THYASIRIDAE (MOLLUSCA: BIVALVIA) FROM THE KEMP CALDERA HYDROTHERMAL SITE, SOUTH SANDWICH ISLANDS, ANTARCTICA

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Abstract   Two species of thyasirid bivalve are described from the Kemp Caldera hydrothermal site, South Sandwich Island back arc system, Antarctica. Spinaxinus caldarium *n. sp. is chemosymbiotic and closely related to* S. emicatus *from the Gulf of Mexico with which it shares the same phylotype of symbiotic bacterium.* Parathyasira cf. dearborni *is not symbiotic and most closely resembles* P. dearborni *a widespread circum antarctic species. The gill anatomy is described for both species and molecular data on the bivalves and the symbiotic bacteria are presented.*

Key words   Thyasiridae, Antarctica, chemosymbiosis, anatomy, new species.

INTRODUCTION

The Thyasiridae is one of the seven bivalve families that are chemosymbiotic and associated with sites of organic enrichment, methane seeps and to a lesser degree hot vents. Unlike most other chemosymbiotic bivalve families the symbiosis is not obligate, some species devoid of symbionts while others are heavily or totally dependent on them (Southward, 1986; Dufour, 2005).

Nine species of Thyasiridae are known from Antarctica and the Magellanic province (Zelaya, 2009, 2010) but only one, *T. falklandica* Smith, 1885 has been shown to host symbiotic bacteria (Dias Passos *et al.*, 2007). By morphological inference from other studies, primarily that of Dufour (2005) it is likely that the following species do not or have only a weak association with bacterial symbionts: *T. (Parathyasira) magellanica* Dall, 1901; *T. (P.) dearborni* Nicol, 1965; *T. debilis* (Thiele, 1912); *Axinulus antarcticus* Zelaya, 2010; *Mendicula sudamericana* Zelaya, 2010. The remaining species may host symbionts: *T. patagonica* Zelaya, 2010; *T. scotiana* Zelaya, 2009; *T. fuegiensis* (Dall, 1890).

All of the above taxa have been taken from shelf to bathyal depths with no association with seep or vent environments. In 2010 hydrothermal vent sites were discovered along the Eastern Scotia Ridge (ESR) (Rogers *et al.*, 2012; Marsh *et al.*, 2012). Rogers *et al.* (2012) describe the fauna associated with these vents as atypical, being devoid of siboglinid worms, mussels and clams and suggest that that this represents a different biogeographical province. However at the

neighbouring hydrothermal site of the Kemp Caldera (KC), bivalves were collected, consisting of vesicomyids and thyasirids (Rogers, 2010). During a later expedition in 2011 siboglinid worms, albeit in poor condition, were collected from the Kemp Caldera as well as from the vent field in the Bransfield Strait (Georgieva *et al.*, 2015). The Thyasiridae are the subject of this paper, which considers their systematics, morphology, symbiosis and biogeography.

MATERIALS AND METHODS

Ethics statement
All necessary permits were obtained for the described field studies. Studies in the East Scotia Sea were undertaken under the permit S3–3/2009 issued by the Foreign and Commonwealth Office, London to section 3 of the Antarctic Act 1994.

Collection
The specimens were collected from the Kemp Caldera during expedition JC42 of the RRS James Clarke Ross in 2010 to the East Scotia Ridge (Fig. 1A). They were extracted from sediment samples taken by the ROV *Isis* and stored in 100% ethanol.

The collection sites were situated close to the base of the north-east face of the caldera at depths between 1421m and 1433m (Fig. 1B). The site has white smoking chimneys but the thyasirids were collected from sedimented areas near to diffuse flow but with no visual shimmering water in the sedimented sites. The thyasirids were collected together with samples of large vesicomyid clams "Calyptogena-type", which are with Heiko
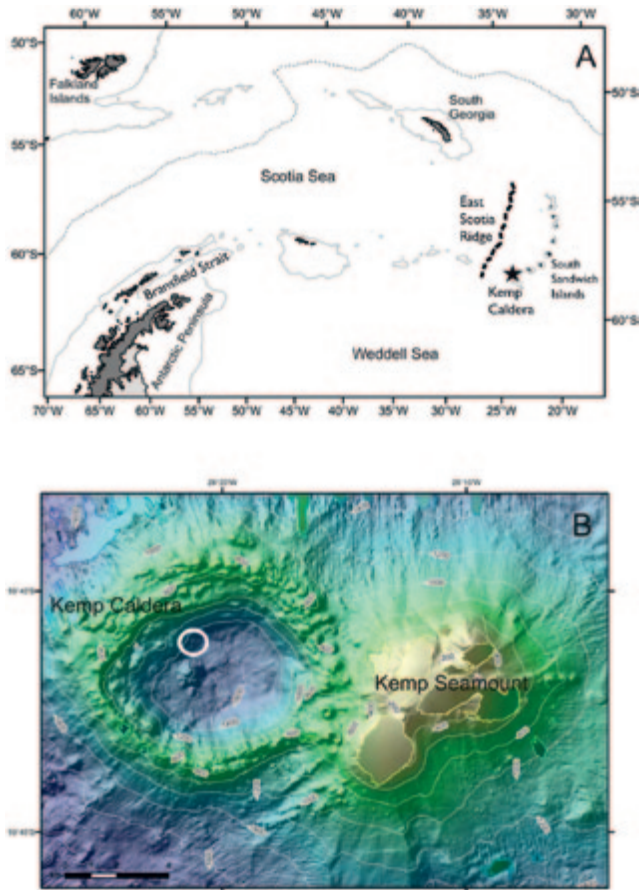
Figure 1 **A**, Map showing the location of chemosynthetic settings in the Southern Ocean, Kemp Caldera, East Scotia Ridge and Bransfield Strait. **B**, Bathymetric map of the Kemp Caldera showing the sampling area of Isis dives 149 and 151 (white circle) and type locality of *Spinaxinus caldarium* n. sp.

Sahling and Elena Krylova for taxonomic work in Bremen.

Morphological examination
Gross morphology was examined with a Leica MZ12 stereo-microscope with images by a Leica Z6 macroscope and modified using stacking software Helicon Focus.

For scanning electron microscopy the shells were air dried and coated with gold. The ctenidia were excised from the body, sliced to expose transverse surfaces, dehydrated in 100% ethanol and critically point dried and examined with a Jeol Neoscope scanning electron microscope.

Abbreviations in anatomical figures and scanning electron micrographs
aa, anterior adductor muscle; **abfl**, abfrontal lamellae; **asc**, ascending lamellae; **bb**, bacterial bundle; **bc**, bacteriocyte; **bs**, blood space; **dg**, digestive gland; **dsc**, descending lamellae; **f(h)**, heel of foot; **f(t)**, toe of foot; **fc**, frontal cilia; **fs**, frontal surface of gill; **glc**, glycocalyx; **id**, inner demibranch; **ifj**, inter filamtar junctions; **ipl**, inner pore layer; **k**, kidney; **lbc**, large bacteriocyte; **lbp**, lateral body pouch; **lc**, lateral cilia; **lfc**, lateral frontal cirri; **lp**, labial palps; **me**, mantle edge; **od**, outer demibranch; **olbp**, openings of lateral body pouch; **opl**, outer pore layer; **p**, pores; **pa**, posterior adductor muscle; **pdg**, protuberance of digestive gland; **pl**, pore layer.

Molecular characterization
DNA was extracted using the QIAamp DNA MicroKit (Qiagen). Fragments of one mitochondrial loci (encoding COI) and two nuclear loci encoding 18S and 28S rRNA were amplified for phylogenetic analysis. The presence of bacteria was tested by PCR of fragments of genes encoding 16S rRNA. Primers and PCR programs are summarized in Table 1. PCR products were purified with ISOLATE II PCR and Gel Kit (BIOLINE) and were sequenced directly at Macrogen Europe (Amsterdam, The Netherlands); as the bacterial sequence chromatograms displayed no ambiguity such as double peaks, no additional cloning step was added.

