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RESEARCH ARTICLE

Macroalgal holdfasts and their interaction with environments from the Neoproterozoic Doushantuo Formation in Guizhou, South China

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Abstract Numerous macro-organisms of the Doushantuo macrobiota, which were found in the black carbonaceous mudstone of the upper Neoproterozoic Ediacraan Doushantuo Formation in Jiangkou County, Guizhou Province, China, are considered to live on sea floor by their holdfasts. The appearance and preserved forms of the macroalgal holdfasts may provide some data to the study of the living and buried environments of macrobiota. They lived in the lower energy and clear environment, and fixed on a soupground with rich water (about 79% water). Currents, possibly ocean currents, could pull out the macroalgal holdfasts from the soupground and break off the macroalgal foliations. After such events, the corpses of macro-organisms would be covered in a reduced environment by the deposits. Afterwards, a new community, including regenerating and undying macro-organisms, lived continuously on a new deposit.

Keywords holdfast, macroalgae, Doushantuo Formation, Neoproterozoic Ediacaran, Jiangkou, Guizhou, China

1 Introduction

A Chinese Ediacaran macrobiota was found on the black carbonaceous mudstone of the upper Doushantuo Formation of the Neoproterozoic Ediacaran in Wenghui Village, Jiangkou County, Guizhou Province, South China. This macrobiota, compression fossils including megascopic algae, possible metazoan and trace fossils, might correlate with the Miaohe biota from Western Hubei and the Lantian flora from Southern Anhui (Zhao et al., 2004; Wang et al., 2005). The Chinese Doushantuoan biota were mainly composed of macroalgae (Bi et al., 1987; Chen and Xiao, 1991; Chen et al., 1994a; 1994b; Ding et al., 1996; Tang et al., 1997; Yuan et al., 1999; Xiao et al., 2002; Yuan et al., 2002; Zhao et al., 2004; Wang et al., 2005). Most of these macroalgae, which were fixed on the sea floor by their holdfast (Chen et al., 1994b; Ding et al., 1996; Chen et al., 2000; Hu, 1997; Xiao et al., 2002; Yuan et al., 2002; Wang et al., 2005), formed a primitive "submarine grassland" (Chen et al., 1994b; 2000; Wang et al., 2005). In morphology, these holdfasts inserting into the deposits could have a relationship with the characteristics of the deposits and rates of sedimentary. The various and preserved-well holdfasts from the Doushantuo Formation of Northeastern Guizhou are better materials for studying the sedimentary and depositing and burying environments during the Neoproterozoic Doushantuo Period.

A 70-m thick section in the Doushantuo Formation near Wenghui village, Jingkou County, Guizhou Province, China (26°50′07″N, 109°01′20″E) directly overlies the tillite of the Nantuo Formation, and conforms the siliceous stone of the Liuchapo Formation (Fig. 1). Its lower part consists mainly of ctenoid dolostone and medium-to-thick beds dolostone (cap carbonate). The middle part is mainly composed of dolostone, muddy dolostone and carbonaceous mudstone. The upper part of the Doushantuo Formation is characterized by its black carbonaceous mudstone with organic-rich matters, and yields abundant macroscopic fossils.

On the basis of bio- and chemo-stratigraphic correlations with well-dated Neoproterozoic sections located throughout the world, the depositional age of the Doushantuo Formation in Yangtze Region is estimated to be between 550 and 600 Ma (Knoll and Xiao, 1999). The U-Pb zircon ages, from the ashes bed above the Doushantuo Formation cap carbonate, and near the boundary of the Doushantuo Formation and the Dengyinag Formation (the topmost Miaohe biota) in Western Huibei, are 621 ± 7 and 555.2 ± 6.1 Ma, respectively (Zhang et al., 2005). In addition, the Doushantuo biota from

