Early post-metamorphic, Carboniferous blastoid reveals the evolution and development of the digestive system in echinoderms

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Abstract

Inferring the development of the earliest echinoderms is critical to uncovering the evolutionary assembly of the phylum-level body plan but has long proven problematic because early ontogenetic stages are rarely preserved as fossils. Here, we use synchrotron tomography to describe a new early post-metamorphic blastoid echinoderm from the Carboniferous (~323 Ma) of China. The resulting three-dimensional reconstruction reveals a U-shaped tubular structure in the fossil interior, which is interpreted as the digestive tract. Comparisons with the developing gut of modern crinoids demonstrate that crinoids are an imperfect analogue for many extinct groups. Furthermore, consideration of our findings in a phylogenetic context allows us to reconstruct the evolution and development of the digestive system in echinoderms more broadly; there was a transition from a straight to a simple curved gut early in the phylum's evolution, but additional loops and coils of the digestive tract (as seen in crinoids) were not acquired until much later.

Keywords:

echinoderms, blastoids, evolution, development, synchrotron tomography

1. Background

Reconstructing the origin and evolution of animal body plans requires a detailed understanding of the developmental processes underpinning changes in adult morphology [1], and echinoderms are a model group in this respect. Select species have been a focus of investigation for over a century, and recent work on developmental gene regulatory networks has revolutionized our understanding of cell specification mechanisms [2]. Most scenarios for the evolution of development in echinoderms are thus founded chiefly on extant taxa [3].

However, living echinoderms have diverged greatly from the latest common ancestor they share with all deuterostomes and, hence, might not closely reflect developmental processes in the earliest forms. Study of the extensive Palaeozoic fossil record of echinoderms could shed light on the early evolution of development in the phylum, but such work is hampered by the scarcity of fossilized early ontogenetic stages (although see [4]). Here, we report an extremely well-preserved, early post-metamorphic echinoderm from the Carboniferous (~323 Ma) of China. The fossil belongs to Blastoidea, an extinct clade of stemmed echinoderms (pelmatozoans) with pentaradial symmetry [5]. Synchrotron tomography was used to study the internal anatomy of this specimen, thereby revealing, for the first time, preserved evidence of the digestive tract in a blastoid echinoderm. This informs on the development of the blastoid gut, with implications for elucidating the evolution and development of the digestive system in early echinoderms in general.

2. Material and methods

The studied specimen (NHMUK EE 15671) comes from the Mississippian (lower Carboniferous) Luocheng Formation, Xinxu, Guangxi, China [6], and is housed in the Natural History Museum, London. Propagation-based phase-contrast synchrotron radiation X-ray tomographic microscopy was performed at the TOMCAT beamline of the Swiss Light Source, Paul Scherrer Institut, Villigen, Switzerland. The fossil was scanned using an X-ray energy of 20 keV, 1501 projections, and an exposure time of 200 ms, and the sample-to-detector propagation distance was set at 40 mm. This gave a tomographic dataset with a voxel size of 0.65 µm (electronic supplementary material, data S1), which was digitally reconstructed as a three-dimensional virtual fossil (electronic supplementary material, data S2, video S1) using the SPIERS software suite [7].

3. Results

The specimen measures 2.85 mm in height and 1.1 mm in maximum width (figure 1). The theca is cone-shaped and consists of three well-developed basal plates and five well-developed radial plates (figure 1*a*,*d*). The mouth is centrally located at the uppermost extremity of the theca (the summit) and is bordered by the deltoid plates, which are small and represented by the deltoid lips (figure 1*a*,*b*). The anus, proximal edges of the spiracles, and terminal food grooves are also situated on the summit. Each of the food grooves leads to three brachiole facets and is presumably supported by an internal lancet plate. Adjacent to the anus, a notch in the CD interray (in the C and D ray radials) marks the future position of the hypodeltoid plate, and a small wedge of calcite in this notch might reflect the nucleation of the plate (figure 1*a*,*b*). Medial notches in the radials likely represent the initiation of the ambulacral sinuses. Each of the basals and radials is covered by distinct external growth lines (figure 1*a*,*b*,*d*).

