Short Communication

First report of brachiopods with soft parts from the Lower Cambrian Latham Shale (Series 2, Stage 4), California

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A R T I C L E   I N F O

Article info

Article history:
Received 9 December 2019
Received in revised form 25 April 2020
Accepted 26 April 2020
Available online 5 May 2020

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Exceptionally preserved faunas have greatly improved our understanding of animal origin and evolution, and systematic investigations of Cambrian sediments around the world during the last two decades have led to a dramatic increase in the numbers of Konservat-Lagerstätten [1]. In particular, these deposits have an abundance of exceptionally preserved ecdysozoans, such as scalidophorans and panarthropods [2,3]. However, soft-bodied fossil lophophrozoans are much less common in Cambrian Konservat-Lagerstätten. The Brachiopoda, which are now firmly nested within the lophophrozoans, are one of the most successful invertebrate phyla in terms of abundance and diversity during the Phanerozoic Eon [4]. The large majority of brachiopod genera are known almost exclusively from their mineralized fossil shells. Our knowledge of brachiopod anatomy, however, relies heavily on their extant relatives. Fortunately, the remarkable discovery of exquisitely preserved soft tissues from exceptional Cambrian deposits, such as the famous Chengjiang and Burgess Shale Konservat-Lagerstätten, has introduced an entirely new line of evidence about shell internal tissues and soft organs, including the lophophore, mantle canals, digestive tracts, pedicle and setal fringes in early brachiopods [4,5].

More than fifty localities of Burgess Shale-type deposits are presently known from Cambrian strata [1], whilst soft-bodied brachiopods are rarely preserved in the fossil state. The Lower Cambrian Latham Shale is one such example, which is well known for its abundant and well-preserved olenellid trilobite fauna accompanied by brachiopods, some hyolithids and examples of soft-bodied preservation of Anomalocaris appendages and palaeoscolecid worms [6]. However, almost nothing is known about the soft-part preservation of the brachiopods in this unit. In this paper, we present the first report of two species of brachiopods, Paterina prospectensis and Mickwitzia occidens, displaying soft part preservation from Lower Cambrian Latham Shale (Series 2, Stage 4), California (Figs. 1, S1 and S2 online).

Paterina prospectensis — The specimen of Paterina prospectensis is represented by a dorsal internal mould with pronounced negative relief (Fig. 1a, b, e, f). The ventral valve is fragmented, and only the posterior ventral margin is preserved, probably due to exfoliation of the shale-hosted specimen. The dorsal valve has an ovate to subcircular shell with a nearly straight hinge line; the valves reach a maximum width of 8.82 mm and a maximum length of 10.91 mm (Fig. 1a). The dorsal internal mould has a well-preserved ornamentation with evenly spaced prominent growth lines (Fig. 1a, e). These concentric growth lines are spaced regularly (12 over a distance of 1 mm). They are interrupted by nick points, and form sets of drapes in the mid-anterior margin (Fig. 1a). The inner large section of the valve has retained its calcium phosphatic shell, while the outer section of valve is impressed as an internal mould with its original composition lost and replicated by aluminosilicates. The setae are remarkably long (maximum length 7.18 mm) in respect to shell size (Fig. 1a, b). The setae fringe the dorsal and ventral valve margins and are generally at their greatest length anteromedially, decreasing in length posterolaterally (Fig. 1a, b). The individual setae are elongated straight without any curve or twist, and seemingly taper distally (Figs. 1b and S2b, g online). These setae are spaced at about 20–40 μm intervals, with an estimated number of more than 50. Some well-preserved individual setae are evidently coated or partially replaced by pseudomorphed frambooidal, octahedral, and cubic pyrite (Figs. 1f and S2c online). The frambooidal microarchitecture varies from disorganized to well organized, and microcrystals can be tightly or loosely packed (Fig. 1f).

