

Microbial mats in the terrestrial Lower Triassic of North China and implications for the Permian–Triassic mass extinction



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ARTICLE INFO

Article history:

Received 25 February 2016

Received in revised form 25 May 2016

Accepted 8 June 2016

Available online 10 June 2016

Keywords:

Microbial mat

Microbially induced sedimentary structures (MISS)

Early Triassic

Terrestrial ecosystem

Permian–Triassic mass extinction (PTME)

North China

ABSTRACT

Evidence for microbial mats has been reported repeatedly from marine Lower Triassic rocks, but scarcely mentioned in post-mass extinction terrestrial facies. Here, we report from the terrestrial Lower Triassic Liujiagou Formation in North China the presence of five kinds of microbially induced sedimentary structures (MISS) or sedimentary surface textures, including “old elephant skin” textures, wrinkle structures, palimpsest ripples, “*Manchuriophycus*” structures and sand cracks. Terrestrial microbial communities that produced these MISS adapted not only to periodically desiccated conditions, but also to the storm-dominated palaeoenvironments in the Liujiagou Formation. The Permian–Triassic mass extinction (PTME) in North China is marked by the die-off of plants, disappearance of coal beds, extinction of pareiasaurs among tetrapods, decreased bioturbation levels and a dramatic change of sedimentary systems through the Sunjiagou Formation. The Sunjiagou Formation recorded the turnover from an ever-wet to a progressively drier and hotter climate and it spans the PTME in North China. Following this mass extinction, MISS became much more common and widespread, suggesting that the mass extinction provided favourable biological and environmental conditions for the development of the MISS in terrestrial ecosystems, especially the decreased bioturbation intensity and grazing pressure associated with increased temperature and climatic drying. In the upper part of the Liujiagou Formation and overlying Heshangou Formation, the disappearance of MISS coupled with increased bioturbation might indicate an improvement of terrestrial ecosystems and the beginning of the Triassic biotic recovery. However, as the investigation of MISS in space and time through the geological record is in its early stages, further geobiologic and geochemical studies, as well as high-precision isotopic dating from Permian–Triassic terrestrial successions, are needed to fully reveal the timing and pattern of the Early Triassic terrestrial ecosystem reconstruction.

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1. Introduction

Microbially induced sedimentary structures (MISS) were produced by the interaction between microbial activities and physical sedimentary processes in ancient siliciclastic and carbonate depositional systems (Hagadorn and Bottjer, 1997; Noffke et al., 2001; Noffke, 2009, 2010). These structures are always preserved on the upper surfaces of the substrate, which now form rock bedding planes, but the original microbial mats are hardly observed because of destruction during diagenetic processes that followed MISS formation. Analysis of the formation mode and internal textures of these sedimentary structures, as well as comparison with modern microbial mat structures suggest that the formation and preservation of these structures have a direct relationship with the presence of microbial mats (Hagadorn and Bottjer,

1997). Furthermore, MISS are common sedimentary features in Proterozoic–Cambrian strata extending back to the Early Archean (e.g. Hagadorn and Bottjer, 1997, 1999; Gehling, 1999; Noffke et al., 2002, 2003, 2006; Schieber et al., 2007; Meyer et al., 2014), most probably due to the lack of bioturbation that inhibits the formation and preservation of biomats and associated structures. In addition, the occurrence of MISS provides valuable evidence for the detection of early life and reconstruction of environments in the Precambrian (Noffke et al., 2003). So far, several authors have studied Precambrian MISS in continental facies (Prave, 2002; Callow et al., 2011; Simpson et al., 2013; Wilmeth et al., 2014; Strother and Wellman, 2015), and they have argued that microbial communities were flourishing and inhabited continental settings at that time.

In the Phanerozoic, most studies have suggested that sedimentary structures related to microbial communities became more common as a response to periods of lower benthic biodiversity and reduced bioturbation, including a variety of unusual sedimentary structures

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(Sepkoski et al., 1991; Schubert and Bottjer, 1992; Grotzinger and Knoll, 1995; Wignall and Twitchett, 1999; Whalen et al., 2002; Sheehan and Harris, 2004; Calner, 2005; Pruss et al., 2006; Mata and Bottjer, 2009; Buatois et al., 2013; Chu et al., 2015; Ibarra et al., 2016; Peterffy et al., in press; Rakociński and Racki, 2016). However, Davies et al. (2016) recently demonstrated that MISS have been reported more from Phanerozoic than Precambrian strata, and exhibit a pan-environmental and almost continuous record since the Archean, while the perception that MISS are restricted to exceptional intervals of Earth history could arise from a sampling and publication bias. In addition, abiotic and physico-chemical sedimentary processes may also create morphologically similar features to MISS, hindering their accurate identification (e.g. McLoughlin et al., 2008; Davies et al., 2016). Therefore, more original observations of MISS from multiple depositional systems should be collected to re-evaluate the relationship between biotic crises and the flourishing of MISS after these events.

As the greatest crisis of the Phanerozoic, the Permian–Triassic mass extinction (PTME) is of particular interest to geologists. This event wiped out over 90% of marine species, and most terrestrial vertebrate and plant species, and brought about a whole-scale restructuring of ecosystems (Erwin, 1993; Retallack, 1995; Looy et al., 1999, 2001; Song et al., 2013; Benton and Newell, 2014; Benton, 2015). The diversity of marine invertebrates declined dramatically (Alroy et al., 2008), and bioturbation returned to Precambrian levels (Knaust, 2010). The terrestrial PTME is confirmed by the significant turnover and loss of life on land from global-scale data, such as tetrapods, insects and plants (Retallack et al., 1996; Grauvogel-Stamm and Ash, 2005; Hermann et al., 2011; Benton and Newell, 2014; Cascales-Miñana and Cleal, 2014; Cascales-Miñana et al., 2015; Yu et al., 2015), though the position of the terrestrial Permian–Triassic boundary is disputed in different regional basins (e.g. Botha and Smith, 2006; Taylor et al., 2009; Gastaldo et al., 2015). Plant diversity had declined substantially through the PTME followed by the Early Triassic “coal gap” (Veevers et al., 1994; Retallack et al., 1996, 2011; Looy et al., 1999, 2001; Rees, 2002; Retallack, 2013). Furthermore, the significant turnover of the terrestrial sedimentary system and the dramatic collapse of soil systems associated with persistent warming, arid climate and enhanced terrestrial weathering have been documented globally during the PTME (Newell et al., 1999; Ward et al., 2000, 2005; Michaelsen, 2002; Miall and Jones, 2003; Arche and Lopez-Gomez, 2005; Retallack, 2005; Algeo and Twitchett, 2010; Algeo et al., 2011; Smith and Botha-Brink, 2014; Metcalfe et al., 2015; Schneebeli-Hermann et al., 2015; Song et al., 2015). Most studies suggest that the destruction of terrestrial ecosystems happened simultaneously with the decline in marine diversity during the Permian–Triassic transition (Twitchett et al., 2001; Shen et al., 2011; Metcalfe et al., 2015; Zhang et al., 2015; Chu et al., in review). Deposits of this unusual period are characterized by the presence of flat-pebble conglomerates (Wignall and Twitchett, 1999), thin-bedded limestones (Pruss et al., 2005), carbonate seafloor fans (Woods et al., 1999), and siliciclastic microbial-mat related wrinkle structures (Pruss et al., 2004; Chu et al., 2015; Tu et al., 2016). Microbial buildups and mats dominated the seabed after the Permian–Triassic crisis, and these microbe-dominated marine ecosystems lasted for about 5–6 Myr in the Early Triassic, linked to the depression of bioturbation and/or to long-term unusual environmental conditions (Chen and Benton, 2012). Most studies that mentioned these unusual sedimentary structures from the Lower Triassic were restricted to marine carbonate and siliciclastic rocks (e.g. Schubert and Bottjer, 1992; Lehrmann, 1999; Wignall and Twitchett, 1999; Woods et al., 1999; Pruss et al., 2004, 2005, 2006; Pruss and Bottjer, 2004; Abdolmaleki and Tavakoli, 2016; Xu et al., 2017). However, less is known about specific changes in terrestrial microbial ecosystems during the PTME and its aftermath, though specific MISS have been reported in terrestrial Lower Triassic rocks (Wehrmann et al., 2012; Chu et al., 2015; Tu et al., 2016).

Terrestrial Permian–Triassic successions are well exposed and widely distributed in the Shanganning Basin and its surrounding area,

such as Shanxi, Shaanxi, Henan, and Ningxia Provinces in North China, characterized by inland fluvial and lacustrine siliciclastic redbeds. Complete terrestrial Permian–Triassic sections in North China have been little studied, and yet these sections contain important clues for a better understanding of terrestrial ecosystems. Following our report of microbial-related wrinkle structures from the Lower Triassic of the Dayulin section, Henan Province, North China (Chu et al., 2015), Tu et al. (2016) described some kinds of MISS from the same section and suggested that microbes also proliferated in terrestrial ecosystems in the aftermath of the PTME. The MISS in terrestrial siliciclastic facies seem to coincide with the “unusual sedimentary record” in marine settings, which were associated with the end-Permian mass extinction events (Pruss et al., 2004, 2005, 2006; Baud et al., 2007; Chen et al., 2014). Consequently, MISS would be expected to be observed in more terrestrial facies and might be taken as an indicator of the Permian–Triassic boundary in terrestrial stratigraphical sequences. Here we present some more evidence for microbial-mat related sedimentary structures from the Lower Triassic shallow-shore lacustrine siliciclastic deposits in North China. In addition, this study presents a more detailed analysis of terrestrial extinction on the basis of previous and new biostratigraphical, sedimentological, and lithological data from the studied area to reveal the timing and pattern of the PTME in North China. Furthermore, we discuss the relationship between the PTME and the Early Triassic flourishing of MISS.

2. General lithostratigraphy and study sections

The Upper Permian to Lower Triassic sedimentary sequence in North China is represented by the Shiqianfeng Group, which is composed of the Sunjiagou, Liujiagou and Heshanggou formations, in ascending order (Fig. 1). The Sunjiagou Formation consists of fine-grained sandstones and thinly interbedded siltstones in the lower part and reddish siltstone beds, mudstone laminae and interbedded sandstone and marlstone beds in the upper part (Fig. 2A, B). Intensive bioturbation and the *Ullmannia bronnii*-*Yuania magnifolia* plant fossil assemblage, which is known as the youngest Palaeozoic flora in North China (Wang and Wang, 1986; Chu et al., 2015), occur in the lower part of the formation. In previous stratigraphic studies, the base of the Sunjiagou Formation was dated variously from middle Wuchiapingian to basal Changhsingian, and the Sunjiagou Formation was considered to cover the entirety of the Changhsingian stage from the evidence of lithostratigraphy, palaeobotany and palynology (Wang and Wang, 1986; Stevens et al., 2011; Zhang et al., 2012; Liu et al., 2015), though no reliable age-diagnostic fossils are found in the upper part of the formation. The overlying Liujiagou Formation comprises reddish and brown-reddish, fine-grained sandstones with siltstones and fine-grained conglomerates, bearing abundant ripple marks and cross bedding (Fig. 2C–F), and characterized by lacustrine wrinkle structures but an absence of bioturbation, and deposited in a lake shore or fluvial environment (Chu et al., 2015; Tu et al., 2016). The typical Early Triassic plant fossil *Pleuromeia* occurs in the upper part of the Liujiagou Formation, and these are more widely distributed in the Lower Triassic strata (Wang and Wang, 1982; Wang, 1996; Retallack, 1997; Grauvogel-Stamm and Ash, 2005). The Heshanggou Formation consists of brown-reddish and purple mudstone laminae and siltstone beds with interbedded sandstone beds with diverse ichnofossils, such as *Planolites*, *Ptilonichmus*, *Scoyenia*, *Skolithos*, and *Taenidium*, deposited in a shallow-shore lake palaeoenvironment.

