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Description and morphology of the "Juan de Fuca vent mussel", *Benthomodiolus erebus* sp. n. (Bivalvia, Mytilidae, Bathymodiolinae): "Phylogenetically basal but morphologically advanced"

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Abstract

The Juan de Fuca vent mussel first found in 1990 is formally described as *Benthomodiolus erebus* **sp. n.** Comparisons are made with the three other species previously assigned to *Benthomodiolus* namely *B. lignocola, B. geikotsucola* and *B. abyssicola*. The anatomies of all four species are examined and are shown to share the arrangement of pedal and byssus musculature, having largely un-fused mantle margins and a hind gut with a very short loop. The ctenidia were examined using both light and scanning electron microscopy. *B. erebus* and *B. geikotsucola* were found to have lamellar filaments with extensive abfrontal expansion and fusion of the ascending and descending arms. In this there is similarity with *Bathymodiolus*. *B. lignocola* and *B. abyssicola* were found to have linear filaments with narrow abfrontal surfaces with little fusion. All four species were shown to have the abfrontal surfaces covered by polygonal cushions of microvilli although these were much less apparent in *B. lignocola* and *B. abyssicola*. Although *Benthomodiolus* was shown by a number of previous studies, using molecular data alone, to be phylogenetically basal to all other Bathymodiolinae the anatomy is highly adapted for chemosymbiosis. Species of *Benthomodiolus* are found on wood-falls, whale-falls and vent sites and thus mirror the habits of the *Bathymodiolus*/*Idas* clade.

Introduction

In a forthcoming paper, Thubaut et al. (in press) rightly highlight the mismatch between molecular data and morphological taxonomy within the Bathymodiolinae. They cite, in particular, the case of the mussel found at the Juan de Fuca vent site in 1990 and listed as *Adipicola* sp. by Juniper et al. (1992). It was later considered to be an un-described species of *Bathymodiolus* by McKiness et al. (2005) then as an un-described species of *Adipicola* by Southward (2008) and as a code number only by Fontanez and Cavanaugh (2013). It has most recently been linked with the clade that includes *Benthomodiolus* (Lorion et al. 2013, Thubaut et al. 2013, Rodrigues et al. 2015).

None of the published literature illustrates this mussel with the exception of the micro-structure of the ctenidium by Southward (2008). In the above molecular studies *Benthomodiolus*, including the Juan de Fuca mussel consistently appears as basal to all other Bathymodiolinae. Fontanez and Cavanaugh (2013) show that the sister group to the bathymodiolines consists of species of *Modiolus* sensu stricto. Gustafson et al. (1998) following Kenk and Wilson (1985) noted that the gill morphology of *Benthomodiolus abyssicola* (Knudsen, 1970) was like that of a typical *Modiolus* suggesting that it was a filter feeding species.

This paper will give a proper taxonomic status to the Juan de Fuca mussel through a description of the shell and anatomy and will make comparisons with other species assigned to Benthomodiolus. The habitat range of *Benthomodiolus* species includes the three major ecotypes, wood-fall, whale-fall and vent; this paper will investigate whether there are any associated morphological characters. Comparisons with other members of the Bathymodiolinae will attempt to elucidate whether the basal position of *Benthomodiolus* is reflected in the morphology.

Materials and methods

The materials examined in this paper are listed under their respective sections in the results section.

The photographic images were made using a Leica Z6 macroscope and image stacking using Helicon Focus™ software. For some anatomical images the tissues were stained with methyl green to enhance contrast. For scanning electron microscopy gill tissues were excised and cut transversely and longitudinally using a thin razor blade. Tissues were dehydrated in 100% ethanol overnight and critically point dried with liquid CO2 as the intermediate fluid in a Quorum K850 critical point dryer. Dried samples were mounted and gold coated before examination using a Jeol Neoscope™ SEM.

Institutional abbreviations

CMN ML	Canadian Museum of Nature, Mollusca
MNNZ	Museum of New Zealand Te Papa Tongarewa
NMW.Z.	National Museum Wales, Zoology
NSMT	National Science Museum Tokyo
ZMUC	Zoological Museum University of Copenhagen

Anatomical abbreviations

aa anterior adductor muscle, **an** anus, **apr** anterior pedal retractor muscle, **au** auricle, **bys** byssus, **ct** ctenidium, **ddd** duct to the digestive diverticula, **eav** exhalant aperture valve, **f** foot, **f(hl)** heel of foot, **f(t)** toe of foot, **fme** fused mantle edge, **h** heart, **hgl** hind gut loop, **ifj** inter filamentar junction, **ilp** inner labial palp, **imf** inner mantle fold, **lp** labial palps, **lps** suspensor muscle for labial palps, **me/ct** mantle edge ctenidial junction, **mef** mantle edge folds, **mmf** middle mantle fold, **oe** oesophagus, **olp** outer labial palp, **omf** outer mantle fold, **ot** oral tube, **pa** posterior adductor muscle, **pbr1** posterior pedal/byssus retractor muscle, **pbr2** anterior pedal/byssus retractor muscle, **per** pericardium, **pms** posterior mantle septum, **ppr** posterior pedal retractor muscle, **psf** polygonal surface, **rt** rectum, **sppr** secondary posterior pedal retractor muscles, **ss/mg** style sac and mid gut, **st** stomach, **vfg** ventral food groove, **vg** visceral ganglion, **vt** ventricle

Results

Class Bivalvia Linnaeus, 1758
Superfamily Mytiloidea Rafinesque, 1815
Family Mytilidae Rafinesque, 1815
Subfamily Bathymodiolinae Kenk & Wilson, 1985

Genus *Benthomodiolus* Dell, 1987

Type species. *Benthomodiolus lignocola* Dell, 1987

Definition. To 43 mm, Thin, umbonate, narrow modioliform, weakly arcuate with beaks about ¼ distance from the anterior, anterior margin rounded only a little narrower than rounded posterior margin. Median area slightly sulcate, widest part behind the umbos. Hinge margin lacking crenulations, ligament sunken, very long. Periostracum persistent, smooth or with sparse hairs. Pedal/byssus musculature in two groups, a posterior set close to the posterior adductor muscle and a median set attached to rear of the umbo. Mantle edge mostly free, poorly frilled, posterior junction short. Hind-gut with a short or very short loop. Ctenidial filaments linear or laminar. Symbiotic bacteria are extra-cellular.

Species included. *B. lignocola* Dell, 1987; *B. geikotsucola* Okutani & Miyazaki, 2007; *B. erebus* this paper; *B. abyssicola* (Knudsen, 1970).

Distribution. Described species are restricted to the Pacific Ocean from New Zealand, Japan, British Columbia and Panama at bathyal to abyssal depths. An undescribed species from the South Atlantic is reported by Thubaut et al. (2013)

Remarks. *Benthomodiolus lignocola*, *B. geikotsucola* and *B. erebus* are regarded as congeneric, based on a combined analysis of COI mtDNA and 28S rRNA (Thubaut et al. in press). In the tree by Thubaut et al. (in press) *B. lignocola* is shown as the sister taxon to *B. erebus* with *B. geikotsucola* and an un-named species from the South Atlantic as sister taxa on a separate branch. Kyuno et al. (2009) and Lorion et al. (2013) show *B. erebus* and *B. geikotsucola* as sister taxa with *B. lignocola* on a separate branch. The tree by Kyuno et al. (2009) is based on the mitochondrial ND4 gene while that of Lorion et al. (2013) is based on combined COI, NADH4, 16S, nuclear 28S and histone 3 data. *Modiolus abyssicola* lacks supporting molecular data and is placed in *Benthomodiolus* primarily on the disposition of the pedal/byssus musculature (Dell 1987, Thubaut et al. in press). Bouchet in WoRMS (2015) also includes *M. abyssicola* in *Benthomodiolus*. However Gustafson et al. (1998) and Kenk and Wilson (1985) reported that the gill of *M. abyssicola* was like that of *Modiolus* and thus probably a filter feeder and suggested that it should be placed in *Modiolus*. This species is revisited below and shown to have a more typical wedge shaped modioliform shell with sparse hairs. The gill filaments are linear and unlike the laminar filaments in *Bathymodiolus* as reported by Kenk and Wilson (1985). However it is shown below that the filaments of *B. lignocola* are also linear but that in both *B. lignocola* and *B. abyssicola* that the abfrontal surface bears polygonal microvillar structures typical of species with symbiotic bacteria. Regardless of the shell form it seems most likely that *M. abyssicola* does belong in *Benthomodiolus* but it remains tentative awaiting confirmation from molecular data.

Consequently the generic diagnosis is based on a combination of characters from *B. lignocola, B. geikotsucola* and *B. erebus*. If *M. abyssicola* is included, then the shell form needs to be expanded to include the more wedge shaped form.

