Contents lists available at ScienceDirect

Precambrian Research

journal homepage: www.elsevier.com/locate/precamres

Phosphatized microfossils from the Miaohe Member of South China and their implications for the terminal Ediacaran biodiversity decline

Qin Ye[a,*], Zhihui An[b], Yang Yu[a], Ze Zhou[a], Jun Hu[a], Jinnan Tong[a], Shuhai Xiao[c,*]

[a] State Key Laboratory of Biogeology and Environmental Geology, School of Earth Sciences, Institute of Advanced Studies, China University of Geosciences, Wuhan 430074, China
[b] Hubei Key Laboratory of Paleontology and Geological Environment Evolution, Wuhan Center of China Geological Survey, Wuhan 430205, China
[c] Department of Geosciences, Virginia Tech, Blacksburg, VA 24061, USA

ARTICLE INFO

Keywords:
Phosphatized microfossils
Multicellular algae
Spheroidal fossils
Miaohe Member
Late Ediacaran
South China

ABSTRACT

The upper Ediacaran Miaohe Member (~550 Ma) in South China is well known for exceptionally preserved macroscopic carbonaceous compression fossils (i.e., the Miaohe biota) that are pivotal in understanding the marine ecology and environment during the terminal Ediacaran Period. However, micro-organisms, which are also important biotic components of marine ecosystems, are poorly documented and largely limited to simple leiospheres and filaments in the Miaohe Member and equivalent strata in South China and around the world. Here we report a moderately diverse assemblage of cellularly preserved microfossils from phosphorites and siliceous phosphorite nodules and bands of the Miaohe Member at the Maxi section, Hubei Province, South China. Ten named species of eight genera, four open nomenclatures, and two unnamed taxa have been identified, including several multicellular algal fossils and various coccoidal and filamentous cyanobacteria. Abundant spheroidal fossils are morphologically analogous to *Megasphaera*, which has previously been interpreted as a putative metazoan embryo. Together with previously described microfossils from equivalent strata of Miaohe Member, these microfossils expand our understanding of the evolution of marine ecosystems prior to the Cambrian explosion. The late Ediacaran Maxi assemblage and the early Ediacaran Weng'an biota, both preserved through phosphatization, share several taxa. Notably, Doushantuo-Pertatataka-type acanthomorphs (DPAs) are absent from the Maxi assemblage but abundant in the Weng'an biota, consistent with a late Ediacaran decline of DPAs, which may have ushered in the terminal Ediacaran decline of soft-bodied macro-organisms of the Ediacara biota during the Kotlin crisis or in the last 10 million years of the Ediacaran Period.

1. Introduction

The marine ecosystem of the middle to late Ediacaran is characterized by Ediacara-type macrofossils such as those preserved in the Ediacara biota in South Australia, as well as macroalgal carbonaceous compressions such as those from the Miaohe biota (Xiao and Narbonne, 2020). The 575–539 Ma Ediacara biota contains a group of large, structurally complex, and phylogenetically diverse multicellular organisms, including various animals (Droser et al., 2017; Narbonne, 2005; Xiao et al., 2021; Xiao and Laflamme, 2009). The Miaohe biota, which is capped by a 550 Ma ash bed (Condon et al., 2005; Yang et al., 2021), consists of a diverse assemblage of macroscopic algae and problematica (Tang et al., 2008; Xiao et al., 2002; Ye et al., 2019; Zhu et al., 2008). These exceptionally preserved fossil assemblages are important archives of the diversity of macroscopic algae and animals. Currently available data seem to show that the diversity of macrofossils begins to decline around 550 Ma (Darroch et al., 2018; Evans et al., 2022). However, the paleontological record of late Ediacaran micro-organisms and particularly microscopic eukaryotes are relatively rare (Ding et al., 2019; Germs et al., 1986; Knoll and Swett, 1987; Moczydłowska, 1991; Palacios et al., 2017; Volkova et al., 1983; Yin and Gao, 1995), hampering a complete understanding of the late Ediacaran marine ecosystem. To extend these records, here we report new cellularly preserved microfossils embedded in phosphorites and siliceous phosphatic nodules/bands from the late Ediacaran Miaohe Member of the Maxi section in Hubei Province of South China. This phosphatized microfossil assemblage consists of 16 recognizable taxa, including morphological analogs of primary producers and putative animal

---

* Corresponding authors.
E-mail addresses: yeqin@cug.edu.cn (Q. Ye), xiao@vt.edu (S. Xiao).

https://doi.org/10.1016/j.precamres.2023.107001
Received 9 November 2022; Received in revised form 12 February 2023; Accepted 14 February 2023

embryos. The Maxi microfossil assemblage thus provides important data on late Ediacaran paleontology and biostratigraphy, offering new insights into the marine ecosystem on the eve of the Cambrian explosion.

2. Geological setting

Ediacaran strata are well exposed around the Huangling Anticline of South China (Fig. 1A) and are composed of the Doushantuo and Dengying formations. As exemplified by the well-studied Jiulongwan section in the southern limb of the Huangling Anticline (McFadden et al., 2008), the Doushantuo Formation is subdivided into four lithostratigraphic members, including, in ascending order, the basal Ediacaran cap dolostone (Member I), alternating black shale and dolostone (Member II), medium- to thin-bedded dolostone and limestone (Member III), and organic-rich black shale (Member IV). The succeeding Dengying Formation consists of three lithostratigraphic members, which are thick-bedded dolostone of the Hamajing Member, thin-bedded limestone of the Shibantan Member, and thick-bedded dolostone of the Baimatuo Member (Zhou and Xiao, 2007). In the western Huangling Anticline where the studied section is located, however, there is a fossiliferous black shale unit known as the Miaohe Member (Fig. 1B; Xiao et al., 2002; Ye et al., 2019), which has been considered as partially equivalent to either the Shibantan Member (correlation “A” in Fig. 1B; An et al., 2015) or the Member IV (correlation “Z” in Fig. 1B; Xiao et al., 2017; Zhou et al., 2017b). In this paper, we follow correlation “A”.

The sample horizons studied here consist of siliceous phosphorite nodules and bands in the Miaohe Member, as well as a phosphorite bed at the base of the Miaohe Member, at the Maxi section, northwestern Huangling Anticline, Hubei Province, South China (Fig. 1; Schwid et al., 2021; Ye et al., 2019). The Miaohe Member is underlain by a dolostone unit and another black shale unit (Fig. 1B), which are denoted as the upper dolostone and lower black shale (Zhou et al., 2017b). Abundant macroscopic carbonaceous compressions have been reported from the basal Miaohe Member (Ye et al., 2019). An ash bed at the topmost Miaohe Member at the Jiuqunao section in the southwestern Huangling Anticline was dated at 551.1 ± 0.7 Ma (Condon et al., 2005; revised as 550.1 ± 0.6 Ma, Yang et al., 2021), placing a minimum age constraint on the Miaohe Member. Additionally, carbon isotope chemostratigraphic data indicate that the Miaohe Member postdates the Shuram negative carbon isotope excursion, which is equivalent to the negative excursion EN3 recorded in the upper Member III of the Doushantuo Formation in South China (e.g., Jiang et al., 2007; Zhou and Xiao, 2007; Zhu et al., 2007). Insofar as the Shuram excursion is constrained between 574.0 ± 4.7 Ma and 567.3 ± 3.0 Ma based on Re-Os ages from northwestern Canada (Rooney et al., 2020), the Miaohe Member is younger than 567.3 ± 3.0 Ma. Thus, the sampled horizons at the Maxi section are between ~ 567 Ma and ~ 550 Ma, regardless of whether the Miaohe Member is partially correlated with the Shibantan Member or Member IV (An et al., 2015; Zhou et al., 2017b).

3. Material and methods

A total of 83 petrographic thin sections, each with a thickness of ~ 50 μm, were prepared for this study. Microfossils were examined under a ZEISS Axioscope.A1 transmitted light microscope and digitally photographed using an Axiocam 506 camera. Their positions were recorded using Zeiss stage coordinates and their dimensions were measured using the Image J software. All thin sections are reposited at the China University of Geosciences (Wuhan), China.

4. Results: Morphological diversity of microfossils

A total of 16 morphological microfossil taxa (Figs. 2–6; Supplementary Material) have been identified from the phosphorite bed and phosphorite nodules and bands of the Miaohe Member at the Maxi section. Of these, coccoidal and filamentous cyanobacterial fossils were found in almost all fossiliferous samples and consist of six species, including *Gloeodiniopsis lamellosa* (Fig. 2A–B), *Polytrichoides lineatus* (Fig. 2C), *Salome nunavutensis* (Fig. 2D), *Obruchevella minor* (Fig. 2E), *Oscillatoriopsis obtusa*, and *Siphonophycus* spp. (Fig. 2F–G). They are typically preserved as individual coccoids and filaments or as small aggregates. These fossils likely represent smooth-walled spheroidal and tubular sheaths, the latter of which were often loosely or tightly intertwined to form microbial mats, which may have been reworked to form mat fragments. In addition, simple leiospheres are present in most fossiliferous thin sections of the Miaohe Member (Fig. 2H).

