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***Ascetoaxinus quatsinoensis* sp. et gen. nov. (Bivalvia: Thyasiroidea)  
from Vancouver Island, with notes on *Conchocele* Gabb, 1866,  
and *Channelaxinus* Valentich-Scott & Coan, 2012**

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**Abstract**

*Ascetoaxinus quatsinoensis* sp. et gen. nov. is described from deep waters off the coast of Vancouver Island, British Columbia, Canada. The shell of this species is quite unusual in that the margin of the lunule is distinctly scalloped, a feature not reported previously for the Thyasiroidea. Further investigation led to the discovery of another similarly scalloped shell, represented by the unique type specimen of *Cryptodon ovoideus* Dall, 1890, herein re-classified as *Ascetoaxinus ovoidea* (Dall, 1890). Results obtained from scanning electron microscopy reveal additional anatomical differences, including distinct gill structure, that distinguish *A. quatsinoensis* from other thyasirids examined. Morphological comparisons of this new species to closely related taxa has resulted in a re-evaluation of the genera *Conchocele* Gabb, 1866, and *Channelaxinus* Valentich-Scott and Coan, 2012.

**Key words:** thyasirid, clam, morphology, new species, deep-water, British Columbia

**Introduction**

Despite recent advances in thyasirid taxonomy and systematics (e.g., Oliver & Killeen 2002, Oliver & Sellanes 2005, Oliver & Levin 2006, Oliver & Drewery 2013, Rodrigues et al. 2008), our understanding of this group remains far from complete. Resolution is often impeded by the lack of anatomical material and appropriately preserved tissues suitable for molecular study. Systematic progress is therefore serendipitous depending on the availability of newly collected specimens for further comparative study.

In 2009, the Royal BC Museum acquired a single specimen of a large, obliquely extended thyasirid bivalve collected from Quatsino Sound, Vancouver Island, British Columbia, Canada at a depth of 1086–1318m. The shell is unusual in that the margin of the lunule is distinctly scalloped, a feature not reported previously for the Thyasiroidea. Given the relatively large size and oblique outline of this specimen it was possible that the specimen represented an aberration of *Conchocele bisecta* (Conrad 1849), which is also known from the Northeast Pacific (Coan et al. 2000).

Both the Vancouver Island specimen and typical *Conchocele bisecta* were loaned to the senior author for research into thyasirid gill morphology. Results quickly indicated that certain anatomical characters were not shared, suggesting that the scalloped specimen was not an aberrant *C. bisecta*, but rather a previously undescribed taxa. This was further supported by the discovery of another scalloped shell, represented by the unique type specimen of *Cryptodon ovoideus* Dall, 1891, from off southeast USA in the Atlantic.

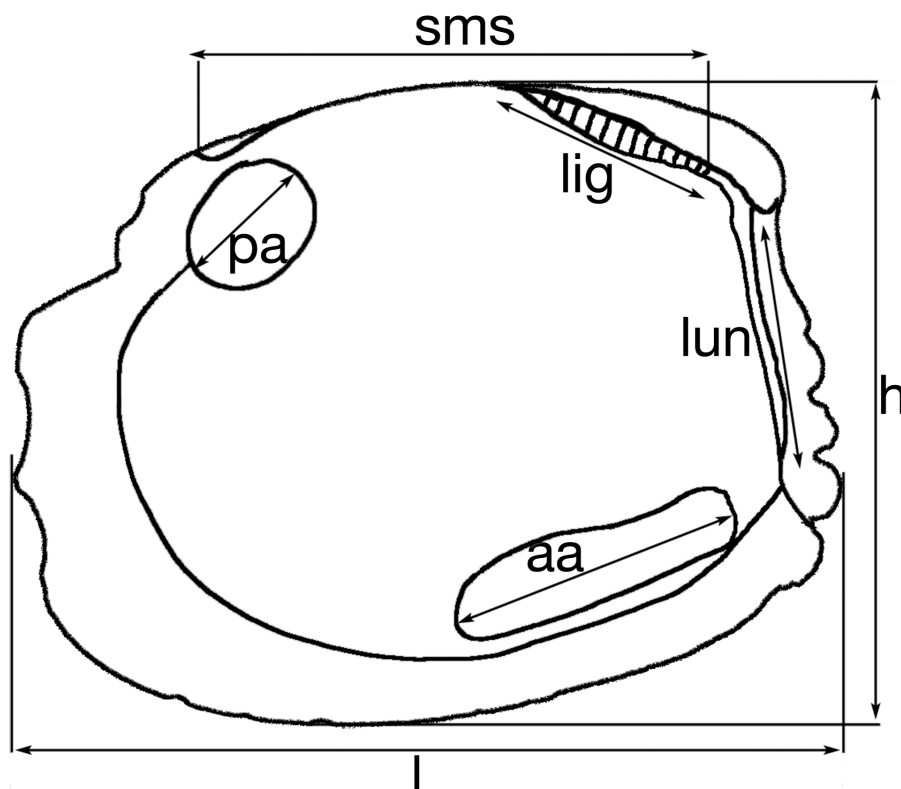
Here we report our findings in detail, including the description of a new genus and species (*Ascetoaxinus quatsinoensis* sp. et gen. nov.). A morphological comparison of this new species to related taxa has also resulted in a re-evaluation of the genera *Conchocele* Gabb, 1866 and *Channelaxinus* Valentich-Scott and Coan, 2012 in Coan and Valentich-Scott, 2012.

## Methods

For comparative study, we examined all extant species from the genus *Conchocele* and other thyasirids considered to be of a similar form (Tab. 1). In general, thyasirids are poorly represented in museum collections and available specimens are mostly in the form of shells only. The larger species are represented by adult shells only in which the characters of the early shell are lost through erosion. This in combination with the absence of juvenile shells precluded the use of prodissoconch and early hinge characters in this study. However, we were able to acquire preserved specimens for two specimens of *C. bisecta* (RBCM 006-00076-001) and a specimen of *C. excavata* (SBMNH). Additional anatomical data was compiled from previously published descriptions of *C. bisecta* (= *C. disjuncta*) (Nakazima 1958, Bernard 1972, Kamenev *et al.* 2001) and *Thyasira perplicata* (= *T. excavata plicata*; in Payne & Allen 1991). Salas (1996) did not regard this Atlantic species as conspecific with the Pacific *C. excavata* and also noted that the name *plicata* of Verrill (Verrill, 1885) was preoccupied, thus giving it the new name of *Thyasira perplicata* Salas, 1996.

Measurements of the shells were made with digital vernier calipers reading to two decimal places (Fig. 1). Gross anatomy was described from ethanol preserved specimens. Although these are not ideal for dissection due to the nature and fragility of the tissues, we were able to acquire detailed images of anatomical structures using computer-aided macrophotography (Leica stereomicroscope and AutoMontage software, following Turner 2008). For scanning electron microscopy, selected tissues were dehydrated in 100% ethanol and critically point dried using a Quorum K850 with CO<sub>2</sub> as the intermediary fluid. Dried tissues were coated with gold and viewed with a Jeol NeoScope SEM.

Abbreviations used in the text are as follows. Those for the anatomical figures are given in the legends: Collections: NMST (National Museum of Science, Tokyo, Japan), NMW (National Museum of Wales), RBCM (Royal BC Museum), SBMNH (Santa Barbara Museum of Natural History), USNM: (National Museum of Natural History, Smithsonian Institution, USA).



**FIGURE 1.** Diagram showing shell parameters. **aa**, anterior adductor scar; **h**, height; **l**, length; **lig**, ligament; **lun**, lunule; **pa**, posterior adductor scar; **sms**, submarginal sulcus.

TABLE 1. Species included in the present study; asterisks indicate species for which anatomical data are available.

Name and Authority	Source of Data	Geographic Range	Depth	Max. Size	Reclassification, Present Study
<i>Ascetoaxinus quatsinoensis</i> sp. et gen. nov.	Described herein	Northeast Pacific	1086–1318m	32mm	<i>Ascetoaxinus quatsinoensis</i> sp. et gen. nov.
<i>Channelaxinus oliveri</i> Valentich-Scott & Coan, 2011	Original designation	Tropical Eastern Pacific	9–120m	13mm	<i>Channelaxinus oliveri</i> Valentich-Scott & Coan, 2012
<i>Conchocele bisecta</i> (Conrad, 1849)*	Coan, Scott & Bernard, 2000	North Pacific	50–750m	130mm	<i>Conchocele bisecta</i> (Conrad, 1849)
<i>Conchocele disjuncta</i> Gabb, 1866	Boss, 1967	Caribbean	421–641m	88mm	<i>Conchocele disjuncta</i> Gabb, 1866
<i>Conchocele koyamai</i> Habe, 1981	Original designation	Northwest Pacific (Japan)		22mm	Genus uncertain
<i>Conchocele novaeguineensis</i> Okutani, 2002	Original designation	Southwest Pacific	470m	74mm	<i>Conchocele novaeguineensis</i> Okutani, 2002
<i>Cryptodon investigatoris</i> Smith, 1895	Knudsen, 1967 (as <i>Conchocele bisecta</i> )	Arabian Sea	260–1102m	32mm	<i>Channelaxinus investigatoris</i> (Smith, 1895)
<i>Cryptodon ovoideus</i> Dall, 1890	Original designation	Northwest Atlantic (SE USA)	646m	25mm	<i>Ascetoaxinus ovoidea</i> (Dall, 1890)
<i>Thyasira excavata</i> (Dall, 1901)*	Coan & Valentich-Scott, 2012 (as <i>Conchocele excavata</i> )	Northeast Pacific	800–2520m	24mm	<i>Channelaxinus excavata</i> (Dall, 1901)
<i>Thyasira fuegiensis</i> (Dall, 1890)	Zelaya, 2009 (as <i>Conchocele fuegiensis</i> )	Magellan	142m	25mm	<i>Thyasira fuegiensis</i> (Dall, 1890)
<i>Thyasira perplicata</i> Salas, 1996*	Payne & Allen, 1991 (as <i>Thyasira excavata plicata</i> )	N & S Atlantic	1277–2044m	15mm	<i>Channelaxinus perplicata</i> (Salas, 1996)

## Systematics

Class BIVALVIA Linnaeus, 1758

Subclass HETERODONTA Neumayr, 1884

Order VENEROIDA H. & A. Adams, 1856

Superfamily THYASIROIDEA Dall, 1900

Family THYASIRIDAE Dall, 1900

*Ascetoaxinus* gen. nov.

