

Hydrospire morphology and implications for blastoid phylogeny

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Abstract.—The external expression of hydrospires in blastoids has provided a basis for major and minor group classification in the clade for over a century. Unfortunately, the complete anatomy of the hydrospires has never been comprehensively studied. This study examined and described the internal hydrospires of six spiraculate species by digitally extracting hydrospire data from a legacy data set of serial acetate peels. Although only six models have been currently generated, hydrospire morphology is variable both within and between previously described spiraculate families. Hydrospires were found to possess novel characters that were incorporated into a phylogenetic analysis of the six digitally modeled species and several related species. The addition of internal morphology into the phylogenetic analysis provides further resolution between groupings of blastoids.

Introduction

Present understanding of blastoid phylogeny is insufficient. The current phylogenetic hypothesis does not include sufficient taxa to make robust interpretations of the evolutionary relationships among previously described groupings or even to verify their monophyly. External character data for blastoids have been accumulating for nearly 200 years and have been used over the past several decades in a variety of morphometric- and phylogenetic-based analyses (Foote, 1991; Waters and Horowitz, 1993; Bodenbender, 1995; Bodenbender and Fisher, 2001; Atwood and Sumrall, 2012; Sumrall and Waters, 2012; Atwood, 2013). A recent study by Atwood (2013) generated a phylogenetic framework to describe the synapomorphies and subclade relationships among blastoids. Unfortunately, our understanding of internal morphology is poor, and consequently, internal character data (with the exception of number of hydrospires) have been largely ignored, limiting character evidence of phylogenetic relationships.

Respiratory structures of blastozoan echinoderms are utilized as synapomorphies for clades and often are used to delineate species. Endothelial respiratory structures such as blastoid hydrospires, parablattoid cataspores, and dichopores of both glyptocystitoids and hemicosmitids are lightly calcified and typically well preserved in specimens with complete thecae (Paul, 1968; Sprinkle, 1973; Sprinkle and Sumrall, 2008; Sumrall and Waters, 2012). These structures can be examined by serially sectioning specimens (Beaver et al., 1967; Breimer, 1988a, b; Dexter et al., 2009; Schmidting and Marshall, 2010) or in some cases through X-ray computed tomography (Rahman and Zamora, 2009; Waters et al., 2014; Rahman et al., 2015). This study focuses on examining the internal respiratory hydrospires of Blastoidea to provide additional character data for subsequent phylogenetic analysis.

Echinoderm homology.—Blastoidea is a diverse clade of Paleozoic stemmed echinoderms with a highly conservative body construction. Unlike many Paleozoic blastozoan echinoderms with irregular plating, blastoid thecal plating consists of 18–21 stable plates that are identifiable among all individuals within the clade. A wide variety of thecal shapes are identified in different blastoid clades (Beaver, 1967), and determining which plates form these morphologies provides a well-constrained framework to understanding the evolution of morphology in the clade. Blastoids are a long-lived clade, extending from the Late Ordovician to the late Permian, providing an opportunity to examine morphological and evolutionary patterns through time (Foote, 1991).

Reconciling blastoid morphologies with those of other blastozoans has been difficult because the morphologies of blastoids are unusually derived and the terminology applied is unique to the clade (Sumrall and Waters, 2012; Kammer et al., 2013). The universal elemental homology (UEH) model (Sumrall, 2010; Sumrall and Waters, 2012) for classifying homologous elements of the oral area and ambulacra among blastozoans provides a theoretical framework for understanding element homology in extinct echinoderms and reduces confusion caused by the unique blastoid terminology. Unfortunately, current character matrices (Bodenbender, 1995; Atwood, 2013) lack the explicit structure outlined by UEH and need to be reexamined to better capture character changes for phylogenetic analysis.

Blastoid systematics.—Traditionally, Blastoidea has been separated into two orders: Fissiculata and Spiraculata. These groupings are based on details of the external expression of the endothelial respiratory structures called hydrospires (Jaekel, 1918; Wanner, 1940; Fay, 1967). There are two common morphotypes of the external expression: fissiculates, which possess hydrospire slits, and spiraculates, which possess incurrent hydrospire pores at the edge of the ambulacra and excurrent spiracles, which are small,

external openings at the end of completely internal hydrosfire folds (Waters, 1988; Fig. 1).

These morphological groups have been examined separately on several occasions over the past 50 years (Breimer and Macurda, 1972; Macurda, 1983; Breimer, 1988a, b; Waters and Horowitz, 1993), but few studies have utilized rigorous phylogenetic methodologies to evaluate evolutionary relationships (Bodenbender, 1995; Bodenbender and Fisher, 2001). The results of a recent phylogenetic analysis by Atwood (2013) suggested that spiraculates are polyphyletic and nested within a larger fissiculate clade, agreeing with previous studies (Waters, 1990; Waters and Horowitz, 1993). In addition, several blastoids, such as *Pentremoblastus* and *Conuloblastus*, appear to be transitions between the fissiculate and spiraculate morphotypes. These genera have hydrosfire slits that lead to bean-shaped or underdeveloped spiracles or have well-developed spiracles and hydrosfire slits only partially covered by ambulacral side plates.

Hydrosfire morphology

Respiratory structures of extinct blastozoan echinoderms are diverse, highly variable, and often clade defining (Paul, 1968, 1972; Sprinkle, 1973; Schmidting and Marshall, 2010). The pores and associated structures of many blastozoans have been examined (Paul, 1968, 1972), but the explicit study of blastoid respiratory structures is lacking. Many studies (not limited to Breimer and Macurda, 1965; Macurda, 1967, 1969, 1975; Breimer and Joysey, 1968; Breimer et al., 1968; Breimer, 1970; Breimer and Dop, 1975; Macurda and Breimer, 1977) incorporated a thorough report of hydrosfire structure into systematic descriptions, but few studies (Beaver, 1967; Dexter et al., 2009; Schmidting and Marshall, 2010; Huynh et al., 2015) primarily discuss function or efficiency of these structures.

