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Dickinsonia from the Ediacaran Dengying Formation in the Yangtze Gorges area, South China

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Abstract

Dickinsonia is an iconic fossil of the Ediacara biota (~575–539 Ma). It was previously known from siliciclastic successions of the White Sea assemblage in Australia, Baltica, and possibly India. Here we describe *Dickinsonia* sp. from the terminal Ediacaran Shibantan Member limestone (ca. 551–543 Ma) of the Dengying Formation in the Yangtze Gorges area of South China. The stratigraphic distribution of Ediacara-type fossils in the Shibantan Member indicates that this biota uniquely preserves both the White Sea and Nama assemblages in stratigraphic succession. The new data presented here suggests that *Dickinsonia* had wider paleogeographic and paleoenvironmental distributions, implying its strong dispersal capability and environmental tolerance.

Keywords: *Dickinsonia*; Shibantan biota; Ediacaran; Yangtze Gorges area; South China

1. Introduction

Macrofossils of the Ediacara biota (~575–539 Ma; Linnemann et al., 2019; Matthews et al., in press) dominated marine benthic communities in the middle to late Ediacaran Period. Most taxa of this diverse, soft-bodied biota have long been considered a phylogenetic conundrum, but some of them are likely metazoans (Fedonkin and Waggoner, 1997; Bobrovskiy et al., 2018; Chen et al., 2019; Evans et al., 2020). Although paleoenvironments play a role in controlling the distribution of Ediacara-type fossils (Gehling and Droser, 2013; Grazhdankin, 2014; Boag et al., 2016), the Ediacara biota has been divided into three successive assemblages of different ages: the Avalon (~571–560 Ma), White Sea (~560–550 Ma), and Nama (~550–539 Ma) assemblages (Waggoner, 2003). However, the dynamics of evolutionary transition among these three assemblages is poorly documented, largely because they are rarely preserved in the same stratigraphic succession to understand how one assemblage progresses to another and whether the transitions are gradual or abrupt. Previous studies have shown that Ediacaran successions in Russia offer an opportunity to investigate the transition from the Avalon to White Sea assemblage (Grazhdankin, 2014), and the Ediacaran Shibantan Member in South China may preserve the transition from the White Sea to Nama assemblage (Xiao et al., 2020b).

Dickinsonia is one of the most recognizable taxa of the Ediacara biota and a potential late Ediacaran index fossil (Muscente et al., 2019). Extensive studies have been con-

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ducted on *Dickinsonia* since its discovery in the 1940s (Sprigg, 1947). There is a general consensus of *Dickinsonia* being a mobile metazoan (Ivantsov and Malakhovskaya, 2002; Gehling et al., 2005; Sperling and Vinther, 2010; Hoekzema et al., 2017; Bobrovskiy et al., 2018; Evans et al., 2019). However, there is little consensus about its exact phylogenetic position within the Metazoa, its growth dynamics, its feeding ecology, and its full environmental and stratigraphic ranges. *Dickinsonia* has been variously interpreted as a relative to ctenophores (Zhang and Reitner, 2006), a placozoan (Sperling and Vinther, 2010), a eumetazoan (Evans et al., 2017), and a bilaterian (Gold et al., 2015). The growth zone of *Dickinsonia* has been hypothesized to be at the anti-deltoidal end (Runnegar, 1982; Gold et al., 2015; Ivantsov et al., 2020) or adjacent to the undivided deltoidal region (Dunn et al., 2017; Hoekzema et al., 2017). In terms of feeding ecology, *Dickinsonia* has been interpreted as a microphagous metazoan with a mouth and a gut (Dzik, 2002) or as an osmotrophic placozoan (Sperling and Vinther, 2010). In terms of environmental and stratigraphic distributions, thus far *Dickinsonia* has only been reported from siliciclastic facies of the White Sea assemblage in Australia (Sprigg, 1947; Gehling and Droser, 2013), Baltica (Keller and Fedonkin, 1977; Grazhdankin, 2014), and possibly in India (Retallack et al., 2021). Here we report a partially preserved specimen of *Dickinsonia* from a limestone facies in the terminal Ediacaran Shibantan Member in the Yangtze Gorges area of South China. Our discovery extends the paleogeographic, paleoenvironmental, and stratigraphic ranges of this genus, and suggests that further investigation of the Shibantan Lagerstätte has the potential to illuminate the evolutionary transition from the White Sea to the Nama assemblage.

