

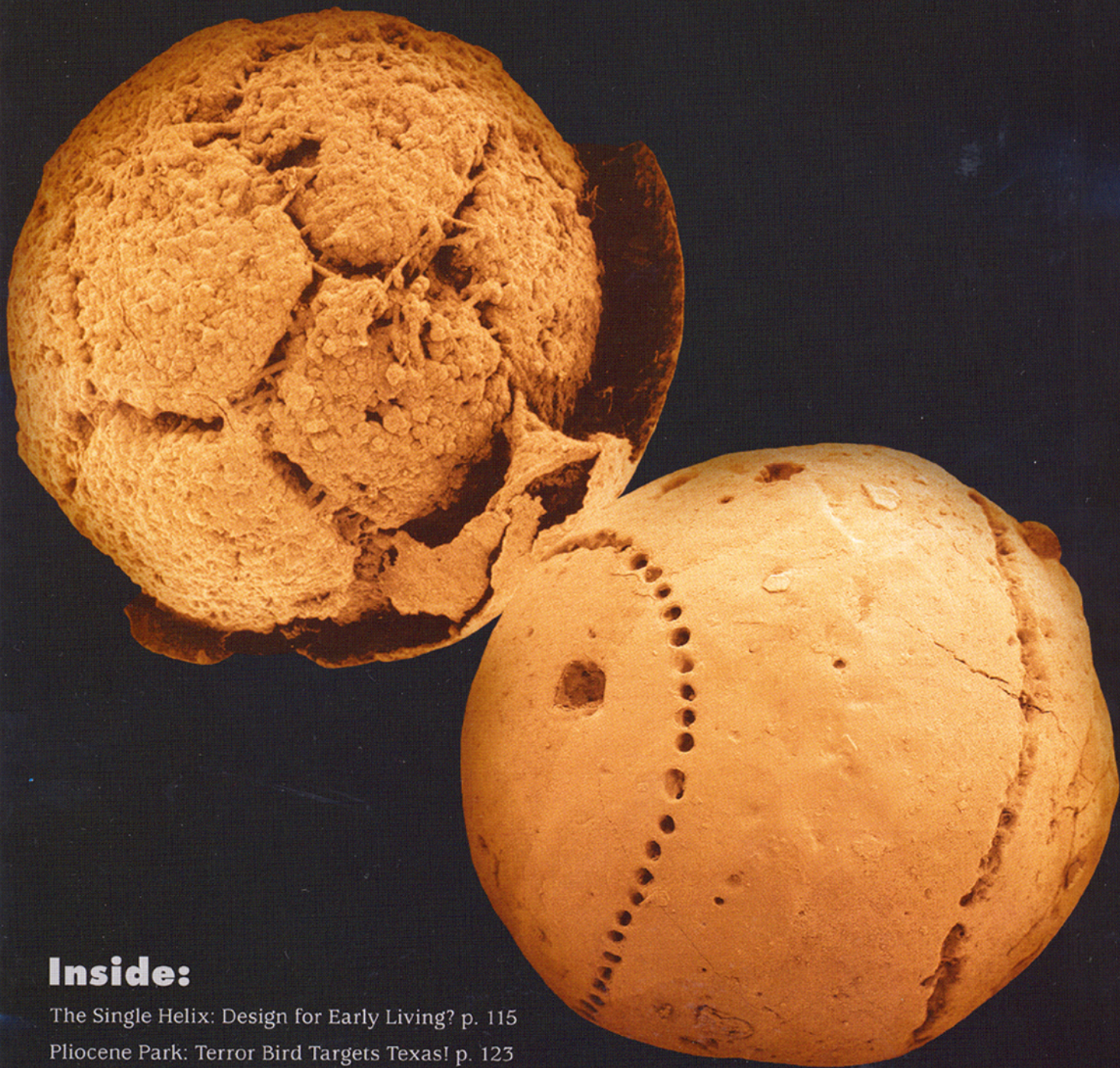


THE
GEOLOGICAL
SOCIETY
OF AMERICA

GEOLOGY

ISSN 0091-7613

FEBRUARY 2007 ■ VOL. 35 NO. 2 ■ P. 97-192



Inside:

The Single Helix: Design for Early Living? p. 115

Pliocene Park: Terror Bird Targets Texas! p. 123

Elemental Sedimentology: Earth, Fire, Air, and Water, p. 151

Where Lightning Strikes Twice in Libya, p. 171

Rare helical spheroidal fossils from the Doushantuo Lagerstätte: Ediacaran animal embryos come of age?