The samples of MISS and other sedimentary surface textures were collected from the Liujiagou Formation of the Dayulin and Liulin sections, which are well exposed in Henan and Shanxi provinces, North China (Fig. 1). The Dayulin section is situated near Yiyang County, Luoyang City, Henan Province (Fig. 1B). It includes successive Late Permian to Early Triassic terrestrial siliciclastic deposits from the Sunjiagou, Liujiagou and Heshanggou formations (Fig. 1C). We collected abundant plant fossils and ichnofossils from the lower part of the Sunjiagou

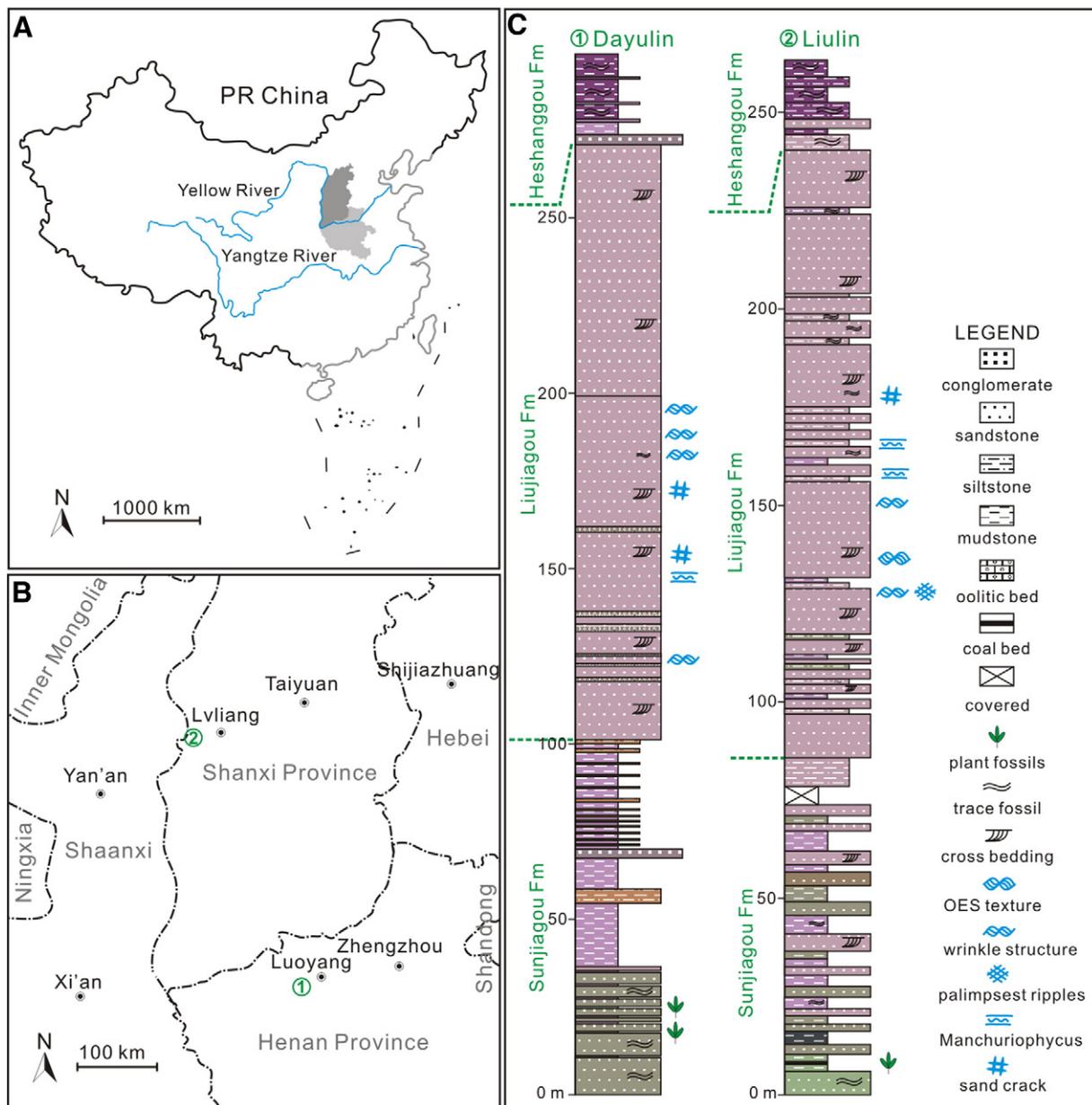


Fig. 1. Investigated localities and columnar sections. (A) Sketch map of China, showing the locations of Henan Province and Shanxi Province (grey shading). (B) Locations of the studied sections. (C) Stratigraphic sections showing lithology and distribution of MISS and fossils. Abbreviations: Fm, Formation.

Formation. Diverse MISS are mainly preserved on sandstone bed tops of the lower to middle part of the Liujiagou Formation, associated with abundant ripple marks and cross bedding, including hummocky cross-stratification and, in some cases, infrequent ichnofossils such as *Planolites*. In contrast, the overlying Heshanggou Formation is characterized by diverse ichnofossils, but the absence of MISS in the massive siltstones and mudstones. The Liulin section outcrops along the highways on both sides of the Yellow River, extending from Wubu County of Shaanxi Province to Liulin County of Shanxi Province (Fig. 1B). It exposes continuous outcrop of the Sunjiagou, Liujiagou, and Heshanggou formations, and the overlying Middle–Upper Triassic strata are also exposed on both sides of the Yellow River (Fig. 2C). The Sunjiagou Formation consists of interbedded sandstones and mudstones or siltstones, with the last appearance of coal beds occurring in its lower part associated with plant fossil fragments (Fig. 1C). MISS were observed and collected on sandstone bedding surfaces from the middle part of the Liujiagou Formation in the Liulin section. Similarly, the overlying Heshanggou Formation is composed of siltstone beds and mudstone

laminae with interbedded sandstone beds, and characterized by diverse ichnofossils, but devoid of MISS.

3. Methods

We measured stratigraphic sections and collected plant fossils in the field. In addition, trace fossils were investigated bed-by-bed and the bedding plane bioturbation index (BPBI) was measured following the method of Miller and Smail (1997). Bedding planes containing MISS were described in detail and samples were collected at each locality. Two detailed lithological logs are provided to mark the positions of the fossils and MISS samples recovered. All the features were photographed with a Canon EOS 7D digital camera. Four samples were slabbed with a cut perpendicular to the bedding surface to study changes in grain size. A total of 29 thin sections were produced for petrological analysis using standard techniques. These were then examined and photographed using a Leica DM-750P microscope equipped with an automatic camera stack-image system. Four slabs and three thin

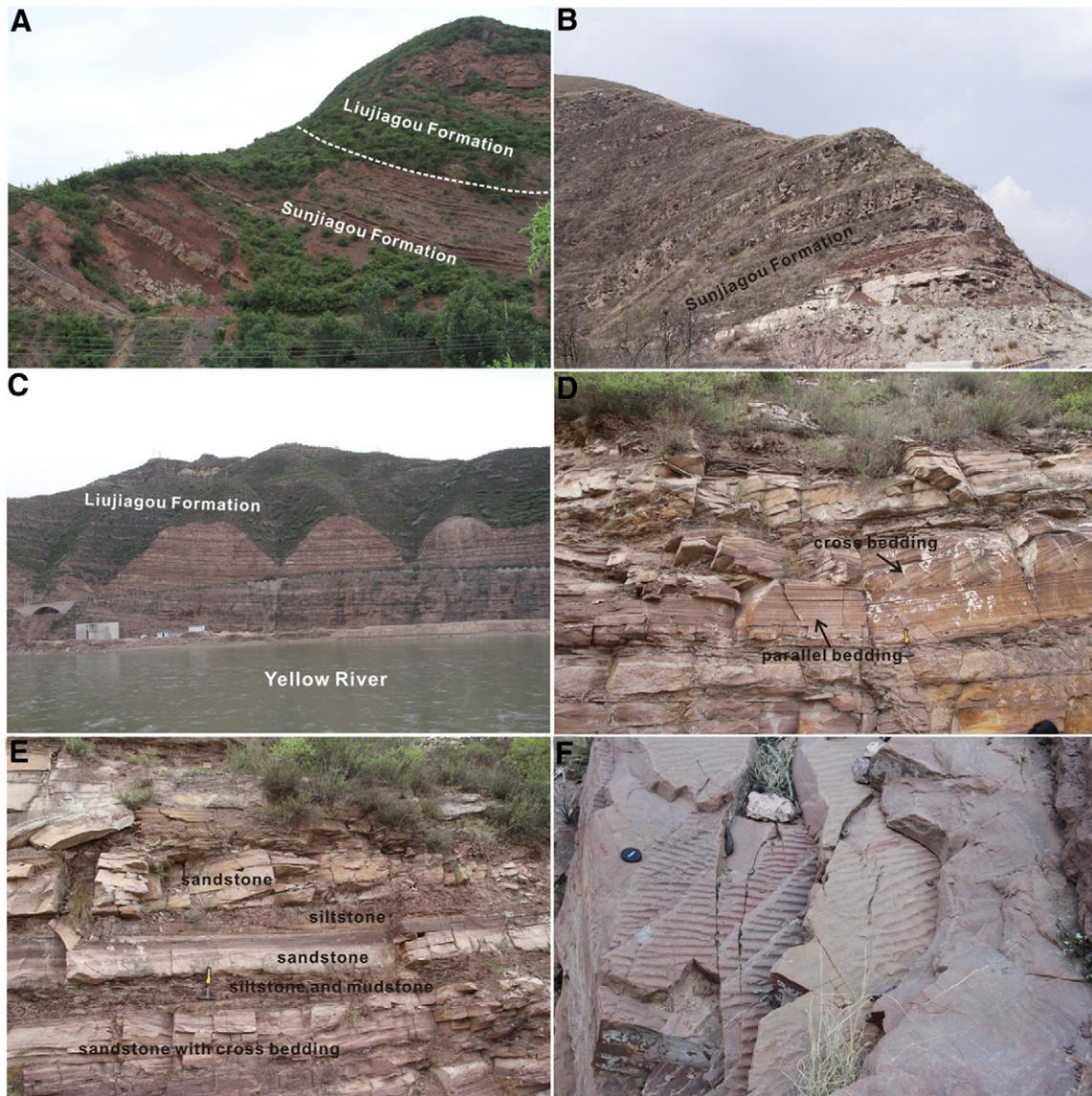


Fig. 2. Field photographs of the studied sections. (A) Field photograph showing the Dayulin section and the boundary between the Sunjiagou and Liujiagou formations. (B) Field photograph showing the Sunjiagou Formation in the Liulin section. (C) Field photograph showing the Liujiagou Formation outcrop of the Liulin section along the eastern bank of the Yellow River. (D) Sandstones of the Liujiagou Formation in the Liulin section showing cross-bedding and parallel-bedding. (E) Brown-reddish fine-grained sandstones and siltstones of the Liujiagou Formation. (F) Ripple marks of the Liujiagou Formation in the Dayulin section, showing the short-wavelength and symmetrical ripples, the parallel and straight ripple crests and consistent crest orientations from bed to bed. Lens cap diameter = 55 mm.

sections were employed for ultramicroscopic studies under a Hitachi SU8010 scanning electron microscope (SEM) with iXRF EDS. All samples in this study are stored in the palaeontological collection of the State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Wuhan (BGE).

4. Major types of MISS and interpretation

Diverse MISS were observed and collected from the Liujiagou Formation in the two sections. Here we document all the types of MISS we observed at the studied sections following the classification scheme of Schieber et al. (2007), including “old elephant skin” textures, wrinkle structures, palimpsest ripples, “*Manchuriophycus*” structures and sand cracks. In addition, we employ the classification scheme proposed by Davies et al. (2016) for distinguishing abiogenic and biogenic sedimentary surface textures in the field, Category A are demonstrably not microbially induced in origin, Category B are demonstrably

microbially induced, and Category ab represents structures for which there is no clear evidence to support either origin.

4.1. “Old elephant skin” textures

4.1.1. Description

“Old elephant skin” (OES) textures were observed on fine sandstone bedding surfaces in the middle part of the Liujiagou Formation at Liulin (Fig. 3, Category B). They are preserved as convex epireliefs with polygonal texture and projecting 2–5 mm from the bedding surface (Fig. 3D). Dark clay laminae overlying the surface have been observed by microscopic study of thin sections (Fig. 4). In addition, SEM images show that the superposed clay laminae wrapped around the quartz grains.