The respiratory structures of blastoids (i.e., hydrosfires) were lightly calcified, porous, and fold-like internally (Beaver, 1967; Sprinkle, 1973). The two main morphotypes, fissiculate and spiraculate, are different both externally and internally. Fissiculates possess hydrosfire slits, which are open to the exterior along the length of the hydrosfire fold but are either covered by side plates or exposed above them and cross the deltoid-radial suture (Fig. 1.2). Spiraculates possess incurrent pores that line the ambulacra and are either positioned between the side plates or penetrate the adjacent radial and/or deltoid plate (Fig. 1.1).

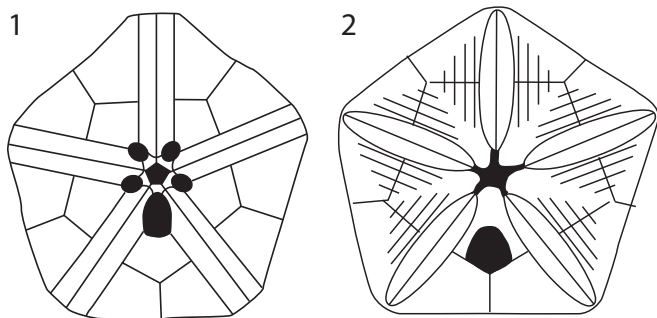


Figure 1. Generalized diagrams of the two primary blastoid morphotypes. (1) Spiraculate morphotype with incurrent hydrosfire pores lining the ambulacra leading to four excurrent spiracles and one large anispiracle. (2) Fissiculate morphotype with four slits on each side of and parallel to the ambulacra crossing the radial-deltoid plate boundary. Modified from Beaver (1967).

The incurrent pores lead to hydrosfire folds (ranging from one to 10 in number; Fig. 2) and finally to the excurrent openings, spiracles, at the summit (Sprinkle, 1973; Waters et al., 2017).

Hydrosfire morphology and terminology can be confusing, specifically with the variation with fold number. Terminology herein follows the morphology outlined in Beaver (1967). In spiraculates, hydrosfire folds occur at pores (Fig. 2.1–2.3) that are visible on the exterior of the organism. The pore leads to a hydrosfire cleft, which is the portion of the fold between the pore and the final termination at the hydrosfire tube (Fig. 2.1–2.3; hydrosfire tube is synonymous with hydrosfire canal in Schmidting and Marshall, 2010). Some hydrosfire clefts may bifurcate early (Fig. 2.2), whereas others are elongate and rest upon plates to accommodate additional folds (Fig. 2.3). At a given pore, multiple folds can be grouped to form hydrosfire groups (Fig. 2.2, 2.3). The hydrosfire tube is the expanded terminus of the fold that eventually leads to the spiracle opening at the top of the theca. Depending on the genus, this tube may reach the summit as a single spiracle or it may combine with adjacent tubes prior to reaching the summit.

Previous interpretations of these structures have either suggested that hydrosfire walls were: (1) open meshworks that allowed for gaseous exchange between the coelomic fluids and ambient seawater (Macurda, 1973; Beaver, 1996) or (2) consisting of tiny calcite crystals (Beaver, 1967). Most workers assumed that the hydrosfire walls were permeable, but the nature of wall preservation leaves little support for permeable folds (Beaver, 1996). The orientation of the section (perpendicular or oblique to the center axis of the blastoid) determines whether the more complex hydrosfire meshwork is uncovered (Beaver, 1996). Macurda (1973) and Beaver (1996) provided evidence on the nature of the stereomic microstructure of blastoids as composed of a meshwork similar to that of modern echinoderms.

The external expression of hydrosfires forms the basis of differentiation between fissiculates and spiraculates (Beaver et al., 1967); however, the internal architecture of hydrosfires has yet to be studied. Typically, hydrosfire data are drawn and reported from one to several sections near the top or center of the theca (e.g., Breimer et al., 1968; Breimer, 1970; Breimer and Dop, 1975; Macurda and Breimer, 1977). This can provide information on general size and number of folds but not on changes in shape and proportion as they pass through the thecal interior. It is, therefore, critical that in-depth examination of these structures be performed to provide a basis for understanding similarities and differences among taxa so that these data can be included into subsequent phylogenetic analyses. Hydrosfires, unlike other internal structures (such as the gut and reproductive organs), are constructed of thin calcareous walls (Beaver, 1967) and are typically preserved within the theca. As the hydrosfires are internal organs, new visualization methodology had to be developed (Waters et al., 2014, 2015) to digitally render and manipulate complete hydrosfire structures. Preliminary work (Waters et al., 2014, 2015; Bauer et al., 2015) suggests that hydrosfires occur in a variety of forms and are likely important in delineating higher taxonomic groupings.

Materials and methods

Paleozoic echinoderm workers have employed techniques such as producing thin sections or acetate peels to study internal

