Middle Cambrian Diplocraterion parallelum from North China:
Ethologic significance and facies controls

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INTRODUCTION

An abrupt increase in the degree and depth of bioturbation occurred during the early Cambrian, corresponding to the rapid radiation of metazoans, which led to the first mixground ecosystems in an event referred to as the “Agronomic Revolution” (Seilacher & Pflüger, 1994; Seilacher, 1999). Major components of this ecological revolution include the first appearance of vertical burrows and the development of tiered infaunal communities (Seilacher & Pflüger, 1994; Mángano & Buatois, 2014, 2016, in press). In addition, the early Cambrian reveals several profound biotic and environmental events that progressively influenced microbialites, such as local occurrence of stromatolites and thrombolites (Dornbos et al., 2005; Riding, 2011).

The well-known ichnogenus Diplocraterion is one of the common trace fossils globally (Fürsich, 1974; Cornish, 1986; Olóriz & Rodriguez-Tovar, 2000; Šímo & Oláhávský, 2007; Rodríguez-Tovar & Pérez-Valera, 2013; Martin et al., 2016). This distinctive trace fossil ranges from early Cambrian to Holocene in age. It occurs in a wide variety of depositional settings, involving carbonate and siliciclastic rocks. This ichnotaxon is often used for environmental characterization of shallow-marine depositional systems (Cornish, 1986; Šímo & Oláhávský, 2007; Mángano et al., 2013; Rodríguez-Tovar & Pérez-Valera, 2013). Diplocraterion typically provides valuable information on environmental factors, such as hydrodynamic energy level, substrate consistency, rates of sedimentation and erosion, and distribution of organic matter (Goldring, 1964; Cornish, 1986; Olóriz & Rodríguez-Tovar, 2000; Rodríguez-Tovar & Pérez-Valera, 2013) and it is regarded as a key ichnotaxon (as are Rhizocorallium and Thalassinoides) to reflect the level of benthic ecosystem complexity and recovery during evolutionary events.
such as the Cambrian explosion and the end-Permian mass extinction (Twitchett & Barras, 2004; Mángano & Buatois, 2014).

The middle Cambrian Mantou Formation (Stage 5) in the Mianchi section (western Henan Province, North China) contains well-preserved Diplocraterion parallelum Torell, 1870. Here we report several macro- and micro-features of Diplocraterion, providing new evidence pertaining to the behavior of the Diplocraterion tracemaker, its ecological significance, and the relationship between tracemaker and substrate in the aftermath of the Cambrian explosion.

**GEOLOGICAL SETTING**

Excellent lower Paleozoic outcrops, particularly of Cambrian strata, occur in the area of Mianchi in Henan Province, North China (Fig. 1). The studied section is located in the northwest part of Henan Province and belongs to the Cambrian western Henan subarea (Pei, 2000). Cambrian strata are exposed along the Rencun Mountain ridge on a ca. 5 km long section. Cambrian strata in this area were deposited along a continental margin, forming laterally extensive tidal flats during times of tectonic quiescence. In the Mianchi section, Cambrian strata are up to 800 m thick and range from Series 2 to Furongian. The trace fossils described in this paper were collected from the Cambrian Series 3 Member II of the Mantou Formation (M2) of the Mianchi section exposed at 34°49’13” N, 111°53’15” E, which mainly consists of muddy siltstone and very fine-grained sandstone and thin-bedded limestone (Fig. 1).

The Mantou Formation is subdivided into three members. Member I (M1) mainly comprises grey-yellow thin-bedded shale and siltstone interbedded with limestone, argillaceous limestone and laminar algal limestone. Member II (M2) consists of grey thick-bedded oolitic limestone and argillaceous limestone intercalating with grey-brown thin-bedded shale and sandstone. Member III (M3) is mainly composed of thin- and medium-bedded oolitic limestone, nodular limestone and thrombolites intercalating with grey-green thin-bedded shale and siltstone. Body fossils are common in the Mantou Formation, especially abundant trilobites, and small shelly fauna in the shale and limestone (Pei, 2000). The trilobite fauna indicates a Series 2 age for M1 and a Series 3 age for M2 and M3 (Fig. 1c; Pei, 2000; Peng, 2009).

