

# Evidence for seafloor microbial mats and associated metazoan lifestyles in Lower Cambrian phosphorites of Southwest China

STEPHEN Q. DORNBOS, DAVID J. BOTTJER AND JUN-YUAN CHEN

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The increase in the depth and intensity of bioturbation through the Proterozoic–Phanerozoic transition changed the substrates on which marine benthos lived from being relatively firm with a sharp sediment–water interface to having a high water content and blurry sediment–water interface. Additionally, microbial mats, once dominant on normal marine Proterozoic seafloors, were relegated to stressed settings lacking intense metazoan activity. This change in substrates has been termed the ‘agronomic revolution’, and its impact on benthic metazoans has been termed the ‘Cambrian substrate revolution’. The shallow marine phosphorites of the Lower Cambrian Meishucun Formation of southwest China contain evidence suggestive of the presence of seafloor microbial mats. This evidence includes abundant and distinctive red-colored bedding planes enriched in heavy iron minerals and mica, interpreted as resulting from mat-decay mineralization and mica trapping by microbial mats. The radular grazing trace fossil *Radulichnus* is also found in this formation, indicating a firm, microbial mat-bound substrate. These radular scratches are always preserved with circular impressions around 10 cm in diameter, possibly the fossils of soft-bodied organisms. The first relatively intense bioturbation in this region is found in this formation and is dominated by horizontal *Thalassinoides* burrows, which could represent undermat mining behavior. The evidence for the presence of microbial mats in the Lower Cambrian Meishucun Formation, and for metazoan lifestyles associated with such mat-bound seafloors, reveals that normal marine environments dominated by typical Proterozoic-style soft substrates still existed during the Cambrian substrate revolution. □ *Meishucun Formation, Radulichnus, Thalassinoides, microbial mats, Cambrian.*

Stephen Q. Dornbos [sdornbos@usc.edu]. (Current address) Department of Geosciences, University of Wisconsin–Milwaukee, Milwaukee, WI 53201, USA; David J. Bottjer [dbottjer@usc.edu], Department of Earth Sciences, University of Southern California, Los Angeles, CA 90089-0740, USA; Jun-Yuan Chen [chenjunyuan@163.net], Nanjing Institute of Geology and Palaeontology, Nanjing 210008, China. 3rd September 2002, revised 30th November 2003.

The increase in bioturbation levels as metazoans began to invade infaunal ecospace is emerging as one of the most significant features of the Proterozoic–Phanerozoic transition. Increases in the intensity and verticality of bioturbation in siliciclastics and carbonates through this transition have been well-documented (e.g. Droser 1987; Droser & Bottjer 1988; Droser *et al.* 1999; McIlroy & Logan 1999). This increase in bioturbation, particularly vertical bioturbation, caused a transition in subtidal siliciclastic environments from typical Proterozoic-style soft substrates to typical Phanerozoic-style soft substrates. Typical Proterozoic-style soft substrates are characterized by low levels of strictly horizontal bioturbation, a low water content, a relatively sharp sediment–water interface, and seafloor microbial mats. Typical

Phanerozoic-style soft substrates, on the other hand, are characterized by intense horizontal and vertical bioturbation, a high water content, a diffuse sediment–water interface, and the lack of well-developed seafloor microbial mats (e.g. Droser 1987; Droser & Bottjer 1988; Seilacher & Pflüger 1994; Droser *et al.* 1999; Hagadorn & Bottjer 1999; Seilacher 1999; Droser *et al.* 2002). A crucial characteristic of these typical Phanerozoic-style soft substrates is the presence of a well-developed mixed layer, the soupy upper few centimeters of seafloor sediment that are homogenized by bioturbation (e.g. Ekdale *et al.* 1984).

This substrate transition was not geologically instantaneous, however, and the dominance of typical Phanerozoic-style soft substrates did not occur with the initial increase in the depth and intensity of

bioturbation, as well as ichnofossil diversity, at the Proterozoic-Phanerozoic boundary (e.g. Droser *et al.* 2002). While the precise duration of this substrate transition has yet to be determined, bioturbation levels reach typical Phanerozoic levels in subtidal carbonates during the Ordovician (Droser & Bottjer 1988, 1989, 1993). This probably means that much of the Cambrian, certainly the Early Cambrian at least, was a unique time interval wherein vestiges of typical Proterozoic-style soft substrates and the beginnings of typical Phanerozoic-style soft substrates co-existed in normal marine subtidal settings. Indeed, this research presents data from phosphorites of the Lower Cambrian Meishucun Formation of southwest China that provides evidence for an Early Cambrian setting in which typical Proterozoic-style soft substrates, complete with microbial mats, existed in conjunction with metazoans adapted to survival on and underneath such substrates. In doing so, this research documents the paleoecology and organism-sediment interactions of Early Cambrian benthic metazoans in a phosphogenic environment, adding to the data already collected from siliciclastic and carbonate environments.

## Previous research

### *Cambrian substrate revolution*

Seilacher and Pflüger (1994) termed the Proterozoic-Phanerozoic boundary substrate transition the 'agronomic revolution', and defined it as a transition from Proterozoic 'matgrounds', with well-developed seafloor microbial mats, to Phanerozoic 'mixgrounds', with intense levels of horizontal and vertical bioturbation and lacking well-developed seafloor microbial mats. They also postulated that Neoproterozoic benthic metazoan lifestyles would center on microbial mats (Seilacher & Pflüger 1994; Seilacher 1999). These lifestyles included: (1) mat encrusters, which lived attached to the microbial mats; (2) mat scratchers, which grazed on the mats; (3) mat stickers, which lived with their lower ends inserted in the mats; and (4) undermat miners, which burrowed horizontally underneath the mats and fed on decomposing mat remnants (Seilacher & Pflüger 1994; Seilacher 1999).

