

The Lantian biota: A new window onto the origin and early evolution of multicellular organisms

YUAN XunLai^{1*}, CHEN Zhe¹, XIAO ShuHai^{1,2}, WAN Bin¹, GUAN ChengGuo¹, WANG Wei¹, ZHOU ChuanMing¹ & HUA Hong³

¹ State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China;

² Department of Geosciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061, USA;

³ State Key Laboratory of Continental Dynamics and Department of Geology, Northwest University, Xi'an 710069, China

Received August 1, 2012; accepted August 28, 2012; published online October 20, 2012

The Lantian biota at the Lantian Town of Xiuning County, Anhui Province, is preserved in black shales of the Ediacaran Lantian Formation. It yields some of the oldest known complex macroorganisms, including fan-shaped seaweeds and possible animal fossils with tentacles and intestinal-like structures reminiscent of modern coelenterates and bilaterians. The Lantian Lagerstätte sheds new light on the origin and early evolution of multicellular organisms in relatively quiet and deep environments soon after the Neoproterozoic Marinoan glaciation. The morphological complexity and diversity of early multicellular organisms may be closely related to sexual reproduction and alternation of generations. The fluctuation of oceanic redox conditions during this period may have played a role in the ecology and preservation of the Lantian biota.

Lantian biota, Ediacaran, multicellular organism, origin and early evolution

Citation: Yuan X L, Chen Z, Xiao S H, et al. The Lantian biota: A new window onto the origin and early evolution of multicellular organisms. *Chin Sci Bull*, 2013, 58: 701–707, doi: 10.1007/s11434-012-5483-6

The rise of multicellularity on Earth is one of the most important innovations in the history of life. Only after the evolution of multicellularity can cell differentiation, organ differentiation, and functional and morphological diversification of macroscopic and complex life evolve. In the Phanerozoic history, such complex macroorganisms played an important role in shaping the Earth's surface environment. But when, where, and how life became macroscopic and complex? To answer these questions, we need to turn to fossils preserved in ancient rocks.

In the long history of life, multicellular organisms have evolved multiple times. A major radiation of multicellular animals took place in between 540–520 Ma [1–3], as evidenced by Early Cambrian small shelly fossils and exceptionally preserved biotas such as the Chengjiang and Burgess Shale faunas. With some exceptions that can be ex-

plained on taphonomic basis, most animal phyla had stem-group representatives in this period, which is commonly referred to as the “Cambrian explosion”. Although prior to the Cambrian, multicellular macroscopic body fossils are relatively scarce, Ediacara fossils, a class of soft-bodied macro-organisms in the late Precambrian (from 580 to 540 Ma), have a wide geographic distribution [4–9]. Although their phylogenetic relationships with Phanerozoic multicellular macroorganisms are controversial [10–15], some of them have been interpreted as coelenterates and mollusks [4,16,17].

So far, the oldest Ediacara fossil assemblage is the Avalon Biota [8] from 579–565-million-year-old deep-water sedimentary rocks in Canada, prompting some to argue that oxygen levels in deep water environment was sufficiently high to support macroscopic multicellular eukaryotes [18]. Prior to this, macroscopic eukaryotic fossils are rare, and it is likely that oxygen levels were not sufficient to support

*Corresponding author (email: xlyuan@nigpas.ac.cn)

significant development of macroscopic eukaryotes.

In the 1980s, phosphatized and silicified fossil Lagerstätte were found in the 635–550 Ma Doushantuo Formation in Weng'an and the Yangtze Gorges areas. Subsequent investigations revealed a great diversity of large acanthomorphic acritarchs, animal embryos, and multicellular algae, which provide important paleontological evidence about the evolution of multicellular eukaryotes following the Marinoan glaciation but prior to the rise of the Ediacara biota [19–34]. In the meantime, sedimentological and geochemical studies have revealed dramatic environment fluctuations in the Ediacaran Period. Deep oceans were probably anoxic in the early Ediacaran, but anoxia was interrupted by periodic oxic events [35–40], whereas shallow waters were mostly oxic. These studies imply a micro-fossil-dominated eukaryotic ecosystem in shallow marine before the advent of the Ediacara macrobiota, and the existence of oceanic redox stratification.

The Lantian biota described herein is from ~600 Ma black shales of the early Ediacaran Lantian Formation, near the town of Lantian, Xiuning county, southern Anhui Province, China (Figure 1). Older than and significantly different from the Ediacara biota in terms of diversity and preservation, this unique macroscopic fossil assemblage opens a new window onto the early evolution of complex multicellular macroorganisms and their environmental backgrounds.

