


A new post-LOME (Late Ordovician Mass Extinction) recovery brachiopod fauna from South China

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Non-technical Summary.—The Late Ordovician Mass Extinction event (roughly 445 million years ago), one of the big five major extinctions, is characterized by a glacial phase followed by a post-glacial warmer phase. Faunas of brachiopods (shelly marine organisms) were affected by the mass extinction, but in the late Rhuddanian (about 441 million years ago; early Silurian), this group became more diverse, recovering from the drastic Late Ordovician event, and a clear change from Ordovician-type faunas to new Silurian-type faunas is clearly observed. In this paper, we discuss such a recovery fauna from the Niuchang Formation (about 441 million years ago), Wanzi section of Zhenxiang, northeastern Yunnan Province in South China. This faunal composition (26 species belonging to 25 genera) indicates shallow-water environments, although some deeper-water species are present, and a clear shift from the previous fauna that was characteristic of post-glaciation shallow-water environments. The presence of such a fauna, only occurring in the early Silurian, indicates that the recovery of the brachiopod faunas after the Late Ordovician extinction took some time to become significant. Throughout the studied section, the succession of brachiopod species found indicates a shallowing of the marine environment, in contrast with the global deepening trend because of local tectonic uplift, which provided a stable environment where faunas could develop and thrive. Finally, the presence of species from the pentameride group of brachiopods, such as the oldest record of the large *Sinostricklandiella*, indicates diversification of this group, earlier than previously thought.

Abstract.—Following the Late Ordovician Mass Extinction event, brachiopod faunas were in a phase of recovery during the late Rhuddanian (early Silurian), documented by a drastic turnover of Ordovician-type to Silurian-type faunas. In this study, we present a recovery brachiopod fauna, from the Niuchang Formation (late Rhuddanian-based graptolite zonation) at the Wanzi section of Zhenxiang in northeastern Yunnan Province, South China. The fossils include 26 species assigned to 25 genera, with a dominance of strophomenides and orthides, but also a diverse suite of atrypides and pentamerides, which exhibit compositional differences compared to the earlier Edgewood–Cathay fauna. The emergence of a more typical Silurian brachiopod fauna suggests a delayed community turnover after the Late Ordovician Mass Extinction event. The shallowing marine environment trend evinced in the brachiopod assemblages in the section indicates a balance between the global transgression and the regional Qianzhong Uplift, which provided a stable environment for the brachiopod recovery. The presence of diverse pentamerides, including the earliest species of the large-shelled genus *Sinostricklandiella*, suggests early diversification of this clade in South China.

Introduction

Following the two pulses of the Late Ordovician Mass Extinction (LOME), the earliest Silurian world gradually returned to a warmer climate (Sheehan, 1973, 2001; Brenchley et al., 1994, 2003; Harper and Rong, 1995; Finnegan et al., 2011; Trotter et al., 2016). After the glaciation, the rising eustatic sea level created vast new habitats in epicontinental seas, within which benthic faunas were established and diversified.

The Rhuddanian was recognized as a recovery interval after the Late Ordovician Mass Extinction event especially for brachiopods in South China (Rong and Harper, 1999; Rong and Cocks, 2014). The recovery brachiopod fauna has been

documented from a number of regions, but the precise age of most of those assemblages is not well constrained (see Cocks and Rong, 2008; Rong and Cocks, 2014, for review). Recently, a highly diverse recovery brachiopod fauna has been discovered in the Niuchang Formation (late Rhuddanian-based graptolite data), Wanzi section, Zhenxiang County, Yunnan Province, South China. Specimens collected from 16 fossil beds in a single section have been identified as 26 species representing 25 genera.

In this study, representative specimens of the brachiopod fauna are illustrated, and their taxonomic composition is analyzed using network analysis (NA), principal component analysis (PCA), and non-metric multidimensional scaling (NMDS). The identification of brachiopod-dominated associations from fossil beds and their paleoecology are discussed. In the context of global transgression, the environmental settings

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of the brachiopod fauna are investigated taking the regional tectonic activity into account. Furthermore, the evolutionary and paleoecological significance of the diverse pentamerides found in the section is explored.

Material and methods

Material and age.—The material was collected from the Lungmachi and the Niuchang formations at the Wanzi section, 5 km west of Wanchang Village, northwest of Zhenxiong County Town, northern Yunnan Province, South China (GPS: 27°39′27.6″N, 104°27′21.5″E) (Fig. 1). The strata yielding the brachiopod specimens in the region were temporarily assigned to the “Lungmachi Formation” (Huang et al., 2016). This formation is overlain by the Huanggexi Formation, primarily composed of limestone (lower-middle Aeronian), and underlain by the Weiba bed (upper Hirnantian, Upper Ordovician) (Rong and Huang, 2023; Wang et al., 2023). The section was measured in great detail based on the collections (YZW-10 to YZW-26). Because the beds above YZW-11 consist of yellow silty mudstone or calcareous mudstone, we designated these as the Niuchang Formation (Rong and Zhan, 2004; Huang et al., 2013). Bed YZW-11 is characterized by brownish silty mudstones with few shale layers yielding abundant graptolites and a few brachiopods and is assigned to the Lungmachi Formation (Fig. 2). The two formations in the section include several fossil groups, such as brachiopods, trilobites, graptolites, a few bryozoans, and gastropods.

The age of the brachiopod fauna is well constrained by graptolites (identified by Chen Xu, Nanjing Institute of Geology and Palaeontology [NIGP]). The specimens of *Korenograptus*

angustifolius (Chen and Lin, 1978) collected from the top of YZW-10 belong primarily to the *Akidograptus ascensus* biozone. Graptolites from YZW-11 can be assigned precisely to the *Cystograptus vesiculosus* biozone. There is a missing biozone in between, which may be due to the scarcity of related specimens in this layer, despite our division of YZW-11 and intensive collecting. Graptolites from YZW-13, -14, -15, -18, and -19a also indicate the *Cystograptus vesiculosus* biozone. Although no graptolites were collected above YZW-19, in spite of the thickness from YZW-11 to YZW-19 (confined within a single graptolite biozone) and the absence of lithological changes from YZW-19 upward, it is likely that the top of the fossil bed in the Niuchang Formation (YZW-26) in the section may not extend beyond the *P. (Coronograptus) cyphus* biozone. Therefore, the age of the brachiopods in this entire section is proposed as late Rhuddanian.