The presence of three basals, five radials, and the configuration of the summit unequivocally demonstrate that the specimen is a blastoid. The small size of the theca and the absence of the anal deltoids, the deltoid bodies, and the hydrospires indicate that the specimen was immature; the presence of the deltoid lips, the most proximal elements of the ambulacral feeding system, and (possibly) the lancets strongly suggests that the specimen had progressed past the passalocrinid stage of blastoid development (as defined by [8]). The passalocrinid stage was inferred to be equivalent to the non-feeding cystidean stage of crinoid ontogeny [8]; the studied specimen represents a more advanced post-metamorphic developmental stage that was capable of feeding (as shown by the presence of brachiole facets associated with the food grooves), analogous to the pentacrinoid stage of crinoid ontogeny. The fossil cannot be identified to the genus or species level because it lacks a number of key adult characters.

The basals and radials are characterized by a core of microperforate stereom, in which the pores are small and circular in cross section (up to about 15 µm in diameter), and frequently filled with pyrite (figure 1*f*). The thecal plates surround a large cavity, oval to pentagonal in cross section, which is occupied by fine-grained sediment (partially pyritized) and connects to the mouth and anus at the summit. A small U-shaped tubular structure is situated within the upper portion of the cavity (figure 1*c*,*e*,*f*). This tube is circular to elliptical in cross section, measuring approximately 80–190 µm in diameter and approximately 2.5 mm in total length. It consists of a thin rim (approximately 5–8 µm in width) surrounding a fill of fine-grained sediment (figure 1*f*). The tube follows a gently undulating course from one end to the other, with occasional sharp kinks, and it decreases in diameter noticeably at the proximal end. Both 'arms' of the 'U' extend towards the summit where the mouth and anus are located; however, no direct connection to these orifices is preserved (figure 1*c*,*e*).

4. Discussion

The U-shaped tubular structure described herein (figure 1*c*,*e*,*f*) has not previously been reported in a fossil blastoid. One possibility is that the tubular structure represents a vertical U-shaped trace fossil; however, there is no evidence of external boring and the U-shaped tube is not connected to the exterior of the specimen (figure 1*c*,*e*), strongly arguing against this interpretation. Instead, the morphology and position of the tubular structure are more consistent with what is described for the digestive tract of extant crinoids [9–11]; in both taxa, the tube is broadly U-shaped and restricted to the central region of the body. Consequently, we interpret the tubular structure in the blastoid fossil as an incompletely preserved part of the digestive system, hitherto unknown in blastoids, and it is inferred that the two upwardly projecting ‘arms’ of the ‘U’ were connected to the mouth and anus in life, as in the pentacrinoid stage of crinoid development [11].

Crinoids are the only extant members of the pelmatozoan clade, which is represented predominantly by a number of extinct Palaeozoic groups (e.g. blastoids, eocrinoids, and rhombiferans). As a result, crinoids are often assumed to be a close analogue for the anatomy and development of fossil pelmatozoans, including blastoids [5], and they have even been taken as an exemplar for basal echinoderms more generally [3]. However, comparisons with the post-metamorphic blastoid described in this study demonstrate that crinoids are unlikely to be a good interpretive model for many fossil groups. In the comatulid crinoid *Antedon*, the digestive tract forms soon after metamorphosis, arising from the enteric sac in the cystidean stage as a looped tubular structure that coils in a clockwise direction. By the pentacrinoid stage, a connection to the anus has been established, and the digestive tract becomes differentiated into oesophagus, stomach, and intestine before the onset of the free-living juvenile stage [9–11]. The post-metamorphic ontogeny of stalked crinoids is less well known, but recent work on the isocrinid *Metacrinus rotundus* is suggestive of a similar developmental history, with the digestive tract (mouth and oesophagus) forming in the cystidean stage [12]. Thus, the developing gut of crinoids differs from what we describe for blastoids, where it takes the form of a simple U-shaped curve, with no evidence of looping, clockwise coiling, or differentiation into distinct organs (figure 1*c*,*e*). Whereas it is possible that differentiation of the digestive tract occurred later in blastoid ontogeny, further structural changes, such as looping and coiling, can be considered highly improbable because these are established before the feeding pentacrinoid stage in modern crinoids [11]. This strongly suggests that the development of extant crinoids involved more radical changes to the organization of the internal organs, including the digestive system, than occurred in blastoid ontogeny, and the same may be true for early pelmatozoans in general.