Taxon	Max shell length AL/TL	Bathymetric range	Distribution	Habitat
B. lignocola	18.1 mm 0.23	810–2670m	Chatham Isds, SW Pacific	Wood
B. geikotsucola	42.5 mm 0.28	4020m	Torishima Seamount, W. Pacific	Whale bone
?B. abyssicola	17.2 mm 0.22	3670–3270m	Gulf of Panama, CE. Pacific	Wood
B. erebus	39.9 mm 0.23	2195m	Juan de Fuca Ridge, NE Pacific	Vent

Benthomodiolus erebus sp. n.

http://zoobank.org/9979FC77-8E46-45E5-908C-7452BD83A435
Adipicola sp. (n. sp.?) Juniper et al. 1992: 1797–1799, shell not illustrated
Bathymodiolus sp. JdeF McKiness et al. 2005: 109–116, shell not illustrated.
Adipicola MV Southward, 2008: 139–146, shell not illustrated

Material examined. *Holotype*. 1 specimen, ROV ROPOS dive R682, Clam Bed, Endeavour Segment, Juan de Fuca Ridge, 47°57.8’N 129°05.5’W, 2195m, 19/August/2002. CMNML 097165

Dimensions in mm. Length 39.9; Height 15.4; Width 13.2; Anterior length 9.5

Paratype. 1 broken and partly dissected specimen, Alvin dive 2803, clam bed, Kini’s Site, Middle Valley, Juan de Fuca Ridge, 48°27.40’N 128°42.52’W, 2416m, 24/July/1994. NMW.Z.2015.013.1. This is the remainder of the material used by Southward (2008) in her description of the fine structure of the ctenidium..

Dimensions in mm. Length 39.2; Height 12.9; Width 10.3; Anterior length 10.1

Shell. Holotype, (Fig. 1a–d). Thin but not fragile (0.45–0.55 mm at margins). Equilateral. Umbos prominent. Inequilateral, beaks towards the anterior, just under ¼ the total length from the anterior. Outline modioliform elongate, posterior a little deeper than anterior, ventral margin slightly concave, dorsal margin gently curved. Median area sulcate, widest behind the beaks. Ligament sunken very long, 17.7 mm, no trace of underlying crenulations visible. Anterior hinge margin extending posteriorly beyond the beaks for a short distance. A small flattened lunule under the beaks. Sculpture of fine commarginal ridges increasing in size towards the margins, periostracum persistent of a golden amber shade and lacking hairs. Internally shiny, pearlescent, muscle scars indistinct. The prodissoconch and juvenile shell are too eroded to give any details here.

Paratype, (Fig. 1e). The shell is of the same proportions as the holotype, but is very much thinner (0.25–0.35 at margins) and more fragile.

Pedal byssus musculature. (Fig. 2a–c). The foot has a long toe and a greatly reduced heel. The byssus gland opens at the base of the heel and a longitudinal groove runs the entire length of the sole. The pedal/byssus retractor is divided into two widely separated bundles; the posterior bundle (pbr1) is greatly elongate, of two primary strands and attaches to the shell just above the posterior adductor muscle; the median bundle (pbr2) is relatively short and extends dorsally attaching in the rear of the umbonal cavity. The posterior pedal retractor is slender and runs anterior and parallel to the median pedal/byssus retractor; associated are three fine strands or secondary posterior pedal retractor muscles that coalesce with median pedal/byssus retractor; the anterior pedal retractor consists of two primary bundles, is elongate and attaches above and separate from the anterior adductor muscle. A slender labial palp suspensor muscle rises from the base of the anterior pedal retractor and is inserted into the anterior adductor muscle.

Adductor muscles. The adductor muscles are of almost equal size, the posterior is circular in section while the anterior is oval (Fig. 2a).

Ctenidium and labial palps. The ctenidia (Figs 2a, 4a–e) run almost the entire length of the mantle cavity, are thick and fleshy but not deep (Fig. 2a). The inner demibranch is a few filaments longer than the outer demibranch, both have reflected filaments the ascending arms slightly shorter than the descending arms and these fused for over half their length. The filaments are extended abfrontally, appearing as lamellae (Fig. 4a). There is a groove along the ventral edge of each demibranch (Fig. 4a). The filaments are held together by a single row of large ciliary junctions.

Scanning electron microscopy reveals that the abfrontal surfaces are extensive giving a triangular plate like form to the largely fused ascending and descending arms of each filament (Fig. 4b, c). The inter filamental junctions are very prominent formed of a large bundle of cilia (Fig. 4d). The frontal surface is ciliated while the abfrontal surface is covered by an epithelium of microvilli arranged in a polygonal structure (Fig. 4c, e). The ultrastructure was described my Southward (2008) where the ctenidia were shown to harbor symbiotic bacteria extra–cellulary among dense epithelial microvilli.

The labial palps (Fig. 3f) are small, triangular with 15 sorting ridges on each, there is a short oral tube extending to the mouth.

Mantle edge and apertures. The mantle edges are free for their entire length (Fig. 2a) except for a narrow septum (Fig. 3b and c, pms) separating the exhalant aperture from the inhalant/pedal aperture. The mantle edge is composed of three major folds (Fig. 3c–e); the outer mantle fold (omf) is smooth and never fused. The middle mantle fold (mmf) is narrow and weakly frilled (Fig. 3d), the stronger frills border the posterior inhalant aperture and a short median section (Fig. 3e), probably marking the pedal aperture. The inner mantle fold is finely digitate

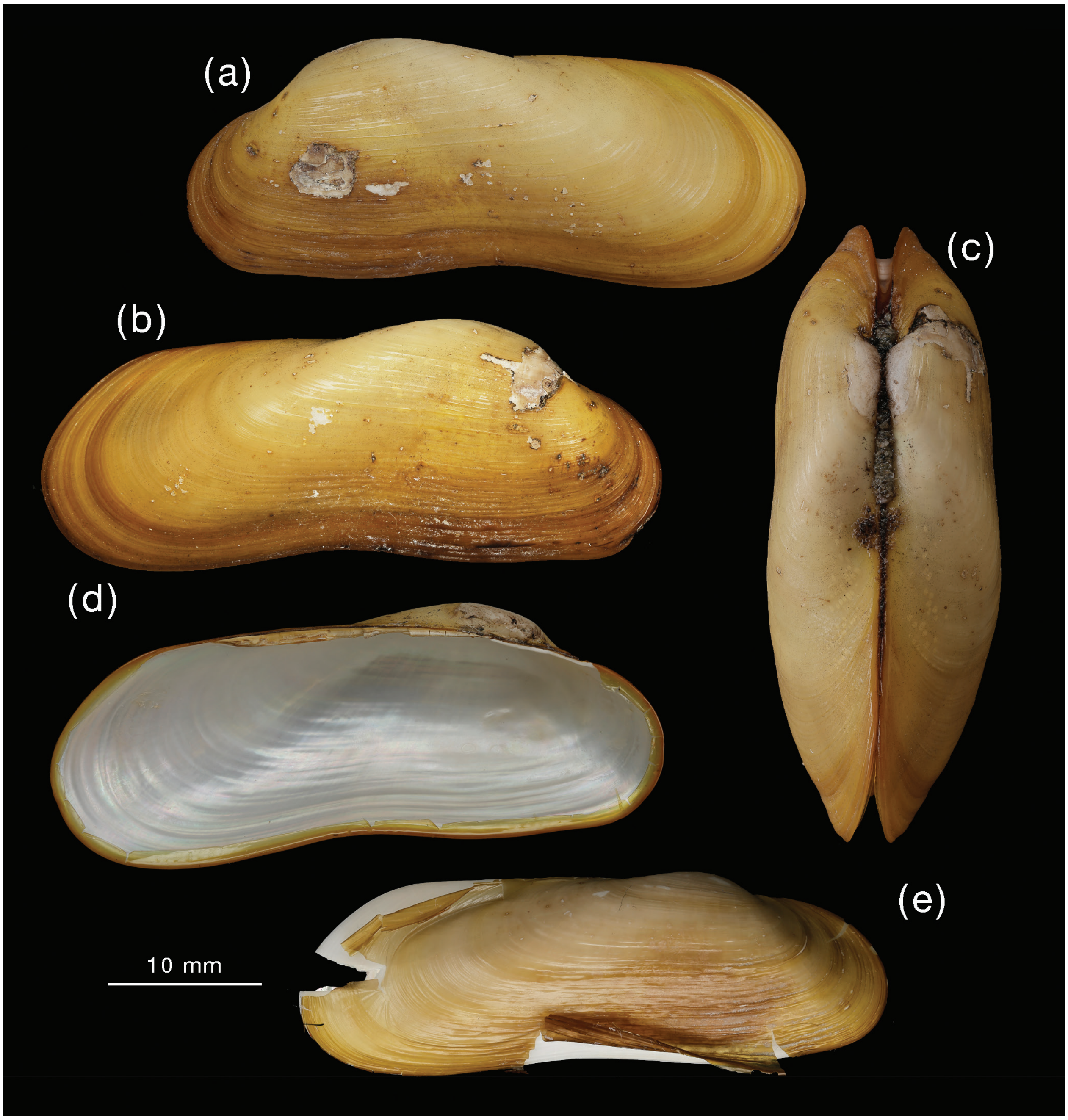


Figure 1. Shells of *Benthomodiolus erebus* sp. n. **a–d** holotype, **a** external of left valve, **b** external of right valve, **c** internal of left valve, **d** dorsal (CMNML 097165), **e** paratype external of right valve (NMW.Z.2015.013.1a).

along the entire length of the pedal/inhalant aperture (Fig. 3d). The exhalant aperture is muscular and smooth edged (Fig. 3b); a pair of folds visible on the inner face probably function as a valve (Fig. 3a, eav).