A preliminary study of the brachiopods (from 16 collections YZW-11 to YZW-22, excluding YZW-19a) revealed the presence of 8 major groups, including lingulides, craniids, orthides, strophomenides, pentamerides, atrypides, productides, and spiriferides, represented by 25 genera. Among these genera, *Levenea*, “*Eostropheodonta*,” *Leptellina* (*Merciella*), *Zygospiraella*, *Aegiria*, and *Sinostricklandiella* are abundant, while *Katastrophomena*, *Thulatrypa*, *Epitomyonia*, and *Dicoelosia* are less common. Strophomenides (6 genera) and orthides (4 genera) dominate both in terms of abundance and generic diversity. Although there are fewer specimens of other major groups, the generic diversity of atrypides (4 genera) and pentamerides (4 genera) is quite high.

After identifying specimens bed by bed, we compiled a range chart for the brachiopod genera from the Niuchang Formation (Fig. 2). The diagram reveals a trend of increasing diversity



Figure 1. Map showing the geographical location of the Wanzi section in Wanchang Village, northwest of Zhenxiong County, northern Yunnan, South China.

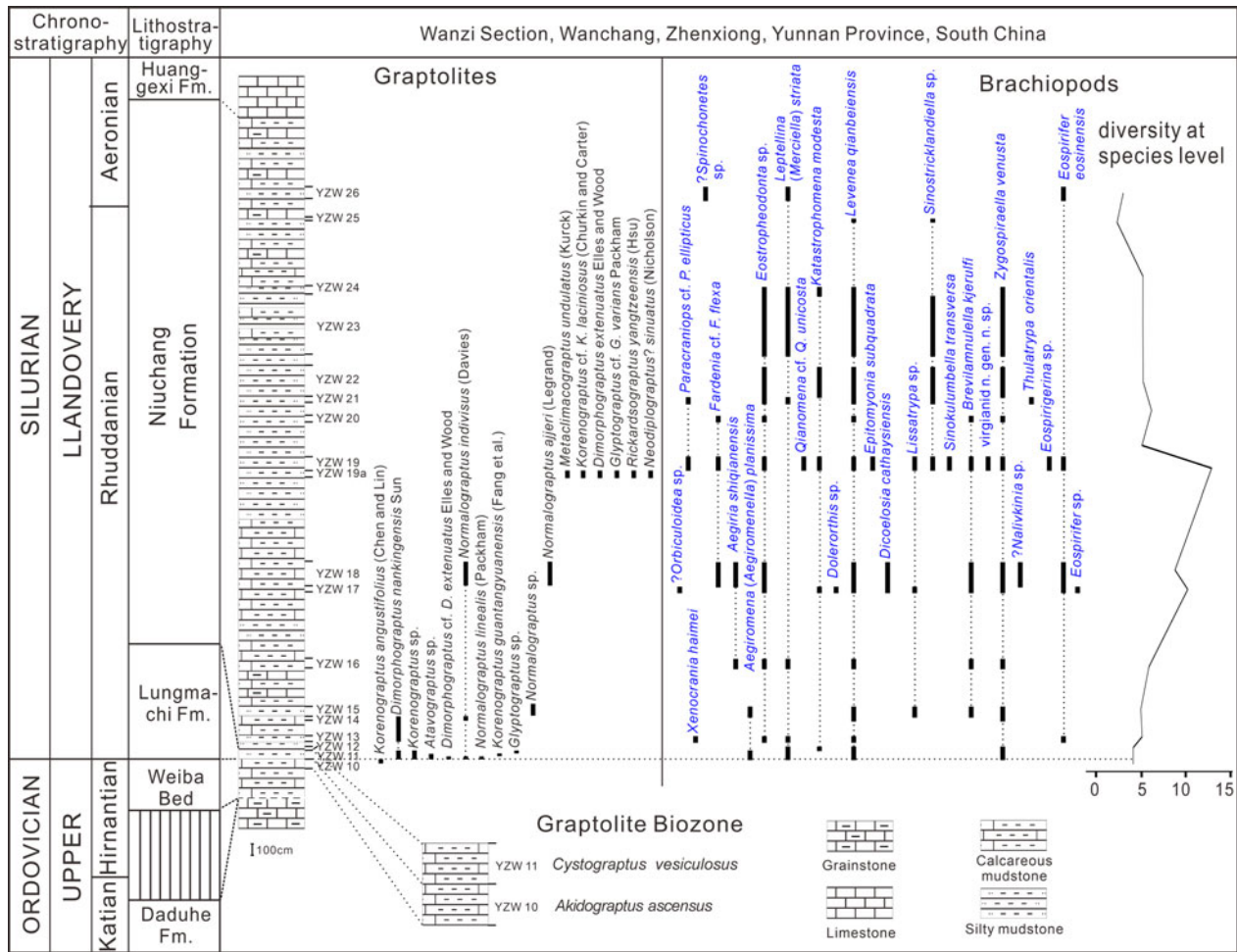


Figure 2. Collections made in the Weiba Bed (YZW-10, upper Hirnantian, Ordovician), Lungmachi Formation (YZW-11, lower Rhuddanian, Silurian) and Niuchang Formation (YZW-12 to YZW-26, upper Rhuddanian, Silurian) at Wanzi section. Range chart shows graptolite and brachiopod composition from YZW-10 to YZW-26.

from YZW-11 to YZW-19, followed by a decrease from YZW-20 to YZW-26, along with variations in brachiopod composition. In this study, we analyzed the binary data for taxon occurrence (Appendix) for the 15 collections.

Methods

To investigate the paleoecology of the brachiopods from the Wanzi section, differentiating brachiopod-dominated assemblages is a crucial step. Network analysis (NA) is widely applied in paleobiogeographical and paleoecological analyses (e.g., Sidor et al., 2013; Huang et al., 2017, 2018; Kiel, 2017). The method was discussed in detail by Vilhena and Antonelli (2015), and the advantages of using NA compared to traditional methods are summarized by Huang et al. (2016). For example, NA can calculate attribute values to detect the structure of the investigated data. More importantly, NA generates a network diagram that indicates the relationships between collections and taxa, along with their relative generic diversity, indicated by the size of the nodes for each collection.

In this study, to visualize the relationships among different brachiopod associations, a genus-collection dataset has been

produced. The bipartite network method incorporates both collection data and the presence-absence information of different taxa, aiming to minimize information loss. R (version 4.3.1) programming with the package igraph (Csárdi and Nepusz, 2006) was used in this study to visualize the bipartite genus-collection networks. The layout used was Force Atlas 2, and the out-degree was used to determine the size of the collection nodes.

