Periostracum and fibrous shell microstructure in the unusual Cambrian hyolith *Cupitheca*

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ABSTRACT

Cupitheca is an enigmatic tubular fossil common in early Cambrian deposits worldwide. It has recently been argued to be a hyolith, probably orthothecid. *Cupitheca* had a dense network of mantle-filled tubules that connected to what we interpret as a continuous organic periostracum. The innermost shell layer consists of horizontal or slightly inclined bundles of fibres elongated along the a-axis and offset from other bundles at aragonitic twin angles, confirming aragonite as the original mineralogy for the shell of *Cupitheca*. This is a similar shell microstructure to that inferred for Cambrian hyoliths, strengthening the claim that *Cupitheca* is a hyolith. This shell microstructure of bundled aragonite fibres and the tubule systems can also be seen in many Cambrian molluscs and other lophotrochozoans. In some lineages this shell texture evolved into fracture-resistant crossed lamellar microstructure and in others nacre. These transitions began to occur sometime between the mid-Cambrian and Ordovician, and nacre and crossed lamellar microstructure were the most common constituents of the inner shell layer of molluscs by the middle or late Palaeozoic Era.

RESUMEN

Cupitheca es un fósil tubular enigmático frecuente en depósitos del Cámbrico inferior de todo el mundo. Recientemente se ha asignado a hiolitos, probablemente un Orthothecida. *Cupitheca* tiene una estructura densa de túbulos, que estaban rellenos por manto y que conectaban con lo que interpretamos como un periostraco orgánico continuo. La capa más interna de la concha consiste en haces de fibras horizontales o ligeramente inclinadas, alargadas según un posible eje cristalográfico a y giradas con respecto a otros haces contiguos a ángulos propios de maclas aragoníticas, lo que confirma la mineralogía original de la concha de *Cupitheca* como aragonítica. Esta microestructura de concha es similar a la inferida para hiolitos del Cámbrico, lo que refuerza la aserción de que *Cupitheca* es un hiolito. Esta microestructura a base de haces de fibras aragoníticas y un sistema de túbulos también se puede encontrar en muchos moluscos del Cámbrico y en otros lofotrocozoos. En algunos linajes esta textura de concha evolucionó hacia una microestructura lamelar cruzada, y en otros, hacia nácar, siendo ambas las más resistentes a la fractura. Estas transiciones comenzaron en algún momento entre el Cámbrico medio y el Ordovícico, de modo que

el nácar y la microestructura lamelar cruzada fueron las más frecuentes en las capas internas de las conchas de los moluscos ya en el Paleozoico medio o superior.

1. INTRODUCTION

Cupitheca Duan in Xing *et al*. (1984) is a widespread early Cambrian fossil known from China (Xiao & Zhou, 1984; Pan *et al*., 2015; Skovsted *et al*., 2016), Australia (Bengtson *et al*., 1990; Skovsted *et al*., 2016), Antarctica (Wrona, 2003), Spain (Fernández-Remolar, 2005), Canada (Peel, 1987; Skovsted & Peel, 2007), and Greenland (Malinky & Skovsted, 2004; Skovsted, 2006). Specimens of *Cupitheca* are typically tiny (usually no more than 2 mm in length), straight to slightly curved tubes with a circular or sub-circular cross-sectional outline. Bengtson (in Bengtson *et al*., 1990) provided the best, most complete, description of *Cupitheca* (as *Actinotheca*) and noted the unusual flat, rounded shape of the shell termination (Figs 1a, c, f), interpreting it as a transverse septum that formed as the earlier shell segment broke off in a decollation process similar to that of the modern gastropod *Caecum* (Fretter & Graham, 1978). Bengtson also noted a concentration of tubules at the transverse wall (see Figs 1d-e), inferring a role of these presumably organic-filled tubes in decollation.

Although *Cupitheca* had earlier been grouped with hyoliths (e.g. Xiao & Zhou, 1984), Bengtson (in Bengtson *et al*., 1990) considered it to be a problematic fossil because there were no clear hyolith features, its unusual pattern of decollation is not known in other hyoliths, and no clear operculum was known. More recently, Skovsted *et al*. (2016) described opercula from the early Cambrian of Australia and China (see Fig. 1b) that he interpreted to be part of the skeleton of *Cupitheca holocyclata* based on its consistent co-occurrence, and similarity in size, sub-circular outline, and ornament, although the transverse ridges are somewhat more prominent in the opercula than in *Cupitheca*.

Hyoliths have been argued to represent an extinct class of molluscs (Marek & Yochelson, 1976; Dzik, 1978) or a separate phylum possibly closely related to sipunculans (Runnegar *et al*., 1975; Runnegar, 1980, 1996). Recently, Moysiuk *et al*. (2017) described exceptionally preserved hyoliths from the Burgess Shale and Spence Shale with an apparent lophophore, suggesting that hyoliths may instead be lophophorates.

Herein we describe and interpret details of the shell of *Cupitheca*, including microstructure, tubules, pathologies, and external ornament. We compare the shell microstructure of *Cupitheca* with that of other hyoliths as well as molluscs, brachiopods and other lophophorates. The shell microstructure of *Cupitheca* is similar in many ways to that of undisputed Cambrian hyoliths, and also to many helcionellids and unusual Cambrian molluscs like *Pelagiella* and *Ocruranus*.

2. MATERIALS AND METHODS

All the specimens described herein were collected by B. Runnegar and S. Bengtson from the Parara Limestone at Horse Gully, South Australia, University of New England, Armidale localities (UNEL) 1852, 1854, and 1856 (Bengtson *et al*., 1990). The Parara Limestone at this section contains a diverse fauna, and the presence of the problematic ecdysozoan *Stoibostrombus crenulatus* and the trilobite *Yorkella australis* indicates the formation correlates with the *Dailyatia odyssei* Zone in the Arrowie Basin, Australia, from Stage 3 of Series 2 of the Cambrian (Betts *et al*., 2016).

Runnegar and Bengtson extracted fossils along with other macerate material from carbonate rock using dilute acetic acid. We sorted the fossils from the macerates, placed them on SEM stubs, and coated the stubs with gold or carbon. Specimens were photographed using: 1) a LEO Gemini 1530 Field Emission SEM with Zeiss Auriga Cross-Beam Station at the Centro de Instrumentación Científica, University of Granada; 2) a Phenom Pro SEM at the Departamento de Estratigrafía y Paleontología, University of Granada; 3) an FEI Sirion model XL30 SEM at the Materials Research Laboratory, University of California at Santa Barbara; or 4) an FEI Quanta 400 Field Emission SEM at the Department of Earth Science, University of California at Santa Barbara. Working distance was typically about 10 mm and voltages ranged from 3 to 10 kV.

