JGS
Journal of the Geological Society

Review Focus

Published Online First

https://doi.org/10.1144/jgs2016-142

The Weng'an Biota (Doushantuo Formation): an Ediacaran window on soft-bodied and multicellular microorganisms

John A. Cunningham[1,2]*, Kelly Vargas[1], Zongjun Yin[3], Stefan Bengtson[2] & Philip C. J. Donoghue[1]

[1] School of Earth Sciences, University of Bristol, Life Sciences Building, 24 Tyndall Avenue, Bristol BS8 1TQ, UK
[2] Department of Palaeobiology and Nordic Center for Earth Evolution, Swedish Museum of Natural History, 10405 Stockholm, Sweden
[3] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

K.V., 0000-0003-1320-4195; S.B., 0000-0003-0206-5791; P.C.J.D., 0000-0003-3116-7463

* Correspondence: John.Cunningham@bristol.ac.uk

Abstract: The Weng'an Biota is a fossil Konservat-Lagerstätte in South China that is *c.* 570 – 609 myr old and provides an unparalleled snapshot of marine life during the interval in which molecular clocks estimate that animal clades were diversifying. It yields fossils that are three-dimensionally preserved in calcium phosphate with cellular and sometimes subcellular fidelity. The biota includes candidates for the oldest animals in the fossil record, including embryonic, larval and adult forms. We argue that, although the Weng'an Biota includes forms that could be animals, none can currently be assigned to this group with confidence. Nonetheless, the biota offers a rare and valuable window on the evolution of multicellular and soft-bodied organisms in the prelude to the Cambrian radiation.

Received 21 November 2016; **revised** 28 February 2017; **accepted** 1 March 2017

The origin and evolutionary assembly of animal body plans comprises one of the most formative episodes in the history of life. Animals are ecosystem engineers and their appearance fundamentally changed our planet's ecology (Butterfield 2011*a*). Despite the importance of this evolutionary episode, many aspects of the timing and nature of the event remain poorly constrained. Molecular-clock analyses estimate that animals originated by the Cryogenian and diversified through the Ediacaran (Peterson & Butterfield 2005; Erwin *et al.* 2011; dos Reis *et al.* 2015), but fossil evidence of animals from before the Cambrian is controversial (Erwin *et al.* 2011; dos Reis *et al.* 2015; Cunningham *et al.* 2017). The Weng'an Biota is one of the few Lagerstätten from the critical interval in which early animals are expected according to molecular-clock studies. In this Ediacaran fossil assemblage, organisms are phosphatized in cellular and even subcellular detail, providing a rare glimpse of soft-bodied and multicellular life at this time. Early research appeared to fulfil expectations of the presence of metazoans with reports of embryonic (Xiao *et al.* 1998), larval (Chen *et al.* 2000, 2002) and adult (Xiao *et al.* 2000; Chen *et al.* 2002, 2004; Yin *et al.* 2015) animals from the Weng'an deposit. However, subsequent analyses have cast doubt on this view, and there is currently much disagreement over these interpretations (Bailey *et al.* 2007*a*; Huldtgren *et al.* 2011; Bengtson *et al.* 2012; L. Chen *et al.* 2014, Xiao *et al.* 2014*a*). Here, we review the stratigraphic position, geological age and environmental setting of the deposit, and present an overview of the biota and an assessment of the phylogenetic affinities of the various taxa.

Stratigraphy and age

The Weng'an Biota occurs within the Ediacaran Doushantuo Formation (551 – 635 Ma, Condon *et al.* 2005) of south China (Fig. 1). In addition to the phosphatized microfossils from Weng'an, this formation has yielded silicified microfossils (Yin *et al.* 2004) and macrofossils that are preserved as 2D carbonaceous compressions including macro-algae (Xiao *et al.* 2002) and the putative ctenophore *Eoandromeda* (Tang *et al.* 2008, 2011). The Weng'an Biota itself is known from localities in Weng'an County, Guizhou Province. The Doushantuo Formation overlies the Marinoan glacial tillites of the Cryogenian Nantuo Formation that can be dated to 635 Ma (Condon *et al.* 2005). It is overlain by the Ediacaran Dengying Formation, which contains fossils of the classical Ediacara macrobiota (Sun 1986; Xiao *et al.* 2005; Z. Chen *et al.* 2014). The base of the Dengying Formation can be dated to 551 Ma (Condon *et al.* 2005). In Weng'an, the Doushantuo Formation is composed of five units that have been described in detail by Xiao *et al.* (2014*b*) and Yin *et al.* (2015). The Weng'an Biota occurs mainly in Unit 4, the Upper Phosphorite Member, but also in Unit 5. Unit 4 is divided into 4A, a black phosphorite, and 4B, a grey dolomitic phosphorite (Dornbos *et al.* 2006; Xiao *et al.* 2014*a*,*b*; Yin *et al.* 2015).

The age of the biota has been debated (Budd 2008; Erwin & Valentine 2013; Xiao *et al.* 2014*a*; Yin *et al.* 2015), with arguments focusing on the correlation of two karstic surfaces, one at the top of Unit 3 and the other within Unit 5 (for detailed discussion of Doushantuo correlation see Zhu *et al.* (2007), Zhu *et al.* (2013) and Yang *et al.* (2015)). If the lower surface is correlated to the *c.* 582 Ma Gaskiers glaciation (Condon *et al.* 2005) then the biota would be younger than 582 Ma. However, the lower surface may be older (Yin *et al.* 2015) and, if the upper karstic surface correlates to the Gaskiers glaciation (Xiao *et al.* 2014*a*), then the biota would be older than 582 Ma. Direct radiometric dates for Unit 4 at Weng'an have been inconclusive, giving Pb–Pb isochron ages of 572 ± 36 Ma for Unit 4A (Y. Chen *et al.* 2009) and 599 ± 4 Ma for Unit 4B (Barfod *et al.* 2002). However, a recent U–Pb date of 609 ± 5 Ma from a tuff immediately above Unit 4 at Zhancunping, in Hubei Province (Zhou *et al.* 2017), suggests that the Weng'an biota is probably older than 609 ± 5 Ma and probably older than the

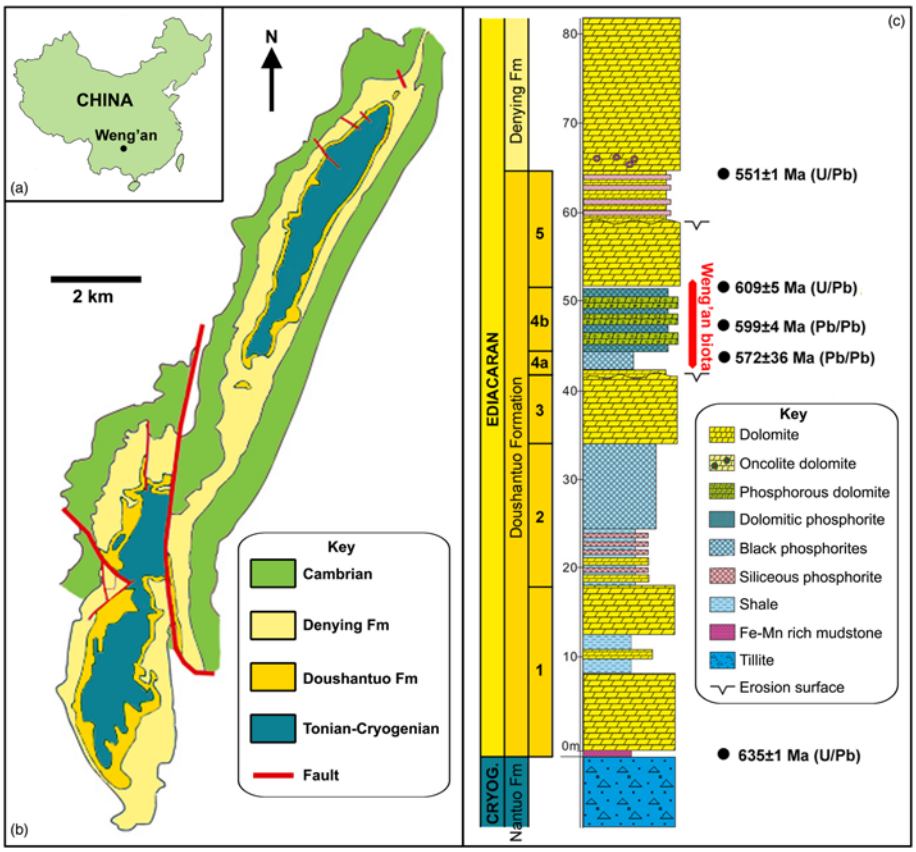

Fig. 1. The location and geological setting of the Weng'an Biota. (**a**) Map of China showing the location of Weng'an. (**b**) Geological map of the Weng'an area. (**c**) Stratigraphic column of the Beidoushan section in the Weng'an area indicating Units 1 – 4 of the Doushantuo Formation, the occurrence of the Weng'an Biota and the radiometric age constraints discussed in the text. Modified from Yin *et al.* (2015).

