A NEW SPECIES OF *AXINUS* (BIVALVIA: THYASIROIDEA) FROM THE BABY BARE SEAMOUNT, CASCADIA BASIN, NE PACIFIC WITH A DESCRIPTION OF THE ANATOMY

P. GRAHAM OLIVER[1] & ANNA M. HOLMES[1]

[1]BioSyB, National Museum of Wales, Cathays Park, Cardiff, CF10 3NP, Wales, UK

Abstract   A second and new species of living thyasirid is added to the genus Axinus. *A.* cascadiensis *n. sp. was collected from the hydrothermal spring site at Baby Bare Seamount, Cascadia Basin, NE Pacific Ocean at a depth of 2592m. The anatomy is described in detail and compared with the Atlantic species,* A. grandis. *A.* cascadiensis *is shown to have highly modified gills that support dense aggregations of bacteriocytes suggesting that this species is highly dependant on the bacterial symbiosis. The mantle is highly modified with a series of partitions and folds that are proposed to function to direct and control the ciliary currents entering and traversing the mantle cavity. The ecological setting is described and thought not to support typical hot vent or cold seep communities due to low levels of sulphides and hydrocarbons. The highly sporadic distribution of both species of* Axinus *suggests that the genus is localised to small-scale environments, the details of which are not understood. Despite the appearance of fossil* Axinus *in the Eocene, modern species display the most highly modified anatomy of any extant thyasirid, suggesting that the Thyasiroidea may be much earlier in origin.*

Key words   Thyasiroidea, Axinus, *new species, functional morphology, hydrothermal springs, deep-sea*

INTRODUCTION

The genus *Axinus* is represented by very few species and only a single living species was known prior to this paper, *A. grandis* (Verrill & Smith in Verrill, 1885). *Axinus grandis* was described from bathyal depths off Delaware and has since been recorded from the eastern and western Atlantic, Mediterranean and Caribbean (Löffler, Janssen, Gürs & Taviani 2005). The anatomy was described by Payne & Allen (1991) and they noted mantle folds and tentacles not seen in any other thyasirids, which they used to support the recognition of the genus *Axinus*. Only a single, small specimen was available to them and they made no comment on the functional morphology. Throughout its range, *A. grandis* appears to be rare and little is known of its ecology. The genus was not included in the review of gill structures made by Dufour (2005) and the role of bacterial symbiosis in *Axinus* is not recorded.

In 1995 exploration of the Baby Bare Seamount began and a large (20mm + in length) thyasirid bivalve was discovered in the sediment surrounding the outcrop (Mottl, Wheat, Baker, Becker, Davis, Freely, Grehan, Kadko, Lilley, Massoth, Moyer & Sansone 1998). This thyasirid was tentatively identified as an *Axinus* and close to *A. grandis* by Eve Southward (Voight & Grehan 2000)

A large numbers of shells and some living specimens have been collected subsequently during expeditions in 1997 and 2002 and this extensive material has allowed us to distinguish the Baby Bare shells from *A. grandis*. The live collected specimens have allowed us to revisit the anatomy, explore the role of chemosymbiosis and add to the findings of Payne and Allen (1991).

The genus *Axinus* is represented in the fossil record back to the Eocene (Löffler, Janssen, Gürs *et al*, 2005), thus making the genus one of the earliest recognisable thyasirids and we discuss the morphology in this context.

MATERIALS AND METHODS

The material from the Baby Bare site was collected by Dr Janet Voight during the period 1995-2002 using the DSRV 'Alvin' and the ROV Jason. The material was collected as dead shells or living specimens that were fixed in formalin and preserved in 70% ethanol. All of the material was deposited in the Field Museum of Natural History, Chicago.

The anatomical dissections were made following light staining in methyl blue to give contrast to the tissues for subsequent photography. Photography of the dissections and the shells was carried out using computer enhanced digital imaging with AutoMontage™ software.

The scanning electron microscopy was made following critical point drying of formalin fixed

Contact author : graham.oliver@museumwales.ac.uk

tissues and using both SEI and BEI methods.

INSTITUTIONAL ABBREVIATIONS

FMNH – Field Museum of Natural History, Chicago
NMW – National Museum of Wales, Cardiff

SHELL ABBREVIATIONS

adm anterior dorsal margin, **am** anterior margin, **esc** escutcheon, **lun** lunule, **pm** posterior margin, **pvm** posterior ventral margin, **vm** ventral margin.

ANATOMICAL ABBREVIATIONS

a anus, **aa** anterior adductor, **apr** anterior pedal retractor, **ddd** digestive divertular duct, **dg** digestive gland, **ex a** exhalant aperture, **f** foot, **g** gonad, **h** heart, **hg** hind gut, **ifj** inter filamental junction, **k** kidney, **lbp** lateral body pouch, **llbp** duct to the left lateral body pouch, **m** mouth, **mg** mid gut, **ps** posterior septum, **rdg** ridge attached to sensory papilla, **rlbp** duct to the right lateral body pouch, **sp** sensory papilla, **s** stomach.

SYSTEMATICS

BIVALVIA: VENEROIDA
THYASIROIDEA
(see Taylor, Williams & Glover, 2007)

Genus *Axinus* Sowerby, 1821

Type species *Axinus angulatus* Sowerby, 1821

GENERIC DEFINITION

Shells pyriform to subquadrate with a large lunule, long shallow escutcheon and a strong anterior median angulation. Posterior sulcus indistinct or well defined. Hinge edentulous. Internally has complex mantle partitions and flaps. Ctenidium of two demibranchs, filaments highly modified to harbour chemosymbiotic bacteria.

Axinus cascadiensis new species

Axinus, near *A. grandis* - Southward in Voight & Grehan 2000: 97

Material Examined   Holotype, One live col-

lected specimen, ALVIN Dive 3152, Baby Bare Seamount, Cascadia Basin, 47°42.65'N 127°47.15'W, 2591m, 14 October 1997, J. Voight, FMNH 308159

Paratypes   11 live collected specimens as holotype, FMNHC 280989. 3sh + 10v as holotype, NMW.Z. and 50+v FMNHC280980

Measurements   Holotype length = 23.6mm : Height = 21.9mm : Tumidity = 13.6mm.

Table 1   Shell dimension ratios for 50 shells from type series of *Axinus cascadiensis* n. sp.

	Mean	Std. Dev.	Min	Max
Length/Height	1.09	0.05	0.98	1.25
Length/Tumidity	1.79	0.12	1.59	2.07

