A Cambrian tommotiid preserving soft tissues reveals the metameric ancestry of lophophorates

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In brief
Guo et al. describe the first known articulated camenellan tommotiid, a group of enigmatic Cambrian animals that have been difficult to classify based on disarticulated microfossils. Camenellans were vagile armored worms, with affinities to living lophophorates (e.g., brachiopods), suggesting a motile last common ancestor.

Highlights
- We describe the first articulated camenellan tommotiid, from the early Cambrian
- Camenellans had seriated, annelid-like chaetal bundles and body outgrowths
- Early lophophorates were armored, vagile animals prior to becoming sessile
- Soft anatomy is vital for understanding the oldest skeletal fossils
A Cambrian tommotiid preserving soft tissues reveals the metameric ancestry of lophophorates

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SUMMARY

Among extant animals, Lophotrochozoa accounts for the majority of phyla. 1 This bilaterian clade radiated rapidly during the Cambrian explosion, obfuscating its phylogenetic relationships and rendering many aspects of its early evolution uncertain. Many early lophotrochozoans are known only from isolated skeletal microfossils, "small shelly fossils," often derived from larger animals with complex multi-element skeletons. 2 The discovery of articulated fossils has revealed surprising insights into the animals from which these skeletal pieces were derived, such as paired shells in the mollusc Halkieria. 3 Tommotiids are a key group of phosphatic early skeletal fossils that first appear in the late early Cambrian. 4, 5 Although their affinities were previously obscure, discoveries of partial scleritomes and investigations of growth and microstructure 6 provide links with Brachio- poda 7, 8 and Phoronida, 9 two of the lophophorate phyla. By contrast, the body plan of camenellan tommotiids remains a palaeontological mystery, with hypothetical reconstructions representing motile, benthic, dorsally armored worms. 4, 10 Here, we describe an articulated camenellans (Wufengella bengtsoni gen. et sp. nov.) from the Cambrian Chengjiang Biota, China, revealing the morphology of the scleritome and the first soft tissues from an adult tommotiid. Wufengella carries two dorsal rows of sclerites in a highly asymmetric arrangement, flanked by smaller, cap-shaped sclerites. The scleritome was fringed by iterated fascicles of chaetae and two layers of flattened lobes. Phylogenetic analysis confirms that camenellans occupy a deep branch in lophophorate phylogeny, prior to the acquisition of a sessile lifestyle. Wufengella reveals direct evidence for a metameric body plan reminiscent of annelids early in the evolutionary history of lophophorates. 11, 12

RESULTS AND DISCUSSION

Lophophorata Hyman 1959
Order Tommotida Missarzhevsky 1970
Wufengella bengtsoni gen. et sp. nov.
LSID urn:lsid:zoobank.org:act:2353549D-7775-40EB-8BD7-31439DA2D572.
Holotype CJHMD00041, Nature Museum of Yunnan, Chengjiang, Yunnan, China. A single specimen as part (Figure 1A) and counterpart (Figure 1C), a composite mold of the scleritome with peripheral soft tissues (see also Figure S1).
Locality Yu’anshan Member, Chiungchussu Formation, Cambrian Series 2, Stage 3, Haikou, Kunming, Yunnan, China. 13
Etymology For Wufeng Hill, Chengjiang. “Wufeng” means dancing/flying phoenix. The species name honors Stefan Bengtson.
Diagnosis for genus and species Dorsal biseriate scleritome of successively overlapping and distinct left (sellate) and right (mitral) sclerites, with superimposed smaller, dorsal, cap-shaped sclerites arranged in rows at the lateral margins of the scleritome. In each row, 12 sellate and 11 or 12 mitral sclerites are preserved. Sclerite surfaces bear growth lines and prominent, regular ribs, without visible radial ornamentation. Flat, rigid lobes flank the body—a longer
and narrower dorsal lobe and shorter and wider ventral lobe. Dorsally, between the scleritome and the lobes, are long capillary chaetae, bundled into fascicles, with some additional spinose chaetae.

