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Authors: Wang, Yue, Du, Wei, Komiya, Tsuyoshi, Wang, Xun Lian, and Wang, Ye

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Macroorganism paleoecosystems during the middle-late Ediacaran Period in the Yangtze Block, South China

YUE WANG[1], WEI DU[2,3], TSUYOSHI KOMIYA[3], XUN LIAN WANG[2] AND YE WANG[2]

[1]*School of Resources and Environments, Guizhou University, Guiyang 550025, China*
[2]*School of Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China (e-mail: duwei@ea.c.u-tokyo.ac.jp)*
[3]*Graduate School of Arts and Sciences, The University of Tokyo, Tokyo 153-8902, Japan*

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Abstract. The evolution of paleoecosystems was often accompanied by the expansion of ecological niches; organismal habitats extended from the sediment surface to the water column, and then to the interior part of the sediment. A major step in ecosystem innovation was recorded in the macrobiota of the upper Doushantuo Formation during the middle-late Ediacaran Period, including the Miaohe biota from western Hubei and the Wenghui biota from northeastern Guizhou, in the Yangtze Block, South China. The macrobiota was dominated by branching and unbranching macroalgae, with abundant metazoans (including worms or vermiform animals, trilobozoans, poriferans, and medusiform animals) and ichnofossils. They lived in a warm and calm tropical ocean, with plentiful sunlight, oxygen, and nutrients. The habitats of the organisms can be subdivided into three layers of morphology and paleoecology: the epibenthic layer, the erect-benthic layer, and the plankton layer. In the case of the epibenthic and erect-benthic layers, the organisms lived on the depositional surface, or were fixed on the seafloor; in the plankton layer, the organisms floated in the water column or on the water surface. In middle-late Ediacaran macroorganism paleoecosystems, the following changes occurred: diversification, the intensification of competition between organisms, a reinforcement of the ability of organisms to change their surroundings, and the effective conversion of bioenergy. The macroorganism paleoecosystem was a key transition in the establishment of a complicated and multilayered ecological pyramid and increasing atmospheric oxygen, and a prelude to the Cambrian explosion.

Key words: bioenergy transformation, environmental factors, middle-late Ediacaran macrobiota, paleoecosystem, South China

Introduction

Ecosystems are a synthesis of abiotic factors, organisms, and the transformation of energy and material in a given time and space (Yang, 1993; Stiling, 1996; Jiang, 2002; Wang and Wang, 2007). Microbial mats were ubiquitous, even on the pre-Ediacaran seafloor, and microbial sedimentary structures consisted of photosynthetic cyanobacteria and aerobic and anaerobic microbes (Schopf, 1992; Seilacher, 1999; Shi *et al.*, 2008), and were distributed on the surface of soft deposits (Seilacher and Pflüger, 1994; Seilacher, 1999; Pflüger, 1999; Bouougri and Porada, 2002; Noffke *et al.*, 2003; Droser *et al.*, 2006; Bottjer and Clapham, 2006; Shi *et al.*, 2008). In the pre-Ediacaran biomat paleoecosystem, only microorganisms inhabited the sediment surface; autotrophs, particularly oxygen-producing photosynthetic organisms, served as primary producers that produced oxygen and organic carbon, whereas aerobic and anaerobic heterotrophs served as consumers and decomposers that consumed oxygen and organic carbon. Therefore, bioenergy transformation in the paleoecosystem was dominated by biochemical reactions in the water (see Seilacher, 1999), and real consumers were absent from the food chain (see Seilacher, 1999) (Figure 1A).

The emergence of planktonic eukaryotes in the Paleoproterozoic (Zhang, 1979; Knoll, 1992; Schopf, 1992; Yan and Liu, 1993; Butterfield, 2000; Yuan *et al.*, 2002; Knoll *et al.*, 2006; Peng *et al.*, 2007) expanded ecological niches. However, eukaryotic microorganisms were mainly photosynthetic autotrophs; therefore, bioenergy transformations between species were still biochemical transformations in water. Even in the plankton-eukaryote paleoecosystem, real consumers were absent and there was little competition between organisms (Figure 1B).

Appearance of macroalgae with obvious organ differ-

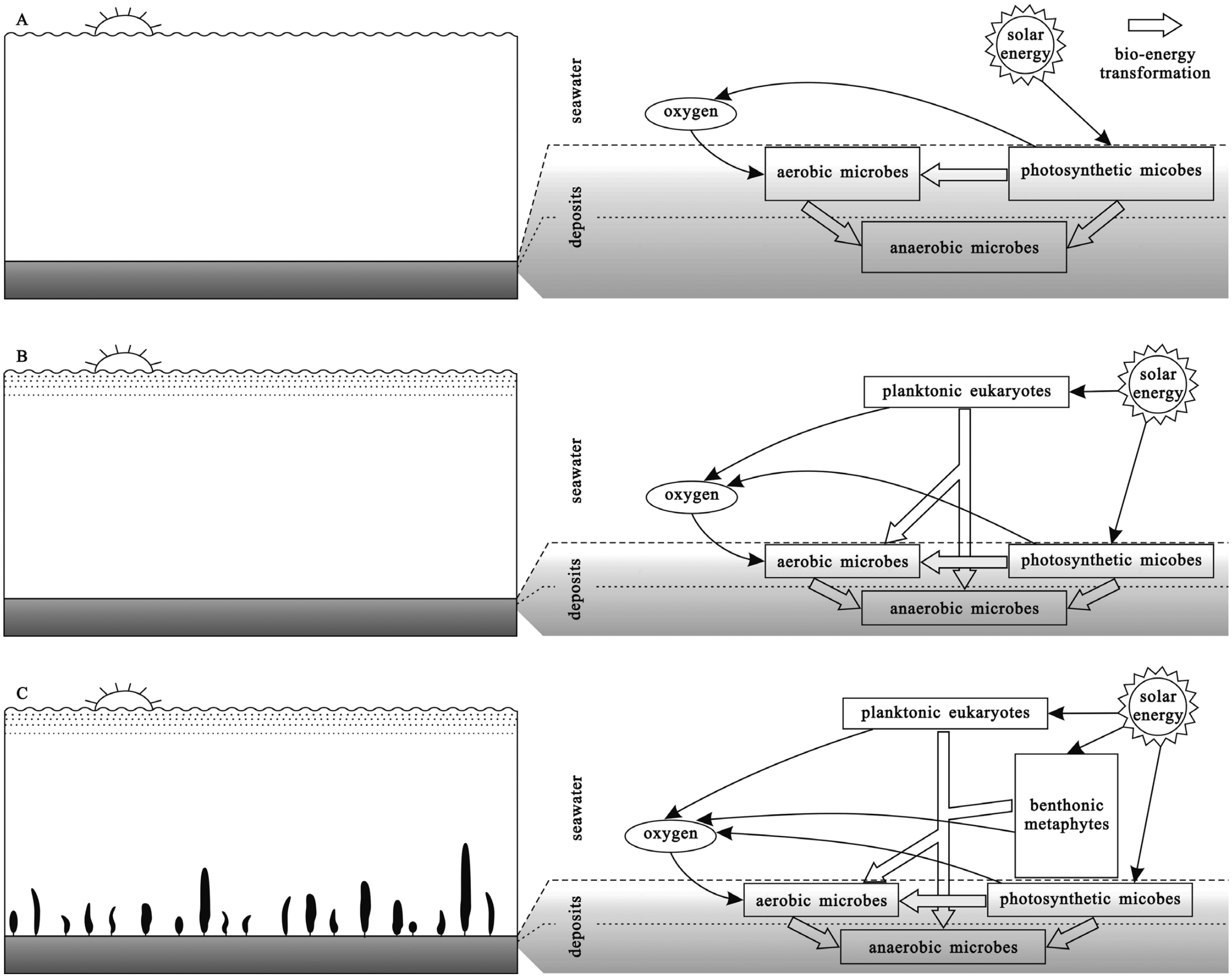

Figure 1. A schematic diagram of bioenergy transformation in paleoecosystems before the Ediacaran Period. **A,** Biomat paleoecosystem, **B,** plankton-eukaryote paleoecosystem, and **C,** macroalga paleoecosystem.

