LETTER

An early Ediacaran assemblage of macroscopic and morphologically differentiated eukaryotes

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The deep-water Avalon biota (about 579 to 565 million years old) is often regarded as the earliest-known fossil assemblage with macroscopic and morphologically complex life forms[1]. It has been proposed that the rise of the Avalon biota was triggered by the oxygenation of mid-Ediacaran deep oceans[2]. Here we report a diverse assemblage of morphologically differentiated benthic macrofossils that were preserved largely *in situ* as carbonaceous compressions in black shales of the Ediacaran Lantian Formation (southern Anhui Province, South China). The Lantian biota, probably older than and taxonomically distinct from the Avalon biota, suggests that morphological diversification of macroscopic eukaryotes may have occurred in the early Ediacaran Period, perhaps shortly after the Marinoan glaciation, and that the redox history of Ediacaran oceans was more complex than previously thought.

The Lantian fossils were collected from early Ediacaran slope-basinal black shales in southern Anhui Province, South China (Fig. 1). The Ediacaran System in southern Anhui consists of two formations—the Lantian Formation and the overlying Piyuancun Formation[3], which are respectively correlated on the basis of regional lithostratigraphy with the Doushantuo (635–551 million years, Myr) and Dengying (551–542 Myr) formations in the Yangtze Gorges area[4,5]. The Lantian Formation is divided into four members that are similar to and can be correlated with the four divisions of the Doushantuo Formation[6]. The lowest Member I is a 1.8-m-thick dolostone ('cap dolostone') conformably overlying a Marinoan-age glacial diamictite. The overlying Member II consists of 35 m of finely laminated fossiliferous black shales (Supplementary Figs 1 and 2). Member III is 34 m thick and characterized by dolostones interbedded with mudstones in the lower part and ribbon rocks (limestone with dolostone intercalations; Supplementary Fig. 3) in the upper part. The uppermost Member IV consists of 20 m of black silty mudstones, which is overlain by siliceous rocks of the Piyuancun Formation and then the early Cambrian Hetang Formation[7].

The correlation of the four lithostratigraphic members between the Lantian and Doushantuo formations is supported by chemostratigraphic data (Fig. 1, Supplementary Fig. 4 and Supplementary Tables 1, 2). The basal Lantian cap dolostone is characterized by sedimentary features and $\delta^{13}C_{carb}$ values[8,9] similar to the 635-Myr-old basal Doushantuo cap dolostone[10]. Lantian Member III dolostones and ribbon rocks record a large negative $\delta^{13}C_{carb}$ excursion (Fig. 1 and Supplementary Fig. 4) that can be correlated with the negative excursion EN3 in Doushantuo Member III in the Yangtze Gorges area[10,11]. In the Yangtze Gorges and neighbouring areas, ash beds within Doushantuo Member II gave a zircon U–Pb thermal ionization mass spectrometry (TIMS) age of 632.5 ± 0.5 Myr (ref. 12) and a zircon U–Pb sensitive high resolution ion microprobe (SHRIMP) age of 614 ± 7.6 Myr (ref. 13), and Doushantuo Member IV is constrained between 593 ± 17 Myr (Re–Os age)[14] and 551.1 ± 0.7 Myr (zircon U–Pb TIMS age)[12]. These dates indicate that the Lantian biota in Member II black shales is probably older than the 579–565 Myr Avalon biota[1].

Regional mapping and palaeogeographic reconstruction indicate that fossiliferous black shales of Lantian Member II belong to a widespread shale-dominated facies that extends along the marginal shelf to the deep basin of the Yangtze Block (Fig. 1)[15]. The fossiliferous black shales are finely laminated, lacking cross-stratification or other wave- or current-influenced sedimentary structures. No grading is found in the fine
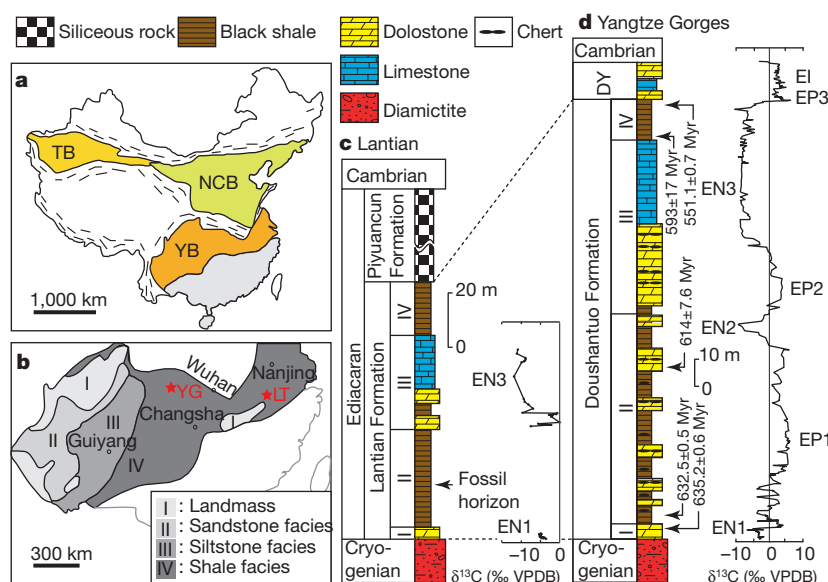

