"TUBULAR GILLS" Extreme gill modification in the Thyasiroidea with the description of *Ochetoctena tomasi* gen. et sp. nov. (Bivalvia: Thyasiroidea)

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Abstract

Three dimensional tubular structures of the ctenidium of some thyasirid bivalves are described for the first time. The classification of the thyasirid gill is modified accordingly into five types based on the number of demibranchs, reflection of the filaments and shape of the filaments, either rod, laminar or tubular. The tubular structure is seen in its most modified form in a chemosymbiotic abyssal species from the south-east Atlantic, which is described here as *Ochetoctena tomasi* gen et sp. nov.

Introduction

Chemosymbiotic bivalves typically host their autotrophic bacteria in tissues of the ctenidium (gill). As a consequence gill morphology is modified and from a gross perspective these gills are thick and fleshy in comparison with those adapted for filter feeding (Taylor and Glover 2010). The fleshy nature of the gills of thyasirids and lucinids was recognised long before their function was discovered and was shown to be a result of elongation of the abfrontal zone of the filaments (Allen 1958). Bacterial symbiosis associated with this modification was confirmed by a number of studies in the 1980s (see review by Taylor and Glover 2010). In the heterodont families Lucinoidea and Vesicomyidae the association is apparently obligate but the Thyasiridae display both symbiotic and asymbiotic taxa. Variation in thyasirid gill structure was first demonstrated by Southward (1986), and later in a wider

ranging study by Dufour (2005). Dufour (2005) classified thyasirid gills into three categories based on the number of demibranchs, the degree of abfrontal extension and the extent of bacterial symbiosis. In all three types the filaments were either rod-like or lamellar, the lamellar form having greatest abfrontal extension and strongest association with chemosymbiotic bacteria. This lamellar gill (type 3 of Dufour 2005) has recently been described from two other heterodont families the Montacutidae (Oliver, Southward and Dando 2012) and the Basterotiidae (Oliver 2013).

A more complex gill, akin to the tubular form of many lucinids (Distel and Felbeck 1987) has been suggested to occur in *Conchocele* (Taylor and Glover 2010; Dufour 2005) and as such was partially described by Nakazima (1958) in *C. disjuncta* Gabb (= *C. bisecta* Conrad). In thyasirids the bacteria are extracellular with the exception of "*Maorithyas*" *hadalis* where an intra-cellular arrangement was described and where the frontal cilia are absent (Fujiwara et al. 2001).

Recently I was sent two thyasirids from the Regab pockmark (Gulf of Guinea) to identify and name following their inclusion in the bacterial study of Rodrigues and Duperron (2011). From a cursory examination it is immediately apparent the gill filaments are not laminar but that the gill is a three dimensional network of tubules.

Using scanning electron microscopy this paper describes the gross structure of these "tubular" gills and compares them with those described by Dufour (2005), especially the lamellar (Type 3) gill associated with chemosymbiotic taxa. Both *Conchocele* and the Regab thyasirid have been shown to be chemosymbiotic (Imhoff et al 2003; Rodrigues and Duperron 2011). Comparisons with the lucinoid gill are made and finally the Regab thyasirid is described as *Ochetoctena tomasi* gen. et sp. nov.

Materials and methods

Specimens examined

Thyasira sarsi (Philippi, 1845). North Sea:- Lyell Oil Field, 60°55'N, 01°14'E, 150 m, National Museum of Wales, 20+ specimens.

Thyasira flexuosa (Montagu, 1803). North Sea, National Museum of Wales, 20+ specimens.

Axinus cascadiensis Oliver & Holmes, 2007. Baby Bare Seamount, Cascadia Basin, 2591m. National Museum of Wales, 5 specimens.*Conchocele bisecta* (Conrad, 1849). Locality unknown, probably Queen Charlotte Sound, British Columbia. RBCM, 006-00076-001., 1 specimen.

Undescribed new genus, single specimen, Off Quatsino Sound, Vancouver Island, British Columbia, Canada, 50°15.482'N, 128°26.400'W to 50°14.519'N, 128°26.567'W, 1086 – 1318m. Coll. J. Boutillier, Fisheries and Oceans Canada, 02 September 2004. RBCM 010-00221-005.

Conchocele excavata, (Dall, 1901). Farallon Islands, San Francisco County, California, , USA, Station J-13 (Benthos 9). SBMNH 83964, 1 specimen.

Ochetoctena tomasi gen. et sp. nov. (this paper), Regab Pockmark, Gulf of Guinea, West Africa, RV Meteor GUINECO cruise, M76/3, Dive 215, 05°47.84'S. 09°42.64'E. 3167 m, 2 specimens.

Parathyasira resupina Iredale, 1930. Holotype, specimen not examined, image from Australian Museum, Sydney. Malacology:C.57834.

Parathyasira subcircularis (Payne & Allen, 1991). Rockall Trough, Scotland, North-east Atlantic, 58°26'N 12°42'W, 1595 m, NMW.Z. 1 specimen.

Parathyasira sp. nov. Owen Basin, Arabian Sea, 19°08'N 58°39'E, Discovery Cruise 211—stn12719#1, 3150m, NMW.Z.1995.009. 1 specimen.

Methods

All specimens had been previously fixed in ethanol or formaldehyde of unknown concentrations. 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 CO_2 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

AMS – Australian Museum, Sydney
NMW.Z – National Museum of Wales
RBCM – Royal British Columbia Museum
SBMNH – Santa Barbara Museum of Natural History

Results

The laminar filament. (Type 3L) in *Thyasira flexuosa*, *T. sarsi*, *Axinus cascadiensis*, "*Conchocele*" excavata and the undescribed genus from Quatsino Sound

Both demibranchs are present, the outer extending over approximately half of the inner (Figs 1A-C). The filaments are fully reflected forming a descending and ascending lamella. The filaments are extended abfrontally giving each a laminar form. The supra-branchial chamber is represented by the large dorsal space (sbc) between the descending and ascending laminae. Ventrally the abfrontal regions extend and fuse to form continuous inter lamellar septae of varying patterns (ils) (Figs 1A-C, 2A, B). Using *Thyasira sarsi* as typical of this group the micro-structure is as follows. All parts of the abfrontal surfaces and the septae (ils) are lined with polygonal bacteriocytes (Fig. 2B). The frontal face of the filaments are fully ciliated (Figs 2C, D) with a median band of frontal cilia (fc) bordered on both sides by a band of lateral frontal cirri (lfc) and behind these a band of lateral cilia (lc). If removed the ciliated surfaces can be recognised by a remaining intricate pattern of scars on the epithelial surfaces (Fig. 2E, arrowed). Immediately behind the ciliated bands there is a network of inter-filament junctions (ifj) (Fig. 2D).

In *"Conchocele" excavata* only alternate filaments fuse to form inter lamellar septae and the middle portions of these septae do not bear bacteriocytes (Fig. 2F).