Many multicellular algal thalli were discovered (Figs. 3–5) and some of them are exceptionally preserved with anatomical details (Figs. 3–4,

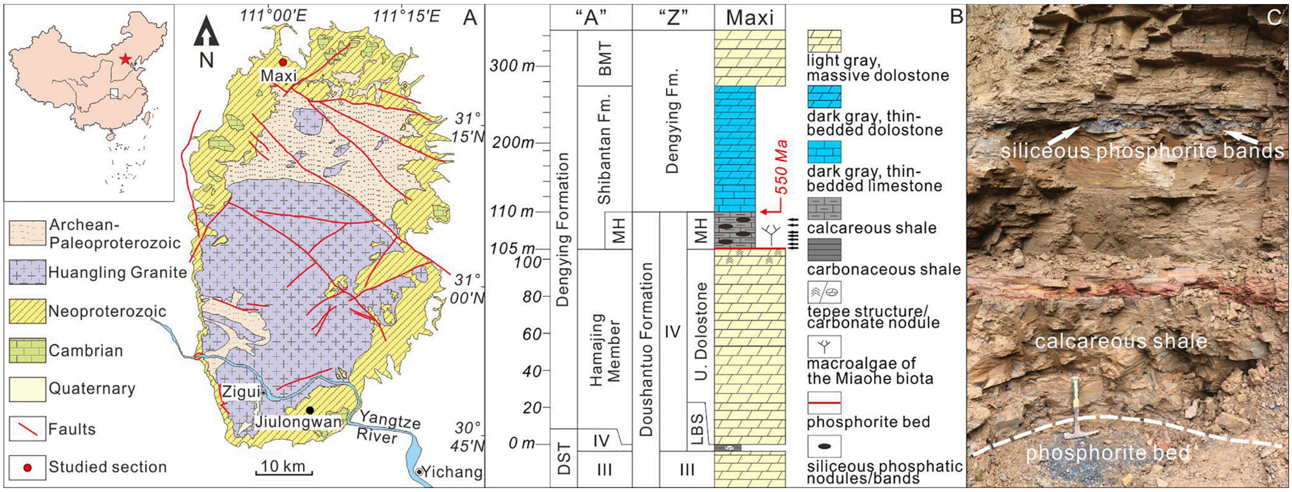

Fig. 1. Simplified geological map, stratigraphic column, and an outcrop photograph of the Miaohe Member at the Maxi section. (A) Locality map of Huangling Anticline (rectangle in inset map of China, where the red star marks Beijing), showing the location of the Maxi section, marked by a red dot. (B) Stratigraphic column of the upper Ediacaran at the Maxi section (Ye et al., 2019), showing the two possible correlation schemes of An et al. (2015; ‘A’) and Zhou et al. (2017b; ‘Z’). Black arrows denote microfossil-bearing horizons, and red arrow denotes the ~ 550 Ma age constraint based on Condon et al. (2005) and Yang et al. (2021). Note scale changes at a stratigraphic height of 105 m. (C) A field photograph of the fossiliferous interval of the Miaohe Member at Maxi. Rock hammer (28 cm) for scale. Abbreviations: DST, Doushantuo Formation; III and IV, Member III and IV of Doushantuo Formation; BMT, Baimatuo Member of Dengying Formation; MH, Miaohe Member; LBS, Lower Black Shale; U. Dolostone, upper dolostone. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

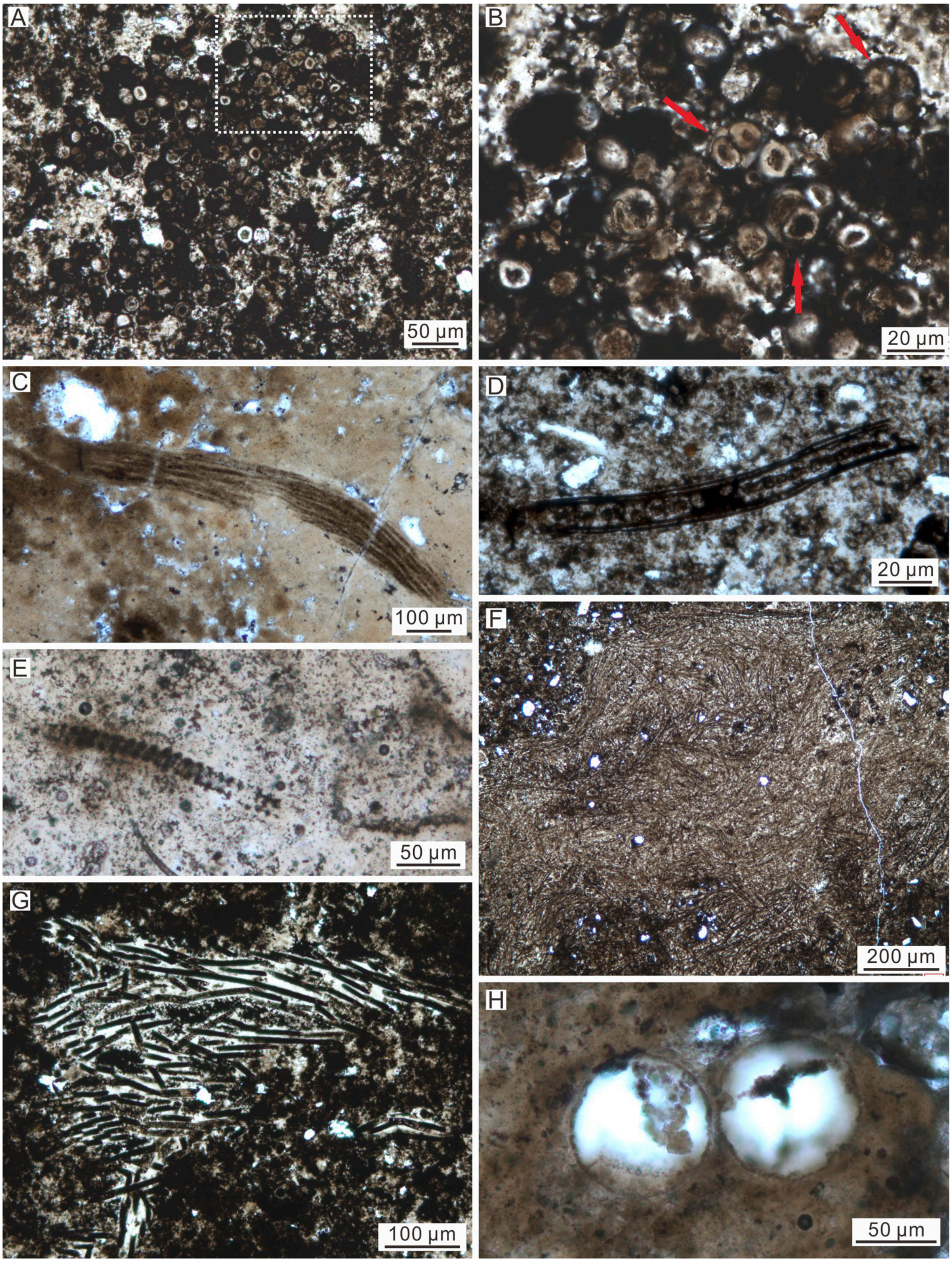

Fig. 2. Prokaryotes from the Miaohe Member at Maxi. A–B: *Gloeodiniopsis lamellosa*, MX-grey-1p-94 (108.2 × 11). B: Magnified view of area marked by white rectangle in (A). Arrows denote cells with sheaths and envelopes. C: *Polytrichoides lineatus*, 21MX-h+1.2 m-2-1 (19.4 × 108.8). D: *Salome nunavutensis*, MX-grey-1p-48 (83.5 × 13.7). E: *Obruchevella minor*, 21MX-h+1.2 m-1-4 (12.3 × 94.6). F–G: *Siphonophycus* spp. F: MX-grey-1-②-20 (93 × 22). G: MX-grey-3-5 (104 × 6.7). H: *Leiosphaeridia jacutica*, 21MX-h+1.2 m-9-4 (11.8 × 97.3).

5A–C). These microfossils are classified as *Archaeophycus yunnanensis* (Fig. 3A–B), *Wengania exquisita* (Fig. 3C–D), *W. globosa* (Fig. 3F–G), *W. minuta* (Fig. 3E), *Thallophyca* sp. (Fig. 4A–D), *Paramecia* sp. (Fig. 4E–H), and two unnamed species (Fig. 5A–D).

Archaeophycus yunnanensis occurs as dyads, tetrads, octads, and loosely to irregularly packed polyhedral to spheroidal cells that form a colony (Fig. 3A–B). *Wengania* is characterized by a globular thallus with tightly packed cuboidal, polyhedral, and irregularly shaped cells (Zhang, 1989; Zhang et al., 1998). Three species are identified in the Miaohe Member: *W. exquisita*, *W. globosa*, and *W. minuta*. *Wengania globosa* is ~ 520.7 μm in diameter and consists of polyhedral or cuboidal cells (3.3–7.4 μm) that are regularly organized in parallel or slightly

