

Running head: Oldest brooding echinoderm

The oldest evidence of brooding in a Devonian blastoid reveals the evolution of new reproductive strategies in early echinoderms

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Brooding of young is a reproductive strategy observed in many extant echinoderms, but the evolutionary history of this behaviour is largely unknown due to the scarcity of examples preserved in the fossil record. Synchrotron x-ray tomography is used to describe an exceptionally preserved specimen of the Devonian blastoid echinoderm *Hyperblastus reimanni*. The coelomic cavity appears completely preserved in a coiled arrangement partially enclosing organs associated with the digestive, haemal and axial systems. The vault region of the coelom surrounds four structures interpreted as three internally brooded larvae and a gonad. The presence of putative larvae brooded internally in this specimen sheds new light on the reproductive strategies employed by blastoids, suggesting they were sexually dimorphic and that internal brooding was acquired early in the group's history. The acquisition of brooding may have

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been linked to high clastic sediment influx associated with the Appalachian Orogeny, which would have been detrimental to the survival of larvae living at the soupy sediment–water interface.

Key words: echinoderm, blastoid, larvae, reproduction, sexual dimorphism, synchrotron x-ray tomography

Echinoderms have been important components of marine ecosystems for over 500 million years (Smith *et al.* 2013). Members of the phylum possess a unique set of distinctive morphological characters, including pentaradial symmetry, a water vascular system and a mesodermal calcite skeleton, which enabled them to fill varied ecological niches (Smith 2005). Modern species display a wide range of reproductive strategies including forms of advanced parental investment (Gillespie & McClintock 2007; Barreto and Bauer 2019), with brooding of young known to occur in all living classes (Gillespie & McClintock 2007). Numerous extant species brood their young externally, with some crinoids protecting juveniles by attaching their bodies to the genital pinnules (Pertossi *et al.* 2021). Additionally, many crinoids (Hyman 1955; Balser 2002; Obuchi *et al.* 2010), starfish (Hyman 1955; McClary & Mladenov 1988), sea cucumbers (Hyman 1955) and brittle stars (Hyman 1955; Landschoff *et al.* 2015) are known to develop larvae internally before releasing them into the water column. Internal or external brooding involves extended parental protection of eggs and young, particularly from the mother, and can reduce the negative impact of factors such as predation pressure or high sediment input. Brooding is an energetically expensive behaviour but can greatly increase the survival rate of offspring (Barreto and Bauer 2019), albeit

brooded individuals are usually deprived of the advantages of broad geographical dispersion (Cohen and Johnston 1987). It is thus assumed to be the result of a wide range of environmental stresses, such as restricted food availability, high risk of predation or ocean acidification (Pearse 1994).

Brooding behaviour is very difficult to infer for extinct taxa. Examples of brooding have been reported in some fossil arthropods (Fortey and Hughes 1998; Caron and Vannier 2016) as far back as the middle Cambrian but very few instances have been documented for early representatives of most animal groups. Generally, brooding is only present in female individuals. The fragility of eggs, embryos and larvae coupled with the short duration of the brooding cycle, greatly reduces the chances of finding fossilized brooded young. The oldest known fossil occurrence of brooding by echinoderms comes from a single specimen of the Early Pennsylvanian blastoid *Pentremites rusticus*, in which several hundred eggs were preserved confined to the group of CD interray hydrospires (Katz & Sprinkle 1976).

Blastoids are an extinct group of stemmed echinoderms with pseudo-fivefold symmetry and a relatively good fossil record owing to their tightly sutured theca (Brett *et al.* 1997). Their closest extant relatives are crinoids, but direct comparisons are commonly regarded as inadequate for inferring blastoid palaeobiology because of important anatomical differences between the two groups. Blastoids possess a good fossil record but little is known about their internal soft tissues. One of the most important internal anatomical features of blastoids is the hydrospire complex, which is formed by elongated folds of a porous meshwork of thin-walled calcite with diverse morphology and is thought to have functioned primarily in respiration (Breimer & Macurda

1972; Bauer 2018), although it has also been suggested to have played a role in reproduction (Katz & Sprinkle 1976). Gonopores and gonoducts are known from approximately 15 genera (Breimer & Macurda 1972), but gonads are known from only a single genus (Donovan *et al.* 2016). Additionally, a gut was described in a single specimen of an undetermined species of a Carboniferous juvenile blastoid (Rahman *et al.* 2015).

