

ONTOGENY AND MICROSTRUCTURE OF THE ENIGMATIC CAMBRIAN TOMMOTIID *SUNNAGINIA* MISSARZHEVSKY, 1969

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Abstract: The tommotiids are a significant component of the earliest skeletal animal remains in the fossil record, occurring in large numbers in the Lower Cambrian. Sclerites of the tommotiid genus *Sunnaginina* have been implicated as integral to hypotheses regarding the evolution of the brachiopod body plan, with a morphology intermediate between the unspecialized sclerites of the tubular *Eccentrotheca* and the specialized sclerites of the tannuolinids. Abundant *Sunnaginina* ?*imbricata* sclerites, of a broad ontogenetic spectrum, were recovered from the Comley Limestone, Lower Cambrian (Stages 3–4), Shropshire, UK and compared to *Sunnaginina imbricata* from the Aldan River, Siberia (uppermost Tommotian). New microstructural data, collected using synchrotron radiation X-ray tomographic microscopy, reveal a unique microstructure for *Sunnaginina* ?*imbricata* sclerites among the tommotiids; interlamellar cavities spanned by a series of continuous pillars, giving a colon-naded appearance contrasting to that of *S. imbricata*. These

data refute the inclusion of *Eccentrotheca* within the Sunnaginiidae and highlight the need for a revision of suprageneric classification of the tommotiids. Rather, structural similarities between *Sunnaginina* sclerites and those of the tannuolinids suggest a close affinity to this group. Recent phylogenetic hypotheses place the tannuolinids as stem-linguliform brachiopods, with *Paterimitra* plus the paterinid (and possibly rhynchonelliform) brachiopods as their sister group. Our new data therefore resolve *Sunnaginina* as close to the node defining crown-Brachiopoda. However, the characters supporting this phylogenetic scheme cannot be consistently applied to all taxa, nor do they define a series of nested clades. We therefore suggest that a more thorough phylogenetic analysis is required in the light of the data presented here and other recent descriptions.

Key words: *Sunnaginina*, Tommotiida, Brachiopoda, small shelly fossils, ontogeny, Cambrian, Comley Limestone.

EARLY Cambrian so-called ‘small shelly fossils’ are among the most ancient skeletal remains known from the animal fossil record. The small shelly faunas include stem representatives of biomineralizing phyla, as well as enigmatic forms of unknown biological affinity (Bengtson 2004). As such, they have a pivotal role to play in resolving whether the Cambrian explosion hypothesis reflects a rapid diversification of animals or, rather, a dramatic increase in the abundance of fossils recording the existence of lineages that had long since diverged (Runnegar 1982). Despite their significance, the small shelly faunas have been relatively understudied.

The tommotiids are a diverse group of small shelly fossils integral to debate over the origin of the brachiopod body plan (Balthasar *et al.* 2009; Skovsted *et al.* 2009a). *Sunnaginina* is an integral taxon, with an apparently transi-

tional morphology between the irregular sclerites of *Eccentrotheca* and the ‘organized’ tannuolinids (Bengtson *et al.* 1990). However, the phylogenetic relationship between *Sunnaginina* and the other tommotiids is unclear, and there has not been a revision of the suprageneric taxonomy of tommotiids subsequent to recent redescrptions of the histology and scleritome reconstruction of several key taxa. The aim of this study is to critically evaluate competing hypotheses for the phylogenetic position of *Sunnaginina* within the brachiopod stem. This will be achieved by first characterizing the ontogeny and internal structure of *Sunnaginina* sclerites for comparison to other tommotiids allied to the brachiopod stem. Ultimately, this will provide a test of the hypothesis that *Sunnaginina* represents a key step in the evolution of the brachiopod body plan.

HISTORY OF RESEARCH

The order Tommotiida Missarzhevsky, 1975, as emended by Landing (1995) contains four families: Tommotiidae Missarzhevsky, 1969, Tannuolinidae Fonin and Smirnova, 1967, Lapworthellidae Missarzhevsky, 1966, and Sunnaginiidae Landing, 1984. The Sunnaginiidae have the widest range of morphologies among the tommotiids. The genera included, *Eccentrotheca* Landing *et al.*, 1980, *Jayceia* Landing, 1995, *Kulparina* Conway Morris and Bengtson *in* Bengtson *et al.* 1990, and *Sunnaginina* Missarzhevsky, 1969, have single or multiunit scleritomes with two broad categories of sclerites; low, broad, left- and right-handed sclerites and high, laterally compressed cap-shaped sclerites. However, a whole spectrum of transitional morphologies has been documented from most genera (Landing 1995).

Sunnaginina, originally described from the Siberian platform (Rozanov *et al.* 1969), is now known from Lower Cambrian deposits of North America (Landing *et al.* 1980; Landing 1988, 1995), England (Brasier 1986; Hinz 1987), Australia (Bengtson *et al.* 1990) and Mongolia (Grigorieva 1982; Esakova and Zhegallo 1996). The described material consists of symmetrical paired (right and left) sclerites defined by up to four lobes, with a broadly pyramidal morphology and generally reconstructed as composing a uni-membrate scleritome. Because of the occurrence of chiral symmetry and approximate equal proportions of each morphotype (Hinz 1987), the scleritome is inferred to be bilaterally symmetrical. Landing (1995) described multisclerite units composed of tiny cap-shaped sclerites fused to larger conoidal plates, thus proposing a bimembrate scleritome. Landing (1995) further suggested that some cap-shaped sclerites described as *Eccentrotheca kanesia* and *Jayceia delatiformis* belong to the *Sunnaginina imbricata* scleritome. Skovsted *et al.* (2008) suggested that *Sunnaginina* represents a stem phoronid and imply a tubular scleritome akin to that for the related tommotiid *Eccentrotheca*. They do not comment on the disposition of sclerites within this scleritome model, further articulated material being required to address this issue.

The ornament of *Sunnaginina* sclerites is dominated by a series of coarse growth ridges. Hinz (1987) identified a polygonal pattern on the underside of a sclerite. Such a pattern has been noted in several other tommotiids including *Lapworthella*, *Tannuolina* (Conway Morris and Chen, 1990), *Kennardia*, *Dailyatia* and *Paterimitra* (Laurie 1986; Bengtson *et al.* 1990). This reticulate pattern has been suggested (in *Kennardia*) to indicate the presence of epithelial tissue that mantled part of the outside of the sclerite, as well as contributing to basal secretion as in other tommotiids (Bengtson *et al.* 1990, p. 134), and used to suggest epithelial cell size, and by inference, genome content (Conway Morris and Chen 1990).

Landing *et al.* (1980) and Landing (1995) described the microstructure of the *Sunnaginina* sclerite from etched sections, as divided into three layers. First-formed parts of the sclerite are composed of finely crystalline apatite ('dense layering'), followed by elongate apatite crystals found on the upper and lower surface of each horizontal septum and on the inner shell surface between septa (the 'prismatic layer'). The prismatic layer is locally deflected 90 degrees to form hollow columnellae extending perpendicularly across the interseptal space. Hinz (1987) also noted transverse 'rods', which support single layers, suggesting that they may represent a means of reducing weight and/or conserving apatite. Neither author comments on the spatial distribution of the 'rods' within the interseptal space. Finally, development of blocky, equidimensional apatite ('coarse-layering'), initiated at outer margin, may or may not fill the interseptal space (Landing *et al.* 1980).

The tommotiids (*sensu lato*) have more recently been interpreted as a paraphyletic ensemble comprising the brachiopod stem (Balthasar *et al.* 2009; Skovsted *et al.* 2009a). The 'camenellans' (consisting of *Lapworthella*, *Dailyatia*, *Camenella* and similar forms) form a sister clade to the remaining tommotiids plus brachiopods and are reconstructed as vagile organisms with a dorsal skeleton (Skovsted *et al.* 2009a). *Eccentrotheca* and *Paterimitra* share microstructural features with paterinid brachiopods and, based on articulated specimens (Skovsted *et al.* 2008, 2009b), are believed to be sessile filter feeders, with *Eccentrotheca* as a candidate stem phoronid (Skovsted *et al.* 2008, 2011). On the basis of the presence of striated setal tubes and other morphological and ultrastructural features (Williams and Holmer 2002; Holmer *et al.* 2008), the tannuolinids (*Micrina* and *Tannuolina*) are proposed as the immediate sister group to crown linguliform brachiopods. *Paterimitra* has been suggested as a stem-rhynchonelliform (Holmer *et al.* 2011). Although the precise topology of the brachiopod stem is in a state of flux, the broad sequence of character acquisition predicted by this hypothesis is a specialization and reduction in number of sclerites, and an evolution in mode of life from vagile to sessile (Skovsted *et al.* 2008, 2009a, b). The position of *Sunnaginina* within this scheme is currently unclear, although it is generally regarded as closely related to *Eccentrotheca* and *Kulparina* (Skovsted *et al.* 2008).

