Animal embryos in deep time

Stefan Bengtson

Discoveries of spectacularly preserved embryos and tissues, in rocks that are about 570 million years old, open a new era in the study of early animal evolution.

A spell seems to have been broken — animals considerably older than the Cambrian are finally being found in the fossil record, and they are preserved in a way that reveals details down to the cellular level. This stirring claim is based on studies of the roughly 570-million-year-old Doushantuo phosphorites in southern China, and is hardly weakened by the fact that it comes from two different groups of palaeontologists. On page 553 of this issue[1], Xiao *et al.* report on exquisitely preserved algae and animal embryos from the phosphorites, while, in *Science*, Li *et al.*[2] describe sponges and animal embryos from the same deposits.

The Cambrian Explosion, the evolutionary radiation of life forms about 550 million years ago, was one of the major turning points in the history of the Earth. Over a period of a few tens of millions of years, practically all of the principal animal lineages (phyla) appeared. At least this is what the fossil record suggests. The dearth of animal fossils below the Precambrian–Cambrian boundary has been one of the main frustrations in studies of early animal history, for there has been very little agreement on how, when and where animals lived and evolved during the Proterozoic — the period of time that ended with the beginning of the Cambrian and the Phanerozoic (see Fig. 1 for a timescale). The celebrated Ediacara biota of the Vendian Period, mostly preserved as impressions and traces in sandstones and shales, provides some clues. But it has so far produced more disputes than data with regard to early animals; most Ediacaran deposits are in any case only slightly older than the Cambrian[3].

For a long time following Darwin, a long interval of hidden animal evolution before the Cambrian used to be assumed. But owing to the influence of Preston Cloud[4,5] and others, the more recent inclination has been not to postulate more hidden evolution than absolutely necessary. An estimate in 1996 by three palaeontologists suggested that the main divergence of animal phyla occurred no earlier than 565 million years ago[6]. At the same time, an attempt[7] to estimate the same divergence times using sequence comparisons of various animal genes landed at figures that were more than twice as high. This analysis has been criticized on methodological grounds, and a date of about 670 million years[8] has been proposed instead. Although most palaeontologists will probably be quite happy with the latter date, the fossil record has hitherto been ominously silent.

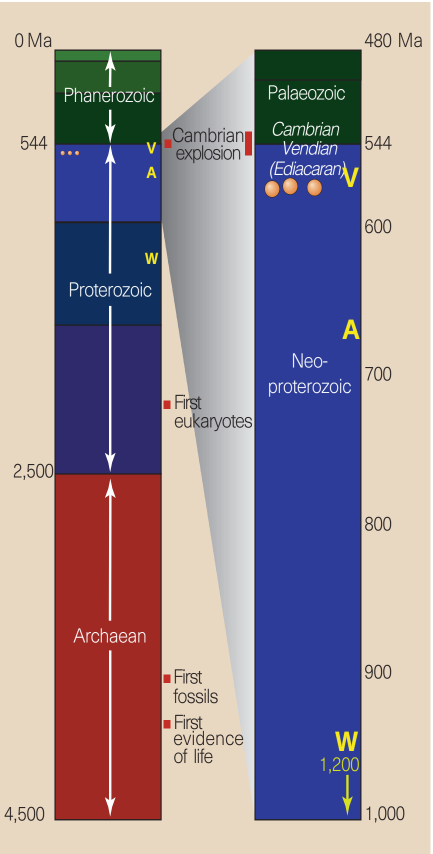

Figure 1 **Timescale of Earth's history (left), and the interval between 1,000 and 480 million years ago (Ma), showing some significant events in the fossil record. The Doushantuo fossils described by Xiao *et al.*[1] and Li *et al.*[2] are indicated by three spherules. V, A and W show the alternative approximate ages (without error bars) of the main radiation of animals as proposed by Valentine *et al.*[6], Ayala *et al.*[8] and Wray *et al.*[7]. Specifically, these are alternative dates for the divergence between protostomes and deuterostomes.**

