

Epibiosis and epifaunal tiering in brachiopods from the Cambrian Xiaoshiba Lagerstätte of China

Yu Wang^a, Paul D. Taylor^b, Jie Yang^a, Xiguang Zhang^{a,*}

^a Institute of Palaeontology, Yunnan University, Kunming 650500, China

^b Department of Science, Natural History Museum, London SW7 5BD, UK

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ABSTRACT

In the early Cambrian, brachiopods quickly became a distinctive group of the marine community and played a key role in the increasingly diversified benthic ecosystem. Based on new material from the Cambrian Stage 3 Xiaoshiba Lagerstätte, we focus on brachiopods displaying epibiotic relationships and tiering attachment to demonstrate: 1) abundant individuals of *Kutorgina chengjiangensis* once acted as the predominant components to construct the cohesive substrate, which were often selected by epibionts as their hosts for shallow-sea inhabitation, exhibiting a symbiotic association; 2) within the same community, the secondary tierers are well recorded at least by some of acrotretoid brachiopods attaching to gregarious tubes of *Tubulella* sp. Our findings give additional evidence for illuminating the unexpected complexity of the palaeoecosystem and clarifying the rapid adaptive radiation and ecological niche expansion associated with early Cambrian brachiopods.

1. Introduction

Epibiosis, the long-lasting association of two taxa, is widespread in extant organisms, and the interactions between the epibiont and its host can be critical for understanding their life habits and the ecosystem of which they are part. In the fossil record, epibiotic associations are broadly recognized, including some significant discoveries that are relied on exceptional material yielded by Cambrian Konservat-Lagerstätten (e.g., Topper et al., 2015; Zhang et al., 2020a). However, such recognition of bio-interaction may not represent the earliest emergence, since nanometer-scale globules preserved together with stromatolites from the Mesoproterozoic Gaoyuzhuang Formation in northern China were argued to be the earliest known occurrence of epibiosis (Seong-Joo et al., 1999). To date, this interpretation has been both doubted and supported in subsequent papers (Kirkland et al., 1999; Lepot et al., 2008). The contradictive viewpoints are partly due to the extremely rare occurrence of fossil material from the Precambrian sediments.

During the Cambrian Explosion, abundant brachiopods unearthed from Cambrian sediments distributed worldwide have exhibited remarkable taxonomic diversity and various life strategies (Wang et al., 2012; Topper et al., 2014, 2015). More significantly, these early brachiopods appear to have played a crucial role in Cambrian benthic ecosystems by forming dense concentrations on the seafloor, stabilizing

the soft substrate, and providing shells that formed secondary substrates for colonization by other organisms (Zhang et al., 2010, 2020a; Chen et al., 2024). The latter include non-conspecific brachiopods, microbial mats and other invertebrates. Consequently, they have acted to promote biodiversity, functioning as both substrate users and substrate creators (Taylor, 2016; Wilson and Taylor, 2017; Vinn et al., 2024). The Cambrian fossil assemblages dealt with here proved to be an important resource for exploring the dramatic evolution of early life on Earth and the increasingly complex ecosystem associated.

Here, we present new fossil material from the Cambrian Age 3 Xiaoshiba biota, which occurs within the Hongjingshao Formation (Yang et al., 2013, 2014; Hou et al., 2019) and contains a unique aggregation of rhynchonelliform brachiopod *Kutorgina chengjiangensis* Zhang et al., 2007. In addition, four more brachiopod taxa have been collected and identified, including *Longtancunella chengjiangensis* Hou et al., 1999, *Yuganontheca elegans* Zhang et al., 2014, *Eoglossa chengjiangensis* Wang et al., 2014 and *Lingulellotreta yuanshanensis* Zhang et al., 2020b (Fig. 1). These exquisite fossils display rare examples of Cambrian epibiosis, in which epibionts of uncertain affinity, as reported here were attached to the host brachiopod *K. chengjiangensis*. The epibiotic relationship may represent the earliest intimate association among all of rhynchonelliformean lineages so far known. Nonetheless, it remains very hard to differentiate parasitism and other interactions in these fossil

* Corresponding author.

E-mail address: xgzhang@ynu.edu.cn (X. Zhang).

colonial organisms (Taylor, 2015). Also, from the same succession at the Xiaoshiba fossil site, some acrotretoid brachiopods attached to colonial tubular organisms have been well documented. These small-sized brachiopods were anchored to different tubes, exhibiting notable variation in distance above the sea floor. Thus, the brachiopods, together with the tubular organisms, furnish a rare example of epifaunal tiering in the Cambrian.

2. Materials and methods

The Xiaoshiba biota comes from the eastern suburb of Kunming in southern China, where the Cambrian (Stage 3) Hongjingshao Formation

is widely exposed (Yang et al., 2013; Hou et al., 2019). The Xiaoshiba fossil assemblage spans two biozones: the lower *Yunnanocephalus-Chengjiangaspis-Hongshiyanspis* Zone and the upper *Yiliangella-Zhangshania* Zone (Yang et al., 2014; Hou et al., 2019). The fossils described here come from both biozones. All of these specimens are deposited in the Collections of the Institute of Palaeontology, Yunnan University (YKLP).