**Description**

The anterior is inferred from posterior overlap of sclerites and lateral lobes as in other cataphract lophotrochozoans. The anterior-most region is missing, but the scleritome appears relatively complete, assuming equivalent tapering at both ends. The scleritome is 14.5 mm in length and 3.6 mm wide at the midbody. Exposed soft tissues extend the body to ~16 mm long and ~11 mm wide. Sclerites are preserved as a mold that forms a depression on both part (Figure 2A) and counterpart (Figure 2B). Tomographic data reveal no additional sclerites within the sediment, confirming a dorsal (rather than tubular) scleritome (Figures S2A–S2D), consistent with the taper observed anteriorly and posteriorly and the bilaterally symmetrical peripheral soft tissues (Figures S1B and S1D). The part preserves the series of mitral and sellate series (Figures 1A, 1B, 2A, 2C–2F, and S3A–S3D), whereas the counterpart mainly preserves the superimposed and smaller cap-shaped sclerites (Figures 1C, 1D, 2G, 2H, and S3E–S3H) and the apical regions of the mitral/sellate series (Figure 2B). Substantial overlap of sclerites obscures their original outlines, but compactional deformation allows their tracing (STAR Methods). Growth lines of sellate sclerites are deflected onto the ventral side on the posterior margin, suggestive of the shell margin doubling over as a duplicature (Figure 2D).

Sclerites vary in shape along the anterior-posterior (AP) axis; their general appearance is summarized here based on the midbody (Figures S2 F–S2H). Mitral and sellate sclerites are both in sinistral/L-form symmetry. The posterior margin of sellate sclerites has a faint sella separating it into left and right lobes (Figures 2C and 2D). The larger left lobe forms a prominent projection beneath the mitral and sellate sclerite anterior to it (Figures 2C–2F). Sellate sclerites have a steep left lateral margin, with the right lobe forming a less steep, laterally projecting slope, displacing the apex to the left (Figures 2C and 2D). Mitral sclerites have a pointed, conical apex (Figures 3I–3L) with four distinct sides during growth. The accrescent and decrescent sides are wide and concave medially (Figures 2E and 2F). Apices of the sellate (Figures 3C and 3D) and cap-shaped sclerites (Figures 3G and 3H) are also conical. The smaller (~1.5 mm near the mid-length of the body), cap-shaped sclerites form irregular marginal rows superimposed onto dorsal surfaces of the mitral and sellate sclerites, only clearly visible on the counterpart (Figures 2G and 2H).

All three sclerite types bear regularly spaced co-marginal ribs best seen on the part for the mitral and sellate sclerites (Figures 3C–3J). No other ornament is visible, except for fine
growth increments between the co-marginal ribs (Figures 3E and 3F). Neither the obplicate nor plicate side exhibits radial folds (plicae) as in Camenella. The dorsal integument extended beyond the scleritone to form a margin between the sclerites, lobes described below, and the chaetal fascicles (Figures 2L and 2M).

Chaetae are preserved as imprints or masses of weathered pyrite, sometimes delineating a single chaeta or few chaetae (Figures 2I–2M). Where pyritized, they can be readily identified using fluorescence microscopy (Figures 2J, 2K, and 2M). Chaetae occur on the dorsal surface as long, slender capillary forms emerging from fascicles that insert in the interface between two body lobes flipping the dorsal scleritone (Figures 2I–2K). There are additional and widespread shorter and stouter chaetae (Figures 2L, 2M, and 2P), as well as chaetae oriented perpendicu lar to the chaetal fascicles, likely arising from the dorsal integument (e.g., Figures 2K, S1K, and S1L). The distance between the distal-most tips and from where the fascicles emerge on the dorsal body suggests a length between 2.4 and 3.6 mm, with each capillary chaeta being less than 20 μm in width (more completely preserved chaetae are shown in Figure S1G).

Two sets of seriated lobes, one short and the other long, project laterally from the body (Figures 1 and 2L–2P). The shorter set of lobes is ventral (Figures 2L–2O) and relatively broad, whereas the longer, more slender lobes are dorsal and best exposed in the counterpart (Figure 2P). The lobes have a slight posterior overlap (Figure S1H), suggesting they were relatively flat in life (Figure 4B). The lobes project from the margin of the body in a consistent, approximately perpendicular orientation without evidence for bending, as if relatively rigid. Anterior and midbody lobes are similarly sized but become successively smaller posteriorly. The number of lateral chaetae cannot be counted with confidence due to variable splitting and exposure but exceeds 16. The number of body lobe pairs seems to correspond to the number of chaetal fascicles.

