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Short Communication

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

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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 pan-arthropods [2,3]. However, soft-bodied fossil lophotrochozoans are much less common in Cambrian Konservat-Lagerstätten. The Brachiopoda, which are now rather firmly nested within the lophotrochozoans, is 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 bra-

chiopods, *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 framboidal, octahedral, and cubic pyrite (Figs. 1f and S2c online). The framboidal 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

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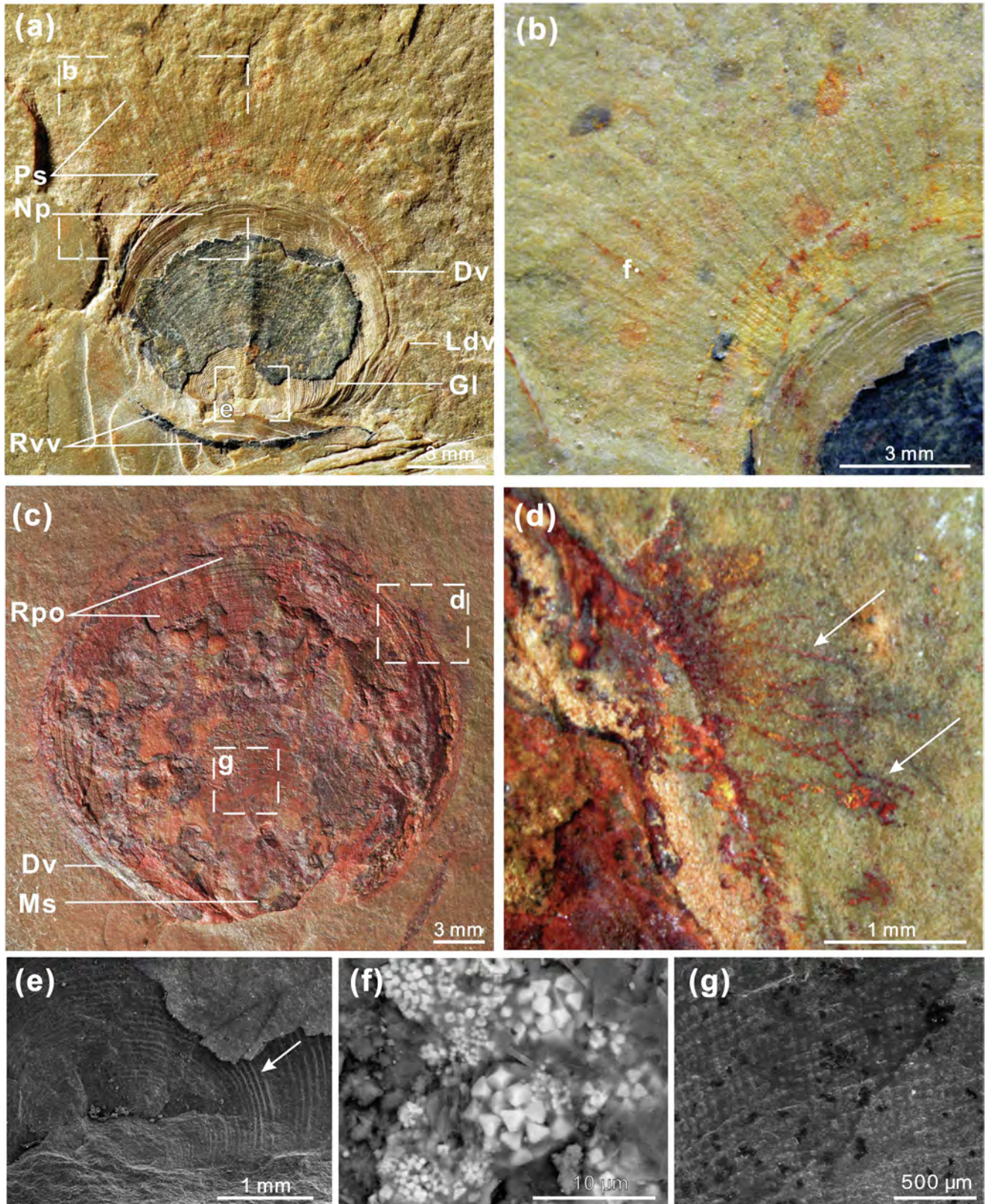