Figure 1 | Locality maps and stratigraphic columns. a, Yangtze Block (YB) in relation to North China Block (NCB) and Tarim Block (TB). **b**, Early Ediacaran facies distribution on Yangtze Block (simplified from ref. 15), with Yangtze Gorges (YG) and Lantian (LT) marked. **c, d**, Ediacaran stratigraphic columns of Lantian and Yangtze Gorges areas. Carbonate $\delta^{13}C$ data for basal Lantian cap dolostone (EN1) from ref. 8, and those for upper Lantian Formation from this study (Supplementary Table 1). Radiometric ages and $\delta^{13}C$ data in **d** from previously published data[11–14,30]. Scale bars apply only to Lantian and Doushantuo formations. DY, Dengying Formation. Ediacaran positive, negative and inertial carbon isotope excursions EP1, EP2, EP3, EN1, EN2, EN3 and EI are based on ref. 10.

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laminae (Supplementary Fig. 1b), indicating that they are not micro-turbidites but were deposited as suspensions settling below the storm wave base. The Lantian fossils are exceptionally preserved—with minimum fragmentation, random orientation (Supplementary Fig. 2), and lack of folded specimens—indicating that they were not transported by density currents and did not sink from surface water; instead, most of them were probably preserved *in situ*. The *in situ* preservation of epibenthic macroalgae[4], some with intact holdfast, suggests deposition in a quiet environment below the storm wave base but within the photic zone.

Previous investigators have described numerous carbonaceous compressions from Lantian Member II (refs 3–5), including simple vesicles such as *Chuaria circularis*, dichotomously branching forms (Fig. 2a), loosely bundled filaments (Fig. 2b), conical structures with densely packed filaments (Fig. 2c), fan-shaped forms with fascicles of filaments and sometimes transverse bands (Fig. 2d–i), and chained rings (Fig. 2j). Our renewed excavation has recovered, from the same fossiliferous interval, more than 3,000 specimens of macroscopic carbonaceous compressions that show a considerable degree of taxonomic diversity and morphological differentiation.

The new fossils can be described under five morphological types. Type A fossils (five specimens; Fig. 3a–e) are 16–40 mm in length and characterized by a fan-shaped structure consisting of a globose holdfast at its base, a lower stalk, and an upper crown. The stalk was originally conical in shape, consisting of a splay of packed filaments and a truncated or slanted upper end. The crown consists of more than ten tentacle-like non-branching ribbons that are of unequal to sub-equal length (2–13 mm) and tend to have a rounded distal end. Type B (20 specimens; Fig. 3f) is similar to Type A but its crown consists of a single broad ribbon, possibly representing a younger ontogenetic stage of Type A, although transitional forms are lacking. Type C (four specimens; Fig. 3g–i) is a centimetre-sized conical fossil, and has a fusiform inner body surrounded by diffuse organic stains. The inner body seems to be ornamented with longitudinal structures that converge distally to form a conical pyramid, which supports a cluster of filaments, each ~3 mm long and ~0.2 mm wide. Type D (one specimen; Fig. 3j) consists of a globose holdfast (0.5 mm in diameter), a thin stalk (1.3 mm long, 0.4 mm wide), and a cylindrical tube (18 mm long, 1.4 mm wide) with an axial dark trace (0.2–0.3 mm wide). Type E (one specimen; Fig. 3k) is similar to Type D in having a stalk and an axial structure, but it lacks or does not preserve a globose holdfast, its stalk is much longer, and its axial structure is encased in a much broader guitar-shaped structure.