Bayesian phylogenetic inference of 479 characters and 173 taxa (STAR Methods; supplemental information) recovered Wufengella bengtsoni as a stem group lophophorate, in a polytomy with other camenellan tomomiids, subsuming a clade that contains Eccentrotheca, Paterinitra, and the extant lophophorate phyla (Figures 4D, S4, and S3I). There is substantial uncertainty regarding interrelationships of the brachiopod crown, with many unresolved nodes in the analysis without topological constraints. This is similar to some previous morphological analyses of brachiopod interrelationships, particularly regarding whether or not inarticulates are a clade. If inarticulated is constrained as monophyletic (as favored by recent molecular analyses), relationships are better resolved (Figure S4B), with fossil brachiopods placed largely congruently with their taxonomic assignments. These constraints do not impact the placement of Wufengella or other tomomiids.

Lophotrochozoans with multi-element skeletons (scleritomes) are familiar components of early Palaeozoic fossil assemblages. They encompass several phyla, including mchaearian annelids,14,17 sachitid molluscs, and tomotomid total group lophophorates.7,15,18 “Tommotiid” here refers to an informal grouping, including camenellans, eccentrotheci morphs, and tannoulinids (following common usage7,9,15), rather than to Tommotiidae. Most early scleritomous animals were originally known from isolated sclerites that offer limited insights into the organisms from which they were derived. For example, while Halkieria sclerites allowed for reconstruction as a cataphact, Wiwaxia-like animal2 with multiple types of dorsal sclerites, articulated Halkieria specimens revealed unexpected sclerite arrangements and anterior and posterior shells. While articulated fossils are vital for testing models of scleritone arrangement, associated soft and non-bio mineralized tissues are critical for understanding the phylogenetic placement of early skeletal taxa.14,18,20

Tommotids have long been allied to brachiopods based on similar microstructures and organo-phosphatic biomineralogy.19 The scleritone construction of tommotids was elusive until Mi cri na was reconstructed as bivalved and brachiopod-like1 and partial scleritomes showed that Eccentrotheca sclerites formed...
a dwelling tube. 9 *Paterimitra* was morphologically intermediate between those two, with two major basal sclerites flanked by many smaller elements. 18 These adaptations for a sessile mode of life and characters shared with either brachiopods or phoronids have led to placement of these taxa in the lophophorate crown, on the stem lineage of these two phyla, 7–9,21 although there have been few formal analyses of these relationships. 21,22

Figure 3. Sclerite ornament and growth characters of *Wufengella bengtsoni* gen. et sp. nov.

All RTI extracts using specular enhancement images except (K and L) SEM backscatter images. Detailed RTI settings in Table S1.

(A and B) Part and counterpart respectively showing locations of details in other panels; (B) rotated to mirror (A).

(C and D) Detail of apical regions of two sellate sclerites; co-marginal ribs indicated by arrowheads.

(E and F) Detail of (C), showing growth lines between co-marginal ribs, marked by overlay in (F).

(G and H) Details of a cap-shaped sclerite indicated in (B); arrowheads in (H) indicate co-marginal ribs.

(I and J) Mitral sclerites indicated in (A), showing co-marginal ribs.

(K and L) Mitral sclerite with well-preserved apex. ap, apex.

Scale bars, 1 mm except in (L) and 0.2 mm.

See also Figure S3.
Camenellan tommotiids have been hypothesized to be vagile organisms with dorsal scleritomes. Their sclerites are more regular in morphology than the taxa discussed above, with asymmetrical sclerite types having left- and right-handed symmetry variants and bilateral morphs formed from early ontogenetic fusion in some genera. Reconstructions include a mixed biseriate to tetraseriate arrangement of sclerites on the dorsum in *Dailyatia*, a biseriate scleritome, or a more complex array of dorsal sclerites in *Lapworthella*. Articulated specimens have been lacking, except for a putative juvenile camenellan from Mongolia. The scleritome of *Wufengella* consists of asymmetrical, phosphatic, serially repeated sclerites that grew continuously via accretion, with a prominent ornament of regularly spaced ribs. These characteristics alone limit the early Palaeozoic sclerite-bearing taxa to which it can be compared to tommotiids and to a lesser extent machaeridians and sachitids. Machaeridian sclerites are also asymmetrical with prominent growth ribs, but they have a narrow attachment to their bodies, and new shell material accreted at a single accreting margin, whereas basal/internal accretion is inferred from *Wufengella*, commencing from a prominent conical apex. Sclerites of machaeridians are calcitic rather than phosphatic. The sclerite arrangements of sachitids (e.g., *Halkieria*) have been compared with reconstructions of camenellan tommotiids, but the sclerites of *Halkieria* and related taxa grew to a finite size and were subsequently replaced during ontogeny, rather than showing continuous growth as in *Wufengella*. Comparisons between *Wufengella* and halkieriids are therefore limited to the accretionary shells. Sachitids are considered to have had an aragonitic biomineralogy, and the shells of sachitids and *Wufengella* share no other characters.