4.1.2. Interpretation

The OES structure was described as “a surface corrugation of a sandstone bed which provides a quasi-polygonal texture in the rock

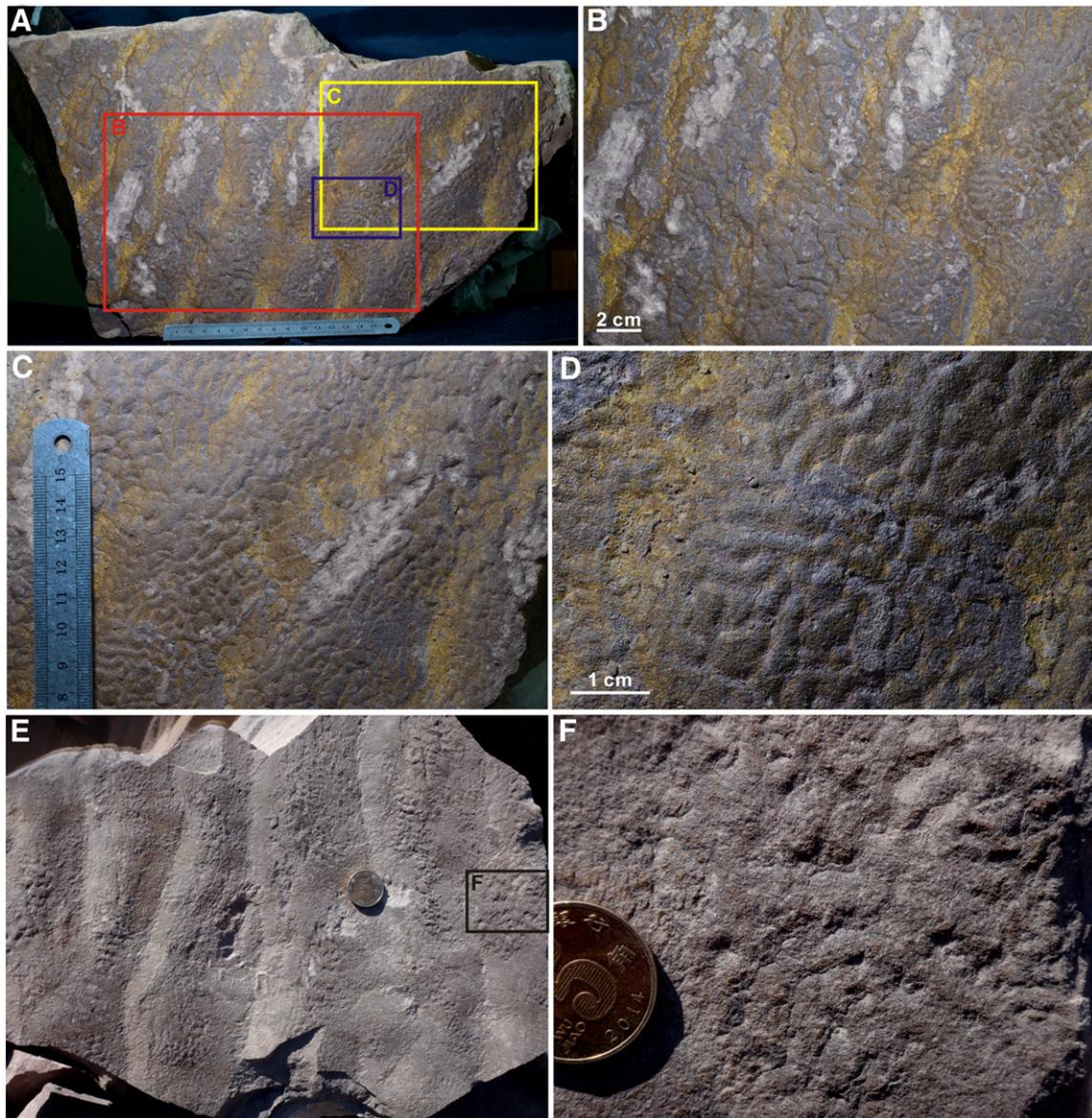


Fig. 3. Old elephant skin (OES) textures. (A) OES textures preserved on rippled sandstone bed tops, collected from the middle part of the Liujiagou Formation in the Liulin section. (B–D) Close-up of (A) showing OES textures are composed of convex epireliefs with polygonal texture or elongate to elliptical bulges. (E) OES textures preserved on rippled sandstone bed tops and confined to the crests of the ripples. (F) Close-up of (E) showing OES textures are composed of convex epireliefs with polygonal texture. Coin diameter = 20 mm.

record” (Bottjer and Hagadorn, 2007), and it was considered as a kind of specific wrinkle structure. Bottjer and Hagadorn (2007) suggested that this type of structure might form when mats provided a veneer between the lithologically identical overlying and underlying beds. The OES therefore should represent microbial mat surface features that have been induced by the microbial mat itself (Hagadorn and Bottjer, 1997, 1999; Gehling, 1999; Gerdes et al., 2000). In this study, the OES preserved as positive epireliefs on sandstone bed tops associated with ripple marks (Fig. 3), and forming in both the ripple crests and troughs, might suggest that a microbial mat protected the areas where the original ripple set is preserved.

4.2. Wrinkle structures

4.2.1. Description

A total of three wrinkle structure types were recognized through studies of morphology and microscopic characteristics, including cross-cutting wrinkle structures, parallel wavy wrinkle structures and

bulge-like wrinkle structures (e.g. Chu et al., 2015). Cross cutting wrinkle structures (Banerjee and Jeevankumar, 2005) are preserved as bifurcating and frequently interconnected crests on bed tops of fine sandstones, while one set of wrinkles cuts across another set at a low angle (Fig. 5A–C). The crests are 2–5 mm in height, and 2–6 mm in width. Opaque laminar clays were observed on the surfaces of the wrinkles in Fig. 5A from thin section microscopic features (Fig. 6C). Fine-grained quartz grains are abundant in the surface laminae as floating grains, and these differ in size from normal grains in the thin sections and slabs (Fig. 6B, C). SEM investigations show that the floating grains are enclosed by curved, continuous and thin laminar clays, while Energy-dispersive X-ray spectroscopy (EDS) shows that these submicroscopic features are highly enriched in silica and aluminium.

Parallel wavy wrinkle structures are preserved as sinuously curved continuous crests, separated by parallel narrow troughs, on the upper surfaces of fine sandstone beds (Fig. 5D–F). The height of individual crests usually ranges from 1 to 4 mm, and their spacing from 10 to

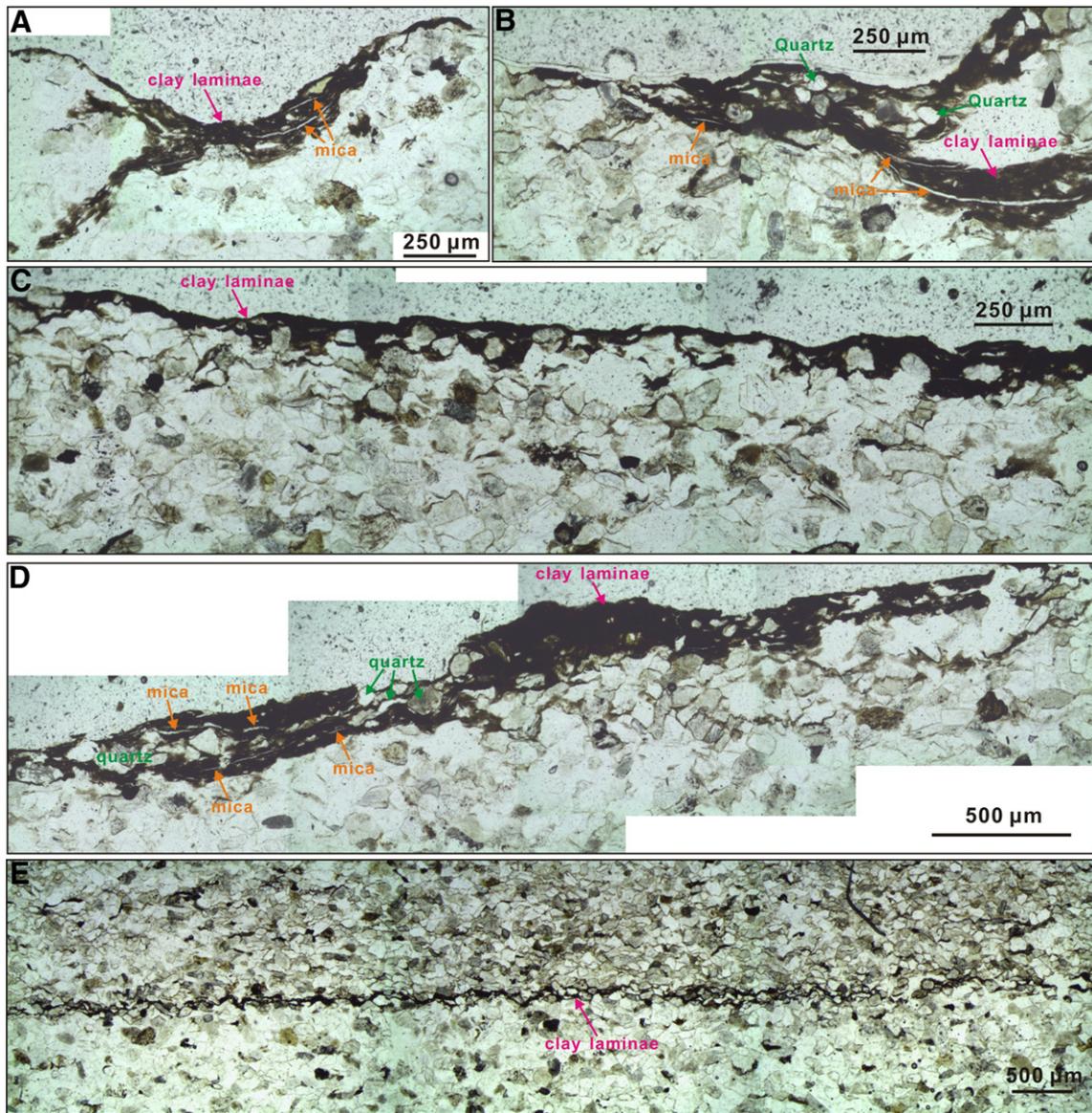


Fig. 4. Thin section photomicrographs of Fig. 3A. (A–D) Photomicrographs showing the presence of thin, wavy, crinkly and dark clay laminae on the bedding surface. (E) Thin section of the dark clay laminae preserved within the sandstone of Fig. 3A, and showing the change in grain size between the upper and lower parts of the thin section.

15 mm. Microscopic thin sections perpendicular to the structural trend show that the clay laminae are completely encased in sediment above and below, representing the complete structure of the wrinkles (Fig. 6D, E). Bulge-like wrinkle structures are preserved as elongated to subrounded bulges, characterized by patches of convex epireliefs, 2–6 mm in width and irregularly distributed, and separated from each other by narrow grooves, on the upper surfaces of fine sandstone beds (Figs. 6F, 7A). Opaque laminar clays are observed on the surfaces of the wrinkles in thin section (Fig. 6G–I). In addition, bulges with similar geometry and orientation are distributed along the extension directions of ripple crests (Fig. 7B), suggesting successful protection by the overlying microbial mats against hydrodynamic damage.

