Accepted Manuscript

Journal of the Geological Society

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DOI: https://doi.org/10.1144/jgs2020-135

To access the most recent version of this article, please click the DOI URL in the line above.

Received 13 July 2020
Revised 4 September 2020
Accepted 7 September 2020

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The Shibantan Lagerstätte: Insights into the Proterozoic-Phanerozoic transition

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Abstract: The Shibantan Lagerstätte (551–543 Ma) in the Yangtse Gorges area in South China is one of the best-known examples of terminal Ediacaran fossil assemblages preserved in marine carbonate rocks. Taxonomically dominated by benthic organisms, the Shibantan Lagerstätte preserves various photoautotrophs, biomineralizing tubular fossils, Ediacara-type macrofossils (including rangeomorphs, arboreomorphs, erniettomorphs, palaeopascichnids, a possible dickinsoniomorph, the mobile bilaterian *Yilingia*, and soft-bodied tubular fossils), abundant ichnofossils, and a number of problematic and dubious fossils. Shibantan fossils provide intriguing insights into ecological interactions among mobile bilaterians, sessile benthic Ediacara-type organisms, and microbial mats, thus offering important data to test various hypotheses accounting for the decline of the Ediacara biota and the concurrent expansion of bilaterian bioturbation and mobility across the Proterozoic-Phanerozoic transition.
Introduction

The terminal Ediacaran stage (TES, ca. 550–539 Ma; Xiao et al. 2016; Xiao & Narbonne 2020) sits at the junction between the Proterozoic and Phanerozoic eons. Thus, it is pivotal in illuminating the Proterozoic-Phanerozoic transition or PPT (Schiffbauer et al. 2016; Darroch et al. 2018; Muscente et al. 2018; Tarhan et al. 2018). As appearing in the fossil record, the TES is characterised by the decline of the Ediacara biota—which is an assemblage of soft-bodied macrofossils and an emblem of the late Ediacaran Period in ca. 575–539 Ma), and the concurrent expansion of biomineralizing animals and mobile bilaterians, both of which exploded during the ensuing Cambrian Period. A number of hypotheses have been proposed to account for the accelerated diversification of animals across the PPT as a result of genetic-developmental innovations, environmental changes, and ecological interactions (Erwin & Valentine 2013). Some of these hypotheses can be directly tested against the fossil record and are relevant to this review. These include (1) the cropping/predation hypothesis that ecological interactions, particularly grazing and predation, triggered a cascade of positive ecological feedback loops that led to the diversification of biomineralizing animals (Stanley 1976; Vermeij 1989); (2) the savannah hypothesis that heterogenous distribution of food resources (e.g., provided by sessile epibenthic Ediacara-type organisms as opposed to microbial mats) stimulated the rise of mobile bilaterian animals that exploited such resources (Budd & Jensen 2017); (3) the dynamic redox hypothesis that spatially heterogeneous and temporally dynamic redox conditions motivated the rise of mobile bilaterians (Wood & Erwin 2018; Xiao et al. 2019).

The TES fossil record is critical in assessing the hypotheses listed above. TES fossil assemblages have been reported from numerous successions around the world (see review in Xiao & Narbonne 2020). Most of these assemblages are preserved in siliciclastic rocks. The TES Shibantan Lagerstätte, which is the focus of this review, is unusual in preserving
macroalgae, Ediacara-type fossils, and abundant trace fossils in a carbonate facies. The Shibantan Lagerstätte, therefore, offers a unique perspective on the PPT and a comparative analog of the Phanerozoic fossil record, which is largely hosted in carbonate facies.

**Stratigraphy, depositional environment, and age constraints**

Ediacaran strata in the Yangtse Gorges area consist of the Doushantuo and Dengying formations (Fig. 1). The Doushantuo Formation consists of a mixture of black shales and carbonate rocks. At Wuhe where the Shibantan Lagerstätte is being excavated, the Dengying Formation consists of three members (Chen et al. 2014; Meyer et al. 2014). The Hamajing Member consists of ~20 metres of light grey peritidal dolostone, with tepee structures and karstification features. The Shibantan Member consists of 100–150 metres of dark grey, thin-bedded, laminated micritic, peloidal, and intraclastic bituminous limestone with diagenetic chert nodules. Sedimentary structures are dominated by fine and crinkled laminae, although hummocky cross beds, rip-up clasts, and graded beds are common (Zhao et al. 2013; Meyer et al. 2014; Xiao et al. 2020a). The overlying Baimatuo Member consists of ~100 metre of light grey massive peritidal dolostone, characterised by abundant dissolution vugs and breccia (Meyer et al. 2014). The Baimatuo Member is unconformably overlain by the Yanjiahe Formation, which contains basal Cambrian microfossils (Dong et al. 2009; Ahn & Zhu 2017; Guo et al. 2020; Shang et al. 2020) and the basal Cambrian negative carbon isotope excursion or BACE (Jiang et al. 2012; Ahn & Zhu 2017).