The ecological and evolutionary effects of this substrate transition on nonburrowing benthic metazoans, particularly if they were adapted to typical Proterozoic-style soft substrates, were termed the 'Cambrian substrate revolution' by Bottjer *et al.* (2000, p. 2). Evidence for the Cambrian substrate revolution is seen in the evolutionary response of Cambrian nonburrowing benthic echinoderms and

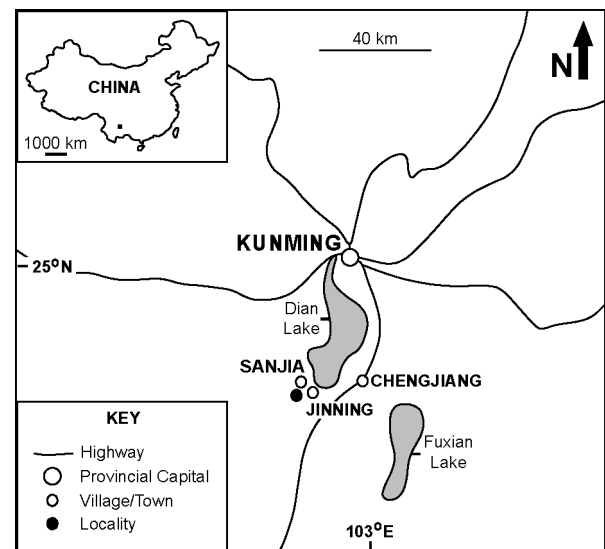


Fig. 1. Location map of Xiaowaitoushan Hill quarry near Sanjia Village, Jinning, Yunnan Province, China (Modified from Chen & Zhou 1997).

the ecological response of early grazing molluscs to these substrate changes (Bottjer *et al.* 2000; Dornbos & Bottjer 2000).

## Geologic setting

Exposures of the Lower Cambrian Meishucun Formation in a quarry on Xiaowaitoushan Hill near Sanjia Village, Jinning, Yunnan Province, China were examined during this study (Fig. 1). This locality was a proposed type section for the Precambrian-Cambrian boundary because of its abundant and diverse small shelly fossils. The Meishucun Formation is a lowermost Cambrian sequence of dolomitic phosphorite, dolomite, and bentonite up to 19 m thick (Chen & Zhou 1997; Zhang *et al.* 1997; Zhu 1997), consisting of the Lower Phosphate, White Clay, Upper Phosphate, and Dahai Members (Fig. 2). The two phosphorite members are separated by the thin (0.5 to 2 m) White Clay Member bentonites (Fig. 2; Chen & Zhou 1997). Field observations indicate that the Lower Phosphate Member is composed of relatively thin, planar beds of dolomitic granular phosphorite, while the Upper Phosphate Member contains thicker, hummocky-cross-stratified beds of dolomitic granular phosphorite (Figs 2, 3, 4). This difference in sedimentary structures indicates a shallowing upward from below storm wave base to between storm and normal wave base from the Lower to Upper Phosphate Members. This shallowing continues into the uppermost cross-bedded Dahai Member dolomites that are capped by a karstic dissolution surface and overlain by black shales

