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

by NIDIA ÁLVAREZ-ARMADA[1],[*] , JENNIFER E. BAUER[2] , JOHNNY A. WATERS[3] *and* IMRAN A. RAHMAN[4],[5]

[1]Independent; nidia.alvarez.armada@gmail.com
[2]University of Michigan Museum of Paleontology, Ann Arbor, Michigan 48109-1085, USA
[3]Department of Geological & Environmental Sciences, Appalachian State University, Boone, North Carolina 28006, USA
[4]The Natural History Museum, London SW7 5BD, UK
[5]Oxford University Museum of Natural History, Oxford OX1 3PW, UK
[*]Corresponding author

Abstract: 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. Here, synchrotron x-ray tomography is used to describe an exceptionally preserved specimen of the Devonian blastoid echinoderm *Hyperoblastus 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 used 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 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 more than 500 myr (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 have a wide range of reproductive strategies including forms of advanced parental investment (Gillespie & McClintock 2007; Barreto & 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 by the mother, and can reduce the negative impact of factors such as predation pressure or high sediment input. Brooding is an energy-expensive behaviour but can greatly increase the survival rate of offspring (Barreto & Bauer 2019), although brooded individuals are usually deprived of the advantages of broad geographical dispersion (Cohen & 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 & Hughes 1998; Caron & 