

*PATERIMITRA PYRAMIDALIS* FROM SOUTH AUSTRALIA: SCLERITOME, SHELL  
STRUCTURE AND EVOLUTION OF A LOWER CAMBRIAN STEM GROUP  
BRACHIOPOD.

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**Abstract:** The tomotiid *Paterimitra pyramidalis* Laurie, 1986, is re-described based on well preserved material from the lower Cambrian Wilkawillina, Wirrapowie and Ajax limestones of the Flinders Ranges, South Australia. The material shows that the scleritome of *Paterimitra pyramidalis* includes three sclerite morphotypes (S1, S2 and L). Detailed shell microstructure studies shows striking similarities with both the paterinid brachiopod *Askepasma toddense*, as well as with the tomotiid *Eccentrotheca helenia*, which strengthens the suggested evolutionary link between tomotiids and brachiopods. Based on partly articulated specimens

and similarities in shell microstructure and sclerite morphology with *Eccentrotheca*, *Paterimitra pyramidalis* is reconstructed as a tube dwelling, epifaunal, sessile, filter feeder with an organic pedicle-like attachment structure. The proposed reconstruction of the scleritome comprises a basal unit composed of one S1 and one S2 sclerite, as well as an unresolved number of L sclerites lining a coniform tubular structure.

**Key words:** Tommotiida, Brachiopoda, *Paterimitra*, scleritome structure, lower Cambrian, South Australia.

## INTRODUCTION

Tommotiids constitute an extinct group of small metazoans represented by variously shaped minute organophosphatic sclerites found in lower Cambrian strata around the world (Rozanov *et al.* 1969; Landing 1984; Missarzhevsky 1989; Bengtson *et al.* 1990; Conway Morris and Chen 1990; Esakova and Zhegallo 1996). Their scientific history dates back to Tate's (1892) report on Cambrian fossils from South Australia, but it was only just over 40 years ago that tommotiids were proposed to represent a unique fossil group (Fonin and Smirnova 1967; Rozanov *et al.* 1969; Bengtson 1970). Since then, several genera of enigmatic, phosphatic small shelly fossils (SSF) from the early Cambrian have been assigned to this group, for example *Micrina* Laurie, 1986, *Dailyatia* Bischoff, 1976, *Eccentrotheca* Landing, Nowlan and Fletcher, 1980, and *Porcauricula* Qian and Bengtson, 1989. Tommotiid sclerites usually occur as distinct sclerite morphs and were originally part of external multicomponent protective shells or scleritomes (Bengtson 1970).

Tommotiids have commonly been regarded as a problematic group, mainly due to the fact that they appear almost exclusively as disarticulated sclerites in the fossil record

(although ontogenetically fused elements do occur, see for example Landing 1984, 1995; Li and Xiao 2004; Demidenko 2004). The cataphract nature of tommotiid sclerites has undoubtedly complicated interpretations of scleritome construction, biology, ecology and systematic position, but they are generally considered to belong to the lophotrochozoan/spiralian clade (Williams and Holmer 2002; Ushatinskaya 2002; Skovsted *et al.* 2008; Kouchinsky *et al.* 2012; Murdock *et al.* 2012).

Although the Order Tommotiida Landing, 1984 has gained wide acceptance, no consensus exists regarding the Family level classification of tommotiids (see discussion in Esakova and Zhegadlo 1996). However, Skovsted *et al.* (2009b) suggested a super-grouping of tommotiids in two major clades: the camenellan clade comprising the families Lapworthellidae, Kennardiidae and Tommotiidae; and another clade comprising the Tannuolinidae and the eccentrothecimorph tommotiids *Eccentrotheca*, *Paterimitra* Laurie, 1986, *Kulparina* Conway Morris and Bengtson (*in Bengtson et al.*, 1990), *Porcauricula* and *Sunnaginia* Missarzhevsky (*in Rozanov et al.*, 1969).

Traditionally, most reconstructions of tommotiid body plans involve vagrant, bilateral, slug-like constructions (Bengtson 1970, 1977; Landing 1984; Evans and Rowell 1990; Holmer *et al.* 2002; Demidenko 2004; Li and Xiao 2004), with the coeval *Halkieria* Poulsen, 1967 (more specifically *Halkieria evangelista* Conway Morris and Peel, 1995) serving as a model (but see Bischoff 1976 for an alternative view). However, Skovsted *et al.* (2008) documented articulated scleritome material of *Eccentrotheca* demonstrating a tubular scleritome, suggesting that the animal was a sessile filter feeder (see Skovsted *et al.* 2011a for a detailed description of this taxon). Following the reinterpretation of *Eccentrotheca*, the eccentrothecimorph tommotiids have been reconsidered as members of the stem group of the lophophorate phyla (*i.e.* Brachiopoda and Phoronida; see Skovsted *et al.* 2008, 2009a-b,

2011a; Holmer *et al.* 2008, 2011; Balthasar *et al.* 2009; Kouchinsky *et al.* 2010; Murdock *et al.* 2012).

Brachiopods are marine filter feeding lophotrochozoans with a mineralized bivalved shell. They have an extensive fossil record and were among the dominant shell-bearing suspension feeders during the early Cambrian (Ushatinskaya 2001, 2008; Zhang *et al.* 2008). As members of the lophotrochozoan clade they have been regarded as forming a monophyletic group together with the Phoronida (Cohen 2000; Cohen and Weydmann 2005; Helmkampf *et al.* 2008; Giribet *et al.* 2009; Santagata and Cohen 2009; Sperling *et al.* 2011), though their exact relationship with other lophotrochozoans is still the focus of ongoing debate (Passamaneck and Halanych 2006; Helmkampf *et al.* 2008; Yokobori *et al.* 2008; Sperling *et al.* 2011). The necessity of combining research fields, *e.g.* palaeobiology, ecology and molecular biology, in order to illuminate the evolution of different animal taxa in relation to each other has been argued by many (Gould and Calloway 1980; Lüther and Bartholomaeus 1997; Carlson 2001; Benton and Donoghue 2007). In this context, studies of morphology and stratigraphic distribution of stem and crown groups (Budd and Jensen 2000) like tommotiids and brachiopods provide essential data for reconstructing the tree of animal life. The oldest known organophosphatic brachiopods are the paterinids, a group that combines a strophic shell with an organophosphatic shell composition (Williams *et al.* 1998; Laurie 2000; Topper *et al.* 2013). Eccentrothecimorph tommotiids show many similarities to early paterinid brachiopods, including morphological (Skovsted *et al.* 2009a, 2011a), ontogenetic (Holmer *et al.* 2011), and microstructural (Balthasar *et al.* 2009, Topper *et al.* 2013) features, suggesting a close phylogenetic relationship.

In this regard, the South Australian tommotiid and proposed stem group brachiopod *Paterimitra pyramidalis* Laurie, 1986 is of particular interest, since it combines both specific tommotiid and brachiopod features. Until recently, only a handful of specimens of a single

sclerite type of *Paterimitra* had been described (Laurie and Shergold 1985; Laurie 1986; Bengtson *et al.* 1990; Gravestock *et al.* 2001). However, Skovsted *et al.* (2009a) documented partly articulated specimens, from collections yielding several hundred disarticulated sclerites including three different sclerite types: symmetrical S1 and S2 and asymmetrical L sclerites from several sections intersecting lower Cambrian (Unnamed Cambrian Stages 2-3) carbonates in South Australia. Based on the striking similarities in shell structure and mineralogy, inferred scleritome construction and, to a certain extent, overall sclerite morphology between *Paterimitra* and *Eccentrotheca*, it has been suggested that these two taxa are closely related sessile filter-feeding stem group lophophorates (Skovsted *et al.* 2009a, 2011a; Balthasar 2009). As noted in Laurie's (1986) original description, the name *Paterimitra* reflects the similarity in structure and ornament between the sclerites and the shells of the paterinid brachiopods *Paterina* Beecher, 1891 and *Micromitra* Meek, 1873. The shell microstructure with polygonal compartments resulting in a fine reticular ornament externally, and first and second order lamination show strong similarities to the paterinid brachiopod *Askepasma* Laurie, 1986 (Balthasar *et al.* 2009; Topper *et al.* 2013 and herein). At the same time, *Paterimitra* also shows morphological similarities to another paterinid, *Salanygolina* Ushatinskaya, 1987 (Holmer *et al.* 2009, 2011) from the lower Cambrian of Mongolia, which will be discussed below.

This paper reports new information on *P. pyramidalis* based on over 1400 specimens derived from more than 60 stratigraphic horizons across twelve stratigraphic sections measured through key carbonate units exposed across the Arrowie Basin in South Australia. All are of early Cambrian age, obtained from both available older collections and recently collected material, parts of which were included in Skovsted *et al.* (2009a). Ontogenetically fused sclerite elements are relatively rare in *Paterimitra*, but the studied material contains several articulated specimens comprising more than one sclerite type. Based on the presence

and characteristics of the two additional sclerite types originally reported by Skovsted *et al.* (2009a), we present a revised diagnosis for *Paterimitra*. Furthermore, we discuss a tubular reconstruction of the *Paterimitra pyramidalis* scleritome and its position in the brachiopod/eccentrothecimorph-tommotiid clade.

## **GEOLOGICAL SETTING, AGE AND STRATIGRAPHY**

Sclerites and partially articulated scleritomes of *Paterimitra pyramidalis* documented herein are derived from a combination of spot samples and systematic sampling along measured stratigraphic sections through transgressive to highstand system tract deposits, which crop out in the vicinity of the Bunkers Range/Graben, Heysen Range, Chace and Druid Ranges, and Mt. Scott Range in the Arrowie Basin (Gravestock and Cowley 1995; Gravestock and Shergold 2001; Zang 2002; Zang *et al.* 2004; Paterson and Brock 2007) (Fig. 1). These thick carbonate-dominated successions represent depositional systems across a wide spectrum of facies representing sheltered upper intertidal to lagoonal environments (Wirrapowie Limestone), shallow water peri-platform with archaeocyath-calcimicrobe bioherms (Brasier 1976; James and Gravestock 1990; Clarke 1990; Paterson and Brock 2007) to intrashelf open depressions and shoals (Wilkawillina and Ajax limestones). The majority of stratigraphic sections mentioned herein have previously been described in some detail by numerous authors (*e.g.* Paterson and Brock 2007; Skovsted *et al.* 2009b, 2011a; Topper *et al.* 2011a-b) and so are summarised in Appendix 1.