2. Geological setting

The terminal Ediacaran Dengying Formation (551–539 Ma) in the Yangtze Gorges area is divided into three units — the Hamajing, Shibantan, and Baimatuo members in ascending order (Fig. 1). The Hamajing and Baimatuo members are both composed of peritidal dolostones, whereas the Shibantan Member consists of subtidal limestones. Ediacara-type macrofossils are confined to the Shibantan Member of the Wuhe section (Chen et al., 2014; Wang et al., 2020; Xiao et al., 2020b).

The Shibantan Member at Wuhe is about 150 m thick. It comprises dark to light grey, medium- to thin-bedded limestones, with intercalated chert bands and chert/calcite concretions. Storm-related deposits, such as hummocky cross-stratification and intraclastic breccias, occasionally occur in the Shibantan Member, indicating depositional environments above the storm-wave base; storm-induced rapid burial also likely facilitated soft-bodied fossil preservation (Xiao et al., 2020a). Dark, organic-rich, crinkled laminae are ubiquitous in Shibantan limestones, and these laminae have been interpreted as fossilized microbial mats (Chen et al., 2013; Xiao et al., 2019). Together with less common stromatolitic structures, the occurrence of laminated microbial mats indicates that Shibantan limestones were deposited in the photic zone. These microbial mats may have also played an important role in the preservation of Ediacara-type macrofossils (Gehling, 1999; Callow and Brasier, 2009; Laflamme et al., 2011; Wang et al., 2020).

The fossiliferous horizons of the Shibantan Member at Wuhe contain a diverse assemblage of macrofossils. Classical Ediacara-type fossils, e.g., *Arborea*, *Rangea*, *Pteridinium*, *Flabellophtyon*, *Hiemalora* (Chen et al., 2014; Wan et al., 2020; Wang et al., 2020; Xiao et al., 2020b) and *Dickinsonia* described herein, are typically found as positive and corresponding negative reliefs. Vendotaenid macroalgae are always preserved as carbonaceous films surrounded by authigenic clay minerals and pyrite (Anderson et al., 2011). Abundant trace fossils which reflect complex behaviors of early metazoans (Chen et al., 2013, 2018, 2019; Meyer et al., 2014; Xiao et al., 2019) and the problematic taxa *Yangtziramulus* (Xiao et al., 2005; Shen et al., 2009) and *Curviacus* (Shen et al., 2017) have also been discovered from the Shibantan Member. Approximate stratigraphic distribution of these fossils was given in Xiao et al. (2020b) and shown in Fig. 1B.

3. Material and methods

The *Dickinsonia* specimen described in this paper was collected from a stratigraphic horizon that is about 1 m above the base of the Shibantan Member at the Wuhe quarry (GPS coordinates 30.789°N and 111.051°E). Both part and counterpart were recovered, but the stratigraphic orientation of the specimen was not marked when it was excavated. The specimen was photographed with a Nikon D810 digital camera. Measurements were obtained from photographs using ImageJ v. 1.52a. The specimen is deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Nanjing, China (NIGP173490).

4. Systematic paleontology

Genus *Dickinsonia* Sprigg, 1947
Type species: *Dickinsonia costata* Sprigg, 1947.

Dickinsonia sp.
(Fig. 2)

2020b dickinsoniomorph – Xiao et al., fig. 5f.

Occurrence: Terminal Ediacaran Shibantan Member, Dengying Formation, Yangtze Gorges area of South China.
Description: The only specimen is incomplete and preserved as a negative relief with a corresponding positive relief. The

