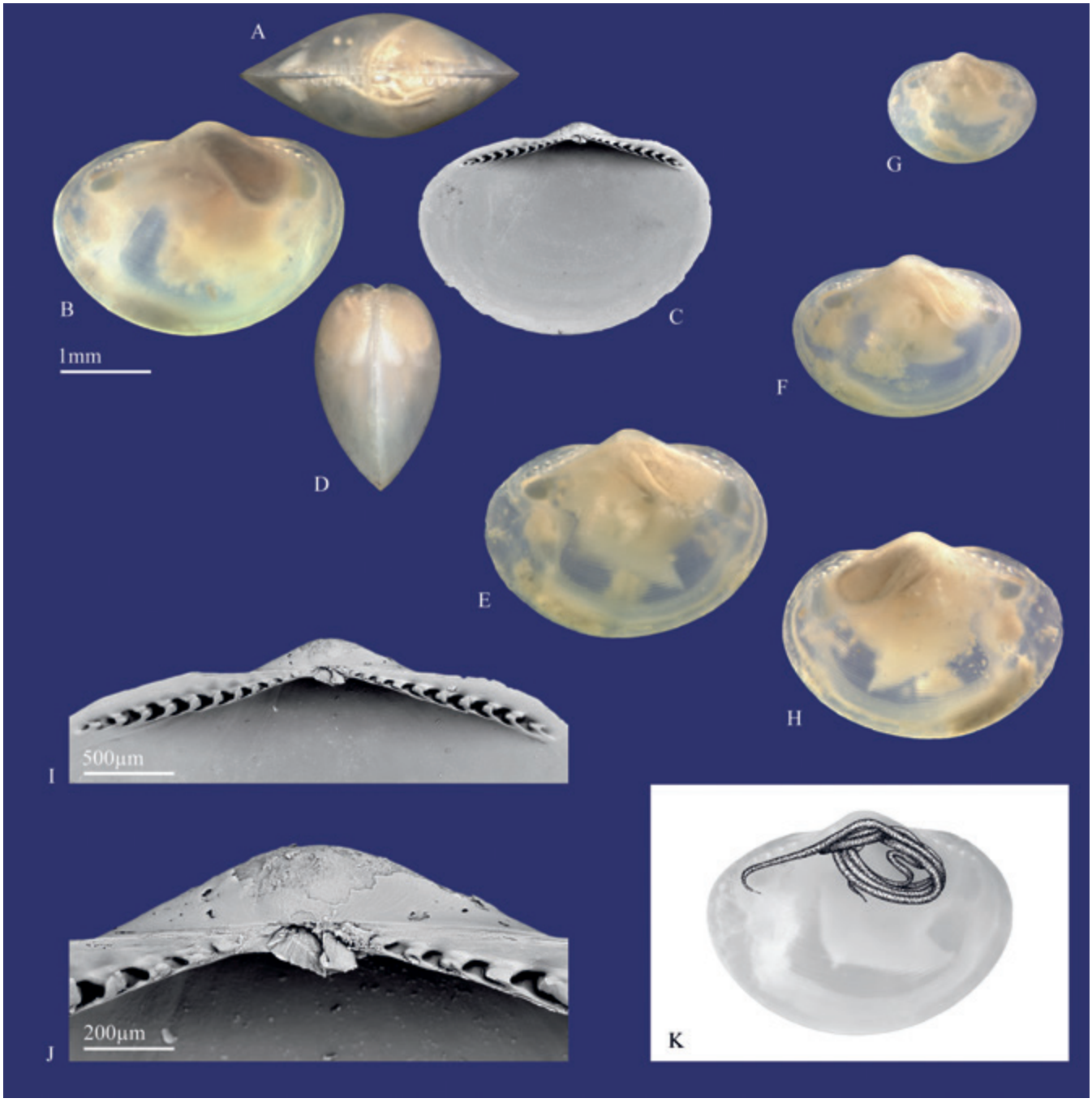

Figure 34 *Yoldiella insculpta* (Jeffreys, 1879) **A-K** *Biogas IV DS62* **A** Dorsal **B** Right valve **C** Left valve internal **D** Posterior **E-G** Right valve **H** Left valve **I-J** Hinge detail **K** Gut loop

Remarks *Y. incala* bears some resemblance to *Y. lucida*. The latter species is generally more elliptical in shape, has a narrower, less prominent and more centrally located umbo, a postero-dorsal margin that is more convex in its curvature. The ventral margin of *Y. incala* is more deeply rounded that found in *Y. lucida*. *Y. lucida* is also rare in depths greater than 1100m.

Yoldiella insculpta (Jeffreys, 1879)

Leda insculpta Jeffreys, 1879: 580

Type locality West of Ireland, 54º19'N, 11º50'W, 1492m.

Type material Lectotype BMNH 85.11.5.459, selected by Allen *et al.* (1995)

Key features

Shell To 3.6mm in length. Thin, moderately tumid. Outline oval; postero- and antero-dorsal margins short, horizontal; posterior and anterior margins broadly rounded; ventral margin deeply rounded. Umbo broad, prominent above the dorsal margin, located at, or very slightly anterior of the mid-line. Sculpture of fine, regular, well-defined concentric striations, feint radial striations are present (particularly on the posterior end) in some larger individuals; periostracum silky. Hinge relatively long, narrow, slightly curved, 8-12 small chevron-shaped teeth on either side of the ligament.

Gut loop The hind-gut lies on both sides of the body, and forms three tight coils on the right side and two on the left.

Figure 35 *Yoldiella insculpta* (Jeffreys, 1879). Gut loop, Biogas DS62

Distribution Allen *et al.* (1995) record *Y. insculpta* from 22 stations in the West European Basin, mostly from a small geographic area around 47º30'N, 08º40'W in depths from 1913-2360m, and 4 stations in the Canaries Basin in depths from1934-3301m. There appear to be very few other records since Jeffreys' original material collected on the *Porcupine* expeditions.

Remarks Individuals of *Y. insculpta* are recognizable by the sculpture and gut loop, but there is a superficial resemblance to young *Neilonella striolata* (Brugnone 1876)

Yoldiella lenticula (Möller, 1842)

Nucula lenticula Möller, 1842: 17
Yoldia abyssicola Torell, 1859: 149
Yoldiella lenticula var. amblia Verrill & Bush, 1898: 866
Type locality Western Greenland

Type material Syntype SMNH 3687; Lectotype BMNH 1843.7.3.31 (see Allen, 1995)

Key features

Shell To 7mm in length. Solid, tumid. Outline elongate-oval; dorsal margins crimped either side of the umbo; antero-dorsal margin short and gently sloping; postero-dorsal margin longer, slightly convex, gently sloping; posterior margin narrowly rounded; anterior margin more broadly rounded; ventral margin long, deeply rounded. Umbo broad, rounded, prominent, projecting just above the dorsal margin, situated distinctly anterior of mid-line. Sculpture of very weak concentric striations and more prominent, irregular growth ridges, periostracum glossy. Hinge long, curved at least 11 chevron-shaped teeth on either side of the type 2 ligament, posterior row of teeth longer than anterior row.

Gut loop The hind-gut forms a simple, rounded loop on the right side of the body.

Distribution Allen *et al.* (1995) record *Y. lenticula* from 4 stations in the West European basin mostly from a small geographic area from 43º-48º N and 3º-10º W in depths from 1400-2245m, and 1 station in the Canary Basin at 27º 44.9'N, 14º 25.0W in a depth of 2129m.

Remarks *Yoldiella lenticula* is most likely to be confused with larger, more posteriorly elongate specimens of *Y. philippiana*. However, *Y. lenticula* has a different teeth arrangement and a more gently sloping, and slightly convex dorsal margin. Both species exhibit a strong inflation across the valves, but in *Y. lenticula* the level of inflation is to a greater degree. *Yoldiella lenticula* is also and Arctic species for which there is no evidence for its modern occurrence within the study area. Records show *Y. lenticula* to be a deep water species found in depths of 1400-2245m (Allen *et al.* 1995), whereas *Y. philippiana* is shallow water species commonly found on the outer continental shelf and upper slope at depths of 25-536m.