DNA sequences obtained during the present study were complemented with data from GenBank and available datasets and aligned using CLUSTALW (Thompson *et al.*, 1994). Phylogenetic reconstructions were performed for single genes using maximum likelihood and a general time reversible model with Gamma distribution of rates and a fraction of invariant sites using MEGA, version 6 (Tamura *et al.*, 2011).

SYSTEMATICS

Class BIVALVIA Linnaeus, 1758
Subclass HETERODONTA Neumayr, 1884
Order VENEROIDA H. & A. Adams, 1856
Superfamily THYASIROIDEA Dall, 1900
Family THYASIRIDAE Dall, 1900

Genus *Spinaxinus* Oliver & Holmes, 2006

Spinaxinus caldarium new species

Material examined
Holotype 1 complete specimen, in 100% ethanol, Kemp Caldera, South Sandwich Islands, Off

Table 1 Primers and PCR parameters used for amplifications and sequencing reactions

	Gene		Primer names	Primer sequences (5'→3')	Reference
Host	COI mtDNA	52°C (40)	BivF4t1	TGTAAAAACGACGGCCAGTGKTCWACWAATCATAARGATATTGG	Batstone et al. 2014
			BivR1t1	CAGGAAACAGCTATGACTAMACCTCWGGRTGVCCRAARAACCA	
	18S rRNA	54°C (40)	5F	CTGGTTGATYCTGCCAGT	Williams et al. 2004
			1100 (R)	CTTCGAACCTCTGACTTTCG	
	28S rRNA	52°C (40)	LSU-900f	CCGTCTTGAAACACGGACCAAG	Williams et al. 2004
			LSU-1600f	AGCGCCATCCATTTTCAGG	
Bacteria	16S	45°C (27)	27F	AGAGTTTGATCATGGCTCAG	Lane (1991)
			1492R	GTTACCTTGTTACGACTT	

Great Wall, JC42-F-0609, *Isis* Dive 149, 59.6933°S 28.3535W, 1431m, 09/02/2010, Natural History Museum London NHMUK 20160416

Paratypes   1 shell, dissected tissues for molecular analysis, Kemp Caldera, South Sandwich Islands, Off Great Wall, JC42-F-0609, Isis Dive 149, 59.6933°S 28.3535W, 1431m, 09/02/2010, Natural History Museum London NHMUK 20160417
1 specimen, Kemp Caldera, South Sandwich Islands, End of glacier, JC42-F-0777, Isis Dive 151, 59.6951°S 28.351W, 1423m, 10/02/2010, National Museum Wales NMW.Z.2016.17.1

Comparative material examined
Spinaxinus   emicatus.   Holotype   1   sp., Louisiana slope, Gulf of Mexico, 27°44.1292'N 91°15.2858'W, 643m, NMW.Z.2013.1.1; Paratypes 4 sp., as holotype; 4 sp., Louisiana slope, Gulf of Mexico, 27°45.9164'N 91°06.7308'W, 584m, NMW.Z.2013.1.2 All leg. R. Carney.

Spinaxinus sentosus, Holotype and paratypes, hold of the cargo ship *Francois Vieljeux* approx. 30 miles west of Vigo, Spain, 42°7.95'N 9°26.95'W, 1160m. 1992. NMW.Z.2002.108.1/2.

Spinaxinus phrixicus Holotype, 1 sp., RV Melville/ ROV Jason cruise TUIM06MV, White Lady Vent Field, Fiji Back Arc Basin, 16.99°S 173.914°E, 1977m, 31 May 2005. Hydrothermal seep with patches of *Alviniconcha*, Swedish Museum of Natural History, SMNH – 78311.

Measurements

	Height (mm)	Length (mm)	Tumidity (mm)
Holotype	18.9	18.1	9.8
Paratype (NHM)	18.7	19.1	11.9
Paratype (NMWZ)	16.3	17.0	8.7

Description

Shell (Figs 2A–H, Holotype Figs 2G–H) To 19.1mm, Thin. Equivalve. Rather variable in outline and tumidity and all heavily eroded around the umbonal region. Height and length approximately equal, beaks at or just behind the midline, slightly expanded anteriorly, anterior slope relatively long, anterior broadly rounded, ventral curved to straight, posterior slope steeply curving with or without a very slight sinus. Surface contours weak, posterior sulcus very shallow, posterior slope somewhat flattened, escutcheon narrow, rather deep. Surface irregular with commarginal lines and growth stops covered with a thin straw-coloured periostracum. Periostracum (Figs 2I–J) of crowded wrinkles around the margins and every where drawn out into short spines some 50mm in length but frequently broken. Hinge eroded, structure unknown; ligament (Fig. 2E) deeply sunken, strong and extending over half the length of the escutcheon. Muscle scars indistinct, (overlain in Fig. 2C) anterior adductor elongate about 3x long as broad with a very short free ventral edge from the pallial line, posterior adductor scar about half the length of the anterior but narrow in proportion, pallial line narrow.

Gross anatomy Figs 3A–C illustrate the gross morphology viewed from the right side after sequential removal of the mantle, ctenidia and lateral body pouch. The mantle is very thin, the mantle edge is narrow and free along its entire length except for a short junction creating a small posterior exhalant aperture. The anterior adductor muscle is large in comparison with the posterior with a short free portion from the mantle edge. The ctenidium is composed of both demibranchs, the outer (od) about one third the size of the inner (id). Labial palps very small. The lateral body pouches (lbp) are massive with multiple cuboidal ended tubules; joined to the digestive gland via two wide ducts (olbp). Kidneys large, filling the posterior third of the visceral mass and obvious due to the mass of rust coloured granules filling the lumen. The foot has a greatly elongated muscular toe (f(t)) and a small indistinct heel (f(h)).

Ctenidium The ctenidium is thick and fleshy and in gross form externally can be seen to have surface cilia with a reticulate structure beneath (Fig. 3D). From the scanning electron microscope study the ctendium is made up two demibranchs (Fig. 4), the outer (od) shorter than the inner (id) but with thicker filaments. In both demibranchs the filaments are fully reflected but the ascending (asc) and descending lamellae (dsc) are fused over half their lengths. The outer, frontal surfaces (fs) are ciliated (Fig. 5A, B) with frontal cilia (fc) bounded on each side by lateral frontal cirri (lfc) and below these lateral cilia (lc).
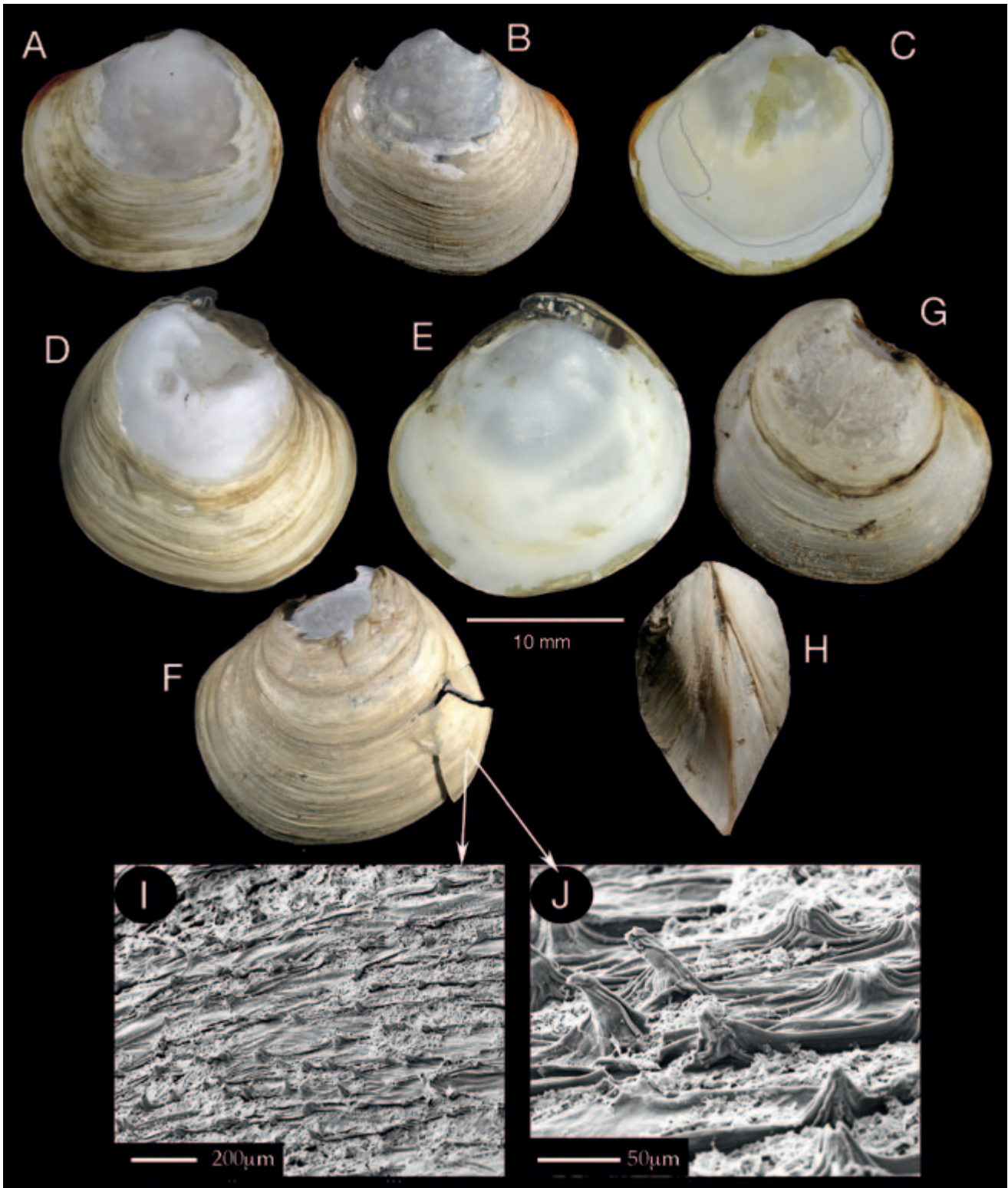
Figure 2 **A–H**, shells of *Spinaxinus caldarium* n. sp. **A–C**, Paratype #1, station JC042 F-0777, 59.6951°S 28.351W, 1423m, NMW.Z. **D–F**, Paratype #2, 59.6933°S 28.3535W, 1431m, NHM. **G–H,** Holotype, 59.6933°S 28.3535W, 1431m, NHM. **I–J** scanning electron micrographs of the periostracum of paratype #2.