4.2.2. Interpretation

Wrinkle structures have been reported repeatedly from shallow marine settings in the Precambrian and the aftermaths of Phanerozoic extinction events (e.g. Hagadorn and Bottjer, 1997; Pruss et al., 2004, 2006; Banerjee and Jeevankumar, 2005; Mata and Bottjer, 2009; Banerjee et al., 2010; Lan and Chen, 2013), but rarely mentioned in

rocks recording terrestrial settings (but see Chu et al., 2015; Tu et al., 2016). In this study, wrinkle structures are one of the most common MISS types in the studied localities. We have found various forms of wrinkle structures in the lower to middle part of the Liujiagou Formation at Dayulin, and in the middle part of the Liujiagou Formation at Liulin. Thin sections show the preservation of a clay veneer and floating quartz grains, which suggest possible grain-trapping and binding from the surrounding environment (Hagadorn and Bottjer, 1997; Banerjee and Jeevankumar, 2005). The preservation of bulge-like wrinkles and their particular peripheries reflect subsurface morphological features developed beneath a microbial mat (Porada and Bouougri, 2007). Recently, Mariotti et al. (2014) described one of the best experimentally constrained mechanisms for the formation of wrinkle structures and similar structures, that “pits form when porous mat aggregates anchor to the bed, oscillate and scour the sand, and ridges form when the oscillatory rolling, dragging and hopping of rounded mat fragments transport sand grains from depressions to bumps”. In addition, observation of the formation of modern ridge- and pit-shaped wrinkle structures indicates that waves with a small orbital amplitude at the bed surface move the microbial fragments and thereby produce linear sand ridges

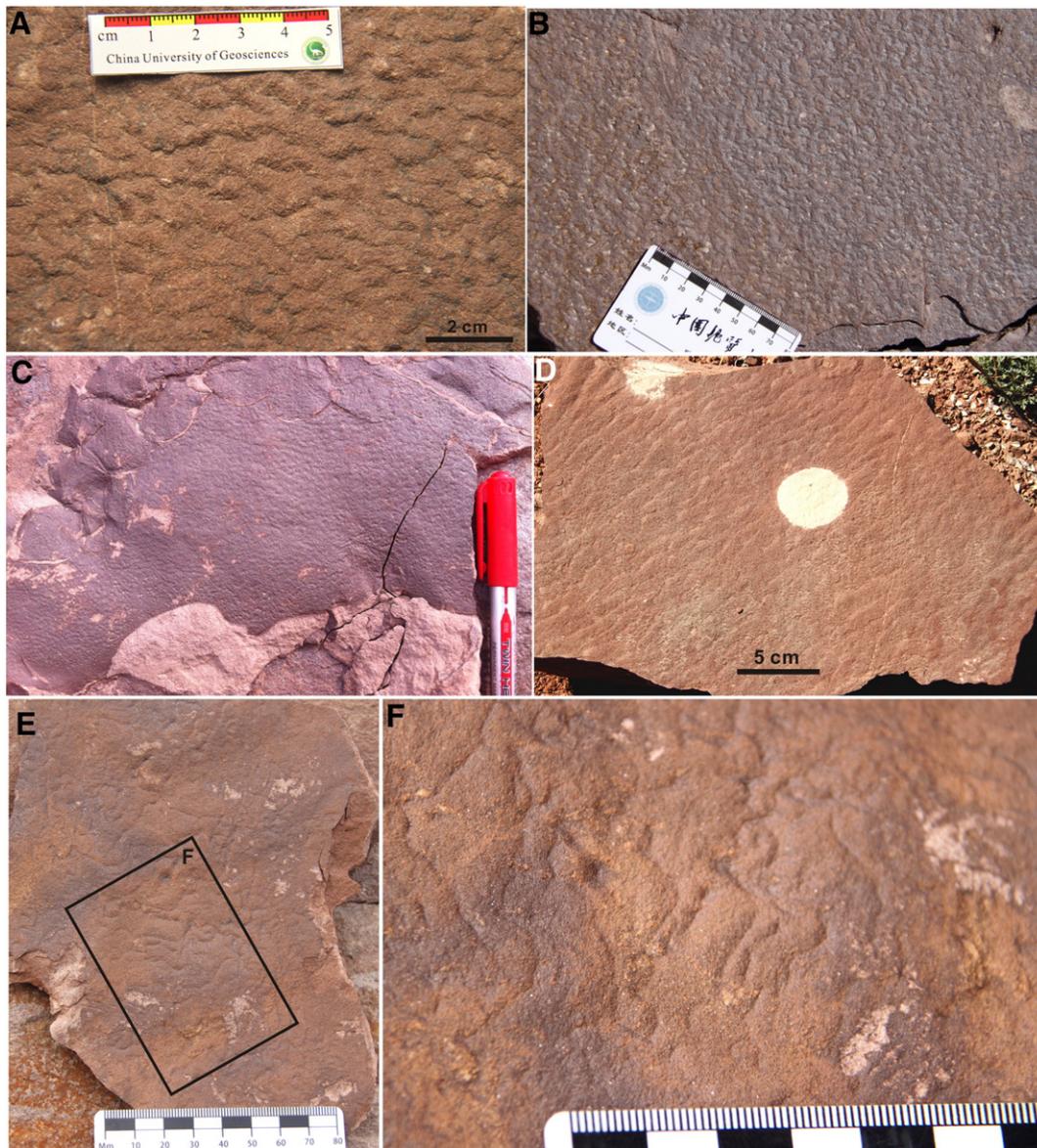


Fig. 5. Photographs of wrinkle structures. (A) Cross cutting wrinkle structures collected from the lower part of the Liujiagou Formation in the Dayulin section. (B, C) Cross cutting wrinkle structures collected from the middle part of the Liujiagou Formation in the Liulin section. (D) Parallel wavy wrinkle structures collected from the lower part of the Liujiagou Formation in the Dayulin section, showing sinuously curved continuous wrinkles. (E, F) Parallel wavy wrinkle structures collected from the middle part of the Liujiagou Formation in the Liulin section, showing sinuously curved continuous crests and narrow troughs of the wrinkles.

and rounded scour pits at wavelengths within hours, but not move sand grains directly.

4.3. Palimpsest ripples structures

4.3.1. Description

Palimpsest ripple structures are preserved as two successive sets of ripples that crossed at a specific angle on the bed tops, and the crests of each set are spaced 20–30 mm apart (Fig. 7C). In these cases, the overlapping of secondary ripples onto primary ripples formed diamond-shaped structures, with isolated patches in which there is no overlap (Fig. 7C, D). The crests of the two sets of ripples are generally flat or subrounded, and coalesced bulges or quasi-polygonal textures resemble bulge-like wrinkle structures or OES in appearance (Fig. 7D). Dark clay laminae overlying the surface are observed in microscopic thin sections, and microbial mats are inferred to have covered these sandy rippled surfaces in the aftermath of the formation of the palimpsest ripple structures, and so protected the lower layers.

4.3.2. Interpretation

The two separate sets of ripples were likely formed by storms or wind-reinforced tides in two depositional events, and a microbial mat must have developed between the two sandy beds with ripples, protecting the earlier ripples from being destroyed by later reworking. This biostabilization or mat binding effect allows two or more sets of ripples to be preserved on the same bedding plane (Pflüger, 1999; Noffke et al., 2001; Bottjer and Hagadorn, 2007; Lan and Chen, 2013). However, multi-directional ripples also can form in modern tidally influenced environments without any microbial mats, generated by different oscillation directions in shallow water (Davies et al., 2016).

4.4. “Manchuriophycus” structures

4.4.1. Description

“Manchuriophycus” structures represent a special type of microbial shrinkage crack, consisting of sinuous, circular, spiral or even figure-of-eight-shaped cracks with curving positive patterns, which are usually

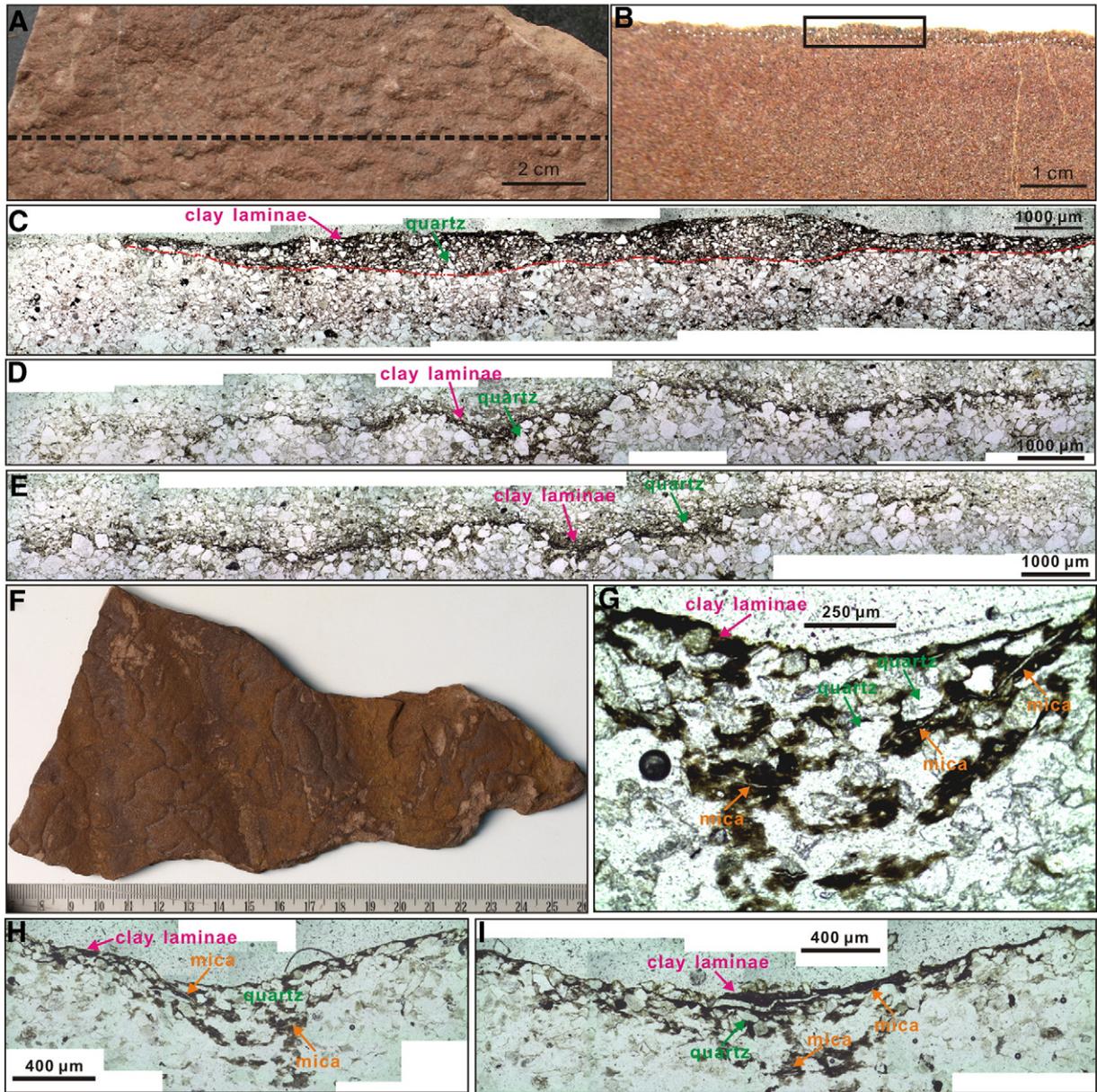


Fig. 6. Details of wrinkle structures. (A, B) Vertical slab of a wrinkle structure cut perpendicular to the bedding surface along the black line in (A), showing the change in grain sizes. (C) Amalgamated thin section photomicrographs showing dark clay laminae and a change in grain size, corresponding to the area of the black box in (B). (D–E) Thin sections of the complete structure of the wrinkles of Fig. 5D. (F) Bulge-like wrinkle structures collected from the middle part of the Liujiagou Formation in the Liulin section. (G–I) Thin section of the wrinkle features in (F), showing the presence of thin, wavy, crinkly and dark clay laminae on the bedding surface.

confined to troughs between ripples on the rippled surfaces of sandstone beds (Fig. 8). They were observed and collected in the lower part of the Liujiagou Formation at Dayulin and in the middle part of the Liujiagou Formation at Liulin. Individual crack fills with tapering ends vary from 2 to 4 mm in width and project 1–3 mm from the bed surface.

