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Source: Acta Palaeontologica Polonica, 54(3) : 525-540

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2008.0082

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# The tommotiid *Camenella reticulosa* from the early Cambrian of South Australia: Morphology, scleritome reconstruction, and phylogeny

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Skovsted, C.B., Bathasar, U., Brock, G.A., and Paterson, J.R. 2009. The tommotiid *Camenella reticulosa* from the early Cambrian of South Australia: Morphology, scleritome reconstruction, and phylogeny. *Acta Palaeontologica Polonica* 54 (3): 525–540. DOI: 10.4202/app.2008.0082.

The tommotiid *Camenella reticulosa* is redescribed based on new collections of well preserved sclerites from the Arrowie Basin (Flinders Ranges), South Australia, revealing new information concerning morphology and microstructure. The acutely pyramidal mitral sclerite is described for the first time and the sellate sclerite is shown to be coiled through up to 1.5 whorls. Based on *Camenella,* a model is proposed by which tommotiid sclerites are composed of alternating dense phosphatic, and presumably originally organic-rich, laminae. *Camenella* is morphologically most similar to *Lapworthella*, *Kennardia*, and *Dailyatia*, and these taxa are interpreted to represent a monophyletic clade, here termed the "camenellans", within the Tommotiida. Potential reconstructions of the scleritome of *Camenella* are discussed and although a tubular scleritome construction was recently demonstrated for the tommotiids *Eccentrotheca* and *Paterimitra*, a bilaterally symmetrical scleritome model with the sclerites arranged symmetrically on the dorsal surface of a vagrant animal can not be ruled out.

Key words: Tommotiida, *Camenella*, scleritome, phylogeny, Atdabanian, Botoman, Cambrian, South Australia.

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Received 28 October 2008, accepted 3 March 2009, available online 22 June 2009.

## Introduction

Tommotiids were amongst the first metazoans to produce mineralised hard parts in the earliest Cambrian. The millimetre-sized cones and plates (termed sclerites) that composed the tommotiid skeleton are phosphatic, presumably by original composition, and are common constituents of "small shelly fossil" (SSF) assemblages found worldwide in early and middle Cambrian strata (Rozanov et al. 1969; Missarzhevsky 1989; Qian and Bengtson 1989; Bengtson et al. 1990; Brock and Cooper 1993; Brock et al. 2000; Bengtson 2004; Skovsted 2006). Since most SSFs are only known from disarticulated elements of multi-component skeletons (termed scleritomes), which lack compelling modern analogues, their taxonomy, functional morphology and biological affinity remain problematic.

Tommotiids (Order Tommotiida Missarzhevsky, 1989) rose to prominence in Newfoundland and Siberia during the eponymous Tommotian Stage and reached maximum diversity in Australia later in the early Cambrian (late Atdabanian–early Botoman equivalents), before their eventual demise in the middle Cambrian. Tommotiid sclerites are formed by basal/marginal accretion and often have characteristic radial and/or co-marginal ribs. The sclerites may be symmetrical or asymmetrical, occurring in dextral and sinistral symmetrical pairs. Indirect evidence that tommotiid sclerites formed a multi-unit skeleton originally came from the association of distinct sclerite types sharing ornament and microstructural details (Fonin and Smirnova 1967; Bengtson 1970, 1977, 1986; Bischoff 1976; Laurie 1986). For several genera (e.g., *Lapworthella*, *Tannuolina*, and *Eccentrotheca*), this model has been confirmed by rare ontogenetic fusion of individual sclerites (Landing 1984; Qian and Bengtson 1989; Bengtson et al. 1990; Demidenko 2004; Li and Xiao 2004). However, no fully articulated specimens were known until recently, and most tommotiid reconstructions have been based on an assumed vagrant, worm- or slug-like model with the sclerites forming a dorsal protective shield (Bengtson 1970, 1977; Conway Morris and Chen 1990; Evans and Rowell 1990; Williams and Holmer 2002; Demidenko 2004; Li and Xiao 2004). The biological affinity of tommotiids has been debated, but compelling evidence of shared shell microstructure and the



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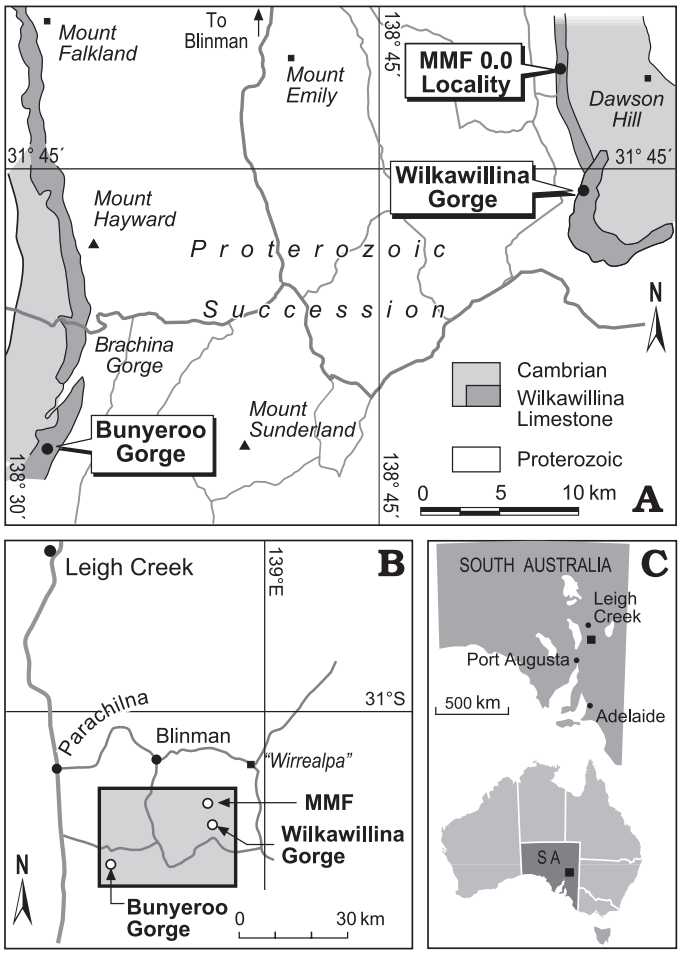



Fig. 1. Simplified locality map showing sample localities within the Wilkawillina Limestone that yielded *Camenella* at Bunyeroo Gorge, Wilkawillina Gorge and the MMF section in the central Flinders Ranges (**A**). The regional context of all localities within South Australia is also depicted (**B**, **C**).

presence of shell penetrating setae indicate that at least one group of tommotiids, the tannuolinids, are members of the brachiopod stem group (Williams and Holmer 2002; Holmer et al. 2002, 2008; Skovsted and Holmer 2003; Balthasar 2004). Thus, being among the earliest biomineralizing metazoans with a possible lophotrochozoan affinity, tommotiids play a crucial role in elucidating the evolution of the deep stem groups of the modern lophotrochozoan phyla.

Skovsted et al. (2008) recently demonstrated that the sclerites of the tommotiid *Eccentrotheca* were fused into a tubular scleritome and that the animal was most likely a fixed sessile filter-feeder, providing additional support for the proposed tommotiid/lophophorate link. The subsequent discovery of articulated specimens of *Paterimitra* reveal that this tommotiid also possessed a modified tubular scleritome composed of two bilaterally symmetrical sclerite types and an unresolved number of small, asymmetrical crescent-shaped sclerites (Skovsted et al. 2009). The structure of the scleritome of other tommotiids remains unknown, but detailed analyses of sclerite morphology, variability, shell structure and ornament provide the best investigative avenues to resolve issues related to scleritome architecture, as well as the phylogenetic relationships of different tommotiid groups. On a broader scale, scleritome reconstructions and resolution of the taxonomic framework of the Tommotiida will be essential for deciphering their biological affinities and thus improve our understanding of the early diversification of modern invertebrate phyla, especially within the lophotrochozoan clade.

In this contribution, the tommotiid *Camenella reticulosa* Conway Morris, 1990 is redescribed based on new collections from the Flinders Ranges (Arrowie Basin) in South Australia. The scleritome of *Camenella* is characterised by two distinct sclerite types without apparent intermediates (bimembrate scleritome sensu Bengtson 1970), and is mainly known from Tommotian and equivalent strata in Siberia, Mongolia and Baltica (Rozanov and Missarzhevsky 1966; Rozanov et al. 1969; Bengtson 1970, 1986). The two sclerite types were originally described as separate genera (e.g., *Camena* [*Tommotia*] and *Camenella*; Rozanov and Missarzhevsky 1966; Missarzhevsky 1970), which were later shown to belong to the same scleritome (Bengtson 1970, 1977). The Australian taxon is the youngest described species of *Camenella* and the new collections reveal novel microstructural information that facilitates an improved understanding of tommotiid shell secretion. In addition, evidence of sclerite wear provides possible clues to the structure and function of the scleritome.

*Institutional abbreviations*.—NMVPL, National Museum of Victoria (locality number), Melbourne, Australia; SAMP South Australian Museum, Adelaide, Australia; UNEL, University of New England (locality number), Armidale, Australia.

# Geological setting

The present redescription of *Camenella reticulosa* is based on material derived from three stratigraphic sections measured through the lower Cambrian Hawker Group succession outcropping in the central Flinders Ranges, Arrowie Basin, South Australia. All specimens are derived from samples collected from the Wilkawillina Limestone outcropping in Bunyeroo and Wilkawillina Gorges and at the base of the MMF (Mernmerna Formation) section in the uppermost Wilkawillina Limestone located 1 km south of Balcoracana Creek on the eastern side of the Bunkers Range (Fig. 1). The material from Bunyeroo and Wilkawillina Gorges are derived from collections made by the late Brian Daily in the late 1960s and early–mid 1970s. These collections, consisting of large numbers of picked (but largely unsorted) microfossil residues, were recently uncovered at the University of Adelaide and were subsequently transferred to the collections of the South Australian Museum. Most of the material is currently being studied by the authors and their postgraduate students (e.g., Smith 2006). Stratigraphic details for most of Daily's collected samples can be pinpointed with a fair degree of accuracy from detailed descriptions found in his com-

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prehensive field note books (also held in the collections of the South Australian Museum). The relevant information relating to the source of the *Camenella* specimens studied herein is summarised below.

*Wilkawillina Gorge*.—Nineteen samples designated A-S (originally collected by B. Daily in 1976) are derived from a short 36 m section measured through the middle part of the Wilkawillina Limestone along a small tributary to the NW of 10 Mile Creek within the Bunkers Graben (Fig. 1). This succession, later nominated as the type section of the Wilkawillina Limestone (Gravestock 1984), is located directly above the iron rich microstromatolitic "reddened" horizon which equates with the regionally significant Flinders Unconformity (James and Gravestock 1990; Gravestock and Cowley 1995). The carbonates are dominated by richly fossiliferous skeletal and peloidal packstones and grainstones (Clarke 1986, 1990), with localised cross laminated ripples and sparry stylonodular bedding. Specimens of *Camenella* were derived from samples A, M, O, P, Q, R, S, which are located respectively 34.82 m, 56.77 m, 58.60 m, 60.43 m, 65.00 m, 66.83 m, and 68.66 m above the base of the section. Approximate coordinates for the base of the section (equivalent with the reddened horizon) are 31°15.7' S; 138°53.5' E; map datum: UTM54J (Fig. 1). Jell (in Bengtson et al. 1990) described the trilobites *Eoredlichia* sp. and *Prouktaspis luta* from locality NMVPL1594 near the top of the Wilkawillina Limestone in the type section (equivalent to section E of Gravestock, 1984), suggesting a *Pararaia tatei* Zone (early Botoman) age for the section.

