

A silicified tommotiid from the lower Cambrian of Greenland

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Three specimens of a new eccentrothecimorph tommotiid are described from the Paralleldal Formation of North Greenland. The specimens are all tubular structures composed of a number of individual sclerites. The sclerites were arranged in rings, which fused to form a rigid tube during ontogeny. The tube has a basal aperture presumably allowing attachment to a hard substrate. In morphology, both individual sclerites and the tubular scleritome are remarkably similar to specimens of *Eccentrotheca* from South Australia. However, the Greenland specimens are silicified and may have been either weakly mineralised or calcareous in original composition. In this respect they differ from all previously known tommotiids, considerably expanding the ultrastructural disparity of the Tommotiida and allowing comparison to a new range of possible lophotrochozoan fossils. • Keywords: Small Shelly Fossils, Tommotiida, eccentrothecimorph, Brachiopoda, silicification, Greenland.

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The earliest skeletal fossils from the terminal Ediacaran and early Cambrian are exemplified by tubes, cap-shaped shells and irregular or cone-shaped fossils that are commonly united under the heading Small Shelly Fossils (SSF's; Bengtson 2004). These fossils represent the oldest known undoubted metazoan fossils and likely include early representatives of the stem lineages of modern phyla (Budd 2003, Kouchinsky *et al.* 2012). One group among the SSF's that have recently attracted considerable attention is the tommotiida. These cap- or cone-shaped fossils are interpreted to be components (sclerites) of multi element external skeletons (scleritomes; Landing 1984). Based on recently discovered tommotiids from South Australia (Skovsted *et al.* 2008, 2009a, b, 2011, 2015b; Holmer *et al.* 2008; Balthasar *et al.* 2009; Larsson *et al.* 2014), tommotiids have been interpreted to be basal members of the stem group leading to the lophophorate phyla Brachiopoda and Phoronida. This interpretation was based both on the morphology of their tubular scleritome structure (Skovsted *et al.* 2008, 2009b, 2011; Holmer *et al.* 2008) and the remarkable similarities in ultrastructure between tommotiids and the earliest brachiopods (Balthasar *et al.* 2009; Murdock *et al.* 2012, 2014; Larsson *et al.* 2014).

In the present contribution I will show that although tommotiids have been thought to be exclusively organophosphatic by original composition (Balthasar *et al.*

2009), silicified specimens from the Cambrian of North Greenland indicate that the range of mineralogical ultrastructures available to tommotiids may have been larger. This observation, and recently presented evidence that not all tommotiids may have had tubular scleritomes (Skovsted *et al.* 2015a), strengthens suggestions that the evolution of the lophophorate stem group was more complex than previously imagined (Murdock *et al.* 2014, Zhang *et al.* 2014). The new material also opens up new avenues for future research into the distribution, structure and affinity of Small Shelly Fossils.

Material and methods

The new material from North Greenland includes a single isolated, 3-dimensional specimen and two partly isolated specimens still attached to silicified limestone surfaces. All specimens were recovered from hydrochloric acid residues derived from silicified, cherty limestones of the Paralleldal Formation in central Peary Land (GGU sample 274907; 82° 17' N 31° 9.2' W; see also Larsson *et al.* 2009 for details). The associated fauna includes calcareous brachiopods (Popov *et al.* 1997), trilobites (Blaker & Peel 1997, Stein & Peel 2008), molluscs (Atkins & Peel 2004, 2008) and the problematic sclerites of *Trachyplax* (Larsson *et al.*

Table 1. Length, width and number of sclerite rings of all specimens of the Greenland eccentrothecimorph. Length and width measurements in mm.

Specimen	Figure	Length	Width	Rings
SMNH X5786	2	7.5	7.2	4
SMNH X5787	3	5.4	5.9	4
SMNH X5788	4	–	8.2	2?

2009). The preserved fauna, and the presence of archaeocyathans (Debrenne & Peel 1986) and *Salterella* Billings, 1861 (Peel & Yochelson 1982) in overlying rocks, indicates a Cambrian Stage 4 age for the fossiliferous horizon.

The two specimens on silicified limestone surfaces were photographed after coating with ammonium chloride at Uppsala University and the single isolated specimen was gold-coated and pictured using SEM at the Swedish Museum of Natural History. All specimens are housed in the palaeontological collections of the Swedish Museum of Natural History in Stockholm (acronym SMNH).

