

Precambrian Animal Life: Probable Developmental and Adult Cnidarian Forms from Southwest China

Jun-Yuan Chen,^{*1} Paola Oliveri,^{†,1} Feng Gao,^{*} Stephen Q. Dornbos,[‡]
Chia-Wei Li,[§] David J. Bottjer,[‡] and Eric H. Davidson^{†,2}

^{*}Nanjing Institute of Geology and Paleontology, Nanjing 210008, China; [†]Division of Biology, California Institute of Technology, Pasadena, California 91125; [‡]Department of Earth Sciences, University of Southern California, Los Angeles, California 90089; and [§]Department of Life Science, National Tsing Hua University, Hsinchu 300, Taiwan, China

The evolutionary divergence of cnidarian and bilaterian lineages from their remote metazoan ancestor occurred at an unknown depth in time before the Cambrian, since crown group representatives of each are found in Lower Cambrian fossil assemblages. We report here a variety of putative embryonic, larval, and adult microfossils deriving from Precambrian phosphorite deposits of Southwest China, which may predate the Cambrian radiation by 25–45 million years. These are most probably of cnidarian affinity. Large numbers of fossilized early planula-like larvae were observed under the microscope in sections. Though several forms are represented, the majority display remarkable conformity, which is inconsistent with the alternative that they are artifactual mineral inclusions. Some of these fossils are preserved in such high resolution that individual cells can be discerned. We confirm in detail an earlier report of the presence in the same deposits of tabulates, an extinct crown group anthozoan form. Other sections reveal structures that most closely resemble sections of basal modern corals. A large number of fossils similar to modern hydrozoan gastrulae were also observed. These again displayed great morphological consistency. Though only a single example is available, a microscopic animal remarkably similar to a modern adult hydrozoan is also presented. Taken together, the new observations reported in this paper indicate the existence of a diverse and already differentiated cnidarian fauna, long before the Cambrian evolutionary event. It follows that at least stem group bilaterians must also have been present at this time. © 2002 Elsevier Science (USA)

Key Words: cnidarian; fossil; Precambrian; embryo.

INTRODUCTION

Over the last decade, an enormous amount of evidence from developmental molecular biology, much of it presented in these same pages, has shown that all Bilateria share a common genetic toolkit for development, and that all Bilateria use the same basic strategies to build their diverse body plans (reviewed in Davidson, 2001; Erwin and Davidson, 2002; Carroll *et al.*, 2001). The Bilateria thus derive from a common ancestor, a point repeatedly substantiated in current molecular phylogenies (reviewed in Adoutte *et al.*, 2000; Peterson and Eernisse, 2001). This ancestor clearly existed prior to the Cambrian, given the famous

diversity of crown group bilaterians already evident in the Early Cambrian fossil record (Fig. 1; Chen and Zhou, 1997; Siveter *et al.*, 2001). At least one well-differentiated adult bilaterian form, *Kimberella*, is also known from the latest Neoproterozoic (Martin *et al.*, 2000), the 10 or 15 million years immediately preceding the Cambrian boundary at 543 million years ago (mya) (see Fig. 1). *Kimberella* was probably a protostomial animal, possibly a mollusc (Fedonkin and Waggoner, 1997), and so the latest common bilaterian ancestor predated this. But of the form of this ancestor, or the time at which it lived, or the nature of the stem group lineage from which it derived, there is yet almost no information in the fossil record (see Erwin and Davidson, 2002 for discussion). The only fossil evidence that would appear to relate to earlier bilaterian forms consists of still enigmatic microfossils of gastrula-stage embryos from the Doushantuo formation of Southwest China (Chen *et al.*, 2000). The age of these microfossils is likely to be between

¹ These authors contributed equally to this work.

² To whom correspondence should be addressed. Fax: (626) 793-3047. E-mail: davidson@mirsky.caltech.edu.

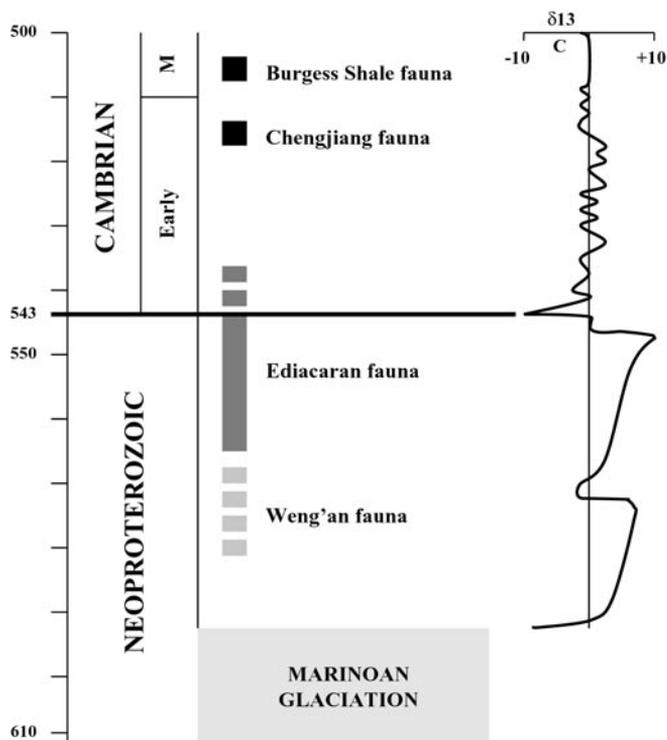


FIG. 1. Global Neoproterozoic–Cambrian time scale and carbon isotope record showing the major fossil faunal assemblages during the early radiation of the Metazoa. Changes in carbon isotopes generally reflect global climatic and oceanographic changes, including those leading to possible Snowball Earth conditions (e.g., Marinoan glaciation) and deposition of cap carbonates, such as the Doushantuo Formation. The great variation in the carbon isotope record during this time interval provides a method for correlating sedimentary rocks between different regions. The fossil assemblages indicated include the Weng'an (Chen *et al.*, 2000) and Ediacaran (Glaessner and Wade, 1966); Chengjiang (Chen and Zhou, 1997) and Burgess (Briggs *et al.*, 1994) faunas. Age of Weng'an fauna lies within range of its "dashed" timeline, youngest age of Ediacaran fauna lies within range indicated by upper "dashed" part of its timeline. The time scale is modified from Martin *et al.* (2000). The carbon isotope curve is from Knoll and Carroll (1999) and Knoll (2000).

570 and 580 mya, i.e., 25–35 my prior to the onset of the Cambrian (Fig. 1).

Molecular and morphological phylogenies agree that the bilaterian stem group emerged from a common ancestor of bilaterians and cnidarians, which probably existed much deeper in time (Peterson and Eernisse, 2001; Medina *et al.*, 2001; Peterson and Davidson, 2000). The cnidarians share with bilaterians many genes encoding transcription factors, signaling pathway components, and cell type-specific proteins (e.g., Yanze *et al.*, 2001; Schuchert *et al.*, 1993; Gröger *et al.*, 1999; Müller *et al.*, 1999; Smith *et al.*, 1999; Spring *et al.*, 2000). But they differ fundamentally from bilaterians: they lack a two-ended gut; they lack bilateral anterior–

posterior body plans; they lack any *Hox* genes of the "middle" class (Finnerty and Martindale, 1999; de Rosa *et al.*, 1999; Yanze *et al.*, 2001); they lack central nervous systems; and perhaps most importantly, they lack the mesodermal sheets and columns on which bilaterian body parts depend for structure, for function, and often for the process of body part development. Cnidarians are also found in the Early and Middle Cambrian (Chen and Zhou, 1997; Briggs *et al.*, 1994), and they may be extensively represented in the late Neoproterozoic Ediacaran fauna as well (Glaessner and Wade, 1966; Brasier *et al.*, 1997; Xiao *et al.*, 1998). Several recent items of evidence support the presence of cnidarian forms in the earlier Doushantuo fossil assemblages. Some embryos from this material putatively identified as cnidarian were published by Chen *et al.* (2000). A fossil adult cnidarian form was also recognized in the Doushantuo phosphorites (Xiao *et al.*, 2000). These fossils were identified as tabulates, an extinct form previously known from Cambrian and later Paleozoic deposits. Here, we describe many new Doushantuo microfossils, that are most probably of cnidarian affinity. Included are larval and some adult stages, though the latter are relatively rare, and both anthozoan and hydrozoan clades are probably represented. We conclude that crown group cnidarians had already appeared by Doushantuo times, which provides a useful constraint with respect to the evolution of the bilaterians.

METHODS

Samples were collected from the lower part of the Weng'an phosphorite in the quarries near Weng'an in Guizhou Province, China. From these, thin sections were prepared by grinding and were mounted on standard microscopic slides for observation. Sections were ground to a thickness of ca. 50 μm , allowing for some three-dimensional visualization at different planes of focus. About 6000 sections have been examined, and nearly 20,000 digital images have been recorded. The images for the present study were obtained by microscopy under direct transmitted and polarized light at 100–1000 \times magnification.

