The Shibantan Lagerstätte: insights into the Proterozoic–Phanerozoic transition

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Abstract: The Shibantan Lagerstätte (551–543 Ma) in the Yangtze 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 photosynthetic, 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.

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The terminal Ediacaran stage (c. 550–539 Ma; Xiao et al. 2016; Xiao and Narbonne in press) sits at the juncture between the Proterozoic and Phanerozoic eons. Thus, it is pivotal in illuminating the Proterozoic–Phanerozoic transition (Schiffbauer et al. 2016; Darroch et al. 2018; Muscente et al. 2018; Tarhan et al. 2018). In the fossil record, the terminal Ediacaran stage is characterized by the decline of the Ediacara biota, which is an assemblage of soft-bodied macrofossils and an emblem of the late Ediacaran Period (c. 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 Proterozoic–Phanerozoic transition as a result of genetic–developmental innovations, environmental changes and ecological interactions (Erwin and 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 heterogeneous distribution of food resources (e.g. provided by sessile ephithetic Ediacara-type organisms as opposed to microbial mats) stimulated the rise of mobile bilaterian animals that exploited such resources (Budd and Jensen 2017); (3) the dynamic redox hypothesis that spatially heterogeneous and temporally dynamic redox conditions motivated the rise of mobile bilaterians (Wood and Erwin 2018; Xiao et al. 2019).

The terminal Ediacaran stage fossil record is critical in assessing the hypotheses listed above. Terminal Ediacaran stage fossil assemblages have been reported from numerous successions around the world (see review by Xiao and Narbonne in press). Most of these assemblages are preserved in siliciclastic rocks. The terminal Ediacaran stage Shibantan Lagerstätte, which is the focus of this review, is unusual in preserving macroalgae, biomineralizing tubular fossils, Ediacara-type fossils and abundant trace fossils in a carbonate facies. The Shibantan Lagerstätte, therefore, offers a unique perspective on the Proterozoic–Phanerozoic transition and a comparative analogue of the Phanerozoic fossil record, which is largely hosted in carbonate facies.

Stratigraphy, depositional environment and age constraints

Ediacaran strata in the Yangtze 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 c. 20 m of light grey peloidal dolostone, with tepee structures and karstification features. The Shibantan Member consists of 100–150 m 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 c. 100 m of light grey massive peloidal dolostone, with alternate dissolution vugs and breccia (Meyer et al. 2014). The Baimatuo Member is unconformably overlain by the Yanjiasset Formation, which contains basal Cambrian microfossils (Dong et al. 2009; Ahn and 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 and Zhu 2017).

In South China, the Dengying Formation represents two and a half transgression–regression sequences (Ding et al. 2019b), but in the Yangtze Gorges area the most prominent subaerial exposure surfaces are recognized in the lower Hamajing and upper Baimatuo members, both of which are also characterized 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. 2019). 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, 2020a; Zhao et al. 2013; Duda et al. 2014; Meyer et al. 2014).

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 terminal Ediacaran stage (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 terminal Ediacaran stage (Tostevin et al. 2018; Zhang et al. 2018), as opposed to about 0.1% in modern oceans (Helly and 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 characterized by negative cerium anomalies (Duda et al. 2014; Wei et al. 2018b) and relatively low Fe$_{\text{carb}}$ contents ($10^3$–$10^5$ 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 c. 551 and c. 543 Ma (Fig. 1). The maximum age constraint comes from a 551.1 ± 0.7 Ma ash bed from the uppermost Miaohe Member at the Jiuqunao section in the Yangtse Gorges area (Condon et al. 2005). The Miaohe 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 c. 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 researchers to refer to the 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 or biota. The Miaohbiota, also in the Yangtse Gorges area, is slightly older than the Shibantan biota. These two biotas are also taphonomically and taxonomically distinct: the Miaoh biota is dominated by macro-algae 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 moulds 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 and Zhao 1978; Yin and Gao 1995; Mason et al. 2017), which has been interpreted as a macroalga (Gnilovskaya et al. 1988; Xiao and 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 probably algae than sulfide-oxidizing bacteria unless the water column was euxinic.

Several dichotomously and trichotomously branching fossils may also represent algal thalli (Fig. 2b and 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*.

*Flabelliphyton 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

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**Fig. 2.** Possible photoautotrophs from the Shibantan Lagerstätte (a–e) and cloudinomorphs from the Baimatuo Member in the Yangtse 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 rectangle in (b). (d) *Flabelliphyton typicum*, courtesy of Bin Wan and from Wan et al. (2020), NIGP-PB22457 (field collection number 15WH-7950), stratigraphic orientation unmarked. (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.
Ediacara Member of the Rawsley 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 and Gao 1995; Ding et al. 2019a). The phylogenetic affinities of these microfossils are uncertain, although similar forms are typically interpreted as photosynthetic eukaryotes and cyanobacteria.

**Biominingeralizing tubular fossils**

Silicified tubular fossils from the Dengying Formation in the Yangtze 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 Yangtze 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 Yangtze 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 Yangtze Gorges area (Fig. 2f). Therefore, both Sinotubulites and Cloudina, which have been widely regarded as weakly biominingeralizing animals (Chen et al. 2008; Wood et al. 2017; but see Yang et al. 2020), are certainly present in the Baimatuo Member and probably also in the Shibantan Lagerstätte.