The tubular/laminar filament (Type 4T/L) in *Conchocele bisecta*

Both demibranchs are present, the outer and inner of approximate equal size (Fig. 1D). The filaments are fully reflected forming descending and ascending lamellae and appear to be narrowly separate along their entire length. At low magnification the filament is seen to be extended abfrontally but rather than appearing to be laminate the frontal region appears as a series of small blocks but these are not apparent abfrontally. Under the SEM the frontal surface appears as a series of vertical bands with rows
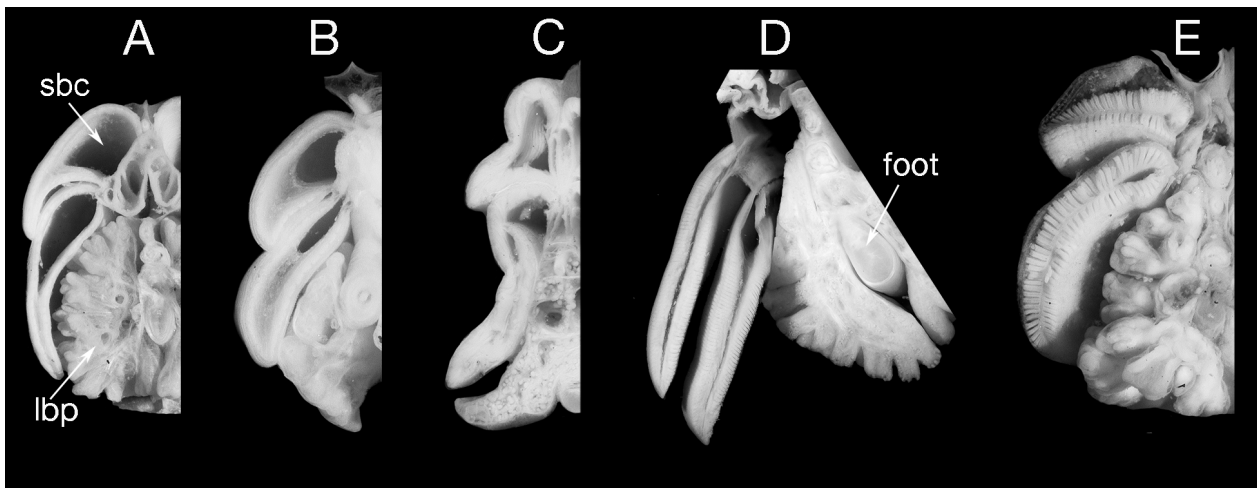
Figure 1. Cross sections through the median area of five species of Thyasiroidea showing the demibranchs on one side in cross section. A *Thyasira sarsi*, B *Thyasira flexuosa*, C *Axinus cascadiensis*, D *Conchocele bisecta,* E *Ochetoctena tomasi*. lbp lateral body pouch; sbc supra branchial chamber.

of openings between the bands (Fig. 3A, openings white arrows) The vertical bands represent the frontal face of each filament and are strongly angulate with no trace of ciliation (Figs 3E, F). Nakazima (1958) assumed that the cilia had been lost through poor preservation but if this was the case the intricate pattern of ciliary 'roots' would remain and be visible under the SEM (see Fig. 2E for comparison). The lateral margins of the frontal bands are smooth (Fig. 3E) but between each band a small projection can be seen sitting on the inter filament junction (Fig. 3F, arrowed).

With the frontal bands ripped off a regular tubular structure is seen (Fig. 3B) with inter filament junctions (arrowed). Viewed from the abfrontal face of a lamella the regular tubular structure is not apparent and replaced by laminar filaments (Fig. 3C abf-lam). Widely separated but torn inter lamellar junctions (ilj) are visible in Fig. 3C, and best seen in cross-section in Fig. 3D (ilj). In cross-section (Figs 3D, 4) it can be seen that the frontal zone (fz) is narrow consisting primarily of the angular bands. The tubular zone (tbz) is a little over half the thickness of the lamella with the remainder being laminar (lz). Inter-lamellar junctions maintain a series of inter lamellar spaces (Fig. 3D, ils). Behind the frontal zone and between the laminar and tubular zones are inter filament junctions (ifj).

The tubes are lined with densely packed bacteriocytes as is the surface of the laminar zone, the inter lamellar junctions do not bear bacteriocytes. Preservation was not sufficient to acquire detailed images of the bacteria.

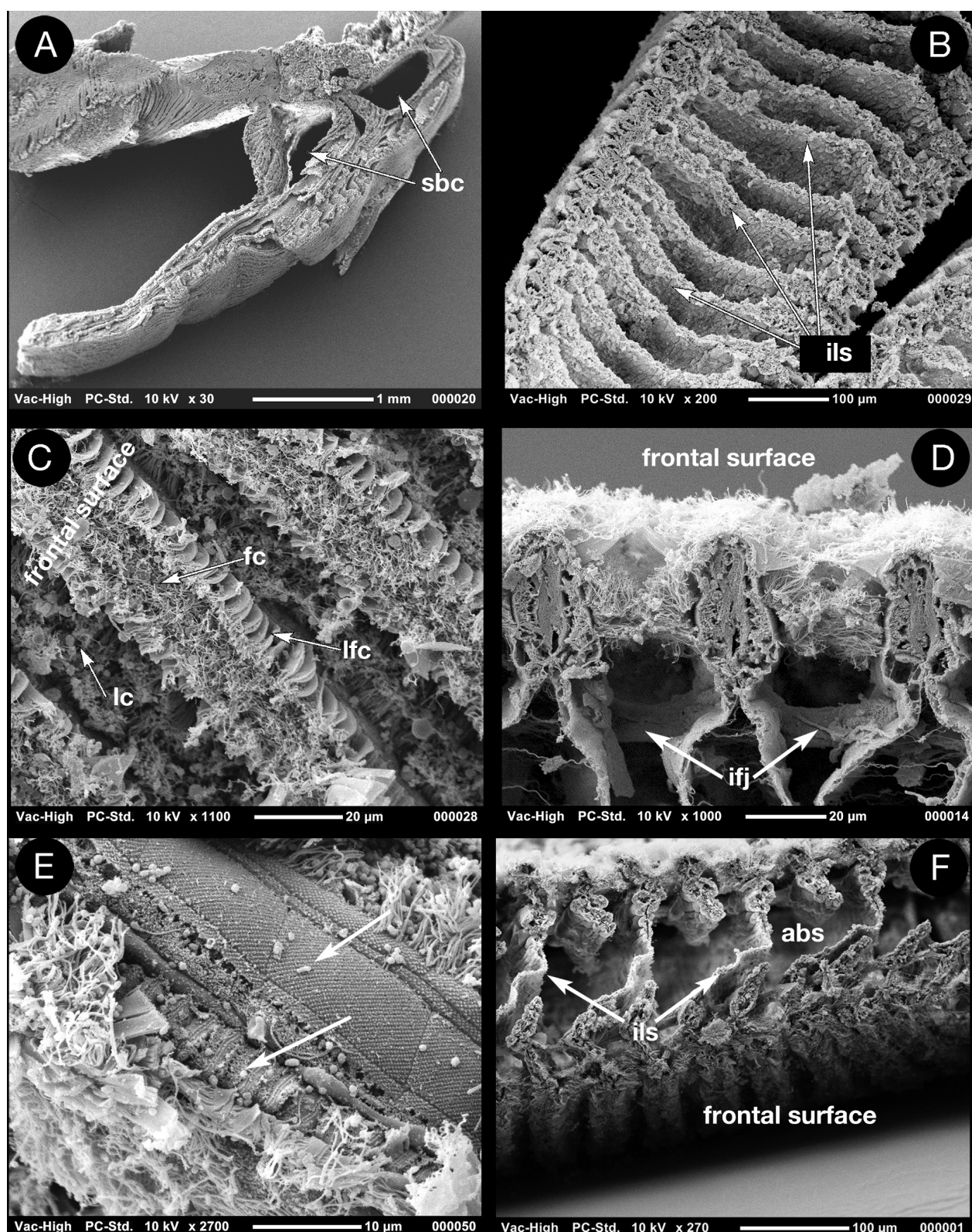**The tubular filament (Type 5T) in *Ochetoctena tomasi***