RESULTS

Geological and Paleontological Setting

The Neoproterozoic (1000–543 mya) is a critical interval in Earth history for the evolution of animal life. Recent work has led to the "Snowball Earth" hypothesis, suggesting that the Earth underwent severe cooling episodes during which much of the globe was covered with ice perhaps as many as four times between 750 and 580 mya (e.g., Hoffman *et al.*, 1998; Hyde *et al.*, 2000). Carbon dioxide from volcanoes would have eventually increased in the atmosphere to the point where a "runaway" greenhouse effect occurred, leading in turn to melting of the ice and torrid climatic conditions. Extensive marine deposition of calcium carbon-

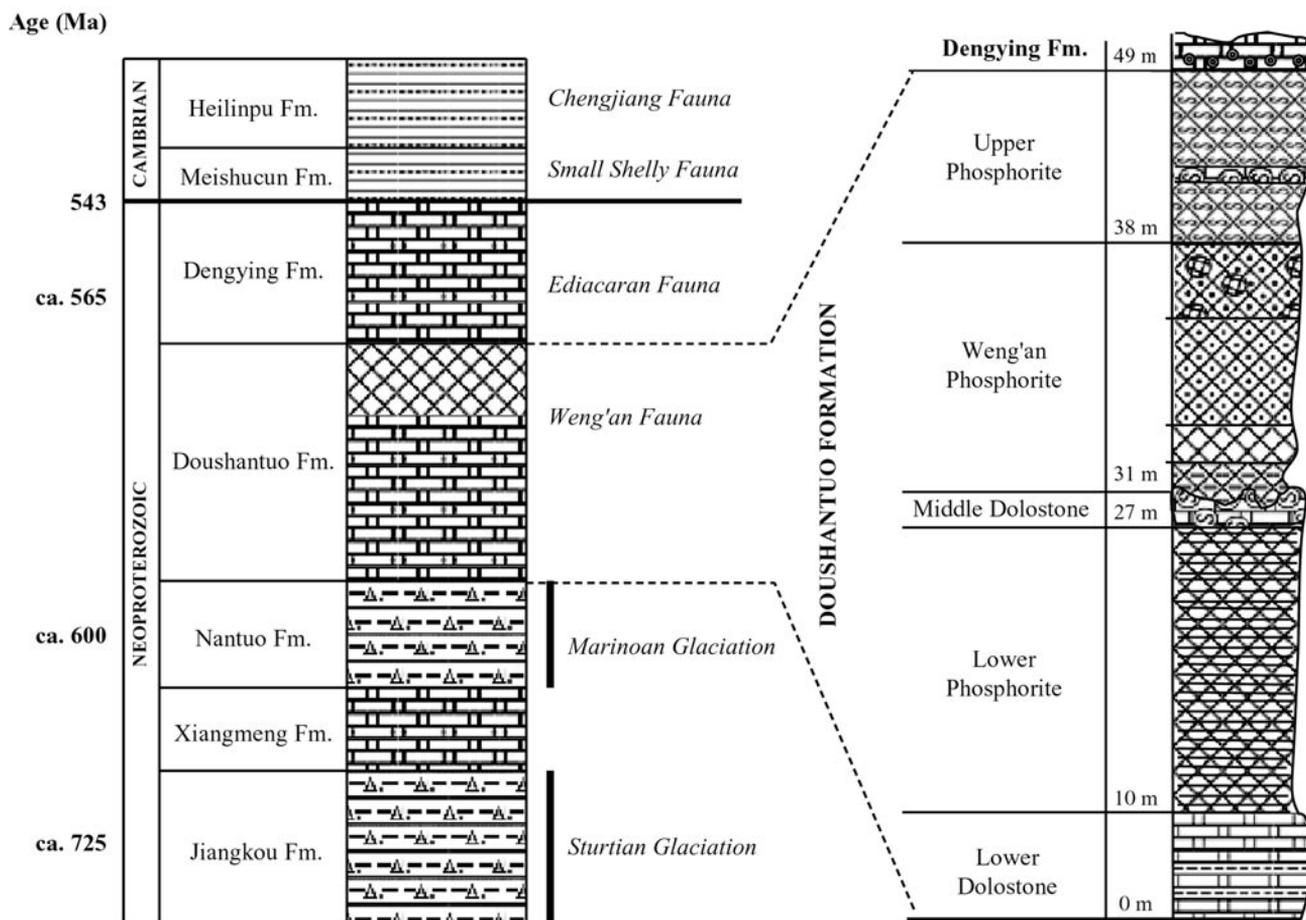


FIG. 2. Neoproterozoic–Cambrian stratigraphy of South China with stratigraphy of the Doushantuo Formation. General Neoproterozoic–Cambrian stratigraphy of South China on left with dates from Knoll (2000) and Martin *et al.* (2000). Significant fossil faunas and Snowball Earth glaciations are labeled in the center of the diagram. On the right is shown the stratigraphy of the Doushantuo Formation as exposed in Weng'an, Guizhou Province, China. The Weng'an fauna occurs in the Weng'an phosphorite. (Ma, million years ago).

ate sediments resulted. The Doushantuo Formation represents the youngest of these “cap carbonates,” deposited during the early phases of a postglacial period, when greenhouse conditions prevailed. Figure 2 shows the stratigraphic sequence of the upper Neoproterozoic rocks in South China, the distribution through time of some significant fossil faunas and Snowball Earth glaciations, and in more detail, on the right, the sedimentary rocks of the Doushantuo Formation. In Fig. 2, this stratigraphic sequence is correlated, on an approximate time scale, with the contemporary glacial episodes and with the successive fossil assemblages. In China, the youngest of the Snowball Earth sedimentary units indicating glacial conditions is the Nantuo Formation. The Nantuo is overlain by the carbonate strata and phosphorites of the Doushantuo.

Strata of Neoproterozoic and Early Cambrian age in South China represent some of the most fascinating sites for understanding the early evolutionary history of animal life. Over the past 20 years, there have been incredible fossil

discoveries in this area, including not only the approximately 570- to 580-my-old Weng'an fauna, but also the early Cambrian Chengjiang fauna that exhibits soft-bodied preservation of Cambrian animals (e.g., Bengtson and Yue, 1997; Chen and Zhou, 1997). Sedimentary rocks and their enclosed fossils in South China have become a focal point for inquiries into the effects of Snowball Earth on life, and on the evolution of metazoans in the period which begins with the Weng'an microfossils and ends with the richness of Cambrian life displayed in the Maotianshan Shale.

The Doushantuo Formation varies in thickness from a few tens of meters up to five hundred meters. In Weng'an, central Guizhou province, the Doushantuo Formation is represented by a phosphorite-dominated sequence, ~40 m in thickness. It is lithologically differentiated into the following five units (Fig. 2):

- Lower Dolostone member, consisting of grayish dolomite with massive bedding; 7.7 m.

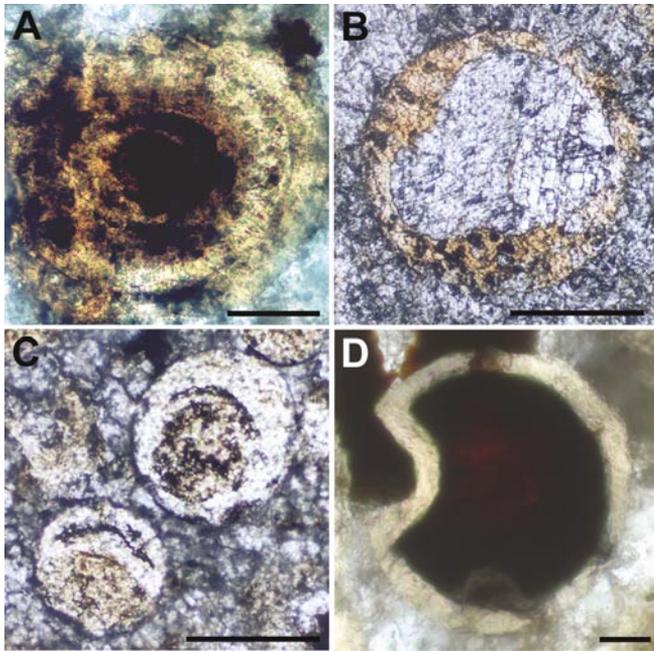


FIG. 3. Examples of probable diagenetic artifacts or uninterpretable structures observed in Weng'an phosphorite sections. (A) Large coated grain composed of multiple concentric layers surrounding a black amorphous core: the structure is $600 \times 530 \mu\text{m}$ (scale bar, $200 \mu\text{m}$). (B) Coated grain with crystalline core. The outside layer varies in thickness from about $5\text{--}50 \mu\text{m}$ (scale bar, $100 \mu\text{m}$). (C) Two asymmetrically coated grains. Both grains show a crescent-shaped structure on one side due to the asymmetric layers of coating. The sizes are different: the top right grain is $130 \times 140 \mu\text{m}$, the bottom left $105 \times 100 \mu\text{m}$ (scale bar, $100 \mu\text{m}$). (D) Homogenous white layer surrounding red-black amorphous core, deformed on one side (scale bar, $50 \mu\text{m}$). While structures such as those in this figure could have formed around biological remains, they have been severely modified by diagenetic processes.

- Lower Phosphorite member, composed of thin-bedded phosphorite with bedding planes that are either smooth or with a surface elephant-skin texture (this kind of texture indicates the presence during deposition of sea floor microbial mats); 17.5 m.

- Middle Dolostone member, consisting of dolomite that has been strongly silicified during diagenesis. It is topped with an erosive surface and bears intensive dissolution features as the result of subaerial weathering; 3.5 m.

- Weng'an Phosphorite member, a phosphate unit deposited in shallow water with high-energy conditions. Erosive surfaces occur commonly. Presence of tidal channels and "herringbone" cross-stratification suggests the influence of tidal currents. Evidence for early phosphatization includes ubiquitous phosphatized crusts and many phosphatized intraclasts, embryos, algae, and other microfossils; 7.4 m.

- Upper Phosphorite member, composed of limestone and phosphatic bands; 7.6 m.

All the fossils illustrated here are derived from the Weng'an phosphorite exposed in the Wusi and Baishakan quarries, near the city of Weng'an. They are preserved either within phosphatic intraclasts (1–5 mm in the greatest dimension), or as small individual phosphatic grains. A number of studies have shown that the Doushantuo phosphorites have a high potential for preservation of very fine biological detail, including cellular and even subcellular structures (e.g., Xiao *et al.*, 1998; Li *et al.*, 1998; Chen *et al.*, 2000). With the aid of seafloor microbial mats, early phosphatization of soft and delicate animal remains within the shallow seafloor sediments led to the formation of phosphatic crusts. These crusts were subsequently broken into pieces and redeposited as intraclasts during storm events. This cycle of phosphatic crust formation, breakage, and redeposition probably occurred many times before final deposition of the sediments.