In South China, the Dengying Formation represents two and a half transgression-regression sequences (Ding et al. 2019b), but in the Yangtse Gorges area the most prominent subaerial exposure surfaces are recognised in the lower Hamajing and upper Baimatuo members, both of which are also characterised by wide distribution of peritidal sedimentary structures such as tepees, dissolution vugs, karstification structures, and possible anhydrite
pseudomorphs (Duda et al. 2015; Cui et al. 2019; Ding et al. 2019c). The intervening Shibantan Member in the Yangtse Gorges area is interpreted to have been deposited in subtidal environments, probably between fair-weather and storm wave bases, given the occurrence of hummocky cross beds, columnar stromatolites, rip-up clasts, and graded beds that are interpreted as tempestite deposits (Xiao et al. 2005; Zhao et al. 2013; Duda et al. 2014; Meyer et al. 2014; Xiao et al. 2020a).

The fossiliferous Shibantan Member in the Yangtse Gorges area was probably deposited in locally oxic environments against the backdrop of a global expansion of oceanic anoxia. Redox-sensitive trace elements and uranium isotopes suggest a global expansion of anoxic seawaters in the TES (Evans et al. 2018; Tostevin et al. 2018; Wei et al. 2018a; Zhang et al. 2018). It is estimated that at least 20% of global ocean floor was bathed in anoxic waters in the TES (Tostevin et al. 2018; Zhang et al. 2018), as opposed to about 0.1% in modern oceans (Helly & Levin 2004). Local redox proxies, however, indicate that the Shibantan Member in the Yangtse Gorges area was deposited in highly dynamic and episodically oxic seawaters (Duda et al. 2014). For example, Shibantan Member limestone is characterised by negative cerium anomalies (Duda et al. 2014; Wei et al. 2018b) and relatively low Fe_{carb} contents (10^{1.2} ppm) (Ding et al. 2019a), indicating oxic benthic environments, which are ecologically relevant because, as shown below, most Shibantan fossils represent benthic organisms.

The Shibantan Lagerstätte is geochronologically constrained between ~551 Ma and ~543 Ma (Fig. 1). The maximum age constraint comes from a 551.1±0.7 Ma ash bed from the uppermost Miaohé Member at the Jiuqunao section in the Yangtse Gorges area (Condon et al. 2005). The Miaohé Member is correlated with the upper part of Member IV of the Doushantuo Formation (Xiao et al. 2017; Zhou et al. 2017). Alternatively, it is regarded as a distinct lithostratigraphic unit below or equivalent to the basal Shibantan Member of the
Dengying Formation (An et al. 2015). Regardless, the ~551 Ma age provides a maximum age constraint for the Shibantan Lagerstätte. The minimum age constraint comes from a 543.4±3.5 Ma tuffaceous layer in the overlying Baimatuo Member in the Yangtse Gorges area (Huang et al. 2020).

**Fossils in the Shibantan Lagerstätte**

**Defining the Shibantan Lagerstätte**

Chen et al. (1981) first introduced the Xilingxia Fauna, referring to the tubular fossil *Sinotubulites* from dolostone of the Dengying Formation (apparently belonging to the lower Baimatuo Member) as well as other fossils presumably from the Shibantan Member and the early Cambrian Tianzhushan Member in the Yangtse Gorges area. Subsequently, the Xilingxia Biota was used by various authors to refer to fossil assemblage in the Shibantan and/or Baimatuo members in the Yangtse Gorges area (Ding et al. 1992; Wang et al. 1998; Zhu 2010). In addition, Sun et al. (2000) also proposed the Xilingxia System as a regional stratigraphic term roughly equivalent to the entire Ediacaran System. To avoid confusion, we follow Zhou et al. (2019) to refer to the fossil assemblage preserved in limestones of the Shibantan Member in the Yangtse Gorges area as the Shibantan Lagerstätte/biota. The Miaohe biota, also in the Yangtse Gorges area, is slightly older than the Shibantan biota. These two biotas are also taphonomically and taxonomically distinct: the Miaohe biota is dominated by macroalgae preserved as carbonaceous compressions in siliceous and carbonaceous shales (Xiao et al. 2002; Ye et al. 2019), whereas Shibantan fossils are mostly preserved as casts and molds in limestones and are numerically dominated by vendotaenids, ichnofossils, and Ediacara-type fossils.