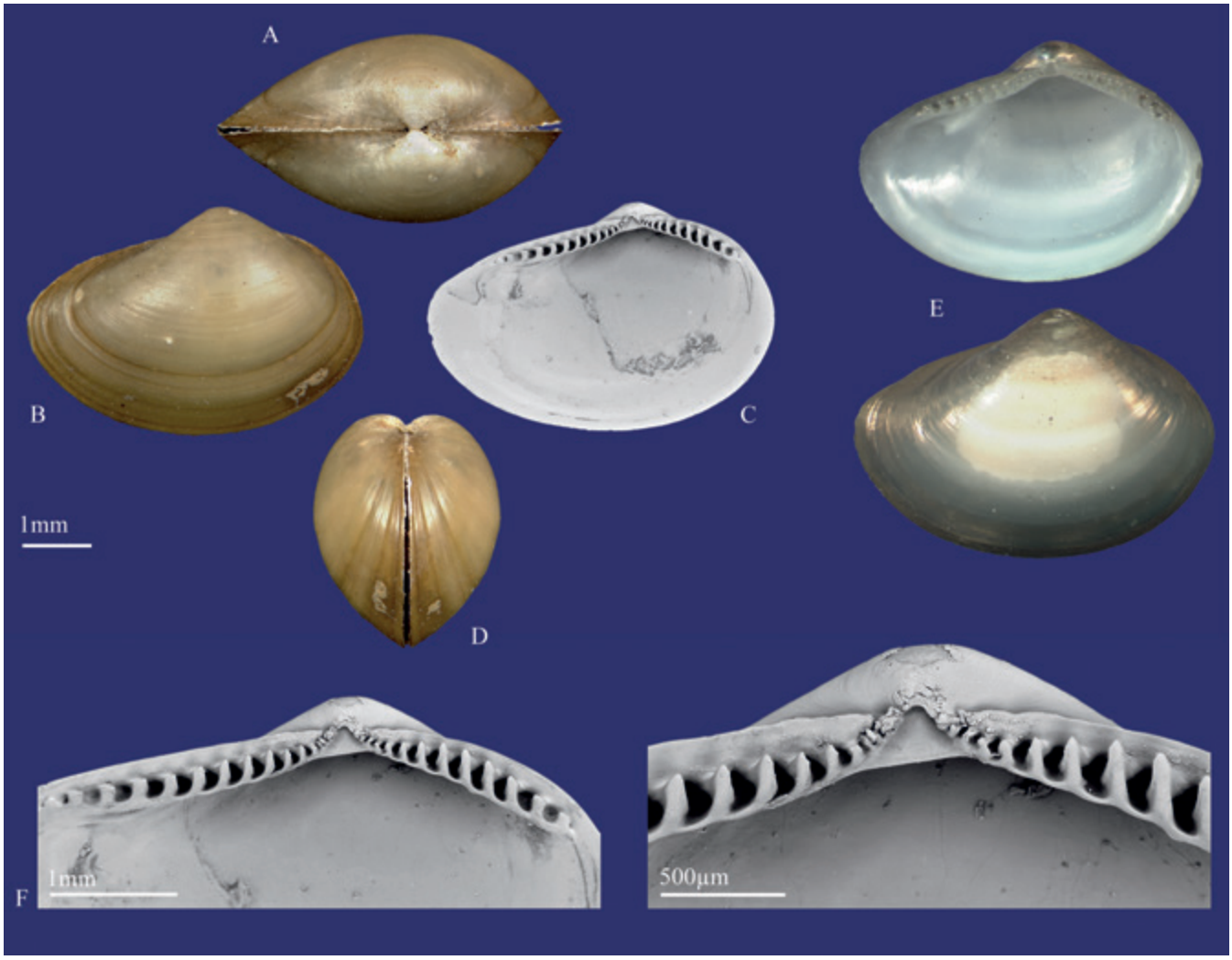

Figure 36 *Yoldiella lenticula* (Möller, 1842) **A-D, F-G** Melvill-Tomlin collection NMW.1955.158, 'E. Finmark' **A** Dorsal **B** Right valve **C** Left valve internal **D** Posterior **E** Syntype SMNH 3687 **F-G** Hinge detail

Yoldiella solidula Warén, 1989

Yoldiella solidula Warén, 1989: 233

Type locality Bell Sound, Svalbard, 54m.

Type material Holotype, SMNH 4085.

Key features

Shell To 3.6mm in length. Very solid, tumid. Outline oval; antero-dorsal and postero-dorsal margins short, almost horizontal; dorsal margin - posterior margin and dorsal margin - anterior margin junctions visible; anterior margin narrowly rounded or slightly pointed at the horizontal mid-line; posterior margin pointed above the horizontal mid-line, lower posterior margin obliquely truncated forming a weakly rostrate posterior margin in larger specimens; ventral mar-

Figure 37 *Yoldiella solidula* Warén, 1989. Gut loop, *SMNH 44935*

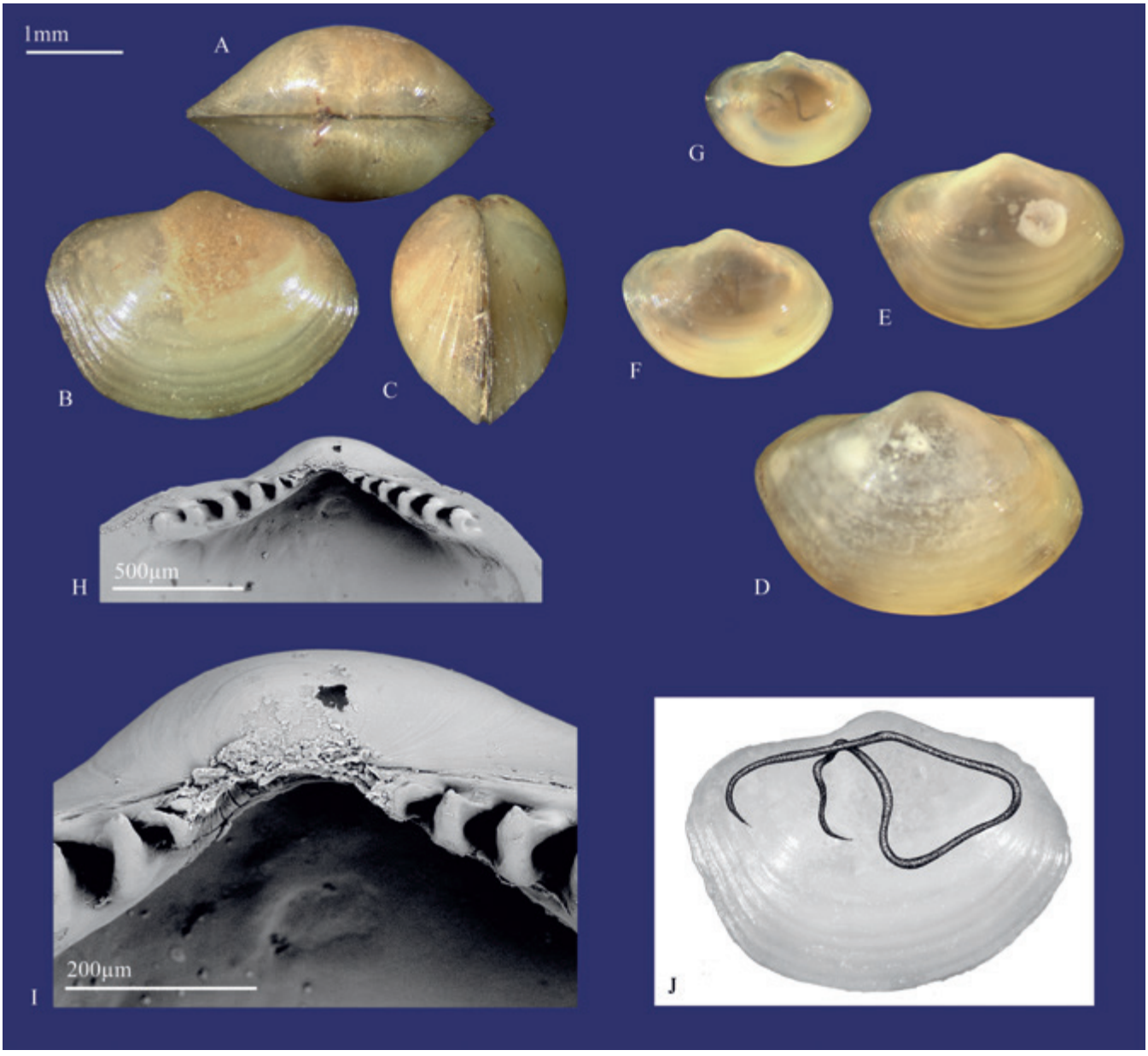

Figure 38 *Yoldiella solidula* Warén, 1989 **A-C** Paratype BMNH 1989137 **D-G, J** SMNH 44935 **A** Dorsal **B** Right valve **C** Posterior **D-G** Right valve **H-I** Hinge detail, Melvill-Tomlin collection NMW.1955.158, 'Spitsbergen' **J** Gut loop

gin deeply curved. Umbo broad, prominent above the dorsal margin, situated at the mid-line. Surface smooth; periostracum glossy. Hinge very solid, broad, v-shaped with 6-8 robust chevron-shaped teeth on either side of the type 1 ligament.