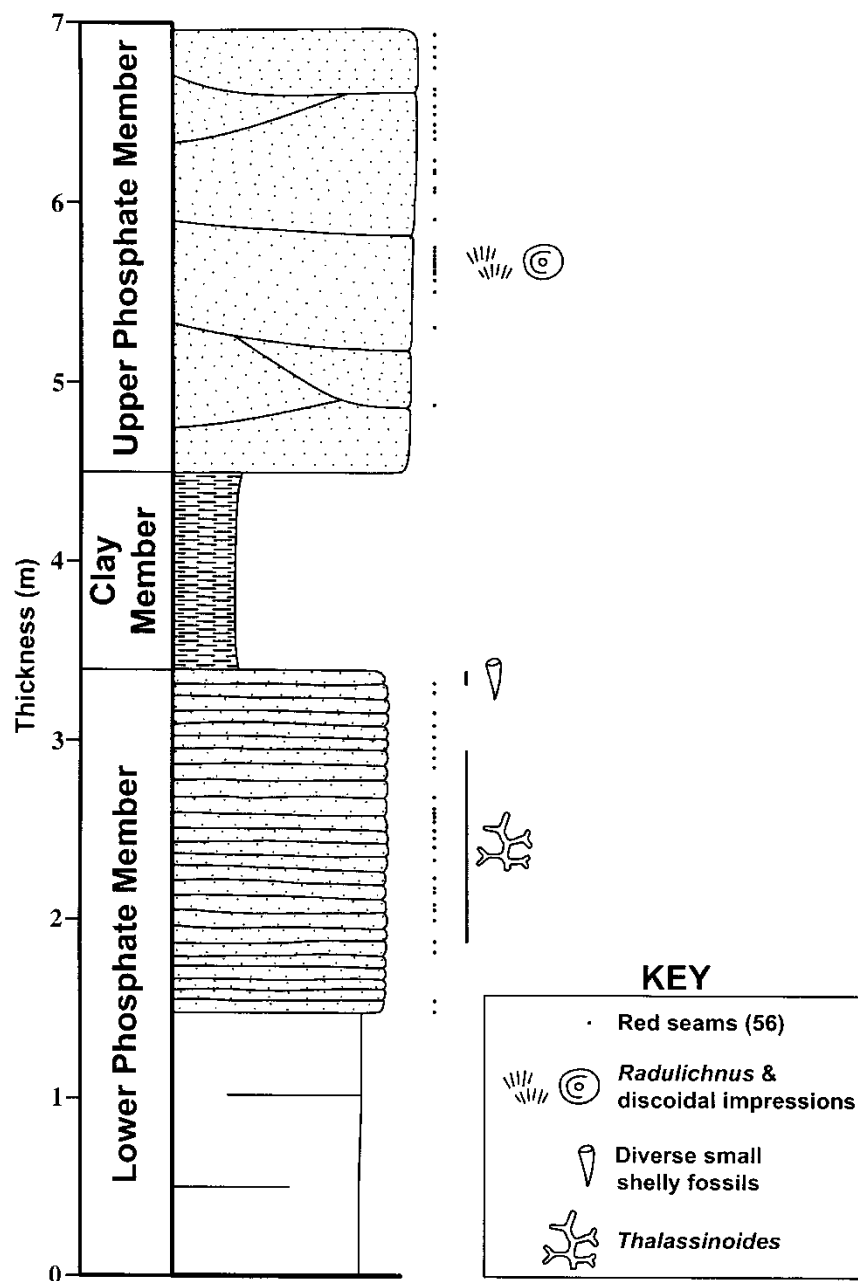


Fig. 2. Composite stratigraphic column of Lower and Upper Phosphate Members of Meishucun Formation as exposed in Xiaowaitoushan Hill quarry near Sanjia Village, Jinning, Yunnan Province, China.

(Chen & Zhou 1997). The Meishucun Formation, therefore, represents a shallowing upward parasequence of dolomitic phosphorite and dolomite disrupted by a central bentonite layer. Both phosphate members contain a diverse array of small shelly fossils as well as abundant phosphatic intraclasts and evidence for mm-scale phosphatic hardgrounds (Chen & Zhou 1997; Zhang *et al.* 1997; Zhu 1997), indicating deposition in phosphogenic environments. Such environments are typically characterized by high energy conditions, low terrigenous sedimentation rates, high organic burial rates, probably due to high export productivity, seafloor microbial mats, and the forma-

tion, erosion, and reworking of phosphatic hardgrounds (e.g. Froelich *et al.* 1988; Lucas & Prevot 1991; Föllmi 1996; Trappe 1998; Soudry 2000).

## Methods

A combination of field observations and thin section analysis produced the data at the core of this study. Field observations focused on metazoan trace fossils, possible evidence for seafloor microbial mats, and diagnostic sedimentary structures. A total of 27 thin sections from the Lower and Upper Phosphate



Fig. 3. Field photograph of Upper Phosphate Member of the Meishucun Formation at Xiaowaitoushan Hill quarry near Jinning, Yunnan Province, China showing thick, hummocky cross-stratified beds. Hammer for scale. Obelisk marks site of once-proposed Precambrian-Cambrian boundary.

Members were examined in order to search for any evidence suggestive of the presence of seafloor microbial mats. Where possible, the paleoecology of Meishucun Formation small shelly fossil genera was also interpreted from the literature. The data resulting from these methods allow for the interpretation of metazoan paleoecology and the characterization of the substrates on which they lived.

## Metazoan behavior and paleoecology

### *Grazing traces*

A key piece of trace fossil evidence for metazoan paleoecology exists in the Upper Phosphate Member. On one *in situ* bedding plane 6 m above the base of the Meishucun Formation and two bedding planes on slabs in float, totaling 2.4 m<sup>2</sup> in area, is the radular-grazing trace fossil *Radulichnus* (Figs 2, 5). One of these float slabs was collected and is stored at the Early Life Research Center in Chengjiang, Yunnan, China. *Radulichnus* was first described by Voigt (1977) from the surfaces of Jurassic, Cretaceous, and Pliocene oyster valves, as well as from Recent bivalve and gastropod shells. These fossil and modern *Radulichnus* are interpreted as the radular grazing traces of gastropods and polyplacophorans created by their feeding on algal films on the surface of the mollusc shells (Voigt 1977). These *Radulichnus* consist of small arcuate sets of scratches less than 1 mm in length that often occur in dense ichnofabrics and occasionally in distinct meandering arrangements (Voigt 1977).

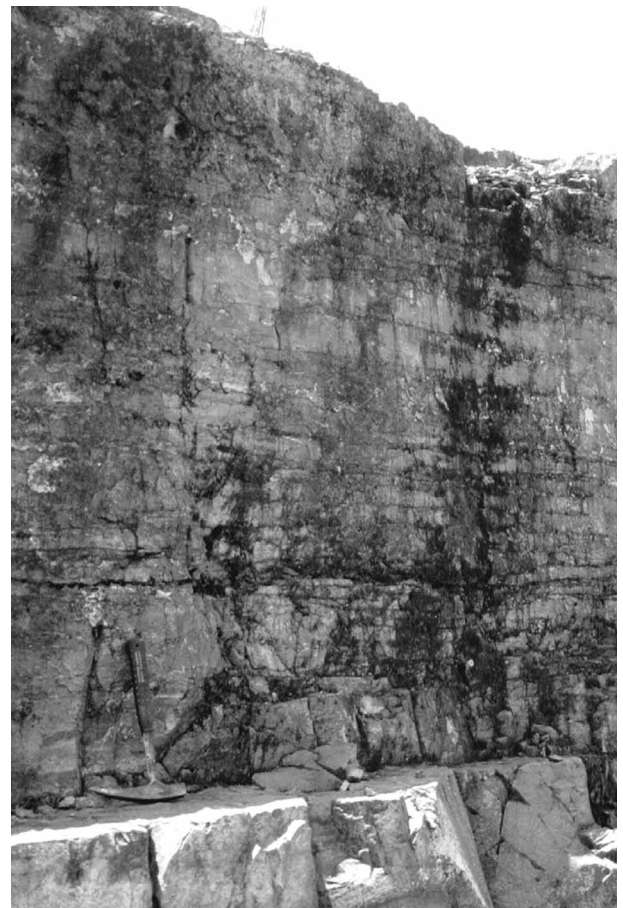


Fig. 4. Field photograph of Lower Phosphate Member of the Meishucun Formation at Xiaowaitoushan Hill quarry near Jinning, Yunnan Province, China showing thin planar bedding. Hammer for scale.