MATERIALS AND METHODS

New material for this study was collected from *ex situ* blocks known to be quarried from the Comley Limestone, Lower Cambrian, Shropshire, UK. The Comley Limestones form the upper part of Stage 3 and Stage 4 (Series 2) of the Cambrian of Shropshire and are dated between

514.45 ± 0.36 and 509.10 ± 0.22 Ma (Harvey *et al.* 2011). Approximately 16 kg of rock was digested using 7 per cent buffered acetic acid following Jeppsson and Anehus (1995). The residue was sieved using $63 \mu\text{m}$ and 1 mm sieves, and the finer fraction was density separated using bromoform to concentrate the phosphatic material. Fossils were recovered by manual picking of the resulting heavy fraction under a binocular microscope. Approximately 80 sclerites or sclerite fragments of *Sunnaginina* ?*imbricata* and *Eccentrotheca* sp. were recovered in roughly equal proportions. In addition, a total of eight other specimens were examined, comprising of five new specimens and three paratypes (Fig. 1) of *Sunnaginina imbricata* Missarzhevsky, 1969, from collections housed at the Swedish Museum of Natural History. These specimens originate from the original collections of Missarzhevsky (Rozanov *et al.* 1969) from the Aldan River, Siberia and are uppermost Tommotian in age. Specimens were mounted on 3-mm brass stubs using clear nail varnish and volumetrically characterized using synchrotron radi-

ation X-ray tomographic microscopy (SRXTM) (Donoghue *et al.* 2006). Measurements were taken using $\times 10$ and $\times 20$ objective lens at 13–17 keV. For each data set, 1501 projections over 180 degrees were acquired, resulting in volumetric data with voxel sizes of 0.74 and $0.37 \mu\text{m}$, respectively. These experiments were performed on the TOMCAT beamline (Stampanoni *et al.* 2006) at the Swiss Light Source, Paul Scherrer Institut, Villigen, Switzerland. Several specimens were mounted in acrylic resin and sectioned before being carbon coated for backscatter electron (BSE) imaging and energy dispersive spectrometry (EDS) and subsequently etched in orthophosphoric acid for 30 s before analysis using secondary electron (SE) using a Hitachi S-3500N scanning electron microscope at University of Bristol. Specimens are deposited at Swedish Museum of Natural History, Stockholm.

Landing *et al.* (1980) devised a nomenclature for *Sunnaginina* sclerites, labelling lobes 'L1–4' and sides 'S1–4'. This was later revised (Landing 1995) to encompass more triangular sclerites and applied to *Eccentrotheca* and

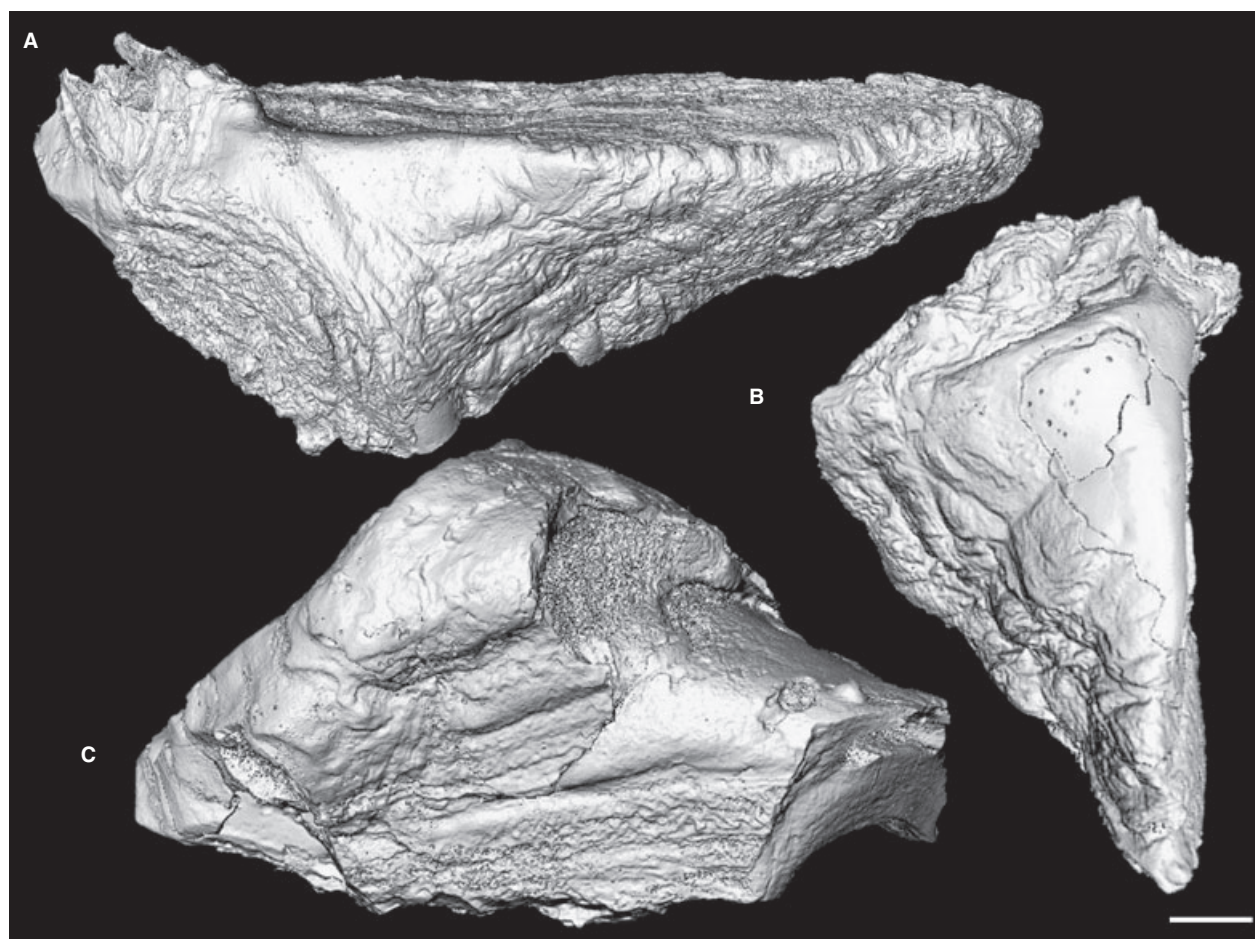


FIG. 1. *Sunnaginina imbricata* Missarzhevsky, 1969 (paratypes) from Aldan River, Siberia, Russia; Uppermost Tommotian, Cambrian. SRXTM renderings of complete sclerites. A. NRM-PZ X 4463 left-handed sclerite in apical view. B. NRM-PZ X 4466 left-handed sclerite in postero-apical view. C. NRM-PZ X 4465 left-handed sclerite in lateral view. Scale bars represent $200 \mu\text{m}$ (A–B) and $150 \mu\text{m}$ (C).

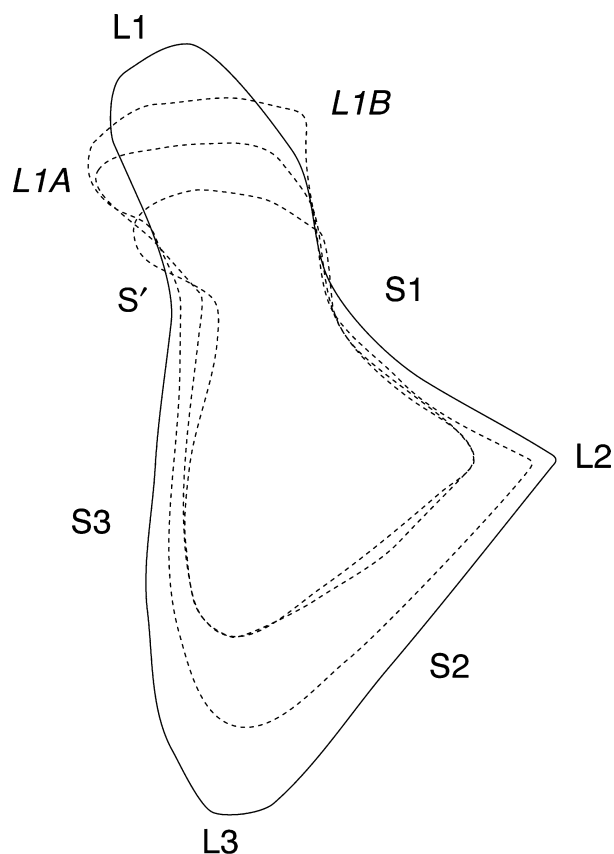


FIG. 2. Apical view of right-handed *Sunnaginina* sclerite with anatomical notations for lobes (L1–4), sides (S1–3) and sulcus (S'), dashed lines represent earlier growth stages, after Landing (1995).

Jayceia, implying restricted growth on side 'S1' and elongation along lobe 'L3'. This modified nomenclature is used herein (Fig. 2).

The genus *Sunnaginina* is nominally divided into five species, for discussion see Hinz (1987, p. 84). Owing to the high morphological variability of the sclerites, such a comprehensive species concept has been refuted (Hinz 1987; Bengtson *et al.* 1990). The Comley specimens studied are superficially indistinguishable from the Siberian material of *Sunnaginina imbricata*; however, the significant differences in internal structure described below bring this affinity into doubt. To reflect this uncertainty, the Comley specimens are here assigned to *Sunnaginina ?imbricata*.