There is very little information about the morphology of the gut in most groups of fossil echinoderms, but the general structure can be inferred from the position of the mouth and anus (figure 2). The most basal stem-group echinoderms (*Ctenoimbricata* and ctenocystoids) have an anterior mouth and a posterior anus [13], suggesting a more or less straight gut. However, in more crownward stem-group taxa (cinctans and solutes), the anus is typically situated closer to the mouth, indicating that the gut had become broadly U-shaped or J-shaped. This shape was likely established early during development, i.e. metamorphosis, as there is no evidence of radical morphological changes during later juvenile development [14]. Our description of the digestive system in a post-metamorphic blastoid suggests that a simple curved gut was also present in basal pelmatozoans; the absence of additional developmental transformations of the gut (i.e. looping or clockwise coiling), such as those seen in crinoids (including fossil forms, see [15]), indicates that these changes are most probably a derived character of some pelmatozoan groups (perhaps restricted to crinoids). This contradicts the hypothesis that the pentaradial organization of echinoderms evolved as a consequence of the formation of multiple loops of the digestive tract [16], as well as the theory that the placement of the anus in the CD interray was the product of clockwise coiling of the gut [17]. Instead, the results presented herein are more compatible with [18], who hypothesized the presence of a simple U-shaped gut in early echinoderms.

Data accessibility. The original slice images, the digital reconstruction, and a video file are available at: http://dx.doi.org/10.5061/dryad.sq134.

Author contributions. I.A.R., J.A.W., and C.D.S. designed the project. I.A.R., J.A.W., and A.A. carried out scans. I.A.R. produced the digital reconstruction. I.A.R. wrote the first draft of the manuscript and all authors contributed to subsequent versions. All authors gave final approval for publication.

Competing interests. We have no competing interests.

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Figure legends

Figure 1. Early post-metamorphic, Carboniferous blastoid (NHMUK EE 15671). (*a*,*b*,*d*) Scanning electron microscope images. (*c*,*e*) Digital reconstructions. (*f*) Slice image. (*a*) Angled upper view. (*b*) Angled upper view, plates given false colour. (*c*) Angled upper view, theca partly transparent. (*d*) Lateral view. (*e*) Lateral view, theca partly transparent. (*f*) Transverse section. Abbreviations: A–E, ambulacra; an, anus; bf, brachiole facets; bp, basal plate; dp, deltoid plates; fg, food groove; gl, growth lines; hd, hypodeltoid; mo, mouth; rp, radial plate; sp, stereom pores; ts, tubular structure. Colours: cyan, radial plate; green, brachiole facets; red, deltoid plates. Scale bars: 0.5 mm.

Figure 2. Phylogeny of extant and extinct echinoderms and hemichordates with reconstructions of the digestive systems (shown in blue). Abbreviations: an, anus; mo, mouth.

Supplementary material

Data S1. Synchrotron tomography scan of the early post-metamorphic, Carboniferous blastoid (NHMUK EE 15671). The slice images are in TIFF format, compressed in a ZIP archive.

Data S2. Interactive three-dimensional digital reconstruction of the early post-metamorphic, Carboniferous blastoid (NHMUK EE 15671). The reconstruction is in VAXML format, compressed in a ZIP archive, and has been downsampled to reduce triangle count. To view: unpack the .zip file, install the SPIERS software suite (program and documentation available from www.spiers-software.org), and double-click the unpacked .vaxml file.

Video S1. Video showing a three-dimensional digital reconstruction of the early post-metamorphic, Carboniferous blastoid (NHMUK EE 15671).

