



Beyond the stony veil: Reconstructing the Earth's earliest large animal traces via computed tomography X-ray imaging



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ABSTRACT

Trace fossils are superb lines of evidence for examining the ancient biologic world because they offer an opportunity to infer behavioral ecology of organisms. However, traces can be difficult to parse from their matrix, which leads to the loss of important morphological and behavioral data. This is especially true for the earliest marine animal traces from the Ediacaran Period (635–541 Ma), which are usually small (<5 mm in diameter) and simple (mostly small horizontal trails and burrows), and are sometimes difficult to be distinguished from co-existing tubular body fossils. There is also evidence that the prevalence of microbial substrates in Ediacaran oceans may have influenced emerging trace makers in non-actualistic ways from a late Phanerozoic perspective (e.g., microbial mats may have facilitated a strong geochemical gradient across the sediment-water interface). Therefore, the discovery of the relatively large traces of *Lamonte trevallisi* from the Ediacaran Shibantan Member of the Denying Formation (~551–541 Ma) in the Yangtze Gorges area of South China provides a unique opportunity to study early bioturbators. These trace fossils are large enough and have sufficient compositional contrast (relative to the matrix) for *in situ* analysis via X-ray computed tomography (CT) and microcomputed tomography (microCT). Each analytical method has its own advantages and disadvantages. CT scans can image larger specimens, but cannot adequately resolve small features of interest. MicroCT scans can achieve higher resolution, but can only be used with small samples and may involve more post-processing than CT scans. As demonstrated in this study, X-ray CT and microCT in combination with other 3D imaging techniques and resources have the potential to resolve the 3D morphology of Ediacaran trace fossils. A new Volumetric Bioturbation Intensity (VBI) is also proposed, which quantifies whole rock bioturbation using 3D analysis of subsurface traces. Combined with the ability to examine trace fossils *in situ*, the VBI can enhance our view of ancient ecologies and life's enduring relationship with sediments.

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1. Introduction

Trace fossils offer a unique insight into the behavior of prehistoric organisms during their lifetime by preserving their activities and behaviors as opposed to just the physical imprint of their bodies (Bertling, 2007; Budd and Jackson, 2016; Miller, 2007; Seilacher, 2007). However, depending on the trace maker, trace size, type of trace, density of traces, and sediment media, it can be challenging to isolate and examine a trace within its matrix (Bednarz and McIlroy, 2009; Jensen et al., 2006; Malpas et al.,

2005; Miller, 2007). Animal trace fossils from the Ediacaran Period (635–541 Ma) are often particularly difficult to examine due to their small size, their simplicity, and their tendency to be preserved on a single plane of preservation (Droser et al., 2005a; Jensen et al., 2005; Sappenfield et al., 2011). Additionally, simple animal traces from the Ediacaran Period are sometimes similar to tubular body fossils and their preservation in microbial substrates renders it difficult to distinguish Ediacaran body and trace fossils based on bedding plane observation alone (Droser et al., 1999, 2002; Jensen et al., 2006; Sappenfield et al., 2011; Tarhan et al., 2015, 2013). *Lamonte trevallisi* is a relatively large Ediacaran ichnospecies that is preserved differently than most trace fossils from the time period. Discovered in the Shibantan Member of the Deny-

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ing Formation (~551–541 Ma) in the Yangtze Gorges area of South China, *L. trevallisi* offers a unique opportunity to study early bioturbators (Chen et al., 2013a,b; Meyer et al., 2014b).

Lamonte trevallisi is a millimeter-scale animal trace fossil associated with microbial mats. It includes three components: surface trackways, vertical traces, and horizontal tunnels. These three components are sometimes connected and they were likely made by the same bilaterian animal, representing locomotion (repichnia), resting (cubichnia/domichnia), and undermat mining behaviors (fodichnia), respectively. The horizontal burrows, relatively large for the time period (up to ~1 cm in diameter) and preserved in full relief, are the most commonly encountered variant of *L. trevallisi* morphology (Chen et al., 2013a,b). *L. trevallisi* burrows occur exclusively within clayey and silty crinkled microlaminated layers that are interpreted as the remnants of amalgamated microbial mats (Chen et al., 2013a; Meyer et al., 2014b). These microbial mats were ubiquitous during the Ediacaran Period, often sealing the sediment from geochemical exchange with the overlying water column (Duda et al., 2014; Gingras et al., 2011; Tarhan et al., 2013; Zakrevskaya, 2014). The high bedding-plane bioturbation densities and close association of *L. trevallisi* burrows with microbial mats implies that the burrowers were actively moving through the mats, possibly exploring them for oxygen and nutrient resources.

The behavior represented by these traces is often obscure, because the burrow networks frequently have a vertical component (taking them away from the exposed plane of preservation), and are thus hidden within the sediment. Hence, an analytical technique is needed to image the trace fossils *in situ* and in three dimensions within their matrix. Targeted petrographic thin sections were of limited utility in earlier *L. trevallisi* studies due to their two-dimensional nature and limited coverage (figs. 3 and 4 in Meyer et al., 2014b). Serial grinding through a hand sample has been used before to examine trace fossils, but this can be time consuming and ultimately destroys the fossil material (Bednarz and McIlroy, 2009; Sutton et al., 2001). Magnetic resonance imaging (MRI) analysis has also been used to analyze trace fossils, but requires a sufficient amount of porosity that the carbonate matrix of *L. trevallisi* lacks.