RESULTS

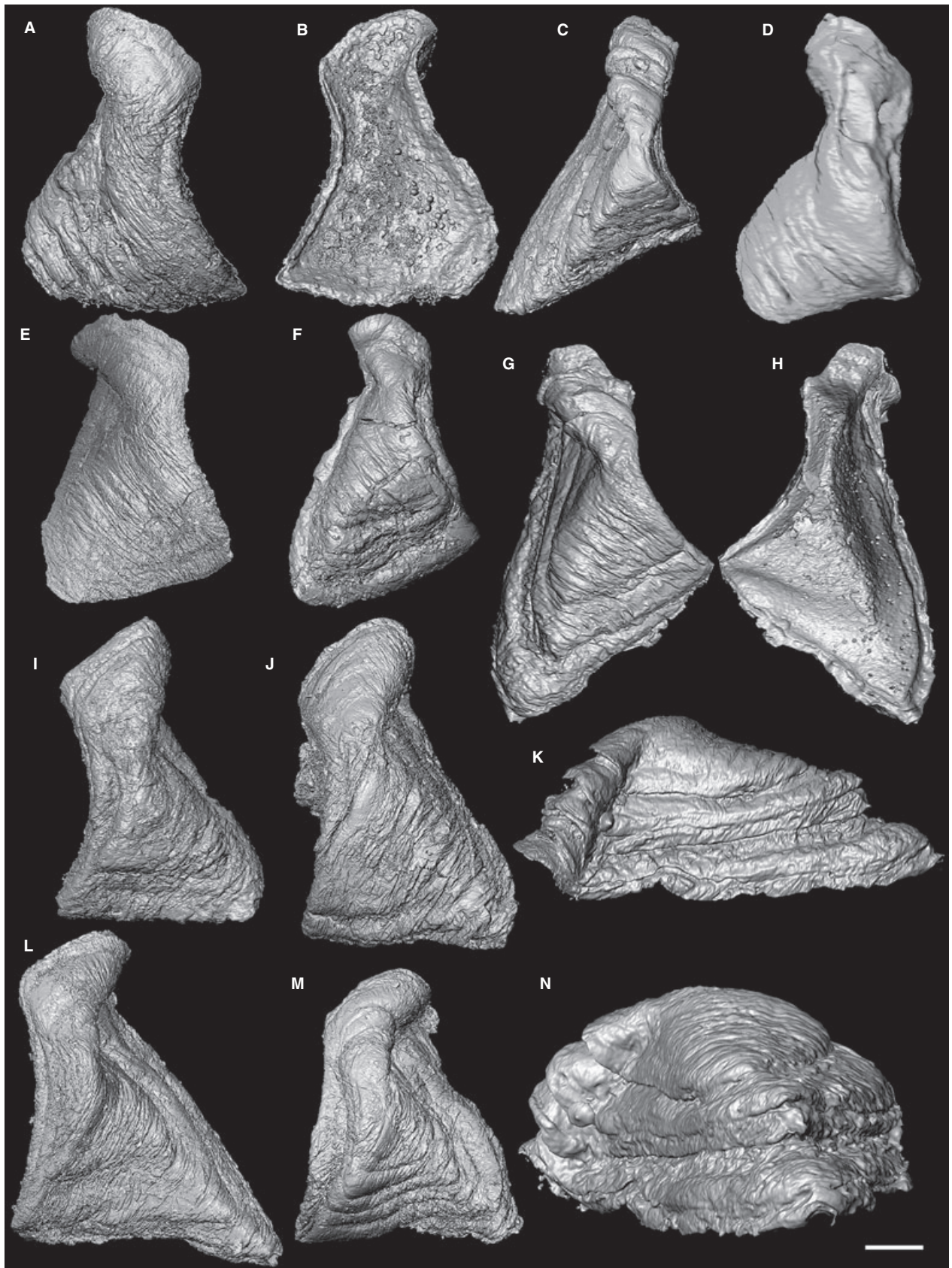
Ontogeny

A number of individual sclerites have been examined with a range of sizes from a single growth stage to more than 15 growth stages and distinguished as dextral or sinistral forms based on whether they exhibit either a strong right or left asymmetry when viewed from above, respectively. After the initial mineralization of the sclerite, the lamellar record indicates that growth continued on the adapical side, and thus a complete ontogenetic sequence is conserved within the sclerochronology of the sclerites. This is corroborated by the closely comparable morphology of the apical growth stage of large sclerites and sclerites composed of a single growth stage (Fig. 3A–D). Sclerites representative of different growth stages show that as growth progresses, the overall morphology of the sclerite changes: the sclerite deepens and becomes increasingly twisted around the anterior-posterior axis. In the majority of specimens, lobe L3 becomes more acute and angular. Consequently, sides S2 and S3 become longer relative to the overall sclerite length, side S1 becomes more concave, and sides S2 and S3 more convex. In later stages lobes L1A and L1B often coalesce into a single lobe (L1), and the sulcus (S') is correspondingly less pronounced, as noted by Hinz (1987). Lobe L2 approximates a right angle throughout ontogeny. These changes result in the development of a broadly triangular outline when viewed from the apex in more mature sclerites (Figs 1A–B, 3E–I, K). A different ontogenetic pathway can be observed in a subset of specimens. Rather than reduction to a single lobe, L1B becomes increasingly acute as the sulcus becomes deeper, and the growth of side S3 is restricted relative to the other morphotype, resulting in an approximately trapezoid outline (Fig. 3J, L–M).

Sclerite architecture

Tomotiids are generally accepted to be composed of lamellar calcium phosphate. EDX analysis of Comley material is consistent with hydroxyapatite. In *Sunnaginina*, this takes the form of alternations of dense and porous laminae, which are observed as light and dark layers respectively,

FIG. 3. *Sunnaginina ?imbricata* Missarzhevsky, 1969 from Comley Limestone, Shropshire, UK; Lower Cambrian. SRXTM renderings of complete sclerites. A, B. NRM-PZ X 4451 right-handed sclerite consisting of a single growth stage in apical (A) and adapical (B) views. C–D. NRM-PZ X 4452 right-handed sclerite in apical (C) view and enlarged initial growth stage (D) to show similarity to (A). E, NRM-PZ X 4453 right-handed sclerite in apical view. F, NRM-PZ X 4454 right-handed sclerite in apical view. G–H, K, N, NRM-PZ X 4455 right-handed sclerite in apical (G), adapical (H), lateral (K) and anterior (N) views. I. NRM-PZ X 4457 left-handed sclerite in apical view. J, NRM-PZ X 4456 left-handed sclerite in apical view. L, NRM-PZ X 4458 left-handed sclerite in apical view. M, NRM-PZ X 4459 left-handed sclerite in apical view. Scale bars represent 100 μ m (A–B, D, F), 360 μ m (C, N), 150 μ m (E, I–J), 450 μ m (G–H, K) and 220 μ m (L–M).



both on SRXTM slices (i.e. lighter tones represents higher X-ray attenuation) and on backscatter electron imaging (i.e. lighter tones represent higher atomic number) of polished sections (Fig. 5A–B). Beyond this, there are some significant differences in internal structure of Siberian *S. imbricata* and *S. ?imbricata* from the Comley Limestone.

The microstructure of *S. imbricata* broadly follows the pattern of alternating dense and porous lamellae noted in other tomotiids; however, they lack the degree of organization reported in *Eccentrotheca* and *Paterimitra* sclerites (Balthasar *et al.* 2009). Rather than being organized into discrete packages of first- and second-order laminations, the laminae occur at irregular intervals and vary in thickness from $>20\text{ }\mu\text{m}$ to just a few microns (Fig. 4A, C–E). Where discrete packages of second-order laminations occur, they are laterally inconsistent, producing cross-cutting relationships, not entirely reflective of the external sclerite morphology. A number of specimens have cracked along laminae resulting in curved sheet-like fractures (Fig. 4E), and in other cases, small ($20\text{--}50\text{ }\mu\text{m}$) approximately spherical holes interrupt the laminae (Fig. 4D–F). In a few cases, these holes are the dominant texture and laminae are difficult or impossible to discern (Fig. 4F).

Sclerites of *Sunnaginina ?imbricata* consist of a number of discrete units expressed as ridges on the external ('outer') surface. Each growth unit consists of these layers of apatite (laminae), which comprise the sclerite wall. At the base of each unit, the final set of laminae extends across the adapical side to form a septum and enclose a cavity (interseptal space). The three-dimensional shape of the interseptal space approximates that of the overall morphology of the growth unit it is within, although it is often not expressed in reduced parts of the sclerite (e.g. 'anterior' of *Sunnaginina*). Laminae show a higher degree of organization than in the Siberian material, with sets up to $20\text{ }\mu\text{m}$ thick (Fig. 5D) and little evidence of cross-cutting relationships, but this second-order lamination is rarely laterally extensive being largely poorly developed.

The interseptal space may be infilled by diagenetic crystalline apatite and silicate mineral grains ($c. 2\text{ }\mu\text{m}$ in diameter), as shown by EDX analysis (Fig. 5C). This material grades between (as well as within) individual specimens from entirely infilling the interseptal space, through lining the margins, to complete absence (Fig. 6). As well as in the interseptal space, silicate minerals have

been identified forming a thin ($1\text{--}2\text{ }\mu\text{m}$) coating around the internal surfaces of the sclerites (Fig. 5E). The presence of silicates in both these positions is consistent with the association of organic material and silicification (Skovsted *et al.* 2009a). Pillars of apatite span the interseptal space. Although apparently randomly arranged throughout the cavity giving a colonnaded appearance, they are often consistent across several growth units, forming a column of apatite perpendicular to the apical surface through much of the sclerite (Fig. 7). The pillars are not hollow, as suggested by Landing (1995), and there is no evidence for a deflected 'prismatic layer'.