Shuhai Xiao Department of Geosciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061, USA
James W. Hagadorn Department of Geology, Amherst College, Amherst, Massachusetts 01002, USA
Chuanming Zhou } State Key Laboratory of Paleobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology,
Xunlai Yuan } Chinese Academy of Sciences, Nanjing 210008, China

ABSTRACT

A small quantity of helically coiled spheroidal fossils has been recovered from acid digestion of phosphorite samples from the Ediacaran Doushantuo Formation, South China. These fossils consist of an internal body enclosed in a sculptured envelope that is very similar to that of Doushantuo animal eggs and blastula embryos such as *Megasphaera ornata*. A hallmark of these fossils is a three-dimensional spiral structure, which always consists of three clockwise coils, and occurs on both the envelope and the internal body. The spiral structure consists of a spiral tunnel or canal flanked by two raised levees, and it is punctured by a series of holes. Some specimens show evidence of uncoiling, invagination along the spiral structure, or bipectinate furrowing on the band between canals. A possible ontogenetic link between these helical spheroidal fossils and *Megasphaera ornata* is suggested by similar size, similar envelope sculptures, and co-occurrence. We tentatively interpret these fossils as postblastula embryos related to *Megasphaera ornata*. Thus, they may represent the most advanced embryonic fossils so far known from the Ediacaran, although their adult morphologies and phylogenetic affinity remain unknown.

Keywords: Ediacaran, Doushantuo Formation, South China, animal embryos, computed tomography.

INTRODUCTION

Phosphatized animal embryos from Ediacaran and Paleozoic rocks provide direct paleontological evidence to test hypotheses about the evolutionary developmental biology of early metazoans. This phosphatization window, however, may introduce temporal, taxonomic, and ontogenetic biases (Donoghue et al., 2006). Ontogenetic stages of early embryos may not be equally represented in Ediacaran to Cambrian phosphorites. For example, cellularly preserved blastulas dominate Ediacaran Doushantuo phosphorites (Xiao et al., 1998) but are comparatively rare in Cambrian Orsten-type deposits (Donoghue et al., 2006), where postblastula embryos, early hatchlings, and cuticular larvae of arthropods are common (Zhang and Pratt, 1994; Bengtson and Yue, 1997; Waloszek, 2003; Dong et al., 2004; Steiner et al., 2004a, 2004b). This ontogenetic incompleteness means that reconstruction of early animal development is necessarily carried out by inferring linkage among unequally preserved stages. In this paper, a rare group of helical spheroidal fossils is reported from the Ediacaran Doushantuo Formation at Weng'an in South China. These fossils are tentatively interpreted as later-stage embryos that may be developmentally linked to Doushantuo blastulas. It is uncertain whether these helical spheroidal fossils are also ontogenetically linked to Doushantuo tubular fossils, which have been interpreted as adult cnidarians (Xue et al., 1992; Xiao et al., 2000; Chen et al.,

2002), but if this possibility holds up to further testing, the new fossils may bridge the developmental gap between two previously described Doushantuo forms.

DESCRIPTION OF HELICAL SPHEROIDAL FOSSILS

Samples were collected from the gray facies (Dornbos et al., 2006) of the upper Doushantuo Formation at Weng'an, Guizhou Province. The age of the samples is 632–551 Ma (Condon et al., 2005) or ca. 600 Ma (Barfod et al., 2002). Approximately 10 kg of dolomitic phosphorite was processed, and 80 specimens of helical spheroidal fossils were recovered using standard acetic acid digestion methods (see Methods section in GSA Data Repository¹). Fifteen specimens were scanned using microfocus X-ray computed tomography (microCT) to assess their compositional variations and internal structure (see Methods in Data Repository; Hagadorn and Nealson, 2001; Hagadorn et al., 2006), and selected animations of X-ray attenuation data are available in Data Repository Figures DR1–DR10 (see footnote 1).

The helical spheroidal fossils (Figs. 1B–1S and 2) are preserved three dimensionally, and

a few show evidence of deflation and flexible deformation (Figs. 2E–2G). Their diameter (493–955 μm ; mean = 722 μm , standard deviation [s.d.] = 89 μm , $n = 80$) is comparable to that of *Megasphaera* (640–844 μm ; mean = 757 μm , s.d. = 69 μm , $n = 16$; Xiao and Knoll, 2000; see Methods in the Data Repository [footnote 1] for discussion on nomenclature of the genus *Megasphaera*). They consist of an internal body enclosed in an ornamented envelope. Unlike *Megasphaera*, however, the helical fossils are distinctively characterized by a spiral structure that occurs on both the internal body and envelope. Several specimens (Figs. 1B–1D) bear a very subtle spiral structure on a sculptured envelope that is otherwise very similar to that of *Megasphaera ornata* (Fig. 1A). Xiao and Knoll (2000) identified five different sculptures on *M. ornata* envelopes: well-seamed polygons, tubercles, dimpled tubercles, anastomosing (or cerebral) ridges, and fractal branches. Interestingly, the helical spheroidal fossils tend to have cerebral (Figs. 1B–1D), fractal (Figs. 1G, 2A–2B, and 2H), and dimpled tubercular (Figs. 1E–1F, 1H–1I, and 2D) ornamentations. This observation strengthens previous suppositions that *M. ornata* may represent multiple biological species (Xiao and Knoll, 2000).

