Microstructure and growth in the problematic Cambrian tommotiid *Lapworthella*: implications for early animal relationships

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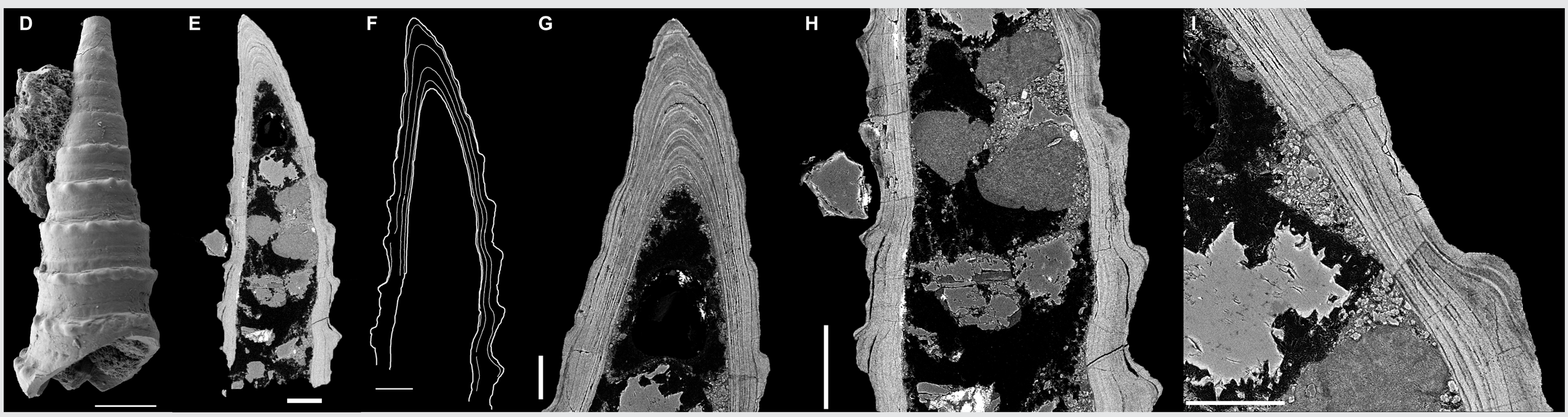
Introduction

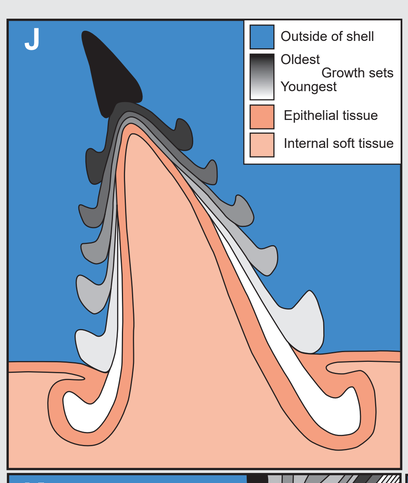
Understanding the relationships between early skeletal fossils is essential to the evolution of modern animal phyla. *Lapworthella* is a camenellan tommotiid, an early-branching ancestor of the brachiopods, whose skeletal fossils are found worldwide in lower Cambrian rocks. We used scanning electron microscopy (SEM) and X-ray micro-tomography (µCT) to examine the microstructure of *Lapworthella* sclerites. We used these observations to develop a revised growth model for *Lapworthella*. Finally, we considered the implications of these new data on the relationships of early biomineralising animals.

Lapworthella microstructure

Lapworthella sclerites are conical with an ornament of transverse ribs. Like all tommotiids, their sclerites consist of alternating dense and porous phosphatic laminae. The dense laminae appear brighter than porous laminae under µCT (A–C) and backscatter SEM imaging (E, G–I).

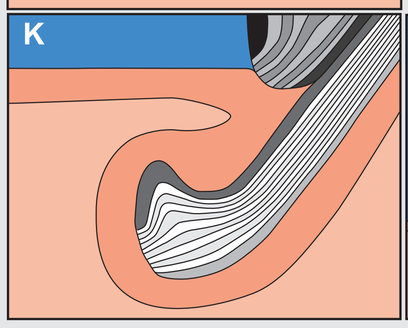
Each lamina can be traced from the sclerite apex to the external margin or sclerite base (C, E–F). Laminae crop out between ribs at the sclerite surface, or at the apertural margin. Each lamina may interact with multiple ribs before cropping out (H–I). Unlike in more derived camenellans, we found no evidence for 'growth sets' (discrete packages of laminae, see also J–L).

