

**Respiratory Structure Morphology, Group Origins, and Phylogeny of
Eublastoidea (Echinodermata)**

**A Dissertation Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville**

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ABSTRACT

Evolutionary relationships of Paleozoic echinoderms have fostered significant debate over the past century. Many early echinoderms have complexly plated bodies with a variety of morphologies, very unlike modern echinoderms (e.g., sea urchins, sea stars). A major clade, Blastozoa, has been subdivided based on the occurrence of specific respiratory structures but these groups have yet to be fully assessed in a quantitative framework. Phylogenetic inference provides a quantitative means to assess trait evolution, respiratory structure modification, or clade origination. Herein, we assess respiratory morphology, evolution, and group origination of Eublastoidea.

The respiratory structures (hydrospires) of eublastoids have been used to separate major subgroups within Eublastoidea but have only been examined externally. Previously only assessed by 2D serial sections of specimens, my research provides 3D detailed anatomical models of these internal structures. Rendering in 3D allows for detailed morphological analysis and functional morphology simulations. Our findings suggest separation by the external expression of hydrospires results in a misleading understanding of evolutionary history.

These insights into eublastoid respiratory structures shed light on an ongoing debate regarding the origins of blastoids. Origins of blastoids are unclear and a series of ancestors has been proposed. A single species of blastoid *Macurdablastus uniplicatus*, was recorded from the Late Ordovician with the next undisputed species in the middle Silurian. We reassessed anatomy and evolutionary relationships through detailed morphological examination, synchrotron imaging, and phylogenetic analyses. Results from our subsequent phylogenetic analyses suggest *Macurdablastus* is not a true blastoid (eublastoid) but is include in the broadly defined Blastoidea that includes coronoids, eublastoids, *Lysocystites*.

The revival of the term Eublastoidea to include species with recumbent ambulacra and hydrospires provided the basis to explore the evolution of this long-lived clade. Following and expanding upon a proposed homology scheme for echinoderms, I produced a comprehensive character matrix for the external and internal morphology of eublastoids. The phylogeny was used to reassess eublastoid classification and as a framework to address the validity of group separation via the external expression of hydrospires. This work provides the first complete assessment of echinoderm respiratory structures and detailed reassessment of eublastoid morphology.

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INTRODUCTION

Our understanding of the early evolution of Paleozoic invertebrates is undergoing a revolution as rigorous, comprehensive, and quantitative analyses become the norm (e.g., Rode and Lieberman, 2003; Congreve and Lieberman, 2010; Hopkins and Lidgard, 2012; Ortega-Hernández et al., 2013; Hopkins, 2016; Bauer and Stigall, 2016; Wright et al., 2017). A phylogenetic framework is required to test questions relating to trait evolution, macroevolutionary processes, and biogeographic patterns.

Echinoderms provide an ideal case study to assess evolutionary relationships throughout the Phanerozoic. Echinoderms first diversified in the Cambrian Explosion, with larger taxonomic groups arising; furthermore, diversity at lower taxonomic levels increased during the Great Ordovician Biodiversification Event (Paul and Smith, 1984; Guensburg and Sprinkle, 2001; Smith, 2004). Blastozoa, a major Paleozoic group of stemmed echinoderms that possess brachioles, and have complex respiratory structures, and are long-lived and quite diverse providing an ideal group to examine morphological and evolutionary trends through time (e.g., Foote, 1991, 1992; Waters, 1988, 1990). Despite this, analyses of their phylogenetic relationships are rare in comparison to those of extant echinoderm groups. Previous divisions within blastozoans have been based on the possession of specific respiratory structures (Paul, 1968, 1972). Current understanding of evolutionary relationships among high-level blastozoan groups lacks consensus, but relationships among and within lineages are currently being assessed. Herein we focus on understanding the evolutionary relationships within Eublastoidea

(eublastoids), a subclade that possesses hydrospires, an elongate lancet plate, and conservative thecal plating.

Most Paleozoic echinoderms have unorganized, mulitplated thecae that disarticulate rapidly, whereas eublastoids possess a conservative thecal plating and well-sutured thecae that does not readily disarticulate. Additionally, the conservative plating is comprised of 18-21 skeletal plates that can be recognized across all species (Beaver, 1967). This makes Eublastoidea an excellent model clade to test morphological and evolutionary questions.

Part I: Three-dimensional reconstruction of respiratory structures

The respiratory structures of Eublastoidea, hydrospires, are arguably the most complex water vascular system of Paleozoic echinoderms. The structures consist of lightly calcified infoldings of the body wall that communicate with the ambient seawater through a variety of pore systems (Fay, 1967). Previously, hydrospires were investigated by creating serial transverse sections of specimens that were examined individually using acetate peels (Fay et al., 1967; Breimer, 1988a, b). This process is destructive and published results often consist of a few isolated sections. Such treatment does not allow for a comprehensive understanding of how the hydrospires form within the theca, for example, the fold number can change depending on the location in the theca. Key features, such as this, can be missed in single isolated sections.

Here we utilize a legacy dataset of acetate peels (Breimer and van Edmond, 1968) to digitally reconstruct the entire hydrospire structures in three dimensions. The resulting hydrospire models provide new data for phylogenetic character generation and

subsequent analyses. Ongoing research associated with this project is also using these digital models to simulate fluid flow and respiration within the eublastoid theca (e.g., Waters et al., 2017).

Part II: Evolutionary relationships

Eublastoid origins

Although Eublastoidea are absent from the Cambrian Explosion and Great Ordovician Biodiversification Event, they are the longest-lived blastozoan echinoderm clade, spanning a 200 million-year interval from the Late Ordovician to the end Permian. A number of hypothetical ancestors, including edrioblastoids, parblastoids, rhombiferans, and coronoids have been proposed for eublastoids over the past 100 years, but little work has been done to reassess the oldest recorded proposed eublastoid species.

Here we present a reexamination of *Macurdablastus uniplicatus* Broadhead, 1984 using a detailed comparative morphological reassessment, high-resolution synchrotron tomography, and phylogenetic analyses, to better elucidate its evolutionary position with respect to eublastoids. This study provides evidence that *Macurdablastus uniplicatus* should not be included in the eublastoid clade but rather is sister taxon of Eublastoidea. The inferred phylogeny suggests *M. uniplicatus* is not a eublastoid or coronoid but part of Blastoidea, a clade defined by the possession of a lancet plate and three defined plate circlets.

Phylogenetic relationships of eublastoidea

Eublastoid morphology has been studied extensively over the past 100 years and recent work has been conducted to assess discrete homologous elements between blastozoan groups (Sumrall, 2010, 2017; Sumrall and Waters, 2012; Kammer et al., 2013). These studies and the conservatively plated thecae of eublastoids provide a valuable starting point for assessing minute changes in skeletal plating across Eublastoidea. This has been particularly useful in identifying character suites to best describe how the skeletal plates evolve and interact with one another and produce the overall shape of the organism.

Here we revise character data, with emphasis on plates around the anal opening, and include new characters determined from the digital reconstruction of the internal respiratory structures building upon the work described in Chapters 1 and 2. The inclusion of assembled internal and external character data in this phylogenetic analysis indicates that a taxonomic revision of the groups is required.

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CHAPTER 1
HYDROSPIRE MORPHOLOGY AND IMPLICATIONS FOR
BLASTOID PHYLOGENY

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My major contributions to this paper include: (1) evaluation of digitally reconstructed hydrosfire anatomy; (2) conducted phylogenetic analyses; (3) writing the manuscript; (4) creating figures and photographs; (5) submitting and revising the manuscript. Colin D. Sumrall and Johnny A. Waters, both co-authors, agreed with interpretations of the data and made revisions of the manuscript before journal submission.