4.4.2. Interpretation

Initially, “*Manchuriophycus*” was named as a Precambrian macrofossil (Endo, 1933; Hofmann, 1967), but then it was reinterpreted as a physical sedimentary structure formed by syneresis shrinkage of clay veneers or by compaction and sediment foundering beneath overlying sediments (Plummer and Gostin, 1981). A related explanation was that they formed by shrinkage of strong and elastic microbial mats, but not the clay veneers (Gehling, 1999, 2000; Koehn et al., 2014). Considering that they are preferentially developed in the troughs of flat-

topped ripples, “*Manchuriophycus*” structures may form if microbial mats selectively grew, or attained a greater thickness, in ripple troughs than on the crests (Schieber et al., 2007; Eriksson et al., 2007; Lan and Chen, 2012; Buatois et al., 2013). In summary, the formation of this structure is thought to relate to the selective growth of the microbial mat and its thickness (Parizot et al., 2005).

4.5. Sand cracks

4.5.1. Description

Sand crack-fills were the most common microbial-induced features in the intertidal-supratidal zones of shallow marine and lacustrine environments in the Precambrian (Schieber et al., 2007; Eriksson et al., 2007; Callow et al., 2011; Lan and Chen, 2012, 2013; Simpson et al., 2013; Lan, 2015 and references therein), but have been less reported in the Phanerozoic. In this study, sand cracks with these peculiar

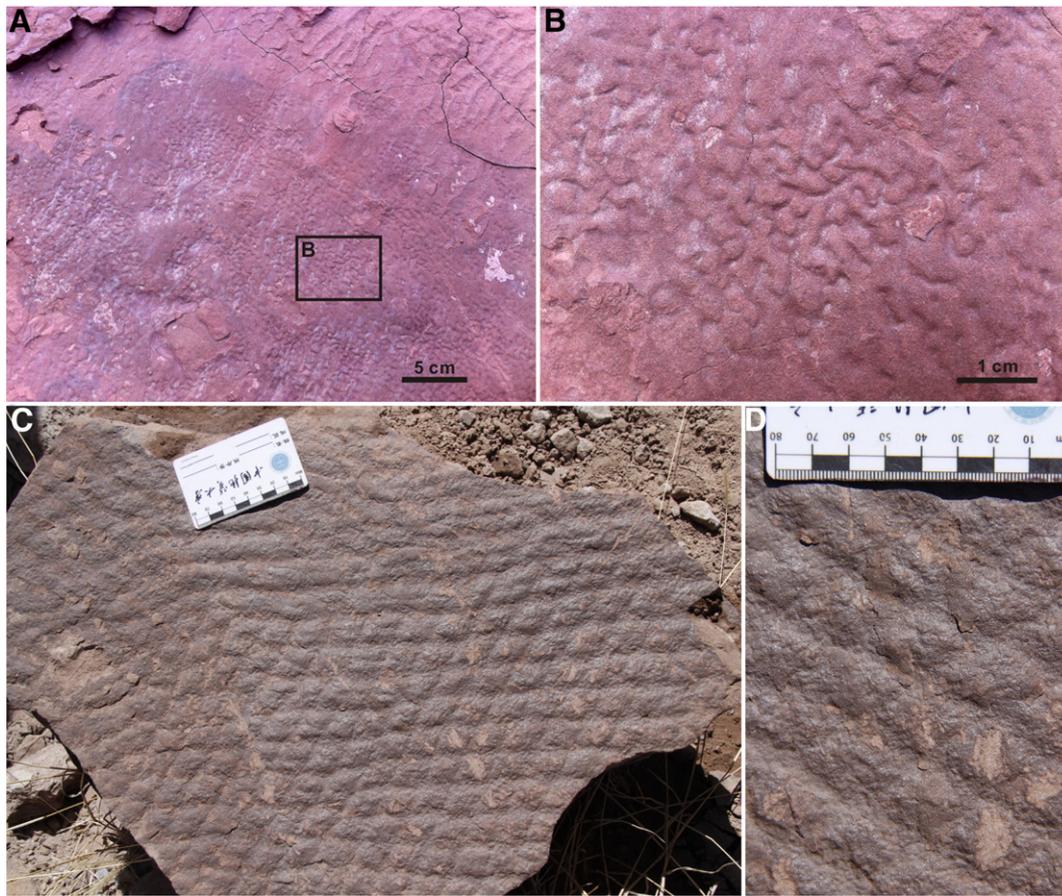


Fig. 7. Details of bulge-like wrinkle structures and palimpsest structures. (A) Bulge-like wrinkle structures collected from the lower part of the Liujiagou Formation in the Dayulin section. (B) Close-up of (A), showing wrinkle features composed of elongate to subrounded bulges. (C) Palimpsest ripple structure preserved as two successive sets of ripples, collected from the middle part of Liujiagou Formation in the Liulin section. (D) Close-up of (C) showing the diamond-like structures with subrounded and coalesced bulges or quasi-polygonal textures.

morphological characteristics have been found in the lower and middle parts of the Liujiagou Formation in the two studied sections, and they exhibit a variety of geometries, such as pedate, mesh-like, spindle-shaped and rectangular to polygonal patterns (Fig. 9). Individual pedate crack fills vary from 20 to 40 mm wide and project 10–20 mm above the bed surface (Fig. 9A). Multiple small, mesh-like cracks are preserved as positive quasi-polygonal features that were formed by the mutual connection among crack-fills on sandstone bed tops. In some cases, multiple sets of crack-fills with specific widths and tapering ends indicate that several generations of shrinkage cracks developed as they formed (Fig. 9B). Spindle-shaped sand cracks are preserved as positive epireliefs within troughs and crests on the upper rippled surfaces of sandstones (Fig. 9C, D, category B). Sometimes, the spindle-shaped crack-fills are slightly deformed with curved patterns. Rectangular to polygonal sphaeresis cracks are preserved on sandstone bed surfaces associated with the ripples, and these form “triple junction” incipient cracks without any cross-cut structure.

4.5.2. Interpretation

Microbial shrinkage sand cracks are easily confused with ichnofossils or purely physical desiccation cracks, unless they present specific morphological characteristics or indirect evidence for the former existence of cohesive biofilms or microbial mats in sandy deposits (Lan, 2015). In our study, no dark clay laminae or changes in grain size are observed in thin sections, which would be indirect evidence for the former existence of microbial mats. However, considering their peculiar morphological characteristics, such as sinuous, doubly tapering, and sand-filled forms, these sand cracks may have been induced

by microbial mat shrinkage, as they are significantly different from purely physical desiccation cracks. Furthermore, spindle-shaped sand cracks developed on wrinkle surfaces of sandstones (Fig. 9C, D), and opaque laminar clays are observed on the surfaces of the wrinkles (Fig. 9E), suggesting that the bedding surface was covered by a microbial mat during formation of the crack fills.

5. The Permian-Triassic terrestrial extinction in North China

We collected some typical Late Permian plant fossils, such as *Taeniopteris*, *Majonica* (?), *Ullmannia* and *Lobatannularia* (Fig. 10A–D), from the lower part of the Sunjiagou Formation, but no plant fossils were recorded in the overlying red sedimentary units at Dayulin. In addition, plant fossils, assigned to the genus *Ullmannia*, were reported by Wang and Wang (1986) in the mid-upper part of the Sunjiagou Formation in the Liulin area, and these represented the last appearance of this typical Late Permian plant genus. Combining a survey of literature with original collections of Permian plant fossils in North China, a total of 19 genera and 32 species of Late Permian plants from the Sunjiagou Formation became extinct (Supplementary of Chu et al., 2015), corresponding closely to the PTME of plants. Furthermore, coal seams observed in the lower part of the Sunjiagou Formation at Liulin represent the last occurrence of coal in the Permian of North China (Fig. 10E). This has been attributed to the extinction of peat-forming plants associated with the arid climate and increasing temperature (Retallack et al., 1996). Among Late Permian tetrapods, six different pareiasaurs have been reported from the Shihezi and Sunjiagou formations in North China (Young and Yeh, 1963; Gao, 1983, 1989; Li and Liu, 2013; Xu

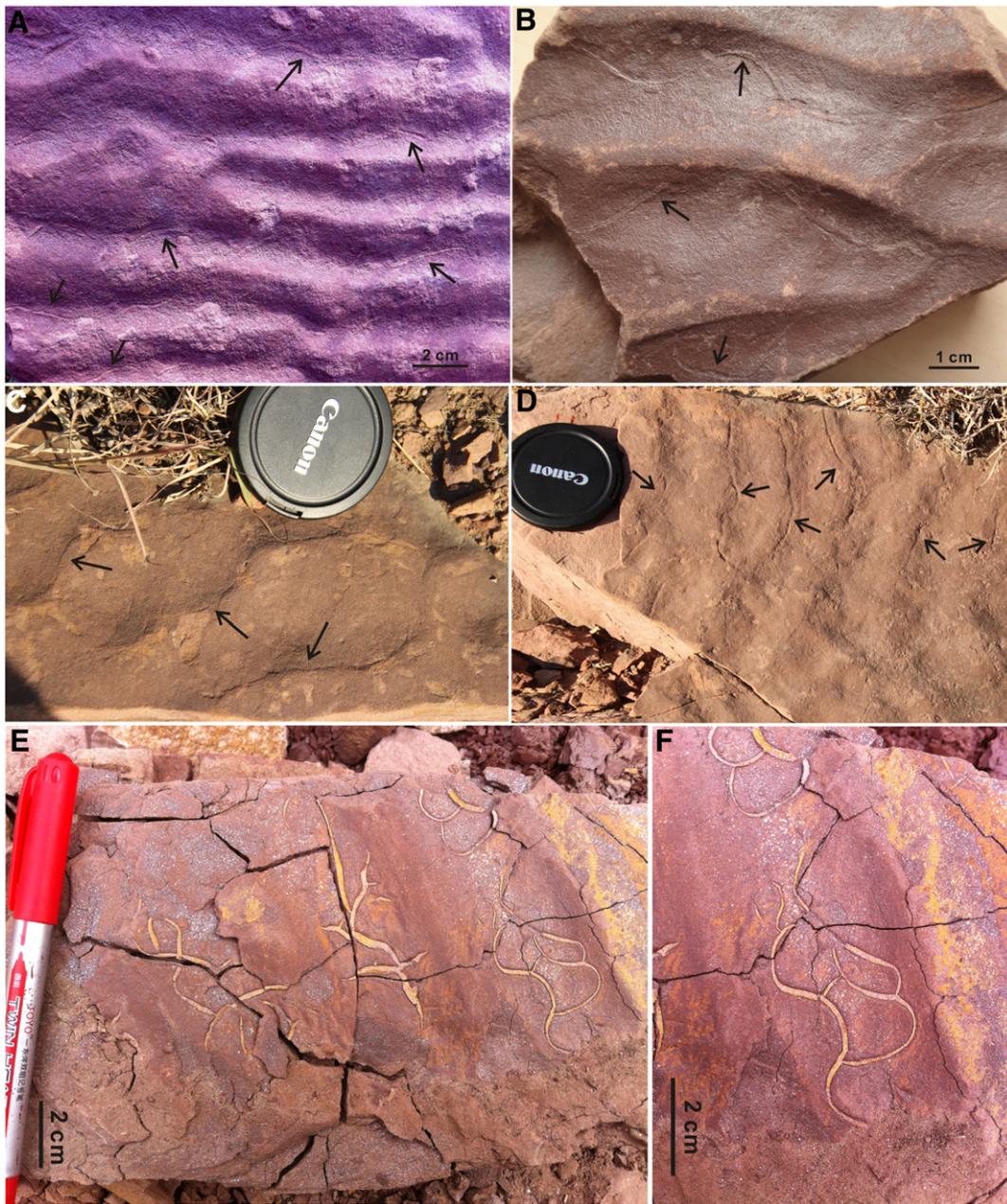


Fig. 8. Photographs of “*Manchuriophycus*” structures. (A, B) Sinuous cracks with positive patterns confined to troughs between ripples on the surfaces of sandstone beds, collected from the middle part of the Liujiagou Formation in the Dayulin section. (C, D) Sinuous cracks with negative patterns confined to ripple crests, collected from the lower part of the Liujiagou Formation in the Dayulin section. Lens cap diameter = 55 mm. (E, F) Photographs showing circular, sigmoidal and figure-8-shaped crack fills, collected from the middle part of the Liujiagou Formation in the Liulin section.

et al., 2015), but re-analysis of all the original specimens shows that only three of these are valid, *Honania* in the Shihezi Formation, and *Sanchuansaurus* and *Shihtienfenia* in the Sunjiagou Formation (Benton, 2016). In fact, pareiasaurs flourished from the Wordian to Changhsingian, but died out during the PTME (Benton, 2016). The level at which pareiasaurs disappear from the Sunjiagou Formation indicates the tetrapod extinction during the PTME. Meanwhile, the absence of metazoans and decreased bioturbation intensity in the upper part of the Sunjiagou Formation and Liujiagou Formation in North China correspond with each other, based on investigation of the fossils collected, literature surveyed and bioturbation index measured (this study; Chu et al., 2015; Tu et al., 2016; Fig. 11).