In transverse section (Figs 5B, C) the ascending and descending arms of the filaments are fused forming entire lamellae with frontal surfaces linked by sheets of extended abfrontal tissue. These abfrontal lamellae (abfl) are composed of a double layer of cuboidal bacteriocyte cells
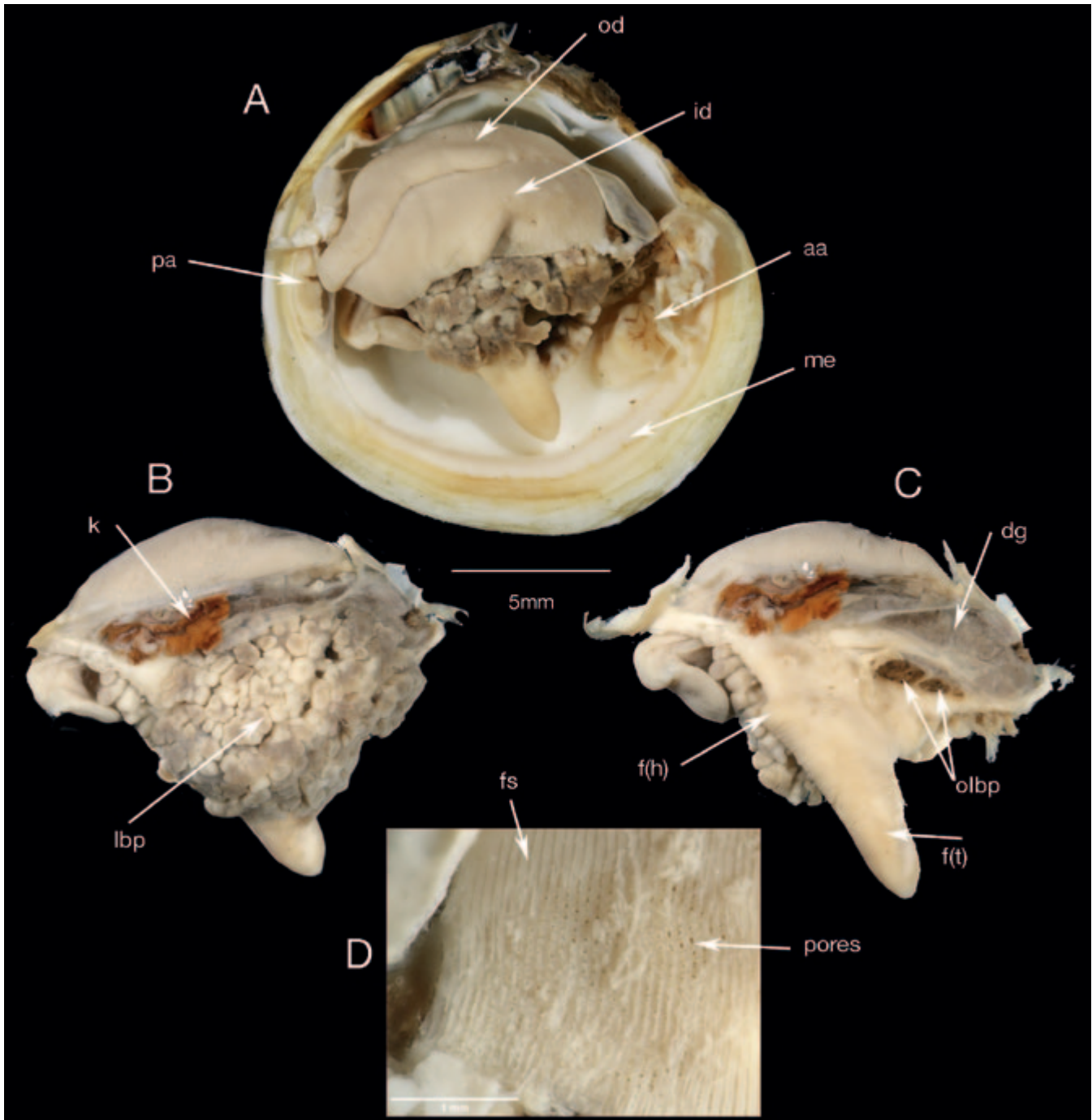
Figure 3   Gross anatomy of *Spinaxinus caldarium* n. sp. **A,** after removal of right valve and mantle. **B,** after further removal of right ctenidium. **C,** after further removal of right lateral body pouch. **D,** section of a ctenidium showing pore structure.

(bc) that line a central blood space (bs) (Fig. 5D). Between the abfrontal lamellae and the frontal surface is a zone of larger bacteriocytes which are part of the reticulate structure seen in gross morphology and is termed here the pore layer (Fig. 5B, pl).