Abstract

The external expression of hydrosfires 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 hydrosfires has never been comprehensively studied. This study examined and described the internal hydrosfires of six spiraculate species by digitally extracting hydrosfire data from a legacy data set of serial acetate peel. Although only six models have been currently generated, hydrosfire morphology is variable both within and between previously described spiraculate families. Hydrosfires 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. Endothecal respiratory structures such as blastoid hydrospires, parblastoid cataspire, 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; Schmidtling 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 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 endothecal 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 the completely internal hydrospire folds (Waters, 1988; Fig. 1).

These morphological groups have been examined separately on several occasions over the past 50 years (Breimer and Macurda, 1971; 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 hydrospire slits that lead to bean-shaped or underdeveloped spiracles or have well developed spiracles and hydrospire slits only partially covered by ambulacral side plates.

Hydrospire morphology

Respiratory structures of extinct blastozoan echinoderms are diverse, highly variable, and often clade defining (Paul, 1968, 1972; Sprinkle, 1973; Schmidtling 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 hydrospire 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., hydrospires) 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 hydrospire slits, which are open to the exterior along the length of the hydrospire 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). The incurrent pores lead to hydrospire folds (ranging from one to 10 in number; Fig. 2) and finally to the excurrent openings, at the summit (Sprinkle, 1973; Waters et al., 2017).

Hydrospire morphology and terminology can be confusing, specifically with the variation with fold number. Terminology herein follows the morphology outlined in Beaver (1967). In spiraculates, hydrospire folds occur at pores (Fig. 2.1–2.3) that are visible on the exterior of the organism. The pores lead to a hydrospire cleft, which is the

portion of the fold between the pore and the final termination at the hydrospire tube (Fig. 2.1–2.3; hydrospire tube is synonymous with hydrospire canal in Schmidting and Marshall, 2010). Some hydrospire 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 hydrospire groups (Fig. 2.2, 2.3). The hydrospire 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 hydrospire 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 they hydrospire 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 hydrospire 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 hydrospires form the basis of differentiation between fissiculates and spiraculates (Beaver et al., 1967); however, the internal architecture of hydrospires has yet to be studied. Typically, hydrospire 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. Hydrospires, unlike other internal structures (such as gut and reproductive organs), are constructed of thin calcareous walls (Beaver, 1967) and are typically preserved within the theca. As the hydrospires are internal organs, new visualization methodology had to be developed (Waters et al., 2014, 2015) to digitally render and manipulate complete hydrospire structures. Preliminary work (Waters et al., 2014, 2015; Bauer et al., 2015) suggests that hydrospires 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 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 hydrospire morphology in 2D (Breimer and Macurda, 1972) as well as 3D (Schmidting and Marshall, 2010; Huynh et al., 2015). A comprehensive investigation of hydrospire 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 hydrospire 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 hydrospires 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 hydrospires vertically through the theca. The image was then compressed and transferred into Rhinoceros, as industrial design program used to render 2D images in 3D. Within Rhinoceros, the images were connected to generate complete hydrospire 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 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 hydrospire 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 plane. 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 able 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 inerray (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). *Ellipticoblatus 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 additionally 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 change 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 characters were removed and the analysis was performed again without hydrospire data in the matrix (Fig. 5.1). An additional analysis was then performed on this matrix with the hydrospire data included (Fig. 5.2).

The tree topology without the hydrospire data (Fig. 5.1) is largely unresolved with a polytomy at the base in the strict consensus of nine equally parsimonious trees, with several small groupings of taxa but relatively little resolution. *Pentremite godoni* and *D. permicus* form a sister pair, but their relationship to other taxa is unresolved. *Ellipticoblastus ellipticus*, *G. granulatus* (Roemer, 1985), 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 hydrospire 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 hydrospire 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 hydrospire fold to spiracle. The wide hydrospire 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 hydrospire data rather than *C. melo* in the data set lacking hydrospire data. This shows that the addition of hydrospire 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 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 Blastoidea. 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 hydrospire 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 hydrospires 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 hydrospire 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 hydrospire 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 to 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, fig. 14, 15.

- 1894 *Cryptoblastus melo*; Keyes, p. 139, pl. 18, fig. 7a, b.
- 1903 *Cryptoblastus melo*; Hamback, 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 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; hydrospace 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 hydrospire 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, fig. 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. 16–9; 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. 24, 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; hydrospire 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 hydrospire duration in the theca. This model is one of two with a reduction in hydrospire folds in the anal area. In addition, the hydrospire 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* Hamback, 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; hydrospace cleft short and stout with apparent increase in length around center of specimen, tapering toward summit; stout cleft provides apparent robustness to hydrospace 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 for 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 hydrospire 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 hydrospire 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 Orbitremiidae 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 *Orbitremities 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; hydrospire cleft thin and long with apparent increase in length around center of specimen, with top half of structure having lower 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 hydrosphere 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; hydrospire 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 hydrospire 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'rbigny, 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.
- 1917 *Pentremites godoni*; Ulrich, p. 254, pl. 5, fig. 26.
- 1917 *Pentremites godoni*; Ulrich, pl. 5, figs. 1–13.
- 1920 *Pentremites godoni*; Weller, p. 319, pl. 4, figs. 31–34, 36.
- 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 increase length around center for specimen, tapering toward summit; each fold group (five folds) merges into a 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 being 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 folds 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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Appendix 1-1

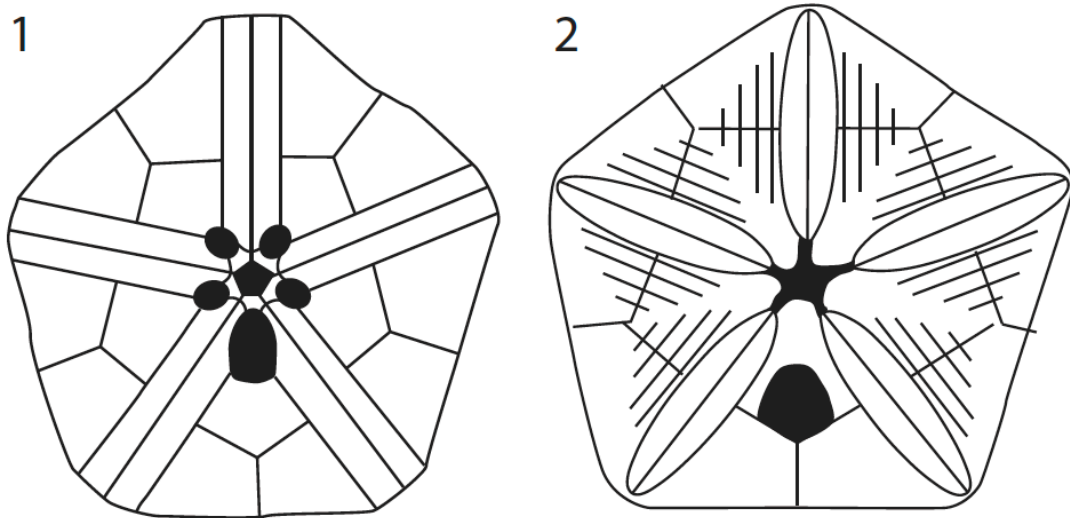


Figure 1.1. Generalized diagrams of the two primary blastoid morphotypes. **(1)** Spiraculate morphotype with incurrent hydrospace pores lining the ambulacra leading to four excurrent spiracles and one large anispiracle. **(2)** Fissiculate morphotype with four slits on each side of and parallel to the ambulacra crossing the radial-deltoid plate boundary. Modified from Beaver (1967).

