Research Advances

A New Fortunian Scyphozoa and its Development

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Objective

The Cambrian fossil embryos of radial animals are represented by taxa of Olivooides, Pseudooides, *Carinachites*, hexangulaconulariids (including Hexaconularia and Arthrochites) and Quadrapyrgites. Liu Yunhuan established a new genus: Qinscyphus Liu 2017 and reconstructed the general morphology of its hatched stages in 2017; this genus has only one species Qinscyphus necopinus. It was interpreted to be a member of Olivooidae Steiner 2014, and was placed besides crown -group Coronatae within Scyphozoa. In 2018, with the discovery of new fragmentary specimens with oral part preserved, the general morphology of *Q. necopinus* have been revised; and at the same time, we found a embryo assignable to Q. necopinus. This embryo has oral part that similar to that of the hatched stages of Q. necopinus, indicating that Q. necopinus underwent direct development.

Methods

The rock samples from the key horizon at Zhangjiagou section were cracked into football-sized pieces, then macerated using diluted acetic acid (~10%). A regular reaction cycle requires three days in summer (around 40° C). Undissolvable residues were dried naturally and then handpicked under a binocular microscope. Selected microfossils were observed under an LEO1530VP environmental scanning electron microscope (SEM) or under a Carl Zeiss Axio Zoom V16 stereo microscope at the Nanjing Institute of Geology and Palaeontology.

Results

(1) Hatched stage of Qinscyphus necopinus

Cup-shaped animal with embryonic tissue and postembryonic tissue, i.e. apical part and abapical part. The embryonic tissue is inverted pentagonal pyramid shape with smooth surface. Post-embryonic tissue tube-shaped with densely spaced and slightly raised annuli. Several circlets of triangular thickenings form five longitudinal rows, pentaradially arranged on perradial belts of post-

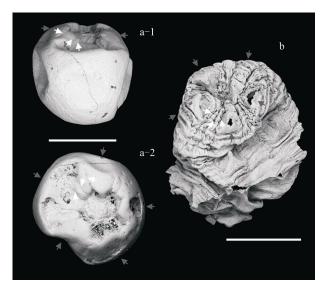


Fig. 1. Hatched stage and embryo of Qinscyphus necopinus. (a-1) embryo of *Qinscyphus necopinus* has surface differentiation only at the oral part, lateral view, egg mambrane omitted, UMCU17CHD0919-001; (a-2) oral view of a-1; (b) hatched stage of *Qinscyphus necopinus*, completely preserved, with annuli and triangular thickenings arranged on perradial belts, UMCU2015XQB086. White arrows denote the two marginal and the single median furrow, gray barrows denote the perradial belts. Scale bar = 500 µm.

embryonic tissue. Each triangular thickening occurs repetitively every four to seven annuli and straddles the next four to five annuli. The interradial belt inserted in between every two adjacent perradial belts, the width of the interradial belts is about two thirds that of the perradial belts. Around the oral aperture, perradial belts and interradial belts demarcated off by marginal furrows, and a median furrow bisecting each interradial belt.

(2) Embryo of Qinscyphus necopinus

The embryo of *Qinscyphus necopinus* has pentaradial symmetry, and it's composed of five perradial belts and five interradial belts arranged pentaradially around the oral aperture, the width of its interradial belts is about two thirds that of its perradial belts, same like their hatched stages. Its interradial belts are demarcated off from the perradial belts by marginal furrows, and a median furrow bisecting each interradial belt. The median and marginal furrows begin from the terminal edges of the interradial

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belts, and extend slightly downwards. The lower part of the embryo is smooth without any recognizable structure. The annuli and triangular thickenings are absent in the embryo, they might are derivatives of the post-embryonic tissue, and they occur only after hatching.

Conclusions

(1) Biological attribute

Oinscyphus necopinus most likely belongs to the Cnidaria, Scyphozoa, Coronatae because of their radial body plan with apical-abapical differentiation, and Qinscyphus has a morphology comparable to that of Olivooides and Quadrapyrgites. Whats more, the presence of triangular thickenings and pentaradial symmetry imply that Qinscyphus might be more closely related to Olivooides. But if triangular thickenings and pentaradial symmetry are the product of later convergent evolution, Qinscyphus might also be more closely related to Quadrapyrgites because of the absence of stellate structures on the apical part. Otherwise, Qinscyphus might be a sister group of the originally defined olivooids (= Olivooides + Quadrapyrgites). If so, the tetraradial symmetry of Quadrapyrgites becomes an advanced feature derived from the pentaradial symmetry of the last common ancestor of Qinscyphus, Olivooides and Quadrapyrgites.

(2) Direct development

The Cambrian fossil embryos reported so far are all underwent direct development without passing a larval phase. The current study demonstrates that *Qinscyphus necopinus* is also a direct developer, following the same development mode of *Olivooides* and *Quadrapyrgites*. The oral part of the embryo has morphology comparable to that of the hatched stages, thus the embryo might represents a prehatching embryonic stage, and the symmetry of their body had been determined at this time. After hatching, the post-embryonic tissue (the annuli and triangular thickenings) begins to develop. Direct development is a ubiquitous development mode of the Cambrian fossil embryos, thus metazoans with direct development are deeply rooted in the Cambrian Fortunian Stage, and thus direct development may be the plesiomorphy of metazoan development.

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