**Kommentar [CL1]:** Fig. 1 about here

## **MATERIALS, METHODS, COLLECTIONS, PRESERVATION**

The material utilised for the present study is composed of acid macerated and picked SSF (small shelly fossil) collections on loan to GAB from the South Australian Museum that includes stratigraphic sections measured through Bunyeroo Gorge (Bun 3\*, 9, 10, 11, 12), and Wilkawillina Gorge (Wilk <6, H, I, K, L, M, P, Q, R, S) originally collected by the late Brian Daily in the late 1960s and early 1970s; the RS sample (RS319) was collected as part of stratigraphic section measured through the Wilkawillina type section by the late David Gravestock in the 1980s. Samples Aus 92-19, 20 (Wilkawillina Limestone type section) and Aus 92- 29 and 30 (Ajax Limestone, Mt. Scott Range) were collected by LEH in 1992. The stratigraphic sections AJX-M, AJX-N, MMF, 10 MS-W, CR1 (Chace Range), and Wirrapowie Limestone (spot sample from Druid Range) were sampled by GAB, CBS, TPT, CML, LEH and co-workers from 2003-2008 (see Appendix 1 for details concerning geological setting, stratigraphy, sample levels *etc*). The collections originate from etching residues obtained from bulk samples dissolved in 10% acetic acid. All sclerites were picked from the residues using a binocular stereomicroscope and Scanning Electron Microscope (SEM) photographs of the illustrated specimens were taken at the SEM-facilities at: the unit for Biological Structure Analysis (BSA), Uppsala University; the Macquarie University Microscopy Unit in the Department of Biological Science, Sydney; and the Swedish Museum of Natural History (Naturhistoriska Riksmuseet, NRM), Stockholm. The height of S1 sclerites was estimated from SEM photographs and under the stereomicroscope.

S1 sclerites with a preserved apex were counted as individual specimens, whereas other S1 parts were regarded as fragments. Altogether, the studied material comprise 1430 sclerites; 1037 x S1 sclerites, 186 x S1 sclerite fragments, 26 x S2 sclerites, 169 x L sclerites, 12 x partly articulated specimens (including 2 to 7 sclerites), and a few additional sclerites of uncertain type (Appendix 2). The sample from the base of the MMF section (Fig. 1)

(MMF/0.0) was the richest sample, comprising a total 640 x S1 sclerites (plus 74 additional fragments), 14 x S2 sclerites and 38 x L sclerites (for details on abundance of sclerites in all samples see Appendix 2). Half of the partly articulated scleritome material (n=6 specimens) is also derived from this sample. The sclerites from MMF/0.0 also represent the best preserved specimens in the collections.

The absence of S2 and L sclerites in many of the Daily and Holmer SSF-collections, as well as in a few of the newer collections, is probably explained by the fact that they were not identified as constituents of the *Paterimitra* scleritome until very recently, and were not recognised in residues from which these collections were retrieved. In cases where the remaining residues have been available, these have been scanned in order to retrieve potentially remaining S2 and L sclerites, but with mostly negative results. The S2 sclerites are considerably smaller than the S1 and L sclerites and are therefore more likely to: 1) be destroyed in taphonomic processes; 2) disappear during the preparation process, depending on how the macerated samples were decanted and the size of sieves used to ensure smaller fractions are not lost; 3) remain undetected in the residues. Once the S2 sclerites were recognized smaller sieve size was used for all new samples. As mentioned in Skovsted *et al.* 2009a and 2011a, the L sclerites of *Paterimitra* and the high, laterally compressed sclerites of *Eccentrotheca* are confusingly similar in size and shape, and in most cases only distinguishable by their external micro-ornamentation. As a result, many L sclerites have probably ended up in *Eccentrotheca* collections, and in order to distinguish between the two taxa specimens would have to be examined using scanning electron microscope, since the micro-ornament is not distinguishable to the naked eye or even under a stereo microscope. A very time consuming project, considering the huge number of *Eccentrotheca* sclerites available in collections described in Skovsted *et al.* (2011a).

All illustrated specimens are housed in the palaeontological collection of the South Australian Museum, Adelaide (acronym: SAMP). In some cases incorrect sample numbers, stratigraphic information and SAMP numbers have been given for illustrated specimens in previous publications. Deviations in terminology and errors concerning sample numbers, stratigraphy and SAMP numbers in previous publications are accounted for in Appendix 3.

Kommentar [CL2]: Fig. 2 about here

### **SCLERITE TYPES: MORPHOLOGY AND TERMINOLOGY**

Due to widely contrasting terminology used in previous publications on *Paterimitra*, we have chosen to redefine and clarify the morphological terminology first outlined in Skovsted *et al.* (2009a). The terms described in the following sections are illustrated in Fig. 2.

Prior to the short report documenting the scleritome of *Paterimitra pyramidalis* in Skovsted *et al.* (2009a), only one sclerite type had been described and assigned to *Paterimitra* (Laurie 1986; Bengtson *et al.* 1990; Gravestock *et al.* 2001). However, judging from available samples it is evident that the scleritome of *Paterimitra pyramidalis* comprises at least three different, clearly distinctive sclerite types (Skovsted *et al.* 2009a): two bilaterally symmetrical sclerites – a high pyramidal, relatively large, sclerite (S1 sclerite; Figs 2A-D; 3-4), and a low, saddle-shaped to triangular, sclerite (S2 sclerite; Figs 2E-F; 5); and highly variable, asymmetrical, laterally compressed and partially twisted sclerites (L sclerites; Figs 2G-I; 6). *Paterimitra* sclerites are apatitic by original composition and grow by basal-internal shell accretion (Balthasar *et al.* 2009). All sclerite types are united by possessing a characteristic reticulate external micro-ornament consisting of regular polygonal compartments (Fig. 3B) which occasionally contain small spherical grains (Fig. 3C). Growth lamellae are distinctly visible from the exterior and sometimes partly exfoliate from each other (Balthasar *et al.*

2009; Skovsted *et al.* 2009a; see also Fig. 3D). The internal sclerite surface is covered by a poorly defined network of pustules or polygonal depressions (Fig. 3D). For details regarding shell microstructure see section below.

Kommentar [CL3]: Fig. 3 about here

### *S1 sclerite*

The relatively large (height ranges from 200-1700 µm) S1 sclerite (Figs 2A-D; 3-4) of *Paterimitra pyramidalis* is bilaterally symmetrical, with a pyramidal outline and a rectangular to trapezoidal cross section (Figs 2A-B; 3A; 4A-B). The S1 sclerite has a rounded *apex* (Appendix 3a) slightly displaced towards one long side (arbitrarily referred to as the *posterior* side; Figs 2C; 4C) which is drawn out into a protruding, laterally compressed *subapical flange* (Figs 2A-C; 4A-C; Appendix 3b) overhanging the *posterior margin* (Figs 2A; 4A; Appendix 3c). The posterior side of the sclerite exhibits a deep *triangular notch* (Figs 2B; 4B). On each lateral side is one *lateral plate* (Appendix 3d) which is long, relatively narrow, and strongly flexured towards the posterior (Figs 2B-C; 4B-C). The anterior exhibits a short, slightly U-shaped *anterior plate* (Appendix 3e), which may be almost flat or convex (Figs 2C-D; 3A; 4A, D), but in some specimens even concave. The anterior plate is sharply circumscribed by two radial *anterior boundaries*, usually developed as furrows (Figs 2D; 3A; 4A, D). These define the anterior edges of the lateral plates. The outline of the anterior plate and the anterior boundaries defines a semi-circular *anterior sinus* (Figs 2D; 4D).

Kommentar [CL4]: Fig. 4 about here

The general size of retrieved S1 sclerites is highly variable. Apart from this, there is a broad variation in terms of proportions of *width* to *height* between different S1 sclerites (Fig. 2A and D). Most of the examined S1 sclerites are quite high and pointed (Figs 3D; 4B, E), but

in some cases the S1 is rather low, even approaching flattened or compressed morphology (Fig. 4F). There is also variation in the proportions of length to width of the lateral plates; most specimens have fairly broad lateral plates (Figs 3D; 4A-C, E-F), some specimens have lateral plates which are very narrow with the flexure towards the posterior weakly developed (Fig. 4G-H).

Yet another parameter that may vary between different S1 sclerites is the development of the subapical flange; in most specimens this structure represents approximately one third of sclerite height (Fig. 2B-C), but several specimens exhibit a strongly extended, extravagantly developed, hood-like, subapical flange (Fig. 4H-I). This kind of variation occurs between separate sclerites within the same sample. Furthermore, judging from the size of the subapical flange in the fragmentary SAMP 47846 illustrated in Figure 4H, this must originally have been a fairly large specimen, indicating that the actual maximum height of S1 sclerites were considerably larger than the one recorded and accounted for above.

