Sclerite fusion in the problematic early Cambrian spine-like fossil *Stoibostrombus* from South Australia

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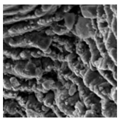

New collections of the problematic spine like fossil *Stoibostrombus crenulatus* Conway Morris & Bengtson from the Mt. Scott Range and Wilkawillina Gorge in the central Flinders Ranges, South Australia contain fused sclerite composites. In each fused specimen the spines are merged along their lateral margins and the orientation of the spines is almost identical. These new specimens confirm that *Stoibostrombus* spines were dermal sclerites, arranged in lateral pairs or transverse rows. The nature of the animal secreting the spines remains elusive, but available evidence suggest that it was an ecdysozoan animal, possibly a palaeoscolecid worm. • Key words: Early Cambrian, South Australia, scleritome, Ecdysozoa, Palaeoscolecida.

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Small Shelly Fossils (SSF) are major constituents of earliest Phanerozoic shelly faunas (Bengtson *et al*. 1990, Gravestock *et al*. 2001, Missarzhevsky 1989, Qian & Bengtson 1989, Rozanov *et al*. 1969, Skovsted 2006). Under this "catch-all" label hides a large number of small scale-, cap- or spine-shaped fossils that often represent disarticulated parts of larger skeletons that remain more or less problematic in terms of zoological affinities. However, some examples can be identified, at least in a broad sense, and may represent early stem group members of modern phyla. In many cases, clues to biological affinity were only provided after exceptional preservation revealed the structure of the complete or partially complete skeleton, or scleritome, of the organism. Such was the case for the net like microfossil, *Microdictyon*, which was discovered to represents dorsal sclerites on a lobopodian (Chen *et al*. 1989, 1995) and the cap-shaped tommotiids (*e.g. Eccentrotheca* and *Paterimitra*) which represent sclerites of stem group brachiopods (Skovsted *et al.* 2008, 2009b, 2011).

Stoibostrombus crenulatus Conway Morris & Bengtson *in* Bengtson *et al*. (1990) has remained one of the most enigmatic Small Shelly Fossils. It is only known from lower Cambrian successions in South Australia (Arrowie and Stansbury basins), but is a relatively common fossil in acid resistant residues ranging from the *Pararaia tatei* trilobite Zone to Toyonian-equivalent horizons in the uppermost lower Cambrian. The cone- or spine-shaped fossils of *Stoibostrombus* are curved to varying degrees and often exhibit an overhanging apex. Each spine is always open at both ends but often do not exhibit any obvious natural or complete margins. The most conspicuous feature of *Stoibostrombus* is the unusual external ornament of pustulose nodes (diagnosed as "pulvinate" by Conway Morris & Bengtson *in* Bengtson *et al.* 1990, p. 145) or crenulated transverse ridges.

Conway Morris & Bengtson (*in* Bengtson *et al.* 1990) compared *Stoibostrombus crenulatus* to *Dimorphoconus granulatus*, a poorly known Ordovician fossil with multiple dorsal spines (Donovan & Paul 1985), suggesting that *S. crenulatus* represented dorsal sclerites of a vagrant benthic animal. Brock & Cooper (1993) noted similarities in general shape and ornament with uthaphosphids suggestive of a palaeoscolecid affinity for *Stoibostrombus*, a hypothesis also supported by Conway Morris (2008). However, Demidenko (*in* Gravestock *et al.* 2001) preferred to compare *Stoibostrombus* to sensory papillae of modern onychophorans. Here, we describe the first occurrence of naturally fused spines of *S. crenulatus*. Although no new unequivocal evidence in favour of any particular phylogenetic hypothesis is presented, the new specimens for the first

