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An early Cambrian agglutinated tubular lophophorate with brachiopod characters

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The morphological disparity of lophotrochozoan phyla makes it difficult to predict the morphology of the last common ancestor. Only fossils of stem groups can help discover the morphological transitions that occurred along the roots of these phyla. Here, we describe a tubular fossil *Yuganotheca elegans* gen. et sp. nov. from the Cambrian (Stage 3) Chengjiang Lagerstätte (Yunnan, China) that exhibits an unusual combination of phoronid, brachiopod and tommotiid (Cambrian problematica) characters, notably a pair of agglutinated valves, enclosing a horseshoe-shaped lophophore, supported by a lower bipartite tubular attachment structure with a long pedicle with coelomic space. The terminal bulb of the pedicle provided anchorage in soft sediment. The discovery has important implications for the early evolution of lophotrochozoans, suggesting rooting of brachiopods into the sessile lophotrochozoans and the origination of their bivalved bauplan preceding the biomineralization of shell valves in crown brachiopods.

Exceptionally preserved Cambrian stem group fossils¹, with novel combinations of character states, are of critical importance in understanding the origin and early evolution of metazoans². The morphological disparity of lophotrochozoan phyla^{3,4} makes it difficult to predict the morphology of the last common ancestor. Only fossils of stem groups can help discover the morphological transitions that occurred along the roots of these phyla^{5,6}. The Brachiopoda is a lophotrochozoan phylum that is characterized by possessing a bilaterally symmetrical bivalved shell composed either of apatite or calcite (rarely aragonite) and secreted by dorsal and ventral mantle epithelia with mantle canals (coelomic extensions). Based largely on shell composition and the type of hinge articulation^{7,8}, the brachiopods are divided into three subphyla; though some molecular trees have indicated the phylum Phoronida may possibly represent a shell-less subphylum or Class within Brachiopoda^{9,10}. However, the original bauplan of the last common ancestor of the brachiopod-phoronid clade has remained shrouded in mystery, not least because of the paucity of early soft-bodied fossil records of phoronids and brachiopods. Living phoronids are benthic, solitary and lacking biomineralization¹¹, and some construct tubes in soft sediment by agglutinating sedimentary grains. The phylum Phoronida has no incontrovertible fossil record until the Devonian¹⁰. Nevertheless, an increasing number of skeletal tommotiids (Cambrian problematica) have been proposed as potential brachiopod/phoronid stem groups^{12,13}, though their soft-part anatomy is hitherto unknown.

Here we report an exceptionally preserved arenaceous agglutinated tubular fossil, *Yuganotheca elegans* gen. et sp. nov. (Figs. 1–2; S2–S6), based on a large number of fossil specimens collected by the Xi'an and Nanjing research groups from the Chengjiang Konservat Lagerstätte around Kunming, China (Fig. S1). This tubular animal displays a previously unknown combination of character states including some found in living phoronids, brachiopods and some manifested in the tubular scleritomes of Cambrian tommotiids, like *Eccentrotheca*¹². The morphological terminology adopted herein mostly follows the revised Treatise on Invertebrate Paleontology⁸. Several terms are introduced to define previously unknown fossil character states. Fossil orientation and description of “upper” and “lower” parts in the animal is based on comparative morphology and its semi-infaunal, sessile life style (Fig. 3).