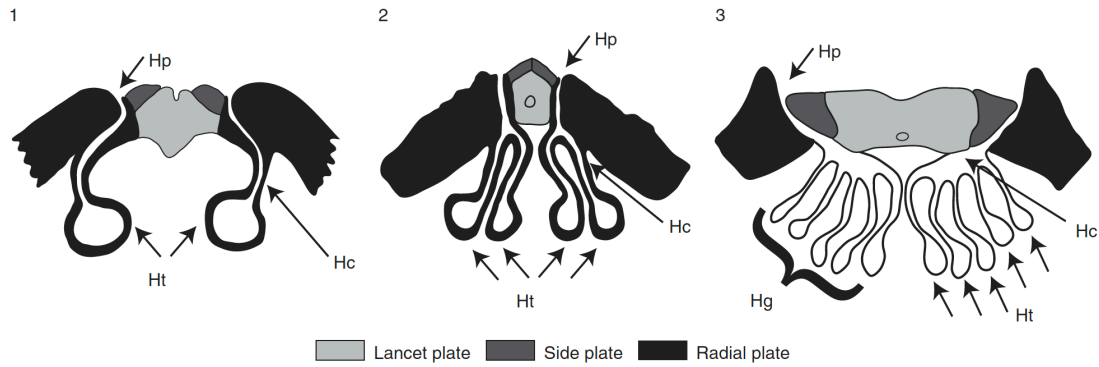


Figure 1.2. Ambulacral plating in relation to hydrospires in several representative spiraculate species. **(1)** *Orbitremites derbiensis* Sowerby, 1825 possessed a single hydrospire fold with a thick hydrospire cleft leading to the hydrospire tube at the end. **(2)** *Globoblastus norwoodi* (Owen and Shumard, 1850) possessed paired hydrospire folds with a bifurcating cleft leading to two hydrospire tubes. **(3)** *Pentremites godoni* (DeFrance, 1819) possessed five hydrospire folds within the hydrospire group; an elongate hydrospire cleft along the plates accommodates the additional folds. Hc = hydrospire cleft; Hg = hydrospire group; Hp = hydrospire pore; Ht = hydrospire tube. Modified from Beavuer (1967).

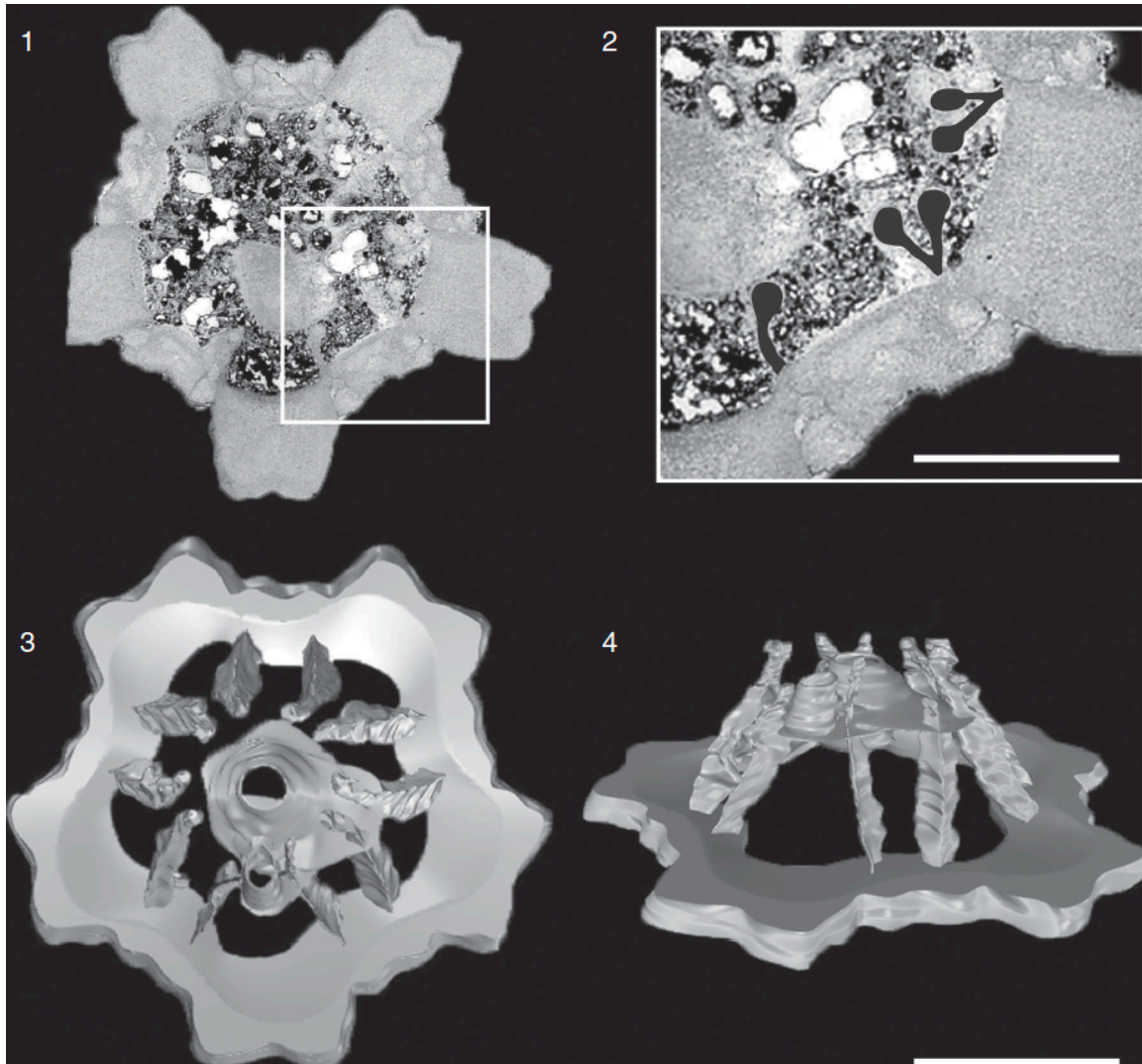
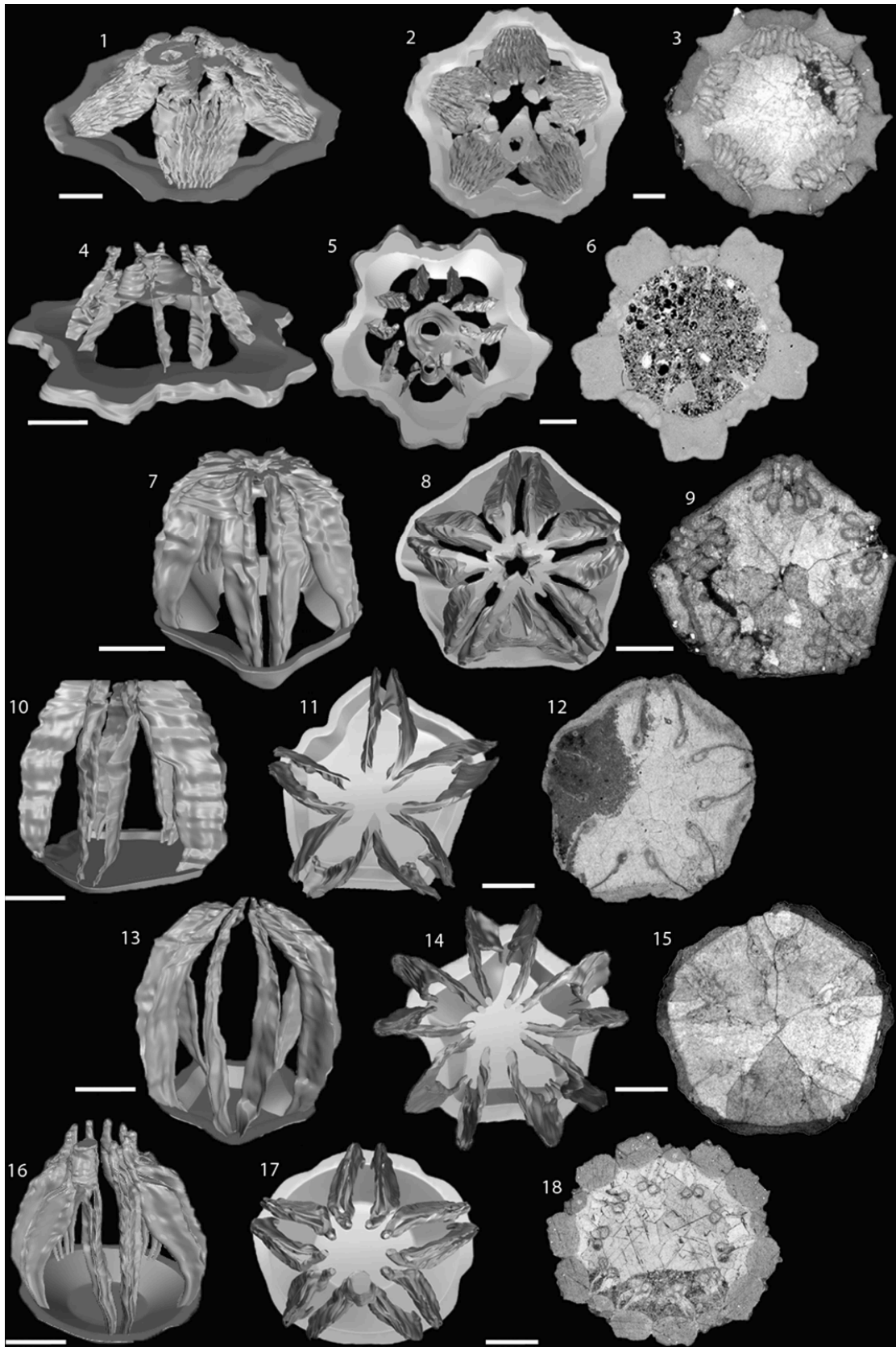