1 The Lantian biota

1.1 Research history

The Lantian biota was first described by Xing et al. [41]. Subsequently several papers on Lantian macrofossils in this region were published [42–44]. In 1992, the Lantian flora was named by Yan et al. [45], and 12 genera and 18 macroalgae fossils were described. In 1997, Tang et al. [46]

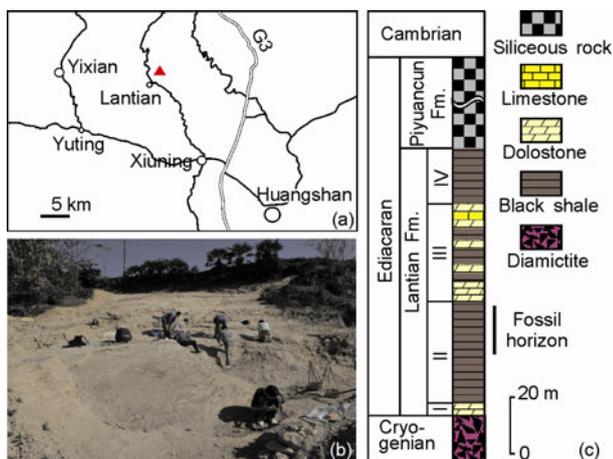


Figure 1 Locality and stratigraphic horizon of the Lantian biota. (a) Locality map, with red triangle marking the fossil locality; (b) excavation site; (c) stratigraphic column. Black vertical bar marks stratigraphic interval where Lantian fossils are preserved.

restudied a group of discoidal or ellipsoidal fossils in this fossil assemblage, and interpreted them as metaphytes with sexual differentiation. Renewed field collection continued in 1994–1999, and a systematic study placed ~50 previously described species in 12–15 species [47,48].

In recent years, Yuan and his colleagues have been restudying this biota and published a paper entitled “An early Ediacaran assemblage of macroscopic and morphologically differentiated eukaryotes” in *Nature* in February 2011, with an accompanying commentary by Narbonne [49].

According to the new data [50], the Lantian biota represents one of the oldest biotas with diverse assemblage of complex multicellular macro-eukaryotes, as well as intriguing fossils with possible hints of animal affinities.

1.2 A brief introduction to the Lantian biota

According to chemostratigraphic, sequence stratigraphic and event stratigraphic data, combined with regional stratigraphic correlation, the Lantian biota is probably older than the Ediacara biota, with an age between 580 and 635 Ma [50]. Lantian fossils are preserved as carbonaceous compressions on bedding surfaces of black shales (Figure 1). The presence of a holdfast in most Lantian fossils indicates that they were benthic sessile organisms.

The biota comprises fan-shaped algae and possible metazoans with tentacles and intestinal comparable with the modern eumetazoans (Figure 2). After a preliminary study, at least 15 different morphological types of macroorganisms were identified (Figure 3). Because the fossils are preserved in shales with fine lamination but without any sedimentary structures indicative of strong hydrodynamic activities or transportation, these macroorganisms are thought to have been preserved *in situ* and have lived below the maximum wave base but within the photic zone. Paleogeographic reconstruction indicates that the Lantian biota lived in a marginal platform or a locally restricted environment with a water depth about 50 to 200 m.

The Lantian biota is quite different from the Ediacara biota in preservational style and biodiversity. Lantian fossils are preserved as carbonaceous compressions on the bedding



Figure 2 (a) Algal fossil in the Lantian biota; (b),(c) part and counterpart of a possible animal fossil with tentacle-like structures. Scale bar is 5 mm for (a) and 10 mm for (b), (c).

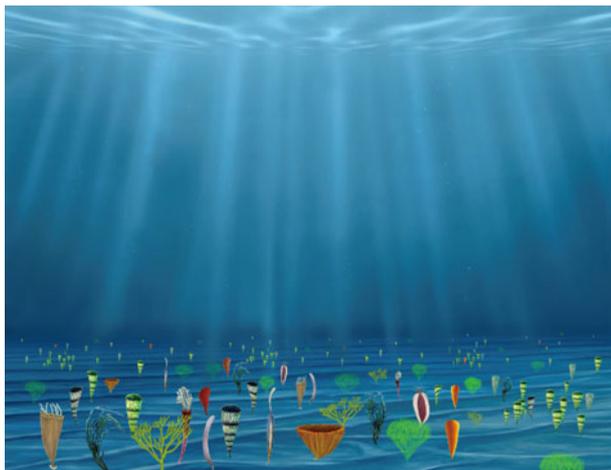


Figure 3 An artist's reconstruction of more than 10 taxa of macroalgae and putative animals in the Lantian biota. Most Lantian fossils have holdfast structures. Coloration is arbitrary. Branching and fan-shaped forms are macroalgae. Conical or cup-shaped forms are putative animals, although they may also represent taphonomic variations of macroalgae.

surface of black shales, whereas the majority of Ediacara fossils are preserved as casts or molds in sandstone or siltstone. Although both biotas are dominated by benthic sessile macroorganisms, they have few species in common. In addition, Ediacara organisms have a broader environmental distribution whereas the Lantian biota is restricted to a quiet water environment.

