



# Evolution of Holdfast Diversity and Attachment Strategies of Ediacaran Benthic Macroalgae

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### Specialty section:

This article was submitted to  
Paleontology,  
a section of the journal  
Frontiers in Earth Science

**Received:** 26 September 2021

**Accepted:** 22 November 2021

**Published:** 08 December 2021

### Citation:

Wang X, Wu M, Wan B, Niu C,  
Zheng W, Guan C, Pang K, Chen Z and  
Yuan X (2021) Evolution of Holdfast  
Diversity and Attachment Strategies of  
Ediacaran Benthic Macroalgae.  
*Front. Earth Sci.* 9:783427.  
doi: 10.3389/feart.2021.783427

Holdfast morphologies and attachment strategies of benthic macroalgae are somewhat flexible and controlled by both the substrate condition and species. Six forms (tapered base, globose holdfast, composite globose holdfast, discoidal holdfast, rhizoids and horizontal rhizomes) of attachment structures of Ediacaran benthic macroalgae are recognized from the early Ediacaran Lantian biota and late Ediacaran Miaohu biota in South China based on functional morphology. Each form is considered either adapted to firm substrates that dominate the Precambrian seafloor, or soft substrates that are more common in the Phanerozoic. The results show a diversification in both holdfast morphology and attachment strategies of macroalgae during the Ediacaran Period. In the early Ediacaran Lantian biota, none of the benthic macroalgae is adapted to soft substrates, while in the late Ediacaran Miaohu biota, a considerable number (41%) of species are adapted to relatively soft substrates. This shift might be an adaptive response to the diversification of macroalgae and a changing substrate condition during the Ediacaran Period: the decline of microbial mats and increase of water content in the sediments in the Ediacaran.

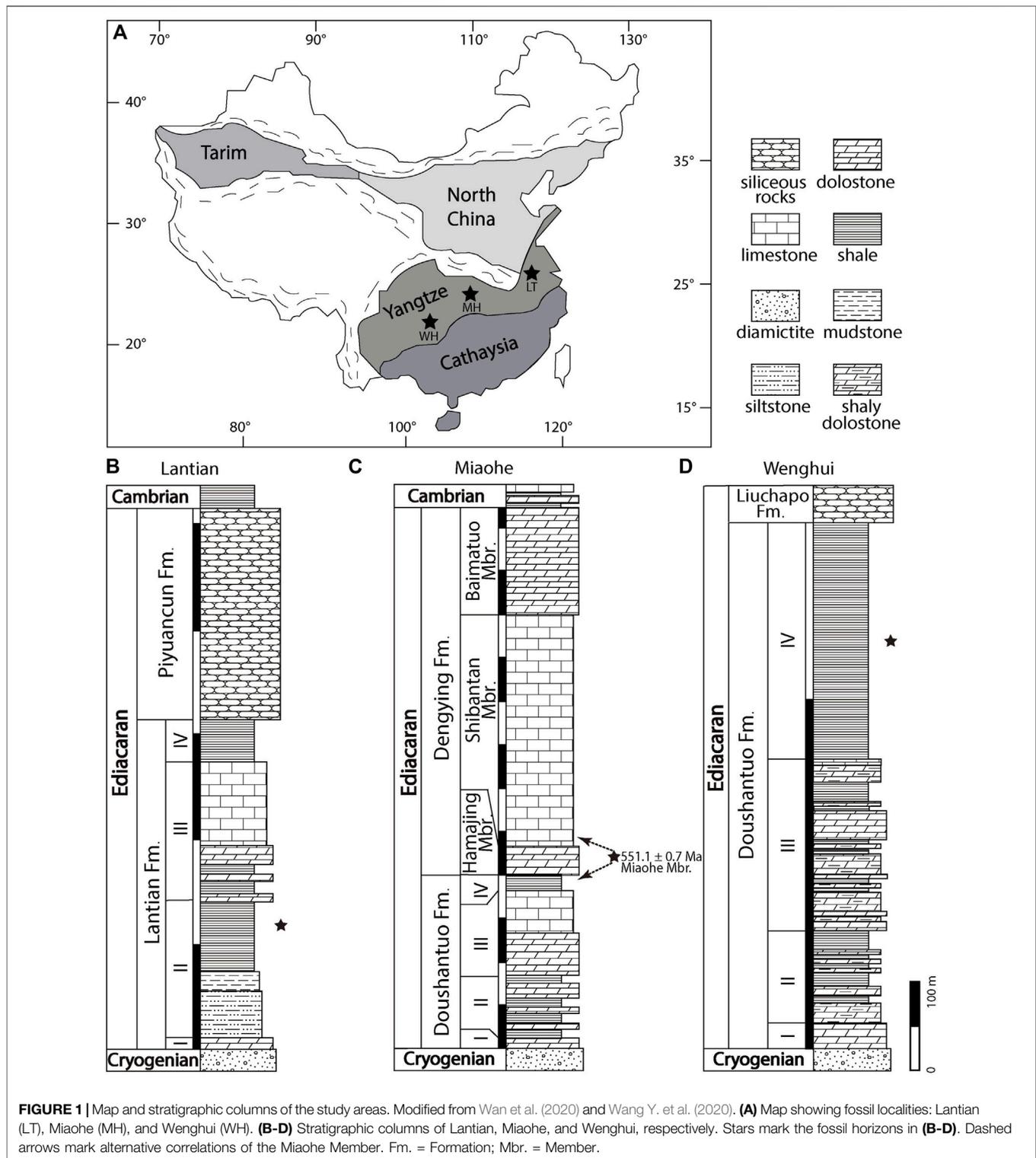
**Keywords:** Ediacaran, macroalgae, holdfast, South China, substrate condition

## INTRODUCTION

Benthic macroalgae are important components of modern and past ecosystems. They are more efficient primary producers than phytoplankton (Bunt, 1975) and provide food and habitats for many other organisms (e.g., Steneck et al., 2002).