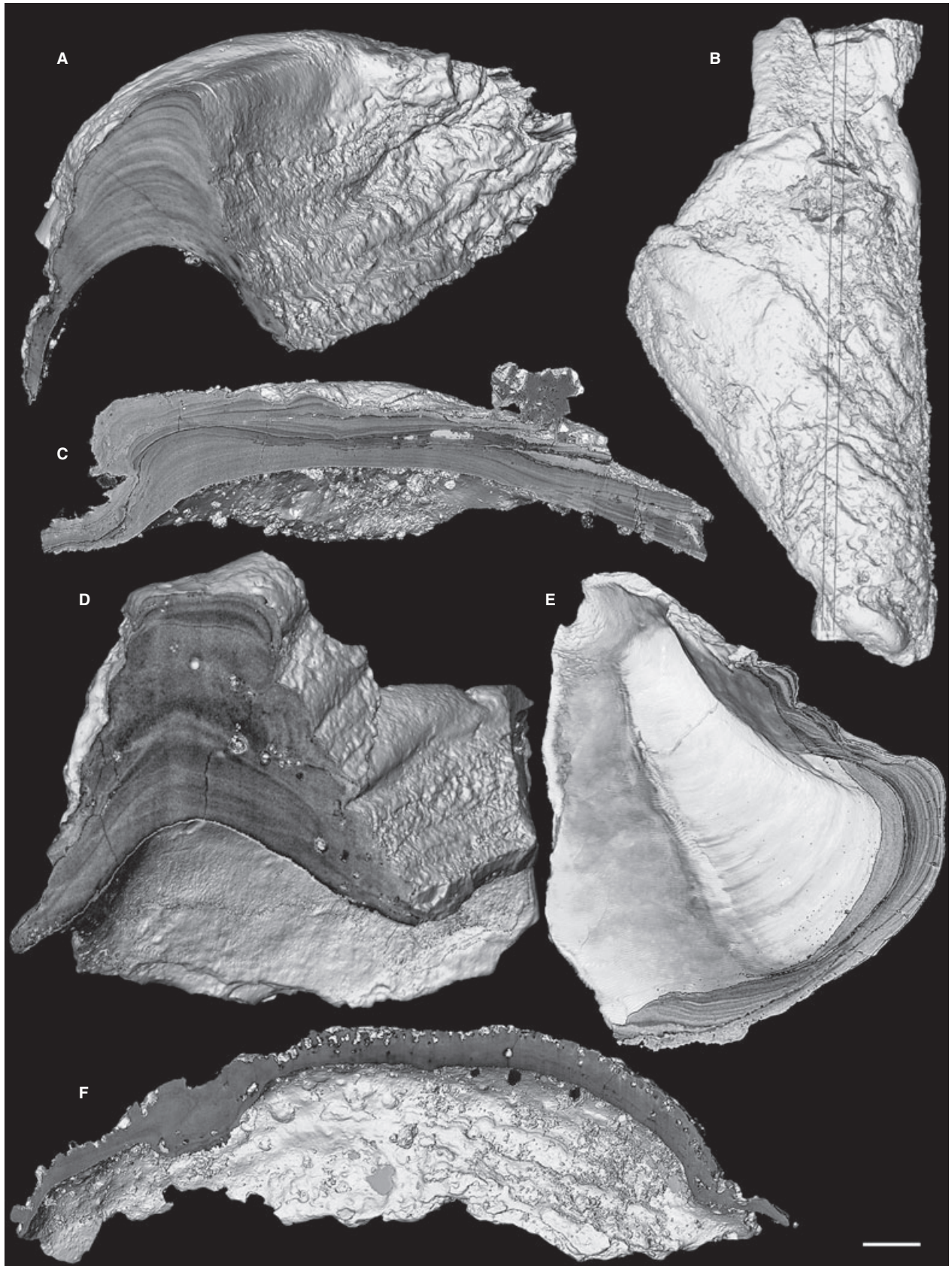
INTERPRETATION

Microstructural variations between S. imbricata and S. ?imbricata

The difference in microstructure between Siberian specimens of *Sunnaginina imbricata* and those previously assigned to the same taxon from the Comley Limestone belies their similarities in external morphology. These differences are sufficient to call into question the synonymy of the Comley Limestone material to *Sunnaginina imbricata*. Instead we assign the Comley Limestone material to *S. ?imbricata* using the nomenclature suggested by Bengtson (1988). The differences may be explained by differences in the preservational or diagenetic history. However, in both sets of sclerites the laminae are consistent with original biological structures and contrast with diagenetic silicate crystals found within cavities of *S. ?imbricata*. The cracks and holes within some specimens of *S. imbricata* probably reflect shrinking and dissolution of globular concretions associated with the loss of an organic-rich material during diagenesis or processing, but this is insufficient to explain the differences between these two suites of *Sunnaginina* sclerites.

An alternative explanation for the observed differences between these sclerites is that the colonnaded microstructure of *S. ?imbricata* is novel and may be derived from the lamellar fabric of *S. imbricata*. This is consistent with the stratigraphic relationship of the two deposits (see Materials and Methods) and the greater similarity between the Siberian material and the microstructure of other tomotiids, for example *Eccentrotheca* and *Paterimitra* (Balthasar *et al.*

FIG. 4. *Sunnaginina imbricata* Missarzhevsky, 1969 from Aldan River, Siberia, Russia; Uppermost Tommotian, Cambrian. SRXTM renderings of complete sclerites. A. NRM-PZ X 4463 sclerite with artificial section to reveal growth lamellae in antero-lateral view. B–C. NRM-PZ X 4464 complete sclerite in apical view with line and section marked (B) and with artificial section to reveal growth lamellae in lateral view (C). D. NRM-PZ X 4465 sclerite with artificial section to reveal growth lamellae in anterior view. E. NRM-PZ X 4466 sclerite with artificial section to reveal growth lamellae in adapical view. F. NRM-PZ X 4467 sclerite with artificial section to reveal loss of lamellar structure in lateral view. Scale bars represent $200\text{ }\mu\text{m}$ (A), $150\text{ }\mu\text{m}$ (B–C, F) and $220\text{ }\mu\text{m}$ (D–E).



