Research Article

Wei Zheng, Xin Xu, Yongan Qi, Zhifeng Xing*, Yunlong Liu, Xiaoyan Li, and Baibing Chen

Characteristic and paleoenvironment significance of microbially induced sedimentary structures (MISS) in terrestrial facies across P-T boundary in Western Henan Province, North China

https://doi.org/10.1515/geo-2020-0285
received January 25, 2021; accepted July 22, 2021

Abstract: We report varied microbially induced sedimentary structures (MISS), and other sedimentary surface textures, from the Induan (Early Triassic) Sunjiagou Formation and Liujiagou Formation in the Xingyang, Dengfeng, Jiyuan and Yiyang areas, western Henan Province, North China. Microanalysis shows that these MISS are characterized by a U-shaped structure, thin clayey laminae, and discontinuous mica sheet that are arranged parallel to the bedding plane, as well as directionally oriented quartz grains floating in lamina, which are indicative of a biogenic origin. The MISS of the studied area were probably affected by four main factors, including the end-Permian mass extinction, the megamonsoon, the adapted sedimentary environment, and the sediment supply, and they possess significant stratigraphic correlation. Abundant microbial-related sedimentary structures from the study area indicate that continental ecosystems were severely devastated in the aftermath of the Permian-Triassic biocrisis. These sedimentary structure assemblages, including MISS, red beds, conglomerate layers, and calcareous concretions in the western Henan Province, show a specific, post-extinction continental ecosystem that was characterized by microflora dominance, monotonous and rare fossils, extreme hot climate, soil ecosystem devastation, and poor vegetation.

Keywords: MISS, continental ecosystem, the end-Permian mass extinction, controlling factors

*** Corresponding author: Zhifeng Xing,** Institute of Resources and Environment, Henan Polytechnic University, Jiaozuo 454003, China; Key Laboratory of Biogenic Traces and Sedimentary Minerals of Henan Province, Henan Polytechnic University, Jiaozuo 454003, China, e-mail: xingzhifeng925@hpu.edu.cn
Wei Zheng: Institute of Resources and Environment, Henan Polytechnic University, Jiaozuo 454003, China; Key Laboratory of Biogenic Traces and Sedimentary Minerals of Henan Province, Henan Polytechnic University, Jiaozuo 454003, China
Xin Xu, Yunlong Liu, Xiaoyan Li, Baibing Chen: Institute of Resources and Environment, Henan Polytechnic University, Jiaozuo 454003, China
Yongan Qi: Institute of Resources and Environment, Henan Polytechnic University, Jiaozuo 454003, China

1 Introduction

According to studies of modern microbial mats, cyanobacteria and its extracellular polymeric substances form sheet-like sedimentary bodies, the microbial mat, by trapping, binding, and biostabilization [1–4]. The strength-toughness properties, cohesiveness, and baffling of the microbial mat enhance the sedimentary surface's resistance to corrosion, smooth its texture, and stabilize it. Additionally, the microbial mat affects surface sediment and environmental properties due to biological activity and biochemistry [2,4]. The microbial community interacts with the sedimentary environment by growing, destroying, decaying, and metabolizing in order to form biomat-related sedimentary structures, which are known as microbially induced sedimentary structures (MISS) [1,4–7]. MISS are primary sedimentary structures that arise syndepositionally from the interaction of biofilms or microbial mats with the physical sediment dynamics of siliciclastic aquatic environments [8]. Biofilms are highly complex assemblages of single celled organisms. In favorable environments, biofilms form around individual sand grains, and these initial biofilms of adjacent grains grow until they form a laterally continuous, organic layer. This layer is a microbial mat [8]. Therefore, MISS are products from the interaction between life and the environment. MISS are usually preserved on the upper surfaces of fine sandstone beds in siliciclastic settings, and the original mat is rarely preserved [8]. They are also common sedimentary features in Proterozoic-Cambrian strata extending back to the Early Archean [2,9–11]. However, after the introduction and influence of bioturbation following the Great Ordovician Biodiversification Event, MISS usually only occur in special periods during the Phanerozoic, such as the Late Permian [7,12–16], the Late Triassic [17], and modern special sedimentary environments [18]. Davies et al. recently demonstrated that the presence of MISS occurs due to metazoan activity and sedimentary environment [19]. Therefore, biomat-related sedimentary structures and their geological processes supply important clues for the rate and mechanisms of ecosystem recovery after Phanerozoic catastrophic events and the coevolution between Earth's environment, microbes, and metazoans.

The largest mass extinction in geological history occurred near the Permian–Triassic boundary, which killed approximately 95% of all marine species and 70% of all continental species on Earth [20,21]. This catastrophic event not only caused a mass extinction, but also formed peculiar biological genus structures and ecological patterns. Microbialites and MISS have been reported from marine strata in the regions surrounding the Paleo-Tethys Ocean and the eastern coasts of the Panthalassic Ocean [12,22–30]. Some geologists systematically study these microbialites and MISS and have summarized four spikes and space distributions following the end-Permian mass extinction event [28,29]. However, less is known about the specific changes in continental microbial ecosystems during the end-Permian mass extinction and its aftermath. So far, continental MISS from the Early Triassic have only been reported in northern Germany, western Morocco, and Liulin, Yiyang, and Xingyang in North China [7,13,14,16,31,32]. These studies have only discussed the type and significance of MISS in sedimentology; the relationship between the end-Permian mass extinction and the Early Triassic flourishing of MISS has not been revealed. Continental Permian-Triassic successions are well-exposed and widely distributed in the western Henan Province, such as the Xingyang, Dengfeng, Jiyuan, and Yiyang areas in North China, and are characterized by inland fluvial and lacustrine siliciclastic red beds. These sections provide many new biostratigraphical, sedimentological, and lithological data and contain important clues for better understanding of continental ecosystems. Here, we analyze sedimentology distribution and contributing factors of biomat-related sedimentary structures and probe the interaction between microbes and the environment in continental ecosystems on the basis of previous and new data.

2 Geologic setting, stratigraphic sequence, and lithofacies features

The western Henan Province, North China, is an independent block located in the southern part of the North China Block. During the middle-late Permian, the North China Block was uplifted and became continental due to the amalgamation of the Qaidam, Tarim, and Siberia-Mongolia paleoplates [33]. As a consequence, fluvial and lacustrine facies deposits have been developed in the upper Permian and Lower Triassic successions of the North China Block, which were formed in the northern part of the Paleo-Tethys Ocean (Figure 1) [34]. The tectonic evolution of the Henan Province was collectively controlled during the Triassic by the Paleo-Asiatic tectonic domain and the Paleo-Tethys tectonic domain [35]. A series of different-sized inland lake basins were formed during this time in the Henan area. In the Early Triassic, western Henan province completely got rid of the influence of sea water and evolved from continental margin offshore deposits to inland fluvio-lacustrine deposits, and western Henan was located in the southwest corner of the large depression basin of North China [36–39]. In addition, fluvial and lacustrine facies deposits, including the Lower Triassic Sunjiagou Formation, Liujiagou Formation and Heshanggou Formation, the Middle Triassic Ermaying and Youfangzhuang Formation, and the Upper Triassic Chunshuyao and Tanzhuang Formation, were formed in the north Pingdingshan-Ruyang area [40].

The continuous continental Permian-Triassic succession is well-exposed in Xingyang, Dengfeng, and Yiyang counties, Jiyuan city, Henan Province, North China (Figure 2). Therein, the late Permian comprises the lower and middle Sunjiagou Formation, while the Early Triassic consists of the upper Sunjiagou, Liujiagou, and Heshanggou Formation [16].

The stratotype section of the Henan Sunjiagou Formation lies in the Nantianmen section, Yiyang county. The lower Sunjiagou Formation, overlying the Shangshihezi Formation, is composed of a thick, greenish-gray sandstone interbedded with greenish, dark mudstones, followed by a reddish mudstone interbedded with thick medium-coarse sandstones in the middle. The upper Sunjiagou Formation, overlying the Liujiagou Formation, is dominated by red mudstone with numerous calcareous-nodular paleosols and thin- to medium-bedded yellow freshwater limestones. The Sunjiagou Formation of four sections that are almost identical, but also have distinctive features. The Sunjiagou Formation of the Cuimiao section (34°40′21.92″N, 113°21′16.81″E), Xingyang county, is approximately 191 m thick. Its lower part is dominated by a red mudstone, followed