### *S2 sclerite*

The S2 sclerite (Figs 2E-F; 5) of *Paterimitra pyramidalis* is acutely triangular or slightly saddle-shaped, and bilaterally symmetrical (Figs 2E; 5A). They are considerably smaller than the majority of S1 sclerites, ranging from approximately 400 to 800  $\mu\text{m}$  in *length* (Fig. 2E). The narrowly pointed posterior end is raised and developed into a more or less well exposed *upturned flange*, giving the sclerite a distinct flexure along in antero-posterior axis (Figs 2F; 5B), although when viewed in lateral cross section the sclerite is convex (Fig. 5C). Some specimens exhibit growth disturbances such that the entire sclerite may be more or less skewed and/or the upturned flange may be displaced (Fig. 5D-F). The *width* (Fig. 2E) of the

S2 sclerite ranges from about 0.5 to 1.0 of the length, but rarely exceeds the length. The degree of concavity varies (Fig. 5B, G), as does the general triangular to saddle-shaped outline (Fig. 5H-I).

Kommentar [CL5]: Fig. 5 about here

### *L sclerites*

The asymmetrical L sclerites (Figs 2G-I; 6) of *Paterimitra pyramidalis* are highly variable, irregular and ridge-shaped units. These are high (Figs 2G; 6A-B), laterally compressed sclerites (Fig. 6C-E, M), which may be moderately to strongly twisted in apical view (Figs 2H; 6F-K), sometimes possessing *multiple apices* (Fig. 6L). The L sclerites have a moderately to strongly curved *basal margin* (Figs 2I; 6M), which often defines a distinct arcuate shape in some specimens (Fig. 6N), whilst others express only modest curvature (Fig. 6O). The *width* of the basal margin and the sclerite *height* were estimated from SEM micrographs of 30 individual L sclerites and two fused L sclerite units (Fig. 2G; Appendix 4). Measurements indicate that L sclerites where the basal margin width is low relative to the sclerite height tend to lack, or possess a very low, curvature of the basal margin (Fig. 6P-Q). These sclerites also lack the characteristic apical twist, although the lateral sides may be slightly bent or even curled up (Fig. 6R). The relatively high L sclerites are represented by one composite of fused sclerites (composite base 900  $\mu\text{m}$ ) and three individual sclerites (basal margin width ranging from 400 to 642  $\mu\text{m}$ , with the exception of one extremely high specimen with a basal margin width of 953  $\mu\text{m}$ ). L sclerites exhibiting a pronounced curvature of the basal margin tend to be very low compared to the basal margin width, with more than half of the measured specimens having a basal margin width exceeding 1100  $\mu\text{m}$  (min 571  $\mu\text{m}$ , max 1 600  $\mu\text{m}$ , Appendix 4) and all possess a relatively strong apical twist.

Kommentar [CL6]: Fig. 6 about here

As mentioned in Skovsted *et al.* (2009a), L sclerites can be confusingly similar to the laterally compressed sclerites of *Eccentrotheca*, a fact clearly illustrated in Skovsted *et al.* (2008: fig. 2 a, b) where a *Paterimitra* L sclerite was incorrectly identified and described as a laterally compressed sclerite of *E. helenia*. The crucial difference is that all *Paterimitra* sclerites possess the same characteristic external micro-ornament of regular polygonal compartments. This micro-ornament is completely absent in *Eccentrotheca* sclerites, which are externally smooth or ornamented by irregular growth lines and simple wrinkles, although they may exhibit a vague, regular polygonal pattern internally (Balthasar *et al.* 2009; Skovsted *et al.* 2009a).

## **ONTOGENY AND GROWTH**

There is a relatively clear trend regarding the proportions of height to width of S1 sclerites during ontogeny. Juveniles (height 200-300  $\mu\text{m}$ ) tend to have relatively low and broad S1 sclerites, with an almost horizontal to semi-horizontal subapical flange (Fig. 7A-B). At a height between 600-900  $\mu\text{m}$  the height to width proportion is close to 1:1 (Fig. 7C-D). At this size, sclerites have attained the subpyramidal shape characteristic for adult *Paterimitra*. The vast majority of S1 sclerites in available collections can be assigned to this early adult ontogenetic stage. Beyond this stage the width is stabilized and remains relatively uniform, while the height continues to increase throughout the life of the organism, resulting in a high and pointed sclerite in older adults (Fig. 7E-F). These sclerites are much rarer in the studied collection and are often fragmentary.

The overall shape of each S2 sclerite is individual. Generally speaking, the S2 sclerite increases in size successively with every growth increment; however, while the increase in

width is rather low (declining with every new increment), the sclerite grows continuously in length. In the L sclerites the overall width/length ratio is individual; the general pattern is that the increase in width reaches a limit and declines, while growth in height appears to be continuous.

Holmer *et al.* (2011) described the early ontogeny of *Micrina* and *Paterimitra*, illustrating evidence for bivalved embryonic and larval stages, which would support a tommotiid origin of the bivalved morphology of brachiopods. However, in the case of *Paterimitra* investigation of a larger set of sclerites herein prompts a reinterpretation of some of the structures discussed by Holmer *et al.* (2011).

The larval shell of S1 sclerites is defined by a 300-500  $\mu\text{m}$  wide growth disturbance of the same overall outline as the adult sclerite but with an open anterior indentation which eventually becomes covered by the anterior plate and a smooth dome or saddle-shaped protegulum forming the start of the subapical flange (Holmer *et al.* 2011: fig. 2A, C-E, H, J). The described larval shell is visible in most S1 specimens investigated (Fig. 8A, C-F). All specimens exhibit a posteriorly extended tongue similar to the protegulum which is more or less clearly demarcated from the rest of the larval shell (Fig. 8A, C-F).

According to Holmer *et al.* (2011) the larval shell of the S2 sclerites is acutely triangular or saddle-shaped and essentially similar in shape to the adult sclerites. The larval shell is 150-200  $\mu\text{m}$  wide with an upturned flange, and a posteriorly located and poorly defined crescent-shaped protegulum with a shallow posterior indentation (Holmer *et al.* 2011: fig. 2B, F-G, K-L). In total, we have studied 26 S2 sclerites, including those illustrated in Holmer *et al.* (2011). Many S2 sclerites display what could be interpreted as a larval shell (Fig. 8B, G-K) of roughly the size and shape described by Holmer *et al.* (2011), although not infrequently the earliest shell-layers seem to be missing, probably due to delamination (Fig. 8L). The presence of the suggested protegulum in the S2 specimen illustrated in Holmer *et al.* (2011: fig. 2B, F;

SAMP46316) is not entirely convincing when the sclerite is viewed from different angles (Fig. 8M-N), and this structure could be interpreted to represent a deformation of a subsequent growth increment along the posterior margin of the specimen. No traces of similar structures could be observed in any of the remaining S2 specimens investigated here (Figs 5A, D, G, I; 8G-L) and the presence of a well-defined protegulum in the S2 sclerites of *Paterimitra* remains to be tested. However, several of the studied S2 specimens exhibit a centrally placed sub-rectangular structure smaller than the larval shell, which we suggest to represent the protegulum (Fig. 8G-I, K, M). Consequently, the ontogenetic model for the S2 sclerite of *Paterimitra* proposed by Holmer *et al.* (2011) must be revised. Rather than being crescent-shaped and posteriorly located, the protegulum was more likely a rounded or rectangular plate situated at the centre of the larval shell.

#### **ABNORMAL GROWTH AND DAMAGE**

All three sclerite types (S1, S2, and L) are very distinct in their shapes and outlines, and generally easily recognized. However, there are some sclerites which deviate substantially from the typical pattern of growth. Both S2 and L sclerites can be theoretically derived from the S1 form by stretching and twisting (L sclerites) or compression of proportions (S2 sclerites). Some sclerites initially identified as S2 sclerites when studied using light microscopy, revealed typical characters comparable to the subapical flange and lateral plates of S1 sclerites when imaged using SEM (Fig. 9A-D). In other instances, some S1 sclerites have such narrow lateral plates and are almost crescent-shaped in anterior or posterior view that they take on the shape of larger L sclerites (Fig. 9E-F). A few abnormal (possibly pathological) sclerites exhibit the same mode of growth and reticulate micro-ornament typical

of *Paterimitra*, but cannot be accommodated with confidence into any of the recognised three sclerite types (Fig. 9G-M).

Kommentar [CL7]: Fig. 9 about here

Several sclerites show clear evidence of disturbance in the normal shell growth. For example, in some S1 sclerites the growth of the subapical flange has been markedly disturbed, resulting in a change in growth direction. In one specimen the flange appears to have been strongly deformed, resulting in an almost 90° shift in direction of growth (Fig. 10A-B). Other specimens display a modest twist of the subapical flange (Fig. 10C-F).

Kommentar [CL8]: Fig. 10 about here

There are also at least two S1 sclerites which have peculiar internal growth disturbances (Fig. 11A-P). These specimens show growth disturbances on the anterior plate, close to the anterior sinus. In SAMP 47876 (Fig. 11A-F) the growth disruption forms a distinct lump with the same texture as the internal sclerite surface (Fig. 11B), indicating that it was secreted by the *Paterimitra* animal during growth. This lump may have been produced to encapsulate or “seal off” a foreign object invading the living chamber from the outside. Externally this is indicated by a break in the growth lamellae and a hole piercing the anterior plate (Fig. 11D-F). In SAMP 47877 (Fig. 11G-P) the S1 sclerite appears to have grown around a circular or cylindrical element (now lost). Whether this reflects a similar internal growth disturbance as the one described above remains unanswered, but, judging from the uneven surface of the edge of this circular ingrowth, something has been broken off (Fig. 11G-K). Externally the inner growth disturbance appears to be opposed by an additional L-like sclerite attached along the anterior sinus of SAMP 47877 (Fig. 11J, L-P).

