nature portfolio

Peer Review File

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

Corresponding Author: Dr Feiyang Chen

This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Attachments originally included by the reviewers as part of their assessment can be found at the end of this file.

Version 0:

Reviewer comments:

Reviewer #1

(Remarks to the Author)
I am pleased to announce that my decision on the manuscript is Accepted, with or without editorial revisions.
In general terms, it is very well written and interesting to read, with clear and concise objectives. Specifically, it has the advantage of having specimens of the Lingulellotreta genus with excellent preservation, where rare details are observed that allow evolutionary and comparative studies with extant representatives, in this case comparing soft parts, which are generally not possible.
Both the amount of material analyzed and the statistical analysis performed are more than sufficient to make the interpretations. At the same time, I consider that the hypotheses raised and the conclusions reached are in accordance with the results obtained from the analyses and samples.
The discovery of evolutionary trends that were, in this case, “discarded by natural selection” is very interesting, and they reveal a degree of variability within a group of organisms that are generally considered conservative when only general characteristics and trends are observed in the hard parts.
Despite finding a few minor errors in the manuscript (noted below), I strongly recommend publishing it.

Reviewer #2

(Remarks to the Author)
Combining soft-bodied and three-dimensional fossils reveal evolutionary novelties in early lingulellotretid brachiopods

by Feiyang Chen, Zhifei Zhang, Lars E. Holmers, Guoxiang Li, Timothy P. Topper, Baopeng Song, Zhiliang Zhang

The subject of the manuscript is interesting and suitable for the wide audience of Communication Biology. The early evolution during the Cambrian Explosion is significant for understanding how animals diversified and evolved into the body plans of modern phyla. This study presents detailed morphologies of two Lingulellotreta species that occurred in the early Cambrian, trying to demonstrate how this ancient genus developed its morphological adaptation as one of the oldest brachiopods and how its shell and anatomical features are distinguished from its modern descendant Lingula, a well-known living fossil. This paper is also exceptional in providing high-resolution images of the well-preserved shell material; the pitting micro-ornamentation on the primary shell layer in Lingulellotreta is identified for the first time and the columnar shell architectures are beautifully demonstrated in the supplementary figures.

However, despite its potential, I don't think the manuscript is ready for publication. Most of the morphological explanations in this manuscript do not show any novelty. Instead, they are taken from earlier publications that also described the same taxa; the pouch-like coelomic cavity under ventral pseudointerarea was explained in detail by Zhang et al. (2007, 2020; Ref. 22 & 28 in your list); and the columnar shell architectures were fully discussed by Zhang et al. (2023; Ref. 37). Unfortunately, these contents are simply repeated without any further discussion. None of the research questions is properly answered,

including: 1) How are these morphological features helpful in explaining the evolutionary trends of the lingulide brachiopods since their first appearance in the Cambrian?; 2) If the pouch-like cavity was developed in the earliest lingulellotretid as a novel body plan, why is the reduction of the pseudointearea already observed in Linguellotreta ergalievi of the Cambrian Stage 4?; 3) If the posterior expansion of the cavity is a morphological experiment only in the very early lineage, how does it help to understand the 540-millions evolution of the lingulide brachiopods? If the authors would like to publish some of the contents in the manuscript, they need to expand their discussions with novel ideas.

I have also provided several minor comments/suggestions on the PDF file annotated and attached. Hope that my comments will be helpful.

Sangmin (Sam) Lee
Research Fellow
School of Science, Faculty of Science, Medicine and Health
University of Wollongong

Reviewer #3

(Remarks to the Author)
The paper is quite interesting and contains new data on the evolution of the soft body and ontogeny of lingulide brachiopods, which previously were considered to be a conservative group. This study is important for the understanding of the evolution and morphology of Brachiopoda. The whole approach is novel and meets modern requirements of the paleontological studies. However, there are few moments that need clarification or correction.

1. The authors describe a pedicle nerve but in recent lingulides it is paired throughout its entire length and it remains unclear why the not paired groove is considered to be a pedicle nerve and why other nerves did not leave imprints.
2. The described halo rings are indistinguishable from the adult ornamentation and there is no reason to recognize them as halo rings, not the first onset of the adult shell.
3. “Compared to the complex musculature in living lingulides, Lingulellotreta has a relatively simple and symmetrically arranged muscle configuration” – this is not explained, the musculature of Lingulellotreta and recent lingulides should be briefly compared and the description of Lingulellotreta musculature possibly should be added to the results.
4. “In brachiopods, the lophophoral cavity (or mantle cavity) and visceral cavity (or coelomic cavity)…” There are generally accepted terms “mantle cavity” and “visceral cavity” and there are three coeloms in lingulides: body coelom, pedicle coelom and lophophoral coelom. Therefore, the newly suggested terms “lophophoral cavity” and “coelomic cavity” are unacceptable as “coelomic cavity” may be applied to all three coeloms and “lophophoral cavity” first of all correlates with the lophophoral coelom. The same concerns captions on the Fig. 3.
5. “Metamorphic shells of Lingulellotreta on both ventral and dorsal valves, characterised by the development of several pairs of fine folds on the protegulum margin (Fig. 2F, Supplementary Figs. 4B-D, 11B and 11C), show great similarity to that of many other early Palaeozoic brachiopods with the ‘paterinate’ type larva that is first discovered on Cambrian paterinates.” It is not described in which features the first-formed shells of Lingulellotreta resemble the paterinate shells and how these fine folds may be interpreted.
6. “Thus, the reduction of the ventral pseudointerarea is a widely observed evolutionary trend in the lingulide lineage, while the novel posterior extension of the coelomic cavity enclosed by ventral pseudointerarea…” Here is a certain contradiction as the posterior extension of the coelomic cavity is declared to be inherited from the tubicolous ancestors and thus cannot be novel.
7. The authors suggest that Yuganotheca is the ancestor of Lingulellotreta but what is the difference in the age of their first findings? Is Yuganotheca younger that first brachiopods including Lingulellotreta? It is an important moment that should be clarified in order to prove that Lingulellotreta could inherited its body plan from Yuganotheca. If Yuganotheca is the ancestor, why other Early Cambrian brachiopods lack pouch-like coelomic cavities?

Figure captions:
Fig. 2F. “Ventral metamorphic shell, show paired fine folds on the protegulum margin (arrows), pronounced halo (tailed arrow) and drip structures on post metamorphic shell (double-headed arrow)”– The drip structures are not visible at this scale.
Fig. 3A – On the reconstruction the foramen is empty while the pedicle protrudes from the umbo.

Supplementary figures
Fig. 2B, C. There are no arrows on the photo but they are in the caption.
2D. There are no double-headed arrows on the photo but they are in the caption.
2H. The arrow does not correspond to any impression or it is invisible at this scale.
4A. “Posterior view of metamorphic shell, noting the prominent halo by tailed arrow and drape structures by arrow” – the proposed halo rings are indistinguishable from the ornamentation. Drape structures are marked but not described in the text and invisible on this photo.
4C. “External view of metamorphic shell, showing paired fine folds on 98 the protegulum margin (arrows)” – no arrows on the photo.
5D. Possibly it is worth adding some arrows for the inner structures and explain them.
5E-H. “Large specimen with developed transmedian 107 muscle scars (arrows) and vascula midia (double-headed arrows)” – there are only simple arrows on 5H.
5I. Right tailed arrow points to the dark spot.

6A. “Oblique view of pseudointerarea and visceral area, noting umbonal muscle scars (arrows) and proximal end of median tongue (tailed arrow).” There are no arrows on the photo.
6B. “Enlarged view of vascula media (arrows) and distal end of median tongue (tailed arrow)”. There are no arrows on the photo.
7A. Tailed arrow seems to point to the third fold of external ornamentation that is probably not halo ring.
7D, E. “Posterior view of metamorphic shell, noting the halo by tailed arrow”. There are no arrows on the photo.
7I. “Internal view of Scale-like structures and growth lines” – internal view of the external surface?
10A. “Dorsal view of columnar shells” – there is a certain mistake in the description of this photo; and where is caption for 10B?
11A, B. No drape structures are visible at this scale.
12H. “Large specimen with median ridge (arrows)” – arrows point to the muscle scars, not median ridge.

Version 1:

Reviewer comments:

Reviewer #1

(Remarks to the Author)
Dear authors, I am pleased to once again share my opinion on the manuscript entitled "Combining soft-bodied and three-dimensional fossils to reveal evolutionary novelties in early lingulellotretid brachiopods." Just as I did the first time I reviewed it, I personally believe it should be accepted for publication, even now with all the improvements and additions made to the first version.
I must also acknowledge and mention the excellent work of reviewers 2 and 3, who made a significant contribution to these improvements.
A small mistake I found that can be corrected is on line 358, which says Lingulellotrate.
I emphasize my interest in the evolution and relevance of new analyses and research on the morphological characters present in Linguliformea, made possible by the discovery of very well-preserved specimens where the soft parts can be appreciated. Furthermore, it can be observed how even in groups considered "conservative", the evolutionary mechanisms "experimented" in the development of characters that appeared and did not last over time, being a common scenario during the Cambrian Explosion.

Reviewer #2

(Remarks to the Author)
Combining soft-bodied and three-dimensional fossils to reveal evolutionary novelties in early lingulellotretid brachiopods by Feiyang Chen, Zhifei Zhang, Lars E. Holmers, Guoxiang Li, Timothy P. Topper, Baopeng Song, Zhiliang Zhang

I think that the authors showed their efforts to improve the manuscript and clarify the issues raised by me and other reviewers, both in the revised main text and the rebuttal letter. However, I feel that the following point still needs to be clarified:

The authors stated that Lingulellotreta has ‘novel’ features derived from soft-bodied stem-group brachiopods (e.g., posterior expansion of visceral cavity). If the feature was derived from the older ancestor, it cannot be a novel character.

In my view, the authors seem to regard the visceral cavity under the elongate pseudointerarea in Linguellotreta as a ‘novel’ feature (or failed experiment) during the Cambrian Explosion, because this feature has not been maintained in younger taxa. However, this view seems to be odd, as we do not treat older forms as novel developments. If it is a novel trait, the authors need to demonstrate the posterior expansion of the visceral cavity between Linguellotreata and its possible ancestors (e.g. Yuganotheca), instead of the comparison with the younger lingulide taxa.

Hope that my comments will be helpful.

Sangmin (Sam) Lee
Research Fellow
School of Science, Faculty of Science, Medicine and Health
University of Wollongong

Ms. COMMSBIO-25-0108A

Reviewer #1 (Fernando Julián Lavié)

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Response: We thank Dr. Lavié very much for his interest in our research and positive comments. All the suggestions have been introduced into the revised version of the manuscript.

Comment 2: Line 238: I think the apostrophe is unnecessary "animals' exoskeletons"

Response: Thanks, we have changed the text to "animal exoskeletons".

Comment 3: Line 284: delete the comma after "provided"

Response: Yes, it is changed accordingly.

Comment 4: Line 326: the last “e” is missing in unbiomineralized

Response: Yes, it is changed as suggested.

Comment 5: Caption figure 1: correct Chengjing for Chengjiang

Response: Yes, it is changed as suggested.

Comment 6: Captions figure 1, 2 and 3, and figure 1: it is written “viscera cavity” or “viscera area”, but in the whole manuscript it is written as “visceral” which I consider to be the correct form.

Response: Thanks, we have changed all terms to “visceral”.

Reviewer #2 (Sangmin Lee)

Comment 1: The subject of the manuscript is interesting and suitable for the wide audience of Communication Biology. The early evolution during the Cambrian Explosion is significant for understanding how animals diversified and evolved into the body plans of modern phyla. This study presents detailed morphologies of two *Lingulellotreta* species that occurred in the early Cambrian, trying to demonstrate how this ancient genus developed its morphological adaptation as one of the oldest brachiopods and how its shell and anatomical features are distinguished from its modern descendant *Lingula*, a well-known living fossil. This paper is also exceptional in providing high-resolution images of the well-preserved shell material; the pitting micro-ornamentation on the primary shell layer in *Lingulellotreta* is identified for the first time and the columnar shell architectures are beautifully demonstrated in the supplementary figures.

