

Revision of the generic placement of two hadal bivalves (Bivalvia: Thyasiridae) from the Japan Trench, with the introduction of a new genus, *Tartarothyas*

P. GRAHAM OLIVER¹ & CHONG CHEN²

¹ Honorary Research Fellow, Department of Natural Sciences, National Museum of Wales, Cathays Park, Cardiff, CF10 3NP, Wales, UK

² X-STAR, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2-15 Natsushima-cho, Yokosuka, Kanagawa Prefecture 237-0061, Japan

Corresponding author: P.G. Oliver (graham.oliver@honorary.museumwales.ac.uk)

Abstract. The hadal bivalves from the Japan Trench originally described as *Maorithyas hadalis* and *Parathyasira kaireiaie* are reassigned to the genera *Tartarothyas* n. gen. and *Spinaxinus*, respectively. The shell, anatomy, and fine structure of the ctenidia are described, and based on these the new genus *Tartarothyas* is introduced. Both species have modified ctenidia to host chemosymbiotic bacteria; those of *Tartarothyas* n. gen. is partly tubular in structure, whereas those of *Spinaxinus* is of fleshy lamellae.

Key words. Taxonomy, deep-Sea, morphology, anatomy, gill structure, periostracum, Thyasiroidea

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INTRODUCTION

In 1999 Fujikura *et al.* reported the discovery of a hydrocarbon seep from the hadal depths of 7326 m in the Japan Trench, the deepest chemosynthesis-based community known. In that year, two species of Thyasiridae were described by Okutani *et al.* (1999), namely *Maorithyas hadalis* Okutani, Fujikura & Kojima, 1999 and *Parathyasira kaireiaie* Okutani, Fujikura & Kojima, 1999. The former species has been recorded at depths of 7326–7434 m, while the latter at 5791–6390 m (Okutani 2008, 2017).

Maorithyas hadalis was shown to be the only species of Thyasiridae in which the symbiotic bacteria were intracellular (Fujikura *et al.* 1999; Fujiwara *et al.* 2001), whereas in all other thyasirids they were found to be extracellular (Dufour 2005). Despite this exceptional discovery, no further anatomical work was done, but the generic placement was changed to *Axinulus* Verrill & Bush, 1898 by Matsuoka (2000) and followed by Sasaki *et al.* (2005), Okutani in Fujikura *et al.* (2008), and Okutani (2017). The generic placement was challenged on several occasions (Oliver & Sellanes 2005; Oliver 2014; Åström *et al.* 2017; Kamenev 2020). Valentich-Scott *et al.* (2014) compared the holotype of *M. hadalis* with the type species of *Maorithyas*, *M.*

marama Fleming, 1950, concluding that the two were not congeneric. However, without further anatomical studies, no alternative placement was given, except that in the online WoRMS and MolluscaBase databases the transfer to the genus *Axinulus* is accepted. The latter placement seems unlikely given that species of *Axinulus* are very small and with a single demibranch (Kamenev 2020), and they are not known to host chemosymbiotic bacteria (Dufour 2005).

Although *P. kaireiaie* has been cited by authors such as Kamenev (2023), the anatomy and shell of this species has not been examined in detail, and its placement in *Parathyasira* has never been verified. The presence of radial rows of minute shell spicules is diagnostic of *Parathyasira*, as shown in the type species, *P. resupina* Iredale, 1930; such spicules are not mentioned in the original description of *P. kaireiaie*.

Here, we were able to select a few specimens of each species from seeps in the Japan Trench for further examination, and this paper describes the shell and anatomy and proposes revised generic placements for both species.

As a matter of correctness, we note here that the bathymetric definition of the hadal zone is beyond 6000 m. While *M. hadalis* was taken in this zone at over 7000 m, *P. kaireiaie* was also taken from depths between 5000 and 6000 m,

which are not strictly hadal, although all were taken from the Japan Trench.

METHODS AND MATERIALS

Methods. Thyasirids were collected by scoop samplers or push cores operated by robotic arms of either the remotely operated vehicle (ROV) *Kaiko* on-board the R/V *Kairei* in 2002 or the deep-submergence vehicle (DSV) *Shinkai 6500* on-board the R/V *Yokosuka* in 2000. In the laboratory, dissections using a stereo light microscope were made by sequentially removing the shell and tissues from the left side in the order: shell, mantle, ctenidium, and lateral body pouch. Once all were removed, dissection of the visceral mass could be made to reveal the route and structure of the gut. In some instances, the tissues were stained with methyl blue to enhance contrast. These observations were supported by scanning electron microscopy of the shell and soft tissues, primarily the ctenidium. Soft tissues were excised, and the ctenidia were sliced into small pieces both transversely and longitudinally. These were dehydrated in 100% ethanol prior to critical point drying using CO₂ as the intermediary fluid in a Quorum K850 critical-point dryer. These were mounted on stubs and gold coated prior to viewing using a Jeol JCM-7000 NeoScope benchtop scanning electron microscope. Specimens studied are deposited in the National Museum of Wales, Cardiff (NMW).

Specimens examined.

"*Axinulus*" *hadalis*:

3 individuals (NMW.Z.2024.008.01), fixed in 10% formalin and transferred to 70% ethanol for preservation, 7324 m deep, Japan Trench (40°2.728'N, 144°16.551'E), 2002/Jul/13, ROV *Kaiko* Dive #252, R/V *Kairei* cruise KR02-09.

Parathyasira kaireia:

4 individuals (NMW.Z.2024.008.02), initially frozen at -80 °C then transferred to 70% ethanol, 5300 m deep, Japan Trench (39°6.5'N, 143°53.4'E), 2000/Jun/15, DSV *Shinkai 6500* Dive #550, R/V *Yokosuka* cruise YK00-04 Leg 2.

5 individuals (NMW.Z.2024.008.03), preserved in 70% ethanol, 5379 m deep, Japan Trench (39°6.34'N, 143°53.52'E), 2000/Jun/18, DSV *Shinkai 6500* Dive #553, R/V *Yokosuka* cruise YK00-04 Leg 2.

Abbreviations.

aam, anterior adductor muscle	dst, lbp, dorsal stem of lateral
aas, anterior adductor-muscle scar	body pouch
arm, anterior retractor muscle	et, entrance to tube
bct, bacteriocyte	exa, exhalant aperture
ct, ctenidium	f, foot
	fz, frontal zone

heel	omf, outer mantle fold
hg, hind gut	ot, oral tube
id, inner demibranch	pam, posterior adductor muscle
ina, inhalant aperture	pas, posterior adductor-muscle scar
k, kidney	per. f, periostracal folds
lbp, lateral body pouch	prm, posterior retractor muscle
lig, ligament	ps, posterior sulcus
lmz, lamellar zone	r, rectum
lp, labial palps	rad. st, radial striations
lun, lunule	s, stomach
me, mantle edge	sms, submarginal sulcus
mg, mid gut	tbz, tubule zone
mms, mantle muscles scars	toe
mo, mouth	vst, lbp, ventral stem of lateral
mv, microvillar surface	body pouch
od, outer demibranch	
oe, oesophagus	

RESULTS

Tartarothyas n. gen.

Monotypic, type species: *T. hadalis* (Okutani, Fujikura & Kojima, 1999).

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Etymology. From *Tartarus* in Greek mythology, the deep abyss used as a dungeon of torment, and used here in reference to the dark region of the ocean floor, especially the hadal zone. It is used in conjunction with *thyas*, a contraction of *Thyasira*.

Definition. Shell medium-sized to 37 mm, subovate; posterior slope long, gently curved; posterior sinus shallow; submarginal sulcus shallow, sharp-edged; auricle lacking; anterior rounded; lunule margin slightly indented; lunule weakly defined. Sculpture of closely spaced, low, commarginal lirae and incised lines. Inner surface radially striate. Periostracum persistent, with minute spines. Hinge edentulous; ligament deeply sunken, short. Ctenidium of two demibranchs; filaments tubular and lamellar. Foot hatchet-shaped. Symbiotic bacteria of two kinds, intracellular.