**Type species.** *Ascetoaxinus quatsinoensis* sp. nov., this paper.

**Type locality.** Quatsino Sound, off of Vancouver Island, British Columbia, Canada; 50°15.482'N, 128°26.400'W to 50°14.519'N, 128°26.567'W; 1086–1318m.

**Species included.** *Ascetoaxinus quatsinoensis* sp. nov.; *Ascetoaxinus ovoidea* (Dall, 1890).

**Diagnosis.** Medium sized shells. Equivalve. Inequilateral, prosogyrous beaks close to the anterior, outline obliquely oval. Anterior margin sloping steeply, almost straight; anterior area defined by a distinct keel, with a deeply impressed lunule encompassing the entire anterior area. Lunule edge scalloped by rounded projections. Posterior margin broadly rounded, indented by a single sinus; posterior sulcus large, deep, distinctly angulated; submarginal sulcus smaller, sharply defining escutcheon but no distinct marginal sinus. Weak angulation between umbo and posterior ventral margin resulting in flattened area adjacent to the posterior sulcus. Anterior adductor muscle scar greatly elongate. Hinge teeth lacking. Ligament partially sunken.

Gill anatomy of Dufour type 3 (Dufour 2005), filaments laminar, frontal surface broad, flat with marginal arrays of cilia. Lateral body pouches large, dense arborescent, dorsal extension of digestive gland prominent with external outgrowths.

**Etymology.** From the Greek *asketos* meaning curiously fashioned and pertaining to the unusual scalloped lunule and the Greek *axinus* meaning like an axe, but also pertaining to the thyasirid genus *Axinus*; gender feminine (Brown 1956).

*Ascetoaxinus quatsinoensis* sp. nov.

Figs. 2–6

**Type material.** Holotype, 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.

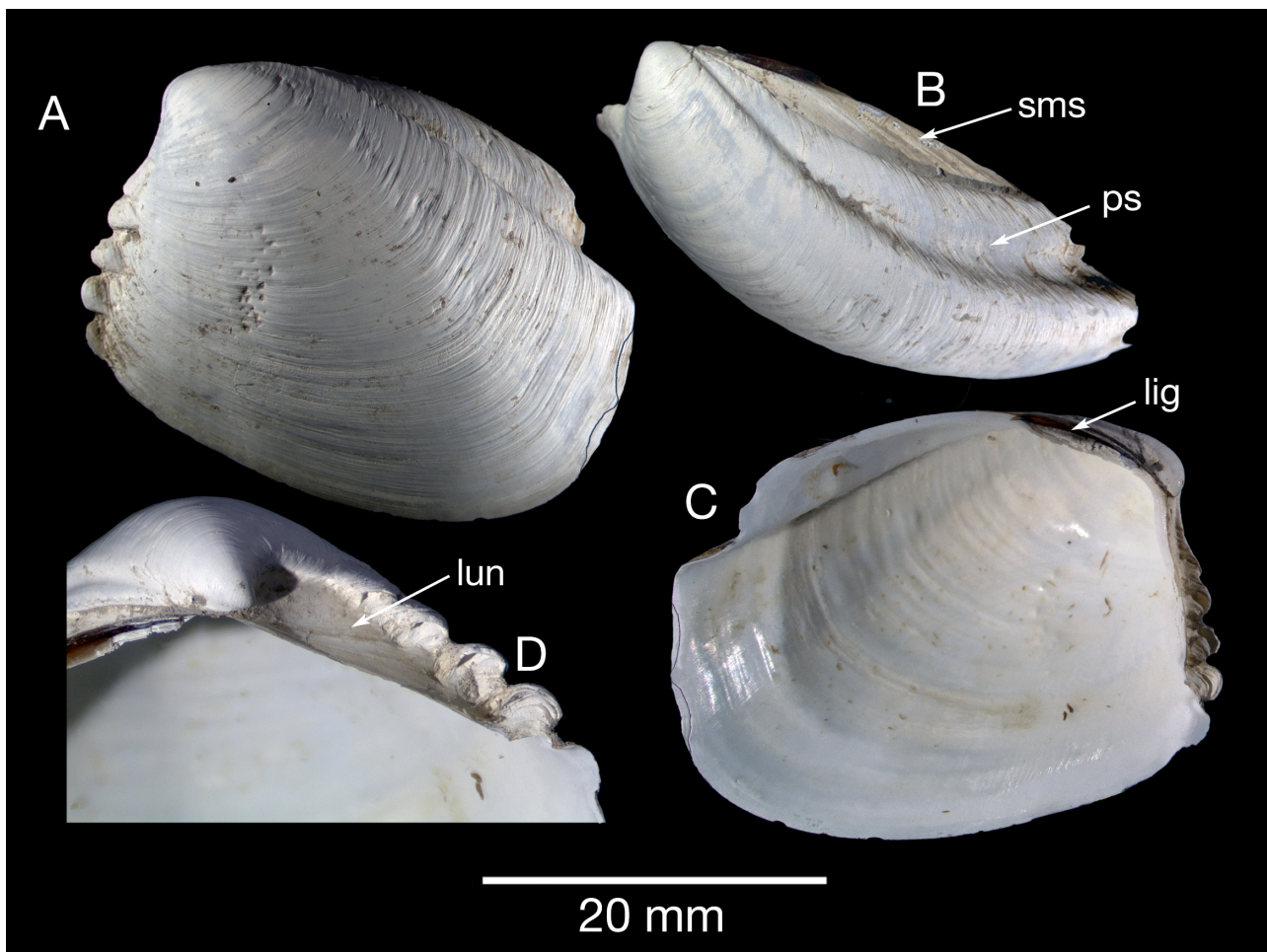
Measurements.

Length (l)	Height (h)	Tumidity Single valve	Lunule (lun)	Ligament (lig)	Anterior adductor scar (aa)
31.3 mm	24.3 mm	9.7 mm	12.0 mm	9.7 mm	10.5 mm

**Description.** *Shell* (Fig. 2). 31.3mm in length. Thin, brittle. Equivalve. Moderately tumid. Strongly inequilateral, prosogyrous beaks close to the anterior margin. Outline obliquely oval; anterior margin almost straight bounding a large excavated lunule; ventral margin long, almost straight; posterior margin broad, sulcate with a distinct posterior dorsal sinus. Posterior sulcus sharply defined, relatively narrow; submarginal sulcus sharply defining a flattened escutcheon. Posterior ventral slope anterior of the posterior sulcus a little flattened, creating a weak secondary ridge. Hinge teeth lacking, ligament partially sunken, relatively short being less than half the length of the escutcheon. Sculpture of well-defined growth lines; edge of lunule drawn out into five



rounded projections. Muscle scars indistinct; anterior adductor scar elongate and parallel with ventral margin. Shell colour white.



**FIGURE 2.** *Ascetoaximus quatsinoensis* gen. et sp. nov., Holotype, RBCM 010-00221-005. **A**, external of left valve; **B**, oblique dorsal view showing posterior and submarginal sulci; **C**, internal of left valve; **D**, oblique view of the lunule. **lig**, ligament; **lun**, lunule; **ps**, posterior sulcus; **sms**, submarginal sulcus.

*Anatomy* (Figs. 3–6). Mantle is thin; unfused except for the formation of a small exhalant aperture (Fig. 3, **ex**). Anterior adductor scar elongate and approximately 4 times longer than posterior adductor scar; free from mantle edge for about one-fifth of its ventral edge; posterior adductor muscle oval. Foot vermiform (Fig. 3), very long, tip not noticeably expanded, heel obsolete, protractor muscles very slender. Labial palps small, narrow with a distinctly grooved dorsal zone and a long tubular portion leading to the mouth (Fig. 5A, B). Alimentary system (Fig. 4) with short oesophagus leading to a relatively small stomach; large digestive ducts leading to the lateral body pouches open into the ventral anterior face (Fig. 5D, **dd**, **np**), smaller ducts open dorsally on the left side and lead to a pair of outgrowths (Fig. 5B, **dg**); walls of the combined style sac and mid gut thickened (Fig. 5D, **ss/mg**), remainder of mid gut coiling back over style sac, passing through heart and coiling towards the posterior as the hind gut; anus opening into exhalant aperture (Fig. 4). Lateral body pouches large, arborescent, terminations cloven or single, blunt (Fig. 5C). Kidney large and packed with golden coloured granules. Ctenidium large, both demibranchs with fully reflected filaments; outer demibranch about half the depth of the inner demibranch (Fig. 3, **od**, **id**). Filaments laminar (Fig. 6A, C), frontal zone narrow, abfrontal zone extended and fused across the ascending and descending arms, creating junctions between the ascending and descending lamellae (Fig. 6A, **abs**). Ventrally every filament is fused. The frontal surface (Fig. 6B) is ciliated with distinct lateral cilia (**lc**) and latero-frontal cirri (**lfc**); frontal cilia not apparent, instead adjacent frontal zone appears wide and smooth (**sfz**). Abfrontal surfaces lined with bacteriocytes that are domed and roundly polygonal with a glycocalyx (Fig. 6C, **bc**). Bacilli bacteria also present in defined bundles, measuring 1.1  $\mu\text{m}$  in length (Fig. 6D, **bct**).