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of the morphological explanations in this manuscript do not show any novelty. Instead, they are taken from earlier publications that also described the same taxa; the pouch-like coelomic cavity under ventral pseudointerarea was explained in detail by Zhang et al. (2007, 2020; Ref. 22 & 28 in your list); and the columnar shell architectures were fully discussed by Zhang et al. (2023; Ref. 37). Unfortunately, these contents are simply repeated without any further discussion. None of the research questions is properly answered, including: 1) How are these morphological features helpful in explaining the evolutionary trends of the lingulide brachiopods since their first appearance in the Cambrian?; 2) If the pouch-like cavity was developed in the earliest lingulellotretid as a novel body plan, why is the reduction of the pseudointearea already observed in *Linguellotreta ergalievi* of the Cambrian Stage 4?; 3) If the posterior expansion of the cavity is a morphological experiment only in the very early lineage, how does it help to understand the 540-millions evolution of the lingulide brachiopods? If the authors would like to publish some of the contents in the manuscript, they need to expand their discussions with novel ideas.

I have also provided several minor comments/suggestions on the PDF file annotated and attached. Hope that my comments will be helpful.

Response: We thank Dr. Lee very much for all the constructive suggestions and helpful corrections. All the comments, including the annotated comments in the pdf file, have been fully considered and introduced into the revised version of the manuscript.

Yes, the pouch-like coelomic cavity under ventral pseudointerarea of *Linguellotreta yuanshanensis* was described in detail from the Chengjiang Lagerstätte by Zhang et al., 2007, 2020. But all the specimens from the Chengjiang Lagerstätte are highly compressed during the diagenesis process, lacking a three-dimensional observation of the pouch-like coelomic cavity. In this paper, we aim to compare the new three-dimensional phosphatic shells of *Linguellotreta* from South China and Kazakhstan with the previously described soft-bodied specimens from the famous Chengjiang Lagerstätte, and provide solid evidence for the existence of the pouch-like coelomic cavity in *Linguellotreta yuanshanensis* and *Linguellotreta ergalievi* for the first time. We try to emphasise the novelty of this paper that the *Lingulellotreta* would be an important link between the soft tubular ancestors and the tongue-shaped descendants.

Furthermore, the comparable study between older *L. yuanshanensis* and younger *L. ergalievi* make it possible to track their evolutionary modifications of anatomical and architecture structures during the Cambrian Explosion, and then to discuss the significance of pseudointerarea reduction in Lingulida.

In this manuscript, we highlight several key morphological features that contribute to understanding the evolutionary trajectory of lingulide brachiopods, including the posterior expansion of the visceral cavity, the development of a large pseudointerarea, and columnar shell structures. Our study further elaborates on how these features influenced the survival and eventual extinction of lingulellotretids while shaping the long-term evolutionary trends in lingulides. The increasing size of the visceral cavity over time (from 13%-26.9% of ventral valve length in Cambrian *Lingulellotreta* to ~59% in modern *Lingula*) 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. The reduction of the pseudointerarea across different lingulide lineages suggests an adaptive shift, potentially reflecting changes in pedicle function and burrowing behaviour.

Our manuscript acknowledges that *L. ergalievi* exhibits a reduction in the pseudointerarea compared to *L. yuanshanensis*, which had a more pronounced posterior expansion. This suggests that even within lingulellotretids, there was a diversification of body plans, potentially reflecting different ecological adaptations or responses to environmental pressures. Comparative analysis with later lingulides (such as Obolidae and Pseudolingulidae) could further clarify whether this trend represents a convergence toward a more efficient body plan that ultimately became dominant in later lineages.

The posterior expansion of the visceral cavity in *L. yuanshanensis* appears to be an early-stage morphological innovation that was not retained in later lingulides. This may suggest that it was an "evolutionary experiment" that did not lead to long-term success, possibly due to inefficiencies or disadvantages in feeding, respiration, or structural stability. However, this feature provides crucial insights into early diversification in lingulide body plans and the selective pressures that shaped their eventual evolutionary trajectory. While posterior expansion was not a persistent trait, it highlights the early plasticity of lingulide anatomical structures and their eventual refinement toward the more successful modern morphology. The evolution from

a posteriorly expanded cavity to a more compact visceral cavity aligns with broader evolutionary trends in lingulides, including increased burrowing capability and a shift in lophophore placement.

In the revised manuscript, we have added the discussion of the evolution of biomineralized shells and anatomic configurations in lingulides, andfurther clarified how these long-term evolutionary trends correlate with ecological transitions and survival strategies through geologic time.

Comment 2: Only shell outline? Or general morphology including soft parts (e.g. pedicle)? (line 21)

Response: Good suggestion, we have changed the text to “general morphology”.

Comment 3: Evolutionary stasis does not require a life form to be uniformly maintained since its first appearance. If the genus is one of the earliest lingulides, the peculiarity in anatomy and shell structure is of course expected. (lines 26-27)

Response: Yes, we agree, and we have changed the text to “Despite the stasis typical of the lingulides in their evolutionary history, new material of well-preserved soft-tissue and phosphatic shells reveal -----”.

Comment 4: How could the columnar shell structures be inherited from the unmineralized taxon? In addition, if the features were inherited, how could they be novel characteristics? (lines 28-30)

Response: Many thanks for picking up this oversight (please also see response to Comment 5). We have rephrased this sentence accordingly.

Comment 5: If the tubular body form in the lingulellotretids is a characteristic inherited from a stem-group brachiopod, why is it regarded as a failed evolutionary experiment? Also, wasn't the tongue-shaped body form evolved from the tubular form? (lines 31-32)

Response: Yes, the tongue-shaped body form likely evolved from the tubular form. However, as we discussed on page 9, lingulellotretids with a tubular form, having an unusual elongate pseudointerarea, only occurred for a relatively short geologic time span, having become extinct during the Early Ordovician. The evolutionary trend for Lingulida was to reduce the ventral pseudointerarea, resulting in the adaptive diversification of lingulides in the Early Palaeozoic. So, in this view, the posterior expansion of the coelomic body with an elongate pseudointerarea in lingulellotretids is regarded as a failed evolutionary experiment compared with the widely developed reduced pseudointerarea in other groups of lingulides. We have added the discussion of an early-stage morphological innovation in *L. yuanshanensis* that was not retained in later lingulides, suggesting an "evolutionary experiment" that did not lead to long-term success. As we explain above, this may possibly due to inefficiencies or disadvantages in feeding, respiration, or structural stability of lingulellotretids.

Comment 6: Why 'however' here? Does this sentence contain contrasting ideas to the previous one? (line 47)

Response: We rephrase this sentence as suggested.

Comment 7: It appears that these sentences include redundant contents. Not really needed. Why are you stating this again? The Cambrian Explosion was already described above. It may be better to focus on the general concept of the 'living fossils' in this paragraph. (lines 49-53)

Response: Thanks, we deleted the redundant contents and rephrase this part as suggested.

Comment 8: This phrase needs to be revised. 'As an example of the most primitive brachiopods,' would be better? Why not lingulides here? Suddenly it changed to the subphylum level. (lines 5-61)

Response: Corrected and revised as suggested.

Comment 9: So, does the 'tongue-shaped body' in the abstract mean the tongue-shaped shell

here? Also, if you confine shell outline to the tongue-shaped shells, linguloids (not lingulides) need to be stated. (line 63)

Response: Yes, we mean tongue-shaped shells that are mainly preserved as fossils. We change to “linguloid brachiopod”.

Comment 10: In which aspects of the rapid evolution? (line 64)

Response: We mean the size of pseudointerareas and architectures of shell structure in lingulellotretids that are added in the Discussion section.

Comment 11: So, did this genus flourish and become extinct during the Age 4? But when did it appear for the first time? It seems there have been its reports (including this article) from the Cambrian Stage 3. (line 66)

Response: Yes, *Lingulellotreta* firstly occurred at the Cambrian Age 3, and flourished in South China and Kazakhstan and became extinct during the Age 4. The occurrence of is added in the Supplementary Figure 15. However, there are big challenges in defining the boundary of the unnamed and undefined Stages 3 and 4 globally.

Comment 12: for example? (line 66)

Response: We added examples of *Palaeobolus* and *Eoobolus*.

Comment 13: Does it mean an anatomical body plan or shell outline? (line 69)

Response: Yes, we mean shell outline and change to “linguloids”.

Comment 14: Better to include their authors and years as well. (line 77)

Response: Corrected and revised as suggested.

Comment 15: recognize or recognise? Need to be consistently used throughout the manuscript. (line 78)

Response: Thanks, we try to use the "recognise" in the whole manuscript consistently.

Comment 16: I am not sure how the Family Lingulellotretidae is revised in this article. (lines)

Response: Yes, we discuss the new characters of *Lingulellotreta* and imply the phylogenetic significance of the family Lingulellotretidae in the section of 'The evolution of biomineralized shells'. But the detailed revision of Lingulellotretidae is a taxonomic work and will be another research task in the future.

Comment 17: Fig. 1A does not show the outline of dorsal valve. (line 89)

Response: Yes, the dorsal valve and ventral valve are highly overlapped as the compression. The boundary between the dorsal and ventral valves is marked by the hinge line in Fig. 1A and Supplementary Fig. 1B.

Comment 18: Instead, reference numbers? Reference 22 (in your list) should also be cited. (line 91)

Response: Corrected and revised as suggested.

Comment 19: Were these anatomical features already demonstrated in Zhang et al. (2020) - reference 22? I am not sure which findings are really novel here. (lines 99-104)

Response: Yes, these anatomical features were previously demonstrated in Zhang et al. 2020 for the phylogenetic purpose, in order to distinguish the similar morphology between soft-tissue preserved *Eoobolus malongensis* and *Lingulellotreta yuanshanensis*. It has been a taxonomic problem since 1974. However, in this paper, we need to redescribe the anatomical features from the type locality for a comparative study with the phosphatic-shelled material retrieved from acid residues. Based on these new materials and observations, we are able to

expand on the discussion of the early evolution of lingulellotretid brachiopods and previous conclusions reached by Zhang et al. (2020).

Comment 20: According to your Supplementary Fig. 14, the shells of *L. yuanshanensis* from the limestone (Shuijingtuo Fm.) are clearly distinguished from its soft-bodied fossils in shell size (not overlapped both in width and length). Then, how could you conclude they would be conspecific? It appears that these two types of the fossils were collected from different stage (one from Stage 3 and the other from Stage 4). In this context, I am not sure if the bivariate plots in Fig. 3B, C is meaningful. (line 109)

Response: Specimens of *L. yuanshanensis* in this study are collected from Cambrian Stage 3, including the Yuanshan Formation and lower Shuijingtuo Formation. The conspecific identification of the limestone fossils (Shuijingtuo Formation) and soft-bodied fossils (Yuanshan Formation) of *L. yuanshanensis* has been done in detail by Holmer et al. 1997 and subsequently revised by Zhang et al. 2020. So we followed their conclusion in this research. The size differentiation between specimens of two-type preservations is likely due to the preservation bias, as only smaller fossils can be preserved as phosphatic casts or coatings in limestones (Yang *et al.* A juvenile-rich palaeocommunity of the lower Cambrian Chengjiang biota sheds light on palaeo-boom or palaeo-bust environments. Nat Ecol Evol, 2021). Moreover, most of the larger specimens are broken into pieces that are not suitable for measurement. Large and complete fossils are largely preserved in the clastic mudstones. The regression analysis in Supplementary Fig. 14 demonstrates the fossils from two different areas are close to one developmental sequence with statistical significance ($P<0.001$), which support the conspecific designation.

Comment 21: Referring to correct figures? (line 113)

Response: Thanks, we have checked and revised accordingly.

Comment 22: Provide a more detailed description about this architecture in your specimens.

(lines 130-131)

Response: More details of columnar shell structures have been provided.

Comment 23: In my view, the data of the small shells are not well-matched with the large soft-bodied fossil data. (lines 134-135)

Response: The significant relevance of the fossils from two areas are demonstrated by the regression analysis of pedicle foramen, pseudointerarea and proparears, although the relationship is not very strong (around 0.7). Please see our response to Comment 20.

Comment 24: Do you mean two patterns shown in the two different species? (lines 137-138)

Response: Yes, we express it more clearly now.

Comment 25: It is very hard to follow your explanation in this paragraph. You have not explained any growth stages in your result section. These growth stages need to be illustrated in detail, clearly evidenced by your fossil images. Otherwise, hard to understand. (lines 168-188)

Response: Thanks for your constructive comment. We have rephrased this paragraph.

Comment 26: How does this citation work? (line 180)

Response: It is not correctly cited, and we delete this citation.