The use of X-ray computed tomography (CT) and microcomputed tomography (microCT) has been growing (Abel et al., 2012) and has proven to be useful for non-invasive examination of the interior of vertebrate fossils (Maisano et al., 2006) as well as some soft-bodied fossil material (Sutton et al., 2001); and more recently Ediacaran body fossils (Hagadorn et al., 2006; Schiffbauer et al., 2012; Meyer et al., 2014a; Wan et al., 2014). This analytical method has thus far been used only a few times to examine trace fossils (Meyer and Polys, 2015; Parry et al., 2015; Yaqoob et al., 2015), and the prospects for the field of ichnology are extremely promising. *L. trevallisi* fossils are large enough and have sufficient compositional contrast (relative to the matrix) for CT and microCT analysis (Meyer and Polys, 2015; Yaqoob et al., 2015). Hence, using this novel fossil processing technique, this research addresses the following questions: (1) Can *L. trevallisi* fossils be virtually extracted from their matrix? (2) Can the amount of bioturbation of the traces be quantified? and (3) What relationships did the *L. trevallisi* trace makers have with the sediments?

2. Geological setting

The geological setting and stratigraphic framework of the Dengying Formation (Fig. 1) in the Yangtze Gorges was presented in detail by Chen et al. (2013a,b) and Meyer et al. (2014b). To summarize, the Dengying Formation overlies the early-middle Ediacaran Doushantuo Formation (635–551 Ma) and underlies early Cambrian Yanjiahe Formation (Dong et al., 2009; Jiang et al.,

2012). The Dengying Formation records the latest ~10% of the Ediacaran Period in South China, but it can have up to three times the thickness of the underlying Doushantuo Formation, which records the preceding 90% (Jiang et al., 2011; Zhou et al., 2017). The Dengying Formation was deposited on a shallow water carbonate platform, and its age is constrained to 551–541 Ma (Condon et al., 2005; Jiang et al., 2009; Zhu et al., 2009). The Dengying Formation is divided into three units, in order of ascending age: the Hamajing, Shibantan, and Baimatuo members (Fig. 1B).

The samples analyzed in this work were collected from the Shibantan Member. This is the most fossiliferous member of the Dengying Formation and contains numerous body and trace fossils. Body fossils include *Vendotaenia* (Anderson et al., 2011), *Paracharnia* (Sun, 1986), *Yangtziramulus* (Shen et al., 2009; Xiao et al., 2005), *Curviacus* (Shen et al., 2017), *Pteridinium* and *Rangea* (Chen et al., 2014), as well as trace fossils such as *Palaeophycus/Planolites*, *Helminthoidichnites*, and *Torrowangea* (Weber et al., 2007; Zhao et al., 1988). The Shibantan Member at the collection site (Fig. 1C and D) is composed of dark gray, thin-bedded, bituminous limestone likely deposited in a shallow subtidal setting. Layers exhibiting cross stratification and rip-up clasts are rare but present, indicating that episodic high-energy events, such as storms, affected the depositional environment (examples of these can be seen in fig. 2E and F of Meyer et al., 2014b). Crinkled microlaminae consisting of organic-rich, calcareous clays and silts are very common, and are often intercalated with thin limestone layers of intraclastic, peloidal, and oolitic packstone and grainstone (Fig. 1B). These crinkled microlaminae are interpreted as microbial mats that trapped silts/clays and were subsequently cemented by diagenetic calcite (Chen et al., 2013a,b; Meyer et al., 2014b). The intraclastic limestone layers range from 0.5 to 20 mm thick, consisting of fine-grained (~50–100 μm) peloidal and oolitic packstone and grainstone. The microlaminated layers are 0.1–2 mm thick and contain more abundant clays and silts compared to the intraclastic limestone layers. Some clayey layers appear to be much thicker, but these are actually many, tightly packed clayey laminae (Fig. 1B). *Lamonte trevallisi* fossils occur exclusively in the microlaminated layers.

3. Methods and materials

The analyzed hand samples, Lt1 and Lt2 (Fig. 2), were collected from a quarry near Wuhe in the Yangtze Gorges area (30° 46'51.61" N, 111°02'24.96" E) where the Shibantan Member is quarried as a raw material for construction purposes. The hand samples were collected as float from the top of the northern most quarry wall (Fig. 1D), ~70 m above the base of the Shibantan Member. The hand samples were selected for their prominent *Lamonte trevallisi* traces, which were partially exposed on their surfaces; and their sizes, which made them appropriate for use with the CT scanner. These trace fossils and associated hand samples have been deposited in the Virginia Polytechnic Institute and State University Geoscience Museum (VPIGM).

3.1. MicroCT analysis of Lt1

Lt1 (VPIGM-4696) was scanned via microCT (Figs. 3 and 4) using a Bruker SkyScan1173 at Micro Photonics in Allentown, PA, USA. Only part of the total hand sample was scanned (Fig. 2A–D). A Hamamatsu flat panel X-ray source operating at 130 kV and 0.61 mA with no X-ray prefilter was employed. An empty container wedge was used. Slice thickness corresponds to one line in a CCD image intensifier imaging system, with a source-to-object distance of 251 mm, resulting in 0.05 mm interslice spacing. For each 2240 × 2240 pixel slice, 1800 views were acquired with 10 sam-

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