Gut loop The hind-gut forms a simple, rounded loop on the right side of the body.

Distribution *Yoldiella solidula* has a wide distribution in the north Atlantic and Arctic from New England and west Greenland, east to the Kara Sea, south to Finmark and northern Iceland (Warén 1989a), and the Laptev Sea (Richling 2000). *Y. solidula* was not found in the AFEN samples or in the *Challenger* material and was not recorded by Allen *et al.* (1995). It was recorded at one of the Biofar stations, 62°41.7'N, 03°37.2'W, 699m (Sneli *et al.* 2005).

Remarks In terms of shell morphology, there seems to be a close relationship between *Y. solidula* and *Y. nana.* However, *Y. solidula* may be distinguished from *Y. nana* due to the former being much more solid and tumid, with a broader umbo and a more deeply rounded ventral mar-

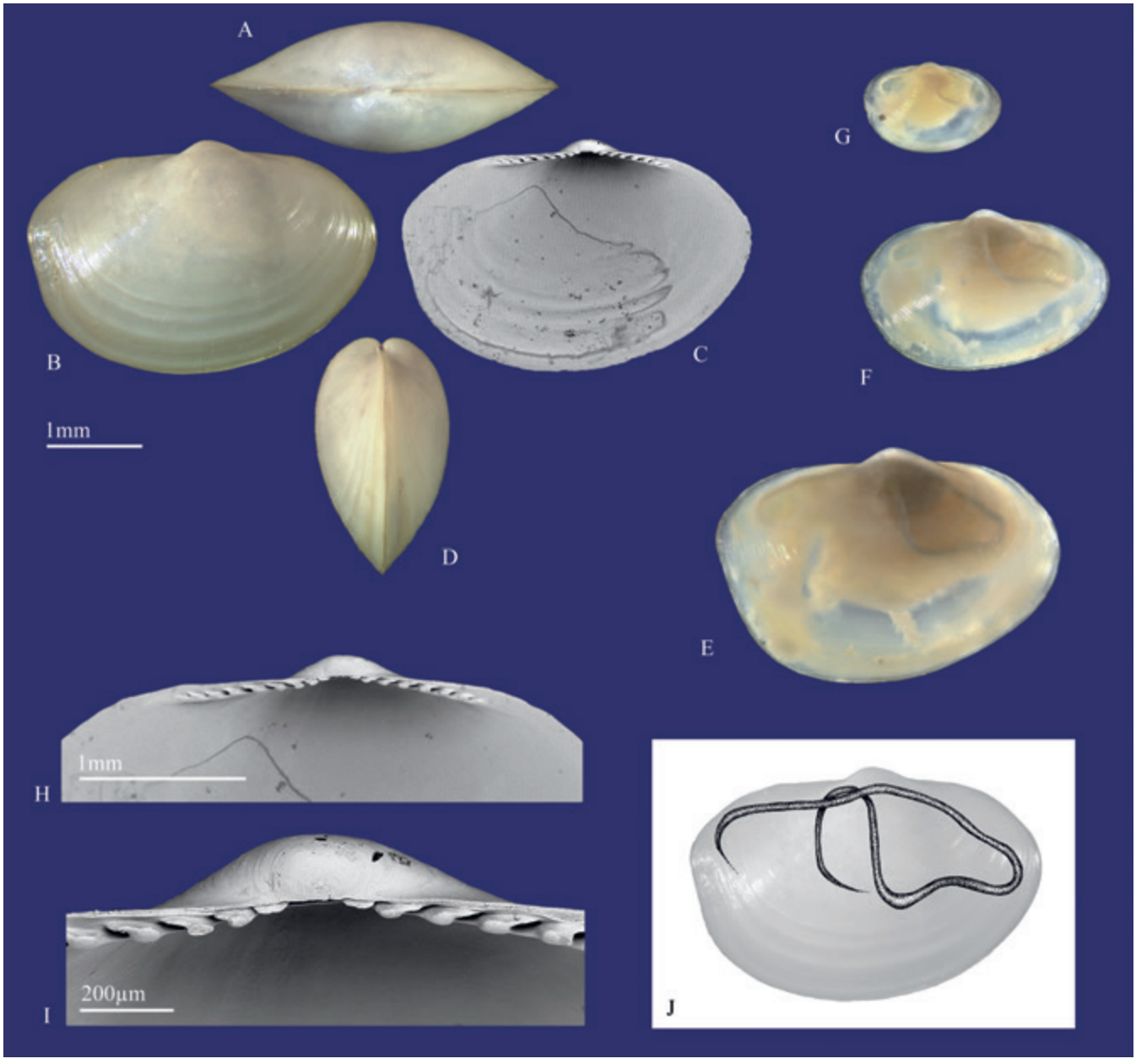

Figure 39 *Yoldiella thaerella n. sp.* **A-D, H-I** Paratypes NMW.2008.057.002 Challenger ES137 **A** Dorsal **B** Right valve **C** Left valve internal **D** Posterior **H-I** Hinge detail **E** Right valve, Holotype NMW.2008.057.001 Challenger ES137 **F-G** Paratypes NMW.2008.057.003, **J** Gut loop, Paratype NMW.2008.057.004 **F-G** Right valve.

gin. The hinge of *Y. solidula* is very solid, broad and with the lower margins forming a more acute angle than found in *Y. nana*.

On examining *Y. solidula* and *Y. nana* specimens, we consider there to be forms of *Y. nana* that closely resemble *Y. solidula* (fig. 25, fig. 26). Richling (2000) also seems to be aware of this complex, as she suggests that there are some forms of *Y. solidula* collected during the Transdrift 1 and ARK IX/4 expeditions in the Laptev Sea, which resembled *Y. nana*. Richling concedes that there is insufficient material with which to make any definitive conclusions regarding these forms.

Yoldiella thaerella n. sp.

Yoldiella inconspicua inconspicua sensu Allen, Sanders & Hannah, 1995: 41
non *Y. inconspicua* Verrill & Bush, 1898

Type locality RSS Challenger Station ES137. Rockall Trough. 54º 34'N / 12º 19'W 2900m

Type material Holotype, NMW.2008.057.001, Paratypes NMW.2008.057.002-5.

Derivation of name Transliteration into Latin of the Greek word "*Thairos*", meaning hinge, suffixed with an adjectival diminutive. The name is given in reference to the weak hinge present this species.

Key features

Shell To 3.6mm in length. Thin, laterally compressed. Outline oval; antero- and postero-dorsal margins almost horizontal; anterior margin rounded with slight oblique truncation of the upper part; upper posterior margin slightly truncated obliquely (smaller specimens the upper posterior margin is rounded); lower posterior margin obliquely truncated or slightly flexuous; ventral margin long, deeply rounded, lowest point posterior of the mid-line. Umbo centrally placed, narrow, not prominent, projecting just above dorsal margin. Sculpture of very weak striations; periostracum silky. Hinge plate characteristically weak, very narrow for the size of shell; teeth blunt, up to 6-7 posterior and 5-6 anterior; ligament type 1, relatively long.

Gut loop The hind-gut forms a rounded triangular shaped loop on the right side of the body, frequently with an indentation along the ventral side.

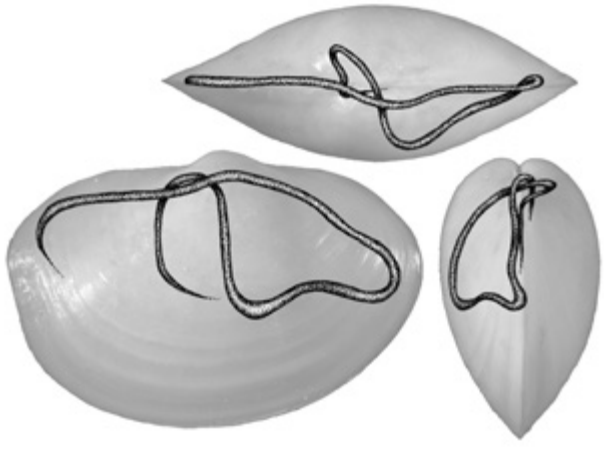

Figure 40 *Yoldiella thaerella* n. sp. Gut loop, Paratype NMW.2008.057.004 *Challenger ES137*

Distribution The species was common amongst the *Challenger* material occurring at a number of stations, in and on the slopes of Rockall Trough in depths ranging from 1270 to 2900m. Allen *et al.* (1995) record this species (erroneously as *Y. inconspicua*) from numerous locations in the Western European Basin (including Rockall Trough) from latitudes of 43ºN to 58ºN, and at depths of 1719-4829m (most commonly in 2400-3000m), and in the North America Basin in depths of 1102-4400m.