Principal component analysis (PCA) and non-metric multi-dimensional scaling (NMDS) also were utilized in our study to map the association affinities, using the software PAST (version 4.01, Hammer et al., 2001). The Raup–Crick (RC) similarity measure was employed with NMDS to detect the groupings of the associations. The RC similarity measure originally was designed for paleobiological studies (Raup and Crick, 1979) and was referred to as SI (Shen and Shi, 2004) and RC (Schmachtenberg, 2008). Huang (2011) extensively discussed RC along with five other similarity measures and recommended RC for sparse data matrices, which are typical in paleobiological studies. Unlike other measures, RC calculations are based on probabilities rather than the functions of the numbers of shared taxa and providing higher resolution.

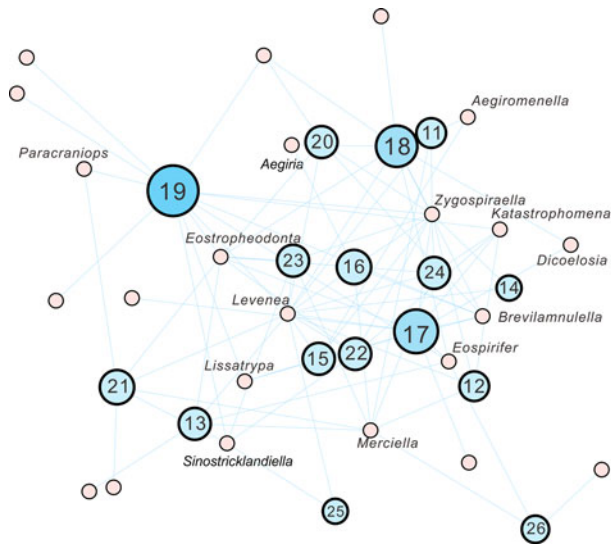


Figure 3. The bipartite network diagram of NA showing brachiopod composition in Wanzi section, with representative genera. Numbers refer to YZW-11 to YZW-26.

Repository and institutional abbreviation.—All figured specimens are housed in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

Results

The bipartite network diagram (Fig. 3) illustrates the structure of the brachiopod fauna in the section. The taxonomic information for each collection is represented by its connected taxa, and the diversity of each collection is visualized by the size of the collection nodes through the “out-degree,” which is determined by the number of edges of each node. For instance, the collection with the highest diversity, YZW-19, contains 13 genera. Furthermore, the connections among collections based on their common taxa (genus level) are displayed. In the network diagram, each node of rare genera in the outer region has a single connection, whereas each node for common genera in the central

part of the diagram is connected to several collections. Genera such as *Levenea*, “*Eostropheodonta*,” and *Zygospiraella* are among the most common genera across the collections. It is also easier to locate specific taxa on the diagram; for example, typical deeper-water taxa such as *Aegiria*, *Aegiromenella*, and *Dicoelosia* can be found in YZW-11 and YZW-15–YZW-18, primarily in the lower part of the section.

While the network diagram offers limited information about the grouping of the collections, the results from PCA and NMDS provide better insights into these associations (Fig. 4). In the PCA plot (Fig. 4.1), three distinct groups are identified. On the right-hand side of the diagram, the group consisting of YZW-17, YZW-18, and YZW-19, with a larger component 1, represents high-diversity collections, each containing 10–13 genera. On the left-hand side of the diagram, the collections can be divided into two groups roughly separated by the horizontal axis. These groups represent collections from the lower (Component 2 ≤ 0.1) and upper (Component 2 > 0.1) parts of the section. Despite variations in the diversity of the collections, the NMDS analysis using the RC measure, with a low stress value (0.201), clearly shows two groups (Fig. 4.2), which correspond to the lower and upper collections in the section, with the exception of YZW-26, possibly due to its very low diversity and the presence of a unique and questionable genus (?*Spinochonetes*). Based on the information from the range chart and network diagram (Figs 2, 3), it is evident that the upper part of the scatter plot (YZW-11 to YZW-18) illustrates that the lower collections of the section increase in diversity from bottom to top. In contrast, the lower part of the scatter plot (YZW-19 to YZW-25) shows that the upper collections exhibit a significant decrease in diversity. To illustrate the transitions within the brachiopod faunas in the section, we have selected representative taxa from the two assemblages (Figs 5–8).

Discussion

Brachiopod faunas following the Late Ordovician Mass Extinction event.—Following the Late Ordovician Mass Extinction (LOME) event, a highly diverse brachiopod fauna

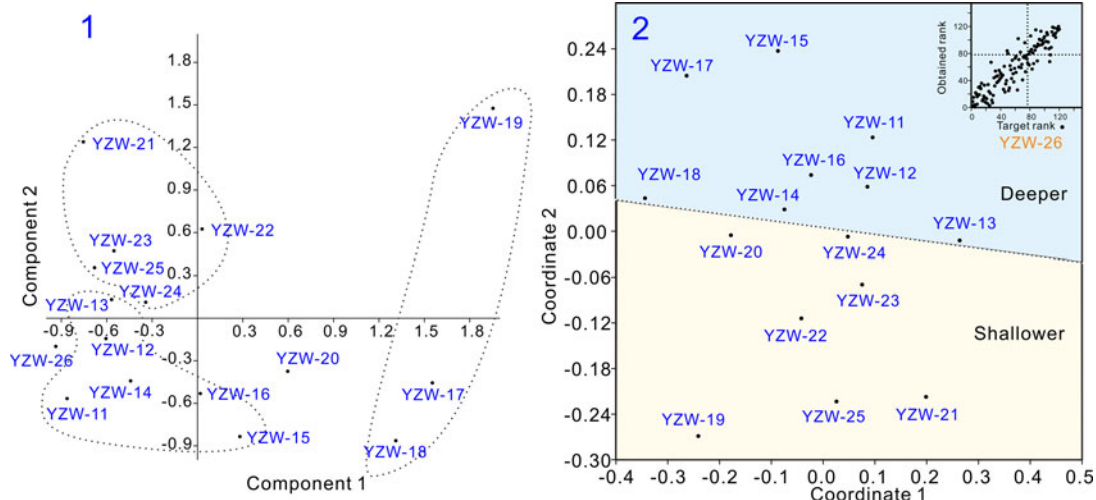


Figure 4. The results of PCA (1) and NMDS (2) for the 15 collections made from the Wanzi section (YZW-26 is not included from the original 16 collections). (2) Two brachiopod assemblages were identified, with relative water depths proposed.