The origin of animals has thus been as elusive as that of life itself: there are many possibilities but few facts to test them against. The Doushantuo fossils promise to change all that — not only do they give the first convincing glimpse of pre-Ediacaran animal life, but the quality of preservation is almost unheard of, even in much younger fossils. This preservation offers insights into cell-level anatomy, embryological development and life cycles — such matters have not normally been considered to be open to investigation in fossils. Above all, the usual explanation for the missing fossil record has been that the animals were soft and small and therefore would not be preserved as fossils. Now such fossils are beginning to appear. Even better, there seems to be nothing very unusual about the Doushantuo phosphorites, and they may therefore show the way to many other such sites.

The key to the exquisite preservation is calcium phosphate. This mineral is known for its faithful replication of delicate tissues[9,10], although early phosphatization in sediments tends to be very patchy and frequently only fossils of millimetre size or below are preserved[11,12].

The specimens described by Li *et al.*[2] are interpreted as sponges. The siliceous or calcareous spicules of sponges are common in the fossil record, and sponges are among the simplest of multicellular creatures. So they would not be unexpected members of the earliest animal assemblages. The needle-shaped spicules in the examples depicted by Li *et al.* are regularly arranged in distinct bodies built up of cell-like objects, some of which adhere to the spicules in the same way as sclerocytes (spicule-forming cells) do in living sponges. Details of the proposed interpretations are open to question, but it will be difficult to disprove that these are indeed sponges.

The Doushantuo sponges are small, about 150–750 µm in maximum dimension. Although Li *et al.* interpret them as fully formed adults, they could also represent propagules or embryos. But the authors quite reasonably interpret other fossils as embryos of different kinds of animals, and here they find themselves in good agreement with Xiao *et al.*[1], who have isolated a suite of globular fossils from the Doushantuo which they identify as animal embryos in the early stages of cell division (cleavage).

Animal embryos are small and delicate. A few years ago, the thought of finding fossilized embryos of anything but bony pre-hatchlings of dinosaurs and the like was preposterous. However, recent discoveries of Cambrian phosphatized embryos of animals in various developmental stages[13,14] suggested that this might be a fruitful search strategy for the missing record of Proterozoic animals[14]. It indeed seems that all we needed was to open our eyes to the possibility: the fossils now identified as embryos had actually been described in the literature but were interpreted as colonial green algae[15].

Xiao and colleagues' fossils are about half a millimetre in diameter, and are compartmentalized into two, four, eight or more bodies which are proposed to be blastomeres (cells in a cleavage embryo; see the stunning picture on the cover and those on page 556 of this issue). The constant size of the fossils, irrespective of the number of compartments, fits a pattern of developing early embryos with a constant cytoplasmic volume. This would not be expected in colonial algae or in objects formed by non-biological processes.

So what information can we get from these kinds of fossils? The two studies[1,2], although preliminary in nature, already yield some insights. The previously known oldest sponges were late Ediacaran hexactinellids (glass sponges)[16,17], but the spicule morphology and cell configuration of the Doushantuo sponges are very different from those of hexactinellids. The early-cleavage embryos have a tetrahedral blastomere configuration that is today known in some animals such as nematodes, flatworms and arthropods. One should be careful about drawing evolutionary conclusions from physically simple patterns like these, but the observation clearly shows the potential of such material. Only finds of later developmental stages will tell in which direction, and how far, these embryos developed.

