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

4  
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## 17 **Abstract**

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

30

## 31 **Keywords:**

32 echinoderms, blastoids, evolution, development, synchrotron tomography

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## 35 **1. Background**

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

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

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55

## 56 **2. Material and methods**

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

67

68

### 69 **3. Results**

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

82 The presence of three basals, five radials, and the configuration of the summit  
83 unequivocally demonstrate that the specimen is a blastoid. The small size of the theca and the  
84 absence of the anal deltoids, the deltoid bodies, and the hydrospires indicate that the  
85 specimen was immature; the presence of the deltoid lips, the most proximal elements of the  
86 ambulacral feeding system, and (possibly) the lancets strongly suggests that the specimen had  
87 progressed past the passalocrinid stage of blastoid development (as defined by [8]). The  
88 passalocrinid stage was inferred to be equivalent to the non-feeding cystidean stage of crinoid  
89 ontogeny [8]; the studied specimen represents a more advanced post-metamorphic  
90 developmental stage that was capable of feeding (as shown by the presence of brachiole  
91 facets associated with the food grooves), analogous to the pentacrinoid stage of crinoid

92 ontogeny. The fossil cannot be identified to the genus or species level because it lacks a  
93 number of key adult characters.

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

106

107

#### 108 **4. Discussion**

109 The U-shaped tubular structure described herein (figure 1*c,e,f*) has not previously been  
110 reported in a fossil blastoid. One possibility is that the tubular structure represents a vertical  
111 U-shaped trace fossil; however, there is no evidence of external boring and the U-shaped tube  
112 is not connected to the exterior of the specimen (figure 1*c,e*), strongly arguing against this  
113 interpretation. Instead, the morphology and position of the tubular structure are more  
114 consistent with what is described for the digestive tract of extant crinoids [9–11]; in both  
115 taxa, the tube is broadly U-shaped and restricted to the central region of the body.  
116 Consequently, we interpret the tubular structure in the blastoid fossil as an incompletely

117 preserved part of the digestive system, hitherto unknown in blastoids, and it is inferred that  
118 the two upwardly projecting ‘arms’ of the ‘U’ were connected to the mouth and anus in life,  
119 as in the pentacrinoid stage of crinoid development [11].

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

141 organization of the internal organs, including the digestive system, than occurred in blastoid  
142 ontogeny, and the same may be true for early pelmatozoans in general.

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

161

162

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

165



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

170

171 **Competing interests.** We have no competing interests.

