

Silicified egg clusters from a Middle Cambrian Burgess Shale-type deposit, Guizhou, south China

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ABSTRACT

Although knowledge of Cambrian fossil eggs and/or embryos has increased dramatically, embryos were previously unknown in siliciclastic settings of coeval strata. Here we report for the first time egg clusters in a fine-grained siliciclastic matrix from the Middle Cambrian Kaili Formation lagerstätte (513–501 Ma), south China. Some were imaged under synchrotron radiation. These spheroids are preferentially preserved as microcrystalline quartz and interpreted as marine invertebrate fossil eggs based on patterns of spheroid arrangement, shape, and analogues of fossil and modern invertebrate eggs. Embryos with cleavage cells are evident in at least one cluster. Detailed element analyses show that eggs are primarily preserved as solid silica replacement, and there is a calcite layer covering the eggs replacing the original organic layer. Silicification of intact invertebrate egg clusters is reported here as a new mode of preservation associated with a Burgess Shale-type deposit.

Keywords: Cambrian, Kaili Formation, fossil eggs, fossil embryos, lagerstätten, silicification, China.

INTRODUCTION

Cambrian fossil lagerstätten, which contain well-preserved fossils in several modes of preservation (Briggs and Nedin, 1997; Orr et al., 1998; Butterfield, 2003; Gabbott et al., 2004), provide invaluable information to understand better the first adaptive radiation of modern animal phyla. In particular, the fossilization of Cambrian eggs and embryos (Zhang and Pratt, 1994; Bengtson and Zhao, 1997; Steiner et al., 2004; Donoghue et al., 2006) provides a taphonomic window with which to understand the early life histories of some extinct metazoans. However, embryos were previously unknown in the silty mudstone of coeval strata. The Kaili Formation lagerstätte (Zhao et al., 2002), Guizhou Province, south China, comprises a significant Middle Cambrian Konservat lagerstätte that shares many genera and a similar ecologic structure with the Burgess Shale lagerstätte (Briggs et al.,

1994). A dozen clusters of uncompact spheroids are reported here from the middle portion of the Kaili Formation (see Lin, 2006), which is composed primarily of silty mudstone. The age of the material is well constrained by trilobite biostratigraphy (Yuan et al., 2002). In the Kaili lagerstätte, Burgess Shale-type taxa, including nonmineralizing arthropods (see Lin et al., 2006), discoidal animals, worms, and algae, are commonly preserved as organic carbon films. Phosphatization is rare and restricted to internal volatile tissues, such as gut glands (Zhu et al., 2004).

METHODS

Synchrotron X-ray microscopy (SXM) was conducted at the National Synchrotron Radiation Research Center in Taiwan. Kaili materials are silicified spheroids embedded in fine-grained sediments primarily composed of clay minerals. There is very little density contrast between spheroids (quartz) and matrix (silicates) that can be detected in other X-ray im-

aging techniques. Synchrotron hard X-rays provide high image resolution with the highest penetration ability. Specimens are trimmed to <3 mm in thickness prior to X-ray radiation. Images of entire clusters are compiled from individual images collected by charge-coupled device (CCD) directly behind the target sample. Concave depressions and hollow spheroids are relatively lighter than solid spheroids and matrix shown in the X-ray images. Energy-dispersive X-ray (EDX) analyses were conducted at the Electron Microscope Unit of Royal Holloway University of London. A qualitative elemental analysis was undertaken across a polished section. Element distributions were then recorded as area maps (25 frames) showing the overall distribution across a single or group of eggs. Brighter color equals higher concentration; black indicates absent. All studied specimens are deposited at the Guizhou University of Technology (GUT), which is now a branch campus of Guizhou University, Guiyang, Guizhou Province, south China.

