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Research article

Taxonomy of some Galeommatoidea (Mollusca, Bivalvia) associated with deep-sea echinoids: A reassessment of the bivalve genera *Axinodon* Verrill & Bush, 1898 and *Kelliola* Dall, 1899 with descriptions of new genera *Syssitomya* gen. nov. and *Ptilomyax* gen. nov.

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Abstract. The type species of *Axinodon ellipticus* Verrill & Bush, 1898 and *Kellia symmetros* Jeffreys, 1876 are re-described. It is concluded that the two species are not conspecific and that *K. symmetros* cannot be placed in the genus *Axinodon*. The family affinity of *Axinodon* is not resolved, although it is probable that this genus belongs to the Thyasiridae. *Kellia symmetros* is the type species of *Kelliola* and is placed in the Montacutidae. *Kelliola symmetros* is most probably associated with the echinoid *Aeropsis rostrata* and is not the species previously recorded from North Atlantic *Pourtalesia* echinoids under the name of *Axinodon symmetros*. This commensal associated with the North Atlantic *Pourtalesia* is here described as new and placed in the new genus as *Syssitomya pourtalesiana* gen. nov. sp. nov., *Syssitomya* gen. nov. differs from all other genera in the Montacutidae by having laminar gill filaments modified for harbouring symbiotic bacteria and it is thus assumed to be chemosymbiotic. A montacutid associated with the hadal *Pourtalesia heptneri* is described as *Ptilomyax hadalis* gen. nov. sp. nov.

Key words. Galeommatoidea, deep-sea, echinoids, commensal, new genera.

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Introduction

The bivalve currently known as *Axinodon symmetros* (Jeffreys, 1876), a commensal associated with the deep-sea echinoid *Pourtalesia* A. Agassiz, 1869, has been found to have a gill structure similar to that of the Thyasiridae Dall, 1900, and to harbour symbiotic bacteria suggesting that it may be chemosymbiotic (Oliver, Southward & Dando in press). In that study, some key taxonomic issues arose that now require resolution before publication of that study can proceed.

Firstly, there has been debate about the family placement of *Axinodon* Verrill & Bush, 1898. Originally, it was placed in the Thyasiridae (Verrill & Bush 1898) and this was followed by Aartsen (1996) and Coan *et al.* (2000). Ockelmann (1965) placed it in the superfamily Galeommatoidea Gray, 1840 and family Montacutidae Clark, 1855; this placement was maintained by Chavan (1969) and is followed in the current European checklist (CLEMAM 2012). The implications of this debate are twofold:

- If *Axinodon* were a thyasirid then the chemosymbiosis might be expected, but the commensalism would be a first for that family.
- If *Axinodon* were a montacutid then *Axinodon* would be the first of that family and the first commensal bivalve shown to harbour symbiotic bacteria.

Secondly, it was also discovered that commensal bivalves were present on the echinoid *Aeropsis rostrata* (Wyville Thomson, 1877), but although similar to that on *Pourtalesia*, they were not identical. Eve Southward (pers. comm.) noted that the type locality and sample number for *Aeropsis rostrata* is the same as that for *Kellia symmetros* Jeffreys, 1876, both from "Station 9" of the "Valorous Expedition" in the Davis Straits. This brought into question the identity of *K. symmetros* and the identity of the *Pourtalesia* commensal. This is further exacerbated by the conflicting descriptions of *Axinodon*, some stating that it is edentulous (Aartsen 1996) other showing a distinct tooth in the right valve (Bouchet & Warén 1979).

Bivalves belonging to the Galeommatoidea and the Montacutidae in particular have long been known to be commensal with species of sea-urchins and some shallow water species have been studied in considerable detail. There are numerous family and subfamily taxa proposed within the Galeommatoidea (Bieler & Mikkelsen 2006) but their distinction and relationships remain controversial (Mikkelsen & Bieler 2007) although the latter authors do recognise the Galeommatidae Gray, 1840 as distinct form all others. Mikkelsen & Bieler (2007) and Carter *et al.* (2011) refer all non-galeommatids to the Lasaeidae Gray, 1842, that being the earliest family name. Many other authors continue to follow the classification of Chavan (1969) and adopt Montacutidae Clark, 1855 for those taxa morphologically similar to *Montacuta* Turton, 1822 (Jespersen *et al.* 2004; Kamenev 2008; Gofas & Salas 2008). Jespersen *et al.* (2004) argue for recognition of Montacutidae on grounds of hinge and anatomical characters in that the Lasaeidae, Leptonidae and Kelliidae have both cardinal and lateral teeth, and the presence of dimorphic sperm is peculiar to species placed in the Montacutidae. Unfortunately, galeommatoids are poorly represented in molecular phylogenies (Taylor *et al.* 2007) and there is no resolution at the family level. Here, Montacutidae is preferred over Lasaeidae, as the species under consideration are morphologically most similar to *Montacuta* and other associated genera that have been grouped in the Montacutidae.

Popham (1940) and Oldfield (1961) studied the morphology of *Montacuta substriata* (Montagu, 1808) [associated with *Spatangus purpureus* (Müller, 1776)] and *Tellimya ferruginosa* (Montagu, 1808) [associated with *Echinocardium cordatum* (Pennant, 1777)]. Gage (1966 a, b, c) studied the behaviour of these species. Ockelmann (1965) studied *Montacuta* (*Decipula*) *tenella* (Lovén, 1846) [now *Tellimya tenella* (Lovén, 1846)] associated with *Brissopsis lyrifera* (Forbes, 1841). From South-east Asia, Jespersen, Lützen & Nielsen (2004) studied the fine anatomy of three species all associated with *Brissus latecarinatus* (Leske, 1778) and created two new genera *Montacutella* Jespersen, Lützen & Nielsen, 2004 and *Brachiomya* Jespersen, Lützen & Nielsen, 2004. Table 1 gives a compilation of galeommatids known to be commensal with echinoids.

Associations with deep-sea echinoids are known, but taxonomic recognition has been restricted to a single taxon associated with North Atlantic species of *Pourtalesia*. Currently this taxon is known as

Table 1. Galeommatoid species attached to[T] or associated with[W] echinoids

Galeommatoid	Associated echinoid	Reference to association	Distribution	Depth range
[W]*Tellimya ferruginosa* (Montagu 1808).	*Echinocardium cordatum* (Pennant, 1777)	Gage 1966a; Oldfield 1961	NE Atlantic	Intertidal Shelf
[W]*Tellimya tenella* (Lovén, 1846)	*Brissopsis lyrifera* (Forbes, 1841)	Ockelmann 1965	NE Atlantic	Shelf
[T]*Montacuta substriata* (Montagu, 1808)	*Spatangus purpureus* (Müller, 1776)	Gage 1966a; Oldfield 1961	NE Atlantic	Shelf
[T]*Scintillona brissae* Morton & Scott, 1989	*Brissus latecarinatus* (Leske, 1778)	Jespersen *et al.* 2004	SE Asia	Sublittoral
[T]*Montacutella echinophila* Jespersen et al., 2004	*Brissus latecarinatus*	Jespersen *et al.* 2004	SE Asia	Sublittoral
[T]*Brachiomya stigmata* (Pilsbry, 1920)	*Brissus latecarinatus*	Jespersen *et al.* 2004	SE Asia	Sublittoral
[T]*Tellimya vitrea* (Hedley, 1907)	*Brissus gigas* (Fell, 1947)	Ponder 1968	S. Australia	Shallow shelf
[T]*Tellimya vitrea aupouria* (Ponder, 1968)	*Brissus gigas*	Ponder 1968	New Zealand	Shallow shelf
[T]*Montacuta echinocardiophila* (Habe, 1964)	*Echinocardium cordatum*; *Lovenia elongata* (Gray, 1845)	Habe 1964: Jespersen *et al.* 2004	Japan	Shallow shelf
Montacuta divaricata Gould, 1861	*Schizaster lacunosus* (Linnaeus, 1758)	Jespersen *et al.* 2004	Japan	Shallow shelf
[T]*Montacuta semiradiata* Tate, 1889	*Echinocardium* sp; *Spatangus* sp.	Ponder 1968; Barel & Kramers 1977	S. Australia	Shallow shelf
[T]*Montacuta semiradiata neozelanica* (Dell, 1956)	*Cyclaster* sp.	Dell 1963	New Zealand	340-620 m
[W]*Neaeromya compressa* (Dall, 1899)	? *Brissaster latifrons* (Agassiz, 1898)	Coan *et al.* 2000	NE Pacific	10-700 m
[T]*Kelliola symmetros* (Jeffreys, 1876)	*Aeropsis rostrata* (Wyville Thomson, 1877)	This paper	N. Atlantic	3000 m
Syssitomya pourtalesiana sp. nov.	*Pourtalesia jeffreysi* & *P. miranda*.	Bouchet & Warén 1979	N. Atlantic	800-3000 m
[T]*Ptilomyax hadalis* sp. nov.	*Pourtalesia heptneri* Mironov, 1978	Mironov 1978	Banda Trench	7340-7335 m
Unidentified	*Sternospatangus sibogae* (de Meijere, 1904)	Mironov pers. comm.		Deep-sea
Unidentified	*Carnarechinus clypeatus* (Agassiz, 1879)	Mironov 1993	S. Atlantic	Deep-sea

Axinodon symmetros (Jeffreys, 1876) and is associated with *Pourtalesia jeffreysi* Wyville Thomson, 1877 and *P. miranda* Agassiz, 1869 (Bouchet & Warén 1979; Gage *et al.* 1985). The synonymy of *Kellia symmetros* and *Axinodon ellipticus* Verrill & Bush, 1898 was first made by Ockelmann in Chavan (1969). Dall (1899) noting discrepancies in Jeffreys original description of *K. symmetros* placed it in a new genus *Kelliola* Dall, 1899; this was synonymised with *Axinodon* by Chavan (1969).