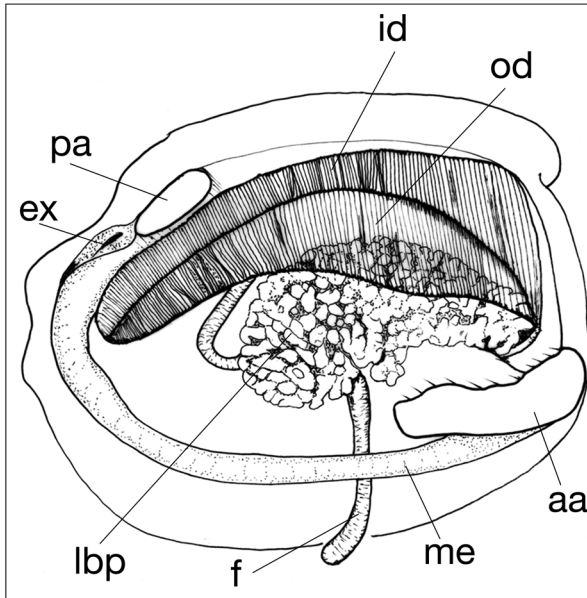


Fig. 3

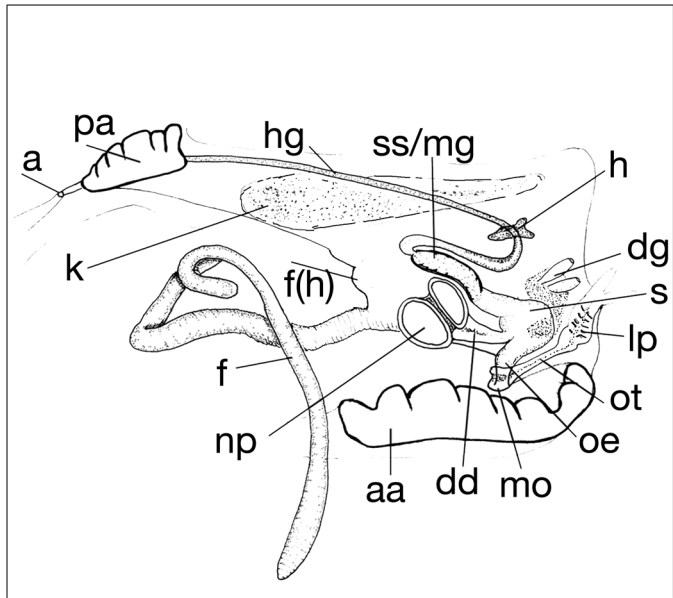


Fig. 4

**FIGURES 3–4.** 3. Diagram of the gross anatomy of *Ascetoaxinus quatsinoensis* viewed from the left side after removal of mantle. 4. Diagram of the alimentary system of *Ascetoaxinus quatsinoensis* viewed from the right side after removal of the mantle and lateral body pouch. **a**, anus; **aa**, anterior adductor muscle; **dd**, duct to digestive gland; **dg**, protrusions of digestive gland; **ex**, exhalent aperture; **f**, foot; **h**, heart; **hg**, hind gut; **id**, inner demibranch; **k**, kidney; **lbp**, lateral body pouch; **lp**, labial palps; **me**, mantle edge; **mo**, mouth; **ss/mg**, style sac and mid gut; **np**, neck of lateral body pouch; **od**, outer demibranch; **oe**, oesophagus; **ot**, oral tube; **pa**, posterior adductor muscle; **s**, stomach.

### *Ascetoaxinus ovoidea* (Dall, 1890)

Fig. 7

**Type material.** Holotype, single specimen, 87 miles off Cape Fear, North Carolina, United States, 646m. Coll. United States Fish Commission. USNM 64226.

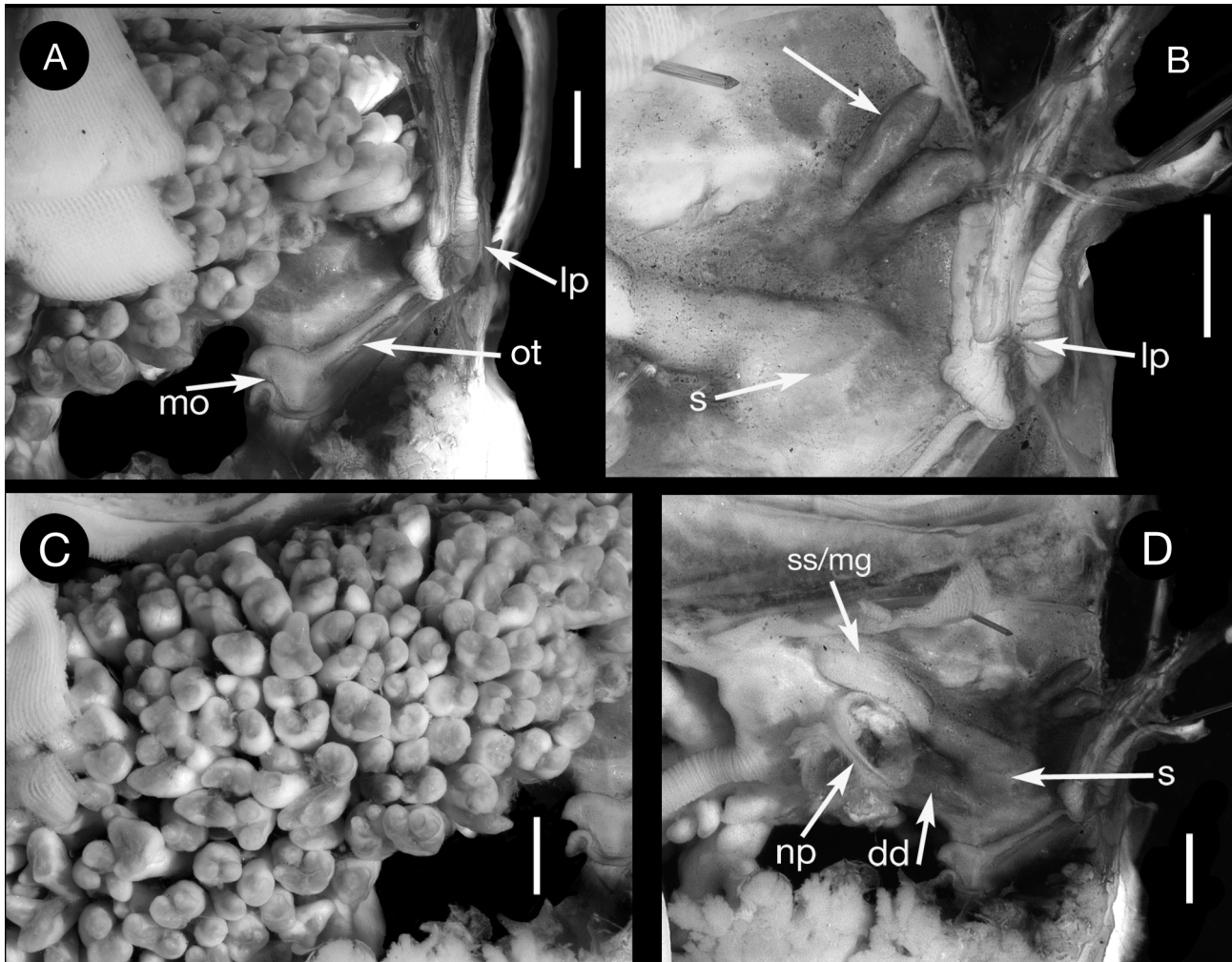
**Synonymy.** *Cryptodon ovoideus*, Dall, 1890; *Thyasira ovoidea* (Dall, 1890).

Measurements.

Length (l)	Height (h)	Tumidity
25 mm	20 mm	14 mm

**Description.** *Shell* (Fig. 7). 25mm in length. Brittle, chalky. Equivalve. Moderately tumid. Strongly inequilateral, prosogyrous beaks close to the anterior margin. Outline obliquely oval; anterior margin almost straight bounding a large excavated lunule; ventral margin long, almost straight; posterior margin broad, sulcate with a distinct posterior dorsal sinus and faint submarginal sulcus. Posterior sulcus sharply defined, relatively narrow; submarginal sulcus sharply defining a projecting escutcheon. Posterior ventral slope anterior of the posterior sulcus a little flattened, creating a weak secondary ridge. Hinge teeth lacking; ligament partially sunken, relatively short with length less than half that of escutcheon. Sculpture of well-defined growth lines; edge of lunule drawn out into two rounded projections. Muscle scars prominent; anterior adductor scar elongate, mostly separate from pallial line, and in parallel with ventral margin. Shell colour, creamy-white.

**Remarks.** Based on putative geographic distributions coupled with obvious biogeographic barriers, it is most unlikely that *Ascetoaxinus quatsinoensis* is conspecific with *A. ovoidea*. Panamic and Caribbean geminate taxa in the Arcoidea have been shown to be distinct species (Marko and Moran, 2009) and this probably applies to most bivalves. Shell morphology differences are present; in *A. quatsinoensis* the scalloping of the lunule is more prominent as is the definition of the escutcheon.