Here, we use synchrotron x-ray tomography to describe the most complete combination of internal organs currently known in any blastoid. *Hyperblastus reimanni* also provides the oldest record of internal brooding by an echinoderm, informing on the evolution of this reproductive behaviour in early echinoderms.

Geological background

The studied specimen of *H. reimanni* was originally collected from the Middle Devonian Silica Shale Formation contained within the Michigan Basin, which is situated two and one-third miles southwest of Sylvania, Ohio, USA. The rocks of the Silica Shale are dominated by blue-grey, soft, highly calcareous shale, which disintegrates rapidly upon exposure. The shale beds are enclosed by two thick beds of blue–grey limestone through gradual contacts, and these contain the same fossiliferous fauna as the central shale beds (Wiedman 1985). Pyrite nodules and pyrite replacement of organisms are widespread throughout the formation (Wiedman 1985).

Method

The specimen of the blastoid *H. reimanni* (CMC IP 37404) was obtained on loan from the Cincinnati Museum Center (CMC). This fossil is three-dimensionally preserved as recrystallized calcite infilled with sediment and partially contained within relatively uncompressed sediments (Fig. 1); elements of the internal anatomy have been replaced with pyrite. Additional blastoid specimens from the University of Michigan Museum of Paleontology (UMMP), UMMP IP 51597, UMMP IP 61796 and UMMP IP 48653, UMMP IP 51593, UMMP IP 54830 were studied to estimate the dimensions of the anal and oral openings of CMC IP 37404 (Table 1).

The fossil specimen was imaged with synchrotron tomography using the TOMCAT (tomographic microscopy and coherent radiology experiments) beamline of the Swiss Light Source, Paul Scherrer Institut, Villigen, Switzerland. The specimen was scanned with a voltage of 37 keV, 1001 projections each with an exposure time of 1000 ms, using the 1.25 × objective. The tomographic datasets were used to digitally reconstruct the internal anatomy of the specimen using the SPIERS software suite (Sutton *et al.* 2012). This was achieved by creating three-dimensional virtual models of the internal structures in SPIERSedit. The reconstruction was based on 2480 slices, with segments assigned to structures with different brightness values, corresponding to variation in x-ray attenuation (correlated with material density) within the sample.

Anatomical description

The theca is cone-shaped and measures *c.* 7 mm in height and 4.5 mm in maximum width (Fig. 1). As typical of blastoids, the theca houses a well-developed system of internal hydrospires (Fig. 1).

The vault accounts for approximately half of the theca (Fig. 2). It is almost entirely occupied by five pairs of structures identified as hydrospires and four vertical tubes associated with a structure exhibiting pseudo-fivefold symmetry in the centre of the vault, with the two central tubes connected at their base (Fig. 2). There are 18 well-preserved calcite folds distributed among the five hydrospire pairs (labelled A–E in Fig. 2). Each pair of hydrospires is located in an ambulacrum, conferring 2–1–2 symmetry (Bauer *et al.* 2017). The aboral deltoid plates are not evident in the reconstruction due to sediment infill, but the theca seems to be intact with no missing plates or other obvious gaps (Fig. 1). There appears to be a reduction of hydrospires opposite to the anispiracle (B in Fig. 2); however, this is most likely to be the result of diagenetic alteration, which is also observable in the displacement of the coiled structure dominating the pelvis region. This is consistent with previous descriptions of specimens of *Hyperblastus*, which do not indicate any reduction of the anal interarea hydrospires (Breimer and Dop 1975).

The mouth leads to a vertical tube, which is bent at the base of the ambulacra to return back aborally, and discharges into the anal opening (Fig. 2). The inner plates of the pelvis are lined with a coiled structure, which is reminiscent of the peripheral subcoelom in adult crinoids (Ezhova and Malakhov 2020). Additionally, there are traces of continuations of the coiled structure preserved above the base of the hydrospires surrounding the gut,

which are consistent with the coelomic cavity; but their incomplete preservation prevented a full reconstruction (Fig. 2).