Alimentary system. The alimentary system (Fig. 3g) runs along the dorsal surface of the visceral mass. The oesophagus (oe) is flattened, relatively short, about the same length as the stomach (st). The mid gut and hind gut run in a straight line except for a very short, tight, loop (hgl) just anterior of the heart ; the hind gut runs through heart and the rectum (rt) runs over the posterior adductor muscle with the simple anus (Fig. 3c) opposite the exhalant aperture.

Stomach. The stomach (Fig. 3g) (st) is situated beneath the umbos, in front of the median pedal/byssus retractors (pbr2) and slightly to the left side. Externally it is elongate somewhat triangular in form, the oesophagus (oe) entering on the anterior face and the conjoined style sac/mid gut (ss/mg) leaving posteriorly, the right side is expanded posteriorly, there is a very slight division into anterior and posterior chambers with a shallow dorsal caecum (ca) projecting on the left anterior dorsal face and the thickening of the dorsal hood behind this (dh). Ducts to the digestive gland are prominent on the right dorsal side (ddd1–3) while a large duct exits on the lower mid left and a smaller

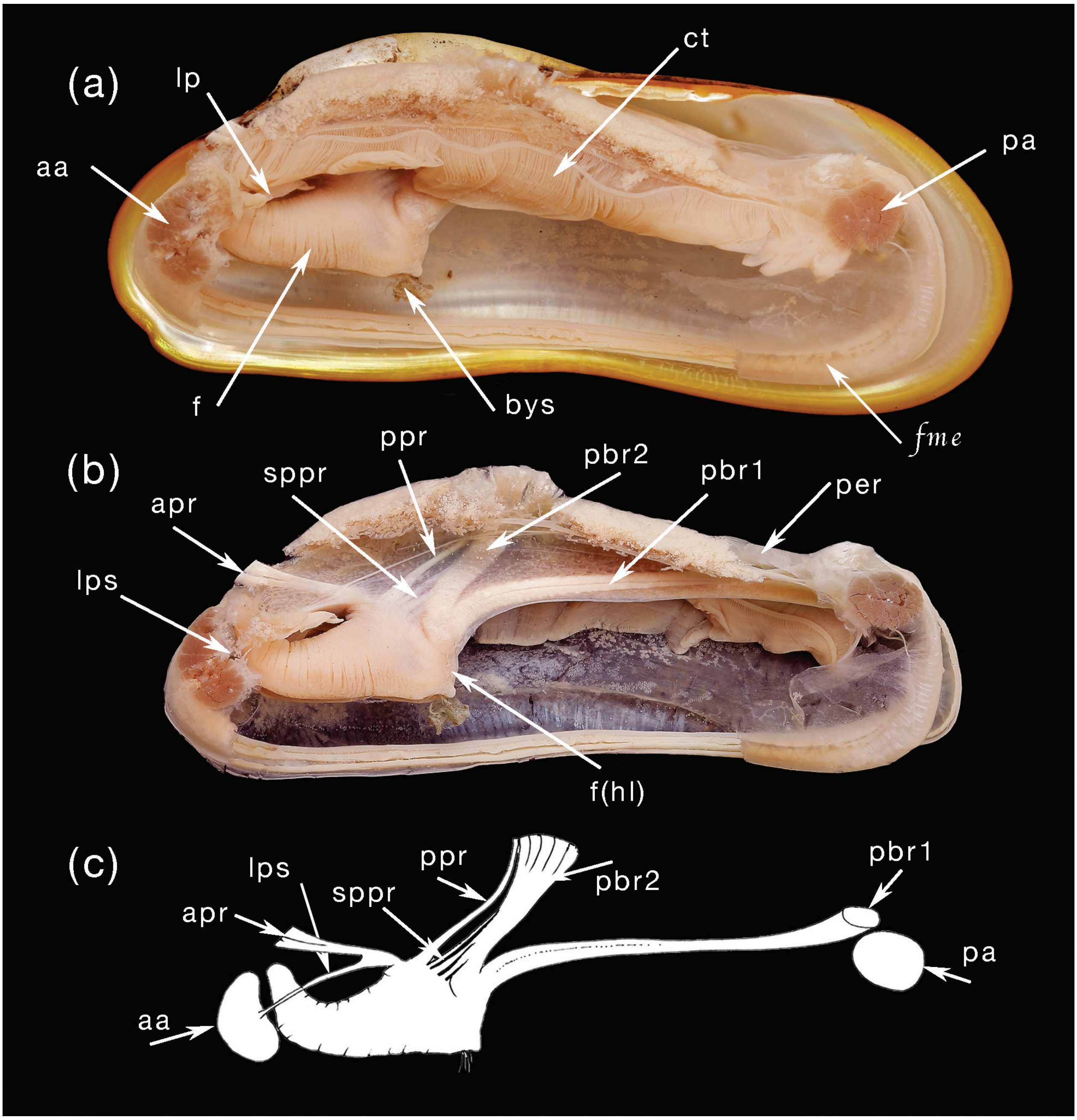


Figure 2. Gross anatomy of *Benthomodiolus erebus* sp. n. **a** after removal of left valve and mantle, **b** after further removal of the ctenidium, **c** diagram of the adductor, pedal and byssal musculature.

on the ventral anterior left, the latter are not visible in Fig. 3g.

Internally the major typhlosole runs longitudinally across the floor, to its right side there is a smooth depression and leading off this are tracts to the right side ducts. There is a deep embayment running from the anterior floor and up the anterior left side into the shallow caecum and sharply curving into the dorsal hood. A small duct exits this trough on the anterior floor and medially it opens into the left pouch where a large duct exits. The gastric shield is shaped into the dorsal hood and extends posteriorly of the left posterior dorsal face. Sorting ridges are nowhere apparent except for a well defined but small area on the posterior edge of the left pouch.

Pericardium. The pericardium (Figs 2b, 3g) (per) is situated immediately anterior of and between the posterior byssus retractor muscles (pbr1). The ventricle (vt) is muscular while the auricles (au) are relatively large and thin walled. The arrangement of the auricular veins could not be elucidated.

Etymology. After *Erebus* (Greek), Noun in apposition, “place of darkness between earth and Hades” alluding to the abyssal, hydrothermal vent, type locality.