Gaskiers glaciation, which cannot be related to the karst surface at the top of Unit 3 if this date is correct. Acritarchs identical to those containing embryo-like fossils are found just above an ash band dated to 632.5 ± 0.5 Ma in Doushantuo sections from the Yangtze Gorges (Yin *et al.* 2007), suggesting that these organisms could have existed at this time. In summary, the biota is probably older than the classical but enigmatic Ediacaran biota and considerably predates the rich animal fossil record of the Cambrian. Putative animals from the assemblage are therefore candidates for the oldest animals in the fossil record.

Depositional environment, preservation and reworking

The Weng'an Biota is interpreted as having been deposited in an outer-shelf environment on a SE-facing passive margin (Jiang *et al.* 2011). Abundant wave ripples and cross-bedding features indicate deposition above fair-weather wave base (Xiao & Knoll 1999). The fossils were probably deposited in oxic conditions (Shields *et al.* 2004), although phosphatization may have occurred in anoxic sediments (Muscente *et al.* 2014; Schiffbauer *et al.* 2014). The soft-bodied organisms of the biota are three-dimensionally preserved in calcium phosphate and can be preserved at a subcellular level (Hagadorn *et al.* 2006; Huldtgren *et al.* 2011). However, even the best-preserved specimens are a complex amalgam of cements, making it challenging to determine which aspects represent preserved biology (Xiao *et al.* 2000; Bengtson 2003; Bengtson & Budd 2004; Cunningham *et al.* 2012*a*; Schiffbauer *et al.* 2012). The preservation of Weng'an fossils is discussed in Box 1. The fossils occur either as, or within, phosphatic grains that have been abraded and rounded, indicating transport from other parts of the basin after initial preservation (Xiao *et al.* 2007*b*). In unit 4A, a *c.* 5 m thick black phosphorite, the fossils occur in reworked phosphatic clasts. As a result, they cannot be released by acetic acid maceration and have generally been studied in petrographic thin sections (e.g. Chen

Box 1: Preservation of Weng'an fossils

The Weng'an organisms, like all exceptionally preserved soft-bodied remains, were subjected to both post-mortem decay and later diagenetic and geological processes (Donoghue & Purnell 2009). These processes alter the morphology of the fossils in ways that can be unpredictable. Palaeontologists must take these factors into account rather than simply comparing the fossils with extant or freshly dead modern organisms. This is particularly true given the simple nature of the biological structures relevant to the interpretation of the Weng'an Biota. In the case of decay, carefully designed experiments can help constrain which features can feasibly be preserved, elucidate likely preservation pathways, and identify biases introduced by the decay process (Sansom 2014). Experiments have shown that animal embryos have a relatively high preservation potential, particularly when enclosed in a fertilization envelope, whereas primary larvae have an extremely low likelihood of being preserved (Raff *et al.* 2006; Gostling *et al.* 2008, 2009). In addition, these experiments have identified the likely mechanism for Doushantuo-type preservation: 3D replication of cells by robust bacterial pseudomorphs followed by phosphate mineralization (Raff *et al.* 2008). The diagenetic and subsequent geological processes that the fossil is subjected to can introduce artefacts (e.g. through crystal nucleation and growth) that have no connection to the original anatomy. These processes are difficult to simulate experimentally because of the timescales involved. An alternative approach is to characterize the mineral phases that preserve biological anatomy v. geological artefacts. This has been carried out in fossils where there is agreement regarding affinity and anatomy, and has allowed textural and chemical criteria to be established and then applied to more contentious Weng'an material (Cunningham *et al.* 2012*a*, 2014). In particular, geological artefacts tend to have larger, euhedral crystals with a preferred orientation, higher X-ray attenuation and characteristic void-filling textures. Geological artifacts typically also have high relative abundances of P, Ca and F, and low abundances of C and S. Failure to consider these processes and/or the 3D nature of the specimens can lead to misinterpretations of the fossils as discussed in Box 2.

Box 2: 2D versus 3D analysis

The Weng'an fossils have been subjected to a wide range of analytical techniques. These include scanning electron microscopy (which provides very high resolution images of the exterior of the specimen), analysis of petrographic thin sections (which affords a single cross-section but destroys the remainder of the fossil) and tomographic approaches (which allow the specimen to be imaged in three dimensions). Analyses of specimens in petrographic sections have yielded important insights, including features that have not been identified using other techniques, such as the cell clusters preserved within 'Megaclonophycus'-stage embryoids (L. Chen *et al.* 2014). However, the 2D nature of the data can make it difficult to make inferences regarding the 3D anatomy of the fossil and caution must be exercised. Reports of gastrulae (Chen *et al.* 2000, 2002), cnidarian larvae (Chen *et al.* 2000, 2002) and adult bilaterians (Chen *et al.* 2004) probably result from misinterpretations of deformed cysts, which are abundant in the deposit, that have been studied only in two dimensions (Xiao *et al.* 2000; Bengtson 2003; Bengtson & Budd 2004; Bengtson *et al.* 2012).

et al. 2004; L. Chen *et al.* 2014; see Box 2 for a comparison of 2D and 3D analytical techniques). In unit 4B, a *c.* 10 m thick grey dolomitic phosphorite, the microfossils are abundant and in places are so concentrated that the layers resemble oolites. This is a grainstone composed largely of microfossils that have been phosphatized before being reworked, transported and winnowed (Xiao & Knoll 1999; Xiao *et al.* 2007*b*). The fossils can be extracted by dissolution of the carbonate constituents of rock samples in weak acetic acid and manual sorting of the resulting residues. Specimens can then be studied using scanning electron microscopy (e.g. Xiao *et al.* 1998) or tomographic techniques (e.g. Hagadorn *et al.* 2006) and can be re-embedded in resin and sectioned for further petrographic and geochemical analyses (reviewed by Cunningham *et al.* 2014).

Overview of the Weng'an Biota

Algae

A variety of algal taxa have been reported from Weng'an (Zhao 1986; Zhang 1989; Zhang & Yuan 1992; Xiao *et al.* 1998, 2004; Xiao 2004). Some simpler forms, such as *Archaeophycus* (Fig. 2j), show interesting similarities to extant bangialean red algae (Xiao *et al.* 1998), although other affinities cannot be ruled out (Xiao *et al.* 2014*a*). More complex forms such as *Thallophyca* and *Paramecia* share characters with floridophyte red algae including pseudoparenchymous construction, differentiated thalli and possible reproductive structures (Xiao *et al.* 2004). However, the putative algae have received relatively little attention because of the focus on the search for animals. Many specimens lack the overall form of a photosynthetic organism. For example, the blades typical of various seaweeds have not been recovered and it is hard to envisage how cells positioned centrally within globular masses would have functioned in a photosynthetic organism (Fig. 3a and b). Algae may have been used as a wastebasket taxon for assorted irregular forms and rejected animal candidates. These fossils merit further study and there is a prospect that they may include developmental stages of other organisms including the embryo-like fossils, especially given their typically larger size.

Acritarchs

The acritarchs (Fig. 2k) from Weng'an have been reviewed comprehensively by Xiao *et al.* (2014*b*) and form part of the Doushantuo–Pertatataka microbiota (Zhou *et al.* 2001, 2007; Liu *et al.* 2014). The phylogenetic affinities of acritarchs are unknown and they probably represent a polyphyletic assortment of eukaryotes (Huntley *et al.* 2006). Some Doushantuo acritarchs contain embryo-like fossils (Yin *et al.* 2007), leading to the suggestion that other Ediacaran acritarchs might be resting cysts of these organisms (Cohen *et al.* 2009). The interpretation of the Doushantuo–Pertatataka acritarchs is therefore at least partially linked to that of the embryo-like fossils, although they may well represent a polyphyletic assemblage. The affinities of taxa should be considered on a case-by-case basis.