entiation in the Mesoproterozoic generated biological competition in ecosystems. *Longfengshania* biota (the Chuaria-Tawuia assemblage represented by microalgae *Longfengshania* and *Paralongfengshania*) has been reported from lower Mesoproterozoic strata in North China (Zhu and Chen, 1995; Yan and Liu, 1997; Zhu *et al.*, 2000). The *Longfengshania* and *Paralongfengshania* macroalgae, from the Mesoproterozoic to the early Neoproterozoic, had developed foliation, stalks, and holdfasts (Du, 1982; Du *et al.*, 1985; Walter *et al.*, 1990; Hofmann, 1992; Tang and Gao, 1999; Xiao and Dong, 2006). The differentiation in length and width of these macroalgal foliations and holdfasts suggests that competition had appeared between the different species for environmental resources such as fixable areas, sunlight, and nutrients. In addition, the Lantian biota, which was found in lower Ediacaran strata in southern Anhui, South China, included large macroalgae (e.g. *Doushantuophyton*, *Huanshanophyton*, *Anhuiphyton*, and *Flabellophyton*) that were dominated by branching macroalgae (Chen *et al.*, 1994a, 2000; Steiner, 1994; Yuan *et al.*, 1995, 1999, 2002, 2011; Tang *et al.*, 1997). The emergence of large macroalgae, particularly the branching macroalgae, suggests that they were in competition for environmental resources, particularly sunlight.

In the central part of the Yangtze Block, abundant microbiotas of Ediacaran age have been reported from two discrete areas; the Miaohe biota at Miaohe, western Hubei (Zhu and Chen, 1984; Steiner, 1994; Chen *et al.*, 1994b, 2000; Ding *et al.*, 1996; Xiao *et al.*, 2002; Yuan *et al.*, 2002; Xiao and Dong, 2006), and the Wenghui biota at Wenghui, northeastern Guizhou (Wang *et al.*, 2005, 2007a, 2008, 2011; Wang and Wang, 2008, 2011; Tang *et al.*, 2008, 2009). In this study, we synthesize the previous reports of the two biotas in order to represent the entire picture in terms of the paleoecological framework of the Yangtze platform, and discuss their significance in evolution of the Proterozoic macroorganism paleoecosystems.

Middle-late Ediacaran Wenghui and Miaohe biotas in Yangtze Block

The upper Doushantuo macrobiota, including the Miaohe biota at Miaohe, western Hubei (Zhu and Chen, 1984; Steiner, 1994; Chen *et al.*, 1994b, 2000; Ding *et al.*, 1996; Xiao *et al.*, 2002; Yuan *et al.*, 2002; Xiao and Dong, 2006), and the Wenghui biota at Wenghui, northeastern Guizhou (Wang *et al.*, 2005, 2007a, 2008, 2011; Wang and Wang, 2008, 2011; Tang *et al.*, 2008, 2009), is preserved as carbonaceous compression fossils in the black shales of the upper Doushantuo Formation in the Yangtze Block, South China (Figure 2A). The lithology of the Doushantuo Formation in both the Miaohe and Wenghui areas is remarkably similar, and consists of cap dolostones overlying the glacial diamictite of the Nantuo Formation; dolostones and muddy dolostones with black shale in the middle, and black shale containing abundant macroscopic fossils in the upper part, in ascending order. The formation is overlain by the dolostones of the Dengying Formation at Miaohe and the bedded cherts of the Liuchapo Formation at Wenghui (Figure 2B, C). The Dengying Formation in the open-shelf facies was temporally correlated with the Liuchapo Formation of the deeper-water slope facies (Qin *et al.*, 1984; Wang *et al.*, 1987; Zhu *et al.*, 2007; Jiang *et al.*, 2011).

It is believed that the middle-late Ediacaran macrobiota in the Yangtze Block, South China, which is found in the black shale of the upper Doushantuo Formation, lived in a low-energy and warm environment that was oxygen-poor and had normal salinity (Ling *et al.*, 2004), and was located near the equator (latitude 3.0±4.5°) (Macouin *et al.*, 2004).

The depositional age of the black shale of the uppermost Doushantuo Formation should be older than the U-Pb zircon age of 551.1±0.7 Ma reported in the Yangtze Gorges area, western Hubei (Condon *et al.*, 2005). A less reliable age of 591±5.3 Ma was estimated by the Re-Os isochron method for the lower part of the shale unit in the Yangtze Gorges area (Zhu *et al.*, 2013) (Figure 2C).

Bio-community

Both the Miaohe and Wenghui biota were dominated by macroalgae, accompanied by metazoans and trace fossils (Wang *et al.*, 2005, 2007a, 2011; Wang and Wang, 2011; see Wang *et al.*, 2012, table 1). The black shales that contain macrofossils in the upper Doushantuo Formation, at both Miaohe and Wenghui, (Wang *et al.*, 2011, 2012; Wang and Wang, 2011; Jiang *et al.*, 2011) are lithologically and stratigraphically equivalent to each other. The bio-communities of both the Miaohe and Wenghui biota are similar in composition to each other, and can be vertically subdivided into three ecological layers: the epibenthic layer, where organisms live on the deposit surface; the erect-benthic layer, where they are fixed on the seafloor by their holdfasts; and the planktonic layer, where they float in the water column and on the surface of the sea.