In the original descriptions of "*Kellia*" *symmetros* (Jeffreys 1876) and *Axinodon ellipticus* (Verrill & Bush 1898) there is no mention of an association with echinoids. The first mention of an association is by Ockelmann & Muus (1978) and is restated by Bouchet & Warén (1979), both giving *Pourtalesia* as the host.

In 1978 Mironov described a hadal echinoid, *Pourtalesia heptneri* Mironov, 1978 from the Banda Trench at a depth between 7340 and 7335 m. He noted that there were montacutid bivalves attached to the spines and figured them (Mironov 1978: plate 1) but they have never been described. Alexandr Mironov (pers. comm.) has also found bivalves attached to *Sternospatangus sibogae* (de Meijere, 1904) and most interestingly internal commensals in intestines close to the peristome of *Carnarechinus clypeatus* (Agassiz, 1879); neither are available for study at this time.

Resolution of the issues raised in this introduction requires examination of type materials but, although available, are restricted to holotypes consisting of shells only. For this paper, the holotypes of the species *Kellia symmetros* and *Axinodon ellipticus* are re-described and their supposed synonymy and family affinities are analysed. This is followed by descriptions of the commensals from *Pourtalesia* and *Aeropsis* Mortensen, 1907 and their relationship to previously described species is reviewed. Finally, the specimens figured by Mironov (1978) are formally described.

Material and Methods

The materials used in this study are all from museum collections derived from late 19th century oceanographic explorations and from recent research studies by British and Norwegian deep water programmes. The modern collections were made by grab or sledge hauls and the bivalves were found attached to the spines of sea urchins. Details of each collection site are given for each specimen examined.

Specimens are of dry shells or whole animals previously fixed in formaldehyde and preserved in 70% ethanol.

Stereo microscope observations were made with Leica M8 or M10 instruments and macrophotography with the latter, attached to a digital camera system, employing enhancement via AutoMontage™ software. Scanning electron micrographs of type material held by the United States National Museum were supplied by that institution and all others were made in the National Museum of Wales using a Jeol Neoscope. Soft tissues were prepared by critical point drying and subsequent gold coating for SEM examination.

Abbreviations used in figures

aa	=	anterior adductor muscle
ad	=	anterior depression
by	=	byssus
cp	=	cardinal peg
ct	=	ctenidium
f	=	foot
ga/me	=	mantle edge/gill axis junction
lig	=	ligament
lv	=	left valve
mef	=	anterior mantle edge folds
mf	=	marginal flange
pa	=	posterior adductor muscle
rv	=	right valve

Results

Phylum Mollusca Linnaeus, 1758
Class Bivalvia Linnaeus, 1758
Superfamily "uncertain"
Family "uncertain"

Genus ***Axinodon*** Verrill & Bush, 1898

Type species

Axinodon ellipticus Verrill & Bush, 1898.

Diagnosis (based on shell characters alone)

Shell small, thin. Equivalve. Inequilateral, beaks behind the midline. Umbos prominent, beaks prosogyrate. Outline obliquely subcircular, distinctly expanded anteriorly. Sculpture of commarginal ridges. Hinge plate narrow, ligament deeply sunken on a groove running from under the beaks posteriorly. Right valve lacking any projecting teeth; left valve with a short, weak. marginal flange beneath the lunule. Isomyarian. Pallial line entire.

Axinodon ellipticus Verrill & Bush, 1898

Axinodon ellipticus Verrill & Bush, 1898: 796, pl. XC figs 5, 6; pl. XCII, fig. 1.

Axinodon symmetros – Aartsen 1996: 30, fig. 5.

Material examined

Holotype
1 shell, North Atlantic, off New Jersey, United States Fish Commission *Albatross*, stn 2096, 39˚22'20"N 70˚52'20"W, 1451 fathoms (2864 m), United States National Museum- USNM35175.

Redescription of holotype (Fig. 1)

Shell small, length 3.5 mm, height 3.3 mm. Thin, fragile. Equivalve. Inequilateral, beaks behind the midline. Umbos prominent, beaks prosogyrate. Outline obliquely subcircular, distinctly expanded anteriorly; anterior dorsal margin short, as a poorly defined lunule; posterior dorsal margin indistinct sloping into broadly rounded posterior, anterior broadly rounded more so than posterior, ventral margin broadly rounded no distinct junctions with lateral margins. Sculpture of dense, fine commarginal ridges most obvious on margins. Prodissoconch II distinct, 754 µm across, with weak commarginal lines (Fig. 1H). Hinge plate narrow, ligament deeply sunken on a groove running from under the beaks posteriorly for about one-third of the posterior dorsal slope. Right valve lacking any projecting teeth, hinge plate slightly and irregularly thickened below lunule. Left valve with a short, weak. marginal flange beneath the lunule; a very weak protuberance is visible below the beak. Adductor scars oval, roughly of equal size; pallial line entire. Interior with feeble radial striae.

Differential diagnosis

At the generic level Chavan (1969) lists *Kelliola* Dall, 1899 as congeneric with *Axinodon* and assigns them to the Galeommatoidea in the family Montacutidae. This is despite Verrill & Bush (1898) describing

Axinodon as edentulous and Dall (1899) describing *Kelliola* with teeth. The hinge of *A. ellipticus* has been examined carefully to ascertain if it is edentulous as stated by Aartsen (1996) or if a cardinal peg was present but has been broken off. The SEM images presented here (Fig. 1A) show no indication of a broken tooth confirming the edentulous condition. Comparisons with figures in Chavan (1969) should not be made as these incorrectly show a shell that is expanded posteriorly and teeth that are not shown in the accurate figures made by Verrill & Bush (1898). From the description below, *Kelliola* is seen to

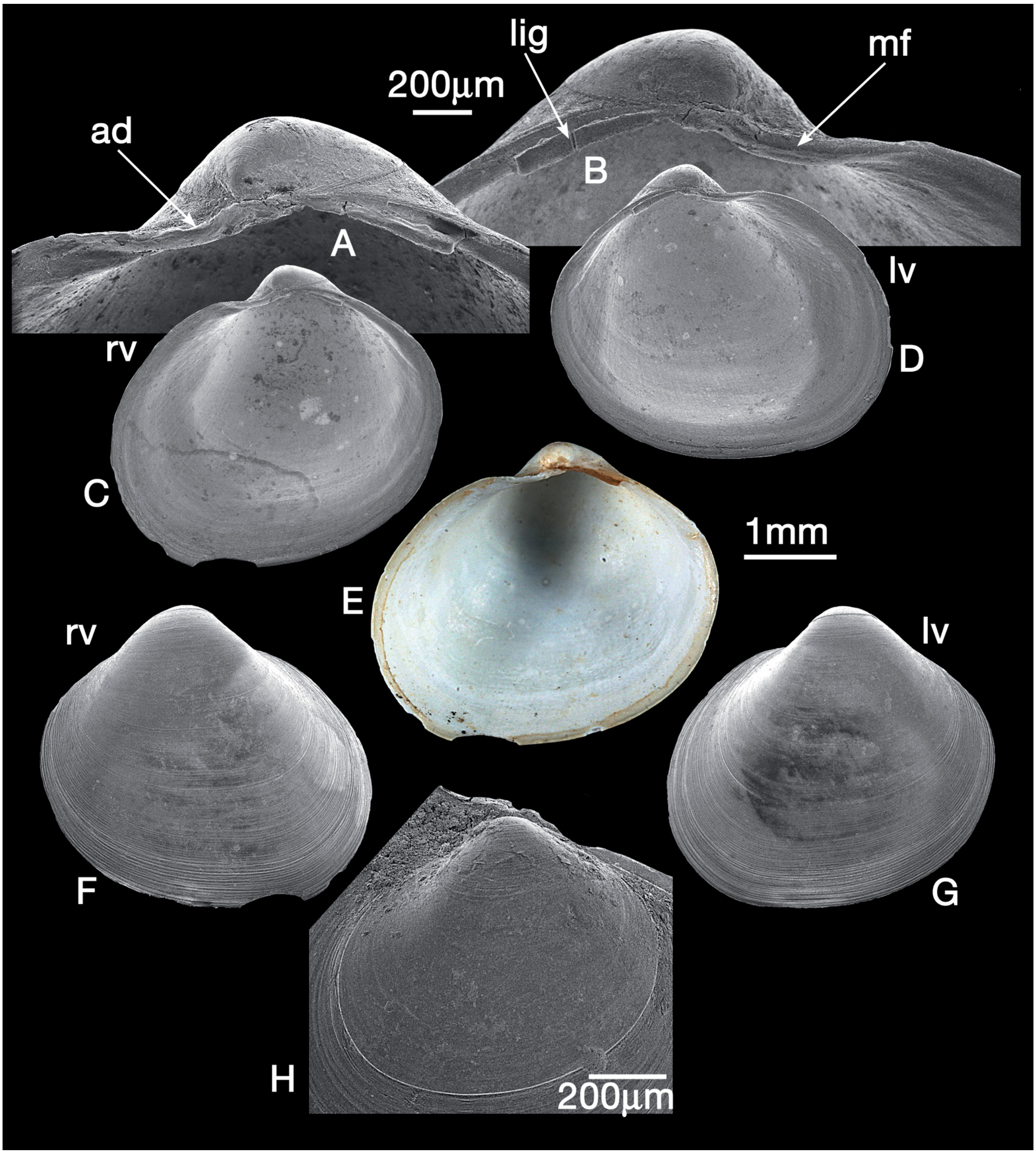

Fig. 1. Holotype of *Axinodon symmetros* Verrill & Bush, 1898, USNM 35175. **A-B**. SEM of hinges of right and left valves. **C-D**. SEM of internal of right and left valves. **E**. Photo micrograph of internal of right valve. **F-G**. SEM of external of right and left valves. **H**. SEM of prodissoconch.