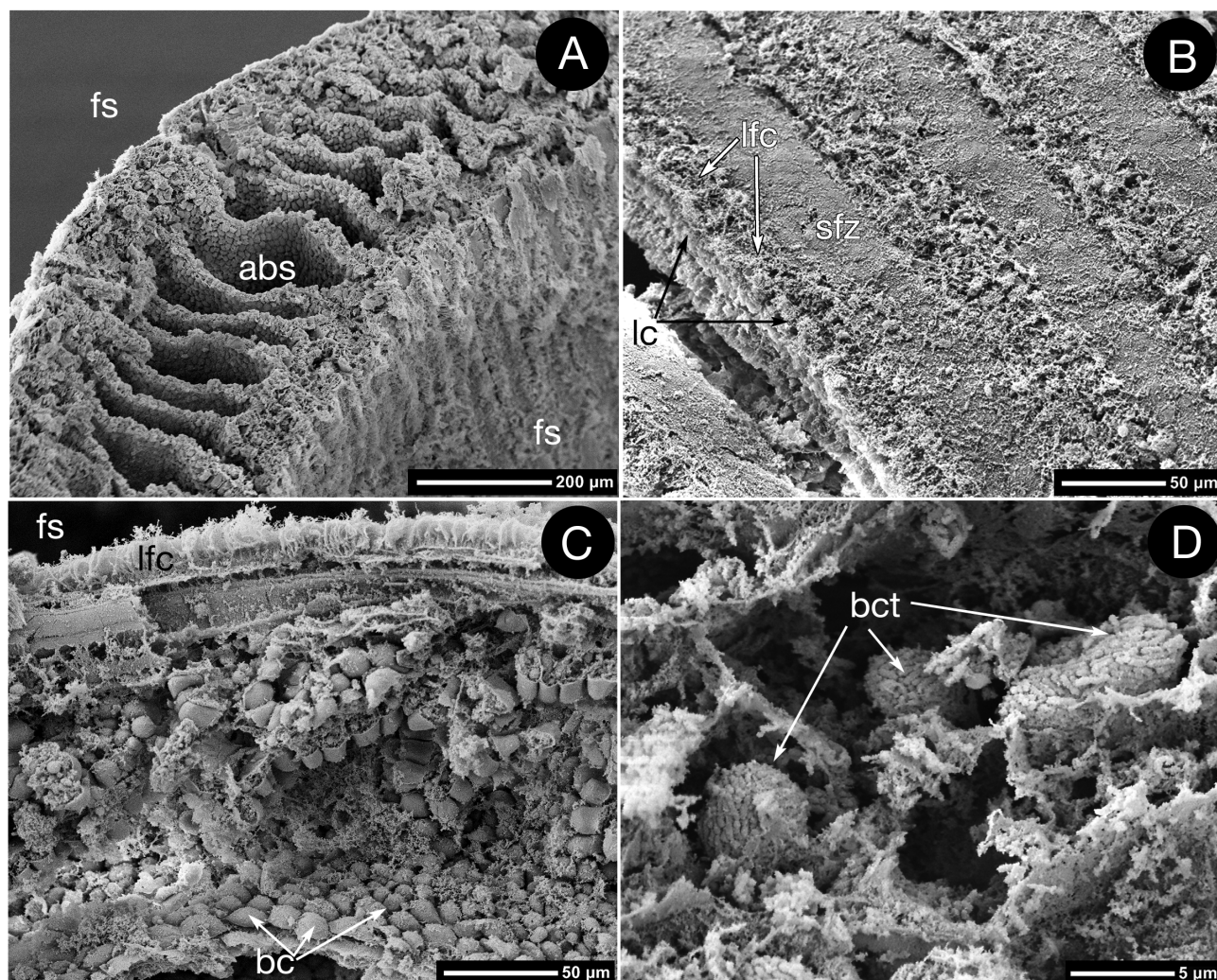
**FIGURE 5.** Photomicrographs of anatomical details of *Ascetoaxinus quatsinoensis*. **A**, mouth and oral tube; **B**, labial palps and protrusions of the digestive gland; **C**, branches of the lateral body pouch; **D**, stomach and style sac/mid gut. Scale bars = 1mm. **dd**, duct to digestive gland; **dg**, protrusions of digestive gland; **lp**, labial palps; **mo**, mouth; **ss/mg**, style sac and mid gut; **np**, neck of lateral body pouch; **ot**, oral tube; **s**, stomach.

## Discussion

**Comparison of *Ascetoaxinus* and *Conchocele bisecta*.** To assess the possibility that *Ascetoaxinus quatsinoensis* was an aberrant *Conchocele bisecta*, detailed comparisons were made between these two taxa. The gill anatomy was the most obvious character that suggested that these taxa were neither conspecific nor congeneric. The gill structure of *A. quatsinoensis* is typical of the larger chemosynthetic thyasirids in that the filaments are greatly extended abfrontally, laminar in form, and fusing to create junctions between the ascending and descending lamellae (Fig. 6A). The frontal surfaces are ciliated with lateral cilia and latero-frontal cirri, but atypically, the frontal cilia appear to be largely absent (i.e., the area they should cover is wide but apparently smooth) (Fig. 6B, **sfz**).

This gill form is in stark contrast with that of *C. bisecta* (Fig. 8). Similar to *A. quatsinoensis*, *C. bisecta* is characterized by a large degree of abfrontal extension (Fig. 8A, **abs**) and the ascending and descending lamellae are joined with regular junctions (Fig. 8, **ilj**). However, these are not derived from every filament and leave distinct inter-lamellar spaces (Fig. 8A, **ils**). Instead of being completely laminar, the filaments have become, in part, tubular (Fig. 8C, **tbz**). When viewed from the frontal surface, the frontal faces appear as strong angulate bars devoid of cilia (Fig. 8A, **fz**; 8B), and between these open a series of entrances to the tubes (Fig. 8B, **et**). The tubular zone (Fig. 8A, **tbz**) comprises half the thickness of each lamella, the inner portion becoming laminar (Fig. 8A, **lz**). Each tube is

densely packed with bacteriocytes (Fig. 8D, **bc**). This tubular structure is described and discussed in a more detailed paper on tubular gills in the Thyasiridae (Oliver in press). The apparent absence of any frontal ciliation may be an artifact of poor preservation but even so the strongly angulate supporting bars are quite different from those in *Ascetoaxinus*.

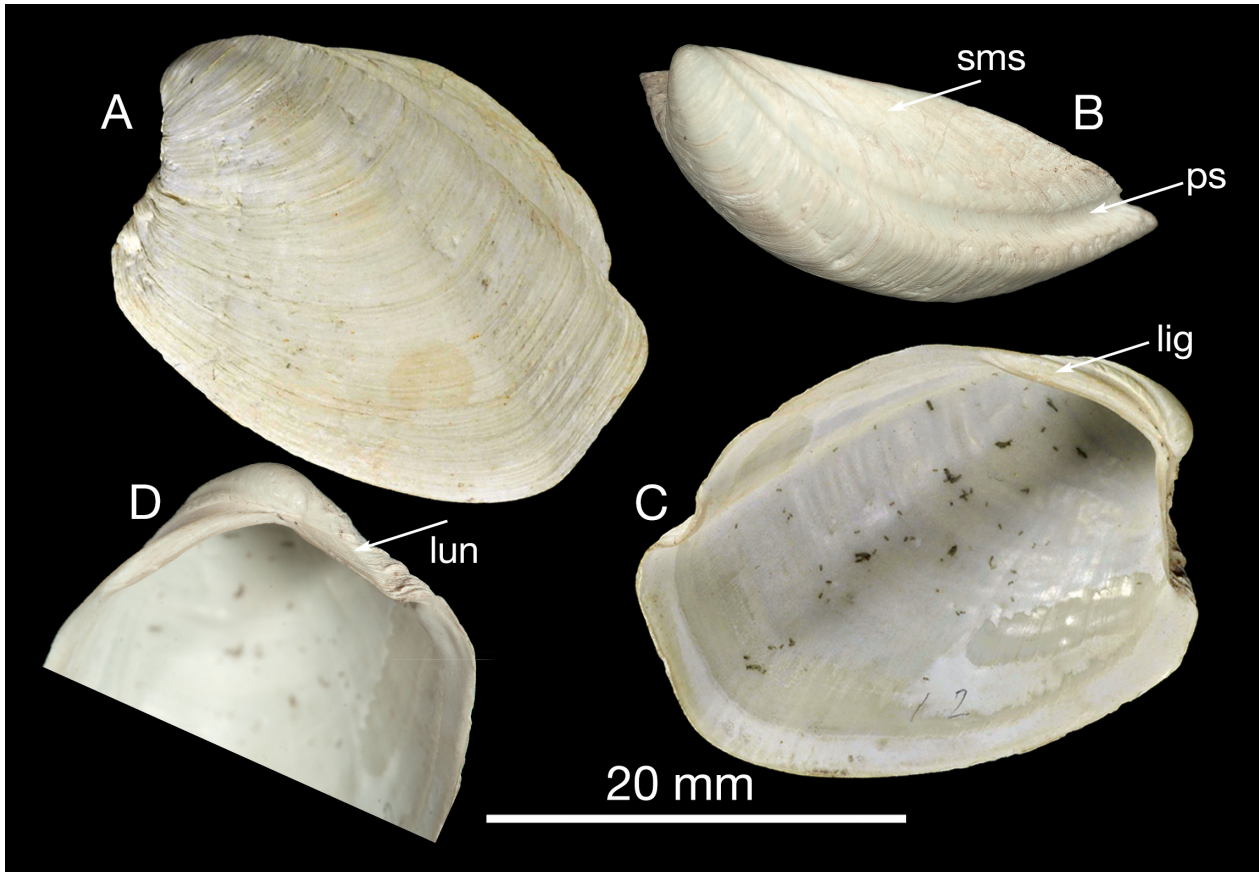


**FIGURE 6.** Scanning electron micrographs of the ctenidium of *Ascetoaxinus quatsinoensis*. **A**, transverse section of a single demibranch; **B**, frontal surface; **C**, lateral view of a filament; **D**, bacterial bundles within bacteriocytes. **abs**, abfrontal surface; **bc**, bacteriocyte; **bct**, bacteria; **fs**, frontal surface; **lc**, lateral cilia; **lfc**, lateral frontal cirri; **sfz**, smooth frontal zone.

Further examination of the anatomy revealed other differences, including the labial palps that are elongate in *A. quatsinoensis* but triangular in *C. bisecta*, and the paired digestive gland protrusions in *A. quatsinoensis* are absent in *C. bisecta*. The arrangement of the digestive ducts leading to the lateral body pouches as illustrated here for *A. quatsinoensis* do not match that shown for *Conchocele* by Bernard (1972, fig. 14) where the ducts are shown to open into the oesophagus and not the stomach. The specimens available to us were not in a sufficient condition to confirm Bernard's observations.