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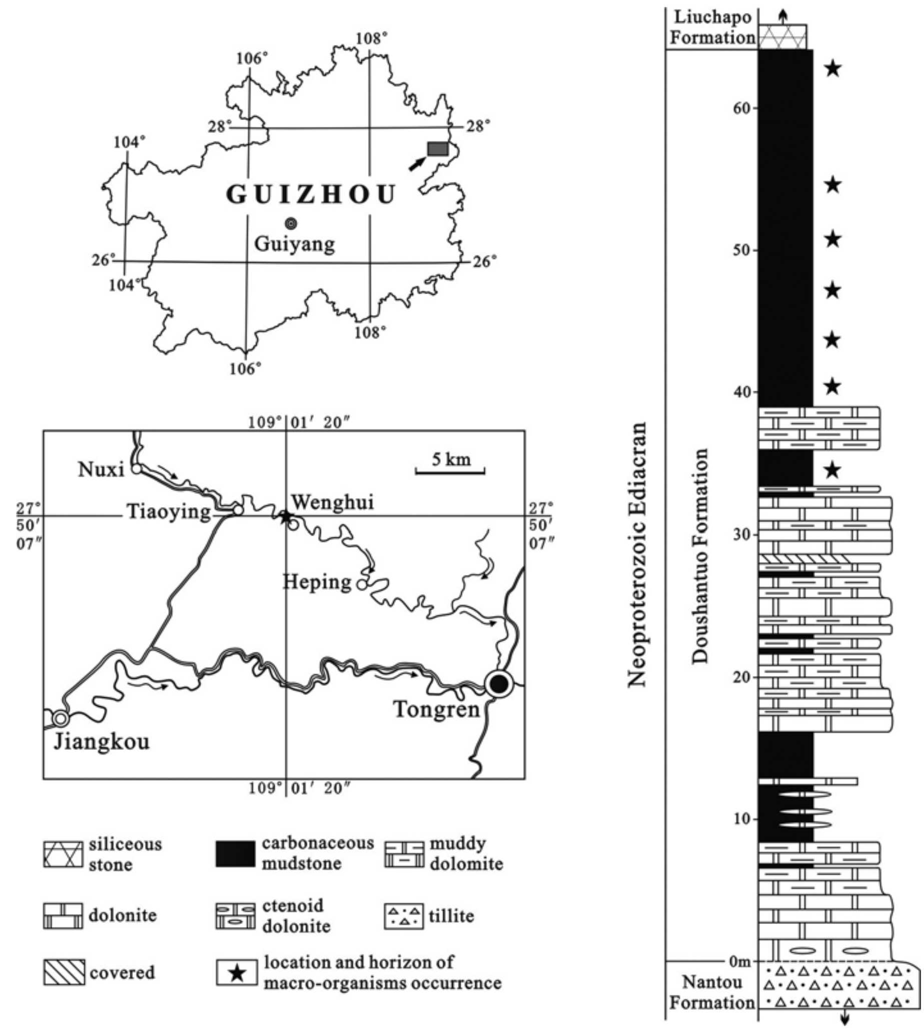

Fig. 1 Locality and horizons of the Duoshantuo macro-biota in Northeastern Guizhou Province

northeastern Guizhou and the Miao biota are both found in the upper parts of the Doushantuo Formation in the Yangtze Region, South China; the Lichapo Formation in northeastern Guizhou is commonly believed to correspond to the Dengying Formation (Qin et al., 1984; Wang et al., 1987).

2 Basic structure and function of macroalgal holdfast

According to morphology, Ding et al. (1996) considered that the megascopic algae in the Miaohe biota can be divided into three parts: holdfast /or rhizoid, stalk /or parastem, and foliation /or lamena. It was believed that the stalk of *Miaohenella* Ding in Ding et al., 1992, a joint between the lamena and holdfast, functions to support lamena. Furthermore, Ding et al. (1996) and Hu (1997) divided these holdfasts into global, coniform, rhombic-shaped and rotundity-shaped by their outline. However, many researchers, in descriptions of the macroalgae from the terminal Neoproterozoic, only divide the marcoalgae into both holdfast (or rhizoid) and foliation (or algal body, or nutritional body); and the stalk or the parastem of Ding et al. (1996) is merged into the foliation (Chen and Xiao, 1991; Steiner et al., 1992; Chen et al, 1994a; 1994b; Steiner, 1994; Yan, 1995; Yuan et al., 1995; 1999; Chen and Wang, 2002; Xiao et al., 2002; Yuan et al., 2002; Wang et al., 2005).

Studies show that the macroalgal holdfast consists of holdfast-stem, holdfast-burl, holdfast-pedicel and filament-rhizoid (Fig. 2).

The holdfast-stem is a joint between the holdfast and foliation. Like a short stick, it gradually minishes upwards in the diameter to differ clearly from the lower foliation that is the same or enlarging upwards in the diameter (Pl. I, figs. b-k; Pl. II, figs. a-j). The carbonaceous film constituting the holdfast-stem thins (light in color) upwards, and is gradually thicker (dark in color) than the foliation. Therefore, it is inferred that the holdfast-stem may be the support for the erect foliation.

The holdfast-pedicel is an organ of macroalgal holdfast and is located under the depositional surface. The holdfast-pedicels from the Northeastern Guizhou are highly varied in outlines: spherical (Pl. I, figs. b, h-k; Pl. II, fig. a), discal

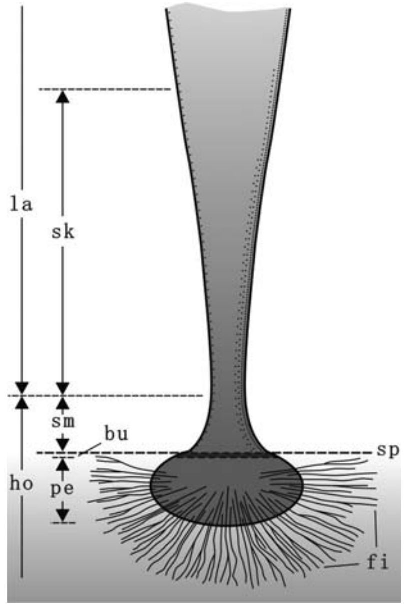

Fig. 2 Sketch showing the structure of the macroalgal holdfast. Note: La) foliation; sk) stalk; ho) holdfast; sm) holdfast-stem; bu) holdfast-burl; pe) holdfast-pedicel; fi) filament-rhizoid; sp) depositional surface.

