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Peduncular attached secondary tiering acrotretoid brachiopods from the Chengjiang fauna: Implications for the ecological expansion of brachiopods during the Cambrian explosion

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ABSTRACT

Brachiopods are usually thought to contribute little to the tiering complexity from the Paleozoic to the Recent, mainly due to the fact that their recent representatives live primarily in lower tiers directly above or below the water–sediment interface. Here we present the first and oldest record of varied levels of secondary tiering in minute brachiopods attached by exceptionally preserved thread-like pedicles around the branched fronds of the algae-like *Malongitubus kuangshanensis* Hu, 2005. The specimens illustrated herein were recovered from the Chengjiang fauna (Series 2, Stage 3) in the Lower Cambrian Heilinpu Formation at the Kuangshan section in Malong County, Yunnan Province, southern China. The micro-morphology and oval outline of the attached brachiopods demonstrate that they can be assigned to acrotretoid brachiopods (Linguliformea, Lingulata, Acrotretoidea), described here as *Kuangshanotreta malungensis* gen. et sp. nov. This is the first report on the occurrence of acrotretoid brachiopods in the Lower Cambrian muddy deposits from southern China. The posterior margins of the *Kuangshanotreta* shells are invariably either in direct contact with, or directed towards, and then in situ attached to the algal frond of *M. kuangshanensis*, indicating a secondary tiering in the ecological structure of Early Cambrian brachiopods. The acrotretoid *Kuangshanotreta*/algae *malongitubus* association represents both the first and oldest evidence into the enigmatic paleoecology of the diverse acrotretoid linguliformean stock that comprises an important component of the Cambrian evolutionary fauna, and sheds light on medium-high levels of secondary tiering (+5 to +10 cm) Cambrian soft substrate suspension-feeding communities. When compared to other Chengjiang brachiopods, the miniature morphology and concomitant weight reduction of the shell of *K. malungensis* may be a good adaption to a suspended epifaunal tiering life style. We infer that the diversification of micromorphic and miniaturized acrotretoids that occurred from the Middle Cambrian to Early Ordovician may be the result of the increased availability of habitable surfaces provided by high levels of tiering in new types of ecological spaces.

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1. Introduction

The study of the vertical distribution of suspension-feeding benthic organisms above and below the seafloor was defined as tiering by Ausich and Bottjer (1982) and Bottjer and Ausich (1986) (see also Ausich and Bottjer, 2001), where secondary tierers are suspension-feeders that use primary tierers for their life above or below the seafloor. Brachiopods were one of the most important marine suspension-feeding benthos, especially in the early Paleozoic sea (Bassett et al., 1999; Harper, 2006). They are, however, usually thought to contribute little to the tiering complexity from the Paleozoic to the Recent mostly due to the view that all brachiopods have been suspension feeders (primary tiering) that were free-living on the substrate, attached by means of a pedicle or by cementation (Rudwick, 1970; Williams et al., 2000).

However, several analyses of skeletal fossil assemblages indicated a possible sponge–brachiopod commensal relationship (Lenz, 1993; Mergl, 2002; Holmer et al., 2005), and indicated that brachiopods exploited and developed more variable levels of ecological structure in Paleozoic benthic communities. Direct evidence of commensalism between sponges and brachiopods in the Cambrian was provided by exceptionally-preserved fossils derived from the Burgess shale (Conway Morris and Whittington, 1985). Nevertheless, exceptionally preserved in situ records of brachiopod associations with other skeletal organisms including sponges are rarely fossilized in the Early

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Cambrian; most previous records are from the Chengjiang fauna (Series 2, Stage 3), Yunnan, southern China, where brachiopods, such as the calcareous-shelled *Kutorgina* and *Alisina* as well as other more problematic forms such as *Longtancunella* and *Xianshanella* represent low secondary tierers (0 to +5 cm tier), and are found still attached by massive pedicles directly to various skeletal organisms including the shell of other brachiopods, hyoliths and trilobite exuviae (e.g. Hou et al., 1999; Zhang et al., 2007a,b, 2008, 2010, 2011a,b).

Here we present the first detailed description of the in situ commensal association of large-scale algae with an assemblage of the micromorphic lingulate *Kuangshanotreta malungensis* gen.et sp. nov. from the Early Cambrian Chengjiang Fauna in Malong County ca. 60 km northeast of Kunming, Yunnan, South China. This is the first record of varied levels of medium–high secondary tiering in brachiopods that developed during the Cambrian explosion interval. Close observation and SEM analysis of the micromorphic brachiopods demonstrate that they represent a taxon of oldest-known acrotretoid brachiopods that diversified and became one of the dominate linguliformeans during the Middle Cambrian–Lower Ordovician interval time (Bassett et al., 1999). The new record of *Kuangshanotreta*/*Malongitubus* association demonstrates that a much higher tiering complexity of linguliformean brachiopods than previously thought was already reached by the Early Cambrian, and provides the first clear evidence on the autoecology of acrotretoids—an extinct lineage of lingulate brachiopods.