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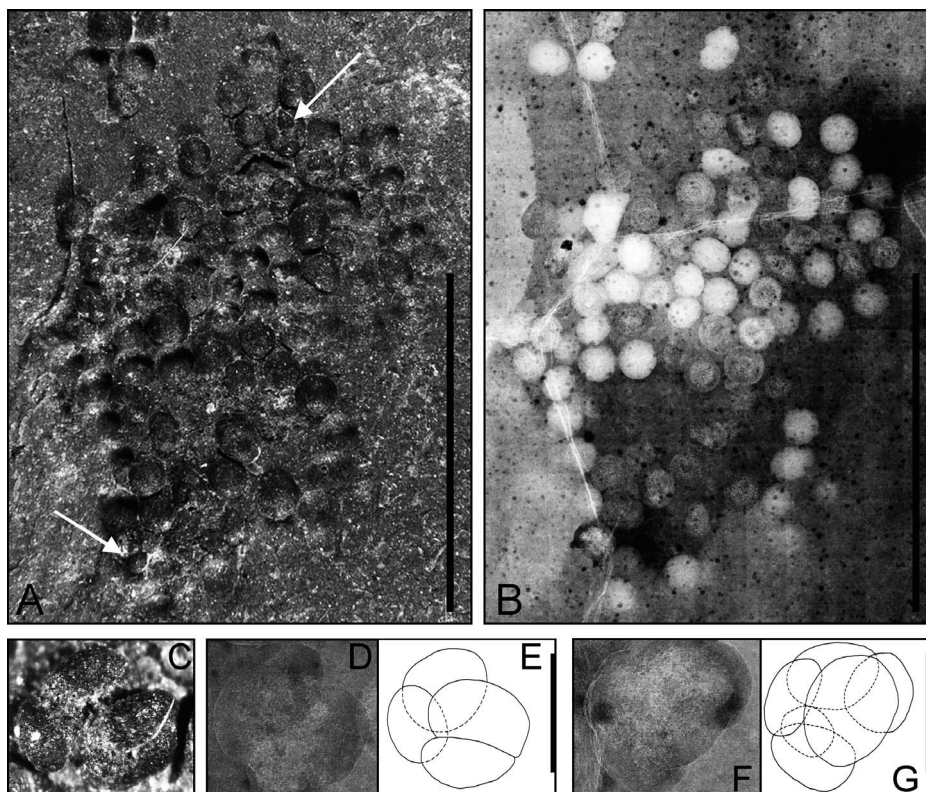


Figure 1. Spheroid cluster GUT 986 from Kaili Formation lagerstätte photographed with light microscopy (A, C) and synchrotron X-ray microscopy (B, D, F). A and B: General view of entire cluster. C–E: Blastomeres of four-cell embryo (indicated by upper arrow in A). F and G: Blastomeres of eight-cell embryo (indicated by lower arrow in A) with only six cells preserved. E, G: Interpretive sketches of embryos with cleavage cells. Relative scale bars, 1 mm (A, B); 500 μm (C–G). Images of four-cell and eight-cell embryos are enlarged in Figures DR1–DR2 (see footnote 1).

EGG CLUSTERS

The eggs are black to dark brown under natural light, externally smooth, mostly spherical, and sometimes slightly elongated. They are always present in clusters with no signs of current alignment or reworking. Some clusters contain spheroids randomly piled together (indicated by multiple layers) with an irregular boundary, whereas in other clusters the spheroids are packed together with a close-packing arrangement in a restricted depression.

Preservation conditions of Kaili eggs vary, ranging from those with a nearly spherical outline to those that are inflated and decayed with only their cases (or chorions) preserved. In the latter case, decayed egg clusters are fossilized essentially as aggregates of microgeodes, which are hollow in the center and contain miniature quartz crystals and iron-stained powders. In some cases silicification allowed the preservation of cleavage cell walls (Figs. 1C–1G). In these well-preserved eggs, silica must have been solid prior to the complete decay of organic matter, which would occur rather slowly but could not be completely eliminated (see Lin, 2006).

SXM imaging strengthens the egg hypothesis. The geometry and internal structure of

individual embryos and cleavage cells can be determined, and deeply buried spheroids can be located precisely (Fig. 1B). This permits us to determine within each cluster the number of spheroids and the spheroid size distribution. For example, cluster GUT 986 (Figs. 1A, 1B) contains 77 spheroids with a size range of 508–945 μm ($d_{\text{mean}} = 767 \mu\text{m}$, $\sigma = 76$). This size range is similar to the egg size of some modern marine invertebrates, such as those of sea urchins with direct development (Raff, 1987). Most important, several embryos with early cleavage cells are evident in the cluster, and cell boundaries can be determined (Figs. 1C–1G; see Data Repository Figs. DR1, DR2¹).