Figure 1.3. *Deltoblastus permicus* is an example of anatomical model reconstruction methodology. **(1)** Digital transverse slices are cut out and aligned in the same direction. Target areas of internal morphology can be identified as seen by the white box. **(2)** This enlarged box of **(1)** shows the hydrospires 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. Scale bar represents 1 cm. Modified from Waters et al. (2014) and Bauer et al. (2015).

Figure 1.4. (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.



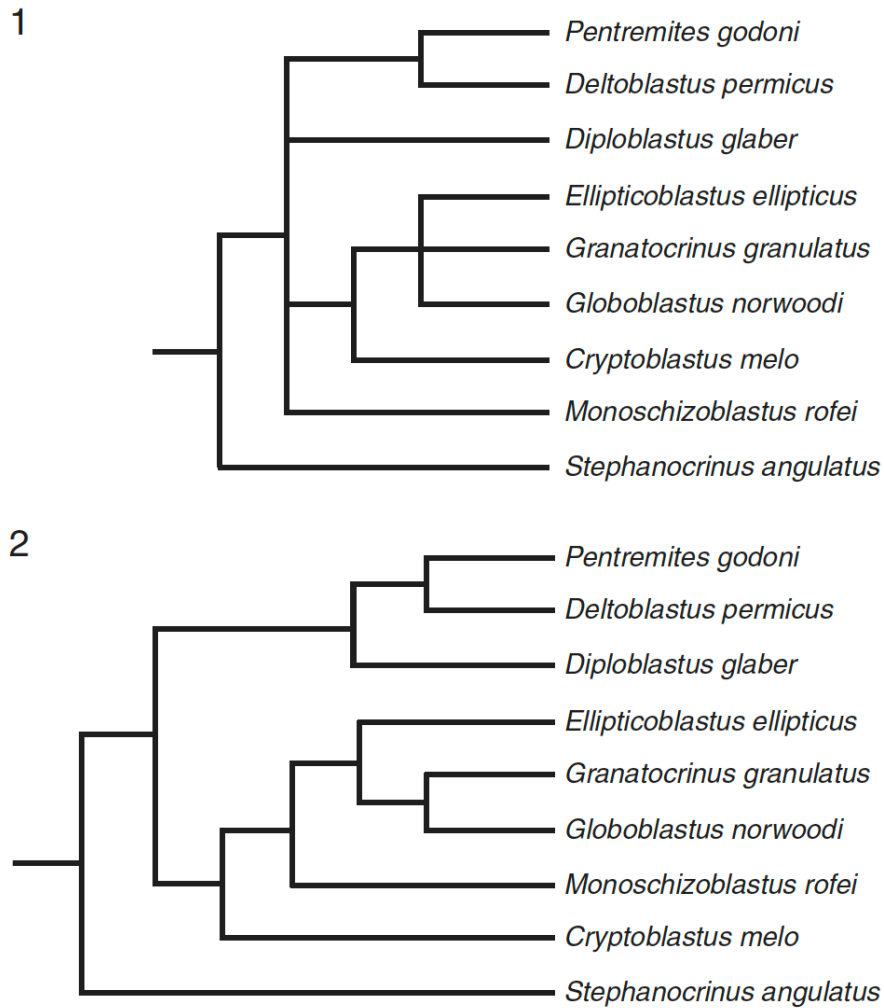


Figure 1.5. (1) Strict consensus tree of seven most parsimonious trees with tree lengths of 52 without the addition of hydrospire data (CI 0.645, RI 0.486, RC 0.309). **(2)** Strict consensus tree of one most parsimonious tree with the addition of hydrospire data with a length of 60 (CI 0.650, RI 0.488, RC 0.317).

CHAPTER 2
REEVALUATION OF *MACURDABLASTUS* WITH IMPLICATIONS
FOR THE ORIGINS OF EUBLASTOIDEA

Abstract

Many echinoderm clades have unclear evolutionary origins. Eublastoids are a large clade of stemmed blastozoan echinoderms diagnosed by their well-organized body plan, the lancet plate supporting the ambulacra, and hydrospire respiratory structures. Although Eublastoidea is a large successful clade it is absent from early echinoderm radiations during the Cambrian and Ordovician. Here we provide a reevaluation of the earliest recorded eublastoid species, *Macurdablastus uniplicatus* using detailed morphological assessment based in advanced synchrotron tomography, and phylogenetic analysis. *Macurdablastus uniplicatus* does not fall within Eublastoidea due to the morphological differences in lancet plate and respiratory structures. These results move the oldest recorded eublastoid from the Upper Ordovician to the middle Silurian and provide a basis for classification revision of Blastoidea.

Introduction

The evolution of complex, skeletal, metazoan body plans began with the notable Cambrian Explosion that expanded high-level diversity in many taxonomic groups (Sepkoski, 1979; Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985). An additional radiation during the Early Ordovician, is recorded by rapid diversification in lower level taxonomic groups (Sepkoski, 1979). Echinoderms radiated during the Cambrian and into the Early Ordovician as a key component of the Great Ordovician Biodiversification Event, several groups (including Eublastoidea) are absent from these radiations and widespread echinoderm bearing deposits and have unclear origins (Barrande, 1887;

Sprinkle, 1973; Sprinkle, 1982; Paul and Smith, 1984; Guensburg and Sprinkle, 2001; Smith, 2004; Guensburg and Sprinkle, 1992; Sprinkle and Guensburg, 2004; Nardin et al., 2010; Lefebvre, et al., 2013; Zamora et al., 2013; Lefebvre et al., 2016).

Unfortunately, many early Paleozoic echinoderm groups do not clearly participate in these radiations, but rather appear suddenly in the fossil record without clear evolutionary lineages. The origin of major blastozoan clades have not received much attention and we rely heavily on the sampling of the fossil record and well-preserved specimens. Blastozoans (stemmed echinoderms that bear brachioles, and complex respiratory structures) provide an ideal focus group to study this phenomenon because this group is long-lived and quite diverse (e.g., Foote, 1991, 1992; Waters, 1988, 1990). Here we focus on subset of blastozoans, Eublastoidea, and re-examine *Macurdablastus uniplicatus* Broadhead, 1984, the oldest recorded eublastoid, using advanced imaging that allowed us to better apply an improved homology scheme.