Both demibranchs are present but the outer is about half the depth of the inner (Fig. 1E). The normal filament structure is not apparent even under low magnification but appears as a series of small blocks (Fig. 8F). In trans-verse view (Figs 5, 7C) the ascending and descending arm of each filament is seen to be made up of a series of tubules (lt), abfrontally these are fused to form a median tube (mt). There is a small dorsal supra branchial chamber (Fig. 5 sbc). In lateral section the tubes can be seen to open between the frontal faces of the filaments (Fig. 6 (te), 7B white arrows). These faces (Fig. 7B black arrows) are composed of a double band of the bases of lateral frontal cirri. Although not well preserved there are indications of lateral cilia and the frontal cilia zone is a deep groove. With the frontal zone ripped off the tubes can be seen in cross-section (Fig. 7D) and long section (Fig. 7E) if cut laterally. The walls are composed mostly of bacteriocytes (bct), the lumen is open and attached to the walls are numerous spherical cells (sph) of unknown function but may be involved with the elimination of waste products as suggested for similar structures observed by Reid and Brand (1986). Sporadically there are bundles of filaments (Fig. 7F ptf), 15 - 20 μm in length, each with a swollen, paddle-shap tip. These are similar in form to structures described as hyphomicrobial cells observed in *Syssitomya* by Oliver et al. (2013). This interpretation is open to question given the observation of paddle shaped artifacts observed on bivlace cilia by Beninger, Potter & St-Jean (1995). Here these structures are not attached to the walls of the tubules and if they are cilia they are probably not in situ.

The bacteria in the bacteriocytes are small, subspherical measuring approximately 0.65 μm in diameter (Fig. 7F bct).

Discussion

The results presented here reveal further modification of the thyasirid gill towards a complex three-dimensional structure. The gill types described by Dufour (2005) can now be added to with two additional types; "tubular/laminar"
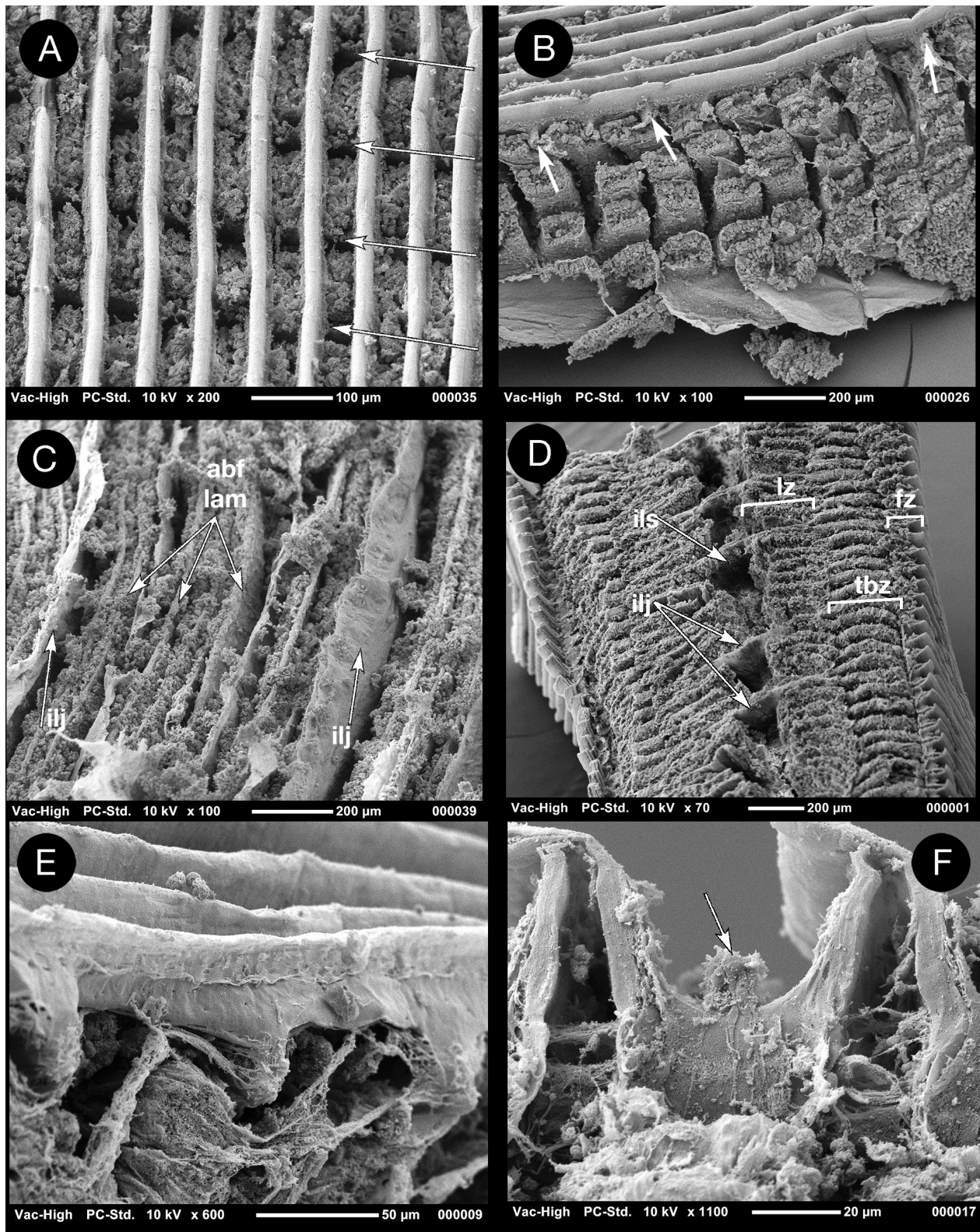
Figure 2A–E. Scanning electron micrographs of the ctenidium of *Thyasira sarsi*; A gross transverse section, B longitudinal section of ventral portion of inner demibranch, C ciliated frontal surface, D transverse section through the frontal zone. E frontal surface with cilia removed. Figure 2F "*Conchocele*" *excavata*, longitudinal section of ventral portion of inner demibranch. abs abfrontal surface; fc frontal cilia; lc lateral cilia; lfc lateral frontal cirri; ifj inter filamental junction; ils inter lamellar septum; sbc supra branchial chamber.

