REVISION OF THE EARLY CAMBRIAN TOMMOTIID *KULPARINA ROSTRATA* FROM
SOUTH AUSTRALIA

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ABSTRACT— The early Cambrian (Terreneuvian, Stage 2) tommotiid *Kulparina rostrata* Conway Morris and Bengtson in Bengtson et al., 1990 is revised. The pyramidal sclerites of *K. rostrata* are shown to be bilaterally symmetrical and homologues of the symmetrical S1 sclerites of *Paterimitra pyramidalis* Laurie, 1986. The scleritome of *K. rostrata* is also shown to include flattened asymmetrical sclerites that were originally described under the name *Eccentrotheca guano* Bengtson in Bengtson et al., 1990 and which corresponds to the L-sclerites of *Paterimitra*. A modified tubular scleritome and a sessile filter-feeding mode of life is envisaged for *Kulparina rostrata*.

Key words: Tommotiida, Stem Group Brachiopoda, Scleritome reconstruction, Early Cambrian, Flinders Ranges,

INTRODUCTION

TOMMOTIIDS ARE an extinct group of metazoans represented by organophosphatic sclerites (individual elements of multi-component skeletons or scleritomes; Bengtson, 1970, 1985) of various shapes that are often very abundant in lower Cambrian deposits around the world (Rozanov et al., 1969; Landing, 1984; Missarzhevsky, 1989; Bengtson et al., 1990; Conway Morris and Chen, 1990; Esakova and Zhegallo, 1996; Skovsted et al., 2009a, b, 2011). The sclerites of tommotiids are generally fairly distinct, but until recently they were exclusively known from disarticulated assemblages, the structure of the skeleton and body plan of the animal remained unknown and tommotiids have commonly been regarded as a phylogenetically problematic group. Reconstructions of the tommotiid animal were largely based on a worm or slug-like model (e.g. Bengtson, 1970, 1977; Landing, 1984; Evans and Rowell, 1990), and the discovery of the vagrant, slug-like and sclerite-bearing mollusc *Halkieria evangelista* Conway Morris and Peel, 1995, from the lower Cambrian Buen Formation of North Greenland provided apparent support for this model (Williams and Holmer, 2002; Demidenko 2004; Li and Xiao, 2004).

The recent discovery and detailed description of articulated specimens of the tommotiid *Eccentrotheca helenia* Skovsted, Brock, Topper, Paterson and Holmer, 2011 from lower Cambrian carbonates in South Australia by Skovsted et al. (2011), demonstrated that the scleritome of this tommotiid was constructed as a tube composed of vertically stacked sclerite rings. The scleritome exhibited an open basal aperture that attached to hard substrates and the animal is interpreted to have been a sessile filter-feeder related to modern lophophorates (i.e. Phoronida and Brachiopoda; Skovsted et al., 2008, 2011). Subsequently, the tannuolinid tommotiid *Micrina etheridgei* (Tate, 1892) has been shown to share many

characters (shell morphology, ultrastructure and larval shell morphology) with Cambrian linguliform brachiopods (Holmer et al., 2008, 2011; Balthasar, 2009), whilst a third tommotiid taxon, *Paterimitra pyramidalis* Laurie, 1986, appears to be closely allied with paterinid brachiopods (Skovsted et al., 2009a; Topper et al., 2013; Larsson et al., 2014), thus further strengthening the proposed tommotiid-lophophorate link.

Paterimitra pyramidalis Laurie, 1986 exhibits three different sclerite types; a bilaterally symmetrical, pyramidal sclerite (S1), a triangular and bilaterally symmetrical (S2) sclerite, and laterally compressed asymmetrical (L) sclerites (Skovsted et al., 2009a; Larsson et al., 2014). Partly articulated specimens of *P. pyramidalis* suggest a cone or tube-like, bilaterally symmetrical scleritome. The basal part of the scleritome consists of one S1 sclerite and one S2 sclerite defining a circular posterior opening, and an unresolved number of L sclerites lining the distal margin of the S1/S2-composite (Skovsted et al., 2009a; Larsson et al., 2014). The similarities between *Paterimitra* L sclerites and laterally compressed sclerites of *Eccentrotheca* suggest a similar arrangement of ring-like sclerites lining the distal margin of the *Paterimitra* scleritome (Skovsted et al., 2009a; Larsson et al., 2014). The similarities in mode of shell formation, scleritome construction and microstructure of *Eccentrotheca* and *Paterimitra* led Skovsted et al. (2011) to informally establish a supergroup of tommotiid taxa referred to as the eccentrothecimorphs (a group that also includes *Porcauricula*, *Sunnaginina*, *Micrina*, *Tannuolina* and *Kulparina*) and are considered to represent a key stem group to the lophophorate phyla Brachiopoda and Phoronida (see Skovsted et al., 2011). The implication of these discoveries is that the brachiopod body plan, with its two bilaterally symmetrical valves, probably evolved through a stepwise specialization and reduction in the number of sclerites (Skovsted et al., 2008, 2009a, 2011), however see Murdock et al. (2014) for a slightly different interpretation.

Kulparina rostrata Conway Morris and Bengtson in Bengtson et al., 1990 is a poorly documented tommotiid, endemic to the Arrowie and Stansbury basins in South Australia, that has recently been suggested to be a close relative of *Paterimitra* (Skovsted et al., 2011). The potentially pivotal role of *Paterimitra* in deciphering the evolution of brachiopods has prompted a detailed re-investigation of *K. rostrata* to help elucidate the evolutionary changes within the tommotiid lineage that led to the establishment of the Brachiopoda.