A distinct shift of lithology of the sedimentary facies can be observed in the Sunjiagou Formation, and the greyish-green, grey and dark grey

alternating mudstones, siltstones and fine-grained sandstones in the lower part contrast markedly with the red, brown and purple mudstones, siltstones and fine-grained sandstones in the upper part. These then contrast with the red, brown and purple siltstone, sandstone and conglomerate beds of the overlying Liujiagou Formation. The lower part of the Sunjiagou Formation is characterized by vertical burrows, small-scale ripple cross bedding, plant fossils and infrequent coal seams (Fig. 10A–F), which indicate deposition in a swampy/lacustrine or river flat environment. The overlying Liujiagou Formation comprises red, brown and purple siltstones, sandstones and conglomerates frequently with large-scale cross-bedding, patches of minor angular poorly sorted green to maroon or red mud rock clasts and desiccation cracks (Fig. 10G, H), which contain a higher proportion of sandstone to shale than in the underlying Sunjiagou Formation. We interpret

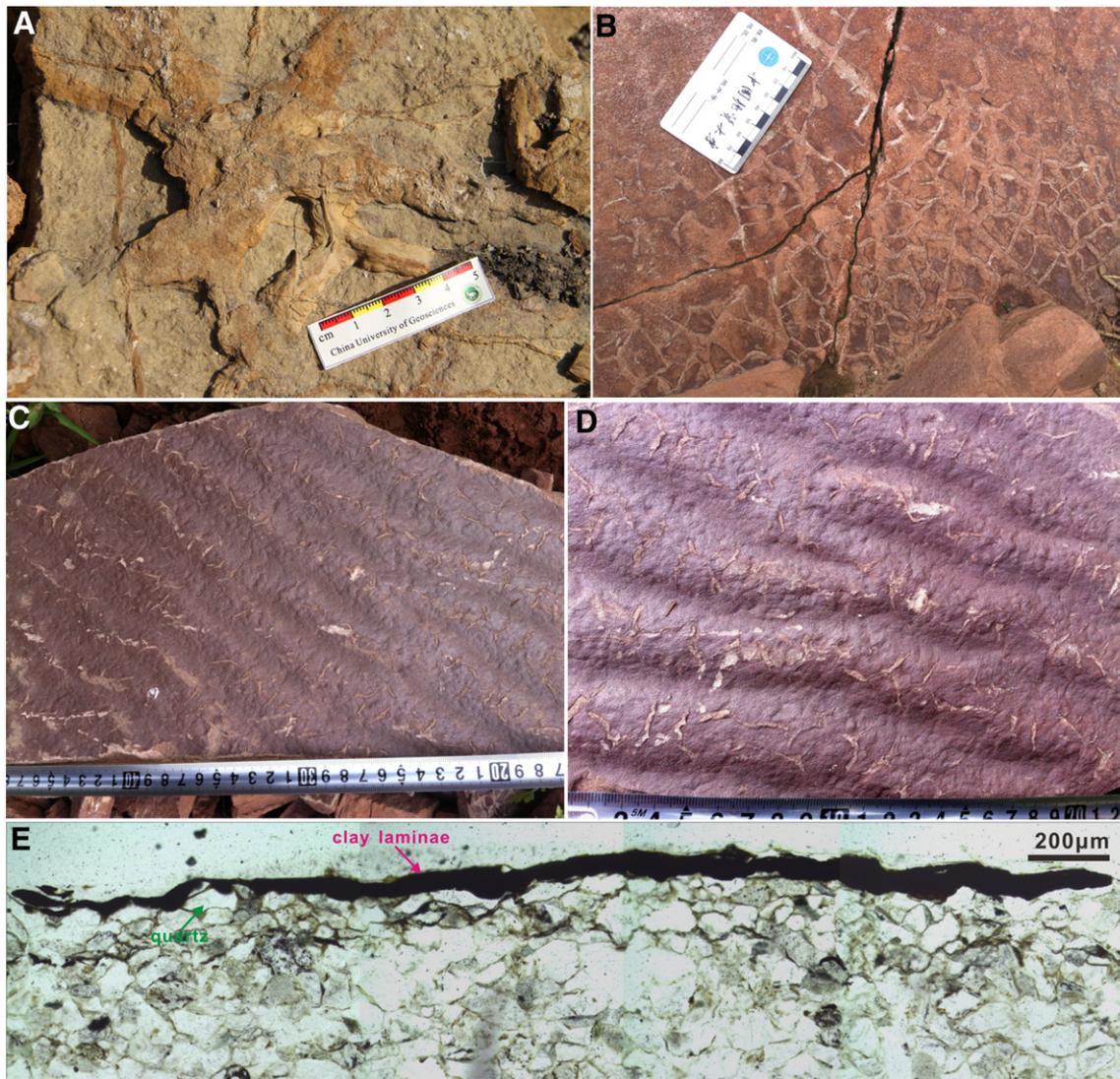


Fig. 9. Sand cracks preserved on sandstone bed tops of the middle part of the Liujiagou Formation in the Dayulin section, and thin section photomicrographs. (A) Pedate cracks. (B) Mesh-like cracks preserved as positive quasi-polygonal structures. (C, D) Spindle-shaped sand cracks confined to ripple crests, preserved as positive epireliefs, and developed on the wrinkle surface of sandstones. (E) Photomicrographs of the thin section in (D), showing the dark clay laminae preserved on the wrinkle surface.

these massive sandstone units as having formed in a very shallow lake to a river flat environment, although the lower part suggests a storm-dominated shallow lake setting (Chu et al., 2015; Tu et al., 2016). The sedimentary record from the Sunjiagou Formation to the overlying Liujiagou Formation indicates a dramatic change of sedimentary system and a collapse of the terrestrial soil system. As mentioned above, the most probable causes of this sedimentary system turnover, associated with enhanced soil erosion and terrestrial weathering, are the widespread die-off of plants and the decrease of vegetation coverage which is attributed to rapid global warming and persistent arid climate (e.g. Retallack et al., 1996; Looy et al., 1999, 2001; Ward et al., 2000; Benton and Newell, 2014; Benton, 2015).

In summary, the end-Permian biotic crisis was represented by the die-off of plant fossils, the disappearance of coal beds, the extinction of tetrapods including pareiasaurs, decreased bioturbation levels and a dramatic change of the sedimentary system coupled with the collapse of the terrestrial soil system in the Sunjiagou Formation, which corresponds to the first lithological unit of the Permian–Triassic red beds in North China (Fig. 11). The Sunjiagou Formation records the turnover from an ever-wet to a progressively drier and hotter climate, indicative of the terrestrial PTME in North China.

6. Discussion

6.1. How did the mass extinction affect the flourishing MISS: favourable conditions or essential conditions?

Following metazoan diversification and increased benthic bioturbation in the post-Cambrian, microbial sedimentary structures are commonly considered to be mainly restricted to exceptional intervals and anomalous environments associated with low levels of bioturbation and grazing (e.g. Calner, 2005; Pruss et al., 2006; Mata and Bottjer, 2009), but some studies suggest that in fact MISS existed in the depositional records of various environments throughout the Phanerozoic (e.g. Noffke and Chafetz, 2012; Carmona et al., 2012; Dai et al., 2015; Xing et al., 2016). However, the flourishing of MISS have been commonly and globally described from post-extinction intervals, suggesting that these occurrences are not coincidental, but do indicate a causal connection.

In most cases, a low level of bioturbation or grazing pressure is one of the most important determining factors in the original formation of MISS, and their later preservation, especially for surface features, due to the absence of destruction from biological interactions. However,

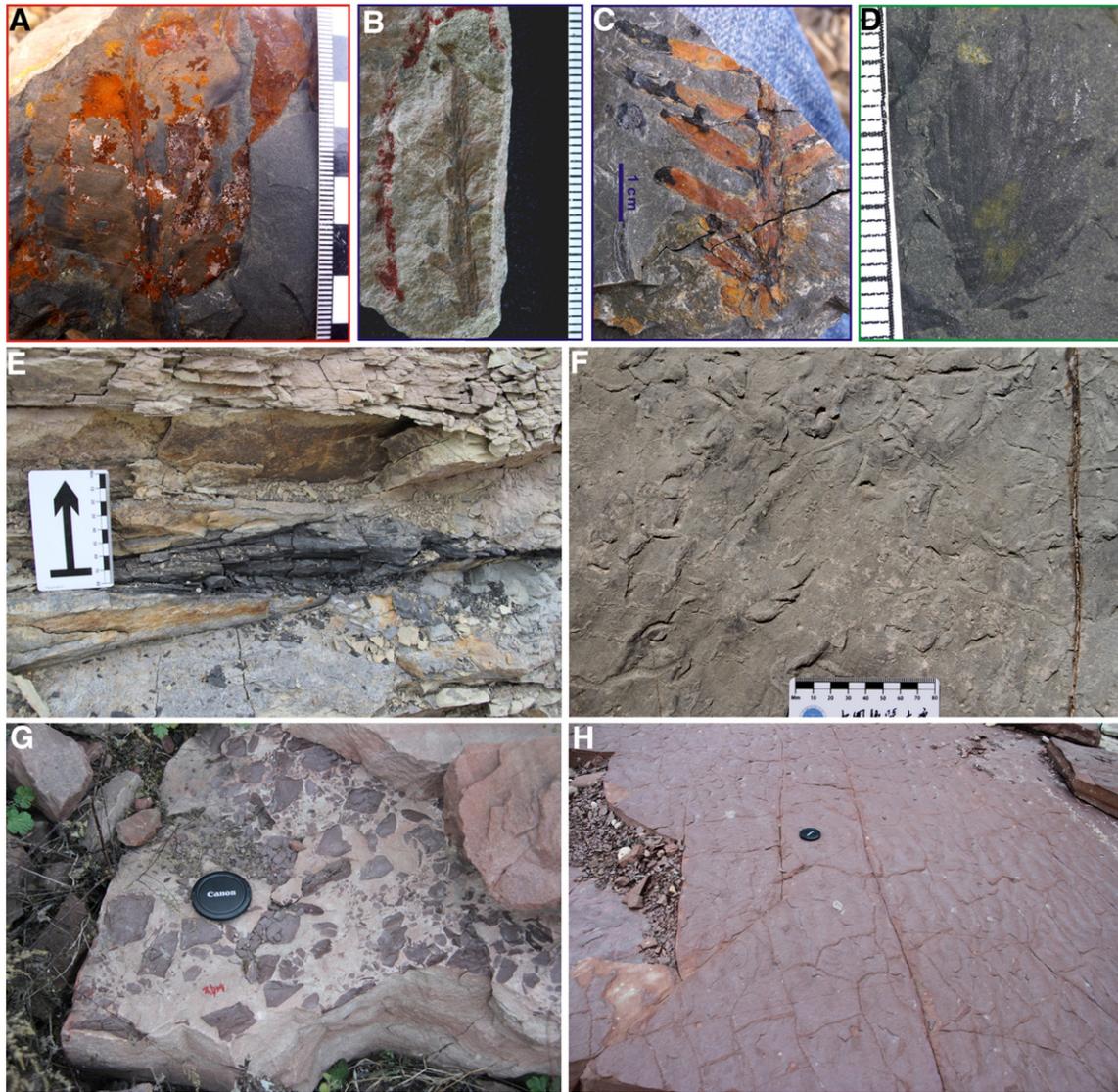


Fig. 10. Plant fossils and trace fossils. (A–D) Photographs of plant fossils collected from the lower part of the Sunjiagou Formation in the Dayulin section, assigned to the genera *Taeniopteris*, *Ullmannia*, *Majonica* (?) and *Lobatanularia*, respectively. (E) The last appearance of a coal bed/seam in the lower part of the Sunjiagou Formation in the Liulin section. (F) Abundant trace fossils preserved on a fine-grained sandstone bedding surface from the lower part of the Sunjiagou Formation. (G) Angular poorly sorted red mud rock clasts within sandstones of the Liujiagou Formation in the Dayulin section. (H) Desiccation cracks preserved on a sandstone bedding surface of the Liujiagou Formation in the Dayulin Section. *lens* cap diameter = 55 mm.