Figure 3. Scanning electron micrographs of the ctenidium of *Conchocele bisecta*; A frontal surface, openings of tubules arrowed; B frontal surface removed to reveal tubules; C abfrontal surface of laminar filaments; D longitudinal section; E edge of a frontal face; F section of the frontal face with projection on the inter filamentar junction arrowed. abf lam laminar abfrontal surface; fz frontal zone; ils inter lamellar space; ilj inter lamellar junction; lz laminar zone; tbz tubular zone.
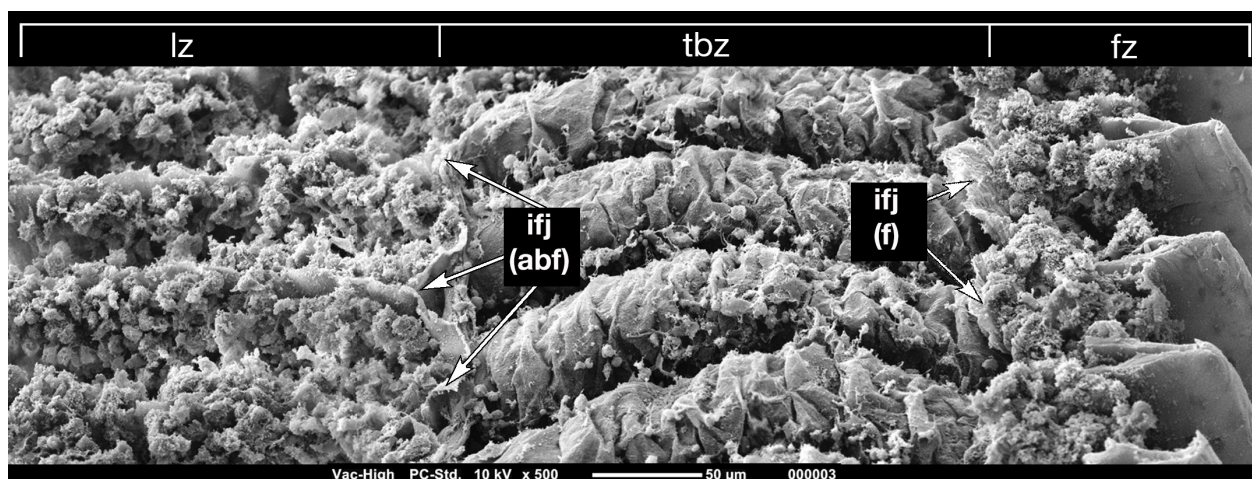
Figure 4. Scanning electron micrograph of the ctenidium of *Conchocele bisecta* showing details of the frontal, tubular and laminar zones. fz frontal zone; ifj (abf) inter filamentar junctions, abfrontal; ifj (f) inter filamentar junctions, frontal; lz laminar zone; tbz tubular zone.

and "tubular". The known gill types can be summarized as follows (Table 1) with a revised nomenclature based on that of Dufour 2005. The revised nomenclature incorporates the shape of the filaments and the number of demibranchs. Filaments that have no or little abfrontal extension are termed rods and these equate to Dufour Types 1 and 2. For Dufour Type 2 those with single demibranchs and non-reflexed filaments are termed "Type 2b (R)" while those with both demibranchs are termed "Type 2a (R)". The letters "L" and "T" refer to the laminar and tubular structures respectively. For each gill type the corresponding genera are listed, but some remain unallocated due to lack of data.

The extent of frontal ciliation is noted but the present observations give rise to difficulties in interpretation of the functioning of the tubular/laminar and tubular gills. All Type 3 (L) gills have complete ciliation of frontal and lateral cilia with eulateral cirri as also seen in the Lucinoidea (Taylor and Glover 2010). Here, it has not been possible to show any similar ciliation in *Conchocele* (Type 4T/L). Without ciliation it is difficult to comprehend how the currents to drive the water flow through the gill tubules are generated. Bernard (1972) records ciliary currents over the gill but gives no details of the ciliation. The lack of the basal structure of the cilia and cirri usually seen when the cilia are removed suggests that the *Conchocele* gill is atypical but its functioning remains enigmatic and requires observation on live material. It seems improbable that the small projections sitting on the frontal interfilamentar junctions, even if motile, could drive water currents into the tubules and could not produce the currents indicated by Bernard (1972).

Although there is an indication of frontal ciliation in *Ochetoctena* this is reduced and in both this genus and *Conchocele* they may be unable to create sorting and feeding currents on the gill.

Thyasirids typically hold their bacteria extra-cellularly (Dufour 2005) but the taxon *Maorithyas hadalis* is reported to hold the bacteria intra-cellularly (Fujiwara et al 2001). This unique condition suggests a further gill type
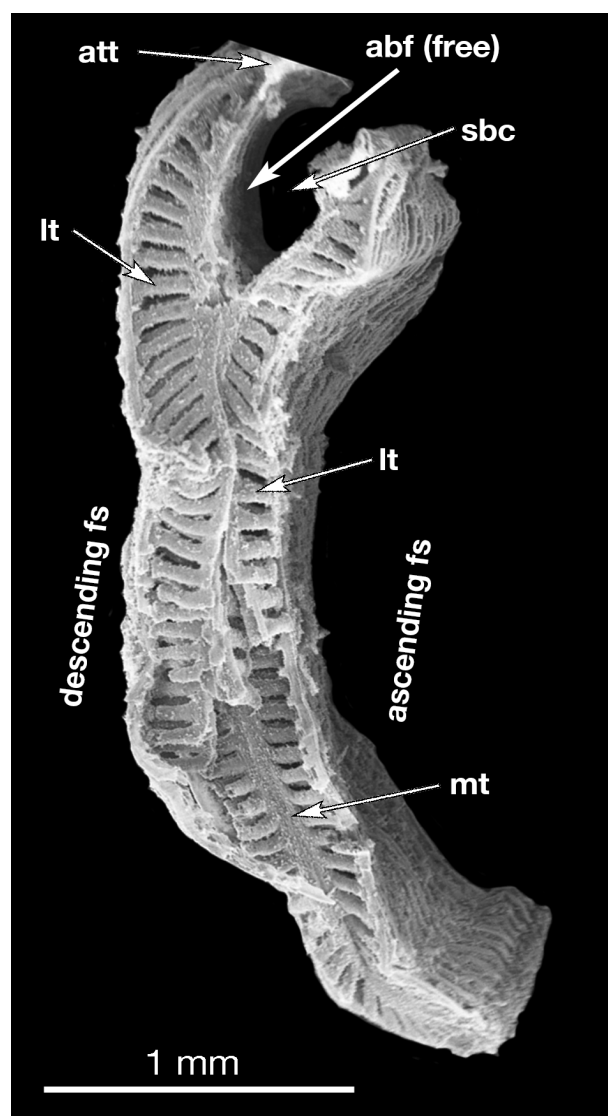
Figure 5. Scanning electron micrograph of the ctenidium of *Ochetoctena tomasi*, lateral view of a filament. abf (free) free abfrontal surface; att attachment point; fs frontal surface; lt lateral tubule; mt median tubule; sbc supra branchial chamber.
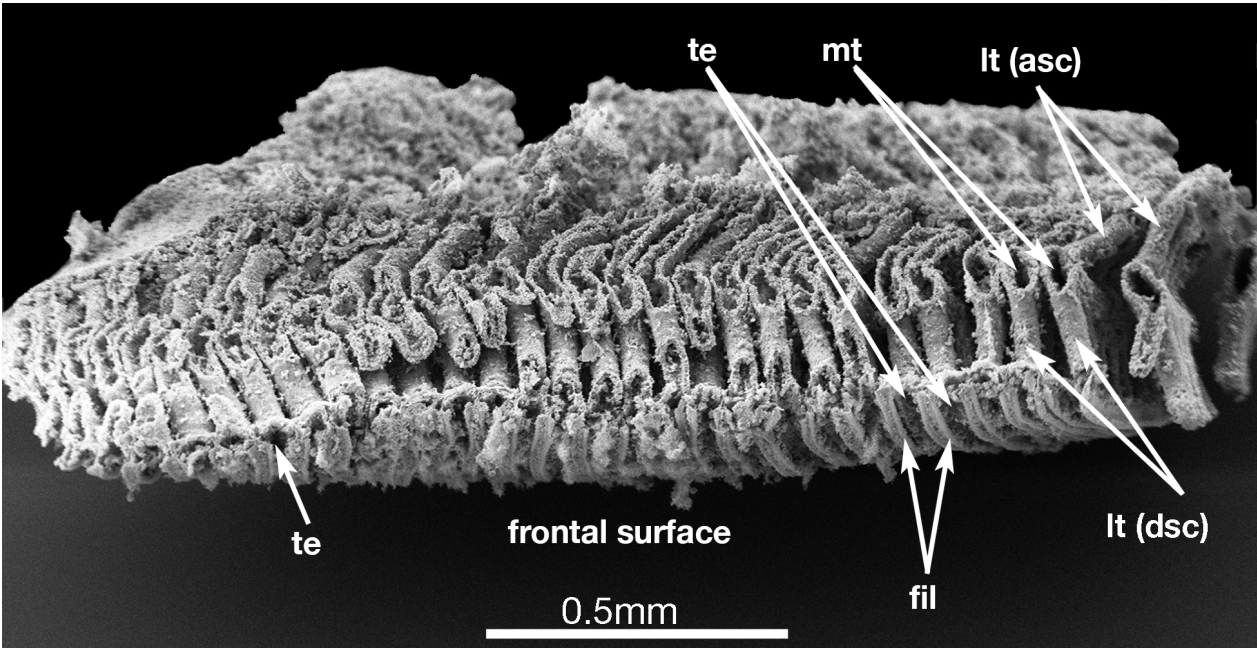
Figure 6. Scanning electron micrograph of the ctenidium of *Ochetoctena tomasi*, oblique section. fil frontal edge of a filament; lt (asc) lateral tubule of ascending arm; lt (dsc) lateral tubule of descending arm; mt median tubule; te tubule entrance.