Remarks. The size and the rather featureless shell that is scarcely sinuous posteriorly and with a very shallow posterior sulcus is unlike most other thyasirids, but the shape is most similar to species of *Spinaxinus* Oliver & Holmes, 2006 (Fig. 12), namely *S. sentosus* Oliver & Holmes, 2006, *S. emicatus* Oliver *et al.*, 2013, *S. phrixicus* Oliver *et al.*, 2013, and *S. caldarium* Oliver & Rodrigues, 2017. In size and form, it is not unlike *Rhacothyas* Åström & Oliver *in* Åström *et al.*, 2017, but here the posterior sinus and lunule are more strongly expressed. The similarity with *Spinaxinus* is further

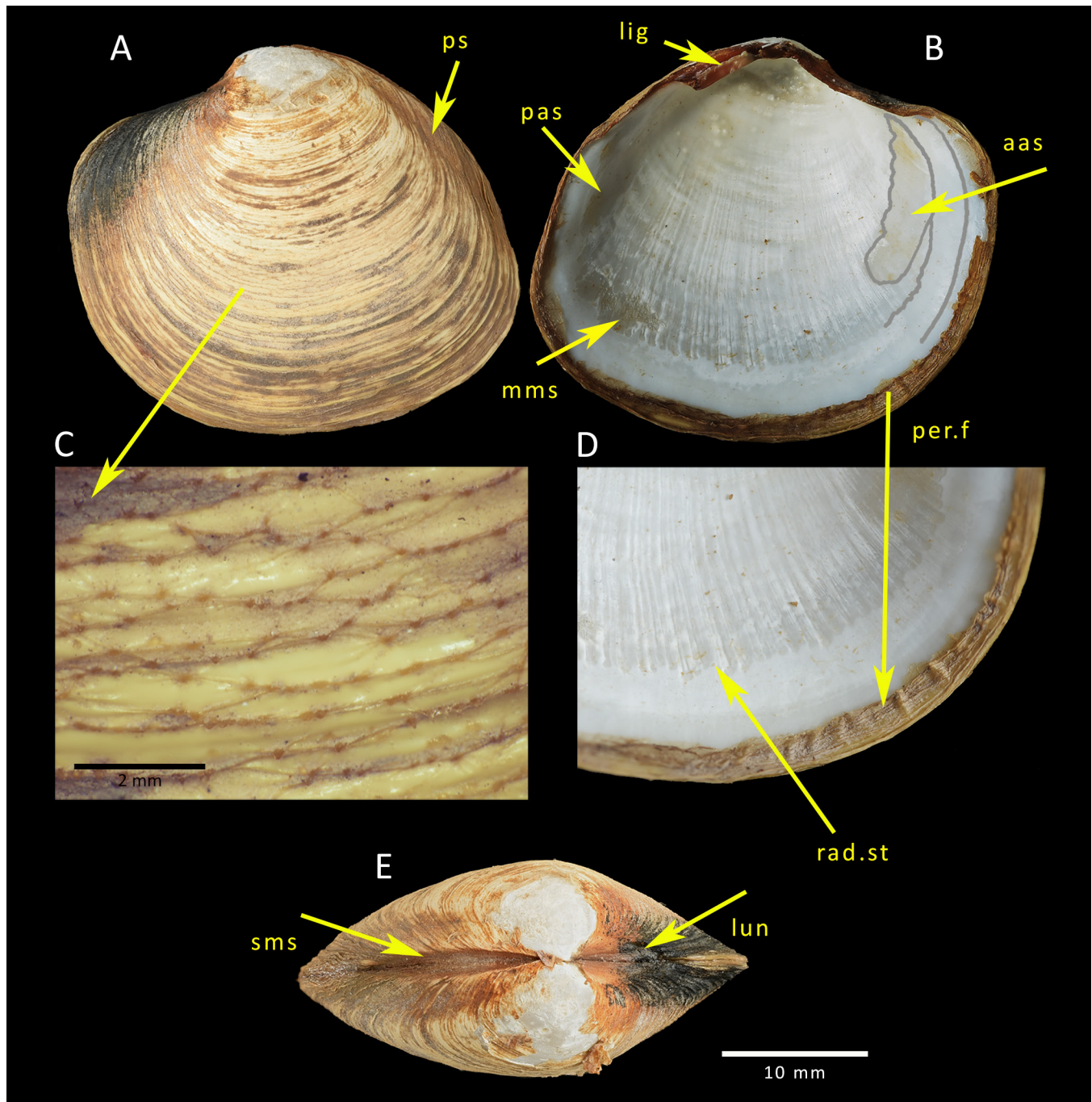


Figure 1. *Tartarothyas hadalis* shell (NMW.Z.2024.008.01). A, left valve external. B, left valve internal. C, periostracum. D, internal margin showing radial periostracal folds and radially striated interior. E, dorsal view of shell.

are *Parathyasira* Iredale, 1930 and *Ochetoctena* Oliver, 2014, but in these genera the spines are calcareous and not periostracal.

Characters not shared with *Spinaxinus* include the hatchet-shaped, rather than vermiform, foot; the convoluted, rather than smooth, mantle edge; the partly tubular, rather than lamellar, gill structure; and the unique feature

setting it apart from all other thyasirids—the intracellular symbionts.

***Tartarothyas hadalis* (Okutani, Fujikura & Kojima, 1999), n. comb.**

Revised species description. Shell (Fig. 1A–E) medium-sized; type series 26.3–36.5 mm in length, specimens exam-

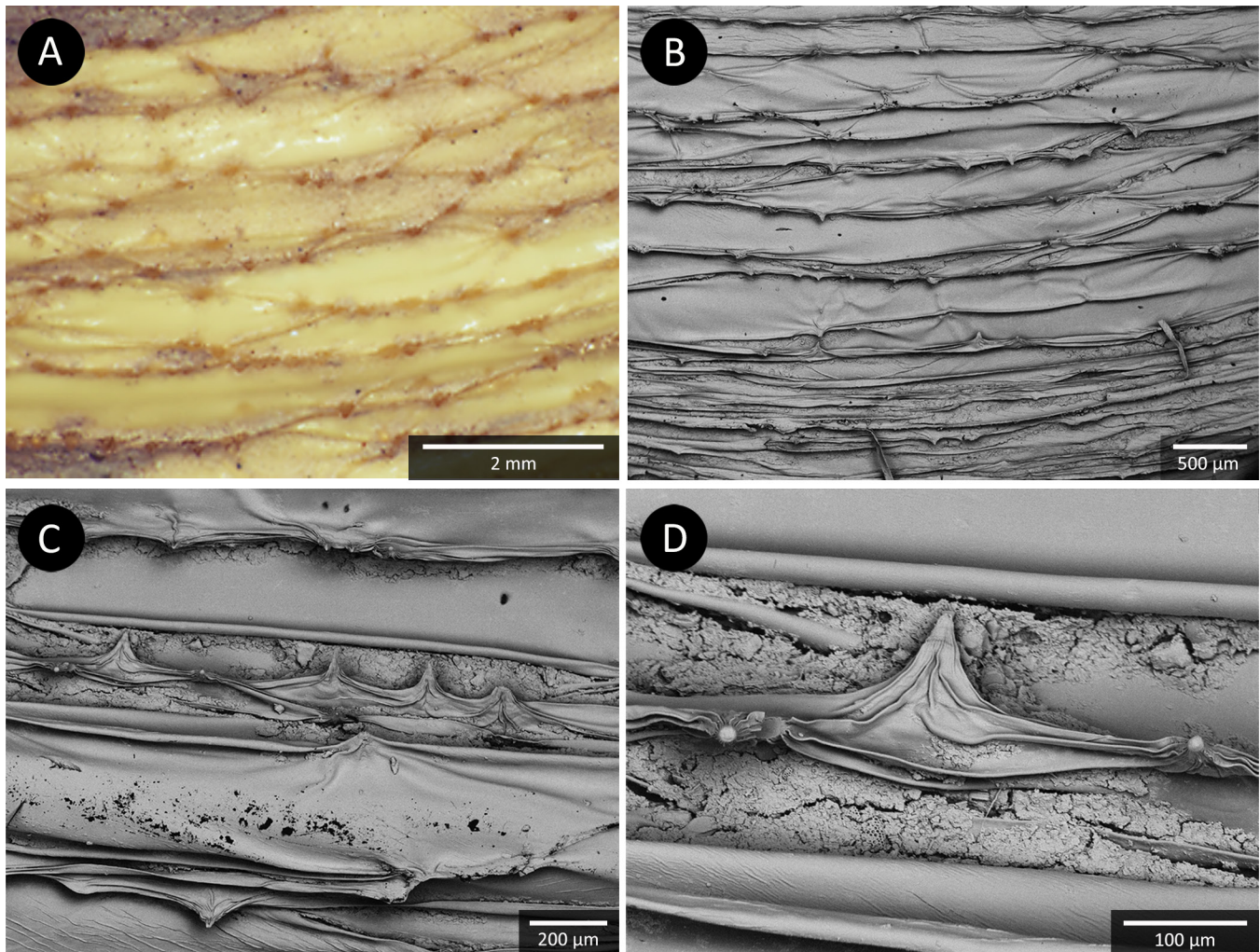


Figure 2. *Tartarothyas hadalis* periostracum (NMW.Z.2024.008.01). A, under natural light. B–D, scanning electron micrographs at increasingly greater magnifications.