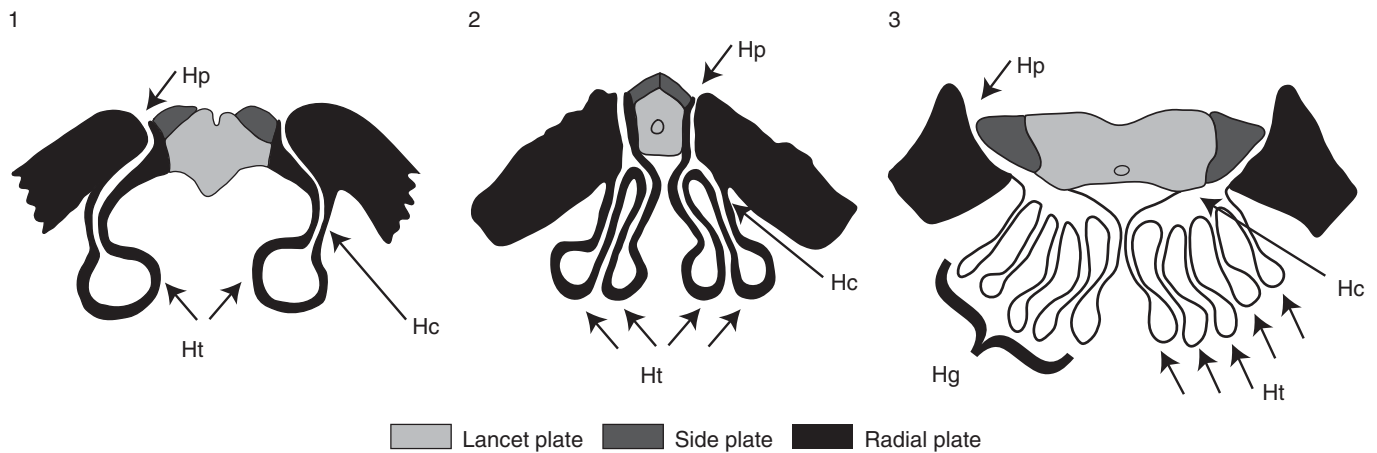


Figure 2. Ambulacral plating in relation to hydrospheres in several representative spiraculate species. (1) *Orbitremites derbiensis* Sowerby, 1825 possessed a single hydrosphere fold with a thin hydrosphere cleft leading to the hydrosphere tube at the end. (2) *Globoblastus norwoodi* (Owen and Shumard, 1850) possessed paired hydrosphere folds with a bifurcating cleft leading to two hydrosphere tubes. (3) *Pentremites godoni* (DeFrance, 1819) possessed five hydrosphere folds within the hydrosphere group; an elongate hydrosphere cleft along the plates accommodates the additional folds. Hc = hydrosphere cleft; Hg = hydrosphere group; Hp = hydrosphere pore; Ht = hydrosphere tube. Modified from Beaver (1967).

morphology of organisms (e.g., Beaver et al., 1967; Beerbower, 1968; Breimer and Dop, 1975; Katz and Sprinkle, 1976, 1977; Broadhead, 1984; Breimer, 1988a, b; Waters and Horowitz, 1993; Dexter et al., 2009; Schmidting and Marshall, 2010). Thin sections and acetate peels of serially sectioned thecae have previously been used to render hydrosphere morphology in 2D (Breimer and Macurda, 1972) as well as 3D (Schmidting and Marshall, 2010; Huynh et al., 2015). A comprehensive investigation of hydrosphere morphotypes has recently begun in three dimensions (Waters et al., 2014, 2015; Bauer et al., 2015). For a more detailed discussion on methodology, see Waters et al. (2014, 2015). Herein, we describe the digital transformation of 2D serial peels into 3D models of hydrosphere morphology for examination and character coding.

Acetate peel data.—A collection of unpublished serial acetate peels contains serial sections of 19 fissiculate species and 27 spiraculate species spanning the taxonomic diversity of Blastoidea. Peels were taken perpendicular to the thecal axis, and some of the peels contain minor flaws (e.g., wrinkles, tears, and bubbles), which can mask internal morphology or result in data loss (Waters et al., 2015). Peels were scanned (by J.A.W.) with a Braun slide scanner at 3,600 dpi and 8-bit grayscale. Once scanned, the peels were resized and compiled in Adobe Photoshop (Fig. 3.1) and the hydrospheres were located and traced on each peel (Fig. 3.2). Once completed, the original photo layers were hidden, and what remained was a series of drawings that traced the hydrospheres vertically through the theca. The image was then compressed and transferred into Rhinoceros, an industrial design program used to render 2D images in 3D. Within Rhinoceros, the images were connected to generate complete hydrosphere structures (Fig. 3.3, 3.4).

Phylogenetic analysis.—As this work is ongoing, a phylogeny incorporating all known blastoid taxa is not currently available. Previously utilized external character data are undergoing large-scale revision to provide a more complete data set to generate character suites that better characterize large morphological change (Supplemental Data 1). Herein, we investigate taxa that

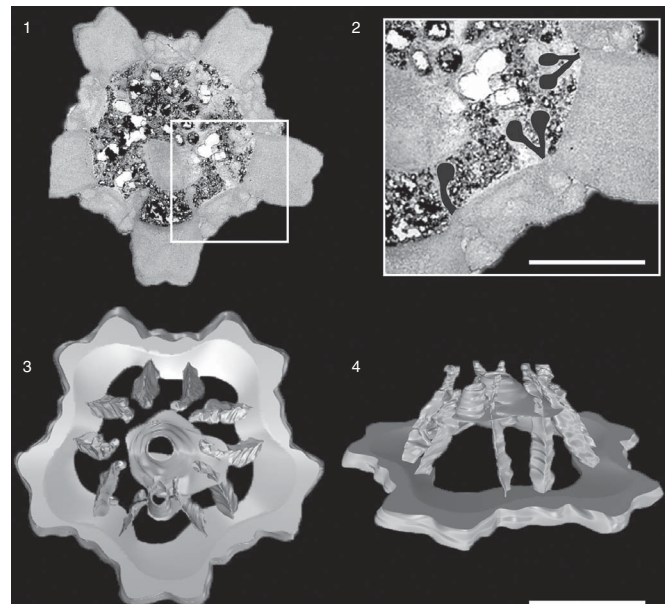


Figure 3. *Deloblastus permicus* is an example of anatomical model reconstruction methodology. (1) Digital transverse slices are cut out and aligned in the same direction. Target areas of internal morphology can be identified as seen by the white box. (2) This enlarged box of (1) shows the hydrospheres in the target area traced in black. Scale bar represents 0.5 cm. (3) Aerial and (4) oblique lateral view of completed *D. permicus* model. (2) Scale bar = 0.5 cm; (3, 4) scale bar = 1 cm. Modified from Waters et al. (2014) and Bauer et al. (2015).

have completed internal models in addition to several other taxa that have been suggested to be closely related (Atwood, 2013). The objective is to assess whether the addition of hydrosphere data, although currently limited, has an effect on tree topology. Phylogenetic analysis was performed via maximum parsimony in PAUP* 4.0b10 (Swofford, 2003). Characters were equally weighted and unordered and examined via exhaustive search parameters (Supplemental Data 2). The outgroup taxon was *Stephanocrinus angulatus* Conrad, 1842 based on sister taxon relationships identified in previous studies (Sprinkle, 1973; Broadhead, 1982, 1984; Brett et al., 1983).

Repositories and institutional abbreviations.—Unpublished serial acetate peels repositied in the Naturalis Biodiversity Center in Leiden, Netherlands, were utilized for this study (Breimer and van Egmond, 1968). Raw scanned peel data are available in Supplemental Data 3–8.