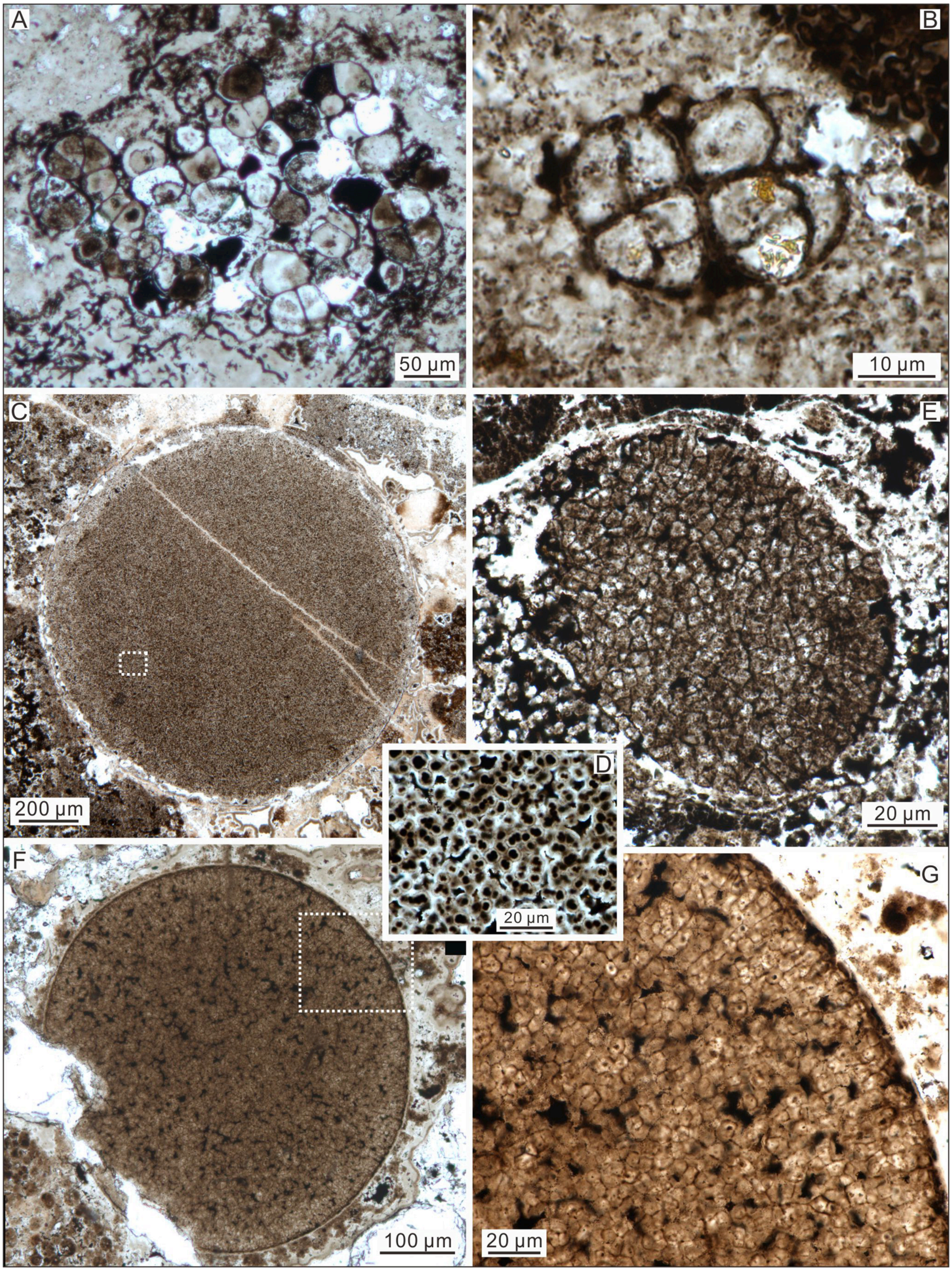

Fig. 3. Multicellular algae from the Miaohe Member at Maxi. A–B: *Archaeophycus yunnanensis*. A: MX-grey-1-③-18 (103.4 × 11). B: MX-grey-3-3 (91 × 21). C–D: *Wengania exquisita*, 21MX-h+40 cm-1-4 (22 × 99). D: Magnified view of area marked by white rectangle in (C). E: *Wengania minuta*, 21MX-grey-1-③-1 (94 × 14). F–G: *Wengania globosa*, 21MX-grey-7-1 (101 × 5). G: Magnified view of area marked by white rectangle in (F).

diverging rows (Fig. 3F–G). *Wengania exquisita* has relatively small polyhedral cells (2.0–5.6 μm) that are tightly and irregularly arranged (Fig. 3C–D). *Wengania minuta* is comparatively smaller than the other two species (Fig. 3E; thallus diameter ~ 97.7 μm, cell diameter 2.8–4.0 μm), and it may represent a juvenile stage of *W. exquisita* since these two taxa are similar in cell arrangement within the thallus (Xiao, 2004).

Two Maxi microfossils, one of which is illustrated in Fig. 4A–D, are tentatively assigned to the genus *Thallophyca*, whose key feature is medulla-cortex thallus differentiation (Zhang, 1989; Zhang et al., 1998). The Maxi specimens, identified as *Thallophyca* sp., are spheroidal to ellipsoidal in overall shape (1546.0–1687.9 μm in thallus diameter) and their medullary cells are arrayed as outward diverging splays of

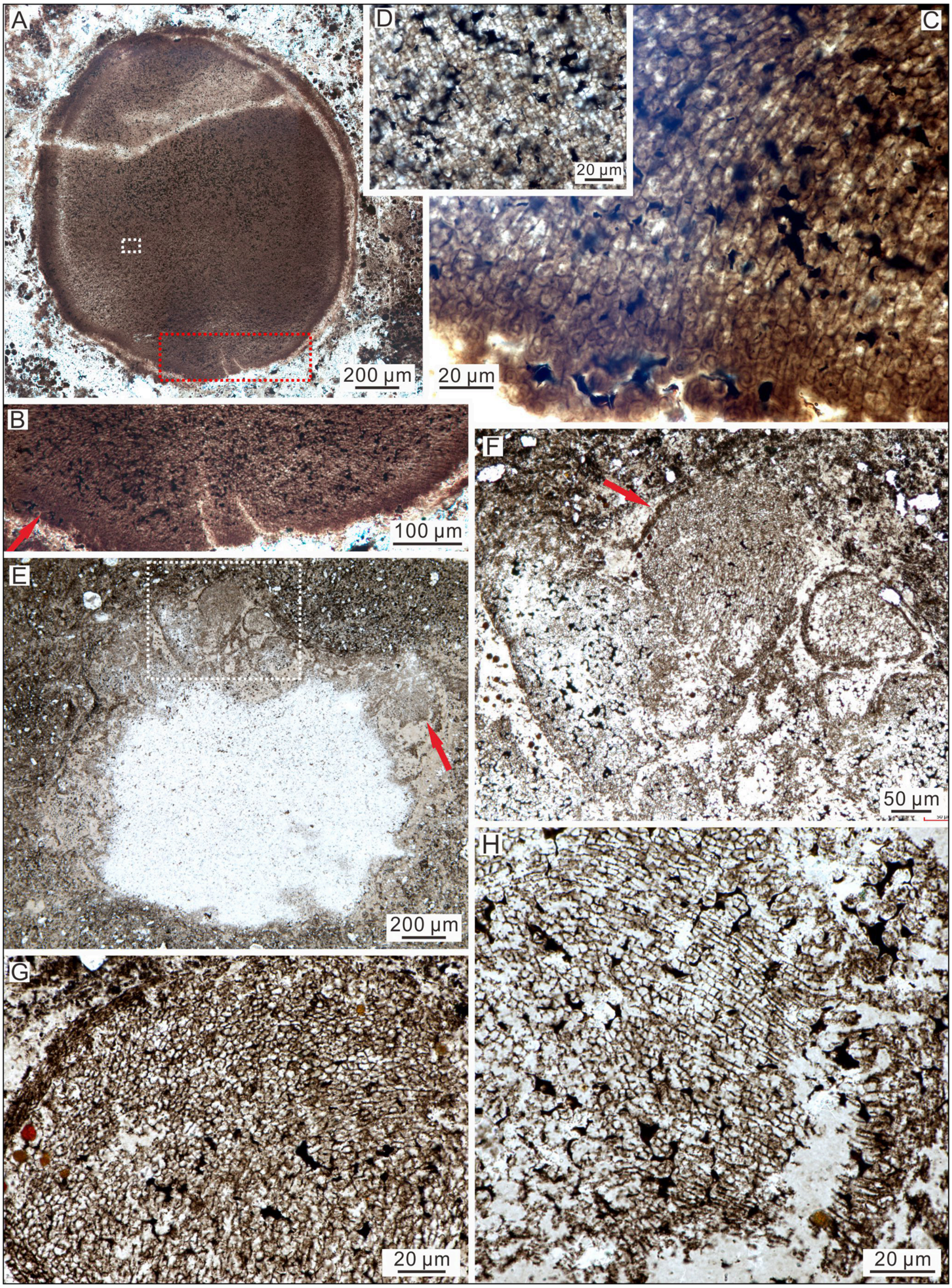

Fig. 4. Multicellular algae from the Miaohe Member at Maxi. A–D: *Thallophyca* sp., 21MX-grey-7-5 (103 × 2.8). B–D: Magnified views of areas marked by red rectangle in (A), red arrow in (B), and white rectangle in (A), respectively. E–H: *Paramecia* sp., 21MX-grey-1-③-7 (95.5 × 3.5). F, H: Magnified views of areas in (E) marked by white rectangle and red arrow, respectively. G, Magnified view of area marked by red arrow in (F). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

filaments or cell fountains (Fig. 4A–C), indicating pseudoparenchymatous thallus organization. The cells at the outer or cortical portion of the thallus in specimens of *Thallophyca* sp. are commonly enlarged (generally 4.5–6.9 μm in diameter vs. 2.3–5.2 μm for the inner or medullar cells), possibly representing meristematic thallus growth (Fig. 4C; Xiao et al., 2004), although we cannot rule out the possibility that the larger cortical cells may be a result of taphonomic mineral coating on the cell walls. Regardless, the boundary between the medulla and cortex is transitional in these Maxi specimens, which can be distinguished from *T. ramosa* and *T. corrugata* where this boundary is relatively sharp