**Photoautotrophs**
The most common fossils in the Shibantan Member are undoubtedly *Vendotaenia* sp. (Cao & Zhao 1978; Yin & Gao 1995; Mason et al. 2017), which has been interpreted as a macroalga (Gnilovskaya et al. 1988; Xiao & Dong 2006; Bykova et al. 2020) or a giant sulfide oxidizing bacterium (Vidal 1989). Shibantan *Vendotaenia* specimens are ribbon-shaped fossils (Fig. 2a) typically preserved as carbonaceous compressions but sometimes replicated by pyrite and clay minerals (Anderson et al. 2011). They do not have a distinct holdfast structure, do not form microbial mats, are typically randomly distributed on the bedding surface, and can be entirely superimposed above or below larger benthic fossils (Wang et al. 2020), suggesting that they were probably planktonic organisms and thus were more likely algae than sulfide oxidizing bacteria unless the water column was euxinic.

Several dichotomously and trichotomously branching fossils may also represent algal thalli (Fig. 2b–c). They are somewhat similar to the problematic fossil *Yangtziramulus zhangi* (see below), except that they do not form massive clusters. Unfortunately, the specimens at hand are few and incompletely preserved. They are tentatively regarded as benthic algae, but we note that they may be related to *Yangtziramulus*.

*Flabellophyton typicum* (Fig. 2d), a probable macroalgal fossil consisting of a globose holdfast and a splay of bundled filaments, has been reported from the Shibantan Member (Wan et al. 2020). This species is also present in the early Ediacaran Lantian Formation in Anhui Province of South China (Wan et al. 2020) and the Ediacara Member of the Rawnsley Quartzite Formation, Flinders Ranges, South Australia (Xiao et al. 2020b).

Chert nodules in the Shibantan Member contain three-dimensionally preserved spheroidal and filamentous microfossils, including *Oscillatoriopsis obtusa* (Fig. 2e) (Yin & Gao 1995; Ding et al. 2019a). The phylogenetic affinities of these microfossils are uncertain, although similar forms are typically interpreted as photoautotrophs such as photosynthetic eukaryotes and cyanobacteria.
**Biomineralizing tubular fossils**

Silicified tubular fossils from the Dengying Formation in the Yangtse Gorges area were first reported by Chen and Wang (1977), who initially placed these fossils under an open nomenclature *Cloudina* sp. but subsequently described them as *Sinotubulites baimatuoensis* Chen et al. (1981). According to Chen and Wang (1977), these fossils came from thick-bedded dolostone in the uppermost “middle member” of the Dengying Formation, which would be part of the Baimatuo Member dolostone. Chen et al. (2013) indicated that *Sinotubulites baimatuoensis* ranges from the upper Shibantan to lower Baimatuo members in the Yangtse Gorges area (their fig. 1b), and Chen et al. (2016) illustrated both *Sinotubulites baimatuoensis* and *Cloudina* sp. in thin sections from the middle Shibantan Member in the Yangtse Gorges area, but a formal description of these tubular fossils from the Shibantan Member has not been published. Recently, Liang et al. (2020) described both *Sinotubulites* and *Cloudina* from the basal Baimatuo Member in the Yangtse Gorges area (Fig. 2f). Therefore, both *Sinotubulites* and *Cloudina*, which have been widely regarded as weakly biomineralizing animals (Chen et al. 2008; Wood et al. 2017; but see Yang et al. 2020), are certainly present in the Baimatuo Member and likely also in the Shibantan Lagerstätte.

**Non-biomineralizing Ediacara-type macrofossils**

What makes the Shibantan Lagerstätte important is the unusual preservation of non-biomineralizing Ediacara-type macrofossils in limestones. Most Ediacara-type macrofossils are preserved in siliciclastic rocks (Fedonkin et al. 2007). Preservation in carbonate rocks is extremely rare (Grazhdankin et al. 2008; Chen et al. 2014). Thus, the Shibantan Lagerstätte provides a unique perspective on the palaeoecology and taphonomy of Ediacara-type fossils.
The first Ediacara-type fossil reported from the Shibantan Member was *Charnia dengyingensis* (Ding & Chen 1981), later transferred to *Paracharnia dengyingensis* (Fig. 3a) and originally interpreted as a pennatulid cnidarian (Sun 1986). Since the 2010s, systematic excavation of the Shibantan Member in the Yangtze Gorges area has recovered a number of Ediacara-type taxa (Chen *et al.* 2014). Some of them have been described in detail, including several species of *Arborea* (*A. arborea, A. denticulata*, and *Arborea* spp. A and B of Wang *et al.*, 2020; Fig. 3b–d), the non-biomineralizing annulated tubular fossil *Wutubus annularis* (Fig. 3e) (Chen *et al.* 2014), the segmented trilobate bilaterian *Yilingia spiciformis* (Fig. 3f) (Chen *et al.* 2019), and several palaeopascichnid taxa (Fig. 4d–e) including *Curviacus ediacaranus* (Shen *et al.* 2017). Others are yet to be described systematically but can be generally identified at the genus or higher taxonomic levels, including the organ-taxa *Aspidella* (Fig. 4a–b) and *Hiemalora* (Fig. 4c) (Chen *et al.* 2014; Shao *et al.* 2019), *Charnia* (Fig. 4f), *Pteridinium* (Fig. 5a), *Rangea* (Fig. 5b), unnamed charnids (Fig. 5c–e), and a partially preserved specimen of possible dickinsoniomorph affinity (Fig. 5f). Overall, we estimate that there are about 20 morphospecies representing arboreomorphs, erniettomorphs, rangeomorphs (including both rangids and charnids), palaeopascichnids, bilaterians, a possible dickinsoniomorph, and other miscellaneous morphogroups.

