Vol. 91 No. 6 pp. 2310–2311 ACTA GEOLOGICA SINICA (English Edition) Dec. 2017

Research Advances

Exceptionally Preserved *Punctatus triangulicostalis* and Its Post-embryonic Development

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Objective

The putative coronatean *Punctatus* flourished at the beginning of the Cambrian explosion, and is significant in the exploration of the origin and evolution of early life. Liu Yunhuan established a new species: *Punctatus triangulicostalis* Liu, 2006. Two questions remain: how was the special body plan of *P. triangulicostalis* formed? How does *P. triangulicostalis* transform from embryo to the long cylindrical mature individual? Although the study of Steiner et al. in 2004 involved the above questions, they did not explain them clearly due to the lack of fossil materials at that time. This article aims to consider the above questions based on new information from several rare specimens.

Methods

The fossils were extracted using standard acetic acid maceration techniques. The rock samples were immersed in 5%–7% acetic acid and residues were retrieved regularly after five days of reaction. The undissolved residues were handpicked under a binocular microscope. The microfossils were picked out and then mounted on aluminum stubs for scanning electron microscopy.

Results

(1) Adult *Punctatus triangulicostalis*

The cone is a pentagonal pyramid in shape with stellate surface structure distributed over the surface (Fig. 1-a1, a2). The body is composed of five rows of triangle-like transverse ridges, which correspond to the cone ridges vertically, making a perfect pentaradial symmetric bodyplan. Each transverse ridge horizontally corresponds to its adjacent transverse ridge, thus forming several parallel annular ridges that gradually enlarge from posterior cone to oral end (Figs. 1c, 1d).

(2) Post-embryonic development stage

The post-embryonic development of *P. triangulicostalis* can be divided into four stages (Fig. 1):

Prehatching stage (Fig. 1a-1, 1a-2): There are 2–3 'central contraction bands' on the center of the sphere, which divide the sphere into two hemispheres. There is a pit at the top of the upper hemisphere, around it form pentaradial fissures, finally forming the corolliform oral rudiment, which is composed of five triangle-like transverse ridges. The lower hemisphere forms a sharp cone.

Hatching stage (Fig. 1b): The diameter of the oral end develops from small to large, and then evaginates to form the oral area—the first circle that is composed of five triangle-like transverse ridges. The oral area at this stage is obviously larger than that of the prehatching stage.

Larva stage (Fig. 1c): The cone now has clear pentaradial symmetry, and the triangle-like transverse ridges evaginate to form a new circle of triangle-like transverse ridges that vertically corresponding to the cone ridges. With the last circle of transverse ridges evaginated to form the body, the oral area then forms a new circle of triangle-like transverse ridges. The body of *P. triangulicostalis* lengthens in this way until the adult stage is reached with many circles of triangle-like transverse ridges.

Adult stage (Figs. 1d, 1e): With the last circle of triangle-like transverse ridges evaginated to form the body, the oral area then forms a new circle of triangle-like transverse ridges. The process stops when adult *P. triangulicostalis* has a certain number of circles (about more than 10 circles).

Conclusions

(1) Biological attribute

P. triangulicostalis most likely belongs to the Cnidaria,

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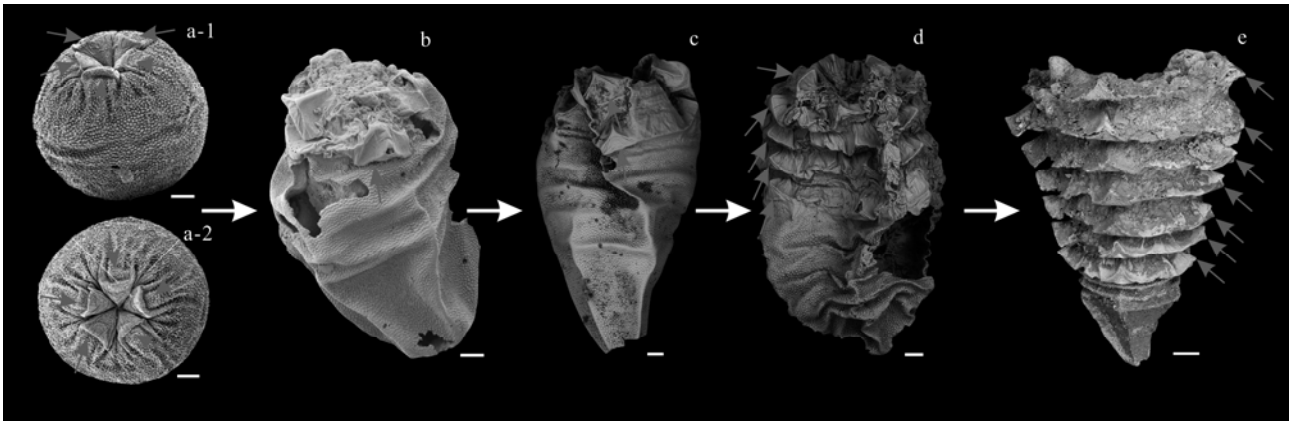

Fig. 1 Growth pattern and post-embryonic development of *Punctatus triangulicostalis*.
(a-1), embryo with obvious stellate surface structure and 'central contraction bands' (see Steiner et al., 2014); (a-2). oral view, corolliform oral rudiment with five triangular transverse ridges (indicated by arrows) at the top of the upper hemisphere (cf. Steiner et al., 2014); (a-1) and (a-2) different perspectives of specimen Kua125-240; (b), larva stage, with stellate spines distributed on the surface; diameter of the oral part larger, a circle of triangle-like transverse ridges evaginated (indicated by arrows); XX16-016; (c), larva stage, with two circles of triangle-like transverse ridges (indicated by arrows), and pentaradial symmetry bodyplan completely developed, XX16-017; (d), adult stage, completely preserved, with five circles of triangle-like transverse ridges (indicated by arrows), 2016XSL036; (e), adult stage, completely preserved, with seven circles of triangle-like transverse ridges, NIGP160499. Scale bar = 100μm.

Coelenterata, Scyphozoa, Coronatae. The *punctatus* is hatch from *Olivooides*, *Olivooides* was first referred to the Coronatae by Bengtson and Yue in 1997; then it was considered possibly to be the sister group of *Quadrapyrgites*; various authors thought it should be classified as stemgroup Cycloneuralia by Steiner in 2014, Coronatae by Liu in 2014 or Cubomedusae by Han in 2016. We consider that *Olivooides* and *Quadrapyrgites* have a similar body type, and which should probably be sister groups.

(2) 'Eversion growth pattern' and body plan

According to our research on many fossils, the growth pattern (we call 'Eversion growth pattern') is presumably as follows: in the pre-hatching stage, the stellate surface structure develops and the transverse contraction bands appear to divide the sphere into two hemispheres. Then a corolliform oral rudiment that is composed of five triangle -like transverse ridges forms. In the hatching, larva and adult stages, the oral area evaginates to form new circles of triangle-like transverse ridges that vertically correspond to cone ridges. As the last circle of triangle-like transverse ridges continually evaginates to form the body, and the oral area then forms a new circle of triangle-like transverse ridges, the body lengthens from one circle to many circles. Through this 'Eversion growth pattern', the body of *P. triangulicostalis* lengthens until it becomes a cylindrical mature individual with many circles of triangle -like transverse ridges.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (grant No.41572009), the State Key Laboratory of Palaeobiology and Stratigraphy (grant No.173121), and the College Students' Training Program of Chang' an University (201610710047, 201710710062, 201710710063, 201710710240).