All the features that we have identified in *Wufengella* are present in tommotiids (or a subset thereof) or likely close relatives. The sclerite arrangements of sachitids (e.g., *Halkieria*) have been compared with reconstructions of camenellan tommotiids, but the sclerites of *Halkieria* and related taxa grew to a finite size and were subsequently replaced during ontogeny, rather than showing continuous growth as in *Wufengella*. Comparisons between *Wufengella* and halkieriids are therefore limited to the accretionary shells. Sachitids are considered to have had an aragonitic biomineralogy, and the shells of sachitids and *Wufengella* share no other characters.

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sclerite morphs (sellate and mitral sclerites, i.e., forms B and C, respectively, in Dailyatia15) are shared exclusively with camenellans. Wufengella has a superficial resemblance to the eccentricid Sunnaginia,35 which can exhibit S-shaped sclerites but otherwise lacks two distinct asymmetrical sclerite types and co-marginal ribs, and grows instead by non-uniform deposition of layers beneath an irregular apical surface as in other eccentricids (Figure S3I). Sunnaginia has a umembrate scleritome that forms a morphological continuum between two end members.32

One genus, Camenella (=Tommotia), belongs to Tommotiidae,15 while two other families (Lapworthellidae and Kennardiidae) are considered closely related and together are informally referred to as “camenellans.”17 Lapworthellids have a single asymmetric and symmetric sclerite morph, whereas kennardiids have two asymmetric morphs along with a third symmetric morphotype (Figure S3I). Both symmetric morphs exhibit multiple (two15,24 or more26) apices, indicative of their derivation from a fusion of multiple sclerites.24

Wufengella lacks bilaterally symmetrical sclerites, therefore limiting its close resemblance to certain species of Camenella. In Wufengella and Camenella the mitral sclerite has four distinct sides, but Wufengella lacks plicae. In both genera, the sellate morphotype forms two lateral lobes often separated by a concave groove (sellae), and the posterior margin deflects ventrally to form a duplicature. Wufengella possesses smaller, asymmetrical cap-shaped sclerites superimposed dorsally, which are unknown in Camenella.

Moldic preservation of the sclerite as a negative impression in both part and counterpart suggests a recalcitrant biomineralogy. While calcium phosphate is occasionally preserved in some inarticulate brachiopods in Chengjiang, moldic preservation due to late dissolution weathering after compaction and lithification is observed variably in brachiopods and some organo-phosphatic ecdysozoans.33,34 Calcium carbonate skele-
ts are unknown in most camenellans, but are at least in Canadiella filigrana, where they were interpreted as juvenile sclerites despite lacking a pointed apex.36

Camenellans are considered closely related and together are informally referred to as “camenellans.”17 Lapworthellids and kennardiids share a close relationship with extant lophophorates, such as annelids and molluscs.20 This body plan observed in Camenella is consistent with a phylogenetic position outside the lophophorate crown group and thus sheds light on the deep

The description of putative camenellan juveniles26 revealed a uniseriate arrangement of pointed sclerite primordia, with a cellular ornamentation identical to that of co-occurring Camenella mongolica, surrounded by smaller sclerite primordia of accessory sclerites. The reconstruction proposed a medial row composed of a symmetric sclerite yet unknown in Camenella, while asymmetric sclerites flank the body.24 Based on our scleritome, we instead suggest that the mitral and sellate sclerites successively overlap each other and are on successive body units that become displaced laterally during growth. This asymmetry results from accommodating rigid sclerites as the body grows, similarly to offsetting the symmetry of certain machaeridians35 where the plates overlap and enclose the body. Peripheral sclerites in Camenella mongolica may correspond to the cap-shaped sclerites described here (Figures 2G and 2H). These smaller sclerites are unknown in most camenellans, but are at least in Canadiella filigrana, where they were interpreted as juvenile sclerites despite lacking a pointed apex.36

Camenellan microfossil assemblages are generally found with mitrals and sellates having both left and right symmetry, whereas our specimen possesses only one symmetry morph (L-form). Bengtson noted that the unbalanced proportions of symmetry forms could be evidence of the organism being biseriately and asymmetrical with frequent reversals in left-right symmetry in individual organisms. Our discovery favors this hypothesis but needs corroboration through the discovery of additional articulated scleritomes. Symmetry reversals are seen in other asymmetrical skeletal fossils, e.g., polychaete jaws, albeit with a much smaller frequency than required for tommotids.

