



## Interactions between Ediacaran animals and microbial mats: Insights from *Lamonte trevallis*, a new trace fossil from the Dengying Formation of South China



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### ABSTRACT

A new ichnogenus and ichnospecies, *Lamonte trevallis*, is formally described from the Shibantan Member limestone of the upper Ediacaran Dengying Formation, Yangtze Gorges area, South China. It is characterized by horizontal tunnels connected with short vertical burrows and surface trails. The horizontal burrows are elliptical or bilobed in transverse cross-section, preserved in full relief, and filled with carbonate intraclasts, micrites, as well as calcite and silica cements. They occur exclusively in silty, crinkled, and microlaminated layers that are interpreted as amalgamated cyanobacterial microbial mats; no burrows have been found in intraclastic layers adjacent to the microlaminated layers. The vertical traces are filled with the same material as the burrows, but they typically project through the crinkled microlaminae and are exposed on the bedding surface. The surface tracks are always preserved in negative epirelief or positive hyporelief and consist of two parallel series of either sharp scratch marks or small knobs. The burrow infill has  $\delta^{18}\text{O}_{\text{carb}}$  and  $\delta^{13}\text{C}_{\text{carb}}$  values distinct from, but intermediate between, microlaminated and intraclastic layers, consistent with petrographic observation that burrow infill consists of a mixture of early carbonate cements, intraclasts, and micrites. Bedding plane bioturbation intensity (20–40%)—measured as percentage of bedding plane area covered by *L. trevallis* traces—is comparable to similar measurements in pre-trilobite Cambrian carbonates. The exclusive occurrence of *L. trevallis* within microbial mats may have both taphonomic and ecological significance. These mats may have provided firm substrates and localized geochemical conditions that contributed to the structural integrity of the burrows, and they may have also facilitated early diagenetic cementation of burrow infill, thus facilitating burrow preservation. The close association of these burrows with microbial mats implies that the trace producers actively mined cyanobacterial mats to exploit oxygen or nutrient resources. The trace makers of *L. trevallis* were better able to utilize the resources around them than many other Ediacaran trace makers and provide an ichnological record of a flourishing benthic ecology in late Ediacaran oceans at the dawn of the agronomic revolution.

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### 1. Introduction

The establishment of burrowing behaviors is a key event in the evolution of bilaterian animals, significantly impacting paleoecological and geobiological dynamics at the Ediacaran–Cambrian transition. Ediacaran burrows and trails are traditionally known for their small size, simple morphology, shallow penetration depth, and relative scarcity when compared to their Phanerozoic counterparts (Droser et al., 1999;

Jensen et al., 2005; Droser et al., 2006; Jensen et al., 2006; Seilacher, 2007). There are several factors that might have contributed to the limited complexity, diversity, and abundance of Ediacaran burrows. First, dissolved oxygen levels were relatively low and uneven in Ediacaran oceans (Kennedy et al., 2005; Fike et al., 2006; McFadden et al., 2008; Shen et al., 2008), which would have limited habitable ranges of burrowing animals. Second, the ubiquitous microbial mats of the time (Hagadorn and Bottjer, 1999; Seilacher, 1999; Bottjer et al., 2000) would likely have maintained a sharp redox gradient across the sediment–water interface such that deeper sediments were poorly oxygenated or sulfidic, and thus generally hostile to burrowers (Gehling, 1999; Fedonkin et al., 2007a; Gerdes, 2007). Third, predation pressures were relatively low, thereby allowing animals to forage along the surface of microbial mats or sediments (Fendonkin and Waggoner, 1997; Ivanstov

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and Malakhovskaya, 2002; Dzik, 2005; Fedonkin et al., 2007b). Finally, it is also possible that Ediacaran animals were not abundant or were physically incapable of making large and complex burrows due to the lack of a strong musculature system (Miller, 2007; Seilacher, 2007). Despite their limited complexity and diversity, Ediacaran trace fossils do offer the only paleontological window onto the mounting importance of bioturbation at a key transition in the history of life.