have a cardinal peg in the right valve (Fig. 2A) and therefore *Axinodon* and *Kelliola* are not congeneric. In outline, *Axinodon* looks like *Kelliopsis* Verrill & Bush, 1898 but the latter has small, distinct teeth (Verrill & Bush 1898). Verrill & Bush (1898) placed *Axinodon* in the Thyasiridae as did Aartsen (1996) and Coan *et al.* (2000), and there are similarities with the thyasirid genus *Mendicula* Iredale, 1924. Without anatomical data, it is not possible to confirm the affinity with the Thyasiridae but it is, however, very doubtful that *Axinodon* is a galeommatid as the latter all display some degree of dentition in the right valve.

Superfamily Galeommatoidea Gray, 1840
Family Montacutidae Clark, 1855

Genus ***Kelliola*** Dall, 1899

Type species

Kellia symmetros Jeffreys, 1876 (OD).

Diagnosis

Small to minute shells, Equivalve. Slightly inequilateral, beaks behind the midline. Outline subovate, anterior a little more expanded than posterior. Hinge with an anterior cardinal peg in the right valve, an anterior marginal flange in the left valve, posterior teeth lacking; ligament internal on a recessed resilifer beneath and posterior of the beaks. Sculpture weak primarily of commarginal lines, faint radial striations may be present along with microscopic notches in the ventral margins. Adductor muscles of approximately equal size; mantle edge with a large pedal gape, fused from mid point posteriorly with a small exhalant aperture; foot with an active byssus. Ctenidia of single, un-reflected, demibranchs.

Kelliola symmetros (Jeffreys, 1876)

Kellia symmetros Jeffreys, 1876: 491.

Kellia (*Kelliola*) *symmetros* – Dall 1899: 890.
? *Kellia symmetros* – Friele & Grieg 1901: 29.
Axinodon symmetros – Warén 1980: 47.

Not *Kellia symmetros* – Locard 1898: 297, pl.XIII, figs 18-20.
Not *Axinodon symmetros* – Bouchet & Warén 1979: 216-217, figs 3A-D. — Aartsen 1996: 30, fig. 5 (is *Axinodon ellipticus* Verrill & Bush, 1898).
Not *Montacuta* (*Axinodon*) *symmetros* – Gage, Billett, Jensen & Tyler 1985: 189.
Not *Axinodon* sp.1 – Olabarria 2005: 20 (is *Mysella* sp.)

Material examined

Holotype

1 shell, North Atlantic, SW of Godthaab, Davis Strait, Valorous stn 9, 59˚10'N 50˚25'W, 1750 fathoms (3202 m), United States National Museum- USNM170626.

Other material

2 specimens, attached to *Aeropsis rostrata*, Bay of Biscay, Shackleton cruise 1977/5, stn D7, 47˚29.7'N 09˚33.3'W, 4250-4265 m, 30 Apr. 1977, leg. E. Southward, National Museum Wales, Zoology- NMW.Z. 2012.015.1; 4 specimens, attached to *Aeropsis rostrata*, Bay of Biscay, Shackleton cruise 1977/5, stn

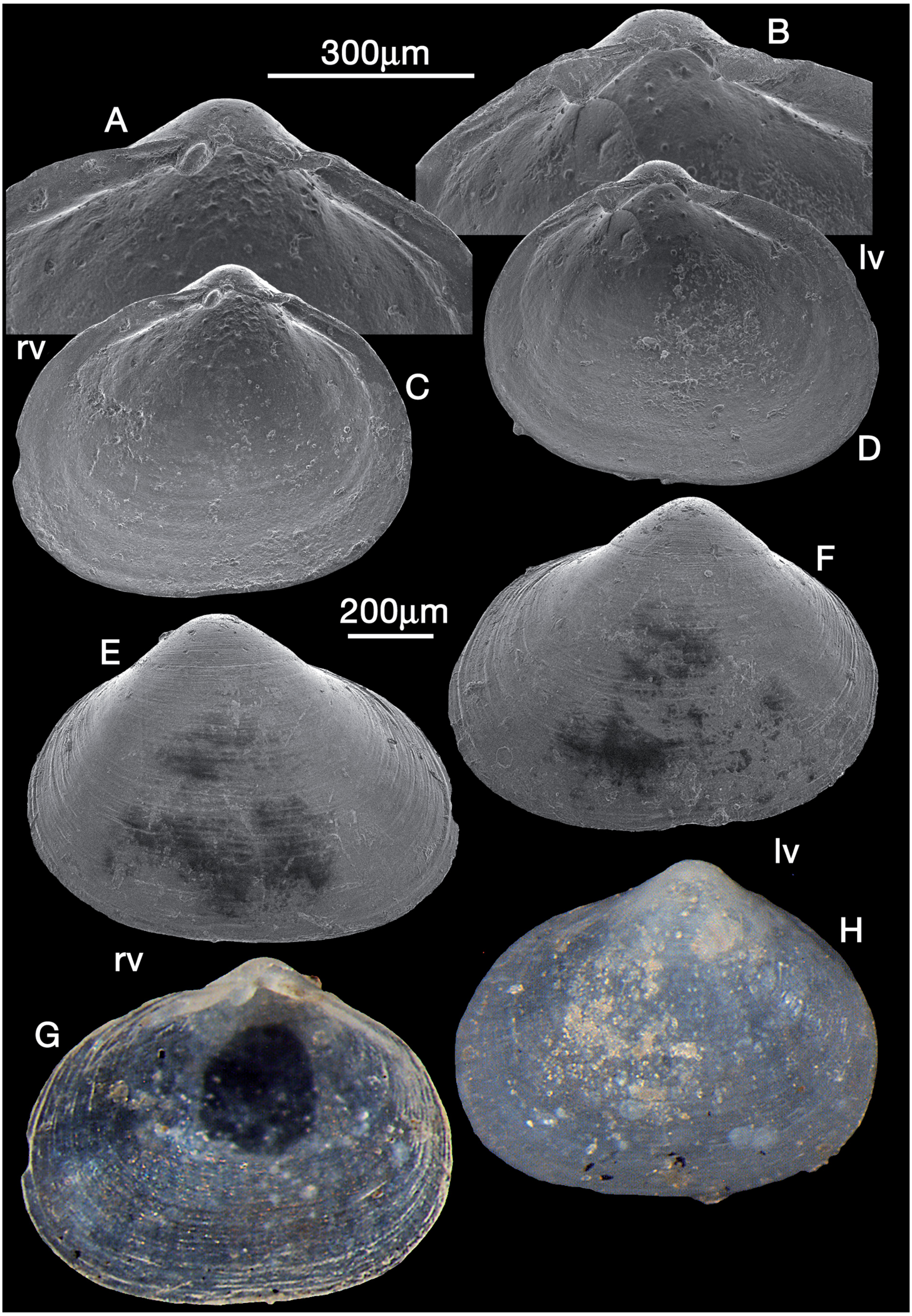

Fig. 2. Holotype of *Kellia symmetros* Jeffreys, 1876, USNM 170626. **A-B**. SEM of hinges of right and left valves. **C-D**. SEM of internal of right and left valves. **E-F** SEM of external of right and left valves. **G-H**. photo micrographs of internal and external of right valve.

D2, 47˚35.52'N 09˚44.07'W, 4120-4165 m, 29 Apr. 1977, leg. E. Southward, National Museum Wales, Zoology- NMW.Z. 2012.015.2.

Type locality

North Atlantic, Valorous St. 9, SW of Godthaab, Davis Strait, 59°10'N 50°25'W, 1750 fathoms (3202 m).

Redescription of the holotype (Fig. 2)

Shell minute, length 1.0 mm, height 0.77 mm. Thin, translucent. Equivalve. Weakly inequilateral, beaks just behind the midline. Umbos prominent, beaks orthogyrate. Outline subovate, slightly extended anteriorly; anterior dorsal margin sloping into broadly rounded anterior margin; posterior dorsal margin indistinct sloping into broadly rounded posterior margin, this slightly less expanded than anterior margin; ventral margin weakly curved. Sculpture weak, of indistinct commarginal lines most obvious on lateral margins. Prodissoconch II distinct, 373 µm across, with weak commarginal lines. Hinge plate weak, Ligament short, internal, attached to a shallow resilifer situated beneath and posterior of the beaks. Right valve with a single, projecting, cardinal peg, immediately anterior to this tooth a slight depression. Left valve with a short, weak, marginal flange in a posterior lateral position. Adductor scars oval, roughly of equal size; pallial line entire.