ined here 27–32 mm in length. Shell thin, brittle; umbos heavily eroded in all. Outline subovate, almost equilateral; beaks slightly nearer to anterior end, slightly longer than high; posterior slope long, gently curved, straightening a little adjacent to posterior sinus, but scarcely indented; ventral margin broadly curved continuous with anterior; lunule margin short, little sunken. Posterior sulcus shallow; submarginal sulcus (escutcheon) long, narrow, shallow, without auricle. Lunule poorly demarcated, shallow, narrow. Sculpture of dense, rounded, commarginal lirae, somewhat variable in expression, fading anteriorly and over posterior sulcus. Hinge edentulous; ligament deeply sunken, extending to one-half length of submarginal sulcus. Periostracum persistent, straw-coloured, with darker anastomosing threads bearing scattered, triangular spines up to 100 µm long (Fig. 2A–D). Periostracum forming widely spaced radial ridges on inner margins of shell. Shell interior white,

with dense, prominent radial striations. Muscle scars weakly impressed; anterior adductor scar elongate, slightly diverging from pallial line for half its length; three times length of posterior adductor scar. Mantle margin muscle scars prominent.

Anatomy (Figs 3–6). Mantle edge free except for short, smooth exhalent aperture. Inner mantle fold expanded, appearing as dissected blocks of tissue (Fig. 5A, B). Anterior adductor muscle elongate, with inhalant aperture on its inner face; Y-shaped ridge and sensory papillae prominent.

Ctenidium (Figs 5C–E, 6A–F) of both demibranchs; outer demibranch approximately one-half depth of inner demibranch; filaments reflected, thick, fleshy. Filaments consisting of three layers: frontal zone of ciliated bands; tubule zone of short tubules, their apertures prominent at low magnification, lying between frontal ciliated bands; inner zone of lamellar extensions of tubules. Tubules lined

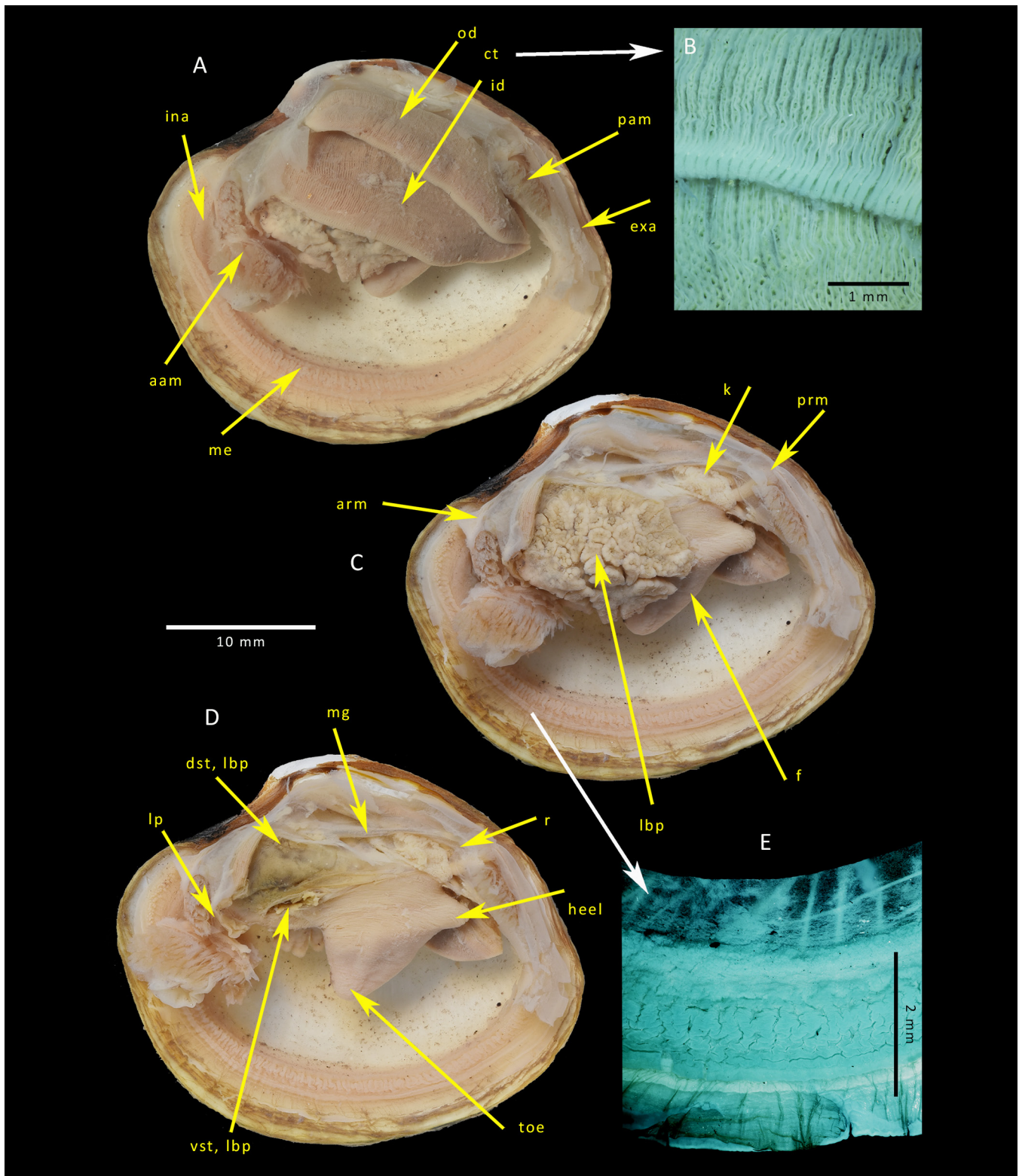


Figure 3. *Tartarothyas hadalis* gross anatomy (NMW.Z.2024.008.01). A, from left side mantle removed. B, fragment of ctenidium showing openings to tubules under natural light. C, from left side mantle and ctenidium removed. D, from left side mantle, ctenidium and lateral body pouch removed. E, detail of the mantle edge folds.

