Life history and autecology of an Ediacaran index fossil: Development and dispersal of *Cloudina*

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Abstract: *Cloudina* is the best-known biomineralizing metazoan and a potential index fossil in the late Ediacaran Period, yet many aspects of its biology remain poorly understood. Previous reports have shown that *Cloudina* tubes grow from a basally closed funnel (or apical element), with occasional dichotomous branching. New material from the Ediacaran Beiwan Member of the Dengying Formation, South China, includes two distinct morphotypes—tubes with rounded versus pointed conical apices. In branching specimens, one of the daughter branches tends to have a conical apex. It is hypothesized that cloudinids with a spherical apex were derived from sexual reproduction, with their spherical termination representing the embryonic shell, whereas those with a conical apex are daughter branches detached from their parent tubes through asexual reproduction. These interpretations imply that *Cloudina* could reproduce both sexually and asexually, producing spherical embryonic shells and conical propagules, respectively. This strategy may have served to enhance dispersal, which was critical for the ecological success of early gregarious and sedentary animals such as *Cloudina*.

Keywords: *Cloudina*, Ediacaran, ontogeny, reproduction, dispersal

1. Introduction

One of the most evolutionarily important events in the early Cambrian was the widespread acquisition of biomineralized skeletons across numerous metazoan groups. The seemingly synchronous rise of biomineralization across multiple animal phyla and involving multiple minerals (calcium carbonate, calcium phosphate, silica) indicates that the genetic toolkit and biomolecular machinery for biomineralization has earlier phylogenetic roots and that the Cambrian radiation of

biomineralizing animals was driven by ecological and environmental factors (Knoll, 2003). The Cambrian radiation of biomineralizing animals was, however, preceded by a small number of late Ediacaran skeletal animals, including *Cloudina*, *Sinotubulites*, *Namacalathus*, and *Namapoikia* (Grant, 1990; Grotzinger et al., 2000; Wood et al., 2002; Hua et al., 2005). Of these Neoproterozoic biomineralizers, *Cloudina* is the first described and perhaps best known, with a wide geographic distribution in Namibia, Oman, South China, Siberia, Mexico, southeast USA, British Columbia, Brazil, Paraguay, and Spain (see Cortijo et al., 2010; Warren et al., 2011) but a restricted stratigraphic range between 549 Ma and 541 Ma (Grotzinger et al., 1995; Amthor et al., 2003). As such, *Cloudina* is a valuable terminal Ediacaran index fossil (Grant, 1990; Hua et al., 2005); but perhaps equally as important, the presence of biomineralizing metazoans, while restricted to only a few taxa, within the last few million years of the Ediacaran Period indicates the evolutionary emergence of mineralized skeletons prior to their phylogenetically widespread appearance in the Cambrian Period (Hua et al., 2003; Xiao and Laflamme, 2009; Peters and Gaines, 2012).

Cloudina is a small tubular fossil characterized by a succession of stacked funnel-shaped elements and interpreted as the biomineralized exoskeleton of an early metazoan (Germs, 1972; Grant, 1990). While widely accepted to have grown by episodic addition of new funnel-shaped elements from an apically-closed basal element, little is known about the early ontogeny of *Cloudina*, perhaps as a result of the susceptibility of *Cloudina* tubes and apices to fragmentation. Some Chinese *Cloudina* specimens, however, are preserved with complete apices, and therefore present an opportunity to examine the ontogenetic growth sequence of this important index fossil (fig. 3A and 3C in Bengtson & Yue, 1992; plate 1, fig. 6 in

Chen and Sun, 2001; fig. 1A–B and 1F in Hua et al., 2005; fig. 6.4 in Hua et al., 2007; fig. 2D in Chen et al., 2008).

Dichotomous branching has been reported in both Chinese (Hua et al., 2005, 2007) and Spanish *Cloudina* specimens (Cortijo et al., 2010). Interpreted as asexual division, a general feature of cloudinid dichotomous branching is that it is irregular, with daughter tubes of different diameters being produced. One of the daughter tubes is always significantly smaller and narrower than the other. Furthermore, when dichotomy starts to develop, the combined diameter of the two daughter tubes is no greater than that of the parent tube, implying that the parent tube embraces both daughter tubes (Cortijo et al., 2010; Vinn and Zaton, 2012). Most reported specimens show an early stage of division, but little is known about the developmental initiation and ontogenetic fate of daughter branches. To address unresolved questions about the life history of *Cloudina*, we examined new material collected from the late Ediacaran Dengying Formation of South China, with a focus on evidence of sexual and asexual reproductive strategies, and the inferred implications for ecological dispersal.

