

Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite

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Phosphorites of the late Neoproterozoic (570 ± 20 Myr BP) Doushantuo Formation, southern China, preserve an exceptional record of multicellular life from just before the Ediacaran radiation of macroscopic animals. Abundant thalli with cellular structures preserved in three-dimensional detail show that latest-Proterozoic algae already possessed many of the anatomical and reproductive features seen in the modern marine flora. Embryos preserved in early cleavage stages indicate that the divergence of lineages leading to bilaterians may have occurred well before their macroscopic traces or body fossils appear in the geological record. Discovery of these fossils shows that the early evolution of multicellular organisms is amenable to direct palaeontological inquiry.

Most of the fossils that document the first 85% of evolutionary history are microscopic. Not until the Phanerozoic eon (<544 Myr BP) do the remains of large animals, algae and, later, plants become conspicuous constituents of the sedimentary record. The most important biological event that connects these palaeobiologically distinct eras is the evolution of complex multicellularity in eukaryotes. Multicellular organisms arose at least six times: in animals, fungi and several groups of algae¹. Macroscopic remains of uncertain systematic affinities occur in rocks as old as 1,800–

2,100 Myr BP² and cellularly preserved microfossils of red, green and stramenopile (brown and related) algae indicate that multicellularity was achieved in these groups by about 1,000 Myr³. Multicellularity may have evolved comparably early in minute ancestral animals, but until now any pre-Ediacaran animal history has been contentious and thought by many to be unrecognized and perhaps unrecognizable by palaeontologists.

Phosphorites of the Doushantuo Formation in southern China contain three-dimensionally preserved fossils that record in exquisite

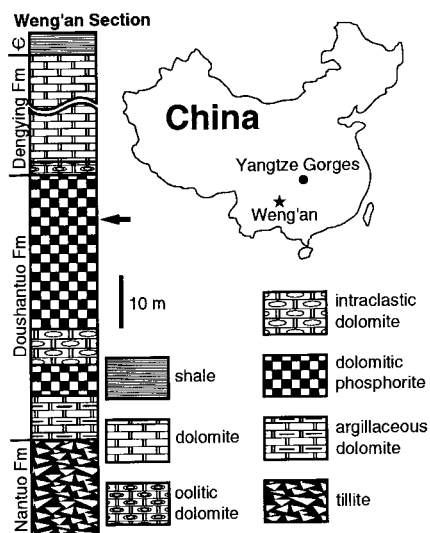
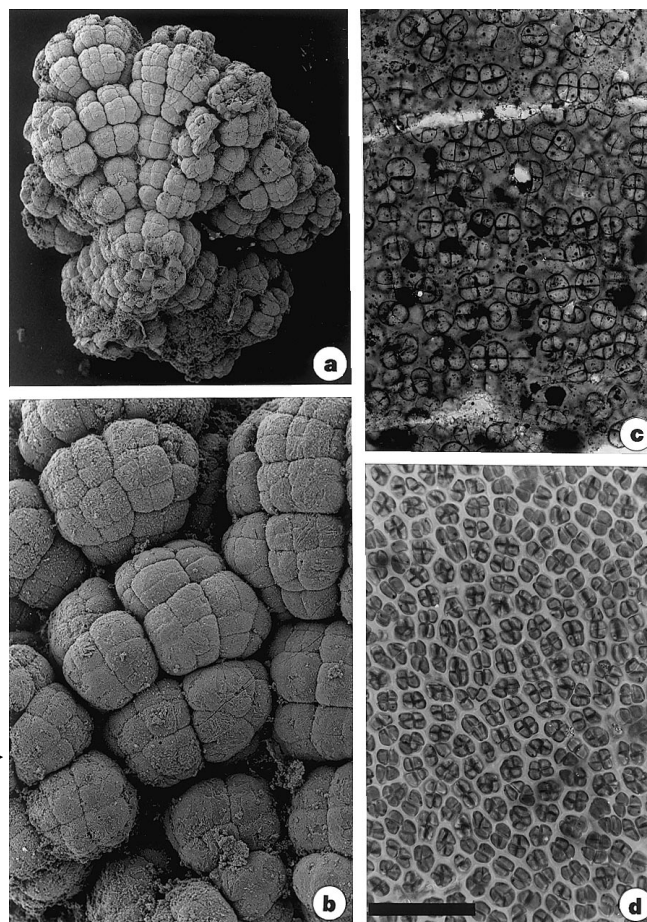


Figure 1 Location and generalized stratigraphy of the fossiliferous Weng'an section in Guizhou Province, South China. The arrow indicates the principal stratigraphic horizon containing phosphatized algae and embryos. Fm, Formation.