Fig. 1. *Paterina prospectensis* (7002-300) and *Mickwitzia occidentens* (10-8-1) from the Lower Cambrian Latham Shale. (a–b) Light image of the well-preserved specimen of *P. prospectensis* showing the dorsal valve (Dv), growth lines (GI), lateral margin of dorsal valve (Ldv), nick points (Np), prolongate 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. occidentens* 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-pustulose 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 fila 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 (Fig. 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 (Fig. 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 orientata*, the setae of this specimen are rather shorter and thinner, about 2 mm long and 10 μm in diameter (compared with up to 4 mm in length and 50 μm in diameter for *H. orientata*) [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 *Iphidea* 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 Wuliuan 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 mickwitzziids 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]. Mickwitzziids have a cosmopolitan distribution and have been reported from the Cambrian Series 2 of west Laurentia, Baltic, and Australia [7]. In South China, mickwitzziids are represented exclusively by *Heliomedusa*

orientata, an enigmatic species recently assigned to stem group brachiopods together with *Mickwitzia*, with a lowermost occurrence in the middle-upper Yu'an-shan Formation (*Eoredlichia* trilobite Zone) ([8,10], Fig. S1 online). Intriguingly, the specimen of *Mickwitzia occidens* collected from Latham Shale discussed here is remarkably similar to specimens of *H. orientata* from the Chengjiang Konservat-Lagerstätte in size, morphology, preservation of setae and the reticulate-pustulose 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 mickwitzziids in Laurentia and Gondwana may be diachronous, and it is also possible that the cosmopolitan mickwitzziids may have first appeared in South China.

Conflict of interest

The authors declare that they have no conflict of interest.

Acknowledgments

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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.



Yue Liang is a Ph.D. candidate at the Department of Geology, Northwest University, China. Her research is aimed to enhance the understanding of evolution and phylogenetics of Cambrian stem group brachiopods and other lophotrochozoans, in combination with knowledges from morphological and anatomical studies of the living cousins. To achieve this, she is undertaking palaeobiological investigations of Cambrian fossils from China, Sweden, USA and Estonia.

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

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Abstract: The exceptionally preserved brachiopods (*Paterina* and *Mickwitzia*) are described for the first time from the Lower Cambrian Latham Shale (Series 2, Stage 4), California, USA. *Paterina prospectensis* is represented more or less with the original mineralized phosphatic valve with distinct concentric growth lines on the shell surface, which is provided with delicate setae preserved extraordinarily around the anterior margin. *Mickwitzia occidens* is represented as a flattened reddish-brown imprint of shell valves, partly preserving the reticulate-pustulose surface ornament. This is the first report of a paterinate brachiopod with long hair-like setae from outside of the Burgess shale which also extends fossil record trace of exceptionally preservation of the paterinids from the Wuliuan 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 have already developed by Stage 4. *Mickwitzia occidens* has a striking resemblance in terms of size, morphology, preservation of setae and the reticulate-pustulose ornament to the enigmatic brachiopod *Heliomedusa orientalis* renowned in the Chengjiang Konservat-Lagerstätte, recently assigned to Mickwitziidae. The occurrence of *Heliomedusa*-like *Mickwitzia* in Latham Shale represents an important geological extension of this taxon to Cambrian Stage 4 in North America and raising a question as if the first appearance datum (FAD) of mickwitziids in Laurentia and pan-Gondwana seems not synchronous, and it is also possible that the cosmopolitan mickwitziids may have first appeared in South China.