Remarks The deep-sea species reported by Allen *et al.* (1995) as *Y. inconspicua inconspicua* is not *Y. inconspicua* Verrill & Bush 1898, but is in fact a new species. Warén (1989a) synonymised *Y. inconspicua* and *Y. fraterna* with *Y. nana*, and from our examination of the type specimens it appears that Warén was correct in this assertion. The species reported by Allen *et al.* (1995) is an abyssal species with a depth range given as 1102-4829m, whereas the type specimen of *Y. inconspicua* Verrill & Bush was found at a depth of 581m – a depth that is well within the range of *Y. nana* which appears to be rarely found below 1000m (see above). We hereby propose the name *Y. thaerella*, and the select a type series for this new deep-sea species.

Allen *et al.* (1995) also described two new subspecies, *Y. inconspicua africana* and *Y. inconspicua profundorum*, based on *Y. inconspicua* sensu Allen *et al.* (= *Y. thaerella* sp. nov.). Following the descriptions given by Allen *et al.* (1995), along with the differences highlighted between these subspecies, we believe there to be sufficient justification in raising these subspecies to species in their own right as *Y. africana* Allen, Sanders & Hannah 1995 and *Y. profundorum* Allen, Sanders & Hannah 1995 respectively. The name bearing type specimens and type localities given in Allen *et al.* (1995) for the two subspecies remain as the name bearing type specimens and type localities for the respective species.

DISCUSSION

The genus *Yoldiella* is known to be species rich in the deep sea (Allen *et al*, 1995) and in boreal and arctic waters (Warén, 1989, 1989a; Richling, 2000). However, there were surprisingly few modern records for the UK Atlantic Margin (Seaward,

Table 1 Geographical and bathymetric distribution of species

Species	Distribution in study area	Depth range (m)	
		AFEN	Other sources
Y. annenkovae	Faeroe-Shetland Channel	725-1623	200-3270
Y. curta	Rockall Trough	1364-2046	1270-2900
P. intermedia	Faeroe-Shetland Channel	428-536	7-520
Y. valorousae	Rockall Trough	1612-1886	1491-3220
Y. lucida	Faeroe-Shetland Channel	543-1158	100-1096
Y. nana	Faeroe-Shetland Channel	450-1200	96-1200
Y. nana form A	Faeroe-Shetland Channel	725-919	?
Y. philippiana	Widespread on shelf and upper slope	152-536	25-300
Y. propinqua	Faeroe-Shetland Channel	417-1624	402-1098
Y. jeffreysi	Rockall Trough	1291	862-4862

1990), this despite the nineteenth century pioneering cruises of HMS Lightning, Porcupine and Triton and the subsequent description of many new molluscan taxa by Jeffreys (1876, 1879).

This paper recognizes nine species from the AFEN surveys and a further eight from adjacent waters, giving sixteen species of *Yoldiella* and one species of *Portlandia*. All of the species covered in this study would have previously been considered as rare (*e.g. Y. philippiana*) or were unknown (*e.g. Y. annenkovae*) in British/Irish waters. Yet these detailed surveys covering a wide area have demonstrated that *Y. propinqua,* for example, is actually the commonest *Yoldiella* species on the continental slope in the area.

The species recorded in the AFEN study area show differences with respect to geographic and bathymetric distribution (Table 1). *Yoldiella philippiana* is found only on the continental shelf and upper slope but is widespread. Of the other 8 species, 5 are essentially found only to the north of the Wyville Thomson Ridge and 3 to the south. *Yoldiella annenkovae* and *Y. propinqua* were found only in the Faroe-Shetland Channel on the mid and lower continental slope. Most records of *Y. annenkovae* were from NE of Shetland whereas *Y. propinqua* was widespread throughout the Channel. *Yoldiella nana* and *Y. lucida* have similar depth ranges and distributions, occurring on the mid and lower slopes but not beyond 1200m, and mostly in the Faroe-Shetland Channel with occasional records around the Wyville Thomson Ridge. The final species *P. intermedia* was recorded only as dead shells and therefore we are unclear as to its distribution or indeed, if it is living within the study area. Three species, *Y. curta*, *Y. jeffreysi* and *Y. valorousae* are restricted to the deeper waters (>1364m) south of the Wyville-Thompson Ridge. Of the 8 species not found in the AFEN material but known to occur in adjacent waters, 2 would be considered northern in distribution (*Y. frigida* and *Y. solidula*), and 5 are essentially southern and deep water species. The biogeography of *Y. lenticula* is less clear.

Much of the pattern seen in the distribution of species can be linked to the physical and hydrographic features of the region, and especially the separation of water masses by the Wyville Thomson Ridge (Bett, 2001; Gage, 2001). The distinction of cold-water species restricted to the Faroe-Shetland Channel from those from the warm water Rockall Trough is reflected in the megafauna (Bett, 2001) and in the Crustacea (Bird, 2004; Shalla & Bishop, 2004). The occurrence of the Arctic *Y. annenkovae* can be explained by the extension of arctic cold water into the Faroe-Shetland Channel but within that channel the patterns are not immediately explicable on water temperature or bathymetry alone.

Three of the four species (*Y. lucida, Y. nana & Y. propinqua*) confined to the Faroe-Shetland Channel range from 450-1600m and thus traverse the thermocline that lies at around 600m. This suggests that temperature alone is not the key feature in determining the distribution of these infaunal,

deposit-feeding bivalves. Similar temperature tolerances have been reported for polychaetes from the Faroe-Shetland Channel (Hughes, Narayanaswamy & Bett, 2003)

Among the protobranchiate bivalves the genus *Yoldiella* is highly species rich but this may be an artifact of poor systematics. The taxonomic separation of the genera *Portlandia* and *Yoldiella* clearly needs to be resolved. The two genera are very similar in form, and within the current literature there is much confusion with regards to the placement of a number of species within these two genera. Within the *Yoldiella – Portlandia* complex, we believe there to be three distinct groups – *Yoldiella* sensu stricto, *Portlandia* sensu stricto and a group that is intermediate of the two, in terms of shell morphology. Molecular studies are needed to resolve the monophyly of *Yoldiella* and *Portlandia*.

ACKNOWLEDGEMENTS

Preparation of this paper would not have been possible without generous financial support from the Atlantic Frontier Environmental Network. We are especially grateful to John Hartley, Hartley Anderson Ltd for his assistance in acquisition of funding and for his continual enthusiastic support for the research. We thank Graham Oliver, National Museum of Wales, Cardiff, for extensive editing, stimulating discussions and encouragement throughout the project. Anna Holmes and Harriet Wood, also of National Museum of Wales have provided logistical support and access to the collections. Sankurie Pye, National Museums of Scotland, Edinburgh has kindly made all of the AFEN molluscan material available to us throughout the project. Thanks are due to Anders Warén, Swedish Museum of Natural History, Stockholm for helpful discussion, loan of material and for comments and advice during the preparation of the manuscript; Jan Soerensen, of the Kaldbak Laboratory, Faroes and Ole Tendal, Zoological Museum, Copenhagen for information and data on the *Biofar* surveys; Shelagh Smith, Carlisle for use of her catalogue of *Challenger* material; John Allen, Millport, for the loan of material. We would also like to thank Rafael La Perna for his helpful comments and advice during the preparation of the manuscript.

APPENDIX

Figured material data

AFEN

Station	Latitude / Longitude	Depth (m)
53757#1	61º 4.49′N / 2º 36.83′W	649
53796#5	61º 10.44′N / 1º 38.13′W	250
53815#4,5	61º 26′N / 0º 49′W	180
53874#1	60º 17.03′N / 4º 41.04′W	721
53903#1	61º 0.53′N / 2º 34.01′W	548
54503#1	62º 15.71′N / 0º 12.10′E	753
54522#1,2	60º 35.99′N / 4º 22.34′W	1074
54579	56º 49.82′N / 9º 36.97′W	1796
54585#2a/b	56º 48.02′N / 9º 45.32′W	1854
54586#2	56º 60′N / 10º 1′W	2046
54587#1	57º 5.5′N / 9º 25.84′W	1498
54591	58º 34.49′N / 9º 55.86′W	1859
54598#1	58º 52.88′N / 9º 53.88′W	1766
54625#1	59º 15.02′N / 8º 11.99′W	1364
55203#1,3	59º 34.66′N / 8º 55.38′W	1389
55207#2,3	59º 48.97′N / 8º 22.1′W	1004
55217#2	59º 55.37′N / 8º 6.54′W	536
55237#1	60º 10.22′N / 6º 32.88′W	1183
55268#1	60º 18.69′N / 5º 27.42′W	937
55292#1,2	61º 36.57′N / 1º 46.26W	1054
55301#1	61º 38.71′N / 1º 48.30W	1146
55337#1	62º 19.01′N / 0º 10.02′E	917
55363#2	62º 5.37′N / 0º 17.21′E	473
55378#1	62º 21.28′N / 0º 5.62′E	992
55387#1	62º 21.30′N / 0º 32.18′E	767
55447#6	61º 54.96′N / 2º 48.06′W	1624
55450#1	61º 13.47′N / 2º 27.87′W	834
55452#1	61º 16.11′N / 2º 19.99′W	829