Results and discussion

Hydrospire morphology.—There have been six models generated thus far: *Monoschizoblastus rofei* (Etheridge and Carpenter, 1882) (Fig. 4.13–4.15), *Ellipticoblastus ellipticus* (Sowerby, 1825) (Fig. 4.10–4.12), *Diploblastus glaber* (Meek and Worthen, 1869) (Fig. 4.7–4.9), *Deltoblastus permicus* (Wanner, 1910) (Fig. 4.4–4.6), *Cryptoblastus melo* (Owen and Shumard, 1850) (Fig. 4.16–4.18), and *Pentremites godoni* (DeFrance, 1819) (Fig. 4.1–4.3). All of these taxa have spiraculate morphologies and represent the late Paleozoic spiraculate gross body plan. Examination and description of hydrospire structure from the completed models show them to be character-rich and allow the identification of several novel characters. The number of hydrospire folds has previously been used to delineate taxa, and by including this character in the analysis, it will be possible to test the validity of using hydrospire count to erect taxa.

The number of hydrospire folds in each group (i.e., the series of folds that form a single respiratory structure) varies between the models. The numerous species of *Pentremites* vary in the number of hydrospires per group, and this number can vary between individuals of the same species and ontogenetically (Macurda, 1967; Macurda and Breimer, 1977; Dexter et al., 2009), although this is exceptional. In most taxa with one or two folds, the number is consistent among individuals. However, some taxa have fewer hydrospire folds on the anal side, likely providing additional space for associated structures such as the gonads and/or anus. This can be seen in two of the six models (Fig. 4.1–4.6). In *D. permicus*, for example, hydrospire folds are paired in each group except for those within the CD interray (the anal side), where single folds are present (Fig. 4.4–4.6). This reduction is also seen in *P. godoni*, where the anal side has four folds per group, whereas other groups all contain five folds (Fig. 4.1–4.3). This reduction is not seen in either *E. ellipticus* or *M. rofei*, and these taxa have a single fold per group whereas *D. glaber* and *C. melo* have two folds per group.

Variation of hydrospire morphology suggests their utility to differentiate taxa. Two of the six completed models, *E. ellipticus* and *M. rofei*, are within the traditionally described family, Orbitremitidae, but show variable hydrospire morphology (Fig. 4.10–4.15). *Ellipticoblastus ellipticus* (Fig. 4.10–4.12) has hydrospire fold pairs that begin nearly the same distance apart as

those of *M. rofei* (Fig. 4.13–4.15) but remain closer together as they extend vertically toward the spiracles. The paired hydrospire folds of *M. rofei* bow outward slightly prior to tapering nearer to the spiracle openings (Fig. 4.13). The number of hydrospire folds in each group also varies between families. *Diploblastus glaber* (Fig. 4.7–4.8) and *D. permicus* (Fig. 4.4–4.5) show two folds within each group, whereas both *E. ellipticus* and *M. rofei* have a single fold per group.

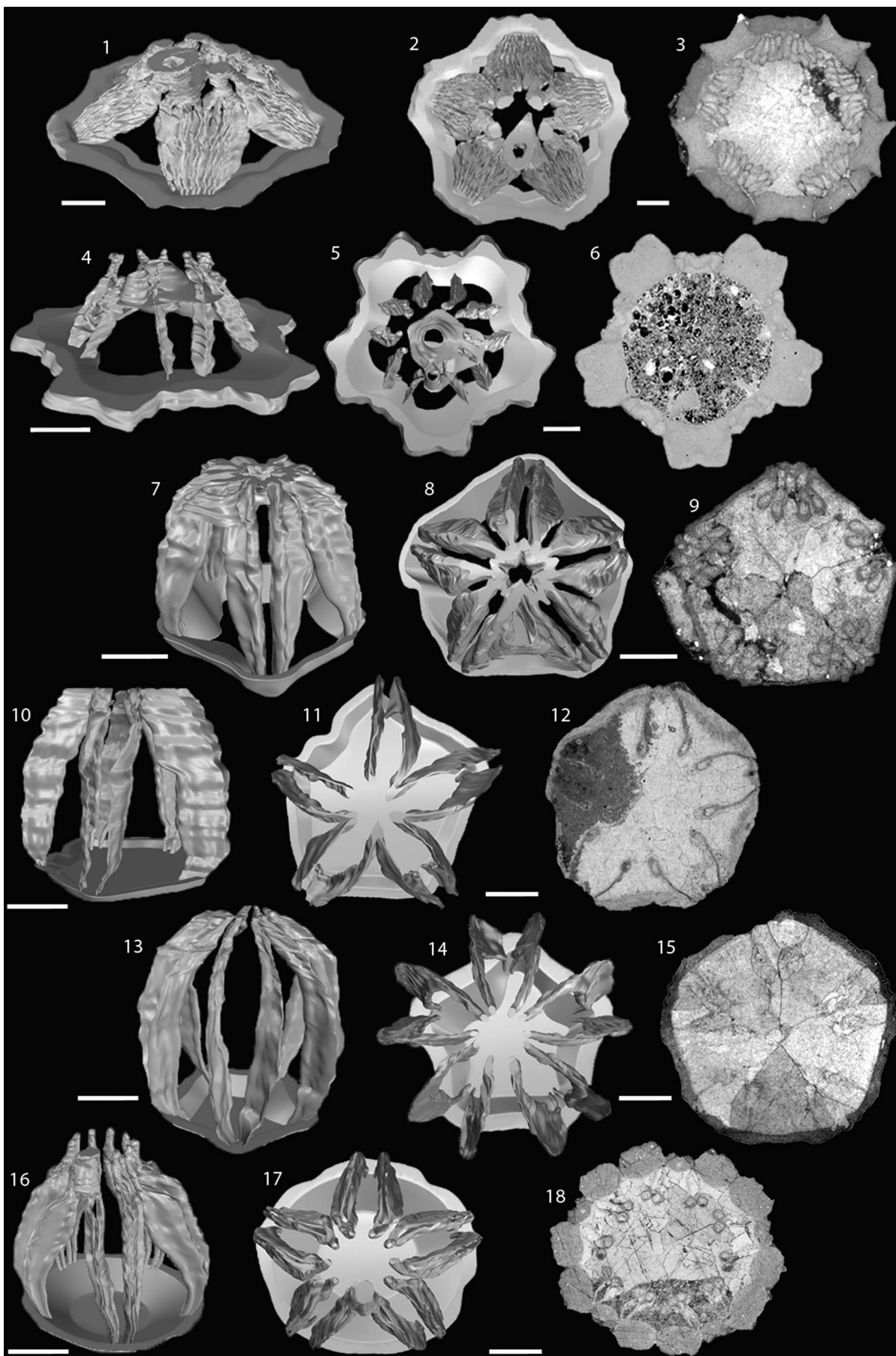
In addition, the surface area of the fold is variable between the generated models. *Deltoblastus permicus* (Fig. 4.4–4.6), *M. rofei* (Fig. 4.13–4.15), and *C. melo* (Fig. 4.16–4.18) all have folds that extend shallowly into the coelomic cavity compared to *E. ellipticus* (Fig. 4.10–4.12) and *D. glaber* (Fig. 4.7–4.9), both of which extend further into the coelomic cavity. Rather than increasing the extent of the folds, *P. godoni* (Fig. 4.1–4.3) has additional narrow folds to increase the surface area. The variation in surface area is likely directly related to gaseous exchange between the hydrospires and the coelomic cavity (Dexter et al., 2009). The hydrospire cleft (Fig. 2) is also variable among these species and may be related to changing the surface area of the fold. *Monoschizoblastus rofei* possesses a long, thin cleft (Fig. 4.14), whereas *D. glaber* has a short, stout cleft (Fig. 4.9). *Pentremites godoni* has an elongate cleft to accommodate the additional folds present at each pore.