The evolution of benthic macroalgae experienced a prolonged stasis since its first appearance (Du et al., 1986; Dong et al., 2008; Xiao, 2013) in the Mesoproterozoic to early Neoproterozoic, and a sudden expansion in morphospace in the Ediacaran (Xiao and Dong, 2006; Bykova et al., 2020). The cause of the increase in morphological disparity might be the drop of  $pCO_2$  in the atmosphere and seawater after the Cryogenian Snowball Earth glaciations (Xiao and Dong, 2006).

The morphology of the holdfast of benthic macroalgae also diversified with the expansion in morphospace. Holdfasts attach macroalgae to substrates, and their morphologies are greatly influenced by the property of substrates and reflect the attachment strategy adopted by the macroalgae. As a result, the morphology of holdfasts may serve as a proxy, to some extent, for



the substrate conditions. For instance, Dornbos et al. (2005) and Lei et al. (2014) have investigated the evolution of attachment strategies of benthic metazoans as a response to the changing substrate conditions in the Cambrian.

The agronomic revolution (AR) or the Cambrian substrate revolution (CSR) is one of the greatest shifts in substrate conditions, transforming from Proterozoic-style substrates to Phanerozoic mixed layers. Typical Proterozoic-style substrates

were firm and well-layered, with low water content and ubiquitous microbial mats; in contrast, typical Phanerozoic-style soft substrates were soupy, water-rich mixed layers (Bottjer et al., 2000). The AR was driven by increasing bioturbation that incorporated water into the sediment (Kloss et al., 2015), but its exact timing and extent have not been yet clearly defined. In the early Cambrian, the AR has already had an effect (Dornbos et al., 2005), and had almost been finished in the late Cambrian (Bottjer et al., 2000). Considering the relatively diverse and abundant trace fossils in the late Neoproterozoic (e.g., Chen et al., 2018; Chen et al., 2019; Xiao et al., 2019), the AR is supposed to have a root back in the Precambrian, but the scarcity of Precambrian biotas restrained the insight to the evolution of substrate conditions during this period. Recently, a large number of specimens of fossil macroalgae with holdfasts preserved intact yielded from the Lantian biota (Yuan and Cao, 1999; Yuan et al., 2011; Bin et al., 2013) and the Miaohe biota (Xiao et al., 2002; Ye et al., 2019a) offered a chance to examine the evolution of substrate conditions in the Ediacaran.

This study focuses on the evolution of macroalgal holdfasts, attachment strategies and substrate conditions during the Ediacaran Period by examining Lagerstätten in South China: the early Ediacaran Lantian biota and the late Ediacaran Miaohe biota. Both biotas are preserved in black shales, and they also share comparable geological settings and depositional environments. We described holdfast morphologies of benthic macroalgae and analyzed their attachment strategies to understand the dynamic of substrate conditions in the early and late Ediacaran.

## GEOLOGICAL SETTING

The Lantian biota is preserved in the Member II black shale of the Ediacaran Lantian Formation in the Anhui province (Figures 1A,B). Underlain by the Cryogenian Leigongwu diamictite and topped by the latest Ediacaran Piyuancun Formation, the Lantian Formation holds the fossil record of life between the end of the Snowball Earth to the eve of the Cambrian Explosion. It consists of four lithological members at the Lantian section (Figure 1B), i.e., in ascending order, Members I–IV. The lowest Member I is the cap carbonate (4 m thick); the Member II consists of siltstone (23 m thick), mudstone (8.6 m thick) and fossiliferous black shale (34 m thick); the Member III consists of dolomite interbedded with black shale (26 m thick) and limestone (40 m thick); the uppermost Member IV consists of black mudstone, 20 m in thickness (Guan et al., 2014; Wan et al., 2014; Wan et al., 2016). The Lantian Formation is the lithostratigraphic equivalent to the Doushantuo Formation in the Hubei Province (Yuan et al., 2011), which has been constrained to be between 635 Ma to 551 Ma (Condon et al., 2005), and therefore the age of the Lantian biota is considered between 635 and 590 Ma (Yuan et al., 2011; Wan et al., 2016).

The sedimentary environment of the Lantian Formation was a restricted shelf basin (Zhu et al., 2007) at low to middle paleolatitudes (Li et al., 2008; Zhang et al., 2015). The *in situ* preserved benthic macroalgae and fine parallel laminations

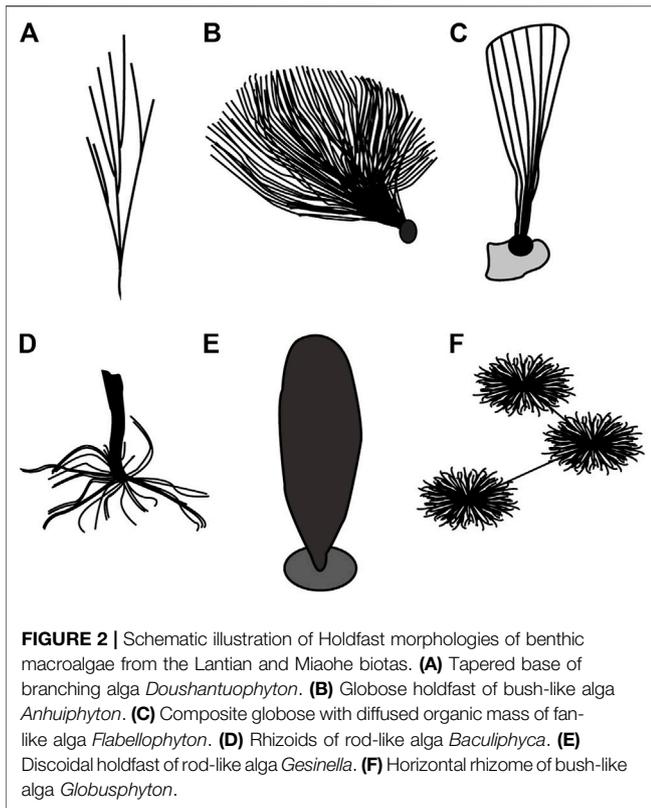
suggest that the deposition probably took place in a quiet environment below the storm wave base but within the photic zone (Yuan et al., 2011). Nevertheless, occasionally alignments of fossils in parallel and/or perpendicular directions indicate relatively weak current or wave movements.