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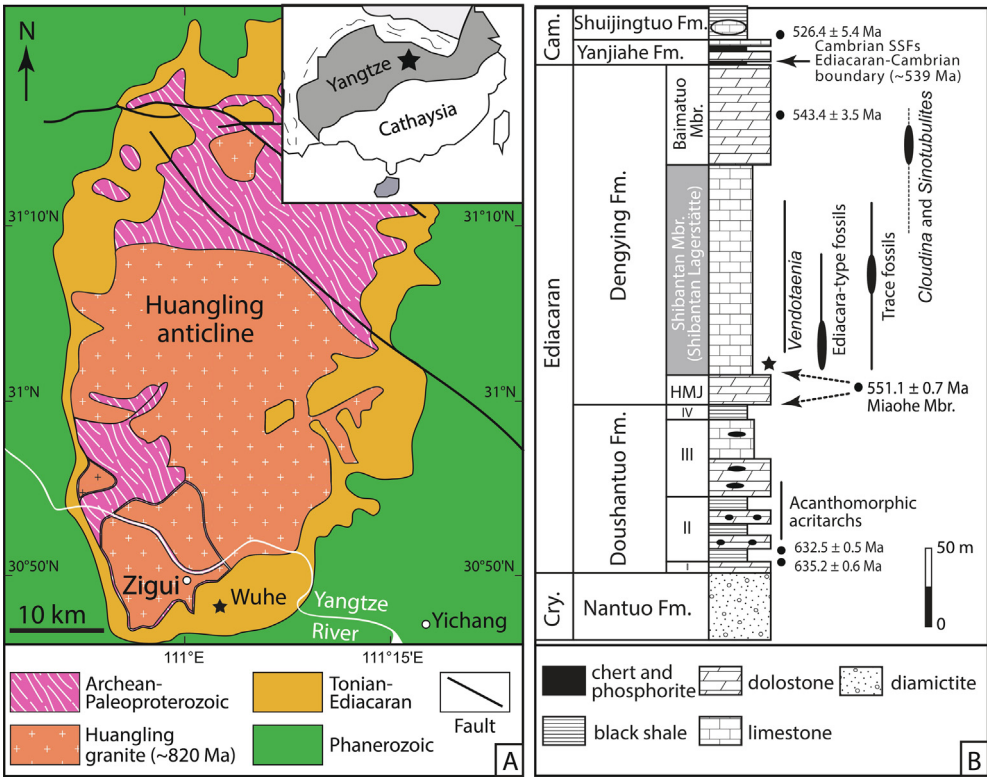

Fig. 1. Geological map and stratigraphic column showing the locality of Wuhe quarry (star in A) and the stratigraphic distributions of Ediacaran fossils. Star in inset map marks the location of the Huangling anticline, which is enlarged in (A). Star in (B) marks the stratigraphic horizon from which the *Dickinsonia* specimen was collected. Modified from Xiao et al. (2020b). Geochronometric data 551.1 ± 0.7 Ma, 632.5 ± 0.5 and 635.2 ± 0.6 Ma from Condon et al. (2005), 543.4 ± 3.5 Ma from Huang et al. (2020), and 526.4 ± 5.4 Ma from Okada et al. (2014). Dashed arrows mark alternative correlations of the Miaohe Member (An et al., 2015; Xiao et al., 2017; Zhou et al., 2017). Cam. = Cambrian; Cry. = Cryogenian; Fm. = Formation; HMJ = Hamajing Member; Mbr. = Member.

preserved part is 81 mm in width and 27 mm in axial length, consisting of 26 modules fanning away from a presumed deltoidal region (the region with the largest, U-shaped modules; see 5. Discussion below), which is traditionally regarded as the anterior end (Evans et al., 2019). The modules appear to be continuous across the midline (Fig. 2C), suggesting a bilaterally symmetrical body plan, although the modules on the one side (right side in Fig. 2A) are better preserved and wider than those on the other side probably due to taphonomic deformation. The serially repetitive modules are bent toward the preserved end, with opposite modules on both sides of the midline forming a U-shaped pair. In the preserved part of the specimen, the angles between the modules and the midline decrease toward the deltoidal end from approximately 77° to nearly 0°. The modules also show a substantial ad-deltoidal decrease in length (or the greater dimension of the modules; Fig. 3A) and ad-deltoidal increase in width (or the lesser dimension of the modules, measured at the margin of the fossil; Fig. 3B). The width of individual modules also increases distally or away from the midline. No trace fossil or contraction rim has been founded in association with the specimen.

Material: One specimen, NIGP173490.

Remarks: Despite its incomplete preservation, the specimen can be identified to the genus *Dickinsonia* on the basis of its terminally bent modules that are arranged on both side of a midline. Furthermore, several lines of evidence — including the U-shaped module pairs, systematic change in module size and shape, and the presence of an undivided region that is often regarded as the deltoidal region (Evans et al., 2017) — indicate that the partially preserved specimen may represent the deltoidal end, which is regarded as the anterior end as defined by the direction of movement (Gehling et al., 2005; Evans et al., 2019; Ivantsov et al., 2020; but see Hoekzema et al., 2017). However, the dramatic increase in module length away from the preserved end is more characteristic of modules at the anti-deltoidal end. Moreover, the diverging angles of *Dickinsonia* module pairs typically decrease more abruptly towards the anti-deltoidal end (from 90° to nearly 0°) than they do towards the deltoidal end; in this sense, the sharply bent modules and the abrupt decrease in diverging angles of the preserved specimen seem to be more consistent with an anti-deltoidal end. At the present, it is difficult to unequivocally determine whether the preserved specimen represents the deltoidal or anti-deltoidal end, although we tentatively consider it as the deltoidal