considering the repeated and widespread presence of local environments with low levels of bioturbation and grazing throughout Earth history, it cannot be said that MISS only appear in the aftermath of biotic mass extinctions. In fact, changes in local sedimentary systems and depositional environments also provide favourable biological and environmental conditions for the formation and preservation of MISS. So, it should be said that a mass extinction, particularly where bioturbation has been reduced, can provide favourable conditions for thriving microbial communities and development of MISS, but not always. The essential factor for the presence of MISS is the amount of bioturbation. That is why MISS are found in brackish, marginal marine, intertidal, supratidal and lacustrine environments in the Precambrian as well as in the Phanerozoic, where metazoan bioturbation is commonly limited by stressful conditions (Hagadorn and Bottjer, 1997; Pruss et al., 2004, 2006; Schieber et al., 2007; Mata and Bottjer, 2009). However, normal marine subtidal environments in the Phanerozoic commonly have substantial bioturbation, and MISS are less common in those conditions. But, when bioturbation is reduced in subtidal environments for some reason, MISS may develop there, such as after a mass extinction, until bioturbation increases again to levels that preclude MISS. Thus, the

essential factor is not mass extinctions but the presence and amount of bioturbation, which can be reduced for a variety of reasons, including mass extinctions.

For this study, the Sunjiagou Formation records the PTME and turnover of the sedimentary system, as well as significant climate change. Bioturbation was much reduced after this mass extinction, as indicated by our measurements of the bioturbation index from the Dayulin section (Fig. 11; Chu et al., 2015; Tu et al., 2016). MISS are widely distributed in the post-crisis lower-middle part of the Liujiagou Formation, but absent in the underlying richly bioturbated Sunjiagou Formation in North China. Therefore, decreased grazing pressure, coupled with low-level bioturbation following the PTME, promoted the formation and preservation of MISS.

6.2. Distribution and depositional conditions of MISS at the studied area

In this study, MISS were confined to the lower-middle part of the Liujiagou Formation in the studied sections, mostly preserved on the reddish silt- to fine-grained rippled sandstone bed tops. Conversely, the deposits of both the underlying Sunjiagou Formation and the

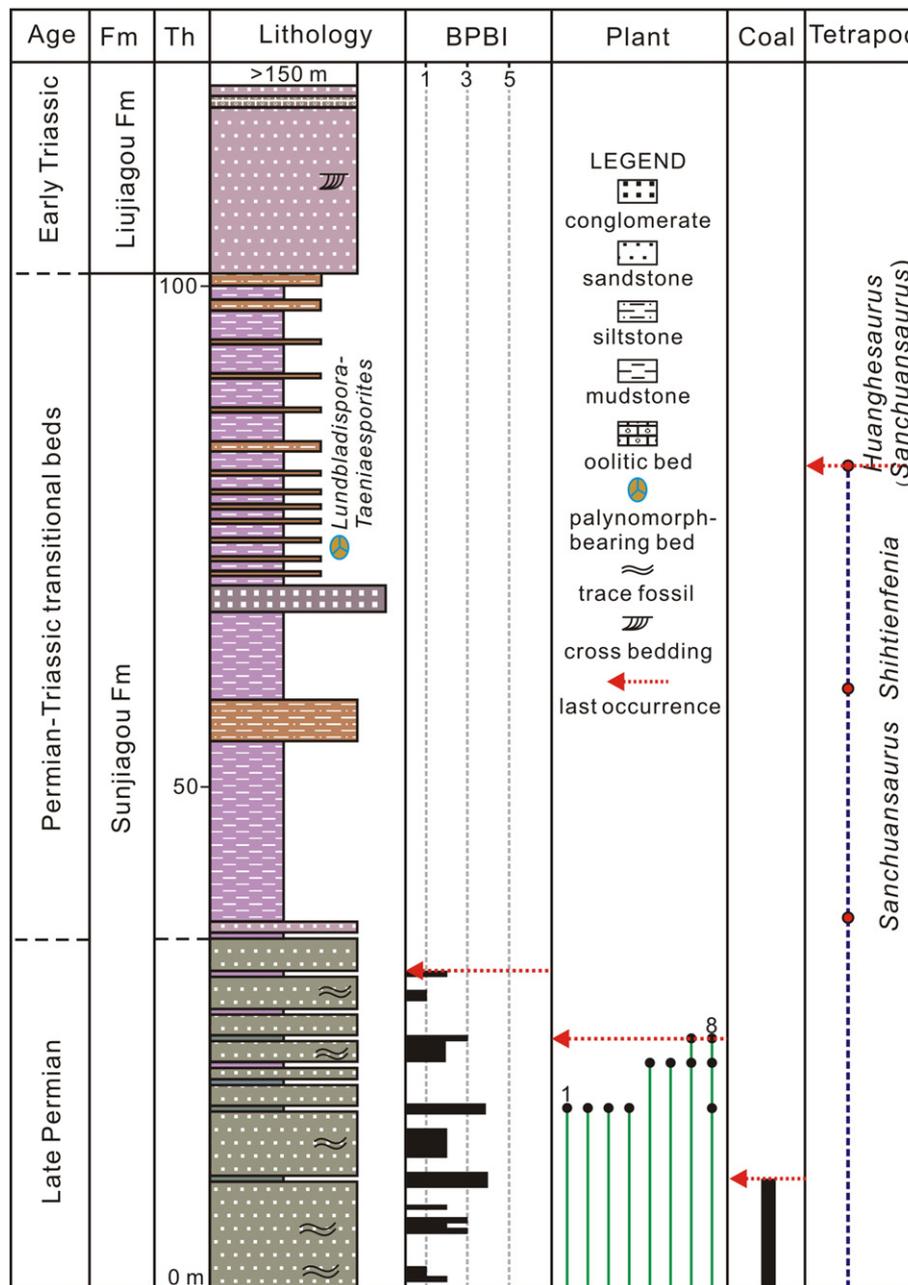


Fig. 11. The distribution of bedding-plane bioturbation index (BPBI), plants, coal, tetrapods (pareiasaurs) and palyomorphs in the Sunjiagou Formation of the studied area, showing the Sunjiagou Formation spanning the PTME. The lithology is on the basis of the Dayulin section; the bioturbation index showing decreased bioturbation intensity in the upper part of Sunjiagou Formation and Liujiagou Formation; the extinction of plants occurred in the lower part of the Sunjiagou Formation in the Dayulin section (this study; Zhang et al., 1987), 1. *Pityospermum junduensis* Wang; 2. *Quadrocladus cf. orobiformis* (Schlotheim) Schweitzer; 3. *Pseudovoltzia cf. liebeana* (Geinitz) Florin; 4. *Pseudovoltzia* sp.; 5. *Sphenobaiera* sp.; 6. *Lobatannularia* sp.; 7. *Ullmannia bronni* Goepfert; 8. *Taeniopteris* sp.; the last occurrence of coal beds occurred in the lower part of the Sunjiagou Formation; the mass extinction of pareiasaurs occurred in the upper part of the Sunjiagou Formation (Benton, 2016); the first appearance of the Triassic-type *Lundbladispora-Taeniaesporites* palyomorph assemblage occurred in the upper part of the Sunjiagou Formation (Hou and Ouyang, 2000). The upper part of the Sunjiagou Formation corresponds to the Permian–Triassic transitional beds. Abbreviations: Fm, Formation; Th, Thickness; BPBI, Bedding Plane Bioturbation Index (Miller and Smail, 1997).

overlying Heshanggou Formation show rich bioturbation, but no MISS. Meanwhile, wrinkle structures were widely found in the Liujiagou Formation in adjoining areas, and show similar characteristics of spatial and temporal distribution (Chu et al., 2015). Similarly, microbial mat-related biosedimentary structures were reported in the red beds of a Lower Triassic siliciclastic playa environment from the central basin of the Middle Buntsandstein (Wehrmann et al., 2012), as well as microbialites and oolites from the Buntsandstein Group in Germany, although its depositional environment is still controversial (Paul and Peryt, 2000; Weidlich, 2007).

Palaeoenvironmental conditions such as water depth, exposure and hydrodynamic energy, control the distribution of MISS within these facies. In fact, specific environmental conditions must exist to allow the corresponding MISS to form and be preserved in the rock record. These conditions provide the habitat for thriving microbial ecosystems to develop and offered long-term preservation potential (Hagadorn and Bottjer, 1997; Noffke et al., 2002; Pruss et al., 2004). In the studied sections, the OES and wrinkle structures are found on sandstone bed tops, which are inferred to have been deposited in storm-dominated or storm-influenced siliciclastic settings from the presence

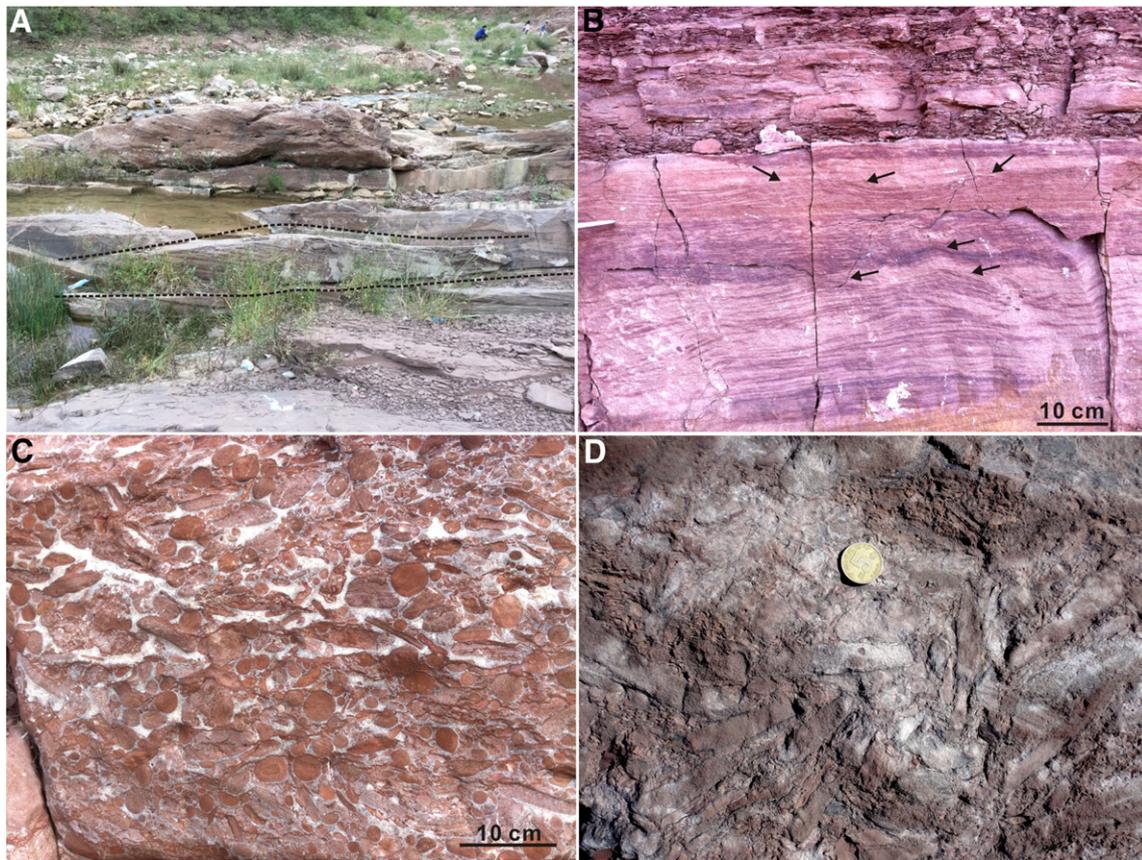


Fig. 12. Sedimentary structures. (A) Field photograph showing large-scale hummocky cross-stratification in the lower part of the Liujiagou Formation in the Dayulin section. (B) Field photograph showing small-scale hummocky cross-stratification in the middle part of the Liujiagou Formation in the Liulin section. (C) Conglomerates with lenticular, rounded and quasi-polygonal shapes. (D) Sandstone with interbed of flat-pebble conglomerates, observed in the lower part of the Liujiagou Formation in the Dayulin section. Coin diameter = 20 mm.

of hummocky cross-stratification and flat-pebble conglomerates (Fig. 12; Myrow et al., 2004; Morsilli and Pomar, 2012). Storm-dominated siliciclastic settings are considered to be appropriate settings for mat growth features where hydrodynamic flow is sufficient to sweep mud from mat surfaces but insufficient to erode biostabilized laminae, so that a microbial-mat-colonized surface trapped and bound the clean, fine-grained, translucent quartz grains (Noffke et al., 2002; Pruss et al., 2004; Schieber et al., 2007).

