

Description and Figures of New Lectotype and Paralectotype Material of Recent Brachiopod *Thecidellina maxilla* (Hedley, 1899)

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ABSTRACT. The material of *Thecidellina maxilla* (Hedley, 1899) from the type locality has only been illustrated as line drawings, no images have previously been published. The illustrations were a reconstruction from more than one specimen and are inaccurate for the size of the cardinal process. Hedley (1899) did not designate a holotype; newly designated lectotype and paralectotype specimens are described and figured and a new diagnosis of *T. maxilla* is provided.

Introduction

The first living thecideide described from the Pacific Ocean was collected from the western slopes of Funafuti Atoll, Ellice Islands (now Tuvalu) in the Mid-West Pacific (Fig. 1). The specimens were attached to sheets of dead coral from a depth of 70–150 m. Hedley (1899) named the species *Thecidea maxilla* and illustrated two valve interiors with line drawings (Fig. 2A,B, reproduced from Hedley, 1899, fig. 57). Thomson (1915) transferred the species *maxilla* into his new genus *Thecidellina* Thomson, 1915.

Since that first publication of Hedley, living and fossil material identified as *T. maxilla* has been described, figured, listed and discussed in many papers (see synonymy below) from localities in the West Pacific and Indian Oceans (Fig. 1). However, until this study, no images of *T. maxilla* from the type locality have ever been published. Hedley's illustrations (Fig. 2A,B) show the interiors of a dorsal and ventral valve; the collection of the Australian Museum, Sydney (AM) holds two valves of a single specimen (AM C.006202) that partially match these illustrations. When the illustrations in Hedley (1899) and images of this specimen

are compared (Fig. 2A,B and Fig. 2C,D respectively), the dorsal valve is clearly the same one, details of the canopy spicules have been copied, but the illustration is also stylized, the dorsal valve is illustrated as being more symmetrical than the actual specimen. The images of these valves (Fig. 2C,D) also show that the posterior part of the dorsal valve, including the cardinal process and many other important taxonomic features, has broken off and is still attached to the ventral valve. Therefore, the illustrations include reconstructions of the dorsal and ventral valve posteriors, based on more than one specimen, a fact not mentioned by Hedley.

A new lectotype and paralectotypes

The specimen AM C.006202 (Fig. 2C,D) is labelled as the holotype of *T. maxilla*. However, the holotype of a new species can only be fixed in the original publication by the original author (ICZN 73.1.3). Hedley (1899) provided a description of the morphological range of multiple specimens of his new species, but did not designate a single specimen as the holotype. Therefore, all the specimens he based his

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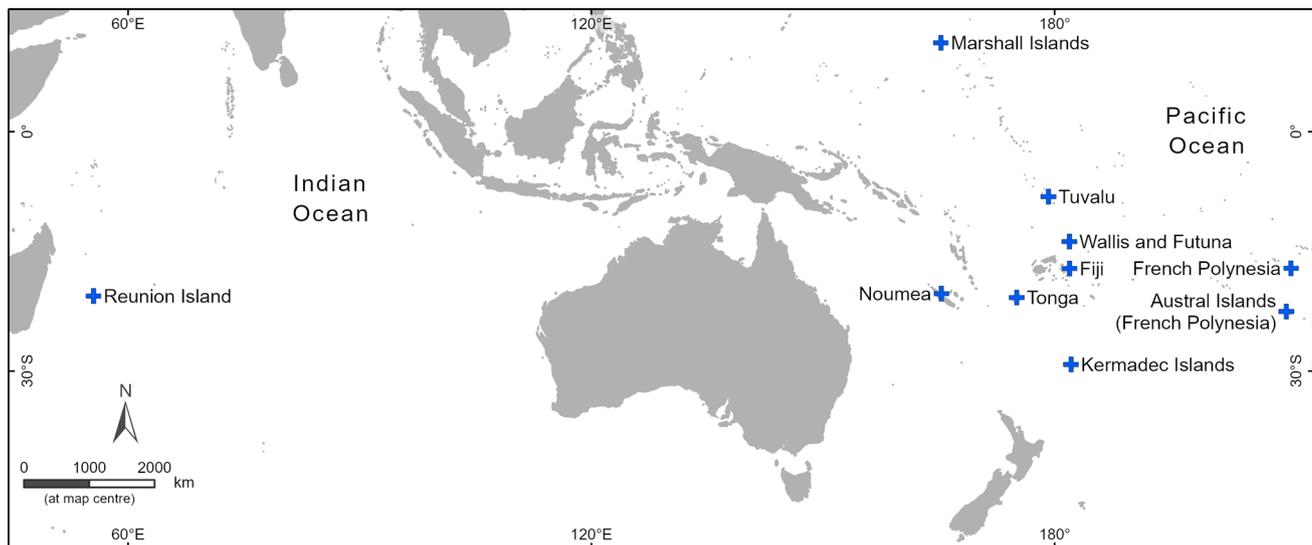


Figure 1. Map of published localities where material has been identified as Recent *Thecidellina maxilla*.

description on must be considered as syntypes (ICZN 73.2). A single specimen from the syntypes may be designated as the lectotype to become the unique bearer of the name of the species and the standard for its application (ICZN 74.1). All other syntypes then become paralectotypes (ICZN 74.1.3).