The actual nature of the Weng'an animal life, i.e., what one would see were it possible to examine it alive, is not yet very well known. In addition to algal and fungal forms, poriferan organisms were undoubtedly present. A variety of sponge eggs and embryos, some apparently including siliceous spicules, as well as small adult sponges, have been observed (Li *et al.*, 1998; Xiao *et al.*, 1998, 2000; Zhang *et al.*, 1998; Yuan and Hofmann, 1998; and our unpublished data). Large sponge eggs, measuring $500\text{--}750 \mu\text{m}$ in diameter, are commonly encountered in sections of Doushantuo phosphorite, and their distinctive early cleavage forms also occur frequently. Geometrically, these are the same cleavage forms as visualized in the spectacular scanning EMS published by Xiao *et al.* (1998), which show eggs extracted from samples of these deposits by acid dissolution of the surrounding limestone. But, with a few exceptions, such as the distinct spiral cleavage geometry of annelids, molluscs and their allies, or the unequal fourth cleavage of regularly developing echinoids, early cleavage forms are notoriously poor discriminators of phylogenetic affinity. While the most likely guess from the morphology and size of these externally visualized cleavage forms is that they are indeed sponge embryos, the same as those seen often in sections, their identity cannot be certainly resolved. Several protostomial bilaterians produce cleavage stages of similar geometry, e.g., certain crustaceans (Kume and Dan, 1968) and also chaetognaths (Shimotori and Goto, 2001). But no other evidence for adult bilaterian forms of such advanced complexity exists for the Weng'an fauna, nor are there any of the trace fossils or bioturbation that characterizes the later benthic habitats of advanced bilaterians.

A variety of smaller embryonic microfossils that do not appear poriferan was also noted by Li *et al.* (1998). Recently, these and some additional new forms were further explored (Chen *et al.*, 2000). Among these are putative gastrulae, which appear to be marvelously preserved, single cell-thick structures the morphology and dimensions of which bear remarkable resemblance to some modern bilaterian gastrulae. The observations are preliminary, in that additional samples of these bilaterian-like gastrulae need to be recov-

ered and examined. Other classes of gastrula-like microfossil reported by Chen *et al.* (2000) resemble the gastrular and planular forms of some modern cnidarians. However, Xiao *et al.* (2000) pointed out that it could not be excluded that these apparent microfossils are of nonbiological origin, i.e., that they are rather products of diagenetic processes, or artifacts of mineralization.

There are indeed many small, more or less spheroid grains that superficially resemble biological objects but which are either of nonbiological origin or are so badly preserved as to be entirely indeterminate. Some typical examples are shown in Fig. 3. Often they have a laminar or concentric structure. But they are different from one another in size and morphology. In what follows, we present multiple examples of fossilized forms that are morphometrically nearly identical to one another, the only reasonable explanation for which is that they are the product of genetic developmental systems. These forms resemble the embryos of certain modern cnidarians. This interpretation is greatly strengthened by the observation of small, adult cnidarian fossils in the same deposits.

Fossilized Embryos and Larvae Resembling Developmental Stages of Modern Anthozoans

Two different kinds of phosphatized microfossil that can be interpreted as anthozoan developmental forms have so far been identified. Examples of a form very commonly encountered in Weng'an rock sections are shown in Fig. 4. The structure of these fossilized embryos is asymmetric. At one end, always facing the top in Fig. 4, a double-layered, tightly-looped fold can be seen symmetrically on either side of a depression, which leads to a solid, amorphous interior. In many specimens, e.g., Figs. 4A, 4C, and 4G and 4H (H is a polarized light image of G), the double-layered nature of the looped structures at the open end is shown by a slit or discontinuity between outer and inner layers. Because

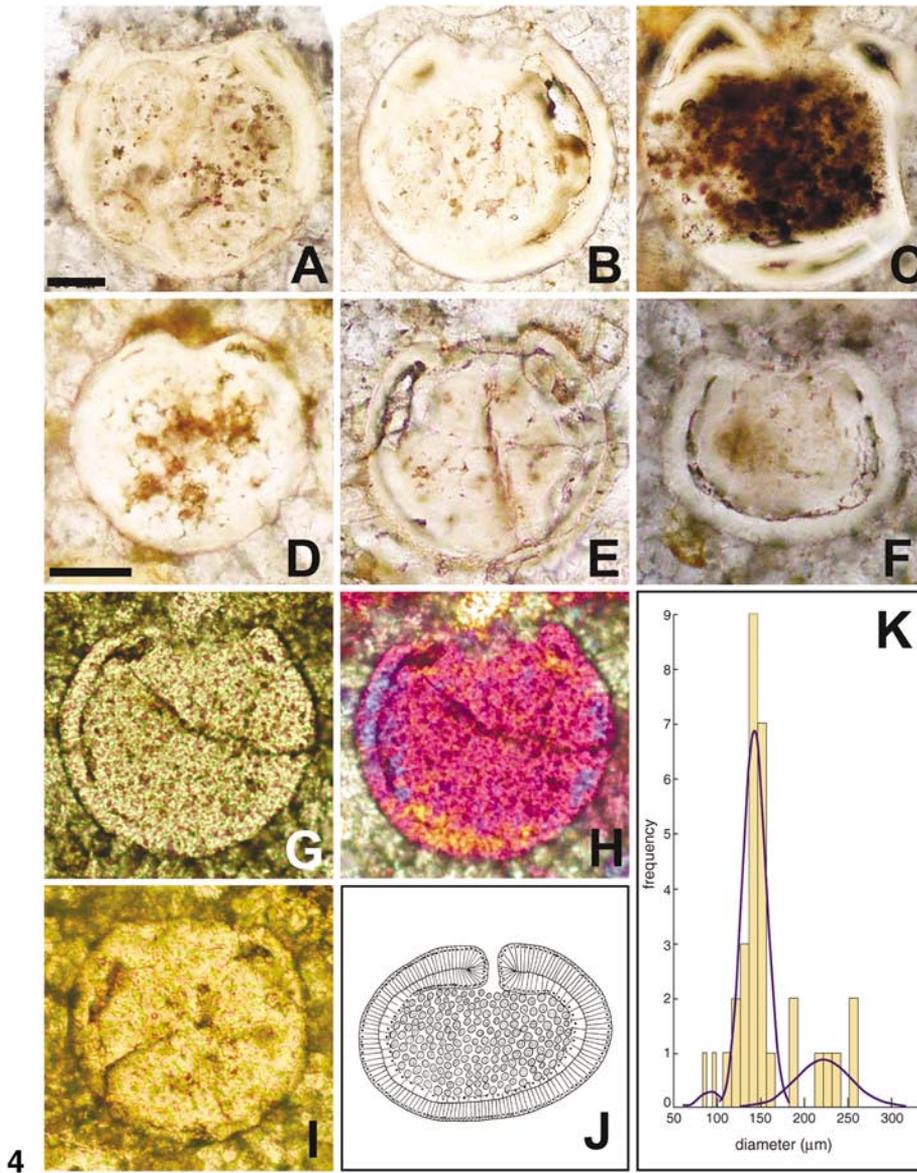
those approximately spherical structures always display the same cross-sectional morphology, the looped structures surrounding the opening at the top are best interpreted as the edges of an embryonic radial pore. The polarized light image in Fig. 4H illustrates further features. The central mass is amorphous phosphate while the two outer layers of the embryo display a similarly oriented crystalline phosphate structure, which is symmetrical with respect to the axis of the putative embryo (see legend). Sometimes, as in Fig. 4C, the amorphous inner mass has a dark orange color which differentiates it from the outer layers even in polarized light. The dark color may indicate the presence of kerogen, an organic carbon-rich residue. A hint of a laminar outer structure in some of the fossil embryos indicates the successive build-up of phosphate layers following the initial phosphatization (e.g., Fig. 4C), while others such as those in Figs. 4G and 4H, look less modified. But the topology of all of them is the same.

The insert in Fig. 4J shows a drawing of a modern anthozoan gastrula, that of *Pachycerianthus multiplicatus* (Nyholm, 1943). The ceriantharia are closely related to the sea anemones. They are solitary anthozoans specialized for life on soft surfaces in which their stalks are embedded. The blastula is filled with a solid acellular mass of yolk granules surrounded with a single layer of ectodermal cells. Gastrulation occurs by a kind of unipolar invagination, leaving the open blastopore at one end, and producing a spheroid with two layers of cells in which the inner layer gives rise to the future gastrodermis. The fossils of Figs. 4A–4I could be gastrular forms similar to that of the modern anthozoan shown in Fig. 4J. Their monopolar invagination, with the thin inner layer applied directly to the outer (ectodermal) layer, and the amorphous filled interior, are particular characters that they share with the *Pachycerianthus* gastrula.

The distribution of size measurements on 32 individual fossils, all of which display similar topologies, is given in Fig. 4K. Most of the putative embryos fall into a single sharp

FIG. 4. Fossil embryos resembling modern ceriantharian gastrulae. (A–I) Fossilized embryos seen in sections of Weng'an phosphorite rock (see Fig. 2). The sections were viewed under the microscope in transmitted light, as described in Materials and Methods. (A–C) are shown at one magnification and (D–I) at a higher magnification; scale bars in (A) and (D) are 50 μm . (H) is the same embryo as (G), but viewed under polarized light using crossed Nicols prisms with a gypsum plate. The organized crystal structures seen under polarized light in the cellular layers (here similar color indicates similarly oriented crystal axes) may reflect the original polarization of cytoskeletal architecture that was preserved in the initial process of phosphatization. Note that the blue color, signifying the same crystal orientation, appears symmetrically with respect to the axis of the embryo. (J) Drawing of a cross-section of late gastrula-stage embryo of the modern anthozoan *Pachycerianthus multiplicatus* (Nyholm, 1943). The small spheres in the interior represent yolk granules; the blastopore is at the top. The embryo consists of a monocellular outer ectodermal layer and monocellular inner endoderm layer. The inner layer, particularly toward the end opposite the blastopore, is not as clearly separated from the yolk mass as at the blastoporal end, just as also in the fossils. (K) Size distribution (diameter) shown for 32 fossil embryos that display the same topology as those shown in (A–I). The frequency distribution has been fit by least squares with Gaussian curves, matching the area under the respective portions of the histogram to that under the curves. For the main peak, the mean is 142 μm and the standard deviation is $\pm 13.7 \mu\text{m}$. The other Gaussians are arbitrary, in that there could be several larger and smaller size classes. The smaller and larger classes of embryo have the same morphology.