The pelvis is occupied by a coiled structure, which extends from the aboral end of the ambulacra to the end of the basals. It is divided into two interconnected compartments and contains five further structures (Fig. 2). The first three are in close proximity to each other (J1, J2 and J3 in Figs. 2 and 3) and located directly below the anal deltoid (D in Fig. 2). These are similar in shape, but approximately 10 times smaller (Table 2) and more elongated than the adult specimen; the flattened portion of the cone occupies two-fifths of the total length of the structure (Figs. 2 and 3). The fourth structure is larger, and is situated between the anal and buccal openings (Go in Fig. 2). The fifth structure is oval-shaped, attached to a wide tube that does not seem to connect to any other structure (S1 in Fig. 2). See Table 2 for more detailed morphological descriptions of these structures.

Discussion

Our digital reconstruction of *H. reimanni* reveals a series of internal structures. Some can be confidently identified as corresponding to previously described internal organs such as the hydrospires (Bauer 2018) and gut (Rahman *et al.* 2015), whereas others are not known in any other blastoids. The mouth of this animal would have been situated centrally in the structure with pseudo-fivefold symmetry, which is interpreted as the peristome (Fig. 2). The anal and oral openings are partially covered by sediment in CMC IP 37404; however, by comparison with other specimens of *H. reimanni* from the UMMP collections, we estimate they measured approximately 0.67 and 0.45 mm in diameter,

respectively (Table 1). The two vertical tubes in the centre of the vault form a well-defined U-shaped structure (Fig. 2), which is interpreted as the gut. This specimen represents the first example of the digestive system preserved in an adult blastoid.

The most prominent of the previously unidentified internal organs is a coiled structure lining the interior of the skeletal plates and potentially enclosing any internal organ present in that region of the theca. The reconstructed morphology of this structure is similar to the peripheral subcoelom found in adult crinoids (Hyman 1955; Haugh 1975; Haugh and Bell 1980; Ezhova and Malakhov 2020). We interpret it as part of the coelomic cavity (Fig. 2). The lateral two of the four vertical tubes preserved in the centre of the vault presumably connected to the peristome surrounding the mouth, and appear to be associated with the coiled coelomic cavity in the pelvis (Fig. 2). Axial and haemal glands with associations to the peristome and mouth, as well as the reproductive and water vascular systems, surround the gut in modern and fossil crinoids and extend into the peripheral subcoelom at the base of the theca (Ezhova and Malakhov 2020; Saulsbury and Zamora 2020; Bargmann and Von Hehn 1968). Consequently, we infer that the two vertical tubes are vestiges of the axial and haemal systems (Fig. 2).

The central chamber at the base of the hydrospires contains five additional structures. These are highly unlikely to be foreign bodies that entered the vault during or after death due to their relatively large sizes (Table 2) and the fact that the theca is preserved intact (Fig. 1). As per our estimation, the size of these structures would not have permitted ingestion (Tables 1 and 2) and they are located outside of the gut (Fig. 2a, h). Structure

S1 is located partially outside of the coelom and is higher in density than other structures; it is interpreted as possible pyrite growth in the pelvic region (Fig. 2). The structures labelled J1–J3 and Go are located close together in the CD interray (Fig. 2), which has been suggested to play an active role in reproduction by housing eggs prior to their release into the water column (Katz and Sprinkle 1976). J1–J3 are similar in morphology and density to the theca of the hosting adult *H. reimanni*; however, they are much smaller and more elongated in shape (Fig. 3 and Table 2). We interpret these as cystidean stage larvae, which are similar in size to the earliest juvenile blastoids reported (Croneis and Geis 1940; Sevastopulo 2005), particularly *Pentremites* (Fig. 3). Although blastoids are expected to display three well-defined basal plates and a rounded vault at the cystidean stage, these characteristics cannot be confidently recognized in our internally brooded larvae (Fig. 3 and Table 2). The presence of putative cystidean stage larvae preserved internally in an adult specimen of *H. reimanni* suggests that this species employed an advanced mode of reproduction involving brooding of young to the larval stage.