*Bunyeroo Gorge*.—The lower Cambrian Hawker Group succession is well exposed in Bunyeroo Gorge and was first described by Dalgarno (1964). Daily originally collected five samples in 1969 from a small section in the gorge that traversed through the Flinders Unconformity represented by the iron rich microstromatolitic "reddened" marker horizon in the Wilkawillina Limestone. Sample Bunyeroo 1* was located some 1.2 m below the "reddened" marker horizon. Samples Bunyeroo 3* and 3 (representing two adjacent samples from the same stratigraphic level) are located 1.2 m above the "reddened" marker horizon, whilst samples Bunyeroo 4 and 4b (representing two adjacent samples from the same stratigraphic level) are located on a "wall like outcrop" (Daily's 1969 unpublished notebook: 24) approximately 2.4 m above the "reddened" marker horizon. Approximate coordinates for the "reddened" marker horizon (sample Bunyeroo 2) in Bunyeroo Gorge are 31°24.7' S; 138°32.1' E; map datum: UTM54J (Fig. 1). Trilobites have not been formally described from the Wilkawillina Limestone at this locality, but based on regional correlation with well dated sections through this marker level at Horse Gully on Yorke Peninsula (Stansbury Basin), Wilkawillina Gorge, Bunkers Range (MMF section, see below), Mt. Scott Range, and the Donkey Bore Syncline, the sample collected from below the "reddened" horizon (Bunyeroo 1*) probably equates with the *Abadiella huoi* Zone (late Atdabanian–early Botoman equivalent), whilst the samples in the limestone just above the "reddened" horizon (Bunyeroo 3*, 3, 4*, and 4) are likely to belong to the *Pararaia tatei* Zone (cf., Bengtson et al. 1990; Paterson and Brock 2007).

*MMF/0.0 Locality*.—Specimens are derived from a single sample horizon MMF/0.0 in the uppermost outcropping Wilkawillina Limestone, just below the iron rich microstromatolitic "reddened" horizon. The sample horizon at MMF/0.0 conforms with the base of the MMF section originally measured by GAB and JRP in 2003 and located approximately 1 km south of Balcoracana Creek on the eastern side of the Bunkers Range (coordinates: 31°11'38.4" S, 138°52'28.7" E; map datum: WGS84; see Fig. 1). Paterson and Brock (2007) described the trilobite *Elicicola calva* Jell, 1990 and reported the presence of the paterinate brachiopod *Askepasma* Laurie, 1986 in horizon MMF/0.0, supporting an age within the *Abadiella huoi* trilobite Zone (late Atdabanian–early Botoman equivalent).

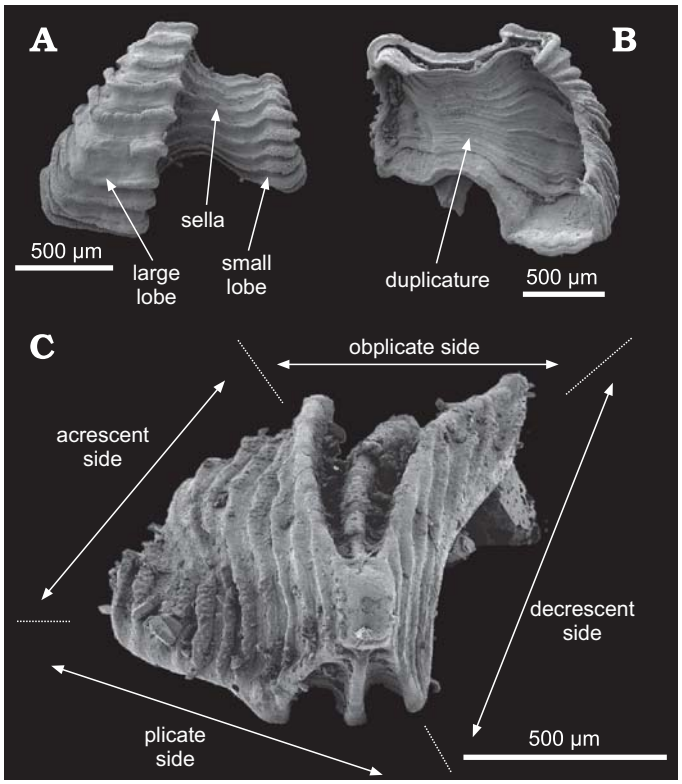



Fig. 2. Tommotiid *Camenella reticulosa* Conway Morris, 1990, from lower Cambrian Hawker Group, Flinders Ranges, Arrowie Basin, South Australia explanation of terminology. **A**, **B**. Sellate sclerites. **A**. SAMP 43172 (dextral), Wilkawillina Q, in dorsal view. **B**. SAMP 43178 (dextral),Wilkawinnina Q, in ventral view. **C**. Mitral sclerite, SAMP 43167 (sinistral), MMF 0.0, in apical view.

# Methods and terminology

In the following description we follow a slightly modified version of the terminology introduced by Bengtson (1970, 1986). All figured specimens were recovered from insoluble

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residues of limestone samples etched by weak (10%) acetic acid and photographed using SEM facilities at Macquarie University, Sydney, Australia and Uppsala University, Uppsala, Sweden. For microstructural studies, individual sclerites were impregnated in blocks of araldite 2020 and sectioned. Cross sections were polished, etched for 30 seconds with 5% HCl, coated with gold-palladium and then studied with SEM facilities at Uppsala University.

# Systematic palaeontology

## Order Tommotiida Missarzhevsky, 1970

## Family Tommotiidae Bengtson, 1970

*Discussion*.—Although Landing (1984) assigned *Dailyatia* and *Eccentrotheca* to the Tommotiidae, we include only *Camenella* in this family. Landing (1984) based his concept of the Tommotiidae on his reconstruction of *Eccentrotheca* as having transverse rows of continually variable sclerites, and his assertion that *Camenella* and *Dailyatia* represent reduced versions of the same model where intermediate sclerite morphologies were lost. We now know that *Eccentrotheca* had a tubular scleritome construction and that sclerite morphology vary vertically with position in the scleritome (Skovsted et al. 2008). The mode of growth of *Eccentrotheca* sclerites also seems to be more similar to that of *Sunnaginia* than to *Camenella* (Landing et al. 1980). We follow Laurie (1986) in placing *Dailyatia* in the Kennardiidae, based on the presence of three fundamental sclerite-types, including one with bilateral symmetry, compared to the two asymmetrical sclerite types in *Camenella*. Missarzhevsky (1989) assigned three genera of lapworthellid-like tommotiids to the Tommotiidae (*Bercutia*, *Geresia*, *Ninella*), but present knowledge suggests that these genera lack distinct sclerite types and probably belong with *Lapworthella* (see also Esakova and Zhegallo 1996).

Based on the shared presence of two sclerite types, Bengtson (1970) suggested that *Camenella* and *Tannuolina* form a natural group (embraced in the concept of the order Mitrosagophora Bengtson, 1970). Later investigations, however, showed that the tannuolinids (*Tannuolina*, *Micrina*) are characterised by a distinct microstructure including open setal tubes and an alternation of thin compact and thicker spacious layers that were probably originally filled with organic compounds (Conway Morris and Chen 1990; Williams and Holmer 2002; Li and Xiao 2004). The microstructure of *Camenella* sclerites is strikingly different with its dense lamination and the lack of setal tubes. The *Camenella* microstructure is much more similar to *Lapworthella* (see Landing 1984) and *Dailyatia* (see Laurie 1986), and for this reason we consider the shared twofold sclerite types of the Tommotiidae and Tannuolinidae to be convergent. As discussed below, the Tommotiidae (e.g., *Camenella*) show similarities to members of the Lapworthellidae and Kennardiidae in morphology, ornamentation and mode of shell growth, and these families probably form a monophyletic clade, here termed the camenellans.

### Genus *Camenella* Missarzhevsky, 1966

1966 *Camena* Missarzhevsky gen. nov.; Rozanov and Missarzhevsky 1966: 93. [non Martens in Albers and Martens 1860; Hewitson 1865]

1966 *Camenella* Missarzhevsky gen. nov.; Rozanov and Missarzhevsky 1966: 95.

1970 *Tommotia* nom. nov.; Missarzhevsky 1970: 100.

*Type species*: *Camenella garbowskae* Missarzhevsky, 1966, Tommotian Stage (*Dokidocyathus regularis* Zone), Chekurovka village, Siberia.

*Emended diagnosis*.—Tommotiids with solid, densely lamellar sclerites. Surface sculpture of fine growth striae, larger co-marginal ribs and occasional transverse ribs radiating from the umbo. Two types of sclerites; pyramidal mitrals and saddle shaped sellates. Mitral sclerites with subquadrate cross-section, a pointed umbo and a system of pronounced radiating folds on one or occasionally two opposing sides. Sellate sclerites strongly asymmetrical and compressed with marginal, sometimes coiled apex, dorsal surface with two lobes of unequal size separated by a depressed sella and ventral surface often with distinct duplicature. Both sclerite types occur in dextral and sinistral symmetry variants. Differs from *Lapworthella* and related genera by the presence of two distinct sclerite types, and from *Dailyatia* and *Kennardia* by the absence of bilaterally symmetrical sclerites.

*Species included*.—See Bengtson (1986) for a comprehensive discussion of the nominal species included in *Camenella*. To this list can be added *Camenella reticulosa* Conway Morris, 1990.

*Discussion*.—The genus *Camenella* appeared in the early Tommotian of Siberia (Rozanov et al. 1969). The genus has also been recovered in lower Cambrian rocks from Baltica (Bengtson 1970), Avalonia (Bengtson and Fletcher 1983), Mongolia (Bengtson 1986) and Australia (Bengtson et al. 1990 and herein). It has two distinct sclerite types (sellate and mitral, Fig. 2; terminology following Bengtson 1970) which were originally described as separate genera by Missarzhevsky (*Camena* [mitrals] and *Camenella* [sellates] in Rozanov and Missarzhevsky 1966). Because of homonymy, the genus *Camena* was later renamed *Tommotia* (Missarzhevsky 1970), resulting in considerable taxonomic and nomenclatural confusion (reviewed in Bengtson 1977, 1986). Although some authors have persisted in separating *Camenella* and *Tommotia* (Meshkova 1969; Repina et al. 1974; Grigorieva in Voronin et al. 1982; Missarzhevsky 1989; Vasilieva 1998), all available evidence, including the new material from South Australia described here, supports the unified model of one scleritome encompassing two distinct sclerite types.