Key Words: Lower Cambrian • Latham Shale • Konservat-Lagerstätte • *Paterina prospectensis* • *Mickwitzia occidens*

Material and Methods

This study is based on two well-preserved specimens, *Paterina prospectensis* and *Mickwitzia occidens*, collected from the fine-grained Lower Cambrian Latham Shale (Series 2, Stage 4), hosted in the collection of University of California, Riverside, USA. The Lower Cambrian Latham Shale is a mixed siliclastic-carbonate unit which crops out prominently in two ranges, the Providence Mountains and the Marble Mountains, in the Eastern Mojave of Southern California (Fig. S1a) (Gaines and Droser, 2002). The shale sequence is about 20 meters thick and lies stratigraphically between the Zabriskie Quartzite and Chambless Limestone (Fig. S1b). Trilobites in the Latham Shale are from the *Bristolia* subzone of the *Bonnia-Olenellus* Zone, indicating that the Latham Shale belongs to the upper Dyeran Stage (Waucoban series) of Laurentia, equivalent to the Toyonian Stage of Siberia (Palmer 1998). The mudstones of the Latham Shale consist of amalgamated event beds, which would have facilitated transport of soft bodied fossils from a living environment to one which favoured their preservation and provide rapid burial of the fossils. Apart from frequency of burial events, lack of coarse-grained sediments from some facies, and proximity of the oxycline were also conducive to soft-bodied preservation. More importantly, ichnologic evidence from the Latham Shale suggests a low depth of bioturbation, which is generally a prerequisite for soft bodied preservation, and most likely the result of low levels of bottom water oxygenation (Allison and Briggs, 1993; Gaines et al., 2005). These factors may have been a crucial factor in the rare soft-bodied preservation in this unit, and that the subsequent secular increase in depth of bioturbation may have restricted soft-bodied preservation in comparable environments (Gaines and Droser, 2002).

Fossils were examined under a Zeiss Stemi 305 microscope and photographed with the Zeiss Smart Zoom 5 Stereo-micrographic system and Cannon camera mounted on a photographic system. Uncoated specimens were examined with a FEI Quanta 400FEG scanning electron microscope at

Northwest University (NWU) and the Swedish Museum of Natural History (SMNH). They were also tested by Bruker M4 Tornado table-top energy-dispersive micro X-ray fluorescence (μ -XRF) to get the characterization of the elemental abundances in samples from the fluorescence spectrum.