I have examined material of *T. maxilla* from the type locality and I designate one specimen as the lectotype (AM C.593654, Fig. 3) and four specimens as paralectotypes (AM C.006202, Fig. 2; AM C.593655, Fig. 4; AM C.593656 Fig. 5; AM C.593657, Fig. 6).

Misleading illustration

The illustrations of Hedley show a dorsal valve with a tiny cardinal process (Fig. 2A), so small that it could hardly have been functional. In contrast, the text of Hedley (1899: 509) described the dorsal valve of *T. maxilla* as having a “stout cardinal process”. The lectotype and three paralectotypes figured herein (Figs. 3–6), from the same pieces of coral that provided the material that Hedley described, all have a large cardinal process. The conclusion must be that the illustrations of Hedley, showing a tiny cardinal process, are not accurate for this feature.

This ambiguity between the illustrations and the text of Hedley has led authors (Cooper, 1954: 317; Hoffmann *et al.*, 2009: 348) to incorrectly state that *T. maxilla* has a “small” or “minute” cardinal process. Another error in a later description of *T. maxilla* (Simon *et al.*, 2018: 493) stated that “the ventral valve floor in *T. maxilla* is not roughly tuberculate (nearly smooth)”. The specimens figured herein often have a strongly tuberculate ventral valve floor.

The purpose of this paper is: to outline the published misconceptions of the morphology of *T. maxilla* from the

type locality; to describe (using modern terminology) and figure the newly designated lectotype and paralectotypes to show (at least part of) the range of morphological variation of *T. maxilla* from the type locality; and to provide a new diagnosis of the species *T. maxilla* based on the lectotype and paralectotypes examined. The terminology follows Hoffmann & Lüter (2009, fig. 2), Hoffmann *et al.* (2009), and Logan & Baker (2013).

The material figured may not encompass the entire range of morphological variation from the type locality, but a distinctive set of morphological features is shown herein. No juvenile specimens were examined and the ontogenetic development of *T. maxilla* is not discussed or figured.

Material and methods

The Australian Museum, Sydney, kindly provided SLR camera images of specimen AM C.006202 and loaned four specimens (AM C.593654–57), from the original material of Hedley, that had been opened to make sure the cardinal process was intact. This material was cleaned with a fine brush and imaged using a Hitachi TM3000 SEM at NIWA, Wellington. One specimen from the type locality held in Canterbury Museum, Christchurch, New Zealand (CM.2006.12.1012, dorsal valve; CM.2006.12.12, ventral valve) was also examined.

The type material is held in the Australian Museum, Sydney and includes the newly designated lectotype (AM C.593654) and paralectotypes (AM C.006202, AM C.593655–57) figured herein. The locality information supplied with the lectotype material was 8°29'S 179°4'E (Funafuti Atoll, Tuvalu).