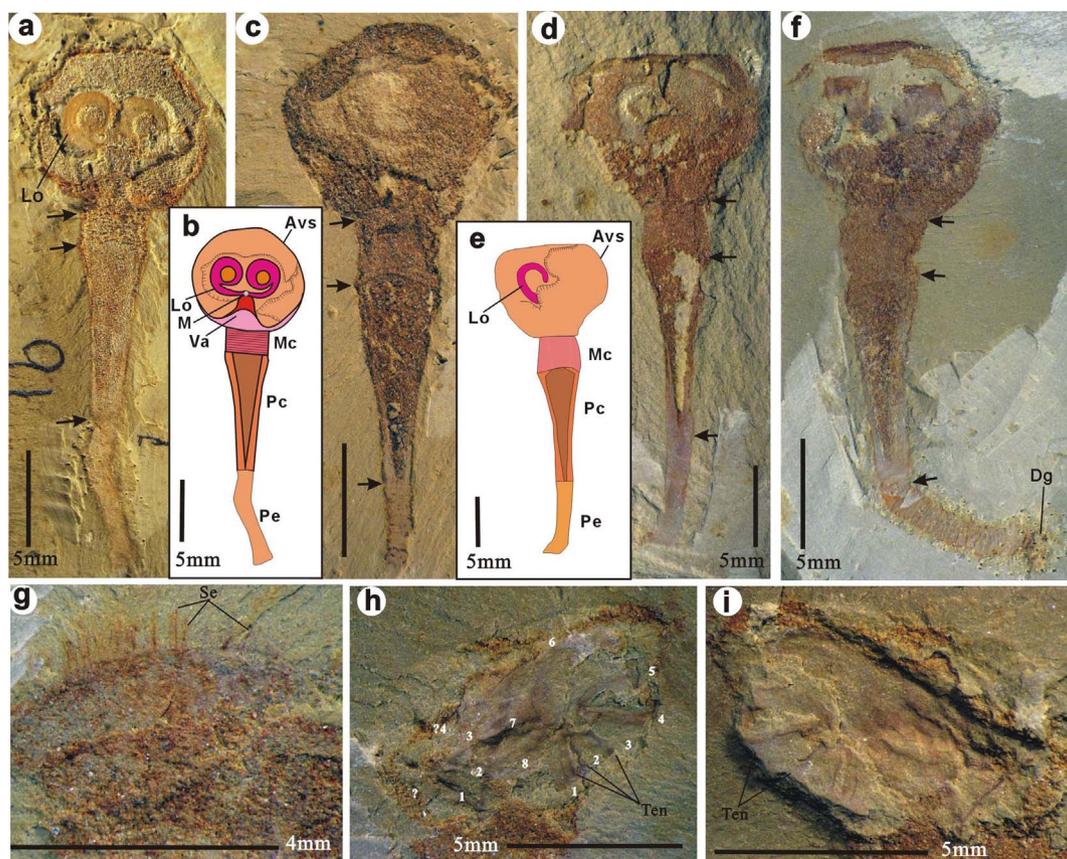


Figure 1 | *Yuganotheca elegans* gen. et sp. nov. from the early Cambrian Chengjiang Lagerstätte, Yunnan, China. Arrows point to the borders between the upper pair of valves (Avs), median collar (Mc), lower conical tube (Pc), and pedicle (Pe); M = mouth; Lo = lophophore; Va = visceral area; Dg = the terminal pedicle bulb with adhered grains; Se = setae; Ten = tentacles. (a), Holotype, ELI BLW-0091, compare to b. (c–d), ELI BLW-0016AB, part and counterpart; note the lophophore imprint in d. (e), compare to d. (f), ELI BLW-0141A, complete individual with well developed pedicle. (g), close-up view of the marginal setae in Fig. S4f. (h–i), enlarged view of the lophophoral tentacles in Fig. S6b and a. The sketch drawings were made and organized together using CorelDraw 9.0 and finally converted to TIF format. Z. Zhang created these images.

