Late Ordovician lingulid brachiopods from the Pingliang Formation (Shaanxi Province, North China): Morphological and ecological implications

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ABSTRACT
Brachiopods first appeared in the early Cambrian and persist till present. They are one of the main lineages of marine invertebrates that diversified throughout the Paleozoic and reached their maximum diversity of high-rank taxonomy during the Ordovician. During this time interval, brachiopods were mainly dominated by the articulated Orthida and Strophomenida, which represent major components of the Paleozoic Evolutionary Fauna; however, the inarticulated lingulid brachiopods (Order Lingulida) were comparatively less abundant and received less attention during this time period. Here, we report a new record of the lingulid brachiopod *Anomaloglossa porca* from the Upper Ordovician (Sandbian) Pingliang Formation of the Xilinggou Section, Shaanxi Province, North China. Collected specimens are preserved as calcium phosphatic shells with highly mineralization which preserve detailed morphology and shell ornamentation of both ventral and dorsal valves. The new occurrence of *A. porca* extends its paleogeographic distribution from Gondwana and Tarim to North China Platform. Moreover, comprehensive geometric morphometric analysis of *A. porca* is performed and the results indicate that both the shell shape and pseudointerarea are very close to the recent infaunal lingulids. If interpreted correctly, the fossils represent the first example of infaunal lifestyles achieved by Ordovician lingulids from North China, exhibiting the ecological complexities of the Late Ordovician benthos composed of epibenthos and infaunas as well.

1. Introduction

Brachiopods are one of the most dominant clades in Paleozoic marine communities, and span the entirety of the Phanerzoic, albeit with greatly reduced diversity following the Permian-Triassic extinction (Holmer and Popov, 2000; Carlson, 2016; Harper et al., 2017). Whilst the Phylum Brachiopoda persists throughout the entire Phanerzoic, only a single Order, Lingulida, spans the entire lifespan of the clade (Carlson, 2016). However, because of their poor extant generic and genetic diversity and lack of modern forms, lingulid brachiopods have long been considered an example of a “living fossil” since Darwin’s “Origins of species” in 1859. The Lingulida first appeared in the lower Cambrian Stage 3 and diversified rapidly during the early Paleozoic (Holmer, 2001; Harper et al., 2017; Zhang et al., 2008, 2020a; Zhang et al., 2021). When the Lingulida reached its maximum diversity, consisting of 36 genera during the Ordovician, the articulated Orthida and Strophomenida rapidly reached their maximum diversity and their generic diversity was doubled as compared to the lingulids; they rapidly became the main components of the Paleozoic Evolutionary Fauna, and thus lingulid brachiopods have received comparatively less attention during this time interval (Sepkoski, 1981; Zhan and Harper, 2006; Carlson, 2016; Harper et al., 2017; Liang et al., 2022).

The relationship between generic and taxonomic diversity in the fossil record has received far more study than morphological and ecological disparity (Erwin, 2007; Cole and Hopkins, 2021). However, there is a general expectation that overall morphological form will correspond to the number of available ecological niches, serving as an effective proxy for understanding the functional ecology of a taxon...
(Foote, 1993; Anderson, 2009; Anderson et al., 2011; Grossnickle and Newham, 2016; Cole and Hopkins, 2021). Recent macroevolutionary research of the “living fossil” lingulid brachiopods presents the morphological diversity of this group throughout the whole entity of Phanerozoic and indicates that the maximum morphospace occupation of this clade is reached during the Ordovician (Liang et al., 2023). Accordingly, it remains important to get a better understanding of how this change happened during the Ordovician period and if morphological and ecological information can be revealed from some specific genera or species.

Here, we report a Late Ordovician (Sandbian) brachiopod Anomalaloglossa porca Percival, 1978 from the Pingliang Formation at the Xilinggou Section, Shaanxi Province, North China. Specimens of A. porca are very abundant with the collected sample number exceed more than 700 in total and most of specimens have highly mineralized shells, with some well-preserved specimens illustrated detailed internal anatomy. In addition to A. porca, the fauna from the Pingliang Formation also yielded numerous graptolites and crinoids. The new occurrence of A. porca has extended the paleogeographic distribution from Gondwana and Tarim to North China Platform. Moreover, a comprehensive geometric morphometric analysis of A. porca was conducted using the whole Phanerozoic linguloid brachiopods dataset, and the results provide important clues for the morphological and ecological information of this clade.