The Miaohe biota refers to the fossil assemblage preserved in a siliceous black shale unit known as the Miaohe Member of the Ediacaran Doushantuo Formation (Figures 1C,D) which crops out in the Hubei and Guizhou provinces. Traditionally, the Miaohe Member is considered the equivalent of the uppermost black shale member of the Ediacaran Doushantuo Formation (Jiang et al., 2011; Xiao et al., 2017; Zhou et al., 2017). The Doushantuo Formation, as mentioned above, is a lithostratigraphic equivalent of the Lantian Formation. In the Miaohe area of the Hubei province and Wenghui area of the Guizhou province, the Doushantuo Formation overlain the Cryogenian Nantuo Formation and is overlaid by the latest Ediacaran Dengying and Liuchapo formations respectively. The Doushantuo Formation is 255 m thick at Miaohe and 79 m thick at Wenghui. Within the Doushantuo Formation, four members are discerned, in ascending order: a cap carbonate unit at the bottom (Member I, 5 m thick at Miaohe and 7 m thick at Wenghui), black shale interbedded with dolomite (Member II, 150 m thick at Miaohe and 10 m thick at Wenghui), laminated dolomite (Member III, 80 m thick at Miaohe and 17 m thick at Wenghui), and black shale and organic-rich mudstone at the top (Member IV, 20 m thick at Miaohe and 45 m thick at Wenghui). Nevertheless, An et al. (2015) proposed an alternative correlation that regards the Miaohe Member as an equivalent of the lower Shibantan Member of the Dengying Formation. The Miaohe Member yields diverse macroscopic fossils in the Miaohe area and several other localities in Hubei (Xiao et al., 2002; An et al., 2015; Ye et al., 2019a), and also in the Wenghui area in Guizhou (Zhao et al., 2004; Wang et al., 2014; Wang et al., 2016). Its age is constrained to 551 Ma (TIMS U–Pb dating, Condon et al., 2005). This black shale member is interpreted as transgressive sediments deposited during sea-level rise (Jiang et al., 2007; Jiang et al., 2011), which may represent a restricted intra-shelf basin setting in the Yangtze Gorges area (Zhu et al., 2013) at low paleolatitudes (Li et al., 2008), and probably represent a continental slope environment in the Wenghui area (Jiang et al., 2011). The surface sediment of the Wenghui area was considered to be soupy (Wang and Wang, 2008).

## MATERIAL AND METHODS

Specimens from the Lantian and Miaohe biotas are deposited in the Nanjing Institute of Geology and Palaeontology, except for the *Gesinella* and *Globusphyton* specimens which are deposited in Guizhou University.

In order to determine attachment strategies of benthic macroalgae in the Lantian and Miaohe biotas, a detailed examination of macroalgal holdfasts was conducted. Observations and measurements were carried out directly on fossil specimens or pictures of fossils from these biotas. Based on



functional morphology, the holdfasts were classified into forms that were either adapted to firm and coherent substrates which dominated the Precambrian seafloor, or soft and soupy substrates that are more common in the Phanerozoic.

As a part of interpreting the adaptive morphology of globular holdfasts, a bivariate Spearman rank-order correlation (Spearman, 1904) was performed to determine if there is a correlation between the size of the thallus and the holdfast of *Flabellophyton*, which is the most representative and abundant taxon in the Lantian biota. A relatively small holdfast compared to the thallus may reflect minimal or no bioturbation (Loduca et al., 2017), hence the correlation (or lack thereof) would indicate if substrate conditions were relevant to the survival of benthic macroalgae or not. We focused on holdfasts instead of the amorphous organic mass here, because the organic mass may represent adhesive polypeptides (e.g., Levi and Friedlander, 2004) exuded from the holdfast rather than an anatomical structure. Two variables used here are the thallus area and the cross-section area of the globular holdfast. The thallus of *Flabellophyton* was an inverted hollow cone originally, and its fan-like fossil represents a projection of a cone on a two-dimensional surface (Wan et al., 2020). The projection is also equal to the frontal area facing into the flow direction, making it an important parameter for benthic macroalgae to withstand moving water. The cross-section area of the globular holdfast is calculated from the diameter which could be directly measured.

Fossil specimens were photographed under a Nikon DSLR D850, a Zeiss stereo microscope Axio Zoom V16. Measurements were made from photos of specimens using ImageJ, version 1.52a

(Rasband, 2018). Statistical analysis was carried out by using SPSS, version 23 (IBM Corp, 2015).

## RESULTS AND DISCUSSION

### Functional Morphology of Holdfasts in the Early Ediacaran Lantian Biota

#### Tapered Base

The base of the macroalgae tapers downwards to a point (Figure 2A; Figures 3A,B), with no differentiated holdfast. This could be an adaptation for shallow insertion into sediments, similar to the strategy adopted by benthic invertebrates referred to shallow sediment stickers (Seilacher, 1999). The tapered base is an uncommon style of attachment for Lantian algae, which only have been found in simple dichotomously branching macroalgae, such as *Doushantuophyton* and *Enteromorphytes*. Fragile structures such as rhizoidal holdfasts can be lost in some fossil specimens (Ye et al., 2019a). However, we have not found any other structures attach to the taper base in all specimens.