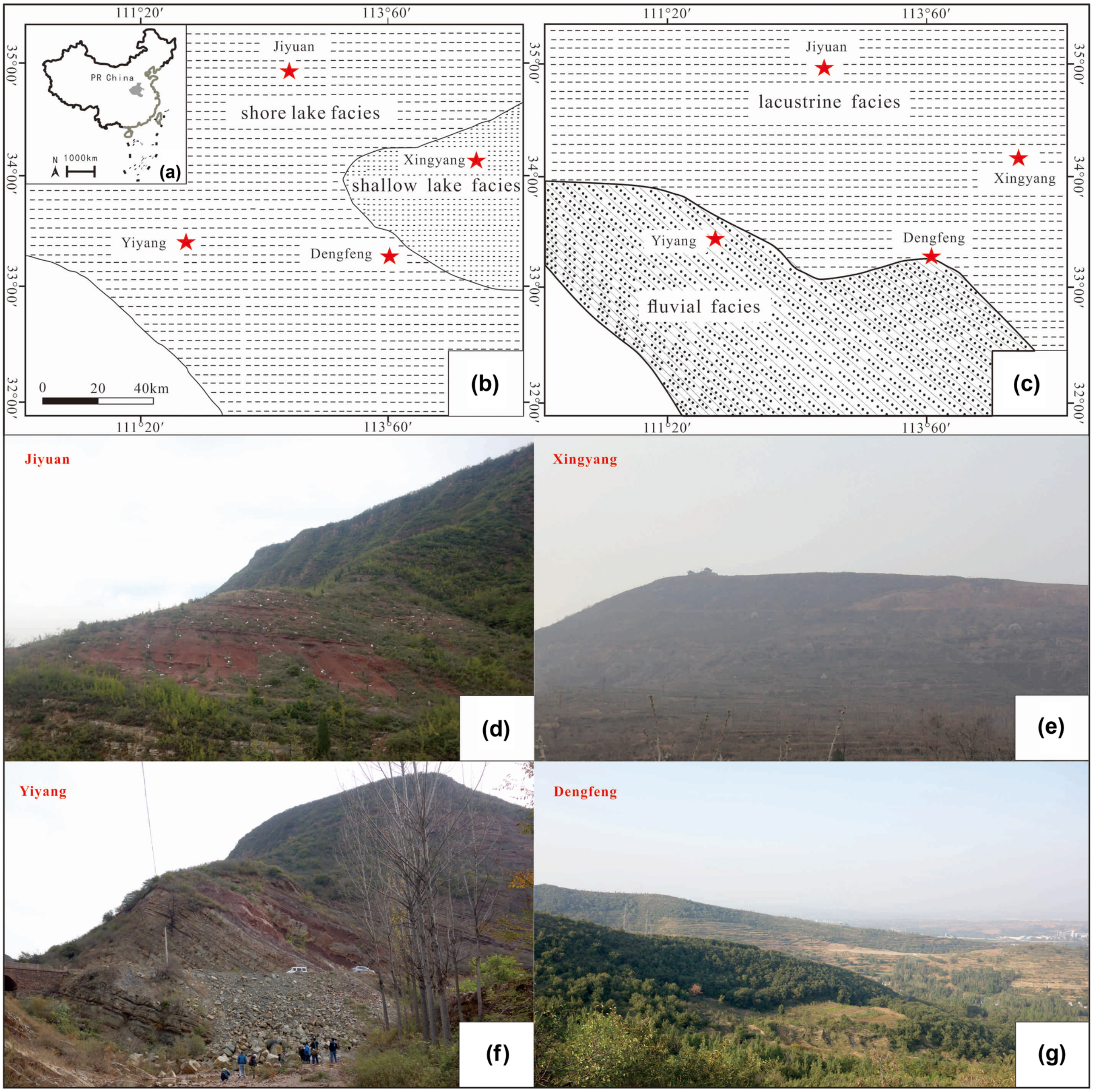

Figure 1: Investigated localities. (a) Sketch map of China, showing the locations of Henan Province (grey shading). (b) A skeleton diagram of the late Permian paleogeography and locations of the studied sections (red star). (c) A skeleton diagram of the early and middle Triassic paleogeography and locations of the studied sections (red star). (d) The photo of the Fangshan section, Jiyuan city. (e) The photo of the Cuimiao section, Xingyang county. (f) The photo of the Ligou section, Yiyang county. (g) The photo of the Baiping section, Dengfeng county.

by a yellow-green sandstone and siltstone at its upper part with well-preserved ripples, cross-bedding, MISS, and conglomerates, which are the typical signs of storm deposits in continental lake basins. The Sunjiagou Formation of the Baiping section (34°19′30.51″N, 113°04′53.89″E), Dengfeng county, is approximately 41 m thick. Its lower part is dominated by red siltstone or mudstone, and the upper part is composed of a thick, greenish-gray sandstone interbedded with yellow-green siltstones and containing well-preserved ripples, cross-bedding, and conglomerates. The Sunjiagou Formation of the Fangshan section (34°58′35.94″N, 112°21′29.69″E), Jiyuan city, is approximately

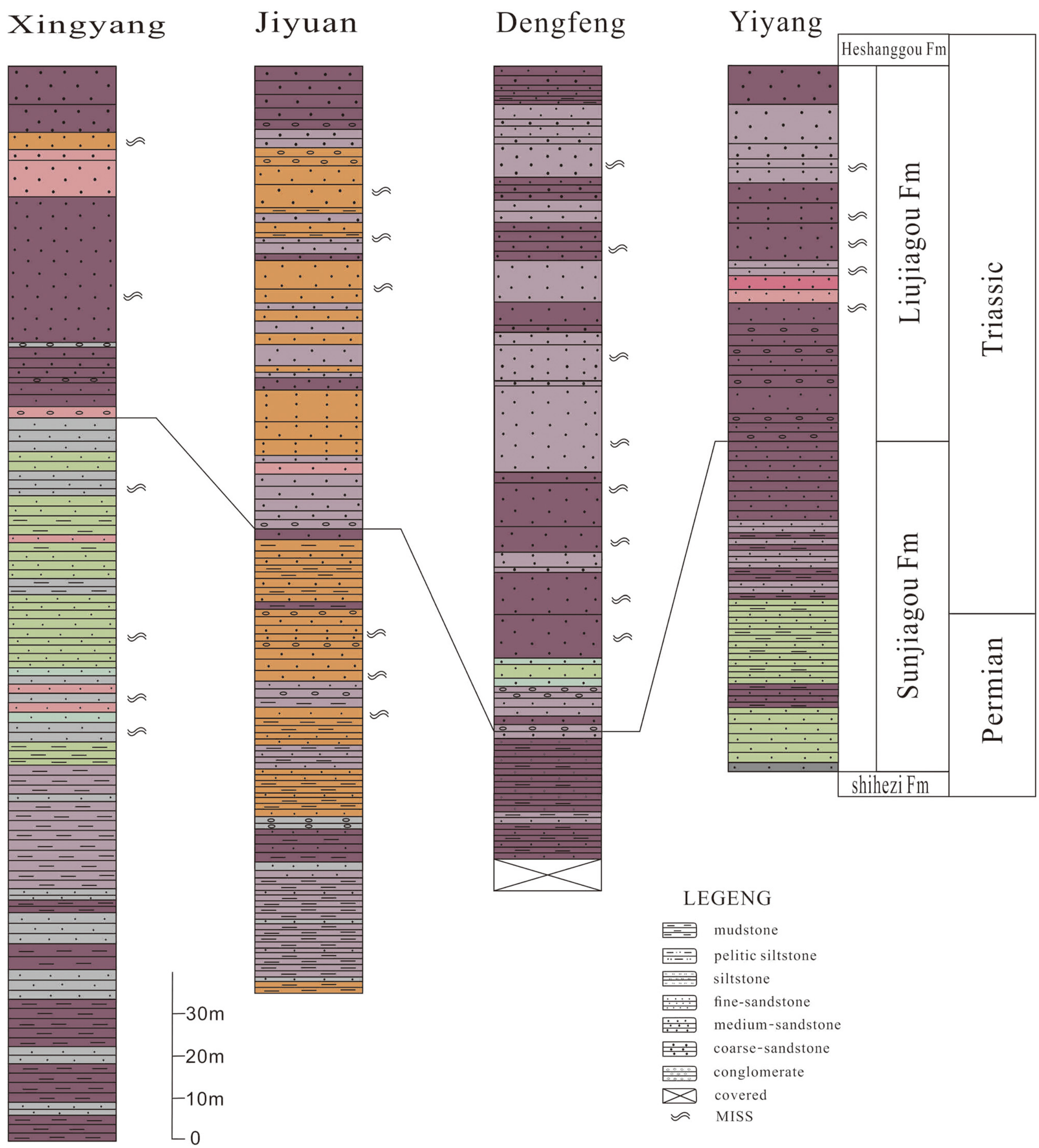

Figure 2: Stratigraphic sections showing lithology and distribution of MISS in Western Henan Province. The middle and upper of Liujiagou Formation were denuded in Xingyang section. The upper of Liujiagou Formation was denuded in Jiyuan section. The lower and middle of Sunjiagou Formation were covered with vegetation in Dengfeng section. Fm = Formation.

