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Combining soft-bodied and three-dimensional fossils to reveal evolutionary modifications in early lingulellotretid brachiopods

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Living lingulide brachiopods are traditionally recognised as representatives of evolutionary conservatism, showing little change in general-morphology from their Cambrian ancestors. However, less attention has been given to their anatomical and ontogenetic modifications since their initial appearance. Among these, lingulellotretids are unique, characterized by their typical elongate pedicle foramen and large pseudointerarea. This study describes exquisitely preserved soft-tissue and phosphatic shells of *Lingulellotreta* from Cambrian Series 2 deposits in China and Kazakhstan. Biomineralized novelties in *Lingulellotreta*, including elongate pseudointerarea forming a pouch-like visceral cavity and columnar shell architecture, probably were evolutionarily modified from the unmineralized tubular ancestor *Yuganotheca* during the Cambrian Explosion. Lingulellotretids, however, faced extinction in the Early Ordovician, exemplifying a short-lived evolutionary experiment with a tubular body form in early brachiopods. Since the early Cambrian, lingulide brachiopods have exhibited a long-term evolutionary trend marked by the reduction of pseudointerarea, reflecting a convergence toward a more efficient body plan that ultimately became dominant in later lineages. The intensification of skeletal defences and the increasing demands of filter feeding within benthic communities likely drove these evolutionary modifications and ecological adjustments, culminating in the development of the distinctive, persistent tongue-shaped body of linguloid brachiopods during the Great Ordovician Biodiversification Event.

The Cambrian Explosion witnessed the emergence of a vast array of animal body plans, including novel anatomical structures and biomineralized skeletons, which proliferated for the first time within a relatively short geologic time span, about half a billion years ago[1–5]. Many animal clades with disparate morphologies were progressively decimated or subsequently modified during their long evolutionary history[3]. Only the adaptive descendants with newly derived forms and functions have survived the continuous extinction events on Earth. In contrast, there are several unique extant animal lineages that retain comparatively more static morphological characters, and exhibit low taxonomic diversity and a certain degree of rarity, compared to their diverse and widespread fossil ancestors[6–8]. Questions remain about when and how certain animal groups underwent fundamental changes, some surviving virtually unchanged, while others eventually went extinct. As a result, every organism embodies a blend of newly evolved traits and characteristics inherited from ancient lineages, shaped by the dynamic interplay between the proliferation of animal body

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plans and episodes of rapid extinction[6,9–11]. Key fossils during this critical period, especially exceptionally preserved material, have provided unparalleled evidence to comprehensively trace evolutionary persistence and change, allowing for comparisons of extant and extinct morphological and anatomical features over long timescales[12–18].

Linguloids are considered to be one of the oldest extant brachiopod lineages, and are traditionally recognised as representatives of extreme evolutionary conservatism, exhibiting little change in general morphology since the Cambrian[19,20]. As an example of the most primitive brachiopods, Lingulellotretidae is one of the most distinctive families in the Linguloidae characterised by the development of an elongate pedicle foramen on a large ventral pseudointerarea[21,22]. To date, only four genera have been described within this family, and there is no reliable fossil record of lingulellotretid brachiopods after the Tremadocian. Without the common tongue-shaped shells, they seemed transient in the linguloid brachiopod history and experienced rapid evolution from the early Cambrian to the Early Ordovician[23]. Among these, *Lingulellotreta* is the earliest genus, flourishing and then becoming extinct during the Cambrian Explosion (Cambrian Epoch 2 Age 4)[21]. Moreover, unlike other contemporaneous lingulides (eg. *Palaeobolus* and *Eoobolus*), the geographic distribution of *Lingulellotreta* is limited to South China and Kazakhstan, which adds to the enigmatic nature of this genus. However, current knowledge on lingulellotretid phylogeny and the early evolution of tongue-shaped body plan in linguloids remains ambiguous.

In light of advanced research on exceptionally preserved brachiopod fossils from Cambrian Konservat-Lagerstätten worldwide, there has been a remarkable growth in knowledge of their feeding, digestion, circulation, muscular systems and ecological (including mimicry and parasitism) relationships within benthic communities[12,14,22,24–33]. In this study, new soft-bodied specimens of *Lingulellotreta* are described from the famous Chengjiang Lagerstätte in South China, along with exquisitely three-dimensional preserved *Lingulellotreta* from early Cambrian Small Shelly Fossil deposits in South China and Kazakhstan. Based on newly obtained ontogenetic data and shell ultrastructures, two species, including *L. yuanshanensis* Zhang, 2020 and *L. ergalievi*, Koneva & Popov, 1983, are recognised, allowing the revision of the family Lingulellotretidae. The anatomic structures, earliest ontogeny and biomineralized shells of *Lingulellotreta* are investigated to enhance our understanding of the heterochronic transformation and evolutionary divergence among early brachiopod lineages during the Cambrian Explosion.

Results

Soft tissue preservation

Soft-bodied specimens of *Lingulellotreta yuanshanensis* from the Chengjiang Lagerstätte are dorsoventrally compressed, making it slightly difficult of distinguishing their original biomineralized shells (Fig. 1A and Supplementary Fig. 1). However, the outlines of both ventral and dorsal valves are distinct with recognisable margins (Supplementary Fig. 1B). The ventral valve is elongate oval, having an acuminate apex posteriorly, while the dorsal valve is subtriangular (Fig. 1A–D). The paired lophophore with ciliated tentacles and long slim pedicle (Fig. 1A and Supplementary Fig. 1B, F) are the most prominent soft tissues, as previously described in detail by Zhang et al.[12,22,26,27]. The average size of the ventral valve is about 6.1 mm in length and 3.4 mm in width, while the maximum length of the well-preserved and strongly annulated pedicle is about 33 mm (Supplementary Table 1). The U-shaped digestive tract featuring an anterior oesophagus, inflated stomach and curved gut in *L. yuanshanensis* was previously reported in specimens from the type locality[22,28]. After scrutinisation of rare (less than 9% of the total sample size) but better-preserved specimens in our collection, a similar morphology of the digestive system is uncovered beneath the prominent elongate pseudointerarea (Fig. 1A and Supplementary Fig. 1A–C). Remarkably, the recurved intestine extends into the ventral pseudointerarea area, and unusually crosses the hinge line (Fig. 1A). This suggests that the visceral area or visceral cavity is greatly extended toward the posterior, indicating the development of a hollow space or cavity beneath the ventral pseudointerarea to accommodate the visceral tissues. The expanding visceral cavity, which houses the extra growth of visceral organs, is best demonstrated in the laterally compressed specimens (Supplementary Fig. 1E). This unique arrangement of soft organs within the biomineralized dorsal and ventral valves has not been observed in stem group and any other extinct or living brachiopods.