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 present only 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. *Hyperoblastus 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 in the Michigan Basin, which is situated $2\frac{1}{3}$ 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 in 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, UMMP IP 48653, UMMP IP 51593 and 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 at a voltage of 37 keV, 1501 projections each with an exposure time of 600 ms, using the ×2 objective. The tomography 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 2479 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. 2A). 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. 2B). There are 18 well-preserved calcite folds distributed among the five hydrospire pairs (labelled A–E in Fig. 2C, E–F, I–J). 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 the anispiracle (labelled B in Fig. 2C, E–F); 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 *Hyperoblastus*, which do not indicate any reduction of the anal interarea hydrospires (Breimer & Dop 1975).
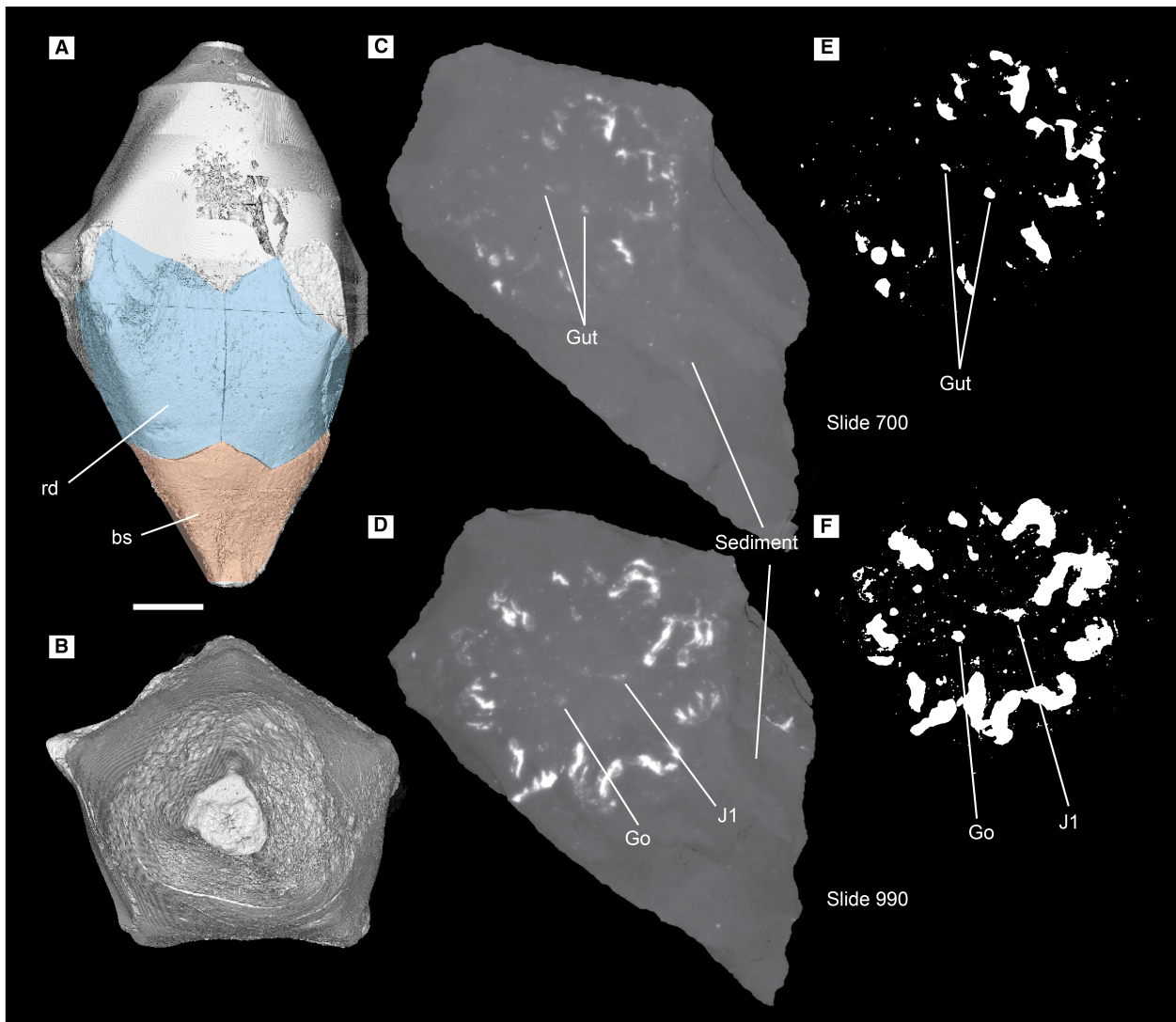
FIG. 1. 3-D reconstructions (A–B) and slice images (C–F) of *Hyperoblastus reimanni* (CMC IP 37404). A, lateral view of the theca showing the basals (red) and the radials (blue). B, aboral view of the theca showing the triangular base. C–D, slices showing internal structures of interest. E–F, thresholded images corresponding to C and D, respectively. *Abbreviations*: bs, basal plate; Go, gonad; J1, juvenile 1; rd, radial plate. Scale bar represents 1 mm.

