

Early Cambrian animal diapause embryos revealed by X-ray tomography

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ABSTRACT

Discoveries of animal embryos have profoundly improved our understanding of the early evolution of animal development. However, the fossil record of early animal embryos is extremely sparse. Here we present some three-dimensionally (3-D) phosphatized *Archaeooides* from the basal Cambrian in southern Shaanxi Province, China. The 3-D reconstructions of a number of specimens, aided by high-resolution X-ray tomography, demonstrate that these soft-bodied fossil organisms have a thick cyst characterized by pustule-like ornaments and vesicular structures. Furthermore, a multicellular inner body undergoing palintomic cell division is enclosed by the cyst. The suite of characters, including submillimeter to millimeter scale, a palintomic pattern of cell division, and a complex cyst wall microstructure, corroborate the hypothesis that *Archaeooides* fossils represent the embryonic remains of animals. More specifically, the structure of the cyst wall bears close comparison to the resting cysts of living invertebrates, allowing us to interpret *Archaeooides* as a diapause embryonic stage adapted to the temporally and spatially heterogeneous redox conditions that extended from the Ediacaran to the early Cambrian. The global distribution of *Archaeooides* indicates that these conditions were geographically widespread. Ultimately, *Archaeooides* provides evidence of the early evolution of this metazoan life history strategy as an adaptation to adverse environmental conditions. Its widespread occurrence in both conventional and exceptional taphonomic windows provides the potential for reconstructing its embryology and, by inference, the developmental evolution of early animals and their body plans.

INTRODUCTION

The fossil record of early animals has documented an early Cambrian explosion of metazoan body plans, evidenced by the stratigraphic first occurrences of fossils of almost all animal phyla in the early Cambrian (Erwin et al., 2011). However, little is known about the embryological evolution of these body plans due to a paucity of fossil embryonic remains of animals. During the past two decades, discoveries of fossil embryos have provided insight into the embryology of early animals and, therefore, the evolution of animal development (Bengtson and Yue, 1997; Xiao et al., 1998; Dong et al., 2004; Steiner et al., 2004; Chen et al., 2006; Yin et al., 2007; Yin et al., 2016). However, fossil embryos are extremely rare, in terms of their diversity, abundance, and stratigraphic distribution (Donoghue et al., 2006). Therefore, the discovery of new fossils of animal embryos from the Neoproterozoic–Paleozoic transitional interval is of great significance.

Four Cambrian taxa of phosphatized spherical fossils, *Archaeooides*, *Olivoooides*, *Pseudoooides*, and *Markuelia*, have all been interpreted as preserving embryonic stages of development (Qian, 1977; Bengtson and Yue, 1997). Among them, *Olivoooides*, *Pseudoooides*, and *Markuelia* have been the focus of most attention (Donoghue et al., 2015), while the more widely distributed *Archaeooides* has been overlooked. Consequently, its biological affinity remains uncertain because little is known of its internal structure, even though some authors have speculated that it may be an animal egg or embryo (Qian and Bengtson, 1989; Pyle et al., 2006).

In an attempt to test previous hypotheses on the nature and biological affinity of *Archaeooides*, we used high-resolution X-ray tomography to characterize the three-dimensional (3-D) structure of a number of specimens. Our results indicate that these specimens preserve not only a complex envelope, but also an inner body with multicellular structure. This is the first report on the 3-D structure of *Archaeooides*, and our data provide strong evidence to test established

hypotheses on the affinity of this enigmatic early Cambrian organism.

MATERIALS AND METHODS

The fossils were collected from the lower Cambrian Kuanchuanpu Formation of the Hexi section in Xixiang County, Shaanxi Province, China (Fig. DR1 in the GSA Data Repository¹). Contemporaneous small shelly fossils indicate that *Archaeooides* occurred in the earliest Cambrian *Anabarites trisulcatus*–*Protohertzina anabarica* Zone dated to 537–532 Ma (Steiner et al., 2014).