A series of major geological events took place in the Neoproterozoic, including the breakup of the supercontinent Rodinia and multiple global glaciations, having a profound impact on the evolution of the biosphere [51–54]. Before the Great Ice Age, shallow water ecosystems were dominated by prokaryotes, which formed stromatolites and microbial mats, although eukaryotes can be traced back to the Paleoproterozoic. The fossil record shows that early eukaryotes were mostly single-celled microscopic algae (e.g. featureless leiosphere acritarchs) or simple globular and tubular forms (e.g. the chuarid-tawuuiid assemblage) [32]. After the Marinoan glaciation, eukaryotes underwent a rapid development, and the Lantian biota record this event in a transgression sequence soon after the Marinoan snowball Earth event.

The accumulation of oxygen in the atmosphere and ocean is a long and slow process in Earth's history. Redox stratification, with an anoxic and even sulfidic bottom water, was common in Proterozoic oceans [36,55]. Shortly after the end of the Marinoan glaciations, the Lantian biota evolved. This implies that sufficient oxygen must have been locally and intermittently available in the Lantian basin to support macroscopic organisms [50]. However, the Lantian basin was probably predominately anoxic [38], which may have facilitated the *in-situ* fossil preservation.

The Ediacaran Period was the turning point in ocean redox evolution, with unstable and fluctuating redox condi-

tions. This unique environmental background may have played a role in the paleoecology and taphonomy of the Lantian biota. The bottom water may have been intermittently oxic to support the Lantian macroorganisms, but reducing condition was prevailing, which may have facilitated to the preservation of Lantian organisms. Such unstable redox conditions may have been a norm in Ediacaran and perhaps Cambrian oceans. It was only until the late Paleozoic was marine completely oxidized [56,57]. The Lantian biota is preserved in many fossiliferous layers in a 15 m-thick black shale, suggesting that repeated switch back and forth between anoxic and oxic conditions. This hypothesis can be tested with high-resolution redox geochemical data.

2 The origin and early evolution of multicellular organisms

2.1 Previous knowledge

The origin of eukaryotes is an innovation event in the history of early evolution of life, and it was closely related to the emergence of free oxygen in the atmosphere. Reliable fossils of unicellular eukaryotes can be traced back to the Paleoproterozoic [58], and major eukaryote lineages might have diverged before Neoproterozoic glaciation. For example, the differentiation of xanthophytes, chlorophytes, and rhodophytes can be dated back to 1300–1000 Ma [59,60], amoebozoans and rhizarians appeared 750 Ma [61]. The fossil record of metazoans is still elusive prior to the Marinoan glaciation, although there are a number of reports [62,63]. However, according to molecular clock estimates, protostomian and deuterostomian animals may have diverged nearly 700 million years ago [64], if not earlier [65–70]. In the 19th century, Haeckel speculated that the early metazoan may have been microscopical organisms morphologically similar to living animal embryos and larvae [71]. Developmental biologists have also speculated that the early metazoans may have resembled modern animal larvae before they acquiring macroscopic bodyplan, and have a long period of early evolutionary history [72].

Relative to microorganisms, multicellular macroorganisms require a greater level of oxygen in the environment. Macroorganisms were widespread in the Middle and Late Ediacaran in shallow marine environments. Many of them had differentiated morphologies. In addition, a moderate number of trace fossils have been reported from the Ediacaran Period [73–76], including the Avalon biota, and macroalgal fossils from the Miaohu biota [77]. Although the exact phylogenetic affinities of many Ediacaran macrofossils remain unresolved, their wide distribution implies that macroorganisms may have initiated a more complex ecosystem in the late Ediacaran, particularly in shallow marine environments where free oxygen levels were sufficiently high.

Multicellular animals may also have had a long evolutionary history prior to the Ediacaran Period. However, no macroscopic animals or reliable trace fossils have been found in rocks older than the late Ediacaran Period. Thus, it is often assumed that the earliest animals may have been microscopic organisms that were unlikely to be preserved in the fossil record [78].

The discovery of the Weng'an biota has shed new light on the evolution of multicellular organisms. This fossil biota is of about 600 million years old [79], older than the Avalon biota. Early diagenetic phosphatization and silicification offer opportunities for exceptional fossil preservation. Multicellular fossils found in this biota are mostly microscopic, including multicellular algae, animal embryos and cnidarian-grade tubular fossils [19–22,32,80,81]. Subsequently, a large number of animal embryo fossils have also been found in the lower Doushantuo Formation (~632 Ma) in the Yangtze Gorges area [82,83]. It has been argued that some large acanthomorphic acritarchs from Ediacaran successions in Australia, Eastern European Platform, and Siberia may represent diapause eggs of early animals as well [84]. Because a complete ontogenetic sequence of the Weng'an embryo fossils is still a matter of debate [30,85], alternative interpretations—including green algae, giant sulfur bacteria, and mesomycetozoon-like protists—have been proposed to account for the morphologies of the Weng'an fossils [30,86–88], but so far animal embryos remain the most plausible interpretation for these fossils [28,31,82,89]. The available data are thus consistent with the hypothesis that animals were probably microscopic before the middle Ediacaran Period.