The list of nominal species of *Camenella* is likely to be substantially inflated due to the lack of appreciation in early systematic works of the multi-component nature of the *Camenella* scleritome and the variability of sclerites (Bengtson 1977, 1986). Only three species, *Camenella baltica*, *C. parilobata*, and now *C. reticulosa* have been described using a scleritome

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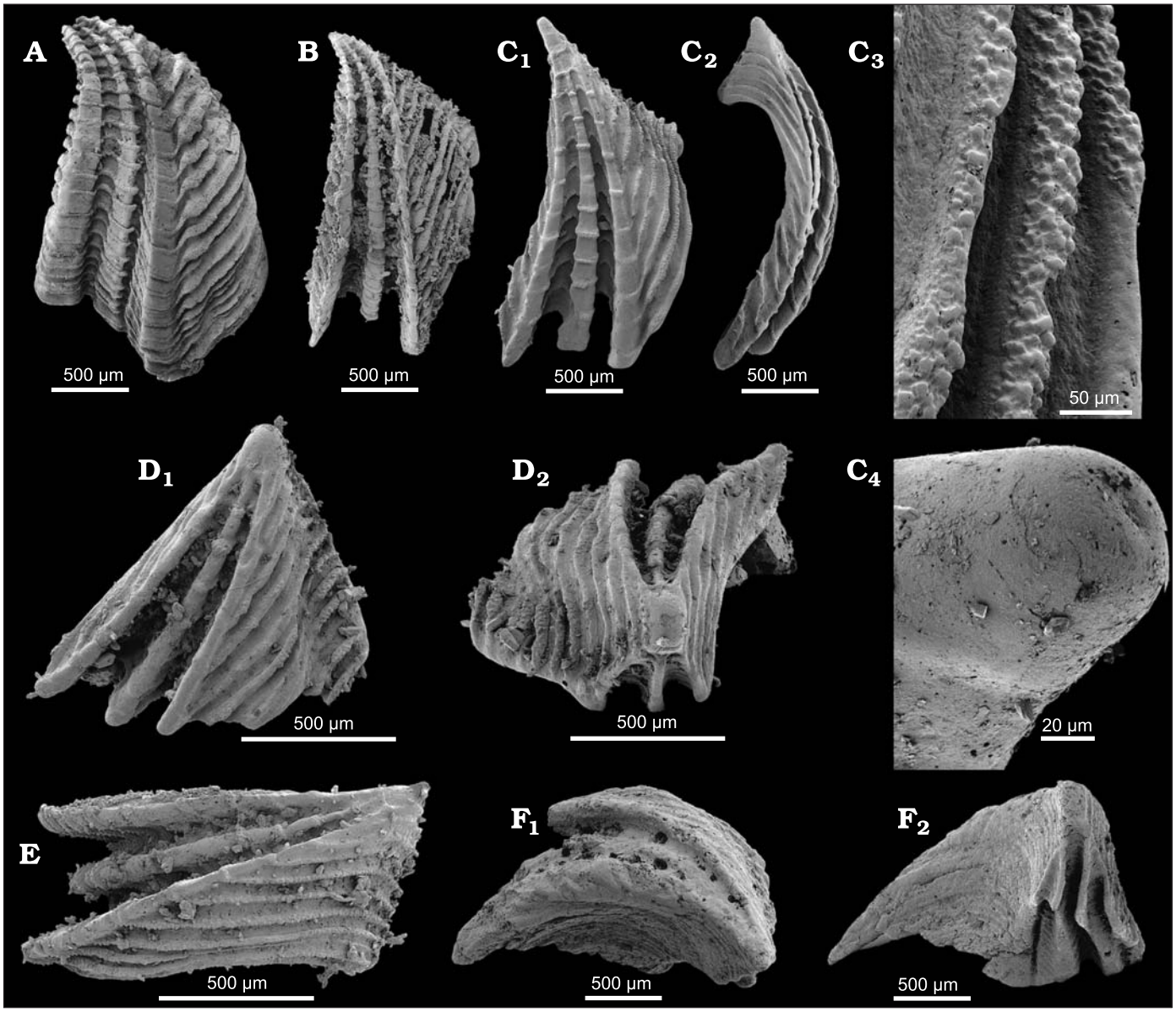



Fig. 3. Tommotiid *Camenella reticulosa* Conway Morris, 1990 from lower Cambrian Hawker Group, Flinders Ranges, Arrowie Basin, South Australia, mitral sclerites. **A**. SAMP 43164 (sinistral), Wilkawillina S; oblicate/accrescent view of sclerite showing wide radial ribs. **B**. SAMP 43165 (sinistral), MMF 0.0; obplicate/accrescent view of specimen with deep radial folds. **C**. SAMP 43166 (sinistral), Wilkawillina Q; $C_1$, obplicate/ accrescent view of specimen with pointed apex; $C_2$, decrescent view showing strong curvature of the aperture; $C_3$, detail of shell ornament on accrescent side showing co-marginal ribs capped by nodes and a superimposed reticulation; $C_4$, detail of smoothly rounded apex showing a circular depression. **D**. SAMP 43167 (sinistral), MMF 0.0; $D_1$, oblique obplicate/accrescent view of small specimen; $D_2$, apical view showing the almost equal development of radial ribs on plicate (lowermost in picture) and obplicate sides. **E**. SAMP 43168 (sinistral), MMF 0.0; oblique obplicate/accrescent view of specimen with minimal helical twist. **F**. SAMP 43169 (dextral), Bunyeroo 4b; $F_1$, oblique apical/obplicate/decrescent view of abraded specimen with strong helical twist; $F_2$, oblique apical/plicate/decrescent view showing angular deflection of strongly developed radial ribs on plicate side.

based model, and all other species require re-evaluation. In the following discussion of *C. reticulosa*, it should be noted that mitral and sellate sclerites of many of these species were described separately under the generic names *Tommotia* (mitral sclerites) and *Camenella* (sellate sclerites), respectively. However, even in these cases it is sometimes possible to identify specific pairs of sclerites that probably belonged to a single scleritome. Until reinvestigations of relevant type material has been carried out, no formal synonymy can be proposed.

*Stratigraphic and geographic range*.—Lower Cambrian (Tommotian to Botoman and equivalents) of the Siberian Platform, western Mongolia, South Australia, Baltica (Sweden) and Avalonia (England, Newfoundland, Nova Scotia).

## *Camenella reticulosa* Conway Morris, 1990

Figs. 2–8.

1990 *Camenella reticulosa* Conway Morris sp. nov.; Bengtson et al. 1990: 131, fig. 81, non. fig. 82.

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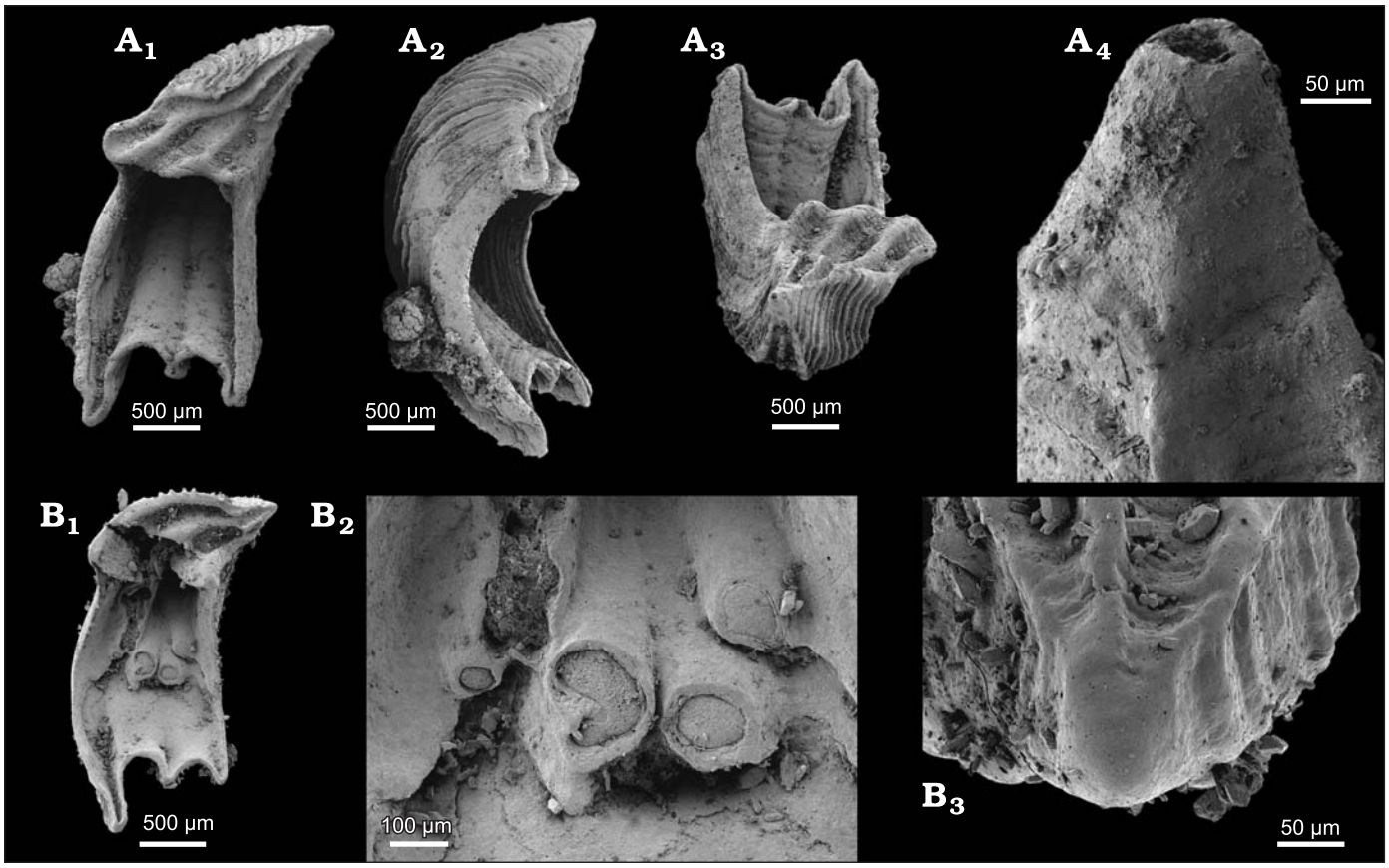



Fig. 4. Tommotiid *Camenella reticulosa* Conway Morris, 1990 from lower Cambrian Hawker Group, Flinders Ranges, Arrowie Basin, South Australia, mitral sclerites. **A**. SAMP 43170 (sinistral), Wilkawillina S; $A_1$, apertural view of large specimen showing deep apertural cavity and angular deflection of radial ribs on plicate side which is developed into a lip projecting under the accrescent side (on left in the picture); $A_2$, view from accrescent side showing strong curvature of the specimen and aperture; $A_3$, apical view showing initial equal development of radial ribs on plicate and obplicate (lowermost in picture) sides, development of the plicate side into a projecting lip and faint co-marginal ornament on the internal surface of the sclerite; $A_4$, detail of apex showing circular perforation (breakage?) and subdued ornament. **B**. SAMP 43171 (sinistral), MMF 0.0; $B_1$, apertural view of specimen showing deep apertural cavity, deflection of radial ribs on plicate side and growth disturbances on plicate and obplicate sides following damage and/or growth retardation at 2/3 of final sclerite length; $B_2$, detail of growth disturbances on internal surface of obplicate side; $B_3$, detail apex showing smoothly rounded apex without perforations.

non 1995 *Camenella* cf. *reticulosa* Conway Morris, 1990; Landing 1995: fig. 7.24.

non 2001 *Camenella* cf. *reticulosa* Conway Morris, 1990; Gravestock et al. 2001: pl. 8: 9.