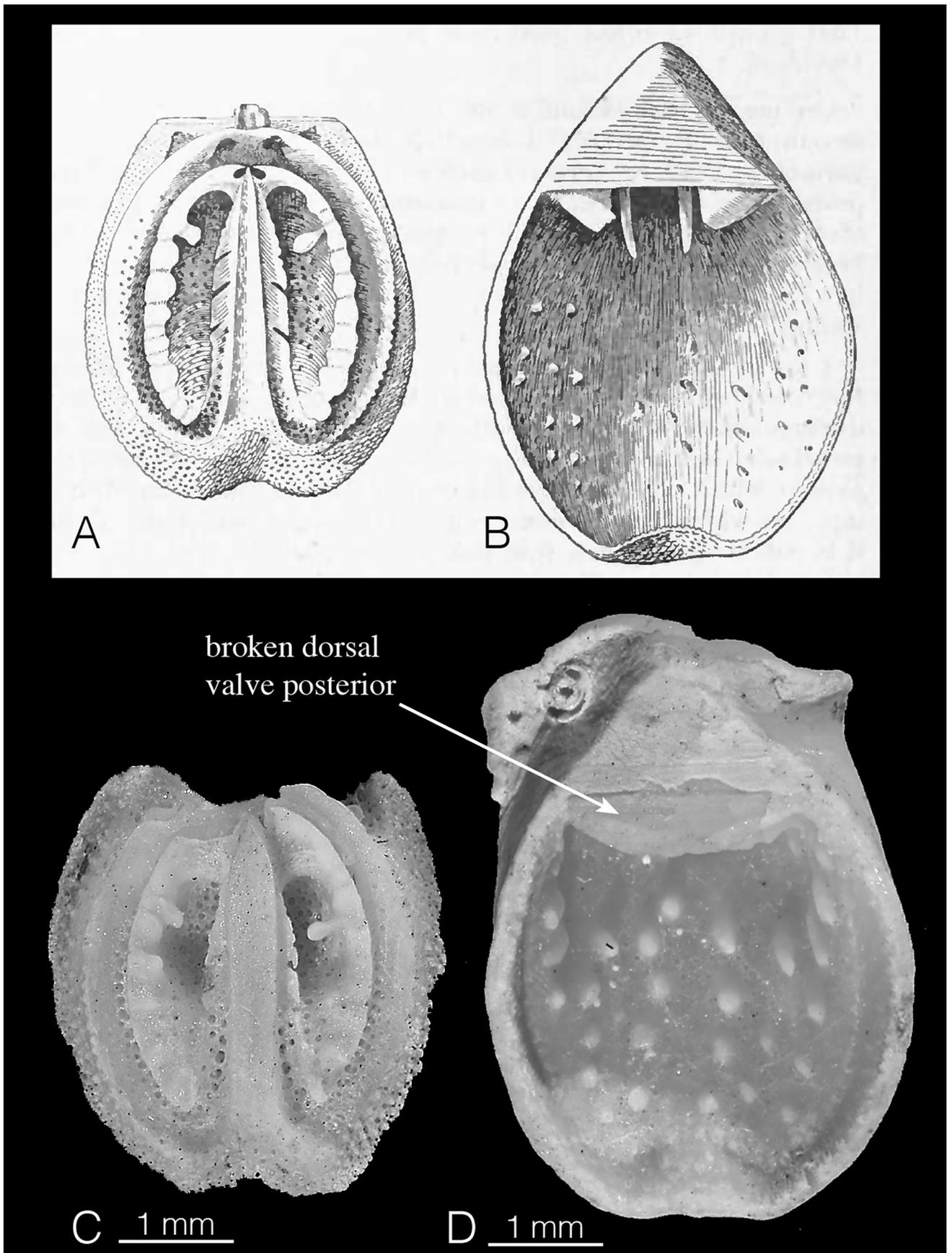


Figure 2. *Thecidellina maxilla*. (A–B) Scan of illustrations from Hedley (1899). (A) Illustration of a dorsal valve interior with tiny cardinal process. (B) Illustration of a ventral valve interior with tubercles on valve floor and long hemispondylium prongs. (C) AM C.006202; SLR camera image of interior of dorsal valve with a wide, concave septum and small canopy spicules (note the missing valve posterior). (D) SLR camera image of interior of the ventral valve showing tuberculate valve floor and the posterior part of the dorsal valve still attached.

Systematics

Superfamily Thecideoidea Gray, 1840

Family Thecidellinidae Elliot, 1958

Genus *Thecidellina* Thomson, 1915

Thecidellina maxilla (Hedley, 1899)

Figs. 2–6

- Thecidea maxilla* Hedley, 1899: 494, 508–510, fig. 57.
Thecidellina maxilla.—Thomson, 1915: 462.—Dall, 1920: 283.—Cooper, 1954: 315, 317–318, pl. 81, figs 1–10.—Cooper, 1964: 1118–1120.—Pajaud, 1970: 240, figs 22, 102B.—Cooper, 1978: 15.—d’Hondt, 1987: 33, 41, pl. 5, figs 1–5.—Lee, 1990: 273, fig. 2.—Laurin, 1997: 412, 413, 416, 453–454, fig. 40a–b.—Brook, 1998: 239, 256.—Lee & Robinson, 2003: 350–352, figs 28–35.—Lüter & Sieben, 2005: 184.—Bitner, 2007a: 498–499, fig. 3a–h.—Bitner, 2007b: 171.—Bitner, 2008: 451, fig. 19.—Bitner, 2009: 12, fig. 12.—Hoffmann, Klann & Matz, 2009: 341, 348, 349.—Hoffmann & Lüter, 2010: 2.—Bitner, 2010: 643, 651–654, fig. 5G–J, tab. 1.—Peck & Harper, 2010: 2209, 2210.—Baker & Logan, 2011: 111, 121.—Simon & Hoffmann, 2013: 402.—Bitner, 2014: 245, 247, 259, 261, fig. 11A–I, tab. 4, appendix.—Bitner, 2015: 42, 43, fig. 5A–E, appendix.—Simon *et al.*, 2018: 482, 492–493, 494, 498.—Bitner, 2019: 600, fig. 7C–E.
Thecidellina cf. *T. maxilla* Cooper, 1964: 1118, pl. 301, figs 15–16, 18–19.—Robinson, 2017: 7–9, fig. 2E–F, tab. 4.
Thecidellina australis maxilla Pajaud, 1970: 47, 240, 241, 312, figs 22, 107.

Stratigraphic range: Miocene to Recent

Material has been identified as *T. maxilla* or cf. *T. maxilla* from the Early Miocene of Java (Cooper, 1978) and of New Zealand (Robinson, 2017), the post-Miocene of the Marshall Islands (Cooper, 1964), the Pliocene of the Chatham Islands (Lee & Robinson, 2003) and the Pleistocene of the Kermadec Islands (Brook, 1998).

Description

The ventral valve outline is drop-shaped, longer than wide, with some variation in width (Figs 2D, 3A, 4A, 5A, 6A). The cicatrix position varies from being beneath the valve (Fig. 3B) to facing posteriorly (Fig. 3C) and this creates variation in the ventral valve exterior, a common feature among thecideoidea. The triangular planodeltidium is often striated (Figs 4A, 6A), the hinge line is straight in unopened specimens. The teeth are large, the ventral valve floor has small to large tubercles (Figs 2D, 3A, 4A, 5A, 6A) and may have short, jagged tubercle-ridges (Fig. 5A), the gonad pits are shallow (Fig. 6A), or just areas of the valve floor free of tubercles (Fig. 5A).