History of Eublastoidea

Eublastoidea Bather, 1899 was erected to include taxa with recumbent ambulacra and hydrospires. We are re-erecting Eublastoidea to include blastoids, as described in Fay et al. (1967). Eublastoidea is therefore part of Blastoidea that includes taxa (coronoids and *Lysocystites*) with conservatively plated thecae and lancet plates (following Donovan and Paul, 1985). Coronoids possess a circular lancet plate that is used as a facetal plate for the erect ambulacra and *Lysocystites* possesses a more elongate lancet plate that also functions as a facetal plate for erect ambulacra.

Eublastoidea, in particular, have an unclear evolutionary history in the early Paleozoic. While the other large echinoderm clades flourish in the Ordovician, only one isolated eublastoid-like plate is known from the Middle Ordovician (Sprinkle, 1973), and from a single locality in the Late Ordovician (Broadhead, 1984). The origins of Eublastoidea have been debated for the past several decades. Previous suggestions include: descent from edrioblastoids (Fay, 1968), which has since been interpreted as a clade of nested within edrioasteroids (Smith and Jell, 1990; Guensburg and Sprinkle, 1994; Zamora and Lefebvre, 2014; Sprinkle and Sumrall, 2015); eocrinoid ancestors assuming that coronoids are closely related to Eublastoidea (Sprinkle, 1973; Sprinkle, 1980; Brett et al., 1983; Broadhead, 1984; Donovan and Paul, 1985). While most authors agree that coronoids and eublastoids are related, there is still debate about whether they represent a distinct class (Broadhead, 1980, 1982; Brett et al., 1983) or are members of a more broadly inclusive Blastoidea (Donovan and Paul, 1985; Paul, 1985; Bodenbender and Fisher, 2001).

Current interpretations that unite eublastoids, coronoids, and *Lysocystites* based on possession of a lancet plate and conservatively plated body. This combination of morphological features is not present in other stemmed echinoderms. Specific morphological evidence uniting these taxa includes the similar thecal plate arrangements, azygous basal in the AB interray, five radials, four individual deltoids with additional deltoid plates in the CD interray, and radial plates encompass an ambulacrum (Brett et al., 1983; Donovan and Paul, 1985; Gil Cid et al., 1996). The lancet plate is shared among these taxa but in modified forms. In coronoids, the lancet plate is small and

semicircular, *Lysocystites* possesses a lancet that is elongated, and the lancet of eublastoid taxa extends for the entire length of the ambulacra. Notable differences, however, exist in the respiratory and feeding structures of these taxa. Eublastoids possess hydrospires, coronoids possess coronal canals, and *Lysocystites* possesses a network of pore structures running through the body plates (Sprinkle, 1973; Donovan and Paul, 1985). Rather than having recumbent ambulacra (as in eublastoids), coronoids have erect ambulacral floor plates with brachioles arising between pairs of primary and secondary floor plates, sometimes referred to as brachiolar trunks (Brett et al., 1983). *Lysocystites* also possesses erect ambulacra.

Macurdablastus as key to understanding Eublastoidea

Macurdablastus uniplicatus is known from two largely complete specimens from the Benbolt Formation of eastern Tennessee. The discovery of *Macurdablastus uniplicatus* moved the first occurrence of Blastoidea from the middle Silurian to the Late Ordovician, slightly closer to the radiations of other early echinoderm groups. Rather than pursuing experimental body plans, as many early echinoderms did during the Ordovician, *M. uniplicatus* possesses the stable plate arrangement that has been considered one of the defining characteristics of Blastoidea (Etheridge and Carpenter, 1886; Fay, 1961, 1967). The conservative plating and increased understanding of homologous elements through Universal Elemental Homology allow for precise examination and testing of morphological hypotheses through time (Sumrall, 2010; Sumrall and Waters, 2012; Sumrall, 2017). At the time of its description, *M. uniplicatus* was not formally assigned to either eublastoid order, Fissiculata or Spiraculata

(Broadhead, 1984). Although this taxon bears the typical plating of blastoids, differences in the size and shape of the lancet plates and in the nature of the respiratory structures differentiate it from other eublastoids, coronoids, and *Lysocystites*.

Here we reexamine *Macurdablastus uniplicatus* using synchrotron tomography to comprehensively examine internal and external morphologies to improve classification and phylogenetic placement. microCT imaging is unable to distinguish between the skeletal calcite and calcite infill of fossil echinoderms. As there are only two complete specimens of *M. uniplicatus*, serially sectioning the specimens was not possible. Synchrotron tomography allowed for a non-destructive alternative and produced increased resolution between skeletal material and infill. Phylogenetic analyses of taxa with complex internal morphology are limited when we can only visualize and code the external morphology. In the case of blastozoans, these complex internal structures, are used as the basis for classification (Fay, 1967; Breimer and Macurda, 1972; Sprinkle, 1973), but there has been little work to digitally reconstruct this anatomy in three dimensions (Schmidtling and Marshall, 2010; Waters et al., 2015, 2017).

Materials and methods

Fossil material

Only two complete specimens are reposit for study with additional isolated skeletal elements. Specimens (USNM 359545 and USNM 359646; Fig. 1) were borrowed from the Smithsonian Institution National Museum of Natural History. These two specimens are the holotype and paratype, respectively, assigned by Broadhead (1984).

The smaller holotype is more complete than the paratype and preserves the major thecal plates. The stem is absent and the basals are crushed, obscuring the details. The ambulacra are poorly documented because the floor plates, cover plates, and brachioles are not preserved. The paratype is slightly larger in size, but only three of the five rays are preserved. The ambulacra are lacking floor plates, cover plates, and brachioles because of poor preservation. Basals are crushed and the crushed rays make it difficult to identify the anal area (CD interray).

Synchrotron tomography

Both specimens of *Macurdablastus uniplicatus* were scanned using propagation-based phase-contrast X-ray tomography on the TOMCAT beamline at the Swiss Light Source (SLS) Paul Scherrer Institut, Villigen, Switzerland. The fossils were scanned using an X-ray energy of 37 keV, 1501 projections, an exposure time of 1000 ms, and the sample-to-detector propagation distance was set at 305 mm. These specifications gave a tomographic dataset with a voxel size of 300 μm which was subsequently rendered as a three-dimensional virtual reconstruction. The phase-contrast method available at the SLS allows small differences in density to be recognized, that are difficult to separate on more typical absorption scans, thereby allowing differentiation between the calcite

The size of the holotype necessitated imaging the specimens in two blocks. Each block contains 482 slices, for a combined total of 964 slices for the complete specimen. Because the two image blocks overlapped slightly, redundant slices were removed when the images were stacked in ImageJ (Schneider et al., 2012). Images were then cropped to reduce empty space and contrast was modified to produce the clearest internal anatomy.

Our focus was to reconstruct the internal respiratory structures as they are lightly calcified infoldings of the body wall whereas the gut and gonads are not skeletonized. Modified images were then imported into SPIERSedit (Sutton et al., 2012) where the internal and external anatomy was reconstructed. To trace the respiratory structures, curves were used with four nodes. Structures of interest were traced using the curve tool throughout the holotype specimen, and the resulting curves were turned into masks to create output objects. SPIERSview was used to remove non-specimen artifacts and to smooth the traced structures. Additionally, SPIERSview was used to render videos of the rotating specimen through the animation panel (Appendix 2-2).