110 m thick. Its lower part is dominated by a red mudstone interbedded with greenish-gray, thin-bedded sandstones or siltstones, and containing MISS and calcareous concretions. Its upper part is composed of a thick fine red sandstone interbedded with conglomerates and displaying well-preserved ripples and cross-bedding. The Sunjiagou Formation of the Ligou section (34°27′03.46″N, 112°20′52.84″E), Yiyang county, is approximately 103 m thick. Its lower part is dominated by a fine greenish-gray sandstone interbedded with mudstones, and its upper part is

dominated by reddish siltstone or mudstone interbedded with numerous calcareous-nodular paleosols and thin- to medium-bedded yellow freshwater limestones.

The Liujiagou Formation, underlying the Heshanggou Formation, is dominated by a massive purple and reddish quartz sandstone, with minor amounts of conglomerates, feldspar sandstones, and calcareous siltstones interbedded with a few thin mudstones. Because of simple and changeless lithofacies assemblages, the thick sandstone of the Liujiagou Formation is called "Jindoushan Sandstone" and usually forms cuesta. The Liujiagou Formation of four sections that are almost identical. The Liujiagou Formation of the Cuimiao section, Xingyang county, is ~93 m thick, dominated by a thick, fine red sandstone containing cross-bedding, ripples, and MISS, and its upper part is denuded. The Liujiagou Formation of the Baiping section, Dengfeng county, is ~212 m thick, dominated by a thick, fine red sandstone interbedded with a thin reddish mudstone and contains cross-bedding, ripples, and varied MISS. The Liujiagou Formation of the Fangshan section, Jiyuan city, is approximately 110 m thick. Its lower part is dominated by a fine red sandstone interbedded with reddish conglomerates and mudstones. Its upper part is composed of a thick, fine red sandstone with well-preserved ripples, cross-bedding, and MISS. The Liujiagou Formation of the Ligou section, Yiyang county, is ~117 m thick and is dominated by a thick, fine red quartz sandstone interbedded with reddish siltstones, thin mudstones, and conglomerates and contains cross-bedding, ripples, and varied MISS.

3 Characteristics and distribution of MISS

3.1 Types of MISS

Many taxonomies of MISS have been studied [2,4,7,11,18,41,42]. Here, we document all types of MISS that we observed at all studied sections following the classification scheme of Schieber et al. and Noffke, including mat growth features, mat destruction features, and mat decay features [2,41]. Fourteen types of typical well-preserved MISS were found from the continental Sunjiagou Formation and Liujiagou Formation in four sections, western Henan Province, including mat growth features (including growth bulges, growth ridges, "old elephant skin" textures, wavy wrinkle structures), mat destruction features (including curved shrinkage cracks, polygonal shrinkage cracks, dendritic shrinkage cracks, "*Manchuriophycus*" structures, fusiform shrinkage cracks, straight shrinkage cracks, cauliflower shrinkage cracks, ripple patches), and mat decay features (including gas blisters, "sand volcanoes").

3.1.1 The mat growth features

The mat growth features were formed due to growth of microbial mats at the sediment-water interface or the interaction of physical processes with biofilm or mat-bound sediment surfaces [2,4,18]. Mat growth features include growth bulges, growth ridges, "old elephant skin" textures, and wavy wrinkle structures in the study area.

Growth bulges (Figure 3a) were formed due to the local extensive growth of microbial mat. These bulges vary from 1 to 5 mm in diameter and project 1–3 mm from bed surface. Occasionally, bulges have grown/merged together. Some clustered low mound-shaped structures are preserved on upper sandstone bed surfaces, and clustered ones may locally amalgamate. Schieber et al. suggest that these structures might form by the vertical accretion and/or binding of quartz sand by localized biofilms [2].

The growth ridges (Figure 3b) are typical mat growth features too. These ridges are preserved on the ripple-marked sandstone bed surfaces and deformed the crests of the ripples. The ridges are 20–40 mm long, 8–12 mm wide. The growth ridges tops are not cracks unlike the shrinkage cracks. Noffke suggested that the growth ridges may form from growth-expansion of the mat, resulting in deformation of the mat surface and concomitant sinuous surface ridge patterns [8].

Wrinkle structures are characterized by abundant bulges and pits (or crests and valleys) of irregular directions which can be categorized into 'transparent wrinkle structures'[10]. Wrinkle structures in western Henan Province include "old elephant skin" textures and wavy wrinkle structures. The "old elephant skin" textures (Figure 3c) comprise elongate to subrounded bulges separated by narrow continuous or discontinuous grooves preserved as positive epirelief on sandstone bedding surfaces. The bulges are commonly 2–8 mm length, 1–5 mm width. Wavy wrinkle structures (Figure 3d) were preserved on the upper surfaces of fine sandstone beds. We can see irregular flow direction, continuous wide crests, and narrow troughs. Tiny ripple structures are millimeter-sized, parallel to one another. The crests are almost round in cross section. The crests are usually 1–2 mm height, 2–3 mm width.

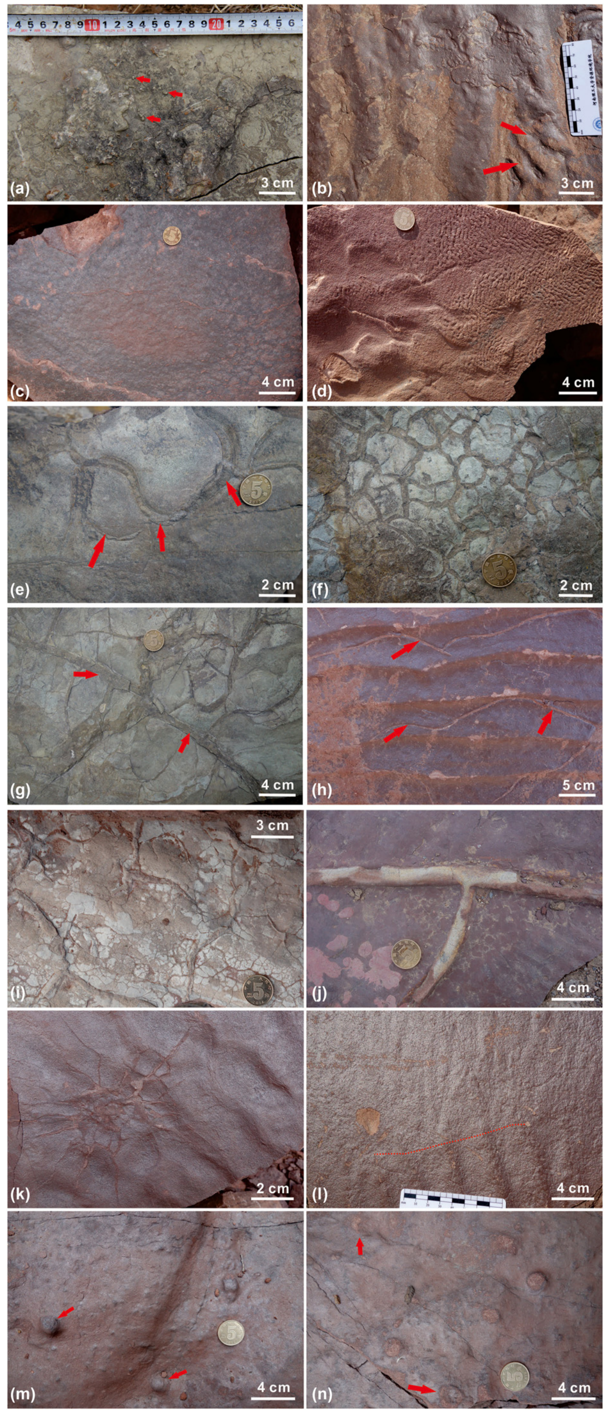

Figure 3: Photographs of MISS from Western Henan Province. (a) growth bulges (red arrow) on the bedding surface of sandstone, Sunjiagou Formation, Xingyang; (b) growth ridges (red arrow) on the ripple-marked sandstone bed surfaces, Liujiagou Formation, Yiyang; (c) "old elephant skin" textures on sandstone bedding surfaces, Liujiagou Formation, Dengfeng; (d) wavy wrinkle structures on the ripple-marked sandstone bed surfaces, Liujiagou Formation, Dengfeng; (e) curved shrinkage cracks (red arrow) on sandstone bedding surfaces, Sunjiagou Formation, Xingyang; (f) polygonal shrinkage cracks on sandstone bedding surfaces, Sunjiagou Formation, Xingyang; (g) dendritic shrinkage cracks on sandstone bedding surfaces (red arrow), Sunjiagou Formation, Xingyang; (h) "*Manchuriophycus*" structures (red arrow) on sandstone bedding surfaces, Liujiagou Formation, Yiyang; (i) fusiform shrinkage cracks on the ripple-marked sandstone bed surfaces, Liujiagou Formation, Jiyuan; (j) straight shrinkage cracks on sandstone bedding surfaces, Liujiagou Formation, Jiyuan; (k) cauliflower shrinkage cracks on the ripple-marked sandstone bed surfaces, Liujiagou Formation, Dengfeng; (l) ripple patches on sandstone bedding surfaces, Liujiagou Formation, Yiyang; (m) gas blisters (red arrow) on sandstone bedding surfaces, Liujiagou Formation, Dengfeng; (n) "sand volcanoes" (red arrow) on sandstone bedding surfaces, Liujiagou Formation, Dengfeng.