2. Geological setting and stratigraphy

The Xilinggou Section (34°42′30.24″N, 108°38′0.13″E) is located in the southern margin of the Ordos Basin, southwestern of North China. This section is cropped out near Cuihuangzhuang village, Jingyang County, Shaanxi Province (Fig. 1). The lithostratigraphic units in the studied section include the Majiagou and Pingliang formations in ascending order and span a stratigraphic interval from the Darriwilian to Sandbian (Fig. 2). The Majiagou Formation mainly consists of light-grayish medium to thick bedded limestones and bears abundant benthic fossils and associated trace fossils (Fu et al., 1993; Niu et al., 2015; Meng et al., 2019), while the lowest boundary is not observed in the studied section. The Pingliang Formation is characterized by thin-

Fig. 1. A sketch-map showing locality of the studied section and facies distribution in the southern Ordos Basin, North China. A, location of the studied area in relative to North China Platform, marked with red rectangle (modified from Jing et al., 2019); B, a sketch map showing facies distribution in the southern Ordos Basin during Late Ordovician; red-star marking the studied Xilinggou Section (modified after Chen et al., 2022). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
bedded micritic limestones, with many interbeds of chert-banded limestones, locally cherty nodules and yellowish silt-mudstones which yielded abundant macro shelly fossils as described and discussed in this paper (Figs. 3-7). Regional stratigraphic correlation suggests that the Pingliang Formation is equivalent to the Jinsushan Formation at the eastern part of the southern margin of Ordos Basin (Dai et al., 2019; Chen et al., 2022; Sun et al., 2023; Liang et al., 2023). Several layers of K-bentonites were observed in the Pingliang Formation, characterized by tuff layers that are easily recognizable in outcrop (Fig. 2); recent Zircon U-Pb dating suggests that the Pingliang Formation was deposited...
Fig. 3. Ventral valves of lingulid brachiopod *Anomaloglossa porca* from the Late Ordovician Pingliang Formation of the Xilinggou Section, Southern Shaanxi. A, ventral exterior, ELI-ZL-206. B-C, ventral exterior view showing the exfoliation of mineralized shell, ELI-ZL-391. D, ventral interior, ELI-ZL-464. E-F, ventral exterior showing with the pseudointerarea preserved and concentric growth lines. G, ventral exterior, ELI-ZL-169. H-I, ventral interior with the metamorphic shell preserved and mineralized, ELI-ZL-042. Scale bar: 1 mm.
Fig. 4. Dorsal valves of lingulid brachiopod *Anomaloglossa porca* from the Late Ordovician Pingliang Formation of the Xilinggou Section, Southern Shaanxi. A-C, dorsal interior with the posterior part preserved as mineralized shell and anterior part preserved as imprints, ELI-ZL-478, ELI-ZL-479, ELI-ZL-325. D-E, dorsal exterior view showing the exfoliation of mineralized shell and the preservation of the metamorphic shell, ELI-ZL-163. F-I, ventral exterior, ELI-ZL-148, ELI-ZL-460, ELI-ZL-368, ELI-ZL-023. E-F, ventral exterior showing concentric growth lines. Scale bar: 1 mm.
during the Sandbian-Katian interval of the Late Ordovician (Wang et al., 2015; Chen et al., 2022) (Fig. 2).

3. Material and methods

In total 787 specimens of Anomaloglossa porca were collected from the Pingliang Formation of the Xilinggou Section, Shaanxi Province, North China, together with abundant graptolites and crinoids awaiting further investigation (Figs. 3-9). Fossils were examined under a Zeiss Stemi 305 microscope and photographed with the Zeiss Smart Zoom 5 Stereo-micrographic system and Cannon camera 5D Mark IV mounted on a photographic system. Specimens were photographed and coated with ammonium chloride ($\text{NH}_4\text{Cl}$) to reduce reflecting light when photographing. Some well-preserved specimens were tested by Bruker M4 Tornado table-top energy-dispersive micro X-ray fluorescence ($\mu$-XRF) to get a characterization of the elemental abundances in samples from the fluorescence spectrum.