MATERIAL AND METHODS

The sclerites and articulated specimens of *Kulparina rostrata* documented in this paper were retrieved from acetic acid resistant residues of samples from measured stratigraphic sections intersecting key lower Cambrian (Terreneuvian Stage 2 to Cambrian Series 2, Stage 3) shallow water platform successions of the Wilkawillina Limestone at Wilkawillina Gorge in the Bunkers Graben (type section) and at Bunyeroo Gorge in the Heysen Range, Arrowie Basin, South Australia (Fig. 1). For detailed descriptions of localities see Paterson and Brock (2007), Skovsted et al. (2011), Topper et al. (2011a, b). The original samples were collected, processed and initially picked by the late Brian Daily in the 1960s with later supplementary sampling undertaken by the late David Gravestock in the 1980s. The material, which includes isolated sclerites and partially articulated specimens, was examined under a binocular microscope. Selected specimens were mounted and coated with gold-palladium for Scanning Electron Microscope (SEM) imaging using a JEOL JSM 6480LA SEM at the Microscopy Unit in the Department of Biological Sciences, Macquarie University, Sydney; a Zeiss Supra35-VP SEM at the unit for Biological Structure Analysis (BSA), Uppsala University; or a Hitachi S-43000 at the Swedish Museum of Natural History

(Naturhistoriska Riksmuseet, NRM), Stockholm. All illustrated specimens are housed in the paleontological collection of the South Australian Museum, Adelaide (acronym: SAMP).

GEOLOGICAL SETTING, SAMPLED LOCALITIES AND ADDITIONAL OCCURRENCES

Wilkawillina Limestone type section (Daily, 1956) + section E (Gravestock, 1984), Wilkawillina Gorge, Bunkers Graben.—The type section for the Wilkawillina Limestone was measured and defined by Brian Daily (1956) near the northwest margin of the Bunkers Graben. The fossiliferous packstones and grainstones of the section have previously been described by Gravestock (1984) and Clarke (1986a, 1986b, 1986c, 1990). Samples yielding specimens of *Kulparina rostrata* were collected in 1982 by David Gravestock along the type section (Gravestock 1984, section E, corresponding to PIRSA (Primary Industries and Regions South Australia) locality register, 6635RS samples; for details see Skovsted et al., 2011: pp. 258 and supplementary material). The L sclerites of *K. rostrata* were retrieved from nine samples from section E; E13 (6635RS310), E15-E22 (6635RS312-6635RS319). At least three of these samples also contain S sclerites of *K. rostrata*; E18 (6635RS315), E21 (6635RS318) and E22 (6635RS319). All these samples predate the *A. huoi* trilobite Zone of South Australian strata and probably correspond to Terreneuvian Stage 2 of the revised Cambrian timescale (Skovsted et al., 2011).

Wilkawillina Limestone, section H, Wilkawillina Gorge, Bunkers Graben.—Section H was collected through the Wilkawillina Limestone less than 2 km south of the type section (=section E of Gravestock 1984), and some of Gravestock's samples from this section contain abundant specimens of *K. rostrata*; samples H81, H83, H86, H87, H88 and H89, located respectively at 83, 125, 135, 146, 156 and 164 m true thickness above the base of the

section. All six samples contain L sclerites, whilst S sclerites are restricted to samples H83, H86 and H87.

Bunyeroo Gorge, Daily sample: Bunyeroo 12.—A single sample (Bun 12) from a suite of samples collected from the Wilkawillina Limestone at Bunyeroo Gorge yielded specimens of *Kulparina rostrata*. These samples were collected by Brian Daily in the early 1970s but, unfortunately, no stratigraphical information exists for the majority of these samples (for details see Skovsted et al. 2009a, 2011). Skovsted et al. (2011, fig. 5a, 5c) described laterally compressed sclerites from this sample as *Eccentrotheca helenia*, stressing the strong resemblance to columnar L sclerites of *K. rostrata*. This is the only sample where possible sclerites of *K. rostrata* and *E. helenia* have been recorded to co-occur, although the identification of these specimens as *E. helenia* may have to be revised (see discussion below).

Additional occurrences of Kulparina rostrata.—In addition to the sections detailed above, sclerites of *K. rostrata* have been reported from several sections, spot locality samples and drill cores in South Australia. These were partially accounted for by Skovsted et al. (2011) and are summarized in Appendix 1.

KULPARINA ROSTRATA AND ECCENTROTHECA GUANO

The tommotiid species *Eccentrotheca guano* Bengtson in Bengtson et al., 1990, and *Kulparina rostrata*, were both originally described from assemblages of disarticulated sclerites from the Kulpara and lower Parara limestones of the Horse Gully section in the Stansbury Basin of South Australia (Bengtson et al., 1990). The two forms share an extremely irregular surface sculpture and the morphological resemblance between them was already noted in the original description of *K. rostrata* (Bengtson et al., 1990, p. 136, figs. 86, 87, 88, 89, 90, 91). The sclerites of *K. rostrata* were originally described as asymmetrical, occurring

in dextral and sinistral symmetry variants, much like the sclerites of *Sunnaginia*. However, recently retrieved material, partly discussed by Skovsted et al. (2011) and described in detail herein, show that *Kulparina* sclerites were actually close to bilaterally symmetrical, with a morphology closely resembling S sclerites of *Paterimitra*. The sclerites described as ‘*E. guano*’ by Bengtson (in Bengtson et al., 1990, figs. 71-73) resemble the L sclerites of *Paterimitra* in general morphology, although the ‘*E. guano*’ sclerites are considerably more irregular and unpredictable in shape and mode of growth. Sclerites of ‘*E. guano*’ and *K. rostrata* exhibit the same kind of irregular mode of growth, surface structure, shell structure (Murdock et al., 2014) and sclerites of both taxa are usually recorded from the same samples. More conclusively though, the new material contains fused specimens representing natural associations of sclerites of ‘*E. guano*’ and *K. rostrata*. Consequently, the two taxa appear to represent two separate sclerite morphs of a single biological species.