Specimens were prepared by manually removing the overlying matrix under a Leica M125-C stereomicroscope. Photographs were taken using a DFC 500 digital camera mounted on a Leica M205-C stereomicroscope and a Leica DFC 7000 T monochrome digital camera mounted on a Leica M205 FA fluorescence stereomicroscope. Energy-dispersive

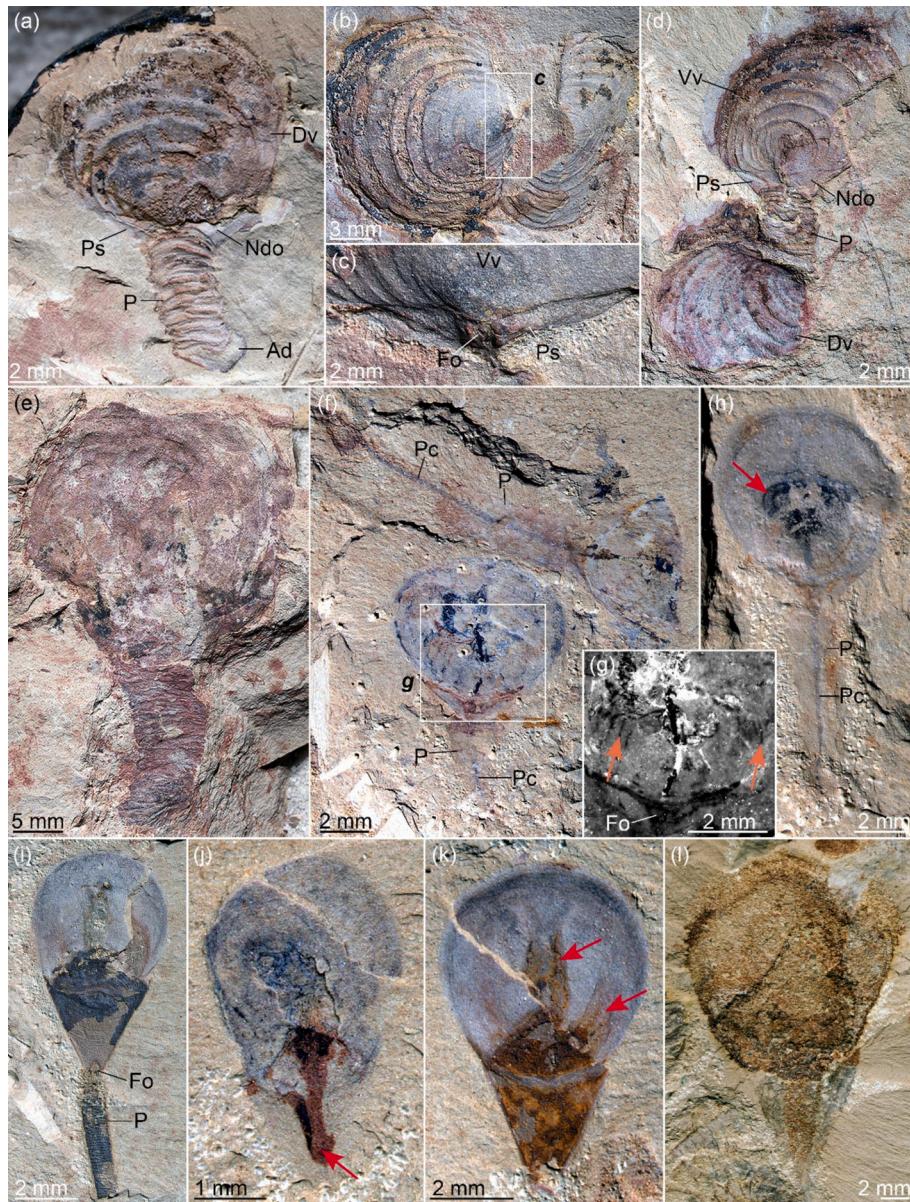


Fig. 1. *Kutorgina chengiangensis* and other co-occurring brachiopods from the Xiaoshiba biota. (a)–(d) *K. chengiangensis*: (a) YKLP 12600: dorsoventrally compressed valves displaying a pedicle, which emerges through the ventral valve and bears a possible terminal disc. (b)–(c) YKLP 12601: (b) an intact ventral valve; (c) close-up of area c in (b) showing the ventral apical foramen located between the pseudodeltidia. (d) YKLP 12602: ventral valve, which with a pedicle attached, was buried aside with its dorsal valve. (e) YKLP 12603: *Longtancunella chengiangensis*. (f)–(h) *Eoglossa chengiangensis*; (f) YKLP 12604, two individuals, the upper one showing pedicle cavity; (g) close-up of area g in (f), fluorescent photograph, showing two sets of lophophoral filaments (arrows). (h) YKLP 12605, showing partially survived lophophoral spirals (arrow). (i)–(k) *Lingulellotreta yuanshanensis*: (i) YKLP 12606, showing foramen and pedicle; (j) YKLP 12607, showing 'U'-shaped gut (arrow); (k) YKLP 12608, showing the dorsal valve with imprints of mantle canals (arrows) on inner surface. (l) YKLP 12609, *Yuganotheca elegans*. Abbreviations: Ad, attachment disc; Ap, apical perforation; Dv, dorsal valve; Fo, foramen; Ndo, notothyrial and delthyrial opening between the outer margins of notothyrium and pseudodeltidium; P, pedicle; Pc, pedicle cavity; Ps, pseudodeltidium; Vv, ventral valve.

Micro X-ray fluorescence (micro-XRF) was performed on uncoated specimens using a Bruker M4 Tornado to trace the elemental distribution on fossil surfaces. Digital figures were processed using Adobe Photoshop CS6 and CorelDRAW 2018. Measurements of specimens were taken using Image J.

3. Results and discussion

3.1. *Kutorgina* and epibiosis

The Class Kutorginata Williams et al., 1996 includes two subgroups: kutorginids and nisusiids, and both are the most abundant rhynchonelliformean brachiopods found in Cambrian Series 2, of which some have been regarded as the oldest known representatives (Williams et al., 1996; Harper et al., 2017; Holmer et al., 2018, 2019). *Kutorgina chengjiangensis* Zhang et al., 2007 collected from the Chengjiang biota, is the

oldest known rhynchonelliformean lineage with well-preserved soft parts, clearly displaying plesiomorphic characters, such as the simple coiled lophophores, primitive articulation without teeth, and robust pedicles (Zhang et al., 2007). In the Xiaoshiba fossil assemblage, of the measured valves of *K. chengjiangensis* approximately 60 % are more than 10.2 mm in length, and occur in lower relief following dorsoventral flattening, like the brachiopods present in the Chengjiang biota (Zhang et al., 2007; Holmer et al., 2018). The pedicle of *K. chengjiangensis* is always subtended between the delthyrium and notothyrium, stretching out from the apical perforation (Fig. 1a, d), which may show as a minute opening (about 0.3 mm in diameter) located near the posterior border of the ventral valve (Fig. 1b, c). A terminal disc is occasionally preserved at the distal end of pedicle (Fig. 1a).