Biomineralized shells

Compared to soft-bodied specimens, *L. yuanshanensis* and *L. ergalievi* obtained from limestone rocks are three-dimensionally preserved and exhibit relatively smaller body size with an average of 2.7 mm in length and 1.9 mm in width, and 2.4 mm in length and 1.9 mm in width, respectively (Supplementary Figs. 1–13, Supplementary Tables 1 and 2). The dorsal and ventral valves are disarticulated with well-developed propareas with a pedicle foramen on the large ventral pseudointerarea (Figs. 1B, D and 2A, C, Supplementary Figs. 2 and 8). Of particular note, is the ventral pseudointerarea is raised above the valve floor (Figs. 1E and 2E) and leaves a large empty space beneath the pseudointerarea, forming a pouch-like structure at the posterior end (Figs. 1E and 2D, Supplementary Figs. 3 and 9), which may imply a tubular construction of the brachiopod body[22]. As the ventral pseudointerarea of *L. yuanshanensis* is relatively large compared to other lingulide brachiopods, the expanding visceral cavity outlined by the internal boundary of the pseudointerarea is quite prominent. In terms of soft tissues, only the imprints of muscles, paired *vascula lateralia* and pedicle nerve are preserved on the internal shell surface (Figs. 1D and 2C, Supplementary Figs. 3A–F, 6A–H and 9D). The musculature of *Lingulellotreta* is symmetric and relatively simple, mainly composed of paired umbonal, transmedian and central muscles of both ventral and dorsal valves. The umbonal muscles are not as distinct as the expanding pseudointerarea (Figs. 1B, D and 2A, C). Transmedian muscles are well developed, directly anterior to the propareas (Supplementary Figs. 2B, D, 3A, B, E, 5D, E and 6A), while central muscles are developed on the median tongue (Supplementary Fig. 6D). The V-shaped impression of pedicle nerve is developed in the visceral area (Supplementary Figs. 2H and 3C), and *vascula lateralia* are straight and divergent in posterior half of valve (Supplementary Figs. 2D, 3B and 5I).

By contrast, shell ultrastructures, noting the earliest ontogenetic characters and biomineralized architectures, are exquisitely preserved (Figs. 1F, G and 2G, Supplementary Figs. 4, 7 and 10), which are usually unattainable from the soft-bodied fossils within the Burgess Shale-type Lagerstätten[34,35]. Abundant micron-sized pitting structures with a diameter of about 0.9 μm are developed on the posterior surface of both dorsal and ventral valves (Fig. 1F, Supplementary Figs. 4C–E and 11C, D), that is outlined by a pronounced halo and referred to as the metamorphic shell with an average size of 200 μm. The drape structures are developed outside the halo, indicating the stress caused by marginal mantle setae. Furthermore, the mound-shape protegulum with lateral fine folds and the brephic shell marked by a pair of symmetrically placed inflated lobes on the anterior margin of ventral valve, are developed inside the halo (Fig. 2F, Supplementary Figs. 4A–C, 7A–E and 11A, B). Most the posterior shell is exfoliated from the dorsal valve, with the partly preserved halo and median sulcus (Supplementary Fig. 7A–E). These earliest ontogenetic structures indicate the existence of a typical paterinide-type larva that experiences metamorphosis during the planktotrophic stage[36]. Based on the cross section of *Lingulellotreta* shells, biomineralized columnar shell architecture is well developed with numerous columns disposed orthogonally between a pair of stratiform lamellae (Fig. 2G and Supplementary Fig. 10), demonstrating a multi-stacked sandwich model, similar to that of the contemporary genus *Eoobolus*[37]. There are about 10 layers of stacked sandwich columnar units developed in *L. yuanshanensis*, with the size of individual columns ranging around 1.6 μm in height and 2.2 μm in diameter (Fig. 1G and Supplementary Fig. 3I–K). By contrast, the columnar architecture is more complex in younger *L. ergalievi*, which has about 20 layers of stacked sandwich columnar unit with the similar size of individual columns, forming a thicker shell than *L. yuanshanensis* (Fig. 2G and Supplementary Fig. 10).