Embryo-like fossils

Weng'an fossils that have been interpreted as the embryos of early animals (Xiao *et al.* 1998) have been the focus of most attention and debate (Fig. 2a–f). They have been interpreted as metazoans (Xiao *et al.* 1998) including bilaterians (Chen & Chi 2005; J. Chen *et al.* 2006, 2009*a*,*b*; Yin *et al.* 2013), as stem-group metazoans (Hagadorn *et al.* 2006; Schiffbauer *et al.* 2012; L. Chen *et al.* 2014) or as members of non-metazoan clades (Bailey *et al.* 2007*a*,*b*; Butterfield 2011*b*; Huldtgren *et al.* 2011, 2012; L. Chen *et al.* 2014; Zhang & Pratt 2014). We consider the various claims below.

Giant sulphur bacteria?

Bailey *et al.* (2007*a*,*b*) proposed an interesting hypothesis that the embryo-like fossils might be giant sulphur bacteria similar to the living *Thiomargarita*. These bacteria can be similar in size and shape to the embryo-like fossils from Weng'an and are capable of undergoing at least a few rounds of palintomic division. However, subsequent analyses have shown that these bacteria cannot account for key morphological aspects of the fossils such as the presence of ornamented envelopes, outer acritarch vesicles, and probable lipid vesicles and nuclei (Donoghue 2007; Xiao *et al.* 2007*b*; Huldtgren *et al.* 2011; Cunningham *et al.* 2012*b*). Moreover, evidence from experimental taphonomy showed that *Thiomargarita* cells are not replicated by biofilm-forming bacteria, meaning that they do not form the stable bacterial pseudomorphs that are thought to be the precursor to exceptional phosphatization (Cunningham *et al.* 2012*b*; see Box 1).

Bilaterians or eumetazoans?

Reports of embryonic bilaterians do not withstand scrutiny. Some are based on identifications of cell geometries argued to be unique to bilaterians. These include specimens purported to preserve endodermal cords (J. Chen *et al.* 2009*b*), polar lobes (J. Chen *et al.* 2006, 2009*a*; Yin *et al.* 2013), embryonic polarity (J. Chen *et al.* 2009*a*,*b*) and duet cleavage (J. Chen *et al.* 2009*a*). In each case, the specimens can be alternatively interpreted as examples of embryo-like fossils that have undergone taphonomic and diagenetic processes (Huldtgren *et al.* 2011; Cunningham *et al.* 2012*a*). Specimens interpreted as possible bilaterian or cnidarian gastrulae and larvae (Chen *et al.* 2000, 2002; Chen & Chi 2005) are more probably deformed cysts filled with phosphatic cements (Xiao *et al.* 2000). The presence of meroblastic embryos (Yin *et al.* 2016) would represent the long sought-after confirmation of the presence of animal embryos. A possible alternative interpretation of these specimens, which are associated with a large population known to undergo asynchronous division (Hagadorn *et al.* 2006), is that they have undergone unequal division. It is currently difficult to test between these possible interpretations.

Total group animals?

The embryo-like fossils probably represent one taxon dividing from a single cell to thousands of cells (Fig. 2a–f). This taxon has been

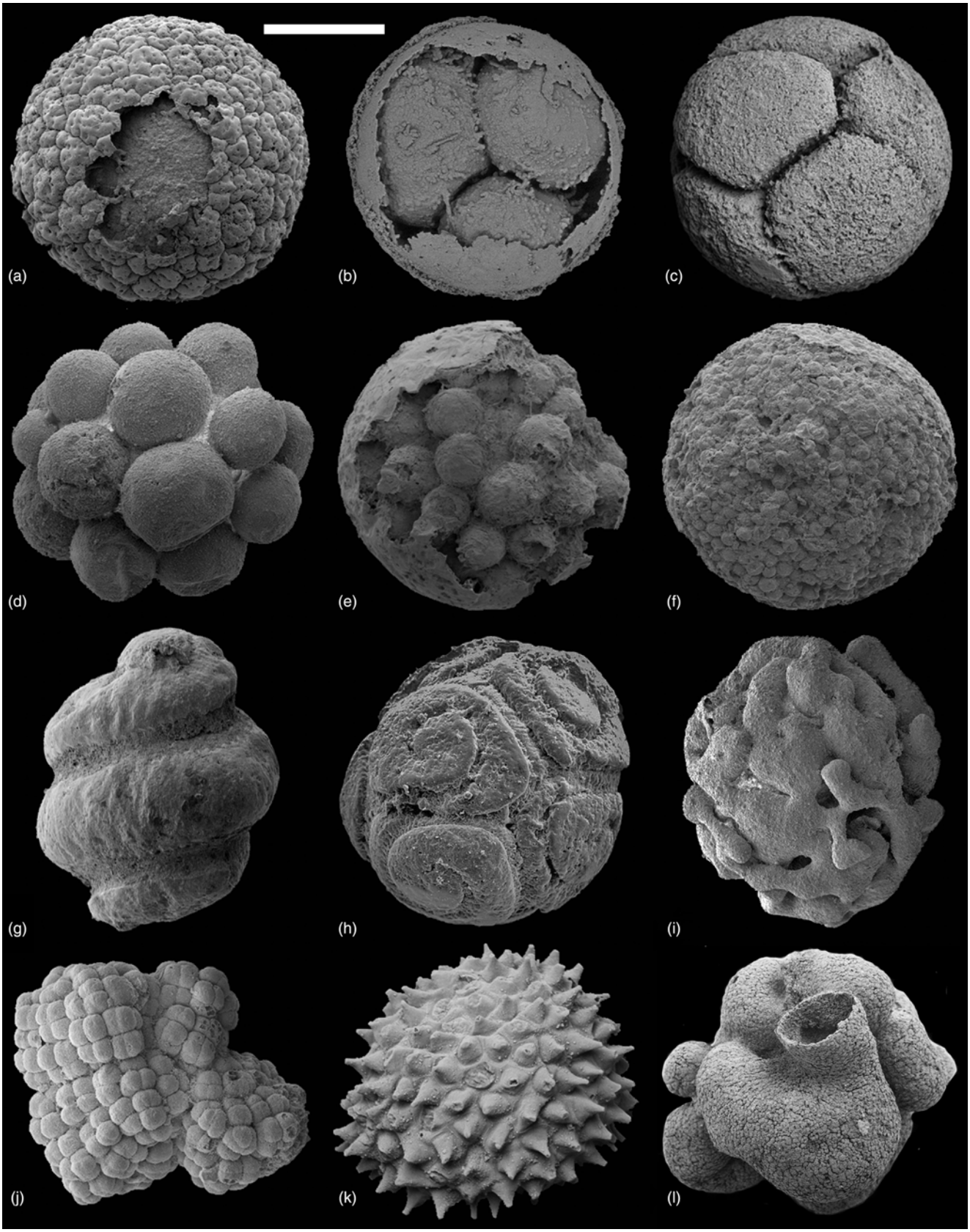

Fig. 2. Scanning electron microscope images of fossils from the Weng'an biota. (**a**–**f**) *Tianzhushania* specimens at various stages of division from a single cell (**a**) to many hundreds of cells (**f**) Swedish Museum of Natural History (SMNH) X 6449–SMNH X 6454. (**g**) *Helicoforamina* SMNH X 6455. (**h**) *Spiralicellula* (from Tang *et al.* 2008). (**i**) *Caveasphaera* SMNH X 6456. (**j**) *Archaeophycus*, a putative red alga SMNH X 6457. (**k**) *Mengeosphaera*, an acritarch SMNH X 6458. (**l**) *Eocyathispongia*, a putative sponge, Nanjing Institute of Palaeontology and Geology (NIGPAS) 161760 (from Yin *et al.* 2015). Scale bar: (**a**) 320 μm, (**b**) 265 μm, (**c**) 265 μm, (**d**) 200 μm, (**e**) 245 μm, (**f**) 280 μm, (**g**) 395 μm, (**h**) 380 μm, (**i**) 250 μm, (**j**) 255 μm, (**k**) 130 μm, (**l**) 415 μm.