Without exception, the spiral structure on the envelope consists of three clockwise coils. The initiation and termination of the spiral structure define two poles, thus transforming a radially symmetrical spheroid into a bipolarized spheroid. The polar coils are only slightly tighter than the equatorial coil; they are not as tightly coiled as gastropod protoconchs. Typically, the spiral structure on the envelope consists of a subsurface tunnel (Figs. 1D and 2J₁) and/or an exposed canal (Figs. 1E₁ and 2A₁), along with a series of open holes (20–40 μm wide and ~40 μm deep; Figs. 1G₁ and 2J₄). It may be flanked by two 20–30- μm -wide levees (Figs. 1E–1I). The holes may be connected with the tunnel (Fig. 2J₄; Fig. DR2) or isolated (Fig. 2K), as illustrated in thin section as well as in X-ray attenuation cross sections. The aperture of the holes is sometimes surrounded by a raised collar that consists of several platelets (Fig. 1H₂), which may or may not be biological in origin. The canal (Figs. 1E₁, 2A–2B, and 2D) may simply be a tunnel exposed by abrasion, although no evidence of abrasion is apparent in some canal-bearing specimens (Fig. 2D₁). The

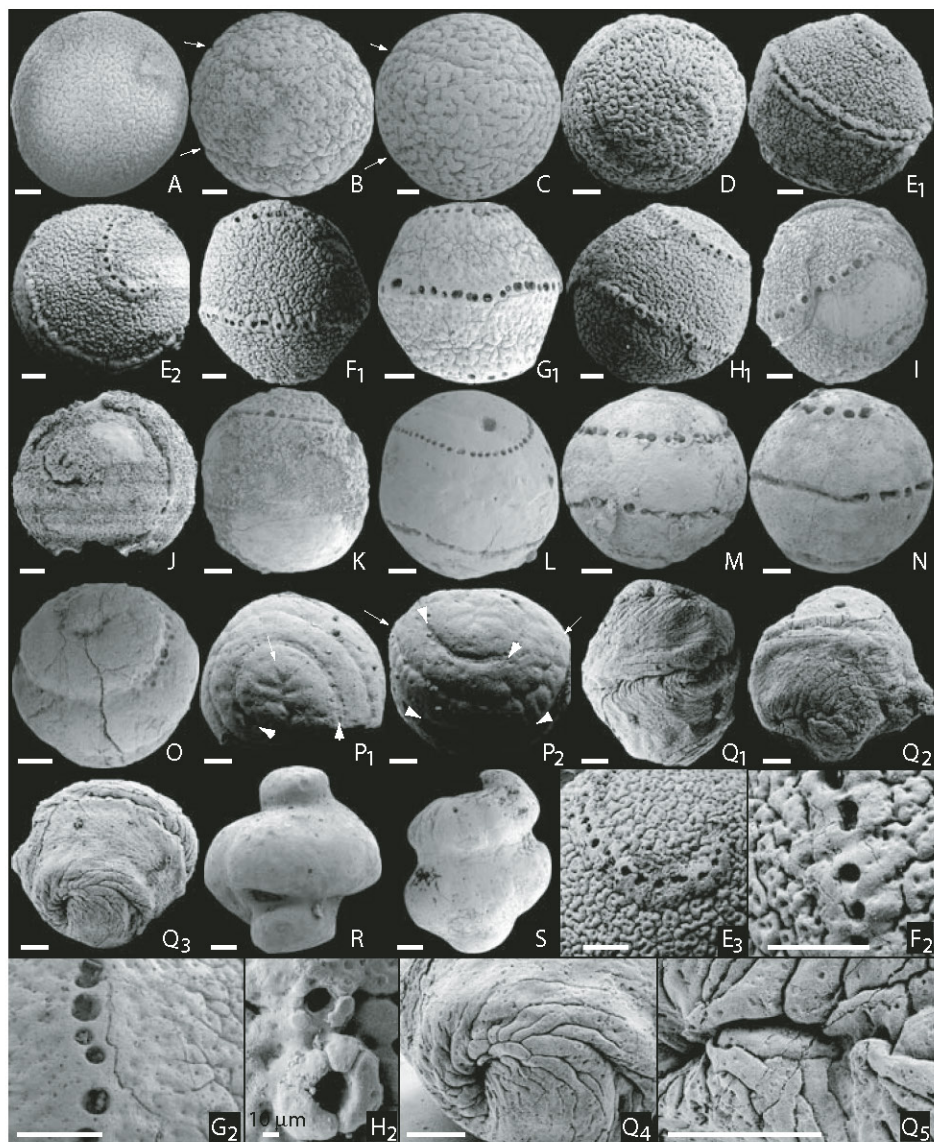


Figure 1. Scanning electron micrograph (SEM) images of *Megasphaera ornata* (A) and helical spheroidal fossils (B–S). A: Cerebral sculpture on *Megasphaera ornata*. B–D: Helical spheroidal fossils with cerebral sculpture and subtle spiral structures (arrows) on envelopes, expressed as shallow grooves (B–C, equatorial views) or a slightly raised ridge (D, polar view). E–I: Helical spheroidal fossils with more pronounced spiral structures on envelopes ornamented with dimpled tubercular (E, F, H, I, equatorial view; E₂ polar view) and fractal sculptures (G, I). E₃, F₂, G₂, and H₂ are close-ups of E₂, F₁, G₁, and H₁, respectively, and show subsurface tunnels with holes and flanking levees (E₃, F₂), subdued sculpture on and adjacent to spiral structure (G₂), and raised collar surrounding a hole (H₂). Note exposed canal along equatorial coil in E₁. J–K: Partially exposed internal bodies, showing spiral structure on internal body just beneath spiral structure on envelope. L–S: Naked internal bodies showing holes and tunnels (L–N), canals (N–P), bipectinate furrow (arrows in P, polar view and P₂ equatorial view; arrowheads pointing to spiral canal), polar invagination (Q, equatorial view, Q₂–S polar views), and partial uncoiling (R–S). Note lack of prominent levees. Scale bars are 100 μm unless otherwise noted.

spiral structure is not ornamented, and adjacent areas have only subdued sculptures; this is particularly apparent in fractal or dendritic envelopes (Figs. 1G and 2A–2B).