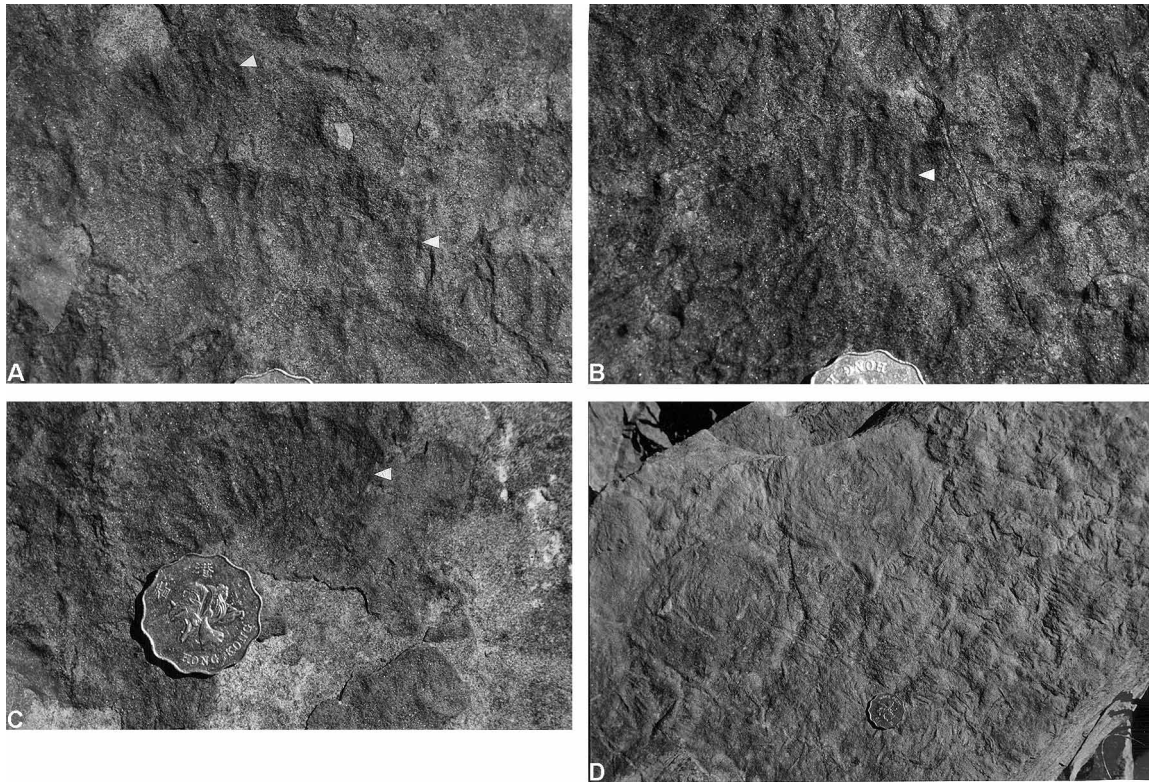


Fig. 5. Field photographs of *Radulichnus* in the Upper Phosphate Member. Coin for scale is 2.7 cm in diameter. □A. Three arcuate sets of scratches (left of arrows) preserved in concave epirelief. □B. A single arcuate set of scratches (left of arrow) preserved in concave epirelief. □C. A single arcuate set of scratches (left of arrow) preserved in concave epirelief. □D. A dense ichnofabric of scratches along with discoidal impressions, all preserved in convex hyporelief.

*Radulichnus* has also been described from the terminal Proterozoic Ediacara Member of the Rawnsley Quartzite and Cambrian sandstones in Saudi Arabia (Gehling 1996; Seilacher 1997). Previously interpreted as arthropod traces, these arcuate sets of hypichnial ridges arranged in fan-shaped arrays are reinterpreted as grazing traces left by an organism which was feeding upon microbial mats on the unconsolidated seafloor (Gehling 1996; Seilacher 1997).

*Radulichnus* is distinguishable from arthropod traces, such as *Rusophycus* and *Monomorphichnus*, because its paired scratches are symmetrical, radially arranged, and its arcuate sets of scratches are not found in pairs (Gehling 1996). The radial arrangement of the scratches indicates that they were created by one organism, which rotated its head as it scratched the microbial mat for nutrition (Gehling 1996). The fact that the traces were left intact as the grazer moved over them, as it would have been required to do, indicates the presence of microbial mats, which would have significantly stabilized the seafloor (Gehling 1996).

*Radulichnus* is often found preserved with Ediacaran fossils, such as *Dickinsonia* and *Kimberella* (Gehling 1996; Seilacher 1997). In one instance, the

possible soft-bodied trace-maker has been preserved with *Radulichnus*. The ovoid body fossil is found in the middle of an array of *Radulichnus* traces with its anterior end near the focal point of the last 3 arcuate sets (Gehling 1996; Seilacher 1997). The fact that the *Radulichnus* traces are still preserved underneath this body fossil provides further evidence for microbial mats (Seilacher 1997). This ovoid body fossil is the proper size and is in the proper position to be interpreted as the possible maker of the *Radulichnus* traces on which it is preserved (Gehling 1996; Seilacher 1997). Although it is unclear exactly what kind of organism made these *Radulichnus*, it was probably an early mollusc because of its radular grazing behavior (Gehling 1996).