All specimens are reposited at the South Australian Museum of Paleontology (SAMP), Adelaide, South Australia. Measurements were made from SEM photographs using ImageJ (Schindelin *et al*., 2012). We use descriptive terminology of the fossils as presented by Bengtson (in Bengtson *et al*., 1990), including 'cylindrical wall' for the tubular shell surface, 'terminal wall' for the apical

end of the shell, and 'tubules' for the protrusions from the steinkern surface, the inferred mantle projections that in better-preserved specimens connect between the surface of the steinkern and the outer phosphatic sheath that we interpret herein as replaced periostracum.

3. RESULTS

3.1. Shell microstructure

Fossils of *Cupitheca* show remarkable variation in features such as degree of shell curvature, length, shell ornament, periostracal thickness, and degree of preservation of tubules. The crystal imprint textures on steinkerns, however, are remarkably consistent, and this along with the fine details of their form and uniqueness compared to other fossils from the Parara Limestone make it clear that these textures reflect original shell microstructure. The shells are interpreted to have been aragonitic, based on angles of offset between adjacent bundles (see below), the fibrous nature of crystallites that are more common with aragonite than calcite, and preservational data. Thin sections of *Cupitheca* from the Parara Limestone show the wall has been replaced with sparry calcite (Bengtson in Bengtson *et al*., 1990) whereas fossils from the same assemblage that had original calcite composition show relatively unaltered shell (Runnegar in Bengtson *et al*., 1990).

Most specimens of *Cupitheca* from the Parara Limestone show some trace of shell microstructure preserved (Fig. 2). Many of the specimens show elongate, fibre-like impressions that are often sub-parallel to the shell margin (perpendicular to the long-axis of the tube) and that extend for at least tens of micrometres and probably much more. The fibres in one broad region of the inner shell surface often occur at an angle to each other within the same horizontal sub-layer (Figs 2a, c-i). The angles between the fibre bundles are highly variable, but the best-preserved cases show angles very close to the 60° and 120° angles (Fig. 2) expected if fibres in adjacent bundles are aragonitic twins. In some instances the bundles of fibres stacked atop each other have different orientations (Fig. 2c), although in other cases vertical tubule fills show borders that match the fibre orientation of the inner shell surface (Figs 2a-b, e-f).

This type of shell microstructure is similar to that named lamello-fibrillar, characterized by successive laminae made up of parallel fibres, with the fibres in different orientations from one stacked layer to the next (Carter *et al*., 2012). The situation in *Cupitheca* seems more complex than that, as in at least some cases the fibres in successive horizontal (parallel to shell surface) levels of the shell appear to occur in the same orientation, but

neighbouring fibre bundles have a different orientation. These aragonite fibres of the innermost shell layer grew orthogonally to the growth front at the margin (rim) of the shell, interweaving with neighboring fibre bundles.

In many regions of the fossils only one edge of the fibres is clearly preserved (Figs 2e-f). These indicate that the long axis of fibres was slightly tilted relative to the internal surface. In some cases the fibres are tilted down towards the terminal end of the shell, and in others toward the aperture. The aragonitic fibres grew all around the cylindrical wall of *Cupitheca*, with periodic twinning. They were grouped in sets that had different lateral dips to each other (Fig. 2g), suggesting a loosely-organized precursor to crossed lamellar where bundles of fibres are inclined to the horizontal shell surface, but with vertical growth along the c-axis as opposed to the horizontal growth along the a-axis as in *Cupitheca*. *Watsonella* shows a nice transition from the type of shell microstructure of *Cupitheca* to something close to foliated aragonite (Kouchinsky, 1999), the inferred precursor to nacre (Vendrasco *et al*., 2011a). In all these shell microstructures (fibrous aragonite as in *Cupitheca*, crossed lamellar, foliated aragonite, and nacre), the c-axis of aragonite is vertical or more or less so (i.e. orthogonal to shell surface). In fact, in some vetigastropods the microstructure changes through the shell from outer to inner layer from fibrous aragonite to crossed lamellar and to nacre, with the crystallographic orientation of the aragonite crystals staying the same throughout.

The outer shell microstructure of *Cupitheca* is unclear. Just above the innermost layer characterized by transverse fibre bundles, one specimen (Fig. 2i) shows longitudinal fibres. This is the opposite pattern to that of some Cambrian hyoliths described by Kouchinsky (2000b), with an inner shell layer divided into sublayers where the top part has transverse fibres and the lower part has longitudinal ones. However, in other Cambrian hyoliths the inner shell layer consists of transverse fibres (Kouchinsky, 2000b), as for *Cupitheca*. Tubule moulds provide some data on microstructures deeper into the shell. These tubule fills (Figs 2a-b, e-f), although partial and only representing a small inner segment of the shell, indicate sub-horizontal fibres in consistent transverse orientations in the shell from the inner shell surface up through a significant thickness of the shell, contrasting with the pattern seen in Figure 2i.