FIG. 5. Putative fossil actinarian planula larva. (A) Cross-sections of a small, complex fossilized organism. The diameter is only about 60 μm , suggesting that the cross-section is toward the narrow end of the planula. The organism consisted of a monocellular outer layer and a monocellular inner layer from which project numerous inclusions and mesenteric septa. (B) Drawing of a modern actinarian planula larva in cross section (*Euphyllia rugosa*, after Chevalier, 1987).



4



5

peak, about $142 \pm 14 \mu\text{m}$ in diameter. These are illustrated in Figs. 4D–4I. There are a larger forms as well, illustrated in Figs. 4A–4C. Given the small dimensions of the blastopore, the majority of possible sections parallel to the central axis of the embryo will be too lateral to reveal the surrounding blastoporal folds, and these would result in smaller images that look like simple discs with a double or single external cellular layer and an amorphous interior. Equatorial sections would look the same. We saw hundreds of circular objects with this very simple structure (not shown). The significance of the measurements in Fig. 4K is that, if they display blastopore-like structures as in Figs. 4A–4I, they must be mid-sagittal sections. Therefore the diameters are comparable, specimen to specimen. What we see is that the dominant class is essentially uniform in size as well as topology.

Chen *et al.* (2000) showed a large planula-like microfossil about $200 \times 300 \mu\text{m}$ in which the interior consisted of what appears to be a highly folded multicellular structure. In Fig. 5A, we show a particularly well-preserved specimen of similar morphology but smaller dimensions. The drawing in Fig. 5B represents a cross-section of a modern actinarian (sea anemone) planula. There is a monocellular outer ectodermal layer and a closely applied monocellular inner endodermal layer. This gives rise to numerous folds, septa, and other multicellular inward projections. The phosphatic fossil in Fig. 5A has a similar topology. There is a regularly striated outer layer, perhaps revealing the periodicity of the cells of which it was composed, as in some of the fossils described earlier by Chen *et al.* (2000). Closely applied to this on the inside, as is particularly clear toward the top in Fig. 5A, is the inner layer. Extending inward from it, e.g., at 9 o'clock, are double-layered septa. Other multicellular projections continuous with the inner cellular layer and several lined cavities can also be seen in the section. Given its structure, if it was a planula larva at this stage the organism was elongate (like that illustrated in Chen *et al.*, 2000), and its slightly flattened, almost circular shape indicates that this is a cross-section similar to that portrayed in Fig. 5B.

The developmental forms shown in Figs. 4 and 5 are unlike bilaterian embryos, which do not produce endodermal linings directly applied to the peripheral ectodermal wall. They are also unlike poriferan embryos, which do not form clear blastoporal invaginations such as seen in Fig. 4, nor planula larvae with complex layered endodermal structures such as seen in Fig. 5. As the drawings in Figs. 4 and 5 show, these microfossils are reasonably interpreted as anthozoan developmental forms.

Evidence for Cnidarian Body Plans of Anthozoan Affinity

Though they are much more rare than the embryo-like forms of Fig. 4, the Weng'an phosphorite also contains fossilized remains of adult cnidarian body parts. These fall into two groups: tabulates, and fossils of animals that might

be related to anemones or soft-bodied coral-like organisms. The species of tabulate recently reported from the Dou-shantuo deposits by Xiao *et al.* (2000), *Sinocyclocyclicus guizhouensis*, was originally thought to be a crinoid (Xue *et al.*, 1992). However, both scanning EMs of three-dimensional fossils etched out of the limestone by acid treatment and images obtained from rock sections reveal the close similarity of this form to Paleozoic tabulates (Xiao *et al.*, 2000). Tabulates are a major extinct cnidarian clade of the Anthozoa (Hyman, 1940; Oliver and Coates, 1987). Many of the reefs of Paleozoic seas were built by tabulates and by animals of another colonial cnidarian order, the Rugosa (Hill, 1981; Stanley and Fautin, 2001). Until the work of Xiao *et al.* (2000), the earliest tabulates known were of Early Cambrian age. Twelve specimens of a tabulate coral were also recognized in our sections, and they appear to be identical to *Sinocyclocyclicus*.

Some details of the structure of this organism are shown in Fig. 6 (see also Xiao *et al.*, 2000). *Sinocyclocyclicus* was a colonial coral-like animal, probably soft bodied, consisting of tubes that are divided into a series of chambers about $10\text{--}16 \mu\text{m}$ apart by cross-walls (tabulae). The individual tabulae were probably about $2\text{--}3 \mu\text{m}$ thick in life, but appear thicker in the sections due to growth of a mineral cement on either side, as can be seen in the image shown in Fig. 6J. The polyp evidently lived in the terminal chamber or calice and it secreted new chamber floors as it grew. The individual tubes are only a few millimeters long and $100\text{--}200 \mu\text{m}$ across, narrower at the bottom. Sometimes the tubes can be seen to branch, and in colonial arrays, adjacent tubes may share a common wall. Figure 6 shows three different specimens. Figures 6A–6D and 6G–6J represent various views of two colonial assemblages, and Figs. 6E and 6F show a single individual. The close-ups in Figs. 6B, 6H, and 6I indicate the general features of the structure of the individual tubes (corallites) and their tabulae. Two neighboring corallites joined by a connecting tube can be seen in Fig. 6B, and two neighboring tubes sharing a common wall are seen in Fig. 6H. The lack of a rigid mineralized corallite wall is shown by its deformability, illustrated in Fig. 6G (see legend). In cross-section, the corallites appear polyhedral (Figs. 6C and 6D), and are penetrated by short septal structures extending inward from the peripheral wall, another cnidarian character. The solitary corallite shown in Fig. 6E preserves the terminal calice, which is an elongate vase-shaped structure that in this slide has been tangentially sectioned and possibly contains an enclosed, withdrawn polyp. The probable soft-bodied polyp, residing on the uppermost complete tabula, is preserved as dark organic remains. The retracted polyp is still tentacular along its distal and lateral margins, with at least six tentacles preserved. Several projections which might be tentacles are tapered and blunt-ended (Fig. 6F). There are four annular structures on the basal outer wall of the calice, that could represent early developmental stages of the tabulae. The presence of these incomplete tabulae suggests that the tabula was formed by horizontal ingrowth.