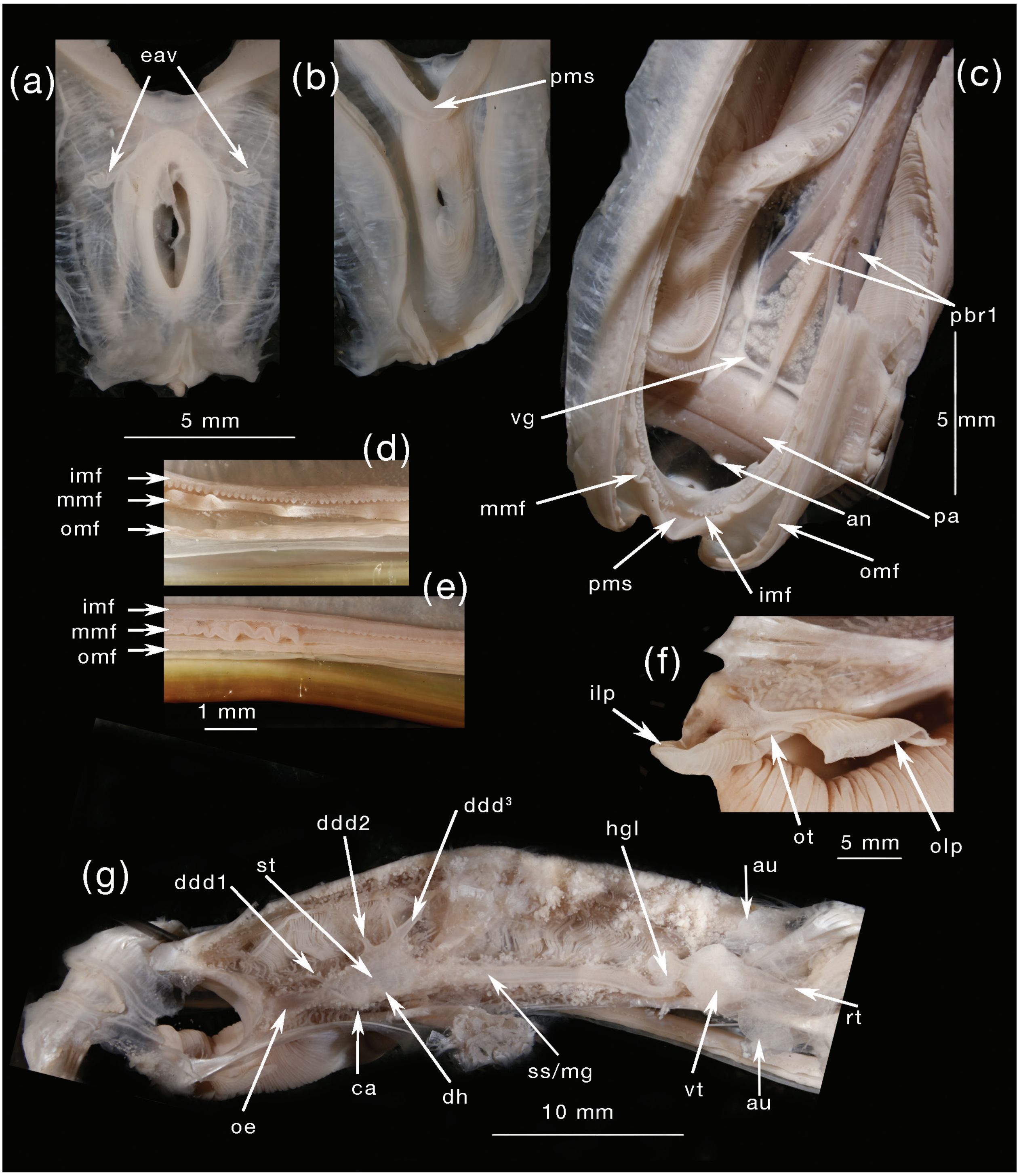
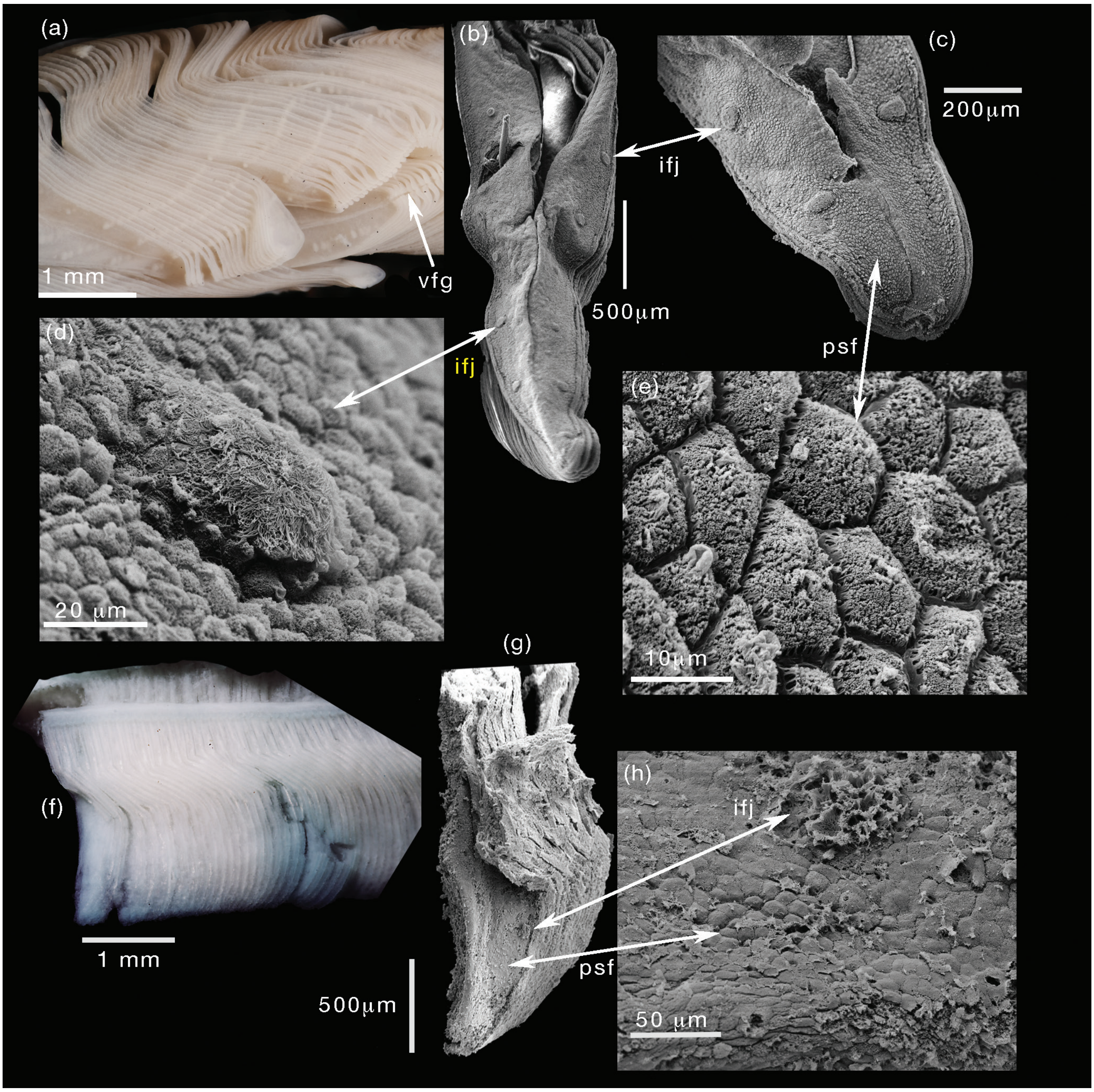


Figure 3. Anatomical details of *Benthomodiolus erebus* sp. n. **a** exhalant aperture interior, **b** exhalant aperture exterior, **c** posterior viewed from the ventral, **d** anterior mantle edge, **e** middle mantle edge, **f** labial palps, **g** the alimentary system and heart.

Habitat. Located in low temperature vent flows (<20 °C) associated with other vent endemic animals but is sparse and rarely collected. At Endeavour, it was recovered in a grab of the siboglinid *Ridgeia piscesae* at the base of the tubeworm cluster. At Middle Valley, it was recovered nestled in crevices of a sulphide block, also colonized by *R. piscesae*. Overall setting at both sites featured sulphide deposits with limited high temperature venting surrounded by ponds of sediment where vesicomyid clams also occurred (Juniper et al. 1992). Although *B. erebus* sp. n. is not visible on ROV imagery the typical habitats are illustrated here (Fig. 5a–b).

Comparative taxa. In the following section the other species assigned to *Benthomodiolus* are described with reference to *B. erebus* rather than in full detail.



Figures 4. a–e The ctenidium of *Benthomodiolus erebus* sp. n. **a** gross anatomy, **b** SEM of whole filament, **c** SEM of tip of a single filament, **d** SEM of inter filamental junction, **e** SEM of polygonal surface of microvilli. **f–h** The ctenidium of *B. geikotsucola*. **f** gross anatomy, **g** SEM of a whole filament, **h** SEM of the polygonal surface.