Mickwitzia occidens — The size of Mickwitzia occidens is relatively large (23 mm long and 26 mm wide) and appears to be more or less flat in lateral profile as other shale-hosted specimens (Fig. 1c, d, g). The outline of the valve is ovoid with the apex located...
Fig. 1. Paterina prospectensis (7002-300) and Mickwitzia occidens (10-8-1) from the Lower Cambrian Latham Shale. (a,b) Light image of the well-preserved specimen of P. prospectensis showing the dorsal valve (Dv), growth lines (Gl), lateral margin of dorsal valve (Ldv), nick points (Np), prolongate setae (Ps) and relics of ventral valve (Rvv); (b) light image of the boxed area in (a) showing the exquisite marginal setae preserved as yellow thin films; (c) light image of the specimen of M. occidens showing the dorsal valve (Dv), metamorphic shell (Ms), reticulate-pustulose ornamentation (Rpo); (d) light image of the boxed area in (c) showing the marginal setae around the lateral part of the shell; white arrows indicate the slim setae; (e) scanning electron microscope image of the enlarged area in (a) showing the concentric growth lines; white arrow indicates the growth lines; (f) backscattered electron image of P. prospectensis from the white dot in (b) showing the setal composition of the pseudomorphed pyrite; (g) scanning electron microscope image of the enlarged area in (c) showing the reticulate-pustulose ornamentation.
at the posterior margin (Fig. 1c). Reticulate-pustule ornament, typical of all known species of Mickwitzia, could also be easily observed on this well-preserved specimen (Figs. 1g and S2e, h online) [7]. The concentric growth lines and radial costellae radiate from the apex at the posterior margin, with about 16 filia and 20 costellae over a distance of 1 mm. The specimen also preserves a smooth metamorphic shell, about 500 μm across, in the posterior part of the dorsal valve (Figs. 1c and S2e, h online). Elemental mappings show that the shell valves have high concentrations of iron, but little phosphate (Fig. S2f online). Some slim setae could be observed along the lateral margin with a posterior-facing tendency (Figs. 1d and S2h online). Unlike the setae of P. prospectensis described above, they are curved and intersected with each other (rather than elongate straight anteriorly), which in turn makes it hard to determine their spacing and total number. Compared to the material of its closest relative Heliomedusa orienta, the setae of this specimen are rather shorter and thinner, about 2 mm long and 10 μm in diameter (comparing with up to 4 mm in length and 50 μm in diameter for H. orienta) [8] (Fig. S3 online). These differences in the development of the setal fringes may be due to the biases in preservation and to the fact that we only have one known specimen from the Latham Shale.

Paterina prospectensis was originally assigned to Kutorgina and Iphides by Walcott, but later he transferred it to Micromitra (Paterina), based on its concentrically striated ornamentation, and subsequently it has been known as Paterina prospectensis [6]. The main difference between Paterina and Micromitra is that the former has an open delthyrium whilst the latter has a homeodeltidium, and they also differ in external ornament (prominent growth lines being a characteristic feature more frequently observed in Paterina species compared with the more elaborate ornamentation in species of Micromitra) [9]. Both genera are representatives of the Paterinata, which were the first brachiopods to emerge from the Cambrian Explosion, and they became extinct in the late Ordovician [9]. The chitinous setae are most likely replicated by calcium in Micromitra burgessensis, and by iron in Paterina zenobia and P. prospectensis; the replacement probably occurred during late diagenesis [5]. The setae preserved in P. prospectensis are very reminiscent of those preserved in specimens of Xianshanella haikouensis from the Chengjiang Konservat-Lagerstätte, South China [4]. They share remarkable similarities in being relatively long, and the maximum length can reach 7.18 and 7 mm in P. prospectensis and X. haikouensis respectively. They are both preserved as reddish imprints, replicated by iron matter, which may suggest a shared similar preservation mode between Latham Shale and the Chengjiang Konservat-Lagerstätte [4]. Moreover, the presence of setae-bearing brachiopod specimens possibly suggests that the individuals were buried alive, having undergone limited or no transportation. The setal preservation in specimens of P. zenobia from Burgess Shale was previously the first report of soft part preservation in this genus, and the setae of P. prospectensis discussed here extends the fossil record of this exceptional preservation from Wulian Stage back to the unnamed Stage 4. In addition, the pronounced similarities of the shell ornamentation and setal morphology between P. prospectensis and P. zenobia may possibly suggest that life strategies of brachiopods (sessile attaching and mimicry [5]) had already developed by Stage 4.