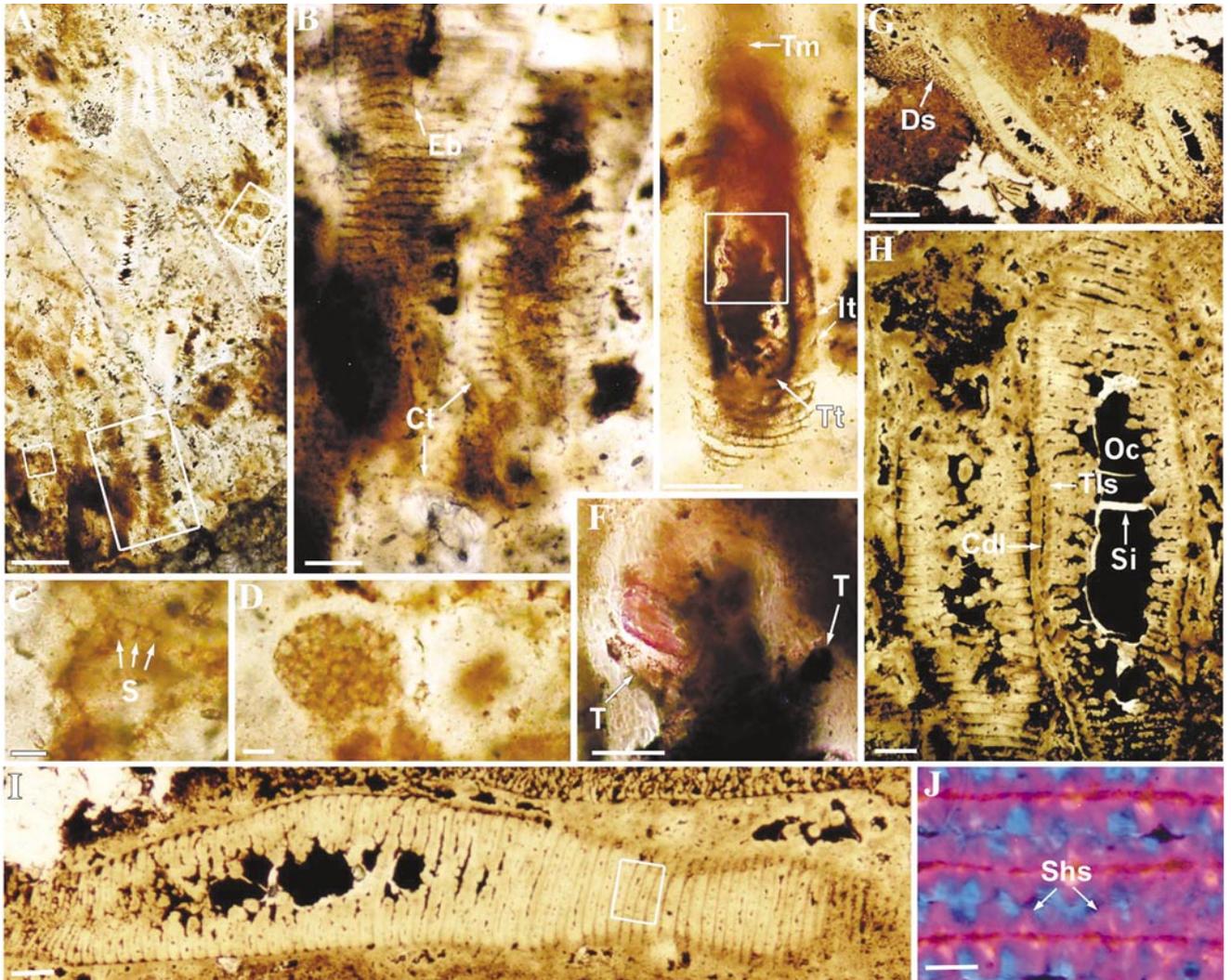
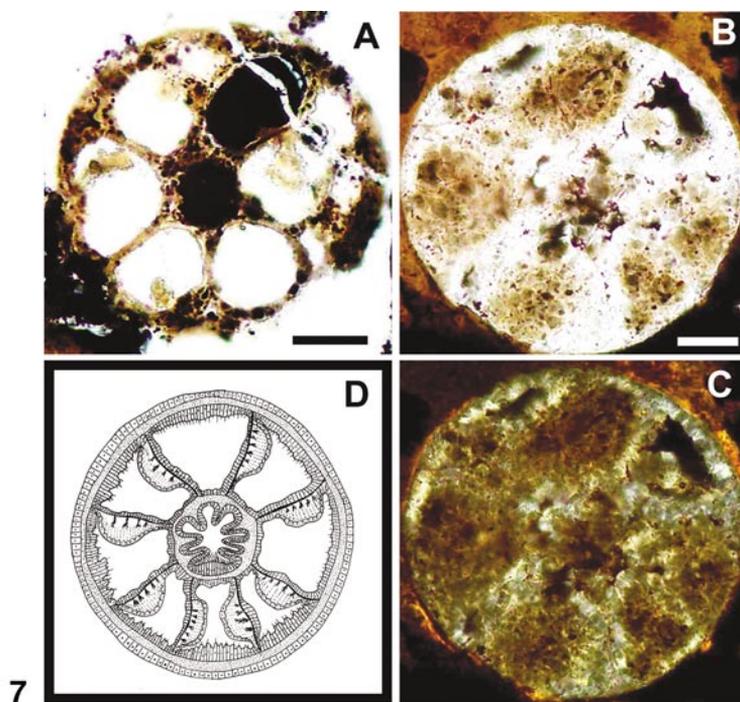
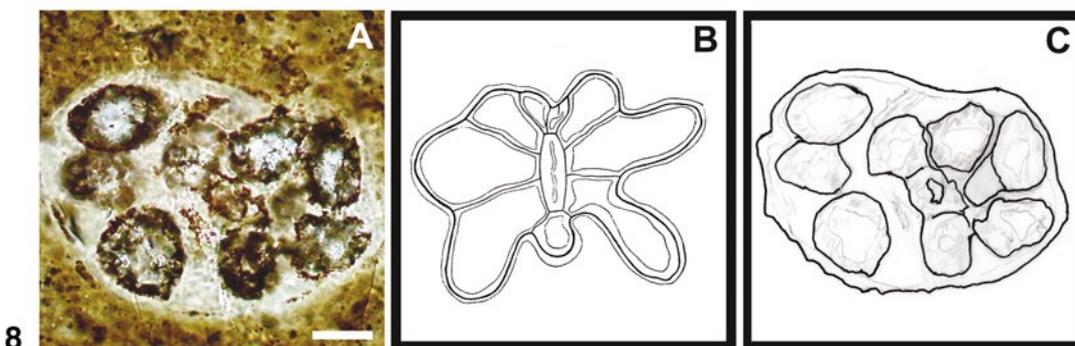


FIG. 6. Sections displaying a colonial, tabulate-like coral *Sinocyclocliticus guizhouensis* (Xue *et al.*, 1992). This microscopic coral originally had nonmineralized, contiguous and sometimes branching tubes. The organism lived in the terminal chamber (calice). Within the tubes are stacks of cross-partitions, the tabulae, secreted successively as the tube is extended. (A–D) A *Sinocyclocliticus* colony (WSB0–60, slice Z0001). (A) Low magnification; 15 corallites are present in this field. The framed areas show regions enlarged in (B) and (C, D); scale bar, 300 μm . (B) Higher magnification, showing a branch present where two tubes have grown out in equal bipartite manner (Eb). This and the adjacent corallite are joined with a connecting tube (Ct). The scale bar is 50 μm . (C) Cross-section of an individual corallite in which some septal elements (S) have been preserved. The perimeter of the corallite is polygonal. (D) Cross-section of two adjacent corallites. (E) A solitary corallite sectioned longitudinally. The calice containing the withdrawn polyp and its tentacles can be seen. The terminal margin (Tm), initial tabulae (It), and terminal tabula (Tt) are preserved. Scale bar, 100 μm . (F) Same corallite, at higher magnification, displaying two tentacular projections (T). Scale bar, 25 μm . (G–J) A colony (BSE, slice 017) with at least 10 corallites preserved. (G) Low magnification view of a second colony; note deformed structure at upper left (Ds), in which a hard external object has forced a concavity in the wall of the tabulate. Scale bar, 300 μm . (H) Higher magnification of a region of (G) illustrating the shared, trilaminar wall of two adjacent corallites. The wall consists of a central dark layer (Cdl) with a structural member on each side (Tls). The dark lumens in the corallites are regions where the tabulae had decayed, leaving cavities filled subsequently with mineral that includes organic carbon (Oc). A fracture was later filled with silica (Si). Scale bar, 50 μm . (I) Another enlarged region of the colony in (G), showing a single corallite crossed by densely packed tabulae. Scale bar, 50 μm . (J) High magnification image of boxed region in (I), viewed with DIC. The remains of three of the original tabulae can be seen as thin darker partitions. The tabulae was then overgrown with fibrous mineral that forms a subhedral structure (Shs), seen here in purple. Scale bar, 10 μm .



7



8

FIG. 7. Fossils resembling anthozoan polyps. (A) Cross-section of a putative polyp, about 200 μm in diameter. (B) Similar specimen, but with six rather than eight chambers, plus a central chamber, possibly the pharynx. (C) Polarized light image of (B): dark regions are amorphous; translucent regions are crystalline and probably represent cellular epithelia. (D) Octocoral polyp (*Alcyonium*) in cross-section (after Hickson, 1895). The central cavity is the pharynx, connected to the gastrodermal wall by septa, each equipped with a set of muscle cells. The outer ectoderm epithelium is separated from the gastrodermis by a mesogleal layer. Scale bars, (A, B) 50 μm .

FIG. 8. Interpretation of a fossilized section as an anthozoan polyp. (A) Oblique section through what could be the pharyngeal area of an anthozoan polyp; about 300 \times 180 μm . Scale bar, 50 μm . (B) Drawing of *Pachycerianthus* polyp (Nyholm, 1943). There are three major chambers on each side, and an elongate pharyngeal structure in the middle, with terminal chambers. (C) Overlay drawing of (A).

The phylogenetic affinities of *Sinocyclocyclicus* are discussed by Xiao *et al.* (2000). Most likely it is a stem-group tabulate which differs from Paleozoic tabulates in its small size and lack of external mineralization. However, Stanley and Fautin (2001) concluded that skeletonization in corals and their relatives is an “ephemeral” trait which has been lost and redeveloped many times, depending on whether environmental conditions favor calcification.

Figures 7–9 show fossils that, with respect to two-dimensional topology, resemble parts of anthozoan polyps

and stalks. The drawing in Fig. 7D shows a section across the polyp of a modern octocoral. This form has eight chambers divided by septa equipped with muscles. In the center is the pharynx. The gastrodermis lines the inner surface of the body wall, and the ectoderm is on the outside. The phosphatic fossil in Fig. 7A bears a great resemblance to this, if allowance is made for the presence of opaque mineral in the chambers of all but one of the peripheral compartments, replaced by a dark amorphous substance in the other chamber and also in what was the pharyngeal

cavity in the middle. Note the well-preserved continuity between the single cell-thick (see Fig. 7D) external lining of the pharyngeal apparatus and the septa, particularly evident in the circumference between about 4 and 9 o'clock in the specimen in Fig. 7A. In the specimen of Figs. 7B and 7C (C is shown in polarized light), the peripheral areas are much less well-preserved and the number of chambers appears to be six rather than eight. However, in this specimen, it is clear that the central structure contains a cavity (i.e., the pharynx) just as does the modern polyp in Fig. 7D. The polarized light image in Fig. 7C shows that the outer wall, the septa, and the wall surrounding the putative pharynx are all of a different constitution than the amorphous material that fills the chambers. We interpret the walls and septa as cellular structural elements, epithelia similar to those that can be seen, e.g., in Fig. 4H or Fig. 5, and the amorphous material as fill within what were the lacunae of the chambers in the living organism.

The fossil in Fig. 8A is shown adjacent to a pharyngeal cross-section (Fig. 8B) of *Pachycerianthus multiplicatus*, the same species as was figured for comparison with the gastrula-stage embryos of Fig. 4J. The tracing shown in Fig. 8C has the same topology as the section in Fig. 8B. There are three large chambers on each side, and what could be the remains of the elongate pharynx in the middle. The similarity suggests that this specimen could come from an adult from the same group as produced the embryos of Fig. 4, i.e., a cnidarian which though miniature in size bears morphological resemblance to modern ceriantharians at both embryonic and adult stages.