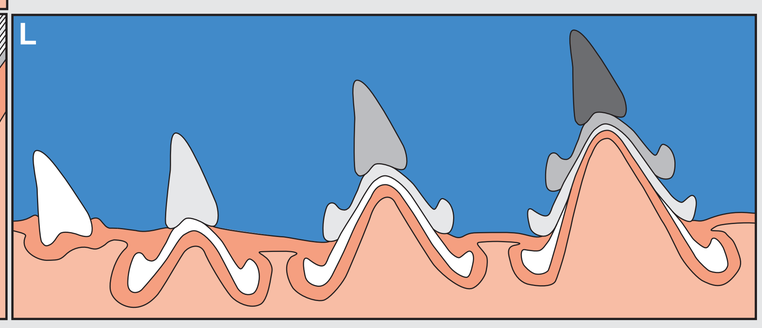


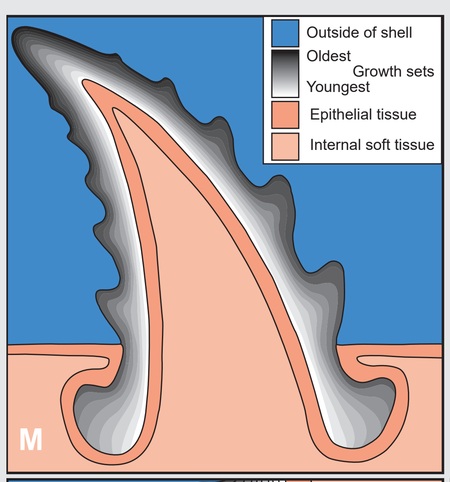


Current growth model

Sclerites grow by adding discrete packages (growth sets) of phosphatic laminae basally and internally (J–L). Each set consists of alternating compact and porous laminae, bounded by a thicker lamina on the internal and external margins (K). Each transverse rib is the external expression of a growth set and each lamina is confined to a single rib. The initial growth set produced is an apical cap (J, L). (J–L) modified after Wrona (2004) and Devaere & Skovsted (2017).