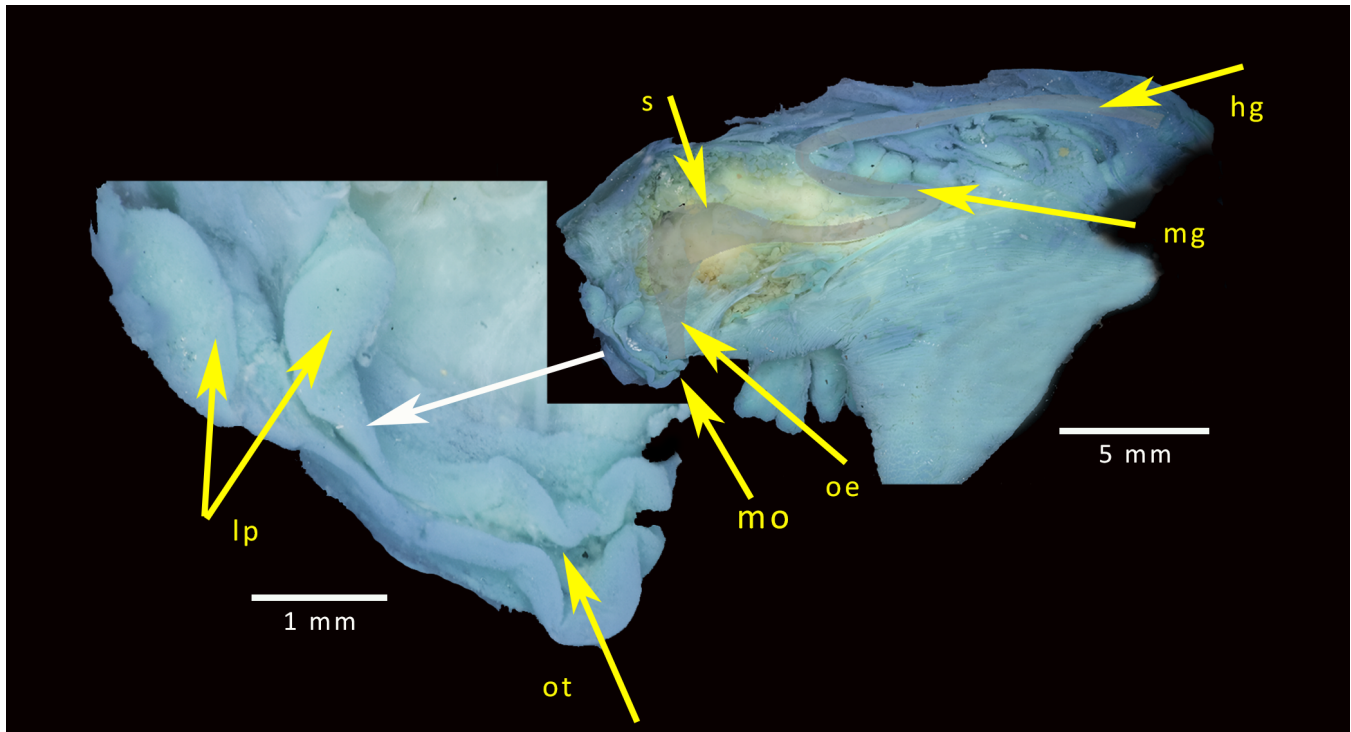


Figure 4. *Tartarothyas hadalis* (NMW.Z.2024.008.01) tracing the route of the alimentary system and labial palps.

with closely packed bacteriocytes, with these less dense on lamellae.

Labial palps very small, with no apparent sorting ridges (Fig. 4).

Lateral body pouches large, of closely packed polygonal processes; these densely granular, with small opaque protuberances at their centres. Large body pouch attached near base on visceral mass; a second very small pouch dorsally. Gut (Fig. 4) simple; short oesophagus entering simple cylindrical stomach; mid-gut exiting posteriorly then forming s-shaped loop before running posteriorly over posterior adductor with anus adjacent to exhalant aperture.

Foot hatchet-shaped, with short, broad toe and small heel.

Remarks. A seabed photograph (Fig. 7) shows living specimens at the surface of the sediment, which is atypical of most thyasirids, which mostly live deep in the sediment. Similar observations have been made for the large, seep-inhabiting *Conchocele* Gabb, 1866 (Okutani in Fujikura *et al.*, 2008; Kharlamenko *et al.*, 2016). *Tartarothyas hadalis* has a hatchet-shaped foot, with a short toe, and lacks the vermiform foot seen in deep-burrowing species. This hatchet-shaped foot is much better adapted to ploughing through sediment rather than the sedentary deep-dwelling habit of other species.

The ctenidial structure is complex, with the filaments modified into tubules close to the frontal surface but as lamellae distally. Tubular structures have been observed in other thyasirids associated with methane seeps. In *Ochetocmeta* Oliver, 2014 from off West Africa, the tubules form a complete network lacking lamellae (Oliver 2014). The structure in *Conchocele* is more similar, with tubules limited to the frontal zone, but the *Conchocele* ctenidium has well-defined interlamellar junctions and spaces as well as elevated frontal ridges (Oliver 2014), none of which are present in *Tartarothyas*.

The inner fold of the mantle edge is unusually thickened and deeply folded. In the preserved state, it takes the form of smooth, cushion-like blocks, but in places the surface is broken and dense, finger-like strands protrude. It is possible that this surface can be expanded and may function as a secondary gill, as seen in many lucinids (Taylor & Glover 2021).

The alimentary system is simple, with the labial palps very small and lacking sorting ridges, which suggests that little suspended material is ingested. The stomach is thin-walled and cylindrical in form, and sorting ridges are not apparent. The mid- and hind-gut are simple tubes, and faecal material was not observed. These observations suggest that suspension feeding is scarcely or never employed, with nutrition relying totally on the symbionts.

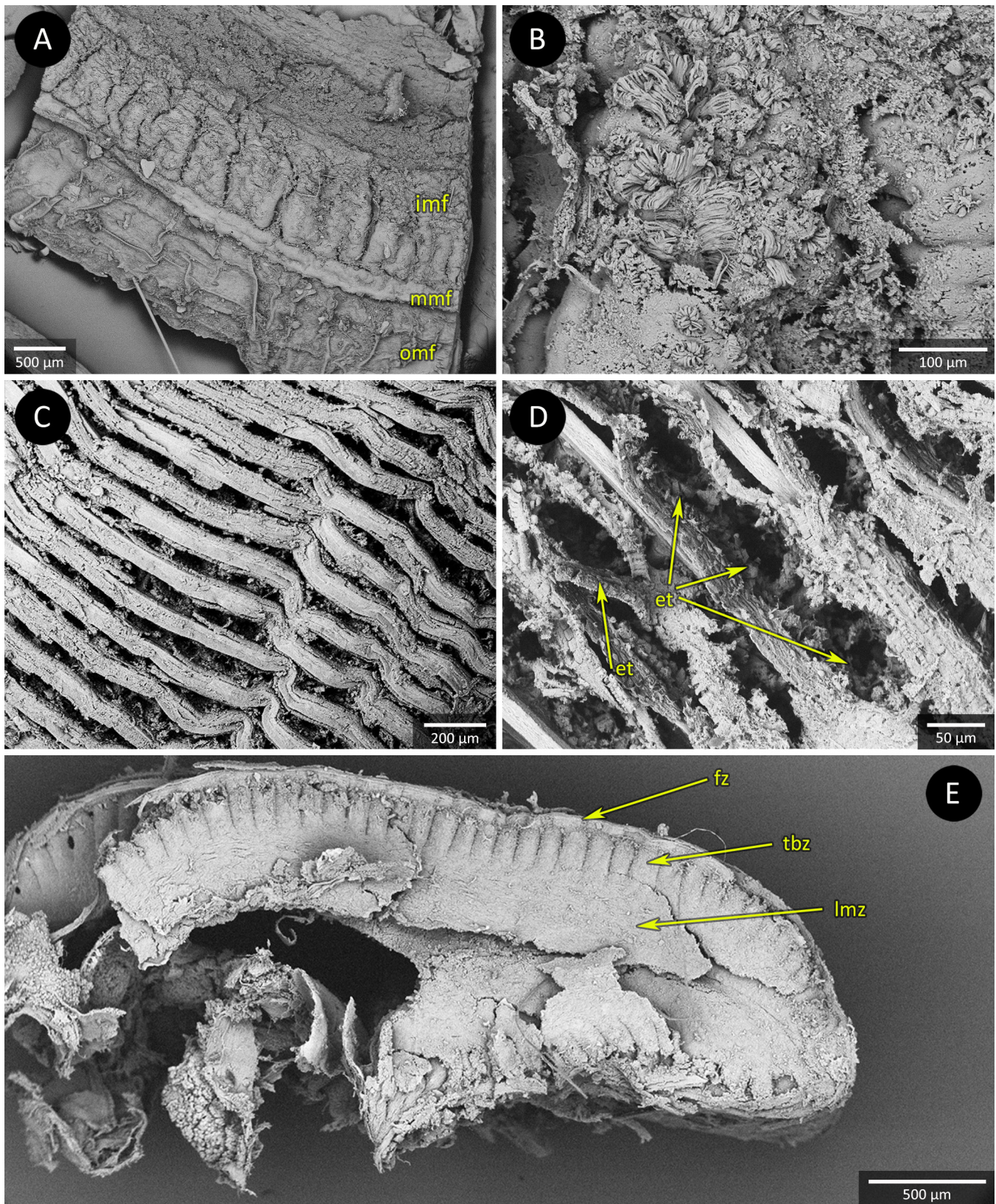


Figure 5. *Tartarothyas hadalis* scanning electron micrographs (NMW.Z.2024.008.01). A, mantle folds. B, erupted surface of inner fold revealing internal strands. C, frontal surface of ctenidium. D, frontal surface with openings to tubules. E, lateral view of filaments showing the frontal, tubule, and lamellar parts.