The degree of morphological differentiation of the Lantian macrofossils suggests that they are multicellular eukaryotes, although their exact phylogenetic affinities are uncertain. Forms with dichotomously branching filaments are likely to be algae. Types A and B also resemble some morphologically differentiated modern algae[16] such as the kelp *Postelsia palmaeformis*, which has a holdfast, a stalk, and a crown of splaying and unbranching blades. Indeed, the Lantian fossil *Flabellophyton lantianensis*, previously interpreted as a macroalga[4], may be related to Types A and B; it consists of a splay of tightly packed filaments but lacks a crown of ribbons, and may represent only the stalk of Type A/B fossils.

The morphologies of Types C–E find no analogues among modern algae. Type C may be interpreted as a cnidarian-like organism, with the fusiform inner body representing a retracted polyp with a gastrovascular
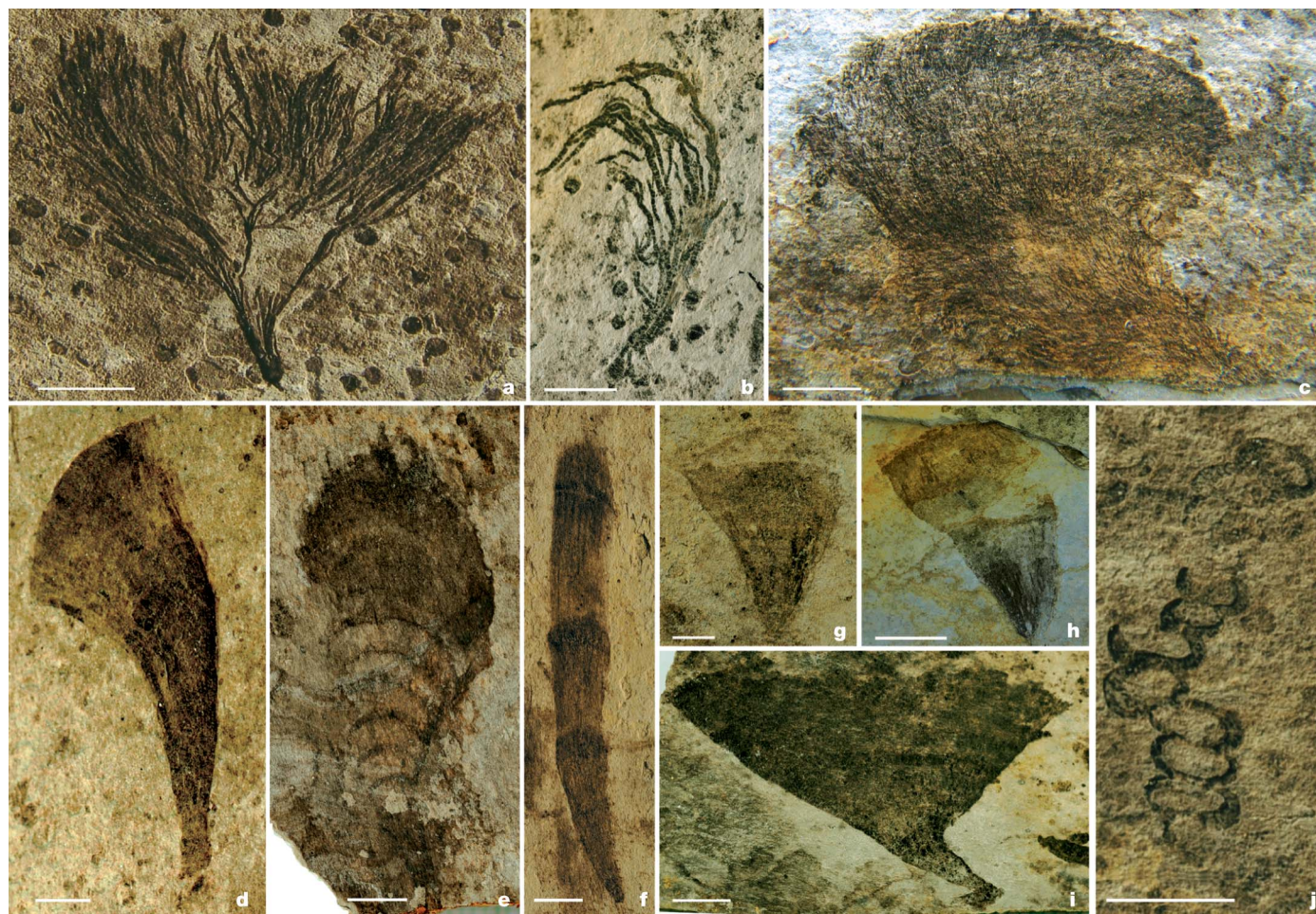