Alternative interpretations of similar-sized spheroids include diagenetically altered fecal pellets, ooids, or impact spherules (microtektites). Unlike the Kaili spheroids, microtektites

¹GSA Data Repository item 2006226, Figure DR1 (enlarged image of a four-cell embryo), Figure DR2 (enlarged image of an eight-cell embryo), and Figure DR3 (solubility diagram of silica and calcite in seawater), is available online at www.geosociety.org/pubs/ft2006.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

tites vary from highly spherical to teardrop or dumbbell shaped and consist of acicular K-feldspar crystals and randomly placed gas voids, quartz, carbonates, and/or sericite (Simonson, 2003). Sedimentary ooids are characterized by either concentric layers and/or radial fabrics nucleated around detrital grains in various sizes and compositions. Ooids are very rare in siliciclastic settings and Kaili spheroids lack any diagnostic features of them. Fecal pellets are produced by planktonic and benthic organisms and occur in concentrations that may be from a single organism or from a mixture of different taxa (Accornero and Gowing, 2003). A cluster of fecal pellets from a deposit feeder would be expected to be composed of the background sediments, in this case fine-grained siliciclastic sediment. Instead, the reported spheroids are composed of silica that is unlike either the composition of the surrounding matrix (Fig. 2) or that of other nonmineralizing taxa preserved in the same beds (Lin, 2006). Most spheroids are uncrushed, indicating that they had structural strength when deposited and/or gained rigidity during precompaction diagenesis, making them immune to compaction. This is unlikely if the pellets were the same lithology as the enclosing sediment. Kremer (2005) concluded that some acritarchs could be phosphatized and preserved in three dimensions in the size range similar to that of the Kaili spheroids. Acritarchs are also present in the Kaili Formation (Yang and Yin, 2001), but these organic-walled fossils are only preserved as organic films. Existing evidence supports the egg hypothesis rather than any alternatives.

TAPHONOMY

An attempt to understand the diagenesis of selectively silicified eggs is based on the following observations. First, modern marine invertebrate eggs are resistant to decay and retain the cell contents for some period of time (months) (Martin et al., 2005). Each Kaili egg probably contained a chorion and cell contents or embryo, based on modern analogues, that were fossilized with predominantly pure silica. Thus, most of the eggs had not ruptured allowing sediment to ingress, while hydrated silica must have diffused into the eggs (see Westall et al., 1995). Calcium carbonate precipitation occurred in the position of the chorion and, in rarer cases, inside the egg, perhaps because some inner cell contents also decayed (calcium and carbon maps in Figs. 2A, 2B). The calcite coatings are interpreted as having occurred either prior to decay or during the decay of the cell contents. Unlike previously reported Cambrian embryos (see Donoghue et al., 2006), which are commonly preserved with phosphate encrustation, it is noteworthy