The base of the hemispondylium is cup-shaped and two long, slender prongs extend from the lateral sides of the cup and reach beyond the cardinal margin (Figs 3A,D, 5B, 6B). The ventral edge of the cup may be clear of the ventral valve floor (Fig. 5B), may be clear but have tubercles touching it (Fig. 3B) or may be connected with the valve floor (Fig. 6B). There is no ventral ridge or septum.

The dorsal valve exterior has faint concentric growth lines (Fig. 3E). Internally, the medium septum is long and narrow; on one specimen it appears to be concave its whole length (Fig. 2A,C) but on the other four specimens the septum is concave anteriorly and has the form of a sharp, blade-like ridge posteriorly (Figs 3F,G, 4B–E, 5C–E,G–I, 6C–D). The anterior edges of the septum, where it flares laterally, may have small to large tubercles (Figs 3I, 5F). Both valve interiors are densely punctate (Figs 3A, 4A,B, 6C). The teeth, lateral margins of the cardinal process and ventral tubercles have a thin covering of secondary shell.

The canopy of spicules over the brachial cavities varies widely; one specimen has stubby spicules directed posteriorly that do not form a canopy at all (Fig. 6C–D,F,G), this may be a male specimen (Hoffmann *et al.*, 2009). In other specimens, the canopy varies from being very sparse (Figs 2C, 5C,D) to being a well-formed open lattice (Fig. 3F,G) to being a lattice that has been partially infilled (Fig. 4B,C,E). Lophophore muscle scars are very faint to absent.

There is a clear visceral gap in two specimens (Figs 3J, 5I) and there are small calcitic connections between the intrabrachial ridge and the brachial bridge in one specimen (Fig. 6C–D,E,G). The intrabrachial ridge has two marsupial orifices beside the tip of the septum (Fig. 3F,H). The calcitic pole is sub-triangular where it attaches to the base of the cardinal process (Fig. 4C,F), flares into an anteriorly-facing, partly-folded or curved sheet (Figs 5H, 6E), then becomes much narrower where it joins the brachial bridge, forming two ovarian notches (Figs 3H, 5C,G,H, 6C). The calcitic pole divides the visceral foramen (Figs 3J, 5I, 6G,H). The peribrachial ridges and the flange are tuberculate (Figs 3G, 4D, 5E,I). All four cardinal processes figured have a very thin spur on the mid-line (Fig. 4F) that joins the folded posterior edge of the calcitic pole (Figs 5I, 6H). Curving lateral adductor scars occur on each side of the cardinal process (Fig. 6H,I).

Remarks

One specimen from the type locality held in the Canterbury Museum, Christchurch was examined. The ventral valve was strongly tuberculate with the cup-shaped hemispondylium well clear of the valve floor. The dorsal valve has a large cardinal process, similar to that in Fig. 5C–E. The dorsal valve has slightly more development of the calcitic connections between the brachial bridge and intrabrachial ridge than the specimen in Fig. 6. The dorsal valve has minimal canopy spicules and the posterior portion of the median septum is flattened and lacking a sharp ridge, similar to the specimen in Fig. 2C.

Revised diagnosis of *Thecidellina maxilla*

The ventral valve has tubercles or tubercle-ridges on the valve floor, the hemispondylium is cup-shaped with two long, curving prongs extending anteriorly, the gonad pits are shallow or just clear areas without tubercles. The dorsal valve has a calcitic pole attached to the cardinal floor and the brachial bridge, dividing the visceral foramen. The calcitic pole flares anteriorly forming a partly-folded or anteriorly curving sheet with ovarian notches, the cardinal process has a very thin medial spur, the dorsal septum is narrow, may be concave its whole length or concave anteriorly and with a curving blade-like ridge posteriorly. The canopy spicule lattice development

