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Microbially-induced sedimentary wrinkle structures and possible impact of microbial mats for the enhanced preservation of dinosaur tracks from the Lower Cretaceous Jiaguan Formation near Qijiang (Chongqing, China)

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ABSTRACT

Recently, a paleosurface with microbially-induced sedimentary wrinkle structures that are associated with abundant, well-preserved, iguanodon-type, tridactyl tracks has been documented at the Lotus tracksite near Qijiang (Chongqing, China) in fluvial deposits of the Lower Cretaceous Jiaguan Formation. Two different wrinkle structure types are identified and described from a macroscopic point of view and also by applying microstructure analysis with a scanning electron microscope (SEM) with energy dispersive spectroscopy (EDS) and other high-resolution instruments, that detected sheath-like and globular organic matter and thus confirm the microbial origin of the observed wrinkle structures. A model for the formation of the two microbial mat induced wrinkle structure types and associated preservation of dinosaur tracks is proposed. Finally, some human footprints were left in comparable modern environments covered with a thin microbial mat, and they are used as a modern analog in order to better understand the track formation and preservation mechanisms of the dinosaur tracks of the Lotus tracksite.

1. Introduction

In 2006, the Qijiang District Bureau of Land Resources and the Southeast Sichuan Geological Team discovered dinosaur tracks within the Lower Cretaceous Jiaguan Formation in the notch named Lotus Fortress that is historically famous as a castle dating back to the Mongol invasions of the late 13th century (Xing et al., 2011). The Lotus tracksite contains nine track levels with both imprints and casts (track fills). The main concentration of vertebrate tracks is on the main track level which is dominated by the tracks of iguanodon and an underlying level (a couple of centimeters below the layer with the iguanodon tracks), which is dominated by pterosaur and bird tracks (Xing et al., 2013). This study focuses on the well-preserved imprints of the main track level and small associated wrinkle structures, that are of a possible microbial origin. Accordingly the presence of a former (thin, superficial) microbial mat may have helped to preserve these tracks, and it is the hypothesis is tested hereafter.

Microbial mats consist of benthic microbial communities, which are usually dominated by photosynthetic prokaryotes, particularly cyanobacteria and photosynthetic bacteria, and occasionally by eukaryotic microalgae such as diatoms (e.g., Bauld, 1984; Cohen et al., 1984; Krumbein et al., 2003; Noffke, 2010; Thomas et al., 2013). Fossil microbial mats data back as far as 345 Ma (Allwood et al., 2006; Noffke et al., 2006a,b) and constitute one of the oldest direct evidence of life. Today, microbial mats can be found in a wide range of environments including tidal flats, lagoons, outer shelf to slope environments, or even in deep ocean basins (e.g., Cohen et al., 1984; Schieber et al., 2007; Noffke, 2010; Mata and Bottjer, 2013). The microbes that created the mats, however, are seldom preserved due to their small size (Noffke and Paterson,

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2008) and tendency to degrade rapidly (Jones, 2000). Since the 1980s (Schieber, 1986; Gehling, 1986; Gerdes and Krumbein, 1987), modern siliciclastic and peritidal, carbonate depositional environments have been extensively investigated to help understand the role of microbes in the formation of microbial mats and the preservation of proxy structures (Cohen et al., 1984; Hagadorn et al., 1999; Noffke et al., 2001; Prave, 2002; Pruss et al., 2004; Noffke, 2005; Schieber et al., 2007; Sarkar et al., 2006, 2008; Noffke, 2010; Lan and Chen, 2012, 2013).

Microbialites (fossil sedimentary structures formed by microorganism communities) can be divided into two main types: those that are found in carbonate dominated environments, and those that are found in siliciclastic environments. In carbonate-dominated, shallow-marine environments, microbial mats can produce stromatolites, which are layered accretionary growth structures that can obtain significant synoptic relief above the seafloor (e.g., Semikhatov et al., 1979; Bauld, 1984; Dill et al., 1986; Reid et al., 2000; Dupraz & Visscher, 2005). On carbonate and siliciclastic tidal flats and other siliciclastic environments, microbial mats are known to be formed by biostabilization, that is by trapping and binding of ambient siliciclastic sediment particles (Noffke et al., 2003a). Various distinctive types of microbial mat features are termed microbially induced sedimentary structures – abbreviated MISS (Noffke et al., 2001). In the first description of MISS from silicilastic environments, Noffke et al. (1996) distinguished MISS that greatly differ in morphology from stromatolites. Stromatolites include planar to updomed features, but MISS constitute a group of sedimentary structures of various morphologies, on the meter to millimeter scale. The most common forms of MISS are wrinkle structures (Hagadorn and Bottjer, 1997), palimpsest ripples (Seilacher, 1999), roll-up structures (Simonson and Carney, 1999), and laminar structures (Noffke et al., 1996). Wrinkle structures (also named wrinkle marks) are among the best documented MISS (e.g., Noffke et al., 2002; Fernández and Pazos, 2013; Zhong et al., 2013), and they are also observed on the main track level of the Lotus tracksite.

Wrinkle structures generally occur on a millimeter scale, and Hagadorn and Bottjer (1999) characterized wrinkle structures as "oddly contorted, wrinkled, irregularly pustulose, quasi-polygonal, commonly oversteepened surface morphologies that can occur on bed tops and bottoms". Many hypotheses have been put forth to explain the formation of wrinkle structures, with nearly all proposed methods requiring the presence of a cohesive microbial mat at the sediment's surface (e.g., Hagadorn and Bottjer, 1997; Noffke et al., 2002). Wrinkle structures have been widely reported from the Precambrian (e.g., Gehling, 1999; Noffke et al., 2002; Noffke et al., 2003b; Parizot et al., 2005; Schieber et al., 2007; Shi et al., 2008a, b, c; Xing et al., 2011; Zhong et al., 2013). The great abundance of Precambrian wrinkle structures has been linked to the absence of grazing animals, which permitted the undisturbed growth of the microbial mats (Fenchel, 1998). Although proportionately rarer, some Phanerozoic wrinkle structures have also been documented (e.g., Noffke and Nitsch, 1994; Fernández and Pazos, 2013).

Microbial mats can either agglutinate sediment particles onto their sticky mucilaginous sheaths or act as bafflers that trap sediment washed in the tangle of filaments (Demicco and Hardie, 1994). Thick microbial mats may form a continuous, strongly cohesive zone of low permeability, separating the underlying sediment from the atmosphere and protecting it against water loss, and therefore the sediment below a dry mat is not necessarily dry ("confined aquifer") (Porada et al., 2007). Today, the important role of microbial mats in the formation and preservation of sedimentary structures (Schieber et al., 2007) as well as in the formation and preservation of (in)vertebrate traces and tracks is more and more recognized (Marty et al., 2009; Carmona et al., 2011; Carvalho et al., 2013; Fernández and Pazos, 2013). Marty et al. (2009) studied the formation and taphonomy of human footprints in microbial mats in various recent tidal flat environments to better understand their influence on the formation and preservation of (fossil) footprints. Marty et al. (2009) observed that a footprint may be consolidated by desiccation or lithification of the microbial mat and/or by ongoing growth of the mat, which may then also modify the initial footprint morphology and lead to the formation of (a stack of) overtracks. More recently, Fernández and Pazos (2013) explained the exceptional preservation of xiphosurid trackways by the presence of filamentous mats and associated binding and biostabilisation of the track-bearing level.

2. Geological and stratigraphical setting

In the Qijiang National Geological Park three bone bearing Upper Jurassic formations (Shangshaximiao, Suining and Pengliazhen) and the Lower Cretaceous track-bearing Jiaguan Formation (Xing et al., 2012) form outcrops. The Qijiang Petrified Wood and Dinosaur Footprint National Geological Park is located in Qijiang County, south of Chongqing Municipality, near the southeastern border of the Sichuan Basin (Fig. 1). According to Xing et al. (2012, fig. 2) the succession at the Lotus tracksite is more than 700 m thick with the Upper Jurassic Pengliazhen Formation (about 340 m) at the base and the Lower Cretaceous Jiaguan Formation (about 390 m) on top with massive sandstones intercalated with thinner mudstone intervals. The track- and wrinkle structure-bearing levels occur in the lower part of the Jiaguan Formation about 30–40 m above the base of the unit, and dinosaur tracks are frequently found in this interval (Xing et al., 2007, 2012, 2013) (Figs. 2 and 3).

The age of the Jiaguan Formation has been indicated between 117 and 85 Ma (Aptian–Santonian) by Li (1995), and between 140 and 85 Ma (Berriasian–Santonian) by Gou and Zhao (2001). Recent pollen studies, however, rather indicate a Barremian–Albian age for the Jiaguan Formation (Chen, 2009), i.e. about 145 to 100.5 Ma.