Epibenthic layer—The middle-late Ediacaran macrobiota contains worm or vermiform animal fossils (Ding *et al.*, 1996; Chen *et al.*, 1994b; Wang *et al.*, 2007a, 2008) and ichnofossils on the sediment surface made by metazoans (Ding *et al.*, 1996; Xiao *et al.*, 2002; Wang *et al.*, 2005, 2007a). The elongated, cylindrical *Wenghuiia jiangkouensis* (Wang and Wang, 2008) (Figure 3A–E) has many homologous metameres: a mouth at the front of the first segment (Figure 3B), an anus at the end of the body (Figure 3D), a clitellum at the 11th or 12th segment (Figure 3B, E), parapodia on the forward venter of the body (Figure 3B), varied setae on the parapodia (Figure 3B) and around the anus (Figure 3D), and a line-like digestive system passing through the center of the entire body, from mouth to anus (Figure 3A–D). *W. jiangkouensis* has been compared to annelids in its morphology and functional biology. Similarly, the curved taenioid *Linbotulichnus* (Li and Ding *in* Ding *et al.*, 1996) (Figure 3J), which crosses the bedding planes, was regarded as a putative trace fossil or an ichnofossil. *Linbotulichnus* consists of many bead-shaped segments with regular crescent-shaped spaces that are regarded as biological structures rather than non-biological structures, which are similar to dehydrated or contracted structures. Moreover, some mastoids are commonly seen on its margins at or near the bends. *Linbotulichnus* is considered to be a trace fossil of a worm-like animal; the segment and mastoid structures were involved in the movement of its body and its head, respectively. In addition, the large discoidal macroscopic fossils, *Cyclomedusa* cf. *radiata* (Sprigg, 1947) with a central tubercle, concentric ridges and veins, and radiating veins (Figure 3H, I), and Trilobozoa (Fedonkin, 1985) with a triradiate symmetry (Figure 3F, G) were collected from the upper Doushantuo Formation at Wenghui. These two macrofossils have also been reported in the Ediacaran fauna of Australia and the White Sea biota in Russia, and are generally regarded as benthic metazoans that lived on the sediment surface (Fedonkin, 1985, 1990; Seilacher, 1999; McCall, 2006; Wang *et al.*, 2011).

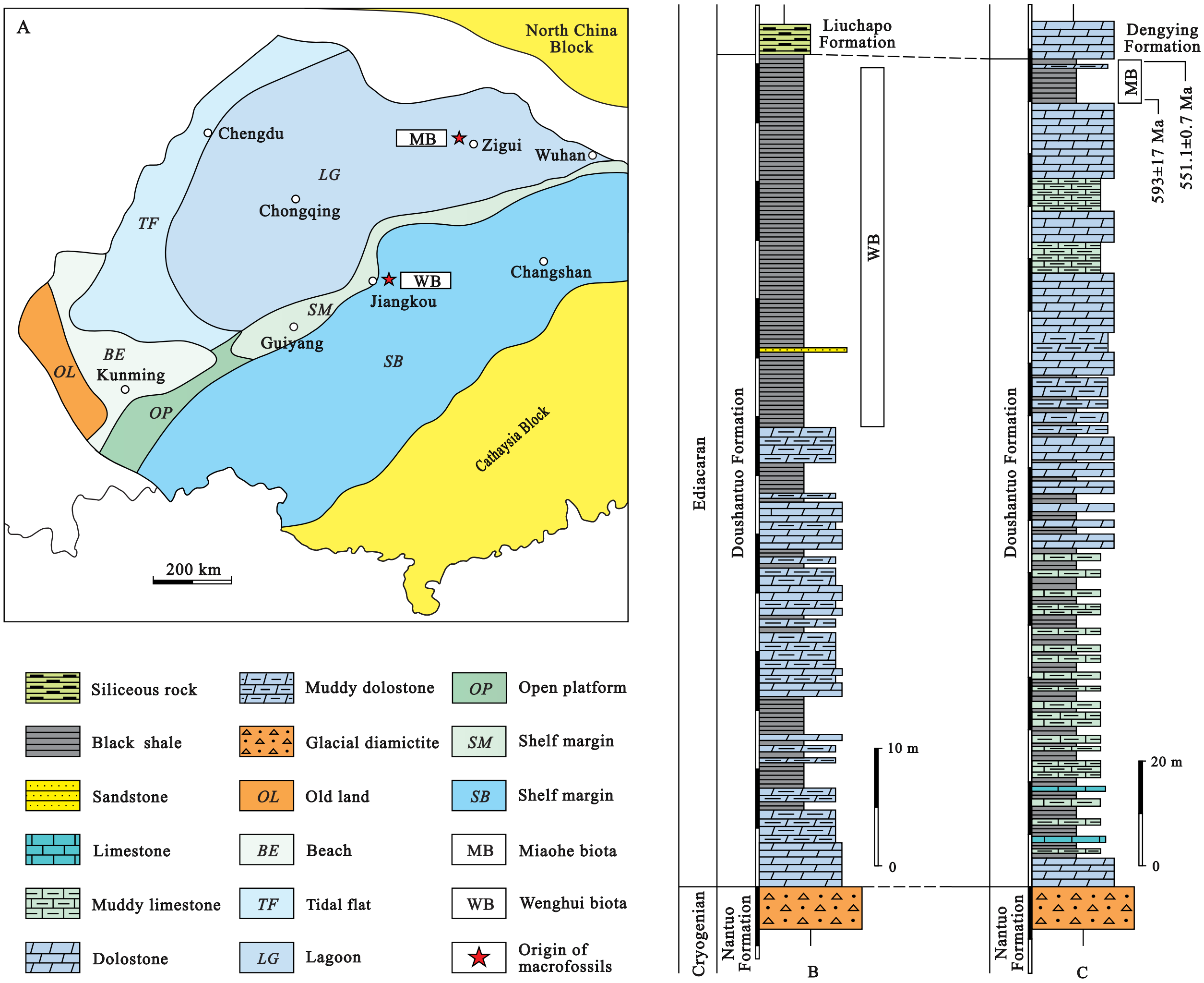

Figure 2. Locations of Miaohe and Wenghui, South China. **A,** Paleogeographical configuration of the Yangtze Block during the Ediacaran Period. **B,** Lithostratigraphy of the Doushantuo Formation of the Wenghui section, northeastern Guizhou. **C,** Lithostratigraphy of the Doushantuo Formation of the Miaohe section, western Hubei.

Regarding macroscopic algae, the coin-shaped *Beltanelliformis brunsae* (Menner *in* Keller *et al.*, 1974) is densely distributed on the bedded surface, but few overlap with each other (Figure 3K). Therefore, *B. brunsae* is not considered as a pelagic macroalga, but as a benthic macroalga on the sediment surface. *Globusphyton lineare* (Xiao *et al.*, 2002; Wang *et al.*, 2007a, 2009, 2011) is characterized by branching filaments scattered radially from small nodes, on a ribbon-like bundle of unbranching filaments (Figure 3L, M) (Wang *et al.*, 2007a). The circular or oval node at the knee-bend of the ribbon-like bundle is regarded as a holdfast, to support the groundling macroalga that lived on the sediment surface (Wang *et al.*, 2007a, 2011).