In some cases the shell microstructure imprints are reminiscent of the elongate growth fronts of laminar shell microstructures like foliated aragonite (Figs 2e-f). However, there are no distinct crystal terminations visible along the long axes of the imprints (the lineations are remarkably straight), they are often very closely spaced together, the lineations run parallel to the shell margin as do the more distinct fibres preserved in other specimens, and there is gradation from these linear traces to distinct fibre imprints. The straight edges are consistent with our interpretation of the basic microstructural units as
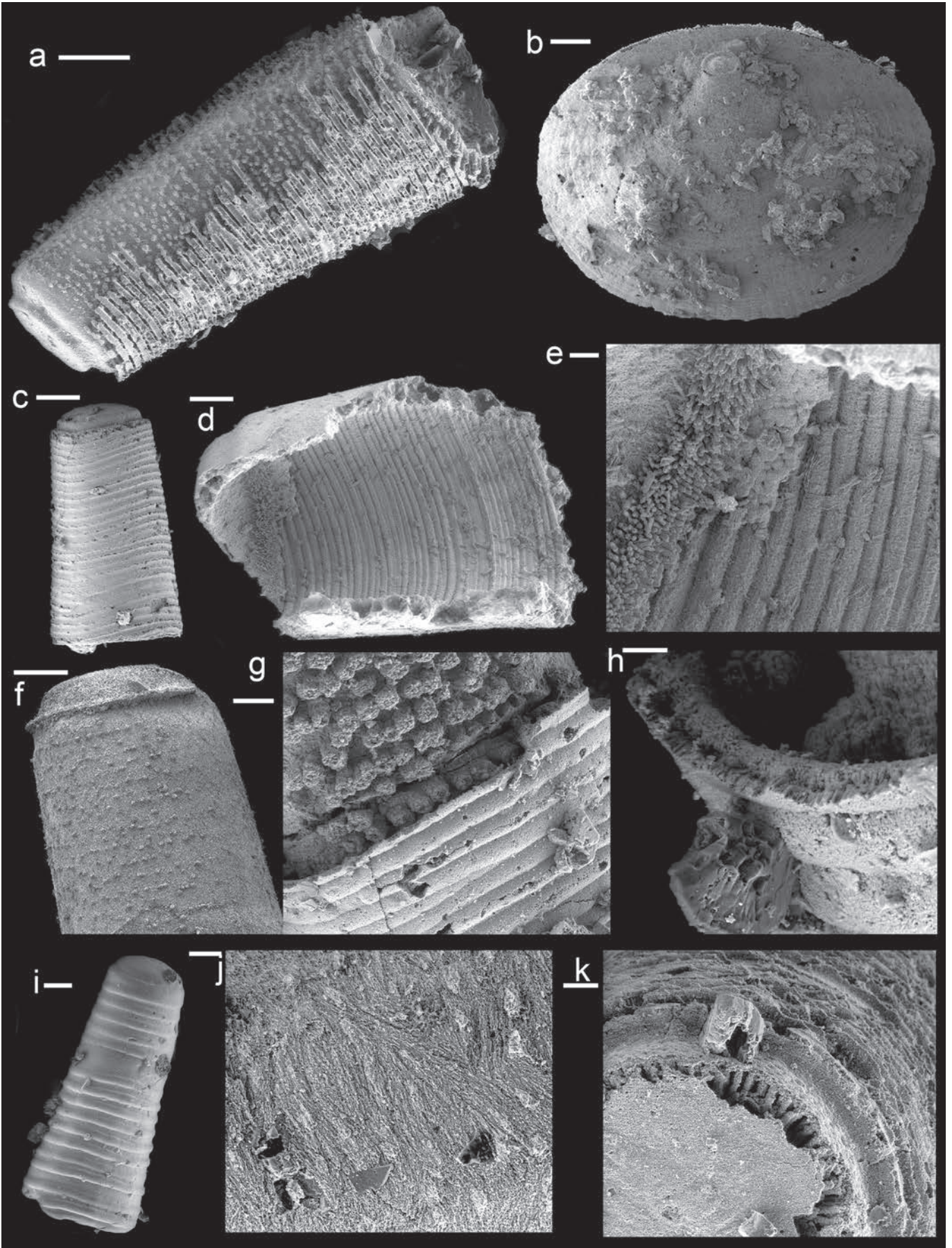
elongate, flat fibres (like very thin blades) of aragonite, as theses straight edges correspond to the lateral margins of the fibres.

3.2. Periostracum

The outer wavy layer of *Cupitheca* is often remarkably well preserved with phosphate (e.g. Figs 1c-e, g-i, 4), in contrast with the underlying shell that was replaced with sparry calcite instead. The consistent thickness and connection to tubules (see below) in the outer wavy layer indicates it is not an external mould. The tiny grains of phosphate that comprise the wavy layer are similar to what Porter (2004) inferred as replaced organic material in the sclerites of halkieriids. The overall form of the wavy layer is similar to that of the periostracum of *Neotrigonia* (Checa *et al*., 2014). For these reasons we interpret the outer wavy layer of *Cupitheca* as representing a phosphatized periostracum possibly homologous to that of molluscs and brachiopods.

3.3. Tubules

Specimens of *Cupitheca* preserve evidence of tubules that extended through the shell, orthogonal to the shell surface. The tubules are preserved in a variety of ways, from tubercles or granules on internal moulds, to fully formed, complete tubes that run from the inner to outer surface of the shell (Figs 1d-g, k, 3, 4a). These tubule casts are in some cases solid but are often hollow (Fig. 3a), indicating they were probably filled with living tissue during life. The tubules have a sub-cylindrical shape and often flare near the external shell surface (Figs 3d-e, j). They align with the valleys on the outer shell surface rather than on the ridges (Fig. 3d).

Views of the inner surface of the outer wavy layer (Figs 1d-e, 3h) show no sign that the tubules extended all the way to the external-most surface of the shell. However they clearly extended nearly to the shell surface (Figs 3d, g-i). Close-up images (Fig. 3d) show a faint boundary between the outer wavy layer and the tubules.

In many specimens tubules may occur in great densities (Fig. 1g), particularly at the terminal wall (Figs 1d-e, 3f-j). Bengtson (in Bengtson *et al*., 1990) noted the common abundance near the terminal wall, and concluded the tubules there were probably involved in decollation. The striking differences in density and morphology (there is more tapering in the terminal wall canals) of canals in the terminal wall versus elsewhere suggest a different function for the different sets of canals.

3.4. Pathologies and other anomalies

Some specimens show growth discontinuities that appear to represent healed scars (Figs 4b-c, f). In addition, one specimen shows an unusual pattern of shell microstructure preservation that appears to reflect damage that was translated even to the inner surface of the shell (Figs 4g-h).

Also, dome-shaped protrusions (Figs 4a-b, f) were seen on more than twenty specimens. These do not seem to represent secondary botryoidal coatings of phosphate, as broken protrusions are as thin-walled as the rest of the outer wall (Figs 4d-e). These protrusions are concentrated in certain regions of the external shell surface, including one specimen with the domes arranged in an oval pattern in the middle of the shell (Figs 4a, d). Other specimens show a concentration of these projections in and around apparent healed scars (Fig. 4f), so they may be related to shell damage repair.