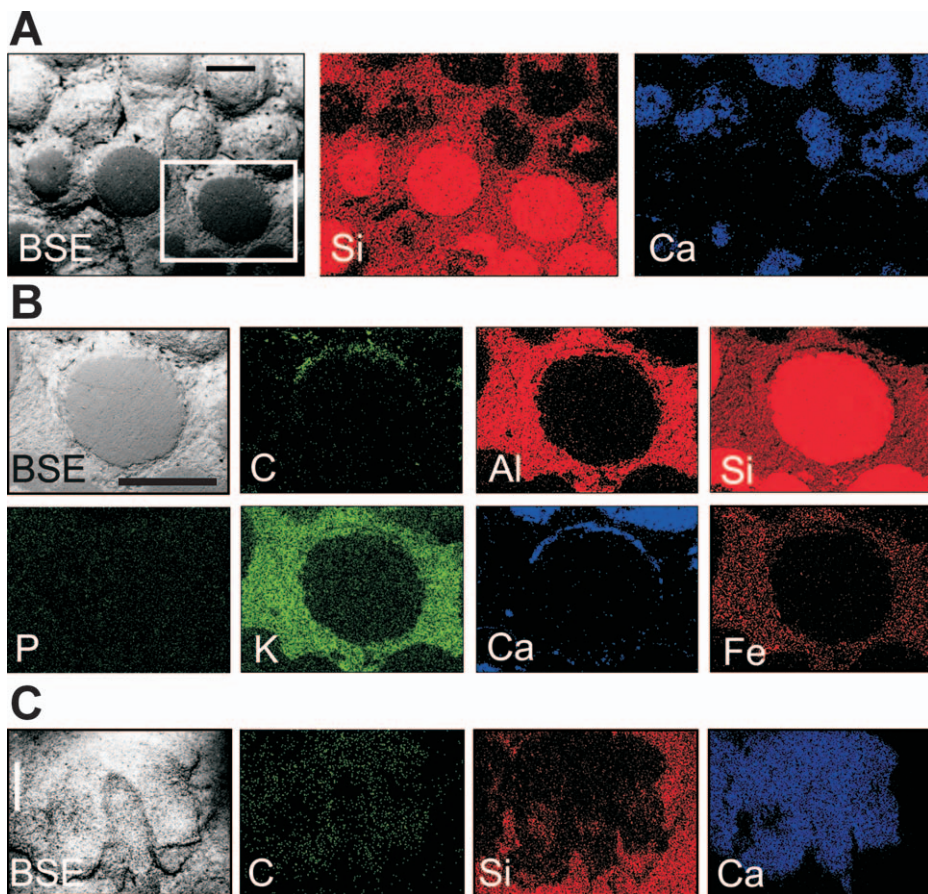


Figure 2. Elemental maps for spheroid cluster GUT 813 from Kaili Formation lagerstätte. A: Partially polished section. B: Close-up of A (indicated as rectangle in A). C: Associated trilobite cephalon. Relative scale bars = 550 μm in all images. BSE—backscattered electron image; SE—secondary electron image.

that no phosphorus peaks were observed during scanning electron microscopy (SEM) and EDX analyses of eggs with calcite coatings (phosphorus map in Fig. 2B).

This study has broader importance for understanding diagenesis in the fine-grained siliciclastic deposits with exceptional preservation exemplified by the Kaili lagerstätte. (1) Although the calcium carbonate–calcium phosphate switch plays an important role in the mineralization of volatile contents (Briggs and Wilby, 1996), here we propose a calcium carbonate–silica switch as a new precipitation control associated with Burgess Shale–type deposits. In order to favor silica precipitation instead of calcium phosphate in low pH conditions, there must have been a ready localized source of silicon predominating over phosphorus in the surrounding sediments and pore water. Co-occurring siliceous sponge spicules (Zhao et al., 2002) or microorganisms may have been this source (Westall et al., 1995). (2) There was partial decay of the chorion but also selective precipitation of calcium carbonate associated with this organic material. In addition, preferential precipitation of the silica must have occurred during early diagenesis

prior to microbial consumption in order to prevent cell collapse and retain a strong three-dimensional structure resistant to compaction by overburden. If eggs and/or embryos were only coated with calcium phosphate, they would mostly likely be crushed due to the high compaction ratio in fine-grained siliciclastic sediments. Thus, the taphonomic window proposed by Donoghue et al. (2006) for the three-dimensional preservation of phosphatized embryos cannot apply in nonconcretionary siliciclastic settings exemplified by the Kaili deposit. (3) Precipitation and dissolution of silica and calcite are sensitive to seawater solubility and pH value (Fig. DR3; see footnote 1), and they can serve as proxies for solubility and pH conditions in ancient environments. This allows us to constrain the geochemistry of the diagenetic environment to some degree. (4) Selective silicification (Holdaway and Clayton, 1982; Schubert et al., 1997), rare in siliciclastics, is a fossilization phenomenon that is currently not well understood and was previously unknown in Burgess Shale–type lagerstätten.