The Mantou Formation conformably overlies the lower Cambrian Zhushadong Formation and underlies the middle Cambrian Zhangxia Formation. The Zhushadong Formation consists of pebble conglomerate, silty mudstone and dolomitic limestone with scarce fossils, most likely deposited in a restricted shallow-marine environment periodically exposed subaerially in a...
seasonally dry, probably subarid, climate. The Zhangxia Formation mainly consists of grey thick bedded oolitic limestone intercalating with thin-bedded oolitic limestone in the lower part and grey-yellow thin-bedded dolostone in the upper part. This unit was formed in an open tidal-influenced carbonate platform.

The trace fossils described in this paper occur in the lower part of M2 (Fig. 1), which records a transition from restricted platform (the Zhushadong Formation and M1) to a storm-affected tidal flat environment (M2 and M3). The ichnofossil-bearing interval (Fig. 2) starts with cross-bedded, very fine-grained sandstone, overlain by a 10 cm-thick siltstone unit with moderate bioturbation (Bioturbation index [BI] = 4), which, in turn, is overlain by a 8 cm-thick, parallel-laminated, mud-rich siltstone. Above this, thinner bedded siltstone is intercalated with abundant mudstone breccia, which, in turn, is overlain by a 4 cm-thick siltstone and a 5 cm-thick, erosively based, wave-ripple cross-laminated and parallel-laminated, silty sandstone, which is interpreted as storm deposits (tempestites). Diplocraterion occurs at the top of this layer.

METHODS

Diplocraterion and the host strata were sampled, cleaned and coated with carbon and gold, respectively. Samples were analyzed both petrographically and chemically in a Quanta 250 field emission gun scanning electron microscope (FEI Quanta 250 FEG-SEM) equipped with a Bruker Quantax 200 XFlash 6/30 EDS at the Key Laboratory of Biogenic Traces & Sedimentary Minerals of Henan Province in Jiaozuo, China. The scanning electron microscope provides element and micro-scale morphological features of Diplocraterion which allows a more detailed discussion of its morphology and ethology.

RESULTS

Diplocraterion parallelum

The investigated Diplocraterion parallelum specimens occur on the bedding plane of silty very fine-grained sandstone with carbonate cement. They consist of perpendicular to bedding, U-shaped, spreiten-bearing burrows with well-developed marginal tube (Fig. 3). On the bedding surface, the spreite consists of alternating layers of dark and light laminae (Fig. 3b). The overall shape of the marginal tube in planar view is semi-circular (Fig. 3e).

Examination of the spreite in thin section shows that the lining is argillaceous, and microscope analysis indicates the presence of illite. Nearly all individuals are truncated upward by erosion surfaces. Specimens are very shallow, penetrating down and up to the top of the overlying muddy layer (Fig. 2). No scratch marks are preserved on the marginal tube. Burrow width is 8-23 mm and burrow depth is 2-4 mm. The diameter of the marginal tube (or limbs) is constant in each specimen (3-5 mm). The maximum depth of Diplocraterion parallelum is difficult to estimate because they were truncated during numerous episodes of erosion. No other trace fossils were found in this layer.

SEM-EDS features

SEM-EDS analysis indicates that light laminae in Diplocraterion parallelum spreite are commonly relatively thin (750μm) and consist of calcareous siltstone with high percentage of calcium (Fig. 4d). Dark laminae are commonly thick (1 mm) and contain more muddy, clay minerals around siliceous spheres, displaying mostly coarse and many empty pores (Fig. 4a) in the surface of dark laminae under the SEM. Through the SEM mapping, dark laminae were dominated by Si, Al and Fe, whereas light laminae were dominated by Ca and Si (Fig. 4c-e). The siliceous spheres were only found within the dark laminae of Diplocraterion (Fig. 4b).

DISCUSSION

Diplocraterion ethology and tracemakers

Diplocraterion typically occurs in Phanerozoic strata formed in the high-energy intertidal and uppermost subtidal zone of tide-dominated shorelines (e.g., Fürsich, 1974, 1975; Cornish, 1986; Mángano & Buatois, 2004a) or in nearshore areas (shoreface sandstones to offshore tempestites) of wave-dominated shorelines (e.g., Stanistreet, 1989; Gaillard & Racheboeuf, 2006). Occurrences in other depositional settings, such as deltaic (e.g., Mason & Christie, 1986), estuarine (e.g., Gingras et al., 1999), deep-marine (e.g., Buatois & López-Angriman, 1992) and even continental (e.g., Kim & Paik, 1997), have been documented as well. Diplocraterion was shown to be common in Phanerozoic examples of the Skolithos and Glossifungites Ichnofacies (Buatois & Mángano, 2011). It
has been extremely useful as an aid to the interpretation of sequence-stratigraphic surfaces, stratal patterns, and depositional environments (Olóriz & Rodríguez-Tovar, 2000; Šimo & Olsavský, 2007; Mángano et al., 2013; Rodríguez-Tovar & Pérez-Valera, 2013; Singh et al., 2014). Diplocraterion probably represents the activity of infaunal, suspension feeding invertebrates (Fürsich, 1974; Häntzschel, 1975; Ekdale & Lewis, 1991; Seilacher, 2007).