Erect-benthic layer—Numerous macroscopic algae in the upper Doushantuo Formation had a branched or unbranched thallus and developed a holdfast or rhizoid, which was associated with greater foliation on the stem structure (see Wang and Wang, 2006). These observations indicate that holdfasts or rhizoids anchored the macroscopic algae on the surface of soft deposits, and a branched or unbranched thallus was suspended in the water column for photosynthesis. The unbranched macroalgae include the elongated, clavate, thallus-bearing *Baculiphyca taeniata* (Yuan *et al.*, 1995) (Figure 4A), *Gesinella hunanensis* (Steiner *et al.*, 1992), characterized by a wide thallus with a developed holdfast (Figure 4B, C), *Liulingjitaenia alloplecta* (Chen and Xiao, 1992),

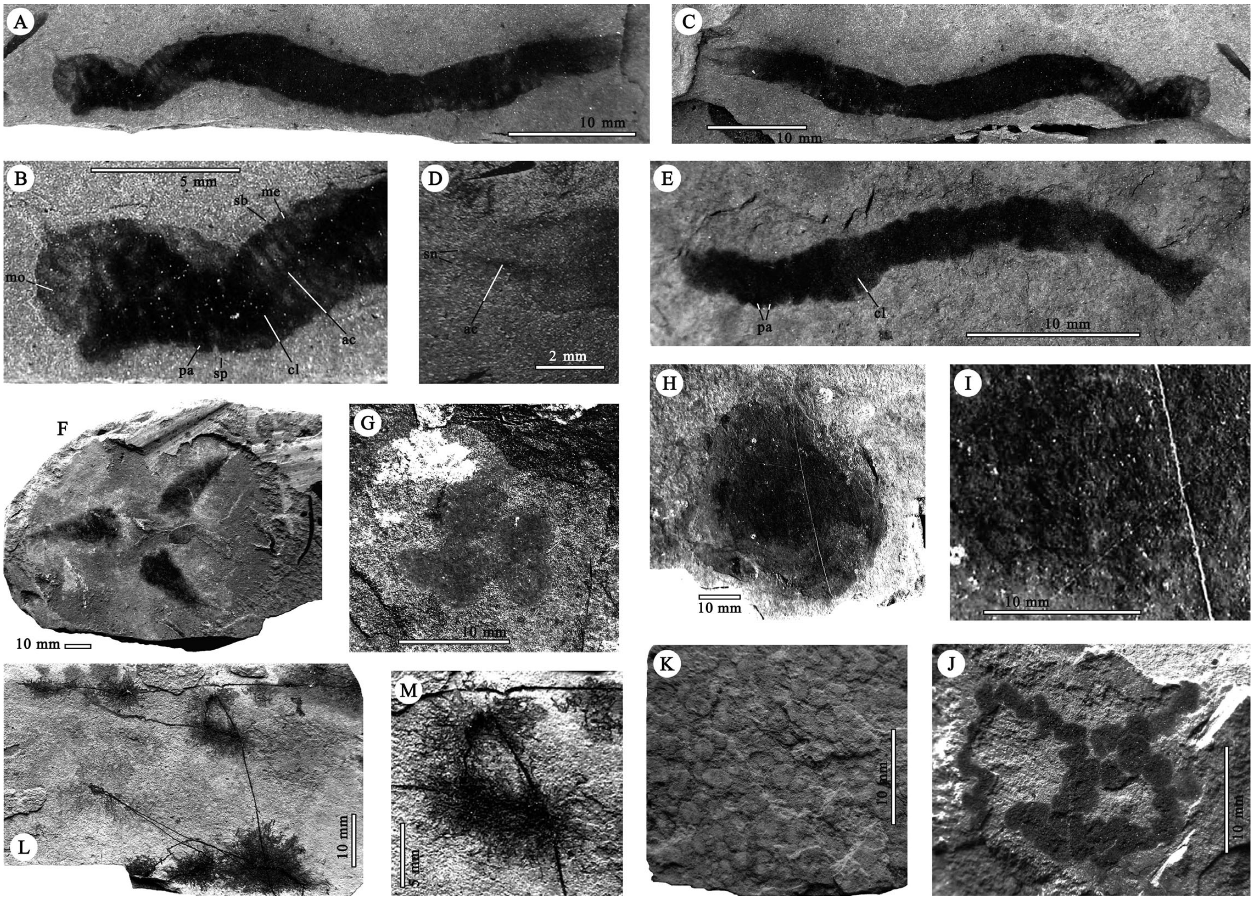

Figure 3. Epibenthic metazoans and macroalgae from the upper Doushantuo Formation (Ediacaran) of the Yangtze Block, South China. **A, C, E,** *Wenghuiia jiangkouensis* (Wang and Wang, 2008); **B,** magnified view of A, showing details of the forepart; **D,** magnified view of C, showing details of the rear end: ac, alimentary canal; cl, clitellum; me, metamere; mo, mouth; sa, seta around anus; sb, seta on body; sp, seta on parapodia; pa, parapodia; **F, G,** unnamed species of Trilobozoa (Fedonkin, 1985); **H,** *Cyclomedusa* cf. *radiata* (Sprigg, 1947); **I,** magnified view of H, showing details of the central part; **J,** ichnofossil *Linbotulichnus* (Li and Ding *in* Ding *et al.*, 1996); **K,** *Beltanelliformis brunsae* (Menner *in* Keller *et al.*, 1974); **L,** *Globusphyton lineare* (Wang *et al.*, 2007a); **M,** magnified view of L, showing branching filaments radially scattered from a node.

which had a helical structure on its rope-like thallus (Figure 4E–G), and *Sinocylindra yunnanensis* (Chen and Erdtmann, 1991), which had a smooth, ribbon-like compression (Figure 4D). In addition, branched macroalgae were the most abundant in the Miaohe and Wenghui biota. They included *Anomalophyton zhangzhongyini* (Chen *et al.*, 1994a), which had a differentiated main axis and side branchlets (Figure 4H, I), *Doushantuophyton lineare* Chen and *D. rigidulum* Chen, which had dichotomous branching (Figure 4N, J), and *Enteromorphites siniansis* (Zhu and Chen, 1984), which was characterized by dichotomous branching and increasing internode length (Figure 4K). Other branching forms were *Jiangkouphyton guizhouensis* (Wang *et al.*, 2007a), which had main and side branchlets, and gemmiform protuberances on its topmost branchlets (Figure 4L, M), *Konglingiphyton erecta* (Chen and Xiao, 1992), which had dichotomous branches and an increase in the width of the branch segments (see Chen and Xiao, 1992, pl. 1, fig. 5; Xiao *et al.*, 2002, figs. 5.13–5.17), *Longifuniculum dissolutum* (Steiner *et al.*, 1992), which possessed a twisted bundle of many dichotomously branching filaments (Figure 4O), *Miaohephyton bifurcatum* Chen (Chen and Xiao, 1991), which had Y-shaped, dichotomous branches (Figure 4S), *Sectoralga wenghuiensis* (Wang *et al.*, 2007a) and *S. typica* Hu (Ding *et al.*, 1996), which had a fan-shaped thallus that was bundled by dichotomous filaments (Figure 4Q, R, U), *Wenghuiphyton erecta* (Wang *et al.*, 2007a), which had dichotomously branching foliation and a complex rhizoid system of the columnar and fila-