Figure 2 Algal thalli from the Doushantuo phosphorite and the modern bangiophyte red alga, *Porphyra suborbiculata*. **a–c**, Thalli from Doushantuo phosphorite. **a**, **b**, Scanning electron micrographs of a thallus composed of cuboidal cell packets similar to those of modern chlorosarcinacean green algae; **b**, the upper left quadrant of **a** at higher magnification. **c**, Photomicrograph of cruciate cell tetrads embedded in a foliose thallus; **d**, Carposporangia within the thallus of living *Porphyra*. Scale bar (in **d**): 200 μ m for **a**; 50 μ m for **b**; and 100 μ m for **c** and **d**.



cellular detail the anatomy and reproductive biology of diverse multicellular algae that lived in the late Neoproterozoic ocean. Doushantuo phosphorites also contain large populations of globular fossils which we interpret to be embryos of early animals. The quality of preservation and evolutionary importance of these fossils rival those of younger Lagerstätten such as the Burgess Shale^{4,5} or Rhynie Chert^{6,7}, and shed unprecedented palaeontological light on the early evolution of multicellular organisms.

Geological setting and fossil preservation

In its type area along the Yangtze Gorges, the Doushantuo Formation comprises a 250-m succession of carbonates, shales and phosphatic shales that lie disconformably above the glaciogenic rocks of the Nantuo Tillite and conformably beneath the carbonates of the Dengying Formation^{8,9} (Fig. 1). Dengying successions contain rare Ediacaran fossils^{8,10} and, in their uppermost part, basal Cambrian shelly fossils¹¹. Depositional age is only broadly constrained by U–Pb dates on volcanic rocks: tuffs in the underlying Liantuo Formation date from 748 ± 12 Myr⁸, whereas bentonites in the overlying Cambrian Zhongyicun Formation have an older age

limit of 539 ± 34 Myr¹². Diverse acritarchs and a distinctive carbon-isotopic signature, however, allow unambiguous correlation with better-dated successions elsewhere, indicating that Doushantuo sediments accumulated 570 ± 20 Myr ago¹³. Most diverse Ediacaran assemblages are younger than ~ 550 Myr^{14,15}, although frond-like fossils in Newfoundland occur in association with 565 ± 3 Myr ash beds¹⁶. Globally, acritarch assemblages of the type found in Doushantuo rocks occur in strata that underlie Ediacaran macrofossils. Thus available data indicate that the Doushantuo Formation is older than the diverse Ediacaran assemblages of South Australia and northern Russia, and may antedate all known Ediacaran-type assemblages, except for the simple centimetre-scale discs reported from pre-Varanger rocks in northwestern Canada¹⁷.

About 600 km to the southwest of the Yangtze Gorges, in the Weng'an region of Guizhou Province (Fig. 1), the Doushantuo Formation has similar acritarchs but markedly different lithologies. Here, Doushantuo sections are only 40–50 m thick and consist predominantly of phosphorites that lie unconformably above older metasediments and, locally, thin Nantuo diamictites¹³ (Fig. 1). Above a thin (0.5 m) basal conglomerate and up to 12 m of massive