3.1.2 The mat destruction features

The mat destruction features result from subaerial exposure and desiccation of microbial mats and include a series of shrinkage cracks [2,18]. Shrinkage cracks are the most common microbial-induced features in the shallow marine and lacustrine environments in the Precambrian or the Early Triassic [2,7,8,13,15,16,18,39]. Because these structures usually occur in siliciclastic sandstone, these shrinkage cracks are also called "sand cracks." Shrinkage cracks in western Henan Province include curved shrinkage cracks, polygonal shrinkage cracks, dendritic shrinkage cracks, "*Manchuriophycus*" structures, fusiform shrinkage cracks, straight shrinkage cracks, and cauliflower shrinkage cracks.

The curved shrinkage cracks (Figure 3e) are preserved as positive epireliefs on bed tops of fine-grained sandstone. These cracks display sinuous morphology and are 2–8 cm length and 2–9 mm width. The outline of these cracks resembles worm, with broad central part and tapering ends. Cracks usually project 1–3 mm up from the bedding plane.

The polygonal shrinkage cracks (Figure 3f) are preserved as positive epirelief on the upper surfaces of fine- to medium-grained sandstone. The varied polygons include tetragonal, pentagonal, hexagonal, subrotund geometries, and so on. Each polygon is composed of 3–5 ridges and most ridges have been flattened. The polygonal ridges width varies from 2 to 8 mm and usually project 0.5–1 mm up from the bedding plane. The host rock is fine sandstone and is dominated by fine quartz grains.

The dendritic shrinkage cracks (Figure 3g) are preserved as positive epirelief on fine sandstone bed tops. They have a main crack that extends into smaller cracks and are similar to polygonal shrinkage cracks except that they differ in shape. Cracks usually project 1–3 mm up from the bedding plane. The main cracks are 8–30 cm long, 4–7 mm wide. These branch cracks are 1–3 cm long, 1–3 mm wide.

"*Manchuriophycus*" structures (Figure 3h) are a special type of microbial shrinkage crack, consisting of sinuous or spiral cracks with curving positive patterns. They are usually confined to troughs between ripples on the rippled surfaces of sandstone beds. Individual cracks with tapering ends vary from 2 to 4 mm in width and project 1–2 mm from the bed surface. Because they are preferentially developed in the troughs of ripples, "*Manchuriophycus*" structures may form if microbial mats selectively grew, or attained a greater thickness, in ripple troughs than on the crests [2,43–45].

A series of fusiform shrinkage cracks (Figure 3i) are preserved as positive epirelief on sandstone bed tops with ripple mark. Spindles are generally 1–5 cm length, 1–5 mm width and stand out 1–2 mm on ripple bed surface. Most of them are randomly aligned with individual spindles meeting, but the shrinkage cracks never form polygons. And, the shrinkage crack fills are composed of the same composition as the host rock. Fusiform shrinkage cracks have also been reported from the Kimberley, northwestern Australia, [43] and from the Ediacaran Sonia Sandstone in India [46]. These structures were interpreted as deformation of cracks resulted from microbial mat [13].

Straight shrinkage cracks (Figure 3j) are preserved as positive epirelief on sandstone bed tops. These ridges are scarce branch and display a straight cracks, 8–30 cm long, 5–10 mm wide. The top of ridges displays half-round and smooth. Straight shrinkage cracks usually project 3–6 mm up from the bedding plane.

Cauliflower shrinkage cracks (Figure 3k) are scarce. Only one occur in Dengfeng area. It preserved negative epirelief on the rippled surfaces of sandstone beds. The crest height of the ripple mark was approximately 4 mm. The cauliflower shrinkage cracks beneath ripple mark were blurry and modified, likely as a result of subaerial central shrinkage. Schieber et al. considered cauliflower shrinkage cracks formed by shrinkage of the microbial mat [2].

The ripple patches are characterized by indented margins (Figure 3l). Ripples have a wavelength of 4 cm, ripple height of 3 mm. These ripple patches are evenly distributed on the bed surfaces. Some crests are deformed towards one direction. Cross section views show that the ripple crests share the same lithological composition with the host rock. The similar ripple patches were described from the Mesoproterozoic Chorhat Sandstone in India [47]. Because of the stepped margins of the ripple patches together with shear erosion of bed surface between ripple patches, Sarkar et al. suggested that the ripple patches were left on bed tops on account of a microbial mat coating origin [47].

3.1.3 The mat decay features

The mat decay features are hypothesized to result from the decay of organic material, often mat-derived, buried underneath mat surfaces [2]. And, of particular interest are mat decay features resulting from the escape of gases or liquids resulting from decay of organic matter buried beneath cohesive biofilms [8]. Mat decay features of the study area are mainly gas domes.

The gas domes are developed on the smooth bedding planes of fine- to medium-grained sandstone and are preserved as positive epirelief (Figure 3m and n). Domes generally have hemispherical or roundly conical tops. Gas domes include gas blisters and “sand volcano” in western Henan Province. The gas blisters (Figure 3m) vary from 2 to 15 mm in diameter and project 1–5 mm from bed surface and have contrasting glossy surfaces. The “sand volcano” (Figure 3n) has an external diameter of approximately 15 mm width and an internal diameter approximately 1 cm width. Wall thicknesses of “sand volcano” structure range from 2 to 5 mm. Gas domes were originally termed “domal upheavals,” but now the more simple term “Gas domes” is used [8]. When these gases break out of the microbial mat cover or surface, a “sand volcano” structure is created, and the domal structures are filled by sand [18]. However, gas blisters form if the gases cannot pierce the mat cover due to thickness, toughness, or biostabilization of the microbial mat [18]. The similar domal structures as domal sand buildups were termed by Bottjer and Hagadorn, and they suggested these gas domes could be resulted from biofilm or microbial mat binding quartz sand grains in vertical direction [48]. Noffke indicated gas domes are typical decomposing mat features, resulting from an upward movement of gases that produce cavities below the decay and decomposition of the microbial mat [8].

3.2 Taphonomy and distribution of MISS

The MISS of four sections are almost identical, but also have distinctive features. In the vertical section, the MISS are found in the Sunjiagou Formation and Liujiagou Formation in Xingyang and Jiyuan. The MISS from the Xingyang area mostly developed in the middle and upper Sunjiagou Formation and the lower Liujiagou Formation, and the MISS from the Jiyuan area occur in the lower Sunjiagou Formation and the middle Liujiagou Formation. However, the MISS of Dengfeng and Yiyang were discovered only in the Liujiagou Formation and run through the entire Formation (Figure 2).

In types, shrinkage cracks have been found in four sections and are the most common and typical MISS, including polygonal shrinkage cracks, curved shrinkage cracks, and dendritic shrinkage cracks. First, only one cauliflower shrinkage crack developed in the Dengfeng. Second, wrinkle structures mostly developed in Xingyang, Dengfeng, and Yiyang, and they are the most typical MISS in the Dengfeng area, including “old elephant skin” textures and wavy wrinkle structures. Third, “sand volcanoes” are present mainly in Xingyang and Dengfeng.

In taphonomy, the MISS of the Liujiagou Formation are well-preserved in four sections on fine-medium red sandstone bedding surfaces and sandstones that have high grain maturity and good sphericity. The MISS of the Liujiagou Formation in Jiyuan have relatively loose cementation and poor sphericity in comparison with those of the other three sections, and they are easily weathered. However, the MISS of the Sunjiagou Formation in Xingyang and Jiyuan are well-preserved on fine greenish-gray or off-white sandstone or siltstone bedding surfaces and sandstone that has relative low grain maturity and sphericity. The MISS of the Sunjiagou Formation in Jiyuan are the most special structures, and they are preserved in thin fine sandstone or siltstone interbedded with thick mudstones. Around the ridges of the shrinkage structures is argillaceous cement, which was captured by the microbial mat.

3.3 The vertical distribution characteristics of MISS

The vertical distribution characteristics of MISS types in the Liujiagou Formation of the Dengfeng and Yiyang areas have a few regular variations. In Dengfeng, the MISS types, in order from bottom to top, are “old elephant skin” textures, little curved shrinkage cracks, polygonal shrinkage cracks, dendritic shrinkage cracks, wavy wrinkle structures, and gas blisters or “sand volcanoes,” which show a change in water depth over time. In order from bottom top, the MISS types in Yiyang are fusiform shrinkage cracks, polygonal shrinkage cracks, wrinkle structures, ripple patches, and polygonal shrinkage cracks. According to an analysis of the sedimentary environment, the variation of MISS types in both Yiyang and Dengfeng changes with water depth, suggesting that an agreeable sedimentary environment is one of the controlling factors of MISS formation [13,19]. It is noteworthy that many conglomerate layers have been found in the Liujiagou Formation in Xingyang and Jiyuan and that MISS are negatively correlated with all conglomerate layers in the stratum.