The fossils in Fig. 9 do not in themselves preserve sufficient morphological detail to afford a unique interpretation, except that they are radially organized, and about 200 μm across (Figs. 9A and 9B) or less (Fig. 9C). However, in light of the evidence foregoing for an anthozoan presence, it is reasonable to interpret them as stalks of some anthozoan form that bore a polyp on the top. Figure 9D shows a section of the subpharyngeal or stalk position of a modern zoantharian, for comparison. Zoantharians include anemones that have other than 8 single, complete septa; often their septa are paired, and are present in multiples of 6 (Hyman, 1940). There are 12 peripheral discontinuities in the fossil in Fig. 9A; that in Figs. 9B and 9C is not well enough preserved all around to count, but the quadrant from about 3 to 6 o'clock is consistent with the presence of 6 septa, oriented centripetally, and separated by chambers filled with dark, amorphous material.

Figures 7–9 all could be sections across a stalk or a polyp (though the plane of section in Fig. 8 is probably oblique). It is possible that the image shown in Fig. 5A is also a cross-section through a polyp. Longitudinal specimens such as the saggital tabulate examples in Fig. 6 are so far lacking, however. This would be a cause for concern, except for the small total number of examples of these forms that we have found in all the thousands of slides examined. There would of course be many more opportunities for cross-sections

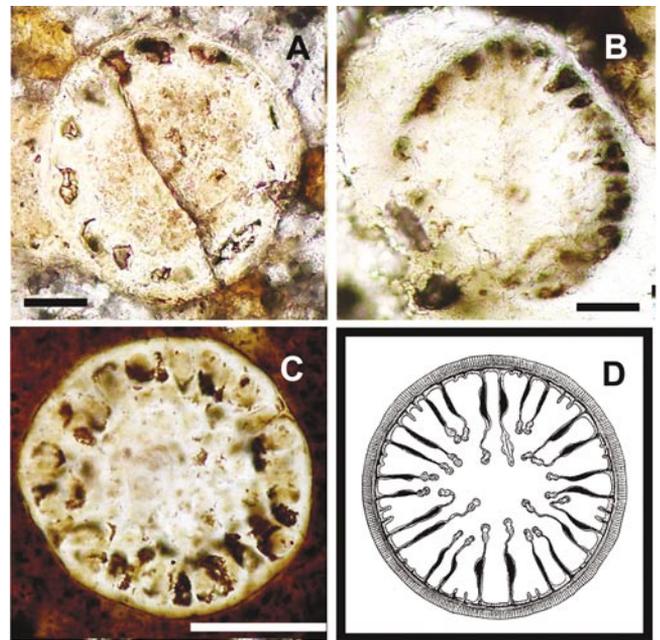


FIG. 9. Sections displaying possible fossilized anthozoan stalks. (A–C) Three separate specimens; (A, B) about 180 μm in diameter; (C) about 100 μm . Scale bars, (A–C) 50 μm . (D) Diagram of modern zoantharian stalk, sectioned at subpharyngeal level (after Hyman, 1940).

than for longitudinal sections if these animals had stalks that are long with respect to their width.

The Likely Presence of Hydrozoan Cnidarians as Well

A set of putative gastrula-stage embryos of morphology different from that of Fig. 4 is shown in Fig. 10. These are the most common of the fossilized embryonic forms that we encountered. They have a partially bilayered structure such as may arise from a unipolar ingression, but they lack the distinctive blastopore of the anthozoan-like gastrulae of Fig. 4. The center is filled with a solid amorphous mass. Figures 10J and 10L are polarized light images, which show clearly that the two peripheral layers at one end of the embryos were each a single cell thick. The crystalline orientation of the cellular layers is again parallel, and everywhere orthogonal to the plane of the epithelium surface. Figures 10Q and 10R summarize the size distribution and the ratio of inner to outer layer diameters for 73 specimens. We see that the morphometric features of this form are highly coherent: the great majority of fossils displaying this morphology are about $141 \pm 8 \mu\text{m}$ in diameter, and the ratio of inner (endoderm) to outer (ectoderm) diameters is very sharply distributed around a value of about 1.4. Such morphological consistency implies that these fossil forms are of biological origin. They could be gastrulae of hydrozoan cnidarians, some of which form by

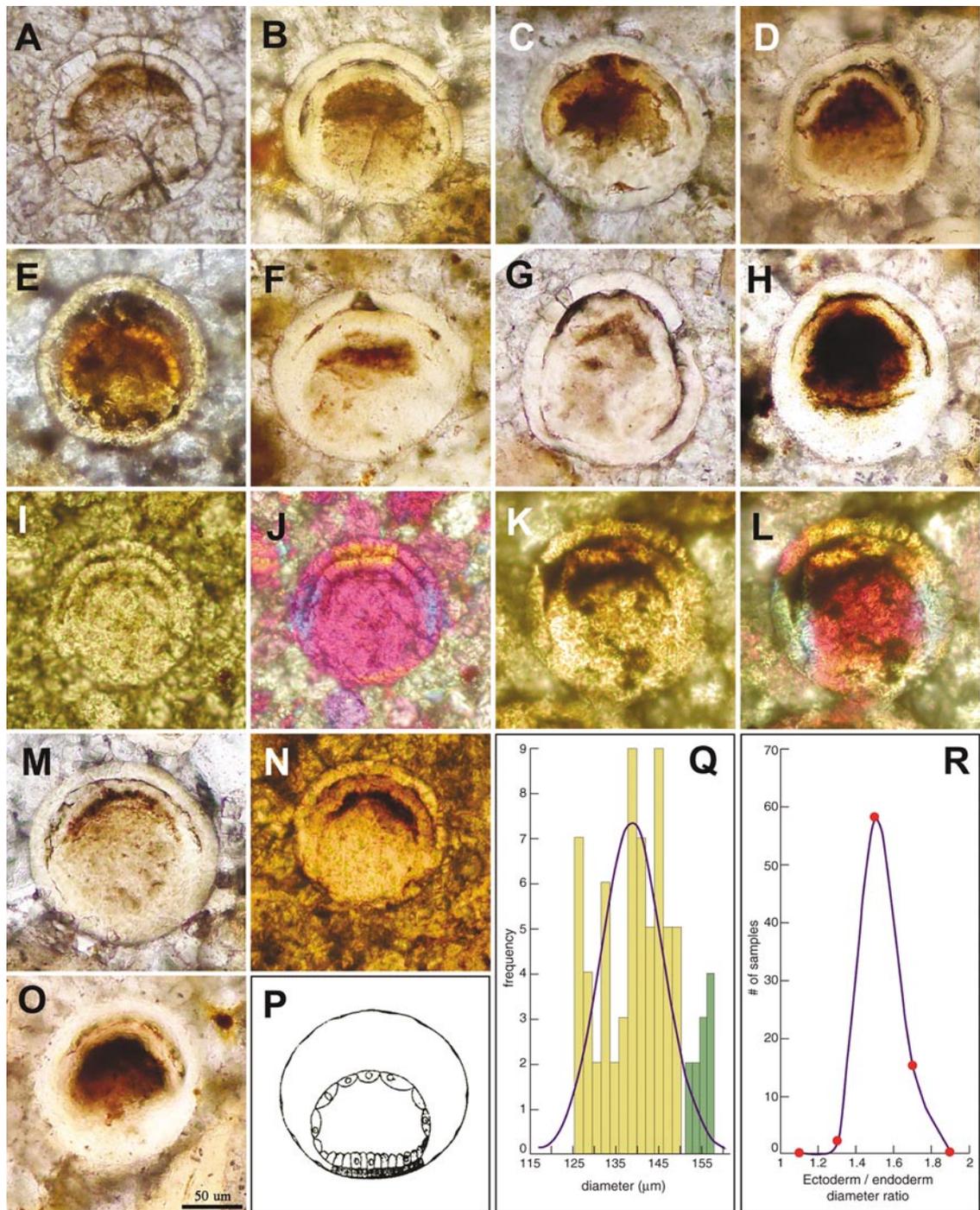


FIG. 10. Putative fossilized hydrozoan gastrulae. A sample of a large number of specimens is shown (A–O). The drawing in (P) illustrates a modern hydrozoan gastrula of similar morphology. (J, L) Polarized light images of (I) and (K), respectively. Note the symmetry of the crystal orientation with respect to the axes of the embryos in both polarized images. We interpret these layers as monocellular epithelia, i.e., the embryonic ectoderm and the embryonic endoderm. This is typical of cnidarian embryos: both ectoderm and endoderm are formed of cuboidal cells (Hyman, 1940). The ingression by which the endoderm is formed marks the future posterior end. (Q) Frequency distribution of outside diameter of 72 specimens of identical overall morphology. The data have been fit by least squares with a Gaussian curve in which the area under the yellow histogram was matched to the area under the curve. The mean is $141 \mu\text{m}$ and standard deviation is $\pm 7.6 \mu\text{m}$. The anterior–posterior and orthogonal diameters were averaged for each specimen. Note that the curve tends to extend on the upper side (green portion of histogram); as can be seen in several examples, such as those in (G) and (H), some of the embryos have begun to elongate in the anterior–posterior direction. (R) Demonstration of the morphometric constancy of the sample. The distribution of ratios of ectoderm to endodermal diameters in the anterior–posterior axis is plotted. This parameter is very sharply distributed: for 90% of the samples, the ratio is 1.3 ± 0.1 .

delamination from one side of the yolk-filled blastula, rather than by invagination (Hyman, 1940; Campbell, 1974). Following gastrulation, the larvae of modern hydrozoans elongates to form the ciliated planula form; perhaps their increased mobility enabled the planulae to escape the sediments in which gastrulae such as those in Fig. 10 were often buried.