Morphology has been assumed to be a proxy for ecology, and evaluating morphological variation can provide valuable insights to reveal ecological information for groups with otherwise poorly known life habits (Stanley, 1970; Cole and Hopkins, 2021; Novack-Gottshall et al., 2022; Liang et al., 2023). To quantitatively evaluate the morphological information of Anomaloglossa porca in order to understand its lifestyles, a total number of 346 Linguloid specimens were collected for geomorphometric analysis to reveal if there remains some resemblance between the Late Ordovician Anomaloglossa porca and recent infaunal ones. The collected data was mainly sourced from the Treatise On Invertebrate Paleontology, Part H Brachiopoda and the published literature (Table S1 with references appended), together with a small number of unpublished specimens deposited in the ELI-NWU collections (Table S1). The pseudointerarea is closely related to the pedicle, and a small pseudointerarea suggests a less functioning pedicle which is more suitable for an infaunal lifestyle (Liang et al., 2023). From this dataset, 65 specimens where a clear pseudointerarea could be distinguished were selected for further morphometric analysis (Fig. 12). We used genera instead of species as related species commonly resemble each other in terms of functional ecology. Morphological data for most genera were collected for 5 ventral valves. For genera with poor records, only 1–4 specimens were collected (Table S1). As for Anomaloglossa porca in this research, 10 ventral valves with complete shell outline were selected to evaluate their shell shape and resemblance to recent infaunal ones.

Landmark-based geometric morphometrics were used to collect shell shape data, employing one homologous landmark defined by the maximum curvature at the posterior position, and 28 equidistant semi-landmarks along the ventral borders (Figs. 10-12). Both landmarks and semi-landmarks were generated with the program TpsDig v. 2.31 (Rohlf, 2015). The definition of landmarks and semi-landmarks for analysis of the pseudointerarea followed the method of Zhang et al., (2020a) and Liang et al. (2023). Landmarks were then appended to curves, and the sliding direction of the semi-landmarks was determined using TpsUtil v. 1.78 (Rohlf, 2015). A generalized Procrustes analysis (GPA) with a minimized bending algorithm was used to remove the effects of size,
location, and orientation of the specimen images. The shape of each specimen was then plotted using the landmark configuration from the GPA. The morphometric data matrix was then analyzed using TpsRelw v. 1.70 (Rohlf, 2015) and PAST v3.25 (Hammer et al., 2001) to explore potential changes in morphospace and to visualize shell shape and pseudointerarea using thin-plate splines. A principal component analysis (PCA) was carried out on the aligned, post-GPA landmarks to show the morphological variation between time bins by PAST v3.25 (Hammer et al., 2001).

4. Systematic paleontology

Phylum  Brachiopoda  Duméril, 1806.
Subphylum  Linguliformea  Williams et al., 1997.
Class  Lingulata  Gorjansky and Popov, 1985.
Order  Lingulida  Waagen, 1885.
Superfamily  Linguloidea  Menke, 1828.
Family  Obolidae  King, 1846.

Etymology. Generic name in reference to inferred unusual shape and life habit (Greek anomalos: abnormal, unusual; Greek glossa: tongue).
Fig. 7. Main faunal components from the Late Ordovician Pingliang Formation of the Xilinggou Section, Southern Shaanxi. A-B, graptolite *Climacograptus bicornis* and its characterized straight needle-like basal spines. ELI-ZL-003. C, undetermined crinoid. ELI-ZL-002. D, co-occurrence of brachiopod and graptolite. E-I, micro X-ray fluorescence maps showing elemental abundances of Mg = manganese, Al = aluminum, P = phosphorus, S = sulphur, K = potassium, Ca = calcium, and Fe = iron. ELI-ZL-340. Scale bar: 1 mm.
Type species: *Anomaloglossa porca* Percival, 1978; the Gunningbland Formation (middle Katian) of Gunningbland and the Malonguli Formation (middle Katian) of Copper Mine Creek, Cliefden Caves, New South Wales, Australia.