Kommentar [CL9]: Fig. 11 about here

## ARTICULATED SCLERITOME COMPOSITES

There are twelve partly articulated specimens of *Paterimitra* in available collections. In most cases where sclerites have been preserved as articulated elements ( $n = 10$ ), the specimens exhibit a fragmentary composite consisting of one saddle-shaped S2 sclerite nested within the triangular notch of a pyramidal S1 sclerite (Figs 12; 13). Of the remaining partly articulated specimens, one specimen represents the association of a S1 sclerite with multiple L sclerites while a second specimen is composed of L sclerites only. Both specimens are described more fully below. In the preserved S1-S2 composite specimens the subapical flange of the S1 sclerite is opposed to the margin of the upturned flange in the S2 sclerite forming a (in some specimens almost perfectly circular) *posterior opening* (Figs 12; 13A-B, D-E). As illustrated in Skovsted *et al.* (2009a: fig. 1.1, n and o), fusion of the S1 and S2 sclerites produces a drawn-out tube-like structure extending from the posterior margin of the S1 sclerite (Fig. 13C, F). However, especially in larger specimens, the triangular notch of the S1 sclerite is not fully covered by the saddle-shaped S2 sclerite and a shallow *posterior sinus* is formed behind it (Figs 12; 13A). All articulated specimens show signs of deformation or growth irregularities: either the subapical flange of the S1 sclerite and/or the upturned flange of the S2 sclerite has been twisted (Fig. 14A-H); or the S2 sclerite appears to have cracked and then partially fused with the S1 sclerite during growth (Fig. 14I-L); or a combination of the previous two (Fig. 14M-P). The somewhat abnormal growth in these specimens seems to have resulted in fusion of the S1 and S2 sclerites, especially the innermost sclerite layer (Fig. 14P), resulting in the preservation of articulated specimens. Consequently, we assume that under normal circumstances, without abnormalities caused by outer disturbances, the sclerites tend to disarticulate and separate post mortem.

Almost all L sclerites in the studied collections were found as individual units (unfused sclerites). Only one sclerite-composite composed exclusively by narrow-based L sclerites was retrieved (Fig. 15A-F). These L sclerites are fused along their basal margins and each sclerite

**Kommentar [CL10]:** Figs. 12-14 belongs somewhere around here

is strongly curved, resulting in a highly recurved plate-like structure. No ring-like L sclerite compounds as described for *Eccentrotheca helenia* has been found in the available collections suggesting L sclerites were generally not naturally fused during ontogeny.

**Kommentar [CL11]:** Fig. 15 about here

One composite specimen (SAMP 43314), briefly described by Skovsted *et al.* (2009a: fig. 2f-l), exhibits narrow-based, compressed, asymmetrical L sclerites fused to the lateral plates of a S1 sclerite (Fig. 16). The S1 sclerite of this composite specimen is slightly deformed and the anterior sinus is not very well defined (Fig. 16A, C); the anterior plate is swollen and partly exfoliated (Fig. 16B, C) and the subapical flange is missing (Fig. 16A-B, D). The posteriorly facing parts of the lateral plates are narrow and slightly depressed with an unusually wide triangular notch (Fig. 16A, D). In spite of the deformation, there are no less than three distinct asymmetrical L sclerites attached to left lateral plate of the subpyramidal S1 sclerite (in Fig. 16B, E-G, J-K labelled *i*, *ii* and *iii*), and one small additional L sclerite is fused to the right lateral plate of the S1 (Fig. 16D, H, J). L sclerite *i* on the left side possesses three apices and is attached directly to the anterior border of the S1 lateral plate along the basal margin, with the apices directed towards the posterior of the S1 sclerite (Fig. 16B-C, G, J). L sclerites *ii* and *iii* are fused along their longitudinal axes, and the composite overlaps the basal margin of L sclerite *i* and the lateral plate of the S1 sclerite (Fig. 16B, G). The curved shape of the basal margin of the L sclerites is apparently accommodating the curvature of the anterior sinus of the S1 sclerite. As described in Skovsted *et al.* (2009a) the internal central cavities of all three L sclerites are easily distinguishable, and show that the sclerites were fused by secretion of sheet-like shell layers partly draping the walls between them.

**Kommentar [CL12]:** Fig. 16 about here

There are a few additional specimens exhibiting what appear to be small L-like sclerites attached to S1 sclerites either posteriorly or anteriorly. In SAMP 43310 (Fig. 17A, D), also illustrated by Skovsted *et al.* (2009a: fig. 1p, q), a narrow, highly tapered sclerite is fused to the margin of the S1 sclerite behind and lateral to the fused S2 sclerite. As mentioned above,

another specimen SAMP 47877 (Fig. 17B-C, E-F) exhibits a small, flattened and pointed, L-like sclerite attached to the anterior plate, along the anterior sinus.

Kommentar [CL13]: Fig. 17 about here

## SHELL STRUCTURE AND EXTERNAL ORNAMENTATION

The shell of *Paterimitra* has a distinct primary and secondary layer. The primary layer includes an ornament of well-defined polygonal compartments that range up to 10 µm in diameter (Fig. 18C). The walls of these compartments are anvil-shaped in cross section with their external face swelling in size and show frequent spinose to granular intrusions (Fig. 19F; see also Balthasar *et al.* 2009: fig. 1E). The external swelling of the walls of some compartments can lead to their partial closure and in L sclerites the swelling often results in bulbous structures that can close off the underlying compartment (Fig. 18D-H). Together with a slightly convex bottom, the cross-section of these polygonal compartments is commonly bowl-shaped (Fig. 19F).

Kommentar [CL14]: Fig. 18 about here

The polygonal compartments continue into the secondary layer and commonly form pillar-like structures normal to the shell surface (Fig. 20B). However, unlike the primary layer, polygonal compartments within the secondary layer are filled by a distinctly laminated deposit of apatite (Fig. 19H-K) and appear as raised structures with depressed walls in etched samples (Fig. 20C). This expression of polygons extends to include the internal surface of etched sclerites (Fig. 20D). The lamination of the secondary shell can be sub-divided into two orders, a first order lamination of up to three laminae per micron and a second-order lamination that can exceed 10 µm in thickness (Fig. 19H-K; see also Balthasar *et al.* 2009). Compartment walls appear as distinct dark lines in backscatter images of polished shell cross sections (Fig. 19H-K), indicating a lower degree of apatite mineralisation along them. The

Kommentar [CL15]: Fig. 19 about here

microstructural differences between primary and secondary shell suggest different modes of shell secretion. Whereas in the primary layer apatite appears to be added along the polygonal walls resulting in the bulbous external extensions and partially closing off polygonal compartments to the outside, the secondary shell is secreted through the continuous deposition of shell material along well-defined laminae.

Along the external surface the shell sometimes peels off to form fringes of primary and secondary shell. In cross section these fringes have the characteristic micro-ornament of polygonal compartments followed by about 10 µm of secondary shell, the equivalent of second-order lamina (Fig. 19A, G, E). When cut transversely and proximally, these fringes can give the impression of longitudinal cavities with a base of polygonal ornament (Fig. 19E). At the lateral margins of S1 sclerites the shell lamination commonly flares out and twists inwards giving a hooked appearance in cross section (Fig. 19A, C-D, J). In some of the studied S1 sclerites the lateral margins were split with finger-like extensions (Fig. 19D). The overall external surface of S1 sclerites frequently shows irregular bulbous and often fringed outgrowths (Fig. 19A-C) whereas the internal surface is much smoother and only in some specimens showed minor changes in growth that corresponded to external irregularities (Figs 4B; 11; 13C).

Kommentar [CL16]: Fig. 20 about here

## FUNCTIONAL MORPHOLOGY AND LIFE-HABIT

*Paterimitra pyramidalis* represents only the second tommotiid taxon where articulated material has been recovered. It is evident that the S1 and S2 sclerites were intimately associated, with the S2 nested within the triangular notch of the S1 to form the basal part of the scleritome (Figs 12-14; 21). The confluence between the upturned flange on the S2

sclerite and the subapical flange of the S1 sclerite (Figs 12, 13) forms a near-circular posterior opening which Skovsted *et al.* (2009a: p. 5) suggested was most likely occupied by some kind of short attachment structure, equivalent to a pedicle (Fig. 21). Evidence from rare articulated specimens (Figs 15-16; 21) indicate that the narrow-based L sclerites, were arranged as closely spaced, imbricating sets along the margins of the lateral plates and the anterior and posterior sinuses of the S1/S2-unit, producing an open tube-like construction (Fig. 21). Broad-based, more arched L sclerites probably dominated the distal portion of this tube, though direct evidence is not available. The soft parts of the organism, (including a presumed lophophore-like feeding apparatus) would have been housed within the central cavity formed by the tubiform scleritome.

**Kommentar [CS17]:** Fig. 20 about here

Although no ring-like elements such as in *Eccentrotheca* are associated with the *Paterimitra* scleritome, the mode of growth characterized by limited increase in width in all sclerite types, but continuous increase in length in the S2 and height in the S1 and L sclerites, favours formation of an elongated scleritome, supporting the interpretation of a fixed, tube-dwelling mode of life for this organism. The absence of articulated broad-based, highly arched L sclerites in the studied material suggests that L sclerites were not naturally fused together but rather separated from each other throughout ontogeny and held together by soft tissue forming the inner body wall. A similar growth pattern, probably enabling some flexibility of the whole scleritome, has been suggested in the reconstruction of the upper portion of the tube in *Eccentrotheca helenia* (Skovsted *et al.* 2011a: p.274, fig. 17). Due to the high degree of morphological variability in S1 sclerites (Figs 4; 14), the orientation of the tube in relation to the S1/S2-unit is interpreted as being fairly variable.