Beneath the frontal surfaces, the pore layer, in lateral view, appears as a dense reticualtion (Figs 6A, B) of filaments and inter filamental junctions (ifj) forming pores (p) around 70mm in diameter. The inner (ipl) and outer pore (opl) layers open between the abfrontal lamellae. The pores (Fig. 6C, p) are approximately 120mm deep and the walls of the filaments and inter filamental junctions are lined with bacteriocytes larger (lbc), up to 20mm (Fig. 6D), than those on the abfrontal
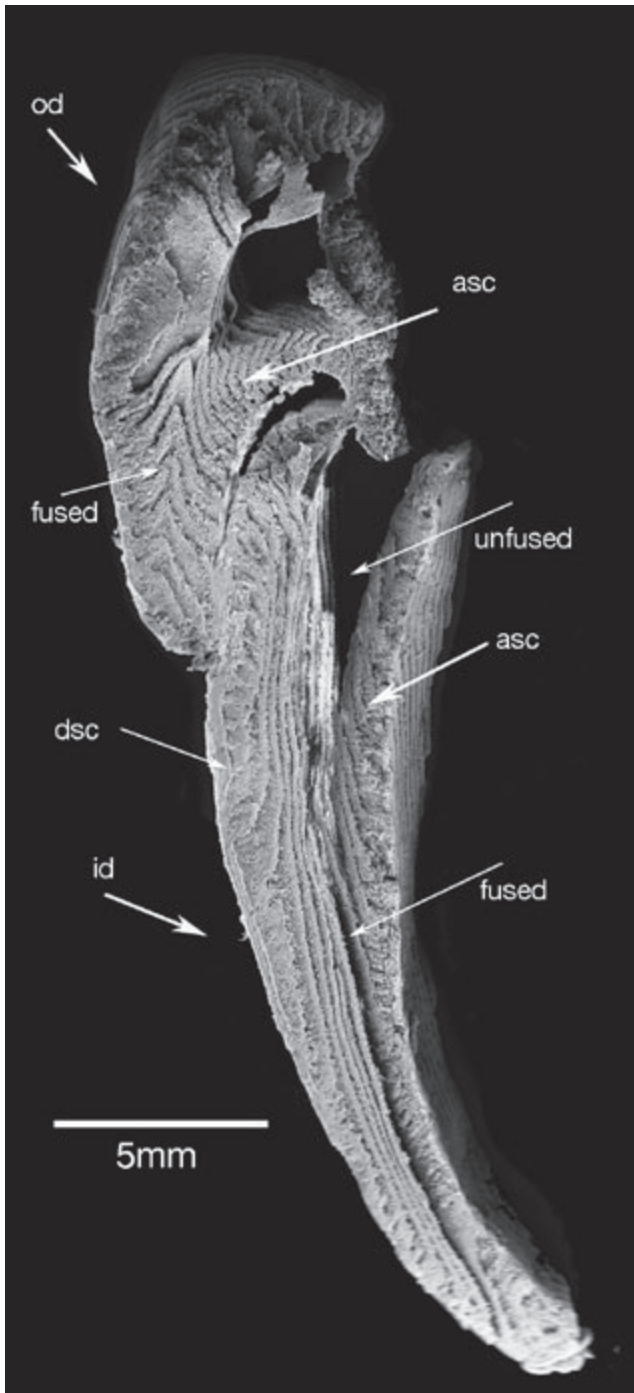
Figure 4 SEM of transverse section of a single ctenidium of *Spinaxinus caldarium* n. sp

lamellae that are typically 10mm in diameter (Fig. 7A, B).

The bacteriocytes have a glycocalyx (glc) (Fig. 7A, B) and are polygonal in section. Each houses a tightly packed bundle of bacteria (bb) (Fig. 7B, C) that number in the thousands per cell. The bacteria are rod-shaped (Fig. 7D) measuring 0.9–1.2mm×0.4mm

Molecular characterization Table 2
For *Spinaxinus caladrium* the 18S rRNA-encoding sequence showed 99% similarity with Thyasira sp. STW-2006 (AM392436)=*Spinaxinus phrixicus*. PCRs on the COI and 28S genes, failed to yield any product and a direct comparison was impossible between *Spinaxinus caldarium* and other *Spinaxinus* species.

Comparisons
The genus *Spinaxinus* is recognised by the unique character of the periostracum that is drawn out into spines. Three species are described; *S. sentosus* Oliver & Holmes, 2006; *S. emicatus* Oliver, 2013 and *S. phrixicus* Oliver, 2013. Separation on shell characters alone is difficult given the eroded nature of the Kemp Caldera material. However these shells have a smaller and weaker posterior sulcus and the posterior area is narrower than in *S. emicatus*. The anterior area is more expanded in *S. sentosus* and *S. phrixicus* is more circular. The more conclusive difference is in the form of the ctenidium, which in *S. caldarium* has a distinct reticulate pore layer below the frontal surface, a structure not present in the other species of *Spinaxinus*.

The molecular data confirms that the Kemp Caldera specimens are congeneric with other *Spinaxinus* species.

Etymology
From *caldarium* Latin "a hot bath" (Brown, 1956) making reference to the type locality of the hydrothermal conditions in the Kemp Caldera.

Parathyasira cf. dearborni Nicol, 1965

Material examined
2 complete specimens, one with a smashed shell, in 100% ethanol, Kemp Caldera, South Sandwich Islands, Off Great Wall, JC42-F-0609, 59.6933°S 28.3535W, 1431m, 09/02/2010. Natural History Museum London NHMUK 20160418

Comparative material examined
Parathyasira dearborni (as *Thyasira bongraini*, re-determined by Diego Zelaya, 2009) All Zoologisches Museum Hamburg. 9 specimens, South Shetland Islands, Elephant Island, 61°13'48"S 54°39'12"W, 280m, ZMH 32977/12. 3 specimens South Shetland Islands, 63°16'48"S 63°44'30"W, 340m, ZMH 32982/4. 7 specimens,
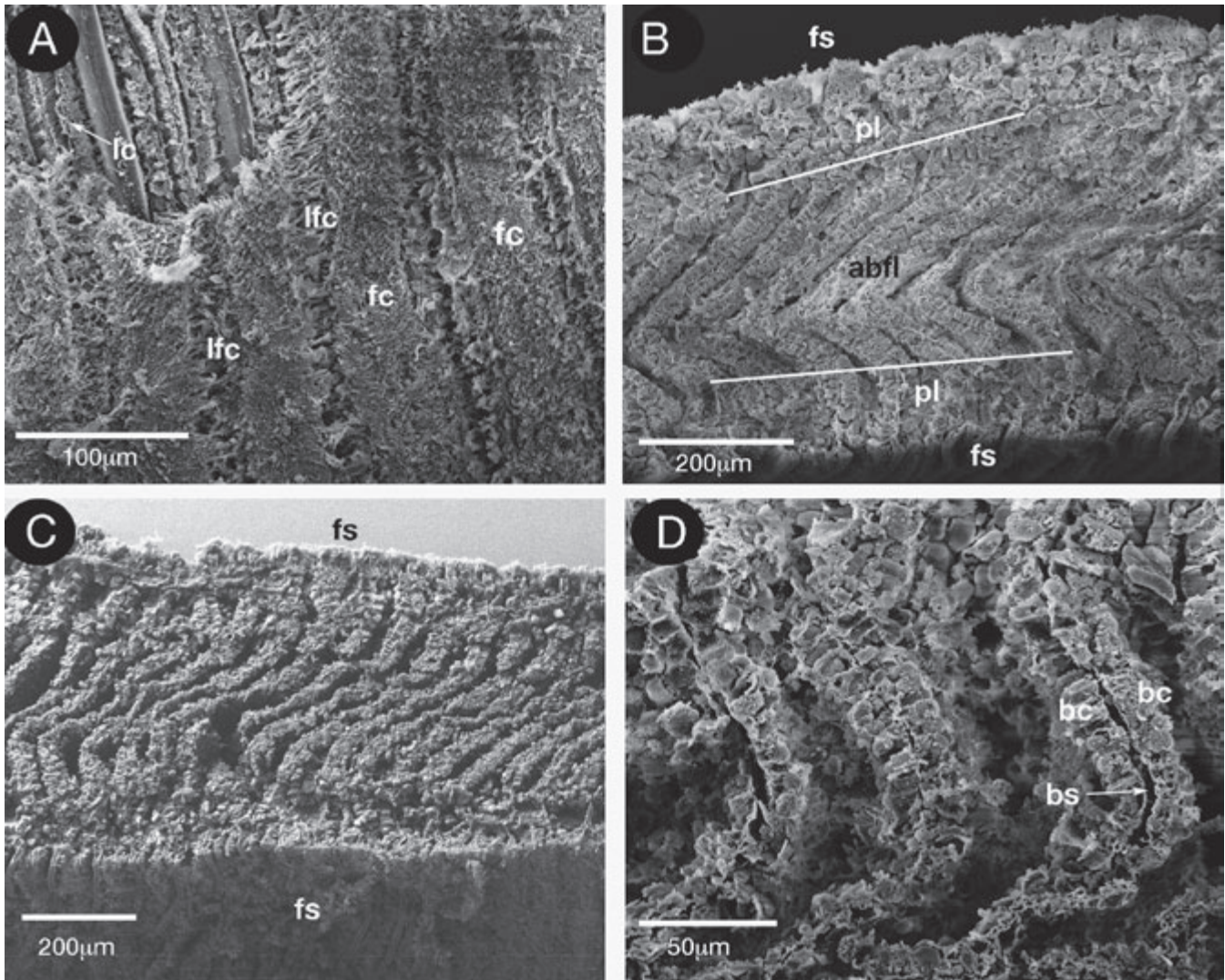
Figure 5   SEM of the ctenidium of *Spinaxinus caldarium* n. sp. **A**, ciliation of the frontal surface. **B–C**, cross section showing pore layer and continuous abfrontal lamellae. **D**, abfrontal lamella showing lining of bacteriocytes and blood space.