*Holotype*: Sellate sclerite SAMP30666 (Bengtson et al. 1990: fig. 81) from UNEL 1856, Parara Limestone, Horse Gully, Stansbury Basin, South Australia.

*Material*.—30 mitral (16 sinistral, 14 dextral) and 31 sellate (16 sinistral, 15 dextral) sclerites from the Wilkawillina Limestone at Bunyeroo Gorge (Bun 1*, 3, 3*, 4, 4b), Wilkawillina Gorge (Wilk A, M, O, P, Q, R, S) and the MMF section (MMF/0.0), 1 km south of Balcoracana Creek.

*Emended diagnosis*.—Species of *Camenella* with sclerites characterised by strong co-marginal ribs ornamented by nodes and a superimposed reticulate pattern. Inter rib areas smooth or with fine transverse growth lines. Sellate sclerite strongly asymmetrical with prominent sella separating large and small lobes. Large lobe with one or two poorly defined subsidiary folds and a weakly developed rib separating the lobe from the sella. Apex tightly coiled (up to 1.5 whorls) with duplicature adpressed to the inside of the sella. Mitral sclerite acutely pyramidal with obplicate and accrescent sides strongly developed. Both plicate and obplicate sides with three pronounced radial ridges separated by two deep folds.

*Description*.—*Camenella reticulosa* has two types of sclerites (Fig. 2), one cone-shaped mitral (Figs. 3, 4) and one narrow, coiled sellate sclerite (Figs. 5, 6). Both sclerite types exhibit broad, strongly raised co-marginal ribs with a micro-ornament of nodes and a superimposed reticulate pattern (Figs. 3E, $5A_3$, $6C_2$; see also Bengtson et al. 1990: fig. 81e). Areas between the ribs are smooth or have faint co-marginal growth lines and occasional radial striae (Fig. $6B_2$, $C_2$). In the current collections, mitral and sellate sclerites are almost always found in direct association and out of the 61 sclerites in the total collection, 31 are sellates (51%) and 30 mitrals (49%). Both sclerite types are asymmetrical with respect to a longitudinal median plane, but occur as dextral and sinistral symmetry variants (D- and L-forms sensu Bengtson 1970),

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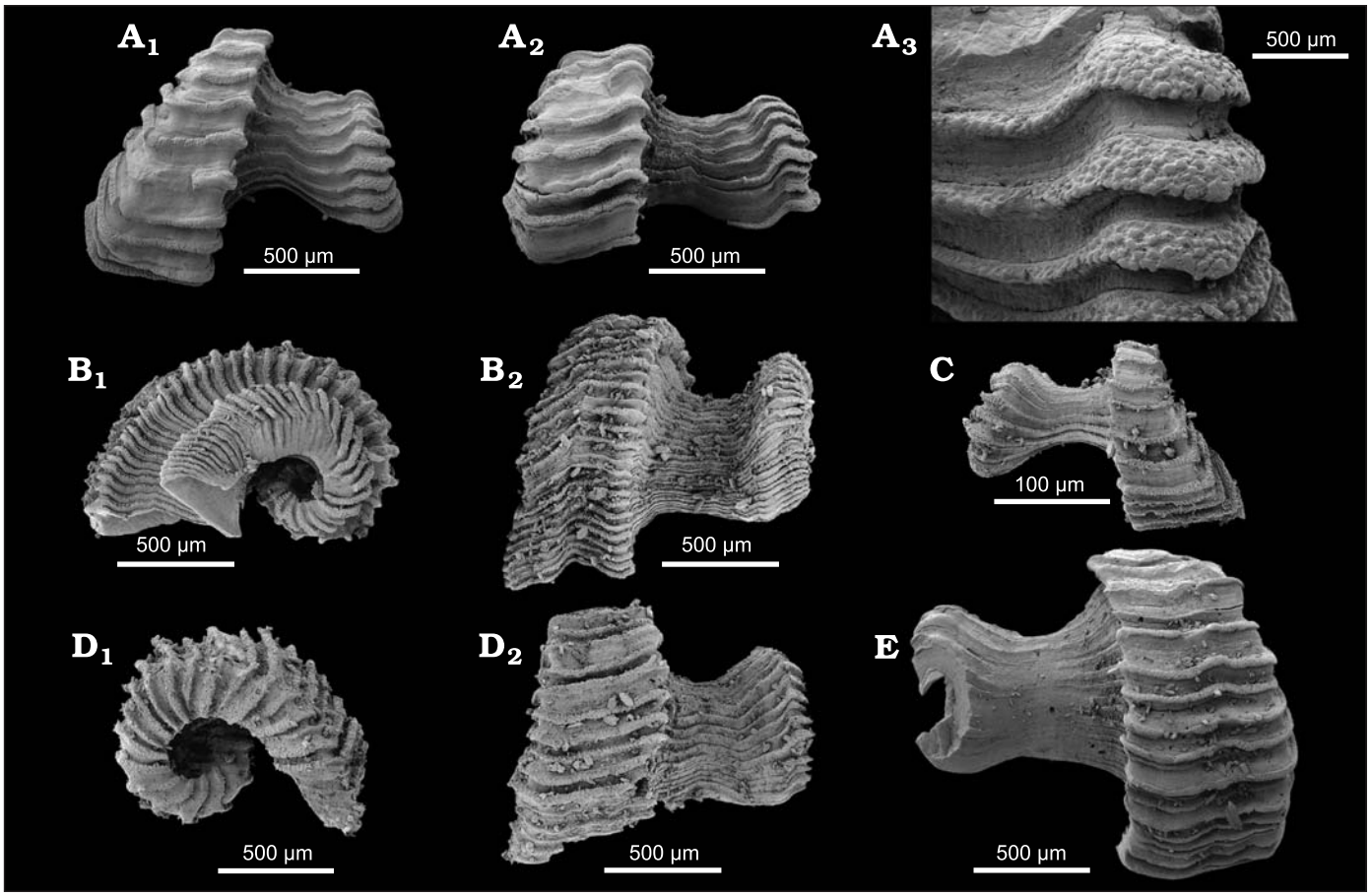



Fig. 5. Tommotiid *Camenella reticulosa* Conway Morris, 1990 from lower Cambrian Hawker Group, Flinders Ranges, Arrowie Basin, South Australia, sellate sclerites. **A**. SAMP 43172 (dextral), Wilkawillina Q; $A_1$, dorsal view of specimen with large and small lobe strongly inclined and ornament of wide co-marginal ribs; $A_2$, oblique dorsal view showing unequal height of the lobes; $A_3$, detail of ornament on small lobe showing wide co-marginal ribs with nodes and superimposed reticulation and fine growth striae between the ribs. **B**. SAMP 43173 (dextral), MMF 0.0; $B_1$, side view (from small lobe) of specimen with narrow and densely spaced co-marginal ribs showing tightly coiled apex; $B_2$, oblique dorsal view showing deep sella, radial rib on large lobe overhanging the sella and faint radial folds on both large and small lobe. **C**. SAMP 43174 (sinistral), MMF 0.0; dorsal view of small specimen showing maximum inclination of large and small lobes. **D**. SAMP 43175 (dextral), MMF 0.0; $D_1$, side view (from large lobe) of specimen with intermediate development of co-marginal ribs showing tightly coiled apex; $D_2$, oblique dorsal view showing unequal development of lobes and relatively narrow sella. **E**. SAMP 43176 (sinistral), Wilkawillina Q; dorsal view of large specimen with damaged small lobe, radial folds on large lobe and wide sella without co-marginal ornament (abrasion?).

which are represented in approximately equal numbers (48% of sellates and 47% of mitrals are of the dextral variant).

*Mitral sclerites*.—Mitral sclerites are strongly asymmetrical cones, up to 2.5 mm long (measured from apex to the margin of the longest [obplicate] side), with a subquadrate cross-section and a slight to moderate helical twist (e.g., Figs. 3, 4). Following Bengtson (1970: 367), the four sides of the cone are termed plicate, obplicate, accrescent and decrescent with the obplicate and accrescent sides more strongly developed than the opposing plicate and decrescent sides. The obplicate and plicate sides each bear three well defined radial ribs separated by deep, narrow folds (Fig. 3A, B, $C_1$, $D_1$, $D_2$, E). On the obplicate side, the ribs are continuous from the apical region to the growing margin of the sclerite; they tend to be straight or gently curved, and the central rib is slightly lower than the marginal ribs (Fig. 3A, B, $C_1$, $D_1$, E, $F_1$). The co-marginal ribs are continuous across the obplicate side, but the ribs are narrower and more widely separated in this region. The accrescent (Fig. $3D_1$, E) and decrescent (Fig. $3C_2$, $F_2$) sides are uniformly curved and exhibit well developed, evenly spaced co-marginal ribs. The radial ribs and folds of the plicate side are initially identical to their counterparts on the obplicate side, but all larger specimens exhibit a marked shift in the growth vector of the ribs which occurred when the plicate side had attained a length of 0.4 to 0.8 mm (Figs. $3F_2$, $4A_1$, $B_1$). The ribs are deflected in the opposite sense of the curvature of the sclerite (Figs. $3F_2$, $4A_1$, $B_1$). This results in wavy ribs and folds on the plicate side, which forms a protruding lip extending beyond the adjacent accrescent side of the sclerite (Fig. $4A_1$, $A_3$).