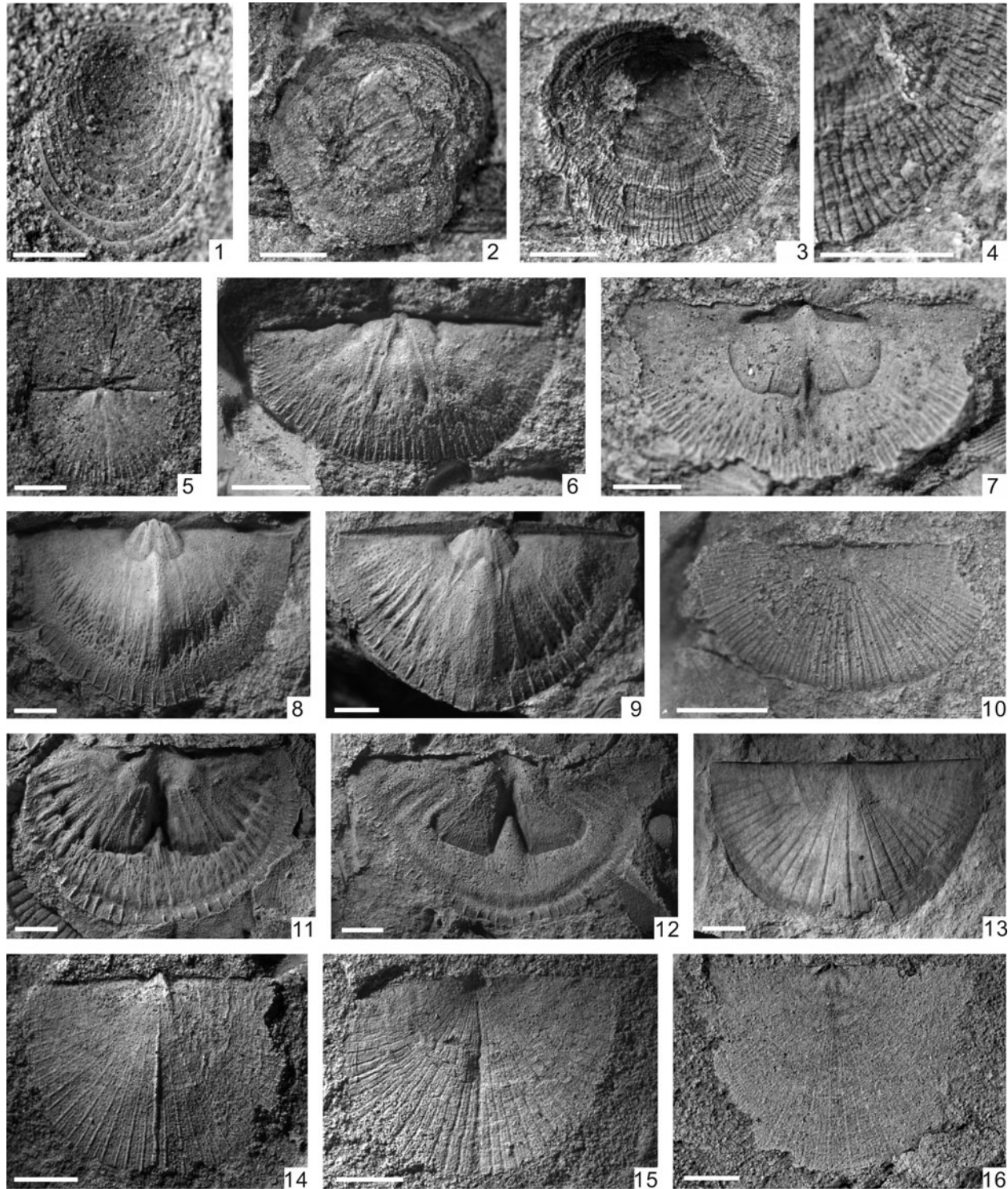


Figure 5. (1) *Paracraniops* cf. *P. pararia* (Williams, 1962): dorsal external mold (NIGP 203390) (YZW-21). (2–4) *Xenocrania haimei* (Reed, 1915) (NIGP 203391): (2) dorsal internal mold; (3) external mold; (4) local enlargement of (3) showing detail of ornamentation (YZW-13). (5) *Aegiromena* (*Aegiromenella*) *planissima* (Reed, 1915): ventral and dorsal internal mold of conjoined valves (NIGP 203392) (YZW-18). (6, 7, 10) *Aegiria shiqianensis* Yang and Rong, 1982: (6) ventral internal mold (NIGP 203393) (YZW-16); (7) dorsal internal mold (NIGP 203394) (YZW-16); (10) dorsal external mold (NIGP 203395) (YZW-16). (8, 9, 11–13) *Leptellina* (*Merciella*) *striata* (Rong and Yang, 1981): (8, 9) two ventral internal molds (NIGP 203396, NIGP 203397) (YZW-21, YZW-24); (11, 12) two dorsal internal molds (NIGP 203398, NIGP 203399) (YZW-24, YZW-21); (13) dorsal external mold (NIGP 203400) (YZW-24). (14–16) *Eostropheodonta* sp.: (14) ventral internal mold (NIGP 203401) (YZW-18); (15) ventral external mold (NIGP 203402) (YZW-18); (16) dorsal internal mold (NIGP 203403) (YZW-18). Scale bars represent: 1 mm (1–4); 2 mm (5–16).