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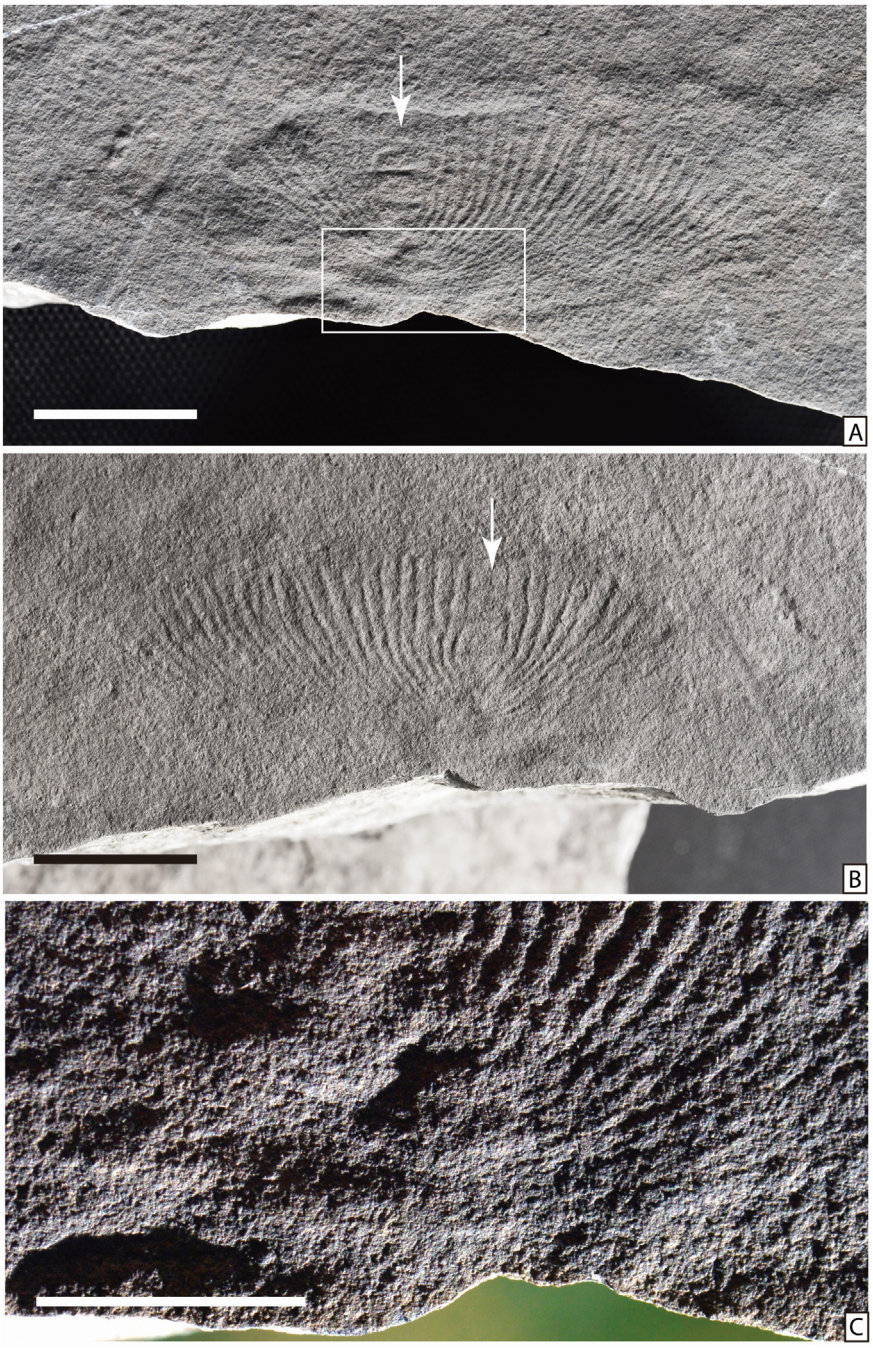

Fig. 2. *Dickinsonia* (NIGP173490) from the Shibantan limestone, part (A) and counterpart (B). Arrows denote the undivided deltoidal region. (C) Magnified view of boxed area in (A), showing details of modules in the middle part. Stratigraphic orientation of the specimen is unknown. Scale bars represent 2 cm (A, B) and 1 cm (C).

end (Fig. 4) but more completely preserved specimens are needed to verify this orientation.