Previously interpreted as arthropod traces by Zhu (1997) in his landmark paper on the Precambrian–Cambrian trace fossils of Yunnan Province, the *Radulichnus* from the Lower Cambrian of China occur in distinctive red bedding planes, visible as red seams in vertical section, within the granular phosphates of the Upper Phosphate Member (Fig. 2). The bedding planes on which they are preserved have an ichnofabric in which few discrete traces are visible, but those that are readily visible are arcuate sets of radially

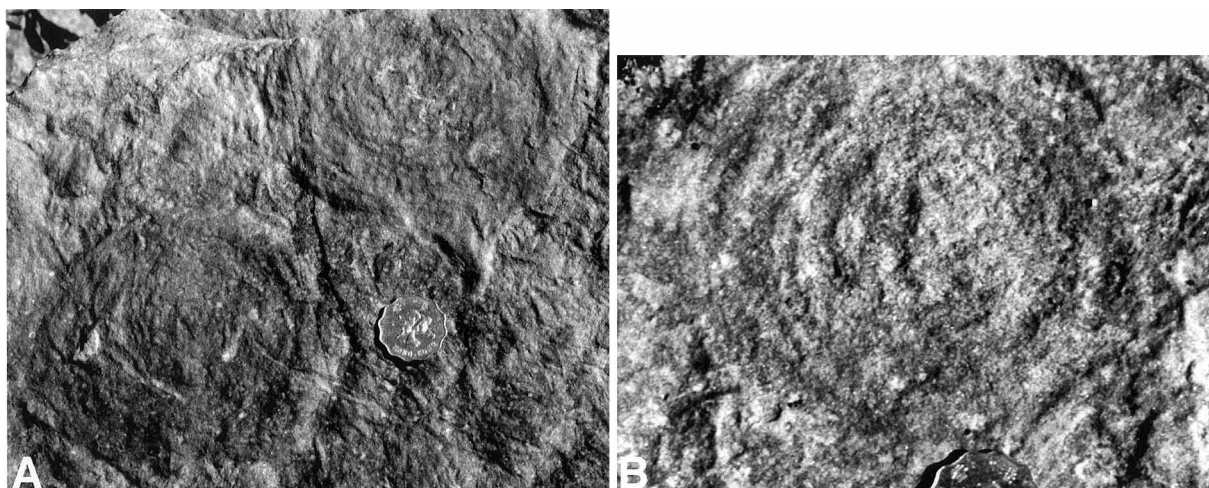


Fig. 6. Field photographs of discoidal impressions in Upper Phosphate Member. □A. Two discoidal impressions preserved in convex hyporelief. Note concentric annulations and pustulose texture. Coin for scale is 2.7 cm in diameter. □B. One discoidal impression preserved in concave epirelief with concentric annulations. Coin for scale is 2.7 cm in diameter.

arranged epichnial grooves or hypichnial ridges (Fig. 5). Because of the obscuring ichnofabric, which is probably the result of extensive radular grazing and other feeding behavior on these red bedding planes, only isolated arcuate sets are visible. Evidence for the arrangement of these sets, either as radial arrays or meandering, is therefore not present. The visible arcuate sets are 2.0 to 3.8 cm wide and contain scratches 1.5 to 2.0 cm in length. The scratches themselves are approximately 1 to 2 mm in width and depth. These traces are clearly not arthropod traces because of their symmetry, radially arranged scratches, and unpaired occurrence. And because they are symmetrical arcuate sets of radially arranged grooves, these Lower Cambrian traces are identifiable as *Radulichnus*.

#### *Enigmatic discoidal impressions*

The Chinese *Radulichnus* are always found preserved with discoidal epichnial impressions with concentric circular lineations and even, in some cases, pustulose texture (Figs 2, 6). Previously interpreted as the resting trace *Bergaueria* (Zhu 1997), these impressions are typically around the same diameter, 10 cm, and are strictly two-dimensional features. Several of these impressions are cut by the edge of the slab on which they are preserved, allowing for confirmation of their two-dimensionality. Their size similarity, sharp outlines, unusual textures, and two-dimensionality indicate that these discoidal impressions could possibly be the fossil remains of soft-bodied organisms, although other interpretations are certainly possible. One even has a somewhat teardrop shape because of what appears to be a pointed extension of the possible

body (Fig. 6A). Considering the close association between these discoidal impressions and *Radulichnus*, it is not unreasonable to suggest that they may be the fossil remains of the *Radulichnus*-maker. Perhaps they are even the impression of a mollusc-grade animal with a broad foot-like organ that was pivoting on the mat-bound seafloor. While their identity remains uncertain, the preservation of these possible soft-bodied organisms was most likely dependent on the presence of microbial mats (Gehling 1999). In fact, the preservation of *Radulichnus* itself in these granular phosphates probably required the presence of microbial mats, which provided a preservative interface, now seen as the red bedding planes between granular phosphate beds. The final step in the preservation of the *Radulichnus* scratches, as well as the possible soft-bodied organisms, was their likely rapid burial in an obrution event.

#### *Comparison with modern grazing traces*

Modern *Radulichnus* from the Sunset Cliffs area of Point Loma, near San Diego in Southern California, closely resemble these Chinese traces. These modern scratches, most likely made by gastropods or polyplacophorans grazing on algal mats on the surface of Upper Cretaceous shales exposed in the intertidal zone, consist of radially arranged scratches less than 1 mm long (Fig. 7). When individual sets of scratches are visible, they are meandering in form, but most of the radular scratches occur in dense ichnofabrics resembling the occurrence of *Radulichnus* in China, making discrete sets of scratches difficult to locate (Fig. 7). In spite of their obvious size difference, with the modern forms being much smaller, the Lower