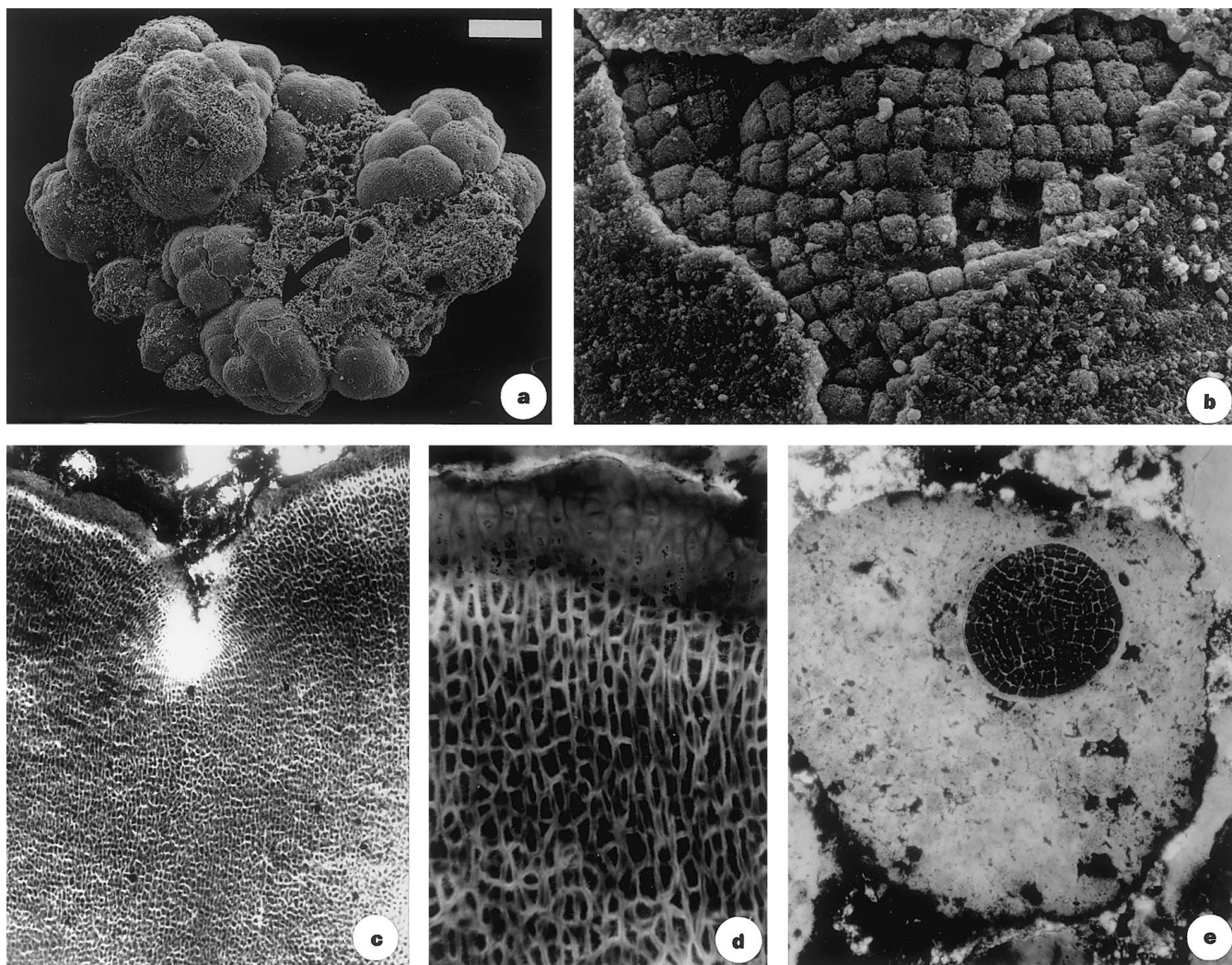


Figure 3 Parenchymatous and pseudoparenchymatous thalli from the Doushantuo phosphorite. **a**, Scanning electron micrograph showing the three-dimensional morphology of a pseudoparenchymatous thallus. **b**, Higher-magnification view of a portion of the same thallus (the arrow in **a** denotes position) showing the cell-surface pattern. **c**, Photomicrograph of a phosphatized thallus in thin section, showing pseudoparenchymatous 'cell fountain' anatomy. **d**, Higher magnifica-

tion of the same thallus, showing the details of the cell arrangement; the apparently distinct cells at the top of the figure reflect taphonomic and not anatomical differentiation. **e**, Parenchymatous thallus preserved within a phosphatic intraclast. Scale bar (in **a**): 140 μ m for **a**; 7.5 μ m for **b**; 55 μ m for **c**; 20 μ m for **d**; and 100 μ m for **e**.

dolostone lie 6–18 m of phosphatic mudstones and subordinate grainstones. The phosphorites exhibit parallel to slightly undulose lamination and are interbedded with fine-grained siliciclastic rocks in the lower part of the unit. Phosphatic beds coarsen upwards, become increasingly dolomitic, and locally contain stromatolites. Phosphatic and dolomitic grainstones, the latter characterized by cross-bedding and phosphorite nodules, are capped by a coarsely conglomeratic unit associated with subaerial erosion. Above this exposure surface, the cycle roughly repeats, with silicified phosphatic dolomitic and dolarenites of the uppermost Doushantuo Formation abruptly overlain by oolitic dolostones of the basal Dengying Formation. The environment of phosphorite deposition is interpreted as a shallow subtidal platform subject to episodic storms.