At least nine species of *Dickinsonia* have been described in the literature, including *D. brachina* Wade, 1972, *D. costata* Sprigg, 1947, *D. elongata* Glaessner and Wade, 1966, *D. lissa* Wade, 1972, *D. menneri* Keller and Fedonkin, 1977, *D. minima* Sprigg, 1949, *D. rex* Jenkins, 1992, *D. spriggi* Harrington and Moore, 1955, and *D. tenuis* Glaessner and Wade, 1966. Among them, *D. spriggi* and *D. minima* have been synonymized with *D. costata* (Glaessner and Wade, 1966). Jenkins (1992) considered *D. brachina* and *D. elongata* as junior synonyms of *D. lissa* and *D. costata*, respectively. The remaining number of species may still be inflated (Evans et al., 2019). For example, *D. tenuis* and *D. costata* could be synonymous and represent different ontogenetic stages (Zakrevskaya and Ivantsov, 2017). *D. tenuis*, *D. brachina*, and *D. lissa* are also highly similar and difficult to distinguish from each another

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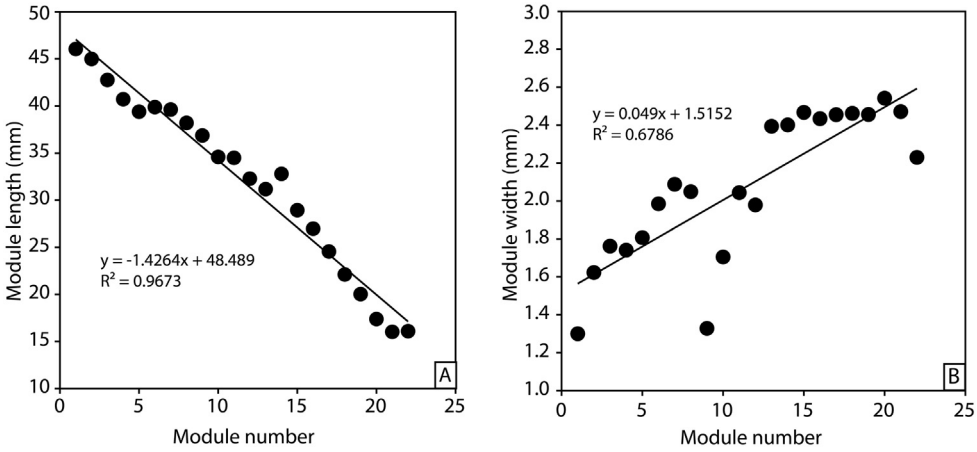

Fig. 3. Module number (counted toward the preserved deltoidal end) versus module length (A) and module width (B), measured on the wider side of the specimen (i.e., right side in Fig. 2A, positive relief; N = 22). Module length was measured along the greater dimension of the modules, and module width was measured along the margin of the fossil.

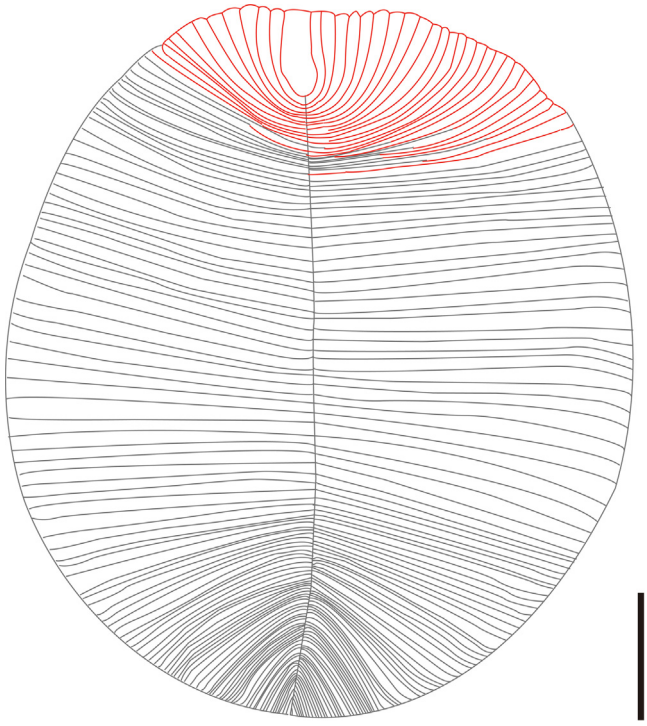

Fig. 4. Hypothetical reconstruction of *Dickinsonia*. Preserved part highlighted in red. Scale bar represents 2 cm.