2.2 New knowledge

New data from the Lantian biota open a unique window onto the early evolution of multicellular organisms. First, it shows that diverse macroscopic multicellular eukaryotes made their appearance before the classical Ediacara biota, and they include algae and possible metazoans. Second, similar to the Ediacara biota, many Lantian elements were sessile benthic organisms. Third, the morphological and taxonomic diversity of the Lantian biota is distinct from that of the classical Ediacara biota, a difference that has either paleoecological or evolutionary implications. Many Lantian fossils, including dichotomously branching algae and fan-shaped algae, have morphological analogues among the younger Ediacaran Miaohu biota and modern algae. Putative animal fossils from the Lantian biota have tentacles and digestive tract structures that can be compared with living animals. In contrast, classical Ediacara fossils lack morphological analogues in younger biotas.

It is generally believed that early metazoans may have evolved in oxygen-rich shallow waters. However, organisms in the Lantian biota probably lived in anoxic environments punctuated by periodic oxicity. Some Lantian elements

(e.g. algae) may have been able to tolerate hypoxia, but it is possible that rapid sexual reproduction and r-selection may have allowed the Lantian organisms to adapt to such variable and challenging environments. Some populations in the Lantian biota contain con-specific individuals with holdfast and of similar size (Figure 4), indicating that these benthic individuals were of the same cohort. Measurements of specimens on a single slab show that the length of fan-shaped fossils in Figure 4 mainly falls within the range of 1.5 to 3.5 cm, and the divergence angle 12° to 32° (Figure 5). These individuals likely represent a reproduction cohort, a reproductive strategy similar to the Ediacara organism *Funisia dorothea* [90].

On the basis of the taphonomic, paleoecological, and paleoenvironmental data from the Lantian biota, one can draw a few general conclusions about the early evolution of the multicellular organisms and its environmental background.

Shallow marine benthic ecosystems before the Neoproterozoic were dominated by prokaryote communities. Although eukaryotes may have originated in the Paleoproterozoic, they were not ecologically dominant and mostly remained microscopic until the Ediacaran Period. Their environmental and physiological restriction may have related to generally low oxygen levels. During the Ediacaran Period, oxygen levels in the atmosphere may have increased, and deep oceans became gradually oxidized although redox conditions were unstable. The rise of oxygen levels made it possible for macroscopic multicellular organisms such as macroalgae and metazoans to colonize benthic ecosystems. Rapid sexual reproduction and r-selection strategies may have assisted the adaptation to Ediacaran environments characterized by variable redox conditions. In the late Ediacaran Period, macroscopic eukaryotes spread to occupy a

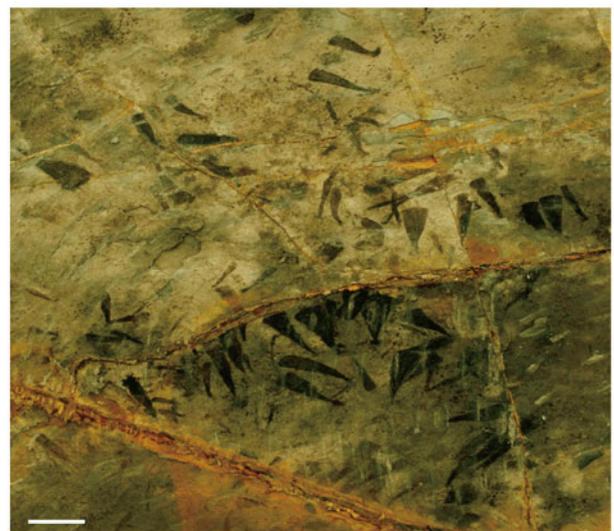


Figure 4 A slab showing the density and orientation of the Lantian fossil *Flabellophyton*. Individuals on this slab may represent a single cohort. Scale bar: 2 cm.

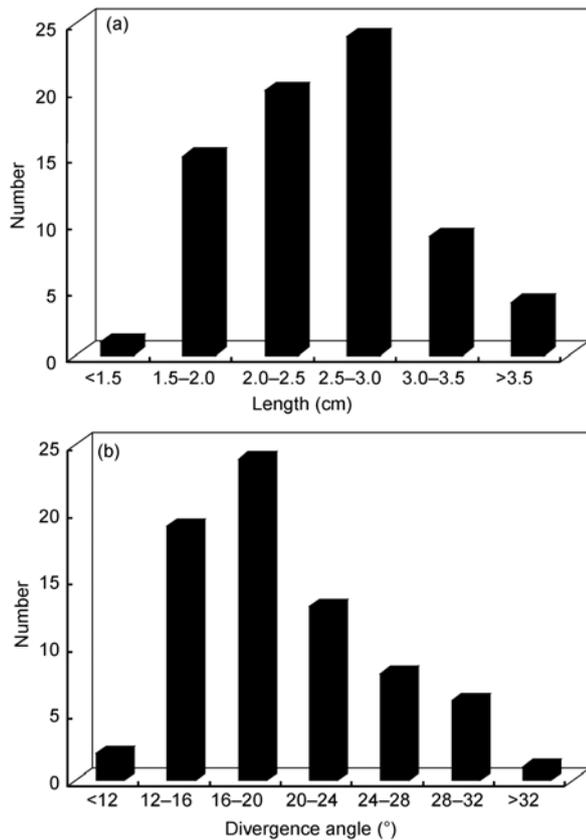


Figure 5 Measurements of fan-shaped fossils shown in Figure 4. (a) Distribution of fossil length; (b) distribution of divergence angles.

much wider environmental spectrum in both shallow and deep water realms.