Our reconstruction also reveals a larger internal structure in the CD interray possibly associated with the reproductive system, which we interpret as the gonad (Go in Fig. 2). The blastoid gonad is assumed to be a singular internal structure connected to the exterior through the gonoduct (Donovan *et al.* 2016), which exits close to the anal cavity either through an individual opening called a gonopore or utilizing the anal opening (Breimer & Macurda 1972; Katz & Sprinkle 1976) and possibly situated in the anal (CD) interray (Sevastopulo 2005). There is only one preceding publication reporting a

preserved gonad in a blastoid (Donovan *et al.* 2016); however, the authors have recognized similar structures to the one described here in other fossil blastoids.

There is only one other known blastoid specimen (*P. rusticus*) preserving evidence of internal brooding. *Pentremites* specimens are known to have a reduced number but greatly enlarged in size hydrospires in the anal area (Bauer *et al.* 2019; Katz and Sprinkle 1976); while this does not occur in *Hyperblastus*, it is possible that the anal hydrospires could increase in volume and were modified specifically for brooding. The larvae within our specimen of *H. reimanni* are positioned in the vault cavity outside of the hydrospire system but in close proximity to the hydrospire pair located in the CD interray. The enlarged hydrospires could plausibly have sustained the larvae in life, providing protection, nutrients and oxygen. These could have then returned to their normal size after death, which might explain the positioning of the larvae in the vault outside of the hydrospire area (Fig. 2). Several species of modern echinoderms brood young inside the mother's body. In some instances, brooding takes place in special chambers within the mother's body, and young acquire nutrients via the coleomic fluid; various species of living Asteroidea, Holothuroidea, Ophiuroidea and Crinoidea are known to display this behaviour (Gillespie & McClintock 2007). Similar to the evidence presented herein, some species of crinoids are known to develop pentacrinoid stage juveniles internally before releasing them into the water (Hyman 1955; Balser 2002). Cystidean stage larvae are fragile (Sevastopulo 2005) and this stage lasts only a few days in modern crinoids (Hyman 1955), which would severely decrease their chances of fossilization. The estimated

size of the anal opening in our specimen is c. 0.67 mm, which is sufficiently large to permit the exit of the brooded cystidean stage larvae. A gonopore, not preserved in our specimen, has been previously described in a specimen of *H. filusus* with comparable body size to our specimen (Breimer and Dop 1975). The size of this gonopore is small, approximately 0.3 mm; however, other species of spiraculate blastoids possess wider gonopores (i.e. 0.5 mm) (Breimer & Macurda 1972). Hence, we hypothesize that the aforementioned specimen of *H. filusus* was a male and that the exit of young from the body in females would have occurred through larger gonopores (yet to be recognized) or alternatively through the anal opening in the anal deltoid.

Sexual dimorphism and possibly internal fertilization must have been developed in all internally brooding blastoid species, such as *H. reimanni* and *P. rusticus*. This morphological variation has been documented in many species of modern echinoderms, including representatives of all five extant classes.

Various types of parental care are known in modern echinoderms, including brooding to juvenile stages, although this is most common in environments characterized by inhospitable conditions or with a high risk of predation (Gillespie & McClintock 2007). The sedimentation and faunal associations in the Silica Shale are indicative of currents with good circulation, periodically affected by stronger currents (Ehlers & Kesling 1970). Open marine communities with an elevated faunal diversity are expected to be tiered and have a strong predation pressure (Scherer *et al.* 2018), which could have had an impact on the reproductive strategies employed by some species. Larvae are susceptible to predation and thus elevated predation