Most Ediacara-type fossils in the Shibantan Lagerstätte are long-ranging genera such as *Arborea, Aspidella, Charnia, Hiemalora, Pteridinium*, and *Rangea* (Xiao & Laflamme 2009). Given its age constrained between 551 Ma and 543 Ma, the Shibantan Lagerstätte is considered by most researchers as part of the TES-aged Nama assemblage (Xiao & Laflamme 2009; Boag *et al.* 2016; Muscente *et al.* 2019), although Laflamme *et al.* (2018; p. 324) regarded it as an example of the 558–550 Ma White Sea assemblage (Grazhdankin 2014). If one accepts An *et al.*’s (2015) correlation, the Shibantan Lagerstätte is stratigraphically close to the 551 Ma ash horizon from the Miaohe Member, and may be
either one of the oldest examples of the Nama assemblage, one of the youngest examples of the White Sea assemblage, or a bridge between these two assemblages. Regardless, the Shibantan Lagerstätte records the youngest occurrence of *Arborea* (Fig. 3b–d) and dickinsoniomorphs (Fig. 5f) known to date. Indeed, some fossils may be identified to genera previously only known from the Avalon assemblage (e.g., Fig. 5c–e, which are somewhat similar to *Frondophyllas* in general morphology and poorly constrained primary branches, but preserves rotated and furled primary and secondary branches) and would greatly extend the younger limit of their stratigraphic ranges.

On-going research of Ediacara-type fossils in the Shibantan Lagerstätte is in progress. Much remains to be learned about the full taxonomic diversity, fossil associations, paleocommunity structures, and similarity to and difference from other Ediacara-type biotas. The strongly preferred orientation of some Shibantan fossils, including *Wutubus* (Chen et al. 2014) and *Arborea* (Fig. 5e) (Wang et al. 2020), means that they were tethered to the substrate and had not been transported, thus ideal for paleocommunity analysis. Preliminary data indicate that Ediacara-type fossils are most abundant and diverse on a fossiliferous bed near the base of the Shibantan Member, where *Charnia*, *Hiemalora*, *Yilingia*, *Wutubus*, and *Aspidella* occur on the same bedding surface. Whereas Ediacara-type body fossils continue to exist upsection and they can co-exist with trace fossils in rare circumstances (e.g., Fig. 6h), they become rare in the lower Shibantan Member (where *Yangziramulus*-like fossils are abundant) and the middle Shibantan Member (where trace fossils are abundant and *Cloudina-Sinotubulites* first appear) (Fig. 1b) (Chen et al. 2016). This stratigraphic succession is consistent with the Shibantan Lagerstätte being a bridge between the White Sea and Nama assemblages, and brings into sharp focus the hypothesized taxonomic turnover between these two assemblages (Darroch et al. 2018) and the debated nature of the Cambrian explosion (Wood et al. 2019).
**Ichnofossils**

Dengying Formation ichnofossils were briefly illustrated and described in Tang *et al.* (1978) and Chen *et al.* (1981). Weber *et al.* (2007) illustrated several simple ichnofossils from the Dengying Formation, including *Helminthoidichnites*, *Torrowangea*, and *Palaeophycus*, but detailed stratigraphic information and systematic description were not provided.

Systematic excavation and description of Shibantan ichnofossils started in the 2010s. Several studies have quantified the bioturbation intensity and documented strong palaeoichnological evidence for animal interactions with microbial mats. The Shibantan Lagerstätte is distinct from other Ediacaran Lagerstätten in the abundance of ichnofossils (Fig. 6a–b). Meyer *et al.* (2014) and Meyer *et al.* (2017) estimated that bedding-plane bioturbation intensity (i.e., percentage of bedding plane area covered by trace fossils) is 20–40% in ichnofossiliferous beds, although vertical bioturbation intensity is low at ~5%. Chen *et al.* (2013) and Meyer *et al.* (2014) described a compound ichnofossil (*Lamonte trevallis*; Fig. 6c), consisting of bilobed horizontal tunnels, surface tracks/trails, and vertical traces that represent the behaviours of under-mat feeding, epibenthic locomotion, and temporary dwelling or resting, respectively. Another Shibantan ichnofossil (Fig. 6d), as yet unnamed, also consists of trackways in association with burrows, possibly produced by a bilaterian animal with paired appendages (Chen *et al.* 2018b). Chen *et al.* (2018a) illustrated a tadpole-like ichnofossil consisting of a spherical “head” connected with a tapering tail (Fig. 6e), interpreted as vertical and horizontal burrows, respectively, produced by bilaterian animals burrowing into and out of microbial mats. *Yichnus levis*, consisting of short and uniserially aligned segments of horizontal burrows (Fig. 6f), was also produced by bilaterian animals that repeatedly burrowed into microbial mats to exploit oxygen and food (Xiao *et al.* 2019).
Most trace fossils are demonstrably associated with microbial mats, as confirmed by thin section observations (Chen et al. 2013; Meyer et al. 2014; Chen et al. 2018a; Xiao et al. 2019).