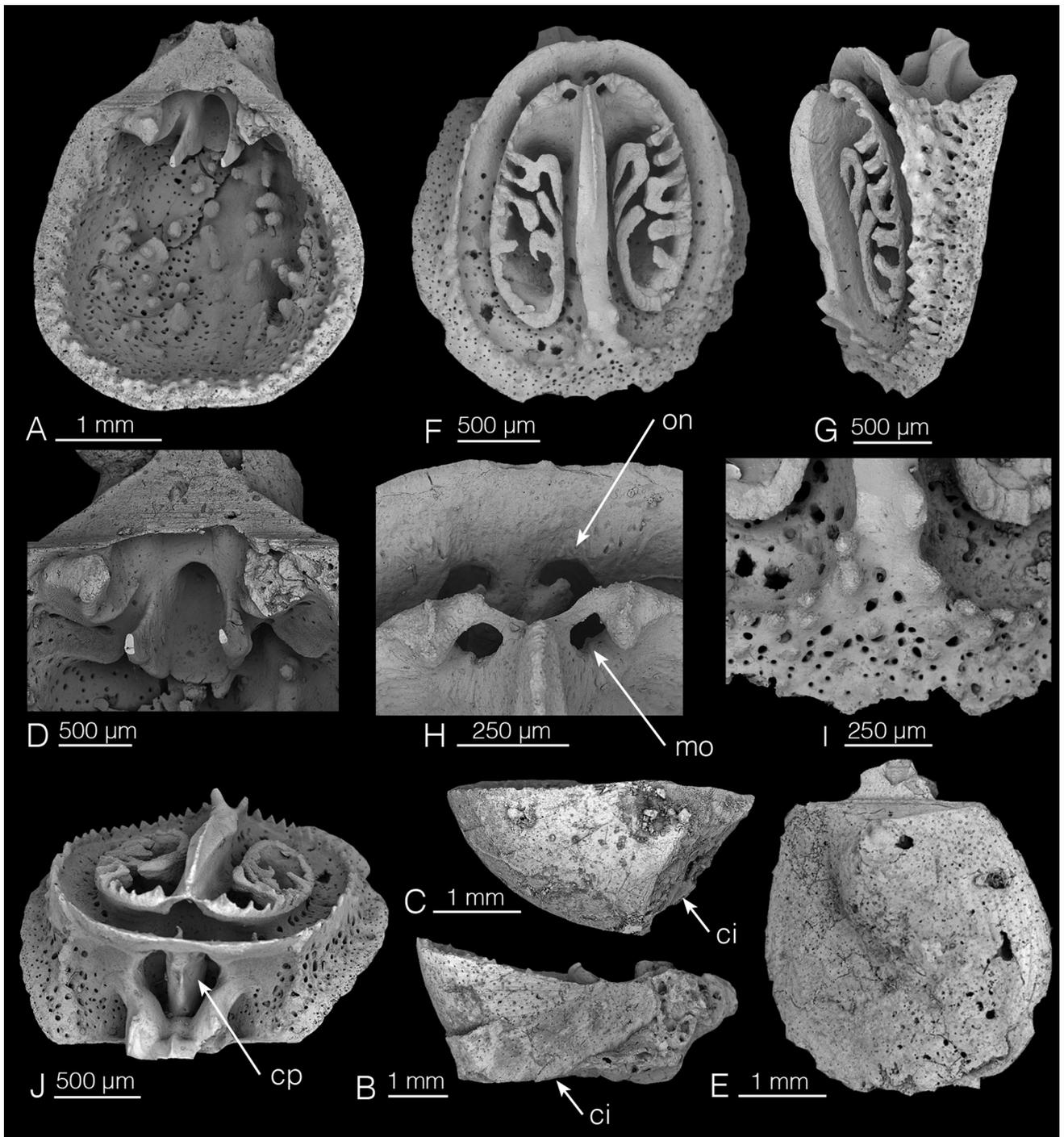


Figure 3. *Thecidellina maxilla* lectotype AM C.593654 (except C). (A) Ventral valve interior with tubercles. (B) Exterior of ventral valve with cementing surface underneath. (C) AM C.593657; exterior of ventral valve with cementing surface at posterior. (D) Close-up of cup-shaped hemispondylium. (E) Exterior of dorsal valve. (F) Interior of dorsal valve with spicules over the brachial chamber and no calcitic connections between brachial bridge and intrabrachial ridge. (G) Lateral view of dorsal valve interior. (H) Close-up of tip of septum, marsupial orifices and ovarian notches. (I) Close-up of tubercles at base of septum and on anterior margin. (J) Posterior view of dorsal interior with calcitic pole attached to brachial bridge and base of cardinal process. Abbreviations: *ci*, cicatrix; *cp*, calcitic pole; *mo*, marsupial orifice; *on*, ovarian notch.