pressure would be expected to have a large negative effect on the development of adult populations (Vieira *et al.* 2012). Throughout the Devonian, the Michigan Basin was subjected to open marine circulation, which permitted the development of rich faunal communities where predation by large pelagic organisms and epizoan settlement were common, and this might have had detrimental effects on the healthy growth of these communities (Kesling and Chilman 1975). An additional factor in the acquisition of brooding may have been rapid sediment influx. The Michigan Basin was commonly subjected to high clastic sediment influx associated with mountain building occurring as part of Appalachian Orogeny (Bird and Dewey 1970). This created an unstable sediment–water interface, which can be described as ‘soupy’ in consistency (Harris and Martin 1979) where tiered or organisms or those with large surface areas could raise or float respectively above the gelatinous sediment and act as ‘hard substrates’ for epizoan attachment (Wiedman 1985); however, larvae and juveniles would have occupied much lower heights close to the unstable substrate, and this could have made it difficult for them to maintain their position in the face of highly energetic currents (Oji 1996) and left them unprotected against predation or parasitism. By internally brooding larvae, *H. reimanni* would thus have enhanced the chances of young surviving into adulthood in a hostile environment. The only other known example of internal brooding in blastoids is reported in *P. rusticus* (Katz and Sprinkle 1976), from the early Pennsylvanian of northeast Oklahoma, which was also subjected to large terrigenous influx during the Pennsylvanian, particularly the Morrowan

(Sutherland and Henry 1977; Heckel 2013), suggesting this might be a common driver in the acquisition of brooding by some extinct echinoderms.

The fossilized evidence of internal brooding of larval blastoids described herein represents only the second known occurrence of this reproductive strategy in blastoids (Katz and Sprinkle 1976) and is the oldest evidence of this behaviour in echinoderms. To the best of our knowledge, this is also the earliest example of brooding within the coelomic cavity by any invertebrate. This has major implications for studying the taxonomy and phylogeny of blastoids, as well as for ecological reconstructions of past marine ecosystems. Anatomical and systematic studies of blastoids currently do not consider sexual dimorphism as a possible morphological trait in blastoid phylogenies, which would have an effect on the identification and classification of representatives of the group. Furthermore, internal brooding in blastoids suggests other environmental stresses, whether biotic or abiotic, were important controls on their palaeocommunities and should be taken into consideration in future reconstructions.

Conclusion

We describe a new specimen of the blastoid echinoderm *Hyperoblastus reimanni*, which preserves internal organs within the coelomic system, as well as three internally brooded larvae. This represents the earliest example of brooding by an echinoderm and indicates that blastoids were sexually dimorphic at least 385 million years ago. Our findings reinforce the utility of synchrotron tomography for studying the internal anatomy of exceptionally

preserved fossils, providing new insights into the palaeobiology of extinct taxa.

Data availability statement

The full dataset associated with this study, including synchrotron raw files and 3D reconstruction, is available from MorphoSource (<https://www.morphosource.org/projects/000490038>). Individual DOIs are listed in Appendix S1

Supporting information

Appendix S1. List of MorphoSource DOIs associated with this study.

Author contributions. NÁ-A, IAR and JEB conceived the study. NÁ-A performed the technical work in collecting and analysing the data. NÁ-A drafted the original manuscript and all other authors contributed to further versions, read and approved the final manuscript.