Shell (Figs 1-11)   To 32mm in length; thin shelled; equivalve; subequilateral, beaks at or just behind the midline, strongly prosogyrate. Moderately tumid but variable, (Length:Tumidity ratio = 1.6:1 to 2.1:1, mean 1.8:1). Outline typically subquadrate with length greater than height, some specimens pyriform with height equal to or greater than length (see below). Subquadrate shells with posterior margin long, steep, gently curved; subacute at junction with short, posterior ventral margin this merging into long straight ventral margin; anterior margin long, straight or slightly incurved, sloping inwards and junction with ventral margin subacute; anterior dorsal margin narrowly rounded merging into long incurved lunule margin this sloping or subparallel with ventral margin. Escutcheon (Fig. 6) running the length of posterior slope, very shallow, demarcated by raised line. Posterior sinus indistinct or as a narrow flattened zone; anterior area demarcated by a strong, roundly angled, ridge running from the beak to the anterior ventral junction. Lunule (Fig. 6) flattened, subcordate, longer than wide, demarcated by a weak ridge. Sculpture of irregular undulations overlain by dense array of concentric raised lines and narrow acute ridges, escutcheon smooth, lunule wrinkled. Prodissoconch, smooth, 220-230μm in diameter (Fig. 8). Periostracum thin, finely wrinkled. Shell white. Ligament deeply sunken, extending for about half the length of escutcheon, visible externally. Hinge edentulous, in very
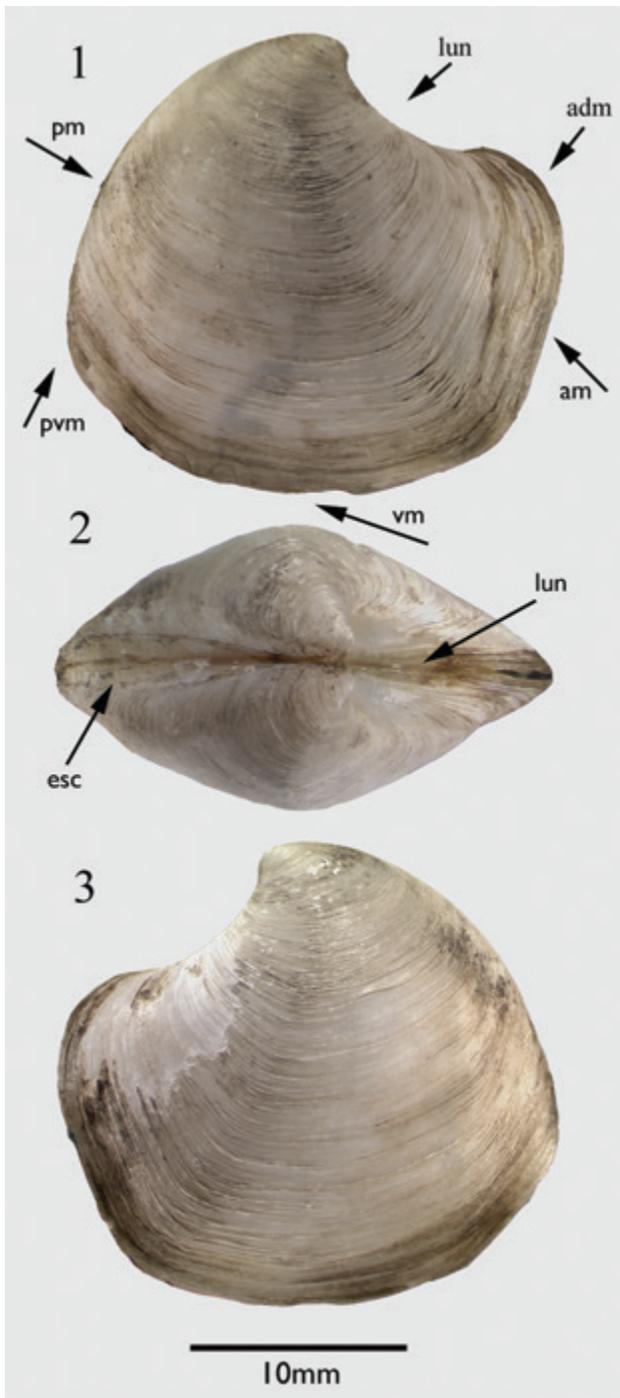
Figures 1-3 *Axinus cascadiensis* n. sp. Holotype, Baby Bare Seamount, 47°42.65′N 127°47.15′W, 2591m, 14 October 1997, J. Voight, FMNHC 280989

small shells there is a notch in the hinge plate below the beak (Fig. 7). Adductor and pallial muscle scars indistinct, anterior adductor oval only slightly larger than posterior.

Variation   The outline is variable (Figs 9-11), this variability generally increasing with the size of

shell. In larger size classes outline can be pyriform, with the ventral margin curved; in some of these the lunule also becomes deeply incurved.

Anatomy   Mantle edge free along the anterior and ventral margins (Fig. 12), fused posteriorly between the termination of the gill axis and the posterior adductor where there is a smooth edged exhalant siphonal opening (Fig. 15). Ventral to this is a short fused area with a translucent oval septum (Fig. 15) in what would be the position of an inhalant aperture. Close to this septate area is the end of a mantle fold (posterior ventral mantle partition) that runs anterior dorsally across the mantle decreasing in size and ending in a mid ventral position (Figs 12, 13). Anteriorly there is a complex arrangement of mantle folds (Figs 12, 13, 31). A long fold of delicate tissue (anterior mantle fold) runs parallel to the anterior margin from the anterior adductor ventrally and bounds an anterior furrow between it and the mantle edge. This fold terminates in a distinct notch and from there is a weak ridge running a short distance to a prominent flap of tissue (anterior ventral mantle flap) in an anterior ventral position. Anterior to this weak ridge is an anterior ventral depression extending to the mantle edge, which is weakly undulating in this region. From the anterior flap, a weak narrow fold (anterior partition) extends dorsally and runs up to the ventral margin of the anterior adductor. On the ventral face of the anterior adductor is a small papilla (Fig. 14).

Ctenidium is large, swollen and of two demibranchs, the outer demibranch is approximately one third the size of the inner demibranch (Fig. 12). The ascending and descending arms of the filaments are widely separated creating open suprabranchial chambers (Fig. 13). The filaments are lamellar and are fused to each other by strong tissue junctions running close to the frontal edge (Fig. 21). The lamellar part of each filament has both faces covered by a layer of bacteriocytes (Fig. 23) giving the surfaces a polygonal pattern (Fig. 22). The exterior of each bacteriocyte is domed and has a micro-villar surface (Fig. 24); beneath is a dense aggregation of short rod shaped bacteria, each approximately one micron in length (Fig. 24).

The labial palps are small (Fig. 13), mostly of a smooth groove but with a small zone of ridges
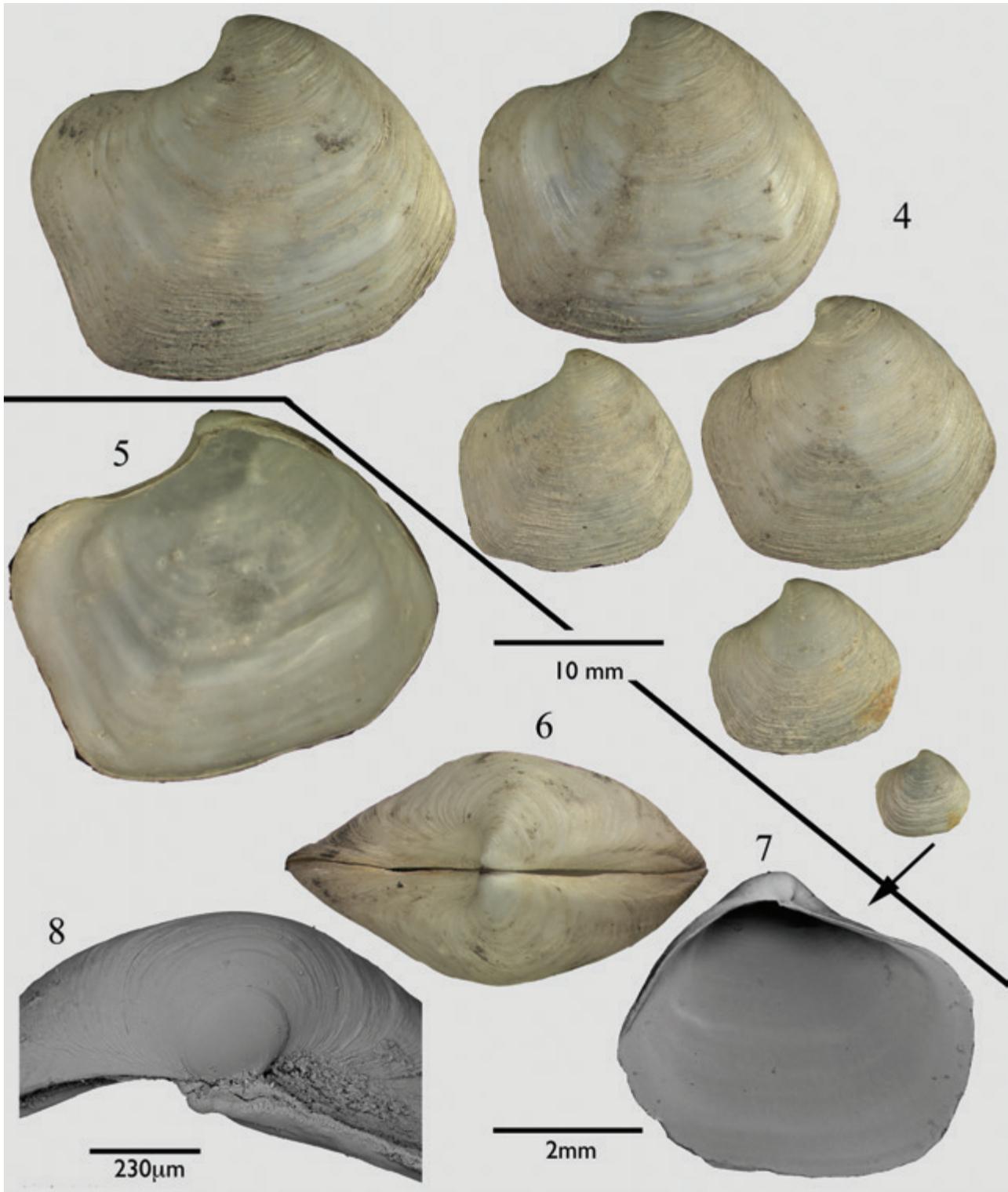
Figures 4-8 *Axinus cascadiensis* n. sp. Paratypes, NMW.Z **Fig. 4** Growth series; **Fig. 5** Internal of right valve; **Fig. 6** Dorsal view; **Fig. 7** Scanning electron micrograph of internal of smallest shell in growth series; **Fig. 8** Scanning electron micrograph of prodissoconch.