Notable variation exists for the ratio of hydrospire pores to hydrospire folds to spiracular openings. In *M. rofei*, there is a single fold per pore, and each of these folds extends through the theca and is expressed as an individual spiracle at the summit (Fig. 4.13, 4.14). Conversely, in *P. godoni*, there are five folds per pore that merge into a single tube that extends toward the summit. Finally, this tube merges with an adjacent tube to be expressed as a spiracle at the summit (Fig. 4.14).

Although only six models were generated for this study, all of the spiraculate morphotype, it is clear there is significant variation both between and within previously described families. Additional models of all morphotypes will result in an increased understanding of variation and similarities between hydrospire structures.

Blastoid phylogeny.—The morphology described in the preceding provides a baseline to evaluate internal character data for blastoids. Preferably, all of the taxa used to infer blastoid phylogeny would be represented by species for which there are both specimens to code external morphology and peel data to code internal morphology. As there were only a few taxa (nine) in this analysis, character data had to be reduced to examine the relationships between these taxa. This was done by examining all character data as a whole and determining characters that were constant and uninformative among the taxa. The uninformative

Figure 4. (1, 2) Anatomical model of respiratory structures of *Pentremites godoni* (DeFrance, 1819) in (1) oblique lateral and (2) aerial views. (3) Representative section of *P. godoni* showing the abundance of folds, elongate cleft, and plate boundaries. (4, 5) Anatomical model of respiratory structures of *Deltoblastus permicus* (Wanner, 1911) in (4) oblique lateral and (5) aerial views; note the reduction of hydrospire folds in the anal area. (6) Representative section of *D. permicus* showing the petite hydrospires and thick plates. (7, 8) Anatomical model of respiratory structures of *Diploblastus glaber* (Meek and Worthen, 1869) in (7) oblique lateral and (8) aerial views. (9) Representative section of *D. glaber* showing paired folds in each group and a stout hydrospire cleft. (10, 11) Anatomical model of respiratory structures of *Ellipticoblastus ellipticus* (Sowerby, 1825) in (10) oblique lateral and (11) aerial views. (12) Representative section of *E. ellipticus* showing the long thin hydrospire cleft of each hydrospire fold. (13, 14) Anatomical model of respiratory structures of *Monoschizoblastus rofei* (Etheridge and Carpenter, 1882) in (13) oblique lateral and (14) aerial views. (15) Representative section of *M. rofei* exhibiting single folds per group. (16, 17) Anatomical model of *Cryptoblastus melo* (Owen and Shumard, 1850) in (16) oblique lateral and (17) aerial views. (18) Representative section of *C. melo* exhibiting short bifurcating hydrospire clefts, circular hydrospire ducts, and clear plate boundaries. All scale bars = 5 mm.



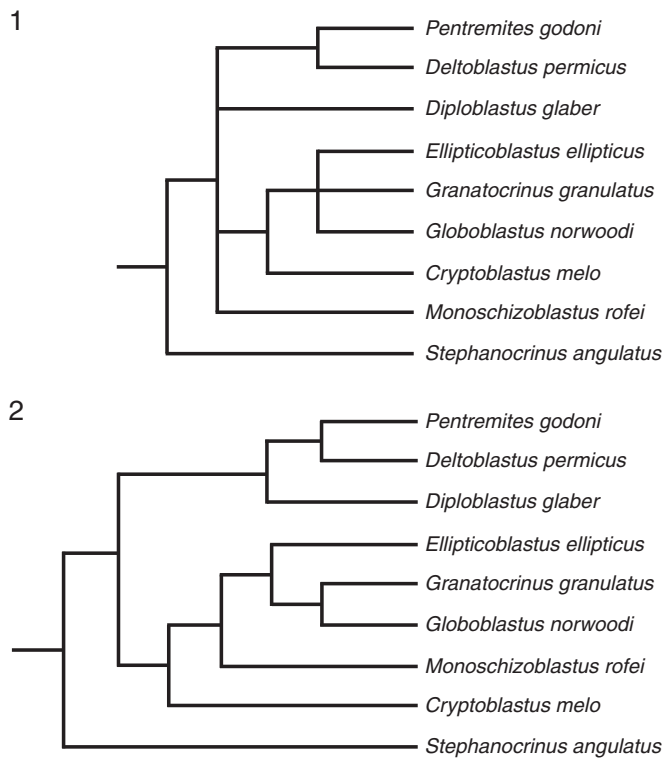


Figure 5. (1) Strict consensus tree of seven most parsimonious trees with tree lengths of 52 without the addition of hydrosfire data (CI 0.645, RI 0.486, RC 0.309). (2) Strict consensus tree of one most parsimonious tree with the addition of hydrosfire data with a length of 60 (CI 0.650, RI 0.488, RC 0.317).

characters were removed and the analysis was performed again without hydrosfire data in the matrix (Fig. 5.1). An additional analysis was then performed on this matrix with the hydrosfire data included (Fig. 5.2).