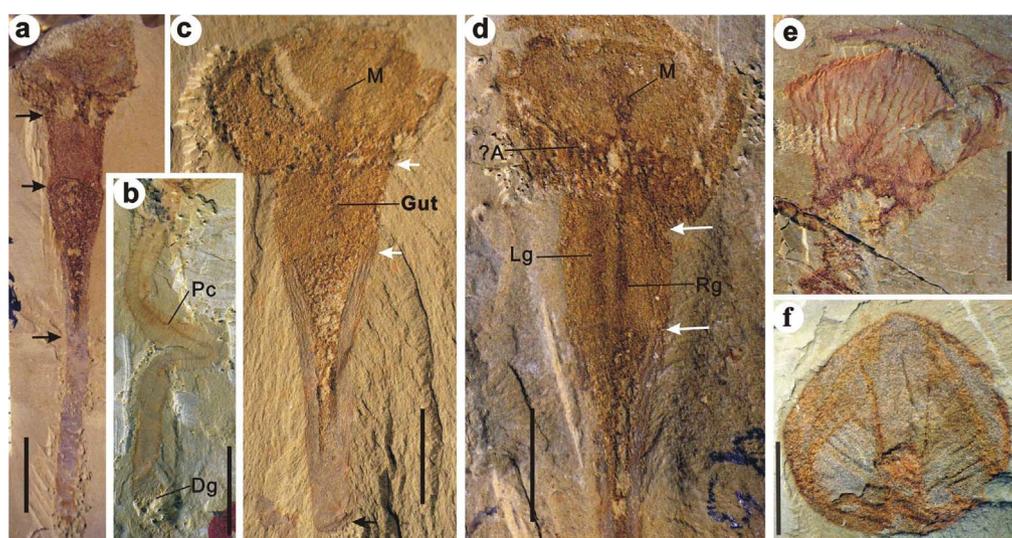


Figure 2 | *Yuganotheca elegans* gen. et sp. nov. from the early Cambrian Chengjiang Lagerstätte, Yunnan, China. Arrows point to the borders between the anterior pair of valves, median collar, lower conical tube, and (in 2a, b, d) pedicle; all scale bars are 5 mm. (a), ELI BLW-0065B. (b), ELI BLW-0101, showing the central lumen (Pc) and the terminal bulb (Dg) of the pedicle. (c–d), showing the oblique growth fila of the lower cone and gut remains. c, ELI BLW-0018A. (d), ELI BLW-0095; note U-shaped lineation interpreted as the digestive tract marked by left (Lg) and right (Rg) parts; note the putative location of mouth (M) and probable anus (?A). (e), ELI BLW-0475A, showing well-preserved ventral mantle canals. (f), ELI BLW-0483B, interior dorsal valve.

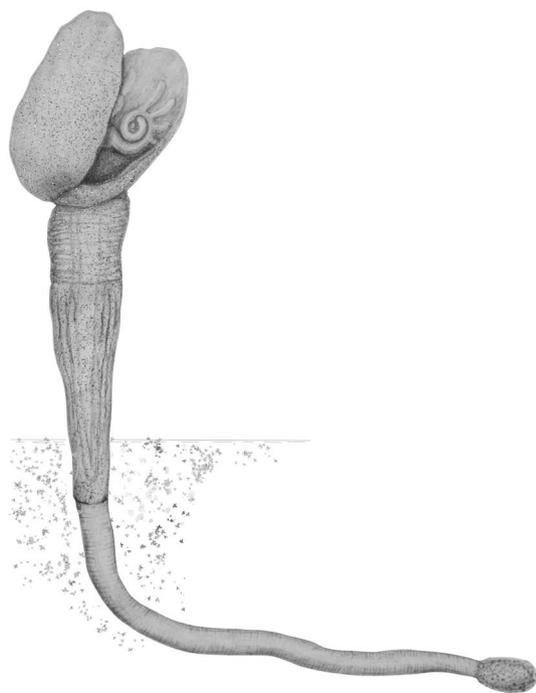


Figure 3 | Artistic reconstruction of *Yuganotheca elegans* gen. et sp. nov. with inferred semi-infaunal life position. The figure was drawn manually by D. Fu using pencil and scanned as TIF format. Z. Zhang created the image.

Results

Systematic palaeontology. Total group Lophotrochozoa

Superphylum Lophophorata

Phylum & Class uncertain

Yuganotheca elegans gen. et sp. nov. Zhang, Li et Holmer

Etymology. Yugan, in honour of the late Prof. Yugan Jin (Nanjing) who pioneered the study of exceptionally preserved brachiopods from the Chengjiang fauna; theca, refers to the conical shape.

Holotype. Early Life Institute, Northwest University, Xi'an, ELI BLW-0091.

Referred material. 710 specimens in Early Life Institute (Prefix: ELI), Northwest university, Xi'an (ELI-BLW 0001-0710), and some in Nanjing Institute of Geology and Palaeontology, Nanjing.

Stratigraphy and locality. Heilinpu (formerly Chiungchussu or Qiongzhusi) Formation, Yu'an-shan Member (*Eoredlichia-Wutingaspis* Trilobite Biozone, ordinarily correlated with the late Atdabanian or Botoman Stage in Siberia), Cambrian unnamed Stage 3. Specimens were collected in Haikou, Erjie, Shankou and Chengjiang areas, around Kunming (Fig. S1).

Diagnosis. Body elongate and quadripartite, comprising an upper pair of unmineralized dorso-ventral valves, median collar region, lower conical tube and a pedicle. Bivalved ventribiconvex, unmineralized "shell" coated with coarse silt to fine sand-sized detrital grains. Dorsal valve circular or subcircular in outline. Ventral valve low conical, with umbo directly connected to a median collar and ornamented by transverse striae or annulations. Mantle canals pinnate, well developed in both valves. Lophophore composed of double crown, bearing unique thick and elongate tentacles. Conical tube, elongate and rigid, progressively stiffening apically, ornamented with longitudinal striae. Vermiform pedicle long and flexible, with a central coelomic canal emerging from apical tip of the conical tube.