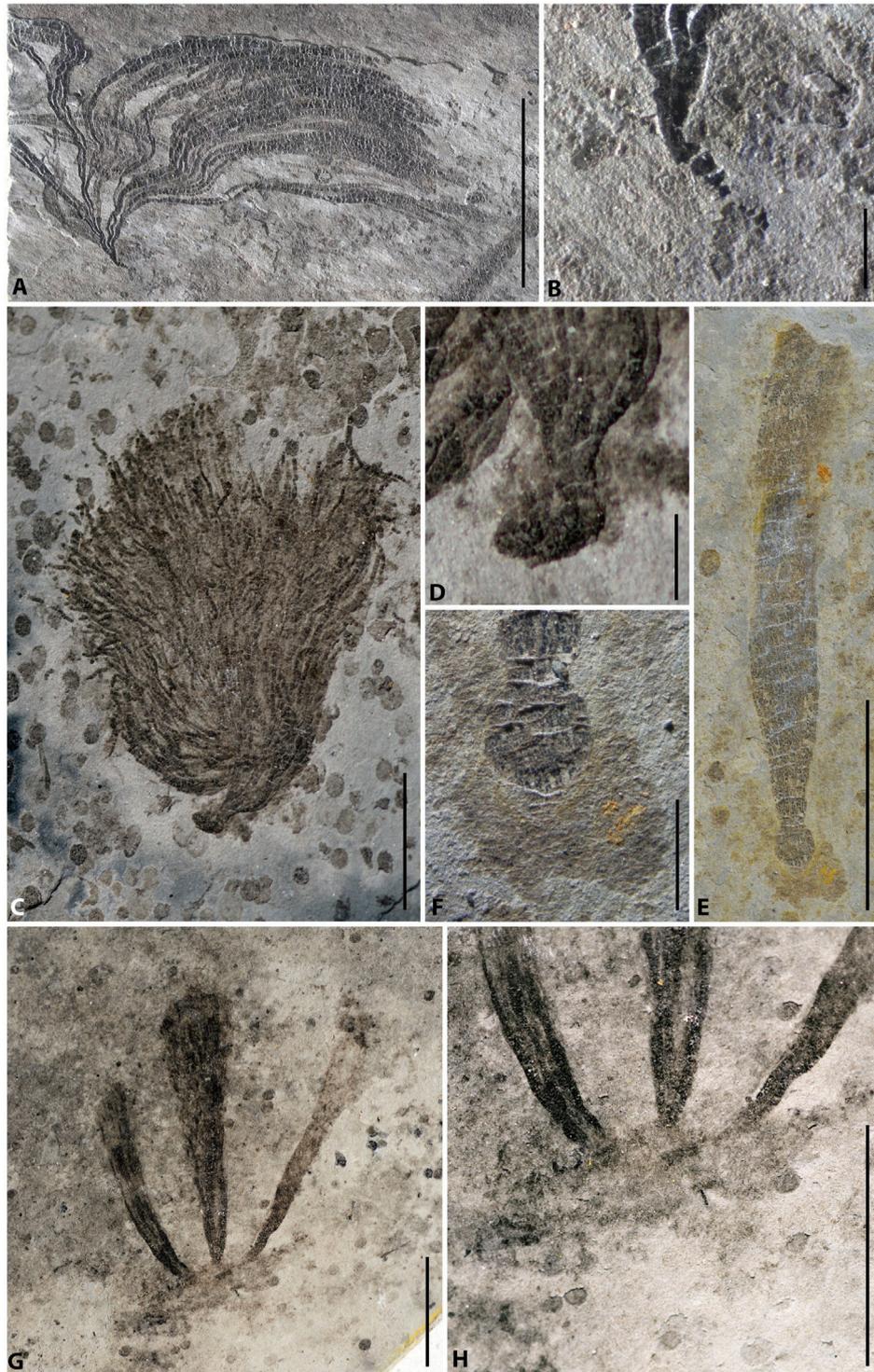
The tapered base can be generally regarded as an analogue to the bare rhizome holdfast (Wang Y. et al., 2020) from the Miaohu biota in the Wenghui area, but the latter may be associated with filamentous rhizoids which have never been found in the tapered base. The possible alga *Protoconites* from the Miaohu biota also bears a tapered base. *Protoconites* is fan-like compression with a tapered basal end, lacking obvious means of attachment. The interpretation of the affinity of *Protoconites* varies from scyphozoan to eukaryotic alga (Xiao et al., 2002). Comparable functional morphology has also been found in Cambrian suspension feeders, such as shallow sediment sticking demosponge *Takakkawia* (Dornbos et al., 2005) and helicoplacoid echinoderms (Dornbos and Bottjer, 2000).

A tapered morphology shows that their entire body mass was centered over a single point, which suggests that the substrates were not a water-rich mixed layer as we expect to find in typical Phanerozoic-style substrates, because these organisms might easily sink into the soupy sediment and die. Hence, shallow sediment stickers and algae that possess tapered bases are considered adapted to Proterozoic-style substrates, which were firm and well-layered and had low water content and ubiquitous microbial mats.

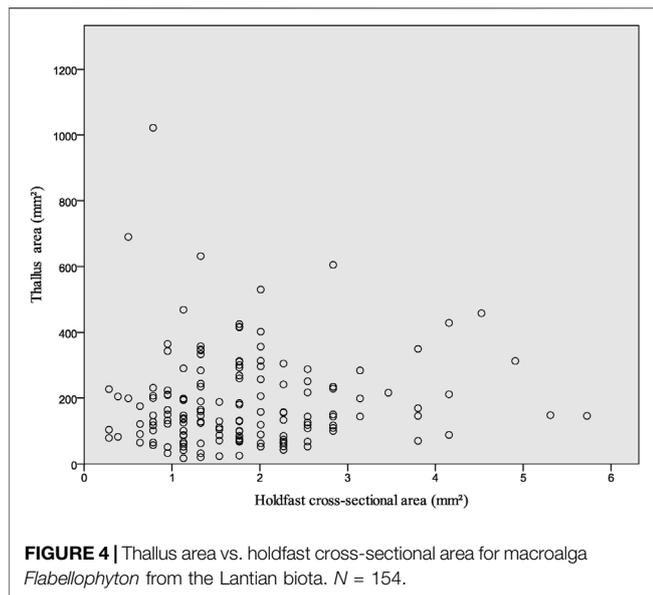
#### Globose Holdfast

A globose holdfast is globular to subglobular and buried shallow in the sediment (Figure 2B; Figures 3C,D). Globose holdfasts are found in bush-like algae, including *Anhuiphyton*, *Huangshanphyton*, and *Marpolia* from the Lantian biota. Occasionally, at the bottom of the globose holdfast, a tiny cone protrudes downwards. Comparable forms have also been found in the Miaohu biota in the Wenghui area and categorized into canopy rhizome holdfast (Wang Y. et al., 2020).