The aperture of the mitral sclerites covers about 50–75% of sclerite length (in apertural view) and is wide, deep and subquadrate in outline (Fig. 4A, $B_1$). The internal surface mimics the various folds and ribs of the exterior surface, but

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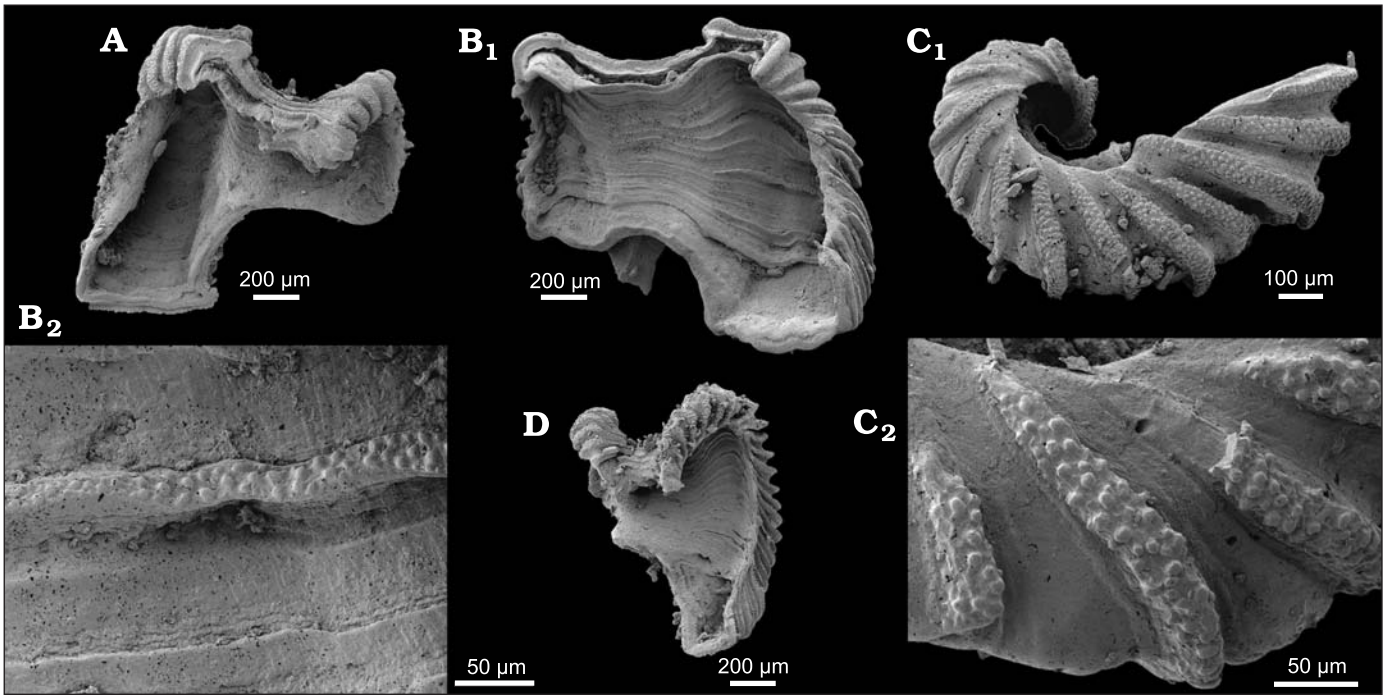



Fig. 6. Tommotiid *Camenella reticulosa* Conway Morris, 1990 from lower Cambrian Hawker Group, Flinders Ranges, Arrowie Basin, South Australia, sellate sclerites. **A**. SAMP 43177 (sinistral), MMF 0.0; internal view of sclerite with damaged apex. **B**. SAMP 43178 (Dextral),Wilkawillina Q; $B_1$, internal view of large specimen with apex removed by co-marginal breakage showing well developed duplicature; $B_2$, Detail of duplicature showing minor co-marginal with nodose ornament and fine co-marginal and radial striae. **C**. SAMP 43179 (sinistral), Wilkawillina S; $C_1$, side view of specimen with preserved apex viewed from the large lobe; $C_2$, detail of lateral flank of large lobe with co-marginal ribs ornamented by nodes and superimposed reticulation. **D**. SAMP 43180 (Dextral), MMF 0.0; internal view of specimen with small lobe damaged showing cavity under duplicature of the large lobe.

is otherwise smooth or with faint co-marginal striae (Fig. $4A_3$). The apex tapers to a subcircular cap approximately 100 µm in diameter. A few specimens display a central circular perforation of the apical cap (Figs. 3F, $4A_4$), but in other specimens the cap is a simple, smooth surface (Fig. $4B_3$).

*Sellate sclerites*.—Sellate sclerites are strongly asymmetrical, up to 1.8 mm long, with a well defined sella dividing the sclerite into large and small lobes (Fig. 5). The sella occupies about 50% of the sclerite width and its margin is marked by a weakly developed ridge on the large lobe that may slightly overhang the floor of the sella (Fig. $5B_2$, E). The large lobe is approximately twice as large as the small lobe in length and width, and is substantially higher (Fig. $5A_2$, $B_2$, $D_2$). The long axis of the lobes may be parallel (Fig. $5B_2$) or form an angle of up to 45° (Fig. $5A_2$, C). The large lobe often has one, occasionally two, poorly defined radial folds, and in one specimen the small lobe has an additional fold (Fig. $5B_2$). In some specimens, these folds are relatively deep, but are more often only visible as a slight deflection of the co-marginal ribs. The co-marginal ribs are expressed over the entire dorsal surface of most sellate sclerites, but width and height of the ribs are reduced on the sella (Fig. $5A_1$, $A_2$). Two large specimens seem to have only very weakly developed ribs in the central portion of the sella (Figs. 5E, 7A). The ventral surface of the sclerite is strongly adpressed to the opposing wall and forms a smooth or weakly ornamented duplicature (Fig. 6A, $B_1$, D). A narrow opening separates the duplicature from the underlying wall under the large lobe, but the duplicature appears to be completely adpressed to the opposing shell surface over the entire width of the sella. The duplicature extends across most of the ventral surface except for a narrow region along the growing margin of the sclerite (Fig. $6B_1$). This region is slightly wider on the ventral surface of the lobes, but never exceeds 0.4 mm in width. The duplicature bears only vestiges of co-marginal ribs, but these occasionally preserve a micro-ornament identical to the ribs of the dorsal surface (Fig. $6B_2$). The apex is coiled through up to 1.5 whorls and the initial growth stages are consequently difficult to examine in detail (Figs. $5B_1$, $D_1$, $6C_1$). Some specimens have lost the apical region by fracturing parallel to the co-marginal ribs of the dorsal shell surface.

*Discussion*.—The sellate and mitral sclerites from the Arrowie Basin are considered conspecific based on the identical surface ornament of coarse co-marginal ridges with nodes and superimposed reticulation, a feature which is shared with the holotype of the species. As in other species of *Camenella*, the distribution of the two sclerite types in the Arrowie Basin is virtually identical and whenever one type of sclerite occurs, the other is also present. The size range and total number of sclerites is also similar (31 sellates [51%] and 30 mitrals [49%]).

*Camenella reticulosa* was originally described by Conway Morris (in Bengtson et al. 1990) on the basis of six specimens from Parara Limestone at Horse Gully and Kulpara in

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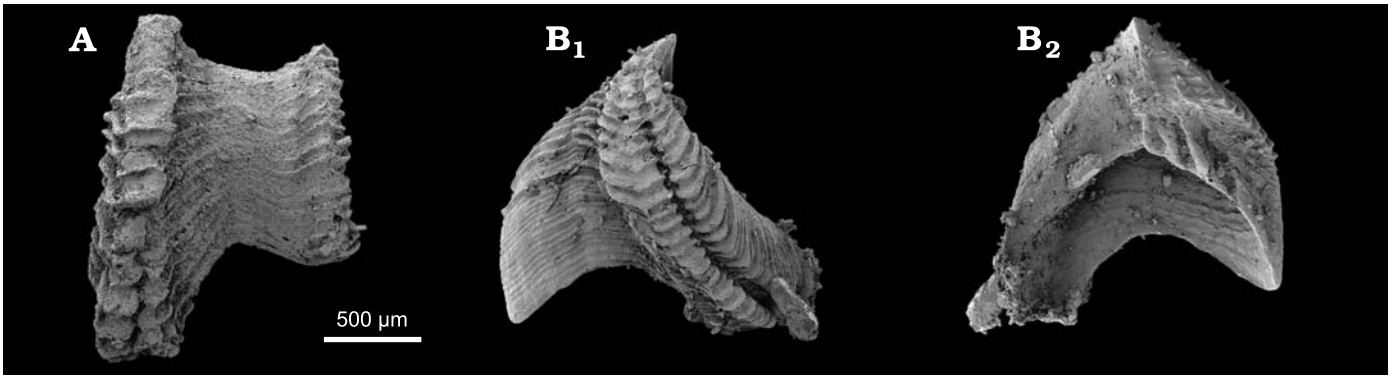



Fig. 7. Tommotiid *Camenella reticulosa* Conway Morris, 1990, from lower Cambrian Hawker Group, Flinders Ranges, Arrowie Basin, South Australia. **A**. Sellate sclerite (dextral), SAMP 43181, Bunyeroo 4; dorsal view showing narrow lateral lobes and wide sella with reduced, possibly abraded ornament. **B**. Mitral sclerite (dextral), SAMP 43182, MMF 0.0; $B_1$, oblique view of deformed oblicate and accrescent sides showing wide through and disturbed radial ornament; $B_2$, oblique view of plicate and decrescent sides showing normal placation, a pointed apex and deep internal cavity.

the Stansbury Basin. One sellate (holotype; Bengtson et al. 1990: fig. 81) and two supposedly mitral (Bengtson et al. 1990: fig. 82) sclerites were illustrated, but the latter show little resemblance to the well preserved mitral sclerites documented herein, and probably represent poorly preserved sclerites of *Dailyatia*. Similarly, the single specimen from Horse Gully referred to *C.* cf. *reticulosa* by Demidenko (in Gravestock et al. 2001: pl. 8: 9) also appears to represent an incomplete sclerite of *Dailyatia*. Landing (1995: table 2) referred four specimens from the Placentian Series of Nova Scotia to *Camenella* cf. *reticulosa*. These specimens were not described and only a single specimen was illustrated (Landing 1995: fig. 7.24), but its relationship to *Camenella* is not clear.

*Camenella reticulosa* can be distinguished from all other species in the genus by the characteristic ornament of strong co-marginal ribs with nodes and superimposed reticulation. In addition, the coiled apex of the sellate sclerite and the presence of three radial ribs and intermittent folds on both plicate and obplicate sides of the mitral sclerite are unique characters of this species. Further, the mitral sclerites are distinguished from those of *C. baltica* and *C. parilobata* by the helical twist (compare Figs. 3 and 4 to Bengtson 1970: figs. 1, 7, 8 and Bengtson 1986: figs. 2–4) and from "*Tommotia*" *kozlowski* and "*Tommotia*" *admiranda* by the lack of radial elements of ornamentation beyond the three plicate and obplicate ribs (compare Figs. 3 and 4 to Rozanov et al. 1969: pl. 5: 2, 3, 9, 17, and Matthews and Missarzhevsky 1973: pl. 3: 14, and Missarzhevsky 1989: pl. 16: figs. 1–8). The sellate sclerites differ from their counterparts in *C. parilobata* by the larger size difference between large and small lobes (compare Figs. 5 and 6 to Bengtson 1986: fig. 1) and from *C. garbovskae* and *C. baltica* by the deeper and wider sella separating the lobes (compare Figs. 5 and 6 to Rozanov et al. 1969: pl. 5: 1, 6, 8, and Bengtson 1970: 2, 10). *Camenella reticulosa* also differ from Tommotiid gen. et sp. nov. described by Skovsted and Brock (in Paterson et al. 2007) by the restriction of the nodose ornament to the ribs and by the well developed asymmetry and radial folds of the mitral sclerite.