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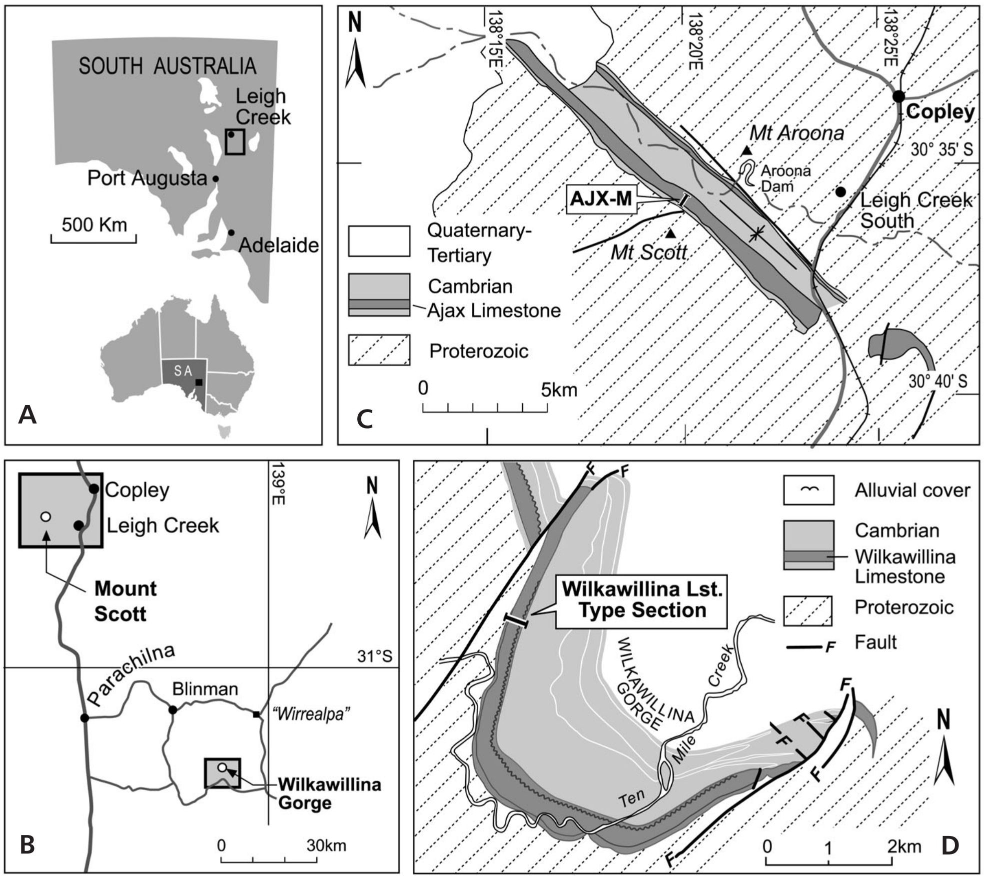

Figure 1. Map figure showing provenance of sampled sections. • A – map showing location in South Australia. • B – generalised map of the Flinders Ranges area showing the location of field areas. • C – detailed map of the Mt. Scott area with the location of section AJX-M indicated. • D – detailed map of the Wilkawillina Gorge area showing location of Wilkawillina type section.

time reveal information on the actual arrangement of spines in *Stoibostrombus*.

Material and geological setting

Large collections of SSF's recovered from multiple sections and localities with exposed lower Cambrian rocks in the Arrowie Basin amassed by the authors during the last decade includes great numbers of *Stoibostrombus crenulatus* (Fig. 1). One of the fused spine pairs described herein (SAMP46285, Fig. 2A–D) is from horizon AJX-M/415, equivalent to 232.07 m (true thickness) above the base of section AJX-M measured through the Ajax Limestone on the northern side of Mt. Scott Range, South Australia. The AJX-M section is located at co-ordinates 30°35´ 49" S, 138°19´ 59.3" E [WGS84] equivalent to section M of Gravestock (1984, fig. 2). The stratigraphy and lithology of the Ajax Limestone at section AJX-M has been summarized by Brock *et al.* (2006), Skovsted *et al.* (2009a, 2011), Topper *et al.* (2011). The carbonate-dominated Ajax Limestone is approximately 280 m thick at AJX-M and conformably overlies the siliciclastic Parachilna Formation. Parts of the rich faunal assemblage of the AJX-M section have been described intermittently over the last few decades including the archaeocyaths (Gravestock 1984), trilobites, molluscs, sponge spicules and SSFs (Bengtson *et al.* 1990, Topper *et al.* 2011). More recently, the stem group brachiopod *Mickwitzia* sp. (Skovsted *et al.* 2009a), the tommotiid *Eccentrotheca* (Skovsted *et al.* 2011), and a bivalved arthropod assemblage (Topper *et al.* 2010b) have been described from this section. The biostratigraphic range of *Stoibostrombus crenulatus* is largely restricted to the *Pararaia tatei* trilobite biozone in this section.