Description (based on material from Bay of Biscay)

Shell. (Fig. 3) Minute, largest of length 1.3 mm, height 1.0 mm. Thin, fragile. Equivalve. Inequilateral, beaks behind midline. Umbos weakly inflated, beaks orthogyrate. Outline subovate, longer than high, length to height ratio 1.3:1, slightly extended anteriorly; anterior dorsal margin sloping, rather straight merging smoothly with rounded anterior; posterior dorsal margin shorter and sloping more steeply than anterior, merging smoothly with rounded posterior margin; anterior slightly more expanded than posterior; ventral margin gently curved. Sculpture weak almost smooth, of fine commarginal lines; radial lines apparent under transmitted light (Fig. 3A) but these very faintly raised (Fig. 3J). Prodissoconch II distinct, 380 µm in diameter sculptured with commarginal lines (Fig. 3I); Prodissoconch I weakly demarcated, 140 µm in diameter with a punctate micro-sculpture (Fig. 3I). Ligament short, internal, attached to a shallow resilifer situated beneath and posterior of the beaks. Right valve with a single, projecting, cardinal peg, immediately anterior to this tooth a slight depression (Fig. 3D). Left valve with a short, weak, marginal flange in a posterior lateral position (Fig. 3E). Adductor scars oval, roughly of equal size; pallial line entire. Ventral margin dissected by minute transverse grooves (Fig. 3K).

Anatomy. (Fig. 4A) Mantle margin free for most of its length, joined and attached to terminal of gill axis, anterior (pedal) aperture extensive, posterior aperture very small. Adductor muscles of approximately equal size. Foot with a large toe and small heel, byssus functional producing a mass of threads arising from a single stalk. Anterior pedal retractor inserted above the anterior adductor, posterior pedal retractor above the posterior adductor. Ctenidium of a single demibranch, with nine non-reflected filaments in the largest specimen. Filaments rod shaped, lacking abfrontal extension or harbouring symbiotic bacteria. Labial palps small but projecting.

Association. Attached by byssus threads to the spines of the echinoid *Aeropsis rostrata* (Fig. 5).

Distribution

Kelliola symmetros is known only from the type locality and from the Bay of Biscay, at abyssal depths. The host echinoid is widely distributed in the North Atlantic (Echinoid Directory 2012).

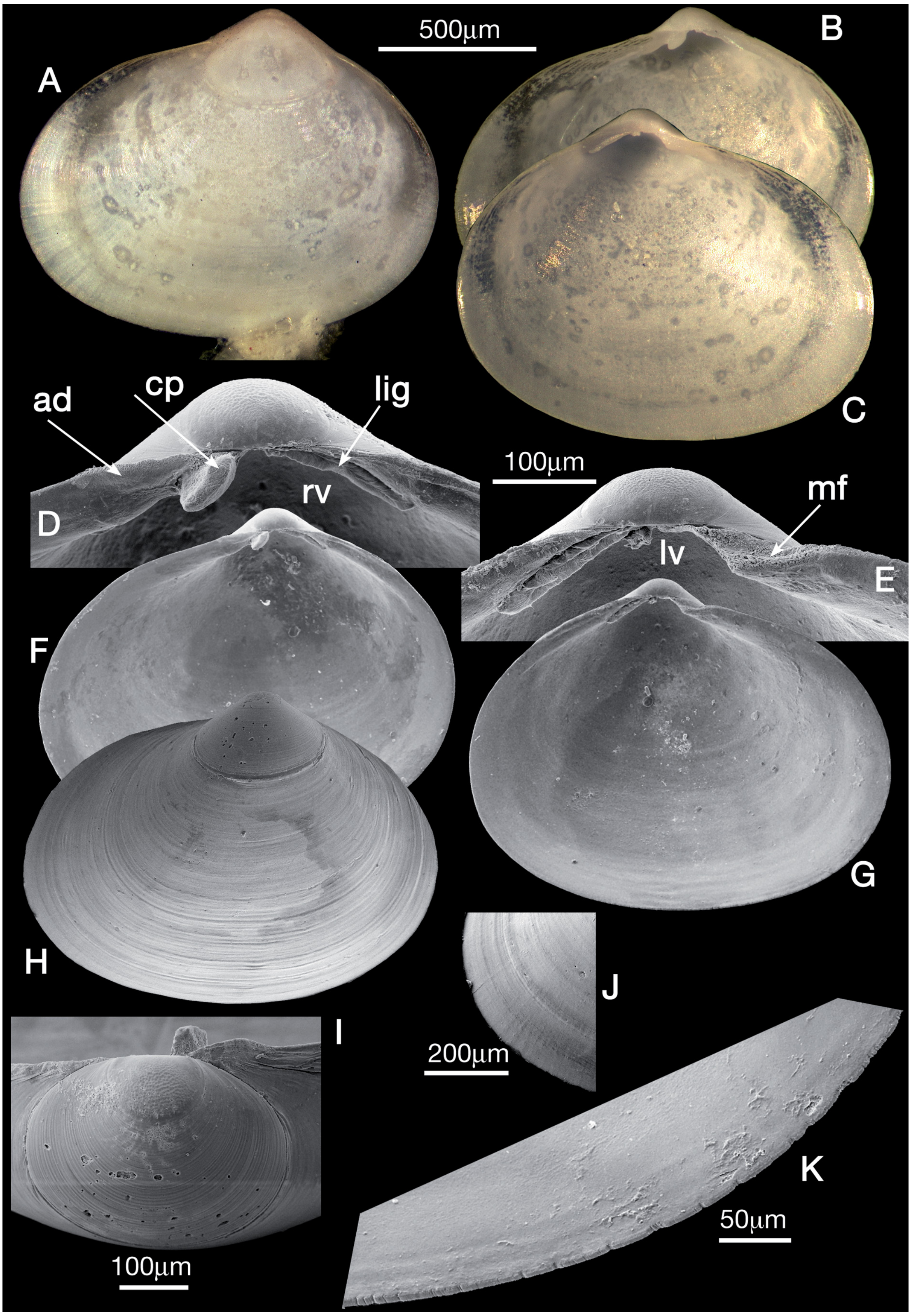

Fig. 3. *Kelliola symmetros* (Jeffreys, 1876) from Biscay. **A-C**. Photo micrographs a external of left valve, internals of both valves. **D-E**. SEM of hinges of right and left valves. **F-H**. SEM of internal of both valves and external of left valve. **I**. SEM of prodissoconch. **J**. SEM of anterior area showing weak radial sculpture. **K**. SEM of margin showing transverse grooves.

Differential diagnosis

The hinges of *K. symmetros* and the *Aeropsis* commensal are almost identical, but *K. symmetros* has slightly more prominent umbos and lacks the marginal transverse grooves. Given that *K. symmetros* was taken in the same sample along with *Aeropsis*, but not attached to it, it is possible that the two are associated. This suggests an ecological affinity with the *Aeropsis* commensal described here. Despite the wide geographical separation of the samples considered here, *Aeropsis rostrata* is regarded as pan Atlantic and having an abyssal bathymetric range (WoRMS 2012). With so few specimens at hand and the poor condition of the holotype of *K. symmetros*, we have chosen to be conservative and regard the *Aeropsis* commensal from Biscay conspecific with *Kelliola symmetros*.