2.3 Discussion

The origin and early evolution of multicellular organisms is a complex process. There is no doubt that eukaryotic multicellularization evolved multiple times in the Proterozoic. For example, xanthophytes, green algae, and red algae diverged in the Mesoproterozoic [59,60,91], when marine benthic ecosystems were dominated by microbial communities and oxygen levels limited the ecological radiation of macroscopic eukaryotes. The Lantian biota may represent the first radiation of complex macro-eukaryotes (perhaps including macrometazoans) shortly after the Marinoan glaciation.

In the late Ediacaran Period, mobile benthic metazoans evolved and left a trace fossil record [92,93]. So far, mobile organisms and trace fossils have not been found in the Lantian biota.

In summary, the Lantian biota marks the transition to an ecosystem where complex and macroscopic multicellular eukaryotes played an increasingly important ecological role. This transition was probably linked to the gradual oxygenation of the Earth's surface environment.

This work was supported by the National Natural Science Foundation of China (41030209, 41130209 and 40625006) and the Chinese Academy of Sciences (KZZD-EW-02, KZCX2-YW-153 and KZCX2-EW-119).

- Shu D. Cambrian explosion: Birth of tree of animals. *Gondwana Res*, 2008, 14: 219–240
- Hou X, Bergström J, Wang H, et al. The Chengjiang Fauna: Exceptionally Well-preserved Animals From 530 Million Years Ago (in Chinese). Kunming: Yunnan Science and Technology Press, 1999. 40–49
- Qian Y. Taxonomy and Biostratigraphy of Small Shelly Fossils in China (in Chinese). Beijing: Science Press, 1999. 27–31
- Glaessner M F. The Dawn of Animal Life: A Biohistorical Study. Cambridge: Cambridge University Press, 1984. 1–244
- Sun W. Late Precambrian pennatulids (sea pens) from the eastern Yangtze Gorge, China: *Paracharnia* gen. nov. *Precambrian Res*, 1986, 31: 361–375
- Grotzinger J P, Bowring S A, Saylor B Z, et al. Biostratigraphic and geochronologic constraints on early animal evolution. *Science*, 1995, 270: 598–604
- Fedonkin M A. Systematic description of Vendian Metazoa. In: Sokolov B S, Iwanowski A B, eds. *The Vendian System, Vol. 1: Paleontology*. Heidelberg: Springer-Verlag, 1990. 71–120
- Narbonne G M. The Ediacara biota: Neoproterozoic origin of animals and their ecosystems. *Annu Rev Earth Planet Sci*, 2005, 33: 421–442
- Xiao S, Laflamme M. On the eve of animal radiation: Phylogeny, ecology and evolution of the Ediacara biota. *Trends Ecol Evol*, 2009, 24: 31–40
- McMenamin M A S. The Garden of Ediacara. *Palaios*, 1986, 1: 178–182
- Seilacher A. Vendobionta and Psammocorallia: Lost constructions of Precambrian evolution. *J Geol Soc Lond*, 1992, 149: 607–613
- Seilacher A. Vendozoa: Organismic construction in the Precambrian biosphere. *Lethaia*, 1989, 22: 229–239
- Retallack G J. Were the Ediacaran fossils lichens? *Paleobiology*, 1994, 20: 523–544
- Peterson K J, Waggoner B, Hagadorn J W. A fungal analog for Newfoundland Ediacaran fossils? *Integ Comp Biol*, 2003, 43: 127–136
- Zhuravlev A Y. Were Ediacaran Vendobionta multicellulars? *N Jb Geol Paläont Abh*, 1993, 190: 299–314
- Conway Morris S. The fossil record and the early evolution of the Metazoa. *Nature*, 1993, 361: 219–225
- Fedonkin M A, Waggoner B M. The late Precambrian fossil *Kimberella* is a mollusc-like bilaterian organism. *Nature*, 1997, 388: 868–871
- Canfield D E, Poulton S W, Narbonne G M. Late-Neoproterozoic deep-ocean oxygenation and the rise of animal life. *Science*, 2007, 315: 92–95
- Zhang Y, Yuan X. New data on multicellular thallophytes and fragments of cellular tissues from late Proterozoic phosphate rocks, South China. *Lethaia*, 1992, 25: 1–18
- Xiao S, Knoll A H, Yuan X, et al. Phosphatized multicellular algae in the Neoproterozoic Doushantuo Formation, China, and the early evolution of florideophyte red algae. *Am J Bot*, 2004, 91: 214–227
- Xiao S, Yuan X, Knoll A H. Eumetazoan fossils in terminal Proterozoic phosphorites? *Proc Natl Acad Sci USA*, 2000, 97: 13684–13689
- Xiao S, Zhang Y, Knoll A H. Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite. *Nature*, 1998, 391: 553–558
- Chen J, Bottjer D J, Li G, et al. Complex embryos displaying bilaterian characters from Precambrian Doushantuo phosphate deposits, Weng'an, Guizhou, China. *Proc Natl Acad Sci USA*, 2009, 106: 19056–19060
- Chen J, Bottjer D J, Oliveri P, et al. Small Bilaterian Fossils from 40 to 55 Million Years Before the Cambrian. *Science*, 2004, 305: 218–222
- Zhou C, Yuan X, Xiao S. Phosphatized biotas from the Neoproterozoic Doushantuo Formation on the Yangtze Platform. *Chin Sci Bull*,