TABLE 1. Measurements of additional specimens of *Hyperoblastus reimanni*[†] and estimates of the size of the anal and oral openings of specimen CMC IP 37404.

Hyperoblastus reimanni	Length (mm)	Diameter (mm)
UMMP IP 51597 Theca/anal opening	10.89	0.79
UMMP IP 61796 Theca/anal opening	7.74	0.66
UMMP IP 48653 Theca/oral opening	14.77	0.83
UMMP IP 51593 Theca/oral opening	6.73	0.43
UMMP IP 54830 Theca/oral opening	5.64	0.32
CMC IP 37404 Theca/estimated anal and oral openings	7.00	Anal 0.67 Oral 0.45

The mouth leads to a vertical tube, which is bent at the base of the ambulacra to return aborally, and discharges into the anal opening (Fig. 2B). The inner plates of the pelvis are lined with a coiled structure, which is reminiscent of the peripheral subcoelom in adult crinoids (Ezhova & 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 prevents a full reconstruction (Fig. 2D).

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. 2E–I). The first three are in close proximity to each other (labelled J1, J2 and J3 in Figs 2H–J, 3) and located directly below the anal deltoid (labelled D in Fig. 2E–F, I–J). These are similar in shape, but approximately 10-fold 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 2H–I, 3).
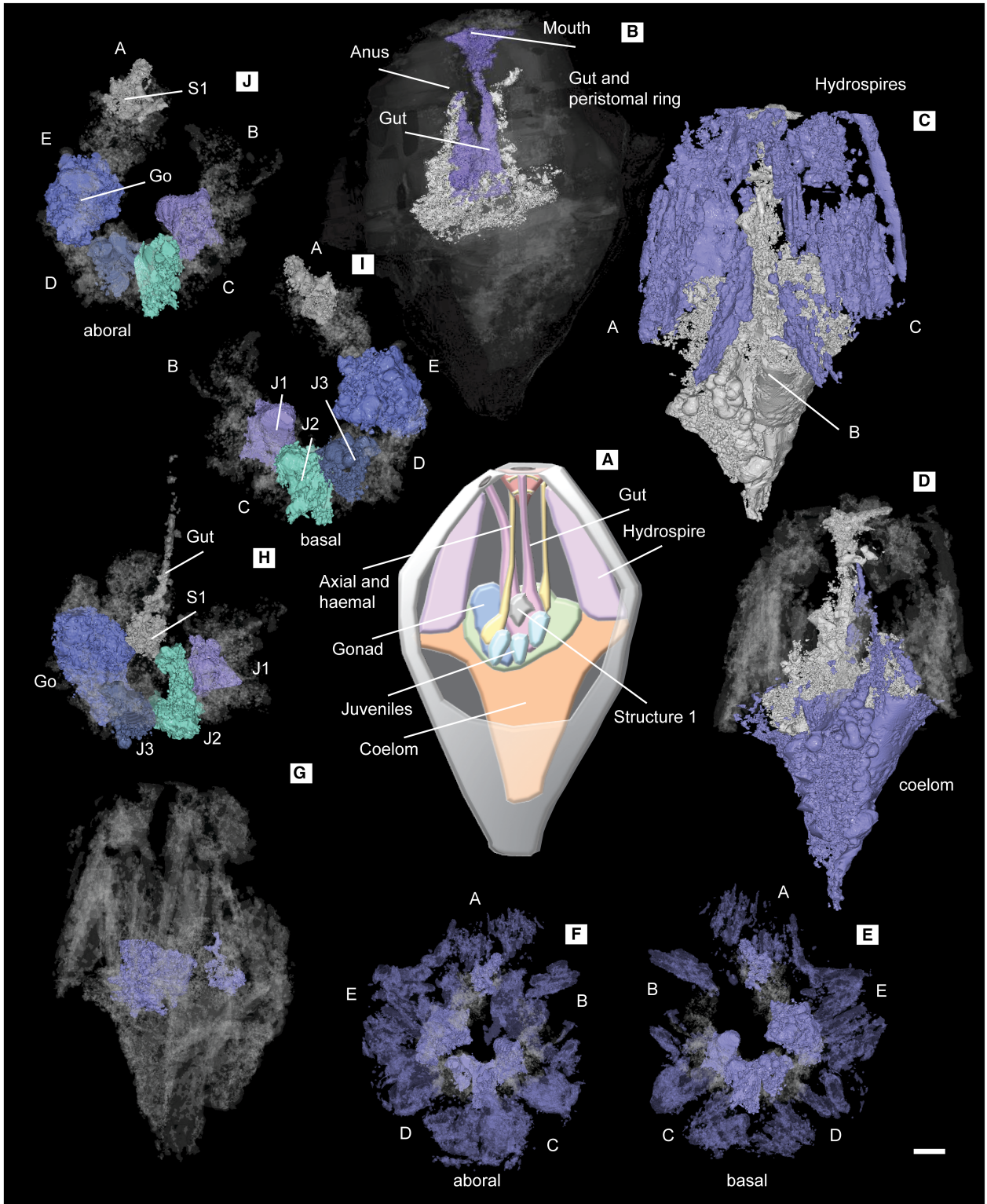
FIG. 2. 3-D reconstructions of the internal structures of *Hyperoblastus reimanni* (CMC IP 37404). A, diagram of the reconstructed internal structures in the thecal cavity: gut (pink), hydrospires (purple), coelom (orange), empty space inside the vault (green), brooded juveniles (light blue), gonad (dark 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 hydrospire system shown in aboral (E) and adoral (F) view; G, position of the brooded juveniles inside 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; J1–3, juveniles 1–3; S1, structure 1. Scale bar represents 1 mm.