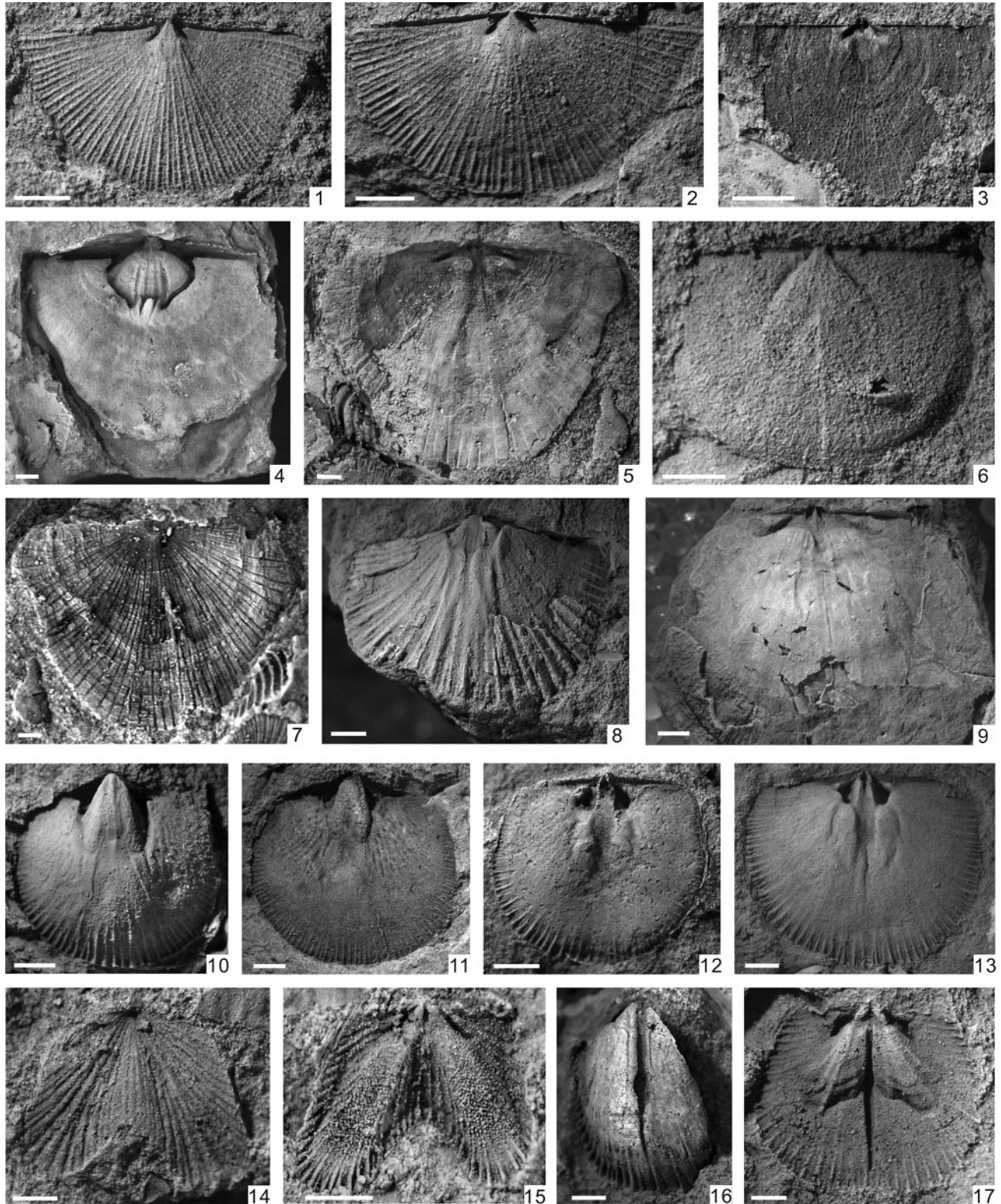


Figure 6. (1–2) *Fardenia* cf. *F. flexa* (Rong et al., 2013): two ventral internal molds (NIGP 203404, 203405) (YZW-20); (3) *Eostropheodonta* sp.: dorsal internal mold (NIGP 203406) (YZW-18). (4, 5, 7, 9) *Katastrophomena modesta* (Rong and Yang, 1981): (4) ventral internal mold (NIGP 203407) (YZW-19); (5, 7) dorsal internal mold and its external mold (NIGP 203408) (YZW-19); (9) dorsal internal mold (NIGP 203409) (YZW-12). (6) *Qianomena* cf. *Q. unicosta* Rong and Yang, 1981: ventral internal mold (NIGP 203410) (YZW-19). (8) *Dolerothis* sp., ventral internal mold (NIGP 203411) (YZW-19). (10–13) *Levenea qianbeiensis* Rong, Xu, and Yang, 1974: (10, 11) two ventral internal molds (NIGP 203412, NIGP 203413) (YZW-20, YZW-12); (12, 13) two dorsal internal molds (NIGP 203414, NIGP 203415) (YZW-17, YZW-24). (14, 15) *Dicoelosia cathaysiensis* Huang, Rong, and Harper, 2013: (14) dorsal external mold (NIGP 203416) (YZW-17); (15) dorsal internal mold (NIGP 203417) (YZW-17). (16, 17) *Epitomyonia subquadrata* Rong et al., 2013: (16) ventral internal mold (NIGP 203418) (YZW-19); (17) dorsal internal mold (NIGP 203419) (YZW-19). Scale bars represent: 2 mm (1–13); 1 mm (14–17).