Fossils occur in both the lower and upper phosphorite sequences. *In situ* collophane crusts contain oriented algal thalli along with generally uncompressed microfossils and fine-grained organic detritus. Fossils also occur in interbedded, locally derived phosphatic grainstones and gravelstones. Phosphatization was contemporaneous with deposition, as shown by the local reworking of phosphatized fossils to form thin bioclastic sandstones¹³.

The chemistry of phosphate permineralization is not well understood, but it has been shown that soft tissues can become phosphatized within days of death¹⁸. In general, phosphogenesis requires both that phosphate be supplied to surface sediments in relatively high concentrations and that physical and/or biological processes operating within sediments further increase pore-water PO_4^{3-} concentration beyond the point of saturation with respect to apa-

tite^{19–21}. Divergent models have been advanced to explain the genesis of bedded phosphorites on ancient shelves and platforms, but most share several features. High biological productivity, commonly related to the upwelling of nutrient-rich deep water, is commonly invoked, as is an ‘iron-pumping’ mechanism in which particulate FeOOH scavenges PO_4^{3-} from the water column and delivers it to sediments, where it is reduced, liberating PO_4^{3-} and increasing pore-water PO_4^{3-} concentration. Dysaerobic bottom waters are thought to facilitate phosphogenesis because of their elevated PO_4^{3-} concentration. On ancient shelves and platforms, delivery of suboxic waters has commonly been attributed to transgression^{19–21}, and the two episodes of phosphorite deposition recorded in Doushantuo successions certainly reflect marked transgressions across the Yangtze Platform¹³. Continental weathering in warm, postglacial environments may also have contributed to regional phosphate enrichment. Low rates of sedimentation, the absence of bioturbation, and extensive cover by microbial mats and thalloid algae would all have facilitated phosphate precipitation.

Multicellular algae

Zhu *et al.*²² first reported fossils in Doushantuo phosphorites, but it was Zhang^{23,24} who established the superb preservation and diversity of this assemblage. In continuing collaborative investigations, we have documented eight cyanobacterial and 31 acritarch taxa in the formation as a whole, as well as eight formally named and numerous other fragmentary remains of multicellular algae¹³. Several other authors have reported evidence of animal remains in Doushantuo rocks. Rare triact spicules in Doushantuo cherts may record early