Protomelission, which has been interpreted variously as a bryozoan (Zhang et al., 2021), a dasycladalean green alga (Yang et al., 2023) or an archaeocyath (Yang et al., 2024), may have been an epibiont of



Fig. 2. *Kutorgina chengjiangensis* and attached organisms. (a) YKLP 12610: Dorsal valve attached by a single tube with slightly inflated node (arrow). (b)–(c) YKLP 12611: (b) Dorsal valve attached by a tube of *Archotuba* sp.; (c) Close-up of area c in (b) showing detail of the attachment between the tube impression (arrow) and the shell margin. (d) YKLP 12612, the anterior margin of the brachiopod was attached by four tubes: two on the dorsal valve (white arrows), two on the ventral one (orange arrows). (e)–(g) YKLP 12613: (e) several *Archotuba* sp. attached to the host: at least one is distinguishable on the dorsal valve (white arrow); one on the ventral valve (orange arrow); (f)–(g) close-up of areas f and g in (e), showing the septum-like structure inside the tube (red arrow) and putative intestine (black arrows). (h)–(i) YKLP 12614: (h) the dorsal valve was attached by a tube; (i) close-up of area i in (h) showing the tube fixed itself to the dorsal valve via its swollen base. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

brachiopods: a rootlike holdfast of a clavate specimen of *Protomelission* is firmly anchored to a discarded shell of *K. chengiangensis* (Yang et al., 2023: fig. 1d, e, h). In previous studies, a tubular organism that may represent the suspension feeder – *Archotuba* clearly displays a connection with the host skeletons (Lei et al., 2014; Hou et al., 2017). Such an intimate relationship is also present in the shells of *K. chengiangensis* reported here. For example, there are up to seven *Archotuba* tubes attached to a shell of *K. chengiangensis*, either isolated or in clusters (Fig. 2a, c, d, e, h). The maximum length of the *Archotuba* tubes is about 37 mm, whereas the maximum width generally occurs at the possible opening and ranges from 0.5 to 2.0 mm; they are usually narrower and longer compared to *Archotuba conoidalis* in the Chengjiang biota (Fig. 2e–g). Some specimens were found to be preserved with the plate-like structures (Figs. 2f, 3f) (Yong et al., 2024). In the Xiaoshiba biota, both *Protomelission* and *Archotuba* have been found attached to shells of the brachiopod *K. chengiangensis* (Fig. 2a, b, d, e, h; Yang et al., 2023: fig. 1d, h) through a series of swollen holdfasts (Fig. 2c, d, i). This indicates that the epibionts utilized a particular kind of brachiopod as a