A closer inspection of the shells showed notable differences among the species in addition to the scalloped edges adjacent to the lunule (Fig. 2, Fig. 7, and Fig. 9). In both *A. quatsinoensis* and *A. ovoidea* the lunule is deeply impressed and fills most of the anterior face, whereas in *C. bisecta* it is weakly defined and covers less than half the anterior face. Although both genera have a strong posterior sulcus, *Ascetoaxinus* has a well defined submarginal sulcus, which is absent in *Conchocele*. Finally, the posterior area is ridged with a flattened zone in *Ascetoaxinus*, but evenly contoured in *Conchocele*. The many significant differences in shell and anatomy justify both specific and generic separation from *Conchocele* as represented by the type species *C. bisecta*.



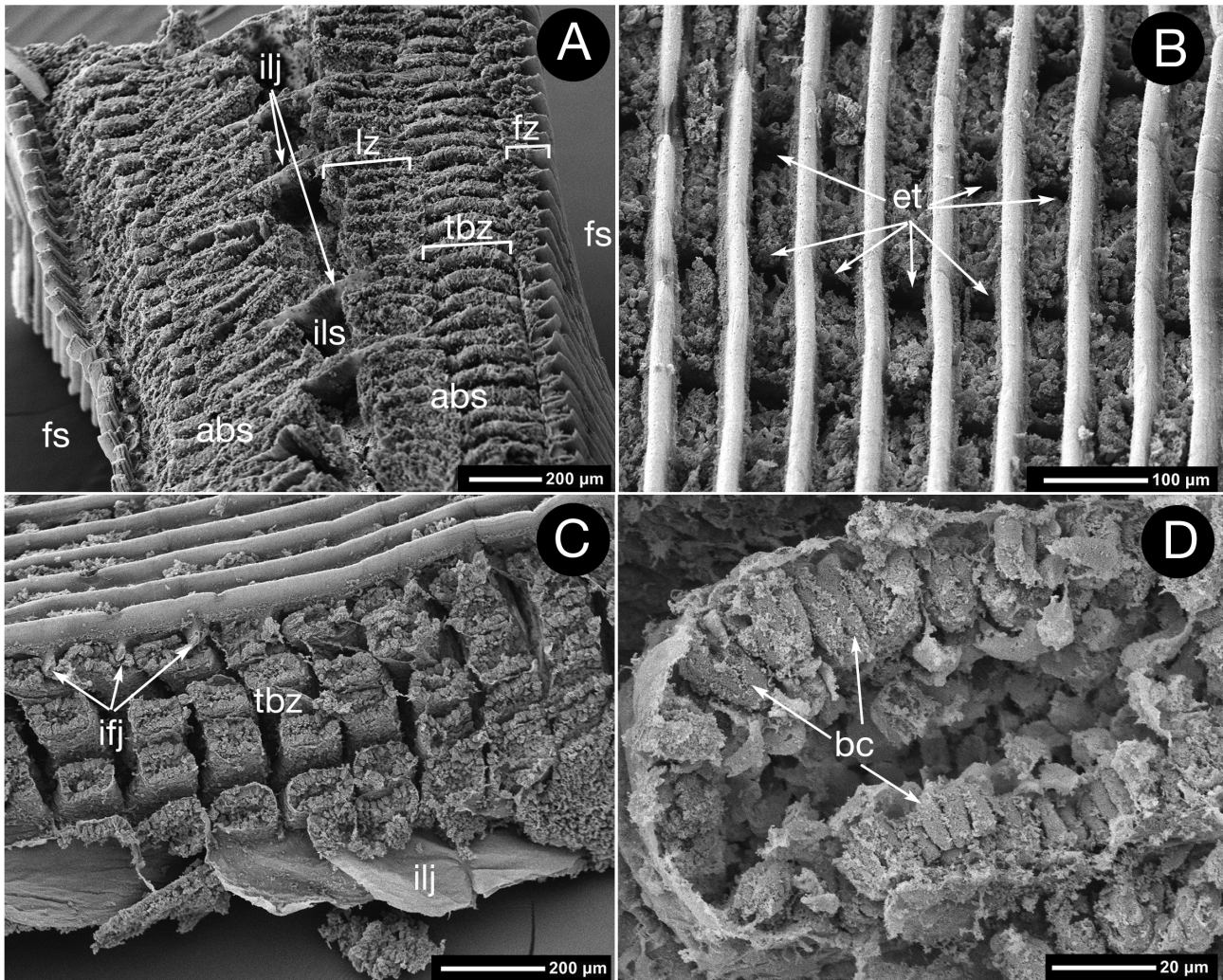


**FIGURE 7.** *Ascetoaxinus ovoidea* (Dall, 1890), Holotype, USNM 64226. **A**, external of left valve; **B**, oblique dorsal view showing posterior and submarginal sulci; **C**, internal of left valve; **D**, oblique view of the lunule. **lig**, ligament; **lun**, lunule; **ps**, posterior sulcus; **sms**, submarginal sulcus.

**Comparison of *Ascetoaxinus* and other species assigned to *Conchocele*.** Examination of other species assigned to *Conchocele* suggested a more complex situation. In addition to *C. bisecta*, three Recent species of thyasirid are classified within *Conchocele* in the WoRMS database (Bouchet 2013): *C. excavata*, *C. fuegiensis*, and *C. novaeguineensis*. *Thyasira perplicata* Salas, 1996 (as *T. plicata* Verrill, 1885) was considered previously to be a subspecies of *C. excavata* by Payne & Allen (1991), but they retained it in the genus *Thyasira*, as does Bouchet (2013). The Arabian species *Thyasira investigatoris* (Smith, 1895) is similar to *C. excavata* but is missing from the WoRMS database although Knudsen (1967) considered it conspecific with *C. bisecta*. Fossil taxa have been described but are not included in the WoRMS database.

***Conchocele sensu stricto.*** The largest and most frequently encountered species of *Conchocele* is *C. bisecta* (Conrad, 1849) from the North Pacific. *Conchocele bisecta* and *C. disjuncta* Gabb, 1866 are both Tertiary fossils and there has been considerable debate on the identity and number of living species in the United States, Canada, Russia and Japan (Bernard 1972, Coan *et al.* 2000, Kamenev *et al.* 2001, Okutani 2000). The current view is that only a single species is extant, with large shells more like *C. disjuncta* and smaller shells like *C. bisecta* (Kamenev *et al.* 2001). Many fossil species and varieties have been described (Krishtofovich 1936). But while there is variation in outline all fossil and recent forms lack a prominent sculpture of any kind.

*Conchocele bisecta*, as *C. disjuncta*, has been reported once from the Caribbean, off Colombia (Boss, 1967). Living *Conchocele* has not been recorded from the Atlantic; however, they are known from Cretaceous and Tertiary deposits in Svalbard and Greenland (as *C. conradii*, Rosenkrantz, 1942), in Brazil (as *C. townsendi* White, 1887), and in the Antarctic (as *C. australosulcata* Stilwell, 2000). The equally large *Conchocele novaeguineensis* Okutani, 2002, from off New Guinea is close to *C. bisecta* as is an unnamed species from off Chile (Oliver & Sellanes 2005). All of these taxa share the shell characters of *C. bisecta* and can be regarded as true *Conchocele*; a revised generic diagnosis is given below.



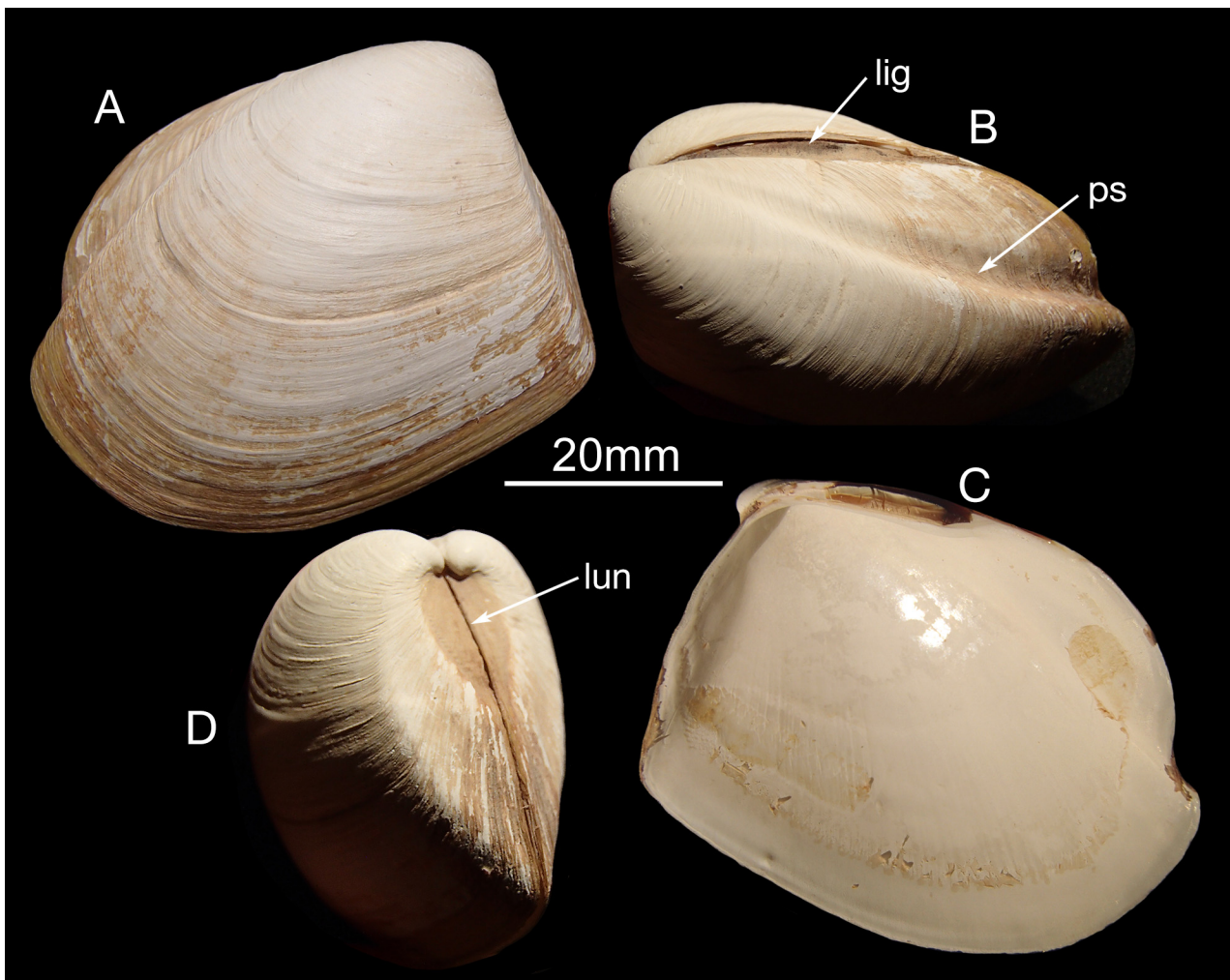
**FIGURE 8.** Scanning electron micrographs of the ctenidium of *Conchocele bisecta* (Conrad, 1849). **A**, transverse section of a single demibranch; **B**, frontal surface; **C**, frontal surface partly torn away to reveal tubes; **D**, a single tube lined with bacteriocytes. **abs**, abfrontal surface; **bc**, bacteriocyte; **et**, entrance to tube; **fs**, frontal surface; **fz**, frontal zone; **ifj**, interfilamentar junction; **ilj**, inter-lamellar junction; **ils**, inter-lamellar space; **lz**, laminar zone; **tbz**, tubular zone.