The fossils were recovered from limestone using acetic acid digestion (acid concentration of 3%) and manual sorting of the ensuing insoluble residue under a binocular microscope. Selected specimens were scanned at the Micro-CT Lab at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), using a Zeiss Xradia 520 Versa. To achieve good contrast, we used a 50 kV operating voltage of the X-ray tube, with a thin filter (LE1) to avoid beam-hardening artifacts. Depending on the sizes of the specimens, two charge-coupled device (CCD)–based optical microscopes (4× and 20×) were applied. This system produces data sets with voxel dimensions ranging between 0.56 μm and 1.63 μm. For each scan, we obtained 3000 equi-angular projections over 360°. The exposure time for each projection was 5–10 s, depending on the density and diameter of specimens. The volume data were processed using VGSTUDIO MAX software (<https://www.volumegraphics.com/en/products/vgstudio-max.html>). All of the specimens are housed at NIGPAS, and the tomographic data are available from the Geobiodiversity Database (<http://www.geobiodiversity.com/>).

¹GSA Data Repository item 2018126, Figure DR1 (locality and stratigraphy of the Hexi Section in Shaanxi, China), is available online at <http://www.geosociety.org/datarepository/2018/> or on request from editing@geosociety.org.

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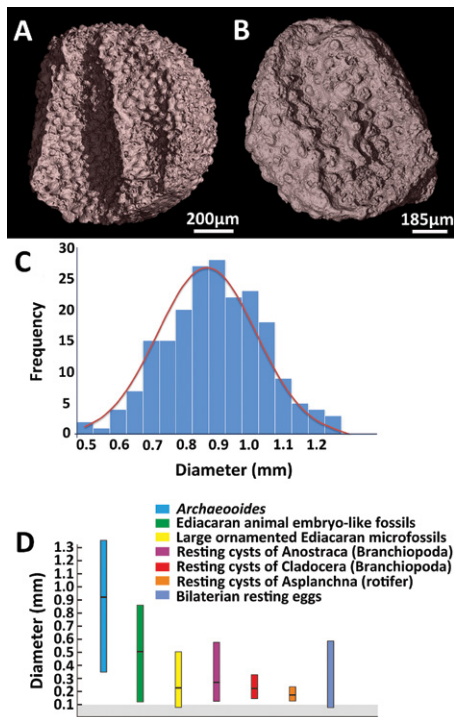


Figure 1. *Archaeooides* from lower Cambrian Kuanchuanpu Formation (China), and diameter histograms. **A, B:** Surface renderings showing ornamented envelopes. **A:** Specimen NIGPAS-CK-F02 (NIGPAS—Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences). **B:** Specimen NIGPAS-CK-F03. **C:** Diameter histogram of 206 *Archaeooides* specimens in this study. **D:** Diameter ranges of *Archaeooides*, Ediacaran embryos, spiny acritarchs, and extant bilaterian resting eggs (data are from: this study; Pyle et al., 2006; Cohen et al., 2009; Hill and Shepard, 1997; Bottrell and Newsome, 1976; Gilbert and Wurdak et al., 1978). Gray horizontal bar highlights the range of 0–100 μm .

RESULTS

Archaeooides is distinguished by subspherical to spherical morphologies and an ornamented envelope (Figs. 1–3). Within our data set, it varies in diameter from 0.487 to 1.380 mm, with a mean of 0.868 mm ($n = 206$) (Fig. 1C). Their minimum diameters could be <0.4 mm as reported by other authors (Fig. 1D; Pyle et al., 2006). The pustule-like external ornament of the envelope varies in shape, size, and density among specimens, all encompassed by the one morphotaxon, *Archaeooides granulatus* (Qian and Bengtson, 1989). In some specimens, the ornament is degraded, presumably by biostratigraphic processes (Fig. 2G). Tomographic data reveal that the pustule-like protuberances are solid, rather than hollow inside (Figs. 2 and 3). They arise from the surface of the envelope with diameters ranging from 15 to 40 μm .