The fourth structure is larger, and is situated between the anal and buccal openings (labelled Go in Fig. 2H, J). The fifth structure is oval shaped and attached to a wide tube that does not seem to connect to any other structure (labelled S1 in Fig. 2H, J). 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
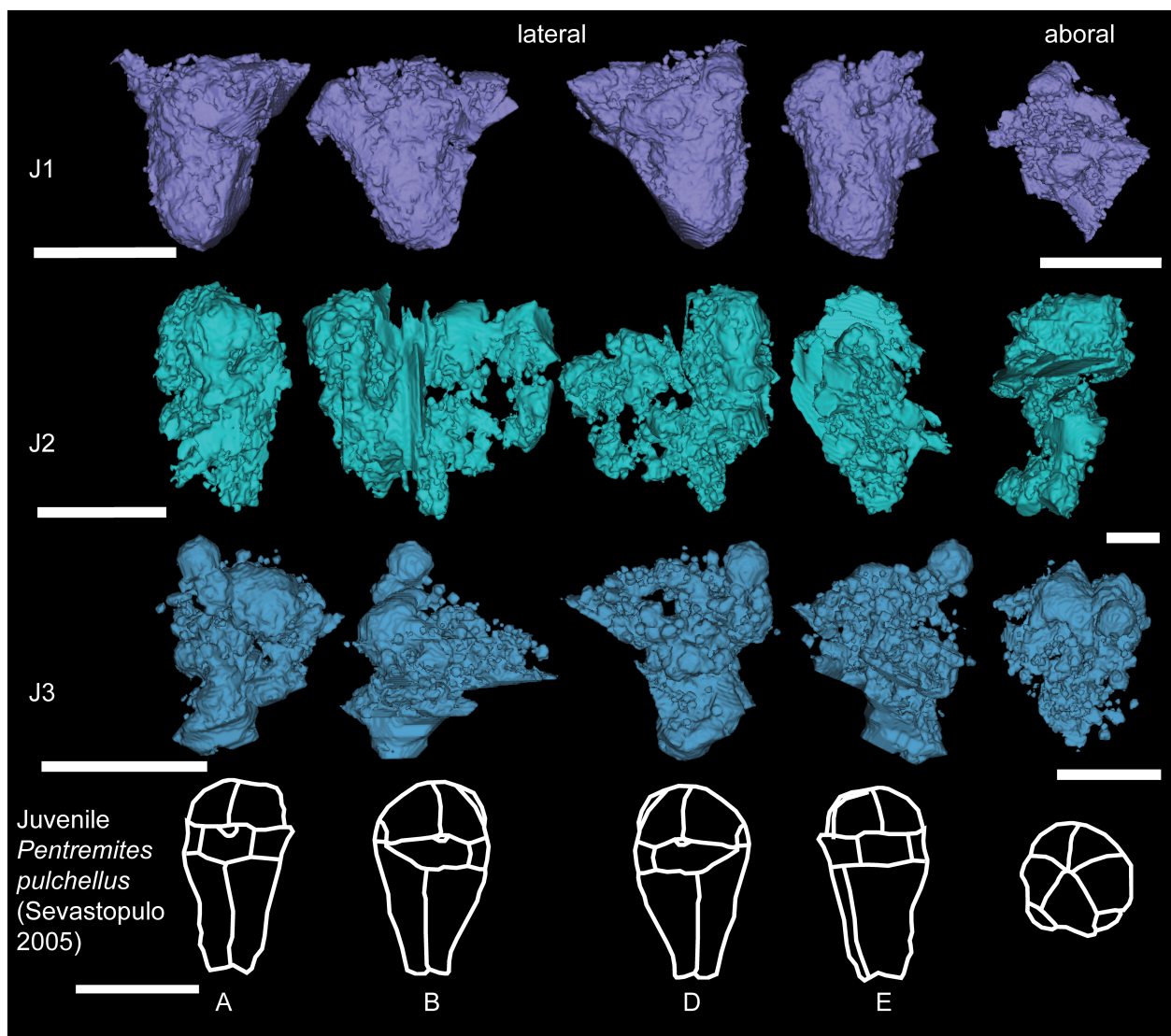

FIG. 3. 3-D reconstructions of brooded juveniles of *Hyperoblastus reimanni* (CMC IP 37404) compared with camera lucida drawings of juveniles of the blastoid *Pentremites pulchellus*. Lowermost set of images redrawn from Sevastopulo (2005). *Abbreviations*: A–B, D–E, ambulacra; J1–3, juveniles 1–3. Scale bars represent 0.5 mm.

TABLE 2. Anatomical description of *Hyperoblastus reimanni*.