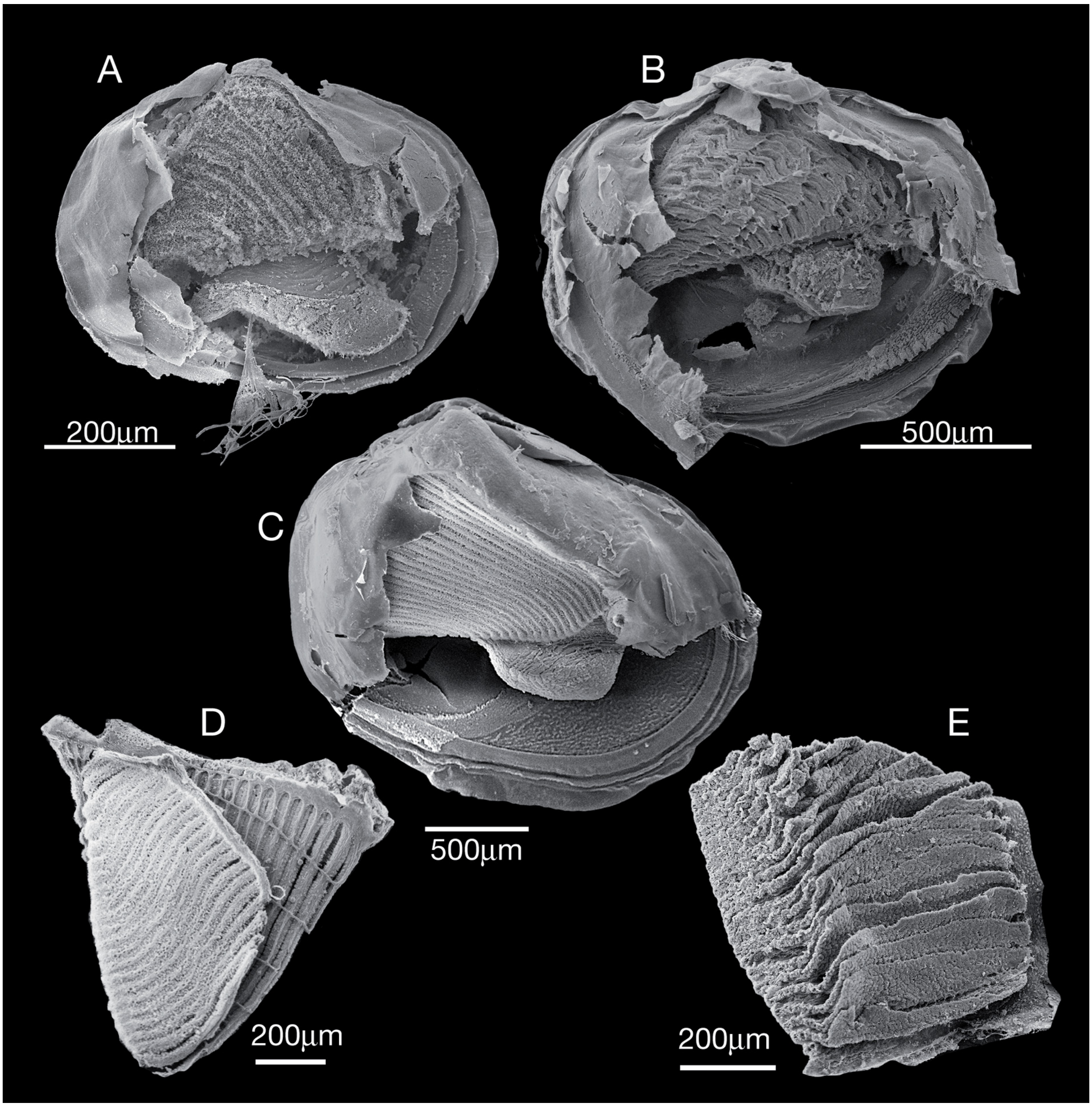

Fig. 4. Scanning electron micrographs of anatomy. **A**. *K. symmetros* (Jeffreys, 1876) from Biscay. **B**. *Syssitomya pourtalesiana* sp. nov. from Norwegian Sea. **C**. *Montacuta substriata* (Montagu, 1808) from North Sea. **D**. Excised ctenidium of *M. substriata*. **E**. Excised piece of ctenidium from *S. pourtalesiana* sp. nov.

Consequently, at the family level the hinge and anatomical characters of *Kelliola* are entirely in keeping with the Montacutidae, consisting of a single cardinal peg in the right valve, a marginal flange in the left valve and an internal ligament. The ligament is attached to an elongate shallow depression extending below the beaks and is therefore most similar to *Montacuta sensu stricto* (Fig. 6). *Montacuta substriata,*

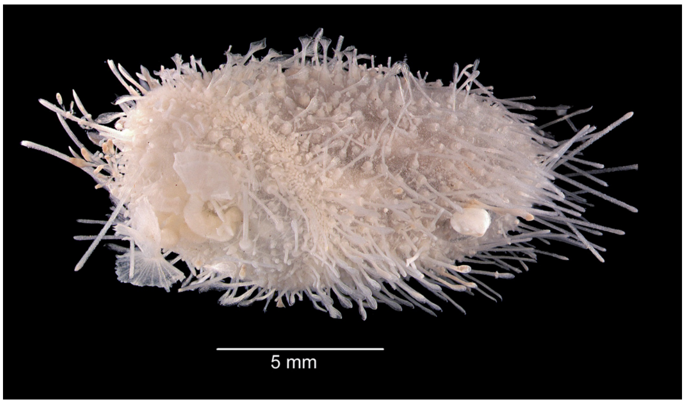

Fig. 5. *Aeropsis rostrata* (Wyville Thomson, 1877) with *Kelliola symmetros* (Jeffreys, 1876) attached, from Biscay.

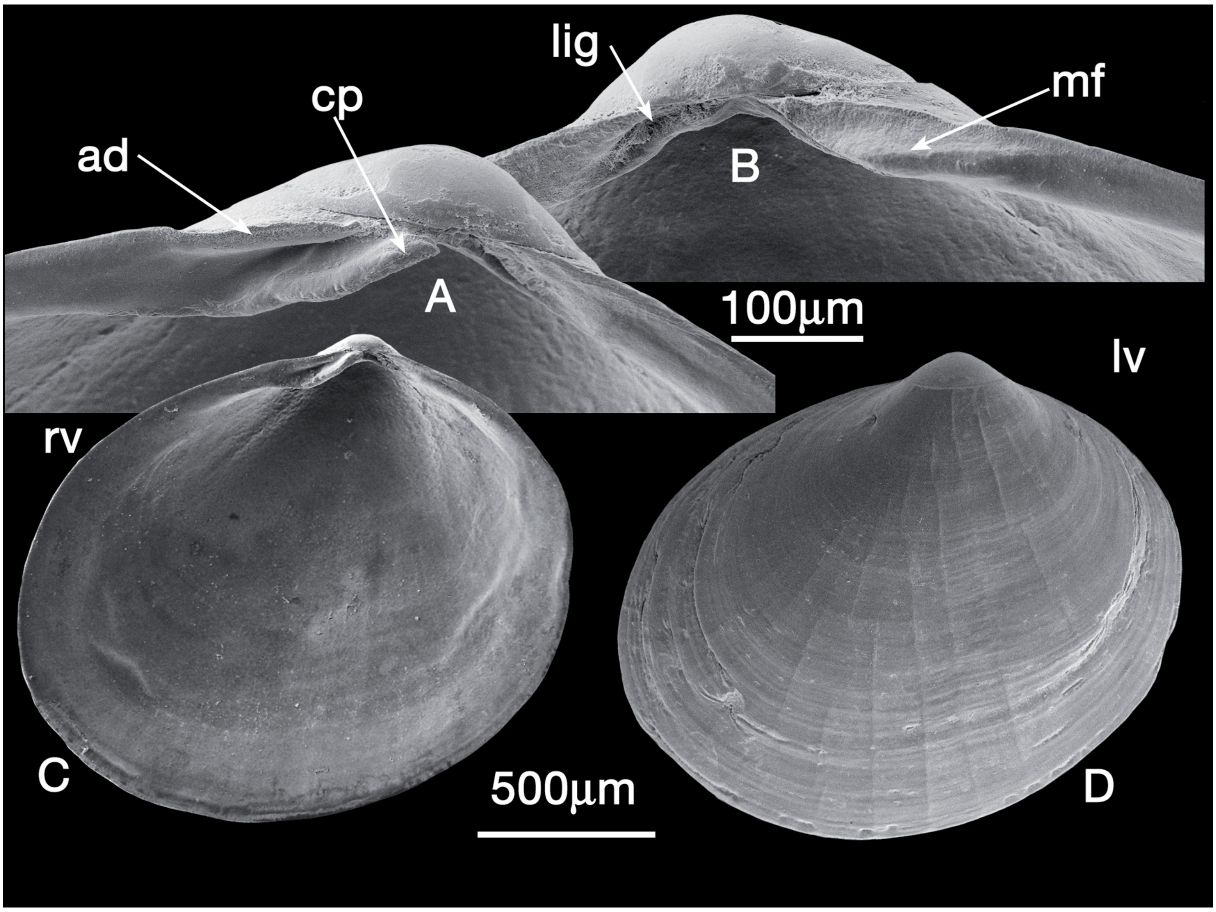

Fig. 6. *Montacuta substriata* (Montagu, 1808), NMW.Z 2000.101.73. Gulfaks Oil Field, North Sea, 217 m. **A-B**. SEM of hinges of right and left valves. **C.** SEM of internal of right valve. **D**. SEM of external of left valve.

the type species of *Montacuta,* has a longer cardinal tooth, has radial ridges and ovate in outline (Fig. 6). Anatomically *Kelliola* is similar to many montacutids, where the ctenidium is reduced to a single demibranch. However, in this genus, the filaments are very few and not reflected (Fig. 4A). This condition could be due to the small size of the specimens.

Dall (1899) noted that Jeffreys' (1876) description of the hinge of *K. symmetros* was incorrect and, in re-describing it, created the new genus *Kelliola* for it. Dall did not make comparisons with other genera but noted that it was similar to *Aligena* Lea, 1846. This is difficult to understand as *Aligena* species have a cardinal peg in each valve (Harry 1969). Comparisons with other montacutid genera are currently complex due to a lack of compatibility in descriptions of characters and the widely varying use of generic names. Such difficulties were amply recognised by Gofas & Salas (2008) in their review of *Mysella* Angas, 1877 and consequent creation of the genus *Kurtiella* Gofas & Salas, 2008. For the purposes of this paper, comparisons are restricted to genera that have a single cardinal peg in the right valve only and left valve with varying degrees of pseudocardinal development. In hinge characters, *Kelliola* is most similar to *Montacuta sensu stricto* (Fig. 6) and *Neaeromya* Gabb, 1873 (Coan *et al.* 2000) in that the development of the posterior teeth is limited to a marginal flange in the left valve and the ligament is attached to a shallow depression beneath and posterior to the beaks. For *N. rugifera* (Carpenter, 1864) Narchi (1969) states that there is a tooth in each valve, although it may be reduced in the left valve (Paul Valentich-Scott pers comm); a further example of the contradictory descriptions found for the montacutid species. In *Tellimya* T. Brown, 1827 the resilifer is developed and the hinge plate thickened accordingly (see Ockelmann 1965, Fig. 2). In *Montacutella* the left valve flange is developed as a small projection (Jespersen *et al.* 2004) and approaches the condition seen in *Aligena*. The shell of *Brachiomya* is like that of *Tellimya* (Jespersen *et al.* 2004).