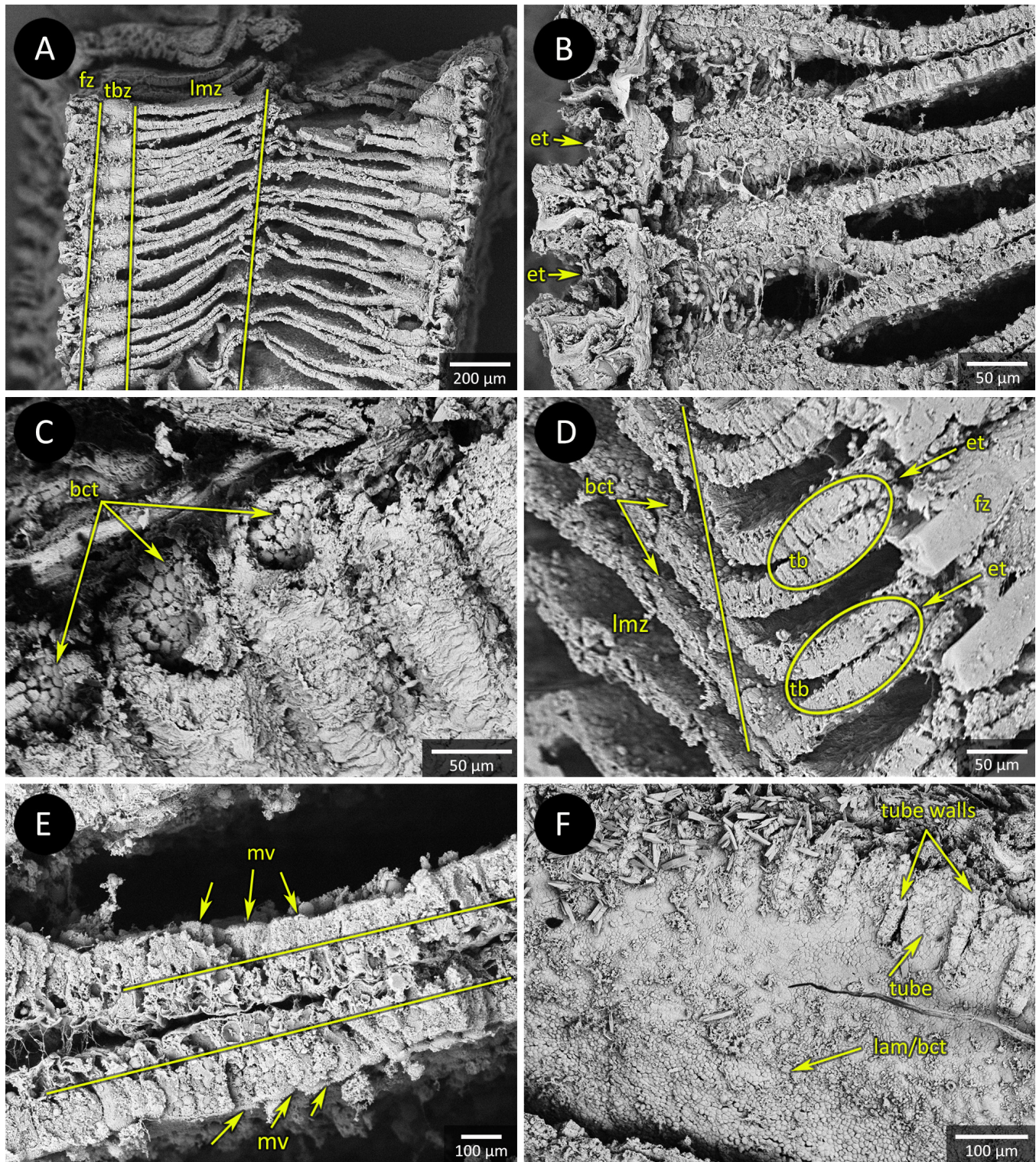


Figure 6. *Tartarothyas hadalis* scanning electron micrographs (NMW.Z.2024.008.01). **A**, transverse section across a demibranch showing filament structure in ascending and descending arms. **B**, detail from **A** showing transition of tubules to lamellae. **C**, fractured tubules showing lining of bacteriocytes. **D**, tubules in section showing dense bacteriocytes. **E**, section of lamella with dense bacteriocytes on their outer surface with a micro-villar lining. **F**, filament split revealing inner surface of tube and lamellar layer.

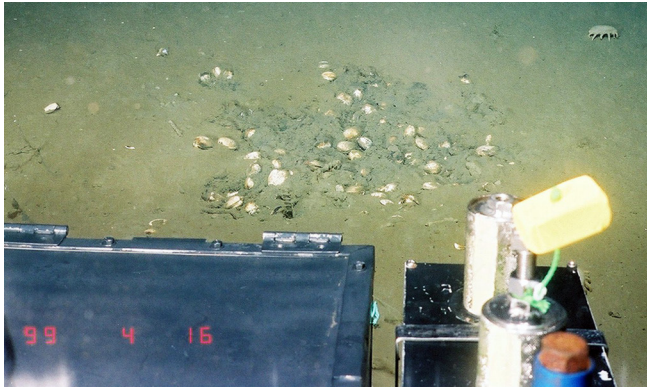


Figure 7. *Tartarothyas hadalis* in life position, 7337 m deep, Japan Trench, ROV KAIKO Dive #110. Image retrieved from the JAMSTEC E-library of Deep-sea Images (J-EDI; <https://www.godac.jamstec.go.jp/jedi/>).

Spinaxinus Oliver & Holmes, 2006

Type species: *Spinaxinus sentosus* Oliver & Holmes, 2006

Other species: *Spinaxinus emicatus* Oliver in Oliver *et al.*, 2013; *S. phrixicus* Oliver in Oliver *et al.*, 2013; *S. caldarium* Oliver & Rodrigues, 2017 (Fig. 12).

Redefinition. Shell 10–25 mm in length, thin-shelled, equi-valve, slightly inequilateral beaks at or slightly behind mid-line; outline subquadrate to subcircular; lunule margin well marked; posterior sulcus shallow to indistinct; submarginal sulcus narrow; auricle lacking. Sculpture weak, of growth line and ridges. Periostracum persistent, with well-developed, dense spines. Foot vermiform; ctenidium of both demibranchs; fleshy filaments lamellar, with dense bacteriocytes.

Remarks. See *Tartarothyas* above.

Spinaxinus kaireiae (Okutani, Fujikura & Kojima, 1999), n. comb.

Revised species description. Shell (Figs 8, 9) small, type series 11.7–12.3 mm long, maximum size of specimens examined here 9.5 mm long. Equivalve, more or less equilateral; beaks prosogyre. Outline subquadrate; lunule margin relatively long, straight, sloping to rounded anterior; posterior-dorsal edge curved; posterior end truncate, very slightly indented; ventral edge broadly curving. Posterior sulcus prominent but shallow; submarginal sulcus narrow, shallow; auricle lacking. Lunule elongate, weakly defined. Hinge edentulous; right valve with a slight cardinal protuberance. Ligament partially sunken, one-half length of submarginal sulcus. Sculpture of commarginal growth lines and low lirae, somewhat variable in thickness; lunule tubercu-

late. Periostracum persistent, laminate, with minute spines most prominent at margins and over posterior sulcus; spines reaching 10 μ m in length.

Adductor scars unequal; anterior adductor scar approximately three times length of posterior, ventral part divergent from pallial line. Inner margin smooth; pallial line broad; adductor-muscle scars indistinct. Shell white but appears pale grey due to sediment trapped by periostracum.