The sequential diagenetic history of silicified egg clusters from the Kaili lagerstätte can

be interpreted in greater detail based on the results from SEM and EDX analyses (Fig. 2). Two scenarios are suggested to explain the presence of calcite envelopes. (1) Initially, changes in pH and Eh (see Scott and Collinson, 2003) triggered the precipitation of silica within the egg. This process probably occurred with decalcification of most calcareous skeletal elements, such as trilobites and echinoderms, in low pH and high solubility conditions (phase I in Fig. DR3; see footnote 1) prior to and/or during shallow burial. Subsequently, calcium carbonate replacing the organic wall or the chorion (calcium maps in Figs. 2A, 2B) was due to the decay of the egg. In that case the cell wall may have begun to break down, but the structural integrity remained. Silica solution must have permeated the wall without bringing in clay. The further breakdown of the cell wall may have promoted precipitation of calcite around the egg. The microbe-induced calcite coatings could occur prior to burial based on taphonomic experiments (Briggs and Wilby, 1996; Martin et al., 2003). (2) Alternatively, the calcite envelopes could be original calcified egg cases, and that is supported by the fact that some of the trilobite fragments associated with egg clusters still retain calcite (Fig. 2C).

CONCLUSIONS AND IMPLICATIONS

Synchrotron techniques provide critical, nondestructive means to image fossilized intact egg clusters of Cambrian metazoans from the Kaili Formation, Guizhou, China. Based on modern taphonomic experiments (Martin et al., 2003, 2005) and the evidence presented here, fossilized invertebrate eggs or egg clusters in the fine-grained siliciclastic environment should be more common in the fossil record than previously reported (see plate 27, no. 1 in Barrande, 1852). This study highlights the potential of a newly reported taphonomic process, a calcium carbonate–silica switch, on the preservation of ancient embryos, which were previously known only from phosphorites (Donoghue et al., 2006). It raises the possibility of discovering fossil embryos in a similar context in both older and younger sediments.