Fig. 3. Synchrotron radiation X-ray tomographic microscopy (SRXTM; **a**–**h**) and light microscopy (**i**–**k**) images of Weng'an fossils. (**a**, **b**) a possible alga SMNH X 6459, comparable with *Paramecia*. (**c**, **d**) a peanut-shaped fossil SMNH X 6460. (**e**, **f**) *Sinocyclocyclicus* SMNH X 5322. (**g**, **h**) *Ramitubus* SMNH X 5326. (**i**–**k**) Light microscopy images of putative algae from Weng'an. Scale bar: (**a**, **b**) 270 μm, (**c**, **d**) 280 μm, (**e**, **f**) 180 μm, (**g**, **h**) 175 μm, (**i**, **j**) 140 μm, (**k**) 115 μm.

Box 3: Taxonomy of the embryo-like fossils

The embryo-like fossils have been described under various genus and species names that are now considered to be different developmental stages or taphonomic variants of a single taxon (Huldtgren *et al.* 2011; Cunningham *et al.* 2012*a*; L. Chen *et al.* 2014; Xiao *et al.* 2014*a*,*b*). The names *Megasphaera* (single-celled specimens), *Parapandorina* (multiple polyhedral cells) and *Megaclonophycus* (large numbers of usually spheroidal cells) are now widely considered to be synonyms (e.g. Huldtgren *et al.* 2011; Cunningham *et al.* 2012*a*; Xiao *et al.* 2014*a*,*b*). However, because of different taxonomic interpretations, different researchers have referred to this taxon as either *Megasphaera* (e.g. L. Chen *et al.* 2014; Xiao *et al.* 2014*a*,*b*) or *Tianzhushania* (e.g. Yin *et al.* 2004; Huldtgren *et al.* 2011; Cunningham *et al.* 2012*a*). The genus *Tianzhushania* and its type species *T. spinosa* were described in 1978 for acanthomorphic acritarchs with cylindrical processes that were known from thin sections (Yin & Li 1978). Yin *et al.* (2001) subsequently described *T. tuberifera* based on specimens with both cylindrical processes and sculptured ornament. *Megasphaera*, with the type species *M. inornata*, was described in 1986 for smooth envelopes (Chen & Liu 1986) and later expanded by Xiao & Knoll (2000) to accommodate specimens with sculptured envelopes (*M. ornata*). Yin *et al.* (2004) showed that *M. ornata* specimens, when viewed in thin sections, could be surrounded by an outer wall identical to that of *Tianzhushania*. They therefore argued that *T. tuberifera*, which had been studied in thin sections, was the same species as *M. ornata*, which had mainly been studied in specimens isolated from acid residues. Yin *et al.* (2004) proposed *Tianzhushania ornata* as the valid name for this taxon. As the various embryo-like stages can be found inside these specimens, Huldtgren *et al.* (2011) argued that *Tianzhushania* is the senior synonym of *Megasphaera*, *Parapandorina* and *Megaclonophycus*. Xiao *et al.* (2014) noted that the diagnosis of *Tianzhushania* had never been formally emended to include specimens with sculptured envelopes. They therefore proposed to retain *Megasphaera* for smooth or sculptured specimens that lack processes and *Tianzhushania* for specimens that have smooth envelopes and processes. The new genus *Yinitianzhushania* (basionym *T. tuberifera*) was erected to accommodate those specimens that have sculptured envelopes and cylindrical processes. However, this classification differentiates *Megasphaera* from the other genera based on the absence of tubular processes, which probably results from taphonomic loss rather than a biological difference. We also find it unsatisfactory to place specimens from acid residues into *Yinitianzhushania* if they have a sculptured envelope and *Tianzhushania* if they do not. This would result in a specimen with a sculptured envelope and tubular processes being placed in one genus (*Yinitianzhushania*) if it had lost only its processes and another (*Tianzhushania*) if it had also lost its sculptured envelope. It is therefore preferable to place all of these taxa in a single genus, *Tianzhushania*, which we consider to be the senior synonym of *Yinitianzhushania*, as well as of *Megasphaera*, *Parapandorina* and *Megaclonophycus*, despite the fact that the diagnosis of *Tianzhushania* has not yet been formally revised to include specimens with sculptured envelopes.

named either *Tianzhushania* or *Megasphaera* according to different taxonomic interpretations (Yin *et al.* 2004; Xiao *et al.* 2014*b*). *Tianzhushania* is preferred here (see Box 3). These specimens were interpreted as animal embryos by Xiao *et al.* (1998) based on the similar size and the presence of palintomic cell division, Y-shaped junctions between cells and an ornate enclosing envelope. More recently, these have been considered as stem, rather than crown, animals because later stages lack evidence for epithelial organization, which is characteristic of modern embryos (Hagadorn *et al.* 2006). However, the placement of these fossils in the animal total-group has also been questioned (Bailey *et al.* 2007*a*; Butterfield 2011*b*; Huldtgren *et al.* 2011; L. Chen *et al.* 2014; Zhang & Pratt 2014).

None of the characters that have been used to justify an animal interpretation are exclusive to animals (see Fig. 4). Features such as palintomic cleavage, Y-shaped cell junctions and an ornate envelope are found in non-animal groups (Huldtgren *et al.* 2011, 2012). They are therefore consistent with an animal interpretation, but they are not diagnostic characters. They are insufficient, either in isolation or in combination, to justify an animal affinity.

It has also been suggested that *Tianzhushania* exhibits characters gained in the animal stem lineage. L. Chen *et al.* (2014) described discrete clusters of cells ('matryoshkas') within embryo-like fossils with hundreds of cells. They interpreted these as reproductive propagules and presented them as evidence for spatial cell differentiation, germ–soma separation and apoptosis. Based on these characters, along with functional cell adhesion, obligate multicellularity and the potential lack of a rigid cell wall, L. Chen *et al.* (2014) argued that *Tianzhushania* might be a stem-animal that had gained some, but not all, of the characters that are present in animals, but not choanoflagellates. The occurrence of dividing cells within the embryo-like fossils is merely an expectation of the existing observation that they exhibit asynchronous cell division (Hagadorn *et al.* 2006). Nevertheless, the interpretation of differentiation and germ–soma separation requires that the clusters are part of the embryo-like organism rather than an exogenous parasite. L. Chen *et al.* (2014) suggested that there is a developmental continuation from the typical cells of these specimens and the clusters, which rules out an exogenous origin. However, there is a discontinuity between monads, dyads and

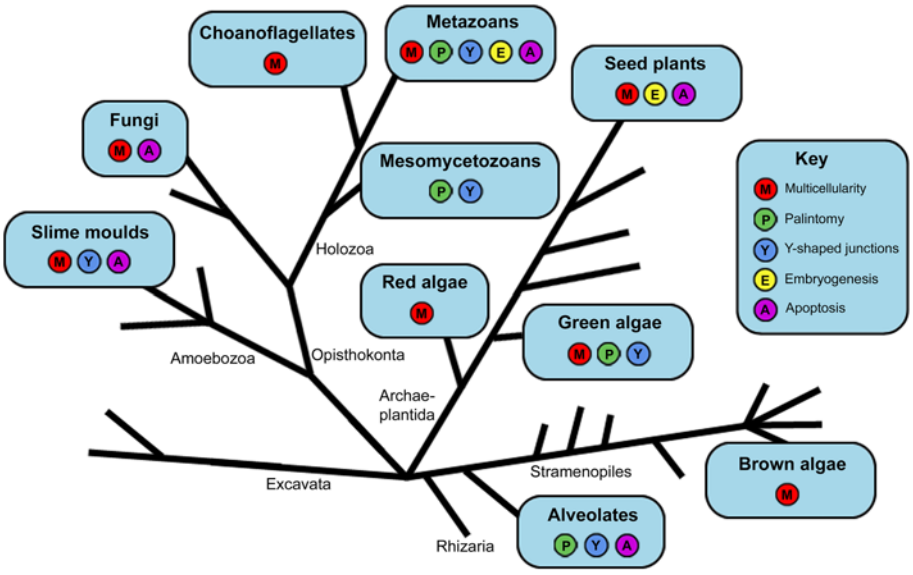

Fig. 4. Schematic representation of eukaryote phylogeny, modified after Rensing (2016), showing the distribution of characters relevant to the interpretation of the embryo-like fossil *Tianzhushania*. Here multicellularity includes both aggregative multicellularity (e.g. slime moulds) and clonal multicellularity (animals, plants, fungi, various algae), as well as both facultative (e.g. choanoflagellates) and obligate multicellularity.

tetrads, which show evidence for palintomy, and larger 'matryoshka' clusters, which do not (Tang 2015; Cunningham *et al.* 2016). Although there must be a switch from palintomy at some point (Chen *et al.* 2017), the lack of intermediates weakens the evidence for an endogenous origin (Tang 2015; Cunningham *et al.* 2016).