3.4 Biogenicity of the Early Triassic continental MISS

Because continental MISS in the study area developed mainly in siliciclastic deposits, it is relatively difficult to distinguish mud cracks by macroscopic view, and they are only classified by type according to features. Therefore, the biogenicity of MISS was analyzed under a microscope

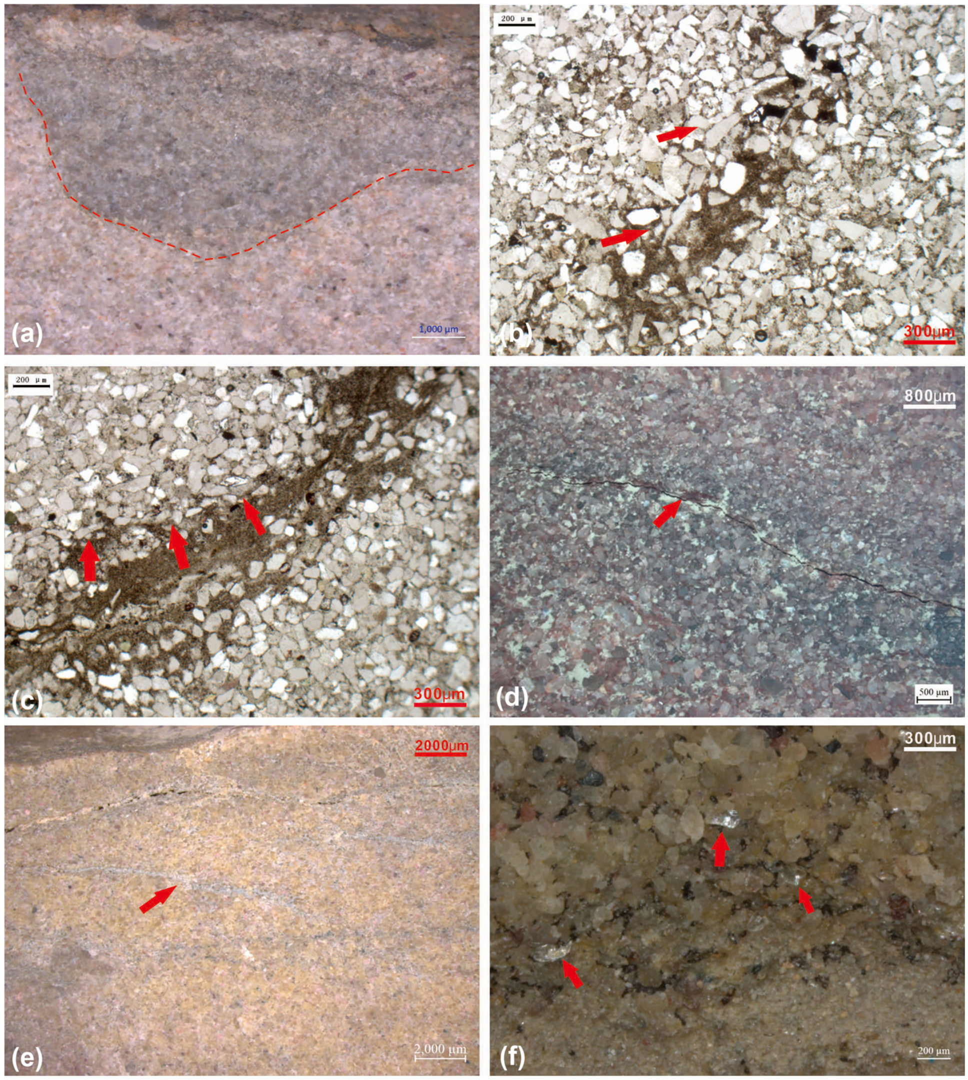

Figure 4: Photomicrographs of MISS from study area. (a) U-shaped structure and clear boundary with clay minerals (red dotted line; longitudinal section of ridges); (b) and (c) direction-oriented quartz grains or relatively large quartz grains that usually float under MISS ridges (red arrow); (d) and (e) dark clayey laminae or seam with a clear boundary in cross section (red arrow; longitudinal section); (f) the mica sheet embedded in the laminated layers (red arrow).

using the MISS research techniques from Meso-Neoproterozoic siliciclastic sandstone [8,10,11,41,49]. The microstructures and biogenicity of the Early Triassic MISS in the study area are assessed and discussed using a polarizing microscope, stereoscope.

3.4.1 The ridge of the shrinkage cracks in the longitudinal section showing a U-shape structure

The ridge of the shrinkage cracks of the MISS in Jiyuan and Xingyang is longwise cut, showing a U shape and clear boundary when compared to that of the surrounding rock, and it contains clay minerals (Figure 4a). Allen suggested that the mud cracks were created by desiccation, as they show characteristic V-shaped morphology in cross section, but it is difficult to form V-shaped cracks in sandstone due to its lack of cohesion [50]. Therefore, the presence of the U-shaped structure is clearly different from the V-shaped morphology in cross section, indicating that these MISS, which are unlikely mud cracks, were created by desiccation and shrinkage of the microbial mat [8,50].

3.4.2 The oriented grains

Under microscope, the MISS sample in Jiyuan, Xingyang, and Dengfeng displays direction-oriented quartz grains or relatively large quartz grains that usually float under MISS ridges (Figure 4b and c) and possess low grain sphericity and better clarity (Figure 4b and c). Modern laboratory experiments show that the mediation of microbial organics has played an important role in the formation of oriented grains [16]. Sand particles were pushed upward by the constantly growing biofilm envelopes and were finally separated from one another, causing the quartz grains to float and align parallel to the bedding planes [8]. Therefore, oriented grains distinctly mark the presence of a microbial mat and also support the presence of a biofilm [13,41,49].

3.4.3 Thin clayey laminae with clear boundary in cross section

Under microscope, the MISS sample from Jiyuan, Xingyang, and Dengfeng has dark clayey laminae with a clear boundary in cross section along the ridge edge (Figure 4d and e), as well as some clayey laminae that have formed a seam due to weathering. Schieber thought that the microbial mat or clayey laminae form MISS by exposure and shrinkage [6]. In the study area, many clayey laminae in cross section indicate that the microbial mat formed in multiple phases and was filled or replaced by clay minerals that formed thin laminae when shrinkage of the mat occurred (Figure 4e). In addition, the seam is probably a residuum of the microbial mat or formed from the weathering of clay minerals.

3.4.4 Mica grains discontinuously arranged parallel to bedding plane

Under the microscope, the samples from Jiyuan and Xingyang show that the mica grains embedded in the laminated layers are discontinuously oriented parallel to bedding plane (Figure 4f). In addition, some mica grains are large and oriented parallel to the clayey laminae, and several mica grains moved upward due to the growth of the microbial mat. Such features are believed to be linked with the capture and binding of the microbial mat [10,11]. Chu et al. and Tu et al. noted that thin clayey laminae and filamentous mica grains arranged parallel to the bedding plane as well as directionally oriented sand quartz floating in lamina are the main identifiable features visible under a microscope, and that these features are linked with capture, binding, and barrier of the microbial mat [15,16]. Therefore, several lines of evidence indicate that the MISS of the study areas were created due to the involvement of ancient microbes.

4 Discussion and conclusions

4.1 The controlling factors of continental MISS

It is well-known that MISS occurred mainly in the Meso-Neoproterozoic siliciclastic shallow sea and have fewer occurrences in continental sedimentary environments. The Early Triassic microbialites and MISS also occur in the marine sedimentary environments of the circum-Tethys Sea. However, the Early Triassic MISS occur in typical sections of Xingyang, Dengfeng, Jiyuan, and Yiyang, indicating that the microbial mat was widely distributed around the continental environment in the western Henan Province. In addition, the MISS in four sections show different characteristics in type, longitudinal changes, and distribution. However, what factors influenced the development of the MISS? We think that the development of continental MISS in the western Henan Province was affected and restrained by four factors.

The first is the end-Permian mass extinction. As the greatest crisis of the Phanerozoic, the end-Permian mass extinction severely devastated continental ecosystems in the western Henan Province, resulting in a sharp decline of metazoans and very low levels of bioturbation, creating an advantage for the formation of microbial communities. Consequently, Microbial communities bloomed in the study area, during which they grew as various MISS.

Second, the megamonsoon is one of strongest events during the Early Triassic, causing strong monsoon cycles and a rise in global temperature [51], as well as wide seasonal drought on land, strong storm-induced currents, and extreme weather conditions, which led to a delay in biotic recovery [51,52]. The presence of laminar structures, storm deposits, and red beds suggests that the megamonsoon affected the study area. Therefore, the biotic recovery delay and extreme weather conditions provided an advantage for the persistent flourishing of microbial communities.