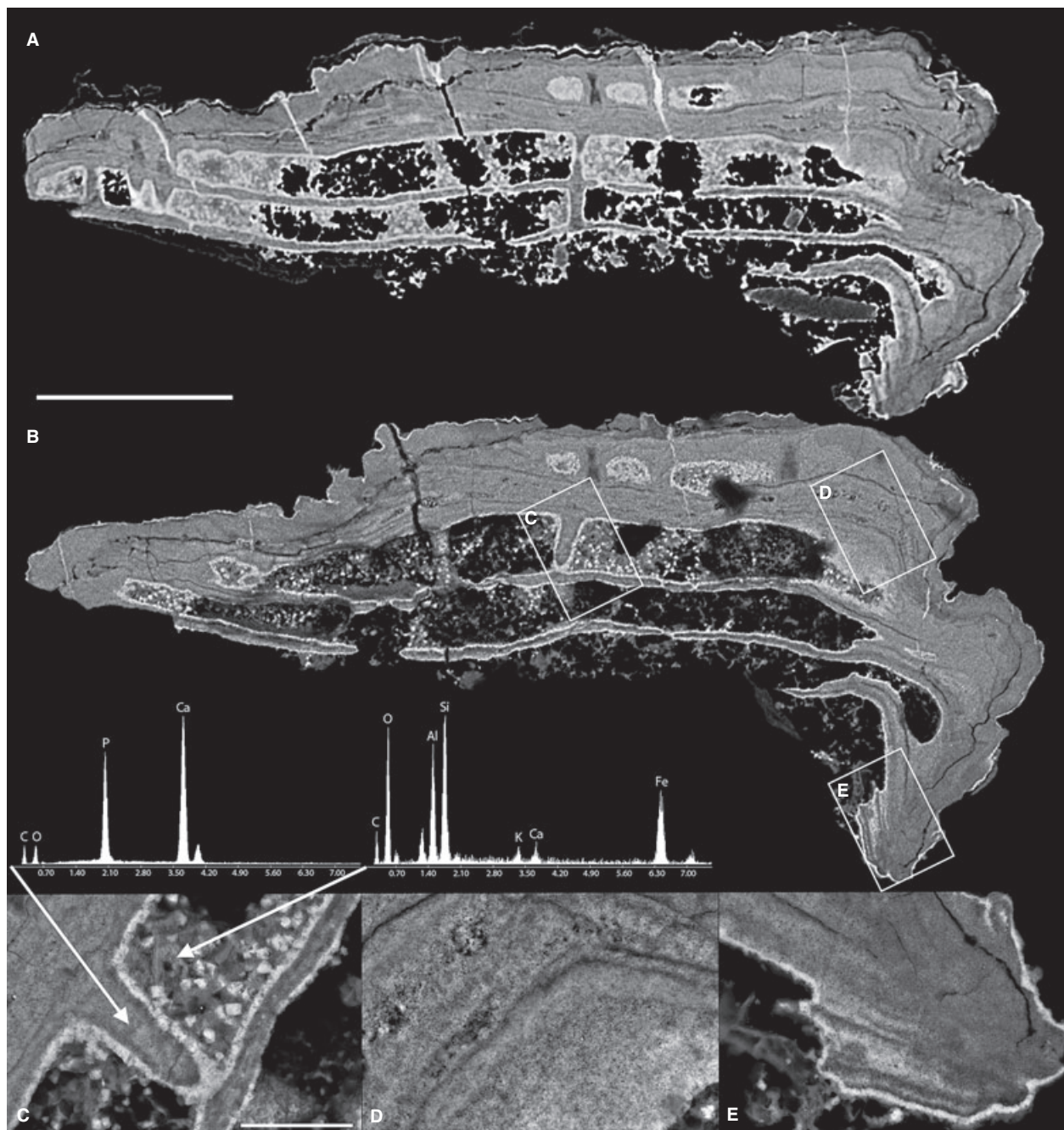


FIG. 5. *Sunnaginia* ?*imbricata* Missarzhevsky, 1969 from Comley Limestone, Shropshire, UK; Lower Cambrian. SRXTM (A) and SEM (B–E) images. A–E, NRM-PZ X 4457 longitudinal sections showing internal structure. A, SRXTM-generated section, in a similar plane to that of B, and showing comparable structures. B, polished section imaged using BSE-SEM. C–E, magnified portions of B, locations denoted by boxes, of pillar structure and interseptal cavity with EDX spectra (C), and laminated structure (D–E). Scale bars represent 100 μm (A–B) and 20 μm (C–E).

2009). Both possess a basic structure of lamellar apatite, resulting in the same gross morphological features. This does not, however, rule out the possibility this morphology was independently acquired. The origin of the small holes within sclerites of *S. imbricata* is unclear and may be due to

diagenesis. It seems unlikely that they are homologous with the large interseptal cavities seen in *S. ?imbricata* as they truncate, rather than deflect, the surrounding laminae, and appear randomly distributed, rather than coincidental with the gross morphology.

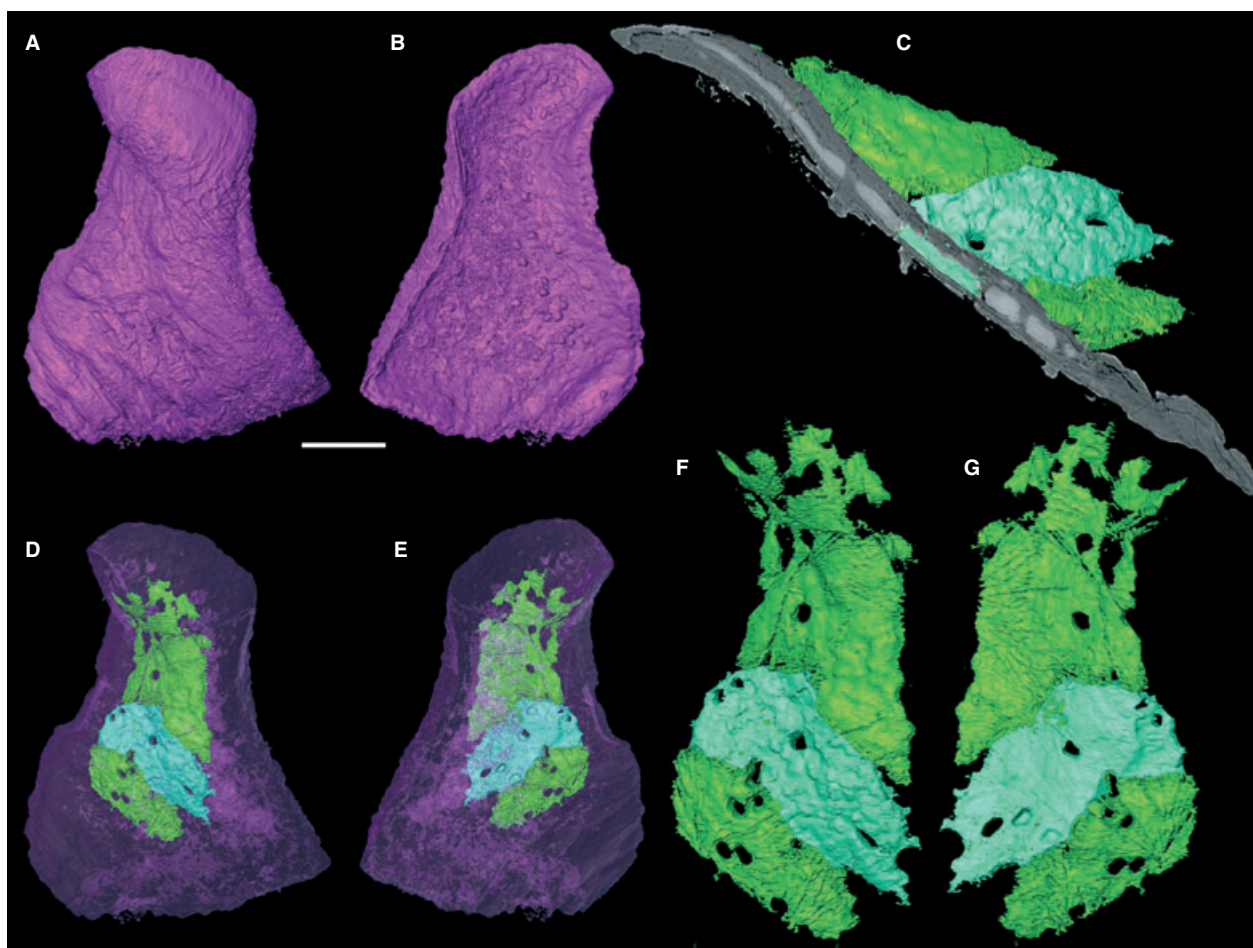


FIG. 6. *Sunnaginia ?imbricata* Missarzhevsky, 1969 from Comley Limestone, Shropshire, UK; Lower Cambrian. SRXTM images. A–G, NRM-PZ X 4451 right-handed sclerite consisting of a single growth stage, with volume rendering of open interseptal cavity (blue) and diagenetically infilled interseptal cavity (green), within surface rendering of complete volume (purple). A–B, rendering of complete sclerite in apical (A) and adapical (B) views. C, SRXTM-generated longitudinal section, showing distribution of open and infilled cavity. D–E, rendering of position of interseptal cavity within complete sclerite in apical (D) and adapical (E) views. F–G, enlarged rendering of complete interseptal cavity in apical (D) and adapical (E) views. Scale bars represent 200 μm (A–B, D–E) and 100 μm (C, F, G).

Growth of *Sunnaginia* sclerites

Sunnaginia imbricata sclerites grow with notably less organization than has been documented in many other tomotiids, such as the tannuolinids (Li and Xiao 2004) and *Camenella* (Skovsted *et al.* 2009a). Individual laminae may laterally fluctuate in thickness and not extend across the complete sclerite. Although the general pattern of basal internal accretion is present, the organic matrix onto which the sclerites were secreted must have been inherently more disorganized. Cracks and holes within some specimens of *S. imbricata*, may reflect shrinking and dissolution of globular concretions, suggesting they may have also had a higher unmineralized organic component.

As in other tomotioid genera, *Sunnaginia ?imbricata* sclerites grow via the alternate addition of dense and

organic-rich porous laminae with some weak organization into second-order laminae, which are periodically deflected to form colonnaded cavities. Some specimens exhibit an incomplete final septum and possess a number of partly formed columns. The septum of the last-formed growth unit (or units) is often incomplete, implying that growth begins at the outer margins and moves across the interseptal space (Landing *et al.* 1980). Skovsted *et al.* (2009a) suggest that interlamellar cavities in sclerites, such as those of *S. ?imbricata*, can be explained by hollowing out of thickened organic-rich layers during decomposition. However, lamellae are not continuous into the interlamellar cavities, rather lamellae are deflected around them. Mineralization of the sclerite progressed in the same manner described from other tomotiids, except where mineralization is locally restricted to the secretion of columns spanning the interseptal cavity only.