3. Methodology

Individual tracks were measured and photographed, and the entire tracksite was mapped on transparent plastic film, based on which a track outline site map was digitized. Aftrewards, the

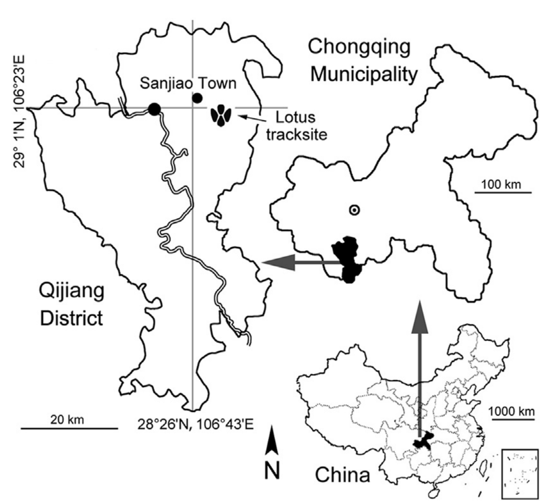

Fig. 1. Geographical map indicating the location with a star icon of the Lotus tracksite (Qijiang National Geological Park) within the Qijiang District, Chongqing Municipality, China.

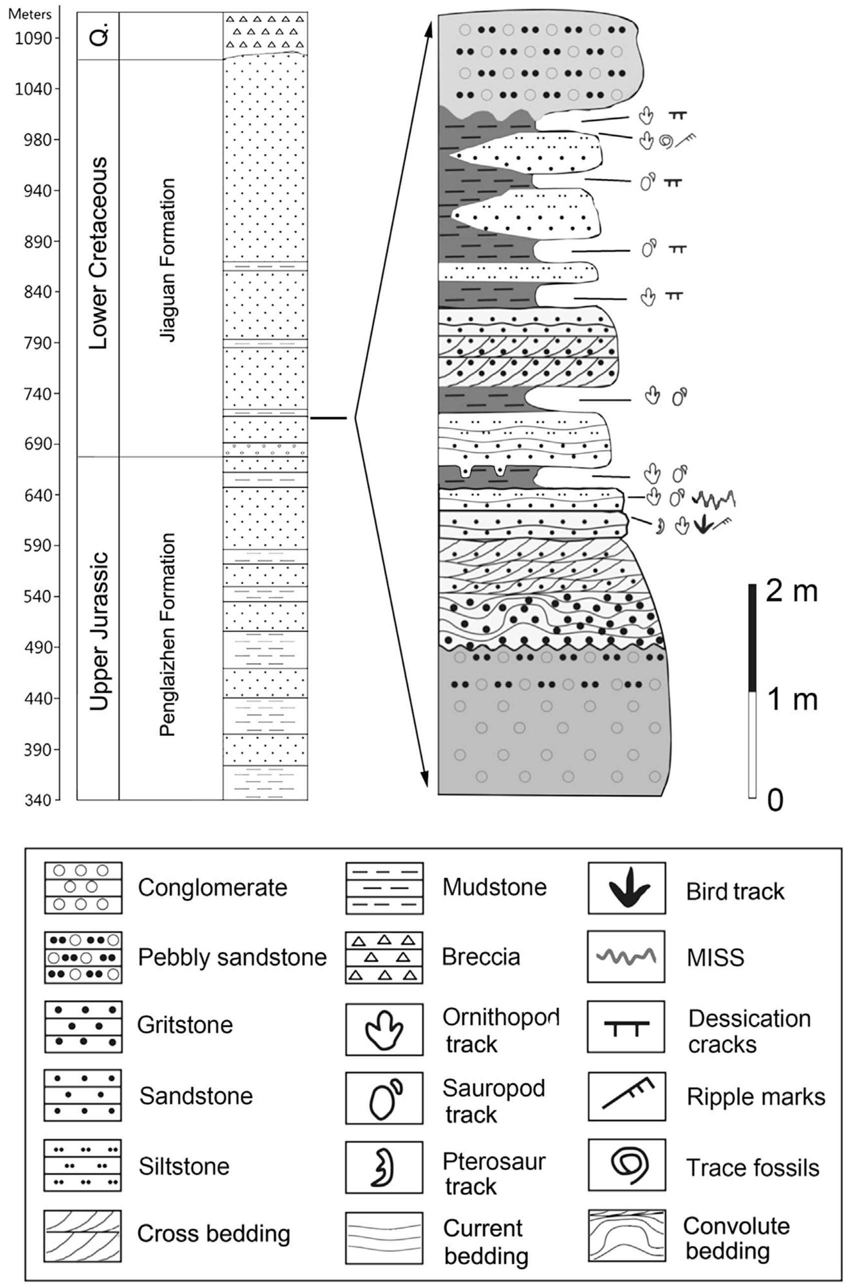

Fig. 2. Stratigraphic section of the sedimentary sequence around the notch that forms the Lotus tracksite. This fluviatile sequence is located in the Jiaguan Formation. The main track level with the MISS-bearing layer and track-bearing layers in the Jiaguan Formation. Abbreviations: Q. = Quarternary.

outline map of the main dinosaur track level was printed and taken to the Lotus tracksite and used to map the areas with wrinkle structures (Fig. 3).

The track-bearing layer was sampled at several localities and the samples were cut with a rock saw and polished. Additionally, thin sections were made and studied using an optical microscope, and an SEM. Platinum plating was applied before SEM and EDS (energy dispersive spectroscopy) analyses. A Supra 55 with ultrahigh-resolution field-emission scanning SEM (produced by Zeiss) equipped with Inca Energy dispersive X-ray spectroscopy analysis attachment was used to photograph microstructures of purpoted microbial structures and to characterize the chemical composition.

Some human footprints were left in comparable recent environments, and they are used for comparison with the fossil tracks. They were left at two different sites, one in Belize (Ambergris Caye) and another in Northwestern China (Yanguoxia) in fine-grained micritic and clayey substrates, respectively, both covered with a thin microbial mat that exhibits wrinkle structures closely resembling the fossil ones observed at the Lotus tracksite.

4. Sedimentology

The probability cumulative grain size curve shows a bi-segment pattern that is composed of a middle slope bouncing population and low slope suspension population but the former is dominant (Fig. 4). The cutoff points of the bouncing population and the suspension population are between 3 and 3.5Φ (Fig. 4). The sedimentary sequence exposed in the notch shows an alternation of thin to thick beds of massive, fine-frained sandstones with fluvial cross bedding, current bedding and convolute