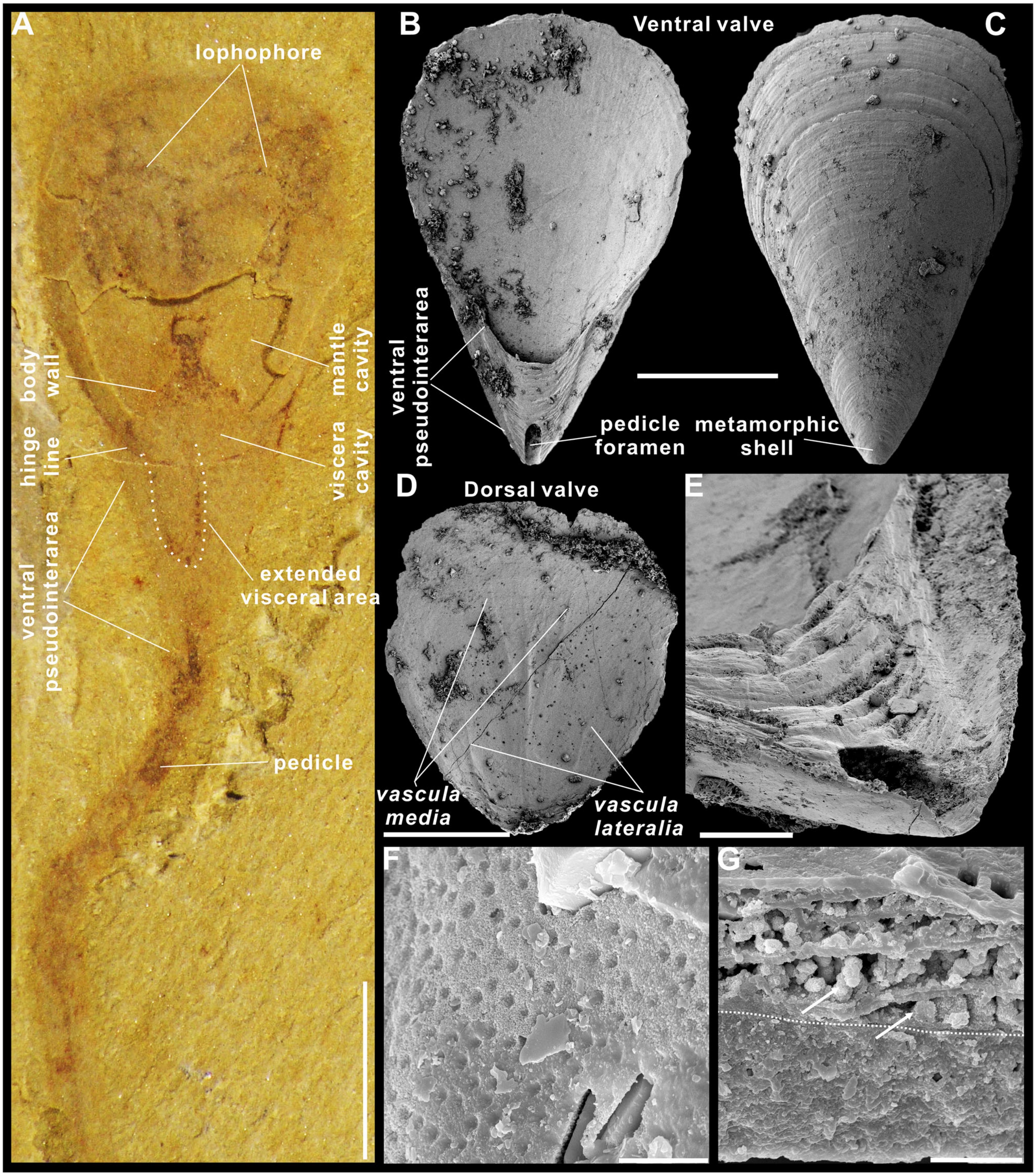

Fig. 1 | Soft-bodied and three-dimensionally preserved *Lingulellotreta yuanshanensis* (Zhang, 2020) from the Yuanshan Formation (Cambrian Stage 3) in Yunnan Province, and from the lower Shuijingtuo Formation (Cambrian Stage 3) in Shaanxi Province, South China, respectively. A Well-preserved specimen, note key anatomical features, including the paired lophophore with ciliated tentacles, body wall separating the mantle cavity and visceral cavity, long slim pedicle, and curved gut extended posteriorly beyond the hinge line (by dotted line), ELI-JS 0357 A. **B** Well-preserved ventral valve, note very large pseudointerarea and elongate pedicle foramen, ELI-XYB 13 CI08. **C** External view of (**B**), noting pronounced metamorphic shell at posterior end. **D** Dorsal valve interior, note mantle canals (including *vascula lateralia* and *vascula media*), ELI-XYB S5-4 CH06. **E** Posterior view of the pouch-like extension of the visceral cavity that will be developed beneath the pseudointerarea., ELI-XYB S5-4 CH03. **F** Enlarged micro-size pitting structures on metamorphic shell, ELI-XYB O02. **G** Shell architecture, composed of laminated primary layer and columnar secondary layer (arrows) bounded by dotted line, ELI-XYB O19. Scale bars, **A** 2 mm; **B**–**D** 1 mm; **E** 100 μm; **F** 5 μm; **G** 20 μm.

Ontogeny

The correlation of valve length versus width of *Lingulellotreta* demonstrates uniform shell growth (Supplementary Fig. 14). However, allometry is revealed when changes in key structures with increasing size are measured during the ontogenetic development (Fig. 3). This enables a more complete understanding of the dynamic growth of the ventral pseudointerarea. Two different allometric patterns of the two species are recognised and compared in the following discussion. Measurements of the ventral and dorsal valves,

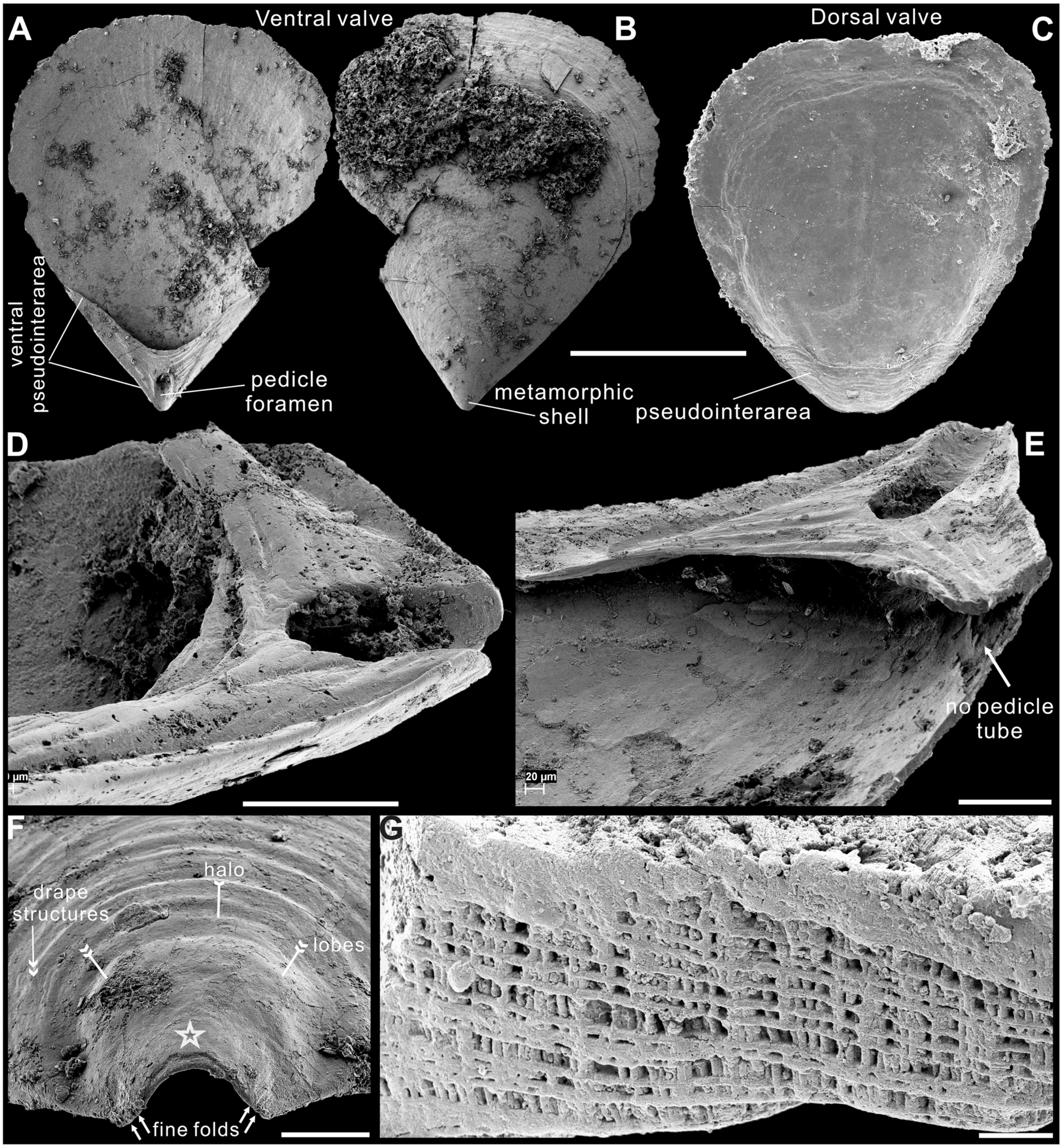

Fig. 2 | Three-dimensionally preserved *Lingulellotreta ergalievi* (Koneva & Popov, 1983) from the upper Shuijingtuo Formation (Cambrian Series 2) in Hubei and Shaanxi provinces, South China. **A** Well-preserved ventral valve, note large pseudointerarea and elongate pedicle foramen, ELI-XYB S5-4 CI01. **B** External view of (**A**), note pronounced metamorphic shell at the posterior end. **C** Dorsal valve interior, note well developed dorsal pseudointerarea, ELI-XYB O25. **D** Lateral view of ventral pseudointerarea and pedicle foramen, ELI-XYB 13 CI04. **E** Anterior view of the raised ventral pseudointerarea, beneath which a small pouch-like cavity is forming, no pedicle tube developed (arrow), ELI-XYB 13 CI07. **F** Ventral metamorphic shell, showing paired fine folds (arrows) on the protegulum (asterisk) margin, paired inflated lobes (double-tailed arrows), pronounced halo (tailed arrow) and drape structures on post-metamorphic shell (double-headed arrow), ELI-XYB 13 CI05. **G** Development of stacked columnar architecture of secondary layer, ELI-AJH 8-2-3 CI11. Scale bars, **A**–**C** 1 mm; **D**, **E** 100 μm; **F** 50 μm; **G** 20 μm.

which were made in most of the complete specimens, are tabulated (Supplementary Tables 1 and 2).