practically. *D. rex* is characterized by its large size and elongate shape, but it has yet to be formally diagnosed and described (Jenkins, 1992), and it may represent large individuals of *D. tenuis* or *D. costata*.

The Shibantan specimen differs from *D. menneri* in its larger number of modules, larger size, and relatively smaller deltoidal region. The overall morphological features of the Shibantan specimen resembles *D. tenuis* and *D. costata* the most. But *D. costata* has fewer and less densely arranged modules. Moreover, *D. tenuis* typically possesses a smaller deltoidal region than *D. costata*, making the former more comparable to the Shibantan specimen. Nevertheless, caution must be exercised in taxonomic placement before more complete material obtained. Hence, we choose to place this specimen to the open nomenclature *Dickinsonia* sp.

5. Discussion

The age of the Shibantan biota is constrained between 551 Ma and 543 Ma by U-Pb zircon ages (Condon et al., 2005; Huang et al., 2020). The 551 Ma age is from the uppermost Miaohe Member which is conventionally thought to be partially equivalent to Doushantuo Member IV (Xiao et al., 2017; Zhou et al., 2017). But An et al. (2015) offered an alternative correlation that the Miaohe Member is regarded time-equivalent to the lower Shibantan Member of the Dengying Formation, rather than the Doushantuo Member IV. If An et al.'s (2015) correlation is correct, it is possible that the Shibantan biota may be closer in age to 551 Ma rather than 543 Ma. Consequently, the Shibantan biota may represent either one of the youngest examples of the White Sea assemblage, one of the oldest examples of the Nama assemblage, or spans these two assemblages (Xiao et al., 2020b). The presence of *Dickinsonia* — which was previously known only from the White Sea assemblage (Xiao and Laflamme, 2009) — in the lower Shibantan Member is consistent with this assessment. Other Ediacara-type taxa in the Shibantan biota, including *Arborea* (Wang et al., 2020), *Charnia* (Xiao et al., 2020b), *Flabellophyton* (Wan et al., 2020), *Pteridinium*, *Rangea*, *Hiemalora*, and *Aspidella* (Chen et al., 2014) are not age-diagnostic. However, the presence of tubular fossils such as *Wutubus*, abundance trace fossils such as *Helminthoidichnites*, *Torrowangea*, *Palaeophycus*, *Yichnus*, *Streptichnus*, and *Lamonte* (Weber et al., 2007; Meyer et al., 2014; Xiao et al., 2019, 2020b), and weakly biomineralized tubular fossils such as *Cloudina* and *Sinotubulites* (Chen et al., 2014; Xiao et al., 2020b) at stratigraphic horizons above the *Dickinsonia* occurrence in the Shibantan

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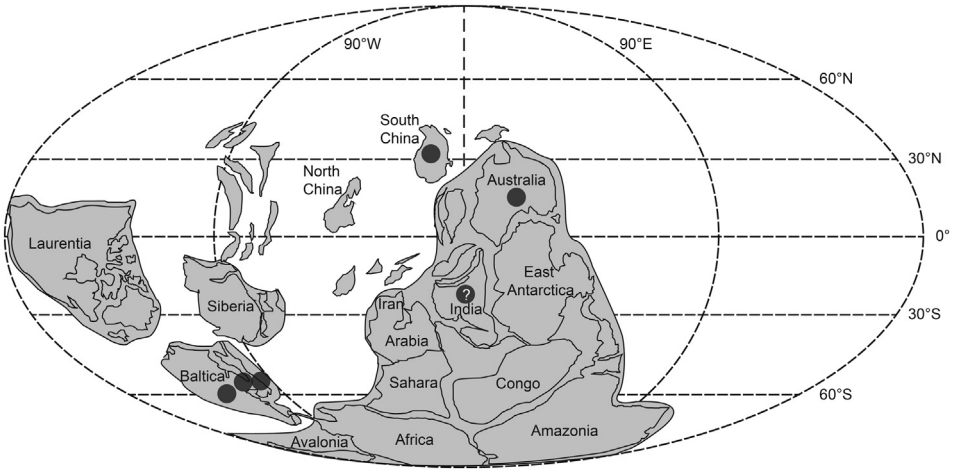

Fig. 5. Paleogeographic distribution (dots) of the Ediacara-type fossil *Dickinsonia*. The paleogeographic map is based on Zhao et al. (2018).