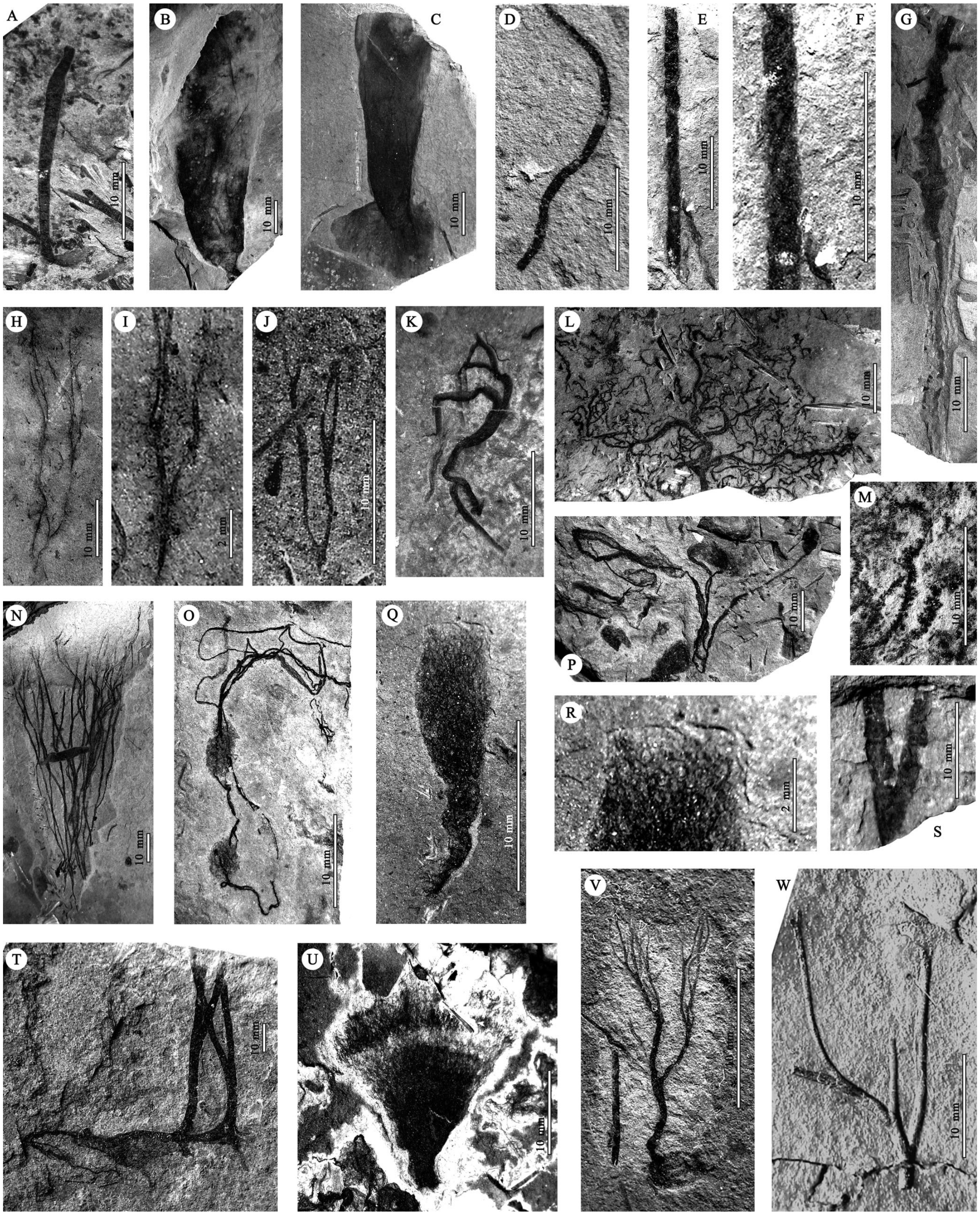

Figure 4. Erect-benthic macroalgae from the upper Doushantuo Formation (middle Ediacaran) of the Yangtze Block, South China. **A,** *Baculiphyca taeniata* (Yuan *et al*., 1995); **B, C,** *Gesinella hunanensis* (Steiner *et al*., 1992); **D,** *Sinocylindra yunnanensis* (Chen and Erdtmann, 1991); **E, G,** *Liulingjitaenia alloplecta* (Chen and Xiao, 1992); **F,** magnified view of E, showing a helical structure on the thallus; **H,** *Anomalophyton zhangzhongyini* (Chen *et al*., 1994b); **I,** magnified view of H, showing the main axis and side branchlets; **J,** *Doushantuophyton lineare* (Chen in Chen and Xiao, 1991); **K,** *Enteromorphites siniansis* (Zhu and Chen, 1984); **L,** *Jiangkouphyton guizhouensis* (Wang *et al.*, 2007a); **M,** magnified view of L, showing gemmiform protuberances on the end branchlets; **N,** *Doushantuophyton rigidulum* Chen (Chen *et al*., 1994a); **O, P,** *Longifuniculum dissolutum* (Steiner *et al*., 1992); **Q,** *Sectoralga wenghuiensis* (Wang *et al*., 2007a); **R,** magnified view of Q, showing the dichotomous filaments; **S,** *Miaohephyton bifurcatum* (Chen in Chen and Xiao, 1991); **T,** *Wenghuiphyton erecta* (Wang *et al*., 2007a); **U,** *Sectoralga typica* (Hu in Ding et al., 1996); **V,** *Zhongbaodaophyton robustus* (Wang *et al*., 2007a); **W,** *Zhongbaodaophyton crassa* (Chen *et al*., 1994b).