During shell development, three growth stages with obvious anatomical changes are recognised. Initially, on the smallest specimens, an obolid-like pseudointerarea[22] was formed with the development of the ventral proparea and pedicle groove just before the enclosing of the pedicle groove (Supplementary Fig. 9A). Secondly, the gradual elevation of the ventral pseudointerarea led to the formation of a pedicle foramen and a small space in the ventral posterior area (Fig. 2E and Supplementary Fig. 8 and 9D–G). This stage is characterised by the development of a short pseudointerarea sealing the obolid-like pedicle groove that is open between dorsal and ventral valves (Fig. 2D and Supplementary Fig. 9B, C), demonstrated by the juvenile specimen of *L. yuanshanensis* and *L. ergalievi* (Supplementary Figs. 2A and 8A). The visceral cavity of *Lingulellotreta* was increased by the

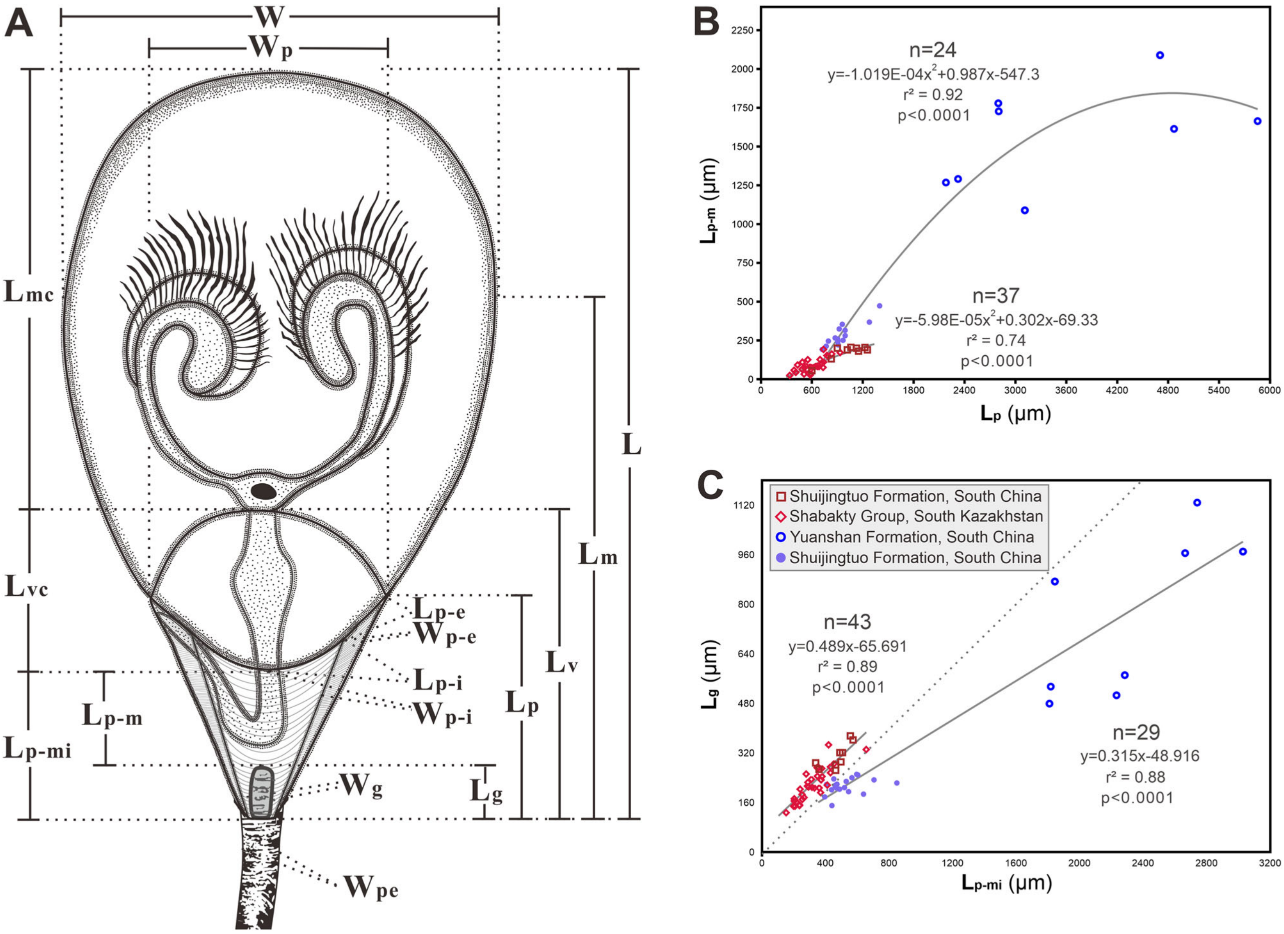

Fig. 3 | Interpretative drawings of *Lingulellotreta yuanshanensis*, and bivariate plots of the ventral valves of early Cambrian *Lingulellotreta yuanshanensis* (red and crimson colours) and *Lingulellotreta ergalievi* (blue and slate blue colours). **A** Key anatomical features shown in Fig. 1, note the curved gut extended posteriorly beyond the hinge line and beneath the raised pseudointerarea, which forms a pouch-like cavity. L length, W width of valve where not specified, and of elements: g ventral pedicle foramen; m valve length at the maximum width, mc mantle cavity, p pseudointerarea, p-m median part of pseudointerarea, p-mi minimum length of pseudointerarea, p-i inner part of propareа, pe pedicle, p-o outer part of proparea, v viscera area, vc visceral cavity. **B** Plots of median part of pseudointerarea length - pseudointerarea length ratio ($L_{p\text{-}m}/L_p$), demonstrating two parabolic curves. **C** Plots of pedicle foramen length—minimum length of pseudointerarea ratio ($L_g/L_{p\text{-}mi}$), the dashed line represents equal pedicel foramen length and median part of pseudointerarea length ($L_g/L_{p\text{-}m} = 1$).

expansion of the visceral cavity posteriorly in response to the adaptation of the newly formed cavity. Thirdly, with the further rapid development of the ventral pseudointerarea, a larger pouch-like cavity was formed to accommodate the expanding visceral organs[26] (Fig. 1B). This positive allometric growth stage is characterised by the increasing development of the elongate pseudointerarea, which is demonstrated by the parabolic curve in Fig. 3B. Thus, the overgrown pseudointerarea cannot be enclosed by the dorsal and ventral valves, which is demonstrated by the mature specimen of *L. yuanshanensis* (Fig. 1A, B and Supplementary Fig. 2E–J). Such a raised process of ventral pseudointerarea is also recognised in the development of another group, the acrotretide brachiopods[38–41], implying a similar but heterochronous development process of marginal accretionary growth of shell from their common ancestor at least from the Cambrian Age 3. However, like the early acrotretides (such as *Palaeotreta*, *Eohadrotreta* and *Linnarssonia*), the early Cambrian *Lingulellotreta* developed the pedicle foramen without a pedicle tube (Fig. 2E and Supplementary Figs. 2 and 8). The pedicle tube was possibly developed by later lingulellotretides (such as *Aboriginella*) through the development of complex conjunction of pedicle and outer epithelia during the late Cambrian[42].