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REFERENCES CITED

- Accornero, A., and Gowing, M.M., 2003, Annual sedimentation pattern of zooplankton fecal pellets in the southern Ross Sea: What food webs and processes does the record imply?: Antarctic Research Series, v. 78, p. 261–278.
- Barrande, J., 1852, *Système Silurien du Centre de la Bohême. Ière. Partie: Recherches Paléontologiques*. Volume I. Crustacés: Trilobites: Prague, Paris, published by the author, 935 p.
- Bengtson, S., and Zhao, Y., 1997, Fossilized metazoan embryos from the earliest Cambrian: *Science*, v. 277, p. 1645–1648, doi: 10.1126/science.277.5332.1645.
- Briggs, D.E.G., and Nedin, C., 1997, The taphonomy and affinities of the problematic fossil *Myoscolex* from the Lower Cambrian Emu Bay Shale of south Australia: *Journal of Paleontology*, v. 71, p. 22–32.
- Briggs, D.E.G., and Wilby, P.R., 1996, The role of the calcium carbonate-calcium phosphate switch in the mineralization of soft-bodied fossils: *Geological Society [London] Journal*, v. 153, p. 665–668.
- Briggs, D.E.G., Erwin, D.H., and Collier, E.J., 1994, The fossils of the Burgess Shale: Washington, D. C., Smithsonian Institution Press, 238 p.
- 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.
- Donoghue, P.C.J., Kouchinsky, A., Waloszek, D., Bengtson, S., Dong, Xi-ping, 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.
- Gabbott, S.E., Hou, Xian-guang, Norry, M.J., and Siveter, D.J., 2004, Preservation of Early Cambrian animals of the Chengjiang biota: *Geology*, v. 32, p. 901–904.
- Holdaway, H.K., and Clayton, C.J., 1982, Preservation of shell microstructure in silicified brachiopods from the Upper Cretaceous Wilmington Sands of Devon: *Palaeontology*, v. 119, p. 371–382.
- Kremer, B., 2005, Mazeuloids: Product of post-mortem phosphatization of acanthomorphic acritarchs: *Palaios*, v. 20, p. 27–36, doi: 10.2110/palo.2003.p03-112.
- Lin, Jih-pai, 2006, Taphonomy of naraoiids (Arthropoda) from the Middle Cambrian Kaili Biota, Guizhou Province, south China: *Palaios*, v. 21, p. 15–25, doi: 10.2110/palo.2004.p04-83.
- Lin, Jih-pai, Gon, S.M., III, Gehling, J.G., Zhao, Yuan-long, Zhang, Xing-liang, Hu, Shi-xue, Yuan, Jing-liang, Yu, mei-Yi, and Peng, Jin, 2006, A Parvancorina-like arthropod from Cambrian strata of south China: *Historical Biology*, v. 18, p. 33–45, doi: 10.1080/08912960500508689.
- Martin, D., Briggs, D.E.G., and Parkes, R.J., 2003, Experimental mineralization of invertebrate eggs and the preservation of Neoproterozoic embryos: *Geology*, v. 31, p. 39–42, doi: 10.1130/0091-7613(2003)031<0039:EMOIEA>2.0.CO;2.
- Martin, D., Briggs, D.E.G., and Parkes, R.J., 2005, Decay and mineralization of invertebrate eggs: *Palaios*, v. 20, p. 562–572, doi: 10.2110/palo.2004.p04-67.
- Orr, P.J., Briggs, D.E.G., and Kearns, S.L., 1998, Cambrian Burgess Shale animals replicated in clay minerals: *Science*, v. 281, p. 1173–1175, doi: 10.1126/science.281.5380.1173.
- Raff, R.A., 1987, Constraint, flexibility, and phylogenetic history in the evolution of direct development in sea urchins: *Developmental Biology*, v. 119, p. 6–19, doi: 10.1016/0012-1606(87)90201-6.
- Schubert, J.K., Kidder, D.L., and Erwin, D.H., 1997, Silica-replaced fossils through the Phanerozoic: *Geology*, v. 25, p. 1031–1034, doi: 10.1130/0091-7613(1997)025<1031:SRFTTP>2.3.CO;2.
- Scott, A.C., and Collinson, M.E., 2003, Non-destructive multiple approaches to interpret the preservation of plant fossils: Implications for calcium-rich permineralizations: *Geological Society [London] Journal*, v. 160, p. 857–862.
- Simonson, B.M., 2003, Petrographic criteria for recognizing certain types of impact spherules in well-preserved Precambrian successions: *Astrobiology*, v. 3, p. 49–65, doi: 10.1089/153110703321632417.
- Steiner, M., Zhu, Mao-yan, Li, Guo-xiang, Qian, Yi, and Erdtmann, B.-D., 2004, New Early Cambrian bilaterian embryos and larvae from China: *Geology*, v. 32, p. 833–836.
- Westall, F., Boni, L., and Guerzoni, E., 1995, The experimental silicification of microorganisms: *Palaeontology*, v. 38, p. 495–528.
- Yang, Rui-dong, and Yin, Lei-ming, 2001, Acritarch assemblages from the Early–Middle Cambrian Kaili Formation of East Guizhou Province and biostratigraphic implication: *Acta Micropalaeontologica Sinica*, v. 18, p. 55–69.
- Yuan, Jin-liang, Zhao, Yuan-long, Li, Yue, and Huang, You-zhuang, 2002, Trilobite fauna of the Kaili Formation (uppermost Lower Cambrian–lower Middle Cambrian) from southeastern Guizhou, South China: Shanghai, Shanghai Science and Technology Press, 423 p.
- Zhang, Xi-guang, and Pratt, B.R., 1994, Middle Cambrian arthropod embryos with blastomeres: *Science*, v. 266, p. 637–639.
- Zhao, Yuan-long, Yang, Ra-dong, Zhu, Mao-yan, Yuan, Jin-liang, and Peng, Jin, 2002, Middle Cambrian Kaili Biota, in Zhao, Yuan-long, ed., *Guizhou—Palaeontological kingdom: Guiyang, China, Guizhou Science and Technology Press*, p. 110–159 (in Chinese).
- Zhu, Mao-yan, Vannier, J., Van Iten, H., and Zhao, Yuan-long, 2004, Direct evidence for predation on trilobites in the Cambrian: *Royal Society of London Proceedings, ser. B*, v. 271, p. S277–S280.

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