The argument for apoptosis is that, because the enclosing envelope imposes a constant volume throughout ontogeny, the only way to create the space required for the putative reproductive structures to grow is for other cells to die off. However, the volume of *Tianzhushania* may well not be constrained in this way, given that early stages often do not occupy the full envelope, and putative later stages provide evidence for distension and then rupture of the envelope (Liu *et al.* 2009; Huldtgren *et al.* 2011). The evidence for differentiation, germ–soma separation and programmed cell death is therefore unconvincing. Moreover, there is also uncertainty regarding the other proposed animal characters. There is no evidence that the walls of *Tianzhushania* are any less rigid than those of non-animal groups such as non-metazoan holozoans (Marshall & Berbee 2011), amoebozoans (Olive 1975), ciliates (Park *et al.* 2005) or volvocalean algae (Hallmann 2006), which also have Y-shaped cell junctions. Nor is there evidence that cell adhesion is different from that seen in groups such as non-metazoan holozoans (volvocalean algae achieve adhesion through cytoplasmic bridges, which are absent in the fossils).

To summarize, *Tianzhushania* does not exhibit characters that are sufficient to identify it as an animal. Evidence for the presence of characters gained in the animal stem lineage is equivocal. There is therefore no justification for an interpretation of *Tianzhushania* as an animal, although a stem-animal affinity cannot be definitively rejected on the basis of current data (Huldtgren *et al.* 2011, 2012). Above all, the available evidence does not yet allow these fossils to be used to substantiate hypotheses on the timing of animal diversification.

Other possibilities

A number of alternative interpretations have been proposed, yet the affinities of these organisms remain uncertain. Comparisons with non-metazoan holozoans (Huldtgren *et al.* 2011), algae (Butterfield 2011*b*; L. Chen *et al.* 2014; Zhang & Pratt 2014) or ciliates are plausible but as yet unsubstantiated and require further investigation. The primary factor that has hindered interpretation of these fossils is poor understanding of the later stages of the organisms' ontogeny. A number of candidates have been proposed, but none are widely accepted. Xiao *et al.* (2007*a*) suggested that helically coiled specimens (Fig. 2g), now named *Helicoforamina*, might be later stages, perhaps representing a coiled vermiform animal. However, this taxon is enigmatic and has also been argued to be an embryo of the ctenophore-like fossil *Eoandromeda*, which has eight spiral arms (Tang *et al.* 2008, 2011), or a single-celled stage of *Spiralicellula* (Fig. 2h), a form that resembles *Tianzhushania*, but differs in having coiled cells (Huldtgren *et al.* 2011). Peanut-shaped specimens with hundreds of thousands of cells (Fig. 3c and d) have also been interpreted as later developmental stages (Huldtgren *et al.* 2011). These have single cells and clusters of cells that are isolated from the main mass of cells and have been argued to be reproductive propagules. L. Chen *et al.* (2014) have also described specimens with putative reproductive propagules. If *Tianzhushania* does reproduce via propagules, then this indicates a lifecycle incompatible with at least crown animals. However, in both cases the interpretation as propagules has proven contentious (Xiao *et al.* 2012; Tang 2015) with a key issue being the incomplete knowledge of the lifecycle of *Tianzhushania*.

Sponge-like fossils

Structures from the Weng'an Biota have been interpreted as siliceous sponge spicules (Li *et al.* 1998). However, these have been shown by subsequent analysis not to be composed of silica and to lack convincing sponge characters (Zhang *et al.* 1998; Antcliffe *et al.* 2014; Muscente *et al.* 2015). More recently, *Eocyathispongia* (Fig. 3c) has been described as a possible sponge from Weng'an (Yin *et al.* 2015). This is known from a single specimen that is preserved at a cellular level. *Eocyathispongia* is considered to be one of the strongest candidates for a Precambrian sponge. However, although it could be a sponge, it has no convincing sponge apomorphies such as pores or spicules, just a generalized sponge gestalt. More detailed characterization of the anatomy of *Eocyathispongia* is required. For example, high-resolution tomography might reveal evidence for the presence or absence of sponge characters and help to constrain the affinity of this enigmatic organism.

Tubular microfossils

A group of tubular microfossils assigned to the genera *Sinocyclocyclicus* (Fig. 3e and f), *Ramitubus* (Fig. 3g and h), *Crassitubus* and *Quadratitubus* have been interpreted as cnidarian-like eumetazoans from the Weng'an Biota (Xiao *et al.* 2000; Chen *et al.* 2002; Liu *et al.* 2008). These genera have regularly spaced cross walls and have been compared with tabulate corals. In a coral-like body plan, the spaces between the cross walls represent the former living positions of the polyp and would be expected to be empty or filled with diagenetic cements. However, the fossils preserve biological structures in these spaces, which is incompatible with a cnidarian interpretation (Cunningham *et al.* 2015). There is no evidence to support a placement of these tubular fossils within eumetazoans or animals.

Vernanimalcula

Vernanimalcula has been described from thin sections as a miniature, adult bilaterian from the Weng'an Biota (Chen *et al.* 2004; Petryshyn *et al.* 2013). It is purported to preserve bilaterian characters such as a mouth, gut, anus and paired coelomic cavities. However, all of the putative bilaterian characters can be alternatively interpreted as artefacts resulting from abiological diagenetic apatite cements, which are ubiquitous in the deposit (Bengtson 2003; Bengtson & Budd 2004; Bengtson *et al.* 2012; Cunningham *et al.* 2012*a*). Moreover, 3D analyses show that Weng'an fossils such as acritarchs and fertilization envelopes that clearly lack bilateral symmetry can exhibit *Vernanimalcula*-like morphology when sectioned in particular orientations (Bengtson *et al.* 2012). There is no evidential basis for interpreting *Vernanimalcula* either as a bilaterian or as an animal of any kind.

Summary and prospects

Research into the Weng'an Biota is currently in a transitional phase. Early research involved many attempts to demonstrate the long-expected presence of animals, including bilaterians, in the Ediacaran. This has been followed by a spell of critical analysis of these claims that has shown that none of these fossils can so far be confidently identified as stem- or crown-group metazoans. The research is now entering a phase where more targeted analysis of the palaeobiology of each taxon is helping to constrain wide-ranging hypotheses of affinity more rigorously. Many fossils are known only from a few specimens and have received limited attention. One such example is the enigmatic fossil *Caveasphaera* (Fig. 2i), which has been tentatively compared with cnidarian embryos (Xiao & Knoll 2000) but requires further investigation. Such taxa betray a cryptic diversity that has been overlooked because of the focus on *Tianzhushania*.

The Ediacaran was a critical interval in the history of life (Butterfield 2007) and the Weng'an Biota offers a unique glimpse of microscopic, multicellular and soft-bodied organisms at this time.

It can provide important insights into Ediacaran biology and the evolution of multicellular organisms at this time, possibly including animal-type multicellularity. Future work constraining the diversity, affinity and ontogeny of the Weng'an organisms is necessary before this potential is fully realized.

Acknowledgements We thank S. Dornbos and an anonymous referee for constructive comments that helped improve the paper. Data statement: There are no data associated with this paper.

Funding This work was funded by the Natural Environment Research Council (NE/J018325/1, NE/F00348X/1, NE/P013678/1), the National Natural Science Foundation of China (41672013), the Science Without Borders Program (CNPq, Brazil), the Danish National Research Foundation (DNRF53), the Swedish Research Council (2010-3929, 2013-4290), the Leverhulme Trust and the Royal Society (Wolfson Merit Award and Newton Advanced Fellowship).