Preservation. All fossils from Chengjiang, including those with a non-mineralized, sclerotized or mineralized (including calcareous or phosphatic) original composition, are almost exclusively preserved as casts and moulds replicated by clays or impressions covered with reddish-brown framboid pyrite¹⁴. However, the preservation of *Y. elegans* is distinctive, varying along the length of the animal from the pedicle, via the conical tube and median collar to the bivalved "shell" (Fig. S3). The most striking preservational aspect of *Y. elegans* concerns the valves + collar, which are invariably preserved as reddish-brown, distorted moulds, covered by aggregated coarse silt to fine detrital sand grains (Fig. S3), in striking colour contrast to the surrounding and infilling fine-grained clay matrix (Fig. S7–10). The aggregated siliceous grains are restricted to the valves, collar and most of the upper of conical tube (Figs. 1a–f, 2a–d, S3a–h, S4a–c and e–f), rather than to the pedicle (Figs. 2b, S3a, S4a–c and e–f). The detrital grains appear mostly to be angular to subangular siliceous coarse silt to fine sand-sized grains (30–120 microns) in contrast to the surrounding host matrix (Fig. S3b–d). Quartz is the major (approximate 83%) constituent, with lesser amounts of feldspar and opaque minerals. Trace element analysis by LA-ICP-MS shows that the detrital grains are composed mostly of silicon dioxide (up to 83%), which is otherwise rare in the surrounding matrix (0.6%); iron accounts for up to 13.5% of the grains cemented by haematitic clay. Such type of preservation and distinct, sharply delineated differences in composition between fossils and host rock does not occur in any other known Chengjiang fossils (Figs. S6a,b,d compared to 6e–h). The exclusive aggregation of grains on the surface of the valves + collar + upper conical tube in *Yuganotheca* (Figs. S7–S10) is most likely bio-induced, and thus very similar to the distribution of agglutinated detrital grains (associated with non-acidic mucous cells) in some living phoronid species where only the uppermost part of the trunk emerging above the substrate is agglutinated¹¹.

Description of fossils. *Yuganotheca* possesses an elongate body plan that consists of an uppermost lophophoral chamber enclosed by a pair of soft, easily deformable valves covered by relatively fine clastic grains, and a tubular attachment structure composed of a median collar and a stiffened conical tube terminated by a long slender pedicle. The "shell" is subcircular to oval in outline, with maximum length ranging between 14.0 mm and 2.3 mm (mean 7.4 mm; n = 207) and maximum width between 17.5 mm and 2.8 mm (mean 9.4; n = 207). The valves appear to be ventribiconvex, with the ventral umbo connecting posteriorly to the median collar. In the fossil state, the valves are distinctly compressed together and preserved as composite impressions or internal moulds (Figs. 1a,c,d,f; 2a,c,d), varying in outline from oval to subtriangular or trapezoidal as a result of variable degrees of post-mortem deformation (Figs. S4a–c and e–f; S5g–h). The intensity and frequency of deformation of the valves suggests a lack of mineralization. The valves are completely coated by a mosaic of abundant siliceous grains (30–120 μm). The valves frequently show a crescent-shaped area close to the posterior margin which is tentatively interpreted as the impression of the visceral area (Figs. 1a,b, 2c,d).

Some specimens preserve a marginal setal fringe (Figs. 1g, S4f–g). As in other Chengjiang brachiopods^{15,16}, the setae are preserved as flat linear impressions along the bedding plane, with a maximum length of ca. 0.76 mm beyond the valve margin. In contrast, their thickness is estimated to be around 38 μm in diameter. When compared with the setae of other brachiopods from the Chengjiang fauna, the setae of *Yuganotheca* appear to be slightly longer and thicker than those in *Lingulelloreta* and *Lingulella*¹⁷, but markedly shorter and thinner than those associated with *Xianshanella haikouensis*^{15,16}.