The third is the adapted sedimentary environment. Most studies have suggested that MISS commonly occur in tidal flat environments with medium turbulence [13,18,41]. The vertical types of MISS change in the Dengfeng and Yiyang and were affected by the hydrodynamic conditions during the time they formed, suggesting that the sedimentary environment of the Dengfeng and Yiyang areas was a shallow-water environment with medium turbulence. Mata and Bottjer concluded that MISS developed on the flooding surface due to underfilling conditions [53]. Paleogeographic patterns with under-filling conditions during the late Permian formed this sedimentary environment, which was beneficial to the development of MISS. During the late Permian, the Qinling block intensified its collision with the North China block and the area north of the Huaiyang old land was uplifted, causing the current to divert northwards [35]. Therefore, the suitable sedimentary environment for MISS was formed with an under-filling condition in study area.

Fourth, sediment supply. Noffke et al. suggested that MISS developed mainly in pure and transparent fine sandstone or siltstone because the cyanobacteria of the microbial community required sunlight for photosynthesis [10]. This conclusion was also confirmed in the study area where MISS occur mainly in the pure sandstone of the Liujiagou Formation. There is a particular sedimentary structure, conglomerate layers, in the four sections of study area. We found a significant inverse correlation between conglomerate layers and MISS in these four sections, showing more conglomerate layers and fewer MISS. The rapid influx of sediments, such as the conglomerates, rapidly destroyed the microbial community habitats, leading to progressive microbe death. This was probably the reason that MISS were not found in the conglomerate layers of study area. Thus, these four factors mainly affected the development of the MISS in the study area.

4.2 Significance of stratigraphic correlation

As the greatest crisis of the Phanerozoic, the end-Permian mass extinction killed over 90% of all marine species and most continental vertebrate and plant species, bringing about a whole-scale ecosystem restructuring [20,54]. As a consequence of the end-Permian mass extinction, microbial proliferation characterized the much degraded marine ecosystems [55,56], and microbial communities bloomed in shallow marine settings, in which they grew as microbialites in carbonate habitats [16,27,57–59]. There are additional evidence for microbial proliferation following the EPE and this comes in several forms: (1) Proliferation of algal cysts in both marine [60] and freshwaters [61]. (2) Proliferation of fungi in both marine and freshwaters [62–65]. (3) Spikes in microbially generated amorphous organic matter (AOM) in palynological residues [66,67]. (4) Spikes in biomarkers characteristic of specific microbes [68–70]. Several geologists suggested that the geologic age of the microbialites was significant for stratigraphic correlation [55,57,71,72]. Zhou et al. thought that the bottom boundary of the microbialites near the Permian-Triassic boundary was accorded with the Permian-Triassic boundary in South China [56]. Therefore, Ezaki et al. concluded that the microbialites were caused by an opportunistic proliferation of microbial communities and became an ecological and biological anachronistic facies after the end-Permian mass extinction [71]. Note that a few recent studies have suggested that extinctions on land were initiated before the major extinction pulse in the oceans [73–75]. Microbial communities bloomed on land, in which they grew as various continental MISS. Tu et al. thought that the siliciclastic MISS could be used as a sedimentary indication for ecosystem devastation following major mass extinctions and were therefore one of most important proxies for environmental stresses in continental ecosystems following major biocrises [16]. As such, continental MISS are also significant for stratigraphic correlation following major biological crisis.

This is to say that abundant microbial communities should occur simultaneously in the study area after the end-Permian mass extinction. However, the MISS developed in the Sunjiagou Formation and Liujiagou Formation in the Xingyang and Jiyuan sections, but only occur in the Liujiagou Formation of the Dengfeng and Yiyang sections. We think this phenomenon was caused by three factors. First, the development of MISS in the study area was affected and restrained by the end-Permian mass extinction, the adapted sedimentary environment, sediment supply, bioturbation, etc., and these factors may have provided favorable conditions for the development of MISS [13]. Chu et al. suggested that the end-Permian mass extinction, particularly less bioturbation, could provide favorable conditions for thriving microbial communities and the development of MISS [15]. Second, the collision between the Qinling block and the North China block intensified, and the area north of the Huaiyang old land was uplifted, causing the current to divert northwards during late Permian. These factors caused these Lower Triassic units to be diachronous. Third, the Sunjiagou Formation and Liujiagou Formation are lithostratigraphic units that were classified by geologists and are not biostratigraphic units. Therefore, based on the features of the MISS and the tectonics of the western Henan Province, we suggest that the Sunjiagou Formation and Liujiagou Formation in study area are diachronous, but the diachronous unit is relatively short for the relatively small area of the western Henan Province.

4.3 Continental ecosystems during the Early Triassic

MISS occurred commonly in the siliciclastic shallow seas of the Meso-Neoproterozoic, indicating the microbes dominated the Meso-Neoproterozoic. Because of the increase in metazoans and bioturbation, microbes such as cyanobacteria were restrained after the Cambrian and especially after the Great Ordovician Biodiversification Event [44]. These unusual biomat-related sedimentary structures were restrained to specific periods and places during the Phanerozoic Eon or the modern sedimentary environment. Red tides in the sea and lake algal outbreaks were seen as a degeneration of aquatic environments. Therefore, these unusual biomat-related sedimentary structures probably represent special sedimentary environments [76]. The widespread MISS of the study area occurred during the Early Triassic indicated they are the special sedimentary structure. Their extensive development in north China region and the lack of metazoan disturbances have a certain relationship with extinction. The transition from metazoan primarily to the microbial mat mainly reflects the changes in ecosystems as a whole. Therefore, research of these MISS and the continental ecosystem are beneficial in order to reveal sedimentary indications of ecosystem devastation following the end-Permian mass extinction.

Based on the research and analysis of lithological characteristics and sedimentary structures, the widespread MISS of the study area indicate a prosperity of microbial communities. Moreover, red beds, conglomerates, and calcareous concretions suggest the presence of soil ecosystem devastation [72,77]. These sedimentary structures indicate the likely occurrence of a special paleoenvironment after a catastrophic event. As these sedimentary assemblages mainly occur in the Permian-Triassic transition period of the study area, we think that the sedimentary assemblages dominated by MISS represent a typical post-extinction continental ecosystem characterized by (1) microflora dominance, (2) monotonous and rare fossils, (3) extreme hot climate, (4) soil ecosystem devastation, and (5) poor vegetation. We refer to the continental ecosystem as a “continental microbial ecosystem” because it has characteristics consistent with regional post-extinction and based-microbe.

The biomat-related structures including microbialites and MISS are one of the main problems in geobiology. Noffke indicated that finding post-extinction, well-preserved microbial mats is one of the important aspects in geobiological research [8]. The continental MISS in the western Henan Province occur during the Permian-Triassic transition period, suggesting that it contains important clues to better understand continental ecosystems. However, specific changes in continental microbial ecosystems during the end-Permian mass extinction and its aftermath are poorly known, although specific continental MISS have been reported in Lower Triassic rocks [7,13–16]. These research primarily analyzed the classification and paleoenvironmental significance of MISS. But, evolution and spatial distribution of MISS were not further studied. Therefore, the MISS from the study area provided evidence for changes in the continental communities and environment after the end-Permian mass extinction, as well as the coevolution between Earth’s environment, microbes, and metazoans.

Acknowledgments: We thank Xi-Yang Zhang, Hu Zhou, and Jia Lin for help with sampling from the studied section. We would like to thank Wen-Tao Yang and Ming-Yue Dai for insightful discussions.

Funding information: This study was supported by the National Natural Science Foundation of China (41772110, 41202071, 41472083), the Key Research Project of Higher Education Institutions in Henan Province (20A170010), and the Foundation of Shandong Provincial Key Laboratory of Depositional Mineralization and Sedimentary Mineral (DMSM2018027).

Conflict of interest: Authors state no conflict of interest.

References

[1] Noffke N, Gerdes G, Klenke T, Krumbein WE. Microbially induced sedimentary structures – a new category within the classification of primary sedimentary structures. J Sediment Res. 2001;71:649–56.

[2] Schieber J, Bose PK, Eriksson PG, Banerjee S, Sarkar S, Altermann W, et al. Atlas of microbial mat features preserved within the siliciclastic rock record. Atlases in Geoscience 2. Amsterdam: Elsevier; 2007. p. 1–311.

[3] Riding R, Liang L. Geobiology of microbial carbonates: metazoan and seawater saturation state influences on secular trends during the Phanerozoic. Palaeogeogr Palaeoclimatol Palaeoecol. 2005;219:101–15.

[4] Shi XY, Wang XQ, Jiang GQ. Pervasive microbial mat colonization on Mesoproterozoic peritidal siliciclastic substrates: an example from the Huangqikou Formation (ca 1.6 Ga) in Helan Mountains. NW China Geol Rev. 2008;54:575–86 (in Chinese with English abstract).

[5] Gerdes G, Klenke T, Noffke N. Microbial signatures in peritidal siliciclastic sediments: a catalogue. Sedimentology. 2000;47:279–308.