Scientific editing by Graham Shields-Zhou

References

Antcliffe, J.B., Callow, R.H.T. & Brasier, M.D. 2014. Giving the early fossil record of sponges a squeeze. *Biological Reviews*, **89**, 972–1004, https://doi.org/10.1111/brv.12090

Bailey, J.V., Joye, S.B., Kalanetra, K.M., Flood, B.E. & Corsetti, F.A. 2007*a*. Evidence of giant sulphur bacteria in Neoproterozoic phosphorites. *Nature*, **445**, 198–201, https://doi.org/10.1038/nature05457

Bailey, J.V., Joye, S.B., Kalanetra, K.M., Flood, B.E. & Corsetti, F.A. 2007*b*. Undressing and redressing Ediacaran embryos – Reply. *Nature*, **446**, E10–E11, https://doi.org/10.1038/nature05754

Barfod, G.H., Albarède, F., Knoll, A.H., Xiao, S.H., Telouk, P., Frei, R. & Baker, J. 2002. New Lu–Hf and Pb–Pb age constraints on the earliest animal fossils. *Earth and Planetary Science Letters*, **201**, 203–212, https://doi.org/10.1016/S0012-821X(02)00687-8

Bengtson, S. 2003. Tracing metazoan roots in the fossil record. *In*: Legakis, A., Sfenthourakis, S., Polymeni, R. & Thessalou-Legaki, M. (eds) *The New Panorama of Animal Evolution. Proceedings of the 18th International Congress of Zoology*. Pensoft, Sofia, 289–300.

Bengtson, S. & Budd, G. 2004. Comment on "Small bilaterian fossils from 40 to 55 million years before the Cambrian". *Science*, **306**, 1291a, https://doi.org/10.1126/science.1101338

Bengtson, S., Cunningham, J.A., Yin, C. & Donoghue, P.C.J. 2012. A merciful death for the "earliest bilaterian", *Vernanimalcula*. *Evolution & Development*, **14**, 421–427, https://doi.org/10.1111/j.1525-142X.2012.00562.x

Budd, G.E. 2008. The earliest fossil record of the animals and its significance. *Philosophical Transactions of the Royal Society of London, Series B*, **363**, 1425–1434, https://doi.org/10.1098/rstb.2007.2232

Butterfield, N.J. 2007. Macroevolution and macroecology through deep time. *Palaeontology*, **50**, 41–55, https://doi.org/10.1111/j.1475-4983.2006.00613.x

Butterfield, N.J. 2011*a*. Animals and the invention of the Phanerozoic Earth system. *Trends in Ecology & Evolution*, **26**, 81–87, https://doi.org/10.1016/J.Tree.2010.11.012

Butterfield, N.J. 2011*b*. Terminal developments in Ediacaran embryology. *Science*, **334**, 1655–1656, https://doi.org/10.1126/science.1216125

Chen, J. & Chi, H. 2005. Precambrian phosphatized embryos and larvae from the Doushantuo Formation and their affinities, Guizhou (SW China). *Chinese Science Bulletin*, **50**, 2193–2200, https://doi.org/10.1360/982004-727

Chen, J., Oliveri, P. *et al.* 2000. Precambrian animal diversity: Putative phosphatized embryos from the Doushantuo formation of China. *Proceedings of the National Academy of Sciences of the USA*, **97**, 4457–4462, https://doi.org/10.1073/pnas.97.9.4457

Chen, J., Oliveri, P., Gao, F., Dornbos, S.Q., Li, C., Bottjer, D.J. & Davidson, E. H. 2002. Precambrian animal life: Probable developmental and adult cnidarian forms from southwest China. *Developmental Biology*, **248**, 182–196, https://doi.org/10.1006/dbio.2002.0714

Chen, J., Bottjer, D.J. *et al.* 2004. Small bilaterian fossils from 40 to 55 million years before the Cambrian. *Science*, **305**, 218–222, https://doi.org/10.1126/science.1099213

Chen, J., Bottjer, D.J. *et al.* 2006. Phosphatized polar lobe-forming embryos from the Precambrian of southwest China. *Science*, **312**, 1644–1646, https://doi.org/312/5780/1644[pii]10.1126/science.1125964

Chen, J., Bottjer, D.J. *et al.* 2009*a*. Phase contrast synchrotron X-ray microtomography of Ediacaran (Doushantuo) metazoan microfossils: Phylogenetic diversity and evolutionary implications. *Precambrian Research*, **173**, 191–200, https://doi.org/10.1016/j.precamres.2009.04.004

Chen, J., Bottjer, D.J. *et al.* 2009*b*. Complex embryos displaying bilaterian characters from Precambrian Doushantuo phosphate deposits, Weng'an, Guizhou, China. *Proceedings of the National Academy of Sciences of the USA*, **106**, 19056–19060, https://doi.org/10.1073/pnas.0904805106

Chen, L., Xiao, S., Pang, K., Zhou, C. & Yuan, X. 2014. Cell differentiation and germ–soma separation in Ediacaran animal embryo-like fossils. *Nature*, **516**, 238–241, https://doi.org/10.1038/nature13766

Chen, L., Xiao, S., Pang, K., Zhou, C. & Yuan, X. 2017. Are the new Ediacaran Doushantuo embryo-like fossils early metazoans? Reply. *Palaeoworld*, **25**, 132–134, https://doi.org/10.1016/j.palwor.2015.06.005

Chen, M. & Liu, K. 1986. The geological significance of newly discovered microfossils from the Upper Sinian (Doushantuo Age) phosphorites. *Scientia Geologica Sinica*, 46–55.

Chen, Y., Jiang, S., Ling, H. & Yang, J. 2009. Pb–Pb dating of black shales from the Lower Cambrian and Neoproterozoic strata, South China. *Chemie der Erde*, **69**, 183–189, https://doi.org/10.1016/j.chemer.2008.12.005

Chen, Z., Zhou, C., Xiao, S., Wang, W., Guan, C., Hua, H. & Yuan, X. 2014. New Ediacara fossils preserved in marine limestone and their ecological implications. *Scientific Reports*, **4**, 4180, https://doi.org/10.1038/srep04180

Cohen, P.A., Knoll, A.H. & Kodner, R.B. 2009. Large spinose microfossils in Ediacaran rocks as resting stages of early animals. *Proceedings of the National Academy of Sciences of the USA*, **106**, 6519–6524, https://doi.org/10.1073/pnas.0902322106

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, https://doi.org/10.1126/science.1107765

Cunningham, J.A., Thomas, C.-W. *et al.* 2012*a*. Distinguishing geology from biology in the Ediacaran Doushantuo biota relaxes constraints on the timing of the origins of bilaterians. *Proceedings of the Royal Society of London, Series B*, **1737**, 2369–2376, https://doi.org/10.1098/rspb.2011.2280

Cunningham, J.A., Thomas, C.-W. *et al.* 2012*b*. Experimental taphonomy of giant sulphur bacteria: implications for the interpretation of the embryo-like Ediacaran Doushantuo fossils. *Proceedings of the Royal Society of London, Series B*, **1734**, 1857–1864, https://doi.org/10.1098/rspb.2011.2064

Cunningham, J.A., Donoghue, P.C.J. & Bengtson, S. 2014. Distinguishing biology from geology in soft-tissue preservation. *In*: Laflamme, M., Schiffbauer, J.D. & Darroch, S.A.F. (eds) *Reading and Writing of the Fossil Record: Preservational Pathways to Exceptional Fossilization*. Paleontological Society Papers, **20**, 275–287.

Cunningham, J.A., Vargas, K. *et al.* 2015. Critical appraisal of tubular putative metazoans from the Ediacaran Weng'an Dushantuo biota. *Proceedings of the Royal Society of London, Series B*, **282**, 20151169, https://doi.org/0.1098/rspb.2015.1169

Cunningham, J.A., Vargas, K., Marone, F., Bengtson, S. & Donoghue, P.C.J. 2016. A multicellular organism with embedded cell clusters from the Ediacaran Weng'an biota (Doushantuo Formation, South China). *Evolution & Development*, **18**, 308–316, https://doi.org/10.1111/ede.12210

Cunningham, J.A., Liu, A.G., Bengtson, S. & Donoghue, P.C.J. 2017. The origin of animals: Can molecular clocks and the fossil record be reconciled? *BioEssays*, **39**, 201600120, https://doi.org/10.1002/bies.201600120

Donoghue, P.C.J. 2007. Palaeontology: embryonic identity crisis. *Nature*, **445**, 155–156, https://doi.org/nature05520[pii]10.1038/nature05520

Donoghue, P.C.J. & Purnell, M.A. 2009. Distinguishing heat from light in debate over controversial fossils. *BioEssays*, **31**, 178–189, https://doi.org/10.1002/bies.200800128

Dornbos, S.Q., Bottjer, D.J., Chen, J., Gao, F., Oliveri, P. & Li, C. 2006. Environmental controls on the taphonomy of phosphatized animals and animal embryos from the Neoproterozoic Doushantuo formation, Southwest China. *Palaios*, **21**, 3–14, https://doi.org/10.2110/palo.2004.p04-37

dos Reis, M., Thawornwattana, Y., Angelis, K., Telford, M.J., Donoghue, P.C.J. & Yang, Z. 2015. Uncertainty in the timing of origin of animals and the limits of precision in molecular timescales. *Current Biology*, **25**, 2939–2950, https://doi.org/10.1016/j.cub.2015.09.066

Erwin, D.H. & Valentine, J.W. 2013. The Cambrian explosion: the construction of animal biodiversity, Roberts & Company, Colorado.