substrate. As a whole, the attachment points are always concentrated along the anterior margins of either the dorsal or ventral valves rather than somewhere centrally situated on the shell surface. Certain epibiont-bearing specimens with pedicles preserved (Fig. 2a, h) and valves articulated may suggest that the colonization of epibionts had endured for some time while the host was alive. This is further supported by the selective settlements of the epibionts, which are always present along valve commissures of the host (Fig. 2a, b, d, e, h), which, in this way, still can open its valves for respiration and feeding. Understanding the complex interactions between the host brachiopods and their epibionts is difficult (Taylor, 2015). Nevertheless, the stable substrate for attachment provided by the host brachiopod *K. chengiangensis* would have undoubtedly been beneficial to the epibionts and it is possible that they also benefited from the enhancement of the flux of food particles caused by the feeding currents of the brachiopod. It is less easy to envisage advantages to the host brachiopods (Zhang et al., 2010). The drag resulting from the epibionts may have increased the chances of the brachiopods becoming dislodged, as is the case of the Recent bivalve

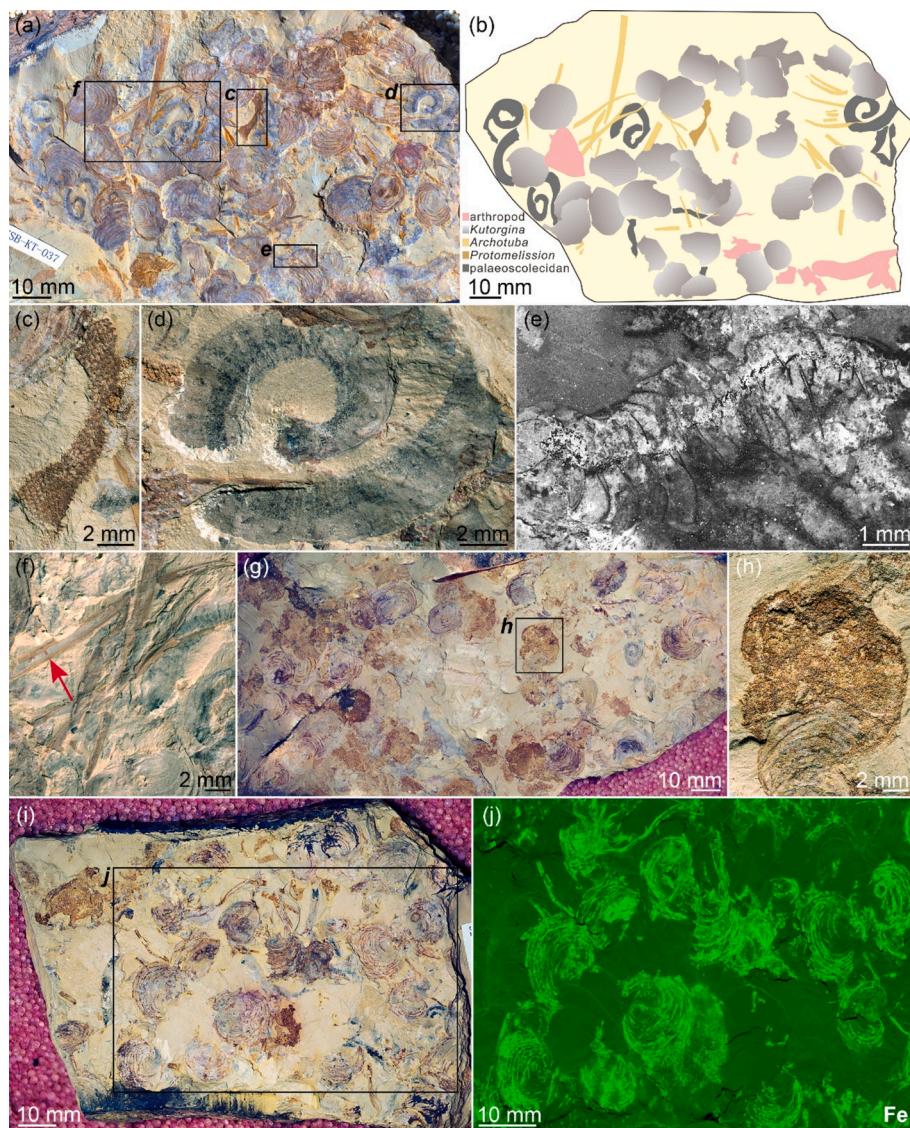


Fig. 3. Mass accumulation of the Xiaoshiba fossil assemblage. (a)–(f) YKLP 12615: (a) Overall view, showing various organisms buried with numerous valves of *K. chengiangensis*, (b) Interpretative drawing of (a). (c)–(f) Close-up of areas c–f in (a): (c) a fragment of *Protomelission*? sp.; (d) a fragmentary paleoscolecid worm gently curved with fine tubercles on its cuticle; (e) fluorescence photograph showing an incomplete euarthropod (*Chengjiangocaris kunmingensis*) with its digestive tract (arrows) partially preserved. (f) *Archotuba* preserved with other organisms, showing a septum-like structure (arrow). (g)–(h) YKLP 12616: (g) overall view of a slab, (h) close-up of area h in (g) showing a valve of *Yuganotheca elegans*. (i)–(j) YKLP 12617: (i) overall view; (j) Micro X-ray fluorescence image of boxed area j in (i) showing the chemical component of buried organisms, which is enriched in iron.