A number of Shibantan ichnofossils remain to be studied in detail but have the potential to illustrate the behaviours and ecological interactions of TES animals. For example, a mortichnial trail preserved as a semi-relief is connected with a body fossil of *Yilingia spiciformis* preserved as a full-relief cast (Fig. 6g; see also Fig. 3f) (Chen et al. 2019); this association helps to establish a link between a group of as yet unnamed ichnofossils and a specific taxon of trilobate and segmented bilaterian animal (Fig. 3f) and to understand its locomotion behaviours. As another example, *Streptichnus* burrows are found in the Shibantan Member in close association with a puckered *Aspidella* holdfast (Fig. 6h); unfortunately, because this specimen is not stratigraphically oriented, we are unable to determine whether the *Streptichnus* burrows are stratigraphically above, below, or penetrate through the *Aspidella* holdfast. If the exact relationship between *Streptichnus* and *Aspidella* can be resolved with additional analysis of stratigraphically oriented specimens, we can determine whether such relationship represents grazing, foraging, predation, or scavenging behaviours of TES animals (Gehling & Droser 2018), thus providing fossil evidence to test the savannah hypothesis (Budd & Jensen 2017).

**Problematic and dubious fossils**

Xiao et al. (2005) and Shen et al. (2009) described the problematic fossil *Yangtziramulus zhangi* from the lower Shibantan Member in the Yangtse Gorges area, and Chen et al. (2016) regarded this taxon as a biostratigraphic index fossil for regional stratigraphic correlation. This fossil was described as a branching system preserved on the bedding surface. The branches are crosscut by stylolites and hence cannot be weathering
structures. They were interpreted as representing vertical walls imbedded in thin layers of sediment and apparently connected by roof and floor walls, thus forming distally open tubes. The ecology of *Yangtziramulus zhangi* was said to be “consistent with osmoheterotrophy or saprotrophy, ecologically analogous to modern fungi” (Xiao et al. 2005). Recent excavation revealed a large number of similar branching structures, some with no roof or floor walls (Fig. 7a), and others with cross-bars connecting neighboring branches and arching toward branching points (Fig. 7b–c). Like *Yangtziramulus zhangi*, these structures consist of two interdigitating and reciprocal components that ramify and diverge at opposite directions: the relatively narrower branches and the relatively wider digitate elements that sometimes bear arching cross-bars (Fig. 7a–c). The digitate elements superficially resemble crustose lichens. The growth of these structures is dictated by the digitate elements, rather than the branches, as evidenced by crustose growth laminae that distally cap the digitate elements (Fig. 7b, arrows). In some cases, *Yangtziramulus*-like forms intergrade to structures with cross-bars and to structures with Liesegang-like rings but no branches (Fig. 7d). Although we are convinced that these structures were formed at the time of host rock deposition or shortly after, we are uncertain whether they represent large-scale microbial structures, eukaryote aggregates (e.g., aggregating *Dictyostelium* cells, which are orders of magnitude smaller), crustose fungi or lichens, or some sort of unusual abiotic structures (e.g., Liesegang or viscous fingering patterns; Li et al. 2009).

Mason *et al.* (2017) illustrated several fossil forms from the Shibantan Member. Two are worth commenting on. One of them was described as three-dimensional discoidal fossils, with depositional laminae go unimpededly from the matrix to the discoid (fig. 7 of Mason *et al.*, 2017). Mason *et al.* (2017) interpreted them as “relatively long-lived organic structures that re-colonised successive layers of carbonate mud on the sea bed.” Although we cannot rule out a biological origin as championed by Mason *et al.* (2017), we also note that the
Shibantan Member is littered with carbonate and chert concretions of various size and shapes, and the relationship between the depositional laminae within and outside of the concretions can be variable depending on the relative timing of concretion formation and compaction (Schwid et al. 2020).