Kelliola is as different from *Montacuta sensu stricto* as are the other genera and a molecular study is required to evaluate the significance of the morphological characters. *Kelliola* is retained here until such a study is undertaken.

Species level comparisons are restricted to the few abyssal galeommatid species that have been described and none other than that described below under *Syssitomya pourtalesiana* sp. nov. have been found attached to echinoids. The shell of *S. pourtalesiana* sp. nov. is more expanded anteriorly, has a more depressed lunule and lacks marginal notches. The ctenidium is highly modified with laminar filaments whereas that of *K. symmetros* is not modified in this manner. Other described, Atlantic, deep-sea, galeommatids have been assigned to the genera *Mysella* (now *Kurtiella*) (Gofas & Salas 2008), *Epilepton* Dall, 1899 (Allen 2007) or *Draculamya* Oliver & Lützen, 2011 (Oliver & Lützen 2011) none having a dentition identical to *Kelliola* or *Montacuta*. Among ten undescribed galeommatoids from the deep Atlantic, Allen (2008) lists two undescribed *Montacuta* species that may or may not be similar to *K. symmetros*.

Genus ***Syssitomya*** gen. nov.

Type species

Syssitomya pourtalesiana sp. nov. (here designated).

Diagnosis

Shell small, thin. Equivalve. Inflated. Inequilateral, beaks behind the midline. Outline roundly subovate, distinctly expanded anteriorly, lunule depression distinct. Hinge with an anterior cardinal peg in the right valve, an anterior marginal flange in the left valve, posterior teeth lacking; ligament internal on a recessed resilifer beneath and posterior of the beaks. Sculpture weak primarily of commarginal lines. Ctenidium of single partly reflected demibranchs; filaments laminar (Fig. 4E), extended abfrontally, abfrontal surfaces lined with bacteriocyte cells densely packed with symbiotic bacteria. A detailed scanning electron and transmission electron microscopy study of the ctenidium is in preparation and is beyond inclusion in this taxonomic paper (Oliver, Southward & Dando in press).

Etymology

From the Greek, *syssitos* a messmate and *mya* a clam, referring to the commensal habit and bacterial symbiosis.

Syssitomya pourtalesiana sp. nov.
Figs 4B, E; 7, 8A-B

? *Kellia symmetros* – Locard 1898: 297, pl.XIII, figs 18-20.
? *Kellia symmetros* – Friele & Grieg 1901: 29.
Axinodon symmetros – Bouchet & Warén 1979: 216-217, fig. 3A-D.
Montacuta (*Axinodon*) *symmetros* – Gage *et al.* 1985: 189.

Not *Axinodon symmetros* – Warén 1980: 47.
Not *Axinodon symmetros* – Aartsen 1996: 30, fig. 5 (is *Axinodon ellipticus* Verrill & Bush, 1898).
Not *Axinodon* sp.1 – Olabarria 2005: 20 (is *Mysella* sp.).

Etymology

After *Pourtalesia*, the host echinoid; and the Latin termination *–iana*, to denote belonging with.

Material examined

Holotype

1 specimen, Norwegian Sea, Ormen Lange gas field, off Sør-Trøndelag, Central Norway, 63°47'N 03°35'E, 815-925 m, Swedish Museum of Natural History SMNH5566.

Paratypes

Same recolt data as for the holotype: 7 specimens, Swedish Museum of Natural History SMNH5567; 1 specimen + 2 shells, National Museum Wales, Zoology- NMW. Z.2012.014.

Other material

8 specimens, Rockall Trough, RRS *Challenger*, stn ES137, 54°40'N 12°19'W, 2900 m, 22 Feb. 1978, leg. I.J. Killeen NMW.Z. 2009.045.2; 6 specimens, Rockall Trough, RRS *Challenger,* stn ES231, 54°42'N 12°12'W, 2898 m, 17 May 1983, leg. I.J. Killeen, National Museum wales, Zoology- NMW.Z. 2009.045.3.

Type locality

Norwegian Sea, Ormen Lange gas field, off Sør-Trøndelag, Central Norway, 63°47’N 03°35’E, 815-925 m, 2009. Swedish Museum of Natural History, det. Anders Warén.

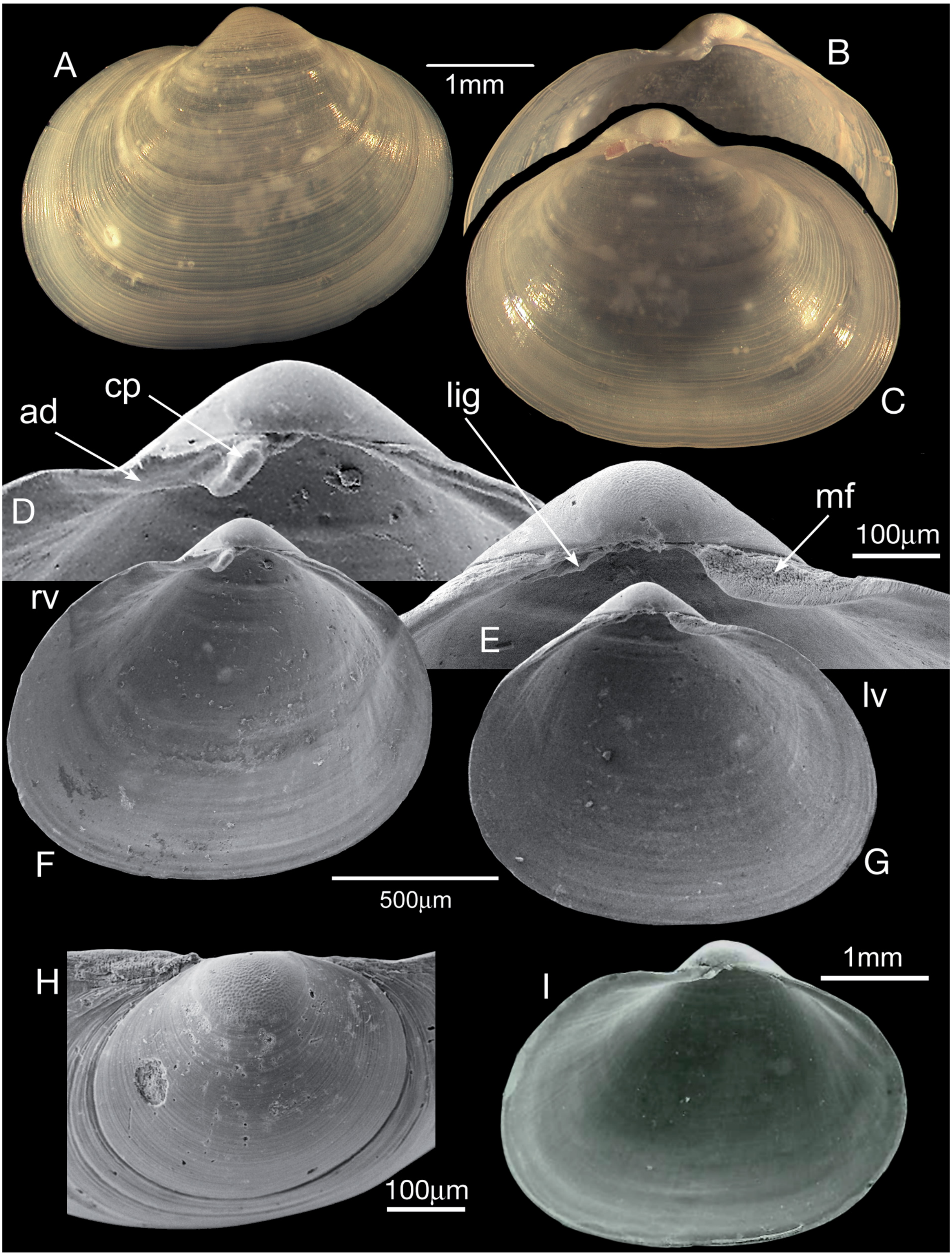

Fig. 7. *Syssitomya pourtalesiana* sp. nov. from Norwegian Sea. **A-C**. Photo micrographs a external of left valve, internals of both valves. **D-E**. SEM of hinges of right and left valves. **F-G**. SEM of internal of both valves. **H**. SEM of prodissoconch. **I**. SEM of internal of right valve from NORBI cruise, abyssal, Courtesy of Anders Warén.