2. Geological setting

The fossils described here were collected from the upper Ediacaran Dengying Formation at the Lijiagou section, near the town of Kuanchuanpu, Ningqiang County, Shaanxi Province, South China (Fig. 1A). The Dengying Formation at Lijiagou is divided in three members (Fig. 1B; Hua et al., 2007): the Algal Dolomite Member (thick-bedded peritidal dolostone), Gaojiashan Member (thin-bedded calcareous siltstone, mudstone, and limestone), and Beiwan Member (a light grey, thick-bedded, peritidal dolostone). Although some authors regard the Beiwan

Member as a part of the Gaojiashan Member (Chen and Sun 2001; Hua et al. 2003, 2005; Chen et al., 2008; Cai et al., 2014), we follow Hua et al. (2007) in separating the upper dolostone unit because it is lithostratigraphically similar to the Beiwan Member and distinct from the more silty and argillaceous Gaojiashan Member at the type section near the Gaojiashan village (Cai et al., 2010; Meyer et al., 2012). The Beiwan Member at Lijiagou section, ca. 20 km WNW of the Gaojiashan section, has yielded abundant secondarily phosphatized *Cloudina* (Bengtson & Yue, 1992; Hua et al., 2005) as well as other fossils, including *Sinotubulites*, “vase-shaped microfossils” or protolagenids, branched tubular fossils and spherical structures of unknown affinities (Hua et al., 2003, 2007; Chen et al., 2008).

3. Material, methods and preservation

The material reported here was extracted from several dolostone blocks collected from the Beiwan Member in Lijiagou. More than a thousand secondarily phosphatized *Cloudina* tubes, the vast majority of which are fragmented and poorly preserved, were isolated from the carbonate matrix using acetic acid maceration techniques described in Jeppsson et al. (1999). Selected specimens were imaged using scanning electron microscopy (SEM; FEI Quanta 600F and Hitachi S-4800; backscattered electron imaging mode). Illustrated specimens are deposited at the Virginia Polytechnic Institute Geosciences Museum (VPIGM).

4. Description and morphological reconstruction

4.1. General description

Cloudina fossils from the Lijiagou section display a relatively wide range of size and morphology, but always fall within the typical range of the genus

(Grant, 1990). Tube diameters range from 100 μm (Fig. 2H) to more than 2 mm (Fig. 3A), and lengths are up to 5 mm in the longest but still incomplete specimens (Figs. 2B, 3A). Cloudinid tubes are constructed by a series of repetitive and successively-stacked funnel-shaped units. Together, these funnel-in-funnel tubes taper only slightly from their aperture to the basal apex, maintaining a largely consistent tube diameter through their overall length (Hua et al., 2005; Cortijo et al., 2010; Cai et al., 2014). As opposed to the open-ended repetitive funnel units, the apical element is basally closed (Chen and Sun, 2001; Hua et al., 2005; Chen et al., 2008; Cai et al., 2014). Rarely, cloudinid tubes show dichotomous branching into two smaller tubes from the larger antecedent tube (Hua et al., 2005; Cortijo et al., 2010).

4.2. Apical element morphology

The Lijiagou *Cloudina* fossils show two distinct morphotypes, and a third less categorizable morphology, of the closed basal element (Fig. 2A–N). In most of the specimens, the basal end is hemispherical and shows no sign of attachment scars or anchoring structures (Fig. 2A–H). The hemispherical basal elements range from 100 μm (Fig. 2H) to 1.5 mm (Fig. 2B) in diameter, and from 200 μm (Fig. 2H) to more than 2 mm (Fig. 2B) in length in well preserved specimens, although some may be incomplete. The exterior surface texture of the basal elements may be smooth (Fig. 2A, C, F, G), wrinkled (Fig. 2B), or exhibit smooth undulations (Fig. 2D, E, H). These surface features have been commonly observed in non-basal *Cloudina* funnels. The basal element has approximately the same diameter as successive funnel-shaped elements in most of the tubes, with a largely consistent, or marginally widening, diameter along the length of tube, a feature which seems to be characteristic of *Cloudina* tubes (Cortijo et al., 2010). The best

preserved specimens consistently show a fold, or partial constriction, occurring just above the hemispherical base (Fig. 2D, E, G, H).

Previously unreported among *Cloudina* fossils are tubes with a pointed, or more conically-shaped, closed base (Fig. 2K–N). This conical morphotype is less abundant than the hemispherical base, with only approximately 10% of the best preserved specimens showing this apical morphology. The length of pointed basal elements ranges from 500 μm (Fig. 2K) to more than 900 μm (Fig. 2L, an incomplete specimen), and its maximum diameter is consistent between 250 μm (Fig. 2K) and 300 μm (Fig. 2L). The exterior surface of the conical basal elements appears smooth, contrasting with the wrinkled or undulated wall of most hemispherical basal elements.