Changes in dimensions of the spreite are interpreted as being a consequence of the growth of the tracemaker (Bromley & Hanken, 1991). Variations in dimensions of the trace fossil reflect the interplays between growth of the animal and variation in rate of deposition and erosion. Goldring (1964) demonstrated the response of the D. parallelum producer to the interplay of erosion and deposition, resulting in yoyo-like combinations of protrusive and retrusive elements of spreite construction. Chakraborty & Bhattacharya (2013) documented the different morphologies of Diplocraterion in cross section and planar view (i.e., the opposite concave laminae in the planar view, which represented the retrusive spreite created by the tracemaker) (Fig. 5). Bromley & Hanken (1991) suggested that downward adjustment would represent a minimal modification of the Diplocraterion tracemaker, whereas upward adjustment behavior might have taken a longer time to become incorporated into the repertoire of the burrower. The occurrence of Diplocraterion parallelum in middle Cambrian strata of North China demonstrates that downward and upward burrow adjustments were attained early in the evolutionary history of this ichnotaxon.

The Diplocraterion studied here are the oldest spreite trace fossils recorded in the Cambrian of North China. Diplocraterion most likely reflects colonization immediately after deposition from a storm event. The absence of the funnel indicates subsequent erosion. Two possible suites of Diplocraterion (D1-D2) have been
The tracemaker burrowed in several stages. First, the burrower constructed the retrusive spreiten during normal equilibrium behavior. All of these features support the interpretation of *Diplocraterion parallelum* as recording the equilibrium behavior of the tracemaker, which adjusted the position of the burrow in response to aggradation and erosion.

Body fossils (e.g., trilobites) are present in the lower part of the Mantou Formation. Well-preserved *Thalassinoides* occurs in the Stage 2 Zhushadong Formation (Zhang et al., 2017). Body fossils in the Member II of the Mantou Formation comprise mainly trilobites (e.g., *Redlichia chinensis* Walcott, 1905, *Yaojiayuella granosa* Walcott, 1905, *Hsuchuangia triangularis* Zhang et Wang, 1985). The presence of *Diplocraterion* suggests that other types of invertebrates, most-likely soft-bodied, were part of the ecosystem. Candidates proposed as possible tracemakers include polychaetes (Schäfter, 1972), echiurids (Schäfter, 1972) and amphipods (Seilacher, 2007). However, U-shaped burrows with spreite have also been attributed to the activities of crustaceans in Triassic and Cretaceous rocks (Olóriz & Rodríguez-Tovar, 2000; Rodríguez-Tovar & Perez-Valera, 2013).

The U-shaped morphology of the Cambrian specimens may have represented a behavioral function similar to modern examples, therefore recording equilibrium traces. The primary ecologic function of U-shaped burrow is most likely for protection in a turbulent environment. Vertical burrowing provides the organism protection from fluctuations in temperature, salinity, and desiccation. These environmental stress factors possibly affected the behaviors of the invertebrate fauna of the Mantou Formation tidal flat.

**Environmental conditions and colonization trends**

The use of trace fossils as a tool to interpret sediment reworking, sedimentation rate, current intensity, and substrate stability and coherence has been known for...
Tidal-dominated estuarine limestone (late Ordovician) Sandstone

Natalin et al., 2014

late Cambrian

Cornish, 1986

Stairway Sandstone (Australia)

Vavrdova et al., 2003

Tidal-dominated estuarine limestone (late Ordovician)

late Cambrian

Olóriz & Rodríguez-Tovar, 2000; Šimo & Olšavský, 2004a, b.