The original descriptions of *Kulparina rostrata* and ‘*Eccentrotheca guano*’ were part of the same publication (Bengtson et al., 1990) with the description of ‘*E. guano*’ on page 120 and *K. rostrata* on page 136. As both taxa are here reinterpreted to represent different parts of the same organism the names are considered to be synonymous. The only applicable generic name for the revised species is *Kulparina* Conway Morris and Bengtson in Bengtson et al., 1990 as the species cannot be accommodated in *Eccentrotheca* Landing, Nowlan and Fletcher, 1980. By strict application of the rule of priority it would seem that ‘*E. guano*’ has precedence over *K. rostrata*. However, according to article 24.2.2 of the International Code for Zoological Nomenclature (ICZN, 1999), the precedence of names published in the same work is the choice of the first reviser. The most characteristic sclerite in the species is the pyramidal S sclerite, which formed the basis for the original definition of *K. rostrata* and precedence is given to this name, with the holotype SAMP 30698 from the Kulpara

Limestone, Horse Gully (Bengtson et al., 1990, fig. 90) as best representing the concept of the revised species.

TERMINOLOGY AND DESCRIPTION

The sclerites of *Kulparina rostrata* show strong resemblance to sclerites of the recently re-described tommotiid *Paterimitra pyramidalis* (see Larsson et al., 2014). This is most obvious for sclerites originally described under the name *K. rostrata*. These sclerites have previously been considered to be asymmetrical (Bengtson et al., 1990, p. 136), but material investigated herein demonstrates that they were bilaterally symmetrical (Fig. 2.1, 2.3, 2.5, 2.7) like the S sclerites of *Paterimitra* (Fig. 2.2, 2.4, 2.6, 2.8). The asymmetry of the sclerites described and illustrated by Conway Morris and Bengtson (in Bengtson et al., 1990, figs 86-91) probably represent fragmentation, as protruding parts of the fragile, poorly preserved sclerites have been broken off on either the left or the right side. This certainly seems to be the case in the holotype (SAMP 30698; Bengtson et al., 1990, fig. 90) where the right lateral side of the sclerite appears to be missing. The previously used terminology (originally defined for and applied to sclerites of *Sunnaginina* by Landing et al. (1980, fig. 5) was developed to illustrate the relationship between the sides (“S1, S2, S3”) and lobes (“L1, L2, L3”) of asymmetrical, essentially triangular sclerites (Bengtson et al., 1990, fig. 91) and is consequently incompatible with the reinterpreted bilaterally symmetrical sclerites of *Kulparina*. Due to the strong similarities with *P. pyramidalis*, it is more appropriate to apply the terminology developed for this tommotiid (see Skovsted et al., 2009a and Larsson et al., 2014) for *Kulparina*. This means that we refer to the symmetrical sclerites (*K. rostrata sensu* Bengtson et al., 1990) as S sclerites and the laterally compressed sclerites (*‘E. guano’ sensu* Bengtson et al., 1990) as L sclerites despite the risk of confusion with the *Sunnaginina*

terminology previously applied to *Kulparina*. In *P. pyramidalis*, the S sclerites occur in two distinct morphs, referred to as S1 and S2, respectively. In contrast, despite showing a large degree of morphological variation, distinct S sclerite morphs are not recognized in *K.*

rostrata. The morphological terminology of S sclerites of *K. rostrata* is illustrated in Figure 2, where specimens, to enhance comparisons, are displayed together with corresponding sclerites of *P. pyramidalis*.

Kulparina rostrata comprises at least two sclerite types, S (Figs 2.1, 2.3, 2.5, 2.7, 3) and L (Fig. 4), both of which exhibit a high degree of plasticity. All sclerites of *Kulparina rostrata* grow by basal-internal accretion in highly irregular intervals, which is reflected externally in irregular, but prominent growth lamellae (Fig. 2.3, 2.5). The external surface is coarsely ornamented by irregular growth-lines (Figs 2.7, 3.2), while the internal surface is smooth to finely granular or pustular (Fig. 3.15).

S sclerites.— Typical S sclerites of *Kulparina rostrata* are characterized by their broad bilateral symmetry (Figs 2.1, 2.3, 3.1, 3.3-3.14). The sclerites are pyramidal to triangular (apical angle approximately 90°) with a concave anterior side, which results in a compressed outline in lateral view and a cross section reminiscent of a broad-based isosceles triangle (Figs 2.1, 2.5, 3.6). The apex (Fig. 2.3) is slightly displaced towards one side (which, in accordance with the *Paterimitra* terminology, is referred to as the posterior (Fig. 2.1); corresponding to the direction of lobe “L3” in Bengtson et al. (1990, fig. 91) and in well-preserved specimens is drawn out into a prominent subapical flange (Fig. 2.1, 2.3, 2.5; rostrum/”L3” *sensu* Bengtson et al., 1990: fig. 91, p 142). The flange may project slightly beyond the posterior side but may alternatively be developed merely as a zone of apically deflected growth laminae on the posterior field (Fig. 3.12-3.14). The posterior side is highly variable in shape but is typically dominated by the sub-apical flange and exhibits a wide triangular notch (Fig. 2.3). Laterally, the sclerite is flanked by two narrow, elongate lateral