Silicified eccentrothecimorph tommotiid from North Greenland

Morphology

All three specimens are tubular structures with a roughly circular cross-section and a diameter of about 6–8 mm (Table 1). The length of the specimens is about 5–8 mm, although the terminations probably represent broken margins. All specimens are composed of multiple sclerites that appear to have been fused during growth of the animal. No isolated sclerites were recovered, potentially due to difficulties in identifying such sclerites among the silicified skeletal debris.

The individual sclerites composing the Greenland eccentrothecimorph tubes are elongate oval to sub-rectangular in outline (Figs 1, 2). In the completely isolated specimen SMNH X5786 the borders between sclerites are formed by narrow furrows (Fig. 1G–I) while the sclerites in specimen SMNH X5787 are separated by wider and deeper furrows (Fig. 2). Individual sclerites are less easy to identify in the poorly preserved specimen SMNH X5788 (Fig. 3). The sclerite surface is generally not well enough preserved to expose fine details but in SMNH X5786 faint furrows running more or less parallel to the boundaries be-

tween sclerites indicate broad growth increments (Fig. 1G). In lateral profile the sclerites of SMNH X5786 are high, conical with height approximately equal to width (Fig. 1H). The apices of all sclerites are inclined towards the same end of the tube. Internally, all sclerites appear to have a shallow cavity (Fig. 1J).

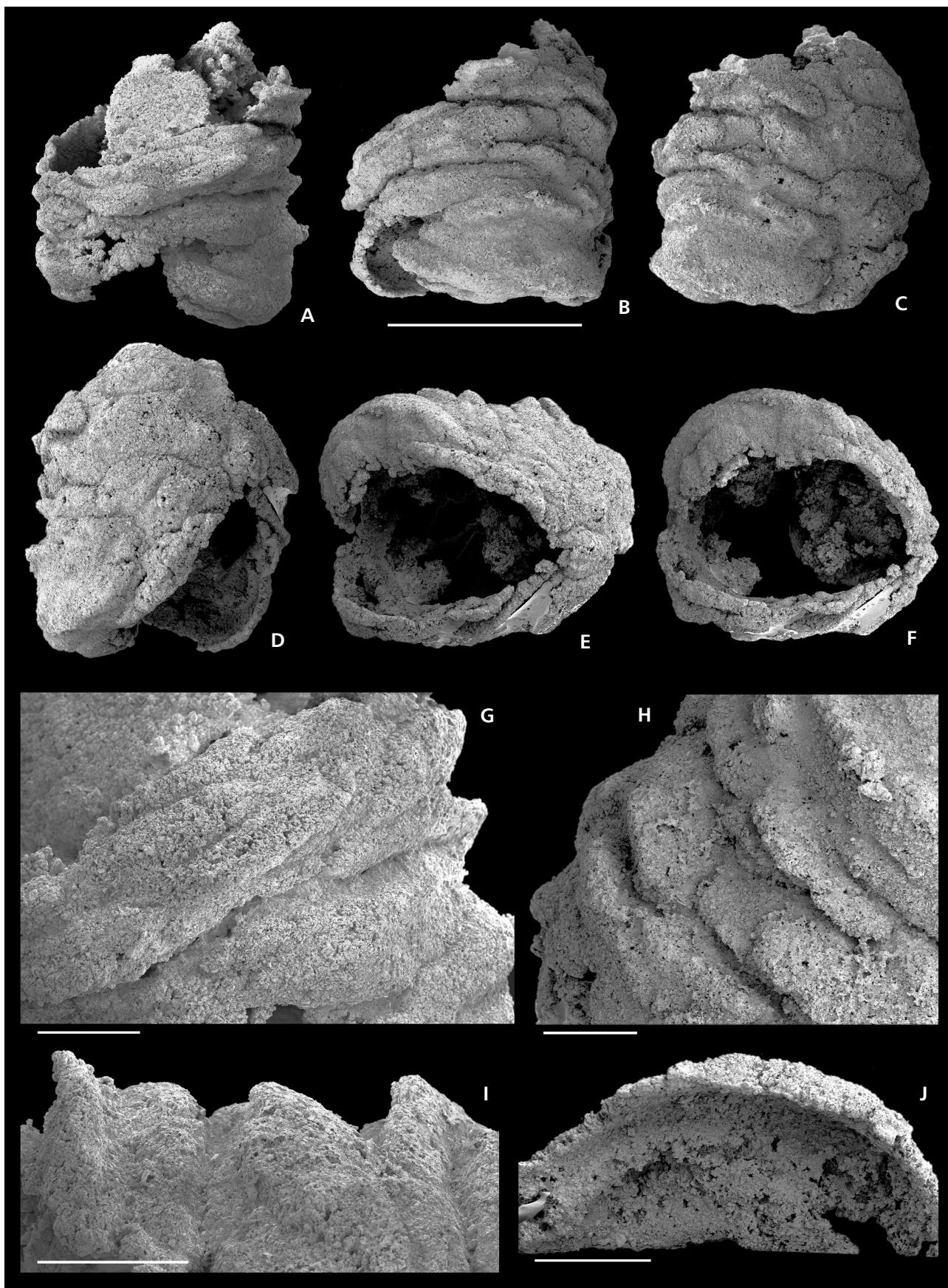
In specimen SMNH X5786 sclerites are clearly arranged in transverse rings that can be followed around most of the circumference of the tube (Fig. 1A–C) although one side of the tube is too poorly preserved to allow sclerites or sclerite rings to be determined (Fig. 1D). The borders between rings are much deeper than between individual sclerites within the rings, suggesting that the sclerites within each ring were amalgamated prior to fusion of the rings (Fig. 1A, B). Although sclerites in specimens SMNH X5787 and SMNH X5788 appear to be arranged in a similar manner, the less perfect preservation of these specimens does not allow detailed definitions of sclerite rings (Figs 2, 3).