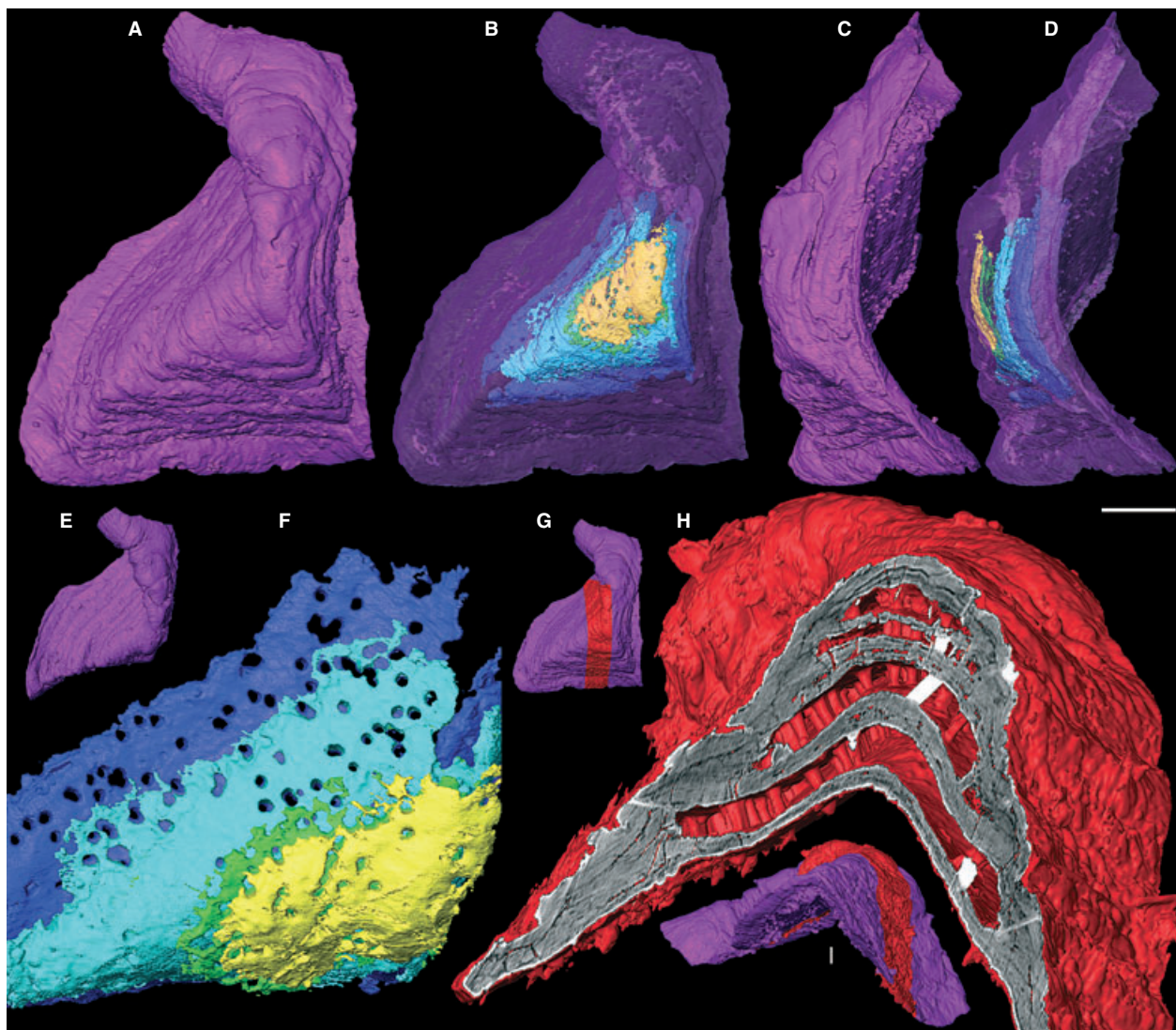


FIG. 7. *Sunnaginina* ?*imbricata* Missarzhevsky, 1969 from Comley Limestone, Shropshire, UK; Lower Cambrian. SRXTM images. A–G, NRM-PZ X 4460 right-handed sclerite with volume renderings of stacked interseptal cavities (blue, cyan, green, yellow) within surface rendering of complete volume (purple). A, C, rendering of complete sclerite in apical (A) and lateral (C) views. B, D, renderings of position of stacked interseptal cavities within complete sclerite in apical (B) and lateral (D) views. E–F, enlarged rendering of stack of interseptal cavities (F) to show consistency of pillars through several growth stages, orientation of sclerite (E). G–I, rendering of thick longitudinal section (red) within surface rendering of complete volume (purple) (H) to show distribution of pillars within cavities, position of sectioned portion of sclerite (G), orientation of sclerite (I). Scale bars represent 200 μm (A–D), 75 μm (E, G), 650 μm (F, H) and 150 μm (I).

The Sunnaginina scleritome

Landing (1995) identified triangular and quadrilateral morphotypes of *Sunnaginina* and suggested two distinct sclerite types. However, specimens of *Sunnaginina* ?*imbricata* from the Comley Limestone display a spectrum of morphologies between these two end-members and are indistinguishable in the earliest ontogenetic stages. Therefore, we do not support a bimembrate scleritome for *Sunnaginina*. The range of morphologies displayed may reflect different positions

within the scleritome, and changes in the overall shape of individual sclerites during morphology may be dictated by adjacent sclerites. For example, lobe L2 approximates a right angle throughout ontogeny, and side S1 is restricted and concave. This may reflect constraints in sclerite growth imposed by their juxtaposition within a scleritome. No fused specimens were recovered from the Comley Limestone samples (cf. Landing 1995, fig. 7.18) but a range of morphologies of *Eccentrotheca kanesia* sclerites are recovered, from broad cap-shaped to high conical specimens,

that (superficially, at least) resemble the small sclerites Landing (1995) recovered fused to one specimen of *Sunnaginina imbricata*. So, although this evidence provides no additional support to the hypothesis that the *Sunnaginina* scleritome incorporated *Eccentrotheca*-like sclerites (Skovsted *et al.* 2011), our findings are not inconsistent with it.

DISCUSSION

Comparisons to other tommotiids

Eccentrotheca, *Paterimitra*, *Jayceia* and *Kulparina*. The microstructure of the sclerites of *Eccentrotheca* and *Paterimitra* has been described as alternations of dense and porous (inferred to be organic-rich) laminae, with varying first- and second-order organizations (Balthasar *et al.* 2009). Our SRXTM data for *Eccentrotheca* (Fig. 8A) and *Kulparina* (unpublished data) demonstrate the same microstructural pattern. However, the mode of growth, with colonnaded interseptal cavities, described in *Sunnaginina imbricata* has not been reported from any of the other members of Sunnaginiidae. Growth lamellae in the Siberian material of *S. imbricata* are much more closely comparable to those observed in other tommotiids yet both taxa differ in their degree of organization. Siberian specimens possess virtually no second-order laminae, and laminae can be observed to cut across one another. In *S. imbricata*, although they show little evidence of cross-cutting of laminae, the second-order lamination is weakly developed and laterally restricted.

There are similarities between the large interseptal spaces within sclerites of *Sunnaginina imbricata* and internal cavities figured by Balthasar *et al.* (2009) in *Askepasma* (Fig. 2H) and *Paterimitra* (Fig. 3C, D). No 'columns' are reported in either taxon, and the nature of the interaction between laminae and the cavities is not possible to resolve for *Paterimitra*. However, the laminae observed in *Askepasma* are deflected around the cavities as in *Sunnaginina imbricata*. Further investigation is required to assess whether the geometric distribution of cavities in *Askepasma* sclerites is similar to that of *Sunnaginina imbricata*.

The polygonal structures observed in *Eccentrotheca*, *Paterimitra* and *Askepasma* (Balthasar *et al.* 2009) are not evident in any specimens of *Sunnaginina*. However, the lack of these structures in coeval specimens of *Eccentrotheca* from the Comley Limestone (our unpublished data) suggests that this may be due to preservational bias. Landing (1995) compared the organization of *Sunnaginina* sclerites with that of the other proposed members of the Sunnaginiidae; these comparisons can be revised in the light of the data presented here. Landing suggested that variation in the preferential growth of certain lobes could have produced the range of morphologies displayed by sunnaginiid gen-

era, such as the relative extension of side S1 in *Kulparina* or the reduction of lobe L3 in *Jayceia* and the corresponding lack of distinction between sides S2 and S3. However, homology of these characters has yet to be demonstrated, and therefore, it is not appropriate to use this model of development as a basis for establishing phylogenetic relationships. An intriguing similarity between *Sunnaginina* and *Paterimitra* is highlighted by their scleritome reconstructions. Skovsted *et al.* (2009b) described a *Paterimitra* 'S1' sclerite fused to smaller *Eccentrotheca*-like 'L' sclerites, in a similar manner to the fused *Sunnaginina* sclerites described by Landing (1995). This similarity remains to be tested with the discovery of further articulated material.

Several authors (Landing *et al.* 1980; Skovsted *et al.* 2008) have suggested that *Sunnaginina* is most closely allied to *Eccentrotheca*. Both genera possess sclerites that are characterized by an irregular apical surface, dominated by coarse growth lines, and known to co-occur in several deposits (Landing *et al.* 1980; Brasier 1986; Hinz 1987; Bengtson *et al.* 1990). Landing (1995) suggests that several larger specimens of the cap-shaped morph of *Sunnaginina imbricata* have been misidentified as *Eccentrotheca kanesia* (and/or *Jayceia deltaformis*). However, we have not recovered any cap-shaped sclerites fused with four- or three-lobed morphs from the Comley Limestone material. Therefore, it seems prudent to reassess the close affinity of these two taxa. Rather, the similarities of (1) sclerite morphology, both broadly pyramidal in shape and twisted about the apical-adapical axis, and (2) the reconstructed scleritomes of *Paterimitra* and *Sunnaginina* suggest a close affinity of these taxa. *Paterimitra* is allied with paterinid brachiopods (Balthasar *et al.* 2009; Skovsted *et al.* 2009b) and *Sunnaginina* may also occupy a similar position. However, *Sunnaginina* lacks the polygonal ornament and characteristic microstructure that allies *Paterimitra* to the paterinids, through comparisons with *Askepasma* (Balthasar *et al.* 2009).