4. DISCUSSION

4.1. Structure and formation of the shell of *Cupitheca*

We interpret the wavy outer layer of fossils of *Cupitheca* as a phosphatic replacement of the periostracum. In cross-sectional views the structure of the wall can be seen to consist of tiny vertical (orthogonal to shell surface) grains neatly arranged (Fig. 1h). This contrasts with laminar

Figure 1. Morphological features of *Cupitheca holocyclata* (Bengtson in Bengtson *et al*., 1990). **a)** SAMP 54965, composite internal/external mould with terminal wall at lower left. The internal mould of another terminal wall is visible on the upper right end of the specimen; this may represent a telescoped additional specimen or a preserved decollation event. **b)** SAMP 54966, inferred operculum of *Cupitheca* (see also Skovsted *et al*., 2016). **c)** SAMP 54967, external view of external mould, terminal wall at top. **d)** SAMP 54968, internal view of external coating and filling of tubule cluster at terminal wall. Apparent internal mould surface external to this may be due to telescoping specimens. **e)** close-up of (d). **f)** SAMP 54969, internal mould with only short length of tubules filled in. **g)** SAMP 54970, composite internal (top) and external mould, showing both tubule infilling and shell ornament. **h)** closeup of (g), oblique view of external coating, showing vertical arrangement of phosphate crystals therein. **i)** SAMP 54971, external mould showing unusually broad ridges. **j)** SAMP 54972, close-up of internal mould showing multiple orientations to fibre imprints. **k)** SAMP 54973, view from the terminal wall side of the specimen, showing tubule fillings and external coat. Scale bars: **(a-d, f, i)** = 100 µm; **(e, g)** = 20 µm; **(h, j-k)** = 10 µm.
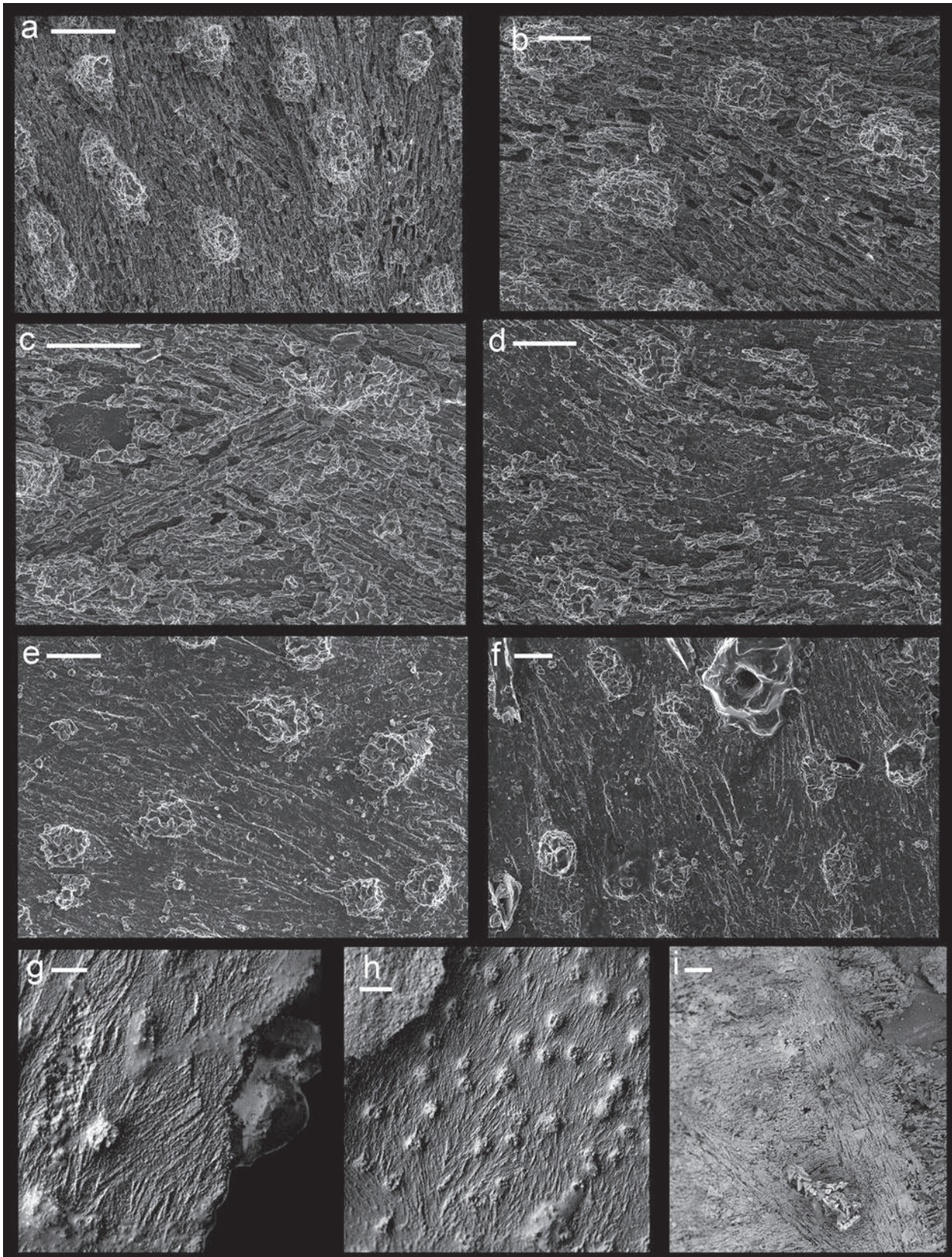
Figure 2. Shell microstructure in *Cupitheca holocyclata*. **(a-d)** SAMP 54974. **(e-h)** SAMP 54975. Views of internal mould surfaces showing partial tubule fills and fibre imprints, as well as partial casts showing shell microstructure details inside the shell. **e-h)** show straight edges interpreted as fibres tilted along their long axis at a low angle to the inner shell surface. **i)** SAMP 54976. The bundle on the right is oriented longitudinally, with aperture in the direction towards the lower left corner of the photograph. Scale bars: **(a, h-i)** = 10 μm; **(b-g)** = 5 μm.

growth expected if the wall instead represents an external coating (mould) of the shell. The thickness of this wall typically ranges from about 1 to 10 microns. The abundant tubules of the shell of *Cupitheca* open at the base of this wall (Fig. 3d).

The shell of *Cupitheca* is probably aragonitic, based on preservational patterns, inferred twinning angles, and the fibrous nature of crystallites. We interpret the lineations on the internal moulds as the sides of aragonite fibres elongated along the a-axis. These occur in bundles at various angles to each other, but in general are transverse (run around the shell) in the innermost layer and at least some cases longitudinal just above it (Fig. 2i). The bundles of fibres probably criss-cross each other and occasionally converge in the same horizontal shell layer in nearly horizontal lamellae. The laminar aspect of the inner shell layer can best be seen in Figures 4g-h, showing first order lamellae that consist of bundles of fibres. The aragonite fibres wound around the *Cupitheca* shell as it grows, with periodic twinning. The fibres may be continuous from old to new shell material, representing very long, spiral elements.

The tubules of *Cupitheca* are interpreted to represent outpocketings of the mantle epithelium that connected straight through the mineral shell to the base of the periostracum. Besides the concentration at the terminal wall, the abundance of tubules elsewhere on the shell indicates they must have had additional functions besides just for decollation. The tubules of *Cupitheca* lack the bulbous ends that correspond to the spaces for eyes in the aesthete canal systems of some chitons, but they do flare out somewhat near the shell surface, so they may have had a sensory role, possibly mechanosensory (through cilia) or visual (with simpler photoreceptors, as for most chitons). Their connection to the periostracum may reflect a role in the replenishment of this outer organic shell layer, or the tubules may have otherwise been involved in repairing damage to the shell.