but the gross structure of the gill remains undescribed. The allocation of this species to *Maorithyas* is incorrect as both shell and anatomy are not in agreement. The type species of *Maorithyas*, *M. marama* Fleming, 1950 is illustrated by Oliver and Sellanes (2005) and can be seen to be similar to *Thyasira sensu stricto* in both shell and anatomy.

This tubular structure increases the surface area of the bacteriocyte zone and creates a more rigid network further facilitating the movement of water from the infra-branchial chamber to the supra-branchial chamber. Similar structures are present within the Lucinoidea; Dando et al (1985) noted the inter-lamellar bridges in *Myrtea spinifera* and Distel and Felbeck (1987) illustrat-ed a complex tubular structure in *Lucinoma aequizonata*. Such complex structures are found throughout the Lucinoidea but this gill differs in consisting of a only a single demibranch (Taylor and Glover 2010). The tubular structure is yet another convergent morphological feature shared by chemosymbiotic thyasirids and lucinids.

The gill structures described here can potentially impact on the systematics of the Thyasiroidea. The observations on the gills of *Conchocele bisecta* and "*C*" *excavata* indicate that these taxa are not congeneric and this is part of the subject of another paper that also describes a new genus containing species previously assigned to *Conchocele* (Oliver and Frey, in press).

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

| Revised type	Dufour type	Demibranchs	Reflection	Abfrontal extension	Frontal ciliation	Filament Form	Genera
Type 1R	Type 1	2	+	–	Complete	Rod	*Axinopsida*
Type 2aR	Type 2	2	+	–/+	Complete	Rod	*Parathyasira*, *Thyasira* s.l.
Type 2bR	Type 2	1	–	–	Complete	Rod	*Axinulus*, *Adontorhina*, *Mendicula*, *Leptaxinus*, *Genaxinus*
Type 3L	Type 3	2	+	++	Complete	Laminar	*Thyasira ss*, *Maorithyas*, *Axinus*, *Spinaxinus*, *Channelaxinus*
Type 4T/L		2	+	++	Absent?	Tubular/ laminar	*Conchocele*