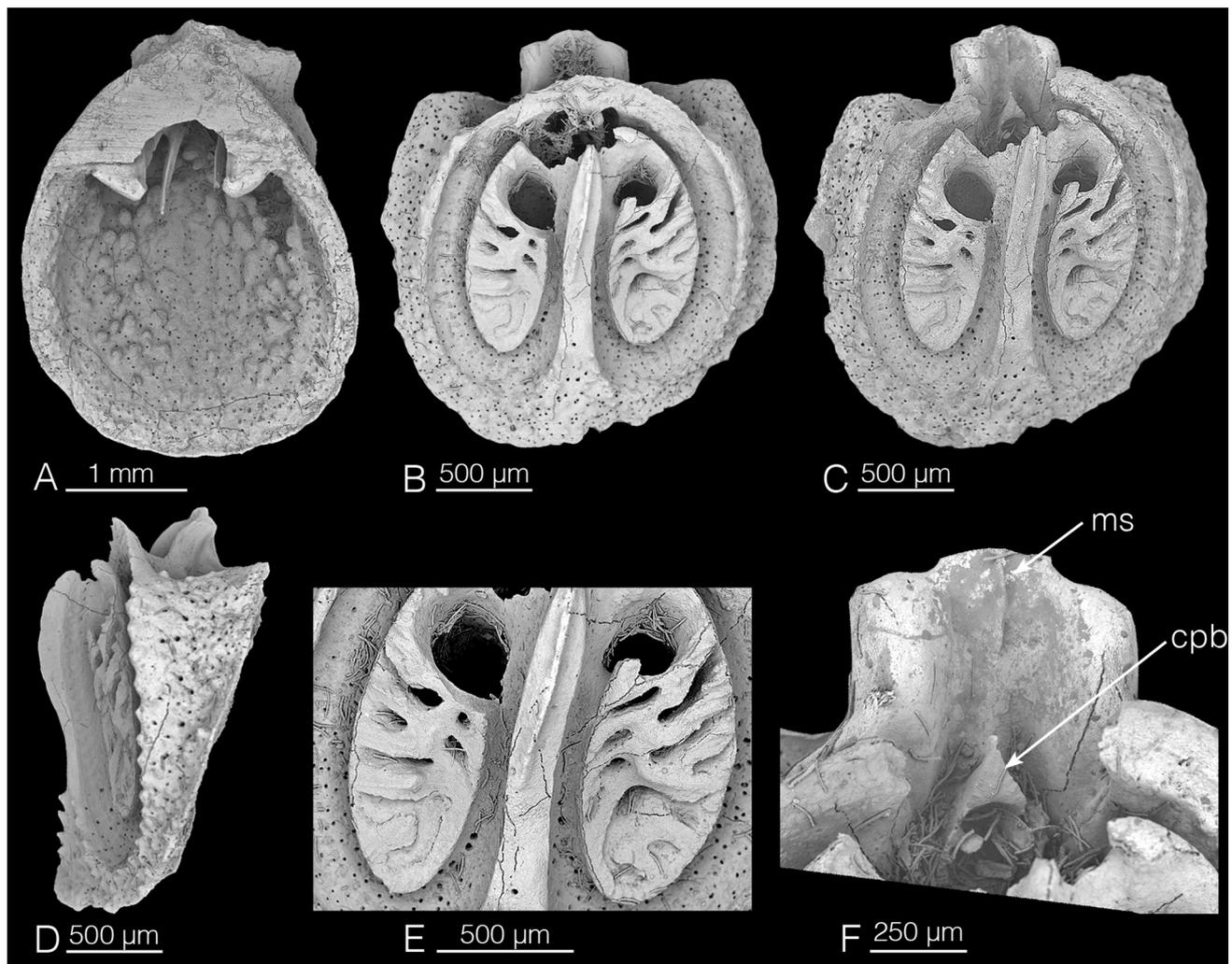


Figure 4. *Thecidellina maxilla* AM C.593655. (A) Ventral valve interior with tubercles on valve floor and long hemispondylium prongs reaching past the teeth. (B) Dorsal valve interior with partially fused spicule canopy. (C) Dorsal valve interior with brachial bridge and calcitic pole broken off showing triangular base. (D) Lateral view of dorsal valve interior with prominent septum blade. (E) Close-up of partially infilled spicule canopy. (F) Close-up of broken base of calcitic pole and very fine median spur on the cardinal process. Abbreviations: *cpb*, calcitic pole base; *ms*, median spur.

may be sparse to extensive and may be infilled. The visceral gap is usually open, calcitic connections between brachial bridge and intrabrachial ridge are small or absent. Marsupial orifices occur on each side of the septum tip.

Discussion

Recent *Thecidellina maxilla* has been reported from at least ten general localities in the Indian and Pacific Oceans (Fig. 1): Tuvalu (Hedley, 1899); the Marshall Islands (Cooper, 1954); Reunion Island (d'Hondt, 1987); Noumea (Laurin, 1997; Bitner, 2007b, 2010, 2015); the Kermadec Islands (Lee & Robinson, 2003); French Polynesia (Pajaud, 1970; Bitner, 2007a, 2014); Fiji (Bitner, 2008); Wallace and Futuna Islands (Bitner, 2008); northern Norfolk Ridge (Bitner, 2009); and Tonga (Bitner, 2019).

However, when comparing the figures herein of material from the type locality with figures in publications that identify Recent material as *T. maxilla* from other localities, none of material from those other localities closely resembles the material in Figs 2–6. The combination of a ventral valve with a cup-shaped hemispondylium and tuberculate floor

and a dorsal valve with a thin spur on the cardinal process, small or no calcitic connections and a thin, concave septum or a septum with a posterior arching blade, was not figured in any other publication.

Lee & Robinson (2003) suggested that most Recent thecideide material in the Pacific Ocean might be variants of *T. maxilla*. However, in published papers on thecideides since then, new taxonomic features and terminology have been introduced and new species have been proposed from the Pacific, Atlantic, Caribbean and Indian Oceans. Lüter *et al.* (2008) and Hoffmann & Lüter (2009) found a high level of diversity among thecideides in the Caribbean among populations previously lumped together under the name *T. barretti* (Davidson, 1864). Hoffmann & Lüter (2010) showed that different species may look similar as adults but certain shell features developed in different ways during their ontogeny.