Understanding tommotiid affinities is crucial for unravelling the origin of the lophophorate phyla, and their sclerite architectures have generated debate over the assembly of the brachiopod and phoronid body plans.4,6-9,21,28 Two major divisions of tommotid-like sclerites have been identified, the camenellans and eccentric which are unknown in most camenellans, but are at least in Canadiella filigrana, where they were interpreted as juvenile sclerites despite lacking a pointed apex.36

Although the phylogenetic position of Bryozoa has previously been highly uncertain, phylogenomic analyses now often show that together with Phoronida and Brachiopoda they belong to Lophophorata.42-45 The monophyly of this group combined with detailed anatomical studies11,46,47 suggests their last common ancestor was a sessile, lophophore-bearing suspension feeder. This contrasts with the body plan observed in Wufengella, which we infer was motile, similarly to that of early representatives of close relatives of lophophorates, such as annelids and molluscs.20 This body plan is consistent with a phylogenetic position outside the lophophorate crown group and thus sheds light on the deep
ancestry of this sessile, filter-feeding clade. Hypotheses involving lophotrochozoans being primitively sessile with U-shaped guts are not supported.

Lophophorates are variably recovered as the sister taxon of one or more phyla, including annelids, nemerteans, or gastrotrichs. Morphological studies have noted similarities between lophophorates and annelids, including chaetae secreted by microvilli; paired, metameric coelomic compartments; and a similar metanephridial architecture. Our phylogeny, depicting annelids and lophophorates as sister taxa, is consistent with homology of these features. Whereas adult brachiopods have mantle chaetae projecting from the aperture, larval brachiopods exhibit paired and sometimes serially repeated chaetae on the dorsal surface, reminiscent of the condition in Wufengella. Seriation along the AP axis in Wufengella involves chaetae, chaetal fascicles, and lobes, and it is integrated to the extent that it can be regarded as metamerism. If involved in sclerite formation, it is likely that the integument of Wufengella is homologous with the mantle of extant brachiopods.

The discovery that camenellans were vermiform, metameric, chaetae-bearing animals corroborates historical hypotheses based on isolated microfossils as well as hypothesized anatomical links between annelids and brachiopods. The body plan of Wufengella deviates from hypothetical intermediates between brachiopods and annelids, however, notably in the arrangement of soft tissues but also the presence of an asymmetrical, phosphatic sclerite. The arrangement of the sclerites in Wufengella also deviates from previous reconstructions based on microfossils alone, mirroring insights provided by articulated specimens of Halkieria. Although Halkieria and related fossils (e.g., Wiwaxia) were previously argued to bridge the gap between the body plans of annelids, brachiopods, and molluscs, subsequent discoveries aligned them to the molluscan stem and crown group. Aspects of the halkieriid body plan may reflect characters primitively shared by molluscs, annelids, and lophophorates (e.g., being vermiform, with chaetae and seriated organ systems). Nevertheless, the hypothesis that brachiopods (and other lophophorates) are derived from armored, vermiform animals finds new support here—but via a lophophorate stem lineage populated by tommotiids rather than halkieriids.

STAR METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2022.09.011.
of Chengjiang, China: The Flowering of Early Animal Life (John Wiley & Sons).

53. Chen, H., Parry, L.A., Vinther, J., Zhai, D., Hou, X., and Ma, X. (2020). A Cambrian crown annelid reconciles phylogenomics and the fossil record. Nature 583, 249–252.

54. Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A., and Huelsenbeck, J.P. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. 61, 539–542.

55. Sperling, E.A., Pisani, D., and Peterson, K.J. (2011). Molecular paleobiological insights into the origin of the Brachiopoda. Evol. Dev. 13, 290–303.