The internal body lacks *Megasphaera ornata*-type sculpture, but it has a spiral structure. The spiral structure on the internal body lies immediately beneath the spiral structure on the enve-

lope; this relationship is visible in several specimens where the envelope is partially removed (Figs. 1J–1K). A number of specimens do not preserve an ornamented envelope at all. These are interpreted as naked internal bodies (Figs. 1L–1S and 2C), which also have a spiral structure consisting of three clockwise coils. The canals, tunnels, or holes on the internal bodies

are approximately the same size as those on the envelope, but they are not flanked by raised levees. The spiral structure does not appear to be connected to any recognizable internal structures, as confirmed by microCT (Figs. DR1–DR9) and thin-section observations. One naked specimen shows evidence of invagination along the spiral structure (Fig. 1Q); the deformation pattern suggests that the surface was pulled inward along the spiral structure. This is particularly apparent near the two poles, where one or two invagination centers are apparent (Figs. 1Q₄ and 1Q₅). Another naked specimen appears to have a bipectinate furrow system along the band between the canals (Figs. 1P and 2F). The furrow system consists of a central axis with alternate side branches. Finally, some naked specimens show signs of slight uncoiling (Figs. 1R and 1S), where the polar coils loosen to become tapering or blunt ends. Thus, the internal body—characterized by spiral structure, bipectinate furrow system, and uncoiling—is morphologically distinct from Doushantuo blastomeres (Xiao and Knoll, 2000).

TAPHONOMY

Previous taphonomic analysis of the Doushantuo embryo fossils concluded that they were phosphatized during early diagenesis, then resuspended and transported intrabasally, and subsequently cemented by dolomite (Xiao and Knoll, 1999; Dornbos et al., 2006). The observation that some holes on the envelope of the helical spheroidal are filled with dolomite cement (Fig. 2H; Fig. DR10 [see footnote 1]) indicates that the spiral structure predates dolomite cementation. Moreover, the spiral structure on the internal body and envelope is often mantled with extremely thin phosphatic laminae (Figs. 2J₃ and 2J₄), which are interpreted as early diagenetic encrustation on organic substrates (Xiao and Knoll, 1999). This observation suggests that the spiral structure predates the phosphatization event. Taphonomic analysis, together with the consistent morphology of three clockwise coils, suggests that the spiral structure is a biological rather than taphonomic structure.