Anatomy (Figs 10, 11). Anterior inhalant aperture adjacent to anterior adductor muscle. Exhalant aperture small, immediately below posterior adductor muscle. Mantle edge slightly thickened, smooth, with weak, radial, mantle muscles on inner edge of margin. Foot vermiform, with toe swollen, heel small. Ctenidium of inner and outer demibranchs; outer demibranch about one-third depth of inner demibranch; filaments fleshy, lamellar, with dense bacteriocytes. Labial palps very small; sorting ridges not apparent. Alimentary system simple; stomach cylindrical, thin-walled; mid- and hind-gut forming simple, S-shaped loop; rectum opening over posterior adductor muscle. Kidney indistinct but marked by presence of small brown granules.

Remarks. The absence of radial rows of shell micro-tubercles is not consistent with placing this species in *Parathyasira*, and the presence of the spiny periostracum is consistent with *Spinaxinus*. Of the known species of *Spinaxinus*, *S. kaireiae* is most similar to *S. emicatus* from the Gulf of Mexico but is smaller and less posteriorly expanded. Furthermore, the lunule of *S. emicatus* is not sculptured.

DISCUSSION

Both species under consideration here have been reassigned to different genera, although they both share a spiny periostracum. They may be closely related, but the ctenidial and anatomical differences of *T. hadalis* and *S. kaireiae* warrant recognition at the generic level. It remains an assumption that *T. hadalis* is the only species of Thyasiridae that has intracellular symbiotic bacteria, but no species of *Spinaxinus* has been examined in this regard.

Fukasawa *et al.* (2017) presented a phylogenetic analysis of Solemyidae and Thyasiridae in which both *T. hadalis* and *S. kaireiae* were included. Most taxa included were from Japanese waters, and these were combined with the data from Taylor *et al.* (2007). The 18S rRNA tree in Fukasawa *et al.* (2017: fig. 5) reflects the tree published by Taylor *et al.* (2007), with the addition of two clusters, one containing *T. hadalis* and the other *S. kaireiae*. The sister taxon to *T. hadalis* was found to be “*Thyasira* sp. Fiji 1977 m” (*sensu*

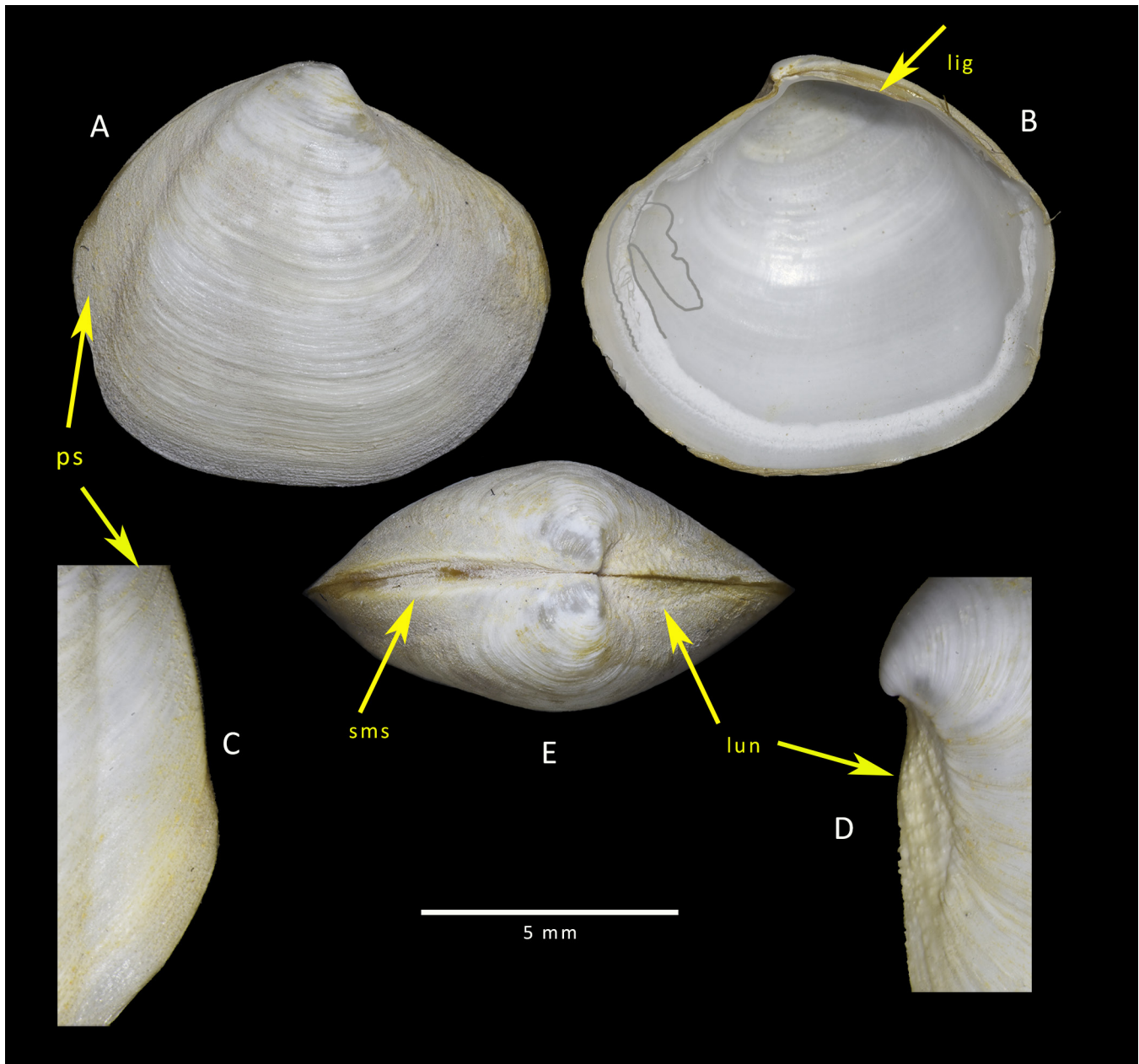


Figure 8. *Spinaxinus kaireiae* shell (NMW.Z.2024.008.02). A, external right valve. B, internal of right valve. C, posterior sulcus of left valve, periostracal spines barely visible. D, lunule. E, dorsal view.

Fukasawa *et al.* 2017), which is *Spinaxinus phrixicus* Oliver, 2013 (Oliver & Rodrigues 2017), thus, confirming the close relationship between *Tartarothyas* and *Spinaxinus*. The second cluster “Cluster A” contains *S. kaireiae* and several unidentified species from bathyal depths. Despite all the *S. kaireiae* coming from the same sample, they do not cluster together, and this is also true for the bathyal species which appear in disconnected parts of the tree. These latter discrepancies throw some doubt on the accuracy of the tree in “Cluster A”, but it does support a not-too-distant link with *T.*

hadalis and *S. phrixicus*, which one might expect, given the similarities in shell form and, notably, the spiny periostracum. Fukasawa *et al.* (2017) also suggested that the bathyal species and the hadal *S. kaireiae* are all the same species. We cannot comment on this, as their bathyal taxa are not named or described and morphological data was not presented in their paper, although we find this unlikely. Both the mitochondrial cytochrome oxidase *c* subunit I (COI) and the concatenated 18S + COI trees in Fukasawa *et al.* (2017) do not resolve the issue of specimens supposedly from the