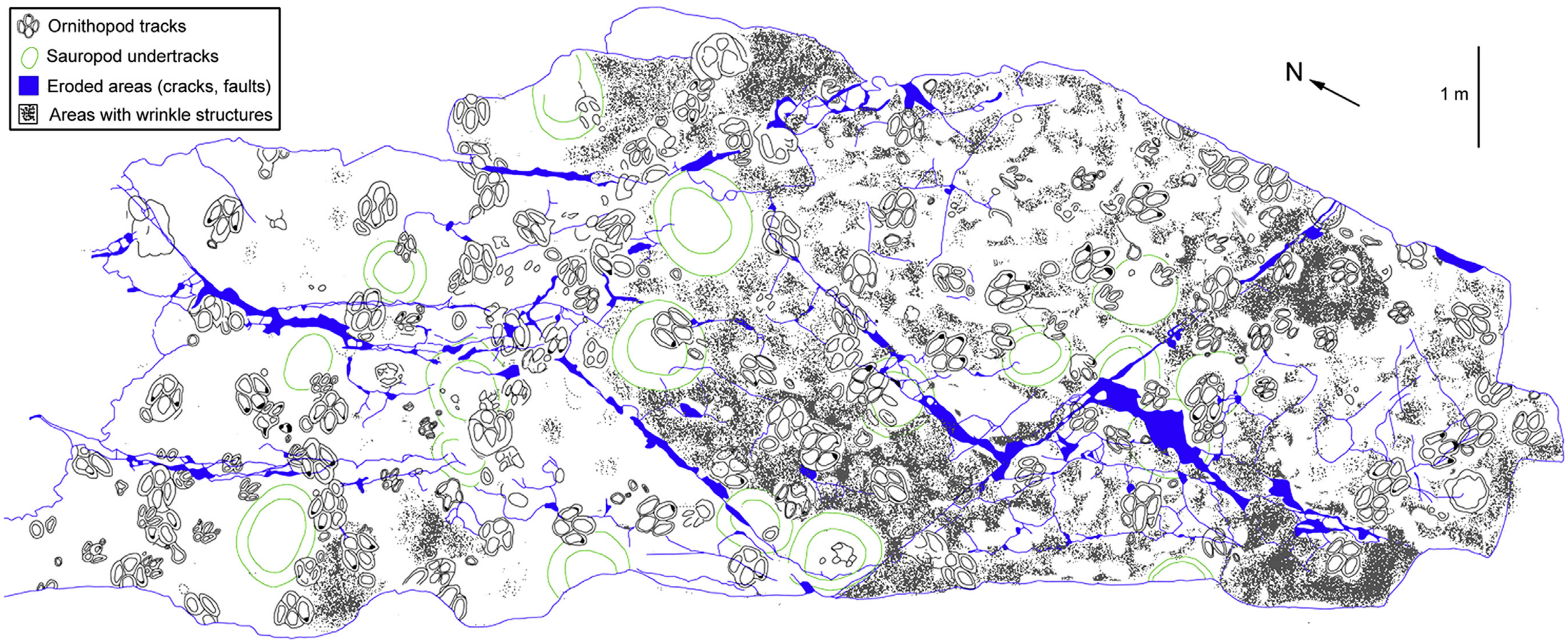

Fig. 3. Outline map of the main dinosaur track level of the Lotus tracksite indicating areas covered with microbial wrinkle structures. 13 trackways of large and 9 of small ornithopods have been identified.

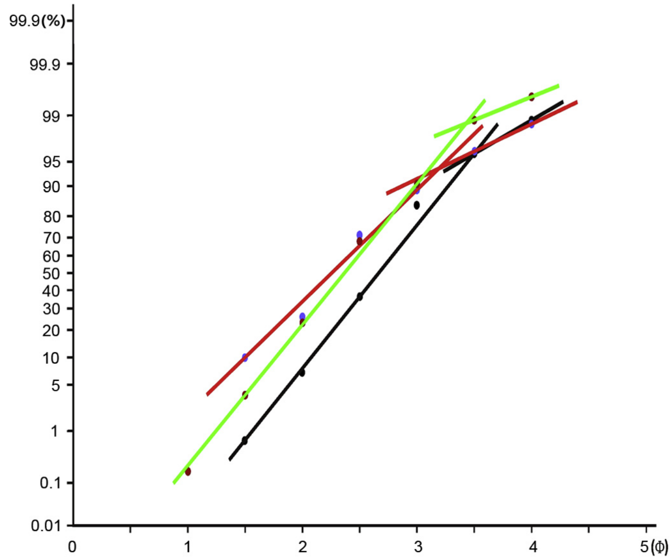

Fig. 4. Probability cumulative grain size curve of the track-bearing and MISS-bearing layers. Three samples have been counted. *X*-axis denote Udden–Wentwoeth scale (Φ) and *Y*-axis denote cumulative probability (%).

bedding and blocky fine-grained siltstones and mudstones. Many of the sandstones are lenticular and contain rip up clasts of the underlying siltstones and mudstones. Some of the sandstone surfaces display current ripple marks, whereas deep-reaching desiccation cracks are common in the siltstones. The track-bearing and MISS-bearing layers were likely deposited in a meandering fluvial system. The main track-bearing level is a siltstone and mostly covered by a thin, micritic, microbial crust. The underlying fine-grained sandstone is dominated by pterosaur and bird tracks while the overlying mudstone contains deep ornithopod and sauropod casts (track fills). Invertebrate traces (e.g., *Scoyenia gracilis* White, 1929; *Beaconites antarcticus* Vialov, 1962; *Planolites beverleyensis* Billing, 1862) are present on the top of the siltstone bed (Fig. 2).

5. Wrinkle structures at the lotus tracksite

5.1. Description

At the Lotus tracksite, two different types of wrinkle structures were observed around the tracks and occasionally a few, compacted wrinkle structures within the tracks, implying that the tracks were left later, when the water just dried of the surface.

Type 1 wrinkle structure is characterized by abundant elliptic, elongated, and crescent bulges preserved in a positive epirelief on the top of the main track level. The bulges are 1–6 mm wide and 0.5–3 mm deep and are brick-red in color (Fig. 5A–B).

Type 2 wrinkle structure is characterized by relatively short, curved, sporadically bifurcating, and flat-topped undulating ripple forms. These ripple-like structures are 2–8 mm wide and about 1 mm high, and separated by parallel, rounded-bottom depressions (Fig. 5C–D). Both types occur as micritic, microbial crusts that are peeling off the underlying sandstone surface (Fig. 5D). The sandstone beneath the thin crust preserves the same wrinkle structures but in less detail. Some authors have termed this type 2 wrinkle structure Kinneyia (e.g. Walcott, 1914; Noffke, 2000; Porada et al., 2008; Thomas et al., 2013).

Macro photographs of cross-sections perpendicular to the bedding surface show that areas with wrinkle structures are characterized by alternating elevations and depressions aligned in an irregular way (Fig. 6A). The upper dense dark lamina (superstratum) is 0.1–0.6 mm thick and has a dense mudstone texture, i.e. grains are only visible in this layer exceptionally. In the sanstone layer below, mineral grains (quartz, feldspar and mica) vary between 0.07 and 0.6 mm in size, but they concentrate in the size range between 0.2 and 0.4 mm. The grains have a subangular to angular shape, but are dominated by the latter. Large mineral grains loosely float in fine grains, exhibiting clearly a floating grain texture. The sorting of the sandstone is good and the grains are in a directional arrangement (Fig. 6B).

Thin sections and fragments of the fresh surficial micritic, microbial crust exhibiting the ripple-like wrinkle structures were palted by platinum. To reduce potential contamination, ultrasonic cleaning was used after drying. The samples were then photographed under the SEM and analyzed by the EDS. Filament-like microstructures are present in the thin in a tanglesome distribution, and filament-like structures are found buried under some sand grains (Fig. 7A). The structures preserved here (Fig. 7B) appear to be the sheaths, and not the filaments. As such, the structures were most likely ensheated forms, one of the most common morphotypes of benthic cyanobacteria involved in mat and biofilm formation (Gerdes et al., 2000). Within the sample, there are extracellular polymer substances (EPS) produced by microbial mats that show heterogenous organic matter with sticky networks that bind to sedimentary grains (Fig. 7C). In the wrinkle structures, there are several globular microbes (maybe sulfate reducing bacteria) together with the filament-like structures. The diameters of these microbes are 2–6 μm (Fig. 7D). Results of the EDS analysis of the sheets indicate that the EPS and globular microbes in the examples have high carbon (C) content and accompanying oxygen (O), silicium (Si), aluminum (Al) and sulfursulfur (S), while the recorded platinum (Pt) is derived from the coating used for SEM studies (see inset in Fig. 7B, D).

5.2. Interpretation

Various types of microbial mat features have been described within the literature, such as wrinkle structures, leveled ripple marks, polygonal sand cracks (crack fills), gas domes, reticulate structures, elongate reticulate structures, 'Arumberia'-like structures, and discoidal structures (e.g., Noffke et al., 2003a; Callow et al., 2011; Zhong et al., 2013), and all formed in a similar way and are termed MISS. However, MISS are not easily differentiated from numerous small-scale MISS-like structures that are non-biogenic structures that formed without the participation of microbial communities, such as rill marks (Reineck and Singh, 1980), rain impact ripples (Robb, 1992), and load structures (Allen, 1985). As a result, two kinds of criteria have been raised by Porada and Bouougri (2007) and Noffke (2009) to distinguish MISS from MISS-like structures. The first of these criteria is tested based on external macroscopic morphologies, and the second is tested based on internal microscopic features.

Wrinkle structures show a preference for heterolithic strata of the offshore transition and mixed tidal flats, where hydrodynamic energy is low (e.g., Fedo and Cooper, 1990; Noffke et al., 2002; Banerjee and Jeevankumar, 2005; Mata and Bottjer, 2009a,b). Mata and Bottjer (2013) stated that wrinkle structures should be most prevalent in environments that consist of heterolithic deposits and are absent from deposits consisting of only siltstone or only sandstone. A further prerequisite for successful mat growth is a sedimentary grain size in the range of 0.02–0.2 mm (silt to fine-grained sand) (Noffke, 1998; Porada and Bouougri, 2007). In this study, wrinkle structures are preserved on a fine-grained sandstone layer surface covered with a siltstone layer (Fig. 2).