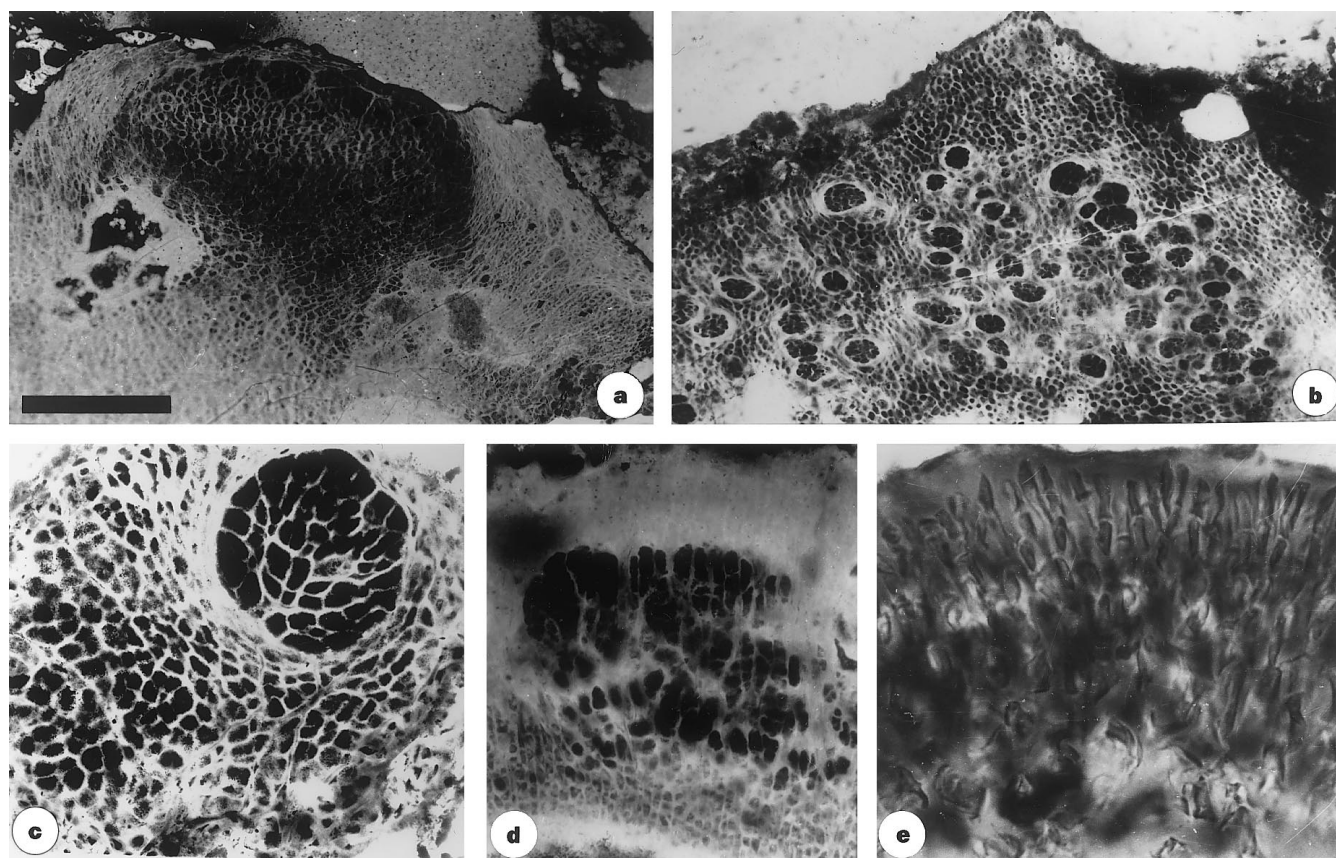


Figure 4 Reproductive structures in Doushantuo thalli and a modern red alga. **a–d**, Doushantuo thalli: **a**, Conceptacle in which carposporangia (clusters of dark, large cells) arise from gonimoblast filaments or supporting cells. **b**, Carposporangia (packets of dark cells) embedded in an anatomically preserved thallus. **c**, Higher-magnification view of carpospores within encompassing vegetative

tissue. **d**, Linearly arranged, dark, elongate cells interpreted as possible spermatangia. **e**, Spermatangial sori of the modern florideophyte red alga *Gracilaria* sp., for comparison with **d**. Scale bar (in **a**): 100 μm for **a**, **b** and **d**; 50 μm for **c**; and 30 μm for **e**.

sponges^{8,9}, but structures originally interpreted as microburrows²⁵ appear to be oblique sections through large, multilamellate cyanobacterial filaments¹³.

Doushantuo algal thalli range from simple colonies of undifferentiated cells to erect, branching forms characterized by tissue differentiation and specialized reproductive structures. Among the simplest multicellular entities are stacked cuboidal cell packets (Fig. 2a, b) of a type referred to as “incipient tissues”²⁶. Very similar structures occur today in several clades of green algae^{27,28}. Discoidal parenchymatous thalli (Fig. 3e) also occur in Doushantuo phosphorites. These fossils are morphologically simple as well, but in this case deceptively so; parenchymatous growth represents an evolu-

tionary departure from the plesiomorphic states in red, green and brown algae, where developmentally regular multicellularity is based fundamentally on filamentous growth^{27,28}.