It has been suggested that mickwitziid occupy a unique position in the brachiopod stem in that they are somehow linked to the even more problematic tommotiids, a suggestion which was primarily based upon the presence of shared characters including shell composition, ultrastructure, and the striated tubes related to the presence of shell-penetrating setae [7,8]. Mickwitziiids have a cosmopolitan distribution and have been reported from the Cambrian Series 2 of west Laurentia, Baltic, and Australia [7]. In South China, mickwitziid are represented exclusively by Heliomedusa orienta, an enigmatic species recently assigned to stem group brachiopods together with Mickwitzia, with a lowermost occurrence in the middle-upper Yu’anshan Formation (Eoredlichia trilobite Zone) [8,10] (Fig. S1 online). Intriguingly, the specimens of Mickwitzia occidentals collected from Latham Shale discussed here is remarkably similar to specimens of H. orienta from the Chengjiang Konservat-Lagerstätte in size, morphology, preservation of setae and the reticulate-pustule ornament. In addition, the preservation mode also bears some overall similarities to the Chengjiang-type preservation in terms of weathering and replication of the shell and soft parts as iron oxides, as well as in the lack of sulphur in both localities. It is possible that Mickwitzia actually is a senior synonym of Heliomedusa, but as pointed out by many authors, it is still very difficult to make detailed taxonomic comparisons between shale-hosted and three-dimensionally preserved material, and more material preserved as well as in the Latham Shale is needed to test this hypothesis. Moreover, the occurrence of Heliomedusa-like Mickwitzia in Latham Shale represents an important stratigraphic extension of this taxon in North America, making it reasonable to suggest that the first appearance datum (FAD) of mickwitziid in Laurentia and Gondwana may be diachronous, and it is also possible that the cosmopolitan mickwitziiids may have first appeared in South China.

Conflict of interest

The authors declare that they have no conflict of interest.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (41721004002, 41890844, 41425008 and 41621003), the Strategic Priority Research Program of Chinese Academy of Sciences (XDB26000000), the Program of Introducing Talents of Discipline to Universities (D17013), Research of L. E. Holmer supported by the Swedish Research Council (VR Project No. 2018-03390) and a Zhongjian Yang Scholarship from the Department of Geology, Northwest University, China. We thank Nigel Hughes and Lauren English (University of California, Riverside) for their permission and assistance with the loan of the specimens of brachiopods from Latham Shale. We also thank Timothy Topper and Luoyang Li (Swedish Museum of Natural History) for their help with photographing. Many thanks to anonymous referees for valuable comments that greatly improved the manuscript.

Author contributions

Zhifei Zhang initiated and designed the project. Yue Liang wrote the draft manuscript with input from Zhifei Zhang and Lars E. Holmer. Yue Liang and Yazhou Hu performed and analysed the SEM and μ-XRF experiments. Lars E. Holmer and Zhifei Zhang revised the draft and edited the final submission.

Appendix A. Supplementary materials

Supplementary materials to this article can be found online at https://doi.org/10.1016/j.scib.2020.05.001.

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Zhifei Zhang is a Changjiang Scholar Professor in the Department of Geology, Northwest University, China. He is interested in exceptionally preserved Cambrian fossils, notably brachiopods and other relative lophotrochozoans, as well as associated Cambrian skeletal fossils from carbonates worldwide.