Mytilus when fouled by epibionts (Witman and Suchanek, 1984).

Direct evidence of epibiont attachment has been well documented in various organisms from the early Cambrian Lagerstätten. For example, numerous linguliform brachiopods from the Guanshan biota confirm an early establishment of the parasite-host system (Zhang et al., 2020a). Brachiopods hitchhiking on *Wiwaxia* from the Cambrian Burgess Shale infer a well-established symbiotic association (Topper et al., 2014). Some co-occurring worms, which, as mobile hosts attached by tiny epibionts, were regarded as a commensal infestation (Cong et al., 2017). Similar epibiotic association seems to have become common in younger strata, such as the association of a Silurian pentastomid with ostracods (Siveter et al., 2015), and encrusting foraminifera and bacteria on decapod crustaceans (Robin et al., 2013, 2015). As demonstrated here, the epibiotic association seen in the Xiaoshiba fossils is similar to that of the Chengjiang biota, in which the highly abundant lingulid *Diandongia pista* is frequently utilized as a hard substrate, hosting epibionts, such as *Longtancunella*, *Archotuba*, and small cementing brachiopods (Zhang et al., 2010). There are some examples of epibiosis observed in rhynchonelliformean brachiopods in the post-Cambrian fossil record (e.g., Alvarez and Taylor, 1987), but the epibiotic attachment in *Kutorgina* reported here represents the earliest known fossil record of epibiosis present in this brachiopod clade.

The Xiaoshiba brachiopods are unusually dominated by two

rhynchonelliformean species *Kutorgina chengjiangensis* and *Longtancunella chengjiangensis* (Fig. 5), both co-occurring with the linguliformean species *Lingulellotreta yuanshanensis* and *Eoglossa chengjiangensis* (Fig. 1f–k). Soft tissues observed from some of these brachiopods include partially intact lophophores (Fig. 1h), lophophoral filaments (Fig. 1g), digestive systems (Fig. 1j), mantle canals (Fig. 1k), and pedicles (Fig. 1a, d–f, h, i). Dense aggregations of brachiopods with attached epibionts occur on bedding planes, and these fossiliferous slabs indicate that the brachiopod *K. chengjiangensis* unusually dominates the fossil assemblage with about 20 individuals per 100 cm² (Fig. 3). These fossil concentrations contain high-proportions of complete shells with minimal fragmentation, and only a small proportion of *K. chengjiangensis* specimens exhibit a pedicle, and these are usually preserved with articulated valves, displaying concentric growth lines and a random orientation on the bedding plane (Fig. 3a, b, g, i).

The taxonomic abundance of the main groups appearing on the bedding surface of five fossiliferous slabs (e.g., Fig. 3) indicates that *K. chengjiangensis* is the commonest taxon in the assemblage, despite the presence of the stem brachiopod *Yunganontheaca elegans*, *Protomelission* sp., *Archotuba* sp., the fuxianhuiid arthropod *Chengiangocaris kunningensis* (Yang et al., 2016) and palaeoscolecidomorph worms (Fig. 3a, b). Micro X-ray fluorescence maps reveal iron enrichment in some specimens from the Xiaoshiba biota, which is inferred to indicate replacement