Comment 27: It seems that the posterior expansion of the coelomic cavity was not the evolutionary trends even within the lingulellotretids. Is the pattern well-presented only in *L. yuanshanensis* (probably, the oldest taxon)? (line 195)

Response: No, the posterior expansion of the coelomic cavity is generally developed with the elevation of ventral pseudointerarea in the lingulellotretids. The interesting phenomenon is that

this pattern is most well-preserved in *L. yuanshanensis*, which is the oldest known taxon. In the slightly younger taxon, *L. ergalievi* has a relatively short pseudointerarea, which means a reduced expansion of the coelomic cavity posteriorly.

Comment 28: If it was only developed in the oldest taxon *L. yuanshanensis*, can it be regarded as a novel feature? (lines 215-216)

Response: As we discuss above, the posterior expansion of the coelomic cavity (it needs the elevation of the pseudointerarea from the valve floor) is generally and uniquely developed in the lingulellotretids, while it is most obvious in *L. yuanshanensis* and *Aboriginella*. This feature in *Lingulellotreta* appears to be an early-stage morphological innovation that was not retained in later lingulides. This may suggest that it was an "evolutionary experiment" that did not lead to long-term success. (please also see response to Comment 42).

Comment 29: The table does not show this value. (lines 222-223)

Response: No, this value is not shown in Supplementary Table 1. But the measurements of the length of lophophore (L_{mc}) and valve length are shown in the table. So, their ratio is calculated by the original data.

Comment 30: Why do you use informal terms here although the formal superfamilial names (Acrotretoidea and Linguloidea) are used in the earlier part? (line 251)

Response: Corrected and revised as suggested.

Comment 31: Similar to which groups? Also, what is the 'micro-size'? In the pitting structures? Now class level! Not Lingulida? (lines 252-254)

Response: Sorry for making the confusion. In the first sentence, we state that the pitted micro-ornamentation is widely developed in Acrotretoidea, Linguloidea, Discinoidea and Acrotheloidea, which is similar to the structures discovered in Lingulellotretidae in the study.

So, we think it implies such structures would be homology in Lingulata, not just in Lingulida. We have revised this part accordingly.

Comment 32: 'pitting structures' vs. 'pitted structures' (lines 261-262)

Response: Actually, both terms are used for describing the micro-ornamentation. We change to “pitting structures” for consistence.

Comment 33: subphylum level? (line 264)

Response: Yes, with the continuous study on the ultra-structures of brachiopods recently, the pitting structures are discovered almost in all Lingulata and Paterinata, revealing it is a plesiomorphic feature of the Linguliformea (subphylum level).

Comment 34: How could you confine the timing of the change to the Early Palaeozoic? You only compared the Cambrian taxa with modern ones. (line 265)

Response: Yes, we compare the Cambrian and living taxa in this study. But, the earliest ontogenetic features of brachiopod larvae were reviewed across the Early Palaeozoic in Zhang 2018. As the metamorphic characters have been gradually modified by different groups since early Cambrian, we then expand the discussion of the living environment of brachiopod larvae to the Early Palaeozoic.

Comment 35: More detailed explanation about this transition (based on your specimens) is required in your result section. (line 285)

Response: We have added the detailed shell structure information of *Lingulellotreta* in the Result section.

Comment 36: I am not sure if this section includes any novel ideas for the evolution of brachiopod shells. It appears that most of the interpretations were already suggested by the

references listed. (lines 249-294)

Response: Given the discovery of well-preserved pitting structures in *Lingulellotreta*, we are quite sure that metamorphic features are here convincedly shown in Lingulellotretidae for the first time. Such characters we believe to be homogenous in Linguliformea at least. On the other hand, the shell architecture of *Lingulellotreta* is not as well documented in a previous paper (Zhang et al. 2024), as that study mainly focused on the description of new eoobolid brachiopods. So, we provide more details in the current study as suggested. Both the pitting structures and shell structures will be very important for the phylogenetic study of lingulellotretids, which is quite uncertain at the moment.

Comment 37: What does it mean? (lines 299-300)

Response: We change it to "which are less obvious when observed solely from the archaic outline of ventral and dorsal valves".

Comment 38: However, the evolutionary transitions in Figure 4 are represented ONLY between Cambrian taxa and a modern species. Which characters do represent the evolutionary transitions in the lingulide brachiopods since the early Ordovician? (line 308)

Response: Yes, we agree that we just have Cambrian specimens for the current study. The body plan of living lingulids possibly originated from the pseudolingulid group during the Ordovician. This makes us state that the tongue-shaped valve outline of living lingulides has been retained since the early Ordovician. During the Cambrian, the shell outline is not standard tongue-shaped. But, the anatomic modifications of lingulides have been discussed in detail by Emig, 1992, 2002, 2008 and Biernat and Emig 1993. So there is no need to include the details of these changes. We have reviewed such transitions in the first part of the Discussion. For Figure 4, the key point is the reduction of pseudoinrerarea that started as early as the Cambrian, and has continued to the present day in lingulides.

Comment 39: So, did this adaptation occur in the Cambrian? (lines 311-312)

Response: Yes, the adaptation of higher ecological tier (attached on the surfaces of other organisms by pedicles) of the benthic community by lingulides is reported from the early Cambrian by Zhang et al. 2010 (Peduncular attached secondary tiering acrotretoid brachiopods from the Chengjiang fauna: Implications for the ecological expansion of brachiopods during the Cambrian explosion) and Wang et al. 2012 (Peduncular attached secondary tiering acrotretoid brachiopods from the Chengjiang fauna: Implications for the ecological expansion of brachiopods during the Cambrian explosion).

Comment 40: in which aspects? Also, how is it linked with their shell concentrations? (line 315)

Response: The large abundance of brachiopods was concentrated to form the shell beds, which served as the pavement of the soft substrate hosting other epi-benthic animals to be attached on the shell beds (Zhang et al. 2020; Chen et al. 2022). So this greatly increased the complexity of the benthic communities.

Comment 41: It means that the evolutionary stasis of the lingulids is obvious since the Great Ordovician Biodiversification. (lines 319-321)

Response: Yes, we point out the tongue-shaped outline when talking about the "evolutionary stasis". As we discussed above, the tongue-shaped valve outline was likely retained in the Ordovician.

Comment 42: Does this make sense? If this body plan is a newly developed in the taxon, it has not been derived from its ancestors. (lines 324-325)

Response: We may need to explain that when we are talking about the novel body plan, we mean the new constitution of the ventral and dorsal valves with completely new structures that is different from any other related groups. But, in the view of evolution, any new forms must be derived from the ancestors. And we are quite sure that the brachiopod ancestors have

no biomineralized valves due to the fossils from the very rare fossil lagerstätte. So, the new body plan (biomineralized ventral and dorsal valves, the posterior expansion of the visceral cavity, the development of a large pseudointerarea) of *Lingulellotreta* would be an important link between the soft tubular ancestors and the tongue-shaped descendants.

Comment 43: More explanation is required how these two taxa are related. (lines 328-329)

Response: Sorry, at present, the relationship between *Lingulellotreta* and *Lingulosacculus* is still in debate (Please see more discussions from Balthasar et al. 2009; Harper et al. 2017; Moysiuk et al. 2017; Zhang et al. 2020). The phylogenetic position of these two genera is very unstable depending on different authors' interpretations. We think more study is needed in the future, as only two specimens of *Lingulosacculus* are discovered, while *Lingulellotreta* has hundreds of specimens from two different preservation windows.

Comment 44: So, how did the lingulides with shorter pseudointerareas have benifits in the microscopic defense and filter feeding? More detailed explanation is required. (lines 332-333)

Response: We have given more explanation in revised manuscript. Compared with the dorsal valve, the pseudointerarea of ventral valve is too long to serve a good cojoin of the valves. Because the main function of pseudointerarea is the articulation of the valves attached by muscles. So, we think a short ventral pseudointerarea can have a better cojoin function of two valves.

Comment 45: Instead of these sentences, more specific evidence in the evolutionary trends of the linguilide brachiopods should be demonstrated. (lines 333-341)

Response: We are providing a case study of novel body plan of *Lingulellotrate*, a key link between the soft tubular ancestor and tongue-shaped shells of lingulide lineage in this study. The explanation of morphological features in *Lingulellotrate* for understanding the evolutionary trends and different survival conditions in the lingulide lineage since early Cambrian has been added in the section of Discussion. What we want to clarify is that the

living fossils *Lingula* is quite different with its earliest ancestors, except of the tongue-shapes outline. Moreover, such anatomic transformation rapidly occurred and preserved as fossils in the early Cambrian. To find more fossil evidence of the evolution trends across Phanerozoic, and compare their details with living representatives would require a much greater sampling effort, and it would be beyond the scope of this paper. We hope we can solve some of the problems with the continuous study of brachiopods in the future.

Comment 46: More detailed stratigraphic information (at least biozones, as mentioned for other fossil localities) needs to be provided. Further, how are the three fossil layers stratigraphically correlated? Which one is the oldest and youngest? But the readers do not know what would be the fossil horizons in the stratigraphic sections. (lines 359-360, 366)

Response: Thanks for his constructive comment. We have added a supplementary figure and biozone information (Supplementary Fig. 15) to show all the details in the Methods section.

Comment 47: However, the shell micro-structures are not described in fine detail. (lines 364-365)

Response: Thanks, detailed shell structures are added in the Results section.

Comment 48: Better to mark these on the specimen (lines 640-641)

Response: Thanks. We have revised Figure 1D as suggested.

Comment 49: This image only provides a posterior view of the large ventral pseudointerarea and pedicle foramen. The pouch-like structure of viscera cavity is supposed to be developed beneath the pseudointerarea. (line 641)

Response: Thank you. We have revised as suggested.

Comment 50: Which one is the columnar layer? Unclearly shown in the image. (lines 643-644)

Response: Thanks. We have revised Figure 1G as suggested.

Comment 51: Mark the dorsal pseudointerarea on the specimen. It appears that its pseudointerarea is well-developed. (line 651)

Response: Thanks. We have revised Figure 2C as suggested.

Comment 52: Ventral pseudointerarea and pedicle foramen. The viscera cavity cannot be seen in the image. (line 652)

Response: Thanks. We have revised as suggested.

Comment 53: In the size data, it is clear that the Yuanshan Fm. specimens are much larger than the Shuijingtuo Fm. shells. I am not sure if the plots are meaningful. (lines 660-661)

Response: As we discussed above (response to Comment 20), the regression analysis in Supplementary Fig. 14 demonstrates the fossils from the two different areas are close to representing a developmental sequence with statistical significance ($P<0.001$), which support the conspecific explanation by Holmer et al. 1997 and Zhang et al. 2020. Based on this analysis, we then plot the data in Figure 3.

Comment 54: Blue? Red? (lines)

Response: We change to “red and crimson colours” and “blue and slate blue colours”.

Comment 55: According to the authors, the viscera cavity in the *Lingulellotreta* is posteriorly extended, occupying the space beneath the ventral pseudointerarea. Then, should the measurement of L_{vc} be extended posteriorly (including $L_{p\text{-}m}$ or $L_{p\text{-}mi}$)? (line 668)

Response: Thanks for your kind suggestion. Yes, the actual size of visceral cavity is longer than the L_{vc}. For most of the specimens, we can not surely observe the posterior end of the

visceral cavity, which hampers the precise measurement of the true visceral cavity. As the boundary of pseudointerarea is prominent, so it provides more chance to measure the L_{vc} on most of the specimens. But we calculate the viscera area (L_v) in our measurement, and then, assess possibly maximum length of viscera area. The off-set of the extended space beneath the ventral pseudointerarea is about 17% and 5% of the valve length in *Lingulellotreta yuanshanensis* and *Lingulellotreta ergalievi*, respectively, which has been calculated in the Supplementary Table 1 and Table 2.

Comment 56: This stem group taxon seems to be drawn as a crown group taxon in this diagram. How did the coelomic cavity evolve in these Cambrian Stage 4 taxa? So, where did the posterior extension of viscera cavity occur? Here? Or it might be a plesiomorphic character for the lingulide brachiopods? It appears that the reduction of ventral pseudointerarea was already done during the early Cambrian (Stage 4). (page 30)

Response: Thanks for the constructive suggestions. For the Figure 4, if we consider all the lingulides group as one crown group, *Yuganotheca* can be considered as a stem group.