Three fused specimens were recovered from samples collected from the Second Plain Creek Member of the Wilkawillina Limestone type section (Daily 1956) in Wilkawillina Gorge by the late Brian Daily in the early 1970s. The section occurs along a small tributary to the north-west of 10 Mile Creek within the syndepositional Bunkers Graben (Fig. 1) and the base of the 69 m section through the Second Plain Creek Member occurs at a karstic boundary associated with the regionally significant Flinders Unconformity (Gravestock & Shergold 2001). The base of the section is estimated at 31° 15´ 44.9˝ S, 138° 52´ 39.8˝ E – WGS84; see also Clarke 1986a, fig. 2; Gravestock 1984, fig. 1). The carbonates of the Second Plain Creek Member range from packstones and grainstones near the base into interbedded wackestones and lime mudstones (Clarke 1986b). One fused specimen (SAMP46288, Fig. 3) was recovered from horizon WILK/N, collected at 58 m above the base of the section and two composite specimens (SAMP46286, Fig. 2E-G; SAMP46287, Fig. 2H–J) are derived from horizon WILK/Q, some 65 m above the base of the section. Trilobites have not been described from the Second Plain Creek Member, but associated SSF and lateral stratigraphic alignments suggest an age equivalent to the uppermost *Abadiella huoi* biozone or lowermost *P. tatei* biozone.

Composite spines

Isolated sclerites of *Stoibostrombus crenulatus* from the Stansbury Basin and Arrowie Basin were described in detail and extensively illustrated by Brock & Cooper (1993), Conway Morris & Bengtson (*in* Bengtson *et al.* 1990) and Topper *et al.* (2009). Beyond the occurrence of the fused specimens described herein, no new information relating to the general morphology, microstructure or composition of *S. crenulatus* was revealed by our studies.

The composite specimens each contain two or three spines fused in a lateral file with their apices oriented in roughly the same directions. However, in other respects the four specimens differ dramatically, and are described separately below.

In SAMP46285 the two spines are long and slender cones with an apical diameter of about 30 μm and an apical angle of 15° and 16° respectively (Fig. 2A–D). Adapically the spines coalesce along an apparently straight line (Fig. 2A). The base of the fused sclerite composite is a dome-like sub-spherical structure bounded by uneven and apparently broken margins (Fig. 2C). The characteristic ornament of serrated nodes and discontinuous transverse ridges is equally expressed on each spine before the zone of fusion and is only weakly deflected adapically at the junction (Fig. 2D). The internal surface of the sclerite composite exhibits a uniform ornament of shallow pits except for the zone of fusion which is clearly demarcated as a wide transverse ridge (Fig. 2B).

SAMP46286 preserves one large spine laterally attached to a smaller spine (approximately half the height and diameter at level of junction; Fig. 2E–G). Despite the size difference the spines have approximately the same proportions and both spines are gently curved in the same direction although they are nearly vertical in relation to the base of the specimen (Fig. 2E). Both spines have broken apices. The spines are joined along a slightly curved line which continues as a gentle fold towards the aperture of the specimen. The ornament of nodes and transverse ridges is only slightly disturbed across the line of junction (Fig. 2G).

Three spines are fused in SAMP46287 (Fig. 2H–J). The spines are arranged in a transverse file of decreasing size with the slightly overhanging apices oriented in the same direction (Fig. 2H). The largest spine is a broad, symmetrical cone (apical angle 42°) and is much larger than the other two spines (Fig. 2I). The second and third spines are of similar dimensions and morphology, but the third spine is broken relatively close to their common base. Both the first and the second spines have well preserved apices with smooth rimmed circular apertures (diameter 35 μm; Fig. 2J). The junctions between the spines are partly obscured but the ornament of the basal areas does not appear to be strongly disturbed across the zones of junction. On the posterior side of the specimen the ornament suggests that the two smaller spines were united first and these were fused to the largest spine as a unit (Fig. 2I).