The globose holdfast in Ediacaran macroalgae would not be an effective anchoring structure on Phanerozoic mixed layers, because a sphere is not the optimal shape to resist upward



**FIGURE 3** | Macroalgae and their holdfasts from the Lantian biota. **(A)** *Doushantuophyton cometa*, PB23767. **(B)** Enlargement of the holdfast in **(A)** showing a simple tapered morphology. **(C)** *Anhuiphyton lineatum*, PB23769. **(D)** Enlargement of the globular holdfast in **(C)**. **(E)** *Flabellophyton lantianense*, PB23768. **(F)** Enlargement of the globular holdfast in **(E)**, with amorphous organic mass. **(G)** Three *Flabellophyton* thalli rise from a common organic mass, PB23770. **(H)** Enlargement of the holdfast in **(G)**. Scale bars represent 10 mm **(A,C,E,G)** and 1 mm **(B,D,F,H)**.



movements. As an uprooting experiment showed (Mickovski and Ennos, 2003), among the common shapes of holdfasts, it was the second easiest to uproot. The force required to uproot the globose holdfast model was very close to the shape of an inverted conical model, which was the easiest shape to uproot. Interestingly, inverted conical is also the shape of attachment structures of the benthic organisms referred to as shallow sediment stickers discussed above.

From the perspective of the holdfast, all the factors that affect attachment [i.e., shape, depth of embedment, the size of the holdfast (Mickovski and Ennos, 2003)] are hardly favorable for effective attachment of a globose holdfast. As a result, the property of the substrate seems to be decisive for the success of globose holdfasts. The substrates had to be relatively firm to provide enough support for the globose holdfast to resist uprooting or sinking, but not completely sealed by microbial mats and had to have ample water content to allow the globose to penetrate the top several millimeters of the substrates. Hence, we consider globular holdfasts are adaptive to less typical Proterozoic-style substrates, potentially represents the transition to soupy substrates.

### Composite Globose Holdfast

In some conical algae, especially in well preserved *Flabellophyton* specimens, an amorphous organic mass may be found surrounding the globose holdfast (Figure 2C). We categorized it into composite globose holdfast, as a variation of the simple globose holdfast discussed above. The mass is usually thinner and has a fainter appearance than the holdfast itself (Figures 3E,F); it probably represents adhesive polypeptides (e.g., Levi and Friedlander, 2004) exuded from the holdfast for agglutinating sediment particles. In other cases, the globose holdfast may attach to a platy carbonaceous structure at its bottom. Moreover, multiple thalli may arise from a common organic mass (Figures 3G,H) reminiscent of some individual *Longfengshania* specimens which can be merged into a

common, irregular carbonaceous mass as well (Hofmann, 1985). Both the amorphous mass and platy structure potentially provide additional anchorage strength for the alga.

Most of the *Flabellophyton* specimens were uprooted from the substrates before being buried, due to the relatively weak current or wave movements. As a result, their holdfasts are preserved as spheres without surrounding amorphous mass. The size of the holdfast is not correlated with the size of the conical thallus, as depicted in Figure 4. Small globose holdfasts are found in both large and small specimens. The correlation analysis also shows there is no statistically significant correlation between the cross-section area of the holdfast and the area of the thallus for *Flabellophyton*,  $r_s(154) = 0.091$ ,  $p = 0.262$ . In contrast, there is a positive correlation between the wet weight/surface area of the above-sediment part and holdfast volume in modern algae (Anderson et al., 2006; Bedinger et al., 2013), possibly due to larger size, which experiences more dragging and have greater attachment strength (e.g., Denny et al., 1985; Wernberg and Thomsen, 2005).