For the Cambrian Stage 4 taxa, we don't have any soft-tissue preserved material. All the information is obtained from the phosphatic shells. For *L. ergalievi*, likely there is a smaller space beneath the ventral pseudointerarea, which can help to host a small part of the visceral organs. But for *P. yunnanensis*, the ventral pseudointerarea is not raised above the valve floor (Chen et al. 2024), so there is no space for the posterior extension of the viscera cavity. Moreover, the ventral pseudointerarea of *P. yunnanensis* is largely reduced, without the development of a pedicle foramen.

The posterior extension of viscera cavity is unique to the lingulellotretid group, which is not discovered in other groups. So, we think it would be an apomorphic character for Lingulellotretidae.

Yes, as we discuss above, the reduction of ventral pseudointerarea was already done during the early Cambrian (Age 4).

Reviewer #3

Comment 1: The paper is quite interesting and contains new data on the evolution of the soft body and ontogeny of lingulide brachiopods, which previously were considered to be a conservative group. This study is important for the understanding of the evolution and morphology of Brachiopoda. The whole approach is novel and meets modern requirements of the paleontological studies. However, there are few moments that need clarification or correction.

Response: We thank the Review #3 very much for the very helpful remarks and constructive suggestions, all the comments have been fully considered and where appropriate introduced into the revised version of the manuscript.

Comment 2: The authors describe a pedicle nerve but in recent lingulides it is paired throughout its entire length and it remains unclear why the not paired groove is considered to be a pedicle nerve and why other nerves did not leave imprints.

Response: Yes, you are right that the impression of pedicle nerve is paired, previously demonstrated by Holmer et al. (1997). We have marked it in the revised Supplementary Figures 2 and 3.

Comment 3: The described halo rings are indistinguishable from the adult ornamentation and there is no reason to recognize them as halo rings, not the first onset of the adult shell.

Response: We have remarked the halo ring in revised Supplementary Figures 4 and 11. Whiles the halo rings in *Lingulellotreta* are not as well-preserved as in some early Cambrian acrotretides demonstrated by our previous study (Zhang et al. 2018 BMC), they are quite distinct as the first transversely semi-oval ring of both dorsal and ventral valves. Because, inside the halo, only pitting micro-ornament and paired fine folds are developed, lacking

growth lines (Supplementary Figs. 4A-E, 11A-D); outside the halo, the nick points or drape structures are developed (Fig. 2F; Supplementary Figs. 4A, G, 11A), and they are the growth disturbances produced by mature marginal mantle setae. The halo size is about 200 μm that can be well compared to that of most of other Palaeozoic brachiopods. All the characters demonstrate the shell inside the halo is the earliest secreted shell before the metamorphosis of the larva (please see more detailed discussions in Williams et al. 1998 Palaeontology; Popov et al. 2007 Lethaia., 2009 Gondwana Research; Zhang et al. 2018 BMC, 2019 Journal of Systematic Palaeontology). So we use the term "halo ring" in this study.

Comment 4: "Compared to the complex musculature in living lingulides, *Lingulellotreta* has a relatively simple and symmetrically arranged muscle configuration" – this is not explained, the musculature of *Lingulellotreta* and recent lingulides should be briefly compared and the description of *Lingulellotreta* musculature possibly should be added to the results.

Response: Thanks, we have added the comparison about the musculature in the sections of Results and Discussion. Yes, you are right that living *Lingula*have a more complicated muscle system (Balthasar, 2009, Liang et al. 2023), compared to Cambrian *Lingulellotreta* (Holmer et al. 1997), because of their burrowing life style. Compared to modern lingulide brachiopods, lingulellotretids exhibit a simpler and more symmetrical muscle configuration. This difference is significant, as it suggests a fundamental shift in locomotion, feeding strategies, and ecological interactions over evolutionary time. The modern *Lingula* lineage has developed a more complex musculature, directly linked to its active burrowing lifestyle, which was absent in Cambrian lingulides. The absence of strong asymmetry in the muscle scars suggests that valve movement in *Lingulellotreta* was relatively limited, in contrast to the powerful closure observed in burrowing modern lingulides.

Comment 5: "In brachiopods, the lophophoral cavity (or mantle cavity) and visceral cavity (or coelomic cavity)…" There are generally accepted terms "mantle cavity" and "visceral cavity" and there are three coeloms in lingulides: body coelom, pedicle coelom and lophophoral coelom. Therefore, the newly suggested terms "lophophoral cavity" and "coelomic cavity" are

unacceptable as “coelomic cavity” may be applied to all three coeloms and “lophophoral cavity” first of all correlates with the lophophoral coelom. The same concerns captions on the Fig. 3.

Response:. Many thanks for picking up this oversight. We change to “mantle cavity” and “visceral cavity”.

Comment 6: “Metamorphic shells of Lingulellotreta on both ventral and dorsal valves, characterised by the development of several pairs of fine folds on the protegulum margin (Fig. 2F, Supplementary Figs. 4B-D, 11B and 11C), show great similarity to that of many other early Palaeozoic brachiopods with the ‘paterinate’ type larva that is first discovered on Cambrian paterinates.” It is not described in which features the first-formed shells of *Lingulellotreta* resemble the paterinate shells and how these fine folds may be interpreted.

Response: Thanks for this kind suggestion. We add more detailed information in the Result section for better comparison (Fig. 2F revised). The fine folds are not described in *Micromitra* by Williams et al. (1998), as the resolution of the image was not very high. New study of the earliest ontogeny of paterinate brachiopods will be investigated in the future. Such fine folds are also well developed in early Cambrian acrotretids (Zhang et al. 2018) and eobolids (Zhang et al. 2024). The fine folds would be the folded surface of the outer epithelium at the time of secretion of the protegulum (Zhang et al. 2018). However, their function remains uncertain.

Comment 7: “Thus, the reduction of the ventral pseudointerarea is a widely observed evolutionary trend in the lingulide lineage, while the novel posterior extension of the coelomic cavity enclosed by ventral pseudointerarea…” Here is a certain contradiction as the posterior extension of the coelomic cavity is declared to be inherited from the tubicolous ancestors and thus cannot be novel.

Response: Sorry for making the confusion. We delete the “novel” and explain it more in the section of “The long-lasting and evolving lingulide brachiopods”. When we are talking about derivation, we mean the similar tubular shape between ancestor *Yuganotheca* and

Lingulellotreta. However, the body plan is quite different, as *Yuganotheca* is completely soft without any biomineralization ability, while *Lingulellotreta* is composed of two phosphatic valves. The novelty in this paper means the posterior expansion of the visceral cavity forming a larger pouch-like cavity, which needs the elongation and elevation of the pseudointerarea from the valve floor. This is a significant change in lingulide brachiopods. Such characters are generally and uniquely developed in the lingulellotretids. We have demonstrated that *Lingulellotreta* would be an important link between the soft tubular ancestors and the tongue-shaped descendants. So, we interpret it as novel feature in lingulellotretids. The evolution from a posteriorly expanded cavity to a more compact visceral cavity aligns with broader evolutionary trends in lingulides, including increased burrowing capability and a shift in lophophore placement.

Comment 8: The authors suggest that *Yuganotheca* is the ancestor of *Lingulellotreta* but what is the difference in the age of their first findings? Is *Yuganotheca* younger that first brachiopods including *Lingulellotreta*? It is an important moment that should be clarified in order to prove that *Lingulellotreta* could inherited its body plan from *Yuganotheca*. If *Yuganotheca* is the ancestor, why other Early Cambrian brachiopods lack pouch-like coelomic cavities?

Response: In the Chengjing lagerstätte, *Yuganotheca* is slightly older than *Lingulellotreta yuanshanensis*, and *Lingulellotreta ergalievi* is much younger. Based on phylogenetic analysis, *Yuganotheca* is a type of stem group brachiopods (Zhang et al., 2014; Harper et al., 2017). It is likely that ancestral brachiopods like *Yuganotheca* would not be discovered in older sediments resulting from the lacking of such 'lagerstätte' to be preserved. Moreover, the relationship between tommotiids and crown brachiopods is not resolved yet. We might be able to answer this question if the phylogenetic analysis of the total group of brachiopods is completed in the future. As we discussed above, the reduction of ventral pseudointerarea is already evolved in the Cambrian lingulides, resulting in the lack of pouch-like coelomic cavities in younger offsprings. So we could consider an elongate pseudointerarea in lingulellotretids is regarded as a failed evolutionary experiment compared with the widely developed reduced pseudointerarea in other groups of lingulides. The posterior expansion of

the visceral coelomic cavity in *L. yuanshanensis* appears to be an early-stage morphological innovation that was not retained in later lingulides, which may suggest that it was an "evolutionary experiment" that did not lead to long-term success. However, this feature provides crucial insights into early diversification in lingulide body plans and the selective pressures that shaped their eventual evolutionary trajectory. While posterior expansion was not a persistent trait, it highlights the early plasticity of lingulide anatomical structures and their eventual refinement toward the more successful modern morphology.

Comment 9: Fig. 2F. "Ventral metamorphic shell, show paired fine folds on the protegulum margin (arrows), pronounced halo (tailed arrow) and drape structures on post metamorphic shell (double-headed arrow)"– The drape structures are not visible at this scale.

Response: Thanks, the enlarged view of the drape structures is shown in Supplementary Fig. 4G.

Comment 10: Fig. 3A – On the reconstruction the foramen is empty while the pedicle protrudes from the umbo.

Response: Very good suggestion. We make some modification of the reconstruction.

Comment 11: Supplementary figures:

Fig. 2B, C. There are no arrows on the photo but they are in the caption.

2D. There are no double-headed arrows on the photo but they are in the caption.

2H. The arrow does not correspond to any impression or it is invisible at this scale.

Response: Thank you very much for the detailed and constructive suggestions. All the corrections are made in the revised Supplementary Figures that are presented below. Sorry for the inconvenience. Arrows are added in Supplementary Fig. 2B, D. The arrows are moved close to the imprints of the paired pedicle nerve in Supplementary Fig. 2H, which might be easier to see on the original high-resolution figure. A more enlarged image is shown in Supplementary Fig. 3C.

Comment 12: 4A. “Posterior view of metamorphic shell, noting the prominent halo by tailed arrow and drape structures by arrow” – the proposed halo rings are indistinguishable from the ornamentation. Drape structures are marked but not described in the text and invisible on this photo. 4C. “External view of metamorphic shell, showing paired fine folds on the protegulum margin (arrows)” – no arrows on the photo.

Response: Yes, we agree that the halo ring and drape structures are not well preserved on this specimen in Supplementary Fig. 4A. It is likely to see them on the high-resolution figure. We add the description of drape structures in the text. There are 4 pairs of arrows are marked on the image in Supplementary Fig. 4C, which would be hard to see on the low resolution image. We revised the position of arrows to make it more visible. Hope readers can see them clearly in the high-resolution image.

Comment 13: 5D. Possibly it is worth adding some arrows for the inner structures and explain them. 5E-H. “Large specimen with developed transmedian muscle scars (arrows) and vascula midia (double-headed arrows)” – there are only simple arrows on 5H.
5I. Right tailed arrow points to the dark spot.

Response: Thanks, we mark the transmedian muscle scars and central muscle scars on Supplementary Fig. 5D, and *vascula lateralia* and central muscle scars on Supplementary Fig. 5E. We change the position of arrows in Supplementary Fig. 5I.

Comment 14: 6A. “Oblique view of pseudointerarea and visceral area, noting umbonal muscle scars (arrows) and proximal end of median tongue (tailed arrow).” There are no arrows on the photo. 6B. “Enlarged view of vascula media (arrows) and distal end of median tongue (tailed arrow)”. There are no arrows on the photo.

Response: The umbonal muscle scars are not clear to see. So mark the transmedian muscle scars in Supplementary Fig. 6A. We mark the central muscle scars and distal end of median tongue in Supplementary Fig. 6B.

Comment 15: 7A. Tailed arrow seems to point to the third fold of external ornamentation that is probably not halo ring. 7D, E. “Posterior view of metamorphic shell, noting the halo by tailed arrow”. There are no arrows on the photo. 7I. “Internal view of Scale-like structures and growth lines” – internal view of the external surface?

Response: Thanks, we revise the arrow position of halo ring, and move the arrow to a new area for better visibility in Supplementary Fig. 7A. Arrows are added in Supplementary Fig. 7D and E. We change the caption of Supplementary Fig. 7I to “Internal view of shell laminae with wrinkled margins”.