The available collection of sellate and mitral sclerites suggests that both sclerite types of *C. reticulosa* are somewhat less variable than sclerites of the other well documented species, *C. baltica* and *C. parilobata*. The sellate sclerites differ mainly in the development of the sella, its relative width and height compared to the lateral lobes, but never to the extreme degree seen in the other two species (compare Figs. 5 and 6 to Bengtson 1986: fig. 1). The difference is even more pronounced when the mitral sclerites are compared. Both *C. baltica* and *C. parilobata* includes straight pyramidal, asymmetrical and laterally compressed mitral sclerites, but in *C. reticulosa* the mitral sclerites differ mainly by degrees in helical twist and development of the radial ribs and folds (compare Figs. 3 and 4 to Bengtson 1986: figs. 2–5). A single, laterally compressed mitral sclerite of *C. reticulosa* (Fig. 7B) has been obliquely compressed from the obplicate/accrescent side, but still exhibits the characteristic three-fold radial ribs of the species. The obplicate side has developed a trough that is somewhat similar to the sella in associated sellates, but the presence of a pointed apex and well developed radial ribs and folds on the plicate side are clearly mitral characteristics. This unusual mitral sclerite of *C. reticulosa* represents a slightly deformed variety of the normal mitral sclerite and may be comparable to the planiform mitral sclerites of "*Tommotia*" *plana*, *C. baltica* and *C. parilobata*. Bengtson (1986) speculated that these simplified, laterally compressed sclerites formed an integrated part of the *Camenella* scleritome.

Another unusual mitral sclerite from the uppermost Wilkawillina Limestone at MMF/0.0 exhibits growth deformations in the form of a wavy ridge on the internal surface of the obplicate side of the sclerite (Fig. 4$B_1$, $B_2$). Shell growth was apparently halted when the sclerite had attained about 2/3 of its final length, and when growth resumed the obplicate ribs and folds were aborted and only reformed at a later stage. The plicate surface is also deformed and exhibits a deep longitudinal split.

*Stratigraphic and geographic range*.—Upper lower Cambrian (*Abadiella huoi* to *Pararaia tatei* Zones), Stansbury Basin: Parara Limestone of Horse Gully and possibly Kulpara.

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Arrowie Basin: Wilkawillina Limestone in Bunyeroo Gorge, Wilkawillina Gorge, near Balcoracanna Gorge, Flinders Ranges, South Australia.

# Shell structure

*Camenella* sclerites are composed of sets of apatitic laminae that bend outwards and fan out along the margin of the sclerite (Fig. $8B_2$, $D_1$, $D_2$). Some of the thickened margins of individual laminae form the prominent ornament of co-marginal ribs that in sclerite cross-sections appear as a saw-tooth pattern (Fig. $8A_1$, $B_1$, C, $D_1$). Depending on the position within the sclerite, the thickness of individual laminae varies from around 1 μm to 40 μm (Fig. $8B_2$, $D_2$). The density of laminae is variable and can be particularly high in stacked thin laminae (Fig. $8A_2$). Thicker laminae can exhibit substantial porosity (e.g., Fig. $8D_4$), but it is unclear to what degree this reflects the primary condition. In one specimen (Fig. $8D_3$), an unusual microstructure of a dense meshwork of cryptocrystalline apatite with submicron pores was found in the marginal thickened portion of a lamina. This microstructure strongly contrasts with other laminae in *Camenella* sclerites which have a microgranular appearance and contain larger pores in the thicker parts of laminae (Fig. $8A_2$, $D_4$). The cryptocrystalline meshwork also contrasts with other primarily apatitic structures found in extant organophosphatic biomineralizing organisms such as linguliform brachiopod shells (e.g., Cusack et al. 1997; Cusack et al. 1999) and probably represents phosphatised organic material.

The dense lamellar microstructure in *Camenella* is similar to that of *Lapworthella* (Landing 1984), whereas it contrasts with that of *Sunnaginia* (Landing et al. 1980) and tannuolinids (Conway Morris and Chen 1990; Williams and Holmer 2002), the etched sclerites of which exhibit repeated sets of thick "hollow" layers that were probably originally filled with organic compounds. However, the *Camenella* microstructure deviates from the pattern of dense lamination along the sclerite margins where individual laminae bend outwards and significantly increase in thickness (Fig. $8B_2$, $D_2$).

This pattern becomes even clearer when taking into account the diagenesis behind the silicified marginal patches of *Camenella*. Previous work on phosphatic shells has shown that silicification primarily replaces calcium carbonate, while apatite remains stable (Balthasar 2007). In cross sections of *Camenella* sclerites, silicified patches have the appearance of "plugs" at the margin of individual layers (Fig. $8D_2$). This pattern of marginally silicified calcium carbonate cement is very similar to the preservation of phosphatic brachiopod shells where organic-rich layers are first hollowed out during decomposition and then cemented with calcium carbonate (Balthasar 2007). For *Camenella*, this interpretation is further supported by possible phosphatised organic material in the immediate vicinity of the silicified areas (Fig. $8D_3$ and asterix in Fig. $8D_2$).

In summary, *Camenella* sclerites were composed of an intercalation of organic-rich and compact apatite-rich laminae. Originally, the organic-rich layers would have had a tendency to hollow out during decomposition and be either filled with calcium carbonate during early diagenesis or retain a high microporosity. However, in most *Camenella* sclerites, both types do not exceed a minimal thickness of 1–3 μm, which makes it almost impossible to distinguish between the truly compact and the more porous laminae. Only along the margins where organic-rich layers increase in thickness can these laminae be distinguished more easily. Importantly, this model of cyclic secretion of organic and apatite-rich layers can be applied to all tommotiids for which microstructural data are available and, in principle, also applies to organophosphatic brachiopods (Williams et al. 1992, 1994; Cusack et al. 1997). The more spacious sclerite structure of tannuolinids and *Sunnaginia* thus simply reflects the presence of thicker organic-rich layers.

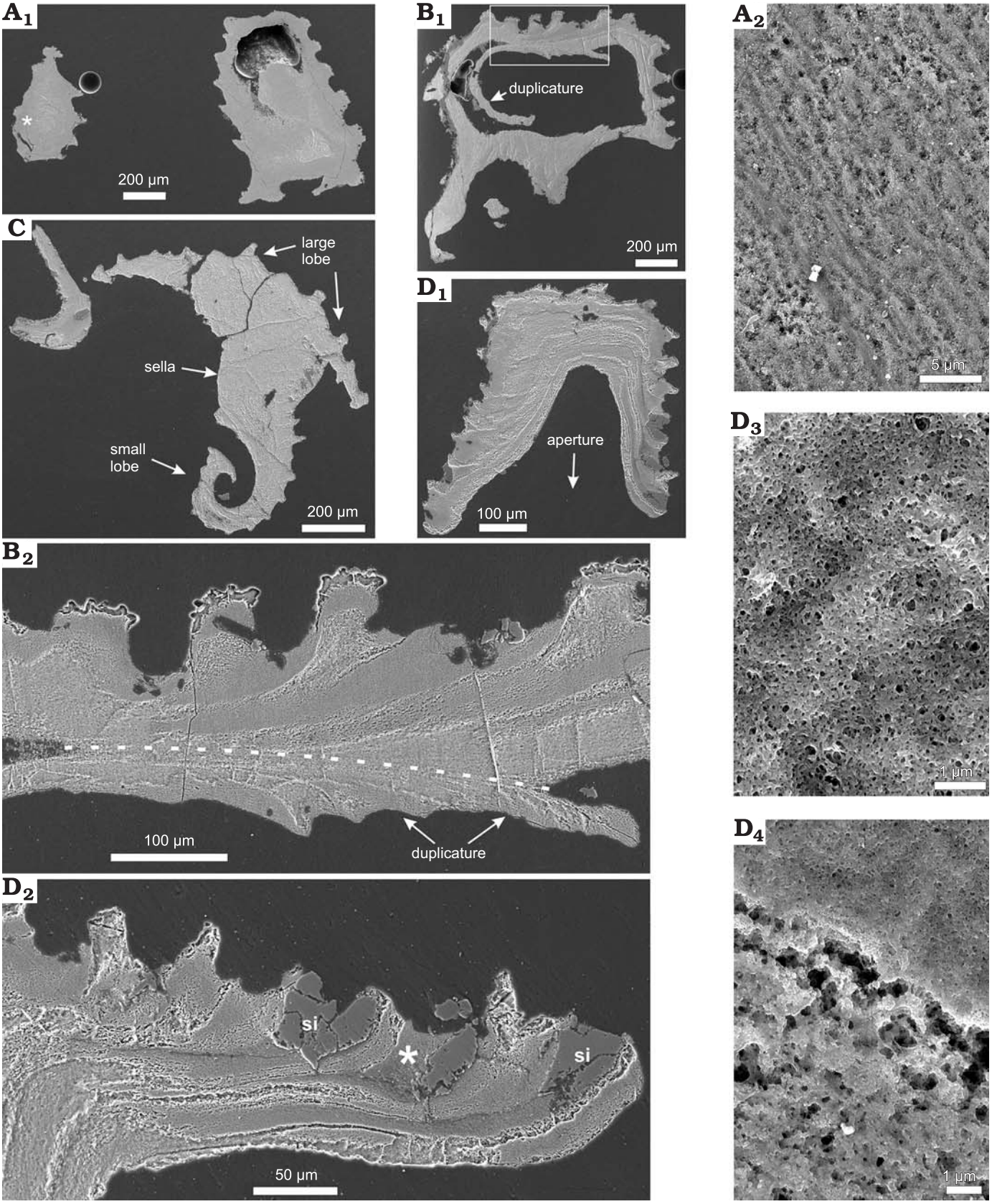
# Discussion

**Tommotiid phylogeny**.—Tommotiids share a scleritome constructed of multiple, essentially cone-shaped sclerites, a laminated shell formed by basal/internal shell secretion and a phosphatic shell composition. An affinity with lophophorates (brachiopods and phoronids) seems most likely, with different tommotiid groups occupying different branches of the lophophorate phylogenetic tree (e.g., Williams and Holmer 2002; Skovsted et al. 2008, 2009; Holmer et al. 2008).