The tube is suggested to extend basically in the same direction as the S1 sclerite. If the scleritome was oriented with the posterior opening towards a vertically inclined substrate (Fig. 21A-B), the S1/S2-unit would form a natural bowl-shaped base to which a cone or tube

could easily fit. The fused elements in specimens SAMP 47877 and SAMP 43310 (Fig. 17), and the seemingly repaired specimen SAMP 43307 (Fig. 14I-J) can all be compared to small but high, untwisted L sclerites. Just like the L sclerites in the articulated specimen SAMP 43314 (Fig. 16) these L-like sclerites are observed abutting directly onto the sinuses of S1/S2-unit both anteriorly and posteriorly. It seems plausible that the narrow-based L sclerites were well adapted to attach to the strongly undulating outline formed by the lateral plates and sinuses of the S1/S2-unit, and to cover uneven areas in a mosaic manner. This would adapt the outline to the curvature of the elongate and strongly arched L sclerites, which would be more suitable for lining a tubular extension. Considering this, it is possible to argue the general pattern to be that high, narrow L sclerites were more proximally associated with the S sclerite complex (S1+S2) attaching to the anterior and posterior sinuses respectively, followed successively in subsequent rows by bigger ones; low, broad L sclerites occupying the more distal parts of the assumed (more or less conical) tube, not fusing with each other to the same extent as the high ones. This would enable the arrangement of large L sclerites into ring-like structures around the tube, slightly inclined in an *Eccentrotheca*-like manner, preferably towards the anterior (Fig. 21A), which in turn might explain the twisting of large L sclerites in both directions. Twisting and curling of sclerites which then end up folding down close/parallel to the tube/cone surface instead of standing out at a right angle from the body wall could offer advantages by reducing the width of the organism, which would be favourable in competition for limited space and enhance balancing of the tube/cone in the water column. The twisting and folding of sclerites would also make them less vulnerable to mechanical breakage.

Skovsted *et al.* (2011a) suggested that *E. helenia* was attached and hanging as pendant forms from ceilings and crevices in cryptic environments or attached to the lateral sides of large archaeocyaths/spongiomorphs. An assumption based on comparisons with the

problematic calcareous cribricyaths – elongate horn-shaped tubes inhabiting cryptic reef environments – and the fact that *E. helenia* co-occur with archaeocyaths (although not yet found *in situ*). The ecology of *Paterimitra* is more complex than *Eccentrotheca*. *Paterimitra* inhabited the same types of biohermal environments as *E. helenia* and was thus exposed to the same selective pressures. However, *Paterimitra* occurs in a wider variety of carbonate dominated facies, including low energy restricted lagoonal systems and open carbonate sand environments. *Paterimitra* is more abundant in biohermal environments, but is not restricted to such environments. The variation and deformation observed in sclerites of *Paterimitra* (in particular S1 sclerites), likely reflect crowding and variation in substrate.

## PHYLOGENY

*Paterimitra* is interpreted herein as a stem-group brachiopod, representing a step in a gradual transition from numerous unspecialized irregular sclerites in early tube-dwelling eccentrothecimorph tommotiids, to a body plan composed of two specialized bilaterally symmetrical valves in brachiopods. The *Paterimitra* scleritome could be interpreted to represent a derived version of the tubular scleritome of a vermiform *Eccentrotheca*-like ancestor; a more crown-ward member of the brachiopod stem, introducing bilateral symmetry to the scleritome coupled with reduction in number and specialization of the basal sclerites (Fig. 22). According to this model, the bilaterally symmetrical S1/S2-unit represents an expanded and larger equivalent to the low, cap-shaped plates in the basal ring of *Eccentrotheca*. The L sclerites correspond to the larger set of high, laterally compressed, triangular sclerites present in the upper portion of the *Eccentrotheca* scleritome. However, as discussed below *Paterimitra* also show distinct similarities to the oldest fully bivalve

phosphatic shelled brachiopods, the paterinids, especially in terms of shell structure and micro-ornament. Consequently, *Paterimitra pyramidalis* is regarded as an intermediate between the tommotiid *Eccentrotheca* and the paterinids (Fig. 22).

Kommentar [CL18]: Fig. 22 about here

#### *Paterimitra and the evolution of brachiopod shell secretion*

Skeletal microstructure is widely recognised as phylogenetically greatly informative at high taxonomic levels (Williams *et al.* 1996). To some extent, skeletal microstructure also records the biological regime of shell secretion, particularly in modern brachiopods where newly-formed epithelial cells first secrete the organic periostracum along the mantle edge and then successively change their secretion regime to form the primary and secondary layers (Williams 1997). Shell secretion in extant organophosphatic brachiopods is characterised by the cyclic deposition of nanometric apatite granules, glycosaminoglycans (GAGs), and collagen or chitin (Williams *et al.* 1992, 1994). The nature of this depositional cycle is evident in the distinct lamination at some 10s of microns that characterise all extant and extinct microstructures of organophosphatic brachiopods (Holmer 1989; Cusack *et al.* 1999). The vastly different diagenetic stability of the various organic compounds and apatite granules creates an environment prone to support very early diagenetic remobilisation of apatite within shell laminae (Balthasar 2007). This principle of localised diagenetic fate within different shell layers is crucial in understanding stem group microstructures where these lack extant representatives. Based on the general occurrence of cyclic deposition in extant organophosphatic brachiopods and the characteristic three-fold succession of periostracum, primary and secondary layer, it must be assumed that these foundations of organophosphatic shell secretion first evolved in the stem group.

*Paterimitra* is the only tommotiid that exhibits a well-defined distinction between primary and secondary layer. Although both primary and secondary layers are characterised by a framework of presumably organic polygonal compartments, the approach to the mineralisation of this polygonal scaffolding differs strikingly between primary and secondary layers. Whereas the polygonal organic walls within the primary layer were mineralized from the walls inwards, mineralization of the secondary shell occurred by incremental deposition of dense laminae within the organic compartments. More than a mere microstructural differentiation of the primary and secondary shell layers, this difference in mineralization points towards a fundamental shift in mineralization strategy between the depositions of both layers.

Apart from *Paterimitra*, this distinctive mode of shell secretion, with a pervasive polygonal network and differential mineralization of primary and secondary layers, is only found in the paterinid brachiopod *Askepasma toddense* (Balthasar *et al.* 2009; Topper *et al.* 2013) (Fig. 23). The only difference between the microstructures of *A. toddense* and *Paterimitra* are the occasional occurrence of elliptical cavities in *A. toddense*. When *A. toddense* and *Paterimitra* co-occur, as in parts of the Flinders Ranges, particularly smaller shell fragments are commonly indistinguishable in polished cross section. Intriguingly, the newly described *Askepasma saproconcha* (Topper *et al.* 2013) suggests that the primary layer might have been covered by an organic periostracum, while its secondary shell exhibits a pronounced reduction in mineralisation similar to that seen in tannuolinids.

**Kommentar [CL19]:** Fig.23 about here

While polygonal imprints are common among tommotiids (see discussion in Conway Morris and Chen 1990), these alone are insufficient to recognize this sequential mode of shell secretion. Indeed, superficial polygonal imprints are known from a variety of phosphatic fossils including other tommotiids (see discussion in Conway Morris and Chen 1990), but also brachiopods (*e.g.* Balthasar 2009; Winrow and Sutton 2012) and conodonts (Conway

Morris and Harper 1988). A pervasive shell-penetrating scaffolding of polygonal layers has only been detected in *Askepasma*, *Salanygolina*, *Eccentrotheca*, *Paterimitra*, and probably tannuolinids (Ushatinskaya 1987; Balthasar *et al.* 2009; Holmer *et al.* 2009; Topper *et al.* 2013).

It should be stressed that the detection of polygonal structures of a pervasive nature is challenging. This either requires unusually preserved material, as in the case of partially silicified specimens of *Salanygolina* (Ushatinskaya 1987; Holmer *et al.* 2009), or the careful study of highly polished cross sections using high-energy backscatter-imaging, a method that is largely underused but has proven to yield unique microstructural information (Balthasar *et al.* 2009; Balthasar *et al.* 2011). In tannuolinids, the reduced mineralization of the secondary shell further complicates the detection of such a pervasive network of polygonal compartments. However, the distribution of polygonal imprints on successive internal laminae in *Micrina* and *Tannuolina* (Conway Morris and Chen 1990; Balthasar *et al.* 2009: suppl. material) suggests the existence of a pervasive network of organic-walled compartments very similar to eccentrothecimorph tommotiids and some paterinids. The characteristic ‘hollowed out’ nature of the tannuolinid shell structure (see for example Williams *et al.* 2002; Murdoch *et al.* 2012) is largely composed of cement (Balthasar *et al.* 2009: Suppl. Figure 1) derived from remobilisation of biogenic apatite within the shell.

Independent of overall morphology, skeletal microstructure provides further evidence for distinct tommotiid clades. The camenellan clade as defined by morphology (see above) lacks a pervasive polygonal framework and members of this clade exhibit a dense micron-scale lamination (1<sup>st</sup> order lamination; Balthasar *et al.* 2009; Skovsted *et al.* 2009). The sclerites of tannuolinids and eccentrothecimorphs, by contrast, contain an organic-walled scaffolding of polygonal compartments. This scaffolding is composed of distinct layers, a few 10s of microns thick (2<sup>nd</sup> order lamination; Balthasar *et al.* 2009), which possibly reflects a

similar mode of cyclic shell secretion in organophosphatic crown-group brachiopods. Within this clade of tomotiids possessing 2<sup>nd</sup> order skeletal lamination, tannuolinids are characterized by their reduced degree of mineralization, whereas eccentrothecimorph tomotiids and *A. toddense* exhibits 1<sup>st</sup> order lamination within 2<sup>nd</sup> order laminae (Balthasar *et al.* 2009; Topper *et al.* 2013).