- 2002, 47: 1918–1924
- 26 Zhou C, Xie G, McFadden K, et al. The diversification and extinction of Doushantuo-Pertatataka acritarchs in South China: Causes and biostratigraphic significance. *Geol J*, 2007, 42: 229–262
 - 27 Yin C, Bengtson S, Yue Z. Silicified and phosphatized Tianzhushania, spheroidal microfossils of possible animal origin from the Neoproterozoic of south China. *Acta Palaeontol Pol*, 2004, 49: 1–12
 - 28 Xiao S, Zhou C, Yuan X. Undressing and redressing Ediacaran embryos. *Nature*, 2007, 446: E9–E11
 - 29 Xiao S. Life on Earth: Precambrian Eukaryote Fossils. In: Selley R C, Cocks R, Plimer I R, eds. *Encyclopedia of Geology*. Amsterdam: Elsevier, 2004. 354–363
 - 30 Hultgren T, Cunningham J A, Yin C, et al. Fossilized nuclei and germination structures identify ediacaran “animal Embryos” as encysting protists. *Science*, 2011, 334: 1696–1699
 - 31 Xiao S, Knoll A H, Schiffbauer J D, et al. Comment on “Fossilized nuclei and germination structures identify Ediacaran ‘animal embryos’ as encysting protists. *Science*, 2012, 335: 1169
 - 32 Yuan X, Xiao S, Yin L, et al. Doushantuo Fossils: Life on the Eve of Animal Radiation (in Chinese). Hefei: China University of Science and Technology Press, 2002. 1–171
 - 33 Schiffbauer J D, Xiao S, Sharma K S, et al. The origin of intracellular structures in Ediacaran metazoan embryos. *Geology*, 2012, 40: 223–226
 - 34 Zhang Y, Yin L, Xiao S, et al. Permineralized fossils from the terminal Proterozoic Doushantuo Formation, South China. *Paleontol Soc Mem*, 1998, 50: 1–52
 - 35 McFadden K A, Huang J, Chu X, et al. Pulsed oxidation and biological evolution in the Ediacaran Doushantuo Formation. *Proc Natl Acad Sci USA*, 2008, 105: 3197–3202
 - 36 Canfield D E, Poulton S W, Knoll A H, et al. Ferruginous conditions dominated later Neoproterozoic deep-water chemistry. *Science*, 2008, 321: 949–952
 - 37 Scott C, Lyons T W, Bekker A, et al. Tracing the stepwise oxygenation of the Proterozoic ocean. *Nature*, 2008, 452: 456–459
 - 38 Shen Y, Zhang T, Hoffman P F. On the coevolution of Ediacaran oceans and animals. *Proc Natl Acad Sci USA*, 2008, 105: 7376–7381
 - 39 Zhao Y Y, Zheng Y F. Stable isotope evidence for involvement of deglacial meltwater in Ediacaran carbonates in South China. *Chem Geol*, 2010, 271: 86–100
 - 40 Li C, Love G D, Lyons T W, et al. A Stratified Redox Model for the Ediacaran Ocean. *Science*, 2010, 328: 80–83
 - 41 Xing Y, Gao Z, Liu G, et al. The Upper Precambrian of China, Volume 3 of “The Stratigraphy of China” (in Chinese). Beijing: Geological Publishing House, 1989. 1–150
 - 42 Bi Z, Wang X, Zhu H, et al. The Sinian of southern Anhui (in Chinese). *Prof Pap Stratigr Palaeontol*, 1988. 19: 27–60
 - 43 Steiner M. Die neoproterozoischen Megaalgen Südchinas. *Berl Geowiss Abh (E)*, 1994, 15: 1–146
 - 44 Chen M, Lu G, Xiao Z. Preliminary study on the algal macrofossils—antian Flora from the Lantian Formation of Upper Sinian in southern Anhui (in Chinese). *Bull Inst Geol Acad Sin*, 1994, 7: 252–267
 - 45 Yan Y, Jiang C, Zhang S, et al. Research of the Sinian System in the region of western Zhejiang, northern Jiangxi, and southern Anhui provinces (in Chinese). *Bull Nanjing Inst Geol Min Resour Chin Acad Geol Sci*, 1992, 12(Suppl): 1–105
 - 46 Tang F, Yin C, Gao L. A new idea of metaphyte fossils from the late Sinian Doushantuo stage at Xiuning, Anhui Province (in Chinese). *Acta Geol Sin*, 1997, 71: 289–296
 - 47 Yuan X, Li J, Cao R. A diverse metaphyte assemblage from the Neoproterozoic black shales of South China. *Lethaia*, 1999, 32: 143–155
 - 48 Yuan X, Xiao S, Li J, et al. Pyritized chuarids with excystment structures from the late Neoproterozoic Lantian Formation in Anhui, South China. *Precambrian Res*, 2001, 107: 251–261
 - 49 Narbonne G M. Evolutionary biology: When life got big. *Nature*, 2011, 470: 339–340