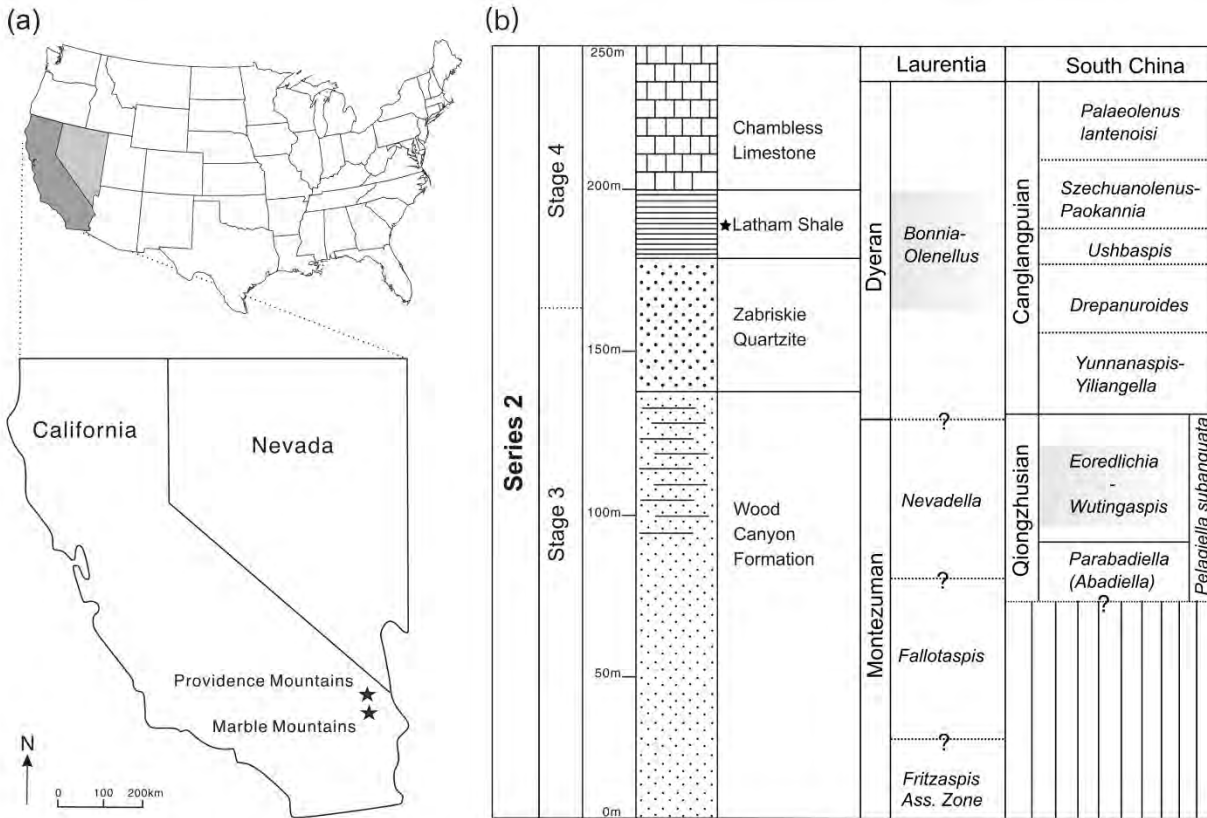


Fig. S1 (a) Location map of the study area; (b) Lower Cambrian stratigraphy of the study area and tentative correlation based on trilobite zonation modified from Stewart and Poole (1975) and Zhang et al. (2017); black star indicates the location of Latham Shale in California and its stratigraphic sequence, while the grey shadow shows the biozones yielding the *Paterina prospectensis* and *Mickwitzia occidens* in Laurentia and *Heliomedusa orientata* in South China, respectively.