Camenellans. The 'camenellans' are characterized by inflated laminae forming repeated co-marginal ribs, and *Camenella* and *Dailyatia* possess differentiated sclerite morphologies (Laurie 1986; Skovsted *et al.* 2009a). The same pattern of alternating dense and porous laminae is found in *Camenella* and *Dailyatia*. These features appear to be incompatible with those of *Sunnaginina* (excepting the suggestion of cap-shaped sclerites; Landing 1995). However, the morphology and microstructure of sclerites of the genus *Lapworthella* and its immediate relatives may have more similarities with sclerites of *Sunnaginina*. Lapworthellids are characterized by high conical sclerites with transverse growth lines and a hollow or septate internal cavity, and they are reconstructed with a unimembrate scleritome (Landing 1984). They show a wide range of morphologies, with various ornament types and degrees of torsion, and often show fusion of two or more individ-

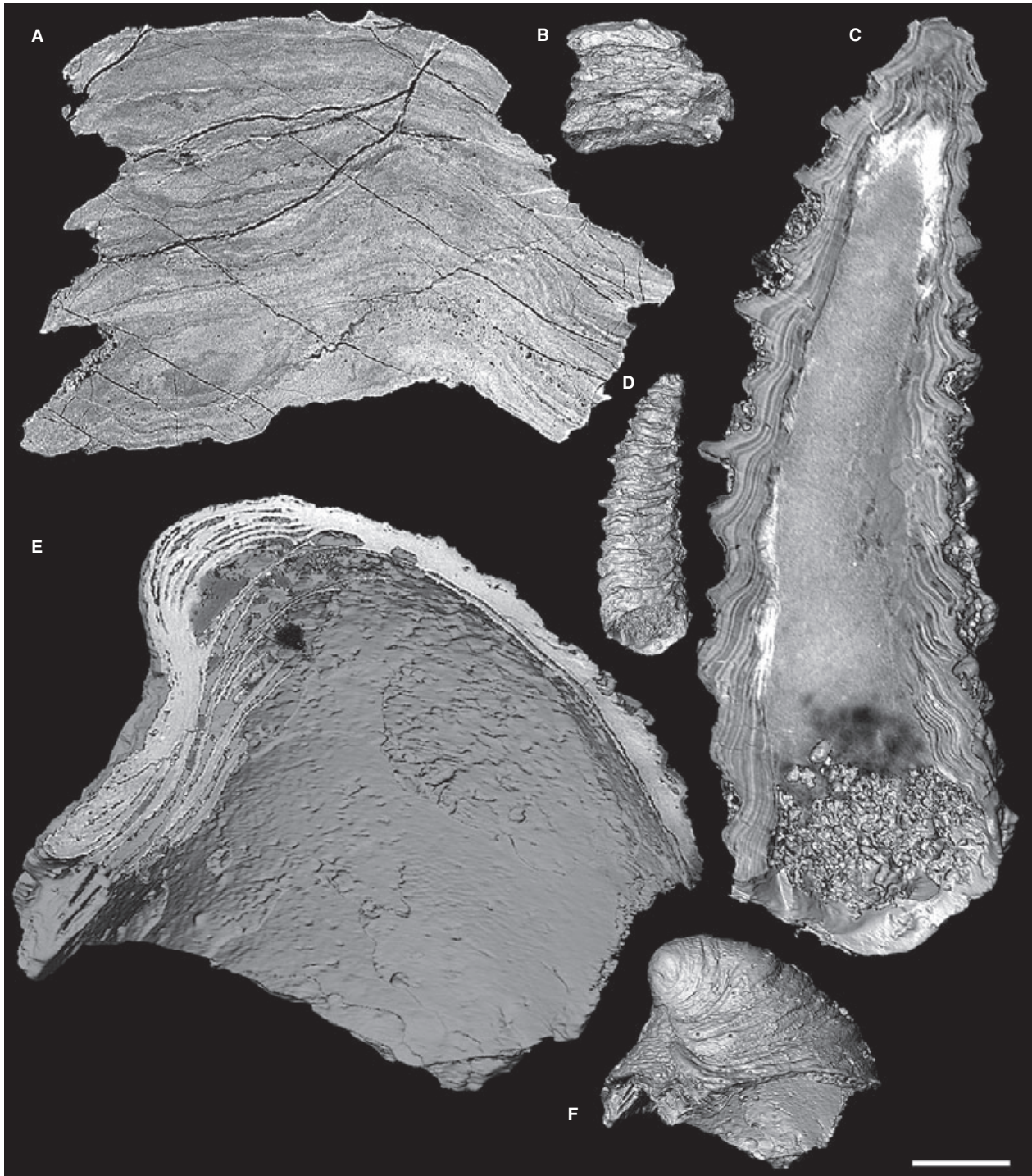


FIG. 8. Internal structure of selected tommotiids, SRXTM images. A–B, *Eccentrotheca kanesia* (Landing *et al.*, 1980) and C–D, *Lapworthella* sp. Missarzhevsky, 1966 from Comley Limestone, Shropshire, UK; Lower Cambrian. E–F, *Micrina etheridgei* Tate 1892 from Early Cambrian, South Australia. A, NRM-PZ X 4461 SRXTM-generated longitudinal section, with orientation of sclerite (B). C, NRM-PZ X 4462 SRXTM-generated longitudinal section, superimposed on volume rendering of complete sclerite, with orientation of sclerite (D). E, NRM-PZ X 4468 SRXTM-generated longitudinal section, superimposed on volume rendering of complete sclerite, with orientation of sclerite (E). Scale bars represent 100 μm (A), 150 μm (C), 200 μm (E) and 500 μm (B, D, F).

ual sclerites (Landing 1984). *Lapworthella* sclerites generally resemble a cone, the outer surface of which is marked by ridges, as in *Sunnaginina* sclerites. South Australian *Lapworthella fasciculata*?, examined here, also possess septa, which have the same pattern of growth as those of *Sunnaginina* though do not show any colonnaded cavities. In specimens of *Lapworthella* sp. from the Comley Limestone, there are no septa that cross the inner surface of the sclerite and therefore no interseptal cavities (Fig. 8C). In cross-section, it is revealed that the sclerite consists of a series of stacked cone-shaped laminae, which thicken towards the distal part of the cone and terminate in a lateral expansion resulting in the ridged pattern observed on the outer surface. This pattern, described also by Landing (1984), is more akin to that of *Camenella* and *Dailyatia*.

The microstructure of camenellan sclerites and sclerites of *Sunnaginina* and *Eccentrotheca* are closely comparable, with the notable exception of the septate sclerites of *Lapworthella*. The inconsistent distribution of septa among species of *Lapworthella* and lack of septa among other camenellans may reflect a possibility that the feature was independently acquired by species of *Lapworthella* and *Sunnaginina*. This is supported by the lack of colonnaded cavities and significant differences in sclerite morphology between these taxa.

Tannuolinids. The architecture of *Sunnaginina ?imbricata* is most closely comparable to the structures found in *Tannuolina* and *Micrina*. Despite the clear differences in overall morphology, the same pattern of alternations of thin, densely laminate and thick, organic-rich layers is apparent. All the sclerites consist of a number of growth units enclosing a cavity, although the units are much more numerous than in *S. ?imbricata* (Fig. 8E). However, *S. ?imbricata* lacks the abundant pores (Holmer *et al.* 2002) or coalescing canals (Kouchinsky *et al.* 2010) that characterize tannuolinid sclerites. Where these pores cross the interseptal space, they resemble ‘pillars’ but are always hollow and open to the outer surface, often penetrating the entire sclerite. Nevertheless, in parts of the sclerites where pores are sparse, the interseptal spaces dominate the microstructure, as in *Sunnaginina*. Some specimens have incomplete final septae suggesting growth proceeded in the same general pattern, beginning at the outer margins and extending to enclose the interseptal space. Nevertheless, it is difficult to reconcile the morphology of *Sunnaginina* sclerites with the scleritome reconstruction of *Micrina* (Holmer *et al.* 2008) and, by inference, *Tannuolina*.

Phylogenetic position of *Sunnaginina*

Microstructural data support a phylogenetic position for *Sunnaginina* that is intermediate of the disorganized sclerites

of *Eccentrotheca* and the specialized sclerite morphology of the tannuolinids (Bengtson *et al.* 1990). Tommotiid phylogeny is still being resolved. However, the hypothesis proposed by Skovsted *et al.* (2011), with the addition of *Paterimitra* as a stem-rhynchonelliform brachiopod (Holmer *et al.* 2011), provides a useful framework. This phylogenetic hypothesis is constructed using a small number of characters, not all of which can be resolved for *Sunnaginina*. Considering that each node is supported by only one (or two) character(s), small changes in the interpretation of features of these taxa can result in dramatic changes in their relative relationships. Therefore, a range of phylogenetic positions for *Sunnaginina* are consistent with this hypothesis (Fig. 9; see caption for details). It is clear that *Sunnaginina* sclerites possess the symplesiomorphic characters that define the tommotiids and do not possess the synapomorphies of the derived clades presented in the phylogeny, but the nodes of interest (defining crown-Brachiopoda) are supported by evidence from scleritome reconstructions, not available for *Sunnaginina*. This highlights a weakness of this phylogenetic scheme, considering that the key characters cannot be consistently applied to all taxa, and that they do not define a series of nested clades. A more thorough phylogenetic analysis is required in the light of the data presented here and other recent descriptions (Skovsted *et al.* 2009a, b, 2011; Kouchinsky *et al.* 2010).