4.2. Comparison with other hyoliths

Runnegar *et al*. (1975) showed evidence that aragonitic crossed-lamellar shell microstructures characterize some hyoliths from the Ordovician and Permian. They inferred an aragonitic composition of the hyolith shell based on preservational patterns. Crossed lamellar texture (bundles of aragonitic fibres highly inclined from the horizontal shell surface, criss-crossing each other) seems clear from their photographs. They described a common shell microstructure in hyoliths where the first order laminae run around the shell in the inner layer and along the shell in the outer layer. Kouchinsky (2000b) described numerous examples of Cambrian hyoliths that show fibre bundles that in the outer layer are longitudinally oriented and dipping

slightly toward the apex, and within the inner layer an outer sublayer with fibre bundles transversely oriented (around the shell) and an inner sublayer with fibre bundles longitudinally oriented and at a slight dip to the tangential plane of the inner shell surface.

As with *Cupitheca*, Cambrian hyoliths show a high density of tubules orthogonal to the shell surface running from the inner shell surface to near the outer shell surface in these Cambrian hyoliths (Kouchinsky, 2000b). As for other hyoliths, *Cupitheca* probably had an original aragonitic composition.

The broad pattern of the shell in *Cupitheca* is very similar to that of other hyoliths, strengthening the claim of a hyolith affinity. The inner shell layer of *Cupitheca* consists of bundles of fibres that differ slightly in orientation but that are more or less tangentially arranged. In one specimen (Fig. 2i), longitudinal fibres can be seen to overlie transverse bundles of fibres in the inner shell layer, a pattern opposite to what Kouchinsky (2000b) found for other Cambrian hyoliths. Nevertheless the tubules in *Cupitheca* are vertically oriented, densely packed, and run nearly the entire thickness of the shell, as they do in other hyoliths.

4.3. Comparison with lophophorates

The shell of *Cupitheca* shares with brachiopods a dense system of organic-filled tubules that have a predominantly vertical orientation and run from the inner shell surface to near the outer shell surface. The tubules of *Cupitheca* typically are about 5-10 µm in diameter, and those of craniiform and rhynchonelliform brachiopods are 5-40 µm in diameter (Taylor *et al*., 2010). Tubules in Cambrian hyoliths (Kouchinsky, 2000b) and *Cupitheca* are straight and unbranching. Caeca typically branch in punctate brachiopods (Williams & Wright, 1970; Taylor *et al*., 2010), but in some pitted brachiopods the caeca are unbranching and flare near the outer shell surface (Wright, 1981) as with the tubules of *Cupitheca*. The Cambrian stem group brachiopods *Micrina* and *Paterimitra* also have a shell with tubules that open at both the inner and outer shell surface (Holmer *et al*., 2008; Skovsted *et al*., 2009). In these cases the tubes are inferred to have contained setae. The problematic calcite-shelled obolellid brachiopod *Mummpikia* (see Balthasar, 2008) has the same distribution, size, and orientation of tubules as does *Cupitheca*. The widespread occurrence of tubules among brachiopods (Williams, 1997a) indicates this feature is probably primitive for the crown group Brachiopoda, and these are probably homologous with similar structures in stem group brachiopods such as *Micrina*, *Paterimitra*, and possibly also hyoliths such as *Cupitheca*.

Brachiopods, like molluscs and *Cupitheca*, have a distinct outer organic shell layer, typically referred to as
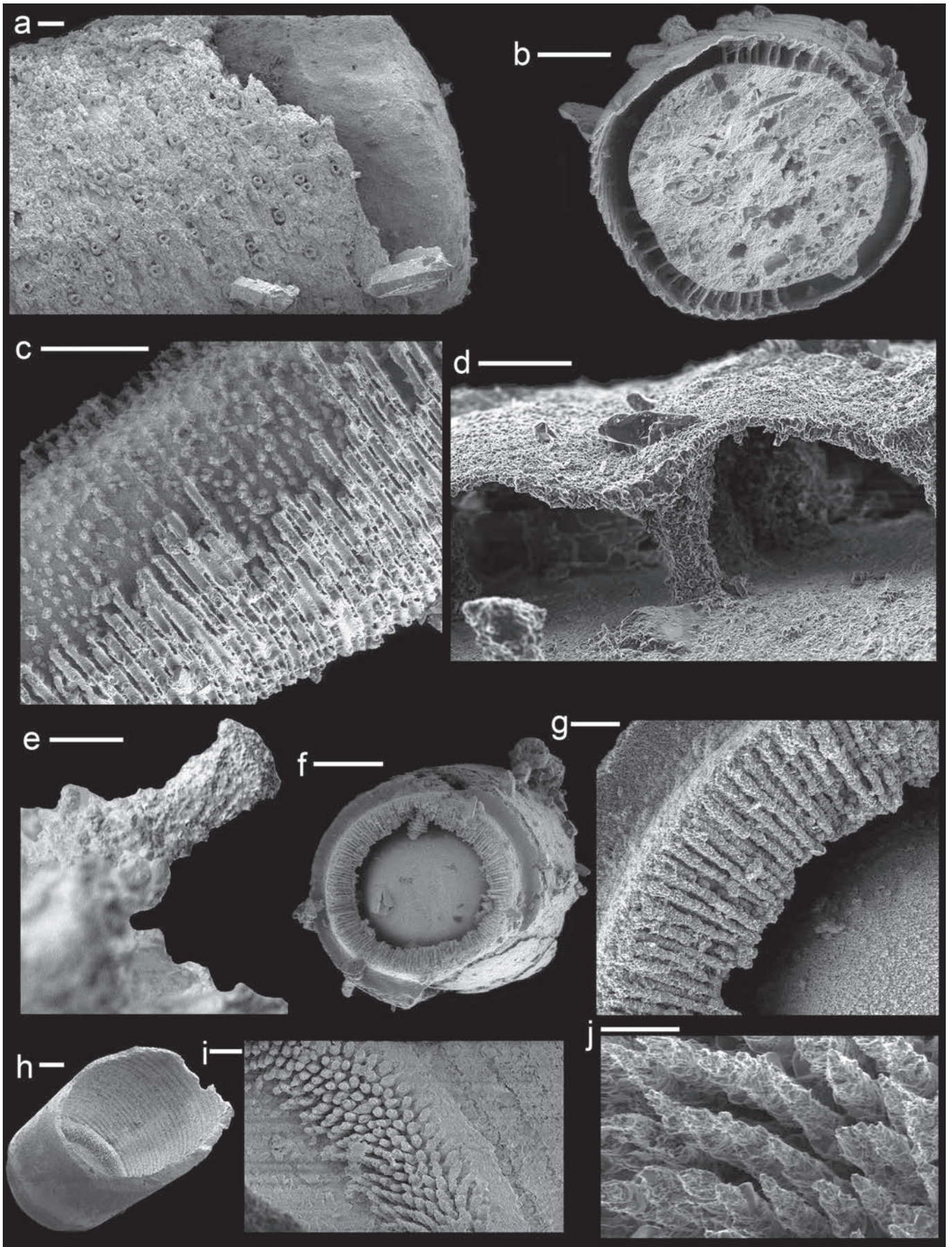
a periostracum. This outermost layer is typically thin in *Cupitheca* (~1-10 μm in thickness), consistent with the range in brachiopods; e.g., the periostracum thickness at first crystallization in *Calloria* is 100 nm, whereas for brachiopods in general, where fully developed, the periostracum can be 5-6 μm thick (Williams, 1997b).