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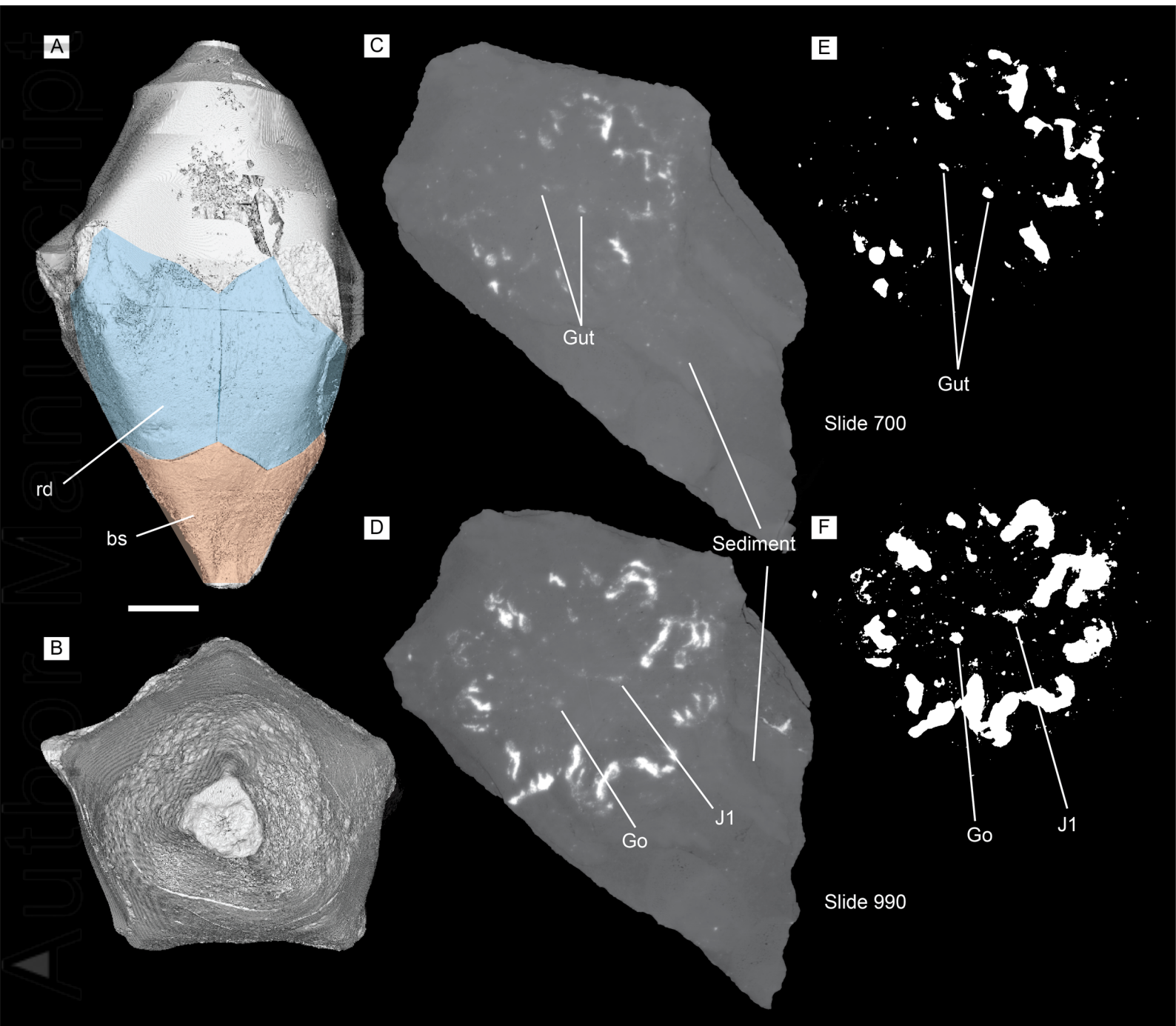
Fig. 1. 3D reconstructions (A, B) and slice images (C–F) of *Hyperoblastus reimanni*. A, lateral view of the theca showing the basals (red) and the radials (blue). B, aboral view of the theca displaying the triangular base. C–D, slices showing internal structures of interest. E–F, thresholded images corresponding to C and D, respectively. *Abbreviations:* bs, basal plate; Go, gonad; J1, juvenile 1; rd, radial plate. Scale bar represents 1 mm.

Fig 2. 3-D reconstructions of the internal structures of *Hyperoblastus reimanni*. A, diagram of the reconstructed internal structures in the thecal cavity: gut (pink), hydrospires (purple), coelom (orange), empty space within the vault (green), brooded juveniles (light blue), gonad (dark blue) and structure 1 (grey). These structures are highlighted in purple: B, gut and the associated organs; C, hydrospire system; D, coelom; E–F, position of the brooded juveniles encased by the hydrospires system shown in aboral (E) and adoral (F) view; G, position of the brooded juveniles within the thecal cavity; H, organs of the reproductive system (gonad and brooded juveniles) with the gut in a central position; I–J, organs of the reproductive system shown in aboral (I) and adoral (J) view. *Abbreviations:* A–E, ambulacra; Go, gonad; J1, juvenile 1; J2, juvenile 2; J3, juvenile 3; S1, structure 1. Scale bar represents 1 mm.