Type 5T		2	+	+++	Reduced	Tubular	*Ochetoctena*
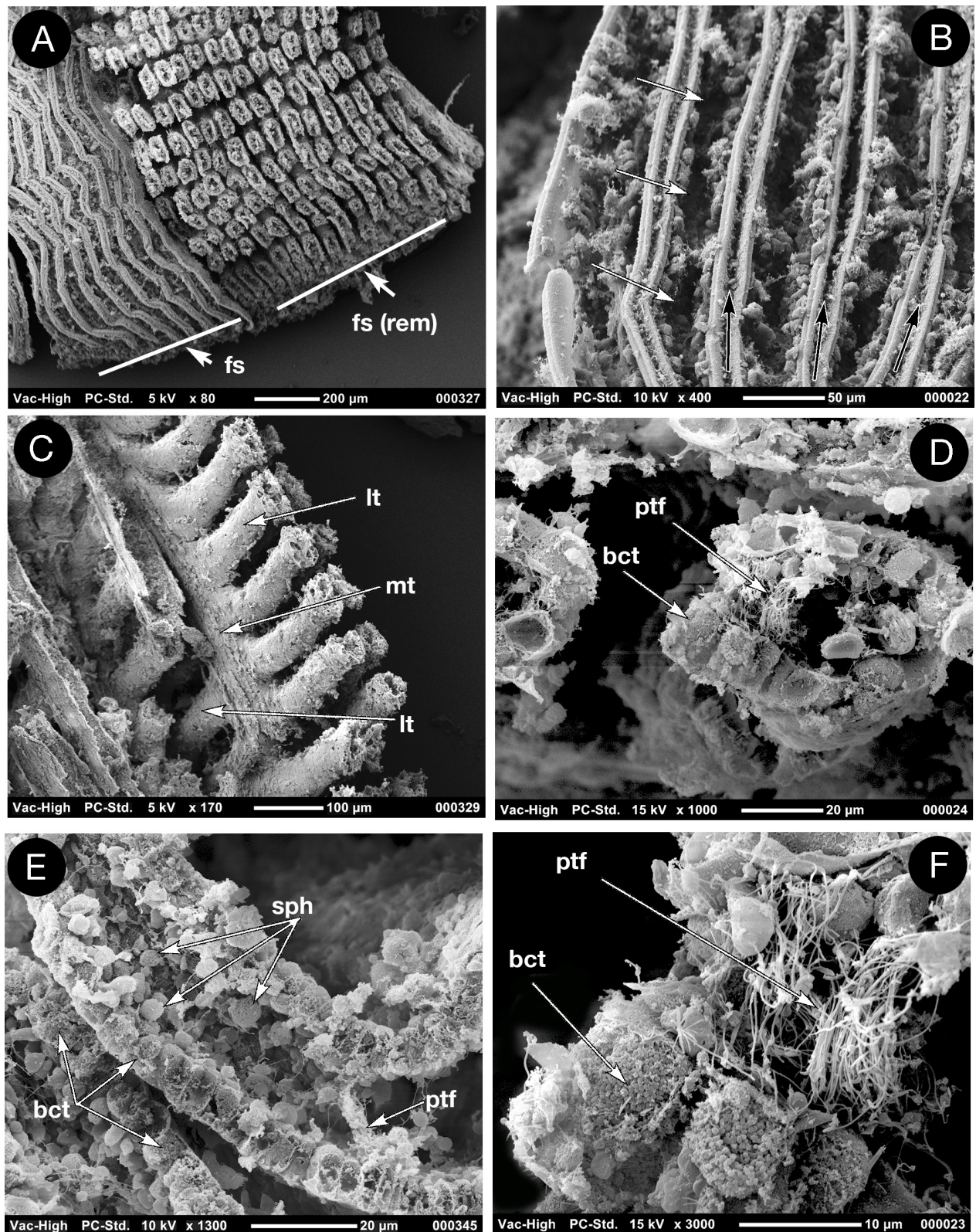
Figure 7A–F. Scanning electron micrographs of the ctenidium of *Ochetoctena tomasi*, A frontal face, frontal surface intact on the left, removed on the right to reveal tubules; B frontal surface with entrances to tubules arrowed; C single filament showing lateral and median tubules; D cross section of a single tubule; E long section of adjacent tubules; F bacterial bundles within bacteriocytes and paddle tipped filaments in the lumen of the tubule. bct bacteriocyte; spb spherical body; ptf paddle tipped filaments; fs frontal surface; fs (rem) frontal surface removed; lt lateral tubule; mt median tubule.
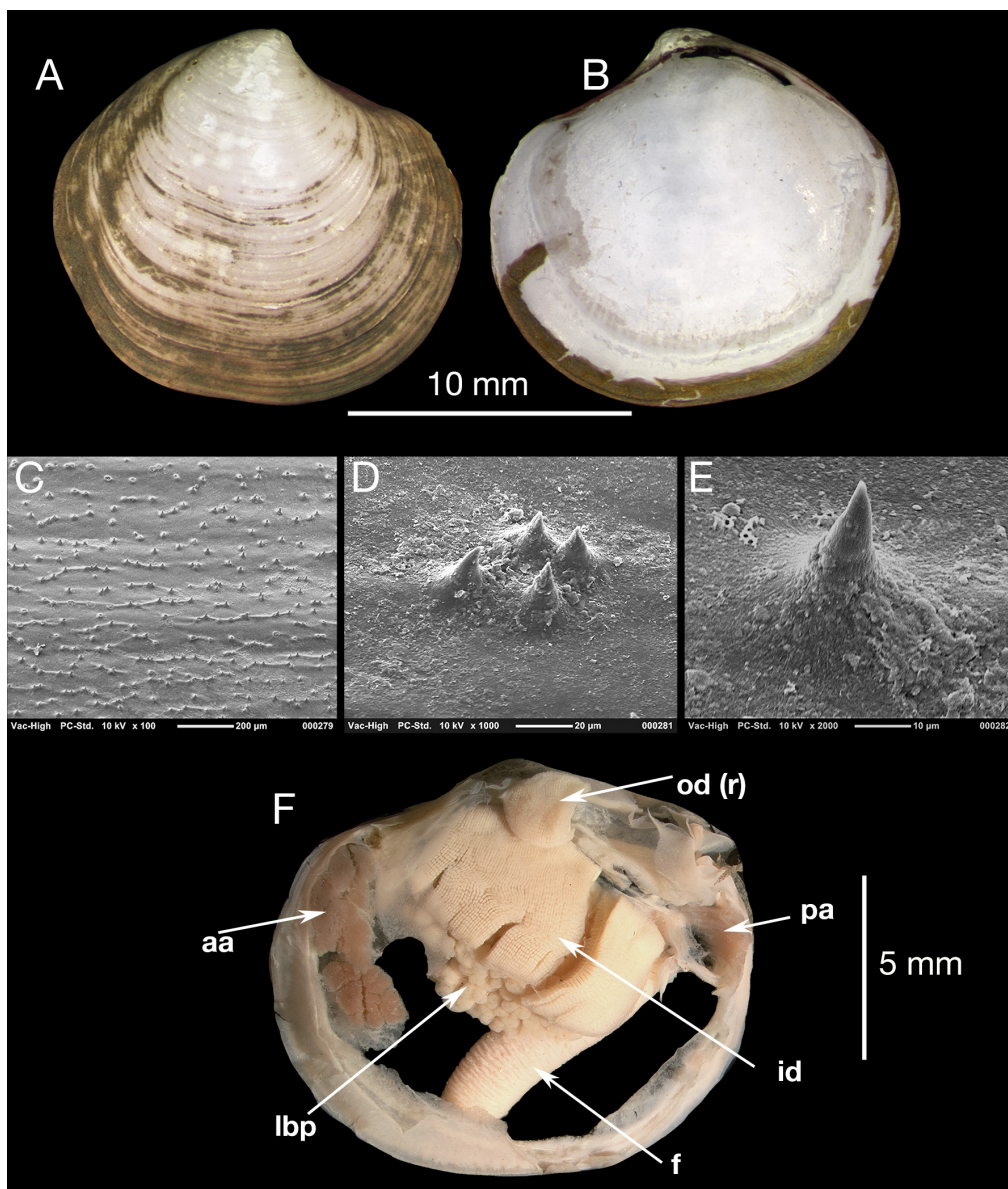
Figure 8 A–F. *Ochetoctena tomasi*, A–B external and internal views of the shell of the holotype, NMW.Z.2014.014.00001; C–E scanning electron micrographs of the shell surface; F gross anatomy viewed from the left side after removal of the mantle. aa anterior adductor muscle; f foot; lbp lateral body pouch; id inner demibranch; od (r) remanant of outer demibranch; pa posterior adductor muscle.

Systematics Appendix

Class Bivalvia Linnaeus, 1758
Subclass Heterodonta Neumayr, 1884
Order Veneroida H&A Adams, 1856
Superfamily Thyasiroidea Dall, 1900
Family Thyasiridae Dall, 1900

Genus *Ochetoctena* gen. nov.

http://zoobank.org/1063B2E8-1D45-49CB-BB5F-2B12FD047BE9

Type species: *Ochetoctena tomasi* sp. nov. this paper. Monotypic.

Definition. Equivalve, Equilateral. Outline subcircular, lunule margin depressed, posterior margin with a single weak sinus. Posterior sulcus shallow but prominent. auricle absent. Escutcheon narrow, shallow. Ligament deeply sunken. Hinge edentulous. External sculpture of commarginal lines and growth stops, overall with microscopic conical, calcareous spines these randomly distributed with some linked by low ridges . Ctenidia of two demibranchs, filaments tubular, "Type 5T".