Presently, no consensus concerning the definitions of the five tommotiid families (Tommotiidae, Lapworthellidae, Kennardiidae, Sunnaginidae and Tannuolinidae) exists and a number of contrasting taxonomic schemes have been proposed (e.g., Landing 1984; Dzik 1986; Missarzhevsky 1989; Conway Morris and Chen 1990; Esakova in Esakova and Zhegallo 1996). Still, a number of tommotiids (i.e., *Paterimitra*, *Porcauricula*) have proved difficult to place within any of the proposed family level groupings. The fundamental

Fig. 8. Microstructure of *Camenella* sclerites. All images from polished and etched sellate sclerites from MMF 0.0, lower Cambrian Hawker Group, Flinders Ranges, Arrowie Basin, South Australia. **A**. Sellate sclerite (sinistral), SAMP 43183; $A_1$, marginal cross section approximately parallel to the aperture showing the larger and smaller lobes; asterix indicates position of $A_2$; $A_2$, showing a dense alteration of dense and somewhat more porous laminae in a central position within a sclerite. **B**. Sellate sclerite (sinistral), SAMP 43184; $B_1$, cross section at high angle to the aperture showing the saw-tooth-like pattern of the co-marginal ribs, the duplicature within the larger lobe and parts of the smaller lobe; box indicates position of $B_2$; $B_2$, reversed bending of shell layers along the duplicature (below the dotted line) and the regular part of the sclerite (above the dotted line). **C**. Sellate sclerite (sinistral), SAMP 43185; oblique marginal cross section showing parts of the small lobe, the large lobe, and the sella in between. **D**. Sellate sclerite (dextral), SAMP 43186; $D_1$, marginal cross section of the larger lobe about 90° to the aperture showing the saw-tooth-like co-marginal ribs and sclerite architecture with marginally bending →

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laminae; $D_2$, detail from $D_1$ showing how some laminae increase marginally in thickness after bending around. Note the silicified areas (si) along the marginal position of some of the thickened lamiae; asterix indicates position of $D_3$; $D_3$, showing a secondarily phosphatized, possibly originally organic microstructure; $D_4$, Detail of $D_3$ showing the margin between the putative organic microstructure (top of image) and the "normal" phosphatic microstructure (bottom of image).

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problem behind the existing taxonomic confusion is the lack of adequate description of variability and microstructure of the sclerites, as well as the unknown construction of the scleritome of most of the taxa included. The suprageneric taxonomy of tommotiids will not be resolved until such descriptions exist.

As discussed in the Systematic Palaeontology section above, we limit the family Tommotiidae to include only *Camenella*. Due to the lack of satisfactory definition of most of the other tommotiid families we will, in the following discussion, refer to the most well studied genera of each family as a basis for comparisons with *Camenella*. The family Lapworthellidae is generally regarded to include species with cone-shaped sclerites that exhibit great variability along a continuous morphological spectrum (Conway Morris and Bengtson in Bengtson et al. 1990). Although a range of genera has been included in the Lapworthellidae (see review in Esakova and Zhegallo 1996), *Lapworthella* remain the only well studied genus (Landing 1984; Conway Morris and Chen 1990). The family Kennardiidae was proposed by Laurie (1986) and includes tommotiids with three different fundamental sclerite types and the best known genus is *Dailyatia* (Bischoff 1976; Laurie 1986; Evans and Rowell 1990; Wrona 2004). The family Sunnaginidae was originally confined to *Sunnaginia* (Landing 1984), but was later expanded to include *Eccentrotheca* and *Kulparina* (Landing 1995) and these genera share a highly irregular mode of shell formation and coarse concentric growth ridges. However, following the discovery of the scleritome of *Eccentrotheca* and *Paterimitra*, this family-level grouping will need re-evaluation. The family Tannuolinidae is probably the best defined tommotiid family, containing the genera *Tannuolina* and *Micrina* which are united by similarities in shell structure and the presence of shell penetrating setae, but differ by the symmetry of the mitral sclerites (Williams and Holmer 2002; Li and Xiao 2004; Holmer et al. 2008).

In terms of general morphology, *Camenella* most closely resembles *Lapworthella* and *Dailyatia*. In particular, the pyramidal mitral sclerites of *Camenella* are closely comparable to wide, pyramidal sclerites of *Lapworthella*, sharing a subrectangular cross-section and possessing well developed co-marginal ribs. However, *Lapworthella* can be differentiated from *Camenella* by lacking sclerites directly comparable to sellates. Like *Camenella*, *Dailyatia* exhibits distinct sclerite types without apparent morphologic intermediates (Bischoff 1976; Laurie 1986), but the number of distinct sclerite morphologies is higher. In *Dailyatia*, three sclerite types are recognised (A–C; sensu Laurie 1986), and while two are asymmetrical (types B and C) like the sclerites of *Camenella*, the third (type A) is bilaterally symmetrical, a morphotype that appears to be absent in the *Camenella* scleritome. Each sclerite type of *Dailyatia* (A–C) is further represented by two well defined subtypes, bringing the total number of sclerite types to six (Laurie 1986). These sclerites include symmetrical pyramidal sclerites (A1 and A2), asymmetrical conical sclerites (B1 and B2) and asymmetrical laterally compressed

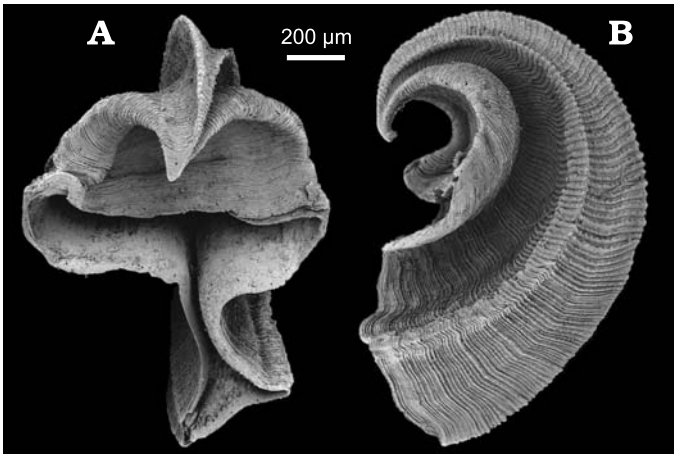



Fig. 9. Tommotiid *Dailyatia* sp., probable C-type sclerite, SAMP 43187 from MMF 0.0, lower Cambrian Hawker Group, Flinders Ranges, Arrowie Basin, South Australia. **A**. Oblique apertural view showing asymmetric twist. **B**. Side view showing open coiling through almost a full whorl.

sclerites (C1 and C2). All B- and C-type sclerites further occur in both sinistral and dextral variants. The C-type sclerites of *Dailyatia* are sometimes strongly coiled and somewhat reminiscent of sellate sclerites in *Camenella* (Fig. 9).

The external ornament of *Camenella* sclerites exhibit a well defined pattern of co-marginal ribs and interjacent low relief areas (Figs. $5A_3$, $6B_2$, $C_1$; Bengtson 1970: fig. 6; Bengtson 1986: fig. 6; Missarzhevsky 1989: pls. 15, 16). Fine growthlines are usually present in low relief areas showing that the sets (ribs and subsequently formed low relief areas) in themselves are ornamental and do not directly reflect growth-increments. This pattern of shell secretion is also evident from the shell structure (see above). The repeated formation of ornamental, co-marginal ribs by inflation of specific shell laminae close to the shell margin is evidently an integrated part of the shell secretion program in *Camenella*. The same pattern of ornamental sets of co-marginal ribs and low relief areas (with superimposed growth increments) is characteristic of *Lapworthella* (Bengtson and Conway Morris in Bengtson et al. 1990: 130) and *Dailyatia* (Laurie 1986: fig. 7c, e, f; Wrona 2004: figs. $8C_5$, $11A_5$). Other tommotiids exhibit very different types of external ornament with undifferentiated co-marginal growth units separated by narrow furrows (e.g., in *Paterimitra*; Bengtson et al. 1990: fig. 92c, f; Skovsted et al. 2009: figs. 1, 2) or more irregular deposits of shell material (e.g., *Eccentrotheca*, Bengtson et al. 1990: fig. 71; *Tannuolina*, Li and Xiao 2004: fig. 4.13; and *Micrina*, Laurie 1986: fig. 4).

These observations strongly suggest that *Camenella*, *Lapworthella*, and *Dailyatia* (and by implication other members of the Lapworthellidae and Kennardiidae) form a natural phylogenetic group, here informally termed the "camenellan" clade. Although the camenellans share a basic cone-shaped sclerite construction, the main synapomorphy of this group is the repeated formation of ornamental, co-marginal ribs by inflation of specific laminae close to the sclerite margin.

Of the remaining tommotiids, at least the tannuolinids (*Tannuolina* and *Micrina*) share characters (e.g., setal tubes

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and microstructure) with some upper stem or basal brachiopods (i.e., *Mickwitzia*; William and Holmer 2002; Holmer et al. 2002, 2008; Skovsted and Holmer 2003). Thus, a paraphyletic Tommotiida appears to form part of the stem of the phylum Brachiopoda with the tannuolinids being the most derived tommotiid members. Holmer et al. (2008) reconstructed the tannuolinid *Micrina* with only two sclerites, partly enclosing the soft parts of the animal and derived this scleritome construction from the tubular scleritome of *Eccentrotheca*. Later Skovsted et al. (2009) demonstrated that the scleritome of *Paterimitra* is less derived, combining two symmetrical sclerites surrounding an organic attachment structure with a large number of *Eccentrotheca*-like sclerites. Based on scleritome construction, as well as similarities in sclerite morphology and growth pattern, *Eccentrotheca* and *Paterimitra* presumably represent more basal members of the same stem group that had already evolved into sessile filter feeders (Fig. 10).

Based on the differences in sclerite construction, ornamentation and morphology outlined above, the camenellans seem to fall outside the *Eccentrotheca–Paterimitra–Micrina* clade of tommotiids and are here interpreted to form their sister group. This conclusion is further supported by the probable differences in scleritome construction between camenellans and other tommotiids discussed below. Fig. 10 summarises the suggested relationships between the tommotiids discussed above and potential synapomorphies separating them.

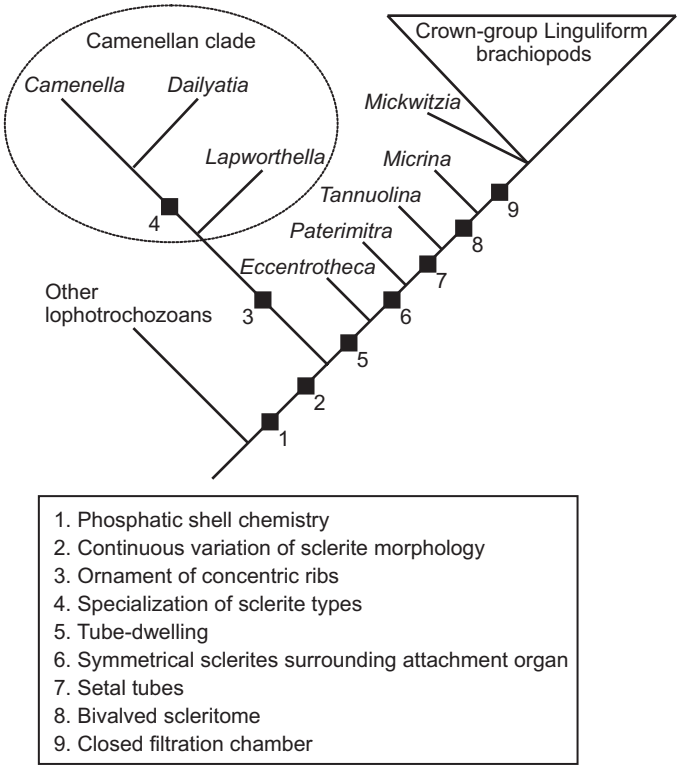



Fig. 10. Suggested relationships between tommotiids and linguliform brachiopods. Camenellans are defined by the ornament of concentric ribs, and diverged from the main tommotiid lineage after the acquisition of phosphatic shell chemistry but before the evolution of a tubular scleritome. The position of the tommotiids *Sunnaginia*, *Porcauricula*, and *Kulparina* is uncertain, but all probably fall close to *Eccentrotheca*. Note that not all potential descendants on each branch are indicated in the diagram. Skovsted et al. (2009) suggested that the branch leading to *Paterimitra* also include paterinid brachiopods.