 - 50 Yuan X, Chen Z, Xiao S, et al. An early Ediacaran assemblage of macroscopic and morphologically differentiated eukaryotes. *Nature*, 2011, 470: 390–393
 - 51 Moore E M. Southwest U.S.-East Antarctic (SWEAT) connection: A hypothesis. *Geology*, 1991, 19: 425–428
 - 52 Dalziel I W D. Pacific margins of Laurentia and East Antarctica-Australia as a conjugate rift pair: Evidence and implications for an Eocambrian supercontinent. *Geology*, 1991, 19: 598–601
 - 53 Hoffman P F. Did the breakout of Laurentia turn Gondwanaland inside-out? *Science*, 1991, 252: 1409–1412
 - 54 Hoffman P F, Kaufman A J, Halverson G P, et al. A Neoproterozoic snowball Earth. *Science*, 1998, 281: 1342–1346
 - 55 Javaux E J, Knoll A H, Walter M R. Morphological and ecological complexity in early eukaryotic ecosystems. *Nature*, 2001, 412: 66–69
 - 56 Gill B C, Lyons T W, Young S A, et al. Geochemical evidence for widespread euxinia in the Later Cambrian ocean. *Nature*, 2011, 469: 80–83
 - 57 Dahl T W, Hammarlund E U, Anbar A D, et al. Devonian rise in atmospheric oxygen correlated to the radiations of terrestrial plants and large predatory fish. *Proc Natl Acad Sci USA*, 2010, 107: 17911–17915
 - 58 Peng Y, Bao H, Yuan X. New morphological observations for Paleoproterozoic acritarchs from the Chuanlinggou Formation, North China. *Precambrian Res*, 2009, 168: 223–232
 - 59 Butterfield N J, Knoll A H, Swett K. A bangiophyte red alga from the Proterozoic of Arctic Canada. *Science*, 1990, 250: 104–107
 - 60 Butterfield N J, Knoll A H, Swett K. Paleobiology of the Neoproterozoic Svanbergfjellet Formation, Spitsbergen. *Fossils Strata*, 1994, 34: 1–84
 - 61 Porter S M, Knoll A H. Testate amoebae in the Neoproterozoic Era: Evidence from vase-shaped microfossils in the Chuar Group, Grand Canyon. *Paleobiology*, 2000, 26: 360–385
 - 62 Maloof A C, Porter S M, Moore J L, et al. The earliest Cambrian record of animals and ocean geochemical change. *Geol Soc Amer Bull*, 2010, 122: 1731–1774
 - 63 Brain C K B, Prave A R, Hoffmann K H, et al. The first animals: ca. 760-million-year-old sponge-like fossils from Namibia. *S Afr J Sci*, 2012, 108: 1–8
 - 64 Erwin D H, Laflamme M, Tweedt S M, et al. The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Science*, 2011, 334: 1091–1097
 - 65 Doolittle R F, Feng D F, Tsang S, et al. Determining divergence times of the major kingdoms of living organisms with a protein clock. *Science*, 1996, 271: 470–477
 - 66 Wray G A, Levinton J S, Shapiro L H. Molecular evidence for deep Precambrian divergences among metazoan phyla. *Science*, 1996, 274: 568–573
 - 67 Ayala F J, Rzhetsky A, Ayala F J. Origin of the metazoan phyla: Molecular clocks confirm paleontological estimates. *Proc Natl Acad Sci USA*, 1998, 95: 606–611
 - 68 Bromham L, Rambaut A, Forsey R, et al. Testing the Cambrian Explosion hypothesis by using a molecular dating technique. *Proc Natl Acad Sci USA*, 1998, 95: 12386–12389
 - 69 Lee M S Y. Molecular clock calibrations and metazoan divergence dates. *J Mol Evol*, 1999, 49: 385–391
 - 70 Wang D Y-C, Kumar S, Hedges S B. Divergence time estimates for the early history of animal phyla and the origin of plants, animals and fungi. *Proc R Soc B*, 1999, 266: 163–171
 - 71 Haeckel E. The gastrea theory, the phylogenetic classification of the animal kingdom and the homology of the germ-lamellae. *Quart J Micr Sci*, 1874, 14: 142–165
 - 72 Davidson E H, Peterson K J, Cameron R A. Origin of bilaterian body plans: Evolution of developmental regulatory mechanisms. *Science*, 1995, 270: 1319–1325
 - 73 Jensen S, Droser M L, Gehling J G. A critical look at the Ediacaran trace fossil record. In: Xiao S, Kaufman A J, eds. *Neoproterozoic Geobiology*. Dordrecht: Kluwer Academic Publishers, 2006. 115–157
 - 74 Jensen S. The Proterozoic and earliest Cambrian trace fossil record: Patterns, problems and perspectives. *Integr Comp Biol*, 2003, 43: 219–228
 - 75 Seilacher A, Buatois L A, Gabriela Mangano M. Trace fossils in the