One of the most important innovations in the early evolution of animal bioturbation was the exploration and penetration of the ubiquitous microbial mats that existed during this time (Gehling, 1999; Hagadorn and Bottjer, 1999; Gehling et al., 2005; Droser et al., 2006). These microbial mats were a major component of the Proterozoic ecosystem (Seilacher, 1999; Hofmann, 2000; Eriksson et al., 2007) and were much more expansive than those found today (Eriksson et al., 2010; Seckbach and Oren, 2010; Gingras et al., 2011). The cohesive nature of microbial mats reduces gas transport into and out of sediments and, in combination with vertical stratification of different microbial communities, creates a steep chemical gradient across the mat–water interface and in the uppermost centimeters of sediment (Moreira et al., 2004; Bosak et al., 2012). The resulting anoxic sediments would likely have hindered or deterred vertical exploration by animals (Seilacher, 1999), although horizontal surface trails and shallow burrows were common in the Ediacaran fossil record (Droser et al., 2005; Jensen et al., 2005, 2006). However, bioturbation did become more pervasive and, with deeper sediment penetration and therefore greater sediment ventilation, had a greater geobiological impact on Earth systems (Canfield and Farquhar, 2009). Bilaterian animals, in the course of interacting with and exploiting the microbial world (Hagadorn and Bottjer, 1999; Seilacher, 1999; Bottjer et al., 2000; Droser et al., 2002), also left increasingly complex burrow systems (Jensen et al., 2000; Jensen and Runnegar, 2005; Seilacher et al., 2005), indicating a more dynamic Ediacaran ecosystem that can be examined by studying the trace fossil record.

In the last decade, the upper Ediacaran Dengying Formation (~551–541 Ma) in the Yangtze Gorges area of South China has become an important stratigraphic unit for the study of Ediacaran trace fossils. Numerous trace fossils, including simple taxa such as *Helminthoidichnites*, *Palaeophycus*, *Planolites*, and *Torrowangea* (Zhao et al., 1988; Ding et al., 1992; Jensen et al., 2006; Weber et al., 2007), as well as more complex forms that represent under-mat feeding, epibenthic locomotion, and temporary dwelling structures of bilaterian animals (Chen et al., 2013), have been reported from the Dengying Formation. In particular, the bituminous limestone of the Shibantan Member in the middle Dengying Formation holds great potential to illuminate ecological interactions between late Ediacaran animals and microbial mats, because of the abundance and exceptional preservation of both trace fossils and microlaminae which have been interpreted as the remnants of microbial mats. Here, we formally describe a new trace fossil, *Lamonte trevallisi*, which can potentially broaden our understanding of trace maker behavior during this time. Building upon our preliminary report of similar trace fossils from the Shibantan Member (Chen et al., 2013), this study synthesizes petrographic and geochemical data in order to better understand the preservation and paleoecology of the Shibantan burrows.

## 2. Geological setting

The geological and stratigraphic background of the Dengying Formation in the Yangtze Gorges area was detailed in Chen et al. (2013). To briefly summarize, the upper Ediacaran Dengying Formation overlies the lower–middle Ediacaran Doushantuo Formation and underlies the Yanjiahe Formation which contains the Ediacaran–Cambrian boundary (Dong et al., 2009; Jiang et al., 2012). It was deposited on a shallow marine carbonate platform (Zhou and Xiao, 2007; Jiang et al., 2011), and its age is constrained between 551 Ma and 541 Ma based on available radiometric dates and stratigraphic correlations (Condon et al., 2005; Jiang et al., 2009; Zhu et al., 2009). The Dengying Formation is divided