Member indicates that at least the upper part of the Shibantan biota can be correlated to the Nama assemblage. In this sense, the Shibantan Member is similar to the Mogilev–Podol'sk and Kanilov groups in Ukraine (Fedonkin et al., 2007) and the Blueflower Formation in the Mackenzie Mountains of northwest Canada (Narbonne, 1994; Carbone and Narbonne, 2014; Carbone et al., 2015) that contain a mixture of body and trace fossils typically found elsewhere in the White Sea and Nama assemblages. Such mixture or transitional biotas blur the boundary between the traditionally recognized White Sea and Nama assemblages (Muscente et al., 2019), but on the other hand, they offer opportunities for more nuanced understanding of biostratigraphic subdivision and evolutionary transition between these two assemblages.

The occurrence of *Dickinsonia* in the Shibantan biota markedly expands its paleogeographic and paleoenvironmental distributions. Previously only known from Ediacaran siliciclastic facies in Baltica (Keller and Fedonkin, 1977; Grazhdankin, 2014), Australia (Sprigg, 1947; Gehling and Droser, 2013), and possibly India (Retallack et al., 2021), *Dickinsonia* from Ediacaran carbonate facies in South China reinforces that, like several other Ediacaran taxa (e.g., *Cloudina*, *Charnia*, and *Pteridinium*; Muscente et al., 2019), *Dickinsonia* may have had a cosmopolitan distribution. It is intriguing to note that Australia and South China share an increasing number of Ediacaran taxa, including *Flabellophyton* (Wan et al., 2020; Xiao et al., 2020c), *Arborea* (Laflamme et al., 2018; Wang et al., 2020), *Eoandromeda* (Zhu et al., 2008; Xiao et al., 2013), and now *Dickinsonia*. This similarity suggests that the paleogeographic proximity of these two continents — which has long been recognized in early Paleozoic paleogeographic reconstructions (e.g., Li et al., 2008; Cawood et al., 2013; Zhao et al., 2018) — may have started in the late Ediacaran Period (Fig. 5). Nonetheless, the wide separation of Baltica from Australia and South China in independently derived paleogeographic reconstructions (Fig. 5; Zhao et al., 2018) suggests that *Dickinsonia* and other cosmopolitan Ediacaran taxa must have had a strong dispersal capability, perhaps through waterborne propagules or planktonic larvae (Darroch et al., 2013; Cortijo et al., 2015; Mitchell et al., 2015).

The Shibantan *Dickinsonia* fossil also represents the first report of its occurrence in carbonate facies. To some extent, this is not surprising because *Dickinsonia* is one of the paleoenvironmentally most widespread taxa in the Ediacara Member of South Australia (Gehling and Droser, 2013). But still, its capability to adapt to both siliciclastic and carbonate substrates implies that *Dickinsonia* was able to colonize a wide range of environments, a phenomenon that has also been observed in several other Ediacara-type taxa such as *Pteridinium*, *Rangea*, *Arborea*, *Charnia*, and *Flabellophyton* (Grazhdankin et al., 2008; Chen et al., 2014; Wan et al., 2020; Wang et al., 2020; Xiao et al., 2020b).

6. Conclusions

A specimen assigned to *Dickinsonia* sp. is reported from the terminal Ediacaran Shibantan Member (ca. 551–543 Ma) of the Dengying Formation in the Yangtze Gorges area of South China. This represents the first report of *Dickinsonia* in South China and in carbonate facies. This discovery extends the paleogeographic and paleoenvironmental distributions of this genus, suggesting that *Dickinsonia* had strong dispersal capability and environmental tolerance. The occurrence of *Dickinsonia* in the Shibantan Member also suggests that this unit uniquely preserves both the White Sea and Nama assemblages in a stratigraphic succession, offering an opportunity to dissect the evolutionary dynamics and possible extinction between these two assemblages (Darroch et al., 2015; Evans et al., 2018; Muscente et al., 2019).

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