56. Lewis, P.O. (2001). A likelihood approach to estimating phylogeny from discrete morphological character data. Syst. Biol. 50, 913–925.
STAR METHODS

KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---------------------|--------|------------|
| Deposited data      |        |            |
| Morphological character matrix in NEXUS format | This study | Data S2 |
| RTI datasets        | This study | Archived at https://doi.org/10.5523/bris.1o4kiwed7uerv2bi7xyihwwjfw |
| CT datasets         | This study | Archived at https://doi.org/10.5523/bris.1o4kiwed7uerv2bi7xyihwwjfw |
| Software and algorithms |        |            |
| MrBayes 3.2.6       | Hou et al.52 | http://nbisweden.github.io/MrBayes/ |
| RTI Viewer          | CNR-ISTI Visual Computing lab | http://vcg.isti.cnr.it/rti/rtiviewer.php |
| Other               |        |            |
| Wufengella bengtsoni specimen | Nature Museum of Yunnan, Chengjiang | CJHMD00041 |

RESOURCE AVAILABILITY

Lead contact
Requests related to fossil specimens should be directed to P.C. (Cong@ynu.edu.cn). All other requests can be directed to L.A.P. (luke.parry@seh.ox.ac.uk).

Materials availability
The single nearly complete specimen is deposited at the Nature Museum of Yunnan, Chengjiang, Yunnan, China with the registration number CJHMD00041.

All data analysed in this paper are available as part of the Report, Figures S1–S4, in the supplemental information or as part of a data repository hosted by the University of Bristol which includes RTI datasets, raw CT datasets and full resolution SEM and light photo micrographs are available at the following repository https://doi.org/10.5523/bris.1o4kiwed7uerv2bi7xyihwwjfw.

Data and code availability
The matrix used for the phylogenetic analysis is available as a nexus file on the online repository https://doi.org/10.5523/bris.1o4kiwed7uerv2bi7xyihwwjfw.

The parameters used for the phylogenetic analysis are described in the STAR Methods section below. The commands necessary to execute the phylogenetic analyses are included in Data S3.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

The single nearly complete specimen was collected from the middle-upper part of the Yu’anshan Member, Chiungchussu Formation, Cambrian Series 2, Stage 3, in a section of Haikou, Kunming, Southwest China.52 The specimens are preserved together with several small myllokunmingiid chordates that were recently reported as a mass gathering in the same beds.13

The fossil was deposited at the Nature Museum of Yunnan, Chengjiang, Yunnan, China with the registration number CJHMD00041.

METHOD DETAILS

Photographs from multiple lighting directions, reflectance transformation images, SEM images, and camera lucida drawings were combined to trace sclerite margins, growth lines and ornament (Figures 2, S2F–S2H, and S3).

SEM images were obtained with a FEI Quanta 650 FEG at working distances of 13.8–16.2 mm, with an accelerating voltage of 15 kv. The specimen was not coated prior to analysis. Composite SEM images were assembled using Adobe Photosop. Fluorescence images were taken with a Leica DFC7000 digital camera mounted on a Leica M205 FA fluorescence microscope. Energy Dispersive X-ray Spectrometry (SEM EDX) of the scleritome and peripheral soft tissue was performed with a Hitachi S-3500N with a Thermo Noran energy dispersive spectrometer. CT scans were produced with a Zeiss Xradia 520 Versa at YKLP.

Details of the camera, lenses and number of images used to produce the reflectance transformation image (RTI) files are given in Table S1 and details of the settings used to generate the images in individual figure panels are detailed in Table S2.
QUANTIFICATION AND STATISTICAL ANALYSIS

Phylogenetic analyses made use of existing datasets for annelids, molluscs and brachiopods\textsuperscript{17,20,22,53} that were supplemented with additional data for tommotids, including the novel observations of \textit{Wufengella} made herein. Phylogenetic analyses were performed in MrBayes 3.2.7.\textsuperscript{54} 10,000,000 generations were requested, with analyses automatically stopped when the standard deviation of split frequencies was <0.01. Convergence was assessed using the ESS (>200) and PSRF (~1.0) reported by the sump command in MrBayes. One analysis (Figure S4A) used the default priors on all parameters (e.g. all topologies have equal prior probability) and a second analysis (Figure S4B) used a soft constraint on annelid internal relationships as employed previously\textsuperscript{53} (Figure 4D) as well as a monophyly constraint on the brachiopod node Inarticulata.\textsuperscript{55} All analyses used the mki + gamma model.\textsuperscript{56}