Hyperoblastus reimanni (CMC IP 37404)	Description	Dimensions (mm)	
		Height	Diameter
Theca	Cone-shaped with visible sutures	*c.* 7	4.5
Gut	Circular to elliptical in cross-section connecting through a bend at the base creating a well-defined U-shape bend	4.1	0.3–0.4
Axial and haemal glands	Not connected to each other and appear to expand at their base	2.4–2.8	0.2–0.8
Coelom	Conical	3.3	2.6
Juveniles 1–3	Cone-shaped with no visible sutures	0.6–0.8	0.5–0.6
Gonad	Oval	1.5	1.0
Structure 1	Oval-shaped basal part attached to a wide tube	0.6	0.3–0.7

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. 2B). 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 mm 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. 2B), 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 & Bell 1980; Ezhova & Malakhov 2020). We interpret it as part of the coelomic cavity (Fig. 2D). 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. 2B, D). 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 (Bargmann & Von Hehn 1968; Ezhova & Malakhov 2020; Saulsbury

& Zamora 2020). Consequently, we infer that the two vertical tubes are vestiges of the axial and haemal systems (Fig. 2B).

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 size (Fig. 2G; Table 2) and the fact that the theca is preserved intact (Fig. 1A). As per our estimation, the size of these structures would not have permitted ingestion (Tables 1, 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 the other structures; it is interpreted as possible pyrite growth in the pelvic region (Fig. 2I–J). The structures labelled J1–J3 and Go are located close together in the CD interray (Fig. 2H–J), which has been suggested to play an active role in reproduction by housing eggs prior to their release into the water column (Katz & 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 & Geis 1940; Sevastopulo 2005), particularly *Pentremites* (Fig. 3). Although blastoids are expected to have 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 used an advanced mode of reproduction involving brooding of young to the larval stage.

Our reconstruction also shows a larger internal structure in the CD interray possibly associated with the reproductive system, which we interpret as the gonad (labelled Go in Fig. 2H, J). 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 through the anal opening (Breimer & Macurda 1972; Katz & Sprinkle 1976), and is 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 of, but greatly enlarged, hydrospires in the anal area (Katz & Sprinkle 1976; Bauer *et al.* 2019); although this does not occur in *Hyperoblastus*, it is possible that the anal hydrospires could increase in volume and were

modified specifically for brooding. The larvae in 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. 2E–F). Several species of modern echinoderms brood young inside the mother's body. In some instances, brooding takes place in special chambers inside the mother's body, and young acquire nutrients via the coelomic fluid; various species of living Asteroidea, Holothuroidea, Ophiuroidea and Crinoidea are known to show 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 (Table 1), 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. filosus* with comparable body size to our specimen (Breimer & Dop 1975). The size of this gonopore is small, *c.* 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. filosus* was male and that the exit of young from the body in female specimens 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 used 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 & 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 the Appalachian Orogeny (Bird & Dewey 1970). This created an unstable sediment–water interface, which can be described as 'soupy' in consistency (Harris & Martin 1979), in which tiered organisms or those with large surface areas could rise or float, respectively, above the gelatinous sediment and act as 'hard substrates' for epizoan attachment (Wiedman 1985). Larvae and juveniles, however, would have occupied much lower depths close to the unstable substrate, and this could have made it difficult for them to maintain their position in the face of high-energy currents (Oji 1996) and left them unprotected against predation or parasitism. By internally brooding their 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 & Sprinkle 1976), from the Early Pennsylvanian of northeast Oklahoma, which was also subjected to large terrigenous influx during the Pennsylvanian, particularly the Morrowan (Sutherland & Henry 1977; Heckel 2013), suggesting that 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 here represents only the second known occurrence of this reproductive strategy in blastoids (Katz & 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 inside 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 that 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 *H. reimanni*, which preserves internal organs inside 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 *c.* 385 Ma. 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 ARCHIVING STATEMENT

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

Editor. Jeffrey Thompson

SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1002/spp2.1493):

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

REFERENCES

BALSER, E. J. 2002. Phylum Echinodermata: Crinoidea. 463–482. *In* YOUNG, C. M., SEWELL, M. A. and RICE, M. E. (eds) *Atlas of marine invertebrate larvae.* Academic Press, 691 pp.

BARGMANN, W. and VON HEHN, G. 1968. Über das Axialorgan ("mysterious gland") von *Asterias rubens* L. *Zeitschrift für Zellforschung und Mikroskopische Anatomie*, **88**, 262–277.