During life the shape and convexity of the valves was probably enhanced by hydrostatic pressure of the pinnate mantle canals which



appear to be optimised for coverage of maximum surface area. In the ventral valve about 4–5 branches emerge from either side of a main trunk which then extend as subparallel canals along the length of the valve (Figs. 2e, S5a–d). In the dorsal valve, subsidiary branches emerge from two central branches that extend anteriorly along the lateral margins of the visceral area (Figs. 2f, S5e–f). The main trunks of canal system are ca. 130 μm in width (Figs. 2e, S5a), in contrast, their distributaries are estimated to range from 50–60 μm in diameter (Figs. 2e–f, S5a,c,e). In the fine muddy infillings between the valves, the imprint of the lophophore is preserved in detail (Fig. 1a–b,d–e); some specimens bear radiating tentacles (Figs. 1h–i, S6a–d). A maximum of eight tentacles can be observed on each lophophoral arm (Figs. 1h–i, S6a–d). The tentacles appear to be parallel-sided and hollow, up to 2.6 mm in length and 0.78 mm in width (Fig. 1h–i).

The median collar connects the upper valves with the lower conical tube. The median collar appears to only connect to the umbo of the ventral valve (e.g. Figs. 2a,c,d, S4f, 5g–h). The median collar ranges between 1.1–7.0 mm in length (mean 3.1 mm; $n = 222$), and from 1.0 to 6.3 mm in width (mean 3.3; $n = 227$) (Table S1) and exhibits a similar preservation and composition to the valves. In some cases (e.g. Fig. S4d), the median collar is preserved as an internal mould, exhibiting fine transverse annulations that suggest flexibility and possible contractibility. The transition between the median collar and the conical tube is abrupt and frequently manifested by a pronounced contrast in preservation and rigidity (Figs. 1, 2a; S4a–c, e–f, 5g–h).

The length of the conical tube varies from 3.1 mm to 21.0 mm with maximum width at the anterior apertural opening, where it is equivalent in width to the median collar. The minimum diameter is located at the posterior-most apical tip of the conical tube, with the apical diameter equivalent to the diameter of the proximal end of the pedicle. The conical tube expands continuously throughout growth with an apical angle of 16–22° (Figs. 1a–f, 2a,c,d, S3f–h, S4a–c,e–f). Many specimens show a prominent internal sediment infill flanked by lateral walls (Figs. 1c–d, S4a–c). The wall exhibits a distinct marginal edge (Figs. 1c,d, S3f–g), demonstrating some degree of rigidity, and possibly reflecting a certain degree of biomineralization. In some specimens, the conical tube is distinctly ornamented by longitudinally inclined lineations (Figs. 2c–d, S4b), which are interpreted here as longitudinal growth increments. The pedicle emerges from the distal tip of the conical tube which suggests that it is provided with an apical opening. The pedicle is flexible, elongate, up to 30 mm in length and 2.1 mm in width (Table S1), and exhibits pronounced annulations (numbering 4–5 per mm) and a coelomic canal (Fig. 2b).

As seen in figures (Fig. 2c,d), a U-shaped darkish lineation can be discerned; we tentatively interpret this as the alimentary canal, possibly arising from an antero-median position at the anterior body wall of the visceral cavity, extending posteriorly through the median collar with the recurved and located in the deep lower conical tube, with a very poorly impressed possible anus at the lateral side of the anterior body wall (Fig. 2d). However, as pointed out by one of the anonymous reviewers, the U-shaped structure is also closely comparable with the U-shaped median and lateral blood vessel of living phoronids¹⁸. Nevertheless, we consider this alternative interpretation less likely due to the lack of any evidence of short diverticula invariably associated with phoronid vessels¹⁸, as well as the fact that similar shaped linear impressions of digestive tracts are well documented in many Chengjiang brachiopods¹⁶, especially *Lingulellotretra malongensis*¹⁹ (also see Fig. S6h).

Discussion

The Lophotrochozoa^{3,4} represents a clade of remarkably diverse and anatomically disparate spiralian animals, especially Annelida, Mollusca (allied as trochozoans) and the Superphylum Lophophorata comprising Bryozoa, Entoprocta, Phoronida and Brachiopoda^{20,21}.

Although the general association of groups within the ‘clade’ Lophotrochozoa has received relatively stable support both from molecular and morphological studies², the exact relationships, origins and morphological transitions of the phyla within this group remain obscure^{4,5,22}.