The assignment of these putative embryos as hydrozoans remains tenuous. Suffice it to say that they are most likely cnidarian, given their double-layered structures, composed of inner and outer epithelial layers surrounding what could be a yolk-filled blastocoel; and their asymmetric organization, which we interpret as anterior–posterior polarity. They differ from the particular anthozoan-like forms shown in Fig. 4. But they are close to the same size as those in Fig. 4, and they could also be another anthozoan-like form, or belong to some other cnidarian group. However, there is an additional item of evidence that suggests the presence of hydrozoans in the Weng'an fauna, shown in Fig. 11. This is a remarkable fossil that resembles a modern adult hydrozoan. Unfortunately, only a single specimen has yet been recovered, and so its interpretation must remain tenuous as well.

As the bar in Fig. 11 indicates, the organism was on the scale of 1 mm or so. It had an external coat, which could be interpreted as a hydrotheca. A large structure projects from its side, which is interpreted as the remains of a reproductive polyp (gonotheca; Fig. 11). The overall branched morphology is like that of a modern hydrozoan. These have an outside chitinous covering (perisarc); within that an epidermal layer; and under that the gastrodermis. Some hint of a laminar structure like this can be seen in this specimen (near "Ps" in Fig. 11).

DISCUSSION

The Weng'an Cnidarians and the Implications of Their Presence

The combined import of the data in this paper is that there is a very strong case for the presence of cnidarian animals in the Weng'an fauna. The animals were in key ways like some forms that are still with us, 580 million years later. At least various kinds of cnidarians with affinities to modern anthozoans were likely present, and possibly hydrozoan-like cnidarians as well. Of course no one would imagine that the animals of this distant fauna could literally be assigned to modern taxa. In essential respects, though, their embryos and aspects of their adult body plans are much like those of Paleozoic and later cnidarians. But there is one characteristic that distinguishes them: even with respect to Ediacaran anthozoans (Glaessner and Wade, 1966), the Weng'an cnidarians are all of microscopic dimensions. The tabulate tubes extend to several millimeters in length, but most of their length is inanimate, consisting of formerly occupied chambers. It might be noted that the embryos we describe here, like those of Chen *et al.* (2000)

are not particularly small; they fall within the range of modern examples.

In some samples, dozens of eggs, embryos, and microscopic sponges in various stages of development can be observed on a single slide. The environment in which these organisms lived evidently supported a certain density and also variety of animal life. This must be true at least for certain niches in this environment, even if the fossilized remains we see in these particularly fortuitous sections are the result of the concentration of biological remains by sedimentary processes, such as repeated winnowing of loose sediment by storm events. So it is not satisfying to imagine that the microscopic size of these cnidarian carnivores could be explained as an adaptation to very sparse food supply. Furthermore, that idea would not explain why the spongiforms of the Doushantuo deposits are also small, as these must have subsisted instead on algae and bacteria. We can begin to envision the environment in which these early animals lived, an environment that has no counterpart in today's world. Microbial mats covered the sea floor providing a relatively firm, cohesive surface with a sharp sediment-water interface (e.g., Bottjer *et al.*, 2000). This would have provided a stable substrate to which microscopic sponges and cnidarians could have attached, or in which they could have lived partially inserted as mat stickers (Seilacher, 1999). The variety of forms indicates a variety of food sources, an environment of some complexity. In sufficient densities, these meadows of tiny sponges and cnidarians would have caused the microbial mat to assume a "fuzzy" appearance. It is interesting to consider this setting as a yet untapped trophic resource awaiting evolutionary exploitation. *Kimberella*, which as discussed above appears at least some 10–15 million years before the "Cambrian Explosion" but millions of years after the Doushantuo, was a fairly large bilaterian animal (possibly as long as 14 cm; Fedonkin and Waggoner, 1997) that likely made its living by scratching the surface of sea floor microbial mats with a radula or radula-like structure (Seilacher, 1999). "Mat scratching" behavior is generally thought to have evolved as a strategy for procuring microbial food resources. Perhaps, however, it was dense populations of microscopic sponges and cnidarians on these mats that rewarded the evolution of this behavior. As bilaterian mat scratchers increased in size, sponges and cnidarians may have found a refuge in larger size as well. Indeed, the Ediacaran sponges and cnidarians that occurred together with *Kimberella* are no longer of the microscopic Doushantuo dimensions. But why this did not happen earlier requires an explanation. The miniature size of sponges and cnidarians that in Paleozoic and later times are all present as much larger forms suggests, as a plausible explanation, that in the Doushantuo environment, conditions required a high surface to volume ratio for survival. The factor(s) responsible could be anything that is generally required by the cells of simple marine metazoans to be absorbed, i.e., oxygen, nutrients, or minerals; or even something that requires surface receptors for detoxification. Whatever the

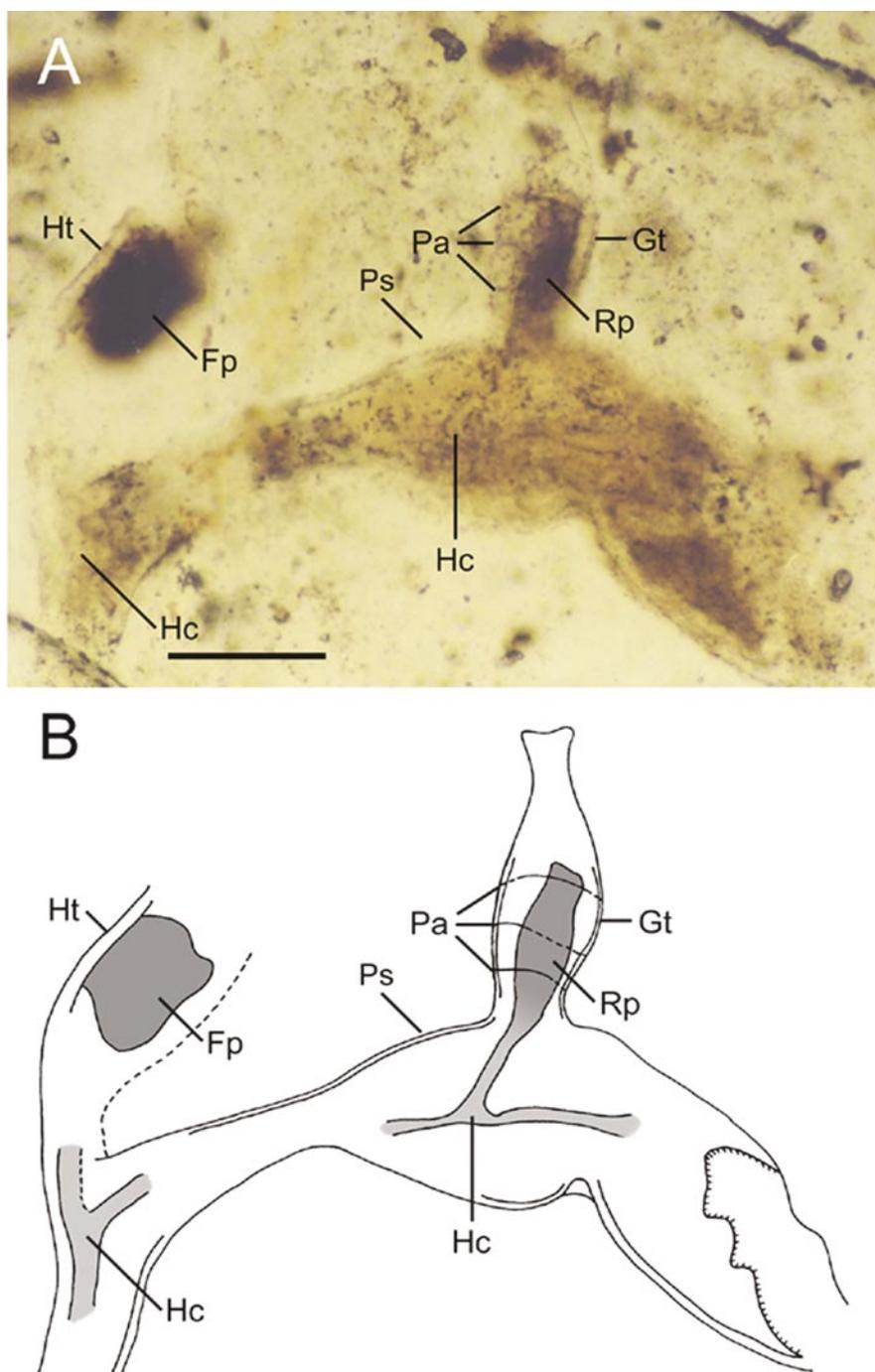


FIG. 11. A new unnamed adult hydrozoan. The fossil shown was found in a section from the Weng'an deposits and is so far unique. (A) The whole organism. Scale bar, 100 μm . (B) Interpretation. Gt, gonotheca; Pa, perisarc annuli; Ht, hydrotheca; Ps, perisarc; Rp, possible reproductive polyp; Fp, possible remains of feeding polyp; Hc, hydrocaulus.

constraints, it must have applied to stem group bilaterians as well.

For these were certainly also present. That is perhaps the most important implication of the discovery of what looks

to be a highly evolved cnidarian fauna in Doushantuo times: since the divergence of the cnidarians from the bilaterian lineage must predate the appearance of fully evolved cnidarians, the two branches were by then clearly

separate, and so bilaterian ancestors also existed. What they were, what they were like, where they lived, and how to recognize them is a major quest of evolutionary biology, the implications of which extend from Neoproterozoic paleontology to developmental biology (Erwin and Davidson, 2002).

ACKNOWLEDGMENTS

We are pleased to acknowledge helpful comments from Daphne Fautin of the University of Kansas on some of the specimens: it was she who first alerted us to the possible similarities of some fossils to octocoral stalks and polyps. We are grateful to Mark Martindale of the University of Hawaii for comments on the manuscript, and to Doug Erwin of the Smithsonian Institution for a very careful critical review of an earlier draft. We also thank Hamid Bolouri of the University of Hertfordshire for the statistical interpretation of the data and George Rossman of Caltech for the expert assistance with polarized light microscopy. This research was generously supported by the grants of NSF of China (Grants 40132010 and 990902), the Minister of Science and Technology of China (Grant 20007700), the Foundation of the National Museum of Natural Science, Taiwan, China (to J.C.), and the National Science Council, Taiwan, China (to C.L.). The research was also supported by NASA/Ames Grants NAG2-1368 and NAG2-1541.