Comment 16: 10A. “Dorsal view of columnar shells” – there is a certain mistake in the description of this photo; and where is caption for 10B?

Response: Sorry for the mistake. We change to “External view, show uneven growth lines” for the caption of Supplementary Fig. 10A. We add caption for Supplementary Fig. 10B.

Comment 17: 11A, B. No drape structures are visible at this scale.

Response: Yes, we agree the drape structures on Supplementary Fig 11B are hard to see. We delete the arrow. But there are small drape structures on Supplementary Fig. 11A. They are visible on the high-resolution figure.

Comment 18: 12H. “Large specimen with median ridge (arrows)” – arrows point to the muscle scars, not median ridge.

Response: Thanks a lot for all the very helpful suggestions. We change to transmedian muscle scars for the caption of Supplementary Fig. 12H.

Ms. COMMSBIO-25-0108A (second revision)

Reviewer #1 (Fernando Julián Lavié)

Comment: Dear authors, I am pleased to once again share my opinion on the manuscript entitled "Combining soft-bodied and three-dimensional fossils to reveal evolutionary novelties in early lingulellotretid brachiopods." Just as I did the first time I reviewed it, I personally believe it should be accepted for publication, even now with all the improvements and additions made to the first version.

I must also acknowledge and mention the excellent work of reviewers 2 and 3, who made a significant contribution to these improvements.

A small mistake I found that can be corrected is on line 358, which says Lingulellotrate.

I emphasize my interest in the evolution and relevance of new analyses and research on the morphological characters present in Linguliformea, made possible by the discovery of very well-preserved specimens where the soft parts can be appreciated. Furthermore, it can be observed how even in groups considered "conservative", the evolutionary mechanisms "experimented" in the development of characters that appeared and did not last over time, being a common scenario during the Cambrian Explosion.

Response: We thank Dr. Lavié very much for his positive comments and helpful suggestion. Yes, we have changed to *Lingulellotreta*.

Reviewer #2 (Sangmin Lee)

Comment: Combining soft-bodied and three-dimensional fossils to reveal evolutionary novelties in early lingulellotretid brachiopods by Feiyang Chen, Zhifei Zhang, Lars E. Holmers,

Guoxiang Li, Timothy P. Topper, Baopeng Song, Zhiliang Zhang

I think that the authors showed their efforts to improve the manuscript and clarify the issues raised by me and other reviewers, both in the revised main text and the rebuttal letter. However, I feel that the following point still needs to be clarified:

The authors stated that *Lingulellotreta* has 'novel' features derived from soft-bodied stem-group brachiopods (e.g., posterior expansion of visceral cavity). If the feature was derived from the older ancestor, it cannot be a novel character.

In my view, the authors seem to regard the visceral cavity under the elongate pseudointerarea in *Lingulellotreta* as a 'novel' feature (or failed experiment) during the Cambrian Explosion, because this feature has not been maintained in younger taxa. However, this view seems to be odd, as we do not treat older forms as novel developments. If it is a novel trait, the authors need to demonstrate the posterior expansion of the visceral cavity between *Lingulellotreta* and its possible ancestors (e.g. *Yuganotheca*), instead of the comparison with the younger lingulide taxa.

Hope that my comments will be helpful.

Response: We thank Dr. Lee very much for his constructive suggestions. Yes, we have compared *Lingulellotreta* with its possible ancestors (e.g. *Yuganotheca*) to demonstrate their tubular bodies are related as suggested. Moreover, we have now tried to clarify our interpretation of morphological novelty in *Lingulellotreta*. Our use of the term "novel" is not intended to imply that the posterior extension of the visceral cavity was entirely unprecedented among all preceding lophophorates or brachiopod-related forms. Rather, we are referring to the emergence of a distinct anatomical configuration within the context of a biomineralized, crown-group brachiopod body plan, as first seen in *Lingulellotreta*.

Specifically, although tubular organization and visceral elongation are present in the soft-bodied stem brachiopod *Yuganotheca*, these features were realized in a biomineralized shell architecture in Lingulellotreta for the first time. The elongate pseudointerarea forming a pouch-like visceral cavity represents a derived modification, not a retained plesiomorphy, and appears to be unique within the early lingulide lineage. We regard this configuration as a "novel combination"—the integration of a tubular body plan with a posteriorly extended coelomic

space enclosed by phosphatic valves, supported by columnar shell architecture.

Furthermore, while similarities with *Yuganotheca* help contextualize the potential ancestry of this morphology, the lack of continuity of this feature in later lingulide taxa strengthens our interpretation of the posterior extension as an evolutionary experiment—a transient innovation during the Cambrian Explosion that was not retained due to possible functional or ecological constraints. The comparison between *Lingulellotreta* and the tongue-shaped descendants is made to investigate the long-term evolutionary trends in lingulides, and clarify the reduction of the pseudointerarea across different lingulide lineages probably represent a convergence toward a more efficient body plan that ultimately became dominant in later lineages.

In the revised text, we have clarified our terminology and now refer to this feature as a morphological innovation or novel integration, rather than implying absolute novelty from a phylogenetic root. We have also added a direct comparison between *Lingulellotreta* and *Yuganotheca* in the Discussion section to address the reviewer's request for a clearer demonstration of anatomical transitions.

We thank the reviewer again, for prompting us to refine our explanation and improve the precision of our evolutionary interpretations.

To the authors of the manuscript entitled “Combining soft-bodied and three-dimensional fossils reveal evolutionary novelties in early lingulellotretid brachiopods”

I am pleased to announce that my decision on the manuscript is Accepted, with or without editorial revisions.

In general terms, it is very well written and interesting to read, with clear and concise objectives. Specifically, it has the advantage of having specimens of the *Lingulellotreta* genus with excellent preservation, where rare details are observed that allow evolutionary and comparative studies with extant representatives, in this case comparing soft parts, which are generally not possible.

Both the amount of material analyzed and the statistical analysis performed are more than sufficient to make the interpretations. At the same time, I consider that the hypotheses raised and the conclusions reached are in accordance with the results obtained from the analyses and samples.

The discovery of evolutionary trends that were, in this case, “discarded by natural selection” is very interesting, and they reveal a degree of variability within a group of organisms that are generally considered conservative when only general characteristics and trends are observed in the hard parts.

Despite finding a few minor errors in the manuscript (noted below), I strongly recommend publishing it.

Line 238: I think the apostrophe is unnecessary “animals’ exoskeletons”

Line 284: delete the comma after “provided”

Line 326: the last “e” is missing in unbiomineralized

Caption figure 1: correct Chengjing for Chengjiang

Captions figure 1, 2 and 3, and figure 1: it is written “viscera cavity” or “viscera area”, but in the whole manuscript it is written as “visceral” which I consider to be the correct form.

Dr. Fernando Julián Lavié

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

Feiyang Chen[1,2]✉, Zhifei Zhang[3], Lars E. Holmer[4], Guoxiang Li[5], Timothy P. Topper[3,6], Baopeng Song[3], Zhiliang Zhang[5]

[1] Key Laboratory of Coalbed Methane Resources and Reservoir Formation Process, Ministry of Education, China University of Mining and Technology, Xuzhou 221008, China.

[2] School of Resources and Geosciences, China University of Mining and Technology, Xuzhou 221116, China.

[3] State Key Laboratory of Continental Dynamics, Shaanxi Key Laboratory of Early Life & Environments, Department of Geology, Northwest University, Xi'an, 710069, China

[4] Institute of Earth Sciences, Palaeobiology, Uppsala University, SE-752 36 Uppsala, Sweden

[5] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

[6] Department of Palaeobiology, Swedish Museum of Natural History, Box 50007, SE-104 05, Stockholm, Sweden

✉ e-mail: feiyang.chen@cumt.edu.cn

Living lingulide brachiopods are traditionally recognized as representatives of evolutionary conservatism, showing little change in outline from their Cambrian ancestors. However, less attention has been given to their anatomical and ontogenetic modifications that ~~occurred after~~ their initial appearance. Among these, lingulellotretid brachiopods are unique, characterized by their typical elongate pedicle foramen and large pseudointerarea. This study describes new and exquisitely preserved specimens of *Lingulellotreta*, a genus within the earliest lingulide groups, from Cambrian Series 2 deposits in China and Kazakhstan. Despite the evolutionary stasis typical of lingulides, ~~soft-tissue and three-dimensional phosphatic fossils~~ reveal the special fecundity of animal forms with anatomical and biomineralized novelties in *Lingulellotreta* during the Cambrian Explosion. These include posterior expansion of pouch-like coelomic cavity, columnar shell structures, and larval metamorphosis, which were likely inherited from the unmineralized tubular ancestor *Yuganotheca*.

However, lingulellotretids quickly faced extinction during the ~~early~~ Ordovician, illustrating a failed evolutionary experiment with a tubular body form in early brachiopods. The escalation of skeletal defence and increasing demands of filter feeding in benthic communities likely drove evolutionary modifications and associated ecological adjustments, leading to the development of the new and persistent tongue-shaped body of lingulide brachiopods during the Great Ordovician Biodiversification Event.

Introduction

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 ~~period~~, about half a billion years ago[1–5]. Many animal clades with disparate morphologies were progressively decimated or subsequently modified ~~by evolved groups~~ during their long evolutionary history [3]. Only the adaptive descendants with newly derived forms and functions ~~survive 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]. However, questions remain unanswered regarding when and how some animal groups underwent fundamental changes, with only a few surviving virtually unchanged while others became extinct eventually. The notion that natural selection acts on every species has been well developed by palaeontologists and biologists after the publication of Darwin's "On the Origin of Species" (Darwin 1859). Thus, every organism is a mixture of newly evolved traits and those retained from an ancient lineage [6]. Amidst this perpetual evolution, the Cambrian is generally considered a time of exceptional fecundity in animal body plans, marked by rapid decimation[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].

Lingulides are considered to be one of the oldest extant brachiopod lineages, and are traditionally recognized as representatives of extreme evolutionary conservatism, exhibiting little change in outline since the Cambrian [19,20]. Although originated in the early Cambrian, Lingulellotretidae is one of the most distinctive families in the Linguliformea characterized 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 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, 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 lingulellotretide phylogeny and the early evolution of tongue-shaped body plan in lingulides 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, parasitism, life strategy) relationships within benthic communities [24–27,12,28,29,14,22,30–33]. In this study, new and soft-bodied specimens of the lingulide *Lingulellotreta* are described from the famous Chengjiang Lagerstätte, South China, along with exquisitely three-dimensional preserved *Lingulellotreta* from the early Cambrian Small Shelly Fossils in South China and Kazakhstan. Based on newly obtained ontogenetic data and shell ultrastructures, two species, including *L. yuanshanensis* and *L. ergalievi*, 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, 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). The paired lophophore with ciliated tentacles and long slim pedicle (Fig. 1A, Supplementary Fig. 1B and 1F) are the most prominent soft tissues, as previously described in detail by Zhang *et al.* (2004*a*, *b*, 2005). 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 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* ~~has been confirmed by fossils form the type locality~~ [22,28]. After scrutinization of rare (less than 9% of the total sample size) but better-preserved specimens, ~~the critical feature of the digestive system~~ is uncovered beneath the prominent elongate pseudointerarea (Fig. 1A, Supplementary Fig. 1A-C). Remarkably, the recurved intestine extends into the ventral pseudointerarea area, and unusually crosses the hinge line ~~of both valves~~ (Fig. 1A). This suggests that the visceral area or coelomic 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 coelomic cavity, which houses the extra growth of visceral organs, is best demonstrated in the laterally compressed specimens (Supplementary Fig. 1E). This novel arrangement of soft organs within the biomineralized dorsal and ventral valves has not been observed in 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). Noteworthily, the ventral pseudointerarea is notably raised above the valve floor (Figs. 1E and 2E) and ~~leaveing~~ 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 coelomic cavity outlined by the internal boundary of pseudointerarea is quite prominent. In terms of soft tissues, only the imprints of muscles, *vascula lateralia* and pedicle nerve are preserved on the internal shell surface (Figs. 1D and 2C, Supplementary Figs. 3A-F, 6A-H and 9). ~~However,~~ shell ultrastructures, noting the earliest ontogenetic characters and biomineralized architectures, are exquisitely preserved (Figs. 1F, 1G 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, 11C and 11D), that is outlined by a pronounced halo and referred to as the metamorphic shell with an average size of 200 μm. Furthermore, the protegulum and brephic shell are developed inside the halo (Figs. 1C, 2B and 2F, Supplementary Figs. 4A-C, 7A-E, 11A and 11B), indicating 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 (Fig. 2G, Supplementary Fig. 10), demonstrating a multi-stacked sandwich model [37].