plates (Fig. 2.3, 2.5), strongly flexed towards the posterior. In some specimens one or both of the lateral plates are often damaged, which results in apparent asymmetry (Fig. 2.1, 2.3, 3.3, 3.8-3.14; Bengtson et al., 1990, figs 86-90). The anterior edges of the lateral plates form two radial, ridge-shaped anterior boundaries bordering a concave, sub-triangular anterior plate (Fig. 2.1, 2.7) with a curved ant-apical edge that defines a widely U-shaped anterior sinus (Fig. 2.7). Some sclerites are strongly flattened in the anterior-posterior direction (Fig. 3.13, 3.14). S sclerites of *K. rostrata* range in width (defined as the distance between the distal edges of the lateral plates) from approximately a few hundred microns up to about 1.5 mm. The height of S sclerites generally ranges up to approximately 1.5 mm, although extremely large sclerites exceeding 2 mm as well as comparably low sclerites (0.6 mm) do occur. The width/height ratio ranges from about 0.6 to 1.8, although most specimens exhibit a width approximately 0.8 of the height.

L sclerites.— L sclerites of *Kulparina rostrata* are typically high, often strongly compressed sclerites that exhibit extremely irregular morphology (Fig. 4). Single sclerites range from simple columnar or triangular forms (Fig. 4.1-4.4, 4.19), through palm- or finger-like (Fig. 4.5-4.9, 4.15), to a somewhat exaggerated and irregular morphology (Fig. 4.16, 4.21, 4.23). Less flattened, almost cone-shaped sclerites also occur (Fig. 4.14). For this reason, general patterns in sclerite morphology are difficult to define. The L sclerites may be straight, but more frequently they exhibit a slight to strong curvature, both in the plane of flattening and perpendicular to it (Fig. 4.1-4.2, 4.8, 4.10-4.12, 4.15-4.16, 4.19). Changes in growth direction occur frequently through the growth of individual sclerites (Fig. 4.3, 4.6, 4.8). The length of the L sclerites usually exceeds the width, occasionally by up to ten times (Fig. 4.3). The width of the sclerite base generally expands evenly throughout growth, but the expansion may in some cases be temporarily halted resulting in straight sclerite sides (Fig.

4.4, 4.9-4.10, 4.17) and some sclerites even exhibit apparent phases of base constriction (Fig. 4.21) or in extreme cases restriction of the basal cavity (Fig. 4.20, 4.22, 4.24). Fusion of adjacent L sclerites during growth into complex, sometimes digitate composites is a common feature and the majority of specimens represent fusion of at least two incipient sclerites and the fused sclerites are often intimately entwined with each other. In flattened sclerites, fusion usually occur in the plane of flattening, resulting in both long, narrow composites (Fig. 4.4-4.5), as well as broad, large sclerites with a curved base (Fig. 4.18, 4.20, 4.23-4.24). Conical or tubular sclerites are usually fused along their shortest sides (Fig. 4.14). L sclerites of *K. rostrata* range in width from approximately 100 μm up to 1.5 mm (small sclerites about 50 μm wide occur in articulation with S1 sclerites, see section below). The length of the L sclerites generally ranges up to approximately 1.5 mm, although extremely large sclerites exceeding 2 mm are known.

ARTICULATED SPECIMENS AND IMPLICATIONS FOR SCLERITOME ARCHITECTURE

The affinity of S and L sclerites of *Kulparina rostrata* is inferred by their co-occurrence in several samples from various sections and by the strong similarities in microstructure (Murdock et al., 2014), growth mode and surface ornament. However, the strongest support is provided by the occurrence of rare articulated specimens exhibiting L sclerites directly attached to the distal margins of S sclerites (Fig. 5). The attached L sclerites in these composites are considerably smaller than any recorded individual L sclerite, but apart from the size discrepancy they exhibit morphological features identical to the isolated L

sclerites described above. The absence of individual small L sclerites may be explained by taphonomic sorting or selective sampling and sorting during the fossil extraction process.

The L sclerites in the composites are attached to the S sclerites either along the posterior margin (Fig. 5.1-5.4) or along the margin of the anterior plate (Fig. 5.5-5.13). This pattern is very similar to the way L sclerites attach to S1 sclerites of *Paterimitra* (Larsson et al., 2014, fig. 16A-H). In SAMP 44787 (Fig. 5.1-5.4) two minute, elongated L sclerites are fused to the distal edge of the posteriorly facing side of the lateral plate in an extremely high *Kulparina* S sclerite (compare Larsson et al., 2014, fig. 16). In SAMP 44787 (Fig. 5.5-5.7), SAMP Z026 (Fig. 5.8-5.10) and SAMP Z027 (Fig. 5.11-5.13) L sclerites of variable morphology, but generally with a broader base, are fused to the margin of the anterior sinus of the S sclerite and appear to overlap the anterior plate (compare Larsson et al., 2014, fig. 17). All L sclerites fused to S sclerites are oriented in the same general direction, towards the apex of the S sclerite. This corresponds closely to the observed direction of L sclerites in composites of *P. pyramidalis* (Fig. 6; Larsson et al., 2014).