close to the junction with the ctenidium.

Foot (Fig. 12) is very long, vermiform, toe swollen, heel absent except for a small protuberance (Fig. 13). Posterior retractor muscle thin (Fig. 12), elongate and attached between the dorsal ends of the adductor muscle. Anterior retractor short (Fig. 12), attached dorsal of the anterior adductor muscle.
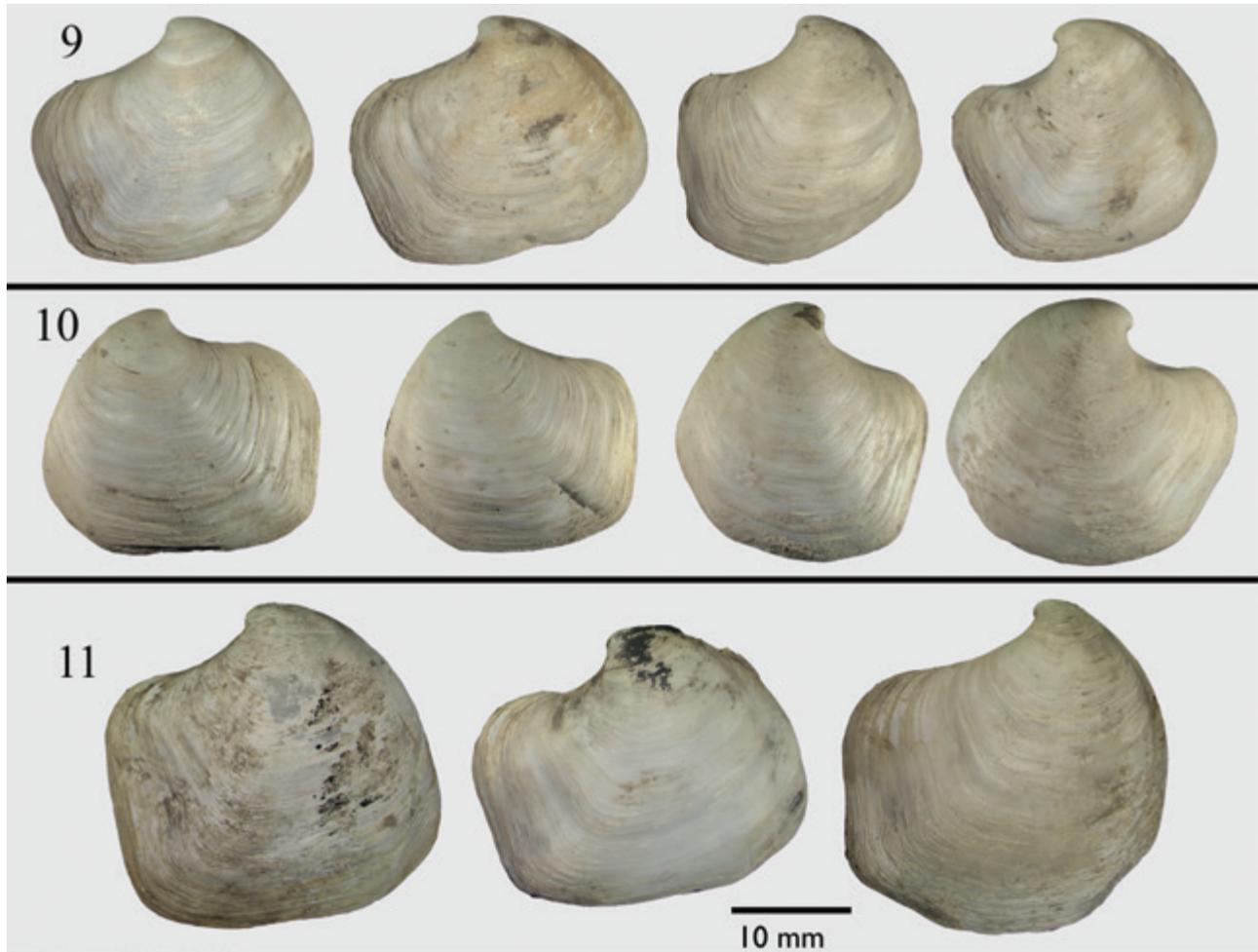
Figures 9-11 *Axinus cascadiensis* n. sp. Variations in shell shape. **Fig. 9** left valves from sample taken in 1997; **Fig. 10** right valves from sample taken in 1997; **Fig. 11** left valves from sample taken in 2002.

Visceral mass: the lateral body pouches are elongate (Figs 13, 16), relatively small, surface smooth, posterior end drawn out to a narrow apex, anterior end also pointed but not elongated. Pouches contain digestive tubules anteriorly and gonad posteriorly (Fig. 17), in the visceral mass the gonad extends over the dorsal extremity of the foot. Digestive diverticulae extend over the anterior under the lunule margin of the shell and surround the stomach, which lies in an anterior dorsal position (Fig. 16). The heart is large, thin walled and situated dorsal of the gonad (Figs 13, 16). The kidney appears as a simple sac situated posteriorly of the heart (Figs 13, 16).

Alimentary system (Fig. 18): the oesophagus is very short and runs dorsally to enter the stomach on its anterior face. The stomach is relatively small and oriented such that the dorsal roof is adjacent to the lunule margin of the shell; diges-

tive ducts leave from both the right and left sides and ducts to the lateral pouches exit on the floor of the stomach (Fig. 19). The mid gut is cylindrical and runs horizontally through the visceral mass and terminates before reaching the heart; the hind gut is narrow and runs in a shallow curve posterior dorsally over the posterior adductor; the rectum is very narrow, rather inconspicuous, and continues around the adductor muscle and travels anteriorly opening in the suprabranchial chamber (Fig. 16).