Despite the excellent preservation of external ornamentation and spiral structure, no internal biological structures are recognizable; most observable internal structures are taphonomic or diagenetic in origin, including multiple generations of phosphatic cements. In addition to the thin phosphatic laminae mentioned already, there are sometimes larger patches of homogeneous collophane that may represent phosphatized organic aggregates within the internal body (Figs. 2A₂ and 2B₂). Relatively late taphonomic features include (1) inward-growing isopachous cements that subtend thin phosphatic laminae; (2) pyrite trails that cut collophane patches and are usually terminated by a euhedral pyrite crystal (Figs.

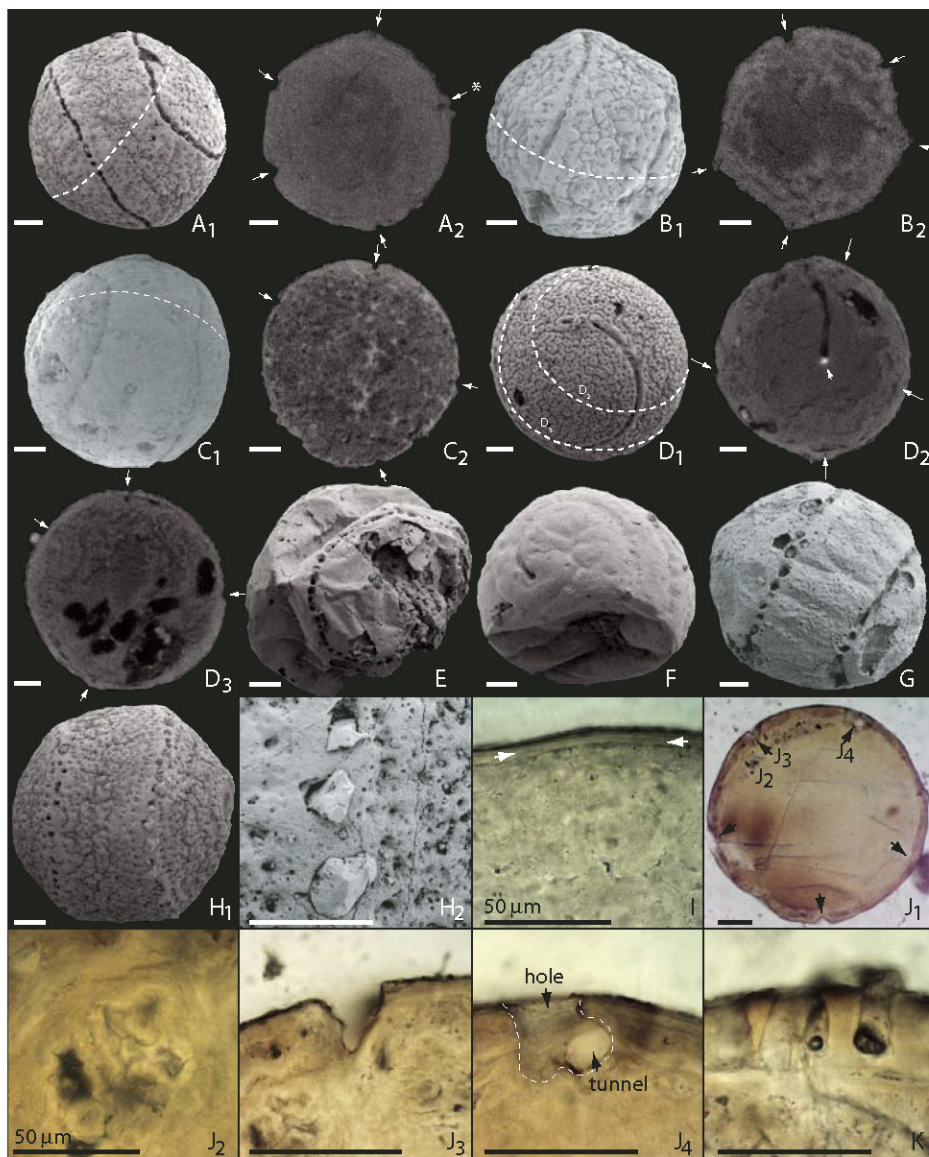


Figure 2. A–D: Scanning electron micrograph (SEM) images (A₁, B₁, C₁, D₁) and corresponding X-ray attenuation cross sections (A₂, B₂, C₂, D₂) of enveloped (A, B, D) and naked (C) specimens. Arrows point to spiral tunnels or canals in sections. Dashed lines denote approximate location of X-ray attenuation cross sections, in which lighter grayscale values represent greater atomic number and/or denser packing. Note large patches of homogeneous colophane located near center of internal bodies (A₂, B₂, D₂), botryoidal cements growing on homogeneous patches (B₂), small spheroidal to ovoidal clots of botryoidal cements (C₂), and pyrite trails (dark areas in D₂, D₃) with a terminal pyrite crystal (arrowhead in D₂). See Figures DR1–DR9 (see text footnote 1) for microCT fly-through animations of these four specimens. Asterisk in A₂ denotes area shown in animation Figure DR2. E–G: SEM of deflated and deformed specimens. F is also illustrated in Figure 1P. H: Spiral structure with a series of holes filled with dolomite. H₂ is magnified view of H₁. I–K: Plane-polarized light photomicrographs of embedded specimens, showing thin phosphatic laminae (arrows in I), clots of botryoidal cements (I), vugs filled with botryoidal cements (J₂), canal (J₃), tunnel connected with a hole (J₄), and a series of isolated holes (K). I is a longitudinal section of Figure 1L, J₁ (arrows pointing to canal or tunnel) is a longitudinal section of Figure 1N, and K is an equatorial section of Figure 1G. Scale bars are 100 μ m unless otherwise noted.

2D₂ and 2D₃; Fig. DR11 [see footnote 1]); and (3) clots of botryoidal or isopachous cements that nucleate on degraded organic matter (Figs. 2C₂, 2I, and 2J₂) or grow on colophane patches (Fig. 2B₂). Thin-section and microCT observations reveal that these clots have irregular spheroidal

to ellipsoidal morphologies, are associated with abundant interclot vugs, and are unlikely to represent biological structures.

The preservation of the helical spheroidal fossils is similar to *Sinocyclocyclicus guizhouensis* from the same deposits, which is a tubular fossil