Two large specimens, consisting of elongate plates with an arcuate base appear to have been formed by the coalescence of multiple L sclerites (Fig. 6). The general morphology of the plates is suggestive of longitudinal sections of a tube and the margins of the plates appear to have continued to grow as a unit after the merging of the constituent sclerites. Individual sclerites in these composites differ dramatically both within and between specimens. In SAMP Z028 a large number of incipient sclerites of vastly differing sizes and morphologies are present in a roughly trapezoidal plate about 1.5 mm long and 1 mm wide (Fig. 6.1-6.6). The majority of sclerites are narrow, almost straight sided, either curved or straight, but a single wide, palmate sclerite with multiple apices are present in the centre of the composite. The sclerites partly overlap, but the larger sclerites are separated quite substantially from each other (about 60-70 μm), often leaving spaces between sclerites and

the plate surface (Fig. 6.2, 6.3, 6.5). Although all sclerites are inclined in the same general direction and are oriented towards the wider of the short sides of the composite, the curvature of longer sclerites appear to be random with sinistral and dextral sclerites overlapping. The roughly quadrate SAMP Z029 is a plate of similar size but is composed of fewer sclerites (Fig. 6.7-6.10). The bulk of the composite is composed of three, large palmate sclerites, each with multiple apices. One side displays two more or less identical and partly overlapping palmate sclerites with two apices while the opposing side is dominated by a single, broad sclerite apparently lacking an apex. Smaller sclerites are also present in two zones at either end of the composite. A very similar sclerite arrangement has been observed in L sclerite composites of *Paterimitra* (Larsson et al., 2014, fig. 15).

The striking similarities between articulated S/L as well as L/L composites of *Kulparina* and *Paterimitra* leads to the conclusion that the scleritome of *K. rostrata* was constructed in a similar sclerite arrangement as suggested for *P. pyramidalis* (Skovsted et al., 2009a, 2011; Larsson et al., 2014). The main difference between the two taxa is the apparent lack of a distinct S2 sclerite morph in *K. rostrata*. S sclerites of *K. rostrata* do vary considerably in morphology and some individual sclerites approach a general shape that may be morphologically comparable to the S2 sclerites of *Paterimitra* (Fig. 3.6, 3.9, 3.13, 3.14). However, morphological variation among S sclerites appears gradational and no distinct morphs can be definitely recognized. There may be a number of potential reasons for their absence; S2 sclerites may potentially be morphologically similar to S1 sclerites and consequently have been misidentified; the absence of S2 sclerite morphs may be because of sampling bias, either by taphonomic factors or during acid preparation, as they may be much smaller in size compared to the S1 sclerite morph, similar to the case in *Paterimitra* (see Larsson et al., 2014); or *Kulparina* does not possess a S2 sclerite morph and the irregular L sclerites may have articulated to form a suitable *posterior opening* (similar to the opening in

Paterimitra) to facilitate attachment to the substrate. Regardless, the morphological similarities between *Kulparina* and *Paterimitra* are compelling and following the *Paterimitra* model, the base of the *Kulparina* scleritome was composed of one or a pair of bilaterally symmetrical S sclerites with the remainder of the scleritome composed of L sclerites which formed a conical or tube-shaped structure. L sclerites lined the anterior margins of the S sclerite/sclerites in subsequent rows and were arranged with the apices directed towards the S sclerite and partly overlapping each other, presumably resulting in a robust scleritome.

DISCUSSION

Partially articulated tommotiid specimens are notoriously rare in the fossil record and *Kulparina rostrata* represents just the third tommotiid taxon (after *Paterimitra pyramidalis* and *Eccentrotheca helenia*) where articulated material has been recovered. The scleritome of *Eccentrotheca helenia* is a slowly expanding tube, constructed through the fusion of discrete basal broad, cap-shaped sclerites and laterally compressed triangular sclerites (Skovsted et al. 2011). The individual sclerites are ontogenetically fused into ring-shaped units that are sequentially stacked vertically forming a tube (Skovsted et al. 2011). The scleritome of *Paterimitra pyramidalis* represents a slightly more complex system, with a small triangular sclerite (S2) seated within the notch of a large pyramidal sclerite (S1) with a currently unresolved number of laterally compressed sclerites (L) flanking the margins and posterior and anterior sinuses of the S sclerites, producing a open tube-like construction (Skovsted et al. 2009; Larsson et al. 2014). Both taxa are interpreted as a sessile filter feeding organism, most likely attaching to hard substrates via organic structures emerging through the apical perforation (Skovsted et al. 2009, 2011; Larsson et al. 2014).

Both *Paterimitra* and *Eccentrotheca* have been directly compared with the Brachiopoda based on overall morphological and skeletal microstructural details (Skovsted et

al. 2009, 2011, Balthasar et al., 2009; Topper et al. 2013; Larsson et al. 2014). The pervasive shell-penetrating scaffolding of polygonal layers has only been detected in eccentrothecimorph tommotiids and the paterinid brachiopod *Askepasma* (Balthasar et al., 2009; Topper et al., 2013) and the possible stem chileate brachiopod, *Salanygolina* (Holmer et al., 2009), suggesting a similar mode of cyclic shell secretion in eccentrothecimorph tommotiids, paterinid brachiopods and perhaps stem rhynchonelliform brachiopods (Holmer et al., 2009, 2011). *Kulparina rostrata* is reported to share the same skeletal architecture as *Eccentrotheca*, *Paterimitra* and *Askepasma*, firmly rooting the taxa within the eccentrothecimorphs and in the stem of the Brachiopoda (Murdock et al. 2014). The overall scleritome configuration of *Kulparina* is not as clear as in *Paterimitra* and *Eccentrotheca* due to the lack of more complete articulated specimens, although the intimate association of S and L sclerites is clear (Fig. 6).

Kulparina, like *Paterimitra*, possesses a combination of *Eccentrotheca*-like sclerites organized in a tubular scleritome displaying specialized S and L sclerite morphs. However, the individual sclerites of *Kulparina*, when compared to *Paterimitra*, display a much more irregular and variable morphology without the distinctive polygonal micro-ornament and the scleritome seems to lack the opposing symmetrical S2 sclerite morph. This implies that *Kulparina* most probably represents an intermediate form on the stem of the brachiopod clade between *Eccentrotheca* and *Paterimitra* (see Skovsted et al., 2011, text-fig. 21), introducing bilateral symmetry to the scleritome, coupled with a reduction in number and the specialization of basal sclerites, however not yet reaching the scleritome complexity and sclerite specialization seen in *Paterimitra*.