Differential diagnosis The anatomy of the Baby Bare species is of the same plan as that of *Axinus grandis* and confirms the generic position. From *A. grandis*, the only other Recent species described, *A. cascadiensis* differs in the following shell characters; posterior sulcus poorly defined, posterior margin never sinuous, outline subquadrate.
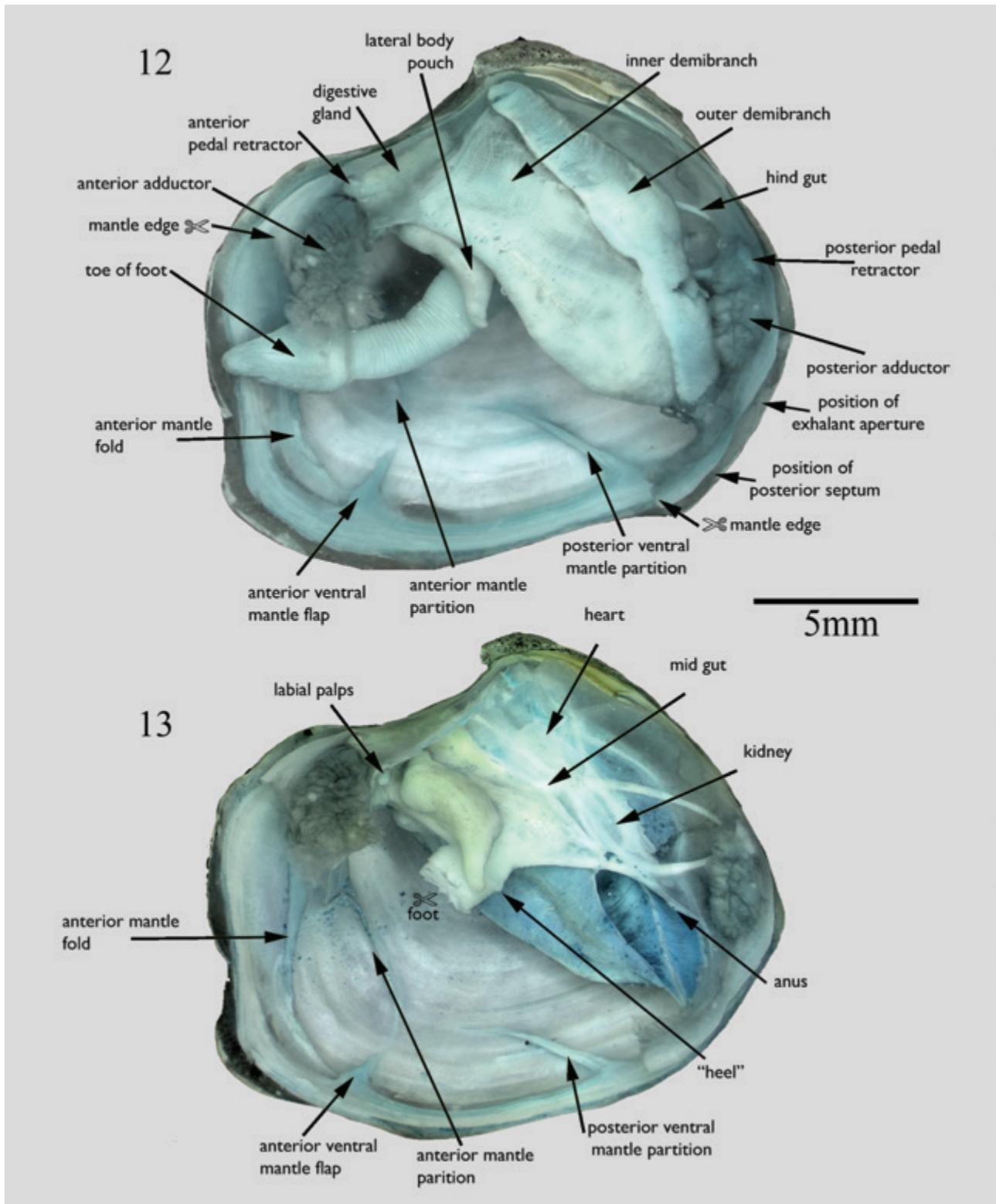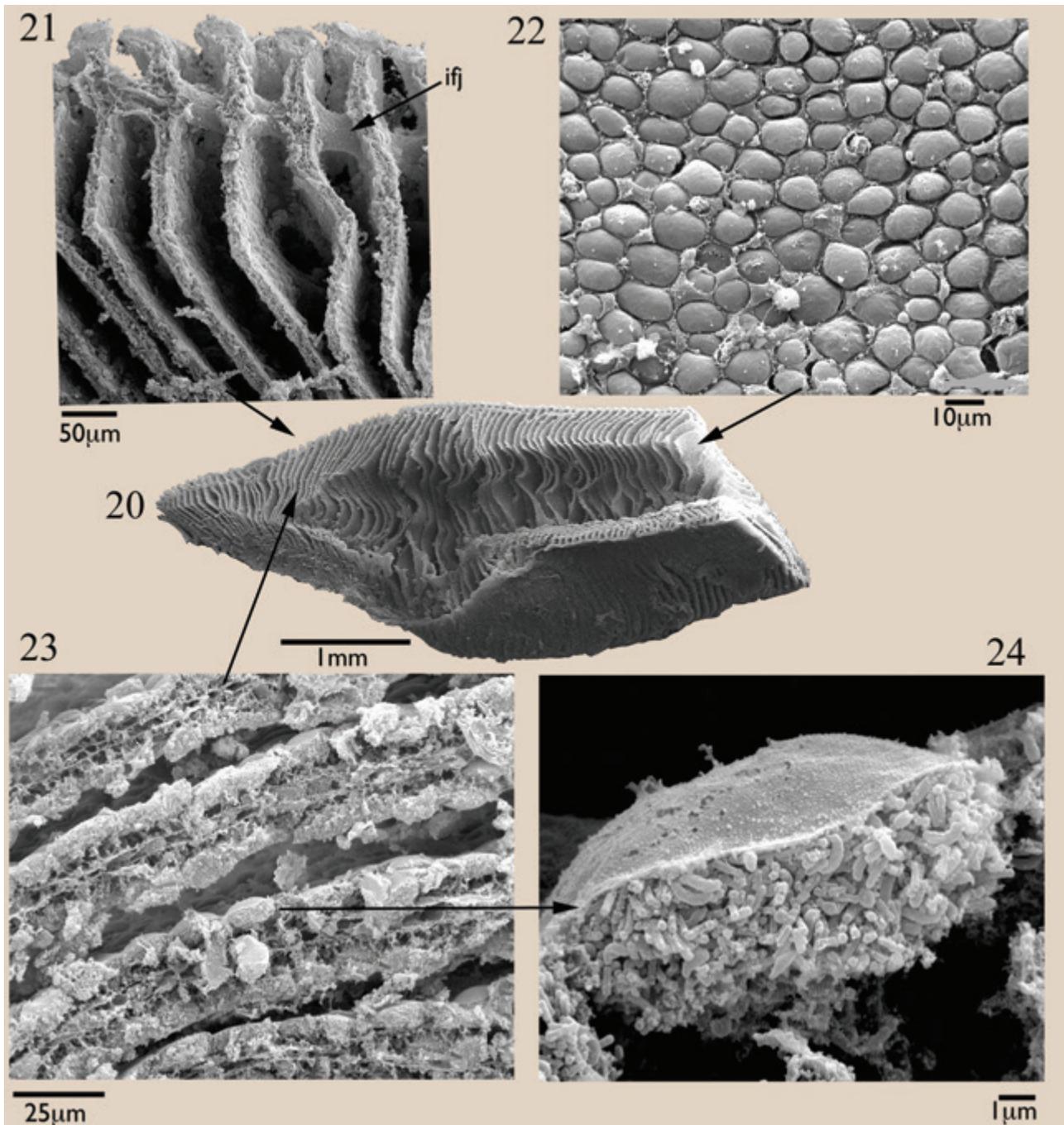
Figures 12-13 *Axinus cascadiensis* n. sp. Gross anatomy. **Fig. 12** After removal of left mantle; **Fig. 13** After removal of mantle and left ctenidium.