172

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224

225

## 226 **Figure legends**

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

235

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

238

239

## 240 **Supplementary material**

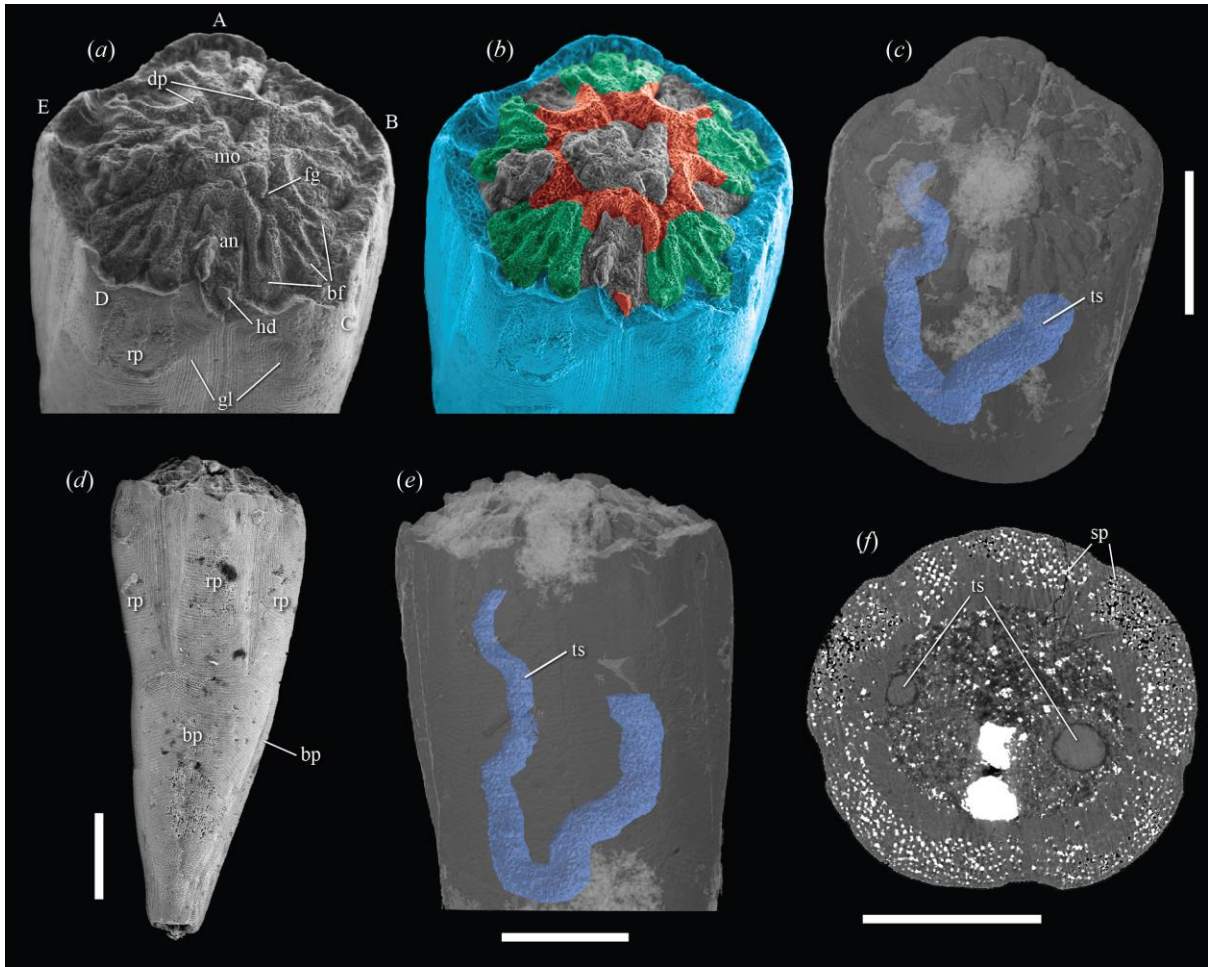
241 **Data S1.** Synchrotron tomography scan of the early post-metamorphic, Carboniferous  
242 blastoid (NHMUK EE 15671). The slice images are in TIFF format, compressed in a ZIP  
243 archive.

244

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

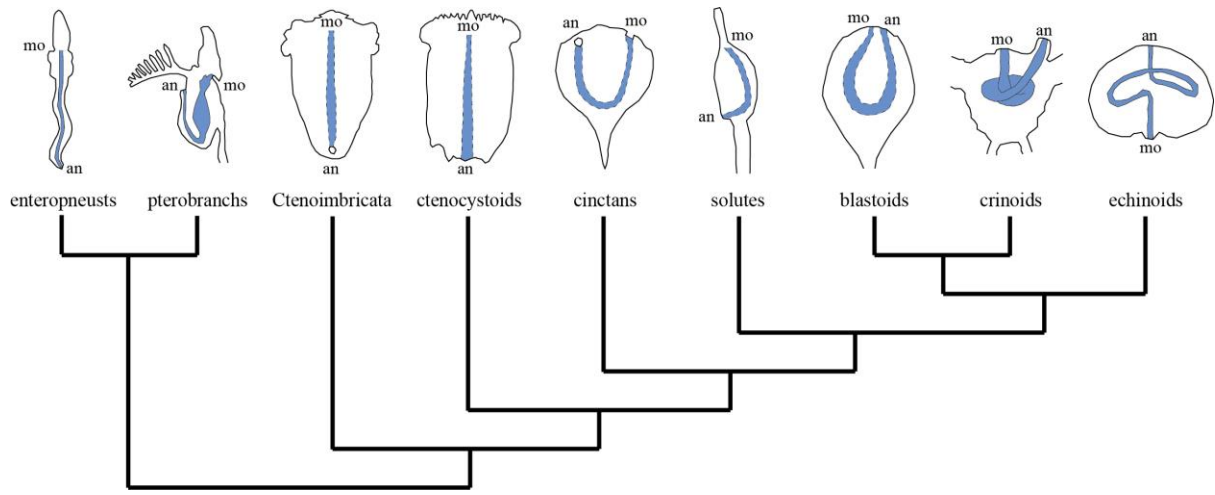
250

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



253

254 **Figure 1.**



255

256 **Figure 2.**