In transverse section, specimen SMNH X5786 is close to circular (Fig. 1E) and the transversely embedded specimen SMNH X5788 appears to have a similar circular cross section (Fig. 3) while specimen SMNH X5787 is too deeply embedded in the silicified limestone to reveal the cross-section of the tube (Fig. 2). The diameter of the tube does not appear to change very much along the length of the tube sections. However, in SMNH X5786 the sclerites of successive rings are inclined towards the same end of the tube, and the opposing end show a distinct depressed oval aperture, potentially representing an attachment scar (Fig. 1D–F). The aperture is oblique in relation to the long axis of the tube and appear to cut across two or three sclerite rings, although this is difficult to establish as this side of the tube is relatively poorly preserved (Fig. 1D).

Preservation

The recovered specimens from North Greenland are derived from silicified limestone samples which also contain brachiopods, trilobites, mollusks and problematic sclerites that have been preserved through silicification of originally calcareous shells (Popov *et al.* 1997; Blaker & Peel 1997; Atkins & Peel 2004, 2008; Stein & Peel 2008; Larsson *et al.* 2009). The eccentrothecimorph specimens described here do not appear to differ in any substantial way from co-occurring calcareous brachiopods or molluscs in terms

Figure 1. Eccentrothecimorph tommotiid SMNH X5786, from the Paralleldal Formation, central Peary Land, North Greenland. Specimen isolated from limestone by hydrochloric acid. • A–D – four different lateral views. • E – oblique apertural view. • F – apertural view. • G – detail of A showing growth bands of individual elongate sclerites. • H – detail of B showing arrangement of sclerites in rings. • I – lateral view of A showing sclerites in successive rings inclined away from basal aperture. • J – internal view of one sclerite close to abapical margin. Scale bar equals 5 mm in A–F. Scale bar in G–J equals 1 mm.



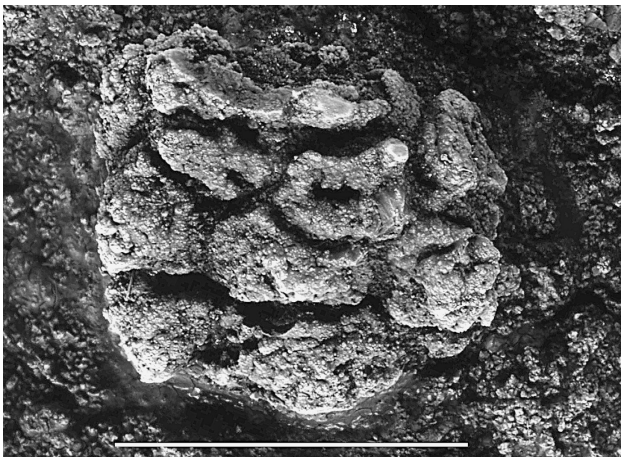


Figure 2. Eccentrothecimorph tommotiid SMNH X5787, from the Paralleldal Formation, central Peary Land, North Greenland. Lateral view of specimen partly embedded in silicified limestone. Scale bar equals 5 mm.