2. Stratigraphy, locality and methods

Lower Cambrian and terminal Proterozoic stratigraphic successions are well developed and widely exposed in eastern Yunnan, South China, where a well-known candidate section for the global stratotype of the boundary between the Cambrian and Precambrian was proposed at Meishucun Section in Jinning County 40 km SW of Kunming, Yunnan Province (Luo et al., 1982). Prior to this proposal, Early Cambrian chronostratigraphic units, in ascending order, the Meishucunian, Chiungchussuan (informally Qiongzhusian), Tsanglangpuian (Canglangpuian) and Lunwangmianoan (Longwangmiaoan) were already established at the stratotype sections, all of which are located around Kunming–Wuding and Malong–Qujing areas (Fig. 1A) (Luo et al., 1994). Until now, the four units were suggested and widely used as the correlation standard not only for China, but also for the rest of the Redlichian Realm (Chang, 1980; Luo et al., 1994; Zhang et al., 2001) both because of their continuous and well developed deposition succession and on account of the richly fossiliferous occurrence of Small Shelly Fossils or trilobites around the Kunming–Wuding and Malong–Yiliang areas of eastern Yunnan Province (Steiner et al., 2005). The widely different sedimentary environments and fossil assemblages of the Lower Cambrian in the eastern Yunnan areas were controlled by the Xiaojiang Fault, resulting from the Tsinning tectonic movement (700 Ma) (Luo et al., 1994) (Fig. 1A). In these areas, the Lower Cambrian, overlying the Ediacarian dolomite (Dengying Formation), comprises fossil-bearing phosphorous dolomite (phosphorite), dolomitic limestone, mudstone, and sandstone. The celebrated Chengjiang fauna was found exceptionally preserved in the upper Chiungchussuan (informerly Qiongzhusian) Heilinpu Formation (well-bedded mudstone) mostly in the areas around Haikou and Chengjiang at both sides of Dianchi Lake (Fig. 1A) (Luo et al., 1999; Hou et al., 2004). In contrast, the Chengjiang-type fossil occurrences are markedly sparse in the coeval muddy deposits of Malong–Yiliang areas, probably due to the high-energy sedimentary environment and extensive bioturbation of mudstone sediments (Hu, 2005; Zhao et al., 2010). Meanwhile, the disparity in trilobite assemblages was recognized in the two regions at both sides of the NE–SW directional Xiaojiang Fault during the Early Cambrian intervals. The Kunming–Wuding area west to the fault yields abundant trilobites composed of *Eoredlichia intermedia*, *Yunnancephalus yunnanensis*, by contrast, Malong–Yiliang area contains *Wutingaspis malongensis*, *Malungia laevigata* (Steiner et al., 2005).

Kuangshanotreta malungensis gen. et sp. nov. described here was recovered from the Kuangshan section of Kuangshan section 13 southwest of Malong County (Fig. 1A). The fossil-bearing strata belong to the *Eoredlichia-Wutingaspis* Zone, Lower Cambrian Chiungchussuan

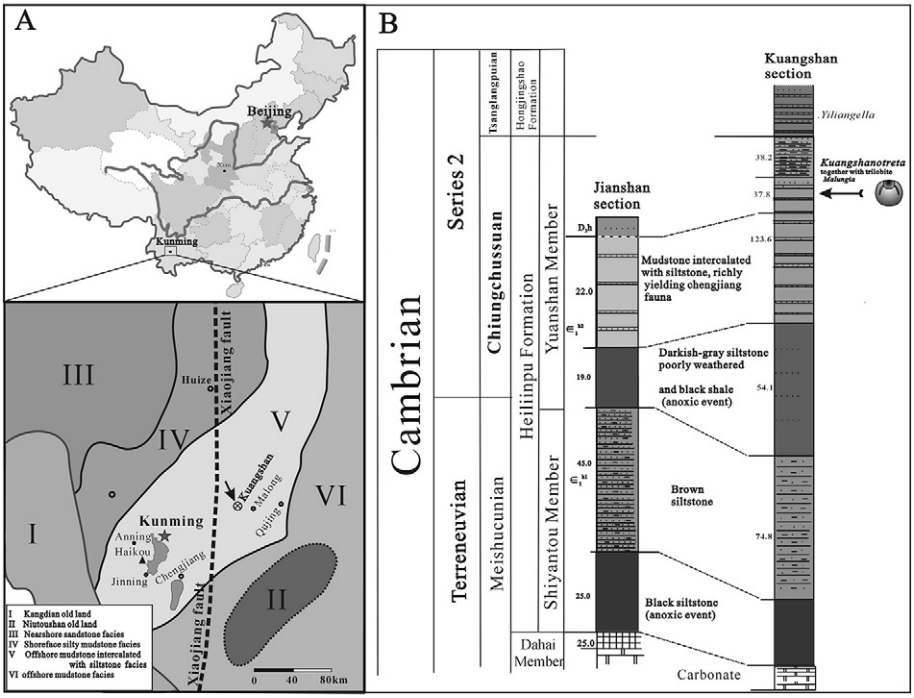

Fig. 1. A. Map showing the location of studied section in China (upper) and the deposition environment of the fossil-bearing strata (arrow) where the brachiopod *Kuangshanotreta malungensis* gen. et. sp. nov. Zhang, Holmer and Hu, was collected. B. Stratigraphical correlations of the muddy deposits yielding the Chengjiang fauna between Kuangshan section in Malong County and Jianshan section at Haikou town of Kunming, southern China; note the stratigraphic level (tailed arrow) containing the assemblage of the algae–micromorphic brachiopod *K. malungensis*, which is absent or eroded in the Haikou area.

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