Eustatic changes (Tichenor et al., 2012) and different climatic conditions (Olóriz & Rodríguez-Tovar, 2000; Šimo & Olšavský, 2004a, b) led to changes in the sedimentary environment. The presence of tidal-flat deposits during the Ordovician period is consistent with the energy gradient along a tidal flat depositional profile, suggesting shoreline progradation (Mángano & Buatois, 2004a, b). Food particles were kept in suspension by uni-directional currents and oscillatory flow, favoring suspension-feeding strategies. However, during times of continuous bedform migration, organisms were not able to colonize the shifting substrate (Desjardins et al., 2012).

The dark laminae consist of Al and Si, whereas the light laminae are composed of Ca and Si. Significant numbers of siliceous spheres are present in the dark
laminae. The components of the light laminae are similar to the surrounding rock. Composition of the spreite suggests that the tracemaker has responded to the interplay of erosion and deposition. The tracemaker penetrated into the sediment during the initial waning phase of the storm, and the spreite was subsequently formed in response to substrate aggradation following the storm event.

The delayed appearance of Diplocraterion, an ichnotaxon present since Cambrian Age 2 elsewhere (Mángano & Buatois, 2014), in the Mantou Formation (Age 5) may have resulted from facies constrains (Tab. 1). The presence of U-shaped vertical burrows underscores the ability of infaunal organisms to colonize sandy shorelines. In contrast, shallow carbonate substrates were apparently not suitable for infaunal colonization by the Diplocraterion producers. Due to long time denudation, deposition in the Mianchi area started during Cambrian Age 3 (Peng, 2009). Following an overall transgression, a carbonate platform (Zhushadong Formation) was first established, then tidal flat were formed (Mantou Formation), and finally deposition took place in a carbonate platform (Zhangxia Formation). Accordingly, carbonate substrates might be suitable for survival of microbial-dominated ecosystems, as indicated by the widespread occurrence of stromatolites and thrombolites in early transgressive carbonate platforms from the Zhushadong Formation and Member I of the Mantou Formation (M1).

Diplocraterion appeared slightly later than Arenicolites in the early Cambrian (e.g., Bromley & Hanken, 1991), with the spreite representing an innovation not present in the latter. Diplocraterion is also as a key ichnoenous to show the dramatic increase in depth of bioturbation in the early Cambrian. The appearance of deep-tier suspension feeders (e.g., the tracemakers of Skolithos, Diplocraterion, and Arenicolites) in Cambrian Age 2 had a major impact in marine ecosystems, coupling the plankton productivity and the benthos, playing a role in the turnover from matgrounds to mixgrounds (Signor & Vermeij, 1994; Butterfield, 2004; Mángano & Buatois, 2014, 2016, in press). Diplocraterion mainly occurs in shallow marine siliciclastics during the early-middle Cambrian (Tab. 1). The oldest Diplocraterion occurrence in carbonate was reported from the late Cambrian Gushan Formation (Furongian) of North China (Zhou et al., 2011). Since the Early Ordovician, Diplocraterion normally occurs in both shallow-marine siliciclastics and carbonates (Pratt & James, 1986). Therefore, the delayed appearance of Diplocraterion in M2 may be due to the lack of suitable siliciclastic facies in the lower Cambrian of North China. Although the pattern of early colonization of siliciclastic sediments by U-shaped vertical burrows during the early Cambrian followed by a subsequent colonization of carbonates during the late Cambrian seems to be quite robust, the underlying reasons are still unclear. It is here suggested the changes in the chemical component from aragonite seas (Ma/Ca > 2) to calcite seas (Mg/Ca < 2) during the transition between the middle and the late Cambrian (Hardie, 1996; Stanley & Hardie, 1998, 1999; Stanley, 2006) may have played a role in the delayed colonization of carbonate substrates by suspension-feeding worms. Calcite seas appear to have favored early seafloor lithification (Palmer & Wilson, 2004). Increased consistency of the sea floor may have favored burrowing by providing a more cohesive sediment, therefore promoting burrow stability.

CONCLUSIONS

The trace fossil Diplocraterion parallelum is described from shallow-marine deposits of the middle Cambrian Stage 5 Mantou Formation in North China. This ichnoaxon comprises shallow, perpendicular to bedding plane, U-shaped spreite burrows enclosed by a marginal tube, with dark and light laminae in planar view. SEM-EDS analysis indicates that the dark laminae of the spreite consist of Al, Si and many silicon spheres, whereas the light laminae and surrounding rocks consist of Ca and Si. The delayed appearance of Diplocraterion in North China was controlled by facies constrains, reflecting the dominance of carbonate deposition in the study area.

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