Some specimens show a basal element that is less easily ascribed to either of the above morphological categories (Fig. 2I–J). These basal elements seemingly appear crushed or flattened, showing similarities to conical apices but with a blunt base. The maximum diameter of the blunt basal elements ranges from 150 μm (Fig. 2I) to 350 μm (Fig. 2J), and their maximum length may exceed 600 μm (Fig. 2J). Like the conical basal elements, the blunt basal elements also exhibit a smooth exterior surface.

4.3. Branching specimen morphology

Branching specimens are very rare in the Lijiagou samples. A total of 7 of >1000 specimens analyzed show signs of branching, with the three best preserved illustrated in Fig. 3A–C. The specimen illustrated in Fig. 3A shows the beginning of the branching process inside the parent tube, with daughter tubes arising from within the narrow portion of the parent funnel. The larger daughter tube

appears to have an open, relatively wide base, while the smaller one shows a narrow, conical, basally tapered apex. It is unclear whether the tapered base is closed or has a narrow opening. Beyond the point of division, the smaller daughter tube expands rapidly (within ~500 μm of tube length) to reach the diameter of the original parent tube. In most instances, branching is associated with a pronounced curvature of the tube, where both parent and daughter tubes may be involved in the curvature (Fig. 3A–C). Once they have extended beyond the parent funnel, the daughter tubes tend to diverge markedly from each other (Fig. 3C; also see fig. 1M–P of Hua et al., 2005, and fig. 6.5 of Hua et al., 2007).

4.4 Isolated spherical structures

Although not abundant (about 25 specimens in our collection), several spherical forms with a diameter of ~300–400 μm have been found in the Lijiagou material (Fig. 4A–C). These spheres are mineralogically comparable to the cloudinid tubes as indicated by comparable greyscales observed in backscattered electron imaging. Some of these spheres have a smooth surface marked by scars (Fig. 4A), whereas others show an orange peel-like siliceous texture and secondary dolomite (respectively, dark-colored patches and rhombohedra in Fig. 4B). Although no obvious intermediate stages have been found, the morphology and physical dimensions of these spheres are similar to the spherical basal elements of *Cloudina*.

4.5 General autecology

Cloudina has been compared to both cnidarians and annelids (Germs, 1972; Glaessner, 1976; Grant, 1990; Hua et al., 2005; Vinn and Zatoń, 2012; Cai et al., 2014). With a lack of preserved soft-tissues, however *Cloudina* has not been yet

confidently positioned phylogenetically. However, morphological and ecological studies have at least reconstructed *Cloudina* as a sessile, epibenthic, and colonial filter feeder (Grant, 1990; Warren et al., 2011; Cai et al., 2014), potentially with the apical end of the tube embedded within the substrate or containing soft-tissues within the apertural end of the tube, as suggested from preferential positioning of predatory borings (Hua et al., 2003). Likely contributing to their cosmopolitan distribution, *Cloudina* shows an apparent plasticity in the types of substrates it can inhabit within shallow marine ecosystems, having been shown in association with matgrounds, biostromes, and bioherms in various localities (Germs, 1972; Warren et al., 2011; Cai et al., 2014). External molds of cloudinid apical elements at the point of substrate attachment (fig. 9A of Cai et al., 2014) in addition to preservation of clustered tubes (fig. 9B of Cai et al., 2014) have bolstered the interpretation of aggregated *Cloudina* populations as gregarious colonies.

5. Interpretations and implications

The range of morphologies observed in the Lijiagou material permits the proposal of an ontogenetic growth series for *Cloudina*. We propose that *Cloudina* started its development from a spherical embryo (Fig. 5A). Although admittedly speculative, this spherical embryo stage was possibly similar to, or even potentially represented by, the isolated spherical structures illustrated in Fig. 4. A spherical embryo would subsequently develop into an embryonic test with a hemispherical base (Fig. 5B, C). If the life mode of *Cloudina* is assumed to be analogous to that of *Conotubus* (Cai et al., 2011; 2014), the fold or constriction that appears directly subsequent to the hemispherical basal element (Fig. 2D, E, G, H) may be interpreted as positional adjustment of the emerging animal to the sea-floor. Following these

early ontogenetic stages, funnel-shaped elements were successively added during the growth of the animal (Fig. 5D–E). The tube may occasionally divide into two daughter tubes, interpreted here as asexual paratomic reproduction by dichotomous branching (Fig. 5F). During division, two different daughter funnels would develop, a smaller one (Fig. 5α) with a conical and closed base, and a larger one with an open base contiguous to the parent tube (Fig. 5G). The new individuals would continue developing as described above (Fig. 5H, β), by adding new funnels to their tubes to accommodate increased body volume.