Benthomodiolus geikotsucola Okutani & Miyazaki, 2007

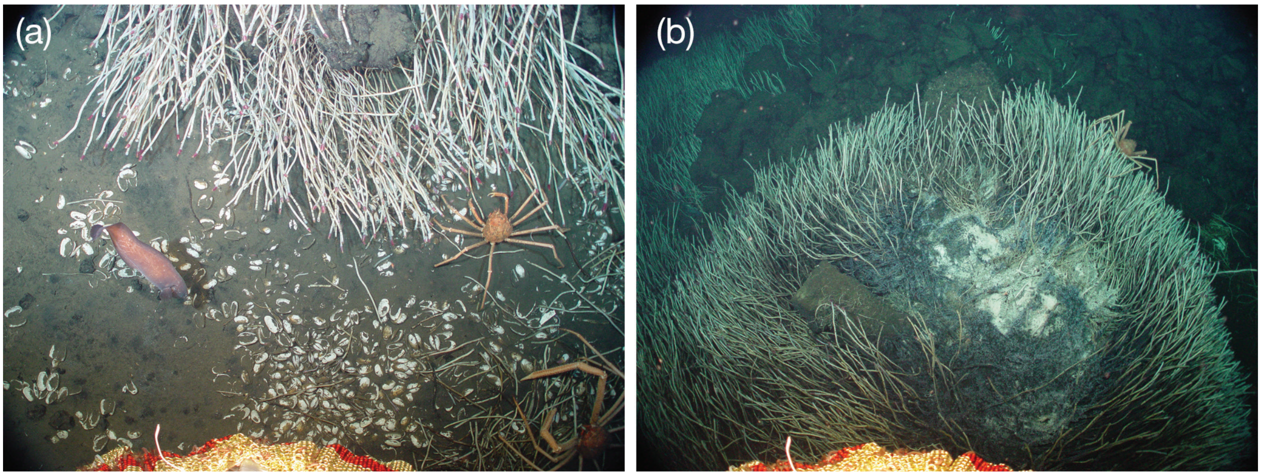
Benthomodiolus geikotsucola Okutani & Miyazaki, 2007: 49–55, figs 2–3.

Material examined. *Holotype*. 1 shell, NSMT-Mo-76703, Summit of Torishima Seamount, 30°55’N 141°49’E, 4020m. Not examined, image courtesy of NSMT.

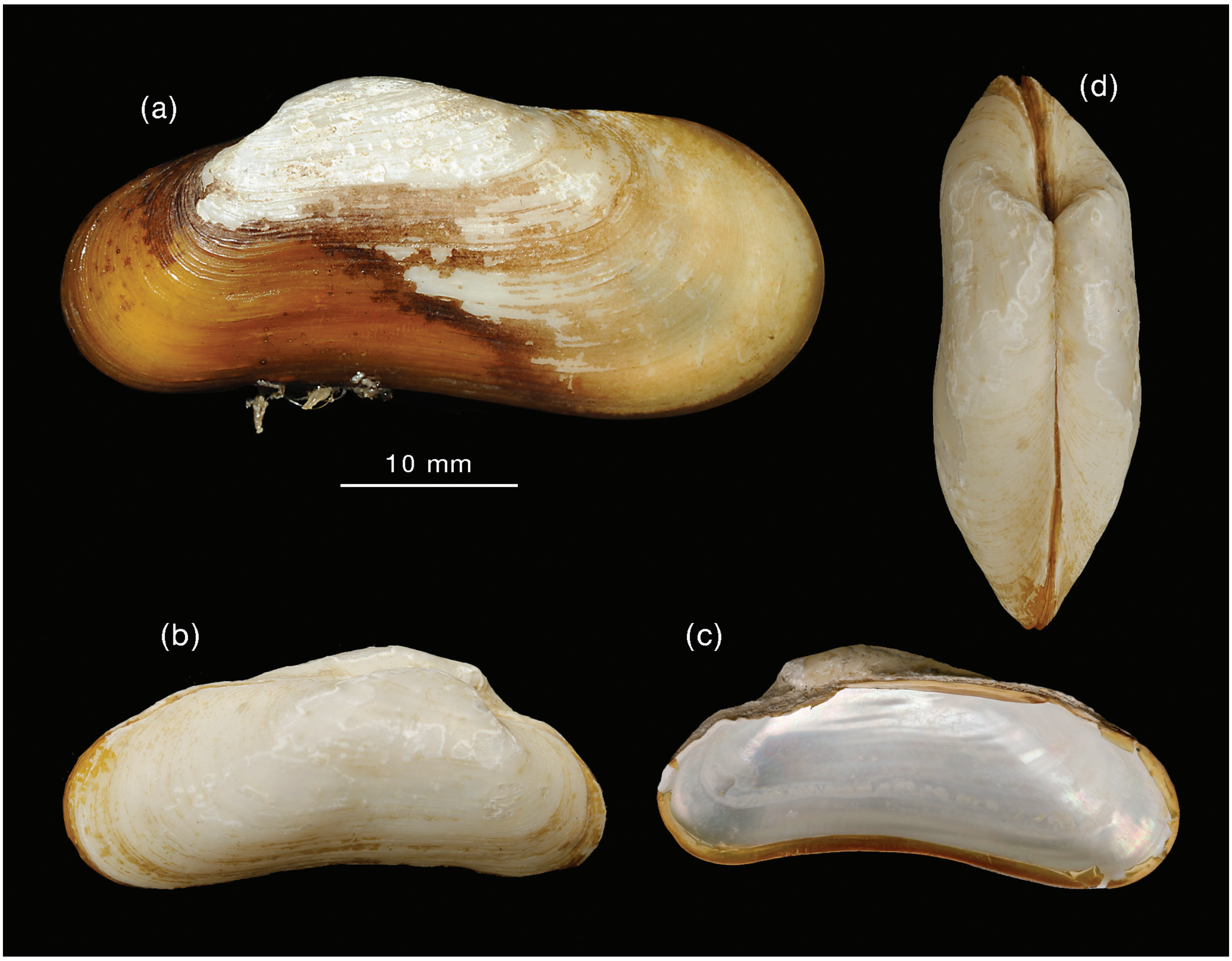
Paratype. 1 specimen, NSMT Mo-76704j as holotype.

Shell. The holotype (Fig. 6a) is slightly larger than any of the shells of *B. erebus* reaching 42.5 mm. The paratype dissected here (Fig. 6b–d) was 28.1 mm in length. The shell is umbonate, narrowly arcuate in outline and medially sulcate; in these there is strong similarity to *B. erebus*. The beaks are rather distant from the anterior margin, more so than in B. erebus with a total length /anterior length of 0.28 compared with a value of 0.24 for *B. erebus*. As in *B. erebus* the periostracum is smooth and devoid of hairs.

Pedal byssus musculature. The arrangement of the pedal and adductor muscles (Fig. 7b–c) is almost identical to that in *B. erebus* in that the byssal retractors (pbr2 and pbr1) are widely separated with pbr2 attached in the rear of the umbonal cavity. Both the anterior pedal retractor (apr) and posterior byssal retractor (pbr1) are slender. The posterior protractor muscle (ppr) in *B. geikotsucola* is very slender and simple and lacking the secondary muscles (sppr) seen in *B. erebus*.



Figures 5. a–b Images of the benthic habitat at the Endeavour segment and Middle Valley. **a** showing a clump of *Ridgeia* and many dead vesicomyid clams, **b** a clump of *Ridgeia* around a sulphide block



Figures 6. a–d Shells of *Benthomodiolus geikotsucola* Okutani and Miyazaki, 2007. **a** exterior of left valve of holotype (NSMT-Mo-7670349), **b–d** of the dissected paratype (NSMT Mo-76704j).

Ctenidium and labial palps. The ctenidium consists of both demibranchs and as in *B. erebus* the filaments are relatively short (Fig. 7a, 4f). The ascending and descending arms of the filaments are fused for over half their lengths and the abfrontal surface is extending creating a triangular laminar form to each filament (Fig. 4g). The filaments have a single row of ciliary junctions on the ascending and descending arms (Fig. 4g–h). The abfrontal surface is composed of polygonal cushions of microvilli.