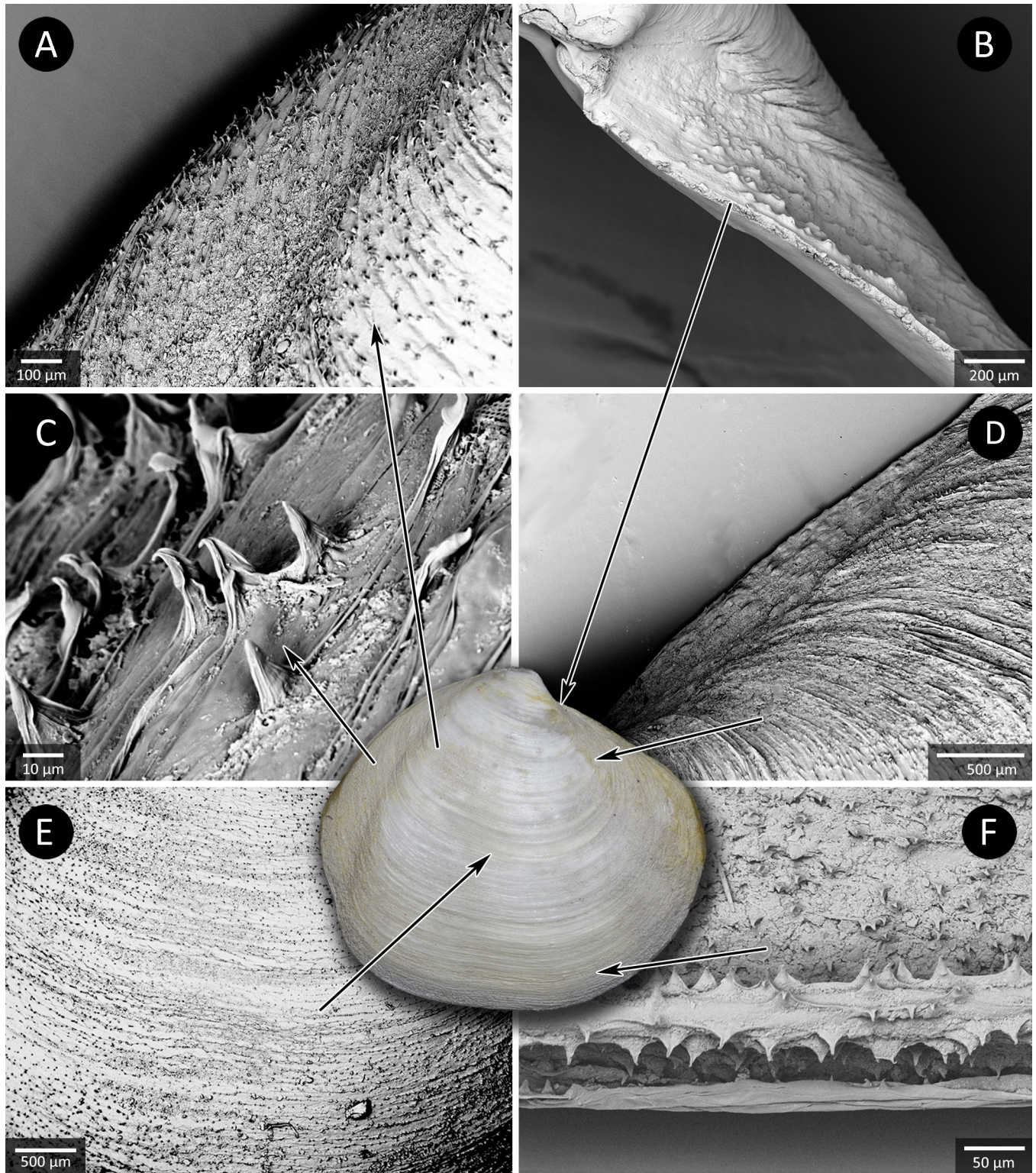


Figure 9. *Spinaxinus kaireiae* periostracum (NMW.Z.2024.008.02). Scanning electron micrographs, shell to indicate areas imaged. A, over posterior angle into sulcus, $\times 100$. B, raised sculpture on lunule. C, individual spines in posterior sulcus, $\times 1,000$. D, over junction with lunule, $\times 43$. E, over middle of valve, $\times 30$. F, at margin, $\times 300$.

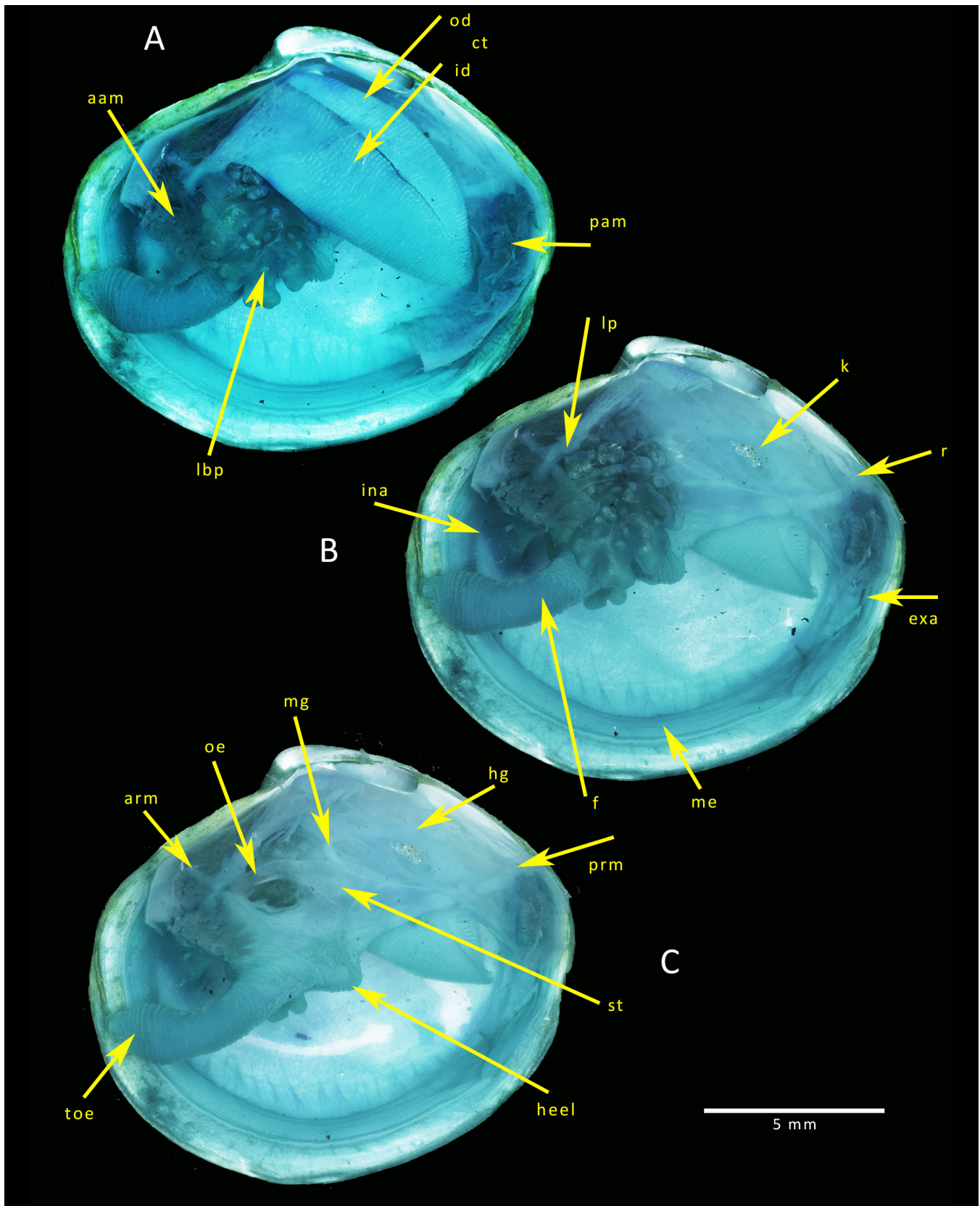


Figure 10. *Spinaxinus kaireiae* gross anatomy (NMW.Z.2024.008.03). A, from left side mantle removed. B, from left side mantle and ctenidium removed. C, from left side mantle, ctenidium and lateral body pouch removed.