[6] Schieber J. Microbial mats in the siliciclastic rock record: a summary of the diagnostic features. In: Eriksson PG, Altermann W, Nelson DR, Mueller WU, Catuneanu O, editors. The precambrian earth: tempos and events. Amsterdam: Elsevier; 2004. p. 663–73.
[7] Zheng W, Qi YA, Zhang ZH, Xing ZF, Chen BB, Li XY. Characteristic and geological significance of microbially induced sedimentary structures (MISS) in terrestrial P-T boundary in Xingyang, West Henan Province. Adv Earth Sci. 2016;31:737–50 (in Chinese with English abstract).
[8] Noffke N. Geobiology: microbial mats in sandy deposits from the archean era to today. Berlin/London: Springer; 2010. p. 1–194.
[9] Hagadorn JW, Bottjer DJ. Wrinkle structures: microbially mediated sedimentary structures in siliciclastic settings at the Proterozoic-Phanerozoic transition. Geology. 1997;25:1047–50.
[10] Noffke N, Knoll AH, Grotzinger J. Sedimentary controls on the formation and preservation of microbial mats in siliciclastic deposits: a case study from the upper Neoproterozoic Nama Group, Namibia. Palaios. 2002;17:533–44.
[11] Noffke N, Gerdes G, Klenke T. Benthic eyanobacteria and their influence on the sedimentary dynamics of peritidal depositional systems (siliciclastic, evaporitic salty, and evaporitic carbonatic). Earth-Sci Rev. 2003;62:163–76.
[12] Pruss SB, Fraiser M, Bottjer DJ. Proliferation of early Triassic wrinkle structures: implications for environmental stress following the end-Permian mass extinction. Geology. 2004;32:461–4.
[13] Zheng W, Qi YA, Xing ZF, Bai WB, Chen BB, Li XY. Characteristic and paleoenvironment significance of microbially induced sedimentary structures (MISS) in continental P-T boundary in Jiyuan, Western Henan Province. Acta Sediment Sin. 2017;35:1121–32 (in Chinese with English abstract).
[14] Chu DL, Tong JN, Song HJ, Benton MJ, Bottjer DJ, Song HY, et al. Early Triassic wrinkle structures on land: stressed environments and oases for life. Sci Rep. 2015;5:1047–50.
[15] Chu DL, Tong JN, Bottjer DJ, Song HJ, Song HY, Benton MJ, et al. Microbial mats in the continental lower triassic of North China and implications for the Permian-Triassic massextinction. Palaeogeogr Palaeoclimatol Palaeoecol. 2017;474:214–31.
[16] Tu CY, Chen ZQ, Retallack GJ, Huang YG, Fang YH. Proliferation of MISS-related microbial mats following the end-Permian mass extinction in continental ecosystems: Evidence from the Lower Triassic of the Yiyang area, Henan Province, North China. Sediment Geol. 2016;333:50–69.
[17] Peterffy O, Calner M, Vajda V. Early Jurassic microbial mats – a potential response to reduced biotic activity in the aftermath of the end-Triassic mass extinction event. Palaeogeogr Palaeoclimatol Palaeoecol. 2016;464:76–85.
[18] Xing ZF. Study on microbially induced sedimentary structures (MISS) from the mesoproterozoic Yunmengshan formation in Western Henan Province. Unpublished M.S. thesis. Jiaozuo: Henan Polytechnic University; p. 2010 (in Chinese with English abstract).
[19] Davies NS, Liu AG, Gibling MR, Miller RF. Resolving MISS conceptions and misconceptions: a geological approach to sedimentary surface textures generated by microbial and abiotic processes. Earth-Science Rev. 2016;154:210–46.
[20] Jin YG, Wang Y, Wang W. Pattern of marine mass extinction near the Permian-Triassic boundary in South China. Sci. 2000;289:432–6.
[21] Erwin DH. Extinction: how life on earth nearly ended 250 million years ago. Princeton: Princeton University Press; 2006. p. 1–296.
[22] Baud A, Richoz S, Marcoux J. Calcimicrobial cap rocks from the basal Triassic units: western Taurus occurrences (SW Turkey). CR Palevol 4. 2005;4(06):569–82.
[23] Baud A, Richoz S, Pruss S. The Lower Triassic anachronistic carbonate facies in space and time. Glob Planet Chang. 2007;55:81–9.
[24] Pruss SB, Bottjer DJ, Corsetti FA, Baud A. A global marine sedimentary response to the end-Permian mass extinction: examples from southern Turkey and the western United States. Earth-Sci Rev. 2006;78:193–206.
[25] Wu YS, Jiang HX, Yang W, Fan JS. Permian Triassic boundary microbialite of anoxic origin. SCI China Ser D. 2007;37:618–28.
[26] Kershaw S, Crasquin S, Li Y, Collin PY, Forel MB, Mu X, et al. Microbialites and global environmental change across the Permian-Triassic boundary: a synthesis. Geobiology. 2012;10:25–47.
[27] Mata SA, Bottjer DJ. Microbes and mass extinctions: paleoenvironmental distribution of microbialites during times of biotic crisis. Geobiology. 2012;10:3–24.
[28] Chen ZQ, Wang YB, Kershaw S, Luo M, Yang H, Zhao LS, et al. Early Triassic stromatolites in a siliciclastic nearshore setting in northern Perth Basin, Western Australia: geobiologic features and implications for post-extinction microbial proliferation. Glob Planet Change. 2014;121:89–100.
[29] Luo M, Chen ZQ, Zhao LS, Kershaw S, Huang JY, Wu LL, et al. Early middle triassic stromatolites from the Luoping area, Yunnan Province, Southwest China: geobiologic features and environmental implications. Palaeogeogr Palaeoclimatol Palaeoecol. 2014;412:124–40.
[30] Lehrmann DJ, Bentz JM, Wood T, Goers A, Dhillon R, Akin S, et al. Environmental controls on the genesis of marine microbialites and dissolution surface associated with the end-Permian mass extinction: new sections and observations from the Nanpanjiang Basin, South China. Palaios. 2015;30:529–52.
[31] Wehrmann A, Gerdes G, Höfling R. Microbial mats in a lower Triassic siliciclastic playa environment (Middle Buntsandstein, North Sea). In: Noffke N, Chafetz H, editors. Microbial mats in siliciclastic depositional systems through time. Vol. 101, SEPM Special Publication; 2012. p. 177–90.
[32] Hminna A, Voigt S, Klein H, Saber H, Schneider JW, Hmich D. First occurrence of tetrapod footprints from the continental Triassic of the Sidi Said Maachou area (Western Meseta, Morocco). J Afr Earth Sci. 2013;80:1–7.
[33] Wang HZ. Atlas of the palaeogeography of China. Beijing: SinoMaps Press; 1985. p. 283 in Chinese.
[34] Peng ZM, Wu ZP. Development features of Triassic strata and analysis of original sedimentary pattern in North China. Geol J China Universities. 2006;12:343–52 (in Chinese with English abstract).
[35] Xu L, Zhang CJ, Jia SH, Zhang JM, Lü JC, Pan ZC, et al. Element geochemistry and palaeoenvironment of Permian–Triassic Stratum in the Huaigeda hill of Dayu town Jiyuan Basin, Henan Province. Acta Geol Sin. 2015;89:137–48 (in Chinese with English abstract).