## Functional Morphology of Holdfasts in the Late Ediacaran Miaohu Biota

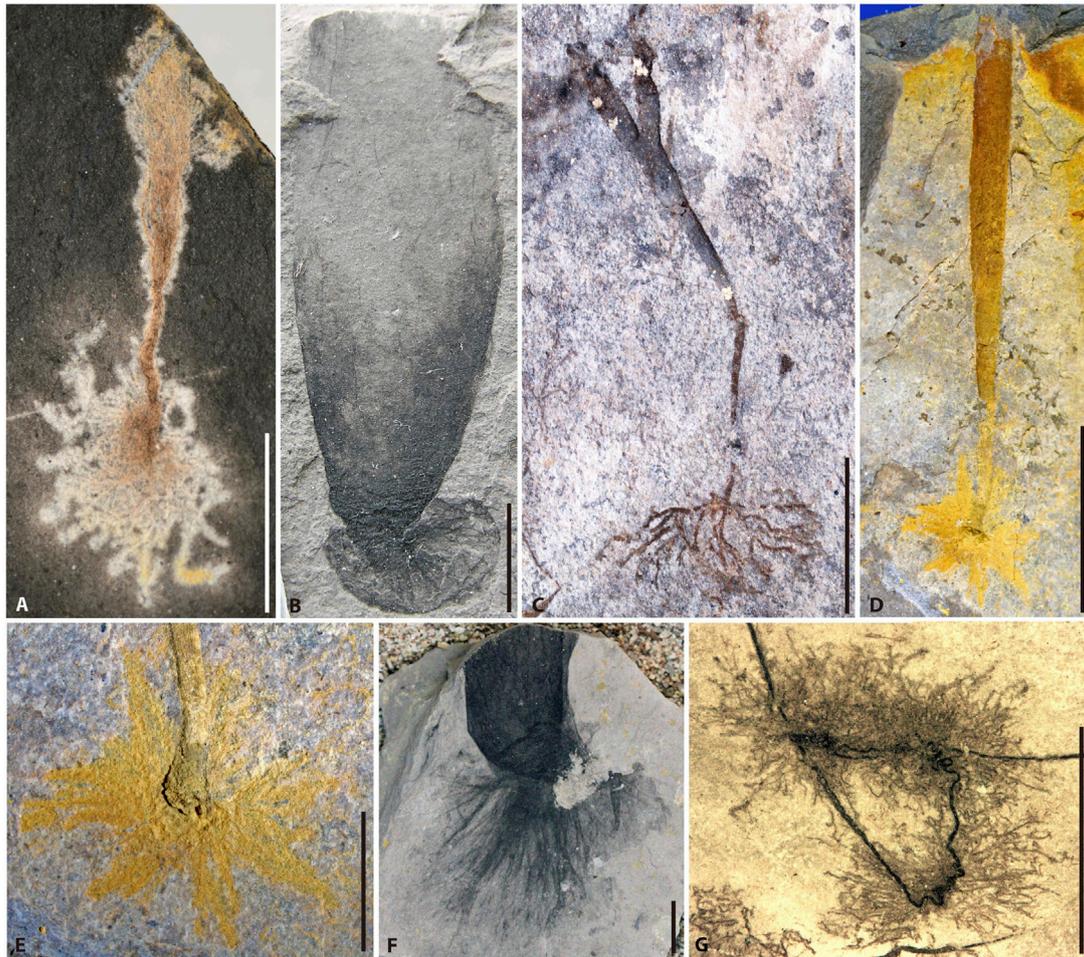
### Rhizoid

Rhizoid holdfasts are the most common type in the Miaohu biota, exhibiting root-like filaments diverging from the base of thallus (Figure 2D). Rhizoid holdfasts are well-developed in algae such as *Longifuniculum* (Figure 5A), *Baculiphyca* (Figures 5C,D), *Konglingiphyton* (Figure 5F), and *Gesinella* (Figure 5E).

Rhizoids are sophisticated structures that increase the surface area of the anchoring device and are common in modern algae living on soft substrate. A larger surface area provides more frictional force between sediment grains and rhizoids (e.g., Yang et al., 2021) to stabilize the alga in soft sediments. Rhizoids also have the ability to bind grains to form clusters. The weight of grains adhered by rhizoids contributes to the anchorage of the alga as well, however, we did not observe any grains coarser than ambient sediments in studied specimens. Similar to rhizoids in morphology, a root-like holdfast is suggested to be an adaptation of benthic metazoans that developed to live on soft mud, and are common in fossil crinoids (Sprinkle and Guensburg, 1995). Root-like holdfasts are considered to be one of the indicators for typical Phanerozoic-style life mode for benthic metazoans (Dornbos et al., 2005) that lived on soupy mixed layers. As this conclusion is based on merely functional morphology, the interaction between the substrate property and holdfast morphology, it is also applicable to organisms with comparable morphology besides benthic metazoans, such as algae.

### Discoidal Holdfast

Discoidal holdfasts are common in the Miaohu biota, displaying a disc-like structure, attached to the base of the thallus (Figure 2E, Figure 5B). Globose structures may be compressed to become discs that resemble discoidal holdfasts. However, discoidal holdfasts are more flattened and often have an elliptical appearance with a stem attached to the center. Discoidal holdfasts also do not exhibit thickened edges as flattened spheres do. Simple basal discs found in the early



**FIGURE 5** | Macroalgae and their holdfasts from the Miaohu biota. **(A)** *Longifuniculum dissolutum* with a rhizoidal holdfast, PB23771. **(B)** *Gesinella hunanensis* with a discoidal holdfast, MH-40-245B. **(C)** *Konglingiphyton erecta*, PB23773. **(D)** *Baculiphyca taeniata*, PB23772. **(E)** Enlargement of the rhizoidal holdfast in **(D)**. **(F)** *Gesinella hunanensis* with rhizoids, MH-57-1058B. **(G)** *Globusphyton lineare* with horizontal rhizomes, MH-40-0248. Scale bars represent 10 mm.

Neoproterozoic macroalgae *Longfengshania* and *Protoarenicola* may represent some of the earliest holdfasts (Du et al., 1986; Dong et al., 2008). In typical Ediacara-type fossil Lagerstätten, disc-like holdfasts are prevalent, for instance, in Ediacaran fronds *Arborea* (Hofmann et al., 2008; Wang X. et al., 2020) and *Primocandelabrum* (Kenchington and Wilby, 2017). Seilacher (1999) suggested that these Ediacara-type organisms were attached on the surface of the seafloor, which was relatively firm due to the presence of microbial mats. Any immobile benthic metazoans that simply lived by attaching to unconsolidated substrates, were well adapted to Proterozoic-style substrates (Dornbos et al., 2005). Considering the resemblance of discoidal holdfasts between macroalgae and other Ediacaran benthic organisms, they probably served as basal attachments in the same manner. As a result, the discoidal holdfast was the adaptation for both macroalgae and Ediacara-type organisms to Proterozoic-style firm substrates.

### Horizontal Rhizome

The horizontal rhizome (Figure 2F) is another anchorage structure found in the Miaohu biota. Several pompom-like individuals of *Globusphyton* are interconnected by horizontal rhizomes which may creep on the seafloor or were shallowly buried within the sediment (Figure 5G). In terms of anchorage capacity, horizontal rhizomes join numerous individuals together, forming a network that provides more effective attachment than a solitary individual could achieve.