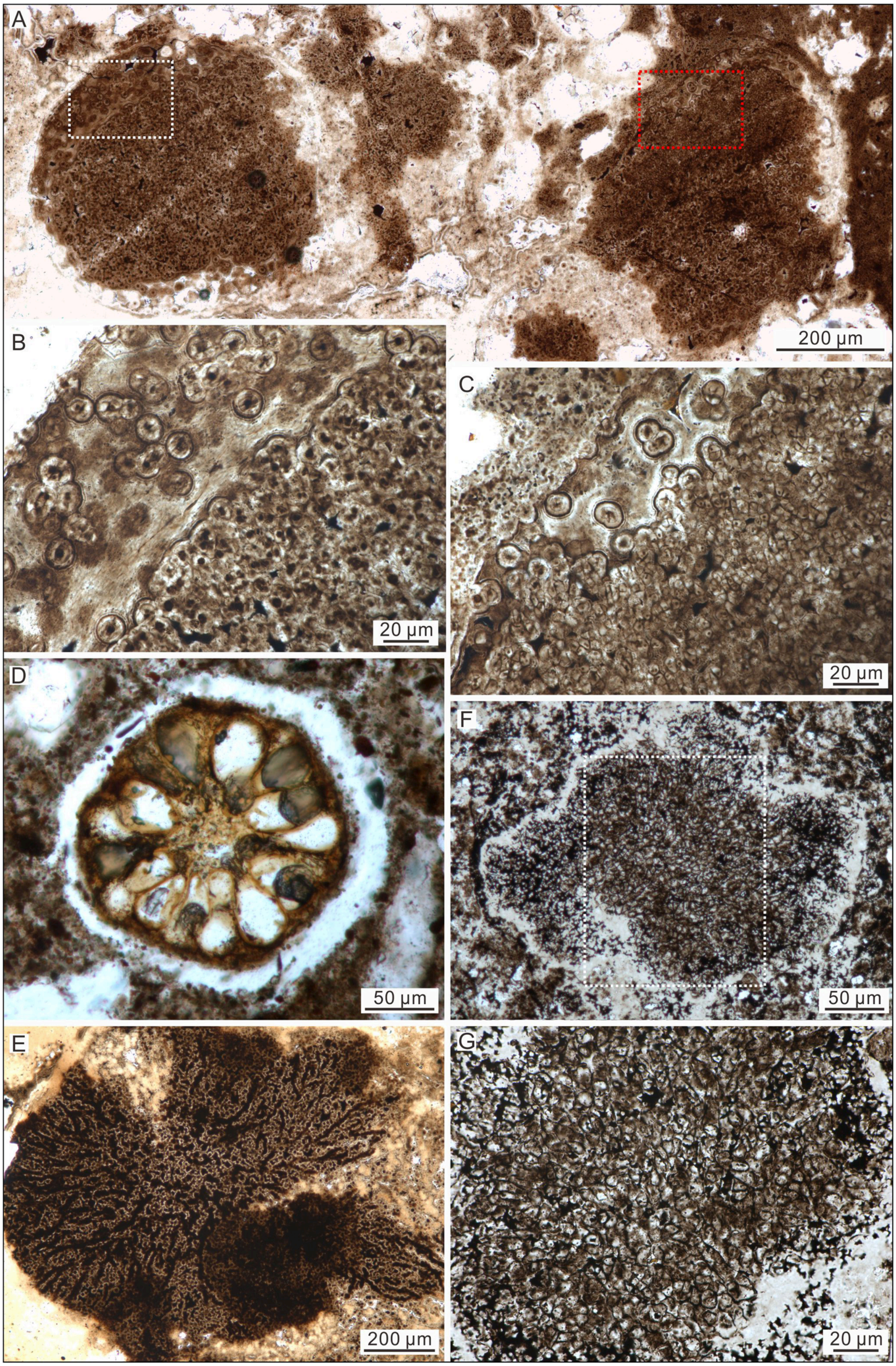

Fig. 5. Multicellular algae from the Miaohe Member at Maxi. A–C: Unnamed species A, 21MX-h+40 cm-1-9 (101.5 × 19). B–C: Magnified views of areas in (A) marked by white and red rectangles, respectively. D: Unnamed species B, 21MX-p-3-9 (84 × 11). E–G: Poorly preserved multicellular algal fossils. E: 21MX-h+40 cm-2-1 (10 × 100.5). F–G: 21MX-grey-2c-2 (109 × 7). G: Magnified view of area marked by white rectangle in (F), with a counterclockwise rotation of 90°. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

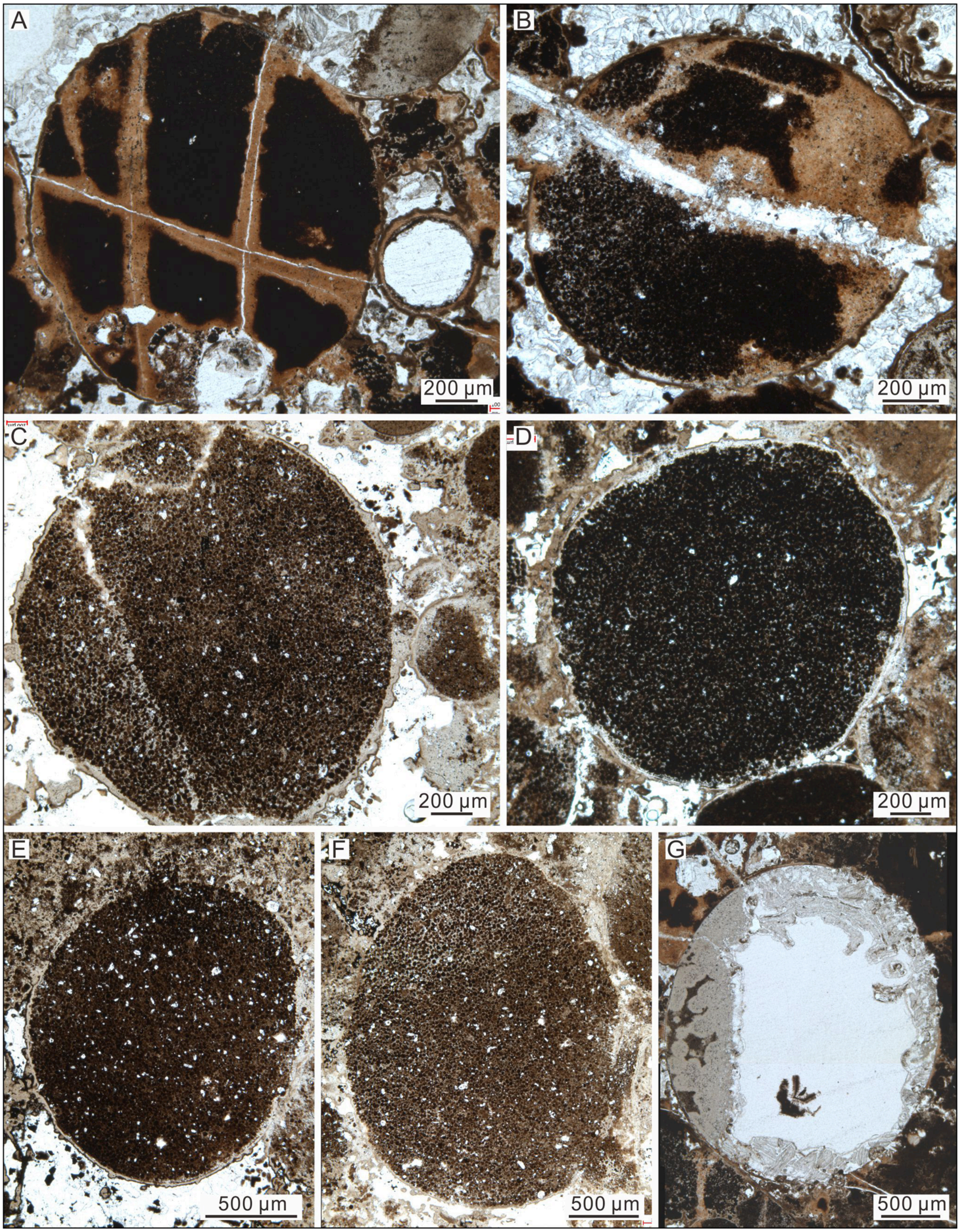

Fig. 6. Spheroidal fossils tentatively identified as *Megasphaera* sp. from the Miaohe Member at Maxi. A: 21MX-h+40 cm-3-8 (17.5 × 103.5). B: 21MX-h+40 cm-3-9 (101 × 12.5). C: 21MX-grey-7-2 (105 × 1.3). D: 21MX-grey-7-4 (97 × 13). E: 21MX-grey-6-1 (97.2 × 2.7). F: 21MX-grey-7-2 (105 × 1.3). G: 21MX-h+40 cm-3-9 (18.5 × 105.8).

(Zhang et al., 1998). However, in terms of thallus size, cell size, and cell fountain structures, the Maxi specimens resemble a specimen from the Weng’an biota identified as possible *Thallophyca* (Xiao et al., 2004, their fig. 22), as well as *Thallophyca* sp. from the Doushantuo Formation in the Zhangcunping area (Ye et al., 2015, their plate III, figs. 1–6) and in the Yangtze Gorges area (Shang and Liu, 2022, their fig.6).

A large specimen up to 2 mm in size is characterized by an ellipsoidal thallus with several irregularly-shaped clusters of rectangle cells (Fig. 4E–H). The clusters are nodular or teardrop-shaped. They show medulla-cortex thallus differentiation, with a peripheral cortex that is 4.0–11.0 μm thick, darker in color, and composed of several layers of smaller and tangentially compressed cells that are 1.8–2.7 μm in length and 0.8–1.9 μm in width (Fig. 4E–F). Medullary cells are generally rectangular in shape, tightly packed in the cluster interior, and larger in size (2.7–3.6 μm in cell length and 1.4–3.0 μm in cell width). Some clusters preserve only the darker cortex whereas the medullary cells are not well preserved (Fig. 4F). The clusters of cells are somewhat similar to *Thallophyca ramosa* in having medulla-cortex zones, but no spheroidal cavities or cell islands are found in the medullary region (Zhang et al., 1998). In addition, the current specimen resembles *Paramecia incognata* since the latter contains many berry-like or spheroidal clusters of cells, known as cell island structures. However, cells in the Maxi specimen are generally rectangular in shape and organized in rows (Fig. 4G), whereas those in cell islands of *P. incognata* are spheroidal, notably larger than those in the surrounding thallus, and sometimes packed in tetrads and octads (see fig. 21.2 and 21.4 of Zhang et al., 1998). Here, the Maxi specimen is tentatively assigned to an open nomenclature *Paramecia* sp.; more specimens are needed to clarify the taxonomical identification.

The thallus of unnamed species A (two specimens, Fig. 5A–C) is spheroidal in shape (542.5–589.9 μm in diameter) and contains numerous small (generally 2.0–3.0 μm), tightly distributed, rectangular cuboidal to polygonal cells. Individual cells typically have a well-defined thin wall and sometimes have a dark inclusion. The thallus periphery is poorly preserved, with no identifiable cells, although sparsely distributed spheroidal structures are present (Fig. 5B–C). These spheroidal structures may represent taphonomically modified cellular structures due to mineral overgrowth. If so, they may represent a cortical zone that is differentiated from the medullary zone with densely packed cells. Morphologically, cells within the thallus of unnamed species A are very similar to those of *Thallophycoides phloeatus* (e.g., fig. 9B, D, F of Zhang and Yuan, 1992), or it may represent a species of *Thallophyca* if its medulla-cortex thallus differentiation can be confirmed.

Unnamed species B (one specimen, Fig. 5D) is circular in overall shape (199.2 μm in diameter) as seen in a thin section. It resembles a flower, consisting of a crown of ~ 15 petaloid structures surrounded by a light-colored corona. The petaloids are teardrop-shaped, with the wider end directed outward. They are 46–67.6 μm in length and 18.7–42.0 μm in width, and are regularly arranged and tightly packed in circlets, with an empty central area in the thallus.

Several fragments found in the Maxi section (24 specimens) possess a discoidal, ellipsoidal, or irregular outline in thin sections, but most of them are poorly or incompletely preserved. One fragment (Fig. 5E) is large (1232.8 × 1075.6 μm) and ellipsoidal in overall shape without an outer membrane. Individual cells are not easily discernable, but there are radiating linear structures (7.0–17.7 μm in thickness) that may represent vestiges of cell arrangement. Another fragment, illustrated in Fig. 5F–G, is irregular in overall shape (327.9 × 243.5 μm) and consists of tightly packed ellipsoidal or polygonal cells (2.5–6.8 μm in size). The cells have a thick wall and sometimes a dark inclusion (Fig. 5G).