South Orkney Islands, 61°07'30''S 46°31'30''W, 289m, ZMH 32969/12.

Description of Kemp Caldera specimens.

Single intact shell (Fig. 8A–C)
Small, H=5mm, L=4.6mm, W=3.7mm, rhomboidal higher than long, rather inflated. Anterior dorsal margin sloping steeply, weakly angulate with anterior margin, lunule not defined. Posterior dorsal margin long, sloping steeply and gently curving to short subtruncate posterior. Ventral margin rounded. Posterior marginal sulcus extending the length of the posterior dorsal margin, narrowly cleft, auricle absent. Posterior sulcus weakly developed. Ligament deeply sunken. Hinge edentulous. Shell greyish white in colour, rust coloured deposits over the posterior and anterior margins.

Gross anatomy (Fig. 8 D–F)
Adductor muscles small, anterior narrow elongate, posterior oval. Mantle edge mostly unfused, except around the dorsal posterior siphonal opening. Mantle edges damaged, could not detect a second posterior aperture. Foot vermiform with a small heel. Lateral body pouches large, spreading over most of the mantle cavity, multi-lobed, dark brown in colour with tips of lobes paler. Digestive gland protruding as a blunt lobe dorsally of the lateral body pouch opening. Labial palps small, narrow with few weak sorting ridges. Kidney large deeply stained with brown granules.
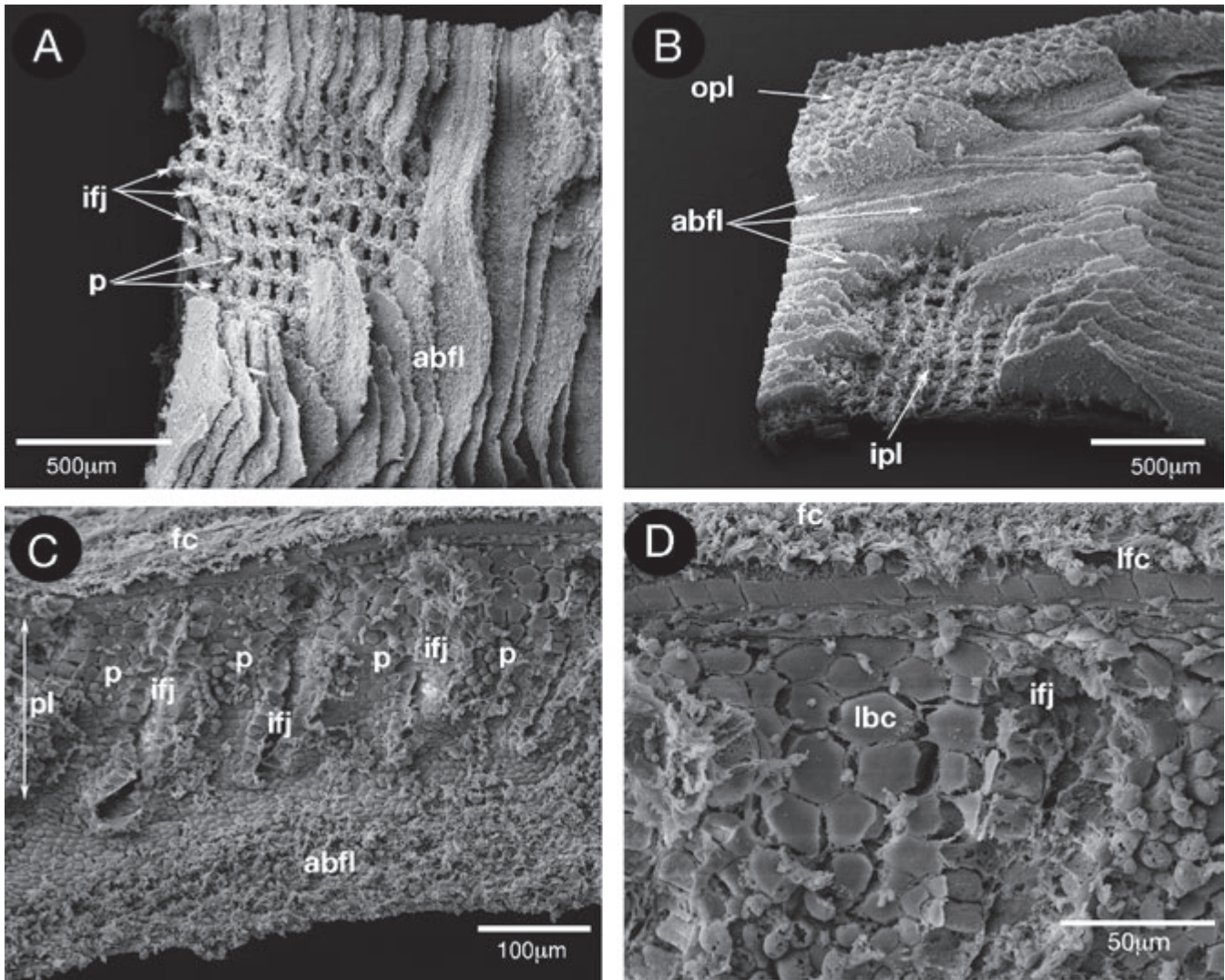
Figure 6 SEM of the ctenidium of *Spinaxinus caldarium* n. sp. **A–B**, filaments pulled open to reveal outer pore layers and arrangement of abfrontal lamellae. **C**, lateral view of a single filament, frontal face at the top, showing individual pores and torn inter filamentar junctions. **D**, large bacteriocytes lining a pore.

Ctenidium (Fig. 9A–D)

Composed of two demibranchs, the outer approximately half the depth of the inner; filament fully reflected. Filaments narrow with the abfrontal surfaces not extended or thickened, bacteriocytes absent. Filaments joined at regular intervals by inter filamental junctions and the ascending and descending lamella by sparse inter lamellar junctions. Frontal surface of filament with frontal cilia and lateral cilia separated by a row of lateral frontal cirri.

Molecular characterization (Table 2)

For *Thyasira dearboni*, the 18S, 28S and COI encoding sequences showed respectively 99%, 95% and 89% with *Parathyasira equalis* (AM774482, AM392437, AM706535).