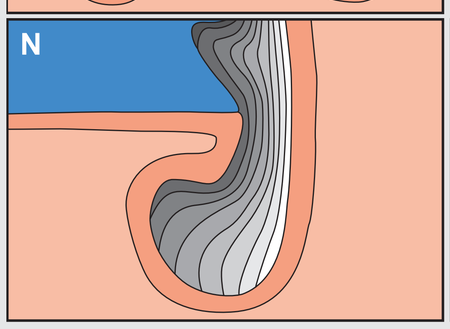


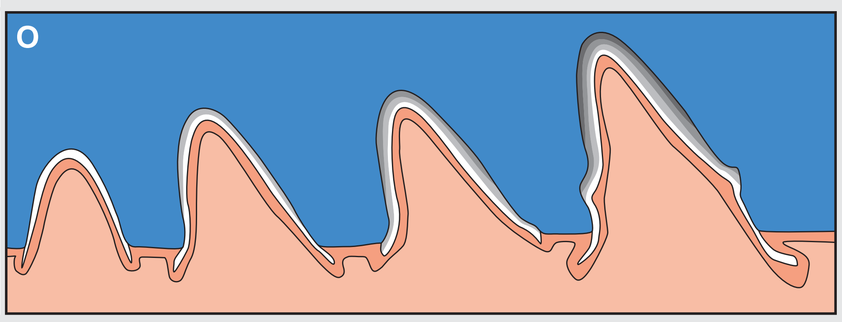




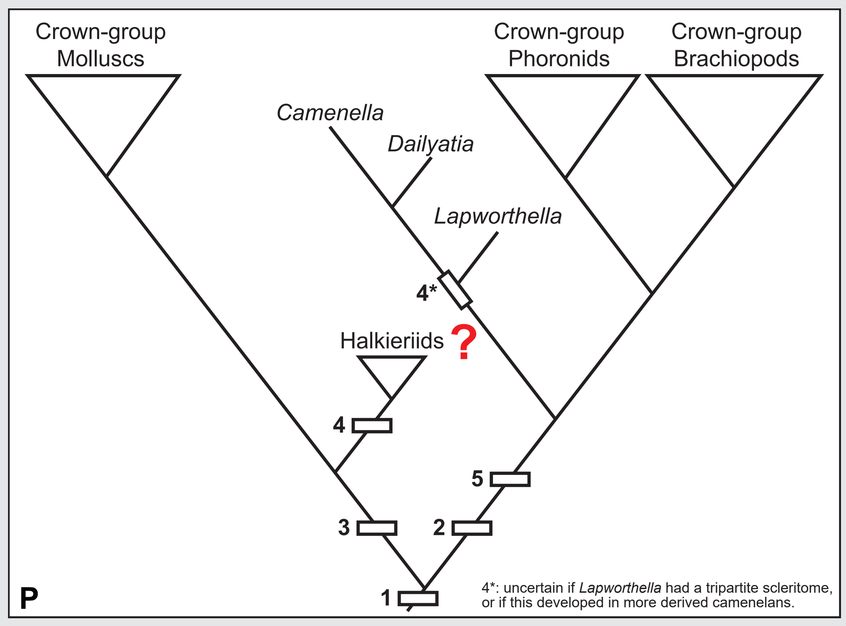
Proposed growth mode

Our proposed growth model comprises alternating compact and porous phosphatic laminae that are continuous from the sclerite apex to either the base or external margin where they crop out (M–N). Laminae are not packaged in growth sets. Each lamina may be deflected at multiple rib crests before cropping out at the surface (M–N); laminae are not confined to a single rib set. Older laminae are towards the external margin and apex. Skeletal material is produced by basal internal accretion (O). No apical cap is produced.

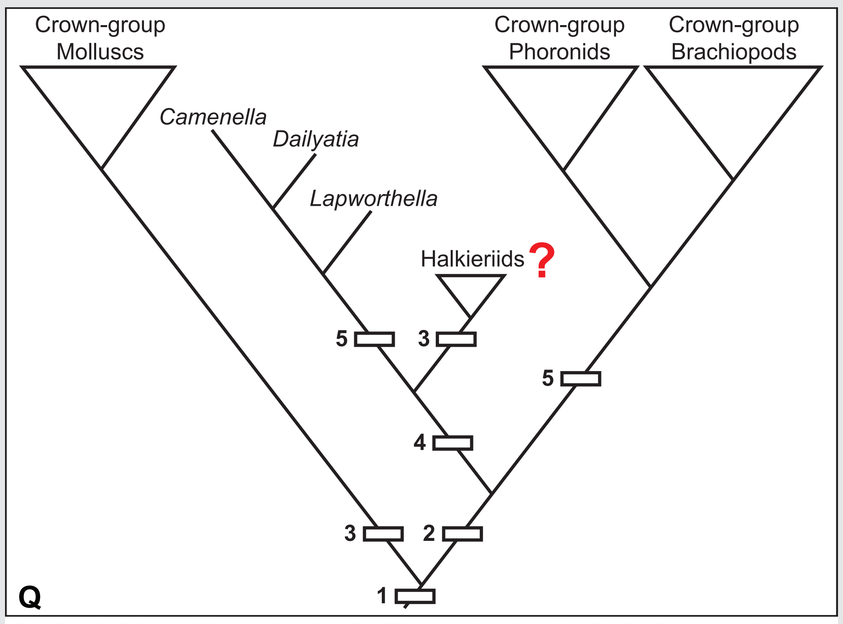




Lophotrochozoan relationships



Camenellans are an early-branching group on the brachiopod stem. Halkieriids are generally thought to be stem-group molluscs (P; Vinther & Nielsen, 2005), though they have also been considered stem-group brachiopods (Conway Morris & Peel, 1990). Recently, camenellans and halkieriids were suggested as sister clades (Q) due to hypothetically similar tripartite scleritomes (Zhao *et al*., 2017). However, halkieriid sclerites were made of aragonitic fibres (Porter, 2008) and grew by basal secretion to a set size before being replaced (Vinther & Nielsen, 2005). Camenellan and halkieriid sclerites are only superficially similar, differing in composition, microstructure, and growth. Differences in skeletal formation argues against a close biological relationship. A camenellan + halkieriid clade on the brachiopod stem (Q) is unlikely.



P–Q. 1: Vermiform body. 2: Phosphatic shell. 3: Aragonitic shell. 4: Tripartite scleritome. 5: Basal internal accretion.

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