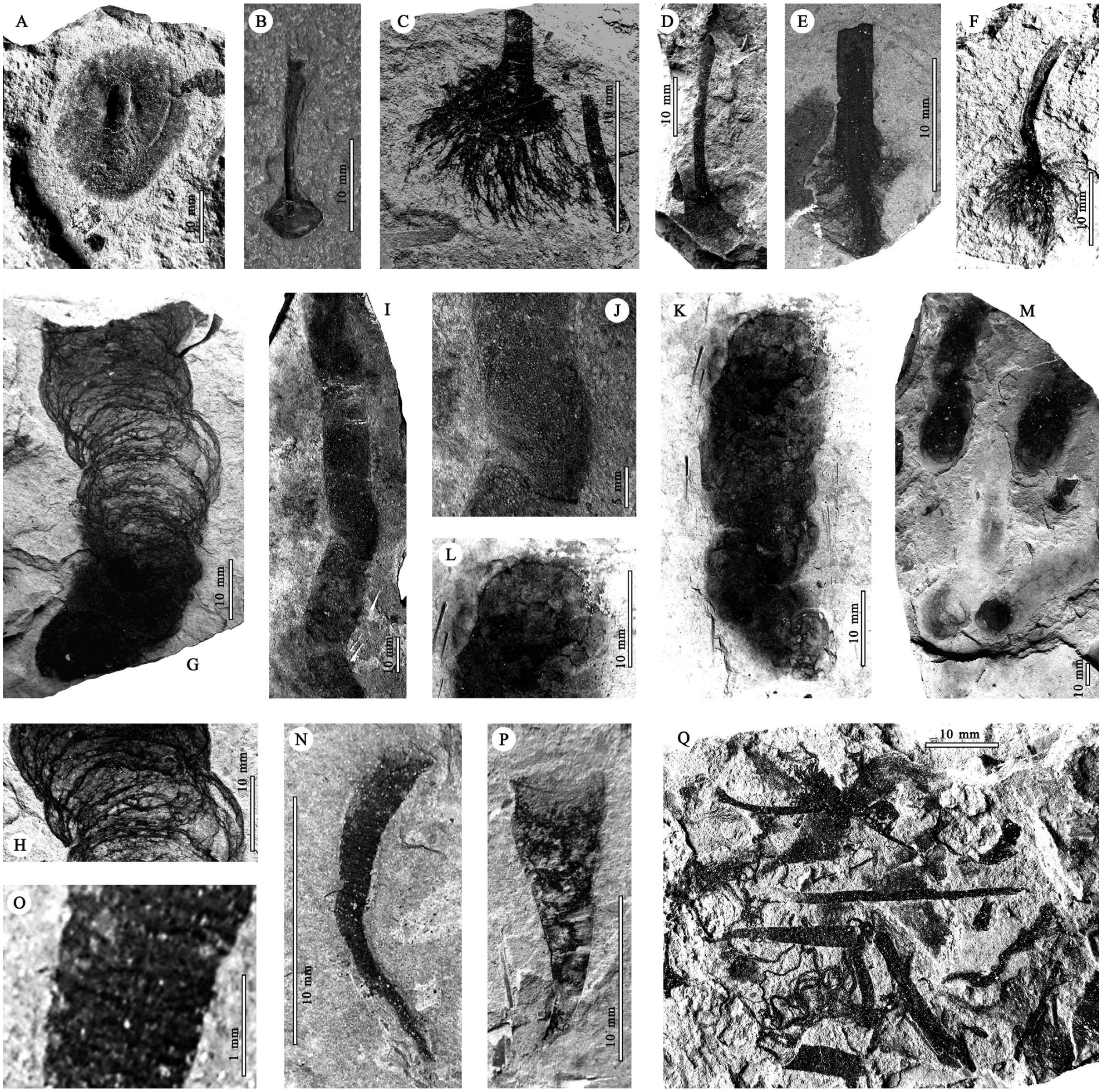

Figure 5. Benthic-fixed metazoans and macroalgal holdfasts from the upper Doushantuo Formation (Ediacaran) of the Yangtze Block, South China. **A, B,** discoidal holdfast; **C,** spherical holdfast;. **D,** asteroidal holdfast; **E, F,** cone-shaped holdfast; **G, I, K,** *Cucullus fraudulentus* (Steiner, 1994); **H,** magnified view of G, showing the complex nonmineralized spongin fiber networks; **J,** magnified view of I, showing the organic wall; **L,** magnified view of K, showing the top pores and the side openings; **M,** two specimens of *Cucullus*; **N, P,** *Protoconites minor* (Chen *et al*., 1994b); **O,** magnified view of N, showing the transverse veins and the longitudinal ridge with tumors; **Q,** distribution of macroscopic algae.

mentous rhizoids (Figure 3T), and *Zhongbaodaophyton crassa* (Chen *et al*., 1994a) and *Z. robustus* (Wang *et al*., 2007a), which had dichotomous branching that was two branchlets in width (Figure 4W, V). In addition, abundant macroalgal holdfasts of unknown affinity have been found, including discoidal (Figure 5A, B), spherical (Figure 5C), asteroidal (Figure 5D), and cone-shaped holdfasts (Figure 5E, F), in both the Miaohe and Wenghui biota. A general feature of the middle-late Ediacaran macroalgae is a large branching or unbranching thallus

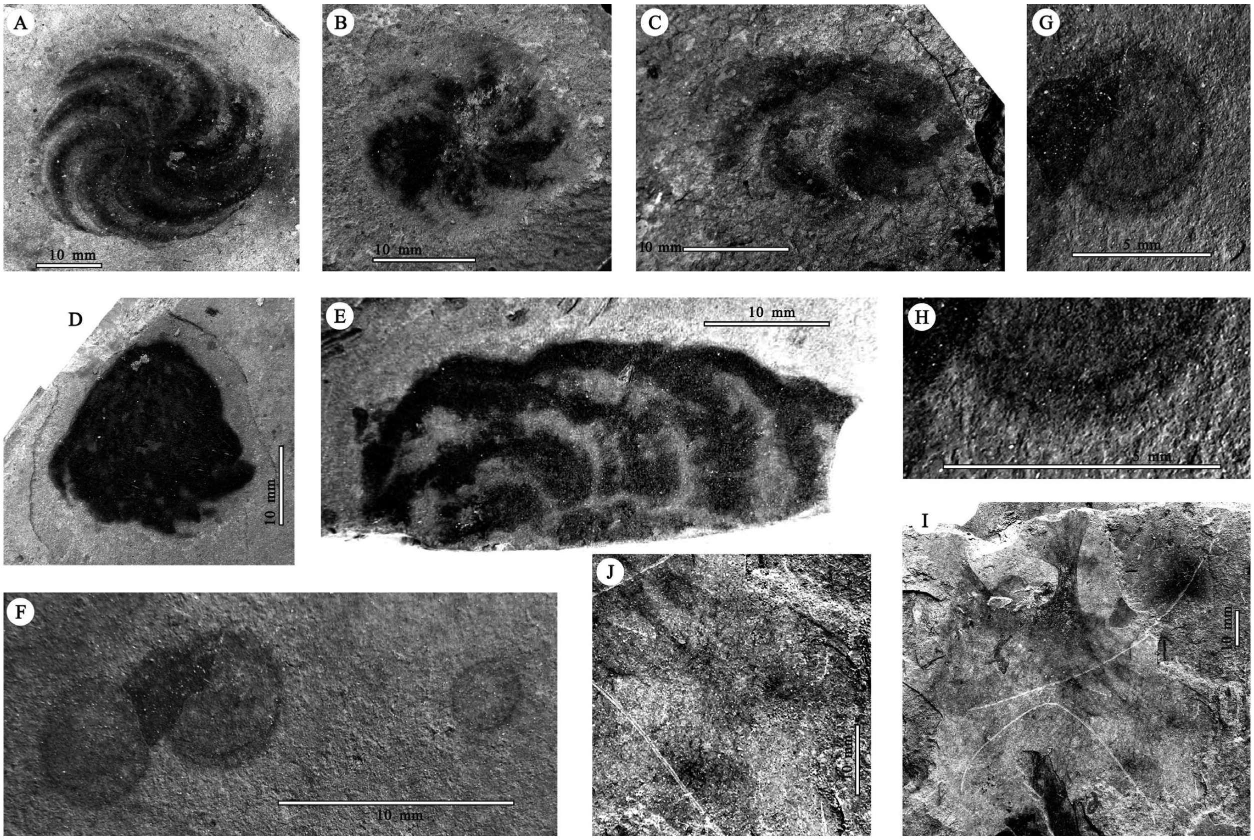

Figure 6. Planktonic metazoans and macroalgae from the upper Doushantuo Formation (Ediacaran) of the Yangtze Block, South China. **A–E,** *Eoandromeda octobrachiata* (Tang *et al.*, 2008), with obverse compressions (A and B), side compressions (C and D), and regularly arranged, feather-like cilia on the eight arms (E); **F,** unknown medusiform metazoan fossil; **G,** magnified view of F; **H,** magnified view of G, showing the tentacles on the discus-body margin; **I,** unknown macroalgal fossil with a wide and large thallus, without a holdfast; **J,** magnified view of I, showing the networks in or on the large thallus.

with a developed holdfast.

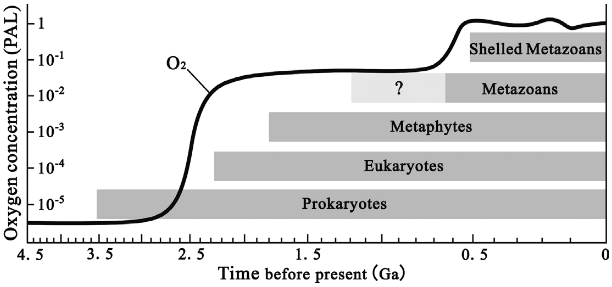

Figure 7. The apparent correlation between changes in atmospheric oxygen and the evolution of life.