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 ventral pseudointerarea. Two different allometric patterns are recognised and compared in the following discussion. Measurements of the ventral and dorsal valves, which were made in most the complete specimens, are tabulated (Supplementary Tables 1 and 2).

Discussion

The heterochronic development of anatomic structures in lingulellotretids

In brachiopods, the lophophoral cavity (or mantle cavity) and visceral cavity (or coelomic cavity) are separated by the anterior body wall, which distinguishes the feeding and digestive spaces in the enclosed dorsal and ventral mantles [38]. The arrangement of these two spaces is vital to the physiology and survival of brachiopods. 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 [12,39,40]. Although compartments of visceral cavity are developed in some living craniiforms [38,41], no separation of the visceral cavity is observed in lingulides. ~~So, the visceral cavity is taken as a whole in the following discussion.~~

The visceral cavity of early Cambrian *L. yuanshanensis* only occupied ~~about 20%~~ of 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* [39,40]. A similarly small visceral cavity is also confirmed in the coeval lingulide *Eoglossa chengjiangensis* [12,26,42]. Thus, there appears to be an evolutionary tendency of size increase of visceral or the coelomic cavity in lingulides, with a consequent reduction in the lophophoral cavity. Furthermore, the relatively small space/volume of the coelomic 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 ~~of dorsal and ventral valves~~, has not been discovered in any other brachiopod groups [22,28]. The large ventral pseudointerarea in lingulellotretids (Fig. 1A, and 1B, Supplementary Figs. 1, 2 and 8) has long been considered a unique feature in brachiopods since the establishment of the Family Lingulellotretidae [21]. However, only *Lingulellotreta* has been preserved in both Burgess Shale-type preservation and three-dimensionally in limestone deposits that has allowed the reconstruction of the evolutionary pathway of anatomical structures in early Cambrian lingulellotretids.

During the development of shells, three growth stages with obvious anatomical changes are recognised. Firstly, the posterior marginal expansion and thickening of shells caused the mantle epithelia to push posteriorly, resulting in the evagination of mantle edge [43,44]. An obolid-like pseudointerarea was formed with the development of ventral propareas and pedicle groove. Secondly, with the continuous elevation of ventral pseudointerarea, the pedicle foramen and a small space was formed in the ventral posterior (Fig. 2E, Supplementary Figs. 8 and 9D-G). This stage is characterized by the development of short pseudointerarea sealing the obolid-like pedicle groove that is open between dorsal and ventral valves (Fig. 2D, Supplementary Figs. 9A-C), demonstrated by the juvenile specimen of *L. ergalievi* (Supplementary Fig. 8A). The coelomic cavity of *Lingulellotreta* was increased by the expansion of visceral cavity posteriorly in response to the adaptation of the newly formed cavity. Thirdly, with the further development of ventral pseudointerarea, a pouch-like cavity was formed to accommodate the expanding visceral organs, resulting in the development of a novel disposition of digestive systems (Figs. 1A and 2A)[26,32]. This stage is characterized by the increasing development of the elongate pseudointerarea that is not enclosed by dorsal and ventral valves, which is demonstrated by the mature specimen of *L. yuanshanensis* (Fig. 1A and 1B, Supplementary Fig. 2E-J). Such raised process of ventral pseudointerarea is also recognised in the development of another group, the acrotretide brachiopods [45–48], 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, resembling the early acrotretides (such as *Palaeotreta*, *Eohadrotreta* and *Linnarssonia*),

early Cambrian *Lingulellotreta* developed the pedicle foramen without a pedicle tube (Fig. 2E, 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 [49].

As discussed above, the continuous increase of the size of the coelomic cavity in lingulides is an evolutionary trajectory since the Cambrian. However, in contrast, the size of pseudointerarea has shown the opposite trajectory, with the length dramatically decreasing over time [12,49] This trend is perhaps most easily observed in living *Lingula*, where only a vestigial pseudointerarea is present (Fig. 4). With the exception of the coelomic cavity expanding posteriorly in lingulellotretids accommodated the growing digestive organs, other lingulide groups (eg. Obolidae and Lingulidae) appear to have adopted a different evolutionary path. With the reduction of the pseudointerarea, resulting in increasingly limited space beneath it (Fig. 4), the coelomic cavity in these groups adapted by moving anteriorly to create more space for the digestive organs in their diversified descendants[12,22,39,40]. Interestingly, regression analysis of key shell 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. Conversely, 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 *L. ergalievi* during Cambrian, Age 4, an evolutionary trend toward reducing the ventral pseudointerarea emerged, continuing in descendants such as *Mirilingula* and *Vaculina* from middle and late Cambrian [49]. The development of a low rhomboidal platform that is slightly raised anteriorly in the ventral valve and the development of an anterior projection that is extended to the mid-valve in dorsal valve indicates

that the coelomic cavity adapted by moving anteriorly. Thus, the reduction of the ventral pseudointerarea is a widely observed evolutionary trend in the lingulide lineage, while the novel posterior extension of the coelomic cavity enclosed by ventral pseudointerarea may have been a failed evolutionary experiment by early Cambrian lingulellotretids, limiting their geographic distribution to Kazakhstan and South China, and leading to their rapid extinction in the Early Ordovician [23].

From a relative perspective, one could speculate that the lophophoral cavity might increase significantly with the dramatic posterior extension of the coelomic cavity. However, the ratio of lophophoral cavity and valve length is largely offset by the extensive increase of ventral pseudointerarea. The lophophore occupies approximately 48% of ventral valve length in the Cambrian *L. yuanshanensis* (Supplementary Table 1), which is similar to the Jurassic *Lingularia* (46%) and recent *Lingula* (46%) [39,40]. It is noteworthy that the ontogeny of lophophore in *Lingulellotreta* is mirrored in the ontogeny of the lophophores of recent lingulides [12,50]. However, with the reduction of pseudointerarea, the relative position of 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 closed to the valve opening in living lingulides [50,51].

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 hard to deduce that the *Lingulellotreta* had a borrowing life, but instead anchored into soft substrate by a bulb-like end to suspend their light shell above the sediment-water interface [29,31,52]. 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 the long pedicle in its living mode. 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 [40,51,53]. This robust type of pedicle has also been described in early Cambrian calcareous-shelled brachiopods, where the distal end was attached to another animals' exoskeletons, demonstrating that pedicle morphology is closely related to the substrate choice [31,54,55]. 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 [12,21,27,40]. This is further supported by the distinctly unequal size of ventral and dorsal valves, and the mismatch of elongate ventral pseudointerarea and short dorsal pseudointerarea (Figs. 1A, 1B, 1D, 2A and 2C). 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 details by [12,22] and [18].

The evolution of biomineralized shells

The pitted micro-ornamentation on the surface of primary layer of metamorphic shells has been widely reported from the superfamilies Acrotretoidea and Linguloidea [43,56] and to a less extent in discinoids [57] and acrotheloids with some variations [56]. The preservation of such pitting structures in *L. yuanshanensis* and *L. ergalievi* confirms the similar morphology and micro-size in the Family Lingulellotretidae for the first time (Fig. 1F, Supplementary Figs. 4D-F, 11B and 11C), and further supports the homology of this pitting ornamentation in Lingulata evolved from early Cambrian [36,43,58]. The mode of formation of these pitted 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 [58]. Based on the restricted distribution of regular pits on metamorphic shell (larval shell) [36], that gradually fades towards the pronounced halo, Lüter [59] argued that the hemispherical pits might be originally filled with rigid tablet-like structures by analogy to Silurian *Opatrilkiella* [60]. These tablets may have been used to protect against ultraviolet radiation penetrating surface waters during the Early Palaeozoic [59]. However, recent lingulides possess a smooth larval shell without pitting structures, with only the living *Discinisca* retaining the pitted structures, an attributed to the development of siliceous tablets [59,61]. The ubiquitous phenomenon of pitting structures preserved on almost all early Cambrian linguliform brachiopods [62] may suggest that the living environment of brachiopod larvae has underwent significant changes since the Early Palaeozoic.

Metamorphic shells of *Lingulellotreta* on both ventral and dorsal valves, characterised by the development of several pairs of fine folds on the protegulum margin (Fig. 2F, Supplementary Figs. 4B-D, 11B and 11C), show great similarity to ~~that~~ of many other early Palaeozoic brachiopods with the ~~'paterinate' type~~ larva that is first discovered on Cambrian paterinates [36,63,64]. 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 ~~stem group brachiopods with subsequent heterochronic changes~~ [36,65,66]. In contrast, living lingulide larvae do not metamorphose, rather they grow by direct development [67–69], demonstrating a dramatic evolutionary modification involving brachiopod larva since the Cambrian. Key points about when such modification happens in different groups, however, need further study of brachiopod ontogeny in the future.

Cusack *et al.* [58] reviewed the shell structures of Cambrian to Recent lingulide brachiopods and concluded that lingulide shells had undergone significant transformations since the early Cambrian. Among these transformations, the complex columnar shells, long been dominantly ~~discovered~~ in acrotretides brachiopods, were actually ~~preserved~~ in early Cambrian ~~stem groups~~ [70,71] and ~~Eoobolidae~~ brachiopods [37,72] prompting more focused studies on shell structures. Holmer et al. described one specimen of *Lingulellotreta* with ~~a~~ columnar shell from the early Cambrian in Kazakhstan [73], however due to ~~the lack of well-preserved specimens,~~ no detailed description was provided,. The columnar shell architecture built with the stacked sandwich model [37] demonstrates an evolutionary transition from the simple ~~type~~ in *L. yuanshanensis* to ~~complex type~~ in *L. ergalievi* (Figs. 1G and 2G, Supplementary Figs. 3I-K, 6J-L and 10). In contrast to another ancient baculate shell structure that conserved in living representatives [58], comparative study of columnar shell is impractical, as such ancient shell structure is completely lost. 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 [12,33,74]. 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 long-lasting and evolving lingulide brachiopods

With the exquisitely preserved fossil material ~~combined from soft-tissue and three-dimensional phosphatic preservations~~, it is important to recognize the dramatic modifications of anatomical structures, larval behaviour and shell architectures between Cambrian and living lingulides, which are masked by the archaic 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 [75].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 they have 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 [19,36,62,76–78]. Their small body size, relatively light shell with columnar architecture, expanded coelomic 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 [29,55,74]. These lingulides brachiopods were commonly preserved as shell beds or shell concentrations as the result of a mass mortality event from the Konservat-Lagerstätten (Supplementary Fig. 1D) [25,30,33], and become an important component of the Cambrian and Palaeozoic Evolutionary faunas [19,79]. In contrast, their living representatives are larger with a body size measured in centimeters, and incorporate all the evolutionary transformations (including anatomical and skeletal features) that have adapted them to an infaunal lifestyle. These anatomical modifications and

associated ecological adjustments likely shaped the new tongue-shaped body of lingulide brachiopods during the Great Ordovician Biodiversification Event, a form that has persisted in living representatives. Additionally, with a larval that directly develops, they have a limited distribution and relatively low diversity[36,69,77,80].

As the Cambrian is considered to be special fecundity in animal forms [11,81], the elongate ~~biomineralized~~ shells ~~with the expansion of coelomic cavity posteriorly~~, in *Lingulellotreta* represent a novel body plan that is likely derived from stem group brachiopods such as soft-bodied *Yuganotheca* [22,52]. This may indicate a tubular origin of brachiopods from unbiomineralizd ancestors ~~by the evolution of biomineralized shells that were displayed by two valves located on their dorsal and ventral sides~~, such as the stem group *Micrina* [82]. The tubular body of *Lingulellotreta* also evokes the "soft shelled" *Lingulosacculus* from early Cambrian Laurentia [83], though its phylogenetic relationship with stem group brachiopods remains unresolved pending further study[22,84]. With the rise of macroscopic defence and high demanding of filter feeding in benthic environments [1,10], the unique Lingulellotretidae is decimated and replaced by modified lingulides (e.g. Obolidae and Pseudolingulidae) with shorter pseudointerareas by the early Ordovician. Due to the different evolutionary rates of various morphological parts, living lingulides are a final mixture of specializations combining both ancient and advanced characters, which have been fixed accumulatively by natural selection over the past half-billion years. Mosaic evolution probably played an important role in the disparity and diversity of brachiopods during the long evolutionary history of brachiopods, especially forging the new and basic body plans in the crucible of the Cambrian Explosion [10,16,75]. Thus, lingulide brachiopods are vivid examples of balancing the evolutionary capacitance and developmental constraints, shaping the organisms with novel modifications and prolonged stasis in a long co-adaptive process.