Measurements (SMNH5566 and part of SMNH5567 paratypes)

	Length (mm)	Height (mm)	L:H
Holotype	4.1	3.2	1.3:1
Paratype	3.0	2.3	1.3:1
Paratype	2.4	2.0	1.2:1
Paratype	1.8	1.4	1.3:1
Paratype	1.3	1.1	1.2:1
Paratype	1.3	1.1	1.2:1

Description based on specimens from the Norwegian Sea

SHELL. (Figs 7, 8) Small, largest length 4.2 mm, height 3.2 mm, breadth 2.7 mm. Thin, fragile, translucent. Equivalve. Inequilateral, beaks distinctly behind midline. Umbos moderately inflated, beaks orthogyrate or marginally prosogyrate. Outline subovate, longer than high, length to height ratio 1.3:1, distinctly expanded anteriorly becoming a little oblique; anterior dorsal margin short as a depressed but ill-defined lunule(Fig. 8A¹); anterior broadly rounded; posterior dorsal margin sloping merging smoothly with rounded posterior margin; anterior distinctly more rounded than posterior; ventral margin gently

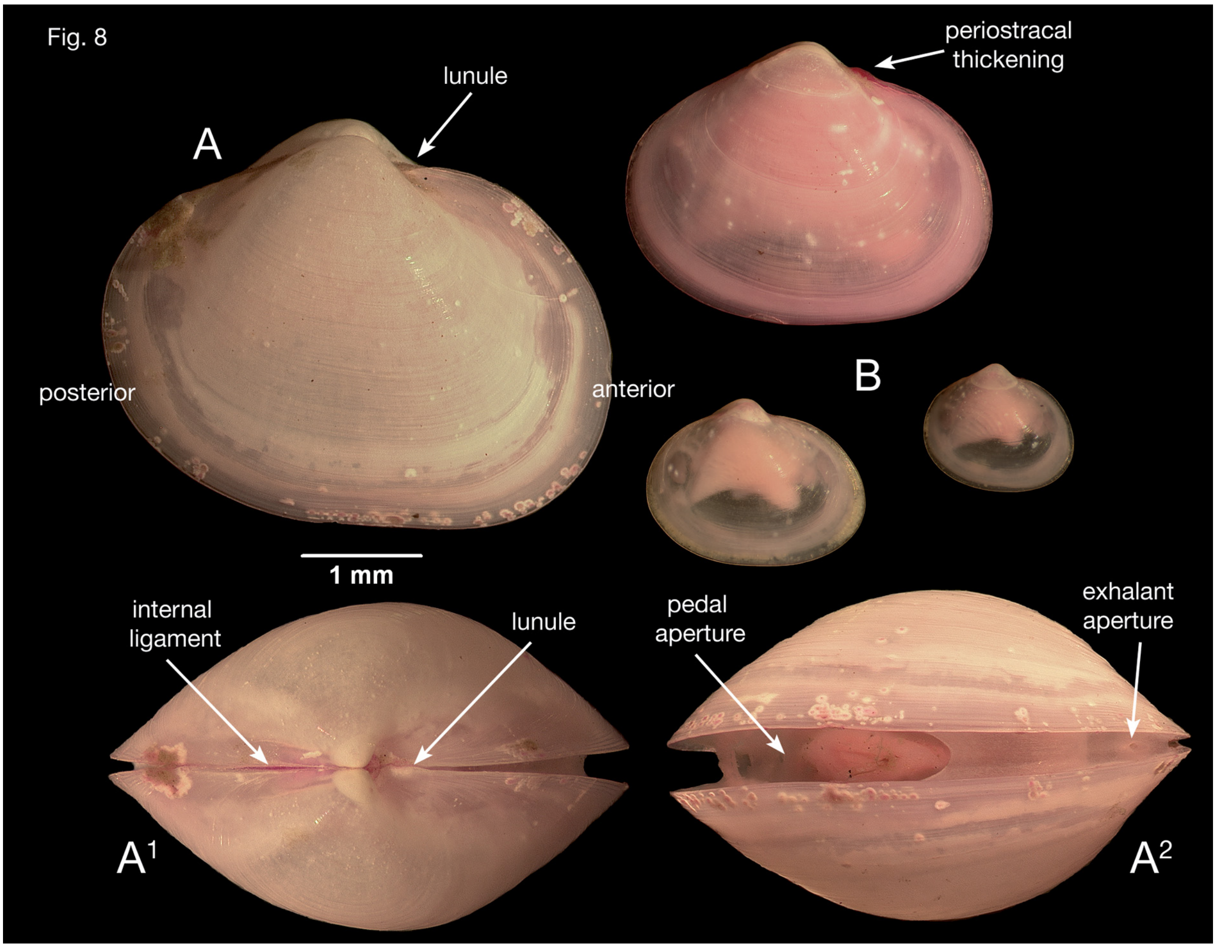

Fig. 8. Computer enhanced photomicrographs of whole specimens of *Syssitomya pourtalesiana* sp. nov. from the Norwegian Sea. **A-A²**. Holotype **A**. Exterior from right side. **A¹**. Dorsal. **A²**. Ventral. **B**. Paratypes, size series.

curved. Sculpture of dense, fine commarginal ridges. Prodissoconch II distinct, 390-410 µm in diameter, sculptured with commarginal lines (Fig. 7H); Prodissoconch I weakly demarcated, 148-150 µm in diameter with a punctate micro-sculpture (Fig. 7H). Ligament short, internal, attached to a shallow resilifer situated beneath and posterior of the beaks (Fig. 7E). Right valve with a single, projecting, cardinal peg, immediately anterior to this tooth a prominent depression (Fig. 7D). Left valve with a short, marginal flange in a posterior lateral position (Fig. 7E). Adductor scars oval, roughly of equal size; pallial line entire. Margin entire.

Anatomy. (Figs 4B, E; 8A^2) Mantle margin free for most of its length, joined and attached to terminal of gill axis, anterior (pedal) aperture extensive, posterior aperture very small (Fig. 8A^2). Anterior mantle edge thrown into folds (Fig. 4B). Adductor muscles of approximately equal size. Foot with a large toe and small heel, byssus functional producing a mass of threads arising from a single stalk. Anterior pedal retractor inserted above the anterior adductor, posterior pedal retractor above the posterior adductor. Ctenidium of single demibranchs, each with up to 30 partly reflected filaments (Fig. 4B). Filaments laminar, extended abfrontally with an extensive bacteriocyte zone (Fig. 4E). Labial palps small but projecting.

Specimens from abyssal depths in the Rockall Trough do not differ significantly from those from the Norwegian Sea except for a large shell that shows greater anterior expansion. The ctenidia of this specimen show the same laminar filaments with abfrontal extension. Specimens collected in the month of February were gravid, the suprabranchial chamber holding hundreds of sub-triangular larvae, on average 112 µm in diameter.

There is no record of any association with an echinoid but these specimens originate from the same sampling programme reported upon by Gage *et al.* (1985) where they were attached to *Pourtalesia miranda*.

Association. Attached by byssus threads to the spines of *Pourtalesia jeffreysi* and *P. miranda* (Fig. 9).

Distribution

Confirmed from the NE Atlantic, Norwegian Sea to Bay of Biscay at depths from 800-3617 m. Records (Allen 2008) from the NW and SW Atlantic have not been confirmed although one of the host species *P. miranda* has been recorded in these areas.

Pourtalesia jeffreysi has two recognised subspecies with both hosting *Syssitomya* gen. nov.: *Pourtalesia jeffreysi gibbosa* Mironov, 1995 has a bathyal range while the subspecies *lata* Mironov, 1995 is abyssal.

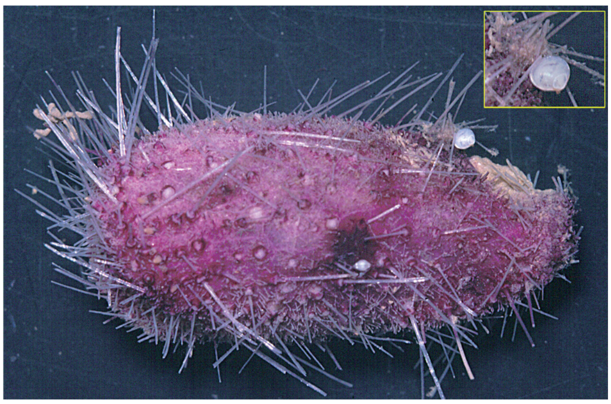

Fig. 9. *Pourtalesia miranda* Agassiz, 1869 with *Syssitomya pourtalesiana* sp. nov. attached, from Biscay. Courtesy of A.J. & E.C. Southward.

The known geographic range for *P. jeffreysi* is the Norwegian Sea and Russian Arctic Ocean (WoRMS 2012).

Differential diagnosis

The shell characters of *Syssitomya* gen. nov. are montacutid in all respects, notably the anterior expansion, internal ligament and the hinge reduced to a single cardinal peg in the right valve and a marginal flange in the left valve. In shell character, similarities are greatest with *Kelliola* but *Syssitomya* gen. nov., uniquely within the Galeommatoidea, has highly modified ctenidia with abfrontally extended, laminar filaments.

At the species level, for comparison with *Kelliola symmetros* see above. The somewhat inflated, anteriorly expanded form of *S. pourtalesiana* sp. nov. is rather distinctive and not like the form of other deep-sea montacutids such as species of *Kurtiella* (Gofas & Salas 2008) or *Epilepton* (Allen 2007) that are more ovate, compressed and have different dentition patterns. From external appearances it more resembles some thyasirids notably *Thyasira subovata* (Jeffreys, 1881) (see Oliver *et al.* 2012) and if not found attached to its host could easily be mistaken for a thyasirid.

Genus ***Ptilomyax*** gen. nov.

Type species

Ptilomyax hadalis sp. nov. (here designated).

Diagnosis

Very small, juvenile shell equivalve, subovate, slightly expanded anteriorly. Adult shell inequivalve dorsal margin of left valve elevated and rolled over, lateral dorsal margins extended, alate. Ligament small, posterior, deeply sunken; dorsal margin with thickened periostracal "ligament". Hinge plate not examined. Sculpture almost smooth with faint commarginal lines. Ctenidium of single reflected demibranchs; byssus of multiple strands; pedal aperture large, exhalant aperture small.