In SAMP46288 two spines of sub-equal size are united (Fig. 3). Both spines exhibit the same morphology, intermediate between narrow spine-shaped and broad cone-shaped (apical angle about 30°; Fig. 3B). However, one of the spines (slightly smaller) is fused to the other at a position somewhat posterior of the other spine, and the directions of the apices diverge by 14° from each other (Fig. 3A). In lateral view it is apparent that the posterior spine is rotated posteriorly in relation to the anterior spine (Fig. 3B). The zone of junction between the spines is a semi-circular arc defined by the posterior spine and exhibits a complicated pattern of folds and crevices affecting the posterior side of the base of the anterior spine (Fig. 3C). However, closer to the aperture the base of both spines are joined more smoothly. The apex of the anterior spine is damaged but the posterior spine preserves a smooth rimmed circular aperture (diameter 25 μm).

Stoibostrombus reconstructed

The recovered specimens, both fused composites and single spines vary extensively in general morphology and ornamentation. Most specimens from the Second Plain Creek Member at Wilkawillina Gorge have an ornament which includes large, nodose plates (Figs 2G, 3D). Such specimens were referred to by Conway Morris & Bengtson (*in* Bengtson *et al.* 1990) as *Stoibostrombus* cf. *crenulatus* but later the new name *Stoibostrombus mirus* Demidenko *in* Gravestock *et al.* (2001) was introduced to accommodate them. We note that within a single collection, specimens of both types occur together, as well as specimens of apparently intermediate morphologies. In the absence of detailed analysis of variability and occurrence patterns we prefer to unite all specimens in a single species.

Although the four specimens with multiple fused spines described above differ from each other they reveal new details concerning the arrangement of the spines in