into three units, in ascending age order: the Hamajing, Shibantan, and Baimatuo Members (Fig. 1). The Hamajing Member consists of peritidal dolostone, with widespread tepee structures (Fig. 2A) and karstification features such as dissolution vugs ranging from a few millimeters to a few meters in size (Fig. 2B) (Zhou and Xiao, 2007). The Shibantan Member is composed of dark gray, thin-bedded, bituminous limestone interpreted to have been deposited in a subtidal environment (Fig. 2C) (Zhou and Xiao, 2007). The Baimatuo Member is composed of light gray massive peritidal dolostone, characterized by abundant dissolution vugs and breccia (Fig. 2G) (Zhou and Xiao, 2007; Chen et al., 2013). Although the Shibantan Member is mostly characterized by thin bedded parallel laminae, cross stratification and rip-up clasts are present (Fig. 2E–F), indicating deposition above storm wave-base. Crinkled microlaminae consisting of organic-rich, calcareous clays and silts are very common, and are commonly characterized with wrinkled bed surfaces. Crinkled microlaminae are often intercalated with thin layers of intraclastic, pelloidal, and oolitic packstone and grainstone (Fig. 2D). These crinkled microlaminae are interpreted as microbial mats (see Section 4) that trapped silts, clays, and micrites, and were subsequently cemented by diagenetic calcite (Chen et al., 2013). No mud cracks have been observed in the Shibantan Member.

## 3. Methods and materials

The Shibantan Member trace fossils were collected from an active quarry near Wuhe in the Yangtze Gorges area (30°46′47.74″N, 111°02′28.89″E). Abundant trace fossils were observed on outcrops where stratigraphic orientation (up direction) was unambiguously identified. Numerous loose slabs and blocks containing trace fossils were collected (Figs. 3–4) from active pits where thin-bedded limestone of the Shibantan Member is quarried for construction and pavement material. A few slabs were also collected from abandoned roofs, but they can be confidently ascribed to the Shibantan Member because of their distinctive lithology (bituminous limestone) and the abundance of vendotaenid fossils characteristic of the Shibantan Member. The stratigraphic orientation of the loose slabs can be inferred using sedimentary structures such as low-angle cross stratification and truncation of microlaminae. Selected specimens were thin-sectioned perpendicular to bedding surfaces in order to petrographically characterize the occurrence of fossils and their relationship with inferred microbial mats (Figs. 5–6).

Polished thin sections and slabs were examined using scanning electron microscopy (Figs. 7–8), conducted on an FEI Quanta 600 field emission environmental scanning electron microscope (ESEM) in high vacuum mode using secondary electron (SE) or backscattered electron (BSE) detectors. Energy dispersive X-ray spectroscopic (EDS) point spectra and elemental maps were generated using an integrated Bruker AXS QUANTAX 400 with a high-speed silicon drift detector. Identical operating conditions were maintained for all EDS analyses: 20 keV accelerating voltage, 5.0 spot size (a unitless measure of beam current and probe diameter), 11.5–12 mm working distance, and X-ray signal count-rates of 25–35 kcps. All elemental maps were acquired for 600 second live-time, and individual point spectra were collected for 100 second live-time. Elemental peaks from point spectra were identified and quantified (with ZAF and Au–Pd coating corrections applied) using Bruker Esprit 1.9.2 software. Initial X-ray point spectra were collected from the burrow infill, intraclastic layers, and clayey/silty microlaminated layers (Table 1, Supplemental Table 1, Supplemental Fig. 1). Elemental maps were subsequently generated (Figs. 7–8) for all elements found at >1% (normalized weight percentage; nwp) in point analysis. Composite elemental maps (Figs. 7C and 8C–D) consist of a montage of individual maps that may vary in relative scales; thus brightness values do not necessarily correspond to the same quantitative abundance across individual maps.

Freshly cut surfaces that intersect burrow infill, intraclastic layers, and microlaminated layers were microdrilled for carbon and oxygen isotope analysis (Fig. 9), using a 1 mm drill bit on a bench press drill. Veins

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