Remarks

The two specimens from the Kemp Caldera have been identified here with *Parathyasira dearborni* by comparison with the Antarctic species redescribed by Zelaya (2009). We were unable to detect the small second posterior aperture considered a species character by Zelaya (2009). While this second aperture is present in the comparative material examined here it was not consistent and its absence in some specimens may be due to the weak mantle adhesion that forms the second aperture. Our reservations stem from the presence of only two specimens in our sample and the considerably greater depth from which they were collected. Zelaya indicates that *P. dearborni* is widely distributed around the Antarctic shelf at depths ranging from 68–752m, much less
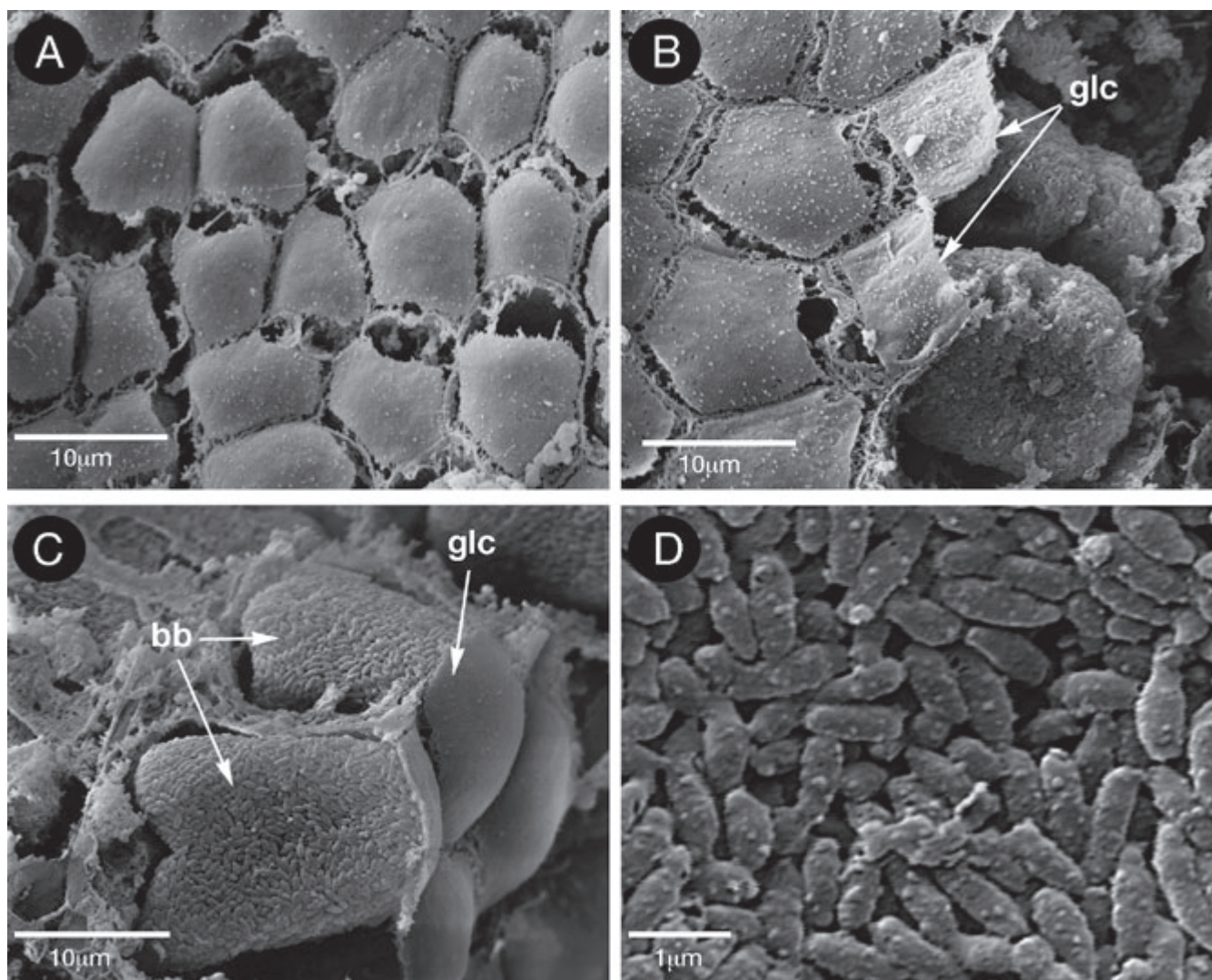
Figure 7   SEM of the ctenidium of *Spinaxinus caldarium* n. sp. **A**, surfac e view of a bacteriocyte layer showing individual polygonal cells. **B–C**, glycocalyx removed to reveal dense bundles of bacteria. **D**, small uniformly rod shaped bacteria.

Table 2   Results of the molecular characterization of *Spinaxinus caladarium* and *Parathyasira cf. dearborni* from the Kemp Caldera.

Species	Gene	Similarity	Blast
Spinaxinus caldarium	18S	99%	*Thyasira* sp. STW-2006 partial 18S rRNA gene, specimen voucher THYA.VENT, SMNH-78311 (= *Spinaxinus phrixicus*)
Parathyasira dearboni	18S	99%	*Parathyasira equalis* partial 18S rRNA gene, specimen voucher BMNH 20070296 (Natural History Museum, London)
Parathyasira dearboni	28S	96%	*Parathyasira equalis* partial 28S rRNA gene, specimen voucher TEQU.SWD.1
Parathyasira dearboni	COI	89%	*Parathyasira equalis* mitochondrial partial cox1 gene for cytochrome c oxidase subunit I, specimen voucher ZMBN77892

than the 1431m for the Kemp Caldera. The inflation of the Kemp shell is greater than that indicated by Zelaya for *P. dearborni* with a height to width ratio of 0.71 as opposed to 0.63. Without an adequate sample no inference can be made from a single measurement.
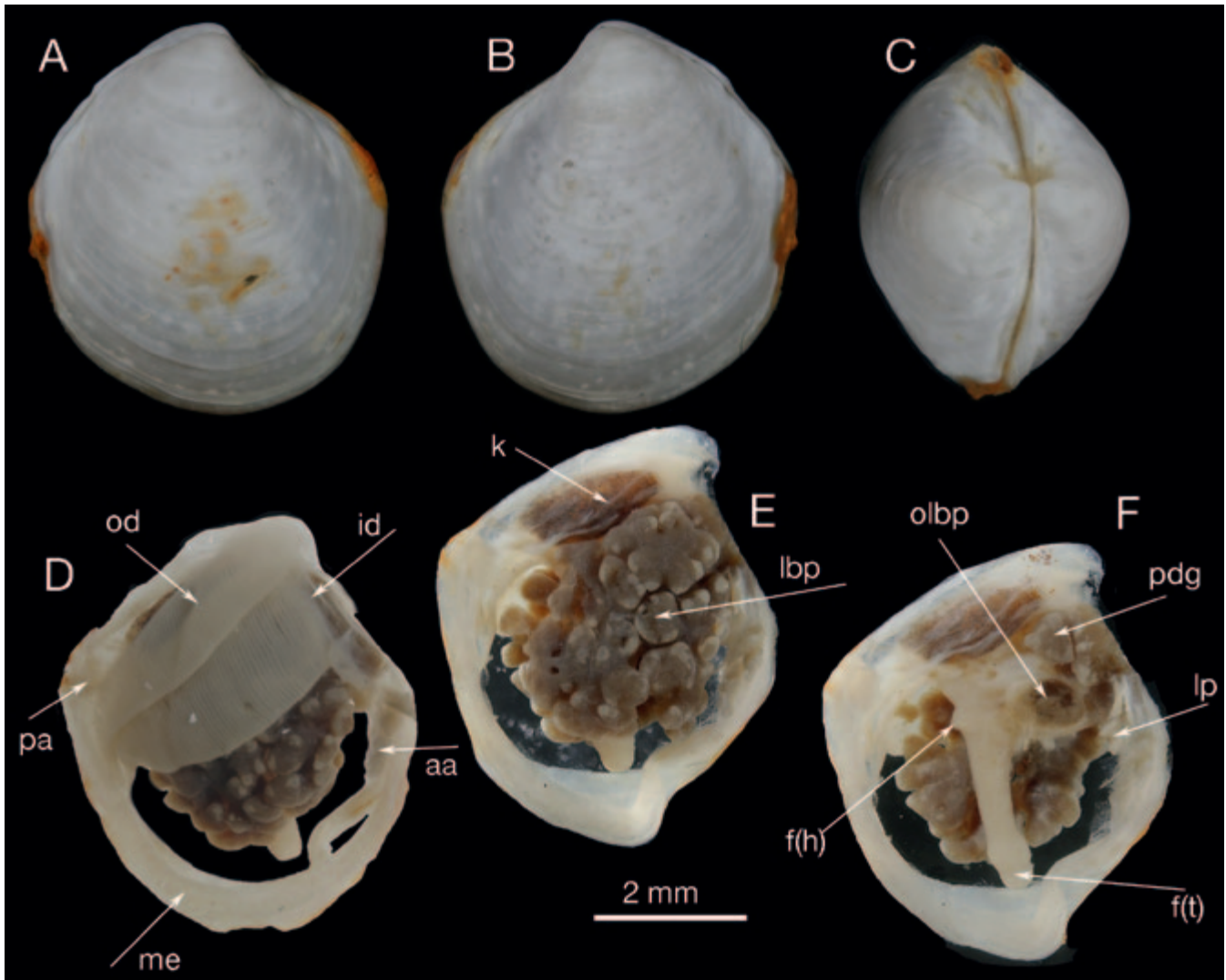
Figure 8 Shell and gross anatomy of *Parathyasira cf. dearborni* Nicol, 1965 from the Kemp Caldera. **A–C**, right, left and dorsal views of the shell. D, gross anatomy after removal of right valve and mantle. **E**, after further removal of the right ctenidium. **F**, after further removal of the right lateral body pouch.