Etymology. *Ochetoctena*, meaning tube-gilled from *ochetos* Greek "a water pipe or conduit" and *ktenos* Greek, "a comb" and the root for ctenidium (Brown 1956).

Distribution. Known only from the Regab pockmark off west Africa.

***Ochetoctena tomasi* sp. nov.**

Thyasira n. sp. Regab – Rodrigues & Duperron, 2011.

Material examined. 2 specimens (1 broken) in ethanol. Regab Pockmark, Gulf of Guinea, West Africa, RV Meteor GUINECO cruise, M76/3, Dive 215, 05°47.84' S. 09°42.64' E. 3167m

Holotype, entire shell from above, NMW.Z.2014.014.00001

Description of holotype. 14.4 mm long, 13.4 mm high, 4.3 mm half t. Equivalve, Equilateral. Outline subcircular. Anterior dorsal (lunule) margin concave, lunule slightly depressed, ovate, smooth, demarcated by a low ridge. Posterior dorsal (escutcheon) margin almost straight; escutcheon narrow, very shallow,
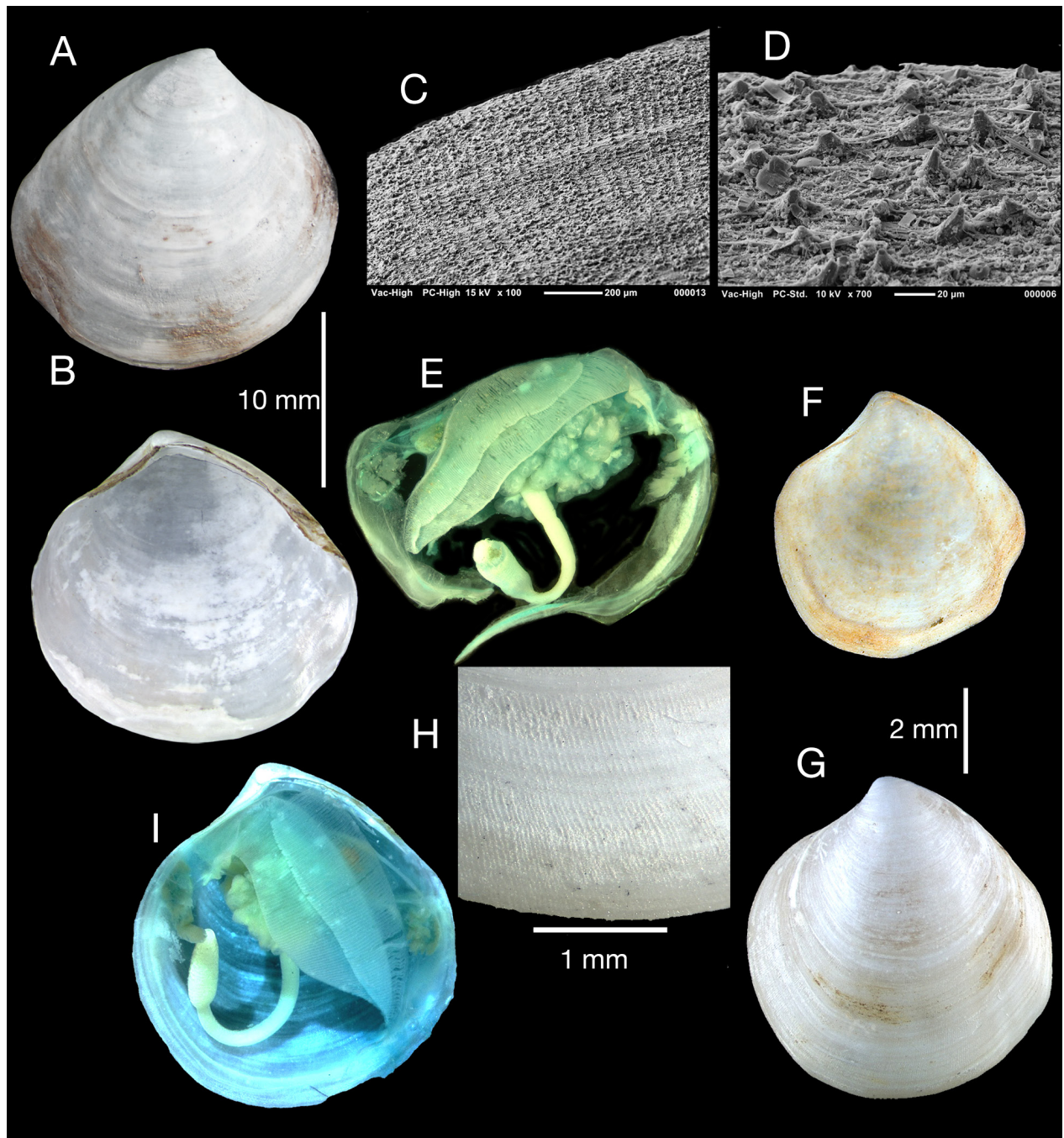

Figure 9. Shells and anatomy of granulose thyasirids of the genus *Parathyasira*. A–E an undescribed abyssal species from the Arabian Sea, NMW.Z .2014, A–B external and internal views of the shell; C–D scanning electron micrographs of the granulose microsculpture; E gross anatomy. F *Parathyasira resupina*, holotype and type of the genus, New South Wales, AMS C57834; G–I *Parathyasira subcircularis*, Rockall Trough, NMW.Z.2013, G external of shell; H gross anatomy; I micrograph showing radial granulose sculpture.

auricle lacking. Posterior ventral margin weakly indented corresponding with a distinct but shallow posterior sulcus. Median area slightly flattened corresponding with slightly straightened ventral margin. Anterior ventral and anterior a continuous broad curve. Ligament prominent but deeply sunken, about half the length of the escutcheon. Hinge edentulous. Sculpture of irregular commarginal lines and growth stops, overall with microscopic conical, calcareous spines emerging through the periostracum, these as isolated individuals, in small clumps or connected by weak sub-concentric ridges. Periostracum relatively thick, brown in colour, shell white. Muscle scars prominent, anterior adductor scar elongate not diverging from the broad pallial line; posterior adductor scar oval.

Anatomy. Mantle edge thick, free except for a junction demarcating the posterior aperture. Foot large, vermiform, toe elongate, heel very small. Lateral pouches large, multi-lobed, lobes cuboid. Ctenidium of two demibranchs, the outer about half the length of the inner; both with fully reflected filaments, these of Type 5T, composed of tubules fused to a median tube with only a small dorsal inter lamellar space.

Etymology. Named for my son Tomas.