Pseudoparenchymatous thalli, formed by the coordinated growth of closely packed filaments, are abundant in the Doushantuo assemblage (Fig. 3a–d). A distinctive characteristic of pseudoparenchymatous growth is the cell fountain, comprising vertical rows of cells that have expanded and diverged upwards to form a fountain-like array in longitudinal section. Cell fountains are common features of Doushantuo thalli, and similar features typify several clades of living red algae, although they also occur in brown algae such as *Ralfsia*²⁶. Rhodophytic affinities are sup-

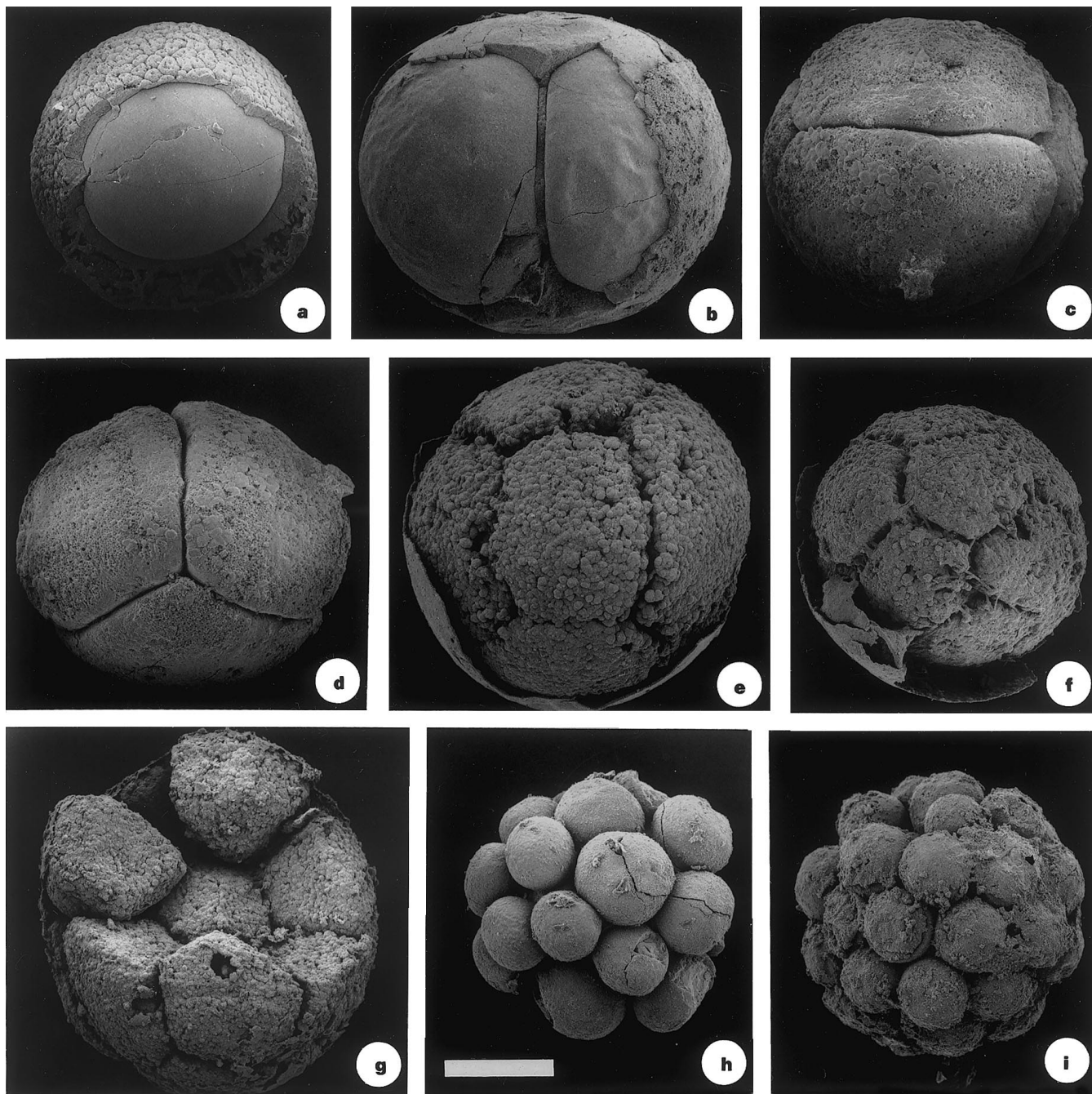


Figure 5 Fossil embryos preserving different stages of cleavage from the Doushantuo phosphorite. **a**, Fertilized (?) egg with thick membrane. **b**, Two-cell stage. **c**, **d**, Four-cell stage, **c** and **d** show different views of the same specimen, illustrating the tetrahedral geometry. **e**, Eight-cell stage. **f**, **g**, Later cleavage stages

showing faceted cell geometry and, in **g**, the three-dimensional distribution of cells. **h**, **i**, Multicellular structures that record later cleavage stages or, especially possible for **h**, colonial protists. Scale bar (in **h**): 200 μm for **a**, **e**, **f**, **g**, **h** and **i**; 150 μm for **b**; and 240 μm for **c** and **d**.