(Pl. II, fig. j), columniform (Pl. I, fig. c; Pl. II, fig. b), star-like (Pl. I, fig. d; Pl. II, fig. f), and coniform (Pl. I, figs. f, g). It commonly grows out of numerous filament-rhizoids (Pl. I, figs. a-k; Pl. II, figs. a, c, f-i).

The holdfast-burl, also a thickened carbonaceous ridge, is an organ connecting the holdfast-stem and holdfast-pedicel (Pl. I, figs. d, e, g-k; Pl. II, figs. b-d, g-i). Possibly, it is formed by uneven or tumefacient macroalgal cells growing up on or near the section between water and deposits.

The filament-rhizoids, bifurcating or solid carbonaceous filaments (Pl. I, figs. a-c, e-j; Pl. II, figs. a, c, h) or films (Pl. I, figs. d, k; Pl. II, figs. f, h, i), commonly grow on holdfast-pedicel. In some specimens, the holdfast-pedicel has no filament-rhizoid (Pl. II, figs. d, j). The filament-rhizoids may absorb nutrients and water, and /or may strengthen the fixation of macroalgae.

The organic and cellular differentiation is regarded as an important symbol of metaphyte (Yuan et al. 1995; Ding et al., 1996; Chen et al., 2000). As for some specimens from northeastern Guizhou, it is evident that the holdfast-stem and the stalk of foliation, similar to *Miaohenella* Ding in the Miaohe biota, bear the differentiation of epidermis, cortex and marrow (Pl. I, figs. e, i-k; Pl. II, figs. a-c). Ding et al. (1996) considered that some macroalgae produced various organs that were differentiated by parenchyma in the Doushantuo Period. They believed that these organic differentiations of the macroalgae are similar to the differentiators of high plants. In addition, the holdfasts of the Doushantuoan macroalgae also bore various differentiating organs: holdfast-stem, holdfast-burl, holdfast-pedicel and filament-rhizoid. The differentiation of holdfast could indicate that the macroalgea have developed into a system to serve various functions, just like the root system. The macroalgal differentiation could imply an evolutional relationship with high plants and the macroalgae during Doushantuo Period (Ediacara).

3 Characteristics of rocks producing macrobiota

The Northeast Gouzhui macrobiota is found in black mudstone in the upper Doushantuo Formation. A small quantity of sporadic pyrites with horizontal beddings can be seen in the black mudstone. Under the microscope, the black mudstone is made up of both micro-layers (Pl. III, figs. e-g), so-called the bright and the dull layers. The bright layer, which is relatively lighter in color, consists mainly of larger-than-grain clay minerals with subangular to subrounded quartzes (commonly 2%–15% in content and 0.03 mm in diameter), between 0.1 and 0.3 mm in gradual thickness, with the thickest in 0.6 mm. On the contrary, a relatively lackluster dull layer is composed of smaller-than-grain clay minerals with rich organic matters, but with few quartzes, and thickness varying from 0.05 to 0.15 mm. Additionally, filament-rhizoids are usually oblique to or subvertical to the micro-bedding in the bright layer, and a number of organic matters in various outline are located in the lower dull layer. Also observed are microcosmic bedded structures (e.g. wavy-bedding and cross-bedding) (Pl. III, fig. f).

4 Relationship between macroalgal holdfasts and sedimentary environments

Many researchers believed that the Chinese Doushantuo macrobiotas, which are also found in the black mudstone with horizontal bedding in Yangtze Region, South China, lived in a reduced, stagnancy, oxygen-anexic and rich-sulfur environment (Chen et al., 1994a; 1994b; Ding et al., 1996; Tang et al., 1997; Xiao et al., 2002; Yuan et al., 2002). Based on the analysis in palaeoecology, Hu (1997) considered that the Miaohe biota lived in a lower-energy sea with rich oxygen. Researches on the fossil characteristics and palaeoecology suggested that the Doushantuo macrobiota from Northeastern Guizhou lived in a clam environment with good-light, poor-oxygen and a measure of energy (Wang et al., 2005).

4.1 Water current

During the late Doushantuo Period, it was a restricted sea with lower energy in the Jiangkou area, Northeastern Guizhou (Luo, 1993; Wang et al., 2005). The macroalgae from the Doushantuo Formation in Northeastern Guizhou are well-preserved as well as their small line-like filament-rhizoids. Moreover, the holdfasts and foliations of the same algae are well-preserved or approximately on same bedded surface (Pl. II, figs. a-k; Pl. III, figs. a-j). The well-preserved fossils not only indicate that they are preserved *in situ*, but also imply that they are in a calm environment with lower water energy.

In a quiet environment, the filament-rhizoids could be gradually preserved around or underline their holdfast-pedicels (Pl. I, figs. a, d, e, k). By contrast, most of the filament-rhizoids appear in bunches and are preserved together with their algal body on the bedded surface (Pl. I, figs. b, h, j; Pl. II, fig. c). Moreover, in some specimens, the holdfast with filament-rhizoids and the algal foliation are preserved like lines on the same surface (Pl. I, fig. c; Pl. II, fig. h). Therefore, these macroalgae were transported by water current before getting buried, and not *in situ*. In addition, many specimens from the upper Doushantuo Formation in Northeastern Guizhou, where fossils are oriented (Pl. III, figs. a-d) and crinkled or broken off (Pl. II, figs. c, e, f), imply that there were measure of water-energy in the sediments. The developed holdfast of macroalgae is also one of the palaeoecological characters to live in the environment with a measure of energy. In an environment of the primitive "submarine grassland", the energy-lower current could contribute to the diffusion of oxygen produced by algae, and could benefit for the growth and propagation of the biota.