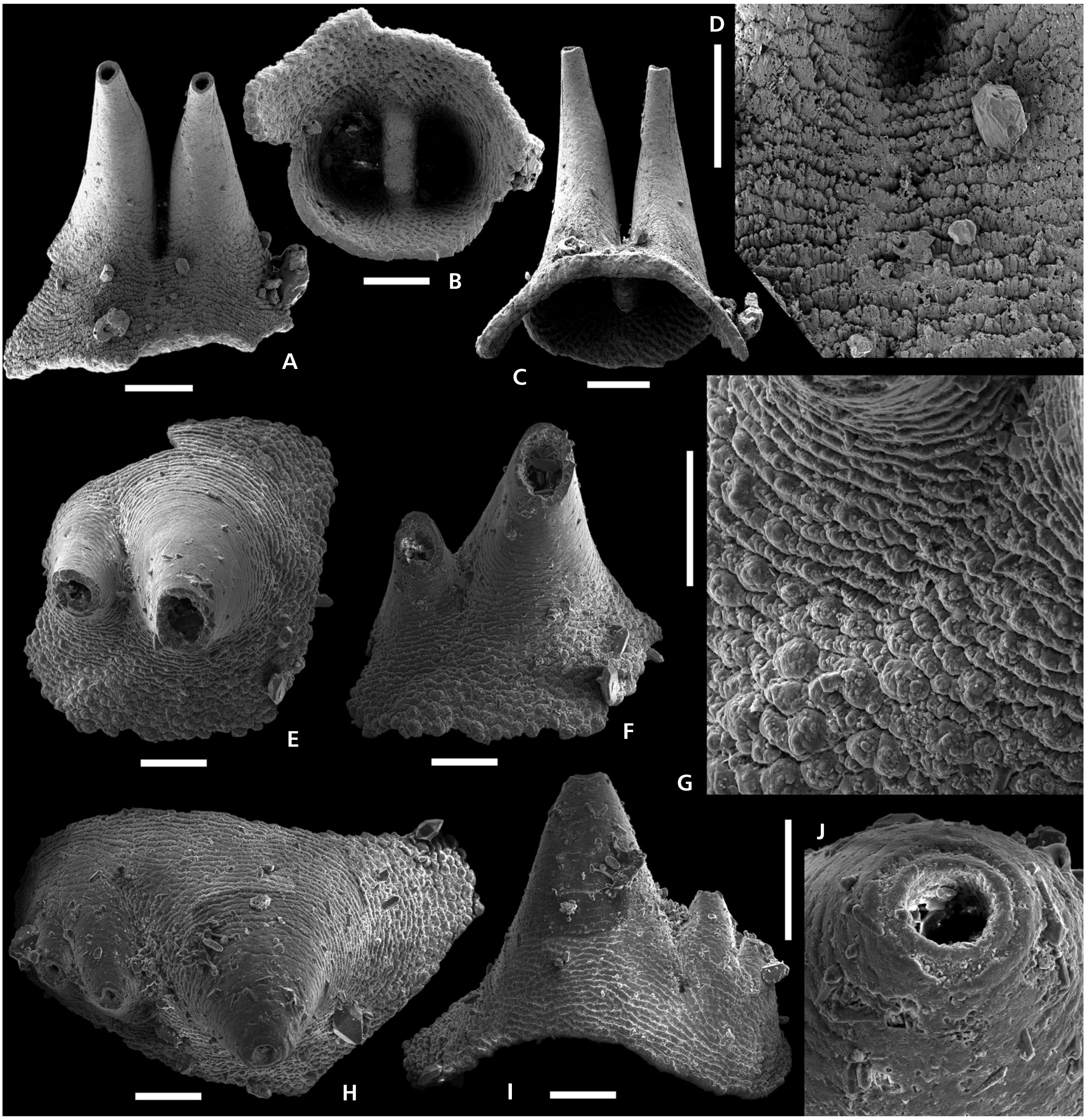

Figure 2. *Stoibostrombus crenulatus* Conway Morris & Bengtson *in* Bengtson *et al.* (1990) from the Arrowie Basin, South Australia. All scale bars except D, G, J equal 100 μm. • A–D – SAMP46285, sample AJXM 415, Mt. Scott. A – oblique anterior view; B – apertural view; C – anterior view; D – detail of junction between spines, scale bar equals 50 μm. • E–G – SAMP46286, Sample Wilk Q, Wilkawillina Gorge. E – dorsal view; F – anterior view; G – detail of junction between spines, scale bar equals 50 μm. • H–J – SAMP46287, Sample Wilk Q, Wilkawillina Gorge. H – dorsal view; I – posterior view; J – detail of apex of largest spine, scale bar equals 50 μm.

scleritome of *Stoibostrombus*. Three specimens have spines joined together side by side or in lateral file with uniform spine orientation (SAMP46285-03). The junctions between spines are smooth and the spines are set on a common dome-shaped base. In SAMP46288 the junction between the spines display evidence of disturbance and spine displacement. In lateral view, this fused specimen suggests that the posterior spine was displaced posteriorly and rotated as it was pressed into the base of the anterior spine. Apically of the zone of junction the posterior spine retains its integrity and seems to have been displaced as a complete solid structure. The anterior spine is more strongly