Abundant spheroidal fossils account for ~ 90 % of Maxi specimens excluding cyanobacteria (Supplementary Material). Some of them (Fig. 6B–F) are characterized by a large vesicle (400–2800 μm in vesicle diameter) enclosing a large number of randomly arranged, dark-colored, micrometer-sized globular structures (9–30 μm in cell diameter); it is uncertain whether these globular structures represent cells or diagenetic artifacts. Others preserve only a vesicle wall, with the interior strongly degraded and filled with secondary cement (Fig. 6G) or cut by veins (Fig. 6A). Considering the possibility that the globular structures may represent cells, which can be lost during degradation, the spheroidal fossils are tentatively assigned to the genus *Megasphaera*, as emended in Xiao et al. (2014b), and they may represent *Megaclonophycus*-stage *Megasphaera* specimens. However, these specimens also bear similarities to the co-existing multicellular alga *Wengania globosa* in overall morphology and cell (or globule) size. But they differ from *W. globosa* in that the latter lacks an enclosing vesicle and is characterized by an outward-diverging arrangement of cells (Fig. 3G). We also note that several leiospheres from the Doushantuo Formation in the Yangtze Gorges area contain one to many cells (Liu et al., 2014), but they are much smaller (50–150 μm in vesicle diameter) than the Maxi specimens. Thus, the Maxi specimens are tentatively identified as *Megasphaera* sp.

5. Discussion

5.1. Implications for late Ediacaran microfossil diversity

When compared with early and middle Ediacaran microfossils, late Ediacaran microfossils are generally low in taxonomic richness. In principle, this difference can be a result of low sampling intensity, poor preservation, or a decline in microfossil diversity in the late Ediacaran. Late and particularly terminal Ediacaran microfossils are dominated by smooth-walled leiospheres (Ding et al., 2019; Germs et al., 1986; Knoll and Swett, 1987; Moczydłowska, 1991; Palacios et al., 2017; Volkova et al., 1983; Yin and Gao, 1995), collectively known as the Terminal Ediacaran *Leiosphaeridia* Assemblage (TELA; Xiao and Narbonne, 2020). Several recent studies, however, reported Doushantuo-Pertatataka-type acanthomorphs (DPAs) and spheroidal specimens identified as *Megasphaera* from late Ediacaran strata in the East European Platform (Golubkova et al., 2015), Mongolia (Anderson et al., 2017, 2019), north-central Siberia (Grazhdankin et al., 2020), and Hunan and Shanxi provinces in South China (Ouyang et al., 2017; Zhang and Zhang, 2017). However, the precise ages of these fossiliferous strata, particularly those from the East European Platform, Mongolia, and north-central Siberia, remain poorly constrained. Therefore, the present materials comprising 16 taxa from the Miaohe Member, which is constrained between 567 Ma and 550 Ma, greatly enrich the microfossil record of the late Ediacaran Period.

In addition to leiospheres, the Maxi microfossil assemblage also contains *Gloeodiniopsis*, *Obruchevella*, *Oscillatoriopsis*, *Polytrichoides*, *Salome*, and *Siphonophycus*, which are common Proterozoic microbial mat builders and dwellers (e.g., Butterfield et al., 1994; Schopf and Klein, 1992). They are traditionally interpreted as photosynthetic cyanobacteria and are thus regarded as primary producers. There are several other taxa in the Maxi microfossil assemblage that can be interpreted as multicellular eukaryotic algae. Among these, *Archaeophycus yunnanensis* has been interpreted as a multicellular alga comparable to extant bangialean red algae or chlorophyte green algae (Shang and Liu, 2022; Xiao et al., 1998; Zhang et al., 1998), although an affinity to the modern chroococcalean cyanobacterium cannot be ruled out (Xiao et al., 2014a; Zhang, 1985). *Wengania* has been assigned to the stem group florideophytes due to its simple undifferentiated pseudoparenchymatous thallus (Xiao et al., 2004). *Thallophyca* has been broadly compared with the fossil and living corallinaleans in the florideophytes, thus it was considered as an early stem group corallinalean red alga (Xiao et al., 2004; Zhang et al., 1998; Zhang and Yuan, 1992). Unnamed species A illustrated in Fig. 5A–C consists of small, polyhedral, and densely packed cells within the thallus, morphologically resembling cellular structures of some florideophyte red algae, particularly if its medulla-cortex thallus differentiation can be confirmed with further evidence. Unnamed species B illustrated in Fig. 5D is characterized by a central area surrounded by circlets of petaloid structures, marginally reminiscent of utricle cells of the modern green alga *Codium* (Cherif et al., 2016; Estevez et al., 2009). However, the Maxi specimen lacks the typical intertwined siphonous tubes in the central area of *Codium* and its size is smaller than *Codium* (Chai et al., 2022). Thus, unnamed species B is considered a possible green alga but its real affinity remains uncertain in the absence of diagnostic features. If *Archaeophycus*, *Thallophyca*, *Wengania*, and the two unnamed species are likely multicellular algal microfossils, they are representatives of eukaryotic primary producers in the late Ediacaran Period.

As to the spheroidal fossil *Megasphaera*, its phylogenetic affinity remains a matter of debate. This genus has been variously interpreted as a green alga, crown-group animal embryo, giant sulfur-oxidizing bacteria, encysting protist, multicellular alga, or stem-group animal embryo (see Xiao et al., 2014a and references therein), although recent analysis converges to a total-group metazoan interpretation, at least for those *Megasphaera* specimens with complex developmental stages (Yin et al., 2022). Maxi specimens of *Megasphaera* are abundant, but unlike those from the Weng'an biota, specimens at the one-cell stage and *Parapandorina*-stage are exceedingly rare and have not been encountered in this study, despite the abundance of *Megaclonophycus*-stage specimens; the lack of a continuous cell division series also characterizes several other occurrences of late Ediacaran *Megasphaera* (e.g., Anderson et al., 2019). Because of the lack of early developmental stages, the taxonomic identification of the Maxi specimens to the genus *Megasphaera* is tentative, and their phylogenetic affinity remains uncertain. Nevertheless, together with macroalgal fossils from the late Ediacaran Miaohe biota (Xiao et al., 2002; Ye et al., 2019) and the Ediacara biota (Xiao et al., 2020), the Maxi microfossil assemblage indicates that the late Ediacaran ecosystem was supported by a wide range of primary producers, including both prokaryotes and eukaryotes and involving both microscopic and macroscopic organisms.

5.2. Comparison between the Maxi and Weng'an assemblages

The moderately diverse Maxi microfossil assemblage prompts us to examine whether the depauperate biodiversity in the late to terminal Ediacaran Period (e.g., the Kotlin crisis; Brasier, 1992; Bykova et al., 2020; Evans et al., 2022) represents a preservational artifact or an evolutionary trend. To assess these possibilities, one needs to compare early and late Ediacaran microfossil assemblages of similar taphonomic mode. To this end, a comparison between the Maxi and Weng'an microfossil assemblages offers an excellent opportunity to assess the evolutionary trends because they represent two snapshots of different times but in a broadly similar taphonomic mode (i.e., microfossils preserved via phosphatization), although the Maxi assemblage may be preserved in relatively deeper-water facies than the Weng'an biota, which is hosted in phosphatic-dolomitic grainstone (Xiao and Knoll, 1999). As discussed above, the Maxi assemblage is constrained between ~ 567 Ma and ~ 550 Ma, thus representing an example of late Ediacaran microfossil biota, whereas the Weng'an assemblage is constrained between 609 ± 5 Ma (Zhou et al., 2017a; re-dated as 612.5 ± 0.5 Ma and considered as a detrital zircon age, Yang et al., 2021) and 576 ± 14 Ma (Barfod et al., 2002), thus representing an example of early Ediacaran microfossil biota.

The early Ediacaran Weng'an biota from phosphorites of the Doushantuo Formation in Guizhou Province, South China consists of various exceptionally preserved microfossils, including spheroidal fossils of *Megasphaera*, multicellular thalli, cyanobacteria, as well as DPAs, providing critical information on the radiation of multicellular eukaryotes (Xiao et al., 2014a, b). Among them, spheroidal microfossils are the most abundant, accounting for more than 90 % of phosphatized specimens in the Weng'an biota, as assessed using controlled sampling and fossil counting strategies (Yin and Zhu, 2008). Similarly, the Maxi assemblage is dominated by *Megasphaera* (Supplementary Material) and has yielded several taxa characteristic of the Weng'an biota, including multicellular algal genera such as *Archaeophycus*, *Paramecia*, *Thallophyca*, and *Wengania*, as well as various coccoidal and filamentous cyanobacteria. These shared microfossil taxa suggest significant similarities between these two assemblages. Together with the report of *Megasphaera* fossils from the late Ediacaran Dengying Formation in Shaanxi Province of South China (Zhang and Zhang, 2017), the Maxi microfossil assemblage expands the biogeographic and temporal distribution of several Weng'an microfossils (e.g., *Paramecia*, *Thallophyca*, *Wengania*). The evolutionary continuity from early to late Ediacaran is also supported by the macrofossil data showing that several carbonaceous compression taxa (e.g., *Doushantuophyton lineare*, *D. rigidulum*, *D. cometa*, *Enteromorphites siniansis*) range from the ~ 602 Ma Lantian biota (Yang et al., 2022; Yuan et al., 2016) to the 576–550 Ma Miaohe biota (Xiao et al., 2002; Ye et al., 2019).

There is also a notable difference between the Maxi and Weng'an microfossil assemblages. No Doushantuo-Pertatataka-type acanthomorphs (DPAs) have been identified in the Maxi assemblage, whereas they constitute a significant proportion of taxonomic diversity in the Weng'an biota (Xiao et al., 2014b) despite their relatively low abundance (less than 10 %; Yin and Zhu, 2008). The Maxi and Weng'an microfossil assemblages share a broadly similar taphonomic mode: both are preserved mainly through phosphatization with localized silicification. The preservational quality of multicellular algal thalli is comparable in the Maxi and Weng'an microfossil assemblages. The Weng'an assemblage has been the focus of numerous monographic studies (e.g., Chen, 2004; Xiao et al., 2014b; Yin et al., 2007; Yin et al., 2011; Yuan et al., 2002), and it is certainly much more intensively sampled than the Maxi assemblage. However, DPAs were among the first fossils reported from the Weng'an assemblage (Chen and Liu, 1986), when this assemblage was first explored in the 1980s and its sampling intensity was rather low. These comparisons between the Weng'an and Maxi assemblages indicate that preservational biases and sampling intensity are unlikely to account for the lack of DPAs in Maxi.