**Non-biominingeralizing Ediacara-type macrofossils**

What makes the Shibantan Lagerstätte important is the unusual preservation of non-biominingeralizing 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 deningensis (Ding and Chen 1981), later transferred to Paracharnia deningensis (Fig. 3a) and interpreted as a pennatulid cnidarian by Sun (1986). Since the 2010s, systematic excavation and description of Shibantan ichnofossils (Xiao et al. 2020), means that they were tethered to the substrate and had not been transported, and are thus ideal for palaeocommunity 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 coexist with trace fossils in rare circumstances (e.g. Fig. 6h), they become rare in the lower Shibantan Member (where Yangtziarmulus-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 by Yang 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 and b). Meyer et al. (2014, 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 c. 5%. Chen et al. (2013) and Meyer et al. (2014) described a compound ichnofossil (Lamonte trevallia; Fig. 6c), consisting of bilobed
horizontal tunnels, surface tracks or 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 short 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, 2018a; Meyer et al. 2014; 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 terminal Ediacaran stage animals (Box 1). 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 a relationship represents grazing, foraging, predation or scavenging behaviours of terminal Ediacaran stage animals (Gehling and Droser 2018), thus providing fossil evidence to test the savannah hypothesis (Budd and 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 embedded 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 neighbouring branches and arching toward branching
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 going 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-colonized 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 the concretions can be variable depending on the relative timing of concretion formation and compaction (Schwid et al., in preparation).

Another interesting form described by 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 organized more or less concentrically, although some do crosscut or overlap (Fig. 7e and 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 and Dunn 2020), whereas others are bundled and are interpreted as macroalgal (Xiao et al. 2020b). It is uncertain whether the Shibantan filaments are related to those described by Liu and Dunn (2020) and Xiao et al. (2020b). Indeed, given their points (Fig. 7b and 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).

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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 c. 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 a groundwater front or Ostwald–Liesegang-type diffusion–precipitation cannot be excluded. These structures are best regarded as dubious fossils at the present.

Fig. 7. Problematic and dubious fossils from the Shibantan Lagerstätte. (a–d) Yangtziramulus-like fossils on bed top. It should be noted that in (a) to (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 overgrow another branching system (upper), in (b) and (c) digitate elements with cross-bars arch 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) changing 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 is 146 mm in length. US coin is 19 mm in diameter. All bedding surface views. All previously unpublished specimens. All are field photographs taken by S. Xiao.
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 palaeoenvironments 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 affinities of the many problematic fossils such as Yangtzeiramulix?

(5) Do substrates and lithologies (e.g. carbonate versus siliclastic deposits) 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, palaeoenvironment and taphonomy? How does it fit in the wider 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?

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, Flabelfophyton, Pteridinium, Rangea and charniards. Some arboreomorphs and rangeomorphs are taphonomically preserved as burrows and tentacles that are tethered to holdfasts and preserved with a preferred orientation (Fig. 5c), suggesting that these erect benthiic 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 synthesis into the wider picture of evolutionary dynamics across the Proterozoic–Phanerozoic transition. 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. Nicholls et al. 2020), direct evidence for grazing, foraging, predation and scavenging (e.g. Gehling and Droser 2018), and repaired wounds (Box 1). Positioned at the junction between the Proterozoic and the Phanerzoic, the Shibantan Lagerstätte can illuminate one of the most significant transitions in Earth history and help us to evaluate the relative importance of biotic versus environmental factors in shaping evolutionary trajectories across the Proterozoic–Phanerozoic transition (Laflamme et al. 2013; Schiiffbauer et al. 2016; Smith et al. 2016; Darroch et al. 2018; Muscente et al. 2018).

Summary and prospects

The 551–543 Ma Shibantan Lagerstätte is a rare example of terminal Ediacaran stage 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 (Cloudina and Sinotubulites), Ediacara-type macrofossils (e.g. rangeomorphs, arboreomorphs, erniettomorphs, palaeopascichnids, a possible dickinsoniomorph, the mobile bilaterian 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), the youngest example of the White Sea assemblage (558–550 Ma), or a transition between these two assemblages. In terms of taxonomic richness of Ediacara-type macrofossils, it seems to be intermediate between the classical Nama assemblage (e.g. Kuibis and Schwarzrand subgroups in southern Namibia) and White Sea assemblage (e.g. Ediacara Member in South Australia). Its trace fossil diversity and abundance is much greater than that of the White Sea assemblage and comparable with that of 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 et al. 2018; Wood 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 terminal Ediacaran stage. 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.

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Author contributions

S.X.: conceptualization (lead), formal analysis (lead), funding acquisition (lead), investigation (lead), project administration (lead), supervision (lead), writing – original draft (lead), writing – review & editing (lead); ZC: formal analysis (supporting), funding acquisition (supporting), investigation (supporting), project administration (supporting); KP: formal analysis (supporting), funding acquisition (supporting), investigation (supporting), visualization (supporting); CZ: investigation (supporting), Y. conceptualization (supporting), investigation (supporting), project administration (supporting), supervision (supporting).

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