Brachiopods typically have a calcitic or phosphatic shell, although some Palaeozoic trimerellid craniiformean brachiopods may have had an aragonitic shell (Jaanusson, 1966), as possibly did some craniopsids, obolellids, and kutorginids (James & Klappa, 1983; Geyer, 1994). Bryozoans typically build their skeleton with calcite although sometimes with aragonite (see review of lophophorate biomineralization in Taylor *et al.*, 2010). *Cupitheca* and other hyoliths, on the other hand, clearly have an aragonitic shell.

4.4. Comparison with early molluscs and other Cambrian taxa

The hyolith-like configuration of bundles of fibres arranged longitudinally and transversely within the shell can be seen in other Cambrian molluscs, including a number of coiled forms such as a shell from the early Cambrian of Yunnan (Feng *et al.*, 2001), as well as *Ocruranus* (Vendrasco *et al.*, 2009) and *Pelagiella* (Runnegar in Bengtson *et al.*, 1990). *Pelagiella* (Fig. 5) also shares with *Cupitheca* a bumpy periostracum (see also Runnegar in Bengtson, 1990; fig. 167) made up of apatite crystals elongated orthogonally to the shell surface and that is in some species porous in places (Vendrasco *et al.*, 2010). Similar lamello-fibrillar patterns in the innermost shell layer can be seen in the coiled molluscs *Protowenella* (Vendrasco *et al.*, 2010) and *Aldanella* (Kouchinsky, 2000a, personal observation), and *Anabarella/Watsonella* (Kouchinsky, 1999; Vendrasco *et al.*, 2015). The similarities with *Pelagiella* are notable, as the latter has been shown to have prominent chaetae (Thomas & Vinther, 2012), which are more characteristic of brachiopods than molluscs.

The system of tubules in *Cupitheca* is likewise similar to what occurs in many molluscs. Particularly striking are the similarities with Cambrian helcionelloids, including relatively dense vertical (orthogonal to shell surface)

canals that occur without branching throughout most or all of the shell thickness (Parkhaev, 2006; Feng & Sun, 2006; Vendrasco *et al.*, 2011b). The coiled early Cambrian molluscs *Barskovia* and *Philoxenella* show a tubule pattern (Kouchinsky *et al.*, in press) the same as that of *Cupitheca*. The aesthete channels of modern chitons are more complex, showing horizontal and vertical components with significant branching, and only penetrating the whole shell thickness in some places (Haas & Kriesten, 1978; Fernandez *et al.*, 2007; Vinther, 2009). Nevertheless chiton aesthete channels typically flare towards the external shell surface as in *Cupitheca*, and primitive chitons, lacking the articulamentum that typically blocks vertical canals (Hoare, 2009), may have had a simpler arrangement of aesthete canals than do modern forms that better resembles *Cupitheca*. Tubules also occur in the shells of other modern molluscs, including arcoid and limopsoid bivalves (Waller, 1980; Reindl & Haszprunar, 1996a), *Corbicula* (Tan Tiu & Prezant, 1989), and fissurellid limpets (Reindl & Haszprunar, 1994). However, differences in fine structure of the pore systems among molluscs that have them led Reindl & Haszprunar (1996b) to conclude they are not homologous. An extensive canal system also occurs in the sclerites of halkieriids (Vinther, 2009), a taxon suggested to belong to the Mollusca (Vinther *et al.*, 2017). In halkieriid sclerites the canals have a prominently horizontal (parallel to shell surface) orientation, contrasting with the vertical configuration of *Cupitheca* and others, although in closely related sachitids such as *Hippopharangites* some of the canals are vertically oriented (Vinther, 2009).

Molluscs, like brachiopods and *Cupitheca*, have an outermost organic shell layer referred to as the periostracum. The thickness of the periostracum of *Cupitheca* (~1 μm) falls within the range of molluscs. Harper (1997) noted a range in thickness from ultra-thin periostraca in oysters and scallops to thicknesses of 30 μm and more.

4.5. Tubules and the early lophotrochozoan

Similar tissue-filled shell pores have been inferred in many Cambrian helcionellids, aculiferans, problematic caps, stem brachiopods, and hyoliths. They maintain prominence in

Figure 3. Tubules in *Cupitheca holocyclata*. **a)** SAMP 54977, partial external coating and internal mould of terminal wall (to right). External coating shows the hollow terminations of tubules concentrated along furrows in the external shell. **b)** SAMP 54978, view from apertural end of specimen showing tubules running vertically all the way through the original shell (dissolved away in this specimen). **c)** SAMP 54965, composite internal/external mould showing organization of tubules in rows corresponding to the furrows of the outer shell. **d)** SAMP 54976, close-up of tubule running from surface of internal mould to external coating. **e)** SAMP 54979, close-up of tubule showing slight flaring towards external surface and possible inclined imprints of shell microstructure. **f)** SAMP 54980, view of terminal wall region of specimen showing high concentration of tubules in that region. **g)** close-up of (f). **h-j)** SAMP 54981, telescoped specimens with external coating and concentrated ring of tubules at apical wall in the innermost specimen. Tubules in this region flare towards the external surface. Scale bars: **(a, d-e, g, i-j)** = 10 μm; **(b-c, f, h)** = 100 μm.

modern chitons and brachiopods. Shell pores occur in other modern molluscs, although possibly they are not homologous (Reindl & Haszprunar, 1996b). Such tubules should have provided greater fracture resistance to early shell-breaking predators, as they prevent easy propagation of cracks. These tubules could also have served a sensory and/or secretory role, as with chiton aesthetes.