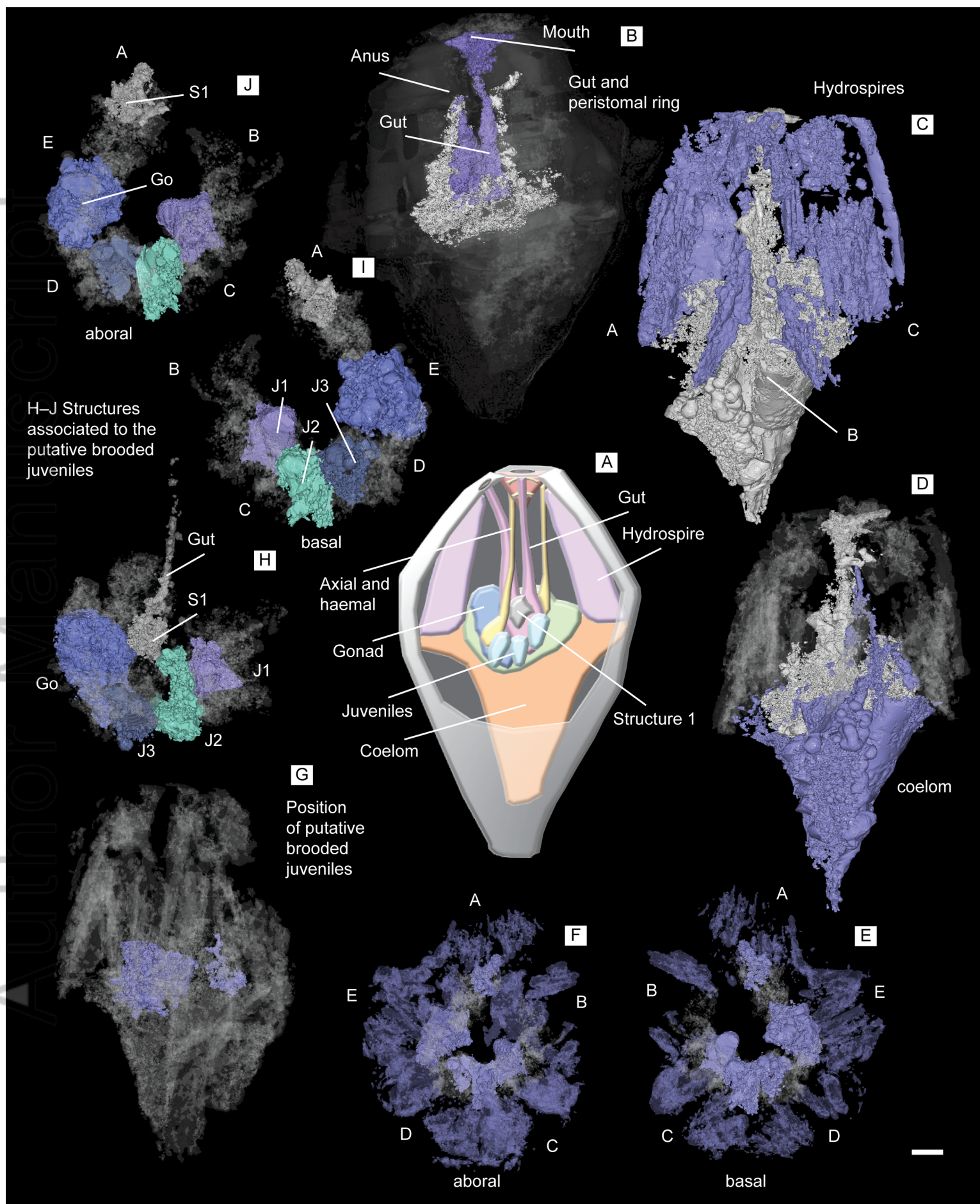
Fig. 3. 3-D reconstructions of brooded juveniles of *Hyperoblastus reimanni* compared to camera lucida drawings of juveniles of the blastoid *Pentremites pulchellus*. Lowermost set of images redrawn from Sevastopulo (2005). *Abbreviations:* A–E, ambulacra; J1, juvenile 1; J2, juvenile 2; J3, juvenile 3. Scale bars represent 0.5 mm.

Table 1. Measurements of additional specimens of *Hyperblastus reimanni* and estimates of the size of the anal and oral openings of specimen CMC IP 37403.

