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Early Cambrian epibolic gastrulation: A perspective from the Kuanchuanpu Member, Dengying Formation, Ningqiang, Shaanxi, South China

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ABSTRACT

The Cambrian explosion is marked by the apparent sudden appearance of diverse metazoan skeletal fossils and an increase in the complexity of both body and trace fossils. Among them, fossil eggs and embryos from the Lower Cambrian Kuanchuanpu Member of the Dengying Formation at Ningqiang in southern China provide a unique window for investigating the ontogeny of metazoans. Gastrulation is the cell migration stage after cleavage, and can be viewed as the embryonic analog of the transition from protozoan to metazoan grades of complexity. As an example, the embryonic developmental sequences of *Punctatus emeiensis* is well-documented because of the stellate spines covering the body surface, that are shared with embryonic stages represented by *Olivooides* and their growth stages represented by *P. emeiensis*. Although *Olivooides* was considered to be a taxonomic mixture, consideration of its variation was neglected. A specific type of embryo with zigzag blastopore lips that differs from typical candidate embryos for *P. emeiensis* is identified; its gastrulation process is reconstructed and is comparable to the epibolic gastrulation of extant metazoans. Both the embryos and adults of this 'type' display radial symmetry, that suggests an affinity distinct from that of echinoderms. Moreover, the body plan of penta-radial symmetry seen widely in Early Cambrian 'Small Shelly Fossils' (SSF's) was probably deep rooted in the Ediacaran.

1. Introduction

During the Ediacaran to Mid-Cambrian time (635–505 Ma), the Earth underwent significant changes in palaeogeography that include the rifting of a possible supercontinent and the formation of a second, slightly smaller supercontinent (Meert and Lieberman, 2004; Jiang et al., 2011). The assembly of the Gondwana supercontinent during the waning stages of the Proterozoic seems to have provided a tectonic backdrop for the myriad biological, climatological, tectonic and geochemical changes leading to, and including, the Cambrian radiation (Meert and Lieberman, 2008). Evidence for this radiation event includes the enigmatic (but widespread) Ediacaran fauna, small Shelly fossils and fossils found in the Chengjiang, Burgess Shale and Sirius Passett lagerstatte (Walcott, 1909; Conway Morris et al., 1987; McCall, 2006; Shu, 2008). In particular, the SSF and the Ediacaran faunas are distinct from each other and the links between the two and their relation to Phanerozoic metazoans is controversial. It is possible that SSF's have the potential to record a mixture of some relicts of Ediacaran faunas and antecedents of the Chengjiang faunas. In particular, the occurrence of fossil eggs and embryos at the transition of the Neoproterozoic/Cambrian provides an exceptional developmental window for bridging the gap between the Ediacaran-SSF's and metazoan life in the Cambrian.

Embryos from the late Neoproterozoic Weng'an biota in the Doushantuo Formation have been described as exhibiting cleavage, blastula and post-blastula stages (Xiao and Knoll, 2000; Xiao et al., 1998). Although some were later interpreted as giant sulfur bacteria (based on concerns of taphonomic bias; Bailey et al., 2007), the Doushantuo fossils contain convincing embryos (Xiao and Knoll, 2000; Xiao et al., 1998; Xiao et al., 2007). Nevertheless, the discovery of possible gastrula embryos from the Doushantuo Formation (Chen and Chi, 2005; Chen et al., 2000; Yin et al., 2001) is hotly debated (Dong, 2009; Xiao et al., 2000). In contrast, embryos, especially the *Olivooides* type, from the Lower Cambrian Kuanchuanpu Member of the Dengying Formation in Ningqiang County, southern Shaanxi Province are generally accepted as embryonic fossils (Bengtson and Yue, 1997; Hua et al., 2004; Liu et al., 2006; Steiner et al., 2004; Yue and Bengtson, 1999, Dong, 2009; Xiao et al., 2000). In spite of this general acceptance, the gastrulation processes in these embryos are poorly characterized. The extraordinarily well-preserved fossil embryos recovered from the Dengying Formation allow us to compare some embryos with the epibolic gastrulation process of extant forms.

Gastrulation is the cell migration stage after cleavage, and can be viewed as the embryonic analog of the transition from protozoan to metazoan grades of complexity. It is the initial process in the formation of embryonic germ layers, especially ectoderm and endoderm, on which all subsequent developments eventually depend

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(Gilbert and Raunio, 1997). There are four major types of gastrulation in extant metazoans, including invagination, epiboly, delamination and ingression (Fig. 1). In epiboly, gastrulation is accomplished by a series of coordinated cellular rearrangements occurring over the surface of the large, yolk-rich macromere(s) that form the bulk of early embryos. Epibolic gastrulation is observed in many extant animals, such as cnidarians, ctenophores, platyhelminthes, sipunculids, echiurans, gastropods, annelids, lophophorates and vertebrates (Anderson, 1973; Gilbert and Raunio, 1997; Wennberg et al., 2008; Werbrock et al., 2001). The general process of epiboly can be represented by the gastrulation of ctenophores: the micromeres born at the future aboral pole move toward the oral pore on the surface of larger macromeres. The blastopore forms where these micromeres meet and corresponds to the position of the mouth. These micromeres were identified as generating exclusively ectodermal derivatives (Martindale and Henry, 1999). Thus, closure of the blastopore can be applied to the recognized different stages of epibolic gastrulation in the Kuanchuanpu fossil embryos.