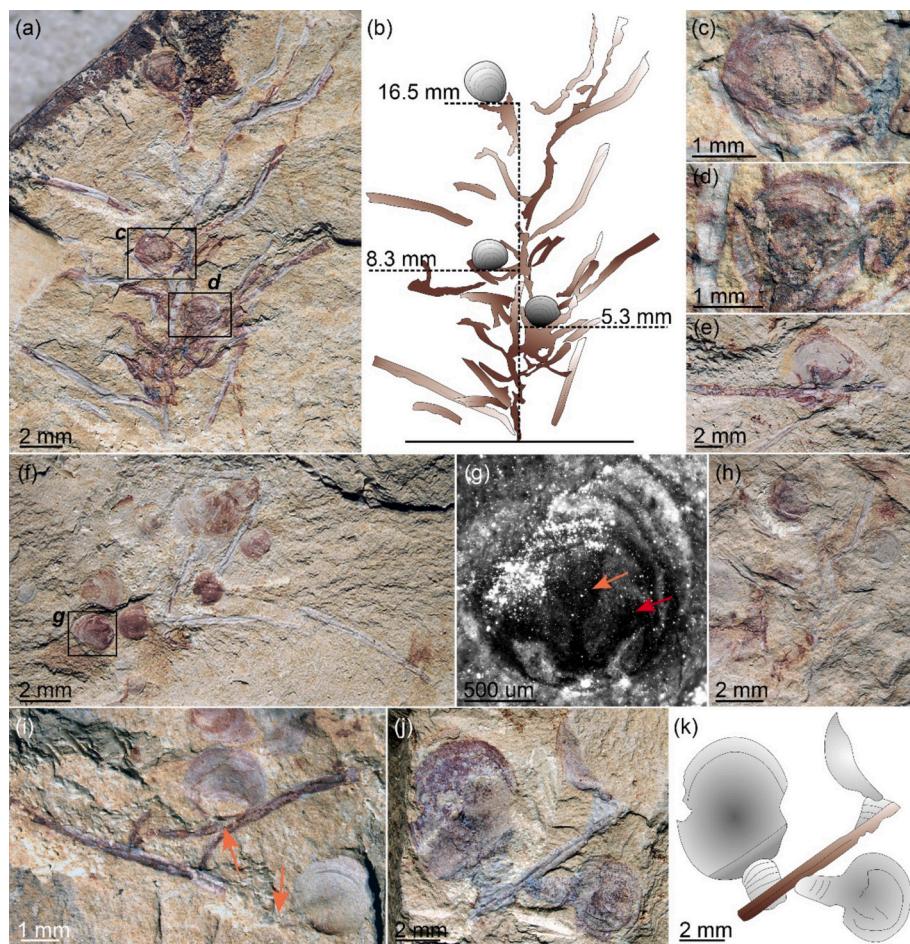


Fig. 4. Secondary tiering of brachiopods from the Xiaoshiba biota. (a)–(d) YKLP 12618: (a) Three acrotretoids attached to a colonial tubular organism; (b) Interpretive drawing of (a); (c)–(d) Close-up of areas c, d in (a), showing the attachments. (e) YKLP 12619, a single brachiopod attached to a tube. (f) YKLP 12620, clustered brachiopods fixed on a tubular organism. (g) Close-up of area g in (f), fluorescent photograph, showing internal imprints of the dorsal valve, median ridge (orange arrow) and submedian ridge (red arrow). (h) YKLP 12621, two individuals connected to fragmentary tubular structures coexisting with other skeletal debris. (i) YKLP 12622, two individuals attached to tube branches (arrows). (j)–(k) YKLP 12735: (j) three individuals of *Longtancunella* attached to a tubular fragment with fleshy pedicles; (k) Interpretive drawing of (j). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of pyrite during the weathering process, resembling that seen in the Chengjiang and Guanshan fossils (Fig. 3i, j) (Chen et al., 2024). The presence of a wide taxonomic variety of soft-bodied animals of different sizes on each slab argues against significant displacement or sorting of the buried organisms (Fig. 3a, b, g, i).

3.2. Epifaunal tiering

Cambrian brachiopods established complex vertical tiering, with co-occurring primary and secondary tierers exhibiting variable levels of tiering in marine benthic communities (Topper et al., 2015). In the Xiaoshiba fossil assemblage, *Kutorgina* represents primary tiering, living directly on the seafloor, and secondary-tiering brachiopods are also present. Some acrotretoid brachiopods with a minute oval shell are often associated with colonial tubular organisms (Fig. 4). These enigmatic tubes may overlap each other and branch radially outward, as though surrounding a central tube. There are three acrotretoids attached to branching tubes at different locations near the central branch, and each is always oriented with the posterior margin toward the frond of a tube and mostly via direct contact (Fig. 4a-d). On another bunch of colonial tubes, there are at least eight brachiopod individuals of varying sizes attached, of which one exhibits a distinct septum impression and demonstrates an acrotretoid affinity (Fig. 4f, g).

There are three observations favouring biological association for an interpretation of epibiotic tiering: 1) The posterior margins of acrotretoids generally align with tube surfaces (Fig. 4a-e, h, i); 2) Absence of acrotretoids lived on other substrates argues against random settling. 3) All available variably-sized shells of acrotretoids are almost complete and articulated with both valves closely fitted together. In addition, three individuals of *Longtancunella* are also attached on either side of a tubular fragment by their fleshy pedicles (Fig. 4j, k). This further supports the symbiotic relationship between the brachiopods and the tubular organisms in the Xiaoshiba Biota. The acrotretid *Kuangshantreta malungensis* from the Chengjiang biota has been found perched on an alga-like *Malongitibus kuangshanensis*, placing it approximately 55 mm above the seafloor (Wang et al., 2012). Acrotretid brachiopods from the Xiaoshiba biota show a similar life strategy in their secondary attachment to tubular-like organism (Fig. 4a, b, h, i).