Methods

All the soft-bodied specimens of *Lingulellotreta yuanshanensis* were from the Chengjiang Lagerstätte. They are mostly dorsoventrally compressed and rarely laterally compressed on the surface of event-deposited claystone beds, demonstrating the typical Burgess Shale-type preservation [85]. Ninety 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 [25] and [86]. 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 [12,22,26–28,31,87].

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. All the specimens are preserved as three-dimensional shells with high fidelity, demonstrating a unique phosphatization window for the preservation of early Cambrian brachiopods [88,89]. 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 [90,91]. Twenty-two ventral and 18 dorsal disarticulated valves of *L. yuanshanensis*, and 34 ventral and 5 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, 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.

Data availability

Specimens studied here are deposited in the Early Life Institute, Northwest University, Xi'an, China (prefixed ELI), and Uppsala University, Sweden (prefixed IGCA), respectively.

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615 **Author contributions**.

616 F.Y.C. and Z.F.Z. conceived the study, Z.F.Z. and Z.L.Z. processed the photograph data. F.Y.C.,
617 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
618 manuscript, to which Z.F.Z., L.E.H., G.X.L., T.P.T. and Z.L.Z. contributed. All authors gave final
619 approval for publication and agreed to be held accountable for the work performed therein.

620

621 **Competing interests.**

622 The authors declare no competing interests.

623

624 **Additional information**

625 The supplementary figures and tables supporting this article have been uploaded as the electronic
626 supplementary material (Supplementary Figs. 1-14, Tables 1 and 2) available at XXX.

627

628 **Correspondence** and requests for materials should be addressed to Feiyang Chen

[Figure captions]

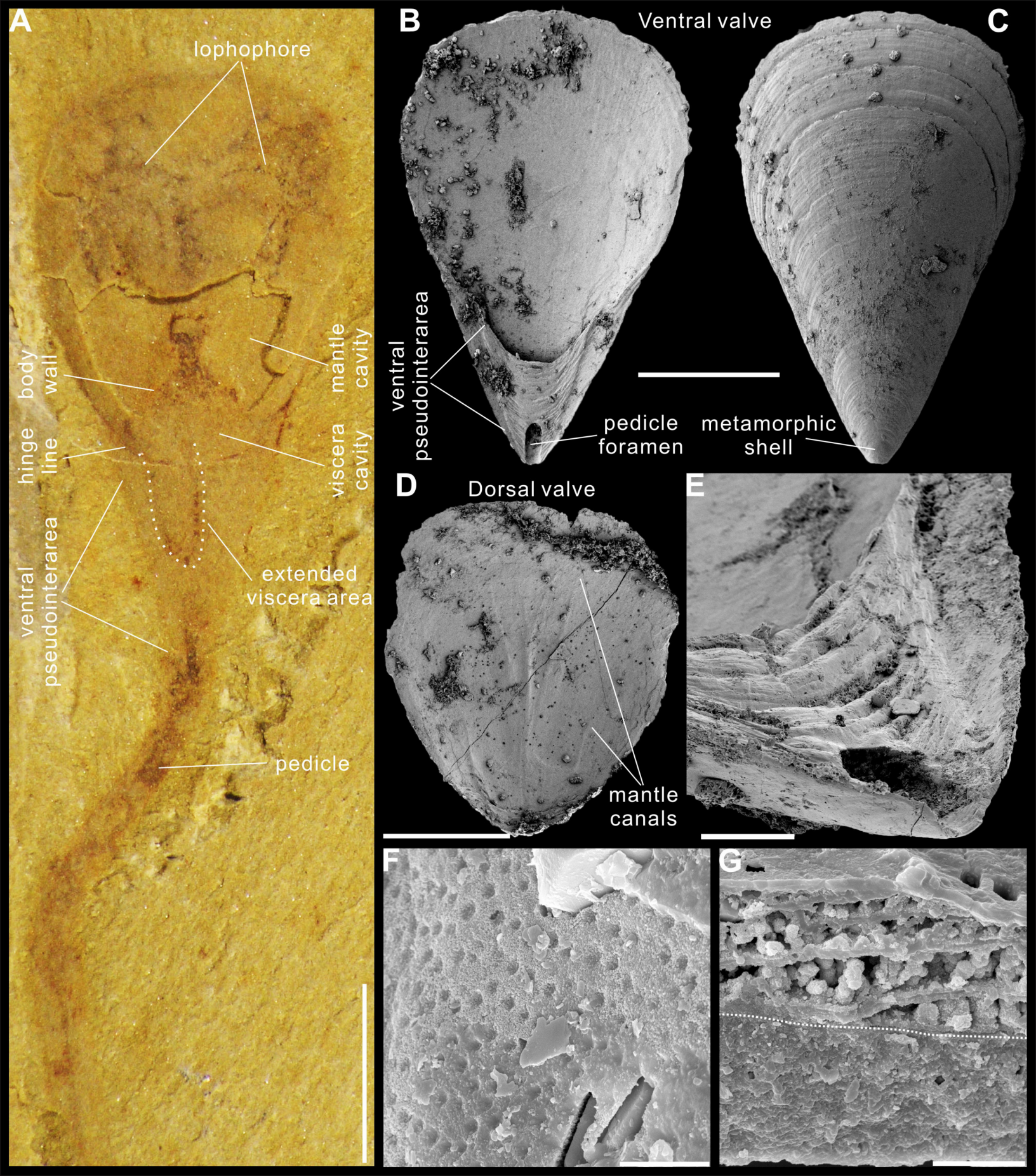
Fig. 1 | Soft-bodied and three dimensional preserved *Lingulellotreta yuanshanensis* from the Cambrian Stage 3 Yuanshan Formation ~~(Chengjing Lagerstätte)~~ in Yunnan Province (A) and from the Cambrian Series 2 Shuijingtuo Formation ~~(Small Shelly Fossils)~~ in Shaanxi Province (B-G), South China, respectively. **A** Well-preserved specimen, note key anatomical features, including the paired lophophore with ciliated tentacles, body wall separating the mantle cavity and viscera cavity, long slim pedicle, and curved gut extended posteriorly beyond the hinge line (by dotted line), ELI-JS 0357A. **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 viscera cavity, ELI-XYB S5-4 CH03. **F** Enlarged micro-size pitting structures on metamorphic shell, ELI-XYB O02. **G** Shell architecture, ~~note the boundary~~ laminated primary layer and columnar secondary layer (dotted line), ELI-XYB O19. Scale bars, (**A**) 2 mm; (**B**-**D**) 1 mm; (**E**) 100 μm; (**F**) 5 μm; (**G**) 20 μm.

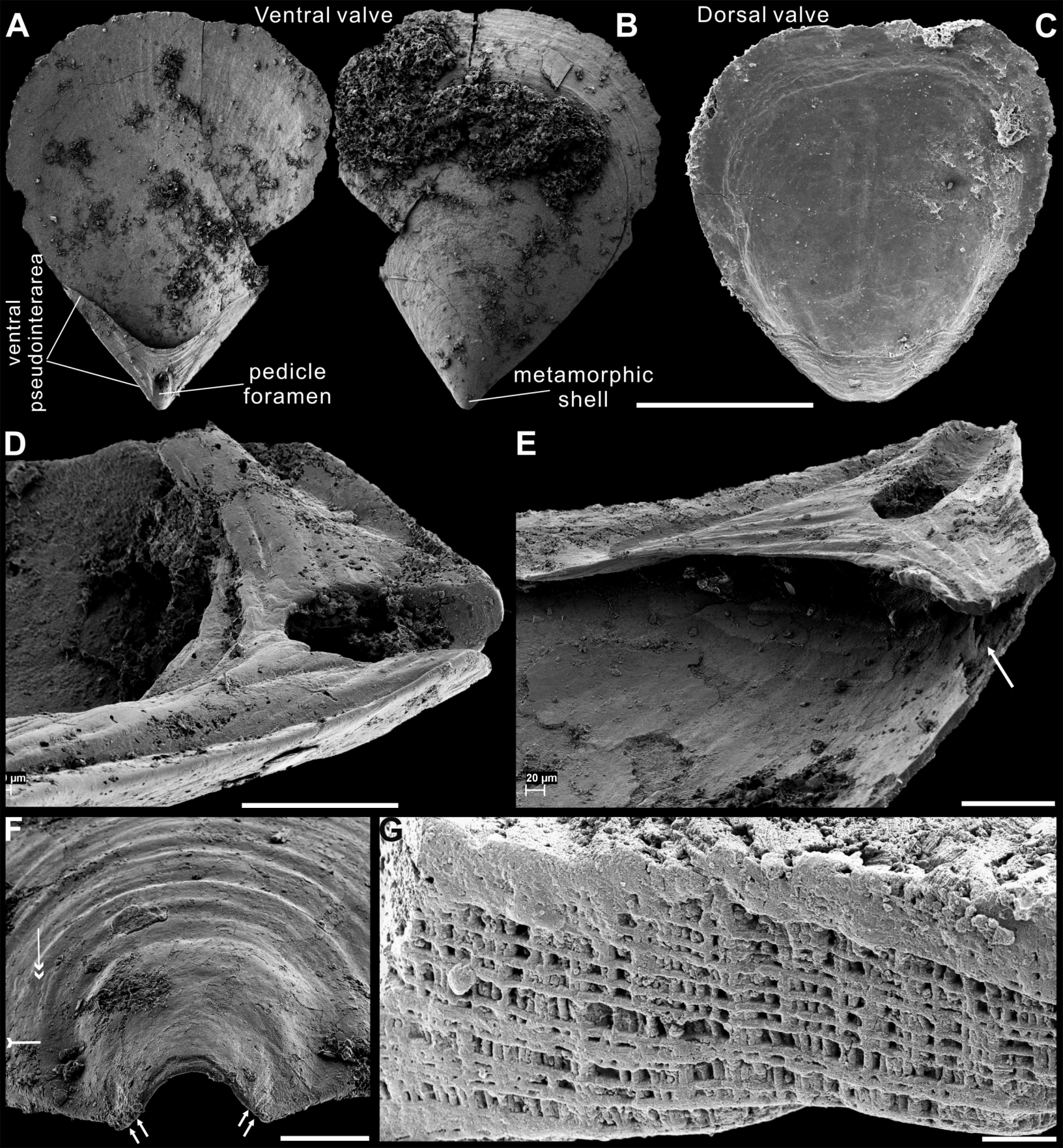
Fig. 2 | Three-dimensionally preserved *Lingulellotreta ergalievi* from the Cambrian Series 2 Shuijingtuo Formation ~~(Small Shelly Fossils)~~ in Hubei and Shaanxi provinces, South China. **A** Well-preserved ventral valve, note large pseudointerarea and elongate pedicle foramen, ELI-XYB S5-4 CI01. **B** External view of (**A**), noting pronounced metamorphic shell at posterior end. **C** Dorsal valve interior, ELI-XYB O25. **D** Lateral view of the pouch-like extension of viscera cavity, ELI-XYB 13 CI04. **E** Anterior view of the raised ventral pseudointerarea, beneath which forming a small pouch-like cavity, no pedicle tube developed, ELI-XYB 13 CI07. **F** Ventral metamorphic shell, show paired fine folds on the