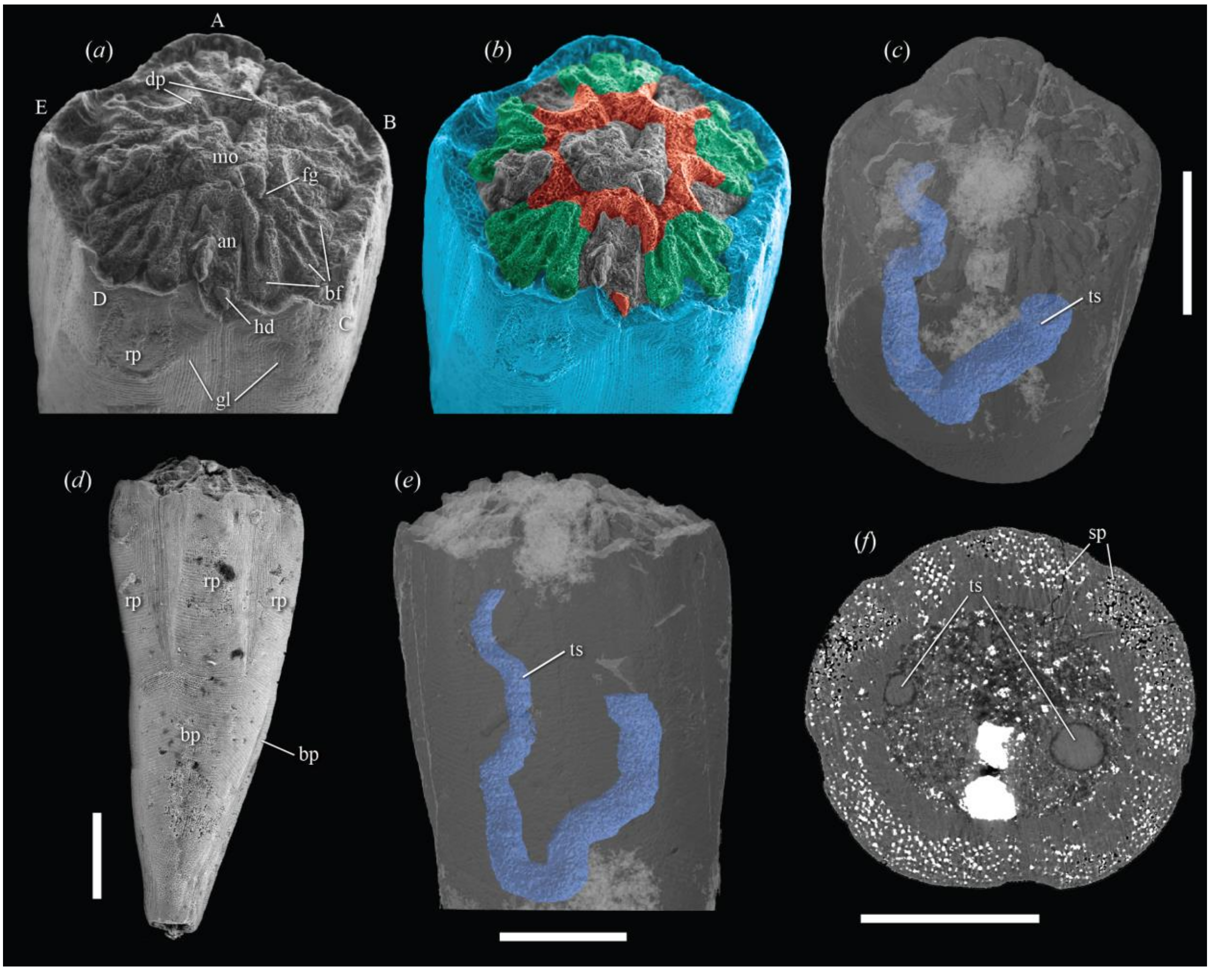

Figure 1.

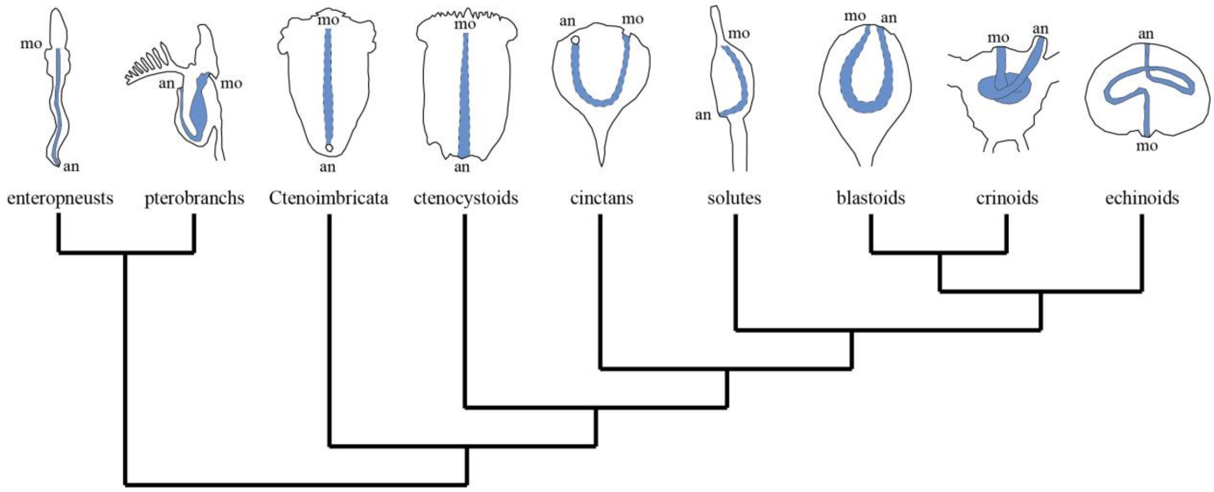
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Figure 2.