In addition, for the beds that developed syneresis shrinkage sand cracks, short-wavelength ($\lambda < 50$ mm) and symmetrical ripples are common, and shrinkage sand cracks are sometimes parallel to ripple troughs or crests (Fig. 2F). These ripples typically have parallel and straight ripple crests and consistent crest orientations from bed to bed (Fig. 2F), indicating deposition in very shallow water across large areas. Meanwhile, the fine-grained sandstone or siltstone beds commonly contain multiple generations of sand-filled polygonal desiccation cracks, indicating periodic exposure (Fig. 10H). So, the occurrences of syneresis cracks and desiccation cracks, coupled with short-wavelength and symmetrical ripples, indicate alternations between subaqueous and subaerial conditions, and deposition in very shallow water.

6.3. Implication for the post-extinction terrestrial ecosystems and the Early Triassic biotic recovery

Blooms of microbial communities in the aftermath of the PTME have been reported worldwide from marine Lower Triassic successions, suggesting that microbial buildups and mats dominated the seabed, preserved in the form of microbialites and wrinkle structures (Kershaw et al., 1999; Pruss et al., 2004, 2006; Mata and Bottjer, 2009). For terrestrial deposition during the post-extinction interval,

MISS-related microbial mats were observed in the Liujiagou Formation of North China and the Detfurth Formation of the Germanic Basin (this study; Wehrmann et al., 2012; Tu et al., 2016), which might imply that microbial communities proliferated both in the sea and on land through most of the Early Triassic. Furthermore, records of terrestrial MISS and microbial organics also indicate extreme environmental stresses following the PTME.

In particular, the detrimental effects of increased temperature and climatic drying, presumably caused/exacerbated the extinction of terrestrial organisms (Benton and Newell, 2014), but provided the habitat for thriving microbial communities and favourable conditions for MISS formation. The degradation of terrestrial ecosystems and turnover from an ever-wet to a progressively drier and hotter climate immediately after the PTME were observed from sedimentological studies in North China, and this promoted the widespread formation of MISS. Furthermore, abnormal hydrochemical and physical environments may also have been responsible for the low-level of bioturbation and flourishing of MISS in the aftermath of the PTME, such as nutrient enrichment associated with enhanced nutrient input, decreased solubility of oxygen associated with reduced atmospheric oxygen content and elevated temperature, strong water energy, and geochemical anomalies associated with the climate turnover (Berner et al., 2007; Algeo and Twitchett, 2010; Sun et al., 2012; Chu et al., 2015).

In the studied sections, MISS were limited in the lower to middle parts of the Liujiagou Formation and not observed yet in its upper part. This phenomenon is also reinforced by our observations of the other sections in Henan, Shanxi and Shaanxi provinces. The investigation of fossils and bioturbation index for these sections in North China demonstrated that the absence of metazoans and decreased bioturbation intensity happened immediately after the severe mass extinction, and only very rare trace fossils occurred in the lower to middle parts

of the Liujiagou Formation (Chu et al., 2015). In the upper part of the Liujiagou Formation, MISS disappeared and burrows and surface traces discontinuously appeared, but significantly were not recovered to the pre-extinction level of bioturbation intensity. Furthermore, the overlying Heshanggou Formation shows diverse ichnofossils and rich bioturbation, with a measured bioturbation index up to 5 (Fig. 13). So, the disappearance of MISS associated with growing bioturbation in the upper part of the Liujiagou Formation and the Heshanggou Formation might indicate an improved terrestrial ecosystem and the prologue of the Triassic biotic recovery. However, the timing and pattern of the recovery of Early Triassic terrestrial ecosystems and correlation between

marine and terrestrial settings requires further geobiological and geochemical studies, as well as high-precision isotopic dating, especially for the terrestrial successions.

7. Conclusions

Five different kinds of MISS or sedimentary surface textures were recognized through studies of morphology and microscopic characteristics. The microscopic features and SEM images showing the presence of crinkly, dark and opaque clay laminae and floating quartz grains, suggest that the microbial mats trapped sand grains from the surrounding

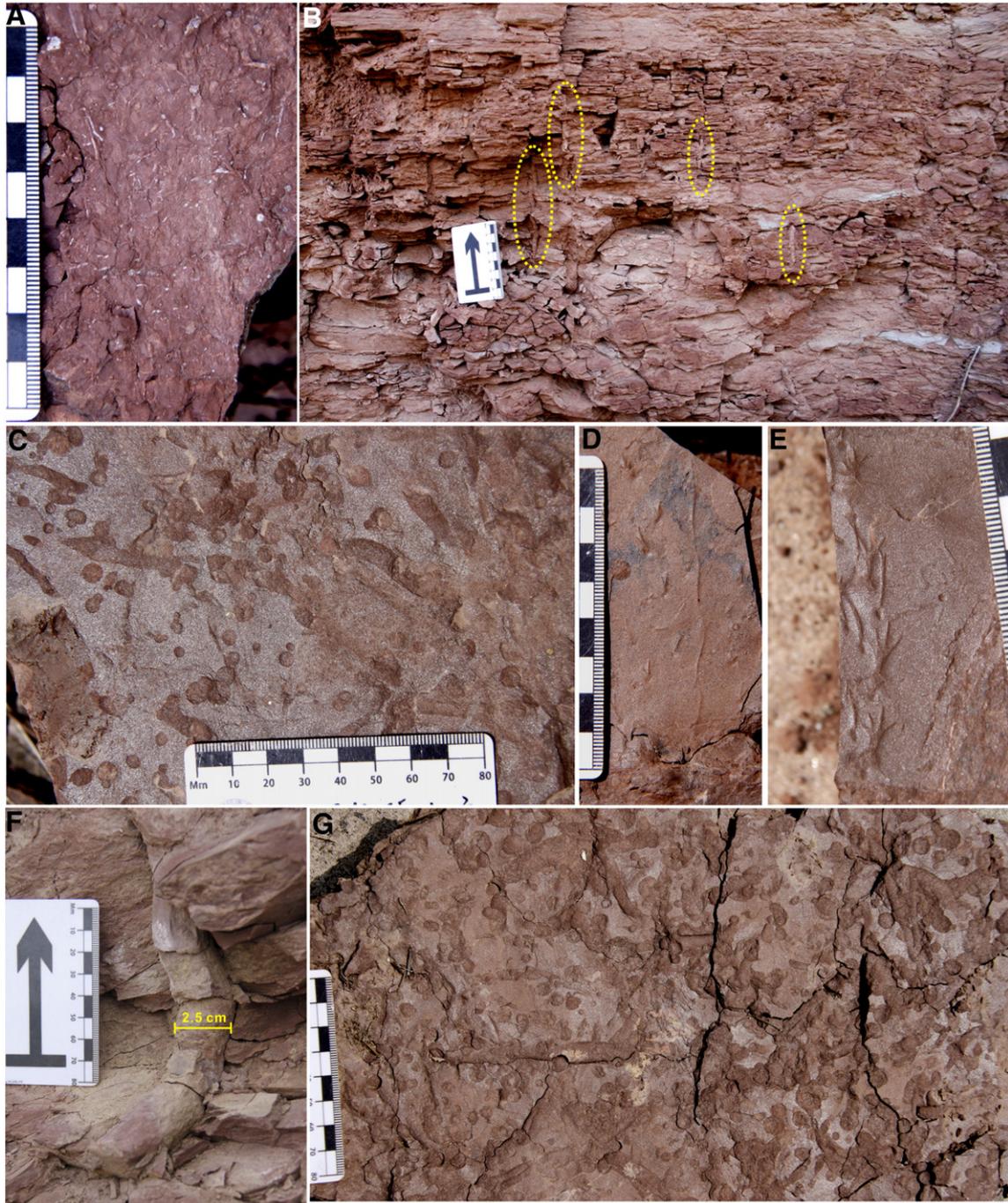


Fig. 13. Burrows and surface traces from the upper part of Liujiagou Formation and Heshanggou Formation. (A) A surface assemblage of slender traces from the upper part of Liujiagou Formation. (B) Vertical burrows extend to a depth of 50–100 mm in the upper part of the Liujiagou Formation. (C) An assemblage of surface traces and burrows, assigned to *Planolites* and *Skolithos*, from the bottom of the Heshanggou Formation. (D, E) Limulid trackways preserved on bedding planes, from the lower part of the Heshanggou Formation. (F) A curved burrow with a maximum diameter of 25 mm, from the lower part of the Heshanggou Formation. (G) A dense assemblage of surface traces and burrows, assigned to *Planolites* and *Skolithos*, collected from the middle part of the Heshanggou Formation.

environment (Hagadorn and Bottjer, 1997). The depositional environments studied here demonstrate that microbial communities in the lakes of the Liujiagou Formation were adapted not only to periodically desiccated conditions, but also storm-dominated palaeoenvironments, which provided the habitat for thriving microbial ecosystem development and offered long term preservation potential.

The Sunjiagou Formation records the turnover of sedimentary systems and climate, and it also records the terrestrial PTME in North China. Following the mass extinction, MISS became much more common and widespread, which suggests that the mass extinction provided favourable environmental and biological conditions for development of MISS in terrestrial ecosystems, such as low-level bioturbation, decreased grazing pressure, and enhanced nutrient input associated with the increased temperature and climatic drying. In particular, the essential factor affecting the presence of MISS is the amount and level of bioturbation. However, a biotic crisis should not be considered as the only condition necessary for the formation of MISS. A full understanding of how MISS form in space and time will require a worldwide survey of original observations from various geological records and a comprehensive explanation should be addressed using large datasets and empirical experimental modelling (e.g. Noffke and Awramik, 2013; Thomas et al., 2013; Mariotti et al., 2014; Davies et al., 2016). In addition, we propose that the disappearance of MISS coupled with growing bioturbation might indicate an improved terrestrial ecosystem and represent the prologue of the Triassic biotic recovery since the deposition of the Heshangou Formation.

Acknowledgments

We thank Xincheng Qiu, Kaixuan Ji, and Wenchao Shu for help with sampling from the studied section. Hao Yang and Ruiwen Zong are thanked for assistance with obtaining SEM and microscope images at the State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences (Wuhan). We would like to thank Zhong-Qiang Chen, Alexander Liu and Qing-Yu Ma for insightful discussions. Steve Zhang is thanked for revising the English of the manuscript draft. The authors are grateful to Sara Pruss, the anonymous reviewer and guest editor Zhong-Qiang Chen for their critical comments and constructive suggestions, which have greatly improved the quality of the paper. This study was supported by the National Natural Science Foundation of China (41272372, 41530104, 41402302), the 111 Project (B08030). It is a contribution to IGCP 630.

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