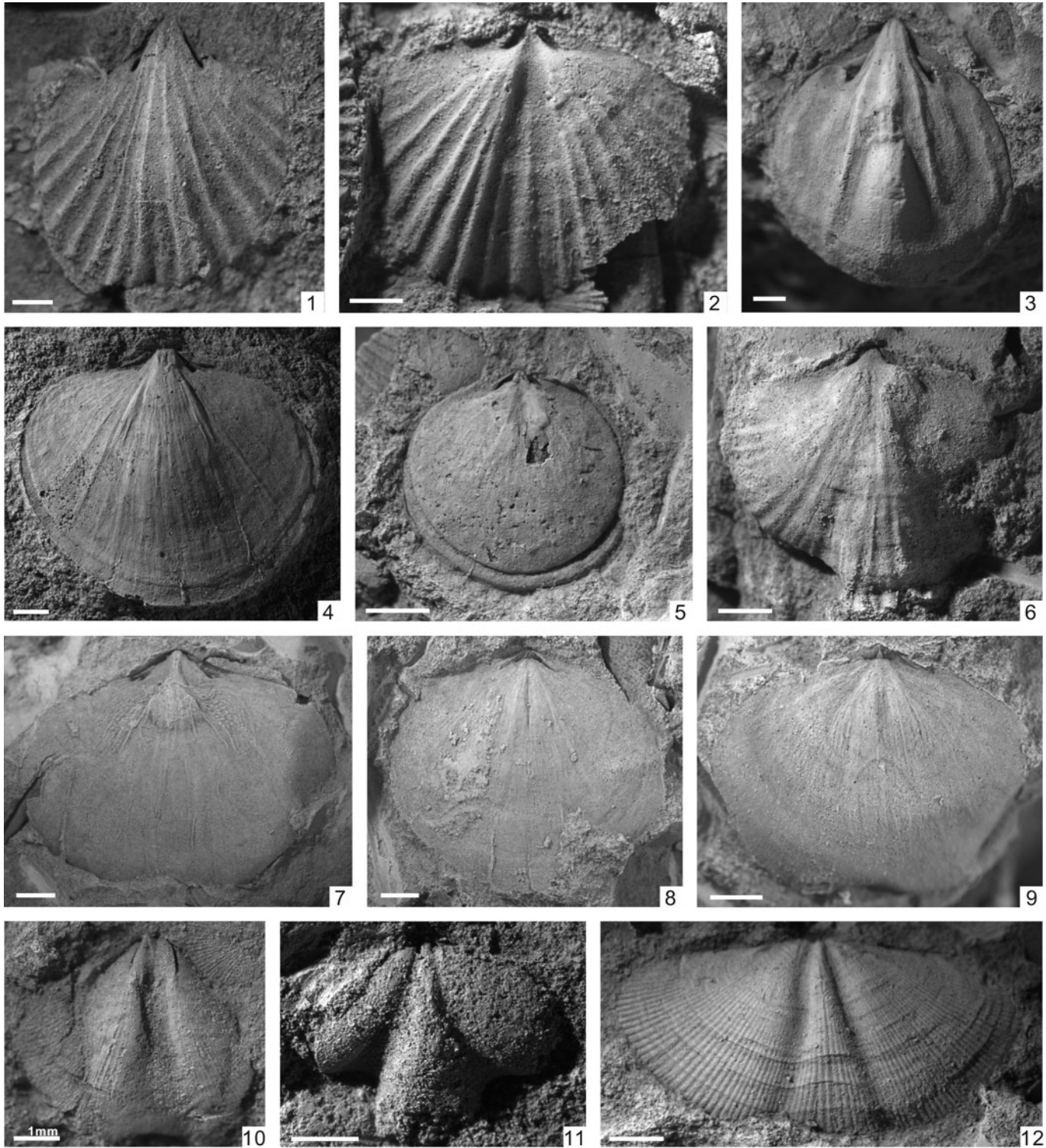


Figure 7. (1–3) *Zygospiraella venusta* Rong and Yang, 1981: (1, 3) two ventral internal molds (NIGP 203420, NIGP 203421) (YZW-19, YZW-23); (2) NIGP 203422, dorsal internal mold (YZW-22). (4, 5) *Lissatrypa* sp.: (4) ventral internal mold (NIGP 203423) (YZW-15); (5) dorsal internal mold (NIGP 203424) (YZW-17). (6) *Eospirigerina* sp.: dorsal internal mold (NIGP 203425) (YZW-19). (7–9) *Thulatrypa orientalis* (Rong, Xu, and Yang, 1974): (7) ventral internal mold (NIGP 203426) (YZW-21); (8, 9), two dorsal internal molds (NIGP 203427, NIGP 203428) (YZW-21). (10, 11) *Eospirifer eosinensis* Rong et al., 2013: (10) ventral internal mold (NIGP 203429) (YZW-13); (11) dorsal internal mold (NIGP 203430) (YZW-19). (12) *Eospirifer* sp.: dorsal internal mold (NIGP 203431) (YZW-17). Scale bars represent 2 mm for images.

known as the Edgewood–Cathay fauna (EC), which developed primarily in the uppermost Hirnantian to lower Rhuddanian of South China (Rong et al., 2013, 2020; Rong and Huang,

2023), may indicate a limited impact of the LOME. The Edgewood–Cathay Fauna (EC Fauna) thrived in post-glacial, warmer, shallow-water regimes with both carbonate and