REFERENCES

- Adoutte, A., Balavoine, G., Lartillot, N., Lespinet, O., Prud'homme, B., and de Rosa, R. (2000). The new animal phylogeny: Reliability and implications. *Proc. Natl. Acad. Sci. USA* **97**, 4453–4456.
- Bengtson, S., and Yue, Z. (1997). Fossilized Metazoan embryos from the earliest Cambrian. *Science* **277**, 1645–1648.
- Bottjer, D. J., Hagadorn, J. W., and Dornbos, S. Q. (2000). The Cambrian substrate revolution. *GSA Today* **10**, 1–7.
- Brasier, M., Green, O., and Shields, G. (1997). Ediacarian sponge spicule clusters from southwestern Mongolia and the origins of the Cambrian fauna. *Geology* **25**, 303–306.
- Briggs, D. E. G., Erwin, D. H., and Collier, F. J. (1994). "The Fossils of the Burgess Shale." Smithsonian Institution Press, Washington DC.
- Campbell, R. D. (1974). Cnidaria. In "Reproduction of Marine Invertebrates" (A. C. Giese and J. S. Pearse, Eds.), Vol. 1, pp. 133–199. Academic Press, New York.
- Carroll, S. B., Grenier, J. K., and Weatherbee, S. D. (2001). "From DNA to Diversity." Blackwell Science, Inc., Malden, MA.
- Chen, J.-Y., and Zhou, G.-Q. (1997). Biology of the Chengjiang fauna. *Bull. Nat. Mus. Nat. Hist. (Taichung, Taiwan, China)* **10**, 11–105.
- Chen, J.-Y., Oliveri, P., Li, C.-W., Zhou, G.-Q., Gao, F., Hagadorn, J. W., Peterson, K. J., and Davidson, E. H. (2000). Precambrian animal diversity: Putative phosphatized embryos from the Doushantuo Formation of China. *Proc. Natl. Acad. Sci. USA* **97**, 4457–4462.
- Chevalier, J.-P. (1987). Ordre des Scléractiniaires. In "Traité de Zoologie" (P.-P. Grassé, Ed.), Vol. 3, Fascicule 3, pp. 403–764. Masson, Paris.
- Davidson, E. H. (2001). "Genomic Regulatory Systems. Development and Evolution." Academic Press, San Diego, CA.
- de Rosa, R., Grenier, J. K., Andreeva, T., Cook, C. E., Adoutte, A., Akam, M., Carroll, S. B., and Balavoine, G. (1999). *Hox* genes in brachiopods and priapulids and protostome evolution. *Nature* **399**, 772–776.
- Erwin, D. H., and Davidson, E. H. (2002). The last common bilaterian ancestor. *Development* **129**, in press.
- Fedonkin, M. A., and Waggoner, B. M. (1997). The Late Precambrian fossil *Kimberella* is a mollusc-like bilaterian organism. *Nature* **388**, 868–872.
- Finnerty, J. R., and Martindale, M. Q. (1999). Ancient origins of axial patterning genes: *Hox* genes and *ParaHox* genes in the Cnidaria. *Evol. Dev.* **1**, 16–23.
- Glaessner, M. F., and Wade, M. (1966). The late Precambrian fossils from Ediacara, South Australia. *Palaentology* **9**, 599–628.
- Gröger, H., Callaerts, P., Gehring, W. J., and Schmid, V. (1999). Gene duplication and recruitment of a specific tropomyosin into striated muscle cells in the jellyfish *Podocoryne carnea*. *J. Exp. Zool.* **285**, 378–386.
- Hickson, S. J. (1895). Anatomy of *Alcyonium digitatum*. *Q. J. Microsc. Sci.* **37**, 343–348.
- Hill, D. (1981). Rugosa and Tabulata. In "Treatise on Invertebrate Paleontology, Part F, Coelenterata, Supplement 1" (C. Teichert, Ed.), Vol. 2, pp. xi–762. Geological Society of America and University of Kansas, Boulder, CO.
- Hoffman, P. F., Kaufman, A. J., Halverson, G. P., and Schrag, D. P. (1998). A Neoproterozoic Snowball Earth. *Science* **281**, 1342–1346.
- Hyde, W. T., Crowley, T. J., Baum, S. K., and Peltier, W. R. (2000). Neoproterozoic "snowball Earth": Simulations with a coupled climate/ice-sheet model. *Nature* **405**, 425–429.
- Hyman, L. H. (1940). "The Vertebrates: Protozoa through Ctenophora." McGraw-Hill Book Co., Inc., New York.
- Knoll, A. H. (2000). Learning to tell Neoproterozoic time. *Precambrian Res.* **100**, 3–20.
- Knoll, A. H., and Carroll, S. B. (1999). Early animal evolution: Emerging views from comparative biology and geology. *Science* **284**, 2129–2137.
- Kume, M., and Dan, K. (1968). "Invertebrate Embryology." NOLIT Publishing House, Belgrade, Yugoslavia.
- Li, C., Chen, J., and Hua, T. (1998). Precambrian sponges with cellular structures. *Science* **279**, 879–882.
- Martin, M. W., Grazhdankin, D. V., Bowring, S. A., Evans, D.A.D., Fedonkin, M. A., and Kirschvink, J. L. (2000). Age of Neoproterozoic bilaterian body and trace fossils, White Sea, Russia: Implications for metazoan evolution. *Science* **288**, 841–845.
- Medina, M., Collins, A. G., Silberman, J. D., and Sogin, M. L. (2001). Evaluating hypotheses of basal animal phylogeny using complete sequences of large and small subunit rRNA. *Proc. Natl. Acad. Sci. USA* **98**, 9707–9712.
- Müller, P., Yanze, N., Schmid, V., and Spring, J. (1999). The homeobox gene *Otx* of the jellyfish *Podocoryne carnea*: Role of a head gene in striated muscle and evolution. *Dev. Biol.* **216**, 582–594.
- Nyholm, K. G. (1943). Zur Entwicklung und Entwicklungsbiologie der Ceriantharien und Aktinien. *Zool. Bidrag.* **22**, 87–248.
- Oliver, W. A., and Coates, A. G. (1987). Phylum Cnidaria. In "Fossil Invertebrates" (R. S. Boardman, A. H. Cheetham, and A. J. Rowell, Eds.), pp. 140–193. Blackwell Science, Cambridge, MA.
- Peterson, K. J., and Davidson, E. H. (2000). Regulatory evolution and the origin of the bilaterians. *Proc. Natl. Acad. Sci. USA* **97**, 4430–4433.

- Peterson, K. J., and Ernisse, D. J. (2001). Animal phylogeny and the ancestry of bilaterians: Inferences from morphology and 18S rDNA gene sequences. *Evol. Dev.* **3**, 170–205.
- Schuchert, P., Reber-Müller, S., and Schmid, V. (1993). Life stage-specific expression of a myosin heavy chain in the hydrozoan *Podocoryne carnea*. *Differentiation* **54**, 11–18.
- Seilacher, A. (1999). Biomat-related lifestyles in the Precambrian. *Palaios* **14**, 86–93.
- Shimotori, T., and Goto, T. (2001). Developmental fates of the first four blastomeres of the chaetognath *Paraspadella gotoi*: Relationship to protostomes. *Dev. Growth Differ.* **43**, 371–382.
- Siveter, D. J., Williams, M., and Waloßek, D. (2001). A phosphatocopid crustacean with appendages from the Lower Cambrian. *Science* **293**, 479–481.
- Smith, K. M., Gee, L., Blitz, I. L., and Bode, H. R. (1999). CnOtx, a member of the *Otx* gene family, has a role in cell movement in hydra. *Dev. Biol.* **212**, 392–404.
- Spring, J., Yanze, N., Middel, A. M., Stierwald, M., Gröger, H., and Schmid, V. (2000). The mesoderm specification factor Twist in the life cycle of jellyfish. *Dev. Biol.* **228**, 363–375.
- Stanley, G. D., Jr., and Fautin, D. G. (2001). The origins of modern corals. *Science Magazine* **291**, 1913–1918.
- Xiao, S., Zhang, Y., and Knoll, A. H. (1998). Algae and embryos in a Neoproterozoic phosphorite. *Nature* **391**, 553–558.
- Xiao, S., Yuan, X., and Knoll, A. H. (2000). Eumetazoan fossils in terminal Proterozoic phosphorites? *Proc. Natl. Acad. Sci. USA* **97**, 13684–13689.
- Xue, Y.-s., Tang, T.-f., Tian, F., and Yu, C.-l. (1992). Discovery of the oldest skeletal fossils from upper Sinian Doushantuo formation in Weng'an, Guizhou, and its significance. *Acta Palaeontologica Sinica* **31**, 530–539.
- Yanze, N., Spring, J., Schmidli, C., and Schmid, V. (2001). Conservation of Hox/ParaHox-related genes in the early development of a cnidarian. *Dev. Biol.* **236**, 89–98.
- Yuan, X., and Hofmann, H. J. (1998). New microfossils from Neoproterozoic (Sinian) Doushantuo Formation, Weng'an, Guizhou Province, Southwestern China. *Acheringa* **22**, 189–222.
- Zhang, Y., Yin, L., Xiao, S., and Knoll, A. H. (1998). Permineralized fossils from the terminal Proterozoic Doushantuo Formation, South China. *Paleontological Soc. Memoir* **50**, 1–52.

Received for publication February 13, 2002

Revised April 29, 2002

Accepted April 29, 2002

Published online June 14, 2002