In addition, numerous metazoans have been found in this ecological layer. Both elongated, sac-shaped *Cucullus* (Steiner, 1994) (Figure 5G–M) and *Sinospongia* Chen (see Chen and Xiao, 1992, pl. 6, Figs. 1–4; Xiao *et al.*, 2002, Figs. 8.8–8.16, 9.1–9.8) are considered as metazoans (Chen *et al.*, 1994b; Ding *et al.*, 1996; Xiao *et al.*, 2002; Finks and Rigby, 2004; Wang *et al.*, 2007a, 2011; Wang and Wang, 2011). They had an organic wall (Figure 5I, J), complex non-mineralized spongin fiber networks (Figure 5G, H), side openings that served as incurrent canals (Figure 5G–K), and top pores that served as excurrent canals (Figure 4K, L). Wang and Wang (2011) and Wang *et al.* (2011) suggested that *Cucullus fraudulentus* (Figure 5G–M) was a primitive member of the Demospongiae, and that the base of *Cucullus* nestled into the muddy substrate (Figure 5G) while the sacciform body floated in the water. Similarly, the conical *Protoconites minor* (Chen *et al.*, 1994b) (Figure 5N–P), which had a thin wall (see Xiao *et al.*, 2002, Figure 7.12, 7.13; Wang *et al.*, 2007b, pl. 1, Figure 4),

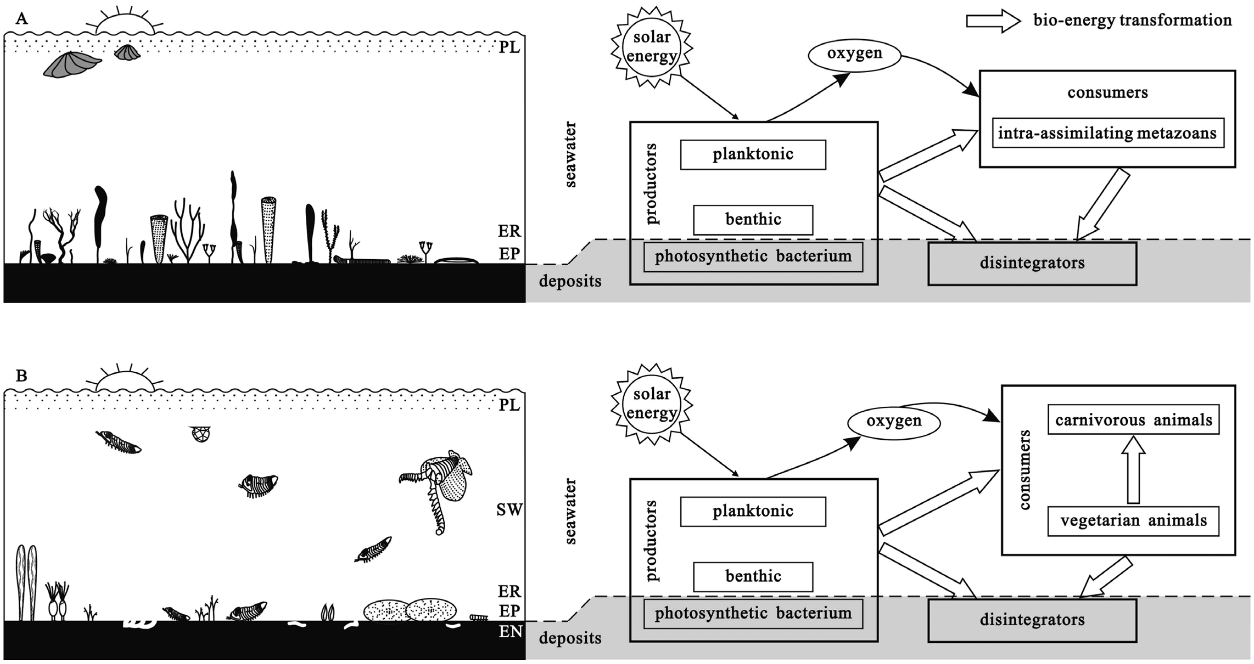

Figure 8. A schematic diagram of Doushantuo paleoecosystems during the Ediacaran and Cambrian Periods, and their bioenergy transformations. **A,** macroorganism paleoecosystem in the Ediacaran Doushantuo; **B,** carnivore paleoecosystem in the Cambrian Period. EN, endogenous layer; EP, epibenthic layer; ER, erect-benthic layer; SW, swimming layer; PL, plankton layer.

an outer sinus opening (Figure 5N), transverse veins (Figure 5N), and a longitudinal ridge with tumors (Figure 5N, O), is considered as a bilateral animal, and that the sharp base was used to insert it into the sediment.

Planktonic layer—Among the upper Doushantuo macrobiota in the Yangtze Block, *Eoandromeda octobrachiata* (Tang *et al.*, 2008), a discoid compression fossil with eight spiral arms (Figure 6A–E), is regarded as a benthic metazoan. However, there are many feather-like cilia arranged on the eight arms (Figure 6B, E); therefore, Wang *et al.* (2008) considered *E. octobrachiata* to be a ctenophore. Wang *et al.* (2011) and Tang *et al.* (2011) showed *E. octobrachiata* as an umbrella-shaped morphotype (Figure 6C, D) with a circular or oval polar field, or a central ring, on the center of its body (see Tang *et al.*, 2011, Figure 1L, 1M), and suggested that the species belongs to the Ctenophora, and had a planktonic lifestyle. A small, unknown medusiform macrofossil in the Wenghui biota (Figure 6F–H) may have been a pelagic metazoan, because it had tentacles on the discus-body margin (Figure 6H) and radial and concentric veins on the surface of the discus (Figure 6G, H). In addition, another unknown macroalga had a wide, large thallus, with filamentous networks and was without a holdfast (Figure 6I, J). It may have been a planktonic macroalga that floated on the surface, using its large thallus and filamentous networks.

Trophic structure and relationships between different species

The food chain is important in maintaining the existence and development of ecosystems (Stiling, 1996; Wang and Wang, 2007). In middle-late Ediacaran paleoecosystems, macroalgae with large thallii flourished in both number and diversity, suggesting that primary producers mainly consisted of photosynthetic microorganisms and macroalgae.

Consumers in the middle-late Ediacaran macrobiota mainly consisted of feeding and filter-feeding metazoans with *in vivo* digestion, and there is no evidence for the chemosymbiotic metazoan proposed by Seilacher (1989) and Buss and Seilacher (1994). *Cucullus*, which possessed top pores and side openings, is considered as a demosponge (Ding *et al.*, 1996; Wang and Wang, 2011; Wang *et al.*, 2011), a filter feeder. The discoidal *Cyclomedusa*, and the Trilobozoa, are thought to have been mat encrusters, which were attached to the biomat and fed by filtration. *Eoandromeda*, a pelagic ctenophore, had regularly arranged feather-like cilia, which have been interpreted as a quivering soft tissue that produced an endocentric current; so it may have been an actively feeding metazoan. A small medusiform metazoan with tentacles may have been a filter feeder. Moreover, the bilaterally symmetrical *Wenghuiia* was an actively feeding animal, because it contained not only a complete digestive system with a mouth, an alimentary canal and an anus, but also some moving organs, such as metameres and parapodia. Therefore, actively feeding and intra-assimilating consumers were already present in the middle-late Ediacaran Period.