The striking similarities in skeletal microstructure between *A. toddense* and *Paterimitra* suggest close phylogenetic relationships. As argued above, the significance of shared microstructure in both taxa reflects the mode of organophosphatic shell formation in crown-group brachiopods, which appears to have been absent in the camenellan clade of tomotiids. While both tannuolinids and eccentrothecimorphs exhibit cyclic skeletal secretion typical of organophosphatic crown group brachiopods, both these clades show different microstructural features linking them to different Cambrian groups of brachiopods. Apart from the connection between *A. toddense* and eccentrothecimorphs, the reduced apatite mineralisation along 2<sup>nd</sup> order laminae is also seen in *A. saproconcha* (Topper *et al.* 2013). Furthermore, partially unmineralized organic shells are known from at least three other problematic Cambrian brachiopod taxa (Balthasar and Butterfield 2009). While the trend to evolve weakly mineralized shells might have been induced convergently by the changing availability of phosphorous in oceans throughout the Cambrian (Porter 2004), a phylogenetic correlation between the evolutionary loss of mineralisation cannot be entirely ruled out. Thus, while current evidence provides strong support for a close relationship between tannuolinids, eccentrothecimorphs and organophosphatic brachiopods, microstructure alone does currently not resolve which tomotiid clade was most proximal to brachiopods.

With respect to the origin of calcareous shells in brachiopods, the existence of a pervasive organic framework might well represent a precursor of the organic envelopes that define the shape of calcite fibres in rhynchonelliform brachiopods as proposed by Holmer *et*

al. (2009). An alternative path of evolving calcareous shells from organophosphatic ancestors has been proposed based on the microstructure of calcareous obolellids (Balthasar 2008) which appear to lack well developed elongate calcite fibres with organic envelopes, a condition closer to the microstructure of modern craniids. While there remains little doubt that the original shell composition of the brachiopod-tommotiid clade was organophosphatic, the evolution of calcareous shells from these origins might have occurred independently along the stems of the two calcareous subphyla.

#### *Identification of brachiopod valve homologies and ontogeny in Paterimitra*

The bilateral symmetry of the basal sclerites (S1 and S2) of *Paterimitra* suggests that these sclerites, in particular in the context of the close similarities in shell ultrastructure and proposed phylogenetic relationship between *Paterimitra* and paterinid brachiopods, are direct homologues of brachiopod valves. In particular the S1 sclerite exhibits similarities to the ventral valves of paterinids. The subapical flange of the S1 sclerite shows strong resemblance to the ventral homeodeltidium of a young adult *Micromitra* (compare Fig. 4A to Williams et al. 1998, pl. 9, fig. 1). The anterior plate of the S1 sclerite is also remarkably similar to the colleplax of the ventral valve of *Salanygolina* (compare Fig. 3A to Holmer et al., 2009, text-fig. 2B). And the larval shell of the *Paterimitra* S1 is very closely comparable to the transversely elongate brephic shell of the ventral valve in *Salanygolina*, with the protegulum and incipient sub-apical flange in *Paterimitra* in the same position as the posterior delthyrium-like projection of the ventral brephic shell in *Salanygolina* (compare Fig. 8D to Holmer et al., 2009, text-fig. 4B). Available evidence thus suggests that the S1 sclerite of *Paterimitra* is homologous to the ventral valve of paterinid brachiopods. Logically, the S2 sclerite could be considered to be homologous to the dorsal valve of brachiopods, but the

morphological evidence for this interpretation is less clear. In particular the position of the S2 sclerite, nested within the triangular notch (interarea?) of the S1 sclerite, is difficult to compare to the position of the dorsal valve in paterinids or other brachiopods. However, the presence of a well defined larval shell and the association of the posterior margin of the S2 sclerite with the pedicle-like attachment structure may support the proposed homology.

As suggested by Holmer et al. (2011), the presence of brachiopod-like larval shells in the opposing symmetrical sclerites suggests that the larvae of *Paterimitra* was effectively bivalved and that L sclerites were added during later stages of ontogeny, perhaps starting only after settlement. Consequently, the bivalved condition in brachiopods may be a retained juvenile character and the bivalved brachiopod body plan a result of paedomorphosis.

## **SYSTEMATIC PALAEOLOGY**

*Repository.* All illustrated specimens are deposited in South Australian Museum, Adelaide (acronym SAMP). Original type specimens are deposited in Commonwealth Palaeontological Collection, Australian Geological Survey Organisation, Canberra (acronym CPC).

Order TOMMOTIIDA Missarzhevsky, 1970

*Remarks.* For a thorough discussion regarding the Order Tommotiida, see Skovsted *et al.* (2011).

Genus PATERIMITRA Laurie, 1986

*Figures 2-21*

\* 1986 *Paterimitra* Laurie, p. 446.

1990 *Paterimitra* Laurie; Conway Morris in Bengtson *et al.*, p. 142.

*Derivation of name:* see Laurie 1986, p. 446.

*Type and only species:* *Paterimitra pyramidalis* Laurie, 1986.

*Emended diagnosis.* Sclerites microscopic, apatitic by original composition, growing via basal-internal accretion. Scleritome comprising at least three clearly distinctive sclerite types: symmetrical sclerite types S1 and S2, and laterally compressed asymmetrical L sclerites. S1 sclerites pyramidal with posterior triangular notch and U-shaped anterior plate. S2 sclerites concave and acutely triangular. External surface with micro-ornament consisting of polygonal compartments. Scleritome consisting of one S2 sclerite nested within triangular notch of one S1 sclerite; multiple L sclerites lining antapical margins in additional rows forming an open tube.

Differs from *Eccentrotheca* by the presence of two specialized bilaterally symmetrical sclerites in the scleritome and the distinct polygonal external micro-ornament. Differs from *Kulparina* by more regular and less compressed sclerite shape and the distinct polygonal external micro-ornament. Differs from *Sunnaginia* by the presence of individual sclerite types, the bilateral symmetry of S1 and S2 sclerites and the absence of right and left hand sclerite pairs, polygonal micro-ornament, and the shell microstructure.

*Discussion.* Laurie (1986) suggested that *Ambonychia macroptera* Tate, 1892 and Plate type III of *Dailyatia ajax* Bischoff, 1976 could be referred to the genus *Paterimitra* as ?*P. macroptera*, based on the external micro-ornament which differs from the type species of

*Dailyatia*, *D. ajax* Bischoff, 1976 and resembles that of *Paterimitra pyramidalis*. This suggestion was questioned by Evans and Rowell (1990), who argued that although there are indeed similarities to *Paterimitra*, the external micro-ornament of *A. macroptera* show strong similarities to the Antarctic species *Dailyatia bradocki* Evans and Rowell, 1990 and *Dailyatia odyssey* Evans and Rowell, 1990. *A. macroptera*, hence, probably represents a poorly known species of *Dailyatia*. Unpublished data from South Australia (Skovsted pers. obs. 2012) supports this interpretation. Consequently, we consider the genus *Paterimitra* to be monotypic.

*Paterimitra pyramidalis* Laurie, 1986

Figures 2-21

- 1985 Problematicum A Laurie and Shergold, p. 88, fig. 7a-b.
- ? 1985 *Eccentrotheca* sp. Laurie and Shergold, p. 88, fig. 7c.
- \* 1986 *Paterimitra pyramidalis* Laurie, p. 446, fig. 9f-j.
- ? 1986 *Eccentrotheca* cf. *konesia* Landing, Nowlan and Fletcher; Laurie, p. 446 fig. 9a-d.
- 1990 *Paterimitra pyramidalis* Laurie; Conway Morris in Bengtson *et al.*, p. 142, fig. 92.
- 2001 *Paterimitra pyramidalis* Laurie; Gravestock *et al.*, p. 116, pl. 8, figs 10, 11.
- part. 2008 *Eccentrotheca* sp. Skovsted *et al.*, fig. 2a, b, figs 1a-n, 2c, d.
- 2009a *Paterimitra* sp. Skovsted *et al.*, figs 1, 2.
- 2010 *Paterimitra* sp. Balthasar *et al.*, figs 1b, d, e, k, 2d.
- 2011 *Paterimitra* sp. Holmer *et al.*, text-fig. 2.
- 2011a *Paterimitra* sp. Skovsted *et al.*, text-fig. 20.

*Holotype*: CPC23676; *paratypes*: CPC23677-23688 (Laurie 1986)

*Emended diagnosis:* as for genus by monotypy.

*Occurrence and age.* Lower Cambrian late Terreneauvean Stage 2 to Cambrian Series 2, Stage 3 (*Pararaia tatei* trilobite zone) of the Wilkawillina, Wirrapowie and Ajax limestones in the Flinders Ranges, South Australia. Cambrian Series 2, Stage 3 of the Todd River Dolomite, Northern Territory. Cambrian Series 2, Stage 3 of the Kulpara Formation, Yorke Peninsula, South Australia. See above for details.

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## Figure and Appendix captions

**FIG. 1.** A-G, locality map showing position of sampled stratigraphic sections and spot localities. A, general position of field area in South Australia; B, geographical position of localities in the Flinders Ranges; C, simplified geological map of Mt. Scott area with positions of sections AJX-M and AJX-N; D, simplified geological map of Bunkers Range showing location of section MMF; E, simplified geological map showing location of Bunyeroo Gorge; F, simplified geological map of the Bunkers Graben, showing location of section 10MS and the Wilkawillina Type Section; G, simplified geological map of the Chace and Druid ranges, showing position of CR1 section through the Chace Range and spot locality in the Druid Range.

**FIG. 2.** A-I, schematic drawing illustrating the morphology of the three different sclerite types of *Paterimitra pyramidalis* (S1, S2, and L) and the terminology used in this study. A-D sclerite type S1. A, apical view showing posterior margin, subapical flange and width, B, posterior view showing subapical flange, triangular notch and lateral plates, C, lateral view showing apex, subapical flange, lateral plate and anterior plate, and D, anterior view showing anterior plate, anterior boundaries, anterior sinus and height. E-F, sclerite type S2. E, planar view showing width and length, and F, lateral view showing upturned flange. G-I, sclerite type L. G, lateral view showing height and width, H, apical view showing apical twist, and I, basal view showing basal margin. Not to scale.