The tree topology without the hydrosfire data (Fig. 5.1) is largely unresolved with a polytomy at the base in the strict consensus of the nine equally most parsimonious trees, with several small groupings of taxa but relatively little resolution. *Pentremites godoni* and *D. permicus* form a sister pair, but their relationship to other taxa is unresolved. *Ellipticoblastus ellipticus*, *G. granulatus* (Roemer, 1851), and *G. norwoodi* (Owen and Shumard, 1850) form a smaller polytomy with a sister taxon of *C. melo*. Both *D. glaber* and *M. rofei* are in an unresolved relationship with these two groupings of taxa.

The addition of hydrosfire data does not significantly alter tree topology (Fig. 5.2) but does provide resolution within the smaller groupings of taxa. The pairing of *P. godoni* and *D. permicus* is now sister group to *D. glaber*, united by the number of respiratory fields. The pairing of *P. godoni* and *D. permicus* is further supported by the shared reduction of hydrosfire folds in the anal area. The grouping of *E. ellipticus*, *G. norwoodi*, *G. granulatus*, and *M. rofei* is supported by the ambulacra being in line with surrounding thecal plates, the number of respiratory folds per field, and the transitions from hydrosfire fold to spiracle. The wide hydrosfire folds of *E. ellipticus* support its separation from the pairing of *G. norwoodi* and *G. granulatus*. The clade of *G. granulatus*, *G. norwoodi*, *M. rofei*, and *E. ellipticus* is sister group to *M. rofei* in the analysis containing hydrosfire data rather than *C. melo* in the data set

lacking hydrosfire data. This shows that the addition of hydrosfire data can support novel relationships that are not supported by external data alone.

This preliminary analysis provides support that the incorporation of internal character data aids in understanding evolutionary relationships among blastoid taxa. Although only five additional internal characters were added to the amended character matrix of 29 characters, these characters appear to provide additional resolution both within and between groupings of blastoids and, in one case, novel relationships.

Future directions

Respiratory structures of blastozoan echinoderms have been long considered synapomorphies for clades and often are used to delineate species (Sprinkle, 1973). While internal character data have previously been successfully incorporated into phylogenetic inference for fossil taxa (Leighton and Maples, 2002; Wright and Stigall, 2013, 2014; Bauer and Stigall, 2016), this study is the first to do so with Blastoida. Although the internal anatomical models used in this study are currently limited, we provided evidence that respiratory structures provide further resolution to a phylogenetic hypothesis because they bring more data to bear in the inferred phylogeny. With more complete taxonomic coverage of blastoid hydrosfire structure, the inferred blastoid phylogeny will provide a basis to support or reject the groupings of Fissiculata and Spiraculata, a framework for taxonomic revision, and a basis for testing evolutionary questions throughout the Paleozoic.

In addition to the hydrosfires being identifiable in serial sections, thecal plate boundaries can be clearly outlined in the peels (Fig. 4.3, 4.6, 4.9, 4.12, 4.15, 4.18). Plates of particular interest for internal anatomy include the lancet, which can occur exposed or concealed along the length of the ambulacra by the side plates. The lancet and adjacent side plates are important as the hydrosfire pores are often found along the plate sutures. Questions concerning plate origination and persistence throughout the theca can be examined. Incorporation of all morphological details will provide a fuller understanding of early echinoderm relationships. Data derived from the evolutionary history of the blastoids can therefore be applied to other echinoderm groups to aid in inferring the relationships among members of this diverse clade.

Systematic paleontology

Remarks.—Descriptions are based on the modeled hydrosfire structures and acetate peel images. As the data set was a legacy collection, the descriptions are based on the peels available for study. The extent of the peels through the specimens was at the discretion of those that generated the peels (A. Breimer), resulting in several models being incomplete (noted in the following). Although it is a variation on normal systematic descriptions, the authors feel that a thorough examination and description of the structures is necessary and provides the framework for understanding subtle similarities and differences between species. The objective, therefore, is to provide descriptions relating the internal anatomy to the external expression of the respiratory structures. These models are

currently being utilized to simulate functional morphology of blastoids (e.g., Waters et al., 2017) but are available on request by contacting the corresponding author.

Class Blastoidea Say, 1825

Family Granatocrinidae Fay, 1961a

Genus *Cryptoblastus* Etheridge and Carpenter, 1886

Cryptoblastus melo (Owen and Shumard, 1850)

Figure 4.16–4.18

- 1850 *Pentremites melo* Owen and Shumard, p. 65, pl. 7, fig. 14a–c.
 1886 *Cryptoblastus melo*; Etheridge and Carpenter, p. 232, pl. 7, figs. 14, 15.
 1894 *Cryptoblastus melo*; Keyes, p. 139, pl. 18, fig. 7a, b.
 1903 *Cryptoblastus melo*; Hambach, p. 40.
 1937 *Cryptoblastus melo*; Cline, p. 636.
 1944 *Cryptoblastus melo*; Cline, p. 137, pl. 51, figs. 32–34.
 1961a *Cryptoblastus melo*; Fay, p. 61, pl. 38, figs. 6–9; text-figs. 98–100.
 1962 *Cryptoblastus melo*; Armstrong, p. 65, pl. 9, figs. 31–40.
 1969 *Cryptoblastus cf. melo*; Macurda, p. 463, pl. 63, figs. 14, 15.

For a complete pre-1937 bibliography of the species synonymies, the reader is referred to Cline (1937, p. 636).

Description.—Two folds in each group; fold pairs remain close together from base to summit; hydrosphere cleft begins small at base, becomes longer toward wider portion of theca, then tapers again as it reaches spiracles, making widest portion of each fold closer to spiracle opening. Overall folds are rather narrow; fold pairs of adjacent groups (same lancet plate) begin close together and bow out slightly, increasing toward top where fold pair becomes closer with fold pair from the adjacent lancet plate. Each group of fold pairs merges to form single spiracle. Anal area reduction absent in *C. melo*, but anal area folds are merged with anus forming anispiracle, ending with eight small openings and one large opening on the summit.