- Ediacaran-Cambrian transition: Behavioral diversification, ecological turnover and environmental shift. *Palaeogeogr Palaeoclimat Palaeoecol*, 2005, 227: 323–356
- 76 Gehling J G, Narbonne G M, Anderson M M. The first named Ediacaran body fossil, *Aspidella terranovica*. *Palaeontology*, 2000, 43: 427–456
- 77 Xiao S, Yuan X, Steiner M, et al. Macroscopic carbonaceous compressions in a terminal Proterozoic shale: A systematic reassessment of the Miaohé biota, South China. *J Paleontol*, 2002, 76: 345–374
- 78 Knoll A H, Carroll S B. Early animal evolution: Emerging views from comparative biology and geology. *Science*, 1999, 284: 2129–2137
- 79 Barfod G H, Albarède F, Knoll A H, et al. Implications for the Neoproterozoic biological and climatic history from dating of the Doushantuo Phosphorites, S. China. *EOS Trans AGU Fall Meeting*, 2002, 83: Abstract B71B–0737
- 80 Chen J, Bottjer David J, Davidson Eric H, et al. Phosphatized polar lobe-forming embryos from the Precambrian of southwest China. *Science*, 2006, 312: 1644–1646
- 81 Zhang Y. Multicellular thallophytes with differentiated tissues from late Proterozoic phosphate rocks of South China. *Lethaia*, 1989, 22: 113–132
- 82 Yin L, Zhu M, Knoll A H, et al. Doushantuo embryos preserved inside diapause egg cysts. *Nature*, 2007, 446: 661–663
- 83 Yin L, Zhou C, Yuan X. New data on *Tianzhushania*—An Ediacaran diapause egg cyst from Yichang, Hubei (in Chinese). *Acta Palaeontol Sin*, 2008, 47: 129–140
- 84 Cohen P A, Knoll A H, Kodner R B. Large spinose microfossils in Ediacaran rocks as resting stages of early animals. *Proc Natl Acad Sci USA*, 2009, 106: 6519–6524
- 85 Xiao S, Hagadorn J W, Zhou C, et al. Rare helical spheroidal fossils from the Doushantuo Lagerstätte: Ediacaran animal embryos come of age? *Geology*, 2007, 35: 115–118
- 86 Bailey J V, Joye S B, Kalanetra K M, et al. Evidence of giant sulphur bacteria in Neoproterozoic phosphorites. *Nature*, 2007, 445: 198–201
- 87 Butterfield N J. Terminal developments in Ediacaran Embryology. *Science*, 2011, 334: 1655–1656
- 88 Xue Y, Zhou C, Tang T. “Animal embryos”, a misinterpretation of Neoproterozoic microfossils (in Chinese). *Acta Micropalaeontol Sin*, 1999, 16: 1–4
- 89 Xiao S, Knoll A H. Embryos or algae? A reply (in Chinese). *Acta Micropalaeontol Sin*, 1999, 16: 313–323
- 90 Droser M L, Gehling J G. Synchronous aggregate growth in an abundant new Ediacaran tubular organism. *Science*, 2008, 319: 1660–1662
- 91 Butterfield N J. A vaucheriacean alga from the middle Neoproterozoic of Spitsbergen: Implications for the evolution of Proterozoic eukaryotes and the Cambrian explosion. *Paleobiology*, 2004, 30: 231–252
- 92 Liu A G, McLroy D, Brasier M D. First evidence for locomotion in the Ediacara biota from the 565 Ma Mistaken Point Formation, Newfoundland. *Geology*, 2010, 38: 123–126
- 93 Pecoits E, Konhauser K O, Aubert N R, et al. Bilaterian burrows and grazing behavior at >585 million years ago. *Science*, 2012, 336: 1693–1696

Open Access This article is distributed under the terms of the Creative Commons Attribution License which permits any use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.