BARRETO, F. S. and BAUER, K. K. 2019. Genetic evidence for alloparental care and frequent multiple paternity in the brooding sea star (*Leptasterias* sp.). *Marine Biology*, **166**, 38.

BAUER, J. E. 2018. Respiratory structure morphology, group origins, and phylogeny of Eublastoidea (Echinodermata). PhD thesis, University of Tennessee, 156 pp. https://trace.tennessee.edu/utk_graddiss/4949

BAUER, J. E., SUMRALL, C. D., WATERS, J. A., ZAMORA, S. and RAHMAN, I. A. 2017. Hydrospire morphology and implications for blastoid phylogeny. *Journal of Paleontology*, **91**, 847–857.

BAUER, J. E., WATERS, J. A. and SUMRALL, C. D. 2019. Redescription of *Macurdablastus* and redefinition of Eublastoidea as a clade of Blastoidea (Echinodermata). *Palaeontology*, **62**, 1003–1013.

BIRD, J. M. and DEWEY, J. F. 1970. Lithosphere plate-continental margin tectonics and the evolution of the Appalachian orogen. *Geological Society of America Bulletin*, **81**, 1031–1060.

BREIMER, A. and DOP, A. 1975. An anatomic and taxonomic study of some Lower and Middle Devonian blastoids from Europe and North America. *Verhandelingen der Koninklijke Nederlande Akademie Van Wetenschappen B*, **78**, 39–61.

BREIMER, A. and MACURDA, D. B. Jr 1972. The phylogeny of the fissiculate blastoids. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen B*, **26**, 13–390.

BRETT, C. E., MOFFAT, H. A. and TAYLOR, W. L. 1997. Echinoderm taphonomy, taphofacies, and Lagerstätten. *The Paleontological Society Papers*, **3**, 147–190.

CARON, J.-B. and VANNIER, J. 2016. *Waptia* and the diversification of brood care in early arthropods. *Current Biology*, **26**, 69–74.

COHEN, A. S. and JOHNSTON, M. R. 1987. Speciation in brooding and poorly dispersing lacustrine organisms. *PALAIOS*, **2**, 426–435.

CRONEIS, C. and GEIS, H. L. 1940. Microscopic Pelmatozoa: part 1, ontogeny of the Blastoidea. *Journal of Paleontology*, **14**, 345–355.

DONOVAN, S. K., WEBSTER, G. D. and WATERS, J. A. 2016. A last peak in diversity: the stalked echinoderms of the Permian of Timor. *Geology Today*, **32**, 179–185.

EHLERS, G. M. and KESLING, R. V. 1970. *Devonian strata of Alpena and Presque Isle counties, Michigan.* Michigan Basin Geological Society, Guide Book for Field Trips, GSA North-Central Section Meeting.

EZHOVA, O. V. and MALAKHOV, V. V. Y. 2020. Axial complex of Crinoidea: comparison with other Ambulacraria. *Journal of Morphology*, **281**, 1456–1475.

FORTEY, R. A. and HUGHES, N. C. 1998. Brood pouches in trilobites. *Journal of Paleontology*, **72**, 638–649.

GILLESPIE, J. M. and McCLINTOCK, J. B. 2007. Brooding in echinoderms: how can modern experimental techniques add to our historical perspective? *Journal of Experimental Marine Biology & Ecology*, **342**, 191–201.

HARRIS, F. W. and MARTIN, W. D. 1979. Benthic community development in limestone beds of the Waynesville (upper Dillsboro) Formation (Cincinnatian Series, Upper Ordovician)

of southeastern Indiana. *Journal of Sedimentary Research*, **49**, 1295–1305.

HAUGH, B. N. 1975. Digestive and coelomic systems of Mississippian camerate crinoids. *Journal of Paleontology*, **49**, 472–493.

HAUGH, B. N. and BELL, B. M. 1980. Fossilized viscera in primitive echinoderms. *Science*, **209**, 653–657.

HECKEL, P. H. 2013. Pennsylvanian stratigraphy of Northern Midcontinent Shelf and biostratigraphic correlation of cyclothems. *Stratigraphy*, **10**, 3–39.

HYMAN, L. H. 1955. *The invertebrates: Echinodermata.* McGraw-Hill, 763 pp.