Figure 2 | Photomicrographs of Lantian macrofossils of probably algal affinities. a, *Doushantuophyton cometa*. **b**, *Huangshanophyton fluticulosum*. **c**, *Anhuiphyton lineatum*. **d**, *Flabellophyton lantianensis* with fan-shaped thallus. **e** and **f**, *Flabellophyton strigata* with fan-shaped thallus and transverse bands. **g–i**, *Flabellophyton* sp. with fan-shaped or conical thallus. **j**, *Orbisiana* sp. Scale bars, 1 cm in **b** and **h**, 5 mm in all others.
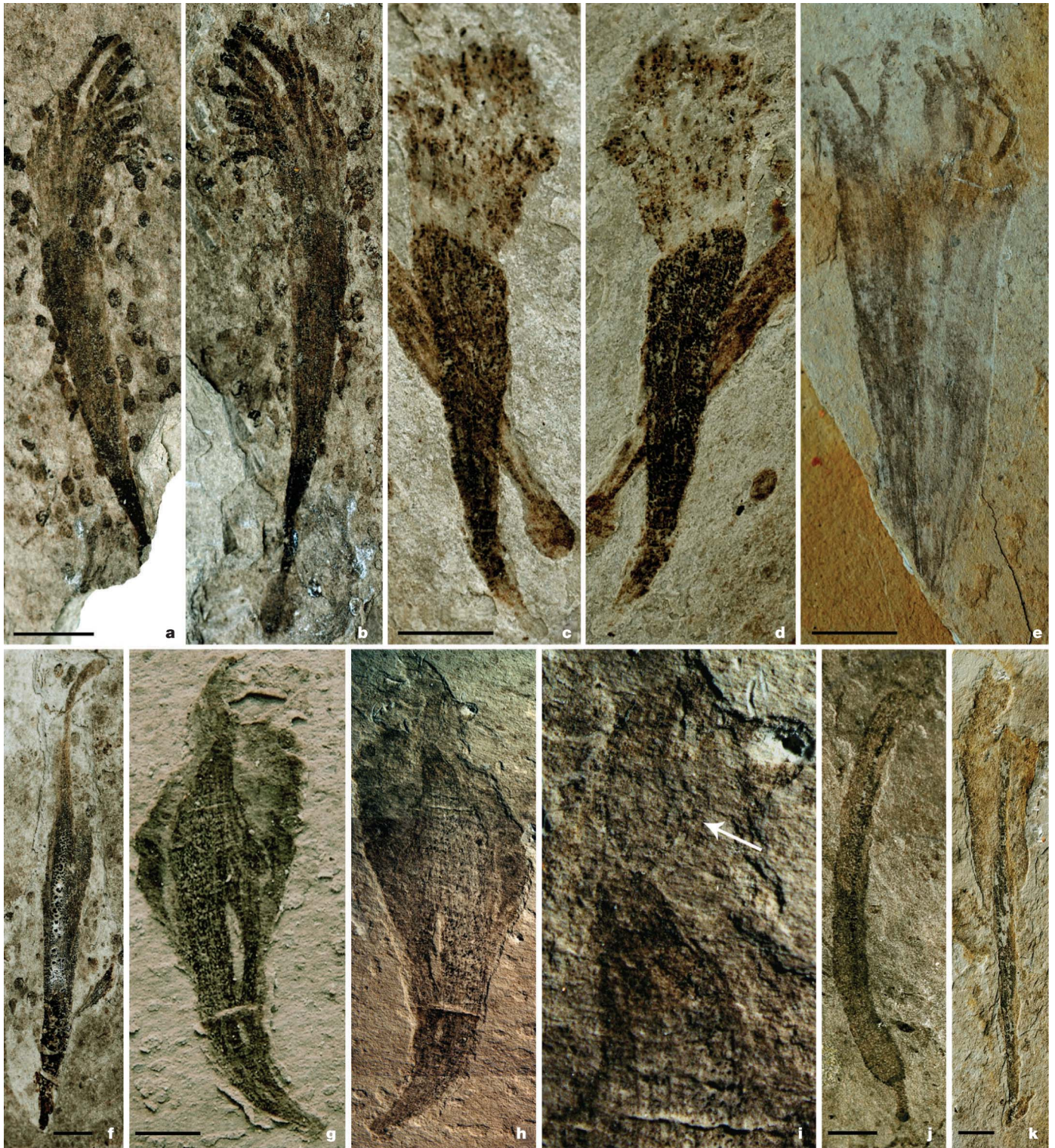
Figure 3 | Photomicrographs of new Lantian forms with uncertain phylogenetic affinities. a–e, f, g–i, j and k represent Type A, B, C, D and E, respectively. a, b, Part and counterpart. Note abundant *Chuaria circularis* fossils (circular carbonaceous impressions ~1 mm in diameter) in background. c, d, Part and counterpart. Scale bar, 3 mm. e, Incompletely preserved specimen. f, Specimen similar to a–e, but with a crown consisting of a single ribbon. g–i, Part, counterpart and magnification of upper part showing a conical pyramid that supports a cluster of filaments (arrow in i). j, Specimen with a holdfast, a stalk, a cylindrical tube, and an axial trace. Scale bar, 2 mm. k, Specimen similar to j in having stalk and axial structure, but with a longer stalk and a broader structure surrounding axial trace. Scale bars, 5 mm unless otherwise noted.