Fig. 5. Wrinkle structures of the main track level. (A) Abundant pits and bulges on a sandstone bedding surface. (B) Close-up of the area shown in A. (C) Relatively short, curved, sporadically bifurcating, flat-topped undulating ripple-like structures on top of the microbial (black) crust. On the underlying sandstone similar structures can be observed. (D) Close-up of the area shown in C. Note the dense, micritic crust that is fragile and slowly peeling off the main track level. (A) (C) represent type 1 wrinkle structures and (B) (D) represent type 2.

Wrinkle structures preserved in the rock are commonly interpreted as indicators of cyanobacterial activity (Hagadorn and Bottjer, 1997). Microbial mats are frequently composed of a cohesive surface layer constructed by ensheathed and sheathless filamentous cyanobacteria, which are photosynthetic autotrophs. Underlying these, there are usually less cohesive zones dominated by coccoid, anaerobic phototrophic, and heterotrophic bacteria. Among which, sulfate-reducing species may play an important role, if sulfate is abundant (Porada and Bouougri, 2007). Nevertheless, Noffke et al. (2003) and Bailey et al. (2009) have noted that other types in mat-forming filamentous bacteria should also be considered when interpreting the origins of MISS. Flood et al. (2014) observed that filamentous representatives of the beggiatoacea, which are sulfur-oxidizing gammaproteo-bacteria, are able to trap and bind sediments in much the same way as phototrophic cyanobacteria, giving rise to many of the same wrinkle structures and reticulate patterns that are commonly attributed to cyanobacteria. Sulfate-reducing bacteria (globular microbes in this paper) have also been found to construct significant microbial mats (Noffke et al., 2006a,b). Some authors consider wrinkle structures as evidence of preserved surfaces with microbial mats (Hagadorn and Bottjer, 1997), whereas others interpret these structures to have formed beneath microbial mats (Noffke, 2010). At the Lotus tracksite, the sandstone layer beneath the superficial thin micritic, microbial crust interpreted as ancient microbial mats also exhibit the same wrinkle structures than on top of the superficial veneer (Fig. 5B, D), suggesting that the wrinkle structures reflect both morphological surface and subsurface features. The mats are less resistant to weathering than most of the sediments, thus the morphology of the microbial mats is only observable if the upper

Fig. 6. Main track level with micritic crust (dark brown) in cross section (A) Macro photograph. Note alternating elevations and depressions aligned in an irregular way. (B) Photograph of the thin section. The grains in the sandstone are quartz, feldspar and mica and the cement is mainly calcareous. Note that the micritic crust is opaque, which also indicates that it contains a lot of iron and/or organic matter. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mats are well preserved, and otherwise the wrinkle structures represent the morphology of sediments beneath the mats.

A model is proposed to demonstrate the formation mode of the two kinds of MISS wrinkle structures observed at the Lotus tracksite (Fig. 8). The growth of the microbial mats occurs under humid conditions either subaerially or under a thin layer of water and during periods of low hydrodynamic energy (Fig. 8A). The wrinkle structures begin to form under water when the energy of a directional flow regime becomes forceful enough, so that microbial mats and the underlying sandstone are deformed into undulating structures similar to ripple marks (Fig. 8B). This may be enhanced by the fact that the microbial mat is loosely attached because of the production of phytosynthetic gas bubbles beneath, so that the mat is readily affected by wind (in areas where it is subaerially exposed) and/or water friction (in submerged areas) (Aref et al., 2014). The 'ripple marks' are anomalous and ramulous due to adhesion forces of the microbial mat. If the 'ripple marks' are buried quickly underwater by ongoing sedimentation in a directional flow regime, the crests may become flattened (Fig. 8C), and ripple-like structures may be preserved. However, if the 'ripple marks' remain exposed subaerially, due to dehydration and the escape of gases produced by the decaying mats, the morphology of the mats and top of the underlying sandstone layer will develop abundant elliptic, elongated and crescent bulges that are preserved as bulge-like structures (Fig. 8D). If smooth mats that have formed under low hydrodynamic energy conditions (Fig. 8A) are directly exposed, bulge-like structures (Fig. 8D) will be preserved similarly.

6. Influence of the microbial mats on the formation and preservation of the dinosaur tracks

Microbial mats favor the preservation of vertebrate tracks and traces in two major ways. First, a microbially-stabilized substrate behaves more plastically, in a way that when a foot produces a track, the microbially-bound sediment preserves the imprint better than pure cohesion-less substrate (notably in the case of fine-grained sand). Second, microbial mats often induce early cementation and enhance the preservation potential of vertebrate tracks (e.g., Genise et al., 2009; Marty et al., 2009; Scott et al., 2010; Carmona et al., 2011; Carvalho et al., 2013). In particular, the decay of the microbial filaments, EPS and other organic matter below the surface (in the anoxic zone) stimulate carbonate precipitation, inhibited by bacteria, in the form of micritic cements, as it can be observed in modern settings (Chafetz and Buczynski, 1992; Schieber, 2007). In addition, ongoing growth of the mat may also enhance the preservation potential of a track by covering-up, and simultaneously (a stack of) overtracks may be formed (Marty et al., 2009).

In order to better understand the preservation of the dinosaur tracks on the Lotus tracksite main track level, we have left some human footprints at two different sites in two different kinds of substrate covered with a thin microbial mat and exhibiting wrinkle structures closely resembling the fossil ones observed at the Lotus tracksite. The first site was located on a supratidal flat near San Pedro Town (Ambergris Caye, Belize), and the second site (name DLF site, Dany–Lida's foots GPS is 36° 3′51.03″N, 103°16′24.97″E) was a small almost dried-up pond in a small valley close to Yanguoxia (Gansu, Northwestern China), where clay and silt eroded from the Lower Cretaceous Hekou Group accumulated during periods of heavy rain. The substrate at both sites were very fine-grained, carbonatic (micritic carbonate mud) at the first, and siliciclastic (clay-silt) at the second site. Even though both sites are not located in a floodplain environment, they are assumed to correspond well to the general environmental and substrate conditions under which the tracks of the Lotus tracksite may have formed. Thus, they are considered to represent a useful modern analog for comparison with the fossil tracks.