More likely, paleoenvironmental, paleoecological, and evolutionary processes are responsible for the difference between these two assemblages. The fossiliferous phosphorites at Maxi are hosted in shales, mudstones, and argillaceous limestone, whereas those at Weng'an are in phosphatic-dolomitic grainstone (Xiao and Knoll, 1999). It is possible that DPAs were ecologically restricted to shallow-water grainstone facies rather than deeper-water mudstone facies. However, Weng'an microfossils were mostly reworked and winnowed in shallow-water environments (Muscente et al., 2015; Xiao and Knoll, 1999; Zhang et al., 2019), and they may have been sourced from deeper-water environments.

Considering that DPAs are generally rare in the last 10–15 million years of the Ediacaran Period, we favor the hypothesis that many of them may have gone extinct in the late Ediacaran. It has been long known that late Ediacaran microfossil assemblages are dominated by leiospheres (Gaucher and Sprechmann, 2009; Grey, 2005; Huntley et al., 2006; Knoll and Walter, 1992; Vidal and Moczydłowska-Vidal, 1997; Xiao and Narbonne, 2020). In South China, with one possible exception (Ouyang et al., 2017), DPAs are restricted to the early-middle Ediacaran Doushantuo Formation, ranging from strata above the basal Ediacaran cap dolostone and below carbonates that host the negative carbon isotope excursion EN3 (Liu and Moczydłowska, 2019; Liu et al., 2013, 2014; Zhou et al., 2007), which is considered to be equivalent to the Shuram negative carbon isotope excursion in Oman (McFadden et al., 2008). The stratigraphic range of DPAs is most thoroughly investigated in the Doushantuo Formation in the Yangtze Gorges area of South China (Fig. 7). The disappearance of DPAs is unlikely an artifact of uneven sampling related to the intensive investigation of the early-middle Ediacaran Doushantuo Formation relative to late Ediacaran strata in terms of microfossils. Outside South China, DPAs also show a major decline in the late Ediacaran Period (Cohen and Macdonald, 2015; Huntley et al., 2006). They are abundant and diverse in lower Ediacaran strata (Cohen and Macdonald, 2015; Xiao and Narbonne, 2020), but are rare in younger rocks (Golubkova et al., 2015; Anderson et al., 2017; Grazhdankin et al., 2020) (Supplementary Material), and their purported late Ediacaran or early Cambrian age remains to be independently confirmed. Thus, we hypothesize that, on a global scale, the diversity of DPAs experienced a sharp decline in the late Ediacaran, probably around 560–550 Ma, even if it was not a total extinction. This hypothesis needs to be tested further with an updated global compilation and a rigorous statistical analysis of Ediacaran DPAs.

The late Ediacaran decline in DPAs harbingers the terminal Ediacaran biodiversity crisis known as the Kotlin crisis (Brasier, 1992) (Fig. 7), which is marked by the decline of soft-bodied macro-organisms of the Ediacara biota during the transition from the White Sea assemblage to the Nama assemblage, approximately around 550 Ma (Darroch et al., 2018; Evans et al., 2022; Grazhdankin, 2014; Xiao and Laflamme, 2009). It is worth investigating whether the diversity decline in micro- and macro-organisms in the late Ediacaran Period was causally coupled or driven by a common cause, possibly related to the dynamic changes in ecological interactions or oceanic redox conditions (Cohen et al., 2009;

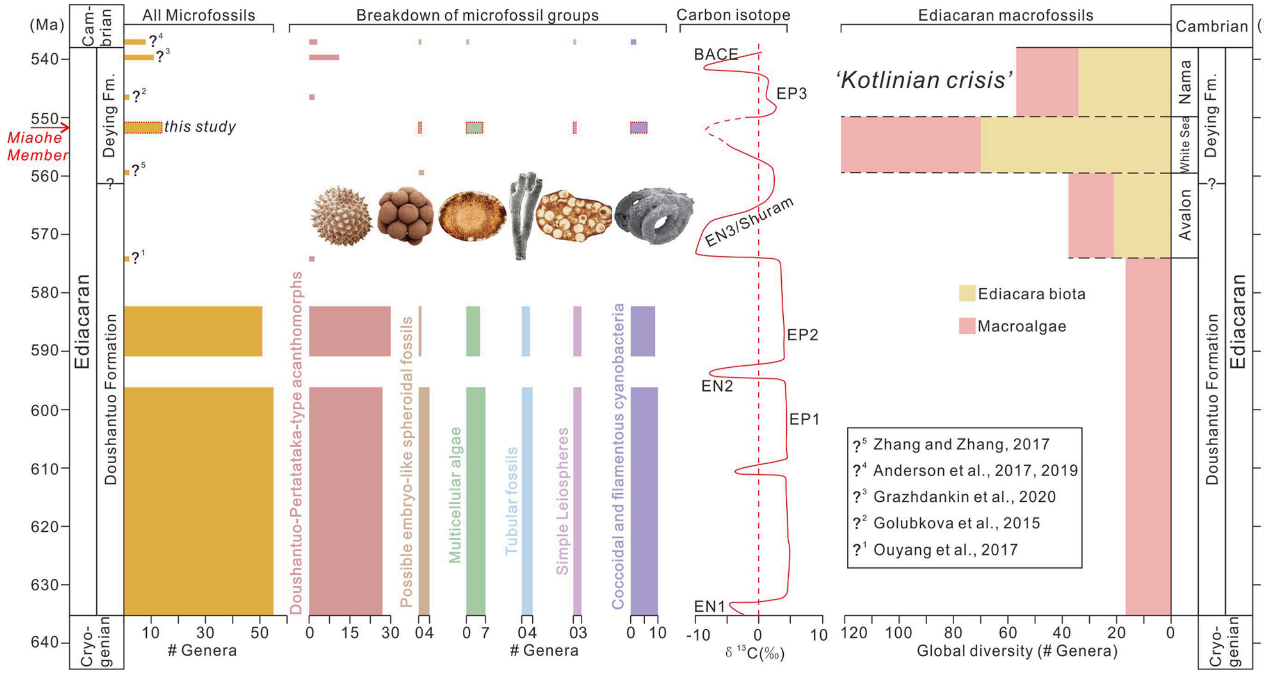

Fig. 7. Compiled genus-level taxonomic richness of Ediacaran microfossils in the Yangtze Gorges area of South China (left), representative Ediacaran carbon isotope curve of South China (center), and genus-level taxonomic richness of Ediacaran macrofossils. Microfossil data are compiled from Liu and Moczydłowska (2019); Liu et al. (2014); Ouyang et al. (2019, 2021); Shang and Liu (2022); Shang et al. (2019); Xiao (2004); Xiao et al. (2014a, b); and Ye et al. (2022). Thumbnail photos are, from left to right, *Mengeosphaera reticulata* (Xiao and Knoll, 1999), *Parapandorina*-stage specimen of *Megasphaera* (Xiao et al., 2014a), *Wengania globosa* (Xiao et al., 2014a), *Ramitubus increscens* (Xiao et al., 2000), *Leiosphaeridia tenuissima* (Liu et al., 2014), and *Obruchevella magna* (Anderson, 2017). Carbon isotope curve is modified from Xiao and Narbonne (2020). Data for the Ediacara biota and macroalgae are from Evans et al. (2022) and Bykova et al. (2020), respectively. See Supplementary Material for details.

Evans et al., 2018, 2022; Johnston et al., 2012; McFadden et al., 2008; Zhang et al., 2018).

6. Conclusions

A moderately diverse assemblage of phosphatized microfossils has been discovered from phosphorite nodules and bands hosted in shales and mudstones of the late Ediacaran Miaohe Member at the Maxi section of Hubei Province, South China. The Maxi microfossil assemblage co-exists with macroalgal fossils (i.e., Miaohe biota) preserved as carbonaceous compressions in shales of the Miaohe Member. The Maxi microfossil assemblage is composed of prokaryotes, multicellular microalgae, leiospheres, and abundant spheroidal vesicles that are tentatively assigned to the genus *Megasphaera*. It adds to a growing list of late Ediacaran microfossils and shares several taxa with the early Ediacaran Weng'an biota. Despite these shared taxa, the Maxi microfossil assemblage is relatively depauperate in taxonomic diversity when compared with the Weng'an biota, and lacks any Doushantuo-Pertatataka-type acanthomorphs (DPAs) that characterize many early Ediacaran microfossil assemblages, including the Weng'an biota. Considering its possible age of 567–550 Ma, the Maxi microfossil assemblage may represent the beginning of the end of DPAs. It is intriguingly possible that the decline of DPAs may be related to the slightly younger Kotlin crisis in the terminal Ediacaran Period (550–539 Ma) during which soft-bodied macro-organisms also suffered diversity loss.

CRediT authorship contribution statement

Qin Ye: Conceptualization, Funding acquisition, Investigation, Resources, Data curation, Visualization, Writing – original draft. **Zhihui An:** Conceptualization, Investigation, Writing – review & editing. **Yang Yu:** Investigation, Writing – review & editing. **Ze Zhou:** Investigation, Writing – review & editing. **Jun Hu:** Investigation, Writing – review & editing. **Jinnan Tong:** Conceptualization, Funding acquisition, Investigation, Writing – review & editing. **Shuhai Xiao:** Conceptualization, Funding acquisition, Investigation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (41902004), the Central Universities Funds (CUGCJ1816, CUG 2106101) to China University of Geosciences (Wuhan), China Postdoctoral Science Foundation (2021M692980, 2022T150600), and State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences) (No. 213125). S.X. was supported by the U.S. National Science Foundation (EAR-2021207). We thank Ke Pang, Li Tian, and Haijun Song for useful discussion, and two anonymous reviewers for constructive comments.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.precamres.2023.107001.

References

An, Z., Jiang, G., Tong, J., Tian, L., Ye, Q., Song, H., Song, H., 2015. Stratigraphic position of the Ediacaran Miaohe biota and its constrains on the age of the upper Doushantuo δ^{13}C anomaly in the Yangtze Gorges area, South China. Precambr. Res. 271, 243–253.

Anderson, R.P., Macdonald, F.A., Jones, D.S., McMahon, S., Briggs, D.E.G., 2017. Doushantuo-type microfossils from latest Ediacaran phosphorites of northern Mongolia. Geology 45, 1079–1082.

Anderson, R.P., McMahon, S., Macdonald, F.A., Jones, D.S., Briggs, D.E.G., 2019. Palaeobiology of latest Ediacaran phosphorites from the upper Khesen Formation, Khuvsgul Group, northern Mongolia. J. Syst. Palaeontol. 17, 501–532.