**Diagnosis.** Large compressed ovoid obolid ornamented by concentric growth lines; ventral pedicle groove bisected by median septum extending anteriorly to divide umbonal muscle scar; dorsal pseudointerarea rudimentary and undifferentiated, dorsal umbonal scar undivided; visceral region (in both valves) coarsely and irregularly pitted, floor of mantle cavity finely and closely pitted.

*Anomaloglossa porca* Percival, 1978
Figs. 3-6
1978 *Anomaloglossa porca* Percival, p. 125, Figs. 3, 4, 5A
1982 *Anomaloglossa porca* Webby and Packham, p. 311 (Webby and Packham, 1982)

**Materials.** 787 specimens; among them, 623 complete specimens were selected to do shell size measurements. 301 specimens were observed as ventral valves, and the rest 322 specimens were dorsal valves.

**Diagnosis.** As for genus.

**Occurrence.** Pingliang Formation, Late Ordovician, Shaanxi Province, North China.

**Description.** Shell ventribiconvex, oval to elongate with sub-parallel shape. 100 μm rounded pits unevenly distributed on the posterior part of the valve. The whole valve presents finely concentric growth lines and drapes. All valves preserved inarticulated with conjunct valves unobserved.

Ventral valve large, with length in 8.8 mm and width in 5.49 mm on

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**Fig. 8.** Interpretative drawings and reconstruction of the lingulid brachiopod *Anomaloglossa porca* from the Late Ordovician Pingliang Formation of the Xilinggou Section, Southern Shaanxi. Abbreviations: CGL = Concentric Growth Lines; DP = Dorsal pseudointerarea; MG = Median Groove; PG = Pedicle Groove; VP = Ventral pseudointerarea.

**Fig. 9.** Global distribution of known Late Ordovician *Anomaloglossa* localities displayed on a paleogeographic reconstruction model redrawn from Cocks and Torsvik (2020). Abbreviations: SC, South China; T, Tarim; W Au, Western Australia.

2016 *Anomaloglossa porca* Percival et al., p. 450, Fig. 2 (Percival et al., 2016)
average ($N = 301$, $SD = 2.63$ for length, and $SD = 1.60$ for width); the maximum value for length and width is 15.69 mm and 10.26 mm; the minimum value for length and width is 3.7 mm and 2.18 mm (Fig. 3). The valve is convex, with elongated shell shape and sub-parallel outlines. Pseudointerarea well developed and triangular, around 48 % longer than wide, occupying 20 % and 41 % of total valves length and width (Figs. 5A-C, 8). Flexure lines weakly defined. Elongate oval pedicle foramen placed at posterior part of the pseudointerarea with apical angle of 31° on average. Foramen up to 1.03 mm long and 0.43 mm wide and extending to about 76 % of the length of pseudointerarea in adults. Pedicle foramen usually preserved as a mud-infilled ridge or groove and continuing as internal pedicle tube (Figs. 5A-C, 8). Densely spaced concentric growth lines developed on the whole valve (Fig. 3).

Dorsal valve large, with length in 8.37 mm and width in 5.66 mm on average ($N = 322$, $SD = 2.23$ for length, and $SD = 1.49$ for width); the maximum value for length is 17.09 mm and 14.81 mm for width; and the minimum value for length and width is 3.98 mm and 2.22 mm (Fig. 4). The valve is convex, with elongated shell shape and sub-parallel outlines. Pseudointerarea small and weakly defined compared to the ventral valve, occupying 5 % to the valve length and 39 % of the valve width (Figs. 5D-E, 8). Median groove sub-triangular, short, and about 31 % of the pseudointerarea width. Median septum vestigial, only developed in some well-preserved adult valve, extending anteriorly for 45 % of the valve length. Muscle Scars symmetrical and observed at the end of the median septum (Fig. 5F).

Some shell aggregation consists of both large and small individuals.
can be observed (Fig. 6A). Both ventral and dorsal valves are moderately thick and lustrous black in color with high contrast to the matrix with yellow to gray-green silt-mudstone. All valves preserved their calcium phosphatic hard shell, and notably enriched in chemical component by calcium and phosphorus, with high elemental contract to the matrix in elemental mapping results (Fig. 6).