Tubular organisms from the Xiaoshiba biota are provisionally assigned to *Tubulella* sp. due to their resemblance to the thin thecae of *Tubulella* from the Burgess Shale, which has been compared to the sessile polyp of a scyphozoan jellyfish (Van Iten et al., 2002). However, the Xiaoshiba tubes are narrower, with a cross-section less than about 0.4 mm in diameter (Fig. 4a, b); the thecae are straight or curved to varying degrees and are always flattened onto the bedding planes (Fig. 4a, h, i). Additionally, its annulations and longitudinal ridges or grooves are visible externally on the thecae (Fig. 4a, e, f, h-j). Even so it remains unavailable to assign it to a species as based on limited material. The tubes are interpreted as projecting vertically into the water column with the terminal blind end adhering to the seafloor (Zhu et al., 2000; Van Iten et al., 2002; Chang et al., 2018).

Wang et al. (2012) proposed that the slender, thread-like pedicle of *K. malungensis* likely coiled around algal fronds. They argued that this hypothesis is supported by the consistent orientation of *K. malungensis* shells, with the posterior ends invariably pointing toward the branched fronds of *M. kuangshanensis*. In contrast, the anterior shell margins point freely downwards. However, specimens from Xiaoshiba do not appear to corroborate this hypothesis. Although none of acrotretoid brachiopods with pedicles have been identified, the anterior margins of their shells are typically oriented upwards, aligned with the direction of divergence of the tubes (Fig. 4a, b).

The Xiaoshiba acrotretoid brachiopods described here are low epifaunal tierers with individuals situated separately across the colonial tubular organism (Fig. 4a, b). The life strategy of acrotretids may be unrelated to tiering height. Topper et al. (2015) pointed out that all examined brachiopods from the Burgess Shale occupy low-tiering levels

– a view which is consistent with our observation.

The disappearance of *Kutorgina* concentrations and the emergence of an acrotretoid-tube association in the fossil-bearing succession provide a brief glimpse into the continuous change of the Xiaoshiba brachiopod communities through time. The alteration representing a key transition was most likely caused by changes in the substrate, which is a primary control of brachiopod distribution (Topper et al., 2015), enabling the rapid occupation of vacant ecospace during the Cambrian substrate revolution.

3.3. Epibiosis and ecosystem

The Chengjiang brachiopod assemblage has been demonstrated as the earliest diverse brachiopod fauna, in which abundant specimens of the linguliformean *Diandongia pista* occasionally have coexisting epibionts, the host-epibiont relationship parallels other evidence of increasingly complex ecosystems through the early Cambrian (Zhang et al., 2010; Zhao et al., 2014). The dense aggregations of the brachiopod *Kutorgina chengjiangensis* with epibionts in the Xiaoshiba biota described here represent one of the early proliferations of Rhynchonelliformea in South China (Fig. 5). In the Wulongqing Formation, some brachiopod genera, such as *Linnarsonia*, *Neobolus* and *Westonia*, occur aggregated to form monospecific shell concentrations (Zhang et al., 2020a; Chen et al., 2024). The Xiaozhuang fossil assemblage (Zeng et al., 2014) in the lower Hongjingshao Formation should represent another occurrence of the formally named Xiaoshiba Lagerstätte (Yang et al., 2013) since the former occurs about 15 km away from the latter, both occurring within the *Yunnanocephalus-Chengjiangaspis-Hongshyanaspis* biozone. The Xiaozhuang fossil site is also known to contain mass accumulations of brachiopod shells, including rhynchonelliformean *Longtancunella* (Zeng et al., 2014; Wang et al., 2022). Together with the dense accumulation of *Kutorgina* shells at the Xiaoshiba succession, this may reveal an early expansion in abundance and ecological adaptation of various brachiopods in southern China during the Cambrian Age 3. Moreover, it indicates that rhynchonelliformeans played essentially the same role as linguliforms did in nutrient cycling and had a similar influence on the composition and diversity of benthic communities in providing more ecospaces for coeval organisms (Harper et al., 2021; Chen et al., 2024).

The diversity of Cambrian hard substrate communities surpasses that of the Precambrian but remains poorly known in comparison to that of the Ordovician and later geological times (Taylor and Wilson, 2003). In soft-bottom environments, hard substrate provisioning was low and restricted to biogenic structures (Wissahak and Neumann, 2006). As one of the earliest groups of skeletonized animals emerged in the Cambrian Explosion, brachiopods quickly occupied a dominant position in Cambrian benthic communities and could become suitable hosts for symbiotic interactions in the marine ecosystem. These demonstrations get supports from our discovery of epibiotic association present in the Xiaoshiba biota.

It has been noted that Cambrian Stage 4 brachiopod shells can form widespread skeletal pavements with a series of thin shell concentrations extending laterally over long distances (Harper et al., 2021). In comparison, the *Kutorgina* skeletal pavements in the Cambrian Stage 3 Xiaoshiba succession, together with the coeval shell concentration of rhynchonelliformeans from the Xiaozhuang fossil site (Zeng et al., 2014; Wang et al., 2022), are restricted to a small area. As a whole, the rhynchonelliformean brachiopods as demonstrated here may have subsequently become dominated component in the associated surroundings. Most likely they have also played an essential role as the linguliforms did in nutrient cycling and influence on the composition and diversity of benthic communities as providing more ecospaces for all coexisting organisms (Harper et al., 2021; Chen et al., 2024).