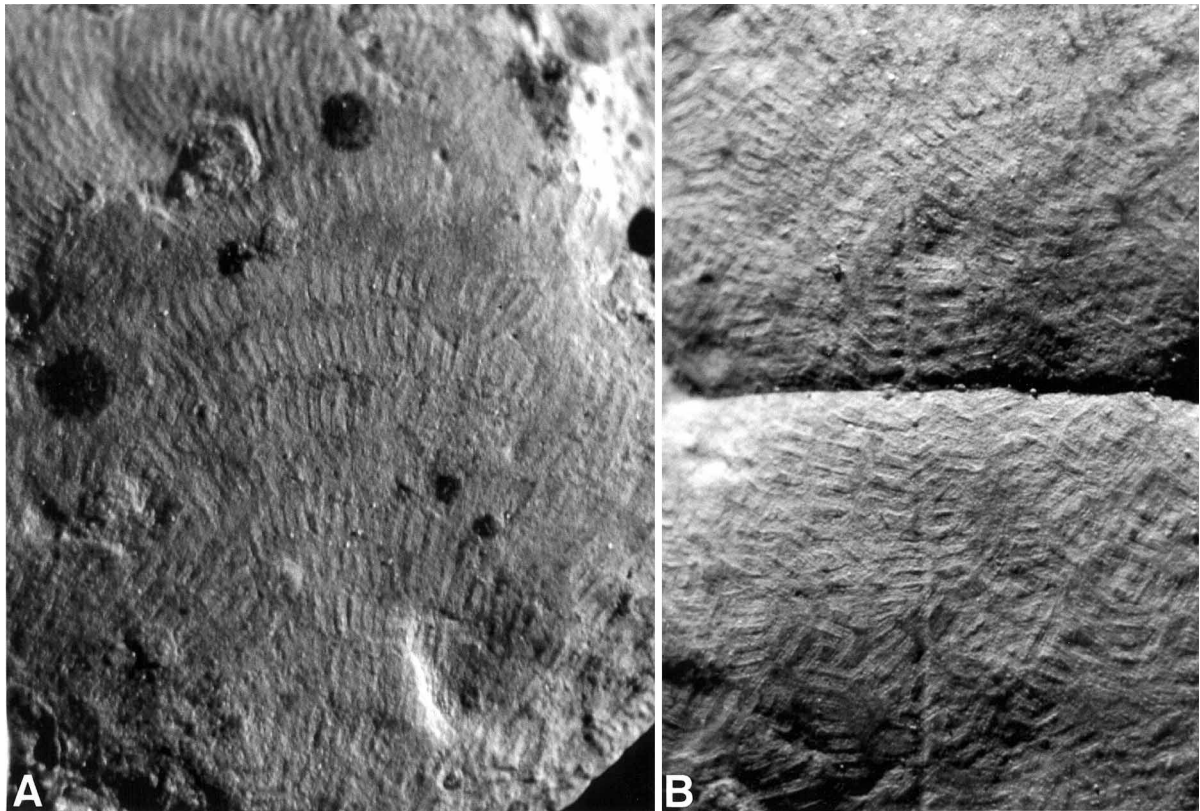


Fig. 7. Photograph of modern *Radulichnus* from Sunset Cliffs, California. □ A. Scratches showing a meandering pattern amidst a somewhat obscuring ichnofabric of scratches. Field of view is 2 cm in width. □ B. A dense ichnofabric of scratches. Field of view is 2 cm in width.

Cambrian and modern *Radulichnus* have highly analogous morphologies consisting of arcuate sets of parallel to sub-parallel scratches.

#### *Evidence for seafloor microbial mats*

Thin section analysis of the red bedding planes in which the *Radulichnus* are preserved reveals ample suggestive evidence for the presence of microbial mats. These bedding planes, which can be seen as red seams in vertical outcrop (Fig. 2), contain dense, bed-parallel, laterally continuous concentrations of heavy minerals, such as hematite and ilmenite, and mica grains (Fig. 8). The heavy minerals are likely the result of mat-decay mineralization, in which the burial and decay of microbial mats below the redox boundary causes the precipitation of heavy minerals along the bedding plane containing the organic material of the microbial mat itself (Schieber 1999). The concentration of mica grains in these bedding planes, which are generally absent in the dolomitic phosphorite matrix, also suggests the presence of microbial mats because their sticky surface would have trapped mica grains from the water column that would not normally

have been deposited in these environments (Schieber 1999). So there is strong petrographic evidence, in addition to the circumstantial evidence discussed above, which suggests the presence of microbial mats in these red bedding planes. These microbial mats would have served as the trophic resource that the *Radulichnus*-maker was consuming.

Field observations also provide evidence suggestive of the presence of microbial mats. In particular, probable microbially-mediated sedimentary structures such as wrinkle structures (Hagadorn & Bottjer 1997) and 'elephant skin' (Gehling 1999) are present on the uppermost bedding plane surface of the Lower Phosphate Member. This bedding plane also happens to be red and enriched in heavy minerals and mica. Both petrographic and field evidence, therefore, strongly suggest the presence of microbial mats in the environments represented by the Lower and Upper Phosphate Members of the Meishucun Formation.

#### *Thalassinoides*

Horizontal *Thalassinoides* in the Lower Phosphate Member also provide a key piece of evidence for