Discussion. The shell of *Ochetoctena* has a weak posterior sulcus and the escutcheon is excavated but lacks any auricle to support the sunken ligament. In this it differs from *Thyasira* sensu stricto where there is a well developed auricle and from *Conchocele* which is oblique with a very strong posterior sulcus. Species lacking an auricle are often placed in the genus *Parathyasira* (Oliver and Killeen 2002; Payne and Allen 1991). The type species of *Parathyasira* is *P. resupina* Iredale, 1930 (Fig. 9F) and has a shell microsculpture of radial rows of calcareous spines. This character is also seen in the Atlantic species *P. granulosa* (Monterosato, 1874), *P. subcircularis* Payne & Allen, 1991 (Fig. 9G-I) and an un-named species from the Arabian Sea (Figs 9A-E). The spines in these species are angular with strongly developed basal connections between the rows (Figs 9C-D). In contrast the spines in *Ochetoctena* are not arranged in rows, are conical and the basal connections are weak or absent (Figs 8C-E). The genus *Spinaxinus* is characterised by having a spiny microsculpture but this is entirely periostracal (Oliver and Holmes 2006; Oliver et al 2013).

Ochetoctena is the only thyasirid known to have ctenidia of the Type 5T structure; *Conchocele* has a partly tubular gills of the Type 4TL morphology. The ctenidia of these *Parathyasira* species show poorly developed abfrontal extension resulting in a flimsy open structure. Dufour (2005) reported that the gills of *P. granulosa* are of her type 2 (type 2aR above) suggesting that the genus *Parathyasira* is characterised by a weak symbiont partnership.

There are, therefore, shell and anatomical synapomorphies that separate *Ochetoctena* from all other known thyasirids.

References

Allen JA (1958) On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). Philosophical Transactions of the Royal Society of London (Ser. B) 684: 421–482.

Beninger PG, Potter TM, St-Jean SD (1995) Paddle cilia fixation artefacts in pallial organs of adult *Mytilus edulis* and *Placopecten magellanicus* (Mollusca, Bivalvia). Canadian Journal of Zoology 73(3): 610–614.

Bernard FR (1972) The Genus *Thyasira* in Western Canada (Bivalvia: Lucinacea). Malacologia 11(2): 365–389.

Brown RW (1956) Composition of scientific words. Smithsonian Institution Press, London and Washington, 882 pp.

Conrad TA (1849) Fossils from northwestern America. In: Dana JD (Ed.) United States Exploring Expedition. During the years 1838, 1839, 1840, 1841, 1842. Under the command of Charles Wilkes, USN Atlas. Geology vol 10, Sherman, Philadelphia, 722–728.

Dall WH (1901) Synopsis of the Lucinacea and of the American species. Proceedings of the US National Museum 23(1237): 779–833.

Dando PR, Southward AJ, Southward EC, Terwilliger NB, Terwilliger RC (1985) Sulphur-oxidising bacteria and haemoglobin in gills of the bivalve mollusk *Myrtea spinifera*. Marine Ecology Progress Series 23: 85–98.

Distel DL, Felbeck H (1987) Endosymbiosis in the lucinid clams *Lucinoma aequizonata*, *Lucinoma annulata* and *Lucina floridana*: a reexamination of the functional morphology of the gills as bacteria-bearing organs. Marine Biology 96: 79–86.

Dufour SC (2005) Gill anatomy and evolution of symbiosis in the bivalve family Thyasiridae. Biological Bulletin 208: 200–212.

Imhoff JF, Sahling H, Süling J, Kath T (2003) 16s rDNA- based phylogeny of sulphur-oxidising bacterial endosymbionts in marine bivalves from cold-seep habitats. Marine Ecology Progress Series 249: 39–51.

Iredale T (1930). More notes on the marine Mollusca of New South Wales. Records of the Australian Museum 17: 384–407.

Fleming CA (1950) New Zealand Recent Thyasiridae (Mollusca). Transactions of the Royal Society of New Zealand 78(2–3): 251–254.

Fujiwara Y, Kato C, Masui N, Fujikura K, Kojima S (2001) Dual symbiosis in the cold-seep thyasirid clam *Maorithyas hadalis* from the hadal zone in the Japan Trench, western Pacific. Marine Ecology Progress Series 214: 151–159.

Montagu G (1803) Testacea Britannica, or natural history of British shells, marine, land and the fresh-water, including the most minute: systematically arranged and embellished with figures, Romsey, London, 606 pp.

Monterosato TA (1874) Recherches conchyliologiques, effectuées au Cap Santo Vito, en Sicile. (Traduz. dall'italiano di H. Crosse). Journal de Conchyliologie 22(3): 243–282.

Nakazima M (1958) Notes on the gross anatomy of *Conchocele disjuncta*. Venus 20(2): 186–197.

Oliver PG (2013) Description of *Atopomya dolobrata* gen. et sp. nov.: First record of bacterial symbiosis in the Saxicavellinae (Bivalvia). Journal of Conchology 41(3): 359–367.

Oliver PG, Frey MA (in press) A new genus (Bivalvia: Thyasiroidea) from Vancouver Island, with notes on *Conchocele* Gabb, 1866 and *Channelaxinus* Valentich-Scott & Coan, 2011. Zootaxa.

Oliver PG, Holmes AM (2006) New species of Thyasiridae (Bivalvia) from chemosynthetic communities in the Atlantic Ocean. Journal of Conchology 39(2): 175–183.

Oliver PG, Holmes AM (2007) A new species of *Axinus* (Bivalvia: Thyasiroidea) from the Baby Bare Seamount, Cascadia Basin, NE Pacific with a description of the anatomy. Journal of Conchology 39(4):363–376.

Oliver PG, Killeen IJ (2002) The Thyasiridae of the British continental shelf and north sea oilfields. 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.

Oliver PG, Rodrigues CF, Carney R, Duperron S (2013) *Spinaxinus* (Bivalvia: Thyasiroidea) from sulfide biogenerators in the Gulf of Mexico and hydrothermal vents in the Fiji Back Arc: chemosymbiosis and taxonomy. Scientia Marina 77(4): 663–676

Oliver PG, Southward EC, Dando PR (2013) Bacterial symbiosis in *Syssitomya pourtalesiana* Oliver, 2012 [Galeommatoidea, Montacutidae]; a bivalve commensal with the deep-sea echinoid *Pourtalesia*. Journal of Molluscan Studies 79: 30–41.

Payne CM, Allen JA (1991). The morphology of deep-sea Thyasiridae (Mollusca: Bivalvia) from the Atlantic Ocean. Philosophical Transactions of the Royal Society of London, series B 334: 481–566.

Philippi RA (1845) Kritische Bemerkungen über einige *Trochus*- Arten und die Gattung *Axinus*. Zeitschrift für Malakozoologie 1845: 87–91.

Reid RGB, Brand DG (1986) Sulfide-oxidising symbiosis in Lucinaceans: Implications for bivalve evolution. The Veliger 29(1):3–24.

Rodrigues CF, Duperron S (2011) Distinct symbiont lineages in three thyasirid species (Bivalvia: Thyasiridae) from the eastern Atlantic and Mediterranean Sea. Naturwissenschaften 98: 281–287. doi 10.1007/s00114–011–0766–3.

Southward EC (1986) Gill symbionts in thyasirids and other bivalve molluscs. Journal of the Marine Biological Association of the United Kingdom 66: 889–914.

Taylor JD, Glover EA (2010) Chemosymbiotic bivalves. In: Kiel S (Ed.) The vent and seep fauna. Topics in Geobiology 33, Springer, Heidelberg, 107–135.