RSS Challenger

Station	Latitude / Longitude	Depth (m)
ES137	54º 34′N / 12º 19′W	2900
ES250	59º 43′N / 12º 33′W	1270
ES252	58º 52′N / 12º 53′W	1510
ES261	57º 24′N / 10º 5′W	1824
ES289	57º 19′N / 10º 25′W	2190
ES399	57º 18′N / 10º 18′W	2200

Jean Charcot - Biogas IV

Station	Latitude / Longitude	Depth (m)
DS62	47º 32.8'N / 8º 40'W	2175

National Museum Wales, Cardiff (NMW)

Cat. No.	Locality	Latitude / Longitude	Depth (m)
NMW.1955.158	'Varanger'	-	-
NMW.1955.158	E. Finmark	-	-
NMW.1955.158	Spitsbergen		216
NMW.1955.158.16638	Norway	-	-

Natural History Museum, London (BMNH)

Cat. No.	Locality	Latitude / Longitude	Depth (m)
BMNH 1992024	Bay of Biscay	50º 4.9'N / 14º 23.8'W	3859
BMNH 1989137	Bell Sound, Spitsbergen	-	54

National Museum of Natural History, Washington DC (USNM)

Cat. No.	Locality	Latitude / Longitude	Depth (m)
USNM 48867	Off Marthas Vinyard, USA	-	581
USNM 159714	Off Marthas Vinyard, USA	-	581

Swedish Museum of Natural History, Stockholm (SMNH)

Cat. No.	Locality	Latitude / Longitude	Depth (m)
SMNH 1533	Hammerfest, Norway	-	-
SMNH 1570	Kara sea	73º 34 'N / 57º 36'E	100
SMNH 1986	Ice Sound, Spitsbergen	-	55
SMNH 3686	Lofoten, Norway	-	148 - 218
SMNH 3687	Western Greenland	-	-
SMNH 35639	Svalbard	78º 37'N / 19º 00'E	9-18
SMNH 38782	-	69º 41N / 19º 01E	40 - 45
SMNH 44935	Svalbard	-	34
SMNH 53404	Faroes	60º 27'N / 5º 00'W	820 - 1180
SMNH 68062	Svalbard		34
SMNH 68072	-	60º 10'N / 5º 10'W	460

REFERENCES

ALLEN JA & HANNAH FJ 1986 A reclassification of the recent genera of the sub-class Protobranchia (Mollusca: Bivalvia). *Journal of Conchology* **32**: 225-249.

ALLEN JA & HANNAH FJ 1989 Studies on the deep sea Protobranchia: the sub-family Ledellinae (Nuculanidae). *Bulletin of the Natural History Museum (Zoology Series)* **55**: 123-171.

ALLEN JA, SANDERS HL & HANNAH F 1995 Studies on the deep-sea Protobranchia (Bivalvia); the sub-family Yoldiellinae. *Bulletin of the Natural History Museum (Zoology Series)* **61**: 11-90.

BETT BJ 2001 UK Atlantic Margin Environmental Survey: introduction and overview of bathyal benthic ecology. *Continental Shelf Research* **21**: 917-956.

BIRD G J 2004 The Tanaidacea (Crustacea, Peracarida) of the North-East Atlantic: the shelf and bathyal *Paratyphlotanais* of the 'Atlantic Margin. *Journal of Natural History*, **38**: (11): 1359 - 1358

BRATTEGGARD & HOLTHE 1997 *Distribution of marine, benthic organisms in Norway: a tabulated catalogue*. Research Report for the Directorate for Nature Management No. 1997-1, Oslo.

CHAMBERS S J & WOODHAM A 2003 A new species of *Chaetozone* (Polychaeta: Cirratulidae) from deep water in the northeast Atlantic, with comments on the diversity of the genus in cold northern waters. *Hydrobiologia* **496:** (1-3):41-48.

CLARKE AH JR. 1963 Arctic archibenthal and abyssal mollusks. Two mollusks dredged from drifting ice station Charlie (Alpha 2). *Bulletin, National Museum of Canada* **185**: 90-109.

COAN EV, VALENTICH SP & BERNARD FR 2000 *Bivalve Seashells of Western North America. Marine Bivalve Mollusks from Arctic Alaska to Baja California.* Santa Barbara Museum of Natural History Monographs Number 2, Studies in Biodiversity Number 2. 764 pp.

FRIELE H 1878 Jan Mayen Mollusca from the Norwegian North Atlantic Expedition in 1877. *Nyt Magazin for Naturvidenskaberne* **24** (3): 221-226.

GAGE JD 2001 Deep-sea benthic community and environmental impact assessment at the Atlantic Frontier. *Continental Shelf Research* **21**: 957-986.

GORBUNOV GP 1946 New and interesting species of Mollusca and Brachiopoda from the Arctic Ocean. *Dreifuiuschaia Ekspeditia Glavseomorputi na Ledokol'nom Parakholi 'G. Sedov' 1937-1940* **3**: 308-322.

HARTLEY JP 2004 The challenge of deep water oilfield environmental monitoring west of Britain pp 450-473. *In* Armsworthy, S L, Cranford P J & Lee K (eds) *Offshore Oil and Gas Environmental Effects Monitoring: Approaches and Technologies.* Battelle Press, Columbus. 631pp

HIDALGO JG 1877 *Moluscos marinos de España, Portugal y las Baleares* **13-14**: 83-84, 113-184. C. Bailly-Baillere, Madrid.

HINDS RB 1843 Description of a new species of *Nucula* from the collections of Sir Edward Belcher, C.B., and Hugh Cumming ESQ. *Proceedings of the Zoological Society of London* **11**: 99.

HUGHES JA, NARAYANASWAMY BE & BETT BJ 2003 SEA4: An overview of the benthic ecology of the Faroe-Shetland Channel. *Report submitted to the Department of Trade and Industry. Strategic Environmental Assessment: SEA 4. Consultation Document.*

JEFFREYS JG 1876 New and peculiar Mollusca of the *Pecten, Mytilus* and *Arca* families procured in the '*Valorous*' Expedition. *Annals and Magazine of Natural History* **18** (4): 424- 436

JEFFREYS JG 1879 On the Mollusca procured during the *Lightning* and *Porcupine* Expeditions. 2. *Proceedings of the Zoological Socitey of London* (**1878**): 553-588

LA PERNA R 2004 The identity of *Yoldia micrometrica* Seguenza, 1877 and three new deep-sea protobranchs from the Mediterranean (Bivalvia). *Journal of Natural History* **38**: 1045-1057.

LA PERNA R 2007 Taxonomy of the family Neilonellidae (Bivalvia, Protobranchia): Miocene and Plio-Pleistocene species of *Pseudoneilonella* Laghi, 1986 from Italy. *The Veliger* **49**(3): 196–208.

LA PERNA R, CEREGATO A & TABANELLI C 2004 Mediterranean Pliocene protobranchs: the genera *Jupiteria* Bellardi, 1875, *Ledella* Verrill & Bush, 1897 and *Zealeda* Marwick, 1924 (Mollusca, Bivalvia). *Bollettino Malacologico* **40**: 25-36.

LAMPRELL K & HEALY J 1998 *Bivalves of Australia*. Backhuys, Leiden. 288pp.

LECHE W 1878 Öfversigt öfver de av svenska expeditionerna till Nvaja Semlja och Jenissej 1875 och 1876 insamlade hafmollusker. *Konigliga Svenska Vetenskapsakademiens Handlingar, ny serie* **10**: 1-86

LOVÉN S 1846 Index Molluscorum litora Scandinaviae occidentalia habitium. *Öfversigt öfver Konigliga Svenska Vetenskapsakademiens Förhandlingar* **3**: 134-160

MAXWELL PA 1988 Comments on "A reclassification of the recent genera of the subclass Protobranchia (Mollusca: Bivalvia)" by J.A. Allen and F.J. Hannah (1986). *Journal of Conchology* **33**: 85-96.

MESSJATSEV I 1931 Molliuski Barentsova Morya. *Memiors of the Academy of the USSR, series 6, Natural Sciences* **1**: 1-167

MÖLLER HPC 1842 Index molluscorum Groenlandiae. *Naturhistorisk Tidsskrift* **4**: 76-97

NORDSIECK F 1974 Molluschi dei fondali della platea continentale fra la Corsica e la Sardegna. *La Conchiglia* **6**: 11-14.