**FIG. 3.** A-D, S1 sclerites of *Paterimitra pyramidalis* from the Flinders Ranges, South Australia. A-C, SAMP 46320. A, posterior view, and B-C, detail of external reticular micro-ornament. D, SAMP 47839, posterior view, delamination of individual shell layers. Specimen

in A-C from sample AJX-M/256, Ajax Limestone, AJX-M section, Mt Scott Range; specimen in D from sample MMF/0.0, Winnitunny Creek Member, Wilkawillina Limestone, Base of MMF section, Bunkers Range (Appendix 3f). Scale bars represent: in A, D 200  $\mu\text{m}$ ; in B-C 5  $\mu\text{m}$ .

**FIG. 4.** A-I, S1 sclerites of *Paterimitra pyramidalis* from the Flinders Ranges, South Australia. A, SAMP 46315, apical view. B, SAMP 47840, posterior view. C, SAMP 47841, lateral view. D, SAMP 47842, anterior view. E, SAMP 43303, posterior view. F, SAMP 47843, posterior view. G, SAMP 47844, posterior view. H, SAMP 47845, lateral view. I, SAMP 47846, lateral view. Specimen in A from sample AJX-M/267.5, Ajax Limestone, AJX-M section, Mt Scott Range (Appendix 3g); specimen in B from sample Bunyeroo 9, Wilkawillina Limestone, Bunyeroo Gorge; specimens in C-D and F from sample 10MS-W/390, Winnitunny Creek Member, Wilkawillina Limestone, 10MS-W section, Bunkers Graben; specimen in E from sample MMF/0.0, Winnitunny Creek Member, Wilkawillina Limestone, Base of MMF section, Bunkers Range; specimen in G from sample CR/449, Wirrapowie Limestone, CR/1 section, Chace Range; specimen in H from sample WILK/Q, Second Plain Member, Wilkawillina Limestone, Wilkawillina Gorge type section (WILK), Bunkers Graben; specimen in I from sample WILK/S, Second Plain Member, Wilkawillina Limestone, Wilkawillina Gorge type section (WILK), Bunkers Graben. All scale bars represent 200  $\mu\text{m}$ .

**FIG. 5.** S2 sclerites of *Paterimitra pyramidalis* from the Flinders Ranges, South Australia. A, SAMP 43306, apical view. B, SAMP 47847, lateral view. C, SAMP 43305, posterior view. D, G, SAMP 47848. D, apical, and G, lateral views. E, SAMP 47849, posterior view. F, SAMP 47850, posterior view. H, SAMP 46316, apical view. I, SAMP 47851, apical view. Specimens

in A from sample WILK/I, Second Plain Member, Wilkawillina Limestone, Wilkawillina Gorge type section (WILK), Bunkers Graben; specimens in B and D-G from sample MMF/0.0, Winnitunny Creek Member, Wilkawillina Limestone, Base of MMF section, Bunkers Range; specimen in C from sample AJX-M/256, Ajax Limestone, AJX-M section, Mt Scott Range; specimen in H from sample Bunyeroo 12, Wilkawillina Limestone, Bunyeroo Gorge (Appendix 3h); specimen in I from sample WILK/Q, Second Plain Member, Wilkawillina Limestone, Wilkawillina Gorge type section (WILK), Bunkers Graben. All scale bars represent 100  $\mu\text{m}$ .

**FIG. 6.** A-R, L sclerites of *Paterimitra pyramidalis* from the Flinders Ranges, South Australia. A, F, SAMP 43311. A, lateral, and F, apical views. B, SAMP 47852, lateral view. C, SAMP 47853, oblique lateral view. D, SAMP 47854, oblique lateral view. E, SAMP 47855, oblique lateral view. G, SAMP 47856, apical view. H, M, SAMP 47857. H, apical, and M, basal views. I, SAMP 47858, apical view. J, SAMP 43313, apical view. K, O, SAMP 47859. K, apical, and O, lateral views. L, SAMP 43314, lateral view, detail of L sclerite with multiple apices. N, SAMP 43312, lateral view. P, SAMP 47860, lateral view. Q, SAMP 47861, lateral view. R, SAMP 47862, lateral view of curled up L sclerite. Specimens in A-F, H-I, K, M and O from sample WILK/Q, Second Plain Member, Wilkawillina Limestone, Wilkawillina Gorge type section (WILK), Bunkers Graben; specimen in G from sample WILK/S, Second Plain Member, Wilkawillina Limestone, Wilkawillina Gorge type section (WILK), Bunkers Graben; specimens in J, N and Q from sample WILK/R, Second Plain Member, Wilkawillina Limestone, Wilkawillina Gorge type section (WILK), Bunkers Graben (Appendix 3i-j); specimens in L and R from sample AJX-N/213, Ajax Limestone, AJX-N section, Mt Scott Range; specimen in P from sample Bunyeroo 12, Wilkawillina Limestone, Bunyeroo Gorge. All scale bars represent 100  $\mu\text{m}$ .

**FIG. 7.** A-F, growth stages of S1 sclerites of *Paterimitra pyramidalis*. A, SAMP 48142, juvenile S1 sclerite, apical view. B, schematic drawing of juvenile S1 sclerite, posterior view. C, SAMP 47863, adult S1 sclerite, posterior view. D, schematic drawing of juvenile S1 sclerite, posterior view. E, SAMP 47839, old adult S1 sclerite, posterior view. F, schematic drawing of old adult S1 sclerite. Specimen in A from sample AJX-M/266, Ajax Limestone, AJX-M section, Mt Scott Range (Appendix 3k); specimen in C from sample AJX-M/262.7, Ajax Limestone, AJX-M section, Mt Scott Range; specimen in E from sample MMF/0.0, Winnitiny Creek Member, Wilkawillina Limestone, Base of MMF section, Bunkers Range. Scale bars in A, C, and E represent 100  $\mu\text{m}$ . B, D, and F, not to scale.

**FIG. 8.** A-M, larval shells and protegula, S1 and S2 sclerites of *Paterimitra pyramidalis* from the Flinders Ranges, South Australia. A-B, schematic drawings of S1 (A) and S2 (B) sclerites (apical views), larval shells enlarged, grey zone representing suggested protegulum. C-F, S1 sclerites. C-D, SAMP 46320. C, apical view, box indicating larval shell enlarged in D. E-F, SAMP 46317. E, apical, and F, lateral views. G-N, S2 sclerites; G-I, K, M, lines indicating suggested protegula on larval shells. G, SAMP 47864, apical view. H-I, SAMP 47865. H, apical, and I, lateral views. J-K SAMP 47866. J, lateral, and K, apical views. L, SAMP 47867, apical view, heavily worn sclerite, larval shell delaminated. M-N, SAMP 46316. M (Appendix 3l), apical, and N, lateral views. Specimen in C-D from sample AJX-N/256, Ajax Limestone, AJX-M section, Mt Scott Range (Appendix 3m); specimen in E-F from sample AJX-N/267.5, Ajax Limestone, AJX-M section, Mt Scott Range (Appendix 3n); specimens in G-L from sample MMF/0.0, Winnitiny Creek Member, Wilkawillina Limestone, Base of MMF section, Bunkers Range; specimen in M-N from sample Bunyeroo12, Wilkawillina Limestone, Bunyeroo Gorge. A-B, not to scale. C-N, all scale bars represent 100  $\mu\text{m}$ .

**FIG. 9.** A-M, sclerites with deviating features and odd specimens of *Paterimitra pyramidalis* from the Flinders Ranges, South Australia. A-B, SAMP 47845, S1 sclerite with unusually large subapical flange. A, apical, and B, lateral views. C-D, SAMP 47868, deformed S1 sclerite. C, apical, and D, lateral views. E, SAMP 47869, S1 sclerite, apical view, unusually wide and high, lateral plates so narrow that it resembles an L sclerite. G-J, SAMP 47870, sclerite of unsure affinity. G, apical, H, lateral, I, posterior, and J, lateral views. K-L, SAMP 47861, unusually irregular L sclerite, lateral views. M, SAMP 47871, gravely disturbed sclerite, probably S1, apical view. Specimens in A-D and G-J from sample WILK/Q, Second Plain Member, Wilkawillina Limestone, Wilkawillina Gorge type section (WILK), Bunkers Graben; specimen in E from sample CR/322.8, Wirrapowie Limestone, CR/1 section, Chace Range; specimen in F from sample CR/449, Wirrapowie Limestone, CR/1 section, Chace Range; specimen in K-L from sample WILK/R, Second Plain Member, Wilkawillina Limestone, Wilkawillina Gorge type section (WILK), Bunkers Graben; specimen in M from sample WILK/A, Second Plain Member, Wilkawillina Limestone, Wilkawillina Gorge type section (WILK), Bunkers Graben. All scale bars represent 200  $\mu\text{m}$ .

**FIG. 10.** A-F, S1 sclerites of *Paterimitra pyramidalis* from the Flinders Ranges, South Australia, with shifted subapical flange. A-B, SAMP 47872, apical views. A, box indicating disturbed posterior area with subapical flange enlarged in B, (line indicating fused, damaged S2 sclerite, for details see Fig.14C-D); B, close up of gravely disturbed subapical flange, showing about 90-degree-shift in growth direction (gd) in subapical flange as indicated by arrows 1 (primary gd) and 2 (secondary gd). C, SAMP 47873, apical view, disturbed growth direction in subapical flange. D-F, SAMP 47874, disturbed growth direction in subapical flange. D, apical view, box indicating area enlarged in E; E, apical view, and F, posterior

view. Specimens in A-B and D-F from sample MMF/0.0, Winnitunny Creek Member, Wilkawillina Limestone, Base of MMF section, Bunkers Range; specimen in C from sample AJX-N/368, Ajax Limestone, AJX-N section, Mt Scott Range. All scale bars represent 100  $\mu\text{m}$ .