We also propose that the rarity of branching *Cloudina* tubes in the fossil record may be due to the release of the smaller “bud” from the parent tube. The reported specimens with a conical base represent the smaller daughter tubes that had originated through asexual paratomy and were then released from the parent tube. The specimen illustrated in Fig. 3D–E shows a wide empty space to the side of the last funnel (arrows); this space may represent a gap that had been occupied by a daughter tube, which had since been released as a propagule. The specimen illustrated in Fig. 3F may represent a released daughter propagule. As can be seen in this and other similar specimens, the conical basal element has a smooth external surface, and the lack of ornamentation may reflect the development of this part of the shell within and under the protection of the parent tube. Distal funnels, on the other hand, show wrinkled walls. These wrinkles may be related to deformation of the flexible organic substrate developing outside the parent tube by water current shearing, suggesting that the shell was weakly mineralized. There is also an abrupt change in orientation between the conical base and subsequent funnels (Fig. 3F); this change is consistent with the divergence of daughter tubes after they emerge

from the parent tube (e.g., Fig. 3C). Thus, the two specimens illustrated in Fig. 3D–F provide strong support to the ontogenetic stages represented in Fig. 5G and β .

Given its global geographic distribution and wide environmental distribution, *Cloudina* must have been able to disperse across large expanses of the oceans, particularly if it lived a gregarious and sedentary life. The afore described propagule stage (Fig. 5 β) may have served to facilitate the ecological dispersion during the cloudinid life cycle, although claims as to passive (density independent) or active (density dependent) dispersal are only speculative without an understanding of either the soft-tissues or phylogenetic affinity of *Cloudina*. With that said, however, the asexual paratomic reproduction of *Cloudina* seems likely to have served as an adaptation for density dependent dispersal in order to relieve pressure of high local population density, limited availability of habitat space, and competition for resources. Regardless of the dispersal mode, the paratomic reproductive strategy of *Cloudina*, as well as its plasticity of substrate type attachment, more than likely promoted its worldwide paleobiogeographic range.

6. Conclusions and summary

From new cloudinid material of the Ediacaran Beiwán Member, Dengying Formation, South China, we have documented two distinct morphotypes of the cloudinid apical element—hemispherical and pointed conical apices. We interpret the hemispherical apices as incipient *Cloudina* derived from the embryonic shell. On the other hand, *Cloudina* tubes that exhibit a conical apex are paratomically-grown daughter branches detached from their parent tubes. The proposed life cycle, supported by surficial textures of these apical element morphotypes and individuals demonstrating dichotomous branching, suggests that *Cloudina* reproduced both

sexually and asexually. Its asexually produced propagules could have assisted in ecological dispersal, therefore facilitating the global distribution of *Cloudina*.

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Figure captions

Fig. 1

(A) Geological map (modified from Cai et al., 2014) of the Ningqiang area, southern Shaanxi Province, South China, showing the locality of the Lijiagou section. Rectangle in inset map shows the location of the Ningqiang area in the northwestern margin of the Yangtze Platform. (B) Litho- and biostratigraphy of the Dengying Formation at Lijiagou (modified from Cai et al., 2014). The upper unit of the Dengying Formation is here recognized as the Beiwang Member (Hua et al., 2007), rather than as part of the Gaojiashan Member (Cai et al., 2014).

Fig. 2

SEM images of *Cloudina* fossils with preserved basal elements. (A–H) Specimens with a hemispherical basal element. This is the most common morphotype in our collection. (F) Specimen apparently with a continuous cylindrical test, rather than a series of nested funnel elements. (D, E, G, H) Specimens with a constriction separating the hemispherical base and subsequent funnel elements. (I–J) Specimens with a conical basal element but a blunt apex. (I) Specimen with a continuous cylindrical test rather than a series of nested funnel elements. (K–N) Specimens with a conical base and a pointed apex.

Fig. 3

SEM images of *Cloudina* fossils with dichotomously branching tubes. (A) Initial branching that produces a larger and a smaller daughter tubes, both nested within the parent tube. (B–C) Specimens with daughter tubes diverging and curving from each other as soon as they emerge from the parent tube. (D–E) Different views of the same specimen, showing dichotomous branching, with one of the daughter tubes released, leaving a wedge-shaped gap in the parent tube (arrows). A poorly preserved tube (arrowheads) is fortuitously attached to the parent tube. (F) Specimen showing the β stage (from Fig. 5) of the proposed *Cloudina* life cycle; note the different ornamentation patterns in the shell, smooth in the basal region and wrinkled in early growth funnels.

Fig. 4

SEM images of spherical fossils interpreted as possible embryos. Note their size and compositions (as indicated by backscattered electron gray scales) are comparable to the *Cloudina* specimens with a hemispherical basal element (Fig 2A–H). Phos: phosphate; Qz: quartz; Dol: dolomite.

Fig. 5

Interpretive diagram showing the proposed ontogenetic sequence of *Cloudina*, from the putative spherical embryo (A) to the hemispherical basal apex (B), through funnel additions (C–E), dichotomous branching (F), and continued growth (G–H) after release of the daughter propagule (α – β).

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Figure 4

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