The origin of the brachiopod bauplan has been the subject of several molecular and palaeontological studies^{23,24}. One hypothesis^{24,25} suggests that brachiopods arose by the folding and shortening of a *Halkieria*-like ancestor, lately summarized as Brachiopod Fold (BF) Hypothesis²⁶. However, this conjecture is challenged by recent discoveries of new fossil and embryonic data^{27,28}, and thus can no longer be considered tenable^{5,29}. Recent molecular analyses^{20,23} are generally in accordance with morphologically based phylogenetic analyses^{7,30,31} which convincingly demonstrate that brachiopods are monophyletic and sister group to the phoronids (see also Cohen³² and Balthasar & Butterfield³³ for an alternative view). The reiteration of monophyly of brachiopods and phoronids could be used to resurrect an early hypothesis that argued brachiopods originated from a tubiculous phoronid-like ancestor^{22,34}. Given that phoronids are most likely a sister group of brachiopods^{20,23}, critical questions about how close phoronids are to a supposed brachiopod stem, how brachiopods acquired a bivalve-shelled body plan from a lophophore-bearing last common ancestor, and the ecological milieu their common ancestor inhabited, are yet to be resolved.

The discovery of *Y. elegans* has important implications for these controversial issues. *Yuganotheca*, with a pedicle embedded in the seafloor for anchorage, can be reconstructed as a semi-infaunal, sessile suspension-feeder (Fig. 3). Additionally, the possession of a horse-shoe-shaped lophophore protected within a lophophoral chamber, formed by paired bisymmetrical but unmineralized “valves” formed by dorsal and ventral mantle lobes with marginal setae and mantle canals (coelomic extensions), unequivocally links *Yuganotheca* to brachiopods. A brachiopod affinity is further supported by the possession of a pedicle with a central coelomic lumen, known from both fossil and recent lingulids¹⁶.

Nonetheless, the agglutinated quadripartite tubular body plan of *Yuganotheca* is markedly distinct from typical crown group brachiopods characterized by bivalved mineralised shells composed of either apatite or calcium carbonate⁷; but is reminiscent, in part, of the agglutinated/chitinous tube-dwelling habitus of extant phoronids. The anatomy of *Yuganotheca* also has anatomical parallels to extant phoronids, such as the deeply U-shaped gut (Fig. 2c–d), a mouth inside and anus outside the helical lophophore fringed with a single row of thick, widely spaced, parallel-sided and hollow tentacles (Fig. 1h–i). The shape, thickness and number of lophophore tentacles also discriminates *Yuganotheca* from known fossil and recent brachiopods (see comparison in Fig. S6a–d to e–h showing the lophophore of associated Chengjiang brachiopods) and may suggest that the mode of filter feeding in *Yuganotheca* differed from the filter-feeding in all crown group brachiopods⁸. It is therefore assumed that *Yuganotheca* directed the gape of the lophophoral cavity into favourable ambient water currents by means of contracting and rotating the annulated median collar, thus achieving a filter-feeding current stirred and directed by the thick and clumsy tentacles towards the mouth, similar to living phoronids. In contrast the laminar filter-feeding current of all crown group brachiopods is directed lateral through the lophophore³⁵, and accordingly, *Yuganotheca* cannot be placed in the currently defined Phylum Brachiopoda^{7,8}. More likely, this taxon represents a key intermediate between phoronids and brachiopods, and this position is also supported by our phylogenetic analysis (Fig. 4). This analysis implies that the valves of *Yuganotheca* and brachiopods are homologous. The evolutionary transition from phoronids to brachiopods is marked by the retention of agglutinated tubular body, the acquisition of an enclosed filtration chamber formed by bilobed mantle extension, and co-opting of a deep extension of U-shaped gut for sessile life habit. The evolution of the