Discussion

In brachiopods, the mantle cavity and visceral cavity are separated by the anterior body wall, which distinguishes the feeding and digestive spaces in the enclosed dorsal and ventral mantles[43]. The arrangement of these two spaces is vital to the physiology and survival of the brachiopod. Lingulide fossils from the Palaeozoic and the Mesozoic have demonstrated a gradual change of utilising the space available, which is even obvious when compared with living representatives[12,44,45]. Although compartments of visceral cavity are developed in some living craniiforms[43,46], no separation of the visceral cavity is observed in lingulides.

The length of the visceral cavity of early Cambrian *L. yuanshanensis* only occupied 13%-27% of the ventral valve length (Supplementary Table 1). This proportion dramatically increased to about 48% in the Ordovician *Pseudolingula*, 54% in the Jurassic taxon *Lingularia*, and finally about 59% in recent *Lingula*[44,45]. A similar small visceral cavity is also confirmed in the coeval lingulide *Eoglossa chengjiangensis*[12,26,47]. Thus, there appears to be an evolutionary tendency of increasing the size of the visceral or visceral cavity in lingulides, with a consequent reduction in the mantle cavity. Furthermore, the relatively small space/volume of the visceral cavity in early Cambrian lingulides, compared to their living counterparts, suggests that their anatomical disposition may have undergone dramatic modifications since the Cambrian. The curved gut of *Lingulellotreta* (Fig. 1A), which extends beyond the hinge line, has not been discovered in any other brachiopod group[22,28]. Although the continuous increase of the size of the visceral cavity in lingulides is an evolutionary trajectory since the Cambrian, the size of pseudointerarea has shown the opposite trajectory, with the

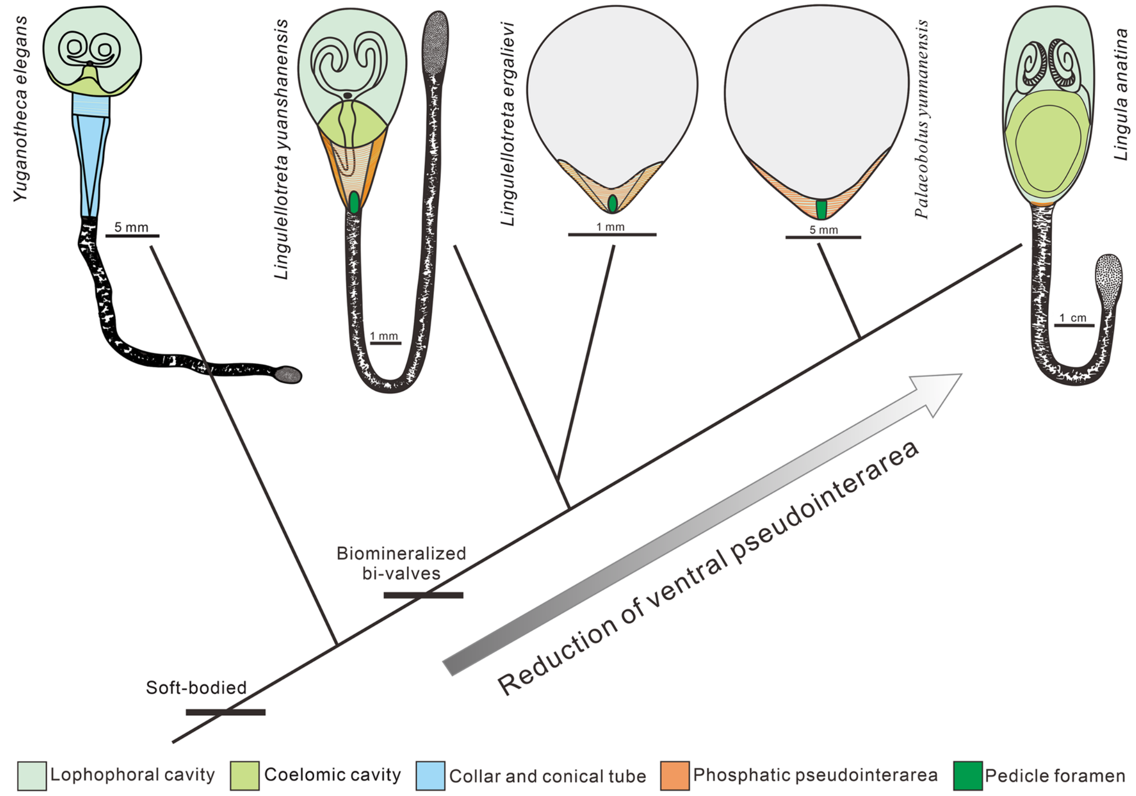

Fig. 4 | Branching structures of the evolution of lingulide brachiopods, demonstrating the relationships between the stem group, extinct ancestral and living lineages. Interpretative drawings of *Yuganotheca elegans* (Cambrian Stage 3 Yuanshan Formation) is modified from ref. 50, *L. yuanshanensis* (Cambrian Stage 3 Yuanshan Formation) is a sketch of Fig. 1A, L. *ergalievi* (Cambrian Stage 4 Shuijingtuo Formation) is a sketch of Supplementary Fig. 8C, *P. yunnanensis* from the (Cambrian Stage 4 Wulongqing Formation) is modified from ref. 89, and Living *L. anatina* is modified from ref. 90.

length dramatically decreasing over time[12,42]. This trend is perhaps most easily observed in living *Lingula*, where only a vestigial pseudointerarea is present (Fig. 4). With the exception of the visceral cavity expanding posteriorly in lingulellotretids accommodated the growing digestive organs, other lingulide groups (eg. Obolidae and Lingulidae) appear to have adopted an opposite evolutionary path. With the reduction of the pseudointerarea, resulting in increasingly limited space beneath it (Fig. 4), the visceral cavity in these groups adapted by moving anteriorly to create more space for the digestive organs in their diversified descendants[12,22,44,45].