ported for at least some Doushantuo thalli by the differentiation of distinct medullary and cortical tissues coupled with reproductive structures similar to the carposporangia and spermatangia of living red algae (Fig. 4).

Compact thalli found abundantly in Doushantuo phosphorites^{13,24} contain ellipsoidal clusters of large (8–18 μm) dark cells distributed along thallus peripheries and occasionally protruding from the thallus surface (Fig. 4a–c). One or more layers of light-coloured, elongate cells (1–4 μm wide and up to 10 μm long) curve around and encompass the clusters. The cell clusters are interpreted as carposporangia and empty spheroidal regions that occupy a similar anatomical position are interpreted as empty conceptacles or cystocarps. Distinctive cell rows at the base of carposporangial clusters compare closely with the gonimoblast filaments that support carposporangial development in living red algae (Fig. 4a). Other thalli contain distinctive tissues of large, dark, oblong or rod-like cells arranged in parallel rows, with apical cells distinctly elongated and separated from subjacent cell rows by transverse septa (Fig. 4d); these structures are interpreted as male reproductive tissues rather like the spermatangial sori of some extant rhodophytes (Fig. 4e).

Such features suggest affinities to the red-algal class Florideophyceae. Other Doushantuo fossils indicate that the class Bangiophyceae had also diversified markedly by the end of the Proterozoic eon: foliose thalli with regularly arranged cruciate cell tetrads (and, less commonly, octads) are indistinguishable from the carposporangial thalli of the extant bangiophyte alga *Porphyra* (Fig. 2c, d).

The oldest known fossil red algae are silicified *Bangia*-like filaments found in 1,200–900 Myr-old tidal flat carbonates from arctic Canada²⁹. Doushantuo fossils show that by the end of the Proterozoic eon the red algae were structurally complex and taxonomically diverse.

A comparable evolutionary pattern seems to characterize the photosynthetic stramenopiles. Compressed seaweeds in uppermost Doushantuo shales in the Yangtze Gorges area include a large population attributable to the Fucales, one of the most derived of all brown algal orders³⁰, whereas microscopic, coenocytic algae in the 1,000–900 Myr-old Lakhanda Group of eastern Siberia³¹ are indistinguishable from species of the extant xanthophyte *Vaucheria*. Similarly, the possible green algae in Doushantuo phosphorites and shales³² complement 750–700 Myr-old compression fossils from Spitsbergen that include populations similar to *Cladophora*³³, among the shallowest branching of all ulvophyte green algae. Thus, by the time large animals enter the fossil record, the three principal groups of multicellular algae had not only diverged from other protistan stocks but had evolved a surprising degree of the morphological complexity exhibited by living algae.

Neoproterozoic embryos

Since Haeckel³⁴ it has been broadly accepted that the earliest metazoans must have been microscopic organisms similar in development and morphology to the embryos or larvae of living animals. Davidson *et al.*³⁵ have expanded this view of animal 'prehistory' by hypothesizing that animals not only originated but underwent substantial early cladogenesis as minute, little-differentiated metazoans similar in form, function and ontogeny to the larvae of living invertebrates. Only later, after developmental toolkits and physiological tolerances had been well established, did macroscopic size and the adult body plans of extant phyla evolve within already discrete clades. Molecular clock estimates have suggested that the divergence of protostome and deuterostome animals took place as early as 1,000–1,300 Myr BP³⁶. These data are currently the subject of intensive methodological scrutiny, although Neoproterozoic algae provide support for the broad hypothesis that animals originated long before they became conspicuous elements of the geological record. As noted above, algal fossils document rapid eukaryotic divergence beginning at least 1,000 Myr BP, and

molecular phylogenies imply that the ancestors of animals diverged from other eukaryotes as part of this radiation³⁷. Three important groups of algae evolved multicellular forms early in their history, and it is reasonable to suggest that animals did so too. The conventional metazoan fossil record can be reconciled with molecular hypotheses by making the simple assumption that clade divergence and the evolution of large size and adult body plans within clades are distinct events separated by a considerable interval of time^{38,39}.