Barfod, G.H., Albaréde, F., Knoll, A.H., Xiao, S., Télouk, P., Frei, R., Baker, J., 2002. New Lu-Hf and Pb-Pb age constraints on the earliest animal fossils. Earth Planet. Sci. Lett. 201, 203–212.

Brasier, M., 1992. Background to the Cambrian explosion. J. Geol. Soc. London 149, 585–587.

Butterfield, N.J., Knoll, A.H., Swett, K., 1994. Paleobiology of the Neoproterozoic Svanbergfjellet Formation, Spitsbergen. Fossils Strata 34, 1–84.

Bykova, N., LoDuca, S.T., Ye, Q., Marusin, V., Grazhdankin, D., Xiao, S., 2020. Seaweeds through time: morphological and ecological analysis of Proterozoic and early Paleozoic benthic macroalgae. Precambr. Res. 350, 105875.

Chai, S., Aria, C., Hua, H., 2022. A stem group *Codium* alga from the latest Ediacaran of South China provides taxonomic insight into the early diversification of the plant kingdom. BMC Biol. 20, 1–10.

Chen, J., 2004. The Dawn of Animal World. Jiangsu Science and Technology Press, Nanjing, pp. 1–366.

Chen, M., Liu, K., 1986. The geological significance of newly discovered microfossils from the upper Sinian (Doushantuo age) phosphorites. Sci. Geol. Sin. 1, 46–53.

Cherif, W., Ktari, L., Bour, M.E., Boudabous, A., Grignon-Dubois, M.J.A., 2016. *Codium fragile* subsp. *fragile* (Suringar) Hariot in Tunisia: morphological data and status of knowledge. Algae 31, 129–136.

Cohen, P.A., Knoll, A.H., Kodner, R.B., 2009. Large spinose microfossils in Ediacaran rocks as resting stages of early animals. Proc. Natl. Acad. Sci. USA 106, 6519–6524. https://doi.org/10.1073/pnas.0902322106.

Cohen, P.A., Macdonald, F.A., 2015. The Proterozoic record of eukaryotes. Paleobiology 41, 610–632.

Condon, D., Zhu, M., Bowring, S., Wang, W., Yang, A., Jin, Y., 2005. U-Pb ages from the Neoproterozoic Doushantuo Formation, China. Science 308, 95–98.

Darroch, S.A., Smith, E.F., Laflamme, M., Erwin, D.H., 2018. Ediacaran extinction and Cambrian explosion. Trends Ecol. Evol. 33, 653–663.

Ding, W., Dong, L., Sun, Y., Ma, H., Xu, Y., Yang, R., Peng, Y., Zhou, C., Shen, B., 2019. Early animal evolution and highly oxygenated seafloor niches hosted by microbial mats. Sci. Rep. 9, 1–11.

Droser, M.L., Tarhan, L.G., Gehling, J.G., 2017. The rise of animals in a changing environment: global ecological innovation in the late Ediacaran. Ann. Rev. Earth Planet. Sci. 45, 593–617.

Estevez, J.M., Fernández, P.V., Kasulin, L., Dupree, P., Ciancia, M., 2009. Chemical and in situ characterization of macromolecular components of the cell walls from the green seaweed Codium fragile. Glycobiology 19, 212–228.

Evans, S.D., Diamond, C.W., Droser, M.L., Lyons, T.W., 2018. Dynamic oxygen and coupled biological and ecological innovation during the second wave of the Ediacara Biota. Emerg. Top. Life Sci. 2, 223–233.

Evans, S.D., Tu, C., Rizzo, A., Surprenant, R.L., Boan, P.C., McCandless, H., Marshall, N., Xiao, S., Droser, M.L., 2022. Environmental drivers of the first major animal extinction across the Ediacaran White Sea-Nama transition. Proc. Nat. Acad. Sci. USA 119. https://doi.org/10.1073/pnas.2207475119 e2207475119.

Gaucher, C., Sprechmann, P., 2009. Neoproterozoic acritarch evolution. In: Gaucher, C., Sial, A.N., Halverson, G.P., Frimmel, H.E. (Eds.), Neoproterozoic-Cambrian tectonics, global change and evolution: a focus on South Western Gondwana. Elsevier, Developments in Precambrian Geology, pp. 319–326.

Germs, J.G.B., Knoll, A.H., Vidal, G., 1986. Latest Proterozoic microfossils from the Nama Group, Namibia (south west Africa). Precambr. Res. 32, 45–62.

Golubkova, E.Y., Zaitseva, T.S., Kuznetsov, A.B., Dovzhikova, E.G., Maslov, A.V., 2015. Microfossils and Rb-Sr age of glauconite in the key section of the Upper Proterozoic of the northeastern part of the Russian plate (Keltmen-1 borehole). Dokl. Earth Sci. 462, 547–551.

Grazhdankin, D., 2014. Patterns of evolution of the Ediacaran soft-bodied biota. J. Paleo. 88, 269–283.

Grazhdankin, D., Nagovitsin, K., Golubkova, E., Karlova, G., Kochnev, B., Rogov, V., Marusin, V., 2020. Doushantuo-Pertatataka-type acanthomorphs and Ediacaran ecosystem stability. Geology 48, 708–712.

Grey, K., 2005. Ediacaran palynology of Australia. Memoirs of the Association of Australasian Palaeontologists 31, 1–439.

Huntley, J.W., Xiao, S., Kowalewski, M., 2006. 1.3 Billion years of acritarch history: An empirical morphospace approach. Precambr. Res. 144, 52–68.

Jiang, G., Kaufman, A.J., Christie-Blick, N., Zhang, S., Wu, H., 2007. Carbon isotope variability across the Ediacaran Yangtze platform in South China: Implications for a large surface-to-deep ocean δ^{13}C gradient. Earth Planet. Sci. Lett. 261, 303–320.

Johnston, D.T., Macdonald, F.A., Gill, B.C., Hoffman, P.F., Schrag, D.P., 2012. Uncovering the Neoproterozoic carbon cycle. Nature 483, 320–323.

Knoll, A.H., Swett, K., 1987. Micropaleontology across the Precambrian-Cambrian boundary in Spitsbergen. J. Paleo. 61, 898–926.

Knoll, A.H., Walter, M.R., 1992. Latest Proterozoic stratigraphy and Earth history. Nature 356, 673–678.

Liu, P., Moczydłowska, M., 2019. Ediacaran microfossils from the Doushantuo Formation chert nodules in the Yangtze Gorges area, South China, and new biozones. Fossils & Strata 65, 1–172.

Liu, P., Yin, C., Chen, S., Tang, F., Gao, L., 2013. The biostratigraphic succession of acanthomorphic acritarchs of the Ediacaran Doushantuo Formation in the Yangtze Gorges area, South China and its biostratigraphic correlation with Australia. Precambr. Res. 225, 29–43.

Liu, P., Xiao, S., Yin, C., Chen, S., Zhou, C., Li, M., 2014. Ediacaran acanthomorphic acritarchs and other microfossils from chert nodules of the upper Doushantuo Formation in the Yangtze Gorges area, South China. J. Paleo. 72 (supplement to No 1), 1–139.

McFadden, K.A., Huang, J., Chu, X., Jiang, G., Kaufman, A.J., Zhou, C., Yuan, X., Xiao, S., 2008. Pulsed oxygenation and biological evolution in the Ediacaran Doushantuo Formation. Proc. Nat. Acad. Sci. USA 105, 3197–3202. https://doi.org/10.1073/pnas.0708336105.

Moczydłowska, M., 1991. Acritarch biostratigraphy of the Lower Cambrian and the Precambrian-Cambrian boundary in southeastern Poland. Fossils Strata 29, 1–127.

Muscente, A.D., Hawkins, A.D., Xiao, S., 2015. Fossil preservation through phosphatization and silicification in the Ediacaran Doushantuo Formation (South China): a comparative synthesis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 434, 46–62.

Narbonne, G.M., 2005. The Ediacara Biota: Neoproterozoic origin of animals and their ecosystems. Annu. Rev. Earth Planet. Sci. 33, 421–442.

Ouyang, Q., Guan, C., Zhou, C., Xiao, S., 2017. Acanthomorphic acritarchs of the Doushantuo Formation from an upper slope section in northwestern Hunan Province, South China, with implications for early-middle Ediacaran biostratigraphy. Precambr. Res. 298, 512–529.

Ouyang, Q., Zhou, C., Xiao, S., Chen, Z., Shao, Y., 2019. Acanthomorphic acritarchs from the Ediacaran Doushantuo Formation at Zhangcunping in South China, with implications for the evolution of early Ediacaran eukaryotes. Precambr. Res. 320, 171–192.

Ouyang, Q., Zhou, C., Xiao, S., Guan, C., Chen, Z., Yuan, X., Sun, Y., 2021. Distribution of Ediacaran acanthomorphic acritarchs in the lower Doushantuo Formation of the Yangtze Gorges area, South China: evolutionary and stratigraphic implications. Precambr. Res. 353, 106005 https://doi.org/10.1016/j.precamres.2020.106005.

Palacios, T., Jensen, S., Barr, S.M., White, C.E., Myrow, P.M., 2017. Organic-walled microfossils from the Ediacaran-Cambrian boundary stratotype section, Chapel Island and Random formations, Burin Peninsula, Newfoundland, Canada: Global correlation and significance for the evolution of early complex ecosystems. Geol. J. 53, 1728–1742.

Rooney, A.D., Cantine, M.D., Bergmann, K.D., Gómez-Pérez, I., Al Baloushi, B., Boag, T. H., Busch, J.F., Sperling, E.A., Strauss, J.V., 2020. Calibrating the coevolution of Ediacaran life and environment. Proc. Nat. Acad. Sci. USA 117, 16824–16830. https://doi.org/10.1073/pnas.2002918117.

Schopf, J.W., Klein, C., 1992. The Proterozoic Biosphere: A Multidisciplinary Study. Cambridge University Press, Cambridge, pp. 1–1348.

Schwid, M.F., Xiao, S., Nolan, M.R., An, Z., 2021. Differential weathering of diagenetic concretions and the formation of Neoproterozoic annulated discoidal structures. PALAIOS 36, 15–27.