Interestingly, regression analysis of key structures reveals two ontogenetic patterns, representing different evolutionary directions in *L. yuanshanensis* and *L. ergalievi* (Fig. 3). The growth of the median part of the pseudointerarea in *L. yuanshanensis* is rapid, as indicated by the steep slope of the parabola-shaped curve in Fig. 3B, while growth in *L. ergalievi* is relatively slow resulting in a shorter pseudointerarea. The morphological similarity between ventral valves (2.5–3.6 mm) of the slightly younger *L. ergalievi* (Cambrian Age 4) and ventral valves (<2.7 mm) of *L. yuanshanensis* (Cambrian Age 3) indicates the paedomorphosis of *L. ergalievi*, with a relatively slow growth rate and development of a short pseudointerarea (Supplementary Figs. 2A and 8). Furthermore, the pedicle foramen of *L. ergalievi* develops quickly, with a steeper slope than that of *L. yuanshanensis* (Fig. 3C), resulting in a relatively large pedicle foramen compared to the median part of the pseudointerarea in *L. ergalievi*. This may suggest that the pedicle in *L. ergalievi* was more robust than in *L. yuanshanensis*. The positive allometry of ventral pseudointerarea in *L. yuanshanensis* supports the expansion of the coelomic which may have contributed to their success during Cambrian Age 3. However, with the origin and dispersal of younger *L. ergalievi* during Cambrian Age 4, an evolutionary trend towards reducing the ventral pseudointerarea emerged, a trend that continues in descendants such as *Mirilingula* and *Vaculina* from the middle and late Cambrian[42]. The development of a low rhomboidal platform that is slightly raised anteriorly in their ventral valve and the development of an anterior projection that is extended to the mid-valve in dorsal valve indicates that the visceral cavity adapted by moving anteriorly. Thus, heterochrony probably played an important role in the differentiation of species and the reduction of the ventral pseudointerarea is a widely observed evolutionary trend in the lingulide lineage, while the posterior extension of the visceral cavity enclosed by the ventral pseudointerarea may have been a failed evolutionary experiment by early Cambrian lingulellotretids. It limited their geographic distribution to Kazakhstan and South China and lead to their rapid extinction in the Early Ordovician[23]. Compared to *L. yuanshanensis*, a reduction in the pseudointerarea of *L. ergalievi* implied that even within lingulellotretids, there was a diversification of body plans, potentially reflecting different ecological adaptations or responses to environmental pressures during the Cambrian Explosion. Comparative analysis with later lingulides (such as Obolidae and Pseudolingulidae)[42] could further clarify that this reduction trend represents a convergence toward a more efficient body plan (short ventral pseudointerarea, lophophore close to the valve opening and robust pedicle) that ultimately became dominant in later lineages.

One could speculate that the mantle cavity might increase significantly with the dramatic posterior extension of the visceral cavity. However, the ratio of mantle cavity and valve length is largely offset by the extensive increase of the ventral pseudointerarea. The lophophore occupies approximately 48% of ventral valve length in the Cambrian species *L. yuanshanensis* (Supplementary Table 1), which is similar to the Jurassic taxon *Lingularia* (46%) and recent *Lingula* (41%)[44,45]. It is noteworthy that the ontogeny of the lophophore in *Lingulellotreta* is mirrored in the ontogeny of the lophophores of recent lingulides[12,48]. However, with the reduction of the pseudointerarea, the relative position of the lophophore is moved forward. As the lophophore cavity is directly connected to the external environment, it may indicate that the increased control of water current as the lophophore is close to the valve opening in living lingulides[48,49].

The pedicle of *L. yuanshanensis* is relatively long and slim, with an average width of 500 µm, and maximum length (33 mm), up to seven times of ventral valve length (Supplementary Table 1). It is difficult to infer that *Lingulellotreta* had a borrowing lifestyle, rather the morphology of the pedicle suggests that it likely functioned to anchor the organism within soft sediment, utilising a terminal bulbous structure to maintain suspension of its lightweight shell above the sediment–water interface[29,31,50]. The expanded pouch-like cavity outlined by the ventral pseudointerarea could precisely hold the growing visceral tissues while standing upright in the water column, anchored by a long pedicle. In contrast, living *Lingula* has a relatively robust and short pedicle (Fig. 4), about 2–3 times that of valve length, which is well-suited for a burrowing lifestyle[45,49,51]. A similarly robust pedicle morphology has been reported in early Cambrian brachiopods with calcareous shells, in which the distal end was affixed to the exoskeletons of other organisms. These examples underscore the close relationship between pedicle structure and substrate preference[31,52,53]. The musculature of brachiopods is a key anatomical feature that reflects their functional adaptations and ecological roles. Compared to the complex musculature in living lingulides, *Lingulellotreta* has a relatively simple and symmetrically arranged muscle configuration, suggesting that the organism has less control over valve movements, including opening and closure of the valves, adjusting valve orientation and attaching to the substrate[12,21,27,45]. This is further supported by the distinctly unequal size of the ventral and dorsal valves, and the mismatch of elongate ventral pseudointerarea and short dorsal pseudointerarea (Fig. 1A, B, D). So, the reduction of the ventral pseudointerarea in *L. ergalievi* likely helped to increase the alignment and fit between the ventral and dorsal valves (Fig. 2A, C). Other evolutionary changes of anatomical features in living lingulides, including the anteriorly extension of mantle canals and the development of three pseudosiphons at the anterior mantle margin associated with infaunal behaviour have been discussed in detail by refs. 12,18,22.

Comparison can be also made between *Lingulellotreta* and the soft-bodied stem brachiopod *Yuganotheca*, which exhibits an unmineralized tubular body and posteriorly elongate coelomic cavity[50]. While both taxa share a broadly tubular axial organisation, *Lingulellotreta* represents a fundamental evolutionary shift in that this architecture is enclosed within rigid, biomineralized valves. Unlike *Yuganotheca*, where the extended visceral cavity is not constrained by a pseudointerarea, *Lingulellotreta* uniquely develops an elongate ventral pseudointerarea that forms a defined, pouch-like cavity to house the extended gut and visceral organs (Figs. 1A, B and 2A). This structural innovation marks an evolutionary transformation of soft-bodied morphology into a mineralized framework, suggesting that *Lingulellotreta* expresses a mosaic of ancestral (tubular organisation) and modified (biomineralized enclosure, columnar shell structure) features (Fig. 4). Thus, the posterior extension of the visceral cavity in *Lingulellotreta* should be viewed not as a retained ancestral trait, but as a different morphological expression of a body plan previously only seen in soft-bodied taxa.