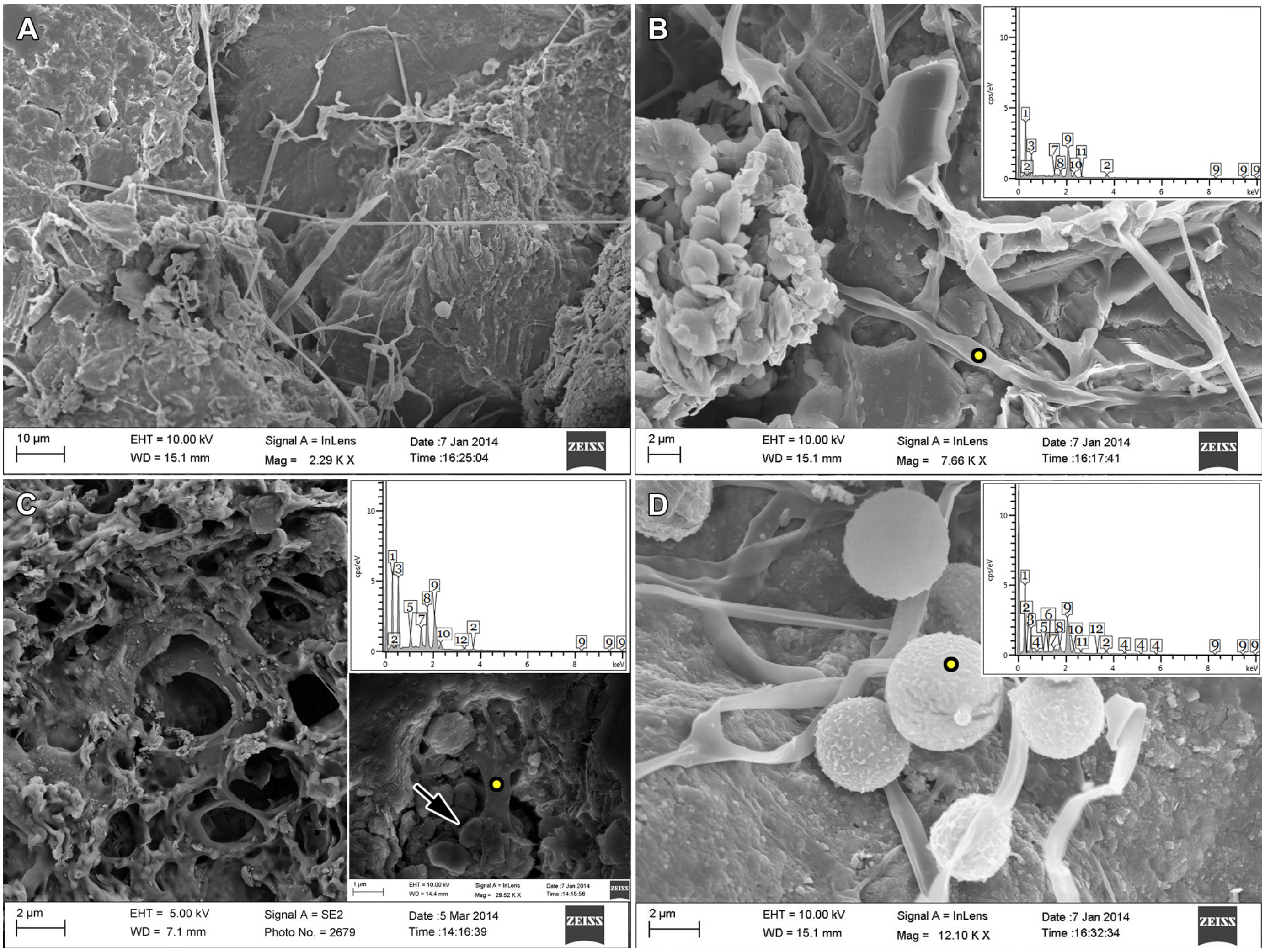

Fig. 7. SEM photographs of the thin section of the fresh micritic crust as well as EDS analysis. (A) Filament-like forms and some buried under sand grains (circle). (B) Detail of the filament-like forms showing a filament sheath. (C) EPS showing heterogenous organic matter with sticky network and they were binding sedimentary grains (lower right corner). (D) Globular microbes. Top right corner are EDS analysis. Points of EDS analysis for each figure are indicated by a dot. In the EDS analyses, the numbers 1–12 respectively means the element C, Ca, O, Ba, Na, Mg, Al, Si, Pt, S, Cl, K.

6.1. *Description of human footprints*

Both human footprints in Fig. 9A and B were left by the third author (DM, 23 cm foot length, 70 kg weight), in moist (water-unsaturated) 2–3 cm thick substrates covered with a thin (<3 mm) microbial mat with wrinkle structures on top of layered, firm sediment with a relatively high yield strength in a way that the underlying sediment was not penetrated but instead, the superficial layer with the microbial mat was compressed (to a varying degree) and pushed into the underlying sediment. In the case of the Belize footprint, the impact of the foot formed a well-defined small displacement rim all around the track, while there is no displacement rim in the case of the Chinese footprint, because of particular properties of the superficial microbial mat that led to cracking around the foot rather than an outward transmitting of the applied force.

Both footprints are well-defined with anatomical details of the toes, even though the footprint from Belize shows better details because compression of the substrate was more important than in the case of the Chinese footprint. In the latter, the microbial mat broke around the foot and was pushed into the underlying sediment by compacting the sediment below the microbial mat but not the mat itself. This is underlined by nice striation marks that can be observed on the toes (Fig. 9B). These striations were created during the foot impact, and therefore can be named entry striation marks. Also, in the case of the Chinese footprint, wrinkle structures that were present prior to track formation were only little affected by the foot impact, as they were only slightly compacted and still are quasi identical to the ones around the footprint (Fig. 9B).

6.2. *Comparison with ornithopod tracks from lotus tracksite*

From a formational and preservational point of view, the fossil ornithopod tracks of the main track level at the Lotus tracksite share many similarities with the two human footprints described above.

Some ornithopod tracks (*Caririchnium lotus* Xing et al., 2007) in this study preserved on areas with microbial mats preserve well-defined digits II, III and IV, a metatarsophalangeal pad, well-defined displacement rims, and wrinkle structures around but also within the tracks (Fig. 9C, D and E). In analogy to the human footprint in Fig. 8B, we assume that the wrinkle structures were present before the tracks were formed and that the mat was pushed by the force of the foot into the underlying sediment without

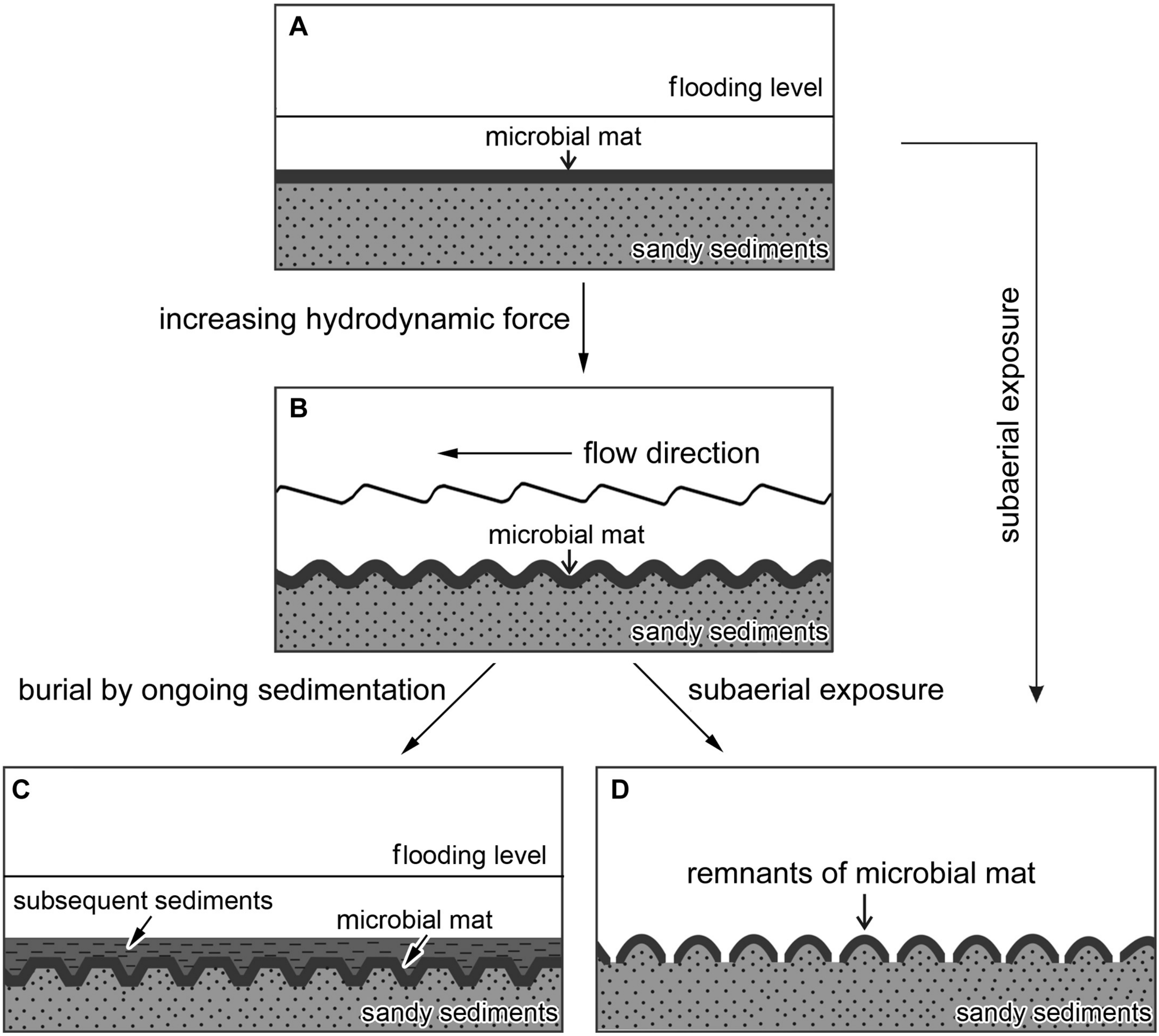

Fig. 8. Formation model for the two types 1 and 2 of microbial wrinkle structures as observed on the main track level of the Lotus tracksite. (C) represents type 2 wrinkle structures and (D) represents type 1.

(completely) obliterating the wrinkle structures, even though they may have been slightly compressed.

A manus print of *Caririchnium lotus* (Fig. 9E) exhibits an anterior part that is deeper than its posterior part, and wrinkle structures are present around as well as within the track. Also, some clasts can be seen on the broken border of the track, and we interpret these clasts as fragments of the original microbial mat, that was broken in this part (Fig. 9E), similar to the human footprint in Fig. 8E, where the mat broke around the foot.