***Thyasira fuegiensis*.** Although the magellanic species *Thyasira fuegiensis* (Dall, 1890) has been attributed to *Conchocele* (Zelaya 2009) this shell is not obliquely extended, and in aspect is more akin to *T. methanophila* Oliver & Sellanes, 2005. Equally large thyasirids of a similar aspect include *T. insignis* Verrill & Bush, 1898, *T. oleophila* Clarke, 1989, *T. southwardae* Oliver & Holmes, 2006, *T. vulcolutre* Rodrigues & Oliver, 2008, and *T. scotiae* Oliver & Drewery, 2013, and are discussed in Oliver & Drewery, 2013. We regard this group of species to be distinct from the oblique forms generally attributed to *Conchocele*.

***Thyasira excavata* and *T. perplicata*.** *Thyasira excavata* Dall, 1901, and the synonymous *T. tricarinata* Dall, 1916 (Fig. 10A–E) recorded from Oregon to the Gulf of California has for many years been placed in *Conchocele* (Coan & Valentich-Scott, 2012). It and its Atlantic counterpart *T. perplicata* (Fig. 10F) are much smaller than *C. bisecta*, rarely exceeding 20mm, and although having a deeply sulcate shell they too lack any prominent ornamentation of the lunule. The presence of a sharp submarginal sulcus, complete occupation of the anterior face by the lunule and posterior-median flattening are, however, shared with *Ascetoaxinus*, although in outline it is much less oblique.

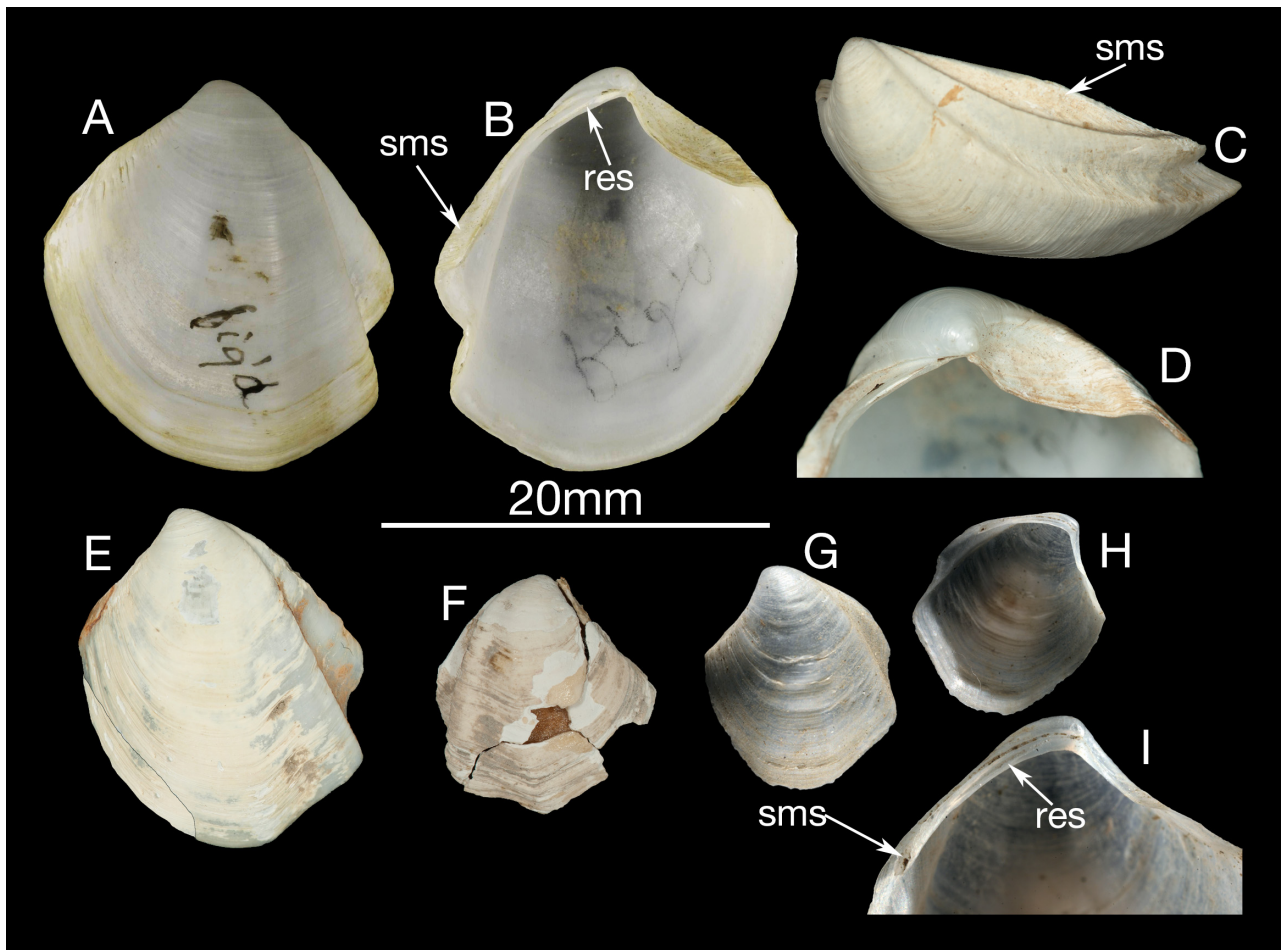
From our examination of the anatomy of *T. excavata* we conclude that it is not congeneric with *Conchocele* but rather is more similar to *A. quatsinoensis*. Since the specimen lent to us is apparently the only preserved example available, our examination has been limited to the removal of a gill for an SEM study and any observations possible on the gross anatomy (Fig. 11–12). The ctenidium consists of both demibranchs with completely reflected

filaments (Fig. 11A). The filaments are laminar (Fig. 11B, D, E) with greatly extended abfrontal surfaces (**abs**) many of these fusing between the ascending and descending lamellae but leaving the dorsal region unfused. Ventrally there is a pattern of alternating filaments developing into inter-lamellar junctions (Figs 11B, D, **ilj**). There are strong inter-filamental junctions lying just behind the frontal zone (Fig. 11D, **ifj**). The frontal surface is ciliated with lateral cilia, latero-frontal cirri and frontal cilia (Fig. 11C). The abfrontal surfaces are densely lined with elongate, lozenge shaped bacteriocytes with a thick glycocalyx (Fig. 11E, **bc**). The bacteriocytes are loosely packed with small cocci bacteria about 1µm in diameter (Fig. 11F, **bct**). The median area of the inter-lamellar junctions are void of bacteriocytes (Fig. 11D, **ilj**). The gross anatomy (Fig. 12) is very similar to that described by Payne & Allen (1991) for *Thyasira perplicata* (as *T. excavata plicata* in Payne & Allen 1991). Payne & Allen note for *T. plicata* “this is the only species of those studied in which the dorsal diverticula are also branched.” In the specimen of *T. excavata* examined in the present study, there is a single small outgrowth (Fig. 12B, **dg**) in the same position as marked by “dg” in figure 15 of Payne & Allen. The bulbous foot is also a shared feature [Fig. 12A, **f(t)**]. Combining our data on *T. excavata* with that of Payne & Allen on *T. perplicata* allows us to confirm that these species do not belong to *Conchocele* and are anatomically closer to *Ascetoximus*. However, conchologically and anatomically they differ from *Ascetoximus* in being less oblique, lacking the lunule sculpture, having a bulbous tip to the foot, having a single and weak protrusion of the dorsal digestive gland, having a complete ciliation of the frontal surface of the gills, and having partial inter-lamellar fusion.



**FIGURE 9.** *Conchocele bisecta* (Conrad, 1849), RBCM 006-00076-001. **A**, external of right valve; **B**, oblique dorsal view showing posterior sulcus and ligament; **C**, internal of right valve; **D**, oblique anterior view showing lunule. **lig**, ligament; **lun**, lunule; **ps**, posterior sulcus.