Phylogenetic inference

Evolutionary relationships were analyzed by reassessing previous character matrices with new information taken from observations and virtual models. External morphological character data was created for all eublastoid taxa and includes 80 characters (Appendix 2-3). Internal character data was compiled from reconstructed internal morphology of *M. uniplicatus*. The other species included in the analysis do not have reconstructed internal morphology. Phylogenetic analysis was conducted in PAUP*4.0b10 (Swofford, 2003) utilizing maximum parsimony and maximum likelihood. The Mk model was utilized for maximum likelihood because it accounts for morphological categorical data and corrects for the exclusion of parsimony uninformative characters (Lewis, 2001). Both algorithms were incorporated for comparison of results to phylogenetic analyses performed only via maximum parsimony. Maximum parsimony utilized TBR and ACCTRAN optimization. In both analyses we treated characters as

unordered and unweighted. *Macurdablastus uniplicatus*, two Silurian eublastoid taxa (*Decaschisma pulchellum* and *Polydeltoideus enodatus*), two Silurian coronoid taxa (*Stephanocrinus angulatus* and *Cupulocorona gemmiformis*), and the enigmatic *Lysocystites nodosus* were incorporated as the in-group in the analysis. Tree stability was assessed via bootstrap support resampling all characters with 100 replicates (Felsenstein, 1978). *Cheirocystis fultonensis*, an Ordovician rhombiferan, was the outgroup.

Results and discussion

Morphology

Macurdablastus uniplicatus was reassessed from the holotype and paratype specimens. Plate boundaries were reinterpreted following the Universal Elemental Homology scheme for the oral area (Fig. 2; Broadhead, 1984; Sumrall, 2010; Sumrall and Waters, 2012). Our interpretation differs from the original in the following ways: The original illustration was missing an oral plate in the CD interray and the lancet plates were interpreted as covering a more restrictive area than it actually appears on the specimen. Unlike eublastoids, which have a lancet plate extending for the full length of the ambulacra, *M. uniplicatus* possesses a lancet plate that extends only to the proximal portion of the ambulacra, where it abuts an axially positioned extension of the radial plate coring the radial cleft near the summit (Fig. 2, 3.5). The morphology of the lancet plate is more similar in outline to the facetal plate found in coronoids (Fig. 3.4) Facetal plates in coronoids are interpreted as homologous to lancet plates serves as the attachment sites for erect ambulacra bearing brachioles extending off the theca (Brett et al., 1983).

Respiratory structures

Clades of Paleozoic blastozoan echinoderms are commonly characterized by their distinctive respiratory structures (Sprinkle, 1973). Eublastoids possess endothelial internal respiratory structures called hydrospires that are thin, calcified infoldings of the body wall, which connect to the outside by pores or slits. Fluids are passed through these structures to the interior of the theca, where gas exchange takes place via membranes supported by hydrospire folds.

Macurdablastus uniplicatus possesses long openings that run parallel to the ambulacra within the radial plate, and lead to infoldings of the radial plate that form single thick internal projections on either side of the ambulacra (Fig. 4). The available specimens have sediment infill within the long opening and making precise assessment of morphology difficult. The thick internal projections, however, are not created from both radial and deltoid plates, as they are in fissiculate blastoids. Deltoids of *M. uniplicatus* are very small and restricted to the summit suggesting lack of participation in the formation of the folds. The digitally reconstructed internal projections of *M. uniplicatus* suggest that within the radial plates the folds are straight adorally, but as they extend aborally toward the radial sinus, they become curved adradially (Fig. 2, 4.2). This occurs on more than one ambulacral ray and is unlikely to be a preservational artifact. Additionally, the reconstructed internal anatomy of *M. uniplicatus* provides evidence of round, elliptical like bulbs at the most adoral end of the ambulacra. These ‘bulb’ structures are not clearly visible from the exterior of the specimen because of sediment covering and the generally poor preservation on the oral surface (Fig. 4.3). Early eublastoids such as *Polydeltoideus*

enodatus and *Decaschisma pulchellum* (Fay, 1967) possess hydrospire slits parallel to the ambulacra concealed by floor plates. Unfortunately, no cover plates remain on the preserved specimens of *M. uniplicatus*, which would provide more information on the external morphology of these structures (e.g., pore development).

Eublastoids have been historically separated into two orders based on the external expression of hydrospire structures. Fissiculates possess slits that run parallel to the ambulacra, across the deltoid-radial suture, and lead to the internal folds. By contrast, spiraculates possess pores that line the ambulacra and lead to the internal folds that culminate as excurrent spiracles on the oral surface. Recent examination and work suggest that these relationships are more complicated than previously considered and these major groups require revision (Atwood, 2013; Bauer et al., 2017; Qualls et al., 2017).

Our comprehensive examination of skeletal elements and internal anatomy suggest that *Macurdablastus uniplicatus* possess critical features to exclude it from Eublastoidea. Specifically, the morphology of the lancet plate being circular and restricted to the oral surface and internal projections of the respiratory structures distinguish *M. uniplicatus* from eublastoids and coronoid taxa.

Phylogenetic inference

Maximum parsimony analysis resulted in two most parsimonious trees (Fig. 5.1, 2). One tree topology has the two eublastoid species in a sister relationship. Sister taxon to the grouping of eublastoids is *Macurdablastus uniplicatus*. The two coronoid taxa group together and are sister taxa to the grouping of eublastoids and *M. uniplicatus*.

Lysocystites nodosus is sister taxon to all aforementioned taxa. The other tree topology results in *M. uniplicatus* nesting within the two eublastoid taxa. The primary difference is in the placement of *Macurdablastus* with the eublastoid taxa, resulting in a polytomy on the strict consensus of the two trees. The clade of *Macurdablastus* and eublastoid taxa is supported by the interambulacral shape, recumbent ambulacra, oral plate septum, widest portion of the radial plate, hydrosphere slit length, and the maximum thecal width. The separation of the two coronoid taxa, *Stephanocrinus* and *Cupulocorona*, is supported by the peristomial cover plate arrangement (PPCP; see Fig. 3.4), lancet plate as a facet plate, oral and radial plates projecting over the summit surface, and coronal canals. Additionally, the position of *Lysocystites* varies from previously proposed evolutionary hypotheses (Donovan and Paul, 1985) by placing *Lysocystites* as sister taxon to the larger coronoid-eublastoid clade. This topology is supported by ambulacral outline, interambulacral shape, small oral plates relative to the radial plates, the widest portion of the radial plate, and exothecal respiratory structures.

The maximum likelihood analysis resulted in a single inferred topology (Fig. 5.4). Similar uniting characters are uncovered with the further separation of eublastoids supported by the lancet shape and the radial sinus development. Additional characters also support the grouping of coronoid taxa including lancet shape and the distal basal shape.

Differences in inferred phylogeny likely resulted from character inclusion within analyses. For the maximum parsimony analysis, of the 80 characters 43 were constant, 21 were variable, and 16 were considered informative. Although the maximum parsimony

analysis removes much of the character data it was retained in this study as it is still commonly used with paleontological datasets. Conversely, the maximum likelihood analysis ignored 10 characters that possessed all missing data. Retention of these ten characters is in their utility in comparing the taxa studied here and other Paleozoic echinoderm groups, including additional eublastoids.

Conclusions

Here we reject *Macurdablastus uniplicatus* as the oldest recorded eublastoid species on the basis of the adorally restricted lancet plate and differences in respiratory structures. The eublastoid group is united by the shape of the lancet plate, defined radial sinus, and the ratio of plates around the ambulacra. These characters are different in *Macurdablastus uniplicatus* excluding it from the eublastoid clade. The digitally reconstructed anatomy of *M. uniplicatus* provided details on the internal and external anatomy that were unclear in previous work. The rejection of *M. uniplicatus* moves the oldest undisputed eublastoid to the middle Silurian (Wenlock; Fay, 1967).

The study of Paleozoic invertebrates has been limited by only being able to examine the external morphology. As evidenced in this study, synchrotron and other advanced imaging techniques can provide a more complete understanding of the entire anatomy. Internal anatomy has been suggested to provide novel characters that aid in better understanding invertebrate organisms (Leighton and Maples, 2002; Bauer and Stigall, 2016; Bauer et al., 2017)

Systematic description

Blastoidea Say 1825

Macurdablastus Broadhead 1984

Diagnosis.—Blastoid with nearly flat summit resulting in little vault in lateral view; aborally restricted lancet plate; expanded radial platform supports recumbent ambulacra; broad respiratory structure openings run parallel to ambulacra.