The pitting micro-ornamentation on the surface of the primary layer of metamorphic shells has been widely reported from the superfamilies Acrotretoidea and Linguloidea[54,55] and to a lesser extent from Discinoidea[56] and Acrotheloidea with some exceptions[55]. The presence of such pitting structures in *L. yuanshanensis* and *L. ergalievi* confirms a similar morphology and micro-size in the Family Lingulellotretidae to the best of our knowledge (Fig. 1F and Supplementary Figs. 4D–F and 11B, C), and further supports the homology of this pitting ornamentation in Lingulata (including all the superfamilies) that evolved from the early Cambrian[36,54,57]. The mode of formation of these pitting structures is still debated and may represent the casts of periostracal vesicles, casts of droplets of mucus or resorption of previously secreted shells by the outer mantle[57]. Based on the restricted distribution of regular pits on metamorphic shell (larval shell)[36], that gradually fades towards the pronounced halo, Lüter[58] argued that the hemispherical pits might be originally filled with rigid tablet-like structures by analogy to Silurian *Opatrilkiella*[59]. These tablets may have been used to protect against ultraviolet radiation penetrating surface waters during the Early Palaeozoic[58]. However, recent lingulides possess a smooth larval shell without pitting structures, with only the living *Discinisca* retaining the pitting structures, a structure attributed to the development of siliceous tablets[58,60]. The ubiquitous phenomenon of pitting structures preserved on almost all early Cambrian linguliform brachiopods[61] may suggest that the living environment of brachiopod larvae has underwent dramatic changes since the Early Palaeozoic.

Metamorphic shells of *Lingulellotreta* on both ventral and dorsal valves, characterised by the development of micro-sized pitting structures and a pronounced halo (Fig. 2F, Supplementary Figs. 4B–D and 11B, C), shows great similarity to those of many other early Palaeozoic brachiopods, including the Cambrian paterinates[36,62,63]. This suggests that during the early Cambrian *Lingulellotreta* had a planktotrophic larval stage before undergoing metamorphosis. This finding further supports the hypothesis that the earliest ontogeny with metamorphosis of planktotrophic larva is plesiomorphic for Brachiopoda and probably first evolved in a stem group brachiopod[36,64,65]. In contrast, living lingulide larvae do not metamorphose, rather they grow by direct development[66–68], demonstrating a dramatic evolutionary modification involving brachiopod larva since the Cambrian. Key points about when such modification happens in different groups, however, requires further study.

Cusack et al.[57] reviewed the shell structures of Cambrian to Recent lingulide brachiopods and concluded that lingulide shells had undergone important transformations since the early Cambrian. Among these transformations, the complex columnar shells, having long been dominant in acrotretide brachiopods, were actually present in early Cambrian stem group brachiopods[69,70] and eoobolid brachiopods[37,71] prompting more focused studies on shell structures. Holmer et al. also described one specimen of *Lingulellotreta* with a similar type of the columnar shell from the early Cambrian in Kazakhstan[72], however due to its limited preservation, no detailed description was provided. The columnar shell architecture built with the stacked sandwich model[37] demonstrates an evolutionary transition from the simple shell architecture in *L. yuanshanensis* to a more complex structure as seen in *L. ergalievi* (Figs. 1G and 2G, Supplementary Figs. 3I–K, 6J–L and 10). The thicker shell layer and more developed columnar architecture with a better alignment of valves and a possible thicker pedicle indicate a better fitness of *L. ergalievi*, that increased their global dispersal during Cambrian Age 4. A comparative study of columnar shell structure with living representatives is impossible, as this type of ancient shell structure is completely lost[57]. The development of columnar shell architectures in early lingulides probably increases the buoyancy of both valves to adapt a pedicle-anchoring life style on soft substrates that is common during early Cambrian[12,33,73]. The evolutionary transition of shell structures across different groups is most probably controlled by the different levels of organic matrix in the outer epithelia, which is responsible for the phosphate-based biomineralization in lingulide brachiopods.

The exceptional preservation of fossil material, encompassing both soft-tissue anatomy and three-dimensional phosphatic shells, provides critical insights into the substantial anatomical, developmental, and structural transformations that occurred between stem-group brachiopods and both Cambrian and extant lingulides. These evolutionary modifications, particularly in anatomical structures, larval behaviour, and shell architecture are not readily apparent when examined solely through the primitive outlines of their ventral and dorsal valves (Figs. 1C and 2B). Therefore, caution should be exercised in assuming that the retention of some phenotypic (external morphological) characters adequately explains the changes—or lack thereof—in other phenotypic characters[74]. The terms ‘evolutionary conservatism’ or ‘morphological stability’ are insufficient to fully describe these ancient-looking animals. For example, the long-lasting lingulide brachiopods may appear unchanged, but the group has been evolving as a whole since the Cambrian.

Aside from the static character of the tongue-shaped valve outline of living lingulides that has been retained since the early Ordovician, almost all other morphological characters demonstrate evolutionary transitions (Fig. 4). With an extended free-swimming period during the metamorphosis of the primary larva, early lingulides quickly achieved a global distribution during the early stages of Cambrian[19,36,61,75–77]. Their small body size, relatively light shell with columnar architecture, expanded visceral cavity, and elongate pedicle enabled early Cambrian lingulides to reach a higher ecological tier, indicating an important adaptation for brachiopods living in the soft substrates of benthic communities[29,53,73]. These lingulide brachiopods are commonly preserved as shell beds or shell concentrations as the result of a mass mortality events observed in Konservat-Lagerstätten (Supplementary Fig. 1D)[25,30,33], and became an important component of both Cambrian and Palaeozoic Evolutionary faunas[19,78]. In contrast, extant lingulide brachiopods are notably larger, with body sizes typically measured in centimeters, and exhibit a suite of evolutionary modifications, both anatomical and skeletal, that reflect adaptation to an infaunal mode of life. These morphological changes, along with associated ecological shifts, likely contributed to the emergence of the characteristic tongue-shaped body plan during the Great Ordovician Biodiversification Event, a form that has been retained in modern taxa. Furthermore, their direct-developing larvae constrain both their geographic distribution and taxonomic diversity, which remain relatively limited to this day[36,68,76,79].

During the Cambrian Period, renowned for its extraordinary morphological diversity and evolutionary experimentation[3,11], *Lingulellotreta* emerged with a novel combination of features that represent important morphological departures from those of soft-bodied stem-group brachiopods such as *Yuganotheca*[22,50]. Here, we define “novel” to refer not to traits without evolutionary precedent, but to features that emerged through substantial modification of ancestral conditions. The elongate shell and posteriorly expanded coelomic cavity, together with the development of an elongate pseudointerarea, apical pedicle foramen, and columnar shell architecture, distinguish this taxon from both its putative stem-group relatives and from later crown-group lingulides. These traits may indicate an evolutionary transition from unbiomineralized tubular forms, such as *Yuganotheca*, toward a biomineralized body plan that ultimately diversified within the lingulide lineage[80]. While the tubular body and elongate pedicle likely reflect ancestral conditions, the biomineralized features noted above are interpreted as morphological innovations within this phylogenetic context. *Lingulellotreta* thus represents a key transitional form linking soft-bodied tubular ancestors to the tongue-shaped shells characteristic of lingulides. The resemblance to the soft shelled *Lingulosacculus* from the early Cambrian of Laurentia[81], further support its intermediate status, although phylogenetic affinities remain unresolved[19,22]. The posterior expansion of the visceral cavity in *L. yuanshanensis*, while modified, was not retained in descendant lingulides, suggesting it may have represented an evolutionary experiment that conferred limited adaptive benefit, perhaps due to functional constrains on feeding, respiration, or mechanical support. Nevertheless, this feature provides valuable insights into early morphological plasticity and the selective pressures that shaped the trajectory of lingulide evolution. The progressive reduction of the pseudointerarea in later lingulide likely reflects an adaptive trend toward more effective burrowing and pedicle use. Thus, the evolutionary transition from a posteriorly expanded to a more compact visceral cavity underscores the refinement of lingulide anatomy into the streamlined morphology of modern representatives.