Through measurements of the macroalgal fragments of about 10 mm in length, the long-axis orientations are primarily northeast to southwest in three different horizons of the upper Doushantuo Formation (Fig. 3). Among 66 specimens found at 40 m from the bottom of the Doushantuo Formation, 39.4% and 24.3% had their long-axis orientations at NNE-SSW and NNW-SSE, respectively (Fig. 3(a)). Of the 23 specimens at 42 m to the bottom of this formation, 47.8% and 26.1% were NE-SW and NEE-SWW, respectively (Fig. 3(b)). Among 81 specimens at 50 m to the formation's bottom, 30.9% and 23.5% were NE-SW and NEE-SWW, respectively (Fig. 3(c)). The results of the measurement imply that the water current orientations transporting these algal fragments are approximately equableness. Moreover, the current orientations accord approximately with the palaeogeographical outline of Yangtze platform (about NE-SW) during the Doushantuo period of the Neoproterozoic (Bi et al., 1987; Sang and Wang, 1987; Liu and Xu, 1994; Xia et al, 1994; Wang et al., 2005). According to the relationship between water current and palaeogeography, the movement of seawater may possibly be the same in Northeastern Guizhou during the Doushantuo Period. In average, the micro-layers consist of both bright and dull layers. Therefore, the water currents are believed to be closely related with the periodic ocean current.

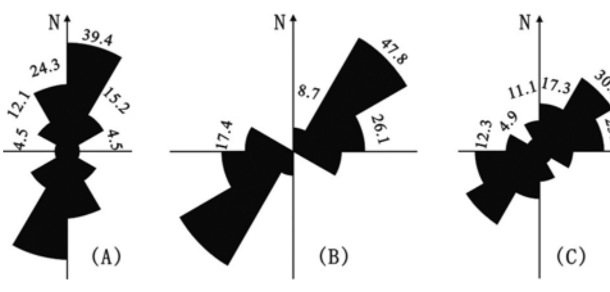

Fig. 3 Rose diagrams showing the orientation of macroalgal fractions. (a) In 40 m distance to the bottom of the Doushantuo Formation; (b) in 42 m distance to the bottom of the Doushantuo Formation; (c) in 52 m distance to the bottom of the Doushantuo Formation; N) north; the Data together shown in percent

4.2 Water energy and ground characters

In the process, the deposits of the black mudstone were formed by an abundance of water. Wang et al. (2005) believed that the Northeast Guizhou macrobiota lived mainly on the soft- to soup-ground with rich-water.

In a life cycle, the macroalgal filament-rhizoids around the pedicel-rhizoid could be oblique to or vertical to the bed, and could be under the surface of deposits. However, in numerous specimens from Northeastern Guizhou, they are preserved together with their algae-body in a bedded surface (Pl. I, figs. a, d, e, k). The presence of filament-rhizoids means that the filament-rhizoids could insert into a water-rich ground.

The distances between holdfast-burls are larger than the thickness of micro-layers. The holdfast-burl could be formed on or near the section between water and deposits, so that it could reflect the regular changes of sedimentary surface. Both micro-layers could show sedimentary periods. Therefore, the differences between the distance of both holdfast-burls and the thickness of micro-layers could be that there was rich water in the deposits. The average ratio in the thickness of both micro-layers and the holdfast-burl distances among the 18 specimens measured is 1 : 3.7; a minimum ratio of 1 : 2.4 and 1 : 5.4 maximum. Not taking into account diagenetic changes means that the water in deposits is an average of 78.54%. The muddy deposits (the soupground) filled rich water into the gaps where few grains came into contact with other each. On the other hand, the macroalgae with disc-shaped holdfast-pedicel (Pl. II, figs. d, j) can adapt on the soupground.

The well-preserved macroalgae together with the filament-rhizoids on the same bed and the orientation of the macroalgal fragments can mean that small water current was able to pull algae out from the soupground. The loose macroalgae floated along the water current and were transported to a distance, without loss of features.

5 Life cycles of macroalgae

Most of macroaglae from the upper Doushantuo Formation settled on the deposits by their holdfast; and their semi-floating foliations erected on sea floor (Wang et al., 2005).

In the Doushantuo Formation of Northeastern Guizhou, there is a common burl-rhizoid (Pl. I, figs. d, e, h, j, k; Pl. II, figs. g-i), or an accidental two to three holdfast-burls (Pl. I, figs. g, h; Pl. II, figs. b-d). The holdfast-burl, which is the dense carbonaceous mass on holdfast, may be on or near the section between the deposits and water, in which case the occurrence of multi-holdfast-burls on the same macroalgal holdfast could be closely relate with the changes of depositional surface.