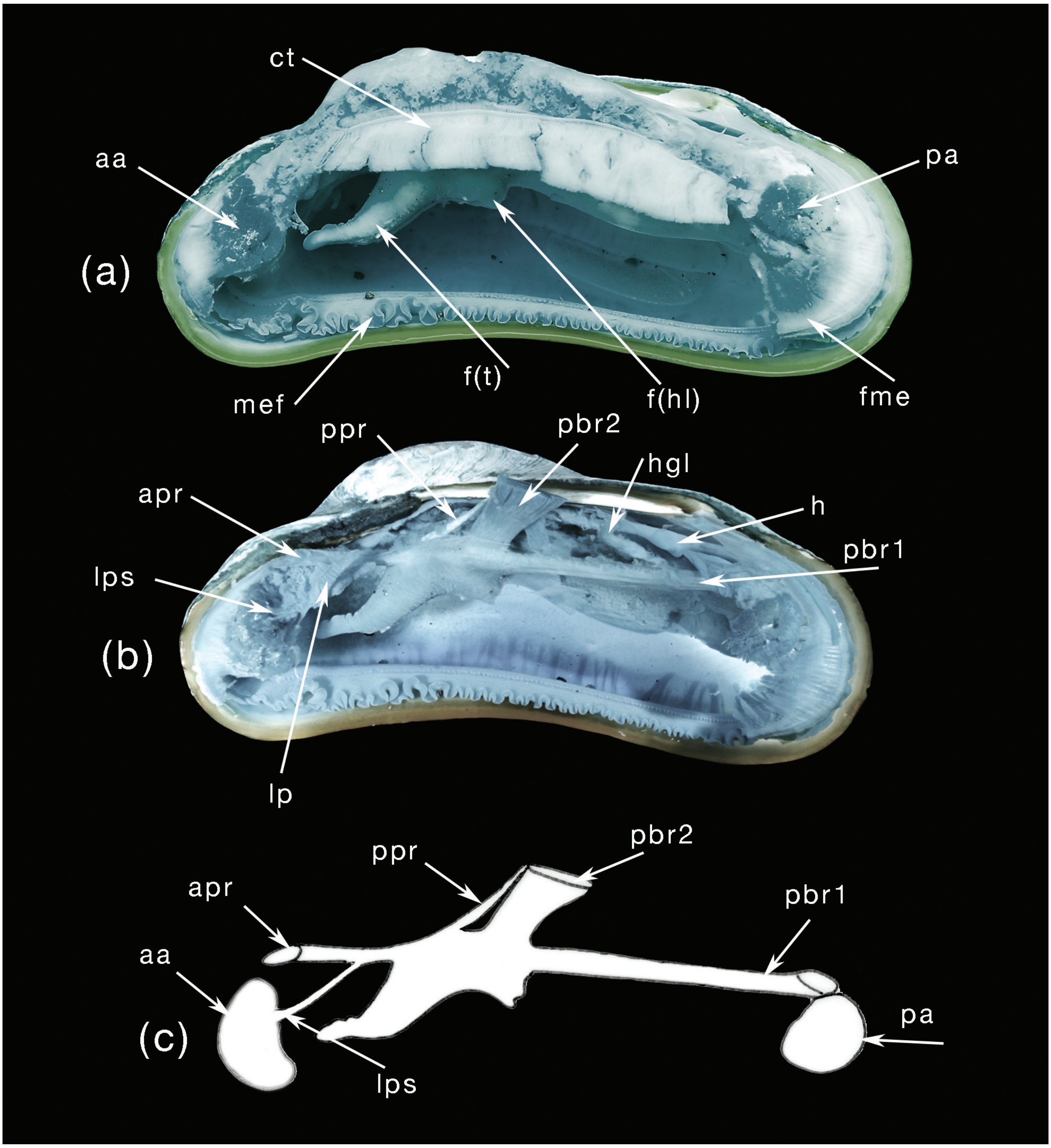


Figure 7. Gross anatomy of *Benthomodiolus geikotsucola* stained with methylene green. **a** after removal of left valve and mantle, **b** after further removal of the ctenidium, **c** diagram of the adductor, pedal and byssal musculature.

Mantle edge and apertures. The mantle edge is free for most of its length and fused only posteriorly to separate the ventral gape for the exhalant aperture. The entire length of the ventral gape the middle fold is thrown into a dense series of folds (Fig. 7a, mef) and in this unlike the almost lack of folding seen in *B. erebus*.

Alimentary system. The stomach was not dissected. The gut follows a similar path to that in *B. erebus* but the hindgut loop is distinct with a short reversed portion (Fig. 7b, hgl).

Benthomodiolus lignocola **Dell, 1987**

Benthomodiolus lignocola Dell, 1987: 33–34, figs. 44, 45, 48, 49, 52, and 53.

Material examined. *Holotype*. 1 shell, NW of Orete Point, White Island, 37°23.7’S 177°39.5’E, 1075–1100m, 23/Nov/1981; Museum of New Zealand Te Papa Tongarewa M.075023. Not examined, image courtesy of NMNZ.

Paratype. 5 specimens, NE of Chatham Islands, 42°47.10’ 175°45.60’W, 1174–1180m, 22/Aug/1984; NMNZ M–075248/1.

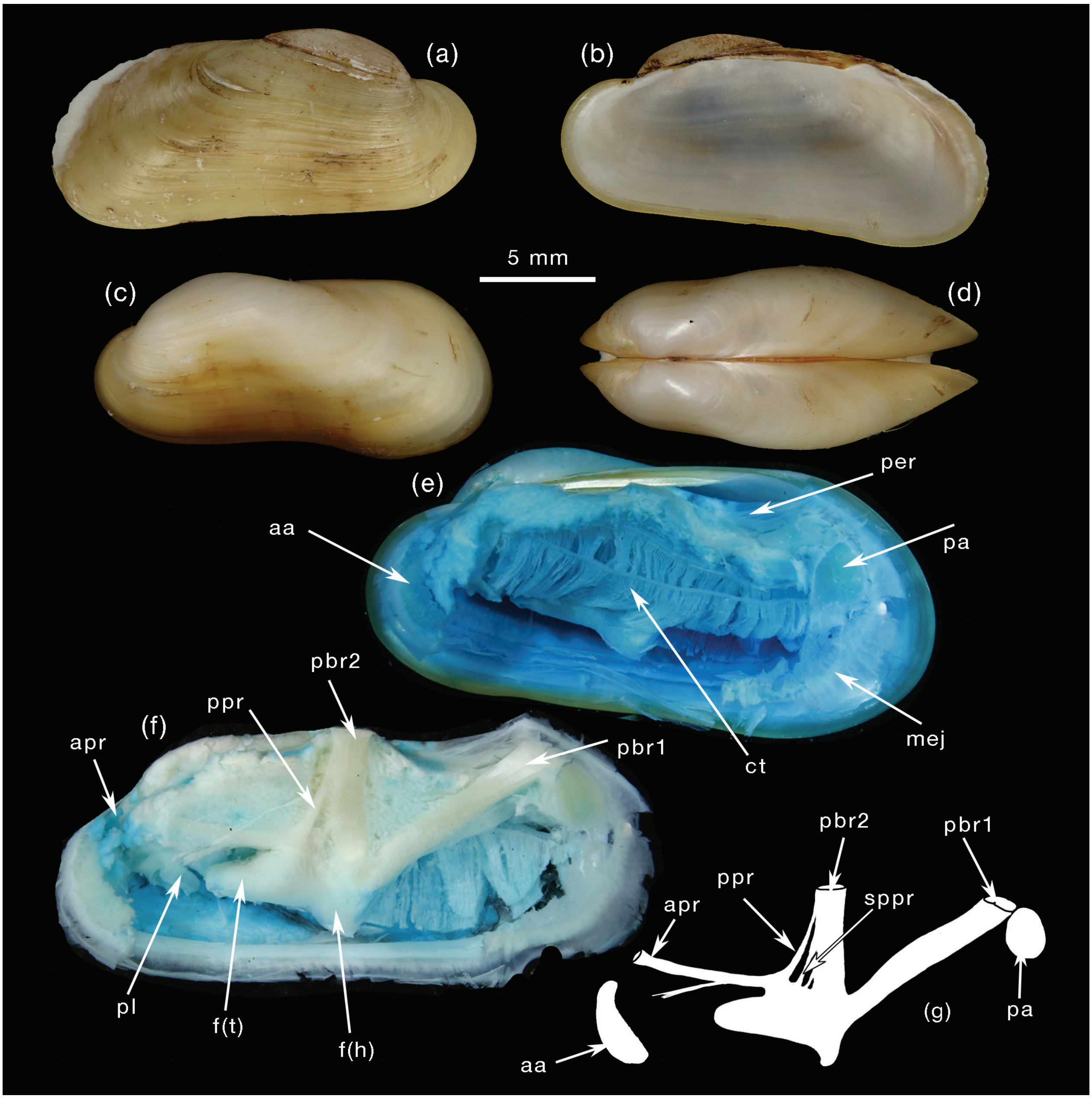


Figure 8. Shells and anatomy of *Benthomodiolus lignocola* Dell, 1987. **a** exterior of the right valve of the holotype (MNNZ M.075023), b-d the shell of the dissected paratype MNNZ M-075248/1, **e–g** gross anatomy stained with methylene green. **e** after removal of left valve and mantle, **f** after further removal of the ctenidium, **g** diagram of the adductor, pedal and byssal musculature.

Shell. The shells have a maximum length of 18.1 mm (Holotype, Fig. 8a–b) and the dissected specimen was 17.4 mm in length (Fig. 8c–d). The shell is umbonate, weakly arcuate with the posterior distinctly deeper than anterior in outline and medially sulcate. The beaks are rather distant from the anterior margin with a total length /anterior length of 0.23. The sculpture is weak of commarginal lines only except over the sulcate zone where faint fine irregular radial creases are present. Fine periostracal hairs are present but worn off in the larger specimens.