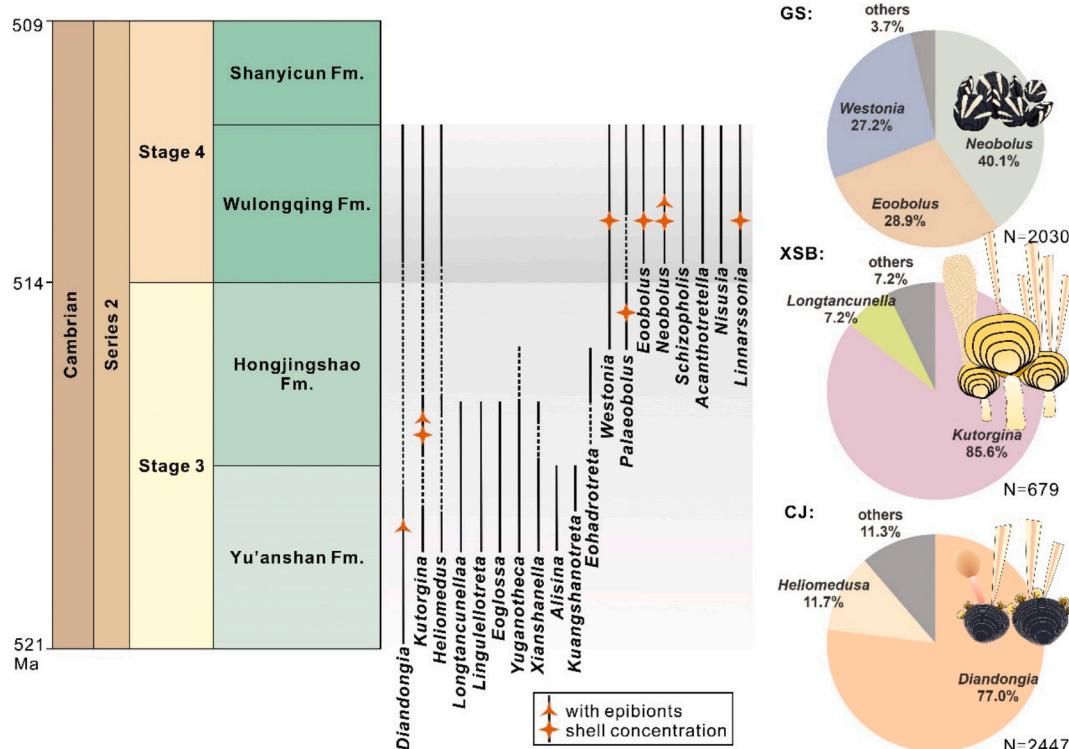


Fig. 5. Stratigraphic ranges, abundance and epibiotic interactions of the three Cambrian (Series 2) brachiopod assemblages from eastern Yunnan. Stratigraphic ranges (genera) based on Chen et al. (2019). Shell concentrations and epibiont marks visualized after Zhang et al. (2010, 2020a) and Chen et al. (2024). The relative abundance of the Chengjiang and Guanshan brachiopods are referred to Zhao et al. (2014) and Chen et al. (2020). Abbreviations: GS, Guanshan biota; XSB, Xiaoshiba biota; CJ, Chengjiang biota.

4. Conclusion

Large numbers of *Kutorgina chengjiangensis* in the Cambrian Age 3 Xiaoshiba biota of eastern Yunnan were, along with other organisms, often buried on bedding planes, with their calcareous shells serving as substrates for epibionts, which often selected the most abundant brachiopods as their hosts.

The exceptionally preserved brachiopod-epibiont association from the Xiaoshiba succession reveals poorly known biotic interactions in marine communities during the Cambrian Age 3.

Additionally, we document the extraordinary preservation of secondary tierers in the Xiaoshiba Lagerstätte, based on the discovery of acrotretoid brachiopods attached to the gregarious *Tubulella* sp. The emergence of the acrotretoid-*Tubulella* association represents another example of epibiosis present in the same biota.

This study contributes to a better understanding of the autecology of rhynchonelliformean (e.g., *Kutorgina*) and acrotretoid brachiopods, the relationships between these brachiopods and other coeval fossil lineages, and the role these brachiopods played in niche expansion within ecosystems during the early Cambrian.

CRediT authorship contribution statement

Yu Wang: Writing – original draft, Visualization, Methodology, Formal analysis, Data curation. **Paul D. Taylor:** Writing – review & editing, Methodology, Formal analysis, Data curation, Conceptualization. **Jie Yang:** Resources, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Xiguang Zhang:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

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