As macroscopic predators emerged and the physiological demands of filter feeding in benthic environments intensified[1,10], the distinctive Lingulellotretidae were decimated and replaced by adapted lingulides (e.g. Obolidae and Pseudolingulidae) with shorter pseudointerareas, allowing for a more effective alignment of the ventral and dorsal valves by the early Ordovician. The increasing size of the visceral cavity in lingulides over time represents a key evolutionary trend that could be more explicitly connected to selective pressures, such as adaptations for improved feeding efficiency, mobility, and burrowing behaviour. Furthermore, dramatic modifications of muscle and lophophore configuration between fossil and living lingulides also suggests a fundamental shift in locomotion, feeding strategies, and ecological interactions over evolutionary time. Owing to the varying evolutionary rates of different morphological features, living lingulides represent a unique blend of primitive and advanced characteristics, gradually refined and fixed by natural selection over the past half-billion years. This mosaic-style of evolution probably played an important role in the disparity and diversity of brachiopods during their long evolutionary history, especially forging the new and basic body plans in the crucible of the Cambrian Explosion[10,16,74]. Thus, lingulide brachiopods are vivid examples of balancing the evolutionary capacitance and developmental constraints, that shape organisms with novel modifications and prolonged stasis in a long co-adaptive process.

Methods

All the soft-bodied specimens of *Lingulellotreta yuanshanensis* were collected from the Chengjiang Lagerstätte (Cambrian Stage 3) (Supplementary Fig. 15). They are mostly dorsoventrally compressed and rarely laterally compressed on the surface of event-deposited claystone beds, demonstrating the typical Burgess Shale-type preservation[82]. Eighty five specimens were collected from the interval of greyish-green mudstone intercalated with silty shale of the Yuanshan Formation (former Yuanshan Member of Heilinpu Formation) at the Erjie section in Jinning area and Jianshan section in Haikou area of Kunming city, Yunnan Province, South China. The stratigraphic range of *L. yuanshanensis* is within the second trilobite zone (*Eoredlichia- Wutingaspis* Zone) of the studied areas. The geological and geographic setting of the studied areas was described in detail by ref. 25 and ref. 83. The fossils appear as a variable degree of reddish to yellowish-brown colour after weathering, with a striking contrast to the surrounding yellowish-green rock matrix. The organo-phosphatic shells seem very thin and preserved as flattened casts or moulds with detectable growth lines, which is usually coated with ferruginous clay[24]. By contrast, the soft anatomic tissues or organs, including the variable lophophore, open digestive track, spine-like setae, branching mantle canal systems and fleshy stalk-like pedicle, are exquisitely preserved as darker colours with black thread-like lines, and their preservation likely took place prior to the breakdown of their soft carcasses[12,22,26–28,31,84].

The phosphatic shells of *L. yuanshanensis* and *L. ergalievi* described here were collected from the Cambrian Series 2 Shuijingtuo Formation at the Aijiahe section in Zigui area of Yichang city, Hubei Province and at the Xiaoyangba section in the Zhenba area of Hanzhong city, Shaanxi Province. *L. yuanshanensis* is from the lower Shuijingtuo Formation (Cambrian Stage 3 *Tsunyidiscus-Wangzizshia* Zone), while *L. ergalievi* from the upper Shuijingtuo Formation (upper Cambrian Stage 3 *Wangzizshia* Zone and Cambrian Stage 4 *Hubeidiscus-Relichia* Zone) (Supplementary Fig. 15). All the specimens are preserved as three-dimensional shells with high fidelity, demonstrating a unique phosphatization window for the preservation of early Cambrian brachiopods[85,86]. Delicate ultrastructures, such as metamorphic characters of free-swimming larva and columnar shell architectures are preserved in fine detail. The geological and geographical setting of the studied areas was described in detail[87,88]. Twenty-two ventral and 18 dorsal disarticulated valves of *L. yuanshanensis*, and 34 ventral and five dorsal disarticulated valves of *L. ergalievi* have been collected from the Shuijingtuo Formation.

Other phosphatic shells of *L. ergalievi* were collected from the Cambrian Series 2 Shabakty Group (*Ushbaspis limbata* Zone and *Redlichia chinensis-Kootenia gimmelfarbi* Zone) at the Ushbas River section and BaBa-Ata River section of Malyi Karatau Range in south Kazakhstan. The geological and geographic setting of the studied areas was described in detail[21]. Seven ventral valves of *L. ergalievi* have been collected from the lower Shabakty Group.

While the soft-bodied fossils were excavated by splitting mudstones directly in the field, the limestone rock specimens were dissolved from applying 10% concentrated acetic acid, with a buffering solution formed after the dissolution of previous samples to avoid chemical damage. Fossils were examined using a Zeiss Stemi 305 stereo microscope. Light photographs were taken using a Nikon camera located at Early Life Institute, Northwest University (Xi’an, China). Scanning electron microscope (SEM) images of coated fossils were taken with a Philips Fei Quanta 400-FEG at State Key Laboratory of Continental Dynamics, Northwest University, Xi'an, and a Zeiss Supra 35 VP field emission at Uppsala University. Measurements of the length, width and angle of different parts of *Lingulellotreta* were performed on light photos and SEM images by TpsDig2 v. 2.16. Scatter plots of different specimens, analysed by PAST v. 3, showing morphological variations, were also constructed.

Statistics and reproducibility

120 ventral valves and 95 dorsal valves of *L. yuanshanensis*, and 43 ventral valves and 7 dorsal valves of *L. ergalievi* are used for the study.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The authors confirm that the data supporting the findings of this study are available within the article. All source data underlying graphs can be obtained in Supplementary data. Specimens studied here are deposited in the Early Life Institute, Northwest University, Xi'an, China (prefixed ELI), and Uppsala University, Sweden (prefixed IGCA), respectively. Measurement data are available as Supplementary Tables 1 and 2 in the Supplementary Information file.

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Author contributions

F.Y.C. and Z.F.Z. conceived the study, Z.F.Z. and Z.L.Z. processed the photograph data. F.Y.C., Z.F.Z., B.P.S. and Z.L.Z. collected fossil, F.Y.C. and Z.L.Z. interpreted data. F.Y.C. drafted the manuscript, to which Z.F.Z., L.E.H., G.X.L., T.P.T. and Z.L.Z. contributed. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests

The authors declare no competing interests.

Additional information

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