KATZ, S. G. and SPRINKLE, J. 1976. Fossilized eggs in a Pennsylvanian blastoid. *Science*, **192**, 1137–1139.

KESLING, R. V. and CHILMAN, R. B. 1975. Strata and megafossils of the Middle Devonian Silica Formation. *Papers on Paleontology*, **8**, 408 pp.

LANDSCHOFF, J., DU PLESSIS, A. and GRIFFITHS, C. L. 2015. A dataset describing brooding in three species of South African brittle stars, comprising seven high-resolution, micro X-ray computed tomography scans. *GigaScience*, **4**, 52.

McCLARY, D. and MLADENOV, P. 1988. Brood and broadcast: a novel mode of reproduction in the sea star *Pteraster militaris*. 163–168. *In* BURKE, R. D., MLADENOV, P. V., LAMBERT, P. and PARSLEY, R. L. (eds) *Echinoderm biology: Proceedings of the Sixth International Echinoderm Conference, Victoria, 23–28 August 1987.* A. A. Balkema.

OBUCHI, M., FUJITA, Y., NAKANO, Y., UEHARA, T. and MOTOKAWA, T. 2010. Reproductive biology and early life history of hermaphroditic feather star *Dorometra sesokonis* (Echinodermata: Crinoidea). *Marine Biology*, **157**, 1191–1201.

OJI, T. 1996. Is predation intensity reduced with increasing depth? Evidence from the west Atlantic stalked crinoid *Endoxocrinus parrae* (Gervais) and implications for the Mesozoic marine revolution. *Paleobiology*, **22**, 339–351.

PEARSE, J. S. 1994. Cold-water echinoderms break Thorson's rule. 26–43. *In* YOUNG, C. M. and ECKELBARGER, K. J. (eds) *Reproduction, larval biology and recruitment in the deep-sea benthos.* Columbia University Press, 336 pp.

PERTOSSI, R. M., PENCHAZADEH, P. E. and MARTINEZ, M. I. 2021. Brooding comatulids from the southwestern Atlantic, Argentina (Echinodermata: Crinoidea). *Marine Biodiversity*, **51**, 59.

RAHMAN, I. A., WATERS, J. A., SUMRALL, C. D. and ASTOLFO, A. 2015. Early post-metamorphic, Carboniferous blastoid reveals the evolution and development of the digestive system in echinoderms. *Biology Letters*, **11**, 20150776.

SAULSBURY, J. and ZAMORA, S. 2020. The nervous and circulatory systems of a Cretaceous crinoid: preservation, palaeobiology and evolutionary significance. *Palaeontology*, **63**, 243–253.

SCHERER, A. E., BIRD, C. E., McCUTCHEON, M. R., HU, X. and SMEE, D. L. 2018. Two-tiered defense strategy may compensate for predator avoidance costs of an ecosystem engineer. *Marine Biology*, **165**, 131.

SEVASTOPULO, G. D. 2005. The early ontogeny of blastoids. *Geological Journal*, **40**, 351–362.

SMITH, A. B. 2005. The pre-radial history of echinoderms. *Geological Journal*, **40**, 255–280.

SMITH, A. B., ZAMORA, S. and ALVARO, J. J. 2013. The oldest echinoderm faunas from Gondwana show that echinoderm body plan diversification was rapid. *Nature Communications*, **4**, 1385.

SUTHERLAND, P. K. and HENRY, T. W. 1977. Carbonate platform facies and new stratigraphic nomenclature of the Morrowan Series (Lower and Middle Pennsylvanian), northeastern Oklahoma. *Geological Society of America Bulletin*, **88**, 425–440.

SUTTON, M. D., GARWOOD, R. J., SIVETER, D. J. and SIVETER, D. J. 2012. SPIERS and VAXML; a software toolkit for tomographic visualisation and a format for virtual specimen interchange. *Palaeontologia Electronica*, **15**, 289.

VIEIRA, E. A., DUARTE, L. F. L. and DIAS, G. M. 2012. How the timing of predation affects composition and diversity of species in a marine sessile community? *Journal of Experimental Marine Biology & Ecology*, **412**, 126–133.

WIEDMAN, L. A. 1985. Community paleoecological study of the Silica Shale equivalent of northeastern Indiana. *Journal of Paleontology*, **59**, 160–182.