2. Localities and stratigraphy

The studied section is located in Shizhonggou (32°58′15.8″N, 106°15′45.0″E), 20 km north of Ningqiang County in southwestern Shaanxi Province, China. It is on the northern margin of the Yangtze Platform (Fig. 2a), where Upper Neoproterozoic and Lower Cambrian sediments were deposited in a shallow-water setting (Steiner et al., 2004). The Precambrian–Cambrian section in this area consists of the uppermost Dengying Formation and the Lower Cambrian Guojiaba Formation.

The Kuanchuanpu Member unconformably overlies the Upper Sinian Gaojiashan Member that yielded phosphatized biota of *Cloudina–Sinotubulites* and numerous microproblematica. It is also in an unconformable relationship to the overlying Guojiaba and Shuijingtuo formations that are characterized by siliceous and phosphatic carbonate yielding trilobites and bradoriids. The Kuanchuanpu Member, consisting of interbedded limestone, chert and phosphatic sandy limestone, is correlated to the Tianzhushan, Yanjiahe, Maidiping, Zhongyicun, and Yangjiagou members in other parts of the Yangtze platform (Liu et al., 2006). The phosphatized globular fossils, namely *Olivooides*, are recovered from the phosphatic limestone ranging from Beds K28 to K61 (Fig. 2b), where they co-occur with such SSF's as *Anabrites trisulcatus*, *Paleosulcachites irregularis*, *Carinachites spinatus*, and *Circotheca* sp., a typical fossil assemblage comparable with the first SSF zone in the Early Cambrian Meishucunian Stage (equivalent to the Nemakit-Daldynian and Tommotian of Siberia) (Luo et al., 1984; Xing and Yue, 1984; Wang et al., 2010; Liu et al., 2006; Yue and Bengtson, 1999; Steiner et al., 2004).

3. Material and methods

After maceration of the phosphatic limestone rock samples with 3–5% acetic acid, several thousand globular fossils were handpicked from the rock residue. Some portions of the fertilized envelopes were picked with needles under the dissection microscope to expose the embryos inside. All specimens examined under scanning electron microscope (SEM) were mounted on slides using double-sided carbon tape. The specimens are registered and deposited at the Early Life Institute (ELI), Northwest University, Xi'an, China.

4. Morphology and classification of stellate embryos

We recognized two types of embryos with sharp stellate spines (Fig. 3); the first type is 600–870 μm in diameter with 3–5 annular folds, most likely corresponding to the lowest 3–5 annular grooves on the apical part of the hatched *P. emeiensis* (Yue and Bengtson, 1999). The second type of embryo of 500–600 μm diameter, being smaller than the first type, features a remarkable circumferential groove (CG)

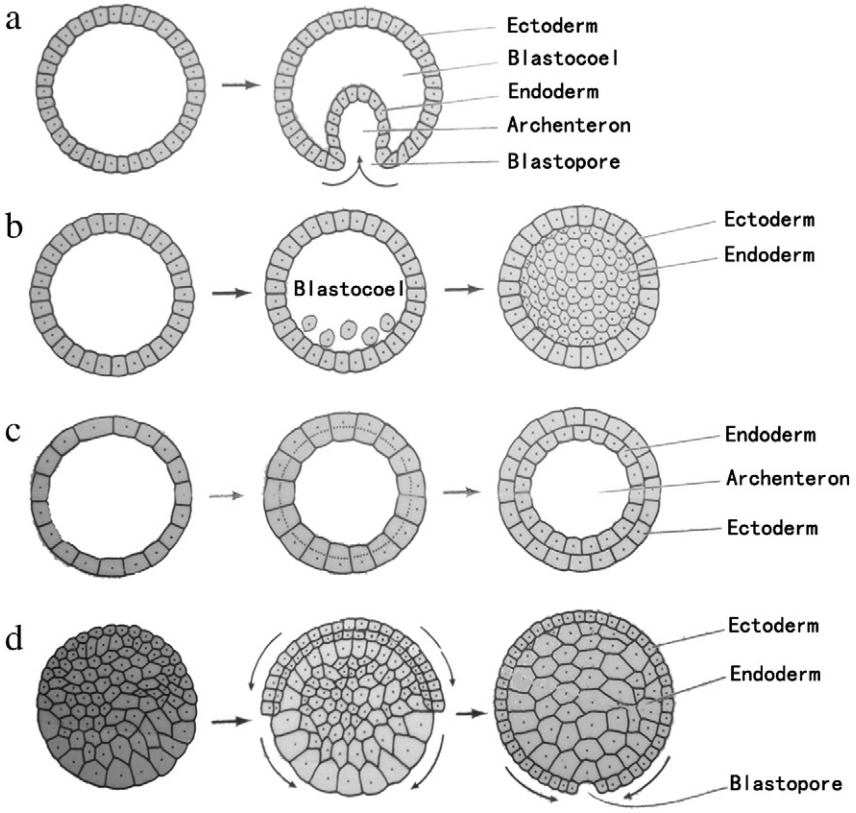

Fig. 1. Form of gastrulation. (a) Invagination of a coeloblastula to form a coelogastrula. (b) Unipolar ingression of a coeloblastula to form a stereogastrula. (c) Delamination of a coeloblastula to form a double-layered coelogastrula. (d) Epiboly of a stereoblastula to form a stereogastrula. (From Brusca and Brusca, 1990; see Gilbert and Raunio, 1997).