The generic placement of *Thyasira dearborni* in *Parathyasira* was first proposed by Zelaya (2009) and follows placements of similar species such as *T. equalis* (Verril & Bush, 1898) by Oliver & Killeen (2002) and Payne & Allen (1991) albeit at the subgeneric level. Payne & Allen (1991) used *Parathyasira* in a wider sense and, with reservation, included oblong species such as *T. tortuosa* (Jeffreys, 1881) and *T. subovata* (Jeffreys, 1881). However, the type species of *Parathyasira* (*P. resupina* Iredale, 1930) has a microsculpture of radial rows of short spines a feature not present in many species assigned to *Parathyasira*. Oliver (2015) discussed this anomaly but declined from giving nomenclatural recognition to smooth, rhomboidal shells with a simple cleft posterior marginal sinus

and poorly developed posterior sulcus. This latter form is typified by the North Atlantic *Thyasira equalis* (Verrill & Bush, 1898) with the following having similar characteristics: the Antarctic *T. dearborni* and *T. magellanica* Dall,1901 the Arctic *T. dunbari* Lubinsky, 1976, and the abyssal Atlantic *T. biscayensis* Payne & Allen, 1991. The molecular data here suggest that the Kemp shell is congeneric with *T. equalis* and it is therefore likely that this shell form does represent a widespread group warranting nomenclatural recognition. The species compliment for *Parathyasira* in WoRMS (accessed, Sept, 2016) includes both smooth and radially sculptured species but is not complete and illustrates the current unsatisfactory generic definitions within the Thyasiridae.
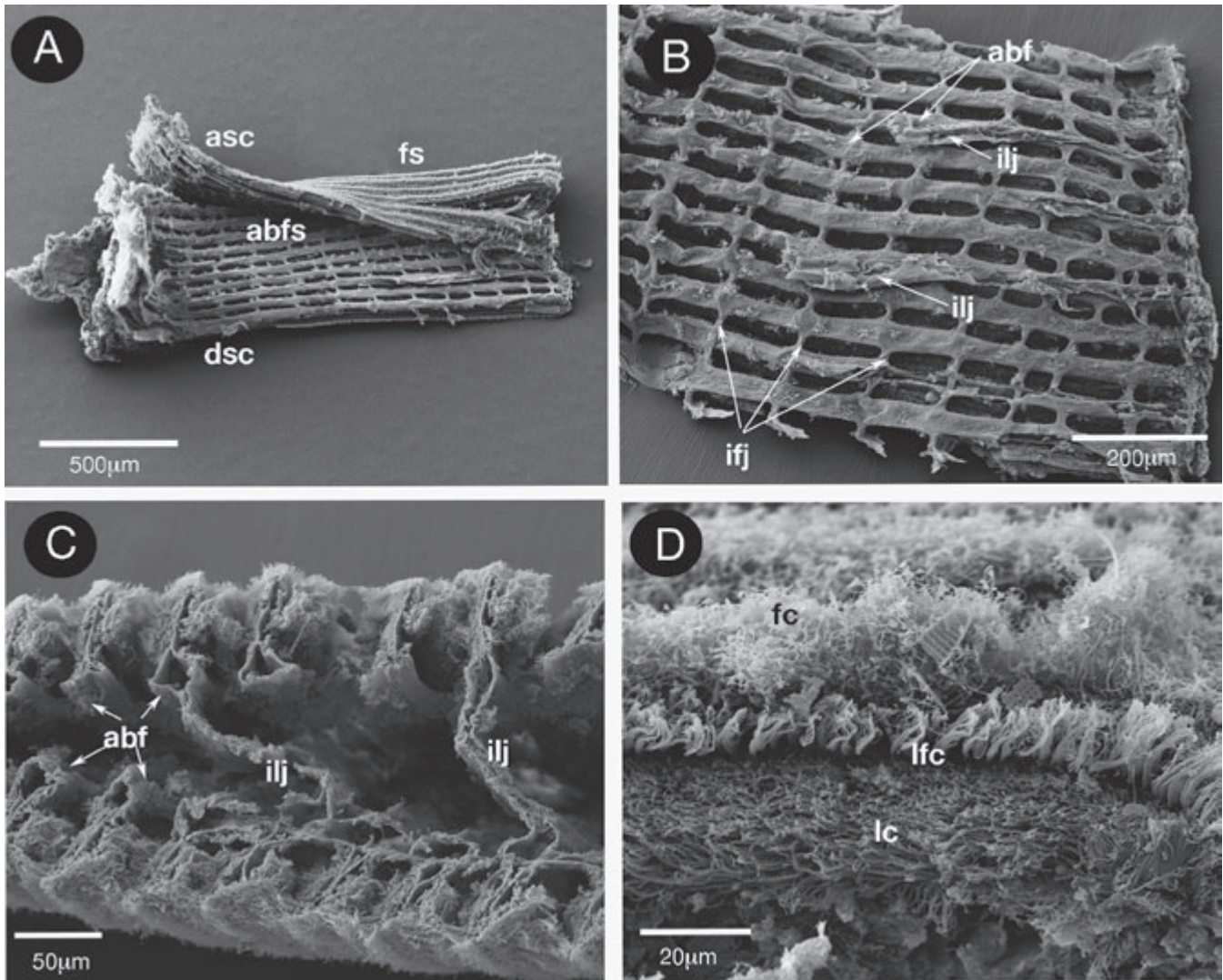
Figure 9   SEM of the ctenidium of *Parathyasira cf. dearborni*. **A–B**, ascending and descending lamellae pulled open to reveal inter filamentar junctions and sparse inter lamellar junctions. **C,** cross section showing lack of abfrontal extensions and sparse inter lamellar junctions. **D**, ciliation of the frontal surface.

BACTERIAL SYMBIOSIS

Bacterial characterization was only possible for those associated with *Spinaxinus caldarium*, no bacterial DNA was detected in *Parathyasira cf. dearborni*. Such findings are in keeping with data available from similar taxa. Bacteria have been found in other species of *Spinaxinus* (Oliver *et al.*, 2013) but not in species similar to *P. dearborni* such as *P. equalis* where there is no abfrontal extension of the gill filaments and lack of bacteriocytes (Dufour, 2005).