cavity surrounded by a hydrotheca-like integument; this interpretation implies the presence of retractor muscles. The longitudinal structures could represent ornamentation, retractor muscles, or mesentery-like structures. The axial structure in Types D and E is puzzling and it could represent the digestive structure of worm-like animals. In an animal model, the holdfast and stalk of Type D would be alternatively interpreted as the proboscis of an early worm-like organism. Intriguingly, a poorly preserved ribbon with an axial trace and a bulbous terminal structure from the Miaohe biota (Doushantuo Member IV) has been interpreted as a 'putative bilaterian metazoan'[17].

Regardless of the phylogenetic uncertainties, the taxonomic diversity and morphological complexity of the Lantian biota are notable. Even considering ontogenetic and preservational factors (see Supplementary Information), we estimate that the Lantian biota consists of ~15 morphospecies, many of which show complex morphological differentiation. This is in sharp contrast to pre-Ediacaran macrofossils, for which diversity is low, morphologies are simple, and eukaryotic affinity and multicellular nature are ambiguous[18]. Indeed, the Lantian biota nearly matches the Avalon biota[19] in taxonomic diversity and morphological differentiation, although the phylogenetic compositions of the two biotas are drastically different, with the former dominated by macroalgae and the latter by modular rangeomorphs[1]. Thus, the Lantian biota implies that some eukaryotic clades had achieved macroscopic and differentiated multicellularity before the Avalon biota, perhaps shortly after the Marinoan glaciation, thus raising the intriguing possibility that Neoproterozoic global glaciations drove the evolution of macroscopic multicellularity[20].

The Lantian macrofossils also place constraints on the redox history of Ediacaran oceans. Because a permissive amount of oxygen is required to maintain the metabolism of complex macroeukaryotes (particularly macrometazoans)[21] and because modern anoxic environments are typically colonized only by microorganisms (including micrometazoans that are mostly derived from aerobic ancestors)[22], the evolution of complex macroeukaryotes sets boundaries for the Ediacaran redox condition. Even the oxygen-producing macroalgae in the Lantian Formation would require free oxygen for respiration and would not have survived an oxygen-free environment, as suggested by the lack of macroalgae (and dominance of cyanobacteria and microalgae) in modern anoxic environments within the photic zone[23]. Thus, the *in situ* preservation of complex macroeukaryotes in the lower Lantian Formation indicates that free oxygen was at least locally available below the storm wave base. If macrometazoans existed in the Lantian biota, their more active metabolism implies an even greater amount of free oxygen.

However, geochemical data indicate that many Ediacaran deep basins were anoxic[24], although some became oxygenated around 580 Myr ago along with the rise of the deep-water Avalon biota[2]. In particular, geochemical studies of black shales in Lantian Member II in southern Anhui[25] and Doushantuo Member II in the Yangtze Gorges area[26] suggest deposition in largely anoxic (and sometimes euxinic) conditions, which would be hostile to benthic macroalgae and macrometazoans. To reconcile the conflicting geochemical and palaeontological indicators of palaeoredox conditions, we propose that the Lantian basin was largely anoxic but punctuated by brief oxic episodes. These oxic episodes were opportunistically capitalized on by benthic macroeukaryotes that were subsequently killed and preserved by frequent switch-backs to anoxic conditions. Brief oxic intervals also occurred in many Mesozoic anoxia events[27], and they are consistent with existing geochemical data from other Ediacaran basins suggesting significant temporal and spatial variations in redox conditions despite overall anoxia[11,24,26,28,29]. This more complex picture of Ediacaran ocean redox history calls for integrated geochemical, palaeontological and sedimentological investigations at ultrahigh stratigraphic resolution.

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