[36] Zheng QG, Zhang YM, Zhao DY, Liu ZQ, Peng GL. Tectonic evolution and preservation and distribution of upper Triassic strata in western Henan. Henan Pet. 1998;02:6–10+59 (in Chinese with English abstract).
[37] Cao GS, Yu SJ, Sun FY, Fang PP, Xu HT. Analysis of carbon and oxygen isotopes of lacustrine carbonate rocks in the Upper Triassic of Sunjiagou Formation in Yiyang area, western Henan Province. Acta Geol Sin. 2019;93(05):1137–53 (in Chinese with English abstract).
[38] Hu B, Lu XH, Song B. Trace fossils and sedimentary environment of lower Triassic in Dengfeng area, western Henan. J Stratigraphy. 2015;39(04):454–65 (in Chinese with English abstract).
[39] Xing ZF, Lin J, Zhou H, Li D, Qi YA, Zheng W. Sedimentary records of the late Permian and early Triassic in Yiyang area, western Henan Province and their response to paleoclimate change. Geol J China Universities. 2019;25(03):401–11 (in Chinese with English abstract).
[40] Bureau of Geology and Mineral Resources of Henan Province. Rock stratigraphic units in Henan Province. Wuhan: China University of Geoscience Press; 1997. p. 116–49.
[41] Noffke N. The criteria for the biogenicity of microbially induced sedimentary structures (MISS) in Archean and younger, sandy deposits. Earth-Sci Rev. 2009;96:173–80.
[42] Sarkar S, Choudhuri A, Mandal S, Eriksson PG. Microbial mat-related structures shared by both siliciclastic and carbonate formations. J Palaeogeogr. 2016;5(3):278–91.
[43] Lan ZW, Chen ZQ. Proliferation of MISS-forming microbial mats after the late Neoproterozoic glaciations: evidence from the Kimberley region, NW Australia. Precambrian Res. 2013;224:529–50.
[44] Lan ZW. Paleoproterozoic microbially induced sedimentary structures from lagoonal depositional settings in northern China. Sediment Geol. 2015;328:87–95.
[45] Lan ZW, Chen ZQ. Exceptionally preserved microbially induced sedimentary structures from the Ediacaran post-glacial successions in the Kimberley region, northwestern Australia. Precambrian Res. 2012;200–203:1–25.
[46] Sarkar S, Bose PK, Samanta P, Sengupta P, Eriksson PG. Microbial mat mediated structures in the Ediacaran Sonia Sandstone, Rajasthan, India, and their implications for Proterozoic sedimentation. Precambrian Res. 2008;162:248–63.
[47] Sarkar S, Banerjee S, Samanta P, Jeevankumar S. Microbial mat-induced sedimentary structures in siliciclastic sediments: examples from the 1.6 Ga Chorhat Sandstone, Vindhyan Supergroup, M.P., India. J Earth SystSci. 2006;115:49–60.
[48] Bottjer D, Hagadorn JW. Mat growth features. In: Schieber J, Bose PK, Eriksson PG, Banerjee S, Sarkar S, Altermann W, Catuneau O, editors. Atlas of microbial mat features preserved within the siliciclastic rock record, atlases in geosciences. Amsterdam: Elsevier; 2007.
[49] Zheng W, Xing ZF. Characteristics and geological significance of microbially induced sedimentary structures (MISS) in Mesoproterozoic Changzhougou formation of Licheng county, Shanxi Province. Geoscience. 2015;29:825–32 (in Chinese with English abstract).
[50] Allen JRL. Sedimentary structures, their character and physical basis. Part II. Developments in sedimentology series. Amsterdam: Elsevier; 1982. p. 1–676.
[51] Qian LJ, Shi ZQ, Ou LH. Research advances in Permian-Traissic Paleoclimate: formation, development and decline of Pangaean Megamonsoon. Mar Pet Geol. 2010;15:52–8 (in Chinese with English abstract).
[52] Shi ZQ, Zeng DY, Xiong ZJ, Zhang H, Zhao AK. Sedimentary records of Triassic Megamonsoon in upper Yangtze area. Bull Mineralogy, Petrology Geochem. 2010;29:164–71 (in Chinese with English abstract).
[53] Mata SA, Bottjer DJ. The paleoenvironmental distribution of Phanerozoic wrinkle structures. Earth-Sci Rev. 2009;96:181–95.
[54] Retallack GJ. Permian-Triassic life crisis on land. Sci. 1995;267:77–80.
[55] Liu JB, Ezaki Y, Yang SR, Wang HF, Adaehi N. Age and sedimentology of microbialites after the end-Permian mass extinction in Luodian, Guizhou Province. J Palaeogeogr. 2007;9:473–86 (in Chinese with English abstract).
[56] Zhou ZC, Luo H, Willems H, Xu B, Wang ZH, Cai HW, et al. The sharp change between the ecosystems of two organic deposits across the Permian-Triassic boundary in the Yudongzi section, Jiangyou, Sichuan, South China. Acta Palaeontol Sin. 2016;55(01):70–86 (in Chinese with English abstract).
[57] Yang H, Zhang SX, Jiang HS, Wang YB. Age and general characteristics of the calim icrobialite near the Perm ian2Triassic boundary in Chongyang, Hubei Province. Earth Sci J China U Geosci. 2006;31:165–70.
[58] Jiang HX, Wu YS. Restudy of the microbialite from the Permian-Tiassic boundary section, Chongqing. Acta Pet Sin. 2007;23:1189–96.
[59] Zhao XM, Niu ZJ, Tong JN, Yao HZ. The distinctive sediments in the early Triassic recovery time: “Anachronistic Facies”. Acta Sediment Sin. 2010;28:314–23 (in Chinese with English abstract).
[60] Haig D, Martin SK, Mory AJ, McLoughlin S, Backhouse J, Berrell RW, et al. Early Triassic (early Olenekian) life in the interior of East Gondwana: mixed marine-terrestrial biota from the Kockatea Shale, Western Australia. Palaeogeog Palaeoclimatol Palaeoecol. 2015;471:511–33.
[61] Mays C, Vajda V, McLoughlin S. Permian-Triassic non-marine algae of Gondwana – distributions, natural affinities and ecological implications. Earth-Sci Rev. 2021;212:103382. doi: 10.1016/j.earscirev.2020.103382.
[62] Looy CV, Twitchett RJ, Dilcher DL, van Konijnenburg-van Cittert JHA, Visscher H. Life in the end-Permian dead zone. Proc Nat Acad Sci. 2001;98:7879–83.
[63] Steiner MB, Eshet Y, Rampino MR, Schwindt DM. Fungal abundance spike and the Permian-Triassic boundary in the Karoo Supergroup (South Africa). Palaeogeog Palaeoclimatol Palaeoecol. 2003;194:405–14.
[64] Spina A, Cirilli S, Utting J, Jansonius J. Palynology of the Permian and Triassic of the Tesero and Bulla sections (Western Dolomites, Italy) and consideration about the enigmatic species Reduviasporonites chalastus. Rev Palaeobot Palyno. 2015;218:3–14.
[65] Vajda V, McLoughlin S, Mays C, Frank T, Fielding CR, Tevyaw A, et al. End-Permian (252 Mya) deforestation, wildfires and flooding – an ancient biotic crisis with lessons for the present. Earth Planet Sci Lett. 2020;529:115875. doi: 10.1016/j.epsl.2019.115875.
[66] McLoughlin S, Nicoll RS, Crowley JL, Vajda V, Mays C, Fielding CR, et al. Age and paleoenvironmental significance of

the Frazer Beach Member – a new lithostratigraphic unit overlying the end-Permian extinction horizon in the Sydney Basin, Australia. Earth Sci Front. 2021;8:600976. doi: 10.3389/feart.2020.600976.
[67] Grice K, Cao C, Love GD, Böttcher ME, Twitchett RJ, Grosjean E, et al. Photic zone euxinia during the Permian-Triassic superanoxic event. Sci. 2005;307:706–9.
[68] Grice K, Twitchett RJ, Alexander R, Foster CB, Looy C. A potential biomarker for the Permian-Triassic ecological crisis. Earth Planet Sci Lett. 2005;236:315–21.
[69] Luo G, Wang Y, Grice K, Kershaw S, Algeo TJ, Ruan X, et al. Microbial-algal community changes during the latest Permian ecological crisis: evidence from lipid biomarkers at Cili, South China. Glob Planet Change. 2013;105:36–51.
[70] He L, Wang YB, Yang H, Liao W, Weng ZT. Palaeogeography and microfacies characteristics of microbialites across the Permian-Triassic boundary in South China. J Palaeogeogr. 2010;12:151–63 (in Chinese with English abstract).
[71] Ezaki Y, Liu JB, Adachi N. Earliest Triassic microbialite micro- to megastructuresin the Huaying area of Sichuan Province, South China: implications for the nature of oceanic conditions after the end-Permian extinction. Palaios. 2003;18:38–402.
[72] Zhang H, Cao CQ, Liu XL, Mu L, Zheng QF, Liu F, et al. The continental end-Permian mass extinction in South China. Palaeogeogr Palaeoclimatol Palaeoecol. 2016;448:108–24.
[73] Chu DL, Grasby SE, Song HJ, Corso JD, Wang Y, Mather TA, et al. Ecological disturbance in tropical peatlands prior to marine Permian-Triassic mass extinction. Geology. 2020;48(03):288–92. doi: 10.1130/G46631.
[74] Fielding CR, Frank TD, McLoughlin S, Vajda V, Mays C, Tevyaw AP, et al. Age and pattern of the southern high-latitude continental end-Permian extinction constrained by multiproxy analysis. Nat Commun. 2019;10:1–12. doi: 10.1038/s41467-018-07934-z.
[75] Gastaldo RA, Kamo SL, Neveling J, Geissman JW, Looy CV, Martini AM. The base of the Lystrosaurus Assemblage Zone, Karoo Basin, predates the end-Permian marine extinction. Nat Commun. 2020;11(1):1–8. doi: 10.1038/s41467-020-15243-7.
[76] Wang YB, Tong JN, Wang JS, Zhou XG. Calcimicrobialite after end-Permian mass extinction in South China and its palaeoenvironmental significance. Chin SciBull. 2005;50:552–8 (in Chinese).
[77] Shen SZ, Crowley JL, Wang Y, Bowring SA, Erwin DA, Sadler PM, et al. Calibrating the end-Permian mass extinction. Sci. 2011;334:1367–72.