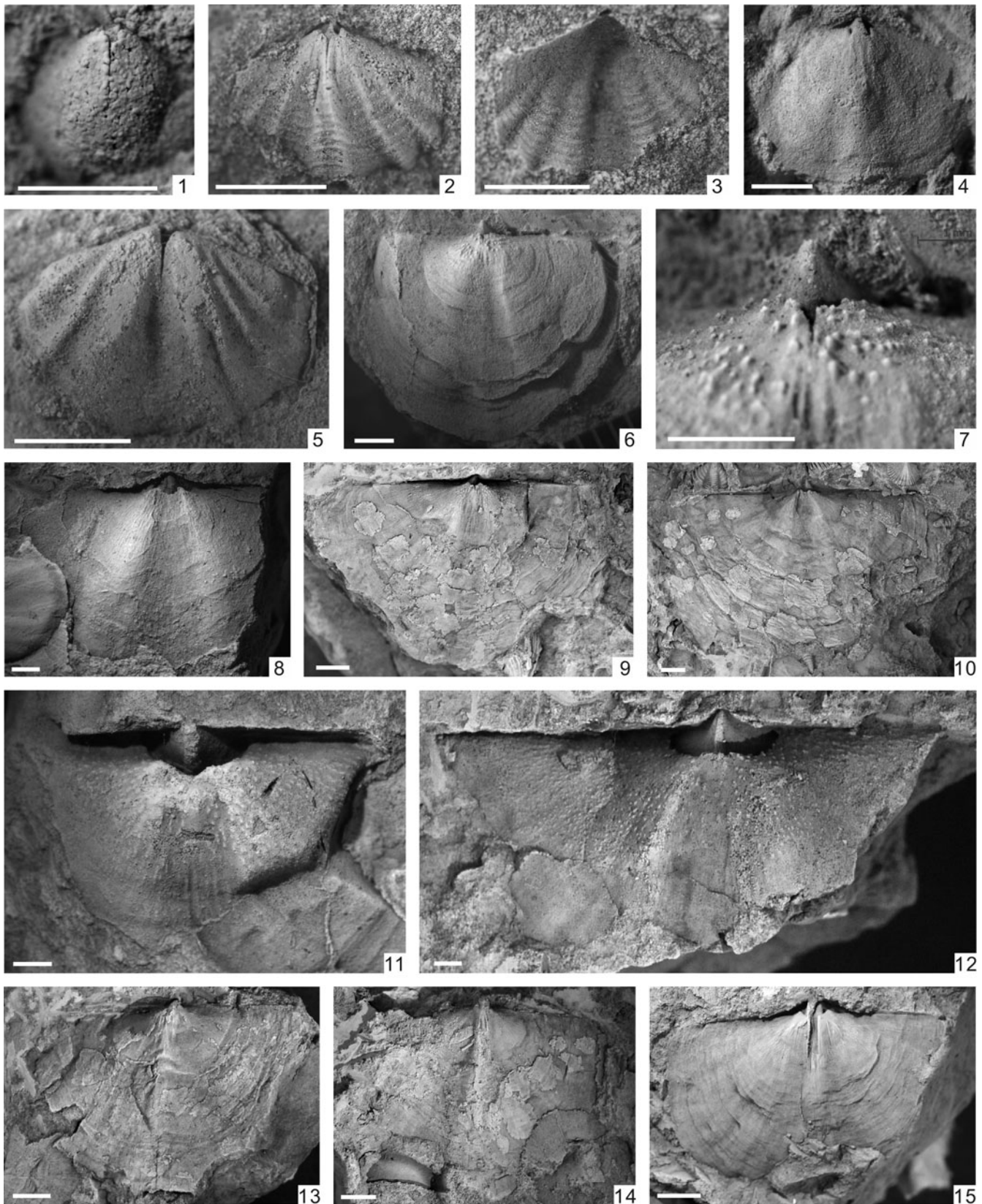


Figure 8. (1, 4, 5) *Brevilamulella kjerulfi* Kiær, 1902: (1, 5) two ventral internal molds (NIGP 203432, NIGP 203433) (YZW-20, YZW-19); (4) dorsal internal mold (NIGP 203434) (YZW-25). (2, 3) virginianid n. gen. n. sp., dorsal internal mold and its external counterpart (NIGP 203435) (YZW-19). (6, 7) *Sinokulumbella transversa* (Grabau, 1925): ventral internal mold and detail of median septum (NIGP 203436) (YZW-19). (8–15) *Sinostricklandiella* sp.: (8–12) five ventral internal molds (NIGP 203437–203441), (8) YGW-23, (9–12) YZW-19; (13–15) three dorsal internal molds (NIGP 203442–203444) (13, 14) YZW-19, (15) YZW-23. Scale bars represent: 2 mm (1–8, 11, 12); 5 mm (9, 10, 13–15).

siliciclastic facies, originating from low latitudes. The EC Fauna significantly differs from the *Hirnantia* Fauna in various aspects, particularly in taxonomic composition. While the highest origination rates in the *Hirnantia* Fauna were observed within the orthides and strophomenides, which are typical Ordovician brachiopods, the EC Fauna exhibited high origination rates for the rhynchonellides and atrypides (Rong et al., 2020), the latter of which (atrypides) together with pentamerides laying the foundation for Silurian brachiopod faunas (e.g., Gushulak and Jin, 2017).

In a recent study conducted on the Dagala section, Zhenxiong County, Yunnan Province, South China, a highly diverse EC fauna (22 identified genera) was discovered. As the fauna immediately above the EC fauna in the same area, the recovery fauna in this study shares eight genera (32%) with the EC fauna, namely *Paracraniops*, *Fardenia*, *Eostropheodonta*, *Dolerorthis*, *Epitomyonia*, *Brevilamnulella*, *Eospirigerina*, and *Eospirifer*. A notable disparity between the EC fauna from Zhenxiong and the succeeding fauna is that the former contains nine orthide genera, whereas the latter only has four orthide genera. In the meantime, the recovery fauna in this study is more characterized by Silurian taxa. This includes four pentameride and four atrypide genera, accounting for 32% of the total diversity. In contrast, the EC fauna consists only of a single pentameride and two atrypide genera, accounting for 11% of the total diversity. These two successive faunas represent a case of delayed turnover occurring nearly 3 million years after the Late Ordovician Mass Extinction event, supporting the limited ecological impact of the biotic event (e.g., Huang et al., 2017).

Shallower trend and community replacement.—The lower assemblages (YZW-11 to YZW-18) and the upper assemblages (YZW-19 to YZW-25) are differentiated by NMDS, which highlights diversity increases and decreases, respectively. Although species richness can be correlated with benthic assemblage (BA) for brachiopods, more information is needed, in particular regarding water depth (Boucot, 1975; Rong, 1986; Brett et al., 1993), to elucidate environmental changes. Bathymetry index taxa are taken into consideration here. Graptolites are associated with deep-water settings, and they were collected only from strata below YZW-19 in the Wanzi section, indicating shallower-water settings for YZW-19 and the collections above. Several deeper-water index brachiopods, such as *Aegiria*, *Aegiromena*, and *Dicoelosia* (Fig. 5), indicative of BA4 environments, have been recorded from the lower part of the section. Among them, *Aegiria* and *Aegiromena* dominate some beds, such as YZW-15 and YZW-16, and the latter extends into YZW-18. Although some deeper-water taxa, such as *Brevilamnulella* and *Epitomyonia*, are still present in YZW-19, the dominant taxa, such as *Levenea* and *Eostropheodonta*, in the layer, alongside large-shelled pentamerid taxa, may indicate lower BA3 environmental settings. Several fossil beds above YZW-19, such as YZW-22 to YZW-26, contain fewer taxa, commonly about five species, indicating shallower water environments (e.g., upper BA3).

Based on the above information, the section can be divided roughly into lower and upper assemblages, representing deeper water (approximately BA4, YZW-11 to YZW-18) and shallower

water (around BA3, YZW-19 to YZW-25) environments. A shallowing-upward trend is evident from the base to the upper part of the Wanzi section. The brachiopod assemblages in this study are of late Rhuddanian age, corresponding to an interval of global transgression. This trend is similar to that observed in the Xinglongchang section (Huang et al., 2016). Although the onset of the Silurian was marked by a significant and rapid eustatic sea-level rise, a regional tectonic movement, known as the Qianzhong Uplift, remained active during the Llandovery (e.g., Rong et al., 2011). The Qianzhong Uplift likely played a more crucial role during the recovery interval following the end-Ordovician mass extinction. This regional tectonic movement contributed to the shallowing-upward trend observed in the Wanzi section, which is situated in the marginal belt of the Qianzhong (central Guizhou) Old Land. The balance between the global transgression and the Qianzhong Uplift ensured a stable regional environment for the development of the recovery brachiopod fauna.

Post-LOME high-diversity recovery brachiopod fauna.—Following the EC fauna, very few high-diversity brachiopod faunas have been reported from the upper Rhuddanian of South China (Rong and Zhan, 2004; Huang et al., 2021). In South China, low to moderately diverse brachiopod faunas have been reported in the upper Rhuddanian (Rong and Cocks, 2014). Among them, a moderately diverse brachiopod fauna (14 genera) from the Niuchang Formation of the Xinglongchang section in Guizhou Province, South China, has been documented by Huang et al. (2013, 2016). The age of this brachiopod fauna is late Rhuddanian to earliest Aeronian, which can be aligned with the brachiopods in this study. Both sections were located on the northwest margin of the Yangtze Platform during the early Silurian. All the genera from the Xinglongchang section, except for *Chrustenopora?* and *Whitfieldella*, are recorded in this study. With three non-articulate brachiopod genera, four pentameride genera, and an additional two strophomenide genera, this study exhibits significantly higher diversity, which is closely associated with the disappearance of graptolite facies in the region.