Another interesting form described in Mason et al. (2017) is “radiating branching strands”, which consist of occasionally bifurcating filaments (preserved as grooves on the bedding surface) that are 0.5–1 mm wide, separated from each other by up to 2 mm, and are bundled to form splays. We have also recovered Shibantan specimens with filaments that are 0.2–0.5 mm in width, 1.0–2.0 mm in spacing, and organised more or less concentrically, although some do crosscut or overlap (Fig. 7e–f). Filaments of similar thickness are common in Ediacaran successions. Some of them are found to connect frondose fossils and are interpreted as stolonic structures (Liu & Dunn 2020), whereas others are bundled and are interpreted as macroalgae (Xiao et al. 2020b). It is uncertain whether the Shibantan filaments are related to those described in Liu and Dunn (2020) and Xiao et al. (2020b). Indeed, given their simple morphologies, microbial and abiotic origins cannot be ruled out for the Shibantan filamentous structures.

Somewhat similar to the filamentous structures are conchoidal structures that occur on the bedding surface and consist of stacked arches, which are 0.5–1.0 mm in width and 3.0–9.0 mm in spacing (Fig. 7g). The arches are curved toward the same direction, and outer (and presumably younger in ontogenetic terms if they are biogenic structures) arches are stacked upon, but do not cross-cut, inner (and presumably older) ones. In cross section perpendicular to the bedding surface, these arches penetrate depositional laminae of ~1 mm in thickness. Like the filamentous structures, the origin of the conchoidal structures is enigmatic. A microbial origin is possible, but an abiotic origin related to the advancement and retreat of
ground water front or Ostwald-Liesegang-type diffusion-precipitation cannot be excluded. These structures are best regarded as dubious fossils at the present.

**Palaeoecology**

The Shibantan Lagerstätte is taxonomically dominated by mobile and sessile benthos. Mobile animals are represented by various ichnofossils (Fig. 6) and *Yilingia spiciformis* (Fig. 3f). Sessile organisms include *Arborea, Flabellophyton, Pteridinium, Rangea*, and charnids. Some arboreomorphs and rangeomorphs are tethered to holdfasts and preserved with a preferred orientation (Fig. 5e), suggesting that these erect benthic organisms were felled by water currents but had not been transported from where they lived. These fronds also show similar taphonomic grades, suggesting little time averaging. Thus, Shibantan fossils offer opportunities for synecological analysis of Ediacaran paleocommunities.

The Shibantan Lagerstätte preserves palaeontological evidence for ecological interactions among different organisms. Importantly, there is abundant evidence for bilaterian-mat interactions, as demonstrated by thin section analysis of trace fossils in association with crinkled microlaminae interpreted as microbial mats (Meyer *et al.* 2014; Chen *et al.* 2018a; Xiao *et al.* 2019). Such interactions offer potential evidence for the cropping hypothesis (Stanley 1976). Similarly, the encounter between *Streptichnus* ichnofossils and an *Aspidella* holdfast (Fig. 6h), if not accidental, may offer direct evidence for grazing, foraging, preying, or scavenging upon Ediacara-type organisms by mobile bilaterian animals, offering evidence for the savannah hypothesis (Budd & Jensen 2017).

**Summary and prospects**

The 551–543 Ma Shibantan Lagerstätte is a rare example of TES fossil assemblages hosted in limestones that were deposited in shallow marine environments between fair
weather and storm wave bases. It contains various photoautotrophs (e.g., vendotaenids, macroalgae, and cyanobacteria), biomineralizing tubular fossils (\textit{Cloudina} and \textit{Sinotubulites}), Ediacara-type macrofossils (e.g., rangeomorphs, arboreomorphs, erniettomorphs, palaeopascichnids, a possible dickinsoniomorph, the mobile bilaterian \textit{Yilingia}, and soft-bodied tubular fossils), abundant ichnofossils that are typically preserved in close association with microbial mats, and a number of problematic and dubious fossils.

The Shibantan Lagerstätte is either among the oldest examples of the Nama assemblage (550–539 Ma) or the youngest example of the White Sea assemblage (558–550 Ma). In terms of taxonomic richness of Ediacara-type macrofossils, it seems to be intermediate between classical Nama assemblage (e.g., Kuibis and Schwarzrand subgroups in southern Namibia) and White Sea assemblage (e.g., Ediacara Member in South Australia). In terms of trace fossil diversity and abundance, it is much greater than the White Sea assemblage and comparable to the Nama assemblage. The overall pattern is consistent with the hypothesized decline of sessile Ediacara-type macro-organisms concomitant with an ecological expansion of mobile and bioturbating animals (Darroch \textit{et al.} 2018; Wood \textit{et al.} 2019).