with perforated cross walls that has been interpreted as a stem group cnidarian (Xiao et al., 2000). Both lack cellular preservation, in striking contrast to the cellularly preserved blastulas of *Megasphaera*. It is possible that the cells in the helical spheroidal fossils are too small to be preserved in recognizable forms; if so, their cells must be smaller than the smallest preserved cells (2–4 μ m; e.g., *Wengania exquisita*) in Doushantuo phosphorites (Xiao et al., 2004). In any case, the lack of cellular preservation is reminiscent of Cambrian Orsten-style phosphatization, in which relatively late ontogenetic stages are preserved by phosphatic coating on more recalcitrant substrates rather than on cell membranes (Butterfield, 2003).

INTERPRETATION AND DISCUSSION

The similar sculptures on the envelopes of the helical spheroidal fossils and *Megasphaera ornata* are striking. This, together with their similar size, stratigraphic co-occurrence, and the transitional forms with faintly developed spiral structures (Figs. 1B–1D), tantalizingly suggests a possible developmental linkage between these two groups of fossils. We propose that the helical spheroidal fossils represent postblastula embryos enclosed within spirally grooved, *M. ornata*-like envelopes. An ultimate test of this interpretation requires the discovery of specimens showing the reorganization of blastomeres to form the spiral internal body.

The adult morphologies of the helical spheroidal fossils are still uncertain. However, the partially uncoiled specimens consist of a loosely coiled tube that has a diameter (~150–250 μ m) comparable to that of the tubular fossil *Sinocyclocyclicus guizhouensis*. If *S. guizhouensis* is an adult form of the helical spheroidal fossils, the polar invaginations (Fig. 1Q) may represent the oral invagination and aboral attachment site that facilitates juvenile settlement; tabulae would not be expected in the helical fossils because tabula development would occur after settlement. This hypothesis implies that previous interpretations of *M. ornata* as arthropod embryos (Xiao et al., 1998; Xiao and Knoll, 2000) need to be reconsidered if *S. guizhouensis* is a stem-group cnidarian. The bipectinate structure (Fig. 1P), if it indeed reflects underlying anatomy, hints at an alternative adult morphology. It is possible that the Doushantuo embryos may be phylogenetically heterogeneous, representing several biological taxa that share similar early embryonic stages. The phylogenetic diversity is further supported by the Doushantuo embryo *Megacolonophycus* which lacks an epithelium and is interpreted as the embryonic stage of a stem-group metazoan (Hagadorn et al., 2006). Given the limited number of specimens with the invagination, uncoiling, and bipectinate structures, it is too soon to draw any definitive conclusion

about the ontogenetic destiny or destinies of the helical spheroidal fossils.