Type species.— *Macurdablastus uniplicatus* Broadhead 1984

Macurdablastus uniplicatus Broadhead 1984

Diagnosis.—Same as generic diagnosis because of monotypy.

Description.—Broad pseudo-fivefold symmetry in summit view with greatest thecal width at top of the organism. Vase-like gross body form in lateral view; summit is flat resulting in little to no vault in lateral view. Conservative body plan includes three primary plate circlets: three basals, five radials, five lancets, and six oral plates.

Ambulacra five, long, thin, parallel sided, tapering aborally. Ambulacra are contained within the radials plates and lay atop projecting radial prongs; interambulacra areas are concave.

Basals three, two zygous and one azygous, in the AB interray. Basal circlet forms broadening conical shape, tapering aborally in lateral view. Basals are approximately 30% of the pelvis height. Stem not preserved, and stem facet shape is not discernible.

Stem facet morphology unknown, bases of holo- and paratype are crushed with secondary calcite overgrowths further obscuring details. The plate boundaries between the basals and radials plates appear abutting.

Radials five, radially positioned, irregular pentagonal shape in lateral view with a low ridge running from the sinus toward the radial-basal suture that becomes less pronounced aborally. Straight, fine, faint growth lines present that parallel plate sutures. Radial prongs project away from primary body axis and produce maximum width of the body. Radial platform (as described in Broadhead (1984)) preserved and appears to be location of main food groove but ambulacral floor plates lacking.

Deltoids (orals) six, small plates. Deltoid body is small, radial-deltoid suture abutting with the plate overlap unclear. Deltoid septum largely hidden by infill, rarely visible. Deltoid crest pentagonal in shape and forms peristomial border. Deltoid body is slightly smaller than the deltoid crest. Anal area deltoids largely missing with O1 (epideltoid) and O6 (subdeltoid) present. O1 borders peristome but not anal opening. Hypodeltoid (O7) missing. Peristome is subpentagonal in shape with no primary peristomial cover plates preserved in place.

Lancet plate, circular and elongate, abuts radial platform distally and two deltoids proximally that preclude it from bordering peristome. Topographically high adorally with a slope aborally. Lower position of lancet would likely have been covered by ambulacral floor plates. The utility of this plate is unknown, no facetar scars present. Main ambulacral groove following shallow dip in radial platform onto the lancet plate and

through the deltoid-deltoid suture near the mouth. Side plates, cover plates, and brachioles unknown

Respiratory structures appear to be a single in-folding on either side of the ambulacra. Folds created by the radial plate, persist for entirety of ambulacra, and narrow from the adoral to the aboral end. Adorally there is a clear 'bulb' that at first glance appears to be an artifact of infill. Reconstruction of these folds suggests this bulb persists into the body cavity but not as deeply penetrating as the folds. The bulb begins at the radial-deltoid suture and a pair of bulbs in the same ray turn inward adorally. Folds are generally parallel to the ambulacra with a slight angle toward the radial platform aborally. The reconstructed data suggest that these folds do not meet underneath the radial platform.

Discussion.—The most notable difference in skeletal plating of *Macurdablastus uniplicatus* with, respect to eublastoids, is the size and position of the lancet plate. In all eublastoids, the lancet plate extends for the entirety of the ambulacra whereas in *M. uniplicatus* it is restricted adorally. Additionally, the lancet is exposed adorally but is concealed aborally. In many eublastoids the lancet can be partially concealed but there is no apparent topographic difference in the plate as seen in *M. uniplicatus*. This was most apparent when examining the reconstructed specimen where the authors could clearly visualize plate boundaries and plate height.

To accommodate the ambulacral floor plates, there is a radially positioned plate that is the support for the recumbent ambulacra. In eublastoids, a hydrospire plate (previously referred to as a sublancet, underlancet, and fused hydrospire plate, see

Beaver, 1967, S235) has been recognized in some species but it is likely that plate is an extension of the radial or deltoid plate depending on thecal position. *Macurdablastus uniplicatus* supports the idea that the hydrospire plate is likely an extension of the radial or deltoid plate. Additionally, eublastoids always possess a lancet plate that is situated atop of the hydrospire plate.

The slits/troughs of *Macurdablastus uniplicatus* adorally look similar to paired spiracles exhibited by several blastoid species (e.g., *Diploblastus glaber*) but this is likely the result of sediment infill in the trough and bulbs. Broadhead (1984) suggested the bulbs to be similar to the hydrospire ducts in eublastoids. Unlike other early eublastoids, *M. uniplicatus* has very simple respiratory structures. Silurian eublastoids possess 3+ thin hydrospire slits covered by ambulacral floor plating. The large exterior opening of the folds in *M. uniplicatus* is more similar to slit structures in *Orophocrinus* (Mississippian) and Permian forms such as *Angioblastus*.

Types.—Holotype USNM 359545 and paratype USNM 359646.

Occurrence.—*Macurdablastus uniplicatus* is known only from the Upper Ordovician Benbolt Formation, Union County, Tennessee, USA.

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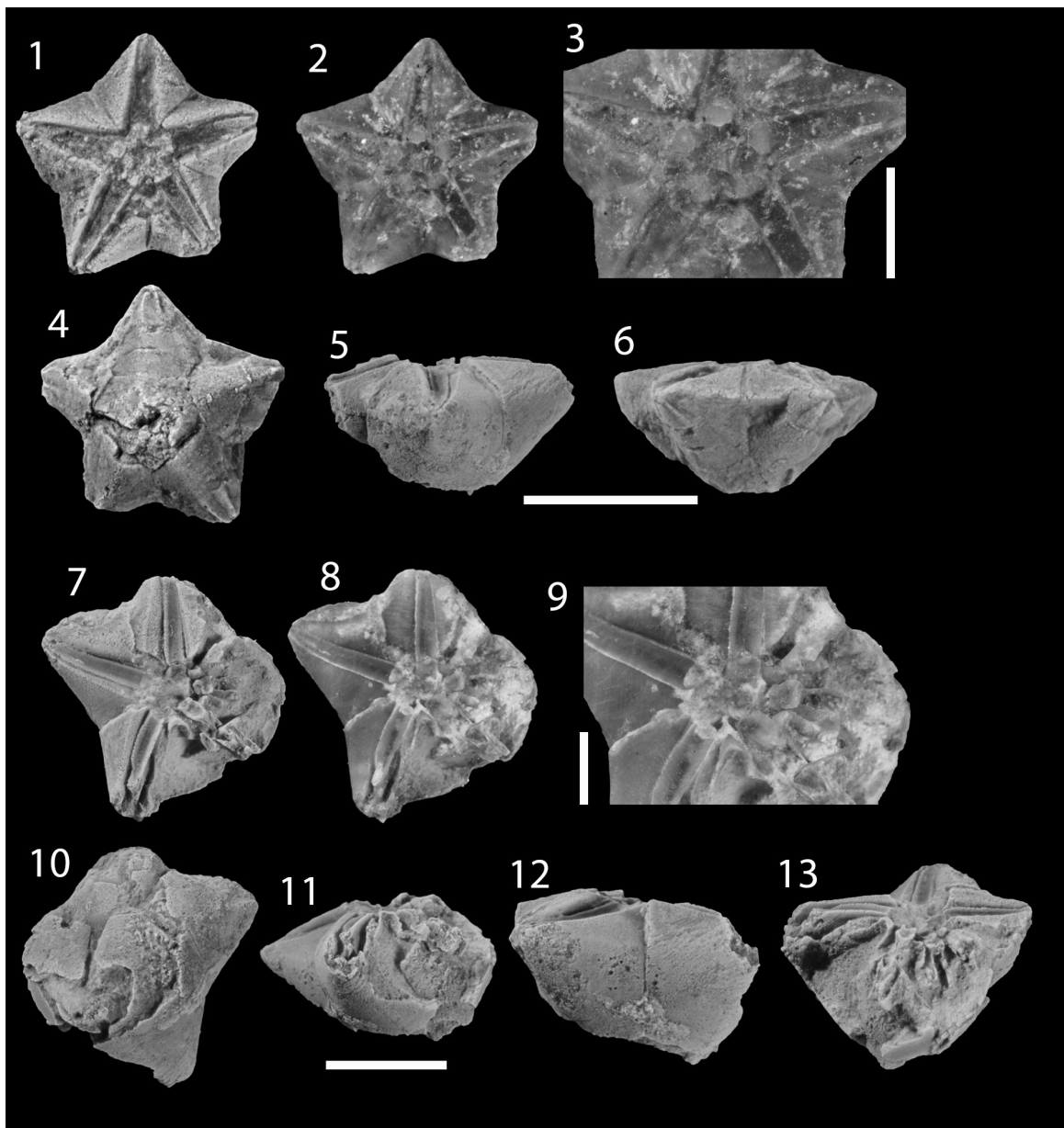
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Appendix 2-1