SYSTEMATIC PALEONTOLOGY

Order TOMMOTIIDA Missarzhevsky, 1970

Family UNCERTAIN

Genus KULPARINA Bengtson in Bengtson et al., 1990

Figures 2, 3, 4, 5, 6

1990 *Kulparina* CONWAY MORRIS AND BENGTSON IN BENGTSON ET AL., p. 136, figs. 86-91.

Type species.—Type and only species *Kulparina rostrata* Conway Morris and Bengtson in Bengtson et al., 1990.

Emended diagnosis.—Tommatioid with scleritome comprising two distinctive sclerite types: symmetrical pyramidal S sclerites and high, laterally compressed and asymmetrical L sclerites. S sclerites with elongated, narrow lateral plates, strongly flexed towards the posterior. Anterior plate sub-triangular to slightly U-shaped. L sclerites high, irregular and extremely variable but generally with strong lateral compression and a tendency towards ontogenetic fusion.

Differs from *Sunnaginia* and *Eccentrotheca* by the presence of bilaterally symmetrical sclerites. Differs from *Paterimitra* by the triangular cross-section and concave anterior plate in S sclerites, the lack of differentiated S2 sclerites, highly irregular morphology of L sclerites and the absence of polygonal surface micro-ornament.

Occurrence.—Lower Cambrian of South Australia (Terreneuvian, Stage 2).

Discussion.— The sclerites of *Kulparina* exhibit many morphological similarities to sclerites of *Paterimitra*, such as the subapical flange, lateral plates with anterior boundaries

and anterior plate of the high, pyramidal S sclerites. The manner in which L sclerites of *Kulparina* are fused to S sclerites (Fig. 5) is also very similar to the way L and S1 sclerites of *Paterimitra* are fused (Larsson et al., 2014). However, there are numerous obvious differences between *Paterimitra* and *Kulparina*. The S sclerite of *Kulparina* is generally angled towards the posterior and the anterior plate is concave resulting in a triangular cross section (Fig. 2.1, 2.7), whilst the S1 sclerite of *Paterimitra* has more anteriorly angled lateral plates and a convex anterior plate resulting in a rectangular to trapezoidal outline in cross section (Fig. 2.2, 2.6). The anterior boundaries of *Kulparina* are generally developed as ridges (Fig. 2.5, 2.7), whereas the anterior boundaries of *Paterimitra* are commonly developed as furrows (Fig. 2.8). *Paterimitra* also possesses a distinct triangular or saddle-shaped S2 sclerite, a sclerite morph absent in *Kulparina*. Of particular note is the absence of the unmistakable *Paterimitra* polygonal surface micro-ornament in *Kulparina* sclerites. The morphology, plasticity and external surface of L sclerites of *Kulparina*, are more reminiscent of the laterally compressed sclerites of *Eccentrotheca*. L sclerites of *Kulparina* also lack the characteristic apical twist possessed by L sclerites of *Paterimitra* and laterally compressed sclerites of *Eccentrotheca*.

KULPARINA ROSTRATA Conway Morris and Bengtson in Bengtson et al., 1990

Figures 2.1, 2.3, 2.5, 2.7, 3-6

1990 *Eccentrotheca guano* BENGTSON IN BENGTSON ET AL., p. 120, figs 71-73.

1990 *Kulparina rostrata* CONWAY MORRIS AND BENGTSON IN BENGTSON ET AL., pp. 136-142, figs 86-91.

2001 *Eccentrotheca guano* Bengtson in Bengtson et al.; DEMIDENKO IN GRAVESTOCK ET AL., pp 230-231, plate VII, fig. 11.

2011 *Kulparina* sp.; SKOVSTED, BROCK, TOPPER, PATERSON & HOLMER, pp. 275-281, text-figs 18-19.

?2011 *Eccentrotheca helenia* SKOVSTED, BROCK, TOPPER, PATERSON AND HOLMER IN SKOVSTED ET AL., text-fig. 5a-c.

Diagnosis.—As for genus by monotypy.

Holotype.—SAMP 30698 (Bengtson et al., 1990: figs 88F, 90A-H) from UNEL1858, Horse Gully, Kulpara Limestone.

Occurrence.—Lower Cambrian pre-trilobitic strata (Terreneuvian, Stage 2) of Wilkawillina and Wirrapowie limestones, Flinders Ranges, Arrowie Basin, and upper Kulpara and lowermost Parara limestones, Yorke Peninsula, Stansbury Basin, South Australia.

Discussion.— Skovsted et al. (2011) previously noted the mutually exclusive stratigraphic ranges of *Kulparina rostrata* (including sclerites originally described as ‘*E. guano*’) and *Eccentrotheca helenia* in all investigated lower Cambrian sections in South Australia. *Kulparina rostrata* has a range which is entirely sub-trilobitic in South Australia and likely correlates with Terreneuvian, Stage 2. Betts et al. (2014) reported that whilst the first appearance of *E. helenia* occurs slightly below the incoming of *Abadiella houi* (eponym of the oldest trilobite Zone in East Gondwana) the majority of its range overlaps with the *A. houi* trilobite zone. The only sample that apparently contains sclerites of both *K. rostrata* and *E. helenia* is sample Bun 12 from Bunyerroo Gorge in the Heysen Range, originally collected by Brian Daily in the 1960s. However, Skovsted et al. (2011) pointed out that the specimens from this sample identified as *E. helenia* are distinctly higher and more columnar than the

majority of specimens from other localities and are very similar to columnar, laterally compressed L sclerites of *K. rostrata*. Consequently, it seems most likely that these sclerites actually represent specimens of *K. rostrata*. The exact stratigraphical position of sample Bun 12 remains difficult to pinpoint, since Daily's original field notebook covering this section is missing (presumed lost). It is thus impossible to re-sample this level to obtain more sclerites which would likely resolve this question. Subsequent sampling along new stratigraphic sections intersecting the Wilkawillina Limestone (and equivalents) in northern and central Flinders Ranges (Betts et al., in prep.) provides clear evidence of a substantial stratigraphical separation between *K. rostrata* and *E. helenia*.