Etymology

Ptilomyax, from the Greek, *ptilo* — winged and *myax*— a small clam (gender masculine).

Ptilomyax hadalis sp. nov.

Montacutid Mironov, 1978: 722, pl. 1.

Etymology

hadalis — referring to the hadal zone of the deep ocean (deeper than 6000 m).

Material examined

Type series of 18 specimens Banda Trench, RV *Vityaz* cruise 57, stn 7271, 5°37'S 131°07.5'E, 7340-7335 m, 21-22 Mar. 1975. Leg. A.N. Mironov.

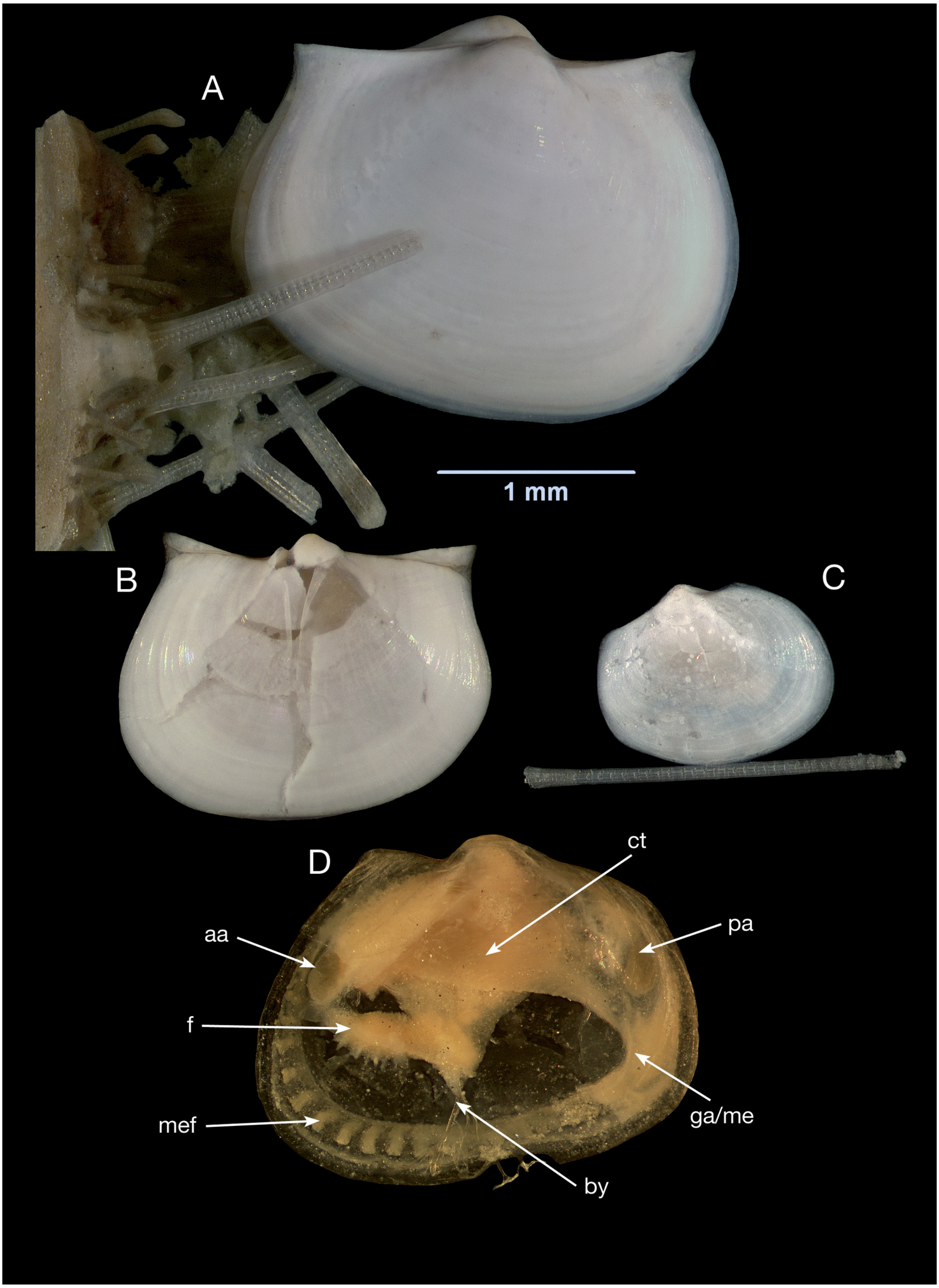

Fig. 10. *Ptilomyax hadalis* sp. nov. **A**. Holotype attached to echinoid spines. **B**. Paratype, left side. **C**. Juvenile paratype lacking "wings". **D**. Anatomy of a paratype as viewed from the left side.

Holotype

1 specimen, Zoological Museum of Moscow State University, Moscow, ZMMU Ld-3043.

Paratypes

14 specimens, Zoological Museum of Moscow State University, Moscow, ZMMU Ld-3044. 2 specimens (1 on SEM stub), National Museum Wales, Zoology- NMW.Z.2012.013.

The material has been poorly preserved, thus the shells are considerably softened, and the tissues are rather contracted. No attempt has been made to examine the hinge, as the valves are so soft that they do not survive being separated. However, the distinctive external form of the shell and the anatomy are sufficient to describe it and place it at the family level.

Description

Shell. (Fig. 10A-C) Small, (largest specimens 2.5 mm L x 1.9 mm H). Inequivalve in adult, lateral dorsal margins of right valve elevated and rolled over projecting beyond left valve. Outline slightly inequilateral, beaks slightly prosogyrate, just behind the mid line, anterior more expanded than posterior; dorsal margins more or less straight, those in adult right valve projecting laterally, becoming alate; forming distinct lateral sinuses with adjacent anterior and posterior margins; lateral margins broadly rounded, anterior more so; ventral margin curved. Ligament small, posterior, deeply sunken; dorsal margin with thickened periostracal "ligament". Hinge plate not examined. Sculpture almost smooth with faint commarginal lines. Prodissoconch I, 105 µm; prodissoconch II, 265 µm, with fine commarginal lines.

Anatomy. (Fig. 10D) Mantle edge mostly unfused with extensive anterior-ventral pedal aperture; fused with terminal of gill axis; exhalant aperture small. Anterior-ventral inner margin raised into series of prominent evenly spaced transverse ridges. Anterior and posterior adductor muscles of similar size, oval in section. Posterior pedal retractor and anterior pedal muscles present. Ctenidium of a single demibranch, ascending and descending lamellae of almost equal size. Labial palps small. Foot with well developed toe, sole flattened and apparently with tissue projections (these may be an artefact of preservation); heel distinct, byssus functional producing numerous thin filaments.

Differential diagnosis

The projecting and rolled over dorsal margins of the right valve are reminiscent of pteriids but *Ptilomyax* gen. nov. is clearly allied with the galeommatids as evidenced by the anatomy. *Ptilomyax* gen. nov. shares many common features with other montacutids associated with echinoids including: a large anterior pedal aperture, mantle fusion limited to junction with gill axis, ctenidium with a single demibranch, foot with prominent toe with a sole and with a functional byssus, ligament internal and weak hinge with poorly developed teeth (Oldfield 1961; Ockelmann 1965; Ponder 1968; Jespersen *et al.* 2004). The Galeommatoidea exhibit an extraordinary range of shell morphologies as can be seen in Chavan (1969) but none have projecting dorsal margins. This unique feature is sufficient to warrant the creation of a new genus and new species.

General discussion

This study has been necessary largely because of inadequate descriptions of small species based on shells alone and from few specimens. Family placement of these taxa cannot be made on shell characters alone and when anatomical data are lacking contemporary studies are compromised. Two key taxa based on unique and poorly preserved shells have been the centre of this paper with the taxonomic crux being their relationship to either of the commensals fully described here from the echinoids *Aeropsis* and *Pourtalesia*. This paper has excluded *Axinodon* but has not clarified the family affinity of that genus. The shell characters of the presence of a single cardinal peg in the right valve, marginal flange in the left valve and an internal ligament attached to a flat or grooved resilifer are shared by the commensals and *K. symmetros*. Although this paper concludes that the *Aeropsis* commensal is *K. symmetros* there was an option to regard *K. symmetros* as a *nomen dubium* because of the poor condition of the holotype and the lack of anatomical data for further comparisons. Despite the holotype of *K. symmetros* being very small and in poor condition, its almost symmetrical outline and lack of lunule distinguish it from the *Pourtalesia* commensal. As a consequence of this decision the *Pourtalesia* commensal was left without a species name and is named here as *pourtalesiana*. The shell characters suggest that it should be placed in *Kelliola* but the highly modified gill and bacterial symbiosis warrant further distinction and the new genus *Syssitomya* gen. nov. is erected for it. The use of anatomical characters to define genera and species within the Galeommatoidea is not novel, most recently Jespersen *et al.* (2004) used anatomical characters to define their montacutid genera *Montacutella* and *Brachiomya* and Oliver & Lützen (2011) did likewise for *Draculamya*. It is accepted that using anatomical characters makes systematic comparisons, with species known from shells alone, difficult but no more so than when applying molecular data to morphological systems. In this case, the adaptive radiation from suspension feeding to bacterial symbiosis represents a considerable change in both morphology and ecology. In my view, this adaptation is of considerably more significance than small changes of shell morphology that have traditionally been recognised by many bivalve taxonomists.

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