4.6. Pathologies and escalation

Healed shell damage can be seen in some of the better-preserved specimens of *Cupitheca* that maintain the outer wall. This indicates the animal was likely under predation pressure, as inferred for early Cambrian molluscs and other taxa (e.g., Conway Morris & Bengtson, 1994; Whittington, 1985; Skovsted *et al*., 2007; Vendrasco *et al*., 2011b). Decollation may have arisen as a response to predation, producing a smaller shell that can move and be hidden more easily than larger forms. The bundles of aragonite fibres occurring in a crossed relationship to each other are reminiscent of the crossed-lamellar shell microstructure of modern molluscs, shown to be resistant to predation (West & Cohen, 1996).

The dome-shaped projections just underneath the external organic shell surface are a mystery, although their distribution over the surface of some specimens indicate they reflect an aspect of the biology of the animal instead a diagenetic overprint. It is possible that these represent infestation by parasites. They may also represent a growth anomaly for another reason, as smaller versions of these seem to make up the ridges in the periostracal coat. A role in damage repair is another possibility, as these enlarged granules often correlate on the shell surface with healed damage (Fig. 4f).

Kouchinsky (2000b) noted that hyoliths have a high concentration of organic matter within the shell, as their shell tended to remain thin even in larger forms. *Cupitheca* is no exception. A similar organic-rich, flexible shell was also inferred for Cambrian molluscs like *Mellopegma* (Vendraco *et al*., 2011b), and is certainly true for early and modern brachiopods as well. The internal flexibility of the shell afforded by organic layers and inclusions may have provided some resistance to early shell breaking predators. However, as slicing abilities improved among predators of the early Palaeozoic, the need arose for thicker and even stronger, more mineralized shells.

4.7. The origin of crossed-lamellar shell microstructure

The evidence for crossed lamellar shell microstructure among Cambrian molluscs is scarce. Runnegar (1985) showed imprints on endolith fillings of fibre bundles with different vertical dip directions (i.e. crossed lamellar structure) in *Yuwenia*, but otherwise no clear crossed lamellar shell microstructure is known from early molluscs. Ordovician molluscs show a preponderance of nacre, but there is a small sample size of species showing original aragonitic shell microstructure. By the middle Palaeozoic crossed lamellar shell microstructure was common in the Mollusca. Among hyoliths the evidence for crossed lamellar shell microstructure from the Cambrian is equivocal (see Runnegar, 1985), but clearly by the Ordovician crossed lamellar microstructure had originated in the Hyolitha and is seen in the later Palaeozoic as well.