Wang Y. et al. (2020) proposed a classification of macroalgal holdfasts in the late Ediacaran Miaohu biota in the Wenghui area. Among the four major types recognized by them, bare and canopy rhizomes resemble tapered and globular holdfasts in the early Ediacaran Lantian biota, whereas pithy and differentiated rhizomes can be roughly correlated to the aforementioned filamentous rhizoids and horizontal rhizomes, respectively.

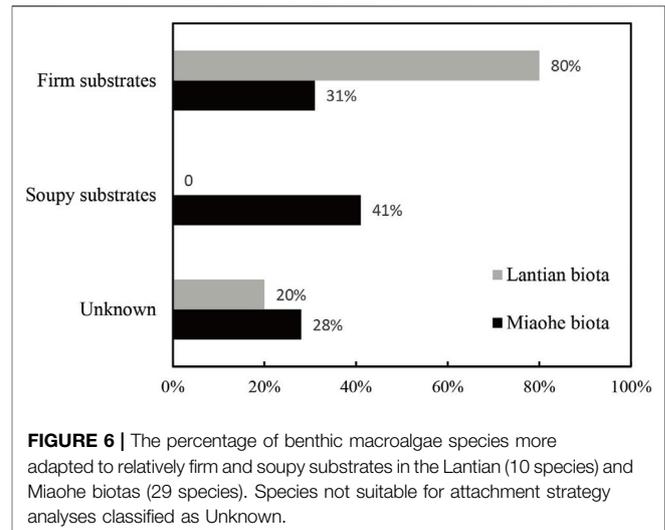
## The Evolution of Holdfast Diversity

Holdfasts of macroalgae that predate the Ediacaran Period were simple and small, the prevalent holdfast type at that period was disc-like. In the Mesoproterozoic, discoidal structures attached to rod-like macroalgae *Tawuia* may represent the first unequivocal holdfast (Kumar, 2001; Xiao and Dong, 2006). Such type of holdfast was also ubiquitous in the Tonian (Dong, et al., 2008; Li et al., 2020) and persisted to the Ediacaran. The simple and invariable holdfast morphology at that time reflects the low diversity of macroalgae and the microbial mat ecosystem was dominant before the Ediacaran. The small discoidal holdfast provided sufficient anchorage to attach on the microbial mat.

During the Ediacaran, holdfasts of macroalgae remarkably diversified, at least six functional morphotypes were recognized. This morphological diversification of macroalgal holdfasts was probably triggered by ocean oxygenation and macroalgae radiation in the Ediacaran Period. The deep sea became intermittently oxic at the beginning of the Ediacaran (Sahoo et al., 2012; Wang et al., 2017; Xiao and Narbonne, 2020). The microbial mat ecosystem declined, and a new ecosystem dominated by erect benthic macroalgae and animals started to establish (Liu et al., 2015; Wan et al., 2020). For example, the benthic macroalga *Flabelliphyton* is a common member of the Lantian, Shibantan, and typical Ediacara biotas distributed in both China and Australia (Wan et al., 2020; Xiao et al., 2020). Through the Ediacaran, the holdfast of *Flabelliphyton typicum* found in both China and Australia (Xiao et al., 2020; Wan et al., 2020) maintained a composite globose shape and was invariable to the significant change of size of the thallus. The morphological stability suggests that the holdfast morphology was at least partially species-specific. As a result, the drastic increase of macroalgae diversity (Ye, 2019b; Bykova et al., 2020) may have also contributed to the diversification of holdfasts during this period.

## Attachment Strategy Innovations for Changing Substrate Condition

One of the major factors that determine the attachment strategy of benthic macroscopic algae is the substrate condition (Verbruggen, 2008). The representative case is the comparison between *Flabelliphyton lantianense* (Figures 3E,F) from the Lantian biota and *Baculiphyca taeniata* (Figures 5D,E) from the Miaohe biota, both of them possess thalli that are very similar in shape and size. The only conspicuous difference between these two species is the morphology of the holdfast: *B. taeniata* possesses rhizoids whereas *F. lantianense* does not. The almost identical above-sediment part and comparable paleoenvironments indicate that the occurrence of rhizoids is a response to changed substrate conditions. Benthic macroalgae have already occurred in the Mesoproterozoic, however, the rhizoids have not been found in any fossil macroalgae that predates late Ediacaran (Ye, 2019b). The absence of rhizoids in such a vast time interval probably indicates the predominance of Proterozoic-style firm substrates in this period. Therefore, the lack of rhizoids in the Lantian macroalgae indicates that they were not necessary for effective attachment at that time because the

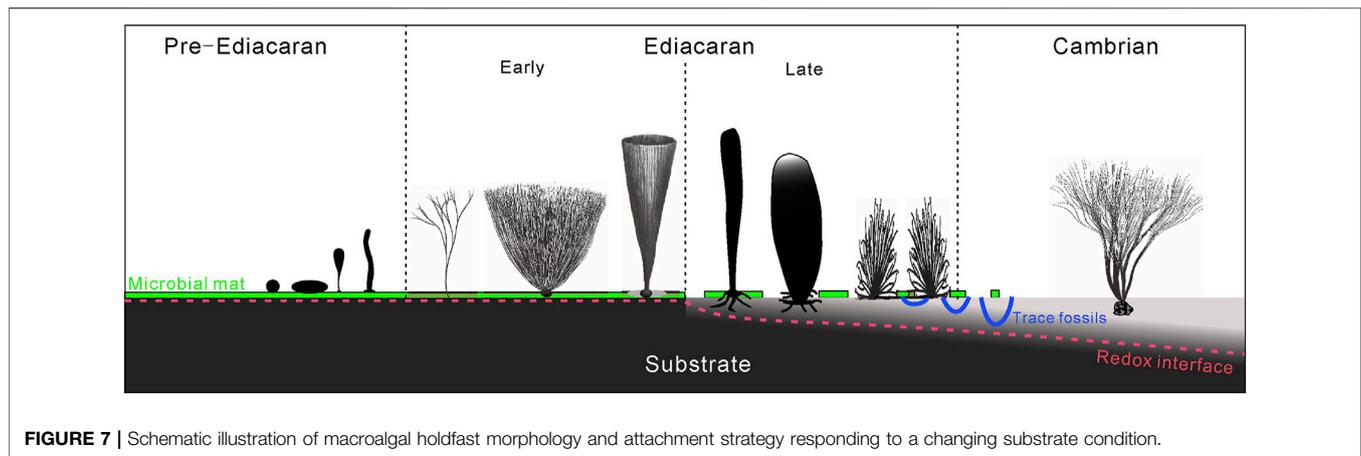


substrates were firm. The ubiquitous rhizoids in the younger late Ediacaran Miaohe biota may represent an adaptation to the changing substrate condition: from Proterozoic-style towards Phanerozoic-style substrates.