Figures 14-19 *Axinus cascadiensis* n. sp. Details of the anatomy. **Fig. 14** Oblique view towards ventral face of anterior adductor muscle to show sensory papilla (*sp*); **Fig. 15** Posterior exhalant aperture (*ex a*) and posterior septum (*ps*); **Fig. 16** Dissection of visceral mass to show disposition of lateral body pouch and digestive gland along with pericardium; **Fig. 17** Excised lateral body pouch showing presence of digestive gland and gonad tissue;
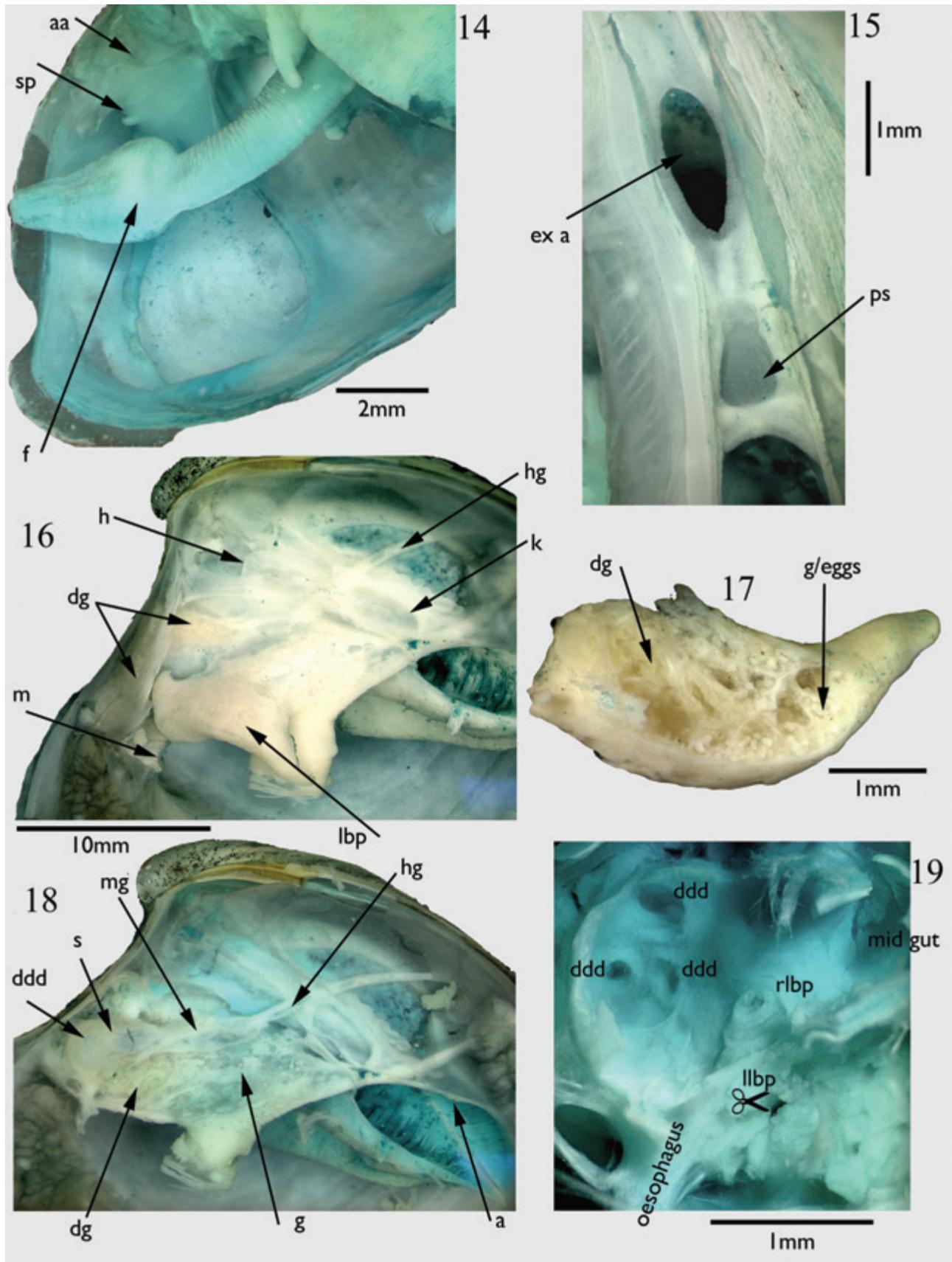
Fig. 18 Dissection of visceral mass to show layout of alimentary system; **Fig. 19** Internal structures of stomach after removal of left side.

Figures 20-24 *Axinus cascadiensis* n. sp, scanning electron micrographs of ctenidium structures. **Fig. 20** excised demibranch; **Fig. 21** cross section of filaments showing strong inter-filamentar junctions close to outer face; **Fig. 22** lateral face of laminar filament showing polygonal bacteriocytes; **Fig. 23** cross section of filament showing bacteriocytes lining both faces; **Fig. 24** split bacteriocyte densely packed with bacteria.

Distribution   Known only from the type locality; Baby Bare Seamount, Cascadia basin, NE Pacific Ocean, 2592m.

Derivation of name   cascadiensis, Latin combination of Cascadia (Cascadia Basin) and suffix *ensis* denoting place of origin.

FUNCTIONAL MORPHOLOGY

The ctenidia are highly adapted to harbour chemosymbiotic bacteria and are of Dufour Type 3 (Dufour 2005) where the abfrontal portion is greatly expanded to harbour dense aggregations of bacteriocytes. The expansion of the abfrontal portion is very large resulting in the ctenidia being
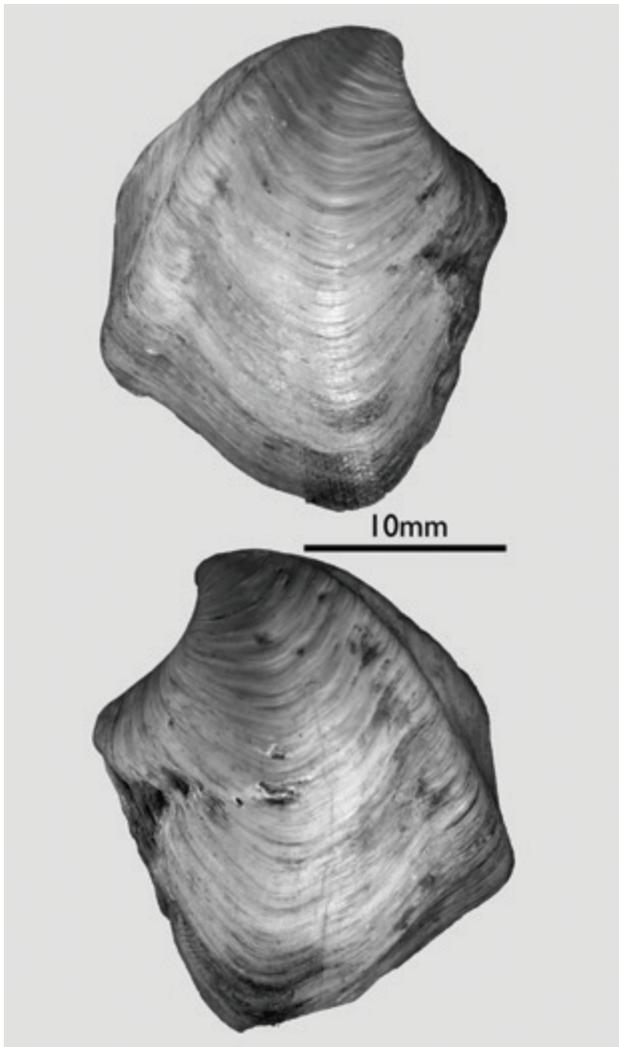
Figure 25 *Axinus grandis* (Verrill & Smith, 1885) left and right valves of syntype, USNM 44824, Photos courtesy of E. Neubert, SMF (Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany).

swollen and basket shaped rather than laminar. This species probably has a strong dependence on the symbiosis. The bacteria appear to be of a single type and are of a similar shape and size to those seen in other species such as *Thyasira methanophila* (Oliver & Sellanes 2005).