5. CONCLUSIONS

Cupitheca had a thick organic periostracum connected to the animal's mantle at the shell margin and via abundant tubules running straight through the shell. The periostracum has a radial (orthogonal to shell surface) texture and ranges from about 1 to 10 µm or more in thickness. The inner shell layer consists of transverse aragonite fibre bundles at aragonite twin angles to each other and in at least some cases overlain by longitudinal fibre bundles. A similar whole shell microstructure characterizes Cambrian hyoliths in general (Kouchinsky, 2000b), adding support to the hypothesis that *Cupitheca* is a hyolith. In Ordovician and Permian hyoliths the shell microstructure appears to be crossed lamellar with high angles of dip to the first-order lamellae (Runnegar *et al*., 1975). Hyoliths independently evolved crossed lamellar shell microstructure with molluscs during the Cambrian-Ordovician. If hyoliths are lophophorates, then this shows one more similarity (crossed-lamellar shell microstructure) in the shells of molluscs and lophophorates (see also Carter, 1979, and Vendrasco *et al*, 2011b). The shell microstructure described as 'lamello-fibrillar' in Cambrian molluscs and other lophotrochozoans may in many cases be the same as that in *Cupitheca*, and thus a precursor to crossed lamellar shell microstructure may have been widespread during the Cambrian radiation. By the end of the Great Ordovician Biodiversification Event nacre was common in the Mollusca and crossed lamellar had originated among hyoliths and probably also molluscs. Nacre and crossed lamellar are the two shell microstructures most resistant to shell breakage, and their abundance at that time reflects the continuing early arms race between predator and prey.
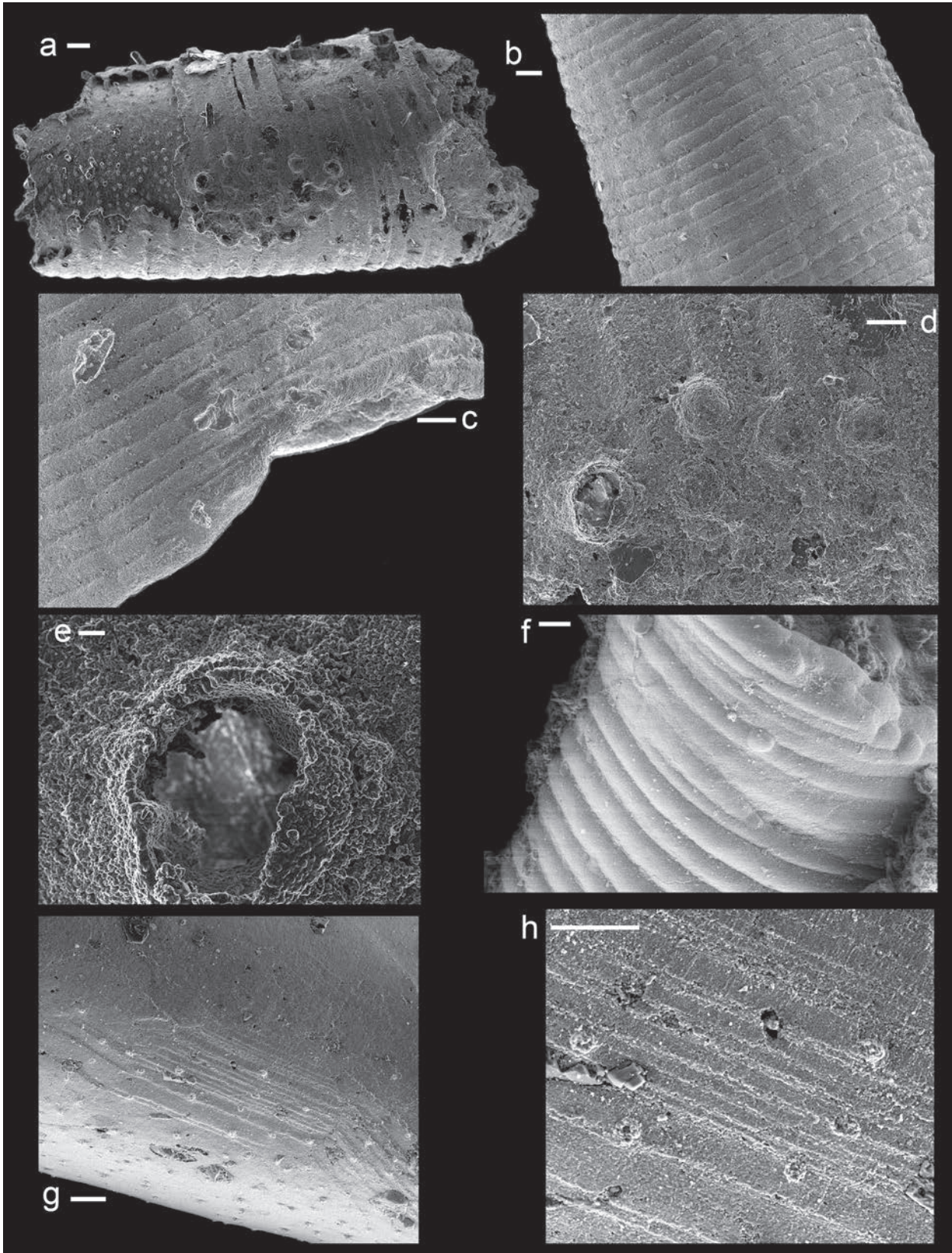
Figure 4. Unusual surface ornament and pathologies in *Cupitheca holocylata*. **(a, d-e)** SAMP 54976, composite internal/external mould showing unusual oval collection of large granules in the shell. **b-c)** SAMP 54982, large granules more sporadically arranged but nevertheless concentrated along ridges in the original shell; **(c)** shows possible damage near the aperture. **f)** SAMP 54983, external mould showing a concentration of granules in a region of healed shell damage. **g-h)** SAMP 54984, internal mould showing unusual linear imprints, possibly reflecting damage that translated through the entire shell. All scale bars 20 μm except in **(d)** (10 μm) and **(e)** (1 μm).
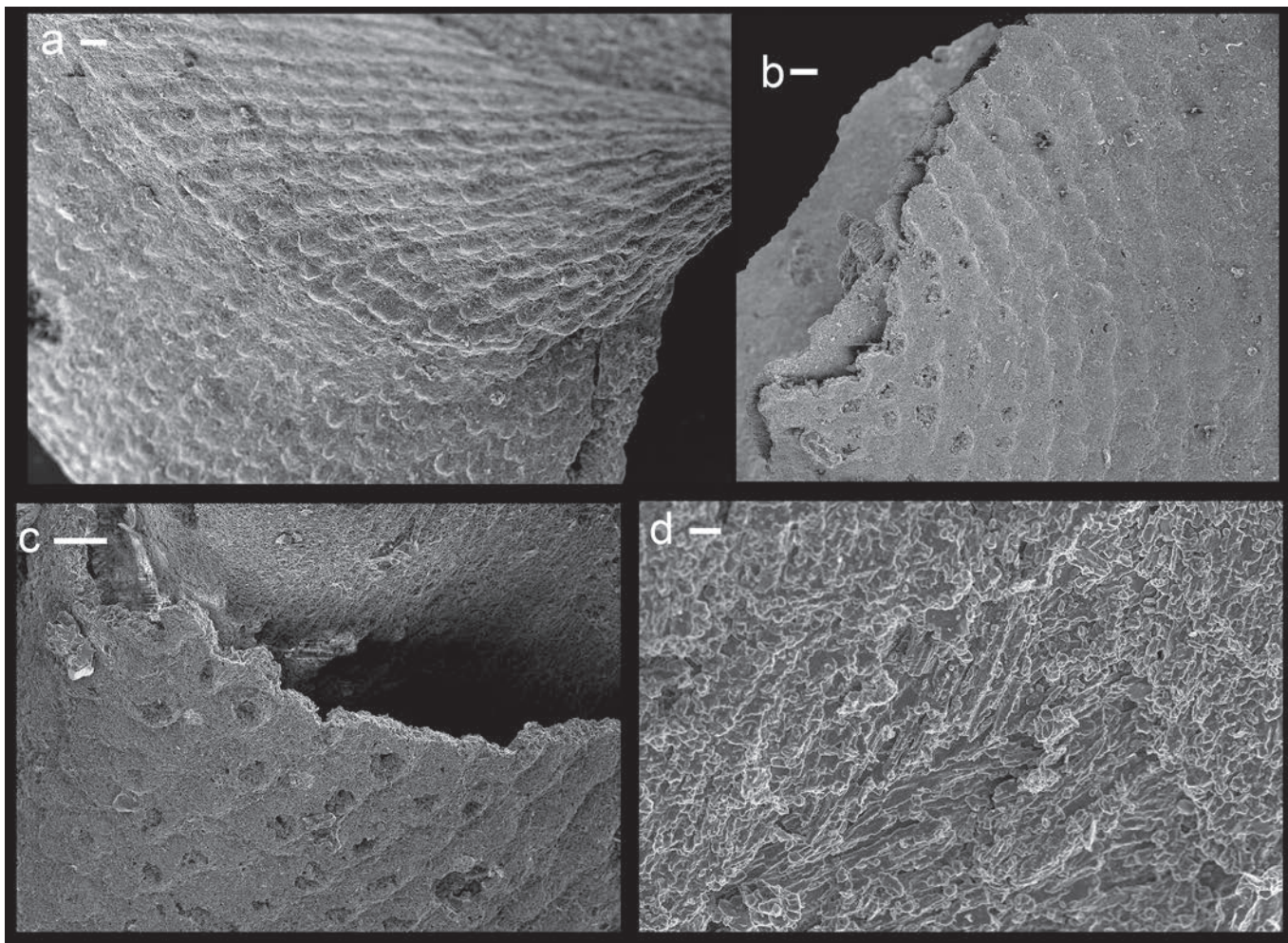
Figure 5. Phosphatized periostracum **(a-c)** and imprints of fibrous aragonite **(d)** in *Pelagiella subangulata* from the Parara Limestone of South Australia, showing an overall shell structure very similar to that of *Cupitheca*. **a)** SAMP 54985, phosphatized periostracum is visible throughout the specimen. **b)** SAMP 54986, phosphatized periostracum and a small section of the steinkern below. **c)** SAMP 54987, phosphatized periostracum with steinkern surface underneath (at top of photo). **d)** SAMP 54988, imprint of fibres in the inner shell of *Pelagiella*. Scale bars: **(a-c)** = 10 μm; **(d)** = 1 μm.

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