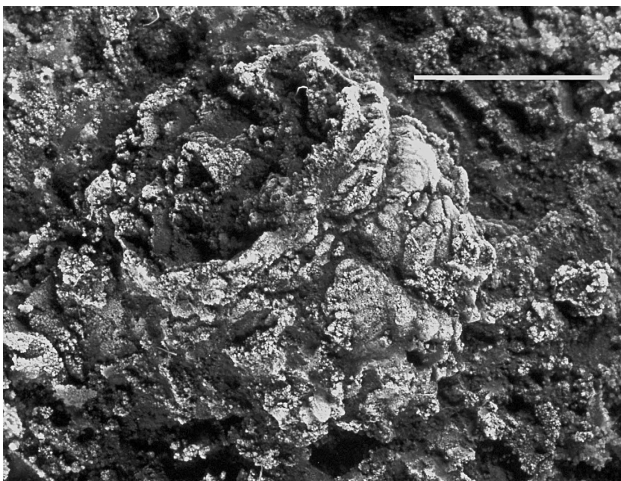


Figure 3. Eccentrothecimorph tommotiid SMNH X5788, from the Paralleldal Formation, central Peary Land, North Greenland. Specimen obliquely embedded in silicified limestone. Scale bar equals 5 mm.

of preservation and have also been silicified. The preparation process, using hydrochloric acid would have destroyed any non-silicified fossils in the sample but preparation of a sub-sample in acetic acid did not result in discovery of any phosphatic fossils (J.S. Peel, personal communication 2015).

In general, the process of silicification appears to most readily affect calcitic fossils (Shubert *et al.* 1997, Baliński 1999) and when originally phosphatic hard parts, such as vertebrate remains, conodonts or lingulid brachiopods are present in silicified marine faunas of the Paleozoic, they are usually not affected by silicification (Baliński 1999, Sun & Baliński 2008). Indeed, the formation of silicified nodules has even been interpreted to facilitate exceptional preservation of phosphatic shell structures in lingulid brachiopods (Zabini *et al.* 2012).

A few reports of originally phosphatic brachiopod shells and tommotiid sclerites from the Cambrian, partly replaced by silica have been published (Balthasar 2004, 2007, 2008; Skovsted *et al.* 2009a; Holmer *et al.* 2009). In the majority of these cases silicified parts of shells appear to have originally been weakly mineralised and first replaced by calcite before silicification of this secondary calcite (Balthasar 2004, 2007, 2008; Skovsted *et al.* 2009a). Exceptional opalization of marine vertebrate bone has also been suggested to be a secondary process after calcite replacement of original phosphate material (Pewklian *et al.* 2008). The exception to this pattern is in the cryptotretid brachiopod *Salanygolina* Ushatinskaya, 1987 from the early Cambrian of Mongolia, where the external surface and parts of the shell interior appear to have been silicified without prior replacement by calcite (Holmer *et al.* 2009). Despite this example, wholesale replacement of phosphatic shells by silica appears to be exceedingly rare. Consequently, it is unlikely that the original shell mineralogy of the Greenland specimens described here was organo-phosphatic. Presumably, the shell material of the sclerites could have been poorly mineralised, but the apparent lack of deformation of the isolated tubular specimen SMNH X5786 would suggest considerable rigidity, and a more likely interpretation is that the sclerites may have been originally mineralised by calcium carbonate.

Interpretation and identification

In general morphology the silicified tubular specimens are closely comparable to tubular specimens of *Eccentrotheca helenia* Skovsted *et al.*, 2011 from the Arrowie Basin of South Australia (Skovsted *et al.* 2008, 2011). This tommotiid exhibits a highly variable scleritome structure with tubular or cone-shaped structures composed of fused sclerites arranged in rings that appear to have coalesced to form a tube during growth, exactly as in the Greenland specimens described here. Individual sclerites in the tubular specimens of *E. helenia* are variable in morphology and include both broad, cap-shaped sclerites and narrowly compressed conical sclerites, again very similar to the Greenland specimens. The tubes of *E. helenia* exhibit a distinct aperture (usually at the narrow end of cone-shaped specimens and sometimes inclined to the long axis of the tube), presumably reflecting attachment to a hard substrate (Skovsted *et al.* 2011). A similar aperture is evident in the best preserved of the Greenland specimens (Fig. 1D). However, the tubular specimens of *E. helenia* from Australia are substantially smaller than the Greenland specimens (maximum diameter not exceeding 3 mm; Skovsted *et al.* 2011 compared to over 8 mm in the Greenland specimens) and individual sclerites also appear to be smaller. The same applies to the sclerites of *E. kanesia* Landing *et al.*, 1980 from

the Terreneuvian of Avalonia (Landing *et al.* 1980; Landing 1988, 1991, 1995) and the related tomotiid *Kulparina* Conway Morris in Bengtson *et al.*, 1990 from South Australia which are also known to have had a tubular scleritome (Skovsted *et al.* 2011, 2015b). *Paterimitra* Laurie, 1986 from South Australia may include sclerites of similar size as in the Greenland specimens, but these exhibit characteristic pyramidal morphologies not obvious in the Greenland material.