**Remarks.** *Anomaloglossa* has been a monotypic since it was first named by Percival in 1978. It was known mainly from the Late Ordovician (Katian) strata in New South Wales, Australia (Percival, 1978), while Zhan et al. (2014) also recorded it from Tarim (Katian), but the latter record was kept under open nomenclature due to the lack of sufficient material, particularly ventral valves. Later Benedetto (2015) and Lavie (2018) discovered *Anomaloglossa* from the Precordillera Terrane (Cuyania) of Argentina at the Middle and Late Ordovician (Darriwilian and Sandbian) in eastern Gondwana, though the specific assignment was kept open.

*Anomaloglossa porca* from the Pingliang Formation is smaller in shell size compared to the Australian and Argentinian specimens. The latter can reach lengths of about 40 mm, which is significantly larger than the Tarim material, measuring approximately 4–6 mm in length. It is worth noting that the size measurement in Tarim may be biased due to the small sample size. The valves from these localities have similar outlines and all preserve well-defined concentric growth lines. Our material has the advantage of preserving the pseudointerarea and pedicle groove in many ventral valves. These features have not been found in materials from both the Tarim and Argentine localities, thus providing additional anatomical information for this taxon. *Anomaloglossa* (including both *Anomaloglossa porca* and *Anomaloglossa* sp.) was originally described from the Late Ordovician (Kantian), and later it was reported from the Middle and Late Ordovician (Darriwilian and Sandbian); our reports remain the second record of its occurrence in Sandbian. Additionally, our reports has expanded its paleogeographic distribution from Gondwana and Tarim to North China Platform.

### 5. Results and discussion

#### 5.1. Faunal composition, biostratigraphical determination and regional correlation

Apart from the abundant lingulid brachiopods, the fauna from the Late Ordovician Pingliang Formation also includes diverse graptolites and crinoids (Fig. 7). Well-preserved *Climacograptus bicornis* were collected from the studied section; they are furnished with an elongate virgellar spine with a slender parasicula, and two short, straight needle-like basal spines, arranged symmetrically and at right angles to the rhabdosome (Fig. 7A-B). The close co-occurrence of brachiopods and graptolites in the same sample makes the graptolites appear almost like pedicles (Fig. 7D). However, detailed examination of the theca structure reveals their true graptolite affinity. The preservation of graptolites differs from that of the calcium phosphatic mineralized brachiopods. Graptolites exhibit high concentrations of sulfur, iron, and manganese, indicating that they have undergone significant pyritization and
endured extensive weathering possibly during the late diagenesis (Fig. 7E). Crinoids are relatively less abundant and collected fossils need to be further investigated (Fig. 7C). In addition to inarticulated lingulid brachiopods observed in the studied section, articulated orthids with diversities for marine biota of the Late Ordovician were concentrated. Anomaloglossa

5.3. Morphological and ecological implications

Life strategies of lingulid brachiopods during the Paleozoic, especially the Cambrian and Ordovician period remains to be a hotly debated topic (Emig, 1992; Emig and Bitner, 2005; Holmer et al., 2018; Topper et al., 2018; Liang et al., 2020a, b; Zhang et al., 2008, 2020a, b); a comprehensive study indicated that the life mode of lingulids has remained remarkably constant at least since the early Paleozoic (Emig, 1997). Lingulid brachiopods exhibited an epi-benthic lifestyle when they first originated during the Cambrian (Zhang et al., 2005, 2008, 2009, 2020a, b; Harper et al., 2017). However, recent lingulids are infaunal, which raises the question of when they became infaunal. Recent research on the morphological and ecological analysis of lingulid brachiopods throughout the Phanerozoic indicates that the maximum morphospace occupation was achieved at the Early Ordovician, together with evidence of soft part preservation and trace fossils, suggesting the initial development of infaunal life strategies while epibenthic ones still exist during this period (Liang et al., 2023). Percival (1978) suggested that Anomaloglossa porca may have had an epi-benthic lifestyle primarily due to its large size. However, recent infaunal lingulid species, such as Lingula and Glottidia, also possess a large shell size, exceeding 40 mm, while still maintaining an infaunal lifestyle (Emig and Bitner, 2005). Additionally, some other giant lingulid species, like Lingula quebecensis, exhibit an epilithic or free-lying lifestyle (Bulman, 1964). These findings indicate that shell size may not be a reliable proxy for inferring the lifestyle of lingulid brachiopods. Considering the relatively “simple” lifestyle of brachiopods, shell shape has been and is herein considered to be directly related to the ecology of brachiopods and is thus reflective of their functional ecology (Harper and Moran, 1997; Topper et al., 2018). Thus, in this study we have quantitatively calculated the shell shape of the Late Ordovician Anomaloglossa porca in order to better understand its morphological and related ecological information in the context of the morphospace occupation of the Superfamily Linguloidae throughout the whole entity of the Phanerozoic (Figs. 9-11).