The envelope is thick (~85–150 μm) and unstratified (Fig. 3). Envelope thickness varies little within specimens, though preservation is not uniform, particularly at the microstructural

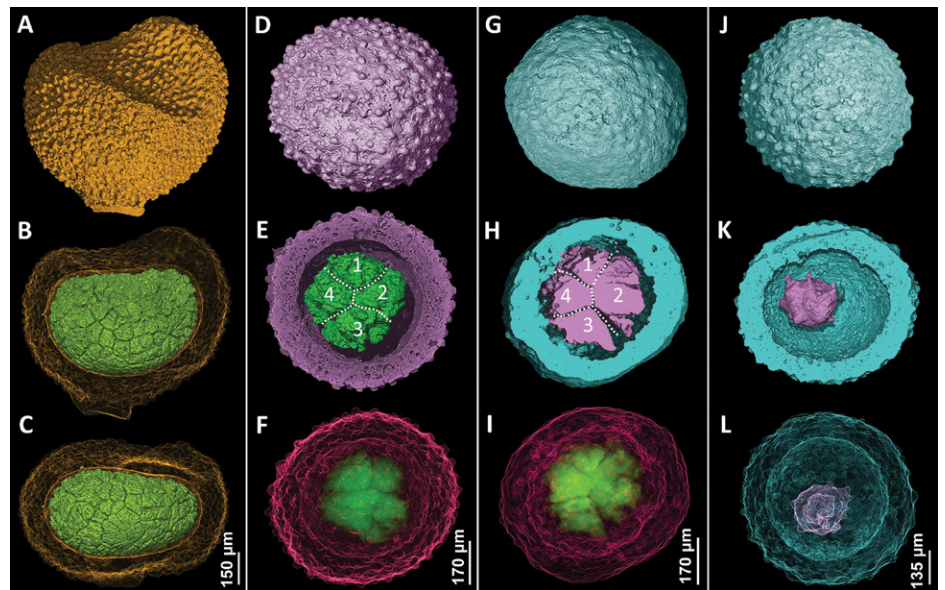


Figure 2. *Archaeooides* from lower Cambrian Kuanchuanpu Formation (China). **A–C:** Specimen NIGPAS-CK-A01 (NIGPAS—Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences). **D–F:** Specimen NIGPAS-CK-E01. **G–I:** Specimen NIGPAS-CK-E11. **J–L:** Specimen NIGPAS-CK-E04. **A, D, G, and J** are surface renderings showing ornamented envelope. **B, C, F, I, and L** are three-dimensional (3-D) renderings with transparent envelope, showing inner bodies. **E** is 3-D rendering showing four-celled inner body enclosed by thick envelope. **H** is 3-D section showing four-celled inner body. **K** is 3-D rendering showing degraded inner body.

scale. Some envelopes betray evidence of post-mortem decay and diagenetic alteration, leaving large secondary cavities with diagenetic mineral linings (Figs. 3D and 3D1). Some specimens are, however, well preserved, without void-filling mineralization, but permeated by microfractures (Figs. 3C and 3C1). Almost all of the well-preserved specimens exhibit large numbers of small vesicular structures (SVSs) that vary within and between specimens (Figs. 3A–3C, 3A1–3C1). In some specimens, the SVSs have been infilled by crystallites or materials with lower X-ray attenuation (Figs. 3B, 3B1–3B3). The envelopes of many specimens are deflated and deformed (Figs. 1A, 1B, and 2A). The plastic deformation suggest that the envelopes were originally flexible and not, therefore, biomineralized, which would have rendered them both brittle and rigid.