Given the rarity of these fossils, it is also worthwhile to consider a radically different hypothesis in which the spiral spheroidal fossils are interpreted as one-celled eggs, rather than postblastula embryos. This interpretation is intriguing because there are two other Doushantuo forms with spiral structures. One of them—*Spirallicellula? bulbifera?*—consists of four coiled structures arranged tetrahedrally (Xiao and Knoll, 2000). The other, *Spirallicellula bulbifera*, consists of eight coiled structures (Xue et al., 1992). Could these represent the cell division products of the helical spheroidal fossils? There are reasons to doubt this interpretation. First, it is unclear why the cells were coiled and how coiled cells might have divided. Second, the style of coiling differs significantly; the helical fossils consistently have three clockwise three-dimensional coils, whereas “cells” of *Spirallicellula bulbifera* and *Spirallicellula? bulbifera?* have less than two planispiral clockwise coils. Third, this interpretation does not provide a satisfactory explanation for the partially uncoiled fossils (Figs. 1R and 1S).

Regardless of the developmental origin and destiny of the helical fossils, it appears that the spiral structure was formed simultaneously along a developmentally predetermined zone, through inward folding and puncturing of the envelope or membrane. No partially formed spiral structures occur, suggesting that the spiral structure did not slowly grow from one pole to the other, from the poles to the equator, or from the equator to the poles. The function of the spiral structure remains highly speculative. It is possible that the spiral structure on the internal body might facilitate uncoiling, and the spiral structure on the envelope may demarcate a zone of splitting to assist hatching of the embryo. Alternatively, holes along the spiral structure may represent cilia insertion pits. This alternative functional interpretation implies that the helical spheroidal fossils represent planktonic larvae, but it does not explain why the spiral structures on the envelope and on the internal body match each other. Still other functions such as gas exchange might also be possible. Thus, the phylogenetic affinity and developmental details of the helical spheroidal fossils remain unclear, because the adult morphologies are uncertain and no modern analogs of helical embryos are known to us (Gilbert and Raunio, 1997; Young, 2002).

CONCLUDING REMARKS

The helical spheroidal fossils reported here are tentatively interpreted as postblastula-stage animal embryos, which possibly represent a step closer to postblastula development. The rarity of the helical spheroidal fossils and tabulated tubular fossils suggests that the Doushantuo phos-

phatization window may be ontogenetically biased against postblastula embryos and adults, in sharp contrast to Cambrian phosphatization windows, many of which bias against cellular preservation of blastulas. Several ecological and biological factors may have affected this preservational bias, including cell size, presence/absence of cuticle, planktonic versus benthic lifestyle, or relative importance of microbial concentration of phosphate in pore water. This taphonomic bias implies that ontogenetic reconstruction of Doushantuo animals requires analysis of a large amount of material using integrated three-dimensional and two-dimensional approaches in order to infer linkage among sporadically preserved developmental stages.

ACKNOWLEDGMENTS

This work was supported by the U.S. National Science Foundation, the National Natural Science Foundation of China, the Chinese Academy of Sciences, the Chinese Ministry of Science and Technology, the National Aeronautics and Space Administration, the Petroleum Research Fund, the National Geographic Society, and the Mellon Foundation. We thank S.R.F. McCartney, M.G. Manning, M. McFeely, and J.D. Schiffbauer for technical assistance, and P. Donoghue, N. Gostling, M. Steiner, and an anonymous reviewer for discussion and constructive comments.

REFERENCES CITED

- Barfod, G.H., Albarède, F., Knoll, A.H., Xiao, S., Télouk, P., Frei, R., and Baker, J., 2002, New Lu-Hf and Pb-Pb age constraints on the earliest animal fossils: Earth and Planetary Science Letters, v. 201, p. 203–212, doi: 10.1016/S0012-821X(02)00687-8.
- Bengtson, S., and Yue, Z., 1997, Fossilized metazoan embryos from the earliest Cambrian: Science, v. 277, p. 1645–1648, doi: 10.1126/science.277.5332.1645.
- Butterfield, N.J., 2003, Exceptional fossil preservation and the Cambrian explosion: Integrative and Comparative Biology, v. 43, p. 166–177, doi: 10.1093/icb/43.1.166.
- Chen, J., Oliveri, P., Gao, F., Dombos, S.Q., Li, C.-W., Bottjer, D.J., and Davidson, E.H., 2002, Precambrian animal life: Probable developmental and adult cnidarian forms from southwest China: Developmental Biology, v. 248, p. 182–196, doi: 10.1006/dbio.2002.0714.
- Condon, D., Zhu, M., Bowring, S., Wang, W., Yang, A., and Jin, Y., 2005, U-Pb ages from the Neoproterozoic Doushantuo Formation, China: Science, v. 308, p. 95–98, doi: 10.1126/science.1107765.
- Dong, X.-P., Donoghue, P.C.J., Cheng, H., and Liu, J.-B., 2004, Fossil embryos from the Middle and Late Cambrian period of Hunan, South China: Nature, v. 427, p. 237–240, doi: 10.1038/nature02215.
- Donoghue, P.C.J., Kouchinsky, A., Waloszek, D., Bengtson, S., Dong, X.-P., Val'kov, A.K., Cunningham, J.A., and Repetski, J.E., 2006, Fossilized embryos are widespread but the record is temporally and taxonomically biased: Evolution & Development, v. 8, p. 232–238, doi: 10.1111/j.1525-142X.2006.00093.x.
- Dombos, S.Q., Bottjer, D.J., Chen, J.Y., Gao, F., Oliveri, P., and Li, C.W., 2006, Environmental controls on the taphonomy of phosphatized animals and animal embryos from the Neo-