NYST P H 1845 Description de coquilles et des polypiers fossils des terrains Tertiaires de la Belgique. *Memoirs couronné par l'Academie de Belgique, Bruxelles, M. Hayes.* 697 pp.

OCKELMANN KW 1959 The Zoology of East Greenland. Marine Lamellibranchiata. *Meddelelser om Gr* **122**: 1-258.

OCKELMANN KW & WARÉN A 1998 Taxonomy of and biological notes on the bivalve genus *Microgloma*, with comments on protobranch nomenclature. *Ophelia* **48**: 1-24.

PHILIPPI RA 1836 *Enumeratio molluscorum Siciliae.* Berolini, Sumptibus Simonis Schropi et Sociorum. 270 pp.

PHILIPPI RA 1844 *Enumeratio molluscorum Siciliae.* Halis Saxonum, Sumptibus Eduardi Anton. 304 pp.

RICHLING I 2000 Arktische Bivalvia – eine taxonomische Bearbeitung auf Grundlage des Materials der Expeditionen Transdrift 1 und ARK IX/4 (1993) in das Laptevmeer. *Schriften zur Malakozoologie* **15**: 1-93.

REEVE L 1871 *Conchologia Iconica* **18**. Pl. 7, species 44. Lovell Reeve & Co, London.

SARS GO 1878 *Bidrag til kundskaben om Norges artiske Fauna 1, Mollusca regionis articae Norvegiae.* W. Brögger, Christiania. 466 pp.

SARS M 1865 *Om de I Norge forekommende fossile dyrelevninger fra Quartäperioden, et bidrag til vor faunas historie.* Christiania, Brögger & Christie's Bogtrykkeri. 217 pp.

SEAWARD DR 1990 *Distribution of the marine molluscs of north west Europe*. Nature Conservancy Council, Peterborough. 114 pp.

SHALLA SH & BISHOP JDD 2004 Four new species of the genus *Leucon* (Crustacea: Cumacea) from the Atlantic Frontier Margin. *Journal of the Marine Biological Association of the UK* **84:** 139-153.

SMITH SM unpublished. A Catalogue of Deepwater Mollusca from the Northeast Atlantic. Specimens held in the collections of the National Museums of Scotland and other selected collections.

SMITH SM & HEPPELL D 1991 Checklist of British marine Mollusca. *National Museums of Scotland Information Series No 11*. 114pp.

SNELI J-A, SCHIØTTE T, JENSEN KR, WIKANDEN PB & STOKLAND Ø 2005 The marine Mollusca of the Faroes. *Annales Societatis Scientarum Faeroensis Supplementum* **42**: 1-170. Føroya Fródskaparfelag.

STIMPSON W 1851a (On several new species from New England.) *Proceedings of the Boston Society of Natural History* **4**: 112-113.

STIMPSON W 1951b *Shells of New England.* Phillips, Samson and Company. Boston. 58pp.

TORRELL O 1859 *Bidrag till Spitsbergens Mollusk-fauna.* Akademisk Afhandling, Stockholm. 154 pp.

VERRILL AE & BUSH KJ 1898. Revision of the deepwater Mollusca of the Atlantic coast of North America with descriptions of new genera and species. Part 1. Bivalvia. *Proceedings of the U.S. National Museum* **20**: 775—901.

WARÉN A 1978 The taxonomy of some North Atlantic species referred to *Ledella* and *Yoldiella* (Bivalvia). *Sarsia* **63**: 213-219.

WARÉN A 1980 Marine Mollusca described by John Gwyn Jeffreys, with the location of type material. *Conchological Society of Great Britain and Ireland Special Publication No. 1*: 1-60.

WARÉN A 1989a Taxonomic comments on some protobranch bivalves from the northeastern Atlantic. *Sarsia* **74**: 223-259.

WARÉN A 1989b Molluscs from east and north of Svalbard, collected by the Swedish *YMER-80* expedition. *Sarsia*: **74**: 127-130.

WINCKWORTH R 1932 The British marine Mollusca. *Journal of Conchology* **19**: 211-252.

WYVILLE THOMPSON J 1874 *The depths of the sea*. Macmillan, London.

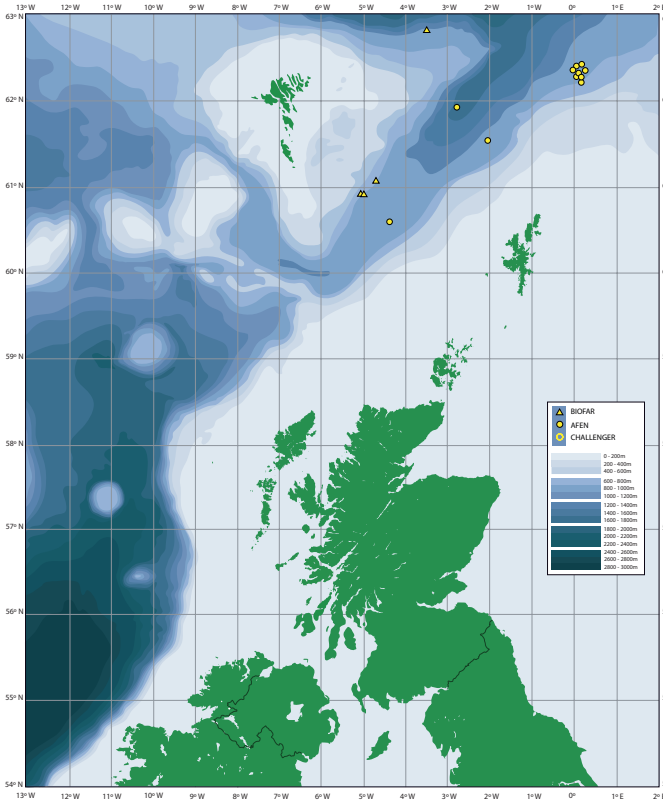

Figure 41 *Yoldiella annenkovae* (Gorbunov, 1946).

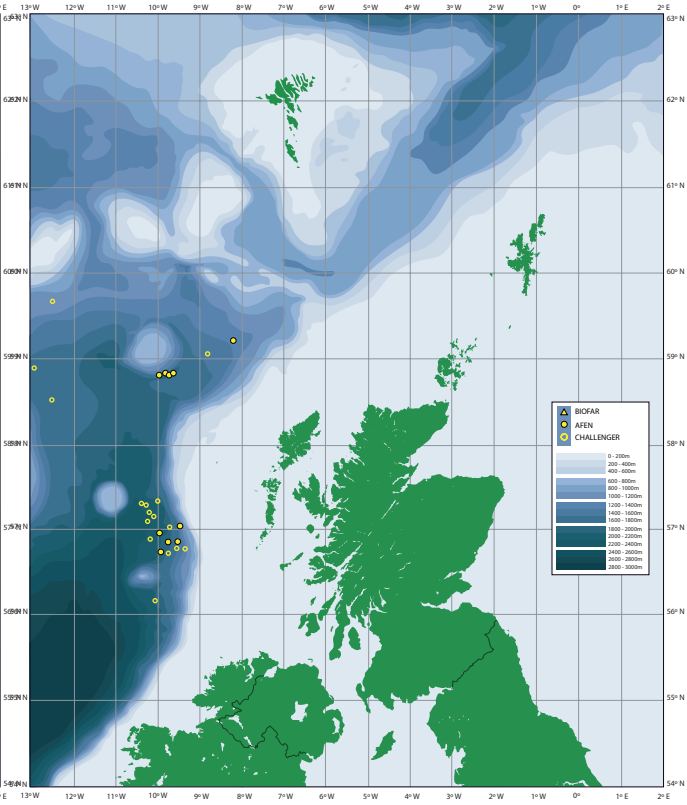

Figure 42 *Yoldiella curta* Verrill & Bush 1898.

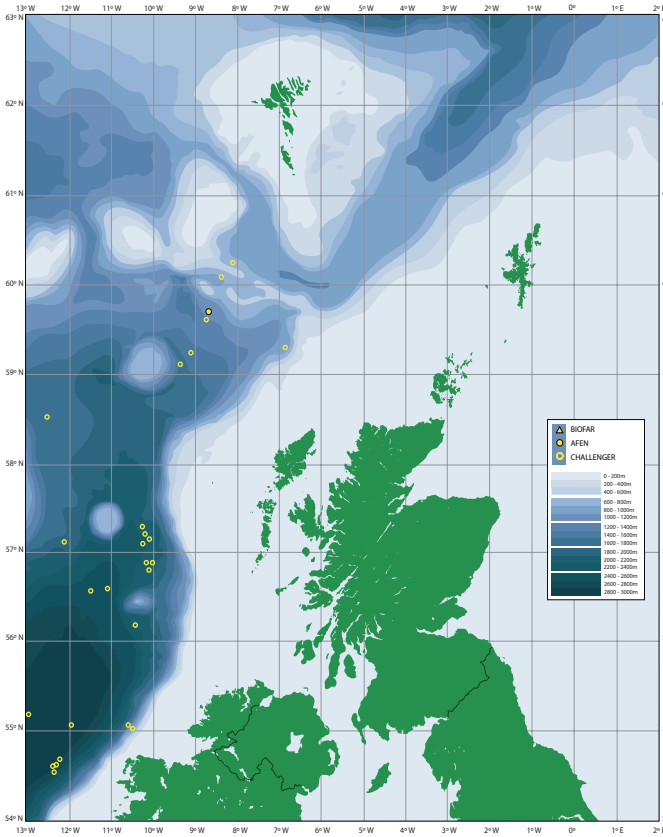

Figure 43 *Yoldiella jeffreysi* (Hidalgo, 1877).