Shang, X., Liu, P., 2022. Diverse multicellular algae from the early Ediacaran Doushantuo chert nodules and their palaeoecological implications. Precambr. Res. 368, 106508 https://doi.org/10.1016/j.precamres.2021.106508.

Shang, X., Liu, P., Moczydlowska, M., 2019. Acritarchs from the Doushantuo Formation at Liujing section in Songlin area of Guizhou Province, South China: Implications for early-middle Ediacaran biostratigraphy. Precambr. Res. 334, 105453 https://doi.org/10.1016/j.precamres.2019.105453.

Tang, F., Yin, C., Bengtson, S., Liu, P., Wang, Z., Gao, L., 2008. Octoradiate spiral organisms in the Ediacaran of South China. Acta Geol. Sin. 82, 27–34.

Vidal, G., Moczydłowska-Vidal, M., 1997. Biodiversity, speciation, and extinction trends of Proterozoic and Cambrian phytoplankton. Paleobiology 23, 230–246.

Volkova, N.A., Kirjanov, V.V., Piscun, L.V., Paskeviciene, L.T., Jankauskas, T.V., 1983. Plant microfossils. In: Urbanek, A., Rozanov, A.Y. (Eds.), Upper Precambrian Palaeontology of the East-European Platform. Wydawnictwa Geologiczne, Warsaw, pp. 7–46.

Xiao, S., 2004. New multicellular algal fossils and acritarchs in Doushantuo chert nodules (Neoproterozoic, Yangtze Gorges, South China). J. Paleo. 78, 393–401.

Xiao, S., Yuan, X., Knoll, A.H., 2000. Eumetazoan fossils in terminal Proterozoic phosphorites? Proc. Nat. Acad. Sci. USA 97, 13684–13689. https://doi.org/10.1073/pnas.250491697.

Xiao, S., Gehling, J.G., Evans, S.D., Hughes, I.V., Droser, M.L., 2020. Probable benthic macroalgae from the Ediacara Member South Australia. Precambr. Res. 350, 105903 https://doi.org/10.1016/j.precamres.2020.105903.

Xiao, S., Knoll, A.H., 1999. Fossil preservation in the Neoproterozoic Doushantuo phosphorite Lagerstätte, South China. Lethaia 32, 219–240.

Xiao, S., Knoll, A.H., Yuan, X., Pueschel, C.M., 2004. Phosphatized multicellular algae in the Neoproterozoic Doushantuo Formation, China, and the early evolution of florideophyte red algae. Am. J. Bot. 91, 214–227.

Xiao, S., Laflamme, M., 2009. On the eve of animal radiation: Phylogeny, ecology and evolution of the Ediacara biota. Trends Ecol. Evol. 24, 31–40.

Xiao, S., Muscente, A.D., Chen, L., Zhou, C., Schiffbauer, J.D., Wood, A.D., Polys, N.F., Yuan, X., 2014a. The Weng'an biota and the Ediacaran radiation of multicellular eukaryotes. Natl. Sci. Rev. 1, 498–520.

Xiao, S., Narbonne, G., 2020. The Ediacaran Period, Geologic time scale 2020. Elsevier 521–561.

Xiao, S., Zhang, Y., Knoll, A.H., 1998. Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite. Nature 391, 553–558.

Xiao, S., Yuan, X., Steiner, M., Knoll, A.H., 2002. Macroscopic carbonaceous compressions in a terminal Proterozoic shale: A systematic reassessment of the Miaohe biota, South China. J. Paleo. 76, 347–376.

Xiao, S., Zhou, C., Liu, P., Wang, D., Yuan, X., 2014b. Phosphatized acanthomorphic acritarchs and related microfossils from the Ediacaran Doushantuo Formation at Weng'an (South China) and their implications for biostratigraphic correlation. J. Paleo. 88, 1–67.

Xiao, S., Bykova, N., Kovalick, A., Gill, B.C., 2017. Stable carbon isotopes of sedimentary kerogens and carbonaceous macrofossils from the Ediacaran Miaohe Member in South China: Implications for stratigraphic correlation and sources of sedimentary organic carbon. Precambr. Res. 302, 171–179.

Xiao, S., Chen, Z., Pang, K., Zhou, C., Yuan, X., 2021. The Shibantan Lagerstätte: insights into the Proterozoic-Phanerozoic transition. J. Geol. Soc. London 178, jgs2020–2135. https://doi.org/10.1144/jgs2020-135.

Yang, C., Rooney, A.D., Condon, D.J., Li, X., Grazhdankin, D.V., Bowyer, F.T., Hu, C., Macdonald, F.A., Zhu, M., 2021. The tempo of Ediacaran evolution. Science Advance 7, eabi9643. https://doi.org/10.1126/sciadv.abi9643.

Yang, C., Li, Y., Selby, D., Wan, B., Guan, C., Zhou, C., Li, X., 2022. Implications for Ediacaran biological evolution from the ca. 602 Ma Lantian biota in China. Geology 50, 562–566.

Ye, Q., Tong, J., An, Z., Tian, L., Zhao, X., Zhu, S., 2015. Phosphatized fossil assemblage from the Ediacaran Doushantuo Formation in Zhangcunping area, Yichang, Hubei Province. Acta Palaeontol. Sin. 54, 43–65.

Ye, Q., Tong, J., An, Z., Hu, J., Tian, L., Guan, K., Xiao, S., 2019. A systematic description of new macrofossil material from the upper Ediacaran Miaohe Member in South China. J. Syst. Palaeontol. 17, 183–238.

Ye, Q., Li, J., Tong, J., An, Z., Hu, J., Xiao, S., 2022. A microfossil assemblage from the Ediacaran Doushantuo Formation in the Shennongjia area (Hubei Province, South China): Filling critical paleoenvironmental and biostratigraphic gaps. Precambr. Res. 377, 106691 https://doi.org/10.1016/j.precamres.2022.106691.

Yin, C., Gao, L., 1995. Microfossils from the Shibantan Member of the Dengying Formation in the Yangtze Gorges, western Hubei. Geological Review 41, 197–204.

Yin, C., Liu, Y., Gao, L., Wang, Z., Tang, F., Liu, P., 2007. Phosphatized Biota in Early Sinian (Ediacaran) – Weng'an Biota and Its Environment. Geological Publishing House, Beijing, pp. 1–132.

Yin, Z., Sun, W., Liu, P., Chen, J., Bottjer, D.J., Li, J., Zhu, M., 2022. Diverse and complex developmental mechanisms of early Ediacaran embryo-like fossils from the Weng'an Biota, southwest China. Philos. Trans. R. Soc. B 377, 20210032. https://doi.org/10.1098/rstb.2021.0032.

Yin, L., Wang, D., Yuan, X., Zhou, C., 2011. Diverse small spinose acritarchs from the Ediacaran Doushantuo Formation, South China. Palaeoworld 20, 279–289.

Yin, Z., Zhu, M., 2008. Quantitative analysis on the fossil abundance of the Ediacaran Weng'an biota, Guizhou. Acta Palaeontol. Sin. 47, 477–487.

Yuan, X., Xiao, S., Yin, L., Knoll, A.H., Zhou, C., Mu, X., 2002. Doushantuo Fossils: Life on the Eve of Animal Radiation. China University of Science and Technology Press, Hefei, China, pp. 1–171.

Yuan, X., Wan, B., Guan, C., Chen, Z., Zhou, C., Xiao, S., Wang, W., Pang, K., Tang, Q., Hua, H., 2016. The Lantian Biota. Shanghai Scientific and Technical Publisher, Shanghai, pp. 1–150.

Zhang, Z., 1985. Coccoid microfossils from the Doushantuo Formation (Late Sinian) of South China. Precambr. Res. 28, 163–173.

Zhang, Y., 1989. Multicellular thallophytes with differentiated tissues from late Proterozoic phosphate rocks of South China. Lethaia 22, 113–132.

Zhang, Y., Zhang, X., 2017. New *Megasphaera*-like microfossils reveal their reproductive strategies. Precambr. Res. 300, 141–150.

Zhang, Y., Yin, L., Xiao, S., Knoll, A.H., 1998. Permineralized fossils from the terminal Proterozoic Doushantuo Formation, South China. J. Paleo. 72 (supplement to No. 4), 1–52.

Zhang, Y., Pufahl, P.K., Du, Y., Chen, G., Liu, J., Chen, Q., Wang, Z., Yu, W., 2019. Economic phosphorite from the Ediacaran Doushantuo Formation, South China, and the Neoproterozoic-Cambrian phosphogenic event. Sed. Geol. 388, 1–19.

Zhang, F., Xiao, S., Kendall, B., Romaniello, S.J., Cui, H., Meyer, M., Gilleaudeau, G.J., Kaufman, A.J., Anbar, A.D., 2018. Extensive marine anoxia during the terminal Ediacaran Period. Sci. Adv. 4, eaan8983. https://doi.org/10.1126/sciadv.aan8983.

Zhang, Y., Yuan, X., 1992. New data on multicellular thallophytes and fragments of cellular tissues from late Proterozoic phosphate rocks, South China. Lethaia 25, 1–18.

Zhou, C., Xiao, S., 2007. Ediacaran d^{13}C chemostratigraphy of South China. Chem. Geol. 237, 89–108.

Zhou, C., Xie, G., McFadden, K., Xiao, S., Yuan, X., 2007. The diversification and extinction of Doushantuo-Pertatataka acritarchs in South China: Causes and biostratigraphic significance. Geol. J. 42, 229–262.

Zhou, C., Li, X., Xiao, S., Lan, Z., Ouyang, Q., Guan, C., Chen, Z., 2017a. A new SIMS zircon U-Pb date from the Ediacaran Doushantuo Formation: age constraint on the Weng'an biota. Geol. Mag. 154, 1193–1201.

Zhou, C., Xiao, S., Wang, W., Guan, C., Ouyang, Q., Chen, Z., 2017b. The stratigraphic complexity of the middle Ediacaran carbon isotopic record in the Yangtze Gorges area, South China, and its implications for the age and chemostratigraphic significance of the Shuram excursion. Precambr. Res. 288, 23–38.

Zhu, M., Zhang, J., Yang, A., 2007. Integrated Ediacaran (Sinian) chronostratigraphy of South China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 254, 7–61.

Zhu, M., Gehling, J.G., Xiao, S., Zhao, Y., Droser, M., 2008. Eight-armed Ediacara fossil preserved in contrasting taphonomic windows from China and Australia. Geology 36, 867–870.