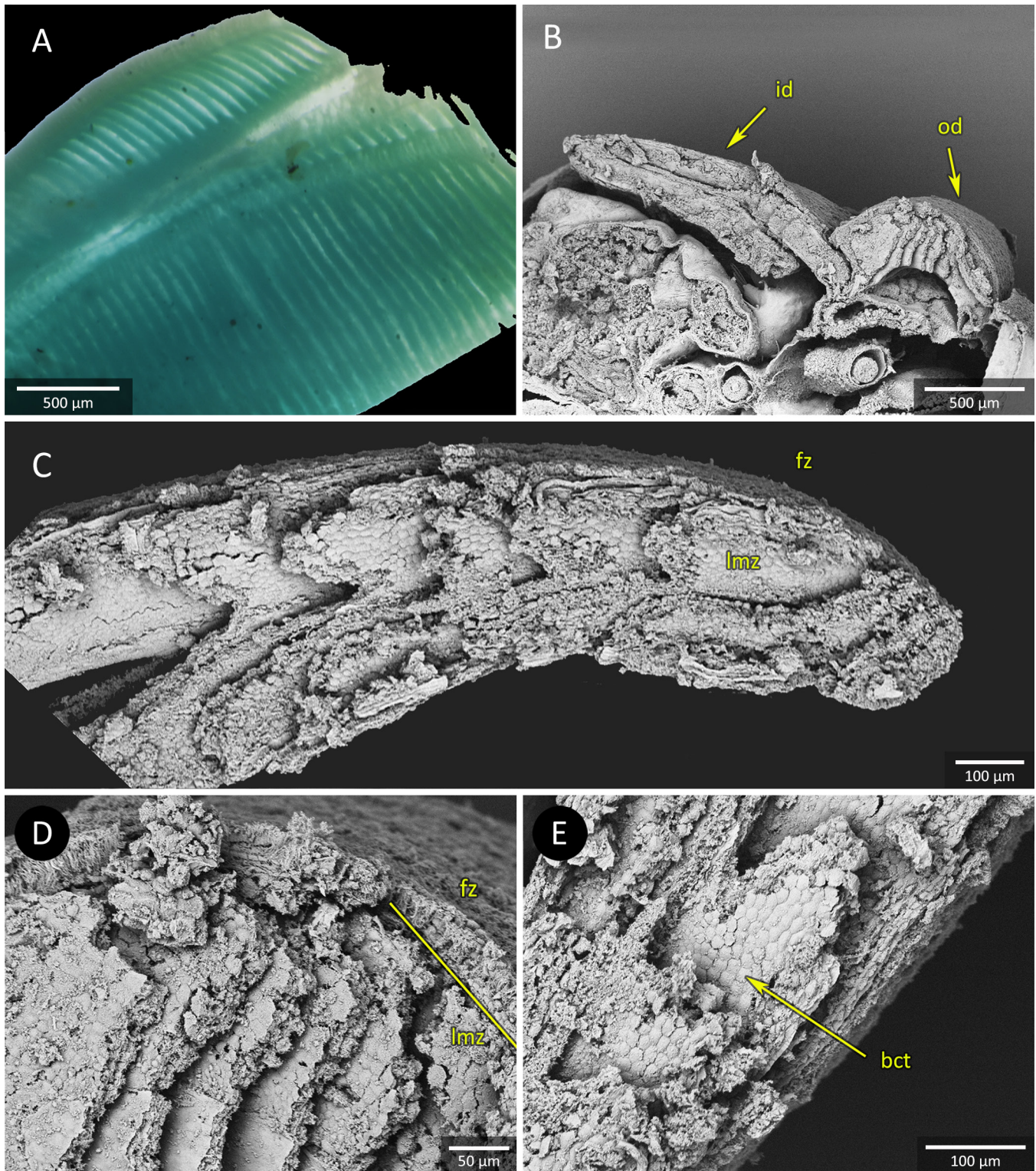


Figure 11. *Spinxinus kaireiae* ctenidium (NMW.Z.2024.008.03). **A**, under natural light, **B–E** scanning electron micrographs. **B**, section across both demibranchs. **C**, lateral view of lamellar filaments. **D**, **E**, magnified areas from **C** showing bacteriocytes.

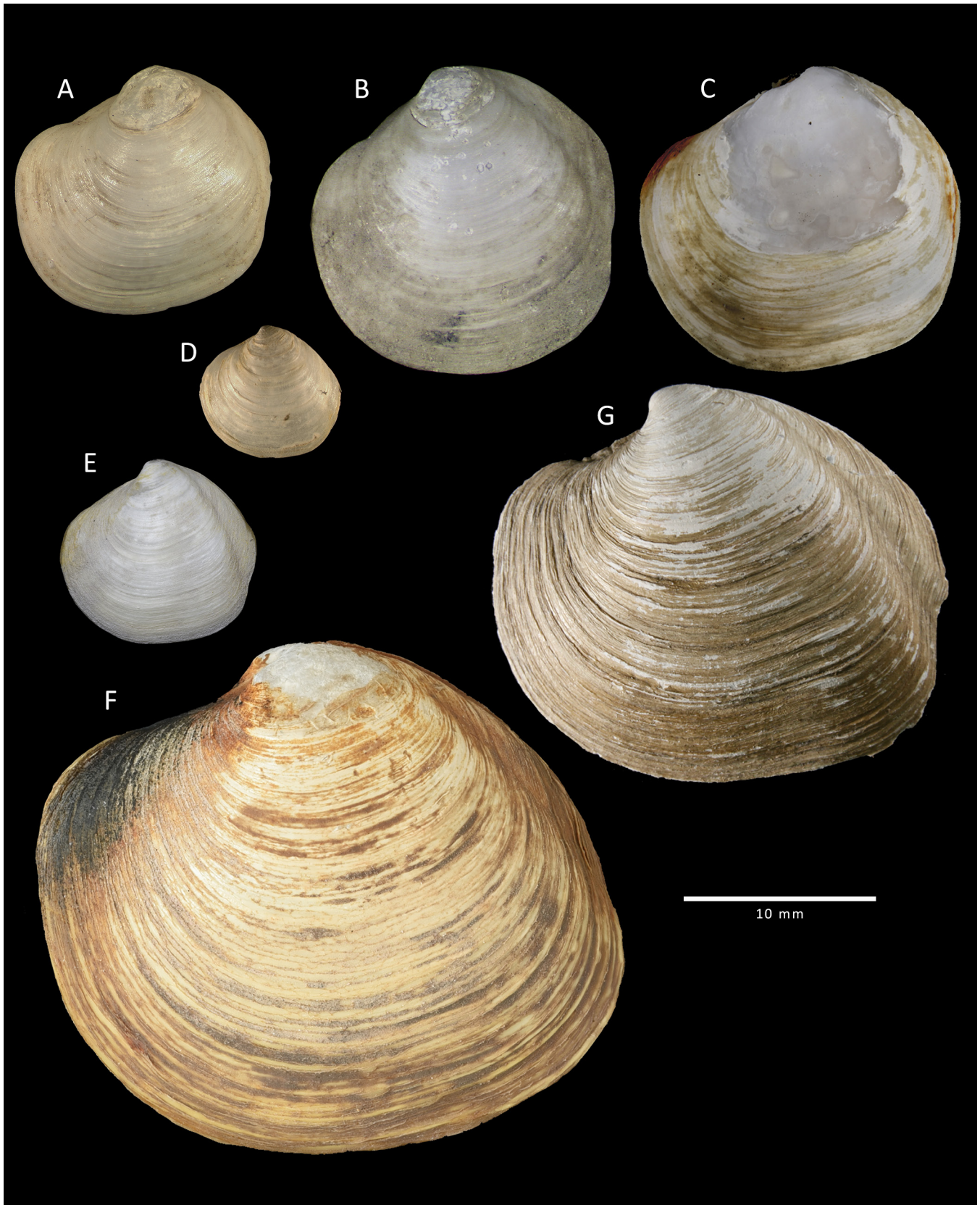


Figure 12. Species of *Spinaxinus* compared to *Tartarothyas* and *Rhacothyas*. A, *Spinaxinus sentosus*. B, *S. emicatus*. C, *S. caldarium*. D, *S. phrixicus*. E, *S. kaireiae*. F, *Tartarothyas hadalis*. G, *Rhacothyas kolgae*.

same species or sample appearing in different parts of the tree. To better assess these trees, information on the morphology of each specimen examined is required.

To conclude, the trees presented by Fukasawa *et al.* (2017) do indicate a phylogenetic link between the two hadal species examined herein and the genus *Spinaxinus*. We place *S. kaireiae* in *Spinaxinus*, but there is sufficient morphological and ecological difference to support the new genus *Tartarothyas* to house *T. hadalis*. Further phylogenetic studies, particularly using nuclear genes, are sought to clarify the evolutionary relationships among these species and the genera *Spinaxinus*, *Rhacothyas*, and *Tartarothyas*.

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