Remarks.—*Cryptoblastus melo* is placed within the family Granatocrinidae; no other models currently exist within this group. Similarities can be drawn from *C. melo*, *E. ellipticus*, and *M. rofei* in that the hydrosphere canal migrates toward the central axis of the theca. The merged canal of fold pairs appears to extend for a distance that is elongate compared to the other models, with the only other ‘elongate’ canal being present in *P. godoni*. Unfortunately, it is difficult to assess whether this is truly a unique feature or whether there are summit data missing from other models. The anatomical reconstruction is consistent with previous studies and information on the internal data of *C. melo*.

Family Schizoblastidae Fay, 1961a

Genus *Deltoblastus* Fay, 1961b

Deltoblastus permicus (Wanner, 1910)

Figure 4.4–4.6

- 1910 *Schizoblastus permicus* Wanner, p. 138, pl. 2, figs. 8, 9.
 1924 *Schizoblastus permicus* Wanner, p. 69, pl. 6, figs. 13–18; pl. 7, figs. 9–12; pl. 8, figs. 1–3.

1924 *Schizoblastus permicus ellipticus*; Wanner, p. 74, pl. 3, figs. 16–19; pl. 4, figs. 1–8.

1924 *Schizoblastus magnificus*; Wanner, p. 62, pl. 5, figs. 12–13.

1932 *Schizoblastus permicus ellipticus*; Wanner, pl. 1, figs. 1–6, 8, 9, 11–13; pl. 2, figs. 14–23, 39; pl. 3, figs. 26–33; pl. 4, figs. 34, 37, 46.

1932 *Schizoblastus permicus* Wanner, pl. 2, fig. 24a, b.

1934 *Schizoblastus permicus* Jansen, p. 823, text-fig. 5.

1961b *Deltoblastus ellipticus*; Fay, p. 37.

1961b *Deltoblastus magnificus*; Fay, p. 38.

1961b *Deltoblastus permicus*; Fay, p. 38, pl. 1, figs. 1–18.

Description.—Two folds in each group; hydrosphere cleft remains relatively stable in length for duration of folds, each fold pair reaching surface as single spiracle. Overall folds rather narrow but uniform; folds do not extend far into coelomic cavity but extend short distance from interior plate walls; groups of adjacent fold pairs (same lancet plate) positioned closely together and angle out very slightly, increasing toward top, where fold pair approaches fold pair from adjacent lancet plate. Anal area reduction present in *D. permicus* but anal area spiracles small and separate from anus, ending with eleven openings on summit.

Remarks.—*Deltoblastus permicus* is placed within the family Schizoblastidae; no other models currently exist for this group. The model for *D. permicus* is incomplete, stopping at or near the deltoid-radial suture. Either the sectioning process was terminated due to ample data from the already sectioned portion of the theca or the structures did not continue or were not visible in the next portion of the theca. The lack of additional sections prevents an understanding of hydrosphere duration in the theca. This model is one of two with a reduction in hydrosphere folds in the anal area. In addition, the hydrosphere canal in this model does not extend far into the body cavity as all of the other models do; this results in narrow folds with decreased surface area. The anatomical reconstruction is consistent with previous studies and information on the internal data of *D. permicus*.

Family Troosticrinidae Bather, 1899

Genus *Diploblastus* Fay, 1961a

Diploblastus glaber (Meek and Worthen, 1869)

Figure 4.7–4.9

- 1869 *Granatocrinus glaber* Meek and Worthen, p. 91.
 1873 *Granatocrinus glaber* Meek and Worthen, p. 537, pl. 20, fig. 11.
 1903 *Granatocrinus glaber* Hambach, p. 65.
 1961a *Diploblastus glaber*; Fay, pl. 48, figs. 1–12; pl. 49, figs. 1–9; text-figs. 113–119.

Description.—Two folds in each group; hydrosphere cleft short and stout with apparent increase in length around center of specimen, tapering toward summit; stout cleft provides apparent robustness to hydrosphere structure; this robustness clouds ability to clearly identify each fold in completed model; each fold increases in width from bottom, which starts as narrow and increases in extent into the coelomic cavity as it approaches

summit, maximum width attained prior to reaching summit, where subsequent narrowing of fold occurs; each fold pair reaching surface V-shaped spiracle around associated deltoid plate. Overall folds are wide; adjacent groups (same lancet plate) begin close together and retain same distance for duration of structures, increasing toward top, where fold pair approaches fold pair from adjacent lancet plate. Anal area reduction absent in *D. glaber*, but anal area spiracles confluent with anus forming anispiracle, ending with four paired spiracles and an anispiracle on summit.

Remarks.—*Diploblastus glaber* is placed within the family Troosticrinidae; no other models currently exist for this group. This species has a single pore leading to two folds that persist to the top and join to form a V-shaped spiracle, seen in the model. The hydrospace canal migrates into the body cavity, similar to the other models, from the base to the summit and produces a relatively wide fold. Although not entirely clear in the model (visible in the peels; Fig. 4.9), the hydrospace cleft is incredibly robust, a feature unique to this model. The anatomical reconstruction is consistent with previously described internal data by Breimer (1988b), where several sections were used to discuss internal morphology and plate arrangements.

Family Orbitremitidae Bather, 1899

Genus *Ellipticoblastus* Fay, 1960

Ellipticoblastus ellipticus (Sowerby, 1825)

Figure 4.10–4.12

- 1825 *Pentremites elliptica* Sowerby, p. 317, pl. 11, fig. 4.
 1863 *Elaeacrinus ellipticus*; Shumard, p. 112.
 1959 *Orbitremites ellipticus*; Joysey, p. 99, pl. 2, figs. 1–9.
 1961a *Orbitremites ellipticus*; Fay, p. 89, pl. 43, figs. 1–3, 10, 11, text-figs. 186, 187.
 1968 *Ellipticoblastus ellipticus*; Breimer and Joysey, p. 181, text-figs. 1, 2.