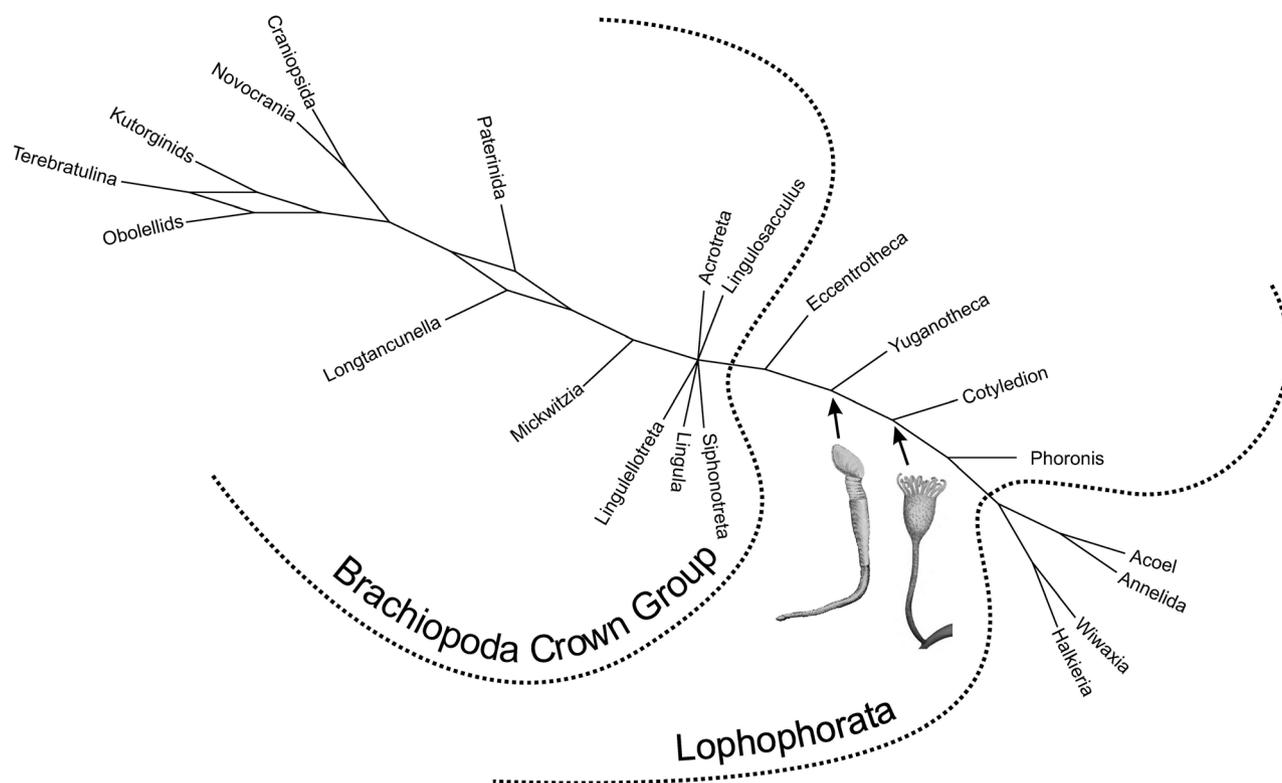


Figure 4 | A splits network of 330 most parsimonious trees retrieved through a TNT new technologies search (10,000 replications; using all four search algorithms built into TNT), suggesting *Yuganotheca* may be the most ancestral brachiopod bearing a tripartite attachment structure that combines characteristics of rhynchonelliform and linguliform brachiopods and features of some tommotiids. The internal phylogeny of the crown groups (calcareous and apatite) brachiopods depend on the assumed polarity of biomineralization of shell, but *Yuganotheca* is invariably basal to the brachiopod crown, and closely allied to phoronids. U. Balthasar created the image.

brachiopod bauplan thus corresponds to reduction and ultimate loss of the deep conical tubular extension of the body cavity beyond shell valves; this feature is apparent in other Cambrian taxa exemplified by the lingulellotretids¹⁹, and notably in *Lingulosaccus*³³, which possessed a drawn-out pocket-shaped ventral pseudointerarea accommodating the bulk of the body cavity while the dorsal valve forms little more than a lid over the filtration chamber. It appears therefore that the linguliform body plan emerged through the loss of the median collar and lower conical tube, while the elongate body was first accommodated in an extended ventral pseudointerarea. In the context of the early evolution of the subphylum Rhynchonelliformea, the annulated median collar of *Yuganotheca* could be pivotal for understanding some key character states present amongst stem group representatives. The median collar, protruding from the ventral valve umbo, provides a link with the circular chitinous pad-like colleplax³⁶, described in the broadly contemporaneous soft-shelled rhynchonelliform chileate *Longtancunella* which was characterised by a stout pedicle that is invariably better preserved than the unmineralized valves³⁷. *Longtancunella* also retained a U-shaped digestive tract and developed a strong, tabular thickened pedicle through elongation of the short median collar in *Yuganotheca*. In a broad sense, the umbonal perforation and colleplax in the chileate-like brachiopods may be homologous with the pedicle sheath in strophomenate brachiopods and the attachment structure (cicatrix) of craniiform brachiopods, a view which is now receiving increasing support³⁸. The discovery of *Yuganotheca* therefore provides a direct bridge between the vermiform phoronids and mineralized brachiopod crown groups, and provides strong support for the view that phoronids and brachiopods are monophyletic. It seems reasonable to infer that each clade evolved separately from a sessile, filter-feeding common ancestor with the body protected within an agglutinated tube; the tubular form and agglutination was retained in extant

phoronids, but lost and replaced separately in organophosphatic and calcareous brachiopods⁷.