- proterozoic Doushantuo Formation, southwest China: Palaeos, v. 21, p. 3–14, doi: 10.2110/palo.2004.p04-37.
- Gilbert, S.F., and Raunio, A.M., 1997, Embryology: Constructing the Organism: Sunderland, MA, Sinauer Associates, 537 p.
- Hagadorn, J.W., and Neilson, K.H., 2001, X-radiographic computed axial tomography of matrix-encased Neoproterozoic fossils: Paleobios, v. 21, p. 60.
- Hagadorn, J.W., Xiao, S., Donoghue, P.C.J., Bengtson, S., Gostling, N.J., Pawlowska, M., Raff, E.C., Raff, R.A., Turner, F.R., Yin, C., Zhou, C., Yuan, X., McFeely, M.B., Stamparoni, M., and Neilson, K.H., 2006, Cellular and subcellular structure of Neoproterozoic embryos: Science, v. 314, p. 291–294.
- Steiner, M., Li, G., Qian, Y., and Zhu, M., 2004a, Lower Cambrian small shelly fossils of northern Sichuan and southern Shaanxi (China), and their biostratigraphic importance: Geobios, v. 37, p. 259–275, doi: 10.1016/j.geobios.2003.08.001.
- Steiner, M., Zhu, M., Li, G., Qian, Y., and Erdtmann, B.-D., 2004b, New Early Cambrian bilaterian embryos and larvae from China: Geology, v. 32, p. 833–836, doi: 10.1130/G20567.1.
- Waloszek, D., 2003, The “Orsten” window—A three-dimensionally preserved Upper Cambrian meiofauna and its contribution to our understanding of the evolution of Arthropoda: Paleontological Research, v. 7, p. 71–88, doi: 10.2517/prpsj.7.71.
- Xiao, S., and Knoll, A.H., 1999, Fossil preservation in the Neoproterozoic Doushantuo phosphorite Lagerstätte: South China: Lethaia, v. 32, p. 219–240.
- Xiao, S., and Knoll, A.H., 2000, Phosphatized animal embryos from the Neoproterozoic Doushantuo Formation at Weng'an: Guizhou: South China: Journal of Paleontology, v. 74, p. 767–788, doi: 10.1666/0022-3360(2000)074<0767:PAEFTN>2.0.CO;2.
- Xiao, S., Zhang, Y., and Knoll, A.H., 1998, Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite: Nature, v. 391, p. 553–558, doi: 10.1038/35318.
- Xiao, S., Yuan, X., and Knoll, A.H., 2000, Eumetazoan fossils in terminal Proterozoic phosphorites?: Proceedings of the National Academy of Sciences of the United States of America, v. 97, p. 13,684–13,689, doi: 10.1073/pnas.250491697.
- Xiao, S., Knoll, A.H., Yuan, X., and Poeschel, C.M., 2004, Phosphatized multicellular algae in the Neoproterozoic Doushantuo Formation, China, and the early evolution of florideophyte red algae: American Journal of Botany, v. 91, p. 214–227.
- Xue, Y., Tang, T., and Yu, C., 1992, Discovery of the oldest skeletal fossils from Upper Sinian Doushantuo Formation in Weng'an, Guizhou, and its significance: Acta Palaeontologica Sinica, v. 31, p. 530–539.
- Young, C.M., 2002, Atlas of Marine Invertebrate Larvae: San Diego, Academic Press, 626 p.
- Zhang, X., and Pratt, B.R., 1994, Middle Cambrian arthropod embryos with blastomeres: Science, v. 266, p. 637–639.

Manuscript received 9 August 2006

Revised manuscript received 7 September 2006

Manuscript accepted 16 September 2006

Printed in USA