In addition, the black mudstone yielding macro-organisms is composed of both bright and dull layers (Pl. III, figs. e-g). The bright layer with larger-than-grain quartzes is composed mainly of clay minerals with micro-cross-bedding (Pl. III, fig. f) and filament-rhizoids subvertical to the bed (Pl. III, figs. e, g). It may be deposited in a water-current environment and may be the main settlement layer of macroalgal filament-rhizoids. By contrast, the dull layer consists of clay minerals with a large number of organic matters that carry certain outlines near the upper part. In the same way, the dull layer may be deposited in the natural environment without current. It may also be a living layer of macro-organisms; and its upper part is, possibly, a buried layer.

Therefore, the life cycle of these macroalgae may correspond with one sedimentary cycle consisting of both bright and dull layers, but few with two more sedimentary cycles (Fig. 4). Every current event, or maybe the end of the regular ocean current in particular, could cause mumerous macroalgae to lie down, or to break off, or to pull up, and even to die.

6 Burying process of macro-organisms

The Guizhou Doushantuo biota lived in a comparatively water-quiet environment with little deposits. The macroalgae fixed on the soft soupground: their holdfasts were under the surface of deposits; and their foliations were half-submerged in the water (Fig. 4(a) and (b)).

When ocean currents happened, an energy-lower water current occurred in Northeastern Guizhou, so most of the soft macroalgae were lain down, or broken off, and /or pulled out all together from their holdfasts, and then floated near the sea floor (Fig. 4(c)). As the water-energy weakened, the floating macroalgal body sank down on the depositional surface. Then the dead macroalgae and the lying part of the live macro-organisms were covered with deposits transported mainly by the current. In the decaying and decomposing process, the dead bodies released out some matters (e.g. H_2S) so that the reduced microenvironment surrounding the dead body increased in the covered state. The macro-organisms could be well-preserved in the reduced environment.

After the current, possible an ocean current, the posterities of macro-organisms grew on a new depositional surface again, and the remaining macro-organisms could form new holdfast-burl on the new interface of deposits and water (Fig. 4(d)).

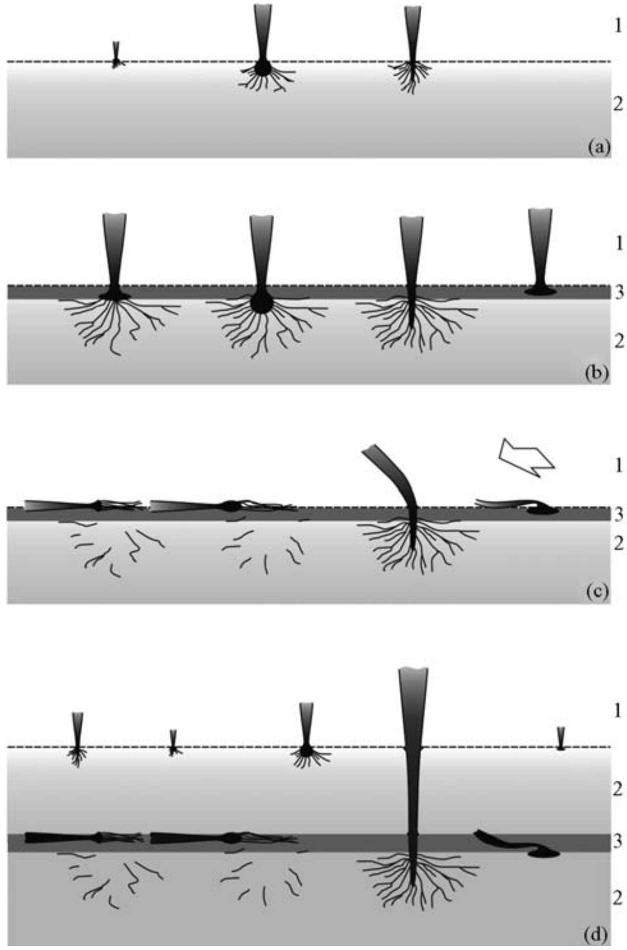

Fig. 4 Sketch showing the life cycle of the marcoalgae during the Doushantuo period. (a), (b) living environment; (b) the macroalgae were lodged down on the surface of deposits or were pulled out from the soupground due to the water-current event, that is possibly ocean current; (c) the deposits transported by the current event covering the dead body; and the new posterities and remaining organisms regenerate on the new depositional surface after the current event; (1) sea-water; (2) event deposits, (3) natural deposits; arrowhead showed the orientation of the current

7 Conclusions

Comparatively, the macrobiota from the black mudstone of the upper Doushantuo Formation in Northeast Guizhou lived in a calm environment with poor oxygen, lower energy and lower sedimentary rate. The macroalgal holdfast fixed on the soupground (about 79% water). The macroalgae could be lain down or broken off or pulled out by a water current, maybe at the end of an ocean current. After the current event, the dead macro-organisms were covered in a stronger reduced environment in deposits, and their posterities and the survival organisms continue to grow on the new depositial surface again. The life cycle of numerous macroalgae could be in between both regular water-currents that may be the end of ocean current.