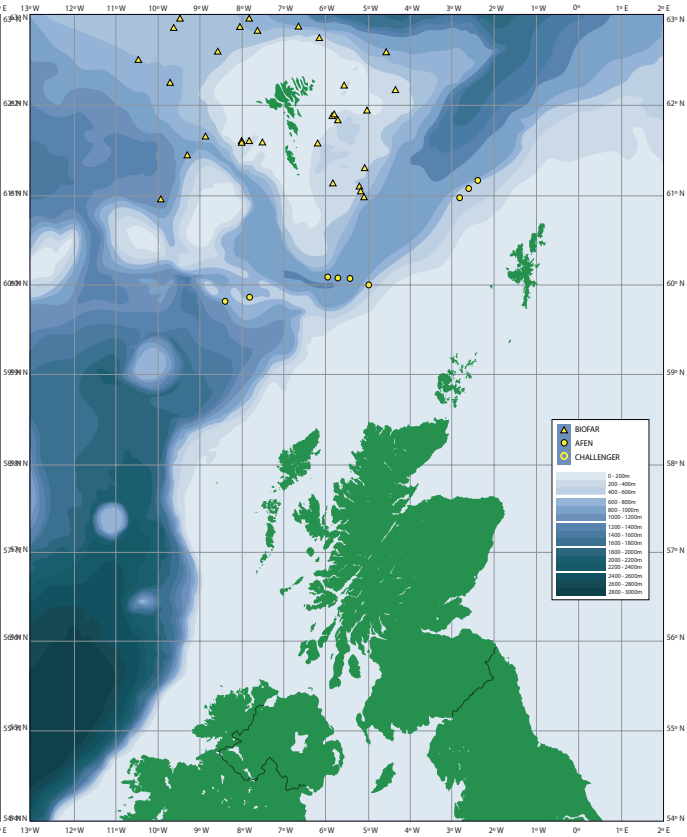

Figure 44 *Yoldiella lucida* (Lovén, 1846).

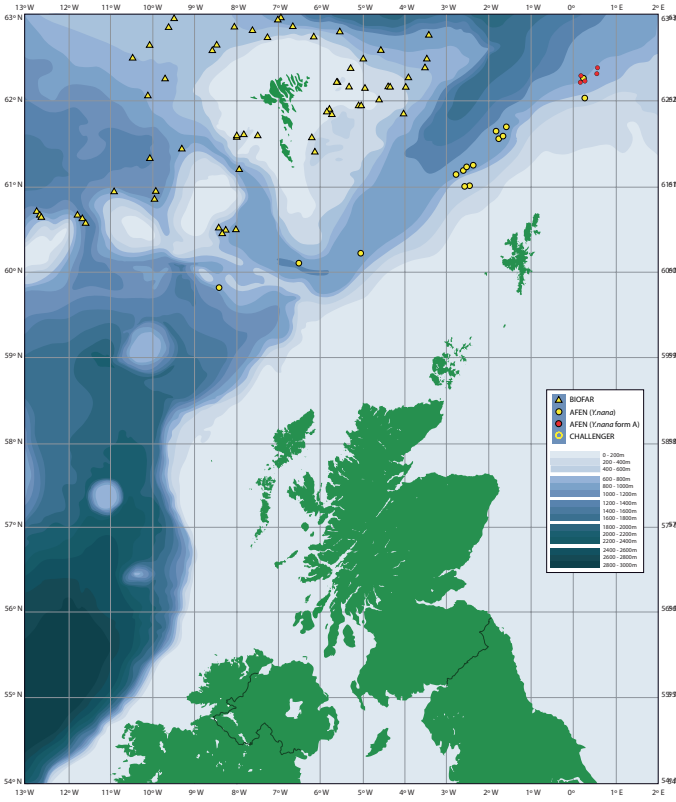

Figure 45 *Yoldiella nana* (M. Sars, 1865).

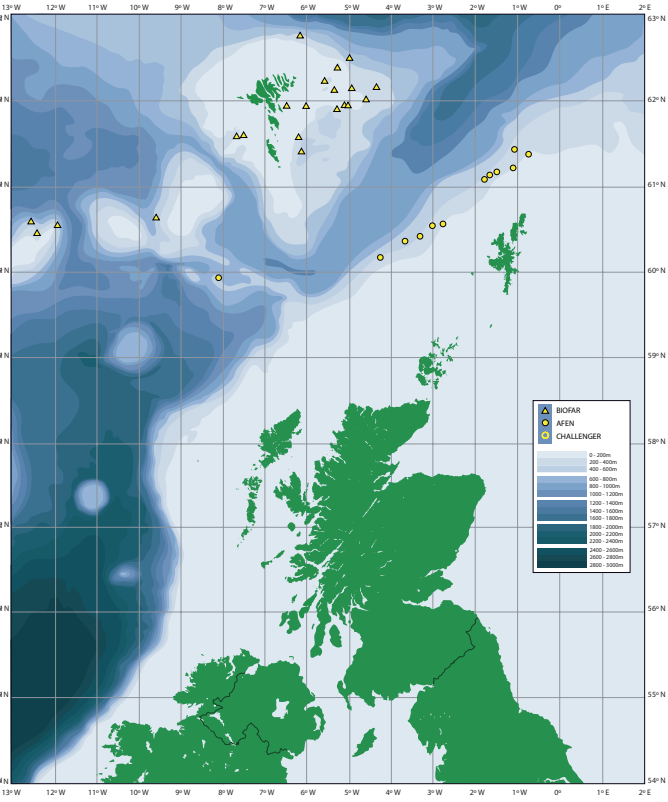

Figure 46 *Yoldiella philippiana* (Nyst, 1845).

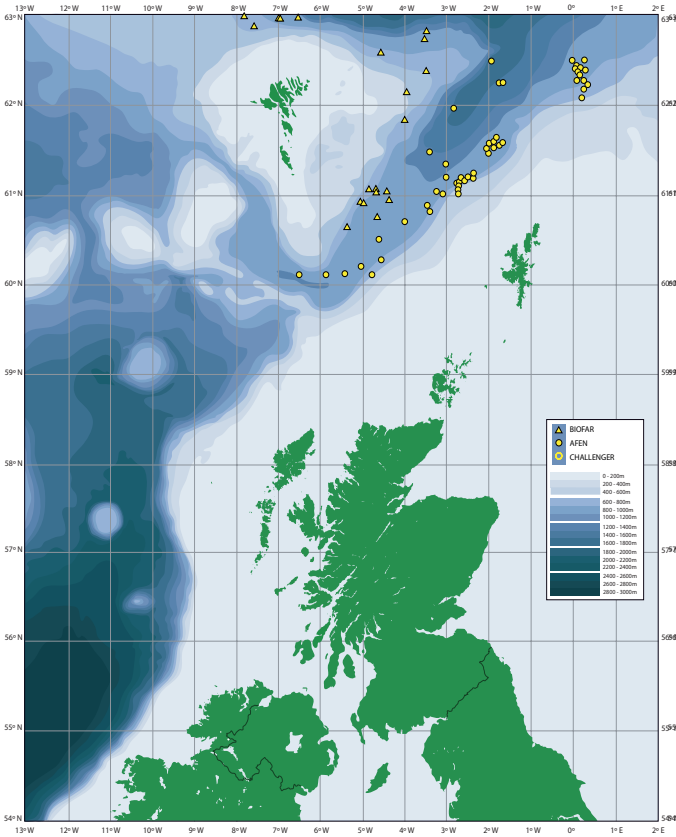

Figure 47 *Yoldiella propinqua* (Leche 1878).