Marty et al. (2009) showed that the formation and morphology of footprints in microbial mats depend not only on the nature (composition, thickness, water content, degree of consolidation, etc.) of the mat itself but also on the characteristics (water content, grain size, lamination, degree of consolidation, presence of a lithified horizon) of the underlying sediment. Consequently, many different combinations are possible, which complicate a thorough description of (fossil) footprints. Nevertheless, it was found that the thickness of the microbial mat and the water content of the mat and of the underlying sediment are the most crucial factors for footprint morphology. In dry mats, poorly defined or no footprints are generally produced, while in water-unsaturated microbial mats the footprints are well defined, often with well-defined displacement rims and anatomical details. The formation of well-defined displacement rims around the prints of large dinosaurs occurs in thick, plastic, moist to water-unsaturated microbial mats on top of moist to water-unsaturated sediment. These features are typical for the dinosaur (ornithopod) tracks of the main track level at the Lotus tracksite.

7. Conclusions

Two different types of wrinkle structures are described from the main track level of the Lotus tracksite and are interpreted to

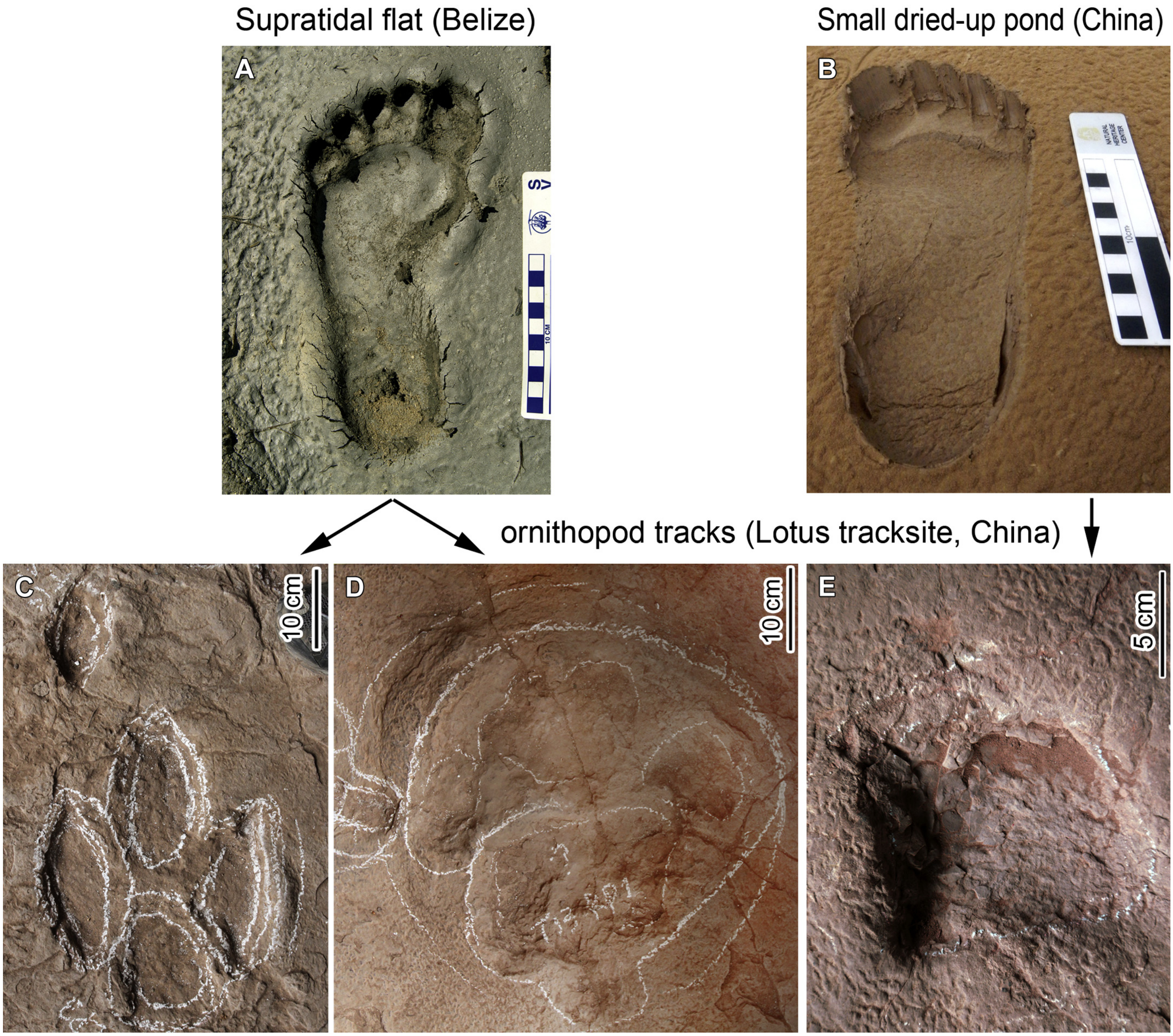

Fig. 9. (A) Left human pes footprint with anatomical details of the toes and a well-defined displacement rim left by the third author (DM) on a thin and water-unsaturated microbial mat on a supratidal flat SW of the airport of San Pedro Town (Ambergris Caye, Belize). Note wrinkle structures to the left of the track. Scale bar is 10 cm. (B) Right human pes footprint without displacement rim but with anatomical details of the toes, left by the third author (DM) on a thin and water-unsaturated microbial mat on top of a 2–3 cm thick moist layer of clay. Note striations on the toe tracks that were created during the foot impact (not exit) and wrinkle structures around the track. Also note that due to the elevated yield strength of the superficial microbial mat, the mat was not penetrated but pushed into the underlaying sediment. As a result, the wrinkle structures, that were present on the surface prior to track formation, are still visible even after the foot impact. Scale bar is 10 cm. (C) Ornithopod (*Caririchnium lotus*) tridactyl pes (T18-LP3) and oval manus track (T18-LM3) surrounded by small displacement rim and wrinkle structures (notably upper right of the pes track) (D) Large ornithopod (*Caririchnium lotus*) pes track (T13-RP1) with a small displacement rim (upper left) and surrounded by wrinkle structures. Tracks in (C) and (D) are outlined with white chalk. (E) Ornithopod (*Caririchnium lotus*) manus track with a deeper anterior than posterior part, and wrinkle structures that are present around as well as within the track. Track is outlined with white chalk. (A) (C) (D) indicate foot impact compresses microbial mat and also leads to formation of displacement rim. (B) (E) indicate foot impact breaks microbial mat breaks and pushes it vertically into substrate without desintegration of original wrinkle structures.

have been produced under two slightly different environmental conditions, that have led to the formation of wrinkle structures both on the surface but also as subsurface features. SEM and EDS analyses have identified elements of the filament sheaths, EPS and globular microbes that are all microtextures and represent ancient microbial mats with a high carbon (C) content and dominance of accompanied oxygen (O), silicium (Si), aluminum (Al) as well as sulphur (S) in their composition. However, not only cyanobacteria but also other bacteria such as beggiatoacea and sulfate reducing bacteria can be considered when interpreting the origin of these "microbial mats". Not only the nature (thickness, water content, degree of consolidation, etc.) of the microbial mat itself but also the characteristics (grain size, lamination, water content, etc.) of the underlying sediment had an important influence on track morphology. However, the presence of a microbial mat was an important if not the crucial factor for the exquisite preservation of dinosaur and other vertebrate tracks at the Lotus tracksite, as they may have enhanced the stabilization and/or early precipitation of Ca-carbonate and hence have consolidated the tracks.

Some human footprints have been left at two different kinds of substrate covered with a thin microbial mat exhibiting wrinkle structures that to better understand the preservation of the dinosaur tracks on the Lotus tracksite main track level. It was found that the formation and morphology of footprints in microbial mats depend not only on the nature (composition, thickness, water content, degree of consolidation, etc.) of the mat itself but also on the characteristics (water content, grain size, lamination, degree of consolidation, presence of a lithified horizon) of the underlying sediment.