There has also been discussion that the cryptic habitat and larval brooding of thecideides means their larvae, once released, have only a short time and a difficult path to reach open water and be carried by ocean currents to new locations. This may lead to localized populations and

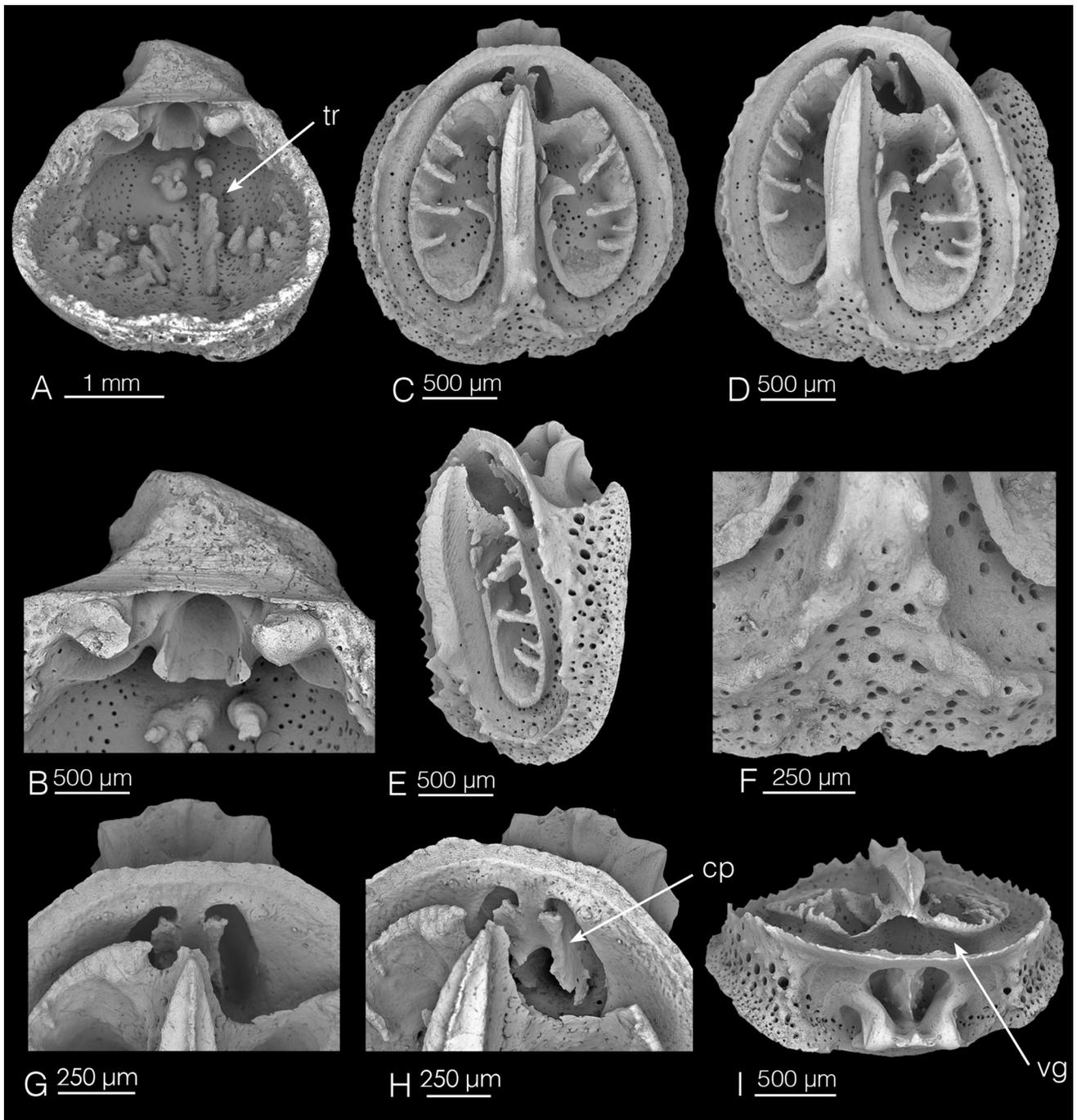


Figure 5. *Thecidellina maxilla* AM C.593656. (A) Ventral valve interior with tubercle-ridges and cup-shaped hemispondylium. (B) Close-up of cup-shaped hemispondylium, free from valve floor. (C) Dorsal valve interior with sparse canopy spicules. (D) Slightly oblique dorsal valve interior. (E) Lateral view of dorsal valve interior with prominent blade on septum. (F) Close-up of tubercles at base of septum and on anterior margin. (G) Close-up of septum tip, marsupial orifice and ovarian notches. (H) Oblique close-up of curved calcitic pole attached to brachial bridge. (I) Posterior view of dorsal interior, calcitic pole divides visceral foramen, wide visceral gap without calcitic connections. Abbreviations: *cp*, calcitic pole; *tr*, tubercle-ridge; *vg*, visceral gap.

speciation within small geographic areas (Lüter *et al.*, 2008; Hoffmann & Lüter, 2009).