In order to determine whether the benthic macroalgae from the early Ediacaran Lantian biota to late Ediacaran Miaohe biota were adapted to the firm or soupy substrates, the morphology of their holdfasts was scrutinized in terms of functional adaptation. These holdfasts were categorized into six general forms which have implications for substrate conditions. As discussed above, tapered base, globose, composite globose, and discoidal forms were interpreted as adaptations to relatively firm substrates which were dominant most of the time of the Precambrian; filamentous rhizoids and horizontal rhizomes are considered to be adaptations to substrates with higher water content comparing to typical Proterozoic-style substrates.

The results show that, in the early Ediacaran Lantian biota, 80% of the benthic macroalga species (10 species in total) are adapted to firm substrates (Figure 6; Supplementary Material S1). The remaining 20% were incompletely preserved and their attachment strategies could not be determined, and were hence classified as unknown. The great majority of firm substrate dwellers suggests that the Lantian biota lived on firm Proterozoic-style substrates. In the late Ediacaran Miaohe biota, 31% of the benthic macroalga species (29 species in total) are adapted to firm substrates (Figure 6; Supplementary Material S1), 41% are adapted to soupy substrates, and 28% are unrecognizable, suggesting the substrates that the Miaohe biota lived on were soupy. Considering the similar depositional environments, the rise of soupy substrate adaptors in the Miaohe biota may indicate the onset of the transformation from firm substrates to soupy substrates had taken place between the age of the Lantian and Miaohe biotas.

During the great transition from the microbial mat to benthic macroscopic ecosystems in the Ediacaran-Cambrian periods (Butterfield, 2007; Wan et al., 2020; Xiao and Narbonne, 2020), the substrate condition also dramatically



**FIGURE 7** | Schematic illustration of macroalgal holdfast morphology and attachment strategy responding to a changing substrate condition.

transformed from the firm, microbial sealed sediments to the soft, water-rich sediments. Moreover, the redox interface migrated downwards to a deeper depth (Figure 7). Although benthic macroalgae (represented by the *Chuarina-Tawuia* assemblage) are not rare in pre-Ediacaran strata, the fossil record of erect benthic macroalgae, such as *Longfengshania* and *Protoarenicola/Pararenicola* (Tang et al., 2021) remains scarce. Macroalgae in the early Ediacaran, despite various shapes of the thalli, e.g., simple dichotomously branching, bush-like, or conical, were adapted to sticking on the surface of microbial mats while mats were still somewhat developed on the seafloor. Attachment innovations in macroalgae in the late Ediacaran, such as developed rhizoids and horizontal rhizomes, are typical adaptations for survival on unstable substrates with a higher water content compared to the early Ediacaran. It may represent adaptive responses to a changing substrate condition in the late Ediacaran, i.e., the decline of microbial mats and the increase of water content in the sediments. Holdfasts of macroalgae became more sophisticated in trapping grains to anchor on mixed substrates in the Cambrian. For example, *Thamnophyton* from the Cambrian Kaili biota show grains coarser than ambient sediments bound in its rhizoids (Yang et al., 2004; Zhao et al., 2011). In summary, the attachment strategy of benthic macroscopic algae became increasingly complex from Pre-Ediacaran to Cambrian, and exhibited some great innovations in the late Ediacaran, adapting to substrate condition and an ecosystem in transformation.

## CONCLUSION

Adaptive morphological analysis indicates there are 6 holdfast forms (tapered base, globose holdfast, composite globose holdfast, discoidal holdfast, filamentous rhizoid, and horizontal rhizome) for benthic macroalgae from the early Ediacaran Lantian biota and late Ediacaran Miaohe biota in South China. The morphological variations between holdfasts

may reflect various attachment strategies and further imply general conditions of substrates. In the Lantian biota, all the benthic macroalgae with attachment structures are adapted to firm substrates, while in the Miaohe biota, a significant number (41%) of species are adapted to relatively soft substrates. The great diversification in holdfast morphology and attachment strategies which was marked by the appearance of complex rhizoidal holdfasts was a response to the diversification of macroalgae and changing substrate conditions during this period, i.e., the decline of microbial mat ecosystem and the founding of a benthic algae-dominated ecosystem. The results also provide evidence that the onset of the agronomic revolution (the Cambrian substrate revolution) likely predates the Cambrian and had a protracted effect on paleoecology and evolution onwards.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/Supplementary Materials, further inquiries can be directed to the corresponding author.

## AUTHOR CONTRIBUTIONS

BW and XW designed the research. XW, MW, WZ, BW, CN, KP, ZC, and XY collected fossils. All authors contributed feedback on drafts, revised and approved the manuscript.

## FUNDING

This research was supported by National Natural Science Foundation of China (41972005 and 41921002), Chinese Academy of Sciences (XDB26000000), National Key Research and Development Program of China (2017YFC0603101), State Key Laboratory of Palaeobiology and Stratigraphy (2102108 and 20201102), and the Youth Innovation Promotion Association of the CAS (grant 2021307).

## ACKNOWLEDGMENTS

We thank Chengxi Wu and Yarong Liu for assistance in fieldworks, and journal reviewers for their constructive feedback.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/feart.2021.783427/full#supplementary-material>

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