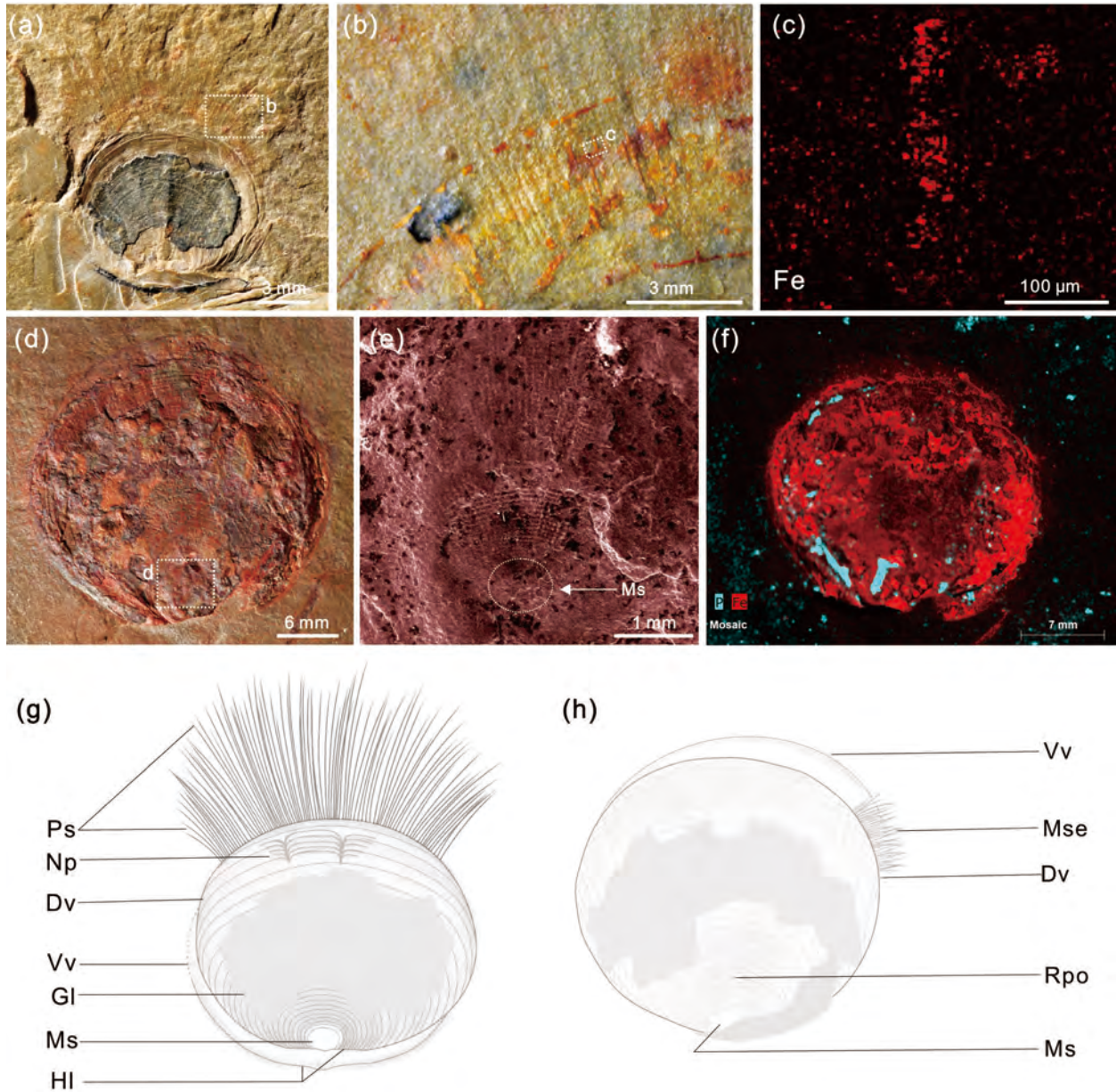


Fig. S2 *Paterina prospectensis* (7002-300) and *Mickwitzia occidens* (10-8-1) from Latham Shale. (a-c), specimen of *P. prospectensis* showing the delicate setal fringe; (b) light image of marginal setae with iron oxides preserved as yellow thin films; (c) EDS elemental mapping of the setae in the boxed area in Fig. S2b indicating the iron oxides composition of setae; (d-f) *Heliomedusa*-like flattened preservation of *M. occidens* with pretty good ornamentation; (e) scanning electron microscope image showing the reticulate-pustulose ornamentation and the metamorphic shell

(Ms); (f) Micro-XRF results indicate the iron rich abundance of the shell and a little phosphorus around the posterolateral margin, Fe = iron, P = phosphorus; (g-h) interpretive drawing of *P. prospectensis* and *M. occidentis* showing the dorsal valve (Dv), hinge line (Hl), growth lines (Gl), lateral margin of dorsal valve (Ldv), metamorphic shell (Ms), marginal setae (Mse), nick points (Np), prolongate setae (Ps) and relics of ventral valve (Rvv).