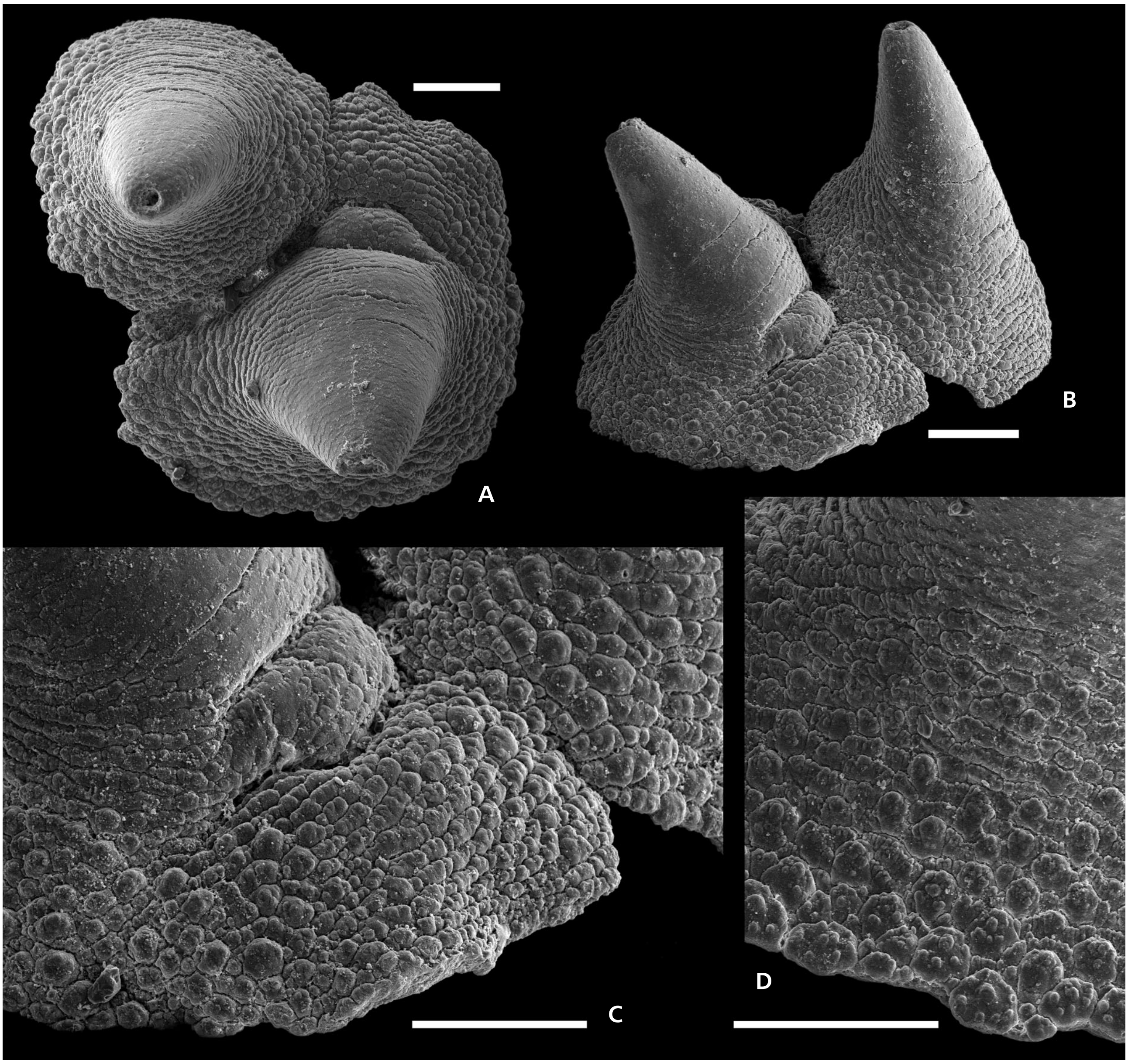

Figure 3. *Stoibostrombus crenulatus* Conway Morris & Bengtson *in* Bengtson *et al*., 1990. • A–D – SAMP46288, Sample Wilk O, Wilkawillina Gorge, Arrowie Basin, South Australia. All scale bars equals 100 μm. A – dorsal view; B – oblique posterior view; C – detailed view of zone of junction between spines; D – detail of shell ornament on posterior part of sclerite base.

deformed and seems to have accommodated the posterior spine by folding of its spine base. However, lateral to the folds the spine bases of both spines seem to grade more smoothly into each other.

The available composite specimens indicate that the spines of *Stoibostrombus* were arranged in lateral rows with all spines oriented in the same direction. Each spine, or spine composites in fused specimens, originally formed a dome-shaped mineralised structure (sclerite) with well-defined margins. The rounded internal ridge in SAMP46285 represents the zone of junction of the fused spines and is situated deep inside the internal cavity of the dome-shaped spine base and clearly demonstrates that fusion occurred in connection with the mineralisation of the sclerites. In the case of SAMP46288 two adjacent spines were affected by lateral compression at the time of sclerite formation, which caused one of the spines to be displaced backwards and rotated. A single specimen of *S. crenulatus* from the Ajax Limestone at Mt. Scott described by Conway Morris & Bengtson (*in* Bengtson *et al*. 1990, fig. 96E, F) preserves a large flat node or plate on the lateral side of the main spine. This structure may also correspond to a second spine, being deformed during an early stage of shell secretion.