The functional morphology of the complex anterior mantle structures (Fig. 32) is related to the control of inhalant currents bringing both oxygenated water from the surface and feeding currents from the sediment, as seen in other thyasirids and lucinids (Taylor & Glover 2000;Oliver & Killeen 2002). The anterior fold is adjacent to the anterior dorsal inhalant aperture created by the foot and bringing oxygenated water from the surface into the mantle cavity. This fold may act simply to direct the water flow ventrally but could also act as a secondary respiratory surface as seen in some lucinids (Taylor & Glover 2000) such as *Codakia tigerina*, *Anodontia philippiana* and *Lucina pensylvanica.* In these lucinids the structures are more complex either multilobed or pleated whereas in *Axinus* the fold is simple (Fig. 32). The ventrally flowing current probably strikes the anterior flaps, which redirect the water dorsally and is channelled by the anterior partitions to pass over the ctenidia (Fig. 33). The mantle edge between the notch at the end of the anterior fold and the anterior flap is undulating, corresponding to the anterior ventral papillate zone seen by Payne & Allen (1991) in *A. grandis*. We propose that this is the pedal gape and inhalant aperture for the feeding current from the sediment (Fig. 33). Water entering here is mixed with the oxygenated water and carried to the front of the ctenidium. The mantle edge between the anterior flap and the posterior ventral partition is smooth and may normally be closed by mantle adhesion. The termination of the posterior ventral partition on the mantle edge we propose is the site for expulsion of pseudofaeces. Figure 34 is presented as our interpretation of the mode of life of *Axinus cascadiensis*. This differs from others in that the aperture for the feeding current is restricted to the anterior ventral position whereas in other species of thyasirids and lucinids the foot is believed to probe the sediment along the entire ventral margin (Taylor & Glover 2000;Oliver & Killeen 2002).

Payne and Allen (1991) also report a second inhalant aperture, created by tissue adhesion, in the same position as the posterior ventral translucent septum described above. We propose that such an aperture will function primarily as the exit for pseudofaeces and that the posterior ventral partition plays a role in guiding and aggregating pseudofaeces at this aperture. They report tentacles associated with this aperture but none are present in *A. cascadiensis*, although they may be analogous to the posterior ventral partitions. Although on first examination the posterior septum, in *A. cascadiensis*, resembles a second siphonal opening, it is entire (Fig. 15) and we are unable to propose a function for this feature.

Payne & Allen (1991) draw attention to a sensory
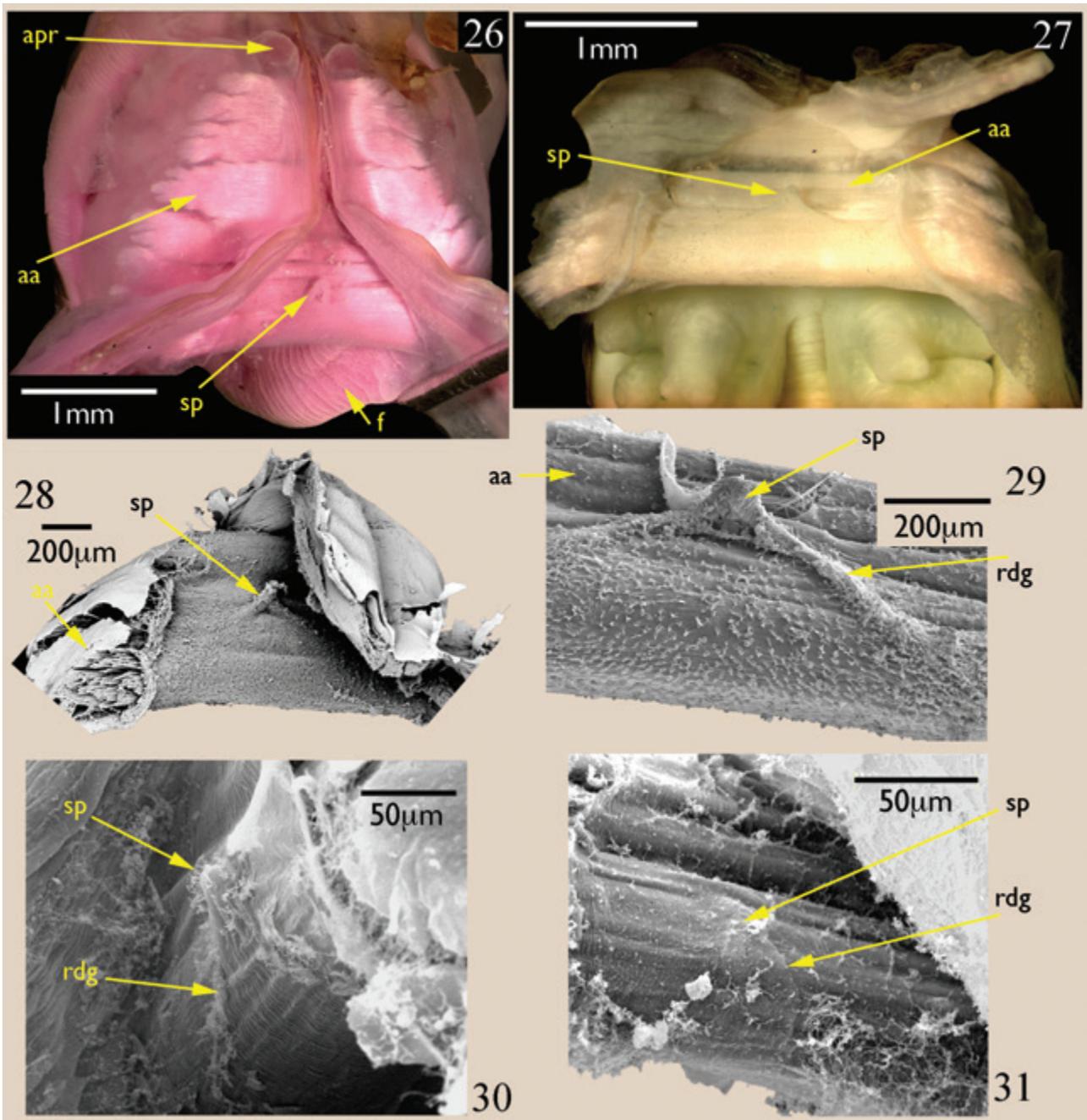
Figures 26-31 Images showing the disposition of a sensory papilla (*sp*) on the dorsal surface of the anterior adductor muscle in a variety of thyasirids. **Fig. 26** *T. sarsi*, North Sea, NMW; **Fig. 27** *T. flexuosa* North Sea, NMW; **Fig. 28** Scanning electron micrograph of *T. sarsi*; **Fig. 29** SEM of *T. flexuosa*; **Fig. 30** SEM of *T. obsoleta*, North Sea, NMW; **Fig. 31** SEM of *Axinulus croulinensis*, North Sea, NMW.

papilla situated on the anterior ventral face of the anterior adductor muscle but do not mention a similar structure in any other thyasirid. Allen (1958) similarly does not mention such a structure in *T. flexuosa*. A similar papilla is present in *A. cascadiensis*, but may not be unique to *Axinus* as a similar papilla can be found, not on the ventral, but on the dorsal surface of the adductor muscle in *T. sarsi*, (Figs 26, 28) *T. flexuosa* (Figs 27, 29), *T. obsoleta* (Fig. 30) and