Our tomographic data demonstrate that a number of specimens have exceptional preservation of inner bodies enclosed by intact envelopes. The two specimens in Figures 2D–2I each have a compacted inner body that comprises four cells with approximately flat adjoining faces, and another (Figs. 2A–2C) has an inner body comprising hundreds of more clearly preserved polygonal cells.

Not all specimens exhibit exceptional preservation of inner bodies. One specimen (Figs. 2J–2L) includes a small irregular inner body within an intact envelope. Secondary cracks have transected the envelope, but do not extend to the internal space enclosed by the envelope (Figs. 2K and 3C). The virtual slices and 3-D

reconstructions illustrate that the inner body has no cell structures, and is hollow with many small, later void-filling crystals inside (Figs. 2K, 2L, and 3C), suggesting that the inner body is likely a mineralized mass of degraded cells or tissues.

DISCUSSION

Biological Affinity of *Archaeooides*

The biological affinity of *Archaeooides* has been poorly constrained largely because knowledge of its biology was limited to cyst morphology. It has been considered to represent animal eggs or embryos, but with little evidence to support these speculations (Qian and Bengtson, 1989; Pyle et al., 2006). Our high-resolution 3-D data of *Archaeooides* reveal dividing cells contained within thick porous cysts, corroborating the hypothesis that *Archaeooides* fossils represent embryonic stages of animals. This inevitably draws comparison to cleavage embryos of living animals, and to the cleavage stages of the early Cambrian cnidarian and ecdysozoan animals, viz. *Olivoides*, *Pseudoides*, and *Markuelia*, as well as to the Ediacaran animal embryo-like fossils (EAEFs) from the Weng'an Biota.

The coordinated arrangement of cell clusters results in tightly sutured cells with flat adjoining faces, giving the component cells a polyhedral shape (Fig. 2). This feature suggests that the cells were bounded together by cell adhesion proteins and formed real multicellular structures rather than a simple colony of cells. Different specimens of *Archaeooides* preserve inner bodies of approximately the same

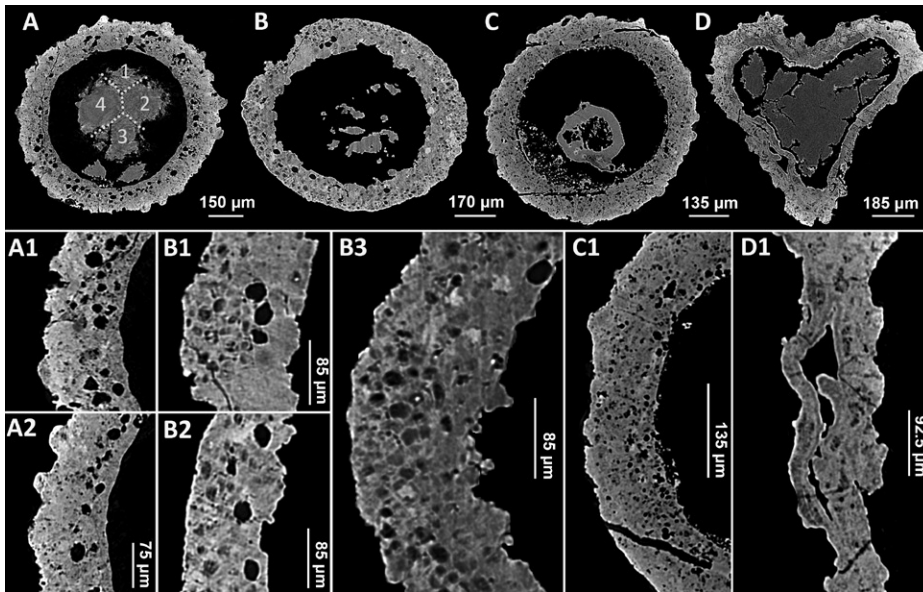


Figure 3. *Archaeooides* from lower Cambrian Kuanchuanpu Formation (China). **A:** Virtual section of specimen NIGPAS-CK-E01 (NIGPAS—Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences). **B:** Virtual section of specimen NIGPAS-CK-E11. **C:** Virtual section of specimen NIGPAS-CK-E04. **D:** Virtual section of specimen NIGPAS-CK-F03. **A1–D1** are magnifications of thick envelopes in **A–D**, respectively, showing small vesicular structures (SVSs) of envelopes.