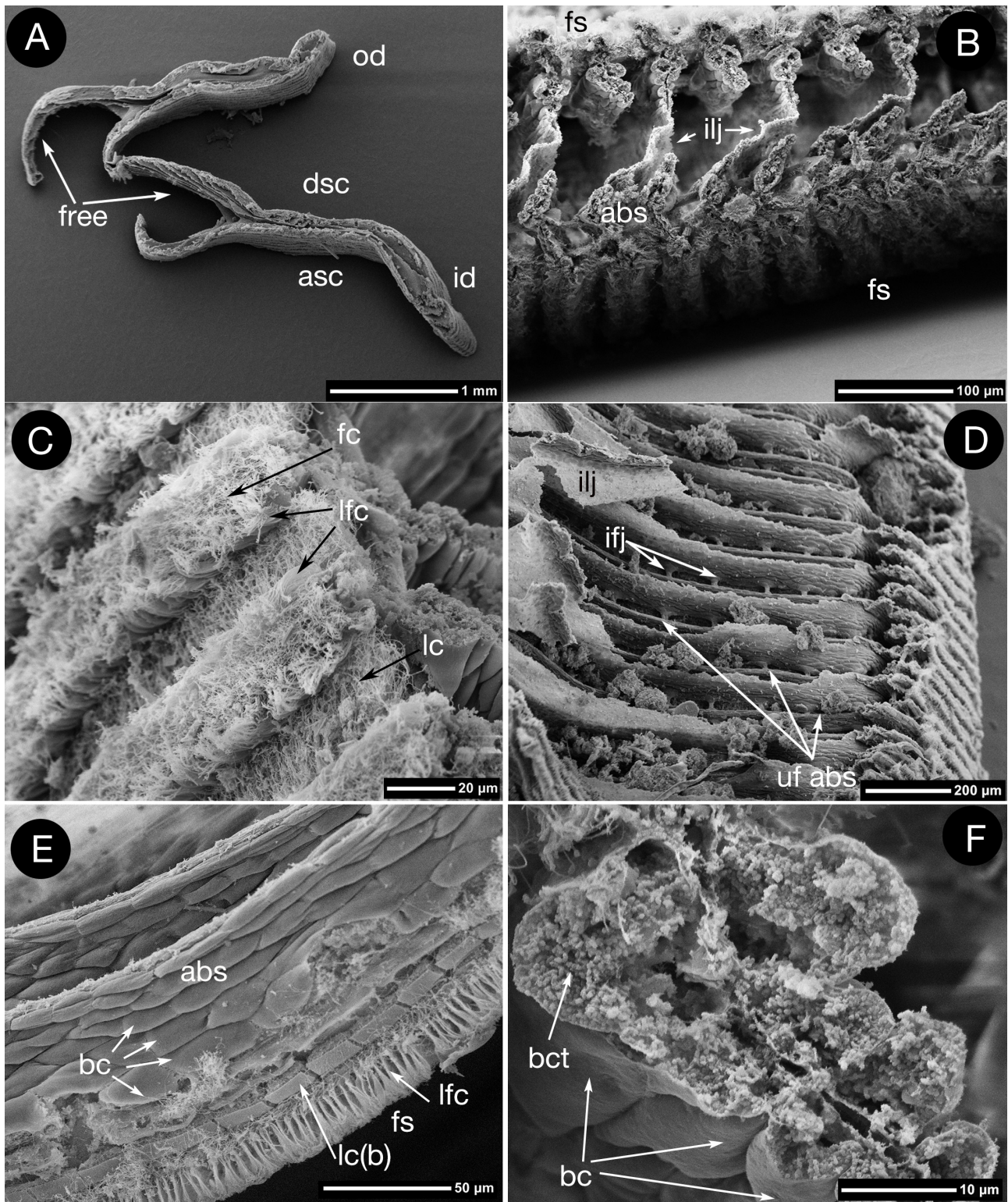


**FIGURE 10.** A–D, *Thyasira excavata* Dall, 1901 [= *Conchocele excavata* (Dall, 1901) in Coan & Valentich-Scott, 2011], Holotype, USNM 107449. A, external of left valve; B, internal of left valve; C, oblique dorsal view showing submarginal and posterior sulci; D, oblique anterior view showing lunule. E, *Thyasira tricarinata* Dall, 1916, nom. nud. (= *Thyasira excavata* Dall, 1901), Holotype, USNM 209321, external of left valve. F, Holotype of *Cryptodon plicata* Verrill, 1885 [= *Thyasira perplicata* (Verrill, 1885) in Payne & Allen, 1991], USNM 44825. G–I, *Channelaxinus oliveri* Valentich-Scott & Coan, 2012, Paratype, SBMNH 149750. res, resilifer; sms, submarginal sulcus.

We cannot leave the generic position of *T. excavata* and *T. perplicata* with no resolution. A re-examination of the genus *Channelaxinus* Valentich-Scott & Coan, 2012, suggests that this is an appropriate tentative placement. When described, the generic diagnosis intimated that “the long, narrow, deep channel that holds the ligament...separates this genus from all others in the Thyasiridae”. A comparison of the hinge plate of *T. excavata* (Fig. 10B) and *Channelaxinus oliveri* (Fig. 10I) reveals that the two are very similar. Personal communication with Paul Valentich-Scott confirms that the deep groove is not the ligament resilifer but rather the submarginal sulcus. *Channelaxinus* and *T. excavata* therefore share many conchological features including a large and excavated lunule, a prominent submarginal sulcus, and flattening of the posterior area (Fig. 10). The shallow shelf habitat of *C. oliveri* is not in keeping with the bathyal ranges of *T. excavata* and *T. perplicata*. Unfortunately, there are no anatomical data for *C. oliveri* as it is known from shells only. The shared shell characters are sufficient to place *T. excavata* and *T. perplicata* in *Channelaxinus* with the proviso that anatomical data may alter this. A revised diagnosis of *Channelaxinus* is given below.

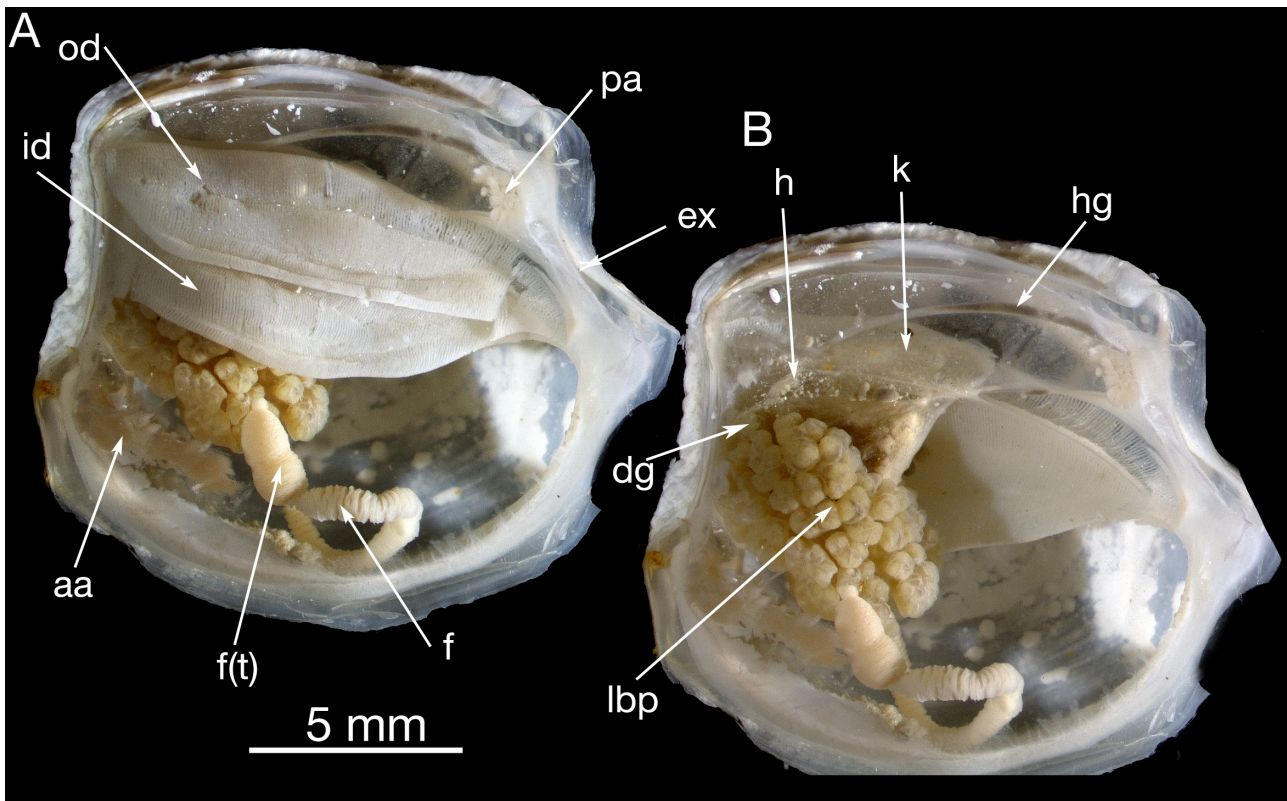
***Cryptodon investigatoris*.** *Cryptodon investigatoris* Smith, 1895 (Fig. 13) was regarded as a subspecies of *Conchocele bisecta* by Knudsen (1967). The shells described by Knudsen (1967) are somewhat different from those illustrated here from the Gulf of Oman, which we regard as true *C. investigatoris*. The identity and affinities of the shells illustrated by Knudsen (1967, pl.2 figs 7 & 8) remain to be clarified as there are a number of described and undescribed Indian Ocean forms that may eventually be assigned to *Channelaxinus* or *Ascetoaxinus*. As illustrated here *C. investigatoris* has all the characters of *Ascetoaxinus* in its size, the deep large lunule, the





**FIGURE 11.** Scanning electron micrographs of the ctenidium of *Thyasira excavatus* Dall, 1901 [= *Conchocele excavata* (Dall, 1901) in Coan & Valentich-Scott, 2012]. **A**, cross section showing full reflection of both demibranchs; **B**, transverse section of a single demibranch; **C**, frontal surface; **D**, frontal surface partly torn away to reveal laminar filaments and inter-lamellar junctions; **E**, lateral view of a filament showing lozenge shaped bacteriocytes; **F**, transverse section through the abfrontal zone showing bacteriocytes and bacteria. **abs**, abfrontal surface; **asc**, ascending lamella of demibranch; **bc**, bacteriocyte; **dsc**, descending lamella of demibranch; **fs**, frontal surface; **ifj**, inter-filamentar junction; **id**, inner demibranch; **ilj**, inter-lamellar junction; **lc (b)**, base of lateral cilia; **od**, outer demibranch; **uf abs**, unfused abfrontal filaments.