**FIG. 11.** A-P, S1 sclerites of *Paterimitra pyramidalis* from the Flinders Ranges, South Australia, exhibiting repaired growth disturbance/damage close to the edge of the anterior plate. A-F, SAMP 47875, with finger-like outgrowth extending inwards from the internal side of the anterior plate. A, posterior view, box indicating area enlarged in B; B, close up of outgrowth exhibiting similar surface structure as the remaining internal surface of the sclerite; C, internal (antapical) view; D, anterior view, box indicating area enlarged in E; E, anteroapical view, line indicating damaged area with hole penetrating anterior plate from the exterior inwards. G-P, SAMP 47876, L sclerite-like ongrowth covering growth disturbance. G, posterior view, box indicating area enlarged in H; H, internal (antapical) view, box indicating area enlarged in I; I, close up of growth disturbance and covering sclerite; J, close up of growth disturbance in I, showing uneven surface around the upper part of the disturbance; K, lateral view, box indicating area with L sclerite-like ongrowth enlarged in L; L, anterior view, box indicating area enlarged in M; M, apical view. Specimens in A-P from sample MMF/0.0, Winnitunny Creek Member, Wilkawillina Limestone, Base of MMF section, Bunkers Range. All scale bars represent 100  $\mu\text{m}$ .

**FIG. 12.** A-B, schematic drawing illustrating the relationship between S1 and S2 sclerites in the scleritome of *Paterimitra pyramidalis* from the Flinders Ranges, South Australia. A, posterior view showing posterior sinus and posterior opening, B, lateral view showing protruding posterior opening. Not to scale.

**FIG. 13.** A-F, articulated S1 and S2 sclerites of *Paterimitra pyramidalis* from the Flinders Ranges, South Australia. A-C, SAMP 43310. A, posterior view, box indicating area with posterior opening enlarged in B; C, lateral view. D, SAMP 47877, posterior view. E-F, SAMP 43308, articulated sclerite compound with subapical flange of the S1 sclerite and the upturned flange of the S2 sclerite fused to form a protruding tube-like posterior opening. E, posterior, and F, lateral views. Specimen in A-C from sample MMF/0.0, Winnitunny Creek Member, Wilkawillina Limestone, Base of MMF section, Bunkers Range; specimen in D from sample AJX-N/213, Ajax Limestone, AJX-N section, Mt Scott Range; specimen in E-F from sample AJX-M/262.7, Ajax Limestone, AJX-N section, Mt Scott Range. All scale bars represent 200  $\mu\text{m}$ .

**FIG. 14** A-P Articulated S1 and S2 sclerites of *Paterimitra pyramidalis* from the Flinders Ranges, South Australia, showing signs of recovery from deformation and/or growth disturbance. A-B, SAMP 43310. A, posterior, and B, antapical views. C-D, SAMP 47872. C, apical, and D, lateral views. E-H, SAMP 47878. E, apical, F, posterior, and G, lateral views, box in G indicating area enlarged in H. I-J, SAMP 43307, S2 sclerite damaged, repaired and fused with S1 sclerite. I, posterior view, box indicating area enlarged in J. K-L, SAMP 47879, S2 sclerite fused with S1 sclerite. K, posterior view, box indicating area enlarged in L. M-P, SAMP 47880, S2 sclerite fused with S1 sclerite, anterior edge of the S2 sclerite constituting a continuous line with the basal edges of the lateral plates of the S1 sclerite. M, posterior view with box indicating area enlarged in N, O, posterolateral, and P, antapical views. Specimens in A-P from sample MMF/0.0, Winnitunny Creek Member, Wilkawillina Limestone, Base of MMF section, Bunkers Range. All scale bars represent 200  $\mu\text{m}$ .

**FIG. 15.** A-F, plate-like sclerite compound consisting of curled up/bent L sclerites of *Paterimitra pyramidalis* from the Flinders Ranges, South Australia, SAMP 47862. A, lateral view with box indicating area enlarged in D, B, lateral, and C, basal, E, planar views, box in E indicating area enlarged in F. Specimen in A-F from sample AJX-N/213, Ajax Limestone, AJX-N section, Mt Scott Range. Scale bars represent: in A-E 200  $\mu\text{m}$ ; in F 50  $\mu\text{m}$ .

**FIG. 16.** A-H, S1 sclerite of *Paterimitra pyramidalis* from the Flinders Ranges, South Australia, with three L sclerites (*i*, *ii*, and *iii*) attached to the left lateral plate and one L sclerite attached to the right lateral plate, SAMP 43314. A, posterior view, box indicating area enlarged in E; B, lateral view exhibiting L sclerites *i*, *ii*, and *iii*, box indicating area enlarged in F; C, anterior view, box indicating area enlarged in G; D, lateral view exhibiting L sclerite, box indicating area enlarged in H; I, posterior, J, antapical, and K, apical views. Specimen illustrated in A-K from sample AJX-N/213, Ajax Limestone, AJX-N section, Mt Scott Range. Scale bars represent: in A-D, I-K 200  $\mu\text{m}$ ; in E-H 100  $\mu\text{m}$ .

**FIG. 17.** A-F, other L-like sclerites fused to S1 sclerites of *Paterimitra pyramidalis* from the Flinders Ranges, South Australia. A, D, SAMP 43310, L-like sclerite fused to base of lateral plate. A, postero-apical view, box indicating area enlarged in D. B-C, E-F, SAMP 47876, L-like sclerite fused to anterior plate. B, anterior view, box indicating area enlarged in E; C, lateral view, box indicating area enlarged in F. Specimens in A-F from sample MMF/0.0, Winnitiny Creek Member, Wilkawillina Limestone, Base of MMF section, Bunkers Range. All scale bars represent 100  $\mu\text{m}$ .

**FIG. 18.** A-H, SEM secondary electron images of isolated L-sclerites of *Paterimitra*. A, SAMP 47881, and B, SAMP 47932, L sclerites of *Paterimitra pyramidalis*, apical views,

boxes indicating positions of figs E and G respectively. C, detail showing the polygonal surface ornament; D, detail of L sclerite showing the co-occurrence of polygonal and bulbous structures in the ornament; E-F, detail of A showing regular appearance of bulbous ornament; G-H, views of the ornament of L-sclerites showing the development of bulbous structures through the swelling of the walls of polygonal structures. Specimen in A and E-F from sample WILK/Q, Second Plain Member, Wilkawillina Limestone, Wilkawillina Gorge type section (WILK), Bunkers Graben; specimen in B and G-H from sample WILK/I, Second Plain Member, Wilkawillina Limestone, Wilkawillina Gorge type section (WILK), Bunkers Graben. Scale bars represent: in A-B 200  $\mu\text{m}$ ; in D-E 50  $\mu\text{m}$ ; in C and H 20  $\mu\text{m}$ ; in F-G 10  $\mu\text{m}$ .

**FIG. 19.** A-K, SEM back scatter images of polished cross sections of isolated *Paterimitra* S1 sclerites that were imbedded in araldite resin. A-C, overview of specimens indicating positions of figures D-K; A1 and A2 are slices of the same specimens separated by a few micron; D, lateral margin with a digitate hooked edge; E, portion of shell with closely spaced proximal sections of external fringes that create the impression of internal cavities; F, Detail of E showing anvil-shaped cross-sections of the walls of the polygonal ornament; G, posterior portion of sclerite with abundant fringes stacked on top of each other; H-K, details of sclerites showing the lamination with cross-sections through polygonal compartments. Scale bars represent: in A 500  $\mu\text{m}$ ; in B, C 200  $\mu\text{m}$ ; in D, G 100  $\mu\text{m}$ ; in E, H, J, K 50  $\mu\text{m}$ ; in I 20  $\mu\text{m}$ ; in F 5  $\mu\text{m}$ .

**FIG. 20.** A-D, SEM secondary electron images of limestone-hosted etched *Paterimitra* S1 sclerite. A, overview with positions of figs B-D; B, detail showing how polygonal compartments form pillar-like structures normal to the sclerite surface; C, detail showing the

pervasive occurrence of polygonal compartments throughout the shell; D, tilted view showing the lamination and the expression of polygonal structures on the internal surface of the sclerite. Scale bars represent: in A 200  $\mu\text{m}$ ; in B-D 50  $\mu\text{m}$ .

**FIG. 21.** A-B, hypothetic reconstruction of *Paterimitra pyramidalis*, schematic drawing illustrating the association between S1 and S2 sclerites, orientation of the L sclerite tube relative to the S1/S2-unit, and the general orientation of the scleritome relative to the substrate. A, lateral view, scleritome oriented in right angle to a vertical substrate, L sclerite tube following the general vertical direction of the S1/S2-unit, and B, posterior view. Not to scale.

**FIG. 22.** Diagram indicating possible phylogenetic relationship between tomotiids and organophosphatic brachiopods. Modified from Skovsted *et al.* 2011.

**FIG. 23.** A-C, SEM secondary electron images of limestone-hosted etched *Askepasma toddense*. A, overview showing the positions of figs. B and C which show the shell lamination and the nature of the distribution of polygonal structures. Scale bars represent: in A 1 mm; in B 50  $\mu\text{m}$ ; in C 20  $\mu\text{m}$ .

## APPENDIX

**Appendix 1.** Detailed description of sampled sections and stratigraphical correlation of sampled horizons.

**Appendix 2.** Sclerite data. Locality. Sample level. Number of sclerites: S1, S1-fragm (S1 sclerites with a preserved apex were counted as individual specimens, other S1 parts were counted as fragments), S2, L, S1+S1, S1+L, L+L,  $\Sigma$ . Ontogenetic stages present in samples (juvenile, young adult, old adult). Height of S1 (approximate height-range of S1 sclerites in mm estimated from SEM pictures and with the stereomicroscope).

**Appendix 3.** Table accounting for deviating sclerite terminology and incorrect sample numbers, stratigraphic information and SAMP numbers given in previous publications featuring *Paterimitra pyramidalis*.

**Appendix 4.** L sclerite data. SEM number; SAMP no; basal margin (BM) width; relative height/width proportions; curved basal margin (BM); apical twist.