The macroalgae in the Neoproterozoic Doushantuoan (Ediacaran) with the organic differentiation are obviously to serve various functions. The holdfast, a primary fixing and absorbing organ, can be divided into four parts: holdfast-stem, holdfast-burl, holdfast-pedicel and filament-rhizoid. Their constructs and outlines are closely related with the sedimentary environment, quality of deposits and rate of deposition.

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Explanation of plates

All specimens are collected from the Neoproterozoic Doushantuo Formation near Wenghui Village, Jiangkou County, Guizhou Province, South China, and are preserved in School of Resources and Environments, Guizhou University. Scale bars equal 1 cm.

Plate I

a: A filament-rhizoids distribute outwardly around the holdfast-pedicel. TY50-472.
b: Bunch of filament-rhizoids and foliation on same bedding surface. TY42-783.
c: *Anomalophyton* (Chen et al., 1994), a linear outline consisting of the foliation and the filament-rhizoids on the same bed. TY50-553.
d: A filament-rhizoid showing a thin film like as star around the pedicel-rhizoid. TY50-348.
e: A foliation with patterned filament-rhizoids around the holdfast-pedicel on or near same bed. TY52-098.
f: A coniform holdfast-pedicel of *Guimenguania* (Chen et al., 1994a). TY50-331.

g: A coniform holdfast-pedicel, and tree burl- holdfasts thickened by carbonaceous mass. TY50-473.
h: A global holdfast-pedicel with bunch of filament-rhizoid. TY52-145.
i: A holdfast can be clearly divided into holdfast-stem, holdfast-burls, holdfast-pedicel, and filament-rhizoid. TY50-327.
j: A filament-rhizoids on the global holdfast-pedicel. TY50-386.
k: A filament-rhizoids around a holdfast-pedicel. TY53-127.

Plate II

a: A holdfast consisting of holdfast-stem, holdfast-burls, holdfast-pedicel, and filament-rhizoid; and the differentiation of epidermis, cortex, and marrow in both holdfast-stem and stalk of *Baculiphyca* Yuan et al., 1995. TY42-067.
b: A coniform holdfast. TY50-514.
c: A holdfast with holdfast-stem, holdfast-burls, holdfast-pedicel, and filament-rhizoid. TY50-427.
d: A discal holdfast of *Gesinella* (Steiner et al., 1992); and three holdfast-burls thickened by carbonaceous mass. TY50-461.
e: A broken foliation. TY50-210.
f: A broken foliation and star-like holdfast-pedicel. TY50-116.
g: A holdfast with a holdfast-burl. TY55-056.
h: Filament-rhizoids and the foliation on same bedded surface. TY50-210.
i: Filament-rhizoids looking like a thin film. TY50-183.
j: A discal holdfast-pedicel. TY42-147.

Plate III

a–c: Orientation of macroalgae. a, TY42-054; b, TY50-120; c, TY42-149.
d: The orientation of *Cucullus* (Steiner, 1994), on a bed. TY50-229.
e: A microcosimic structure of black mudstone bearing both bright layer and dull layer. TYR5001.
f: A micro-layer of black mudstone is composed of both bright layer and dull layer, from the microcosmic wavy-bedding and cross-bedding can be observed. TYR5001.
g: A micro-structure with cross-bedding on the lower bottom. TYR5001.