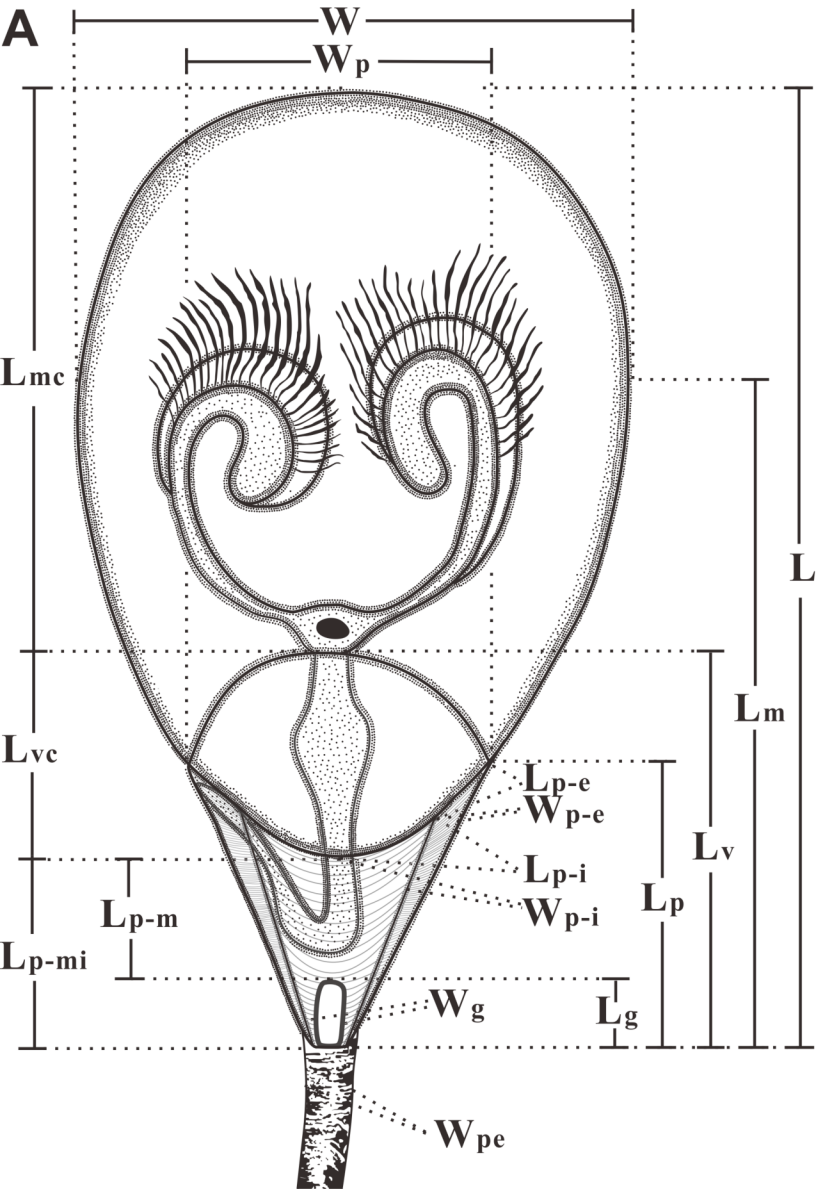
protegulum margin (arrows), pronounced halo (tailed arrow) and drip structures on post-metamorphic shell (double-headed arrow), ELI-XYB 13 CI05. **G** Development of tacked columnar architecture of secondary layer, ELI-AJH 8-2-3 CI11. Scale bars, (**A**-**C**) 1 mm; (**D**, **E**) 100 μm; (**F**) 50 μm; (**G**) 20 μm.

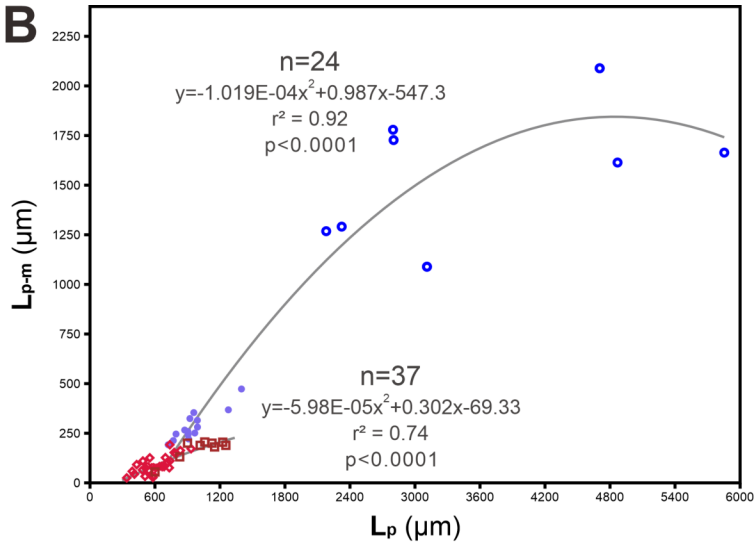
Fig 3 | Interpretative drawings of *Lingulellotreta yuanshanensis*, and bivariate plots of ventral valve of early Cambrian *Lingulellotreta yuanshanensis* (red colour) and *Lingulellotreta ergalievi* (blue colour). **A** key anatomical features shown in Fig. 1, noting the curved gut extended posteriorly beyond the hinge line and beneath the raised pseudointerarea, which forms a pouch-like cavity. Abbreviations: 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 proparea; pe, pedicle; p-o, outer part of proparea; v, viscera area; vc, viscera 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 ($L_g/L_{p\text{-}m} = 1$).

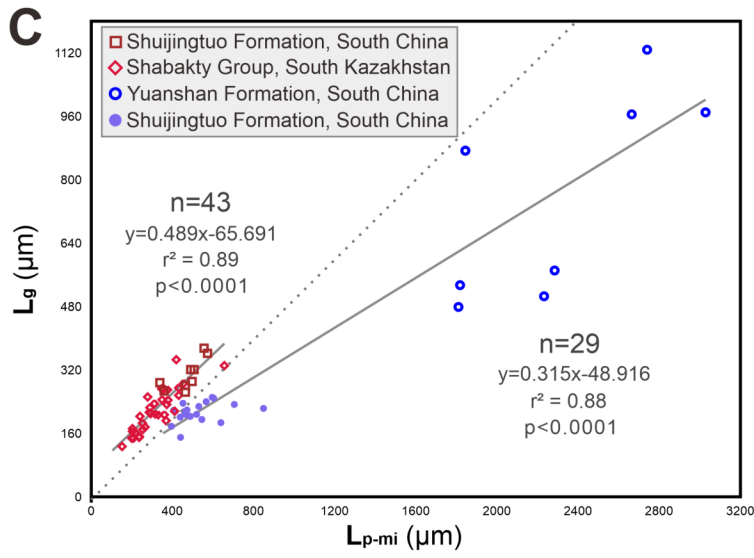
Fig. 4| Branching structures of the evolution of brachiopods, demonstrate the relationships between the stem group, extinct ancestral and living lineages. Interpretative drawings of *Yuganotheca elegans* (Cambrian Age 3 Yuanshan Formation) is modified from[52], *L. yuanshanensis* (Cambrian Age 3 Yuanshan Formation) is a sketch of figure 1(A), *L. ergalievi* (Cambrian, Age 4 Shuijingtuo Formation) is a sketch of Supplementary Fig. 8C, *P. yunnanensis* from the (Cambrian, Age 4 Wulongqing Formation) is modified from [92], and Living *L. anatine* is modified from [93].

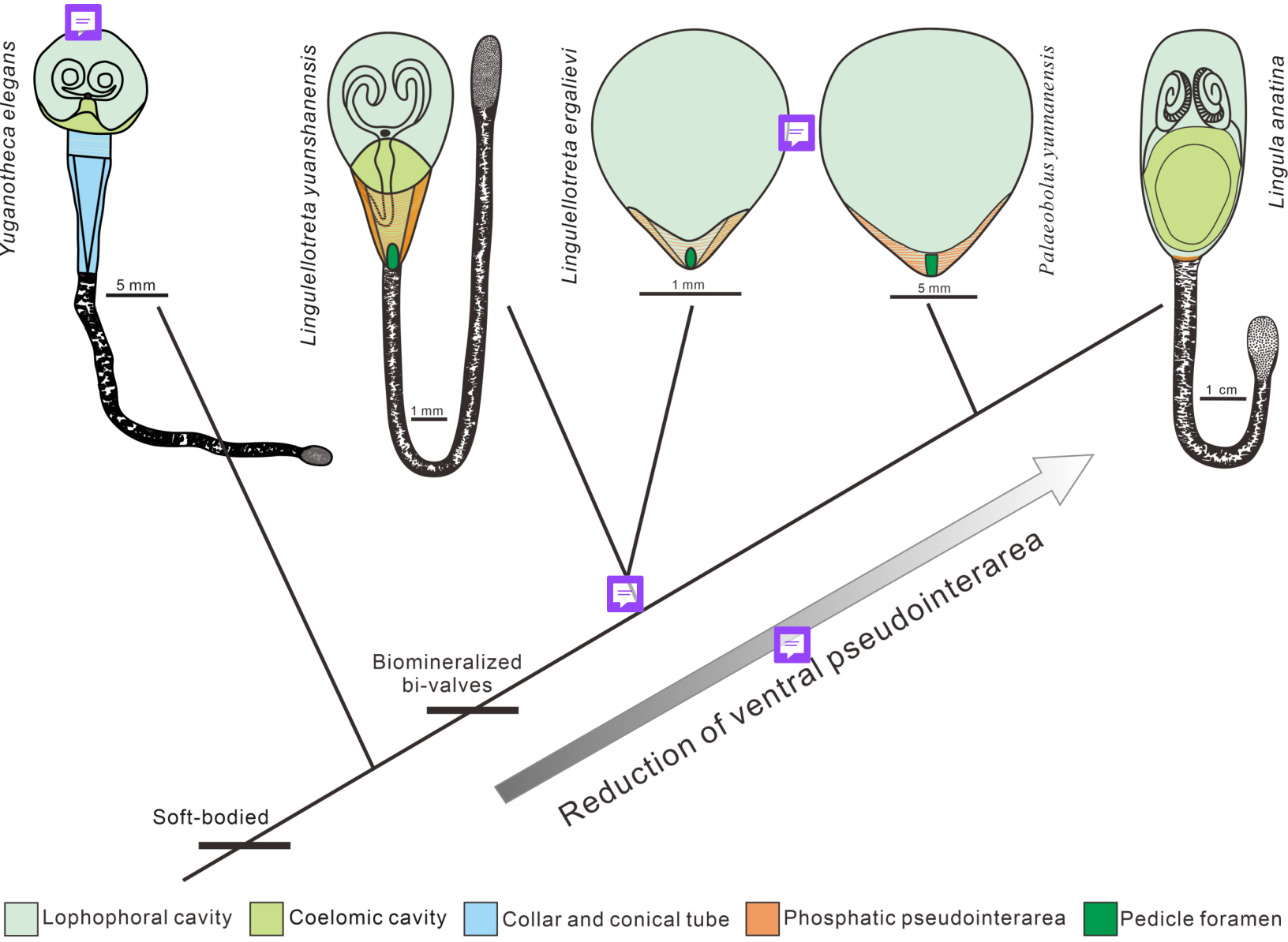

A
lophophore
body wall
mantle cavity
hinge line
viscera cavity
ventral pseudointerarea
extended viscera area
pedicle
B
Ventral valve
C
ventral pseudointerarea
pedicle foramen
metamorphic shell
D
Dorsal valve
E
mantle canals
F
G


A
Ventral valve
B
Dorsal valve
C
ventral pseudointerarea
pedicle foramen
metamorphic shell
D
E
20 µm
F
G


A
W
Wp
Lmc
Lvc
Lp-m
Lp-mi
Lp-e
Wp-e
Lp-i
Wp-i
Wg
Lg
Wpe
Lp
Lv
Lm
L


B
n=24
y=-1.019E-04x²+0.987x-547.3
r² = 0.92
p<0.0001
n=37
y=-5.98E-05x²+0.302x-69.33
r² = 0.74
p<0.0001
Lp-m (μm)
Lp (μm)
0
250
500
750
1000
1250
1500
1750
2000
2250
600
1200
1800
2400
3000
3600
4200
4800
5400
6000


C
Shuijingtuo Formation, South China
Shabakty Group, South Kazakhstan
Yuanshan Formation, South China
Shuijingtuo Formation, South China
n=43
y=0.489x-65.691
r² = 0.89
p<0.0001
n=29
y=0.315x-48.916
r² = 0.88
p<0.0001
Lg (μm)
Lp-mi (μm)
0
160
320
480
640
800
960
1120
400
800
1200
1600
2000
2400
2800
3200


Yuganotheca elegans
5 mm
Lingulellotreta yuanshanensis
1 mm
Lingulellotreta ergalievi
1 mm
Palaeobolus yunnanensis
5 mm
Lingula anatina
1 cm
Biomineralized bi-valves
Soft-bodied
Reduction of ventral pseudointerarea
Lophophoral cavity
Coelomic cavity
Collar and conical tube
Phosphatic pseudointerarea
Pedicle foramen