Axinulus croulinensis (Fig. 31). The papilla is situated in the inhalant flow and we agree with Payne & Allen (1991) that it probably functions in a sensory manner to monitor flow or water chemistry of the inhalant current. The ventral position of the papilla in *Axinus* may allow monitoring of the flows from both the dorsal inhalant aperture and the anterior ventral aperture, while in other thyasirids only the dorsal inhalant flow could be monitored.
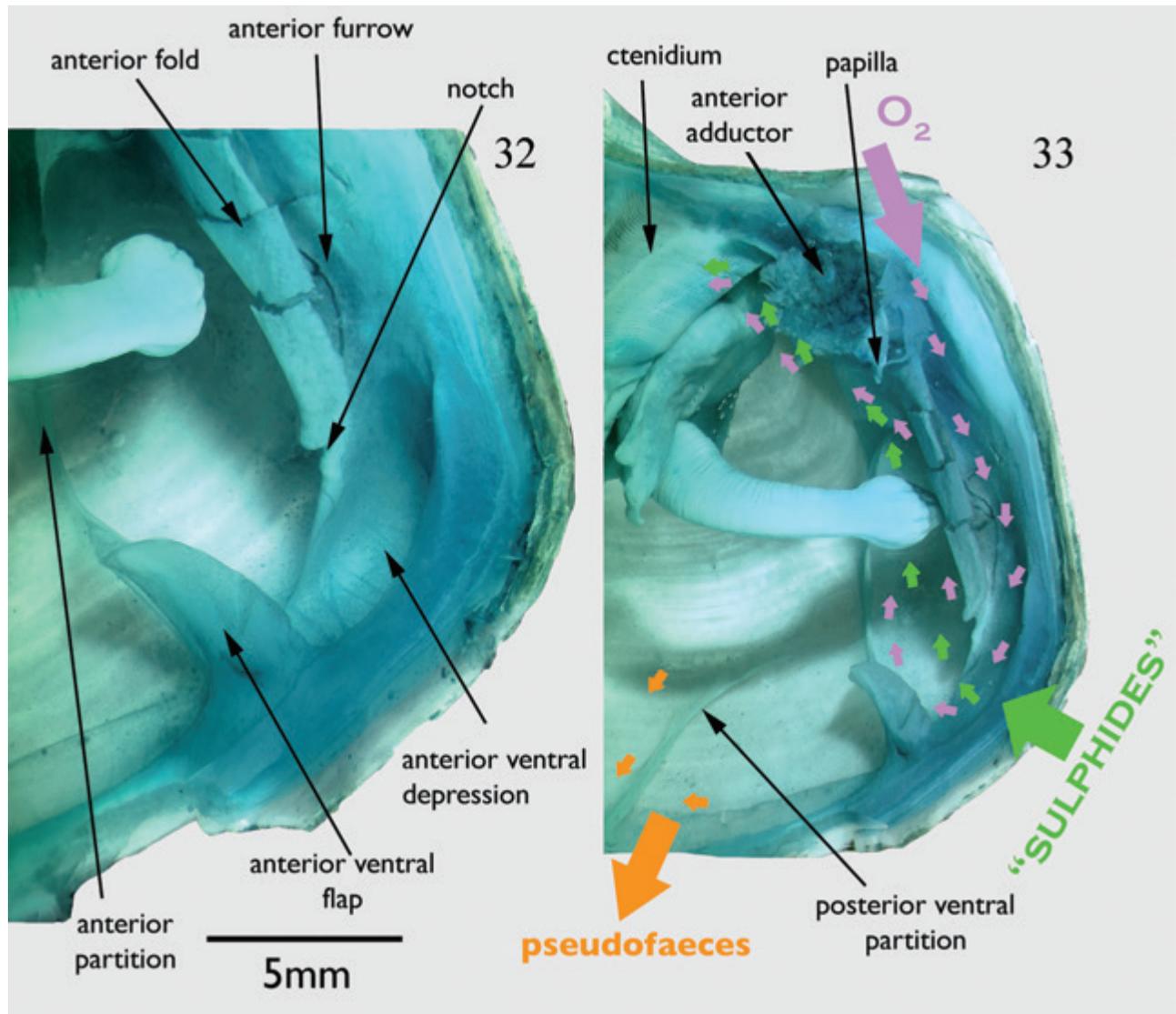
Figures 32-33 *Axinus cascadiensis* n. sp. anterior mantle structures. **Fig. 32** Details of anterior mantle structures; **Fig. 33** Conjectured arrangement of inhalant currents into anterior mantle cavity.

ECOLOGICAL SETTING

The Baby Bare Seamount is the smallest (3-5 km across) of three basaltic outcrops that rise above the basement ridge some 100 km east of the Juan de Fuca Ridge. Baby Bare is 300 m high, but its lower 230 m are covered by turbidite sediments, consequently only the upper 70 m rises above the turbidite plain and are expressed over an area of about 500m across. On the steeper slopes basalt outcrops are present but elsewhere the seamount is covered by hemipelagic sediment, typically to a depth of less than 1 m. The summit lies some 2592 m below the sea surface. The site is now renowned for the hydrothermal circulation of seawater, via adjacent extinct volcanoes, that

results in the presence of warm springs through the rock and sediment at Baby Bare (Mottl, Wheat, Baker *et al.* 1998;Fisher, Davis, Hutnak, Spiess, Zühlsdorff, Cherkaoui, Christiansen, Edwards, Macdonald, Villinger, Mottl & Becker 2003). The temperature of the spring-water is up to 25°C, but in the sediment temperatures are around 2° to 3° as compared with a normal bottom temperature of 1.8°C. Chemical composition of the spring water is greatly altered, concentrations of sulphide (H_2S) are 1.3μmol/kg (Mottl, Wheat, Baker *et al.* 1998) and although not measured in the sediment are probably below 1.0μmol/kg (G. Wheat pers. comm.). Methane is present in the area but is contained in the sulphate minimum zone some 70-150m below the seafloor (G. Wheat
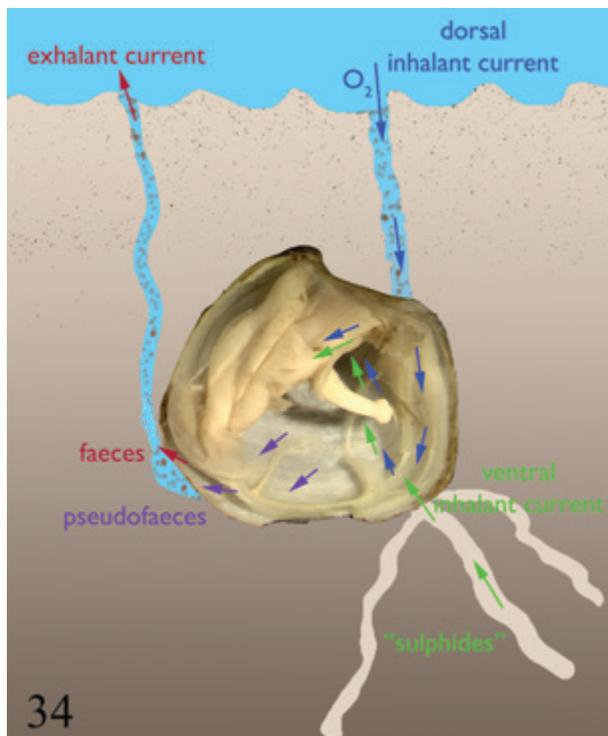
Figure 34 Conjectured life position with inhalant and exhalant currents of *Axinus cascadiensis* n. sp.

pers. comm.). Levels of dissolved iron and manganese are high in the spring water. These values of H_2S and methane are much lower than those that are found at typical hot vent and cold seep sites.