Pedal byssus musculature. The byssal retractors (Fig. 8f, g pbr2 and pbr1) are widely separated with pbr2 attached in the rear of the umbonal cavity. The angle between the byssal retractors is acute. The anterior pedal retractor (apr) is more slender than the posterior byssal retractor (pbr1). The posterior protractor muscle (ppr) is slender with secondary muscles (sppr).

Ctenidium and labial palps. The ctenidium consists of both demibranchs with relatively short strap-like filaments and has a flimsy appearance with weak inter-filamentar junctions (Fig. 10a). The ascending and descending arms of the filaments are fused for only a short distance (Fig. 10b, d). The filaments have a single row of ciliary junctions on the ascending and descending arms

(Fig. 10c). The frontal cilia are present but the abfrontal surfaces are largely devoid of epithelium, probably a consequence of poor fixation. Where present a weak polygonal pattern can be seen (Fig. 10e).

Mantle edge and apertures. The mantle edge (Fig. 8e) is free for most of its length and fused only posteriorly to separate the ventral gape for the exhalant aperture. The mantle edge along the ventral gape is smooth.

Alimentary system. The stomach was not dissected. The gut follows a similar path to that in *B. erebus* but the hind gut loop is distinct with a short reversed portion.

Benthomodiolus abyssicola **(Knudsen, 1970)**

Modiolus abyssicola Knudsen, 1970: 92–94, text figs 55–57, pl. 14, fig. 6.
Benthomodiolus abyssicola (Knudsen) — Dell 1987: 31-33.
Benthomodiolus abyssicola (Knudsen) — Coan et al. 2000: 162, pl. 24.
Benthomodiolus abyssicola (Knudsen) — Coan and Valentich-Scott 2012, 123, pl. 39.

Material examined. *Holotype*. Gulf of Panama, E. Pacific, 05°49’N 78°52’W, 3670-3270m. ZMUC, not examined.

Paratype. From type locality, 10 specimens examined, ZMUC-BIV-30.

Illustration.Paratypes were dissected by Vita Kenk and her drawing was published in Coan and Valentich-Scott (2012). A copy of the original drawing was sent to me by Paul Valentich-Scott and is reproduced here (Fig. 9f).

Shell. The shells have a maximum length of 17.2 mm and the dissected specimen was 17.1 mm in length (Fig.9a–b). The shell is weakly umbonate, wedge shaped with the posterior distinctly deeper than anterior in outline and medially narrowed but weakly sulcate. The beaks are close the anterior margin with a total length /anterior length of 0.22. The sculpture is weak of commarginal lines only. Fine periostracal hairs are present (Fig. 9c) but worn off in the larger specimens.

Pedal byssus musculature. The byssal retractors (pbr2 and pbr1) are widely separated with pbr2 attached immediately behind the umbonal cavity (Fig. 9e–f). The angle between the byssal retractors is acute. The anterior pedal retractor (apr) is more slender than the posterior byssal retractor (pbr1). The posterior protractor muscle (ppr) is slender and incorporated into the anterior byssal retractor (Fig. 9e–f).

Ctenidium and labial palps. The ctenidium consists of both demibranchs with relatively short strap-like filaments and has a flimsy appearance with weak inter-filamentar junctions (Figs 9d, 10f). The ascending and descending arms of the filaments are fused for only a short distance (Fig. 10f). The filaments have a single row of ciliary junctions on the ascending and descending arms (Fig. 10g). The frontal cilia are present but the abfrontal surfaces are largely devoid of epithelium, probably a consequence of poor fixation. Where present a weak polygonal pattern can be seen (Fig. 10h).

Mantle edge and apertures. The mantle edge is free along its entire length except for a small junction with the gill axis of the ctenidium to form a small exhalant aperture (Fig. 9d, f). The mantle edge bears weak folds posteriorly but smooth ventrally and anteriorly.

Alimentary system. The gut follows a simple route with the oesophagus, stomach and mid gut in a line running across the dorsal surface of the visceral mass (Fig. 9f). The hindgut descends into the visceral mass and returns to form a distinct loop (Fig. 9f, hgl) before passing through the heart.

Discussion

Benthomodiolus erebus is regarded as a distinct species but does bear close resemblance to *B. geikotsucola,* which differs in having the shell more extended anteriorly, having a distinct hind-gut loop and strongly folded mantle edge. The molecular data also confirm *B. erebus* and *B. geikotsucola* to be sister taxa (Lorion et al. 2013).

The molecular data link *B. erebus*, *B. geikotsucola* and *B. lignocola* but there are some distinct morphological difference that sets the latter apart from the former two. *Benthomodiolus lignocola* is much smaller; the shell is not quite so umbonate and bears periostracal hairs. The byssal retractor muscles although widely separated are less so than in the other species and reflects the more expanded posterior of the shell.

The ctenidial filaments are linear, strap-like, and unlike the triangular laminar forms seen in *B. erebus* and *B. geikotsucola*. In this, the ctendium of *B. erebus* and *B. geikotsucola* resembles that of *Bathymodiolus* and is highly adapted to host symbiotic bacteria. Although laminar the symbionts are extracellular unlike the intracellular condition of many species of *Bathymodiolus* and *Gigantidas* (Lorion et al. 2013)

Kenk and Wilson (1985) suggested that the ctenidium of *M. abyssicola* was unlike that of *Bathymodiolus* and thus retained *abyssicola* in *Modiolus*. Here the difference in filament form is confirmed but the polygonal epithelium of the abfrontal surface does suggest that *B. abyssicola* is chemosymbiotic. The ctenidial structures of *B. lignocola* and *B. abyssicola* are very similar and both are known from wood-falls. The pedal/byssus musculature is also similar and this suggests that they are indeed congeneric as listed by Bouchet in WoRMS (2015).

Morphologically one might propose *B. erebus* and *B. geikotsucola* to be in a separate genus from *B. lignocola* and *B. abyssicola*, based on the shell shape, lack of periostracal hairs and laminar gill filaments. However, there is currently no molecular support for any generic distinctions within the *Benthomodiolus* clade and there is as yet no molecular data for *B. abyssicola*.