Based on the close similarity in morphology of individual sclerites and in the tube construction, the Greenland specimens would appear to represent a tomotiid species closely related to *Eccentrotheca helenia* and it seems quite clear that the specimens represent an eccentrothecimorph tomotiid. However, the small number of specimens available and the peculiar preservation and uncertain (possibly calcareous) original composition of the Greenland specimens presently precludes identification at the generic level.

Conclusions

The suggestion that the Greenland eccentrothecimorph specimens may have been originally calcareous in composition is clearly at odds with the previous hypothesis that all tomotiids were organophosphatic (Landing 1984, Balthasar *et al.* 2009, Skovsted *et al.* 2009a). However, Cambrian fossils with non-mineralised or calcareous sclerites of comparable size and morphology to the Greenland specimens are known. The fauna of the Paralleldal Formation in central Peary Land includes abundant sclerites of the possible multiplacophoran mollusk *Trachyplax* (Larsson *et al.* 2009) co-occurring with the new eccentrothecimorph. *Trachyplax* exhibit a number of quite distinctive sclerite morphologies (Larsson *et al.* 2009) and although its scleritome structure remain unknown, no direct comparison between *Trachyplax* and eccentrothecimorph tomotiids can be made. The problematic fossil *Cotyledion* Luo *et al.*, 1997 from the Chengjiang fauna of Yunnan Province in South China, recently redescribed as a stem group entoproct (Zhang *et al.* 2013), represents another early Cambrian taxon with somewhat similar sclerites. *Cotyledion*, which may belong to the same total group as eccentrothecimorph tomotiids, exhibits a large number of rounded oval or rectangular sclerites covering its narrow stalk and wide calyx. As noted by Zhang *et al.* (2013), the sclerites are not arranged in transverse rings but rather in longitudinal files and do not appear to fuse to form larger composite sclerites like in eccentrothecimorphs. However in other respects the scleritome construction of *Cotyledion*, particularly in the stem, can be compared to the scleritome construction of the tomotiid *Eccentrotheca* and the non-mineralised or calcareous composition of the sclerites appear comparable

to the new Greenland eccentrothecimorph (Zhang *et al.* 2013).

Based on the close comparison in morphology and shell structure, it has been suggested that different brachiopod groups evolved from different tomotiid lineages (Skovsted *et al.* 2009b) and that calcareous shell mineralogy in brachiopods evolved secondarily from phosphatic bivalved ancestors (Balthasar *et al.* 2009). However, the find of tomotiids with calcareous sclerites suggests that transitions from phosphatic to calcareous shell mineralogy could have happened earlier in tomotiid-brachiopod evolution than previously thought. The extremely close morphological similarity between the (phosphatic) *Eccentrotheca* from Australia and Avalonia and the new (calcareous?) eccentrothecimorph from Greenland further indicates that such transitions in early Cambrian biomineralising taxa could have been much more frequent than assumed.

In summary, the new tubular specimens from Greenland appear to show that the disparity of eccentrothecimorph tomotiids in the Cambrian may have been larger than previously imagined and include forms that were calcareous in original composition or weakly mineralised. It is not inconceivable that calcareous or weakly mineralised cap-shaped sclerites of eccentrothecimorph type were more widely distributed in early lophotrochozoans than hitherto appreciated, as exemplified by the new Greenland tomotiid and the stem entoproct *Cotyledion* and more such sclerites may in the future be identified in SSF assemblages.

The relationship of these sclerite-bearing tubular fossils to tubiculous fossils such as *Cambrocornulithus* Yang *et al.*, 2013 and calcareous Paleozoic tubeworms such as tentaculitids and cornulitids (Vinn & Mutvei 2009, Taylor *et al.* 2010) or the Ediacaran fossil *Namacalathus* Grotzinger *et al.*, 2000 (Zhuravlev *et al.* 2015), all of which have recently been suggested to represent lophophorates, is at present uncertain. However, the discovery of silicified tomotiids will open new avenues to study this enigmatic fossil group in the future and may allow more broad comparisons to other biomineralising lophotrochozoans.

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