The epifauna on the outcrop is diverse and dominated by sponges (Mottl, Wheat, Baker *et al.* 1998) and ophuroids are frequently seen on the video images taken by the ROV "Jason" during the 2002 Juan de Fuca cruise "atlv 7|20" (http://www.whoi.edu/marops/vehicles/jason/van_cruises.html). The fauna of the sediment is less well known, the video images showing little on the surface except for *Axinus* valves. Bivalves, other than *Axinus*, recorded within the sediment consist mainly of shells only, are small and dominated by protobranch taxa. Typical vent and seep chemosymbiotic Bivalvia are not present; such as *Acharax* and *Calyptogena* which are found at the Hydrate Ridge within the Cascadia Basin (Sahling, Rickert, Lee, Linke & Suess 2002) or *Solemya*, *Idasola*, *Adipicola* and *Calyptogena* found at the hydrothermal vent at Middle Valley on the Juan de Fuca Ridge (Juniper, Tunnicliffe & Southward 1992).

These observations indicate that the infauna at Baby Bare is not typical of chemosynthetic communities seen elsewhere at hot vent or cold seep

sites and begs the question of the exact source of nutrients for the symbiotic bacteria. Biotic derived organic detritus from the epifauna may provide sufficient sulphides for the bacterial symbiosis. This process may be enhanced by the high concentrations of dissolved iron that can cause subsurface precipitation of iron sulphides, and these are known to be 'mined' by other thyasirids and lucinids (Dando, Ridgeway & Spiro, 1994; Dando, Southward & Southward, 2004). Such detritus enriched sediments are widespread in the world's oceans and therefore, one would expect *Axinus* to be widely distributed. Data for *Axinus grandis* in the Atlantic is not informative, except that it also appears to be similarly sporadic as evidenced by the few, recorded occurrences. To date none of the Atlantic records are associated with unusual environments but then most records are of dead shells only. The sporadic occurrences of *Axinus* would appear to indicate that it is highly specialised and restricted to an unusual environment, however the environmental data from the Baby Bare site suggest that high levels of sulphides or hydrocarbons are not the controlling factors. The warm and metal rich spring water may therefore be creating the specific nature of the environment upon which *Axinus* depends.

Geological history

The genus *Axinus* was described by Sowerby (1821) from the London Clay, Eocene and was thought until recently to represent the earliest appearance of the genus in the fossil record. Taylor, Williams & Glover (2007) report a similar form from the Lower Cretaceous '*Lucina*' *sculpta* Philipps, 1829, which they attribute to *Axinus* and therefore the earliest known thyasiroidean. The anatomy of both extant species of *Axinus* is highly modified in comparison with other recent taxa such as *Thyasira*, especially those species which lack sulcate shells, have both demibranchs and have weak or no bacterial symbiosis, such as *T. (Parathyasira) equalis*. Despite *Axinus* being present in the Lower Cretaceous it should not be regarded as primitive or representing early thyasirids. Species resembling typical *Thyasira* are present in the Upper Cretaceous (Campanian) (Kauffman, 1969) indicating that the Thyasiroidea had undergone a considerable radiation by this time. The origins of the Thyasiroidea are prob-

ably much earlier (Taylor *et al*. 2007) and their shells probably lacked the sulcate form so representative of *Thyasira s.s.*, *Axinus* and *Conchocele* , which are those genera with the strongest bacterial symbiosis.

REFERENCES

ALLEN J 1958 On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). *Philosophical Transactions of the Royal Society of London B* **241**: 421-484

DANDO PR, RIDGEWAY SA & SPIRO B 1994 Sulphide 'mining' by lucinid bivalve molluscs: demonstrated by stable isotope measurements and experimental models. *Marine Ecology Progress Series* **107**: 169-175.

DANDO PR, SOUTHWARD AJ & SOUTHWARD EC 2004 Rates of sediment sulphide oxidation by the bivalve mollusc *Thyasira sarsi*. *Marine Ecology Progress Series* **280**: 181-187.

DUFOUR S 2005 Gill anatomy and the evolution of symbiosis in the bivalve family Thyasiridae. *Biological Bulletin* **208**: 200-212

FISHER AT, DAVIS EE, HUTNAK M, SPIESS V, ZÜHLSDORFF L, CHERKAOUI A, CHRISTIANSEN L, EDWARDS K, MACDONALD R, VILLINGER H, MOTTL MJ & BECKER CGWK 2003 Hydrothermal recharge and discharge across 50 km guided by seamounts on a young ridge flank. *Nature* **421**: 618-621

JUNIPER SK, TUNNICLIFFE V & SOUTHWARD EC 1992 Hydrothermal vents in turbidite sediments on a Northeast Pacific spreading centre: organisms and substratum at an ocean drilling site. *Canadian Journal of Zoology* **70**: 1792-1809

KAUFFMAN EG 1969 Cretaceous *Thyasira* of North American Interior. In: Moore R. ed. *Treatise on Invertebrate Paleontology, Part N, Mollusca 6, Vol. 1. Bivalvia.* pp N184-202. Boulder: Geological Society of America & University of Kansas.

LÖFFLER S-B, JANSSEN R, GÜRS KR & TAVIANI M 2005 The genus *Axinus* Sowerby, 1821 in the Mediterranean Basin (Bivalvia: Thyasiridae). *Journal of Conchology* **38 (5)** : 581-597

MOTTL MJ, WHEAT G, BAKER E, BECKER N, DAVIS E, FREELY R, GREHAN A, KADKO D, LILLEY M, MASSOTH G, MOYER C & SANSONE F 1998 Warm springs discovered on 3.5 Ma oceanic crust, eastern flank of the Juan de Fuca Ridge. *Geology* **26**: 51-54

PAYNE CM & ALLEN AJ 1991 The morphology of deep-sea Thyasiridae (Mollusca: Bivalvia) from the Atlantic Ocean. *Philosophical Transactions of the Royal Society of London B* **334**: 481-562

SAHLING H, RICKERT D, LEE RW, LINKE P & SUESS E 2002 Macrofaunal community structure and sulfide flux at gas hydrate deposits from the Cascadia convergent margin, NE Pacific. *Marine Ecology Progress Series* **231**: 121-138

Oliver PG & Killeen IJ 2002 The Thyasiridae (Mollusca: Bivalvia) of the British Continental Shelf and North Sea Oilfields. An Identification Manual. *Studies in Marine Biodiversity and Systematics from the National Museum of Wales, BIOMÔR Reports* **3**: 1-73

OLIVER PG & SELLANES J 2005 New species of Thyasiridae from a methane seepage area off Concepción, Chile. *Zootaxa* **1092**: 1-20

TAYLOR J & GLOVER E 2000 Functional anatomy, chemosymbiosis and evolution of the Lucinidae. In: Harper E, Taylor J, Crame J (eds) The Evolutionary Biology of the Bivalvia. *Geological Society, London, Special Publications*, **177**: p 207-225

Taylor JD, Williams ST & Glover EA 2007 Evolutionary relationships of the bivalve family Thyasiridae (Mollusca: Bivalvia), monophyly and superfamily status. *Journal of the Marine Biological Association of the United Kingdom* **87**: 565-574.

VERRILL AE 1885 Third catalogue of Mollusca recently added to the fauna of the New England coast and the adjacent parts of the Atlantic, consisting mostly of deep-sea species, with notes on others previously recorded. *Transactions of the Connecticut Academy of Arts and Sciences* **6**: 395-452

VOIGHT JR & GREHAN AJ 2000 Egg brooding by deep-sea octopuses in the North Pacific Ocean. *Biological Bulletin* **198**: 94-100