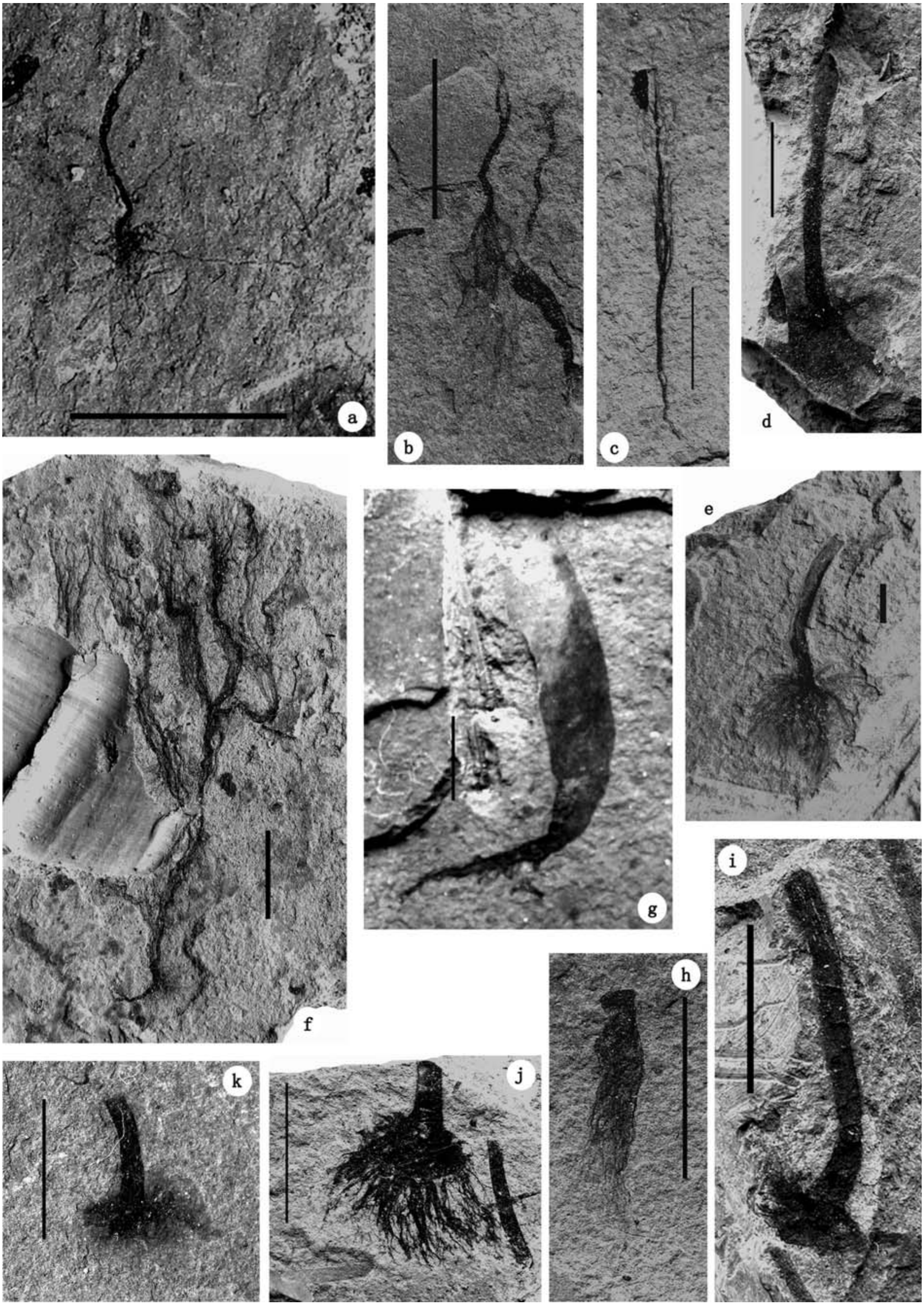

Plate I Wang and Wang, Macroalgal holdfasts and their interaction with environments from the Neoproterozoic Doushantuo Formation in Guizhou, South Chin