**FIGURE 12.** Gross anatomy of *Thyasira excavatus* Dall, 1901 [= *Conchocele excavata* (Dall, 1901) in Coan & Valentich-Scott, 2011]. **A**, from the left side after removal of the mantle; **B**, as in A, but with ctenidium removed. **aa**, anterior adductor muscle; **dg**, protrusions of digestive gland; **ex**, exhalant aperture; **f**, foot; **f(t)**, toe of foot; **hg**, hind gut; **id**, inner demibranch; **k**, kidney; **lbp**, lateral body pouch; **od**, outer demibranch; **pa**, posterior adductor muscle.

prominent submarginal sulcus, and the flattened posterior area. However, it too lacks the distinct scalloped edge to the lunule. It is larger and more oblique in outline than either *Channelaxinus oliveri*, *C. excavata* and *C. perplicata*. Again this is a species known from shells only, so we can only surmise as whether this is an *Ascetoaxinus* lacking lunule sculpture or an oblique *Channelaxinus*. As we have defined *Ascetoaxinus* as having the sculptured lunule margin we tentatively place *C. investigatoris* in *Channelaxinus*.

***Conchocele koyamai*.** *Conchocele koyamai* Habe, 1981 (Fig. 13) is a relatively small species (21mm in length) known only from the type material taken from off Cape Shionomisaki, Kii Peninsula, Honshu, Japan. The exact depth was not recorded, but it was collected by prawn dredging and is likely to be from the shelf. The shell has a prominent raised auricle and is sculptured with radial striations and minute raised conical granules (Fig. 13D); the character of these granules has been confirmed (Hiroshi Saito, the National Science Museum, Tokyo, pers. comm.). These characters are not shared by *Conchocele*, *Channelaxinus* or *Ascetoaxinus*; however, it is not appropriate here to further consider its generic placement.

## Revised generic diagnoses

### Genus *Conchocele* Gabb, 1866

**Type species.** *Conchocele disjuncta* Gabb, 1866, = *C. bisecta* (Conrad, 1849) after Kamenev *et al.* 2001.

**Type locality.** *C. disjuncta*: Pliocene, Dead Man's Island, San Pedro, California; *C. bisecta*: Miocene, Astoria, Oregon.

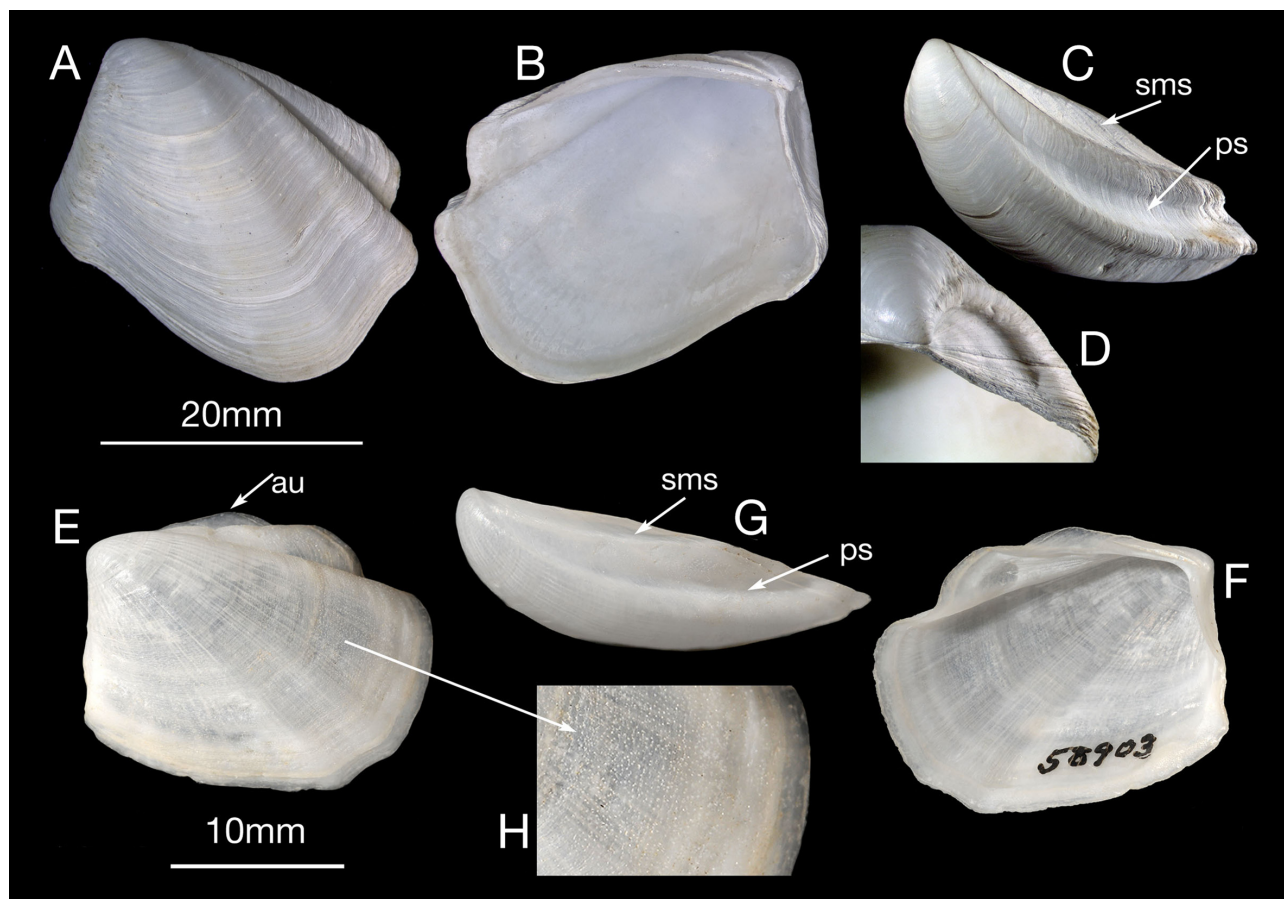
**Species included.** *C. bisecta* (Conrad, 1849), *C. novaeguineensis* Okutani, 2002,

Tertiary fossil taxa in Krishtofovitch (Kamchatka), *Thyasira conradi* Rosenkrantz, 1942 (Svalbard).

**Diagnosis.** Medium to very large shells. Equivalve. Inequilateral, prosogyrous beaks close to anterior, outline

obliquely oval. Anterior margin sloping steeply, almost straight; anterior area defined by a distinct keel; lunule weakly impressed approximately half the length of the anterior area. Posterior margin broadly rounded and indented by a single sinus; posterior sulcus deep, distinctly angulated; escutcheon weakly defined; no distinct marginal sulcus. Anterior adductor muscle scar greatly elongate. Hinge teeth lacking. Ligament partially sunken.

Anterior adductor muscle much longer than posterior; mantle unfused except for a small exhalant aperture; foot vermiform; ctenidia of two fully reflected demibranchs, filaments highly modified with the abfrontal zone divided into a tubular framework and a laminar zone with regular inter-lamellar junctions; tubes lined with bacteriocytes; lateral body pouches densely arborescent.



**FIGURE 13.** A–D *Cryptodon investigatoris* Smith, 1895, NMW, 1955.158, A, external of left valve; B, internal of left valve; C, oblique dorsal view showing submarginal and posterior sulci; D, oblique anterior view showing lunule. E–H *Conchocele koyamai* Habe, 1981, Holotype, NMST-58903. E, external of left valve showing auricle; F, internal of left valve; G, oblique dorsal view showing submarginal and posterior sulci; H, enlargement of median area showing punctate sculpture. au, auricle; ps, posterior sulcus; sms, submarginal sulcus.

### **Genus *Channelaxinus* Valentich-Scott & Coan, 2012 in Coan and Valentich-Scott, 2012**

**Type species.** *Channelaxinus oliveri* Valentich-Scott & Coan, 2012 in Coan and Valentich-Scott, 2012

**Type locality.** Bahía Santiago, Colima, México; 19°06'24''N, 104°22'28''W; 10fm (=18m).

**Species included.** *Channelaxinus oliveri* Valentich-Scott & Coan, 2012; *Thyasira excavata* Dall, 1901 [= *Conchocele excavata* (Dall, 1901) in Coan & Valentich-Scott, 2012]; *Thyasira perplicata* Salas, 1996; *Cryptodon investigatoris* Smith, 1895 (tentative placement).

**Diagnosis.** Moderate to large shells. Polygonal, higher than long. Beaks small, pointed, strongly prosogyrous. Anterior margin sloping long with a deeply impressed lunule, filling much of the anterior area. Posterior sulcus prominent and deep; submarginal sulcus well developed, very narrow to prominent. Median slope flattened, bounded by low ridges. Sculpture of commarginal striae. Hinge edentulous. Ligament long, narrow, sunken.

Anatomy of type species unknown. Following diagnosis based on *C. excavata* and *C. perplicata*. Anterior adductor muscle much longer than posterior; mantle unfused except for a small exhalant aperture; foot vermiform with a bulbous toe; ctenidia of two fully reflected demibranchs, filaments laminar with fully ciliated frontal faces, abfrontal surfaces lined with bacteriocytes; lateral body pouches densely arborescent; dorsal digestive gland slightly protruding.

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