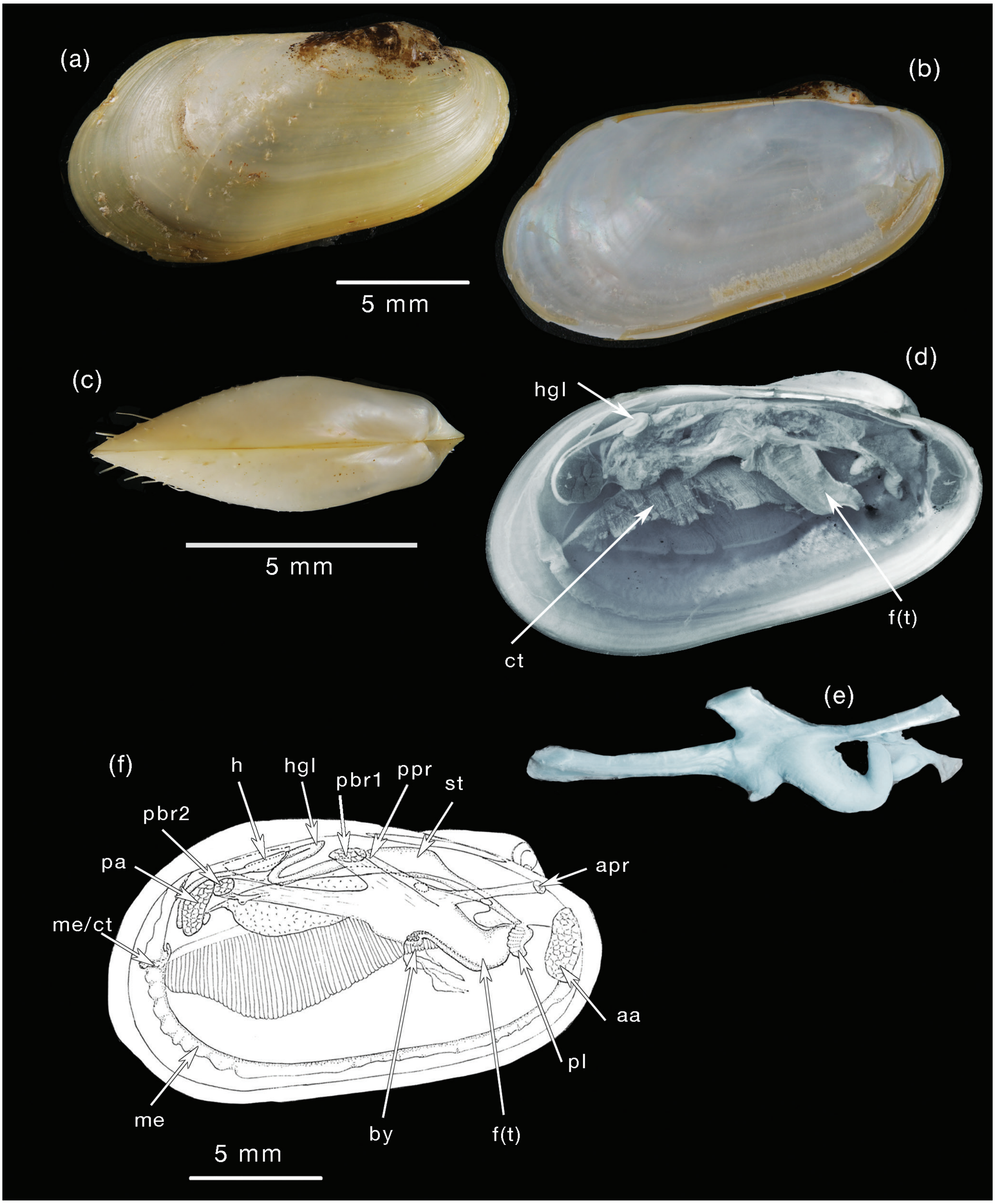
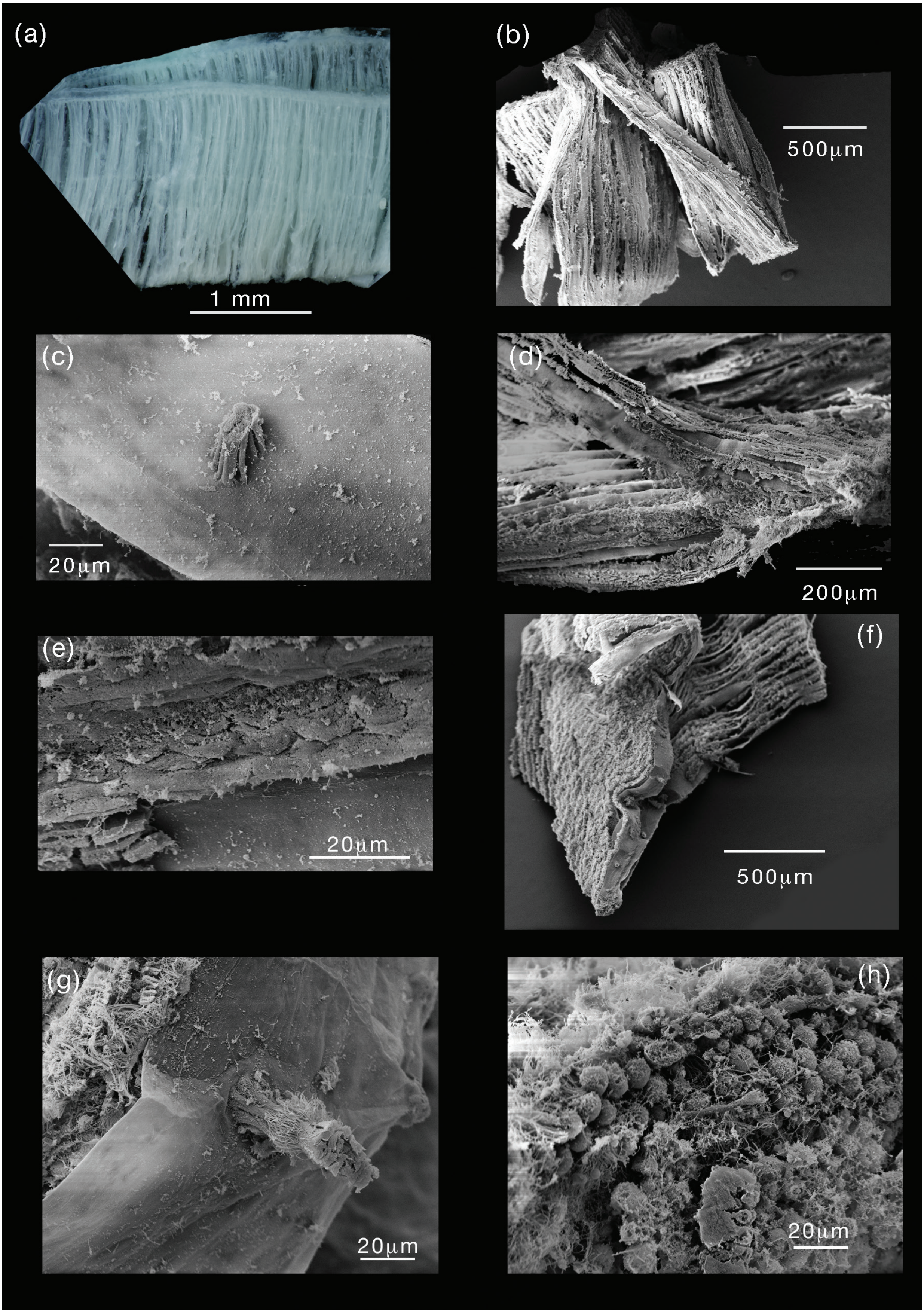


Figure 9. Shells and anatomy of paratypes *Benthomodiolus abyssicola* Knudsen, 1970 (ZMUC-BIV-30). **a** exterior of the right valve of the dissected specimen, **b** interior of left valve, **c** dorsal view of a small specimen with well preserved periostracal bristles, **d** gross anatomy, stained with methylene green after removal of right valve, mantle and ctenidium, **e** pedal and byssal musculature, **f** diagram of the gross anatomy of a paratype after Kenk in Coan and Valentich-Scott 2012.

The morphological basis to the generic systematics of the Bathymodiolinae has been shown by Thubaut et al. (in press) to be unreliable but the number of detailed morphological studies is few. The recent paper on *Idas argenteus* (Rodrigues et al. 2015) shows that quite different feeding strategies can be adopted by sister taxa, *I. argenteus* lacking symbionts and its sister taxon *I. washingtonia* being chemosymbiotic (Southward 2008). With



Figures 10. a–e The ctenidium of *Benthomodiolus lignocola* **a** gross anatomy, **b** SEM of whole filaments, **c** SEM of inter filamentar junction, **d** SEM of tip of filament, **e** SEM of polygonal surface of microvilli (Knudsen 1970). **Figures 4f–h.** The ctenidium of *B. geikotsucola*. **f** SEM of a whole filaments gross anatomy, **g** SEM of inter filamentar junction, **h** SEM of the polygonal surface.

so few morphological studies and the known variance in feeding strategies, no new generic taxa are proposed here. From morphology there is no single affinity with other bathymodioline genera although the pedal byssus musculature and largely unfused mantle margins are most similar to that seen in *Bathymodiolus*.

The shell form *B. erebus* and *B. geikotsucola* is rather unusual with the narrow arcuate outline and relatively long anterior portion, as such they can scarcely be described as modioliform where the outline is more wedge shaped. Although scarce this shell form occurs in other genera notably *Terua* but also in some species of *Bathymodiolus* and *Gigantidas*. The smaller *B. lignocola* and *B. abyssicola* are more modioliform and resemble *Idas*. Shell shape has no consistency within *Benthomodiolus* a situation mirrored in the other clades such *Bathymodiolus* and *Gigantidas* (Thubaut et al. in press).

The *Benthomodiolus* clade is considered to be the sister to the entire remainder of the bathymodiolines and occupies a basal position in all published phylogenetic trees (Thubaut et al. in press, Rodrigues et al. 2015, Lorion et al. 2013, Kyuno et al. 2009). Despite an apparent early origin in the late Cretaceous the origins of the known species are more recent in the Miocene (Lorion et al. 2013). By this time the clade had radiated into the three major ecotypes of wood-fall, whale-fall and vent suggesting a parallel radiation to the remainder of the bathymodiolines but lacking any species associated with cold seeps. The majority of species inhabiting vents and seeps have intra-cellular symbionts and belong to the *Bathymodiolus* and *Gigantidas* clades, the exceptions are *Benthomodiolus erebus* (Southward 2008) and *Vulcanidas insolitas* (Cosel and Marshall 2010) both having rather basal positions in the phylogeny but illustrating the widespread capacity for any clade to inhabit a wide range of chemosynthetic settings. All the morphological data suggest that the affinity of *Benthomodiolus* is with the Bathymodiolinae and not with the Modiolinae as indicated by Kyuno et al. 2009. All *Benthomodiolus* are chemosymbiotic, some with more highly adapted ctenidia than others, but there is no indication that they are in any way more morphologically primitive than other Bathymodiolinae, except perhaps in having extra cellular symbionts. Here again however this condition is found throughout the various clades (eg. *Idas*, see Rodrigues et al. 2015) and is perhaps more related to feeding ecology than phylogeny.

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