Description.—One fold in each group; hydrospace cleft thin and long with apparent increase in length around center of specimen, with top half of structure having longer cleft length than base; each fold combining with adjacent fold to produce five spiracles. Folds wide and occupy significant portion of the coelomic cavity; adjacent groups (same lancet plate) begin close together and bow out slightly, tapering again toward summit where fold pair approaches fold pair from adjacent lancet plate because of increased cleft length allowing folds to meet in center; this produces external expression of single spiracle openings. Anal area reduction absent in *E. ellipticus*; anal area spiracles are confluent with anus, ending with five openings on summit.

Remarks.—*Ellipticoblastus ellipticus* is placed within the family Orbitremitidae; one other model (*M. rofei*) currently exists for this group. The hydrospace canal migrates far into the body cavity producing thin but wide folds unlike the other models. The fold pairs in *E. ellipticus* remain relatively equidistant from one another throughout the theca whereas those of *M. rofei* bow outward in the center of the theca. The anatomical reconstruction is consistent with previously described (Breimer and Joysey, 1968) internal data of *E. ellipticus*.

Genus *Monoschizoblastus* Cline, 1936

Monoschizoblastus rofei (Etheridge and Carpenter, 1882)

Figure 4.13–4.15

- 1882 *Granatocrinus rofei* Etheridge and Carpenter, p. 239.
 1886 *Schizoblastus rofei*; Etheridge and Carpenter, p. 228, pl. 6, fig. 17; pl. 8, figs. 9–11; pl. 17, fig. 2.
 1886 *Schizoblastus bailyi*; Etheridge and Carpenter, p. 223, pl. 16, figs. 12, 13.
 1936 *Monoschizoblastus bailyi*; Cline, p. 265.
 1936 *Monoschizoblastus rofei*; Cline, p. 265.

Description.—One fold in each group; hydrospace cleft thin and does not extend far into coelomic cavity; tapering toward summit becoming narrow again; each fold reaching surface as spiracle with exception of those in anal area. Overall folds are narrow; adjacent groups (same lancet plate) begin close together and bow outward three times distance at origination, tapering toward summit where each fold subsequently approaches fold at adjacent lancet plate. Anal area reduction absent in *M. rofei*; anal area spiracles are confluent with anus, ending with nine openings on summit.

Remarks.—*Monoschizoblastus rofei* is placed within the family Orbitremitidae; one other model (*E. ellipticus*) currently exists for this group. Similar to *E. ellipticus*, *M. rofei* had a single pore leading to a single fold, but unlike *E. ellipticus*, each fold (except those in the anal area) terminates as a spiracle. As with the majority of the models, the hydrospace canal migrates toward the center axis of the body cavity but does not extend as far in as the folds of *E. ellipticus*. The anatomical reconstruction is consistent with previous studies and information on the internal data of *M. rofei*.

Family Pentremitidae d'Orbigny, 1852

Genus *Pentremites* Say, 1820

Pentremites godoni (DeFrance, 1819)

Figure 4.1–4.3

- 1819 *Encrina godonii* DeFrance, p. 467.
 1821 *Encrinites florealis*; von Schlotheim, p. 339.
 1825 *Pentremites florealis*; Say, p. 295.
 1826 *Pentremites florealis*; Goldfuss, p. 150, pl. 50, fig. 2a–c.
 1851 *Pentremites florealis*; Roemer, p. 353, pl. 4, figs. 1–4; pl. 5, fig. 8.
 1858 *Pentremites godoni*; Hall, p. 692, pl. 25, fig. 13.
 1881 *Pentremites godoni*; White, p. 511, pl. 7, figs. 10, 11.
 1886 *Pentremites godoni*; Etheridge and Carpenter, p. 157, pl. 1, fig. 11; pl. 2, figs. 1–13; pl. 12, figs. 16, 17; pl. 16, figs. 19, 22, 23.
 1898 *Pentremites godoni*; Weller, p. 414.
 1920 *Pentremites godoni*; Weller, p. 319, pl. 4, figs. 31–34, 36.
 1917 *Pentremites godoni*; Ulrich, p. 254, pl. 5, fig. 26.
 1917 *Pentremites planus*; Ulrich, pl. 5, figs. 1–13.
 1957 *Pentremites godoni*; Galloway and Kaska, p. 48, pl. 3, figs. 11–13; pl. 11, figs. 20–30; pl. 13, figs. 9–12.
 1961a *Pentremites godoni*; Fay, p. 90, text-fig. 188.
 1961c *Pentremites godoni*; Fay, p. 871, text-fig. 1, figs. 1–4.

Description.—Five folds in each group; fold groups tightly packed making it difficult to distinguish folds in model; original peels provide a clear distinction of each fold; hydrospire cleft thin and elongate to accommodate each of five folds with apparent increased length around center of the specimen, tapering toward summit; each fold group (five folds) merges into single canal, then adjacent canals (separate lancet plates) merge to form single large spiracle opening. Folds narrow but numerous; fold groups at same lancet plate begin close together and angle out slightly, increasing toward top, where fold group approaches fold group from adjacent lancet plate. Anal area reduction present in *P. godoni* and anal area spiracles confluent with anus forming anispiracle, ending with five openings on summit.

Remarks.—*Pentremites godoni* is placed within the family Pentremitidae; no other models currently exist for this group. The model for *P. godoni* is incomplete, missing the lower portion of the theca; the spiracle and anal openings are clear in the model. The sectioning process was likely terminated because the portion that had already been sectioned was enough to address what was being investigated. It should also be noted that although this is an individual within the species *P. godoni*, it has been noted that fold number is variable within a species. The extent of the hydrospires through the theca is not clear as a large portion of the specimen is missing from this reconstruction.

As with the other models, it appears that the hydrospire canal is migrating toward the center axis. Unfortunately, since this is only the top of the specimen, it is not clear whether the remainder of the structure would follow a similar pattern to the other models. Each hydrospire pore leads to four (in the anal area) or five folds, which form a single canal near the summit and finally combine with an adjacent fold group to produce a single spiracle. The folds of *P. godoni* are narrow but numerous, unlike any of the other models.

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Accessibility of supplemental data

Supplemental data available from the Dryad Digital Repository: doi:10.5061/dryad.1d1m6.

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