Biological affinity of *Stoibostrombus*

A subset of early Cambrian SSF's are believed to be phosphatic by original composition. Among these groups, such as the cap-shaped tommotiids (see Skovsted *et al.* 2008, 2009b) or the tubular *Hyolithellus* (see Skovsted & Peel 2011), grew by marginal accretion and most likely represent early stem group members of the lophotrochozoan clade. Other phosphatic SSF's lack evidence of incremental growth and are more likely to represent early members of the Ecdysozoa. *Microdictyon* (see Chen *et al.* 1995, Topper *et al.* 2011), net-like sclerites from a lobopodian, belong to this group. In the case of *Stoibostrombus* the original composition is uncertain, but is likely to be phosphatic. This hypothesis is supported by the fact that the spines themselves are much more frequently preserved in acid residues than their internal moulds, which is opposite the case for the superficially similar hyoliths (cone-shaped, mollusc-like calcareous problematica; see Bengtson *et al*. 1990). The external ornament of transverse ribs which are often present on parts of the spines or spine bases in *Stoibostrombus* may be superficially similar to comarginal growth increments of shells growing by marginal accretion. However, the ribs are often discontinuous, and adapically disintegrate into discrete 'pulvinate' nodes or plates. This type of ornament is similar to the cancellate ornament of *Mongolitubulus* Missarzhevsky, 1977 (see Skovsted & Peel 2001). However, *Mongolitubulus* specimens are now known to represent broken carapace spines from bradoriid arthropods (Skovsted 2005, Topper *et al*. 2007).

Unfortunately, the new information on sclerite arrangement in *Stoibostrombus* does not reveal much concerning the gross scleritome morphology of the animal secreting the spines or its biological affinity. Conway Morris & Bengtson (*in* Bengtson *et al.* 1990) compared *Stoibostrombus* to *Dimorphoconus* Donovan & Paul, 1985, known from aggregates of cone-like shells from the lower Ordovician of Shropshire. The granular cones of *Dimorphoconus* were arranged in a central zone with broad cones and a lateral rim with densely spaced long and narrow cones (Donovan & Paul 1985, fig. 3). This arrangement is quite different from that of *Stoibostrombus* as interpreted herein, and the two fossils are probably not closely related. The characteristic ornament of *Stoibostrombus*, especially forms incorporating large plates, is reminiscent of a host of organophosphatic caps and plates (including *Uthaphospha* Müller & Miller, 1976, *Kaimenella* Märss, 1988 and *Hadimopanella* Gedik, 1977 *etc*.) that are generally thought to represent dermal plates of palaeoscolecid worms (see review in Topper *et al.* 2010a). Of these taxa *Stoibostrombus* is most closely comparable to *Chalasiocranus* Brock & Cooper, 1993 from slightly younger, Toyonian-equivalent rocks of South Australia and the widespread *Uthaphospha* (see review in Hinz *et al*. 1990). In palaeoscolecids, phosphatic sclerites are usually arranged in transverse rows defined by the distinct annulations of the vermiform body (Hinz *et al.* 1990, Topper *et al.* 2010a).

The transverse arrangement of the spines could be explained if *Stoibostrombus* was interpreted as a palaeoscolecid worm. However, the dome-shaped spine base of both single *Stoibostrombus* spines and the fused composite specimens described above, suggest that the scleritome would be much more strongly ornamented than in any bona fide palaeoscolecids known from the fossil record (see Conway Morris 2008 and Topper *et al*. 2010a for recent reviews). At the present time we can only conclude that the proposed relationship of *Stoibostrombus* with ecdysozoans is supported by the available evidence and that *Stoibostrombus* may be most closely related to palaeoscolecid worms.

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