The different trajectories of late Ediacaran body and trace fossils, if proven to be true, have fundamental meanings. One possibility is that locomotion may have played a role in differentiating the evolutionary fates of different Ediacaran organisms. The Ediacara biota, largely consisting of organisms (including stem-group animals or even stem-group bilaterians) with limited mobility, may have faded out in the TES. Highly mobile bilaterian animals, on the other hand, arose in abundance and diversity during the same time interval, as evidenced by the trace fossil record. The ecological and environmental underpinnings of the contrasting evolutionary trajectories, however, are not fully understood but the savannah hypothesis may offer some insights. This hypothesis can be further tested by quantitatively documenting the stratigraphic and spatial distribution of trace fossils and Ediacara-type body fossils in the
Shibantan Lagerstätte (e.g., Mitchell et al. 2020), direct evidence for grazing, foraging, predation, and scavenging (e.g., Gehling & Droser 2018), as well as repaired wounds. Positioned at the junction between the Proterozoic and the Phanerozoic, the Shibantan Lagerstätte can illuminate one of the most significant transitions in Earth history and help us to evaluate the relative importance of biotic vs. environmental factors in shaping evolutionary trajectories across the Proterozoic-Phanerozoic transition (Laflamme et al. 2013; Schiffbauer et al. 2016; Smith et al. 2016; Darroch et al. 2018; Muscente et al. 2018).

Acknowledgements We would like to thank Dr. Phil Donoghue for his invitation and encouragement to write this review paper; Xiang Chen, Lin Dong, Kathleen McFadden, Mike Meyer, Jim Schiffbauer, Yefei Shao, Bing Shen, Qing Tang, Bin Wan, Xiaopeng Wang, and many others for field assistance; and Charlotte Kenchington and Frankie Dunn for constructive reviews.

Funding S.X. acknowledges support from the U.S. National Science Foundation (EAR-2021207). Z.C., K.P., C.Z., and X.L. were supported by Chinese Academy of Sciences (QYZDJ-SSW-DQC009, XDB26000000, and XDB18000000) and National Natural Science Foundation of China (41921002).

Box 1. Outstanding questions

(1) How did trace-making animals ecologically interact with Ediacara-type organisms and microbial mats? Is there evidence for grazing, foraging, predation, and scavenging? Is there evidence in support of the cropping and savannah hypotheses?
(2) How are Shibantan species associated with each other in spatial and stratigraphic distribution? Are ichnofossils and Ediacara-type fossils negatively correlated in terms of distribution, species richness, and abundance? Do paleoenvironments play a role in controlling Shibantan fossil distribution?

(3) Are there crown-group bilaterians or even protostomes in the Shibantan Lagerstätte?

(4) What are the phylogenetic affinity of the many problematic fossils such as *Yangtzialamulus*?

(5) Do substrates and lithologies (e.g., carbonate vs. siliciclastics) play a role in controlling the distribution and preservation of Ediacara-type fossils? How does the Shibantan Lagerstätte compare with other Ediacara-type biotas in terms of taxonomic richness, ecological diversity, paleoenvironment, and taphonomy? How does it fit in the big picture of evolutionary dynamics across the Proterozoic-Phanerozoic transition? Is the extinction of Ediacara-type macro-organisms gradual, stepwise, or abrupt in the terminal Ediacaran stage?

References


Figure captions

**Fig. 1.** Geological map and stratigraphic column. (a) Simplified geological map of the Huangling anticline, showing the location of Wuhe (white star) in the Yangtze Gorges area where the Shibantan Lagerstätte is excavated. Inset map shows major tectonic units of China and location of the Huangling anticline (red rectangle). (b) Stratigraphic column of the Ediacaran Doushantuo and Dengying formations in the Yangtze Gorges area, showing approximate fossil distributions, radiometric ages, and the stratigraphic occurrence of the Shibantan Lagerstätte. Radiometric ages from the Doushantuo Formation (including the Miaohe Member), Baimatuo Member, and Shuijingtuo Formation are from Condon *et al.* (2005), Huang *et al.* (2020), and Okada *et al.* (2014), respectively. The alternative correlations of the Miaohe Member with Member IV of the Doushantuo Formation (Xiao *et al*. 2017; Zhou *et al*. 2017) or with the basal Shibantan Member of the Dengying Formation (An *et al*. 2015) are marked by dashed arrows.

**Fig. 2.** Possible photoautotrophs from the Shibantan Lagerstätte (a–e) and cloudinomorphs from the Baimatuo Member in the Yangtze Gorges area (f). (a) *Vendotaenia* sp., interpreted as a possible macroalga. Stratigraphic orientation unknown. Field photograph of a float by S. Xiao. (b) Two specimens of branching fossils, interpreted as possible macroalgae. We note that these specimens, particularly the left specimen, are somewhat similar to *Yangtziramulus zhangi*, although they do not occur in massive clusters as the latter typically does. Bed top view, previously unpublished specimens, photograph by S. Xiao. (c) Magnification of (b, rectangle). (d) *Flabellophyton typicum*, courtesy of Bin Wan and from Wan *et al.* (2020), NIGP-PB22457 (field collection number 15WH-7950), stratigraphic orientation unmarked but probably bed top view. (e) *Oscillatoriopsis obtusa*, courtesy of Lin Dong and from Ding
et al. (2019a). (f) *Cloudina* sp. (white arrows) and *Sinotubulites baimatuoensis* (black arrows), courtesy of Yaoping Cai and Dandan Liang.