Although, *Kulparina rostrata* precedes *Eccentrotheca helenia* in all known stratigraphic sections in South Australia, *Eccentrotheca* sclerites (see Skovsted et al., 2011 for discussion) have been documented from probably older Terreneuvian (Fortunian or basal Cambrian Stage 2) strata in Newfoundland (*Eccentrotheca kanesia* Landing, Nowlan and Fletcher, 1980; Landing et al., 1980, 1989, 2013; Bengtson et al., 1983; Hinz, 1987; Landing, 1995), supporting its potential basal position on the brachiopod stem. The majority of sclerites of *E. kanesia* are high, triangular and laterally compressed sclerites that are similar to L sclerites of *K. rostrata* in ornament and general morphology (compare for example the specimens in Fig. 4 with Hinz 1987, pl. 15, figs 1-7, 12). However, sclerites of *E. kanesia* differ from *Kulparina* L sclerites in the more regular triangular shape and the lower height/width ratio. In Avalonia, *E. kanesia* also typically occurs together with broader, cap-shaped sclerites (Landing et al. 1980, pl. 1, fig. 13; Landing 1984, fig. 4B; Landing 1995, fig. 7.23 and fig. 6.1-6.13 [cap-shaped sclerites referred to the potentially synonymous genus *Jaycea* Landing, 1995]). These are closely comparable to the low, cap-shaped sclerites of *E. helenia* (Skovsted et al. 2011, text.fig. 7). No such sclerites have been recovered in association with *K. rostrata* in our collections.

The relatively poor preservation of the material in our collections hinders studies of the internal shell microstructure, but SRXTM data presented by Murdock et al. (2014, p. 20, fig. 4) shows that the internal shell structure of *K. rostrata* and '*E. guano*' is identical, supporting the synonymy herein. The shell structure is closely comparable to the microstructure documented for *Paterimitra*, *Eccentrotheca* and *Askepasma* (Balthasar, 2009; Topper et al., 2013; Murdock et al., 2014; Larsson et al., 2014), strengthening the suggested relationship between eccentrothecimorph tommotiids and paterinid brachiopods (Skovsted et al., 2009a, b, 2011).

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Fig caps

Figure 1—Locality map. A, overview map of Australia, marking South Australia. B, South Australia, dark shaded areas indicating Arrowie and Stansbury Basins respectively, ★1-5 indicating approximate positions of sampled sections and spot samples. ★1 area includes CD2, SYC101 and Minlaton-1. ★2 represents Horse Gully section. ★3 represents Bunyeroo Gorge. ★4 represents Wilkawillina Gorge and includes Wilkawillina limestone type section/section E and section H, and 10MS-W and 10MS sections. ★5 area includes Elder Range, Chase Range (CR-1) and Druid Range spot sample locality. YP= Yorke Peninsula. Modified from Bengtson *et al.* (1990); Gravestock *et al.* (2001); and Jago *et al.* (2006, 2012).

Figure 2—Terminology, S1 sclerites of *Kulparina rostrata* Conway Morris and Bengtson in Bengtson *et al.*, 1990 and *Paterimitra pyramidalis* Laurie, 1986 from the Flinders Ranges, South Australia. 1, S1 sclerite of *K. rostrata* (SAMP 44786), apical view; 2, S1 sclerite of *P. pyramidalis* (SAMP 46315), apical view; 3, S1 sclerite of *K. rostrata* (SAMP Z001), posterior view; 4, S1 sclerite of *P. pyramidalis* (SAMP 47840), posterior view; 5, S1 sclerite of *K. rostrata* (SAMP 44786), lateral view; 6, S1 sclerite of *P. pyramidalis* (SAMP 47846), lateral view; 7, S1 sclerite of *K. rostrata* (SAMP Z002), anterior view; 8, S1 sclerite of *P. pyramidalis* (SAMP 47842), anterior view. Specimens in 1, 3, 5, and 7 from sample E22 (6635RS319), Wilkawillina Limestone type section (Daily, 1956)/section E (Gravestock, 1984), Wilkawillina Gorge, Bunkers Graben. Specimen in 2 from sample AJX-M/267.5, Ajax Limestone, AJX-M section, Mt Scott Range. Specimen in 4 from sample Bunyeroo 9, Wilkawillina Limestone, Bunyeroo Gorge. 6 from sample WILK/S, Second Plain Creek Member, Wilkawillina Limestone, Wilkawillina Gorge type section (WILK), Bunkers

Graben. Specimen in 8 from sample 10MS-W/390, Winnitunny Creek Member, Wilkawillina Limestone, 10MS-W section.