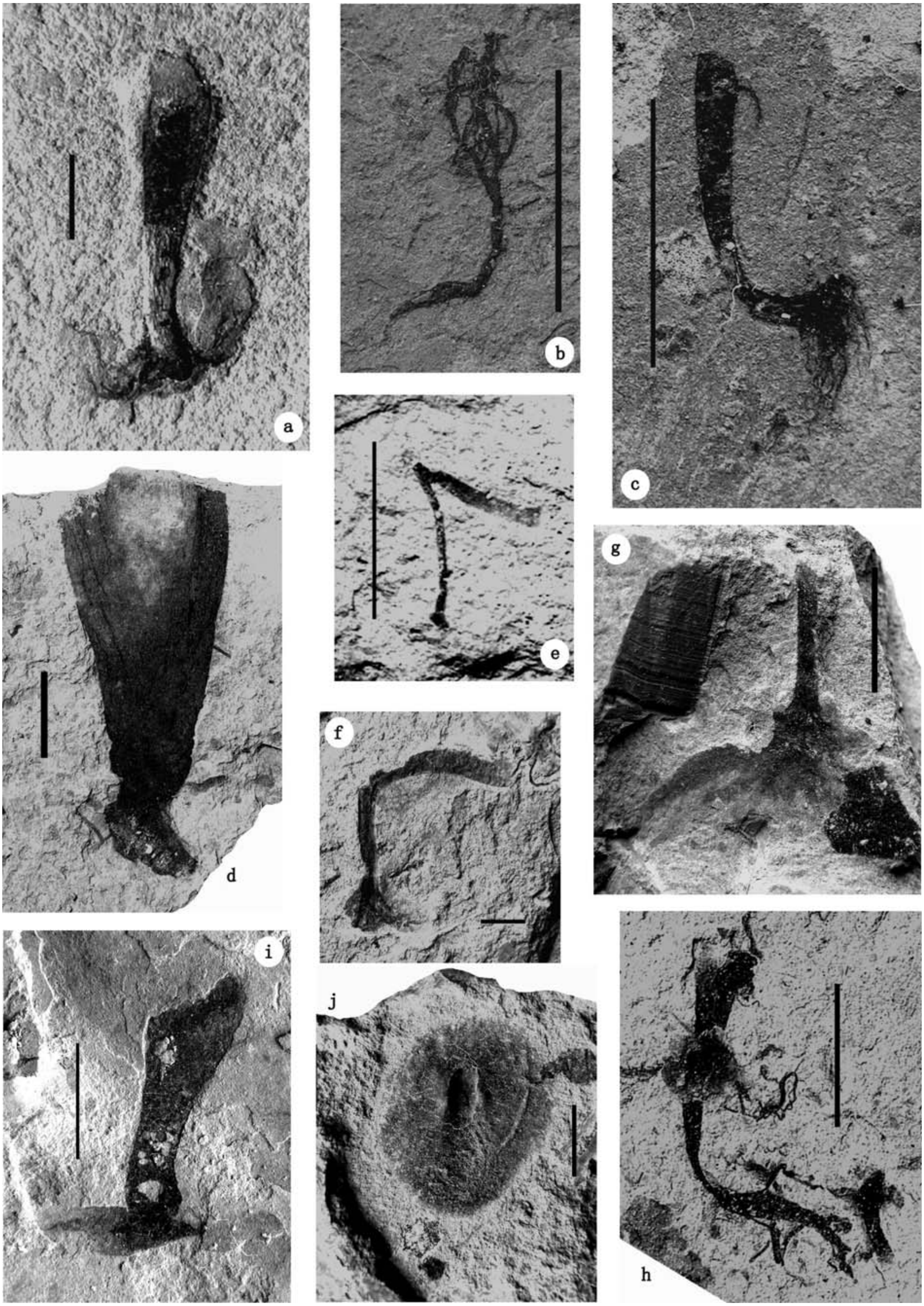

Plate II Wang and Wang, Macroalgal holdfasts and their interaction with environments from the Neoproterozoic Doushantuo Formation in Guizhou, South Chin

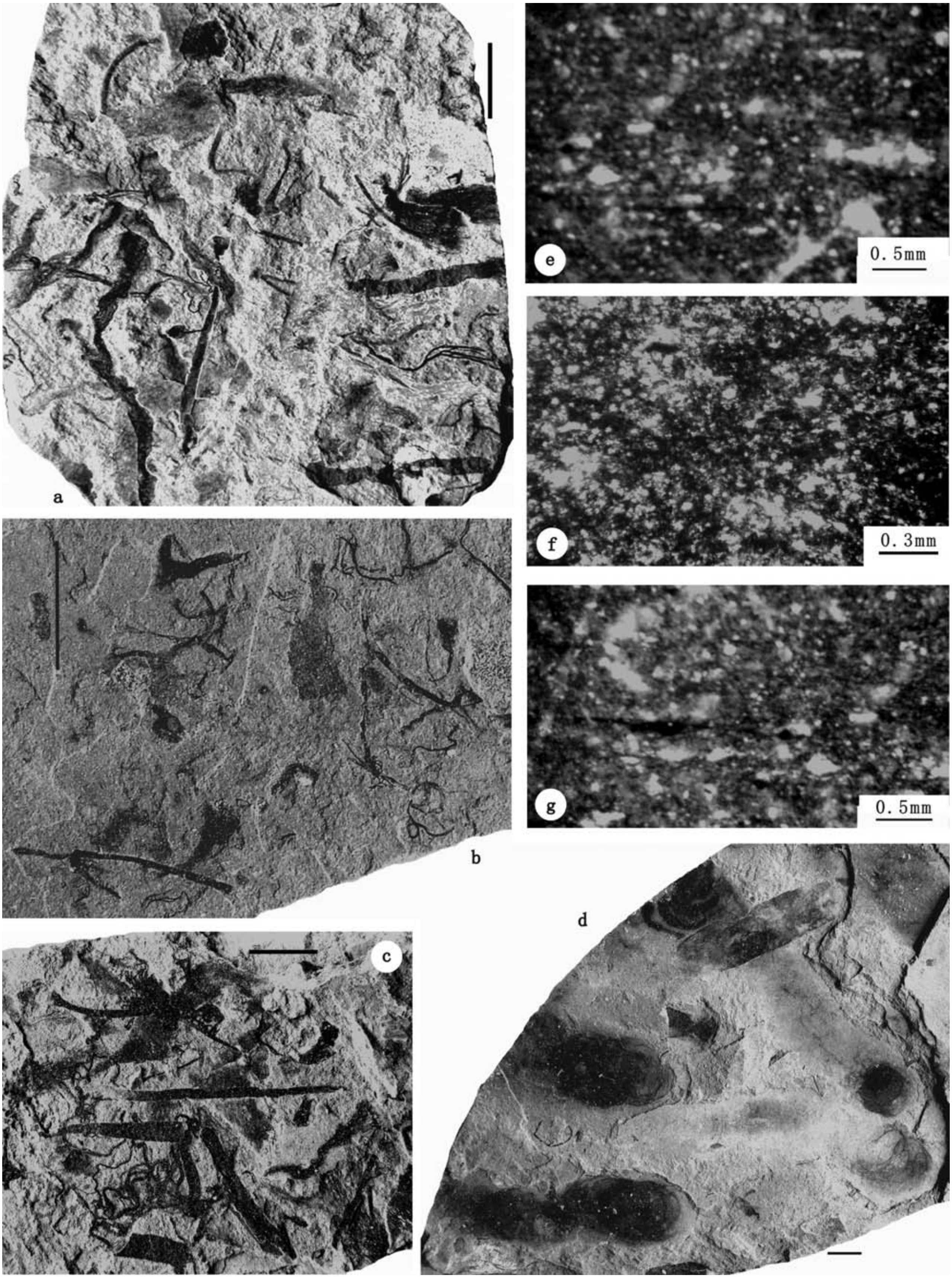

Plate III Wang and Wang, Macroalgal holdfasts and their interaction with environments from the Neoproterozoic Doushantuo Formation in Guizhou, South China