Results of PCA indicate that 98 % of the shell shape variance can be explained by the first two principal components (PC1 = 91.0 %, and PC2 = 6.4 %) (Figs. 10A-C, 11; Table S1). PC1 captures the overall shell shape, with higher values representing a rounded shell outline, whilst lower values correspond to a sub-rectangular shell shape, as demonstrated by the transformed thin-plate splines (TPS). Values for PC2 primarily reflect the relative convexity of the posterior margin; with lower values representing an acute posterior margin, and higher values corresponding to a more rounded posterior (Fig. 11). The convex hull of Anomaloglossa porca in this study falls within the overall convex hull of the Ordovician period and concentrate especially in the area of lower PC1 and higher PC2 value. This represents rather elongate shell with rounded posterior margin which is very close to the recent individuals owing an infaunal lifestyle (Fig. 11). Apart from the shell shape analysis, we also performed morphospace occupation analysis for pseudointerarea (Fig. 12). The pseudointerarea connects the mantle cavity to the posterior pedicle and makes up a sizeable amount of the total shell form, which may provide important clues about the life strategies of lingulid brachiopods (Holmer et al., 2018; Zhang et al., 2008, 2020a). PCA results indicate that 93.4 % of the variance can be explained by the first two principal components (PC1 = 74.4 %, and PC2 = 19.0 %) (Figs. 10D-F, 12; Table S2). Low PC1 and high PC2 values indicate the large pseudointerarea, while high PC1 and low PC2 values represent the relatively small and vestigial pseudointerarea as demonstrated by the transformed thin-plate splines (TPS). Similarly, the convex hull of A. porca in this study falls within the morphospace of the Ordovician forms and especially area of high PC1 and low PC2 values, which is close to the recent lingulids processing an infaunal lifestyle (Fig. 12).

Our geometric morphometric results demonstrate that the overall shell shape and pseudointerarea of the studied species A. porca sets well within in the morphospace of the Ordovician and particularly at the area represented by the elongate shell shape and reduced pseudointerarea.
interested or personal relationships that could have appeared to influence
Declaration of competing interest

Resources, Data curation.
and well-preserved valves show the elongate shell shape and detailed
from the Late Ordovician (Sandbian) Pingliang Formation, North China,
6. Conclusions
more well-preserved specimens, especially those with delicate internal tissues, such as lophophore, mantle canals, setae and some other important characters which can provide more
clues of lifestyles can be employed to better understand the ecological
information of lingulid brachiopods during the Late Ordovician (Westbroek et al., 1980; Emig, 1992; Zhang et al., 2009, 2020a).

Abundant lingulid brachiopod Anomaloglobosa porca were discovered from the Late Ordovician (Sandbian) Pingliang Formation, North China, together with diversified graptolites and crinoids. Highly mineralized and well-preserved valves show the elongate shell shape and detailed internal anatomical information. The new discovery of this genus has extended its paleogeographic distribution from Gondwana and Tarim to North China Platform. Quantitative geometric morphometric analysis of shell shape and pseudointerarea using the whole Phanerozoic dataset indicate an infanlal rather than epibenthic lifestyle of this taxon. Accordingly, this study further suggests that the morphological and ecological diversity of lingulid brachiopods reached its maximum in the Ordovician and indicates the complexity and diversity of marine benthic ecosystems in the early Paleozoic.

CRediT authorship contribution statement


Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

I have shared the link to my data at the Attach File step.

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Appendix A. Supplementary material

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