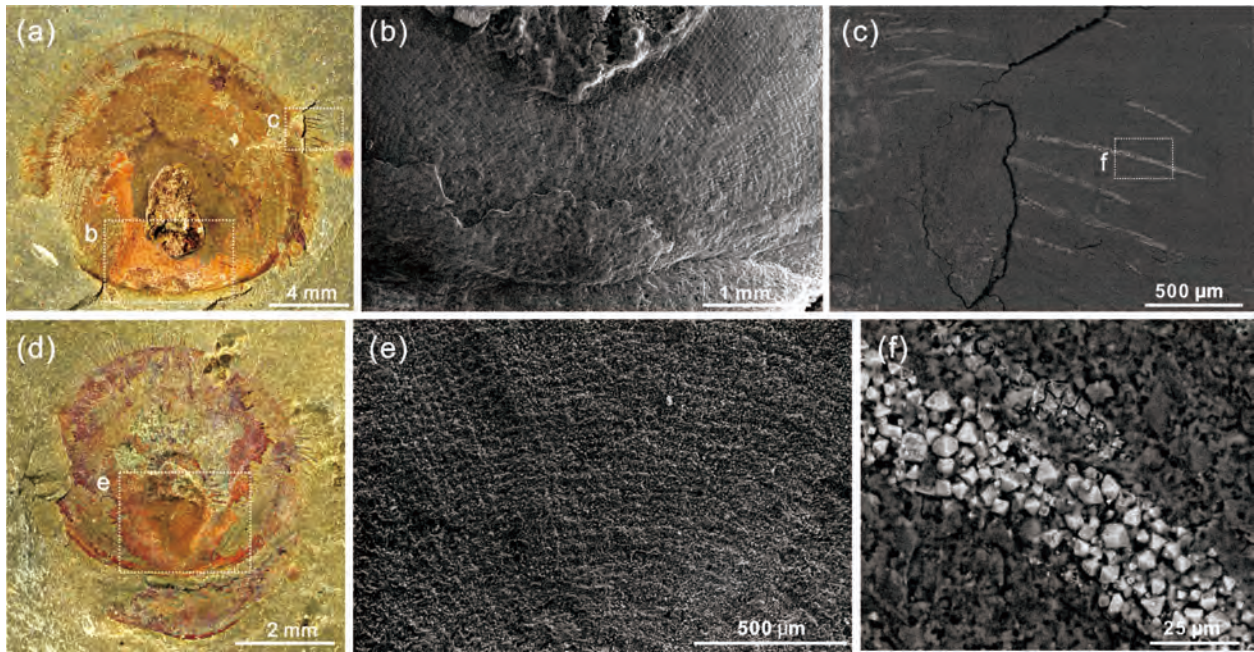


Fig. S3 *Heliomedusa orientata* from the Chengjiang Lagerstätte. (a-c) SJZ 2337; (b) scanning electron microscope image showing the reticulate-pustulose ornamentation; (c) backscattered scanning electron microscope image showing the marginal setae; (d-e) SJZ 2232; (e) scanning electron microscope image showing the reticulate-pustulose ornamentation; (f) enlarged view of boxed area in Fig. S3c showing that setae are composed dominantly of subhedral to euhedral pseudomorphed pyrite crystals.

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美国加利福尼亚州寒武纪早期莱瑟姆页岩（Latham Shale）中首次发现软躯体保存的腕足动物

梁悦, Lars E. Holmer, 胡亚洲, 张志飞*

美国加利福尼亚州寒武纪早期莱瑟姆页岩（第二世, 第四期）作为国际上著名的布尔吉斯页岩型化石库之一, 以保存了大量精美的小油栉虫类（olenellids）三叶虫著称, 同时伴有丰富的腕足动物和软舌螺类化石。但迄今未发现任何腕足动物软组织化石。本文首次报道了该化石库发现的软躯体保存的 2 个腕足动物属种——前瞻型神父贝（*Paterina prospectensis*）和意外迈克威仔贝（*Mickwitzia occidentis*）。前瞻型神父贝壳体边缘保存精细、排列致密、长达 7 mm 的刚毛, 刚毛呈细线状、红褐色, 扫描电镜分析发现保存为次生的莓状黄铁矿。前瞻型神父贝腕足动物的刚毛和壳体与布尔吉斯页岩中发现的底栖固着的神父贝十分相似, 表明腕足动物神父贝中发现的拟态状底栖固着生活方式可以追溯到寒武纪第四期。意外迈克威仔壳体纹饰和向后排列的纤细刚毛与我国澄江化石库发现的东方日射水母贝（*Heliomedusa orientalis*）极为相似, 因此该发现表明干群类腕足动物迈克威仔类（Mickwitziiidae）在劳伦大陆和泛冈瓦纳大陆的首现可能并不同时, 很有可能迈克威仔类在寒武纪早期起源于包括我国华南在内的东冈瓦纳地区, 随后开始向全球扩散。