Palaeontological tests of such conjectures require Lagerstätten of the first order. Reports of phosphatized invertebrate embryos in Cambrian carbonates suggest that older phosphatic Lagerstätten may be the best places to search for early records of animal evolution^{40,41}. The exquisite preservation of Doushantuo algae specifically invites a search for microscopic animal remains, and this search has yielded positive results.

Xue *et al.*⁴² have described spheroidal microfossils containing geometrically arranged cells from Weng'an phosphorites, interpreting them as volvocacean green algae similar to extant *Pandorina*. Our collections, however, demonstrate that comparisons to volvocacean or any other algae are unlikely, given the size, geometry of cell division and structure of encompassing vesicles in the fossil population. Instead, we argue that these fossils are preserved embryos.

The specimens in our sample population are globular, measuring about 500 μm in diameter ($\bar{x} = 584 \mu\text{m}$, $s_x = 12 \mu\text{m}$, $n = 115$). Individuals contain one, two, four, eight or more closely packed internal bodies, the size and orientation of which suggest they are cells that underwent successive binary divisions with little or no intervening growth (Fig. 5). The diminishing size of internal bodies as their number multiplies is suggestive of early embryonic development. The geometric arrangement of the internal bodies is precise and is strikingly similar to the early cleavage stages of metazoan embryos⁴³. An ornamented external covering 10 μm thick encompasses single cells, which we interpret as resting zygotes within egg cases. We further interpret fossils containing two, four, eight or more internal bodies with polygonal or faceted geometries as cleaving embryos, with the internal bodies being blastomeres. Cross-sections (Fig. 5g) suggest that they are stereoblastulas. Developing embryos are not enveloped by a thick egg case, but instead are bounded by a thin wall rather like the zygotic membrane of living invertebrates. Judging from their egg size, we infer that the Doushantuo embryos underwent direct or lecithotrophic larval development.

At the four-cell stage, blastomeres are arranged in a modified tetrahedron, with opposite pairs of cells meeting across cross-furrows oriented perpendicular to one another at either end of the embryo (Fig. 5c). Structures similar to the cross-furrows of early embryos can also be seen at the 8- and 16-cell stages (Fig. 5e–f). Therefore, we interpret the Doushantuo fossils as holoblastic and equally cleaving stereoblastulas. Gastrulas or later developmental stages have not yet been identified.

The Doushantuo fossils could be broadly equivalent to blastaea or planuloids *sensu* Haeckel³⁴, embryos of microscopic animals as envisioned by Davidson *et al.*³⁵, or the earliest developmental stages of some as yet unrecognized macroscopic metazoan. Tetrahedral geometries comparable to those in the Doushantuo population are unusual in modern animal embryos, but not unknown^{43–46}. In fact, some living crustacean arthropods⁴³, have large eggs, direct development, a tetrahedral four-cell stage, and equal holoblastic cleavage in combination. Thus, the Doushantuo fossils are most probably bilaterian, and they may document cladogenesis within the Bilateria before the appearance of diverse Ediacaran assemblages. Given the age and architectural simplicity of these remains, however, phylogenetic interpretation is best approached with caution.

Despite the many uncertainties that surround the interpretation of the Doushantuo embryos, they provide the first direct geological evidence in support of the hypothesis that the main metazoan clades

diversified before the emergence of a conspicuous animal fossil record. More generally, they show that palaeontological investigation can tell us a great deal about the early history of metazoan evolution.

Conclusion

More than a century ago, Agassiz⁴⁷ recognized the 'three-fold parallelism' of patterns in ontogeny, systematics and biostratigraphy. The remarkable phosphatic thalli and embryos of the Doushantuo Formation show that unanticipated palaeontological observations, together with insights from molecular phylogeny and developmental genetics, can facilitate a modern integration of phylogeny, development and palaeontology that extends deeply into evolutionary history to address the early evolution of multicellular life. □

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