A single bacterial 16S rRNA phylotype was retrieved from *S. caladarium* and presented 99% (1336/1342 bp) similarity with the bacterial phylotype associated with *Spinaxinus emicatus* (HG008045), the species described from the Gulf of Mexico (Oliver *et al.*, 2013). Both sequences presented a high similarity with bacterial phylotypes associated with some species of thyasirid and lucinid bivalves but also with several tubeworms such as *Lamellibrachia* sp., *Sclerolinum contortum* and *Escarpia spicata* (95–98%) (Fig. 10). Within the Thyasiridae there is no apparent specificity with any bacterial clade (Fig. 10). This led Oliver *et al.*, (2013) to propose that the bacterial symbionts found in *Spinaxinus emicatus* from the Gulf of Mexico likely originated from a host shift from tube-worm bacteria or from free free-living forms of relatives. This resulted from the observation that the *Spinaxinus* symbionts were more closely related to the above than to
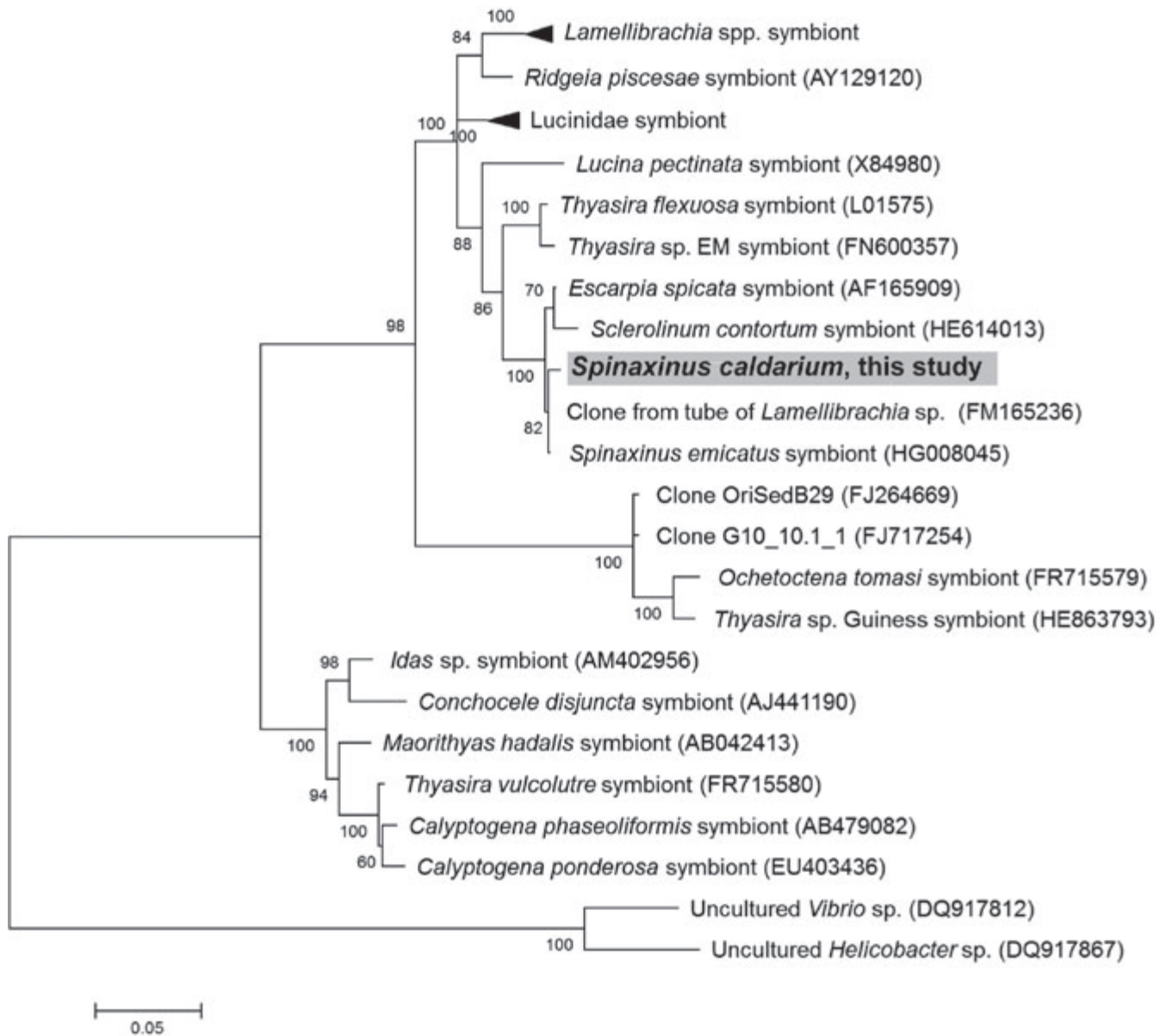
Figure 10 Phylogenetic tree for bacterial symbionts based on the analysis of the bacterial 16 rRNA-encoding gene (1250 nucleotide positions analysed). Bootstraps calculated from 500 NJ replicates (>50 shown). Scale bar represents 5% estimated divergence.

symbionts found in other Thyasiridae species. The discovery here of an almost identical phylotype in *S. caldarium* located some 13,000km from the Gulf of Mexico may rather suggest that in *Spinaxinus* there is a degree of host specificity. However, it has been shown that the population of the siboglinid from Bransfield Strait is conspecific with the North Atlantic *Sclerolinum contortum* Smirnov, 2000 (Georgieva *et al.*, 2015), a species that co-occurs with *S. emicatus* in the Gulf of Mexico. Georgieva *et al.* (2015) were unable to determine the species of *Sclerolinum* found in the Kemp Caldera but suspect that it is *S. contortum*.

In fact *Sclerolinum contortum*, presents a global distribution, have been reported from hydrocarbon seeps in the Arctic Sea and in the Gulf of Mexico, as well as from an arctic hydrothermal vent field (reviewed in Eichinger *et al.* 2014). The host *S. contortum* from the Gulf of Mexico and the Northeast Atlantic show no genetic diversity at the 16S rRNA gene level (Eichinger et al., 2013). Similarly, the bacterial phylotyopes retrieved from specimens collected at both sites (Gulf of Mexico and HMMV) presented a consensus sequence 100% identical (Lösekann *et al.*, 2008). These results indicate a specific and conserved

association between *S. contortum* and its symbionts and a wide geographic distribution of this association. Siboglinids-bacteria symbioses are dictated by horizontal transmission. This high level of homogeneity between symbionts may reflect a limited genetic variability of these symbionts in the environment or a highly selective colonization process (Dubilier *et al.* 2008). The bacterial symbionts from the Antarctic *Scerolinum* have not been characterised but the presence of siboglinids with *Spinaxinus* in both locations suggest that the associations can be maintained and occur over great distances. To date all species of *Spinaxinus* have been found at locations also inhabited by siboglinids of either the genus *Lamellibrachia* or *Sclerolinum* (Dando *et al.*, 1992; Desbruyères *et al.*, 1994; Oliver *et al.*, 2013) but *Spinaxinus* does not occur at all sites inhabited by siboglinids. Relationships between thyasirids and their extracellular symbionts may be relatively less specific or complex than in other groups where symbionts are intracellular. In the past it was suggested that the symbiont distribution showed no pattern of relationship with the thyasirid host, the environmental setting or the geographical location (Oliver *et al*. 2013). However this new finding shows that this may not so straightforward with a clear relationship between *Spinaxinus* and Siboglinidae associated bacteria.

DISCUSSION

The presence of thyasirid bivalves at vent/seep settings is not unusual although at vents they are rare or perhaps just rarely collected. They are generally much smaller than vesicomyids and bathymodiolids and typically deep burrowing. Consequently, they are not seen by ROV operators and this may account for the small numbers collected here and at other sites such as Anyas Garden at the Logatchev site (Oliver & Holmes, 2006). Given that the Thyasiridae are represented by a number of shelf species it is surprising that they have not yet been found at any other vent site on the East Scotia Rise or in the Bransfield Strait. Roterman *et al*. (2016) found for one decapod and two gastropods species that there was little genetic differentiation along the East Scotia Ridge but between the ESR and the Kemp Caldera there was considerable differences. As they suggest, the difference in bathymetry (2400m at the

ESR and 1400m at the KC) may function to isolate populations but may also affect the faunal composition.

Spinaxinus caldarium is the fourth species of this genus to be described and further confirms the close association of this genus with seep and vent settings. It has now been found in the North Atlantic, West Pacific and Antarctic Oceans. The Kemp shells are severely eroded, much more so than any from the other localities. The observation that the *Sclerolinum* from Kemp were in poor condition and Giorgieva's (2015) supposition that this was due to high acidity associated with the high sulphur content of the environment would also explain the eroded condition of the *Spinaxinus* shells.

The co-occurrence of a chemosymbiotic species (*S. caldarium*) with a non-symbiotic species (*P. cf. dearborni*) is not unusual, at least at cold seep sites. Both types are found at the Cadiz mud volcano fields (Rodrigues *et al.*, 2008) and at vent sites off Svalbard (Aström, Oliver & Carroll in press). The non-symbiotic species are not confined to chemosynthetic settings and as in the case of *P. cf. dearborni* may be widely distributed (Zelaya, 2009).

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