With respect to soft anatomy, *Y. elegans* exhibit a combination of ancestral brachiopod characters: the horseshoe shape lophophore bearing up to eight thick and elongate tentacles (Figs. 1a–b,h–i); pinnate mantle canal system (Figs. 2e–f, S5a–f), also found the stem taxa within the Chileata and some paterinates³⁹; and U-shaped gut with separate openings for the mouth and anus. These characters could be regarded as sympleisomorphies of both calcareous and phosphatic crown brachiopods as a whole.

Apart from the upper “shell” and collar structures, *Y. elegans* also possesses a rigid lower funnel-shaped conical tube that has no convincing analogues in any living or fossil brachiopods or phoronids. Apparently, it functioned to elevate the agglutinated lophophoral chamber above the sediment-water interface. The lower conical tube of *Yuganotheca* is generally reminiscent of the tommotiid *Eccentrotheca*, though the construction of the tubular scleritome in *Eccentrotheca* occurs via stacked fused rings of phosphatic sclerites¹² quite distinct from *Yuganotheca*. In contrast to other lophophore-bearing animals, brachiopods possess a specialized and enclosed filtration system in an isolated cavity and fully developed complex organization of tissues and organs⁷. The fact that an enclosed lophophoral chamber had been acquired in *Y. elegans* (albeit with an inferred phoronid-type filtration) could suggest *Yuganotheca* is more derived (Fig. 4) than the phosphatic tommotiids *Micrina* and *Paterimitra* but our cladistic analysis indicates that *Yuganotheca* may be basal in relation to the tommotiids including *Eccentrotheca*¹², *Micrina*²⁷ and *Paterimitra*¹³. The relationships depicted in Figure 4, though crucially depending on assumed polarity of selected taxa, suggests that the body plan of *Eccentrotheca*, and even *Paterimitra*, may also have possessed a filtration chamber made up of similar unmineralized (?agglutinated) valves above the tubular



scleritome. Critically this would mean that the acquisition of a bivalved brachiopod body plan may have preceded the development of mineralized shells. Therefore, it is not improbable that the brachiopod/phoronid clade may have evolved from a common stem group of lophotrochozoan progenitor that was not entirely armoured¹⁰.

Methods

The fossils of *Yuganotheca* were examined by Z. Zhang with a binocular Olympus Zoom Stereomicroscope and photographed with a Nikon camera mounted on a photomicrographic system, with different illuminations for particular views when high contrast images are required. Measurements were directly made by means of a millimeter ruler. The SEM microphotographs of uncoated fossils were taken with Zeiss Supra 35 VP field emission Scanning Electron Microscope at the Evolutionary Biology Centre of Uppsala University, kindly assisted by Gary Wife. BSEM and Elemental EDS analyses were carried out by Z. Zhang and L. Holmer at Uppsala University and some by U. Balthasar at the University of Glasgow. The interpretative drawings of fossils were drawn in CorelDraw 9.0 and converted to TIF format by Z. Zhang. Major and trace element analyses were conducted by LA-ICP-MS at the State Key Laboratory of Geological Processes and Mineral Resources, China University of Geosciences, Wuhan. The preferred values of element concentrations for the USGS reference glasses are from the GeoReM database (<http://georem.mpch-mainz.gwdg.de/>).

Nomenclatural acts. This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature (ICZN). The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix 'http://zoobank.org/'. The LSID for this publication is: urn:lsid:zoobank.org:pub:E1443FFB-9447-42DB-91C3-131FAB223054.

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Author contributions

All authors participated in the discussion and analysis of these fossils. Collection of material was made by Chinese members (Z.Z., G.L., X.Z., H.W., C.C., J.H., J.L. and D.S.). All authors reviewed the manuscript. Z.Z. designed the study and made statistics of these fossils. Z.Z. prepared Figures 1–3 and U.B. prepared figure 4. Z.Z., L.H., C.S., G.L. and U.B. prepared the earlier manuscript, and G.B. corrected the English and improved the final version. Z.Z., U.B. and A.B. made the cladistic analysis and D.F. made the artistic reconstruction of *Yuganotheca*.



Additional information

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