size but comprising different numbers of cells. This presumably reflects palintomically dividing cells, which increase in number without a change in the overall volume of the cell mass, as seen in cleavage embryos of living animals. These features have been observed in cleavage embryos of the Cambrian *Olivoides*, *Pseudooides* (Bengtson and Yue, 1997; Steiner et al., 2004), and *Markuelia* (Zhang et al., 2011), as well as in EAEFs, such as *Tianzhushania*, that are enclosed by a large acanthomorphic cyst (Yin et al., 2007).

The envelope of *Archaeooides* was initially described as a thin shell (Qian, 1977; Pyle et al., 2006), however our data demonstrate that it was originally thick proportional to its radius. This is not an artifact of later diagenetic mineralization and infilling, because the cyst wall preserves biological structure throughout its thickness (Fig. 3). This is manifest as the SVSs, which we interpret as original biological structures rather than artifacts of post-mortem degradation, based on their regular shape, permineralized texture, and consistent preservation across a number of specimens. Envelopes with this character, enclosing palintomically dividing cells, are closely comparable to the enveloping cysts of resting eggs and embryos of some living aquatic invertebrates, such as branchiopods and rotifers (Fig. 4). In these organisms, the majority of the resting cysts are proportionally thick and ornamented (Alekseev et al., 2007), and characterized by a meshwork of interconnecting round chambers (Figs. 4A, 4C–4E) or scattered bullules (Fig. 4B) (Gilchrist, 1978; Wurdak et al., 1978; Maeda-Martínez et al., 1993),

exhibiting a striking similarity to the envelopes of *Archaeooides*.

In addition to cleaving inner bodies and complex thick cysts, the millimeter- and submillimeter-scale sizes of *Archaeooides* fall within the size range of living animal embryos, and overlap the size range of resting eggs of many aquatic invertebrates (Fig. 1D). Taken together, our data corroborate the hypothesis of an animal embryo interpretation of the enigmatic *Archaeooides* and suggest, further, that they represent the encysted diapause stage in the embryology of a Cambrian metazoan.

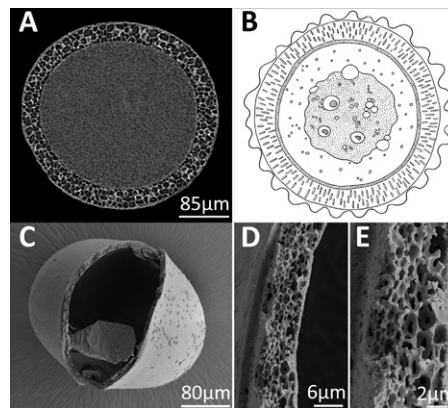


Figure 4. Cysts of extant animal resting eggs. **A:** Resting cyst of tadpole shrimp *Lepidurus* (Branchiopoda, Notostraca), showing thick porous cyst. **B:** Resting cyst of *Asplanchna sieboldii* (rotifer, 120 μm in diameter; after Wurdak et al., 1978). **C:** Resting cyst of brine shrimp *Artemia* (Anostraca, Branchiopoda). **D, E:** Close-up views of porous cyst in **C**.

Evaluation of Candidate Hypotheses

Some EAEFs enclosed by complex cysts have been interpreted as diapause embryos of early metazoans (Yin et al., 2007; Cohen et al., 2009), while competing hypotheses including sulfur bacteria (Bailey et al., 2007) and mesomycetozoean-like protists (Hultgren et al., 2011) were also proposed for them. Our new data and recent advances in the study of EAEFs suggest that the latter two hypotheses, however, are incompatible with *Archaeooides* and the EAEFs.