Among camenellans, *Camenella* and *Dailyatia* share the presence of specialised sclerite types, although further studies are required to propose specific homologies between the sclerite types. Like *Eccentrotheca*, *Lapworthella* lacks specialised sclerite types (i.e., show continuous variation in sclerite morphology), suggesting that the last common ancestor of tommotiids had simple, undifferentiated cone-shaped sclerites and that *Lapworthella* occupies a basal position within the camenellan clade. In this context it might be of some interest to point out that the tommotiid assemblage from the *Watsonella crosbyi* Zone of Southeastern Newfoundland (Member 4, Chapel Island Formation)—predating the oldest tommotiid assemblages from the base of the Tommotian and Meishucunian Stages of Siberia and China, respectively (Geyer, Peng, and Shergold in Shergold and Geyer 2003)—includes both the camenellan *Lapworthella ludwigseni* and *Eccentrotheca kanesia* (Landing et al. 1989).

**Reconstructions of the *Camenella* scleritome**.—The lack of known examples of tommotiids with soft-part preservation means that it is only possible to deduce morphological information from their biomineralised remains which, with only a few exceptions, are confined to isolated sclerites of an originally composite scleritome. In the first described articulated tommotiid scleritome, that of *Eccentrotheca*, individual sclerites form rings that fuse ontogenetically and stack up to form a rigid and somewhat irregular open cone-shaped tube that was probably attached to a hard substrate via an irregular perforation close to the apex of the tube (Skovsted et al. 2008). In *Paterimitra*, a similar scleritome construction is apparent, but the presumed attachment organ protruded through a circular opening between two specialised, bilaterally symmetrical sclerites (Skovsted et al. 2009). The morphology and position (enclosing a presumably organic attachment organ) of these sclerites led Skovsted et al. (2009) to hypothesise that they are homologous with the valves of brachiopods. The evolution of brachiopods from tommotiid ancestors could thus be explained as a gradual decrease in sclerite number coupled with specialisation of the remaining sclerites. Based on this model, Holmer et al. (2008) reconstructed the tannuolinid *Micrina* as a bivalved tommotiid where the two remaining sclerites were connected by muscular attachment, although they did not fully enclose the animal. In the absence of more articulated material of other tommotiids, it seems appealing to use the tubular construction of the scleritomes of *Eccentrotheca* and *Paterimitra* as a blueprint for all tommotiid scleritomes. But given the enormous morphological diversity of tommotiid sclerites, it may be premature to adapt this scleritome organisation uncritically for all tommotiids, particularly *Camenella*.

The well defined morphotypes of sellate and mitral sclerites of *Camenella* contrast with the wide morphological range of

DOI: 10.4202/app.2008.0082

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sclerites seen in *Eccentrotheca*. The apical region of the *Eccentrotheca* scleritome is characterised by a mosaic of low cap-shaped sclerites that vary extensively in shape, resulting in the occupation of a continuous morphospace that includes oval, rectangular, triangular and irregular sclerites (Skovsted et al. 2008). The occurrence of sinistral and dextral sclerite symmetries in *Camenella* and the equal distribution of both types in acid residues suggest a scleritome with pairs of sinistral and dextral sclerites of each morphotype (i.e., sellate and mitral) arranged along a bilateral axis of symmetry. Bilaterally symmetrical composites of fused dextral and sinistral sclerites in *Lapworthella* (Demidenko 2004) and the presence of bilaterally symmetrical sclerites in *Dailyatia* (Bischoff 1976; Laurie 1986) supports the idea that camenellans probably possessed a bauplan arranged along a bilateral axis of symmetry. This variation in sclerite morphology, plus the lack of any obvious articulation mechanism or muscle attachment scars also argues against a bivalved reconstruction, which would be the numerically easiest way to reconstruct a two-component scleritome with equal proportions of both sclerites, as was recently demonstrated for *Micrina* (Holmer et al. 2008).

Before the discovery of articulated specimens of *Eccentrotheca* and *Paterimitra*, most scleritome reconstructions of tommotiids (e.g., Evans and Rowell 1990; Williams and Holmer 2002; Ushatinskaya 2002; Li and Xiao 2004) were based on the articulated scleritomes of *Halkieria evangelista* (Conway Morris and Peel 1990, 1995) or machaeridians (Dzik 1986; Högström and Taylor 2001). Both halkieriids and machaeridians possess a dorsal scleritome composed of imbricating sclerites, which is reflected in relatively flattened sclerite shapes. The phylogenetic position of halkieriids is not fully resolved, but Vinther and Nielsen (2005) suggested a molluscan affinity and machaeridians were recently shown to represent annelids (Vinther et al. 2008). However, for *Camenella*, it is functionally improbable that its coiled and cap-shaped sclerites were arranged in a partially overlapping, imbricating fashion. Based on the variable morphology of *Camenella* sclerites, it also appears unlikely that they covered the integument without leaving some gaps in between neighbouring sclerites, thus making it much more flexible than the rigid tubiform *Eccentrotheca* scleritome. It thus seems that the *Camenella* scleritome was probably unlike *Eccentrotheca* or any other described articulated scleritome and the scleritome was most likely bilaterally symmetrical as is the case for most known stem group lophotrochozoans (Butterfield 2006; Conway Morris and Caron 2007; Caron et al. 2007).

Important insights into the sclerite arrangement can be gained from patterns of mechanical wear. In *C. reticulosa*, the two largest sellate sclerites show signs of abrasion on the central portion of the sella, whereas the raised and more exposed lateral lobes exhibit a well preserved ornament (Figs. 5E, 7A). The same pattern is also observed in smaller specimens, albeit less pronounced with the ornament of co-marginal ribs being subdued but still visible in the depression of the sella (Fig. $5A_2$, $B_2$, C, $D_2$). These patterns may be explained by localised mechanical wear through a second structure that frequently moved across the sella. One possibility is that in the course of scleritome growth the apices of neighbouring mitral sclerites increasingly projected into the space above the sella. Another possibility is that in addition to mineralised sclerites, the scleritome possessed non-mineralised setae that were intercalated between the sclerites. Setae are probably deeply plesiomorphic for lophotrochozoans (Peterson and Eernisse 2001) and given their appearance in the probably more derived tommotiids (*Tannuolina*, *Micrina*), their probable descendants (brachiopods) and possible sister groups (annelids, molluscs; Leise and Cloney 1982; Brocco et al. 1974), it is not unreasonable to assume their presence in *Camenella*.

The possible existence of mobile components within the scleritome, as indicated by the patterns of mechanical wear, contradicts a sessile tubular reconstruction of the *Camenella* scleritome and instead suggests that *Camenella* was a vagrant vermiform organism with a bilateral dorsal cover of symmetrically arranged sclerites. A functional consequence of the partially overlapping sclerites or setae would be to prohibit extensive dorsal flexing. Ventral flexing, however, would have resulted in an effective defensive mechanism as the structures that were resting on the sellae would have fanned out in a protective array.

# Conclusions

Recent discoveries of the first articulated tommotiid scleritomes have turned our concept of this group of early Cambrian problematic organisms around by demonstrating that both *Eccentrotheca* (Skovsted et al. 2008) and *Paterimitra* (Skovsted et al. 2009) had tubular scleritomes and were probably sessile filter feeders. Following these finds, the evolution of the Brachiopoda from tommotiid ancestors via a successive shortening of the tube and specialisation of the sclerites (e.g., *Micrina*; Holmer et al. 2008) appears to be relatively straightforward. However, extending the tubular scleritome construction to all tommotiids may be premature. Although the structure of the *Camenella* scleritome remains elusive in the absence of articulated material, the sclerites were probably arranged along a bilateral axis of symmetry and were less tightly integrated than in *Eccentrotheca* or *Paterimitra*. We consider a vermiform reconstruction of *Camenella* with a dorsal cover of sclerites and a vagrant mode of life most likely. This assertion is based on the presence of well defined sclerite morphologies in almost exactly equal proportions, the lack of articulating surfaces and the probable presence of mobile components within the scleritome (setae or the sclerites themselves). Lapworthellid and kennardiid tommotiids (i.e., *Lapworthella* and *Dailyatia*) share a number of characters with *Camenella*, including details of shell structure and a surface ornament of prominent comarginal ribs, and these tommotiids are interpreted to constitute a monophyletic clade, the camenellans, occupying a basal position within tommotiids.

Given the predominance of vermiform body plans and vagrant life styles in lophotrochozoans and their possible stem

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groups, it must be assumed that the bivalved or tubiform sessile existence of *Eccentrotheca*, *Paterimitra*, *Micrina*, and brachiopods is a derived condition. The possible vermiform body plan and vagrant mode of life outlined above for *Camenella* is consistent with the proposed basal position of camenellans within tommotiids. In our view, this reconstruction and phylogenetic position may be an important piece in the puzzle of reconstructing the complex morphological transformations from a deep lophotrochozoan root through one of its derived branches (tommotiids) to an actual phylum (brachiopods).

# Acknowledgements

Ian and Di Fargher, owners of Angorichina Station are thanked for access to the MMF field locality and for providing excellent field accommodation. Jim Jago (Adelaide, Australia), Bob Morgan, Bo Jonak, Peter Cockle, Brett Pyemont, and Tom Bradley (all Macquarie University, Sydney, Australia) are thanked for assistance in the field. Dennis Rice (SAMP) is thanked for making specimens from the Brian Daily collections available for study. Tim Topper (Macquarie University, Sydney, Australia) helped with SEM work and Mitchell Smith (Macquarie University, Sydney, Australia) picked some of the studied specimens. Lars E. Holmer, Graham E. Budd, and Michael Streng (all Uppsala University, Uppsala, Sweden) provided valuable discussions of tommotiid phylogeny and Lars E. Holmer also read and commented on an early version of the manuscript. We are indebted to Dean Oliver (Dean Oliver Graphics, Sydney, Australia) for drafting Fig. 1. Financial support from the National Geographic Committee for Research and Exploration (grant 7918-05 to GAB, CBS, and JRP), a Macquarie University Development Research Grant to CBS and GAB, and grants from the Swedish Research Council (VR) to CBS and UB are gratefully acknowledged. Constructive reviews by Susannah Porter (University of California, Santa Barbara, USA) and one anonymous reviewer greatly improved the manuscript.

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