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References

Allen, J.R.L., 1985. Wrinkle marks: an intertidal sedimentary structure due to aseismic soft-sediment loading. Sedimentary Geology 41, 75–95.
Allwood, A.C., Walter, M.R., Kamber, B.S., Marshall, C.P., Burch, I.W., 2006. Stromatolite reef from the early Archaean era of Australia. Nature 441, 714–718.
Aref, M.A.M., Basyoni, M.H., Bachmann, G.H., 2014. Microbial and physical sedimentary structures in modern evaporitic coastal environments of Saudi Arabia and Egypt. Facies 60, 371–388.
Bailey, J.V., Orphan, V.J., Joye, S.B., Corsetti, F.A., 2009. Chemotrophic microbial mats and their potential for preservation in the rock record. Astrobiology 9, 843–859.
Banerjee, S., Jeevankumar, S., 2005. Microbially originated wrinkle structures on sandstone and their stratigraphic context: palaeoproterozoic Koldaha Shale, central India. Sedimentary Geology 176, 211–224.
Bauld, J., 1984. Microbial mats in marginal marine environments: Shark Bay, Western Australia, and Spencer Gulf, South Australia. In: Cohen, Y., Castenholz, R.W., Halvorson, H.O. (Eds.), Microbial mats: Stromatolites. MBL lectures in biology, 3. Alan R. Liss, New York, pp. 39–58.
Callow, R.H.T., Battison, L., Brasier, M.D., 2011. Diverse microbially induced sedimentary structures from 1 Ga lakes of the Diabaig Formation, Torridon Group, northwest Scotland. Sedimentary Geology 239, 117–128.
Carmona, N.B., Bournod, C.N., Ponce, J.J., Cuadrado, D.G., 2011. The role of microbial mats in the preservation of bird footprints: a case study from the mesotidal Bahia Blanca estuary (Argentina). Society for Sedimentary Geology Special Publication 101, pp. 37–45.
Carvalho, I.S., Borghi, L., Leonardi, G., 2013. Preservation of dinosaur tracks induced by microbial mats in the Sousa Basin (Lower Cretaceous), Brazil. Cretaceous Research 44, 112–121.
Chafetz, H.S., Buczynski, C., 1992. Bacterially induced lithification of microbial mats. Palaios 7, 277–293.
Chen, H.X., 2009. Research of Paleoenvironment and Paleoclimate of Cretaceous in Ya'an area of western Sichuan Basin. Chengdu University of Technology, China.
Cohen, Y., Castenholz, R.W., Halvorson, H.O. (Eds.), 1984. Microbial mats: Stromatolites. MBL lectures in biology, 3. Alan R. Liss, New York, p. 498.
Demicco, R.V., Hardie, L.A., 1994. Sedimentary structures and early diagenetic features of shallow marine carbonate deposits. SEPM (Society for Sedimentary Geology) Atlas Series 1, 265 pp.
Dill, R.F., Shinn, E.A., Jones, A.T., Kelly, K., Steinen, R.P., 1986. Giant subtidal stromatolites forming in normal salinity waters. Nature 324, 55–58.
Dupraz, C., Visscher, P.T., 2005. Microbial lithification in marine stromatolites and hypersaline mats. TRENDS in Microbiology 13, 429–438.
Fedo, C.M., Cooper, J.D., 1990. Braided fluvial to marine transition: the basal Lower Cambrian Wood Canyon Formation, southern Marble Mountains, Mojave Desert, California. Journal of Sedimentary Petrology 60, 220–234.
Fenchel, T., 1998. Formation of laminated cyanobacterial mats in the absence of benthic fauna. Aquatic Mcirobial Ecology 14, 235–240.
Flood, B.E., Bailey, J.V., Biddle, J.F., 2014. Horizontal gene transfer and the rock record: comparetive genomics of phylogenetically distant bacteria that induce wrinkle structure formation in modern sediments. Geobiology 12, 119–132.
Fernández, D.E., Pazos, P.J., 2013. Xiphosurid trackways in a Lower Cretaceous tidal flat in Patagonia: Palaeoecological implications and the involvement of microbial mats in trace-fossil preservation. Palaeogeography, Palaeoclimatology, Palaeoecology 375, 16–29.
Gehling, J.G., 1986. Algal binding of siliciclastic sediments: a mechanism in the preservation of Ediacara fossils. In: Bureau of Mineral and Resources, Geology and Geophysics, Canberra, Sediments down-under. 12th International Sedimentology Congress, 24–30 August, Canberra, Abstract, p. 117.
Gehling, J.G., 1999. Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks. Palaios 14, 40–57.
Genise, J.F., Melchor, R.N., Archangelsky, M., Bala, L.O., Straneck, R., de Valains, S., 2009. Application of neoichnological studies to behavioural and tapoonomic interpretation of fossil bird-like tracks from lacustrine setting: The Late Triassic-Early Jurassic? Santo Domingo Formation, Argentina. Palaeogeography, Paleoclimatology, Palaeoecology 272, 143–161.
Gerdes, G., Krumbein, W.E., 1987. Biolaminated deposits. Lecture Notes in Earth Sciences. Springer, Berlin.
Gerdes, G., Klenke, T., Noffke, N., 2000. Microbial signatures in peritidal siliciclastic sediments: a catalogue. Sedimentology 47, 279–308.
Gou, Z.H., Zhao, B., 2001. The Cretaceous and Tertiary systems in Dayi and Chongzhou Regions, Sichuan. Journal of Stratigraphy 25, 28–33.
Hagadorn, J.W., Bottjer, D.J., 1997. Wrinkle structures: microbially mediated sedimentary structures in silicilastic settings at the Proterozoic-Phanerozoic transition. Geology 25, 1047–1050.
Hagadorn, J.W., Bottjer, D.J., 1999. Restriction of a late Neoproterozoic biotope: Suspect- microbial structures and trace fossils at the Vendian-Cambrian transition. Palaios 14, 73–85.
Hagadorn, J.W., Pfluger, F., Bottjer, D.J., 1999. Unexplored microbial worlds. Palaios 14, 1–2.
Jones, B., 2000. Microbial sediments in Tropical Karst Terrains: a model based on the Cayman Islands. In: Riding, R.E., Awramik, S.M. (Eds.), Microbial Sediments. Springer-Verlag, Berlin, pp. 171–178.
Krumbein, W.E., Paterson, D.M., Zavarzin, G.A., 2003. Fossil and recent biofilms a Natural history of life on earth. Kluwer Academic Publishers, Dordrecht, p. 504.
Lan, Z.W., Chen, Z.Q., 2012. Exceptionally preserved microbially induced sedimentary structures from the Ediacaran post-glacial successions in the Kimberley region, northwestern Australia. Precambrian Research 200, 1–25.
Lan, Z.W., Chen, Z.Q., 2013. Proliferation of MISS-forming microbial mats after the late Neoproterozoic glaciations: evidence from the Kimberley region, NW Australia. Precambrian Research 224, 529–550.
Li, Y.L., 1995. Daxi conglomerate and its geological time. Journal of Chengdu University of Technology 22, 11–14.
Marty, D., Strasser, A., Meyer, C.A., 2009. Formation and taphonomy of human footprints in microbial mats of present-day tidal-flat environments: Implication for the study of fossil footprints. Ichnos 16, 127–142.
Mata, S.A., Bottjer, D.J., 2009a. Development of Lower Triassic wrinkle structures: implications for the search for life on other planets. Astrobiology 9, 895–906.
Mata, S.A., Bottjer, D.J., 2009b. The paleoenvironmental distribution of Phanerozoic wrinkle structures. Earth-Science Reviews 96, 181–195.
Mata, S.A., Bottjer, D.J., 2013. Facies control on lower Cambrian wrinkle structure development and paleoenvironmental distribution, southern Great Basin, United States. Facies 59, 631–651.
Noffke, N., 1998. Environmental requirements for microbial mat formation in Recent tidal systems. Sedimentary Geology 98, 9–13.
Noffke, N., 2000. Extensive microbial mats and their influences on the erosional and depositional dynamics of a siliciclastic cold water environment (Lower Arenigian, Montagne Noir, France). Sedimentary Geology 136, 207–215.
Noffke, N., 2005. Geobiology: objectives, concepts and perspectives. Palaeoclimatology, Palaeooceanography, Palaeoecology 219, 1–3.
Noffke, N., 2009. The criteria for the biogeneicity of microbially induced sedimentary structures (MISS) in Archean and younger, sandy deposits. Earth-Science Reviews 96, 173–180.
Noffke, N., 2010. Geobiology: Microbial Mats in Sandy Deposits from the Archean Era to Today. Springer, p. 194.
Noffke, N., Nitsch, E., 1994. Sedimentology of Lower Ordovician clastic shelf deposits, Montagne Noire (France). Géologie de la France 4, 3–19.
Noffke, N., Eriksson, K.A., Hazen, R.M., Simpson, E.L., 2006a. A new window into Early Archean life: Microbial mats in Earth's oldest siliciclastic tidal deposits (3.2 Ga Moodies Group, South Africa. Geology 34, 253–256.
Noffke, N., Gerdes, G., Klenke, T., Krumbein, W.E., 1996. Microbially induced sedimentary structures – examples from modern sediments of silicilastic tidal flats. Zentralblatt fur Geologie und Paläontologie 1, 307–316.
Noffke, N., Gerdes, G., Klenke, T., Krumbein, W.E., 2001. Microbially induced sedimentary structures—a new category within the classification of primary sedimentary structures. Journal of Sedimentary Research 71, 649–656.
Noffke, N., Knoll, A.H., Grotzinger, J.P., 2002. Sedimentary controls on the formation and preservation of microbial mats in siliciclastic deposits: a case study from the Upper Neoproterozoic Nama Group, Namibia. Palaios 17, 533–544.
Noffke, N., Gerdes, G., Klenke, T., 2003a. Benthic cyanobacteria and their influence on the sedimentary dynamics of peritidal depositional systems (siliciclastic, evaporitic salty and evaporitic carbonatic). Earth-Science Reviews 12, 1–14.
Noffke, N., Hazen, R., Nhleko, N., 2003b. Earth's earliest microbial mats in a siliciclastic marine environment (2.9 Ga Mozaan Group, South Africa). Geology 31, 673–676.
Noffke, N., Beukes, N., Gutzmer, J., Hazen, R., 2006b. Spatial and temporal distribution of microbially induced sedimentary structures: A case study from siliciclastic storm deposits of the 2.9 Ga Witwatersrand Supergroup, South Africa. Precambrian Research 146, 35–44.
Noffke, N., Paterson, D., 2008. Microbial interactions with physical sediment dynamics, and their significance for the interpretation of Earth's biological history. Geobiology 6, 1–4.
Parizot, M., Eriksson, P.G., Aifa, T., Sarkar, S., Banerjee, S., Catuneanu, O., Altermann, W., Bumby, A.J., Bordy, E.M., Louis van Rooy, J.L., Boshoff, A.J., 2005.