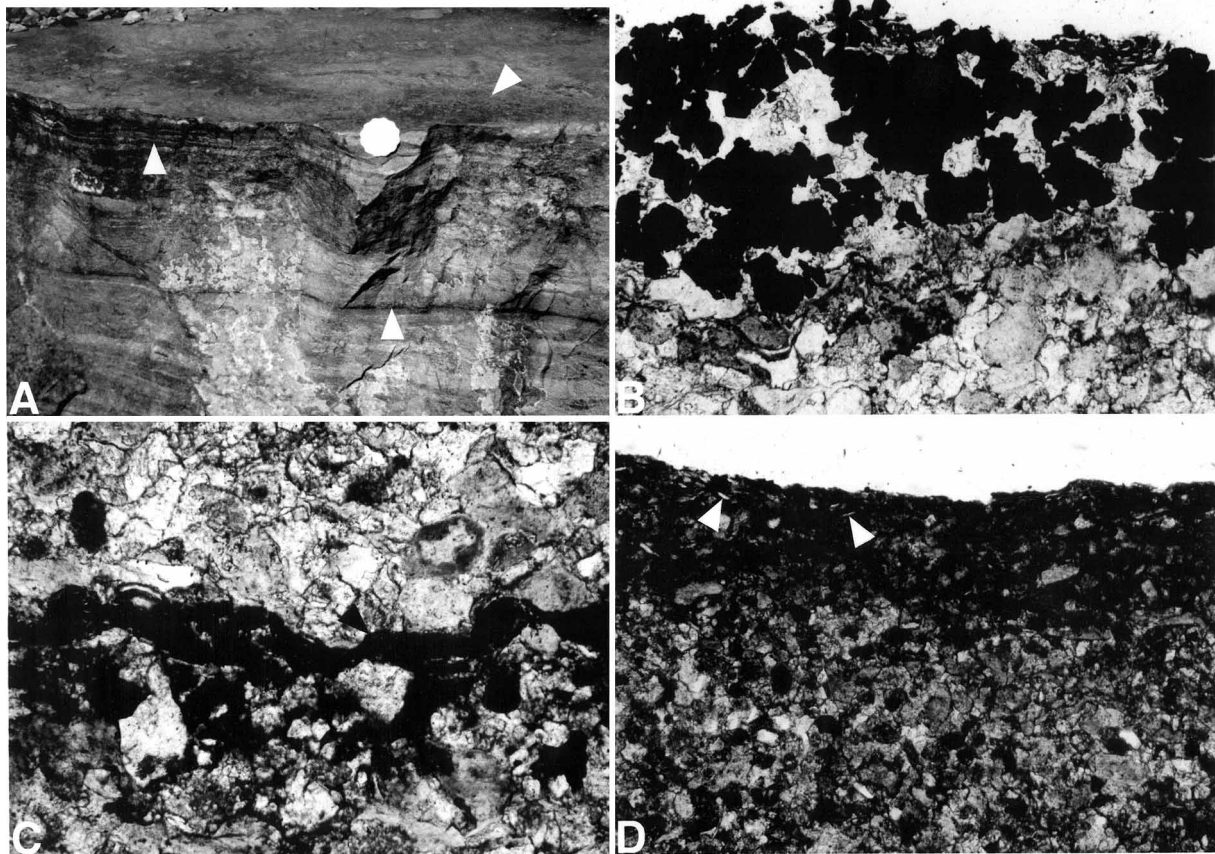


Fig. 8. Photographs and photomicrographs of red bedding planes, or seams, in outcrop and thin section. □A. Photograph of red bedding plane containing *Radulichnus* (uppermost arrow) and red seams in vertical outcrop (lower arrows). Coin for scale is 2.7 cm in diameter. □B. Photomicrograph of red bedding plane showing abundant iron-rich minerals, seen here in black. Field of view is 1.5 mm in width. □C. Photomicrograph of red seam (arrow) between event beds in the phosphorite. Note its wrinkled form. Field of view is 3 mm in width. □D. Photomicrograph of red bedding plane showing enrichment in iron-rich minerals and mica grains (arrows). Field of view is 6 mm in width.

metazoan paleoecology. These *Thalassinoides*, previously interpreted as cross-cutting *Palaeophycus* (Zhu 1997), are abundant in a 109 cm interval of the

Lower Phosphate Member (Fig. 2) and are the first evidence for intense bioturbation in Yunnan Province (Zhu 1997). They are visible on nearly all exposed

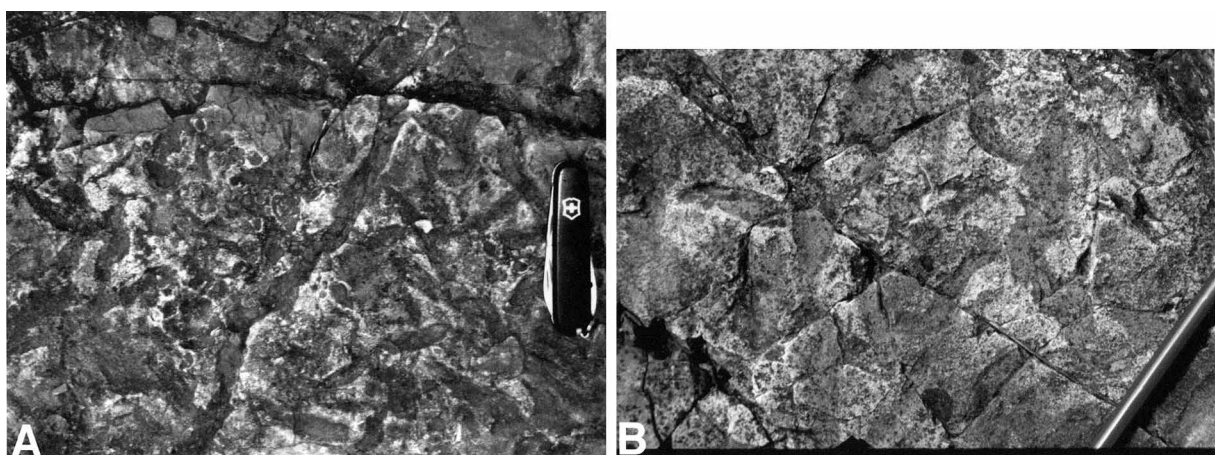


Fig. 9. Field photographs of horizontal *Thalassinoides* in Lower Phosphate Member. □A. Pocket knife for scale is 10 cm in length. □B. Pencil for scale is 8 mm in width.



bedding planes in this interval, typically produce a bedding-plane ichnofabric index (ii) of 3 (Miller & Smail 1997), and contain both T- and Y-branches (Fig. 9). The burrows range from 8–15 mm in diameter and form branching frameworks of unlined horizontal burrows, the ‘maze’ geometry of Droser and Bottjer (1988). While post-Paleozoic *Thalassinoides* are typically considered to be the traces of decapod crustaceans, the identities of early Paleozoic *Thalassinoides* producers remain enigmatic (Myrow 1995).

Considering that these *Thalassinoides* occur within abundant red bedding planes containing strong suggestive evidence for the presence of microbial mats (Fig. 2), their formation may be related to microbial mats. Although the animals that made these *Thalassinoides* lived within these burrows, they may have also fed on buried organic material, including buried microbial mats, for nourishment. If this was the case, then the makers of these traces were engaging in undermat mining behavior (Seilacher 1999). In addition, the unlined nature of these *Thalassinoides* indicates that the coarse-grained matrix in which they were formed was relatively firm, perhaps due in part to the stabilization of microbial mats.