A unique atrypid genus, *Thulatrypa*, which dominates the upper part of the Xinglongchang section, has also been found in the upper part of the Wanzi section. This indicates a similar horizon for the two faunas. However, the significantly higher diversity observed in this study suggests more favorable environmental conditions in this area, possibly heralding an early radiation for some Silurian clades, such as pentamerides and atrypides (e.g., Huang et al., 2021).

Significance of the pentamerides in the fauna.—In comparison to the recovery brachiopod fauna following the Late Ordovician Mass Extinction event in South China, as discussed in previous case studies (Huang et al., 2013, 2016) and reviewed data (Rong and Cocks, 2014), the presence of diverse pentamerides in this fauna completes our knowledge. Globally, the Rhuddanian Age is characterized by only 12 genera of pentamerides, which are sporadically distributed, with no more than three genera occurring in major paleo-plates (Huang et al., 2018). However, in the Wanzi section, four species representing four

genera (including one as gen. and sp. indet.) have been documented, indicating a collection with the highest diversity of pentamerides. The early diversification of pentamerides in this section suggests suitable environmental conditions for the evolution of this clade.

Among the pentamerides, the large-shelled genera have drawn our attention. For example, the warm-water *Virgiana* fauna was extremely well developed in carbonate basins of Laurentian, Siberia, and Tian-Shan, with the largest shells and most abundant shell beds closer to the paleo-equator (see summaries in Jin et al., 2019, 2023). The fauna was absent from most parts of Baltica, Avalonia, and South China. However, the large-shelled *Sinostricklandiella* sp. is abundant in South China, especially in the study section. A few specimens assigned to this taxon differ by having notably short median septa and smaller size. Taxonomically, these specimens should be reassigned to *Sinokulumbella transversa* (Grabau, 1925). Both genera are endemic to South China, and their species have been documented in the upper Xiangshuyuan Formation (lower-middle Aeronian) of northeastern Guizhou Province and in the lower Lojoping Formation (upper-middle Aeronian) in the Yichang area of western Hubei Province. Species of these two genera are found in stratigraphic horizons closely associated with the closure of graptolite facies in the region. In this study, since the graptolites found in the bed immediately below the two pentamerid species are assigned to the *Cystograptus vesiculosus* biozone, the horizon where the pentamerides were collected cannot be higher than the *P. (Coronograptus) cyphus* biozone. Therefore, these species are regarded as the earliest representatives of *Sinostricklandiella* and *Sinokulumbella* (e.g., Rong et al., 2005). These two endemic genera likely evolved from *Stricklandia mullochensis* (Reed, 1917), which is characterized by a wide hinge line, and originating in the early Rhuddanian of Avalonia and Baltica (Cocks, 2008). While the evolution of the *Stricklandia* lineage differs from that of *Kulumbella* (Rong et al., 2005), considering that specimens of both species are from the same collection, it is possible to infer a relationship between *Sinostricklandiella* and *Sinokulumbella*. The new material of *Sinostricklandiella* sp. will support the description of a new species and will be discussed elsewhere. The two youngest representatives of the two genera also indicate the early recovery of the pentamerides.

In addition to the large-shelled stricklandiids, only very few specimens of the small-sized *Brevilamnulella kjerulfi* Kiær, 1902, were collected. It should be noted that there is a unique specimen (Fig. 8.2, 8.3) resembling species of *Brevilamnulella* in dorsal interior, but the presence of clear concentric growth lamella, indicates a new generic character. The establishment of a new genus will require additional specimens for further study.

Katian pentamerides such as virgianids were confined largely to the paleo-northern hemisphere and concentrated close to the paleo-equator (Jin et al., 2022), whereas the Rhuddanian counterparts became widespread in both the northern and southern paleo-tropics, down to the subtropics of southern hemisphere Laurentia (Jin et al., 2023). Rhuddanian pentamerides are commonly considered to have occupied primarily shallow, relatively high-energy waters, ranging from BA2 to upper BA3 (Huang et al., 2018). In South China, particularly in the northern Guizhou to western Hubei area, pentamerides such as *Borealis*

are commonly found in carbonate facies within the upper Rhuddanian to lower Aeronian strata. In these strata, one can even observe species typically associated with higher horizons, such as species of *Pleurodium* and *Paraconchidium*. However, in the clastic facies of the Wanzi section, the pentamerides exhibit significant differences and are predominantly represented by *Sinostricklandiella* sp. Stricklandiids are commonly associated with relatively deeper-water settings, ranging from BA3 to BA4 substrate environments (e.g., Jin et al., 2006; Rong et al., 2007; Rong and Cocks, 2014), which aligns with the bathymetry observed in this study. Despite the shallowing trend observed in the section, the pentamerides identified here lived in BA3 environments.

Furthermore, although a large body size can correspond to both warm- and cold-water environments (e.g., Rong et al., 2017), the large-shelled pentamerides, commonly regarded as typical warm-water taxa (Jin et al., 2006; Huang et al., 2018), diversified during the Aeronian in South China. The size of the *Sinostricklandiella* sp. specimens from the Wanzi section does not exceed 70 mm in width, which is much smaller than the largest representatives of the genus, which can reach 100 mm (e.g., Rong et al., 2017). Their presence in these upper Rhuddanian strata may still suggest an earlier warm environment in the region compared to the habitats of *Sinostricklandiella* species in the Aeronian of South China (Rong and Cocks, 2014).

Conclusion

We report a novel brachiopod fauna from the upper Rhuddanian (lower Llandovery, Silurian) Niuchang Formation, Wanzi section of the Wanchang region in the northeast Yunnan Province of South China. The highly diverse fauna includes 25 genera dominated by strophomenides (6 genera) and orthides (4 genera) in both abundance and diversity, atrypides (4 genera), and pentamerides (4 genera). Compared with the Edgewood–Cathay (EC) fauna in the same region, the more diverse pentamerides and atrypides in this study showed a community replacement and emergence of a more typical Silurian brachiopod fauna.

A shallowing-upward trend was deduced and might be related to the balance between the global transgression and the regional Qianzhong Uplift, which ensured a stable environment for the recovery brachiopods. The presence of diverse pentamerides, including the earliest species of the large-shelled genus *Sinostricklandiella*, indicates similar habitat conditions to those of the genus in the Aeronian of South China. This suggests an early diversification of the clades in this region.

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Declaration of competing interests

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.

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