Figure 3—S1 sclerites of *Kulparina rostrata* Conway Morris and Bengtson in Bengtson et al., 1990 from the Flinders Ranges, South Australia. 1-2 (SAMP Z003): 1, posterior view, box indicating area enlarged in 2; 2, close up of 1, external shell structure. 3, (SAMP Z004) posterior view. 4, (SAMP Z005) posterior view. 5, (SAMP 4486) posterior view. 6, (SAMP Z006) cross section, ant-apical view. 7, (SAMP Z007) posterior view. 8, (SAMP 44788) posterior view. 9, (SAMP Z008) posterior view, damaged subapical flange. 10, (SAMP Z009), antero-apical view. 11, (SAMP Z010) posterior view. 12, (SAMP Z011) posterior view. 13, (SAMP Z012) posterior view. 14-15, (SAMP Z013): 14, posterior view; 15, close up of boxed area in 14, internal surface structure. Specimens in 1-2, 9 from sample Bunyeroo 12, Wilkawillina Limestone, Bunyeroo Gorge. Specimens in 13-15 from sample E18 (6635RS315), Wilkawillina Limestone type section (Daily, 1956)/section E (Gravestock, 1984), Wilkawillina Gorge, Bunkers Graben. Specimens in 3, 5-8 and 11 from sample E22 (6635RS319), Wilkawillina Limestone type section (Daily, 1956)/section E (Gravestock, 1984), Wilkawillina Gorge, Bunkers Graben. Specimens in 4 and 10 from sample H83, Wilkawillina Limestone, section H (Gravestock, 1984), Wilkawillina Gorge, Bunkers Graben. Specimen in 12 from sample E21 (6635RS318), Wilkawillina Limestone type section (Daily, 1956)/section E (Gravestock, 1984), Wilkawillina Gorge, Bunkers Graben.

Figure 4—L sclerites of *Kulparina rostrata* Conway Morris and Bengtson in Bengtson et al., 1990 from the Flinders Ranges, South Australia. 1, (SAMP 44770) lateral view. 2, (SAMP

44769) lateral view. 3, (SAMP 44773) lateral view. 4, (SAMP 44772) lateral view. 5, (SAMP 44771) lateral view. 6, (SAMP 44775) lateral view. 7, (SAMP Z014) lateral view. 8, (SAMP 44777) lateral view. 9, (SAMP Z015) lateral view. 10, (SAMP 44776) lateral view. 11, (SAMP Z016) oblique lateral view. 12, (SAMP Z017) oblique lateral view. 13, (SAMP Z018) lateral view. 14, (SAMP Z019) lateral view. 15, (SAMP Z020) lateral view. 16, (SAMP Z021) lateral view. 17, (SAMP 44779) lateral view. 18, (SAMP 44782) lateral view. 19, (SAMP Z022) lateral view. 20, (SAMP Z023) lateral view. 21, (SAMP Z024) lateral view. 22, (SAMP 44780) lateral view. 23, (SAMP Z025) lateral view. 24, (SAMP 44783) lateral view. Specimens in 1-6, 8, 10, 16-18, 22 and 24 from sample E22 (6635RS319), Wilkawillina Limestone type section (Daily, 1956)/section E (Gravestock, 1984), Wilkawillina Gorge, Bunkers Graben. Specimens in 7, 11-12, 14-15, and 19-21 from sample H83, Wilkawillina Limestone, section H (Gravestock, 1984), Wilkawillina Gorge, Bunkers Graben. Specimens in 9 and 23 from sample H87, Wilkawillina Limestone, section H (Gravestock, 1984), Wilkawillina Gorge, Bunkers Graben. Specimen in 13 from sample H81, Wilkawillina Limestone, section H (Gravestock, 1984), Wilkawillina Gorge, Bunkers Graben.

Figure 5—Articulated S and L sclerite composites of *Kulparina rostrata* Conway Morris and Bengtson in Bengtson et al., 1990 from the Flinders Ranges, South Australia. 1-4 (SAMP 44787) two L sclerites fused to lateral plate of S1 sclerite: 1, posterior view, box indicating area enlarged in 2; 2, close up of 1; 3, antapical view, box indicating area enlarged in 4; 4, close up of 3. 5-7 (SAMP 44785), L sclerites fused along anterior sinus of S1 sclerite: 5, anterior view; 6, apical view, box indicating area enlarged in 7; 7, close up of 6. 8-10 (SAMP Z026), L sclerite fused along anterior sinus of S1 sclerite: 8, apical view; 9, anterior view; 10, lateral view. (SAMP Z027), three L sclerites fused along anterior sinus of S1 sclerite: 11, anterior view, box indicating area enlarged in 12; 12, close up of 11; 13, apical view.

Specimens in 1-4 and 8-13 from sample E22 (6635RS319), Wilkawillina Limestone type section (Daily, 1956)/section E (Gravestock, 1984), Wilkawillina Gorge, Bunkers Graben. Specimen in 5-7 from E18 (6635RS315), Wilkawillina Limestone type section (Daily, 1956)/section E (Gravestock, 1984), Wilkawillina Gorge, Bunkers Graben.

Figure 6—Articulated L sclerite composites forming arched plate-like structures of *Kulparina rostrata* Conway Morris and Bengtson in Bengtson et al., 1990 from sample 6635RS319, Wilkawillina Limestone type section, Wilkawillina Gorge, Bunkers Graben, Flinders Ranges, South Australia. 1-6 SAMP Z028, 1, ‘dorsal’ view, 2, right ‘lateral’ view; 3, oblique ‘anterolateral’ view; 4, oblique ‘posterior’ view; 5, left ‘lateral’ view; 6, oblique ‘anterior’ view. 7-10, SAMP Z029, 7, ‘posterior’ view; 8, ‘dorsal’ view; 9, oblique ‘anterior’ view; 10, ‘anterior’ view. Both specimens.

Arrowie
basin

RANGES

FLINDERS

★6

★3

★4

★5

Ardrossan

yp

★2

★1

yp

Adelaide

Stansbury
basin

South
Australia

200 km

1

2

3

4

5

6

7

8