First, sulfur bacteria are much smaller than *Archaeooides* in diameter. As prokaryotes, they have no nuclei, and cannot produce thick cysts with complex ornaments like *Archaeooides* and the EAEFs (Xiao et al., 2007). On the contrary, *Archaeooides* and the EAEFs have been widely accepted as eukaryotes because of their large sizes, complex cysts, multicellular structures, and well-preserved nuclei within cells of many EAEFs (Yin et al., 2017).

Second, the size of extant mesomycetozoeans is much smaller than *Archaeooides* and the EAEFs (Fig. 1D), as most of them are no more than 100 μm in diameter. As unicellular eukaryotes, some mesomycetozoean protists use palintomic division to produce propagules within a cyst (Hultgren et al., 2011). However, their cysts are very thin and have no SVSs or complex ornaments. Their propagules aggregate loosely without cell adhesion, forming just a simple colony rather than real multicellular structure.

Third, the cleavage patterns of *Archaeooides* and the EAEFs show distinctive spatial relationships between cells. For example, the spatial relationships of the four cells in the two aforementioned specimens of *Archaeooides* (Figs. 2E and 2H) can be found commonly in some living arthropod and spiralian embryos at the four-cell stage (Gilbert, 2013). Furthermore, tri-lobed and J-shaped embryos with polar lobe formation (Chen et al., 2006; Yin et al., 2013), bilateral symmetrical arrangement of cells (Chen et al., 2009), and meroblastic cleavage pattern (Yin et al., 2016) have been observed in the EAEFs. All of these cleavage features cannot be found in bacteria or mesomycetozoean protists but do occur in living animal embryos. In summary, the *Archaeooides* and the EAEFs with complex cysts can be better understood as diapause embryos of early metazoans rather than bacteria or protists.

Insights into the Evolution of the Environment at the Proterozoic–Phanerozoic Transition

Diapause and resting cysts are invariably an adaptation to environmental stresses in which the organism assumes a reduced metabolism awaiting the amelioration of environmental conditions. The discovery of the early Ediacaran animal embryo-like stages preserved within large ornamented cysts (Yin et al., 2007) inspired the reinterpretation of the diverse contemporary

assemblage of large ornamented Ediacaran microfossils (LOEMs) as a resting stage in the life cycle of early metazoans (Cohen et al., 2009). The late Ediacaran disappearance of LOEMs from the stratigraphic record has been correlated with the decline of marine anoxic conditions on continental shelves and platforms, and the diapause stage has been interpreted as an adaptation to the temporal and spatial heterogeneity of shallow marine environments earlier in the Ediacaran (Cohen et al., 2009).

The interpretation of *Archaeooides* as metazoan resting cysts and their widespread paleogeographic distribution during the early Cambrian (Pyle et al., 2006) indicate that while LOEMs may have disappeared in the late Ediacaran, this life history strategy did not, and it remained as relevant an adaptation to adverse environmental conditions in the early Cambrian. This correlates with the more nuanced view of the evolution of the marine environment during the Proterozoic-Phanerozoic transition, in which the temporal and spatial heterogeneity of redox conditions extended deep into the Cambrian, notably in some of the successions in which *Archaeooides* is encountered (Bowyer et al., 2017). We anticipate that the identification of *Archaeooides* as a metazoan resting cyst will provoke the evaluation of the Cambrian acritarch record, like that of the Ediacaran, as a redox proxy.

The widespread occurrence of *Archaeooides* also anticipates that it will be possible to reconstruct more completely the embryology of this early Cambrian marine invertebrate and, thus, better constrain its phylogenetic affinity. In the interim, *Archaeooides* further evidences the early evolution of this life history strategy that would have afforded advantage to metazoans living within the challenging physical conditions associated with the gradual change from the Proterozoic to the Phanerozoic biosphere.

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