### Small shelly fossils

The diversity and abundance of small shelly fossils in the Meishucun Formation warrants further discussion because they provide more evidence of metazoan paleoecology. Many of these small shelly genera are part of an unknown or poorly known scleritome and therefore provide no paleoecological information (Qian & Bengtson 1989). There are many genera found in the Meishucun Formation, however, that are amenable to paleoecological interpretation. An example of one such genus is the tubular fossil *Conotheca* (Qian & Bengtson 1989). Hyolithids such as *Conotheca* have been previously interpreted both as mobile benthic animals (e.g. Missarzhevsky 1989) and sessile suspension feeders (e.g. Kouchinsky 2001), some with their lower end inserted in the substrate (Landing 1993). In the environments represented by the Meishucun Formation these genera probably lived as mat stickers, with their lower end inserted into the mat-bound substrate. The taxonomically enigmatic *Chancelloria*, a roughly conical to sac-shaped coeloscleritophoran, and the likely conularid *Arthrocites* (Qian & Bengtson 1989) also are best interpreted as mat stickers in these environments. This agrees with previous interpretations of *Chancelloria* as a sessile sediment sticker (e.g. Janussen *et al.* 2002). Another Meishucun small shelly fossil for which a paleoecological interpretation is possible is the planispirally coiled, univalved genus *Xianfengella* (Qian & Bengtson

1989). These tiny animals probably lived as surficial grazers on microbial mats, much like many early helcionelloid molluscs (e.g. Gubanov & Peel 1999, 2001). Other Meishucun cap-shaped fossils, including genera such as *Aegides* and *Canopoconus* (Qian & Bengtson 1989), probably were part of a coeloscleritophoran scleritome (Bengtson 1992; Siegmund 1997). These examples illustrate that, where paleoecological interpretations are possible, the benthic metazoans represented by the Meishucun Formation small shelly fossils were well adapted for survival on microbial mat bound seafloors. While further work is certainly necessary, perhaps it is not premature to suggest that much or all of the Early Cambrian Tommotian Fauna was adapted to such seafloors, or at least to the relatively firm substrates of the time (Droser *et al.* 2002).

## Discussion

The trace fossils of the Meishucun Formation provide evidence for both mat scratching and undermat mining by metazoans, behaviors that are ecologically centered on seafloor microbial mats. Considered with the associated direct evidence for microbial mats, these traces indicate that the metazoans living in this particular depositional environment were adapted for survival in settings dominated by microbial mats. The paleoecology of Meishucun Formation small shelly fossil genera, when interpretable, is consistent with this interpretation. In this way, this environment served as a subtidal refuge for metazoans with Neoproterozoic-style adaptations to microbial mats.

Careful consideration of the depositional environment in which these metazoans lived is necessary in order to better understand the environmental conditions that shaped their paleoecology, allowing for such a Neoproterozoic-style refuge. As described earlier, the Meishucun Formation is a shallowing upward, condensed sequence of dolomitic phosphorite that contains abundant phosphatic intraclasts and evidence for mm-scale phosphatic hardgrounds (Chen & Zhou 1997; Zhang *et al.* 1997; Zhu 1997). The Lower Phosphate Member is planar-bedded and was probably deposited below storm wave base. The Upper Phosphate Member, however, consists of thick, hummocky cross stratified beds and was probably deposited between storm and normal wave base. No evidence for intertidal or supratidal environments is found in these members. Seafloor microbial mats are generally thought to play a crucial role in phosphogenesis (e.g. Briggs & Kear 1993; Föllmi 1996; Wilby *et al.* 1996; Soudry 2000), so their presence in this environment is to be expected.

It seems quite likely, based on these characteristics, that the lifestyles of these metazoans were made possible by the phosphogenic environment in which they lived. The presence of microbial mats allowed for mat scratching behavior to take place, and the relatively rapid formation of phosphatic hardgrounds may have aided in the preservation of these grazing traces. It is likely that the formation of the scratches preceded hardground formation, but the seafloor must have been relatively firm for the scratches to be created, probably because of stabilization by microbial mats. In addition, these microbial mats and phosphatic hardgrounds probably aided in the formation of the horizontal networks of *Thalassinoides* by providing a relatively firm substrate as well as buried trophic resources. It is important to note that while these thin phosphatic hardgrounds probably contributed to the formation and preservation of these traces, seafloor microbial mats were probably the most important influence on the paleoecology of these metazoans. In this way, Early Cambrian phosphogenic environments appear to have allowed for the dominance of typical Neoproterozoic benthic lifestyles (Seilacher 1999), while siliciclastic and carbonate environments were probably more advanced in the transition to typical Phanerozoic benthic lifestyles.

## Conclusions

The trace fossils and small shelly fossils of the Lower Cambrian Meishucun Formation of southwest China provide evidence for metazoan behavior and paleoecology that centered around microbial mats, the presence of which is supported by both field and petrographic evidence. The paleoecology of these metazoans is comparable to typical Neoproterozoic lifestyles associated with seafloor microbial mats, including mat scratchers, mat stickers, and undermat miners (Seilacher 1999). The presence of these lifestyles in a subtidal Early Cambrian environment indicates that the increase in bioturbation levels characteristic of the Proterozoic–Phanerozoic transition was spatially and temporally variable, resulting in a mosaic of soft substrate types during much of the Cambrian. As a result, the effect of this Proterozoic–Phanerozoic increase in bioturbation levels on the paleoecology of non-burrowing benthic metazoans, termed the Cambrian substrate revolution (Bottjer et al. 2000), was also highly variable, with benthic metazoans adapted to typical Proterozoic-style soft substrates coexisting with those adapted to typical Phanerozoic-style soft substrates.

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