Contrary to the suggestion of Lee & Robinson (2003), it may be that the apparently widespread species *T. maxilla* is a species complex, as suggested by Hoffmann *et al.* (2009), and that *T. maxilla* *sensu stricto* may be restricted to a relatively small geographical area. Tuvalu (the type locality of *T. maxilla*) includes nine reef islands and coral atolls that have developed on top of steep-sided Late Cretaceous

volcanic seamounts. The surrounding seafloor is on average 2,000 m deep (Krüger, 2008). The widely-scattered island groups of the Pacific Ocean would seem to be ideal places for speciation of organisms with short larval stages that prefer shallow-depths and cryptic habitats.

If *T. maxilla* *s.s.* is restricted to a small part of the Mid-West Pacific Ocean then fossil material identified as *T. maxilla* or *cf. T. maxilla* from localities such as New Zealand and the Chatham Islands needs to be revised.

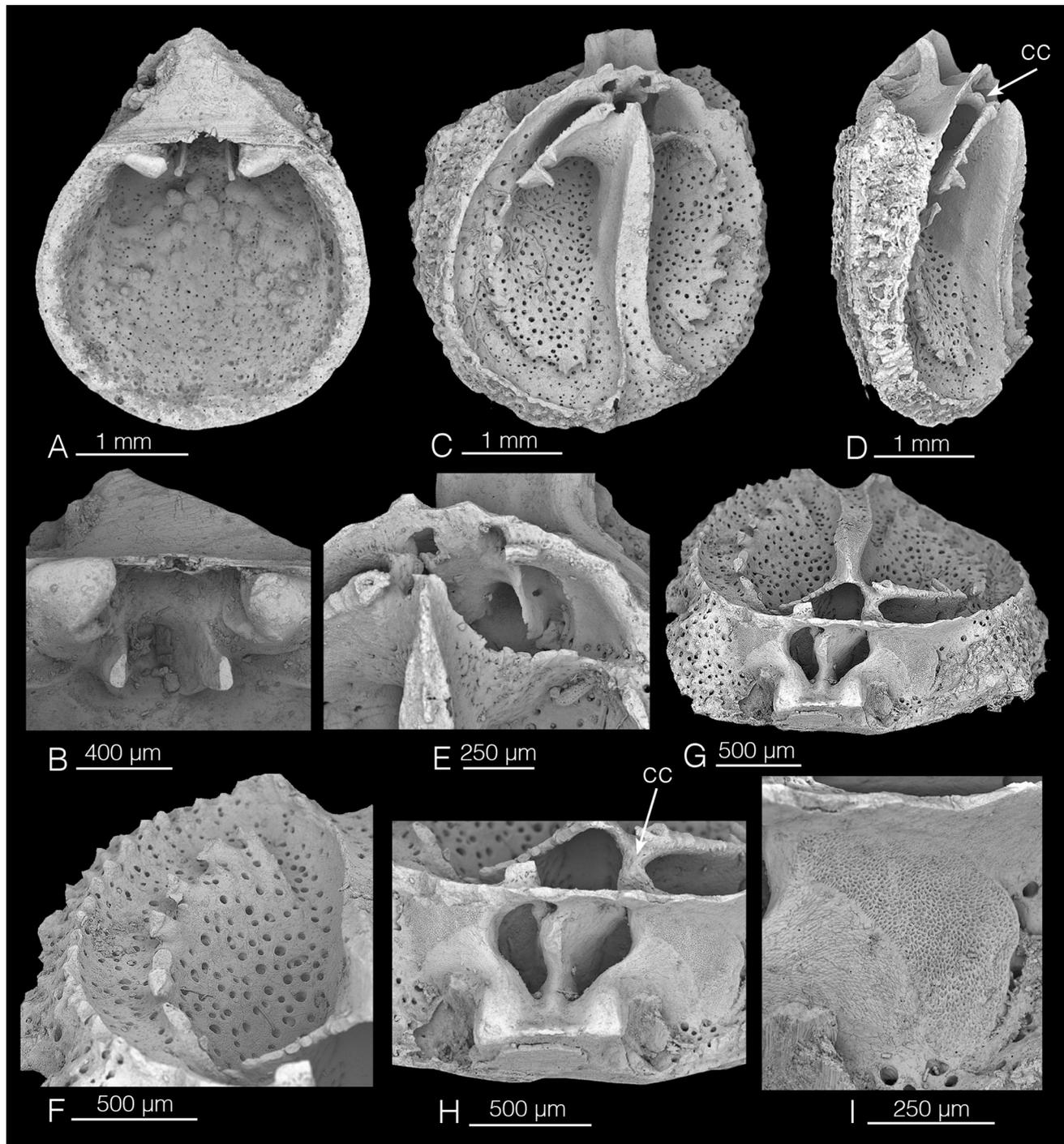


Figure 6. *Thecidellina maxilla* AM C.593657. (A) Ventral valve interior. (B) Close-up of hemispondylium. (C) Slightly oblique view of dorsal valve interior. (D) Lateral view of dorsal valve interior. (E) Close-up of tip of septum, marsupial orifice, calcitic pole and ovarian notches. (F) Brachial cavity with stubby spicules (male specimen?). (G) Posterior of dorsal valve. (H) Close-up of calcitic pole joining the thin median spur on the cardinal process. (I) Lateral adductor muscle scar on right of cardinal process. Abbreviations: *cc*, calcitic connections.

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