To resolve this problem, the analysis must be supplemented with microstructural data. The data presented here highlights differences in microstructure of sclerites belonging to *Eccentrotheca* and *Sunnaginina*. Therefore, the close affinity of *Eccentrotheca*, *Kulparina* and *Jayceia* with *Sunnaginina* is brought into doubt, and the suprageneric taxonomy of the tommotiids needs to be readdressed in the light of this data, as well as a range of recent redescrptions of key taxa.

Given the gradual acquisition of microstructural complexity implicit within this phylogenetic scheme, the disorganized lamellae of *Sunnaginina imbricata* suggest this taxon occupies a basal position, having a lower degree of organization than both the camenellans and *Eccentrotheca*. However, this is inconsistent with the gross morphology of the sclerites when considering the high degree of variability of *Eccentrotheca* sclerites compared to relatively well-conserved *Sunnaginina* sclerites with a clear predictable ontogeny. If the more complex microstructure of *S. ?imbricata* is derived from that of *S. imbricata*, then the sequence of character acquisition it suggests is inconsistent with that suggested in this phylogenetic scheme.

The colonnaded construction of *Sunnaginina ?imbricata* is most akin to that of *Micrina* and *Tannuolina*. However, the lack of other key characters such as shell-penetrating pores and a clear separation into two sclerite morphologi-

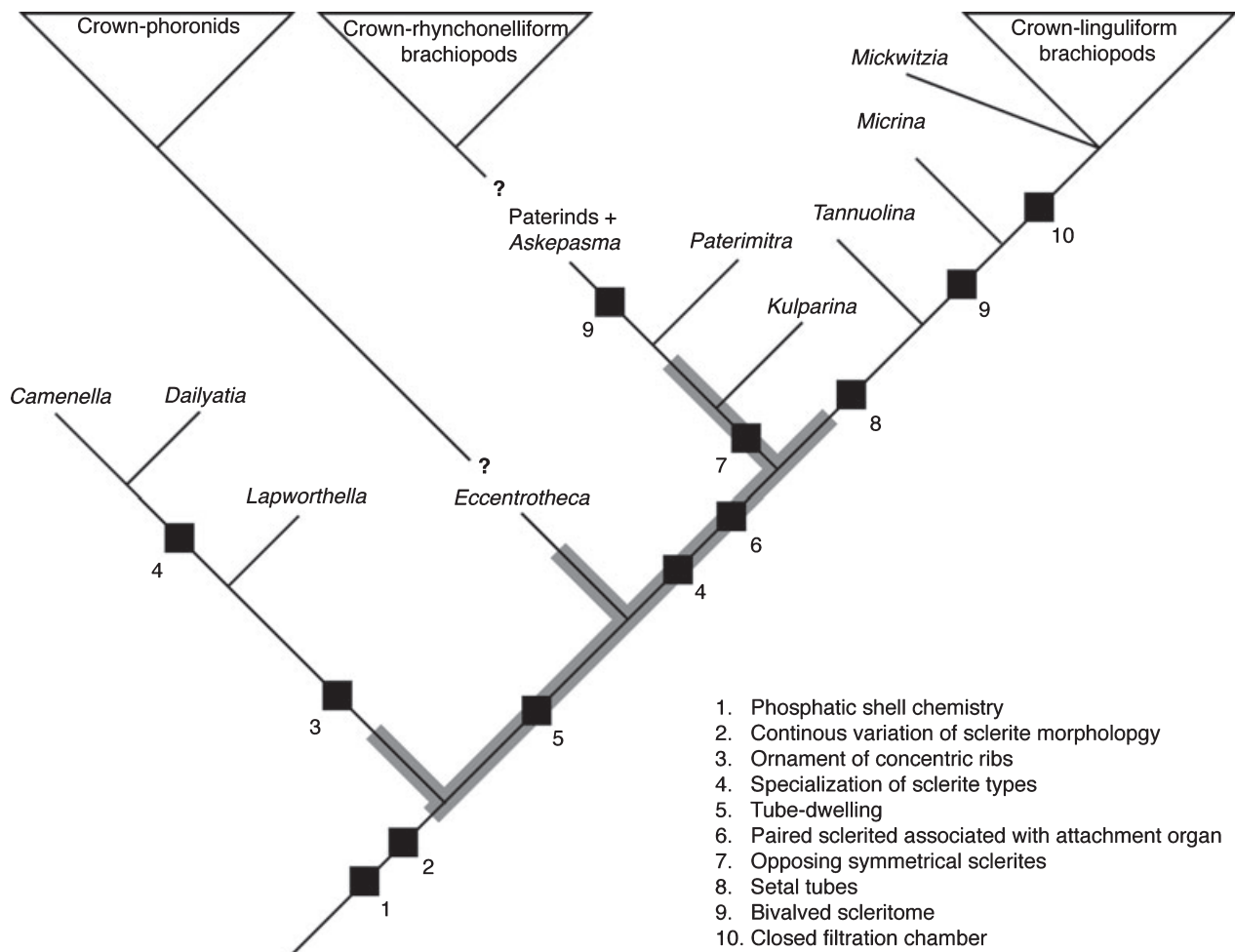


FIG. 9. Hypothetical reconstruction of the phylogenetic relationships between the tommotiids and crown-brachiopods, based on Skovsted *et al.* (2009a; 2011) modified by Holmer *et al.* (2011). Phylogenetic positions for *Sunnaginina* consistent with the data presented here and characters suggested by Skovsted *et al.* (2009a; 2011) shown in the grey box. *Sunnaginina*, like all tommotiids, possessed phosphatic sclerites [1] and shares continuous variation in shell morphology [2] with *Eccentrotheca*, but lacks the ornamented concentric ribs [3] of the camenellans [3,4], linguliform brachiopods [8–10] or paterinid brachiopods [9]. As no articulated scleritomes for *Sunnaginina* are known, it is uncertain whether characters [5], [6] and [7] were present or absent for that genera, and it has been suggested the *Sunnaginina* scleritome may have possessed differentiated sclerites [4] (Landing 1995).

es (mitral and sellate) preclude *Sunnaginina* from lying within the tannuolinids. A position as a sister taxon to the tannuolinids would be consistent with this set of characters, and, under the framework outlined by Skovsted *et al.* (2009a), would imply a close affinity for *Sunnaginina* with linguliform brachiopods.

However, the gross morphological similarities between *Sunnaginina* and *Paterimitra* cannot be ignored, including the presence of large internal cavities in sclerites of *Paterimitra* and *Askepasma* (Balthasar *et al.* 2009), bearing similarities with the interseptal spaces of *Sunnaginina* *?imbricata*, and the (albeit weakly developed) second-order lamination. Close association of second-order lamination suggests a contradictory affinity, that of a stem-rhynchonelliform

brachiopod. In conclusion, the position of *Sunnaginina* within this phylogenetic hypothesis cannot be resolved beyond a placement stem-ward to the node subtended by *Paterimitra* and the tannuolinids plus linguliform brachiopods, prior to the evolution of setal tubes and the bivalve scleritome. However, these data bring into doubt the level of resolution presented in the phylogenetic scheme. There is clearly a high degree of character conflict, not least because the most phylogenetically informative characters cannot be resolved for a number of taxa. The relative placement of individual tommotiid taxa within the brachiopod stem is unclear, and greater taxon sampling is required before a phylogenetic scheme of this level of resolution can be supported.

CONCLUSIONS

1. The *Sunnaginina* scleritome is unimembrate, consisting of dextral and sinistral sclerites up to 15 growth stages in size. They lie on a morphological spectrum from broadly triangular sclerites with a reduced lobe L1 to approximately trapezoid morphs (cf. Landing 1995).
2. *Sunnaginina imbricata* has an apparently primitive microstructure with a derived gross morphology.
3. The complex colonnaded structure of *Sunnaginina* ?*imbricata* may derive from the irregular lamellar microstructure seen in the Siberian material of *Sunnaginina imbricata*.
4. The microstructure of *Sunnaginina* ?*imbricata* sclerites is similar to that of *Eccentrotheca* and *Paterimitra*. The complex colonnaded structure of *Sunnaginina* ?*imbricata* may derive from the irregular lamellar microstructure seen in the Siberian material of *Sunnaginina imbricata*; however, they possess a unique architecture among the tommotiids; colonnaded interseptal cavities that deflect laminae around them can be found in each growth stage.
5. The close affinity of *Sunnaginina* and *Eccentrotheca* is refuted by the colonnaded architecture found in *Sunnaginina* ?*imbricata* sclerites, and the suprageneric taxonomy of the tommotiids should be readdressed.
6. The most consistent phylogenetic position for *Sunnaginina* within the framework proposed by Skovsted *et al.* (2009a; 2011) is sister to the tannuolinid plus linguliform brachiopod clade, close to the node that defines crown-Brachiopoda. However, we suggest the degree of character conflict in this phylogenetic reconstruction precludes any conclusions of affinity to such a high level of resolution.

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