The process of *in vivo* digestion more effectively utilizes the bioenergy available to organisms, and decreases bioenergy loss during energy transformation. The macroorganism paleoecosystems of the middle-late Ediacaran Period in the Yangtze Block, which were dominated by branching and unbranching macroalgae and were characterized by the emergence of actively feeding metazoans, represent the development of more efficient bioenergy transformation and multilevel trophic structures, or ecological pyramids (Figure 8A).

Discussion

In the biomat paleoecosystem on the sediment surface, microorganisms inefficiently used bioenergy and there was little or no competition. The habitats of organisms in the plankton-eukaryote paleoecosystem extended to the water column and the water's surface. Macroalgae in the macroalgal paleoecosystem overcame active competition by greatly increasing the sunlight-receiving area of their thalli, in order to increase photosynthesis. Active competition could accelerate evolution; however, bioenergy transformation in the water, biomat, plankton-eukaryote, and macroalgal paleoecosystems resulted in greater bioenergy loss.

During the middle-late Ediacaran Period, numerous macroorganisms, including abundant macroalgae and feeding and filter-feeding metazoans such as sponges (e.g. Du and Wang, 2012; Du *et al.*, 2015), were distributed from the sedimentary surface to the water's surface in the Yangtze Sea, and formed a new paleoecosystem, the macroorganism paleoecosystem, which was characterized by the emergence of feeding metazoans (Figure 8A).

The significant reduction in microbial mats (Olcott *et al.*, 2002) during the Ediacaran Period may have been due to the emergence of metazoans (Awramik, 1971; Bottjer and Clapham, 2006). In contrast to the chemosymbiotic metazoans in the Ediacaran fauna from Australia and Russia (Seilacher, 1989; Buss and Seilacher, 1994), feeding and filter-feeding metazoans lived side-by-side with macroalgae in the middle-late Ediacaran macrobiota, and the abundant macroalgae provided the main food source for the metazoans (Chen *et al.*, 1994a; Wang *et al.*, 2007a, 2011). The food chain in the middle-late Ediacaran macrobiota allowed consumers to transform bioenergy more efficiently, and to decrease bioenergy loss during assimilation. In addition, macroscopic algae and metazoans could support themselves using their holdfasts and bases, consequently changing their ecological niches, directly or indirectly.

Most modern macroorganisms depend on oxygen to metabolize and reproduce, so their evolution and development are closely related to increases in atmospheric oxygen levels (Figure 7). Nursall (1959) suggested that the increase in oxygen in the atmosphere accelerated the evolution of multicellular organisms during the Proterozoic. Some researchers (see Berkner and Marshall, 1965; Towe, 1970; Kasting *et al.*, 1992) have suggested that the increase in atmospheric oxygen improved the metabolism of multicellular organisms. Runnegar (1982) suggested that *Dickinsonia*, a bilateral metazoan of the Ediacaran fauna from South Australia, required atmospheric oxygen levels of at least 6–10% present atmospheric level. The emergence of benthic metazoans, such as *Wenghuiia*, *Protoconites*, and the ichnofossil *Linbotulichnus*, suggests that the oxygen concentration at the bottom of the sea had risen to a relatively high level in the middle-late Ediacaran Period. In addition, geochemical studies on the Doushantuo Formation support an increase in oxygen during the Ediacaran Period (Zhang *et al.*, 2003; Wu *et al.*, 2006; Halverson and Hurtgen, 2007; McFadden *et al.*, 2008; Li *et al.*, 2010). The interaction between the environment and life, particularly the oxygen increase and the appearance of abundant and diverse macroalgae, resulted in many consequences. In the middle-late Ediacaran Period, the emergence of numerous macroalgae on the seafloor had broken the domination of microorganisms on the depositional surface, and greatly increased photosynthetic efficiency, which increased the oxygen concentration in the water (Chen *et al.*, 1994b, 2000; Wang *et al.*, 2005, 2007a, 2011). Moreover, the branching of macroalgae increased competition for sunlight, and increased the oxygen content of water more effectively. With increasing competition, the macroalgae in the middle-late Ediacaran Period developed more branches and enlarged their thallii (such as the planktonic macroalga with a wide thallus), in order to increase oxygen production through photosynthesis.

In the middle-late Ediacaran macroorganism paleoecosystems, organisms extended their habitat to the water column and surface from the sediment surface, mainly because of competition for sunlight, and enhanced their ability to change their surroundings and decrease their bioenergy loss during bioenergy transformations.

In the Cambrian Period, the emergence of shelled organisms and large carnivorous animals (Hou *et al.*, 1995; Chen *et al.*, 1996; Jiang, 2002; Wang and Wang, 2007) suggests that intensive competition between organisms strengthened the multilevel ecological pyramid. In addition, the fossil records of abundant nektonic and infaunal animals suggest that a swimming layer in the water column and an endogenous layer under the seafloor had been added to the paleoecosystem (Banks, 1970; Crimes, 1987; Chen *et al.*, 1996; Droser *et al.*, 1999, 2002; Jiang, 2002; Wang and Wang, 2006, 2007). The emergence of carnivorous paleoecosystems in the Cambrian Period (Figure 8B) was accompanied by more intense competition between organisms and further environmental change, which accelerated evolution and the increase in atmospheric oxygen that resulted in the Cambrian explosion (Berkner and Marshall, 1965; Chen *et al.*, 1996; Chen, 2002; Kump, 2008). Therefore, the macroorganism paleoecosystems of the late Ediacaran Period, when feeding metazoans and a multilevel ecological pyramid emerged, were a prelude to the Cambrian explosion.

Conclusions

The early paleoecosystems developed from biomat paleoecosystems, through plankton-eukaryote, macroalgal, and macroorganism paleoecosystems, to carnivore paleoecosystems. In the biomat paleoecosystem, only microbes were distributed on the depositional surface, whereas the ecological niches of the organisms extended to the water surface in the plankton-eukaryote paleoecosystem. The macroorganism paleoecosystem was characterized by the presence of macroalgae and filter-feeding metazoans. In the early paleoecosystems, atmospheric oxygen gradually increased, which enhanced more efficient metabolism and increased competition, and further accelerated evolution.

In the macroorganism paleoecosystem of the Yangtze Block, in the middle of the Ediacaran Period, abundant and diverse macroscopic organisms, including branching and unbranching macroalgae and bilaterally and radially symmetrical metazoans, lived in a warm and calm tropical ocean with ample sunlight, oxygen, and nutrients. The habitats of the organisms can be subdivided into three ecological layers in morphology and paleoecology: the epibenthic layer, the erect-benthic layer and the planktonic layer. The actively feeding and filter-feeding metazoans stood at the top of a multilevel ecological pyramid and the appearance of macroorganism paleoecosystems during the deposition of the upper Doushantuo Formation accelerated the evolution of the entire paleoecosystem, and was a prelude to the Cambrian explosion.

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