Table 2. Anatomical description of *Hyperblastus reimanni*.



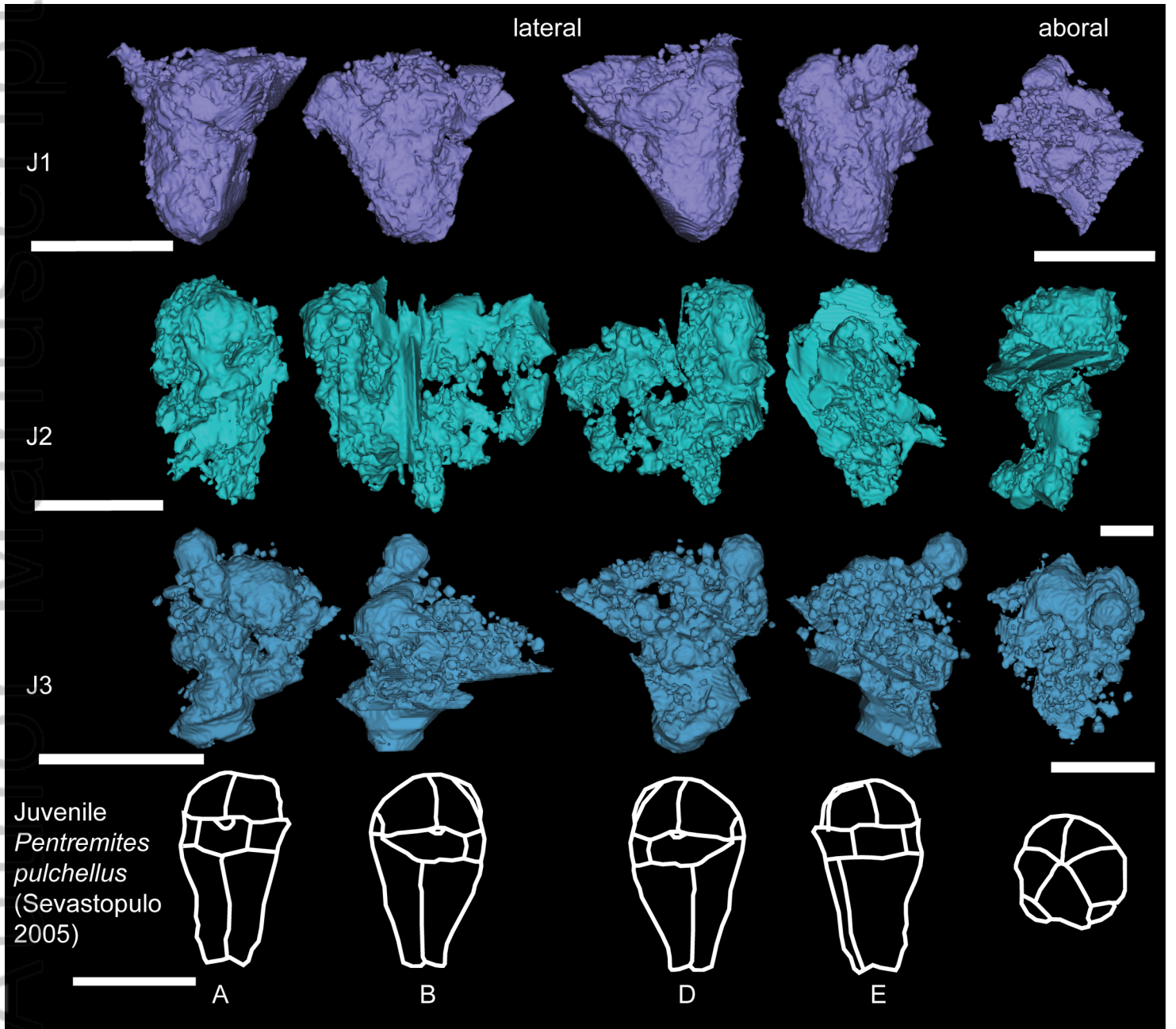
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H-J Structures associated to the putative brooded juveniles

G
Position of putative brooded juveniles

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SPP2_1493_Figure3_166.tif