**Fig. 3.** Ediacara-type macrofossils from the Shibantan Lagerstätte. (a) *Paracharnia dengyingensis*, Zn F0011 (Hubei Institute of Geology), float with unknown stratigraphic orientation (Sun 1986), photograph by S. Xiao. (b) *Arborea aborea*, from Wang et al. (2020), field specimen, bed top view. (c) *Arborea denticulata*, from Wang et al. (2020), holotype, NIGP-170067, bed top view. (d) *Arborea* sp. A of Wang et al. (2020), with a *Hiemalora*-like holdfast, NIGP-169472, bed sole view. (e) *Wutubus annularis*, from Chen et al. (2014), NIGP-159084, inferred bed top view. (f) *Yilingia spiciformis*, from Chen et al. (2019), holotype, NIGP-166252, bed top view. (b–f) Photographs by Z. Chen.

**Fig. 4.** Ediacara-type macrofossils from the Shibantan Lagerstätte. (a–b) *Aspidella* holdfasts with remnant of stalk. Note pleated structures in a (unknown stratigraphic orientation) characteristic of the puckered taphomorph of Tarhan et al. (2015), and peripherally arranged radial structures in b (bed top view). (c) *Hiemalora pleiomorpha*, from Chen et al. (2014), NIGP-159077, inferred bed top view. (d) *Curviacus ediacaranus*, from Shen et al. (2017), holotype, VPIMG-4675, float with unknown stratigraphic orientation. (e) Unnamed palaeopascichnid, unknown stratigraphic orientation. (f) *Charnia* sp., bed sole view. (a–b, e–f) Previously unpublished specimens. (d) Photograph by S. Xiao, and all others by Z. Chen.

**Fig. 5.** Ediacara-type macrofossils from the Shibantan Lagerstätte. (a) *Pteridinium* sp., from Chen et al. (2014), NIGP-159071, float with unknown stratigraphic orientation. (b) *Rangea* sp. with major primary branches and secondary branches (arrows), from Chen et al. (2014),
NIGP-159074, unknown stratigraphic orientation. (c–e) Unnamed charnids on bed top (c) and bed sole (d–e). Note preferential orientation of the three specimens in (e), where arrows point to discoidal holdfasts. (f) A partially preserved specimen of possible dickinsoniomorph affinity, unknown stratigraphic orientation. (c–f) Previously unpublished specimens. All photographs by Z. Chen.

**Fig. 6.** Ichnofossils from the Shibantan Lagerstätte. (a–b) Field photographs showing high intensity of *Streptichnus* ichnofossils on bed sole. (c) *Lamonte trevallis*, showing a bilobed trail terminated by a circular plug-like structure (arrow) interpreted as a resting or temporary dwelling trace, inferred bed top view. (d) Unnamed compound ichnofossils consisting of trackways and burrows, from Chen *et al.* (2018b), NIGP-166148, bed top view. (e) Unnamed tadpole-like compound ichnofossils consisting of a trail/burrow terminated by a circular plug-like trace (arrows), from Chen *et al.* (2018a), bed sole view. (f) *Yichnus levis*, showing uniserially aligned burrow segments on bed top, from Xiao *et al.* (2019), NIGP-169664. (g) Body fossil of *Yilingia spiciformis* (left) followed by mortichnial trail (right) on bed sole, from Chen *et al.* (2019), NIGP-166253. (h) *Streptichnus* ichnofossils (left) and a puckered taphomorph of *Aspidella* (right), unknown stratigraphic orientation. (c–e, h) Previously unpublished specimens. All photographs by Z. Chen.

**Fig. 7.** Problematic and dubious fossils from the Shibantan Lagerstätte. (a–d) *Yangtziparamus*-like fossils on bed top. Note in (a–c) light-coloured branches and dark-coloured digitate elements bifurcate and diverge in opposite directions, in (b) crustose growth laminae (arrows) distally cap digitate elements (lower central) that overgrows another branching system (upper), in (b–c) digitate elements with cross-bars arching toward
bifurcation points of branches and away from bifurcation points of digitate elements that resemble “stromatolites” on the bedding surface, and in (d) Yangtziramulus-like branching system (left) transitioning into digitate elements with cross-bars (central left) and Liesegang-like rings without branches (upper right). Rectangle in (b) marks area magnified in (c). (e–f) A float slab showing curved and bundled filaments that are largely parallel to one another but occasionally crosscut or overlap. Rectangle in (e) marks area magnified in (f). (g) A float slab showing a conchoidal structure. Pencil = 146 mm in length. American penny = 19 mm in diameter. All bedding surface views. All previously unpublished specimens. All are field photographs taken by S. Xiao.