Suspected microbial mat-related crack-like sedimentary structures in the Palaeoproterozoic Magaliesberg Formation sandstones, South Africa. Precambrian Research 138, 274–296.
Porada, H., Bouougri, E., Ghergut, J., 2007. Hydraulic conditions and matrelated structures in tidal flats and coastal sabkhas. In: Schieber, J., Bose, B.K., Eriksson, P.G., Banerjee, S., Altermann, W., Catuneau, O. (Eds.), Atlas of microbial mat features preserved within the clastic rock record. Elsevier, Amsterdam, pp. 258–265.
Porada, H., Bouougri, E.H., 2007. Wrinkle structures-a critical review. Earth-Science Reviews 81, 199–215.
Porada, H., Ghergut, J., Bouougri, E.H., 2008. Kinneyia-type wrinkle structures-critical review and model of formation. Palaios 23, 65–77.
Prave, A.R., 2002. Life on land in the Proterozoic: evidence from the Torridonian rocks of northwest Scotland. Geology 30, 811–814.
Pruss, S., Fraiser, M., Bottjer, D.J., 2004. Proliferation of Early Triassic wrinkle structures: implications for environmental stress following the end-Permian mass extinction. Geology 32, 461–464.
Reid, R.P., Visscher, P.T., Decho, A.W., Stolz, J.F., Bebout, B.M., Dupraz, C., Macintyre, I.G., Paerl, H.W., Pinckney, J.L., Prufert-Bebout, L., Steppe, T.F., DesMarais, D.J., 2000. The role of microbes in accretion, lamination and early lithification of modern marine stromatolites. Nature 406, 989–992.
Reineck, H.E., Singh, I.B., 1980. Depositional Sedimentary Environments. Springer-Verlag, Berlin, p. 551.
Robb III, A.J., 1992. Rain-impact microtopography (RIM): an experimental analogue for fossil examples from the Maroon Formation, Colorado. Journal of Sedimentary Petrology 62, 530–535.
Sarkar, S., Banerjee, S., Samanta, P., Jeevankumar, S., 2006. Microbial mat-induced sedimentary structures in siliciclastic sediments examples from the 1.6 Ga Chorhat Sandstone, Vindhyan Supergroup, MP, India. Journal of Earth System Science 115, 49–60.
Sarkar, S., Bose, P.K., Samanta, P., Sengupta, P., Eriksson, P.G., 2008. Microbial mat mediated structures in the Ediacaran Sonia Sandstone, Rajasthan, India, and their implications for Proterozoic sedimentation. Precambrian Research 162, 248–263.
Schieber, J., 1986. The possible role of benthic microbial mats during the formation of carbonaceous shales in shallow Mid-Proterozoic basins. Sedimentology 33, 521–536.
Schieber, J., 2007. Mat features in sandstones: diagenetic features related to mat metabolism and decay. In: Schieber, J., Bose, P., Eriksson, P.G., Banerjee, S., Altermann, W., Catuneanu, O. (Eds.), Atlas of Microbial Mat Features Preserved within the Siliciclastic Rock Record. Elsevier, pp. 72–75.
Schieber, J., Bose, P.K., Eriksson, P.G., Banerjee, S., Sarkar, S., Altermann, W., Catuneau, O., 2007. Atlas of Microbial Mat Features Preserved Within the Siliciclastic Rock Record, Atlases in Geosciences. Elsevier, Amsterdam, p. 311.
Scott, J.J., Renaut, R.W., Owen, R.B., 2010. Taphonomic controls on animal tracks at saline, alkaline Lake Bogoria, Kenya Rift Valley: impact of salt efflorescence and clay mineralogy. Journal of Sedimentary Research 80, 639–665.
Seilacher, A., 1999. Biomat-related lifestyle in the Precambrian. Palaios 14, 86–93.
Semikhatov, M.A., Gebelein, C.D., Cloud, P., Awramik, S.M., Benmore, W.C., 1979. Stromatolite Morphogenesis-progress and problems. Canadian Journal of Earth Sciences 16, 992–1015.
Shi, X.Y., Wang, X.Q., Jiang, G.Q., Liu, D.B., Gao, L.Z., 2008a. Pervasive microbial mat colonization on Mesoproterozoic peritidal siliciclastic substrates: an example from the Huangqikou Formation (ca. 1.6 Ga) in Helan Mountain, NW China. Geological Review 54, 577–586.
Shi, X.Y., Zhang, C.H., Jiang, G.Q., Liu, J., Wang, Y., Liu, D.B., 2008b. Microbial mats in the Mesoproterozoic carbonates of the North China Platform and their potential for hydrocarbon generation. Journal of China University of Geosciences 19, 549–566.
Shi, X.Y., Jiang, G.Q., Zhang, C.H., Gao, L.Z., Liu, J., 2008c. Sand veins and MISS from the Mesoproterozoic black shale (ca. 1.7 Ga) in North China: implication for methane degassing from microbial mats. Science in China Series D-Earth Sciences 51, 1525–1536.
Simonson, B.M., Carney, K.E., 1999. Roll-up structures; evidence of in situ microbial mats in late Archean deep shelf environments. Palaios 14, 13–24.
Thomas, K., Herminghaus, S., Porada, H., Goehring, L., 2013. Formation of Kinneyia via shear-induced instabilities in microbial mats. Philosophical Transactions of the Royal Society A-Mathematical Physical and Engineering 371.
Walcott, C.D., 1914. Cambrian geology and palaeontology III, no. 2: Precambrian, Algonkian algal flora. Smithsonian Miscellaneous Collections 64, 77–156.
Xing, L.D., Wang, F.P., Pan, S.G., Chen, W., 2007. The Discovery of Dinosaur Footprints from the Middle Cretaceous Jiaguan Formation of Qijiang County, Chongqing City. Acta Geologica Sinica (Chinese edition) 81, 1591–1602.
Xing, L.D., Mayor, A., Chen, Y., 2011. Lianhua Baozhai (Lotus Mountain Fortress, Qijiang County of Chongqing City): a direct evidence of co-existing ancient Chinese and dinosaur tracks. Geological Bulletin of China 30, 1530–1537.
Xing, L.D., Bell, P., Harris, J.D., Currie, P.J., 2012. An unusual, three-dimensionally preserved, large hadrosauriform pes track from "Mid"-Cretaceous Jiaguan Formation of Chongqing, China. Acta Geologica Sinica (English edition) 86, 304–312.
Xing, L.D., Lockley, M.G., Piñuelac, L., Zhang, J.P., Klein, H., Li, D.Q., Wang, F.P., 2013. Pterosaur trackways from the Lower Cretaceous Jiaguan Formation, Qijiang District, Chongqing Municipality, China. Palaeogeography, Palaeoclimatology, Palaeoecology 392, 177–185.
Xing, Z.F., Qi, Y.A., Zheng, W., Yuan, Y.Y., 2011. Microscopic characteristics of extensive microbial mats in Mesoproterozoic Era: an example from the Yunmengshan Formation, Western Henan. Acta Sedimentologica Sinica 29, 857–865.
Zhong, W.L., Zhong, Q.C., Xian, H.L., Kaiho, K., 2013. Microbially induced sedimentary structures from the Mesoproterozoic Huangqikou Formation, Helan Mountain region, northern China. Precambrian Research 233, 73–92.