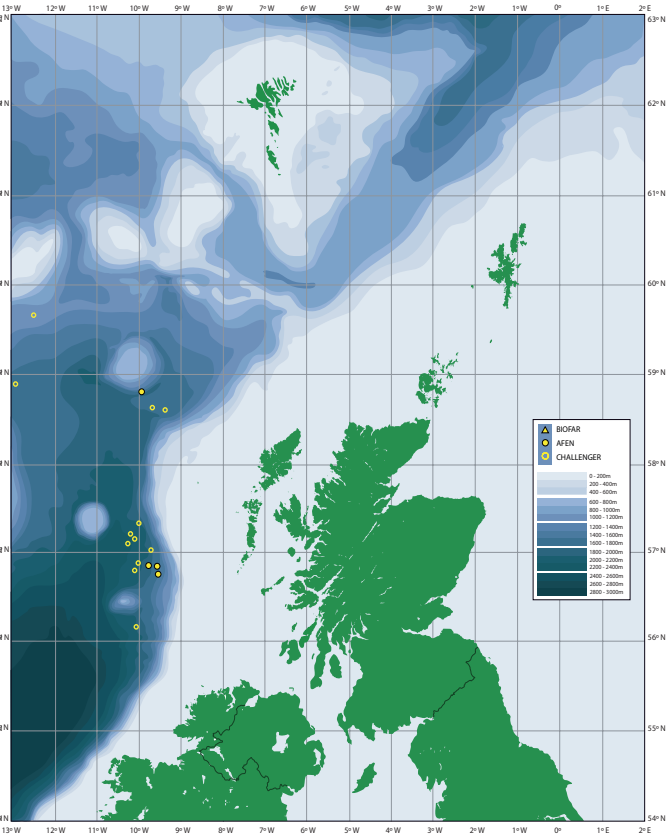

Figure 48 *Yoldiella valorousae* nom. nov.

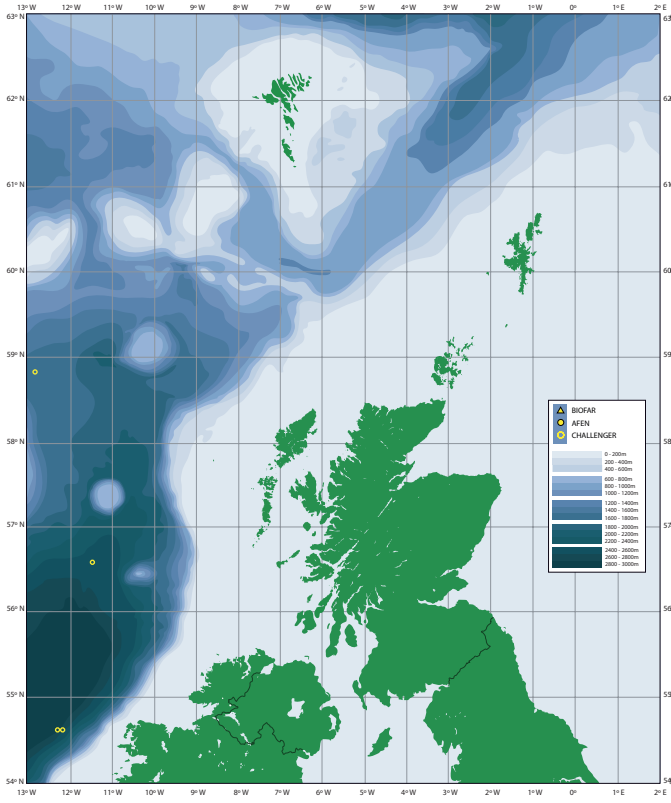

Figure 49 *Yoldiella fabula* Allen, Sanders & Hannah, 1995.

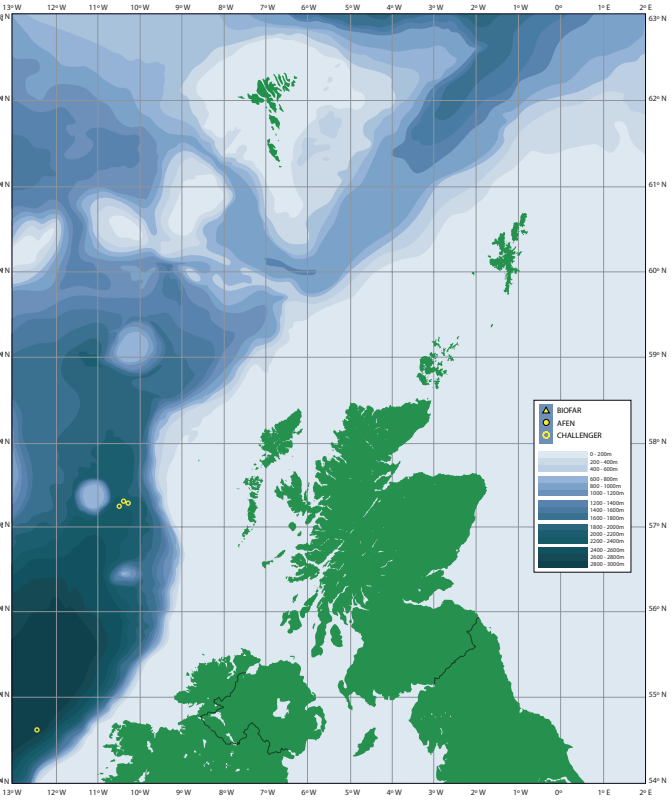

Figure 50 *Yoldiella incala* Allen, Sanders & Hannah, 1995.

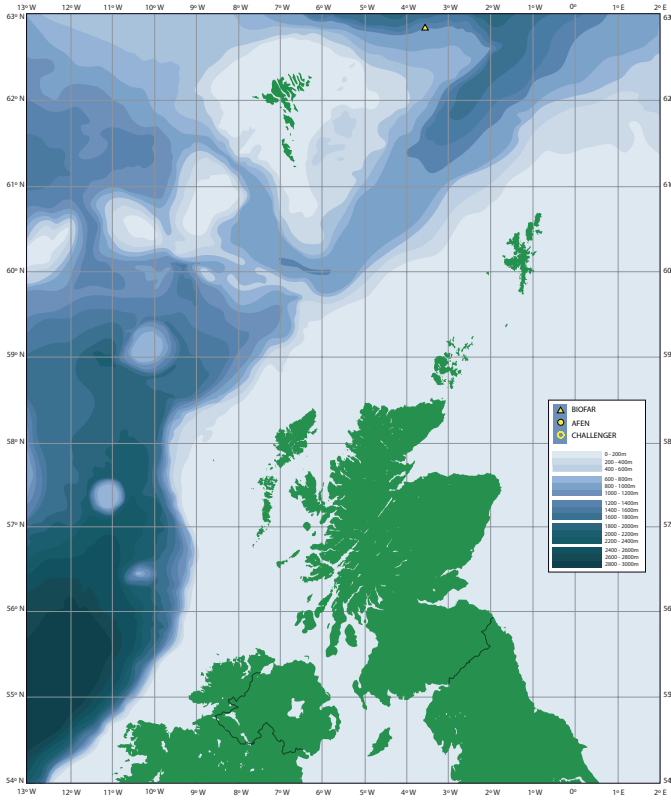

Figure 51 *Yoldiella solidula* Warén, 1989.

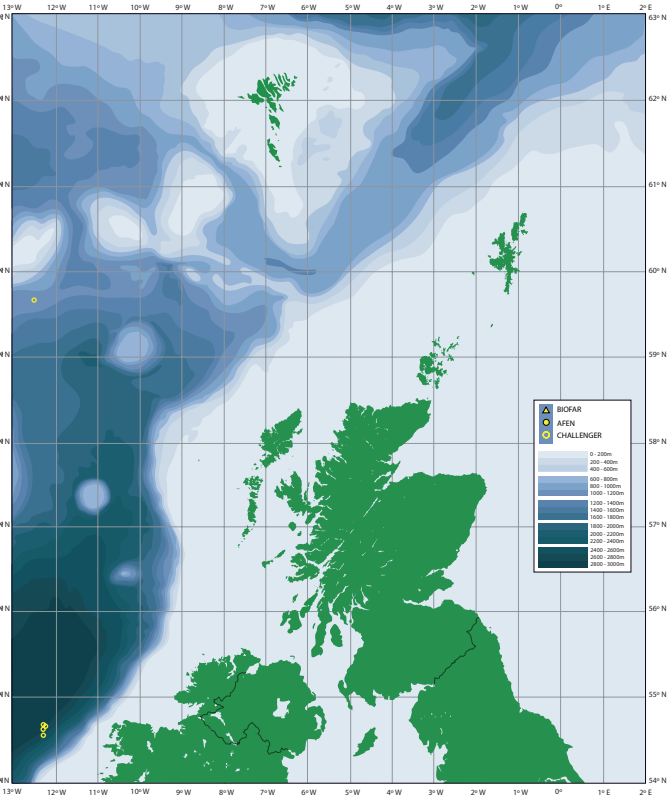

Figure 52 *Yoldiella thaerella* n. sp.