Erwin, D.H., Laflamme, M., Tweedt, S.M., Sperling, E.A., Pisani, D. & Peterson, K.J. 2011. The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Science*, **334**, 1091–1097, https://doi.org/10.1126/science.1206375

Gostling, N.J., Thomas, C.W. *et al.* 2008. Deciphering the fossil record of early bilaterian embryonic development in light of experimental taphonomy. *Evolution & Development*, **10**, 339–349, http://doi.org/10.1111/j.1525-142X.2008.00242.x

Gostling, N.J., Dong, X.P. & Donoghue, P.C.J. 2009. Ontogeny and taphonomy: an experimental taphonomy study of the development of the brine shrimp *Artemia salina*. *Palaeontology*, **52**, 169–186, https://doi.org/10.1111/j.1475-4983.2008.00834.x

Hagadorn, J.W., Xiao, S. *et al.* 2006. Cellular and subcellular structure of Neoproterozoic animal embryos. *Science*, **314**, 291–294, https://doi.org/10.1126/science.1133129

Hallmann, A. 2006. Morphogenesis in the family Volvocaceae: Different tactics for turning an embryo right-side out. *Protist*, **157**, 445–461, https://doi.org/10.1016/j.protis.2006.05.010

Huldtgren, T., Cunningham, J.A., Yin, C., Stampanoni, M., Marone, F., Donoghue, P.C.J. & Bengtson, S. 2011. Fossilized nuclei and germination structures identify Ediacaran 'animal embryos' as encysting protists. *Science*, **334**, 1696–1699, https://doi.org/10.1126/science.1209537

Huldtgren, T., Cunningham, J.A., Yin, C.Y., Stampanoni, M., Marone, F., Donoghue, P.C.J. & Bengtson, S. 2012. Response to Comment on "Fossilized nuclei and germination structures identify Ediacaran 'animal embryos' as encysting protists". *Science*, **335**, 1169, https://doi.org/10.1126/science.1219076

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

Jiang, G., Shi, X., Zhang, S., Wang, Y. & Xiao, S. 2011. Stratigraphy and paleogeography of the Ediacaran Doushantuo Formation (*ca*. 635–551 Ma) in South China. *Gondwana Research*, **19**, 831–849, https://doi.org/10.1016/j.gr.2011.01.006

Li, C., Chen, J. & Hua, T. 1998. Precambrian sponges with cellular structures. *Science*, **279**, 879–882, https://doi.org/10.1126/science.279.5352.879

Liu, P., Xiao, S., Yin, C., Zhou, C., Gao, L. & Tang, F. 2008. Systematic description and phylogenetic affinity of tubular microfossils from the Ediacaran Doushantuo Formation at Weng'an, South China. *Palaeontology*, **51**, 339–366, https://doi.org/10.1111/j.1475-4983.2008.00762.x

Liu, P., Yin, C., Chen, S., Tang, F. & Gao, L. 2009. New data of phosphatized globular fossils from Weng'an biota in the Ediacaran Doushantuo Formation and the problem concerning their affinity. *Acta Geoscientica Sinica*, **30**, 457–464.

Liu, P., Xiao, S., Yin, C., Chen, S., Zhou, C. & Li, M. 2014. Ediacaran acanthorphic acritarchs and other microfossils from chert nodules of the upper Doushantuo Formation in the Yangtze Gorges area, south China. *Paleontology Memoir*, **72**, 1–139, https://doi.org/10.1666/13-009

Marshall, W.L. & Berbee, M.L. 2011. Facing unknowns: living cultures (*Pirum gemmata* gen. nov., sp nov., and *Abeoforma whisleri*, gen. nov., sp nov.) from invertebrate digestive tracts represent an undescribed clade within the unicellular opisthokont lineage Ichthyosporea (Mesomycetozoea). *Protist*, **162**, 33–57, https://doi.org/10.1016/j.protis.2010.06.002

Muscente, A.D., Hawkins, A.D. & Xiao, S. 2014. Fossil preservation through phosphatization and silicification in the Ediacaran Doushantuo Formation (South China): a comparative synthesis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, https://doi.org/10.1016/j.palaeo.2014.10.013

Muscente, A.D., Michel, F.M., Dale, J.G. & Xiao, S. 2015. Assessing the veracity of Precambrian 'sponge' fossils using *in situ* nanoscale analytical techniques. *Precambrian Research*, **263**, 142–156, https://doi.org/10.1016/j.precamres.2015.03.010

Olive, L.S. 1975. *The Mycetozoans*. Academic Press, New York.

Park, K.H., Park, J.K., Lee, J. & Choi, K.S. 2005. Use of molecular markers for species identification of Korean *Perkinsus* sp. isolated from Manila clams *Ruditapes philippinarum*. *Diseases of Aquatic Organisms*, **66**, 255–263.

Peterson, K.J. & Butterfield, N.J. 2005. Origin of the Eumetazoa: testing ecological predictions of molecular clocks against the Proterozoic fossil record. *Proceedings of the National Academy of Sciences of the USA*, **102**, 9547–9552, https://doi.org/10.1073/pnas.0503660102

Petryshyn, V.A., Bottjer, D.J., Chen, J. & Gao, F. 2013. Petrographic analysis of new specimens of the putative microfossil *Vernanimalcula guizhouena* (Doushantuo Formation, South China). *Precambrian Research*, **225**, 58–66, https://doi.org/10.1016/j.precamres.2011.08.003

Raff, E.C., Villinski, J.T., Turner, F.R., Donoghue, P.C.J. & Raff, R.A. 2006. Experimental taphonomy shows the feasibility of fossil embryos. *Proceedings of the National Academy of Sciences of the USA*, **103**, 5846–5851, https://doi.org/10.1073/Pnas.0601536103

Raff, E.C., Schollaert, K.L. *et al.* 2008. Embryo fossilization is a biological process mediated by microbial biofilms. *Proceedings of the National Academy of Sciences of the USA*, **105**, 19360–19365, https://doi.org/10.1073/Pnas.0810106105

Rensing, S.A. 2016. (Why) does evolution favour embryogenesis? *Trends in Plant Science*, **21**, 562–573, https://doi.org/10.1016/j.tplants.2016.02.004

Sansom, R.S. 2014. Experimental decay of soft tissues. *In*: Laflamme, M., Schiffbauer, J.D. & Darroch, S.A.F. (eds) *Reading and Writing of the Fossil Record: Preservational Pathways to Exceptional Fossilization*. Paleontological Society Papers, **20**, 259–274.

Schiffbauer, J.D., Xiao, S., Sen Sharma, K. & Wang, G. 2012. The origin of intracellular structures in Ediacaran metazoan embryos. *Geology*, **40**, 223–226, https://doi.org/10.1130/G32546.1

Schiffbauer, J.D., Wallace, A.F., Broce, J. & Xiao, S. 2014. Exceptional fossil conservation through phosphatization. *In*: Laflamme, M., Schiffbauer, J.D. & Darroch, S.A.F. (eds) *Reading and Writing of the Fossil Record: Preservational Pathways to Exceptional Fossilization*. Paleontological Society Papers, **20**, 59–82.