The Doushantuo phosphorites cover an area of 57 km^2, and they undoubtedly contain further secrets. Phosphate is thus pay dirt. But whereas digging up the basal roots of animals may have its particular appeal, let's not forget about the rest of animal history. Developmental and evolutionary biology are complementary but largely separate sciences, and the fossil record might help in bringing them together. Palaeoembryology may be a science of the past, but it could have a brilliant future. □

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Marine colloids

A neglected dimension

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Marine colloids are the most abundant particles in the oceans[1,2]. They account for 30–50% of the 'dissolved' organic carbon in sea water[3,4] , and they also contain biologically essential metals[5] . Although great strides have been made in assessing the bulk composition of the marine colloidal phase, there is little consensus about what processes regulate colloid cycling, or even what the ultimate fate of these substances is. The work of Chin *et al.* (page 568 of this issue[6]) adds a fresh perspective to these basic questions by invoking polymer gel theory to explain the behaviour of marine colloids. This insight is important because emerging evidence suggests that the marine colloidal phase is intrinsic to a variety of oceanographic processes, with potential ramifications running from the modulation of metal ion uptake by algae to global climate change.

Colloids lie at the boundary between soluble chemical species and sinking particles, and are defined as substances sized between about 1 and 1,000 nm in diameter. Particles in this range are large enough to acquire an interface (that is, the interior is chemically distinct from the surrounding medium) but small enough for gravity not to be the dominant force acting upon them. So removal of colloidal substances from sea water depends upon either their degradation to soluble components or their aggregation to form sinking macroparticles.

It has long been recognized that colloids strongly affect the behaviour of carbon and metals in estuaries[7]. But their role in coastal and offshore sea waters had been largely overlooked, mainly because oceanographers have traditionally employed filters of 0.2–0.7 μm pore size to arbitrarily partition sea water into 'dissolved' and 'particulate' phases. Only recently have concerted efforts begun to discriminate colloidal from truly soluble components within the 'dissolved' phase. Given the early evidence that the marine colloidal phase may account for upwards of 250 gigatonnes of potentially bioreactive organic carbon, it is not surprising that new emphasis is being placed on understanding the sources, cycling and fate of these substances.

Tracer studies using highly surface-active metal isotopes show that the marine colloidal phase is very dynamic, with high colloid aggregation rates being sustained even in nutrient-poor surface waters[8,9]. These findings imply that colloid production rates must also be high, presumably through a combination of cell exudation and lysis, microbial degradation of particulate organic matter, and 'sloppy' feeding and excretion by zooplankton[1,10]. Colloidal concentrates obtained by cross-flow ultrafiltration contain carbohydrates, proteins and lipids[3], as well as significant quantities of the biologically essential metals iron, copper, zinc, nickel and cadmium[5].

So what factors control colloid residence times in sea water? Most recently, interest has largely centred on the biodegradation removal pathway. Indeed, size-fractionation experiments suggest that colloidal organic matter supports the bulk of heterotrophic microbial production in sea water, rather than truly soluble sustances[11]. In this case, colloid 'removal' rates would be primarily a function of enzyme-specific reactions which, in turn, would be strongly influenced by the composition and steric accessibility of molecules within colloidal matrices.

However, the results of Chin *et al.*[6] show the importance of nonspecific surface interactions in colloid cycling. They find that discrete natural polymers coalesce spontaneously to form large, sinking conglomerates (Fig. 1); from the results, it seems that the process has second-order kinetics, with aggregation reaching apparent equilibrium after about 80 hours under the authors' abiotic test conditions. This period is similar to estimates of colloid turnover times in surface waters from ^{234}Th modelling[8,9]. Ion-bridging between biopolymers seems to be the primary driving mechanism because the process is reversed by chelation of Ca^{2+} and Mg^{2+}. As with colloidal concentrates, histological staining indicates that the aggregates are composed of carbohydrates, proteins and lipids — which is particularly interesting, because it suggests that the stability of a wide range of biocompounds within the dissolved-organic-matter component of sea water may depend less on their chemical composition than on their interfacial characteristics.

Chin *et al.* go on to show that these aggregates undergo reversible swelling and condensation as a function of hydration, a behaviour characteristic of gels formed by tangled networks of polymers. Although similar behaviour has been shown for terrestrial humic matter[12], this is the first report for marine aggregates. These changes were observed under chemical conditions very different from those characteristic of sea water, but Chin *et al.* suggest that similar transitions might occur over natural ranges of temperature and pressure or in chemically