Shields, G., Kimura, H., Yang, J. & Gammon, P. 2004. Sulphur isotopic evolution of Neoproterozoic–Cambrian seawater: new francolite-bound sulphate $\delta^{34}S$ data and a critical appraisal of the existing record. *Chemical Geology*, **204**, 163–182, https://doi.org/10.1016/j.chemgeo.2003.12.001

Sun, W. 1986. Late Precambrian pennatulids (sea pens) from the eastern Yangtze Gorge, China: *Paracharnia* gen. nov. *Precambrian Research*, **31**, 361–375, https://doi.org/10.1016/0301-9268(86)90040-9

Tang, B.L. 2015. Are the new Ediacaran Doushantuo *Megasphaera*-like acritarchs early metazoans? *Palaeoworld*, **25**, 128–131, https://doi.org/10.1016/j.palwor.2015.06.005

Tang, F., Yin, C., Bengtson, S., Liu, P., Wang, Z. & Gao, L. 2008. Octoradiate spiral organisms in the Ediacaran of South China. *Acta Geologica Sinica, English Edition*, **82**, 27–34, https://doi.org/10.1111/j.1755-6724.2008.tb00321.x

Tang, F., Bengtson, S., Wang, Y., Wang, X. & Yin, C. 2011. *Eoandromeda* and the origin of Ctenophora. *Evolution & Development*, **13**, 408–414, https://doi.org/10.1111/J.1525-142x.2011.00499.X

Xiao, S. 2004. New multicellular algal fossils and acritarchs in Doushantuo chert nodules (Neoproterozoic; Yangtze Gorges, south China). *Journal of Paleontology*, **78**, 393–401, https://doi.org/10.1666/0022-3360(2004)078<0393:NMAFAA>2.0.CO;2

Xiao, S. & Knoll, A.H. 1999. Fossil preservation in the Neoproterozoic Doushantuo phosphorite Lagerstatte, South China. *Lethaia*, **32**, 219–240, https://doi.org/10.1111/j.1502-3931.1999.tb00541.x

Xiao, S. & Knoll, A.H. 2000. Phosphatized animal embryos from the Neoproterozoic Doushantuo Formation at Weng'an, Guizhou, South China. *Journal of Paleontology*, **74**, 767–788, https://doi.org/10.1666/0022-3360(2000)074<0767:PAEFTN<2.0.CO;2

Xiao, S., Zhang, Y. & Knoll, A.H. 1998. Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite. *Nature*, **391**, 553–558, https://doi.org/10.1038/35318

Xiao, S., Yuan, X. & Knoll, A.H. 2000. Eumetazoan fossils in terminal Proterozoic phosphorites? *Proceedings of the National Academy of Sciences of the USA*, **97**, 13684–13689, https://doi.org/10.1073/pnas.250491697

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. *Journal of Paleontology*, **76**, 347–376, https://doi.org/10.1666/0022-3360(2002)076<0347:MCCIAT>2.0.CO;2

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. *American Journal of Botany*, **91**, 214–227, https://doi.org/10.3732/ajb.91.2.214

Xiao, S., Shen, B., Zhou, C., Xie, G. & Yuan, X. 2005. A uniquely preserved Ediacaran fossil with direct evidence for a quilted bodyplan. *Proceedings of the National Academy of Sciences of the USA*, **102**, 10227–10232, https://doi.org/10.1073/pnas.0502176102

Xiao, S., Hagadorn, J.W., Zhou, C. & Yuan, X. 2007*a*. Rare helical spheroidal fossils from the Doushantuo Lagerstatte: Ediacaran animal embryos come of age? *Geology*, **35**, 115–118, https://doi.org/10.1130/G23277A.1

Xiao, S., Zhou, C. & Yuan, X. 2007*b*. Undressing and redressing Ediacaran embryos. *Nature*, **446**, E9–E10, https://doi.org/10.1038/nature05753

Xiao, S., Knoll, A.H., Schiffbauer, J.D., Zhou, C. & Yuan, X. 2012. Comment on "Fossilized nuclei and germination structures identify Ediacaran 'animal embryos' as encysting protists". *Science*, **335**, https://doi.org/10.1126/science.1218814

Xiao, S., Muscente, A.D. *et al.* 2014*a*. The Weng'an biota and the Ediacaran radiation of multicellular eukaryotes. *National Science Review*, **1**, 498–520, https://doi.org/10.1093/nsr/nwu061

Xiao, S., Zhou, C., Liu, P.J., Wang, D. & Yuan, X. 2014*b*. Phosphatized acanthomorphic acritarchs and related microfossils from the Ediacaran Doushantuo Formation at Weng'an (South China) and their implications for biostratigraphic correlation. *Journal of Paleontology*, **88**, 1–67, https://doi.org/10.1666/12-157R

Yang, A., Zhu, M., Zhang, J., Zhao, F. & Lü, M. 2015. Sequence stratigraphic subdivision and correlation of the Ediacaran (Sinian) Doushantuo Formation of Yangtze Plate, South China. *Journal of Palaeogeography*, **17**, 1–20, https://doi.org/10.7605/gdlxb.2015.01.001

Yin, C., Gao, L. & Xing, Y. 2001. Discovery of Tianzhushania in Doushantuo phosphorites, in Weng'an, Guizhou Province. *Acta Palaeontologica Sinica*, **40**, 497–504.

Yin, C., Bengtson, S. & Yue, Z. 2004. Silicified and phosphatized *Tianzhushania*, spheroidal microfossils of possible animal origin from the Neoproterozoic of South China. *Acta Palaeontologica Polonica*, **49**, 1–12.

Yin, L. & Li, Z. 1978. Precambrian microfloras of southwest China with reference to their stratigraphic significance. *Memoirs of the Nanjing Institute of Geology and Palaeontology,* Academia Sinica, **10**, 41–108.

Yin, L., Zhu, M., Knoll, A.H., Yuan, X., Zhang, J. & Hu, J. 2007. Doushantuo embryos preserved inside diapause egg cysts. *Nature*, **446**, 661–663, https://doi.org/10.1038/nature05682

Yin, Z., Zhu, M., Tafforeau, P., Chen, J., Liu, P. & Li, G. 2013. Early embryogenesis of potential bilaterian animals with polar lobe formation from the Ediacaran Weng'an Biota, South China. *Precambrian Research*, **225**, 44–57, https://doi.org/10.1016/j.precamres.2011.08.011

Yin, Z., Zhu, M., Davidson, E.H., Bottjer, D.J., Zhao, F. & Tafforeau, P. 2015. Sponge grade body fossil with cellular resolution dating 60 Myr before the Cambrian. *Proceedings of the National Academy of Sciences of the USA*, **112**, E1453–E1460, https://doi.org/10.1073/pnas.1414577112

Yin, Z., Zhu, M., Bottjer, D.J., Zhao, F. & Tafforeau, P. 2016. Meroblastic cleavage identifies some Ediacaran Doushantuo (China) embryo-like fossils as metazoans. *Geology*, G38262.1, https://doi.org/10.1130/G38262.1

Zhang, X. & Pratt, B.R. 2014. Possible algal origin and life cycle of Ediacaran Doushantuo microfossils with dextral spiral structure. *Journal of Paleontology*, **88**, 92–98, https://doi.org/10.1666/13-014

Zhang, Y. 1989. Multicellular thallophytes with differentiated tissues from Late Proterozoic phosphate rocks of South China. *Lethaia*, **22**, 113–132, https://doi.org/10.1111/j.1502-3931.1989.tb01674.x

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, https://doi.org/10.1111/j.1502-3931.1992.tb01788.x

Zhang, Y., Yuan, X. & Yin, L. 1998. Interpreting late Precambrian microfossils. *Science*, **282**, 1783, https://doi.org/10.1126/science.282.5395.1783a

Zhao, D. 1986. The discovery of phosphatic red algae in the Sinian Doushantuo Formation. *Acta Sedimentologica Sinica*, **4**, 126–127.

Zhou, C., Brasier, M.D. & Xue, Y. 2001. Three-dimensional phosphatic preservation of giant acritarchs from the Terminal Proterozoic Doushantuo Formation in Guizhou and Hubei provinces, south China. *Palaeontology*, **44**, 1157–1178, https://doi.org/10.1111/1475-4983.00219

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. *Geological Journal*, **42**, 229–262, https://doi.org/10.1002/gj.1062

Zhou, C., Li, X., Xiao, S., Lan, Z., Ouyang, Q., Guan, C. & Chen, Z. 2017. A new SIMS zircon U–Pb date from the Ediacaran Doushantuo Formation: age constraint on the Weng'an biota. *Geological Magazine*, https://doi.org/10.1017/S0016756816001175

Zhu, M., Zhang, J. & Yang, A. 2007. Integrated Ediacaran (Sinian) chronostratigraphy of South China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **254**, 7–61, https://doi.org/10.1016/j.palaeo.2007.03.025

Zhu, M., Lu, M. *et al.* 2013. Carbon isotope chemostratigraphy and sedimentary facies evolution of the Ediacaran Doushantuo Formation in western Hubei, South China. *Precambrian Research*, **225**, 7–28, https://doi.org/10.1016/j.precamres.2011.07.019