Figure 2.1. *Macurdablastus uniplicatus* holotype USNM 359545 **(1–6)** Scale bar represents 5 mm. **(1)** Summit view of the holotype specimen; **(2)** Summit view of the holotype specimen under water to better elucidate plate boundaries; **(3)** Enlarged summit view under water, scale bar indicates 2 mm; **(4)** Basal circlet view of holotype specimen; **(5)** Ambulacral view; **(6)** Interambulacral view. *Macurdablastus uniplicatus* paratype USNM 359646 **(7–13)** Scale bar represents 5 mm. **(7)** Summit view of the paratype specimen; **(8)** Summit view of the paratype underwater; **(9)** Enlarged summit view underwater, scale bar 2 mm; **(10)** Basal circlet view of paratype; **(11)** Oblique ambulacral view to visualize the respiratory folds; **(12)** Interambulacral view; **(13)** Oblique view of damaged area. All images are whitened with ammonium chloride except where noted.



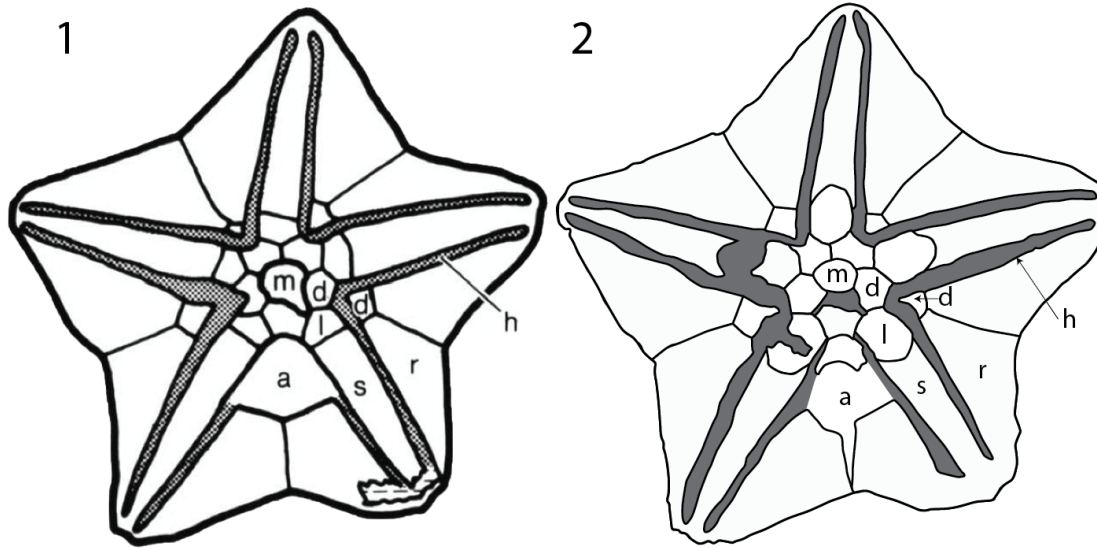


Figure 2.2. (1) The original line drawing of *Macurdablastus uniplicatus* from Broadhead (1984), compared to **(2)** the revised plate boundaries of *Macurdablastus uniplicatus*. M = mouth, d = deltoid/oral, l = lancet, r = radial, s = radial platform, a = anus, h = hydrospire. Specific differences lie within the recognition of an additional plate in the anal area and the elongation of the lancet plate from the pentagonal plate described in Broadhead (1984).

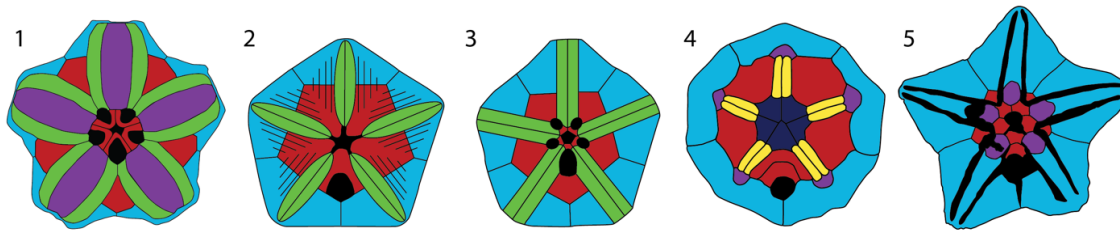


Figure 2.3. Universal Elemental Homology scheme described by Sumrall and Waters (2012) interpreted on line drawings of (1) *Pentremites* (eublastoid, spiraculate); (2) *Heteroschisma* (eublastoid, fissiculate); (3) *Devonoblastus* (eublastoid, spiraculate); (4) *Stephanocrinus* (coronoid); (5) *Macurdablastus*. Red = oral plates; light blue = radial plates; green = ambulacral floor plates; yellow = cover plates; dark blue = primary peristomial cover plates; purple = lancet plates.

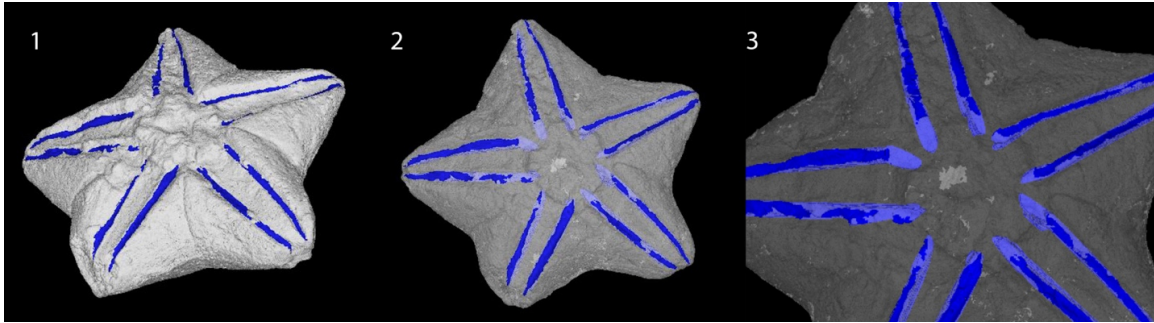


Figure 2.4. SPIERSview of the reconstructed anatomical model of the holotype of *Macurdablastus uniplicatus*. **(1)** Shows the external expression of the respiratory structures, in blue, with an opaque body. **(2)** Slightly transparent body reveals the bulbs in the adoral position to the respiratory structures. **(3)** Close up view with very transparent body to see the structures in more detail. Note the slight adradially curvature of the bulbs.

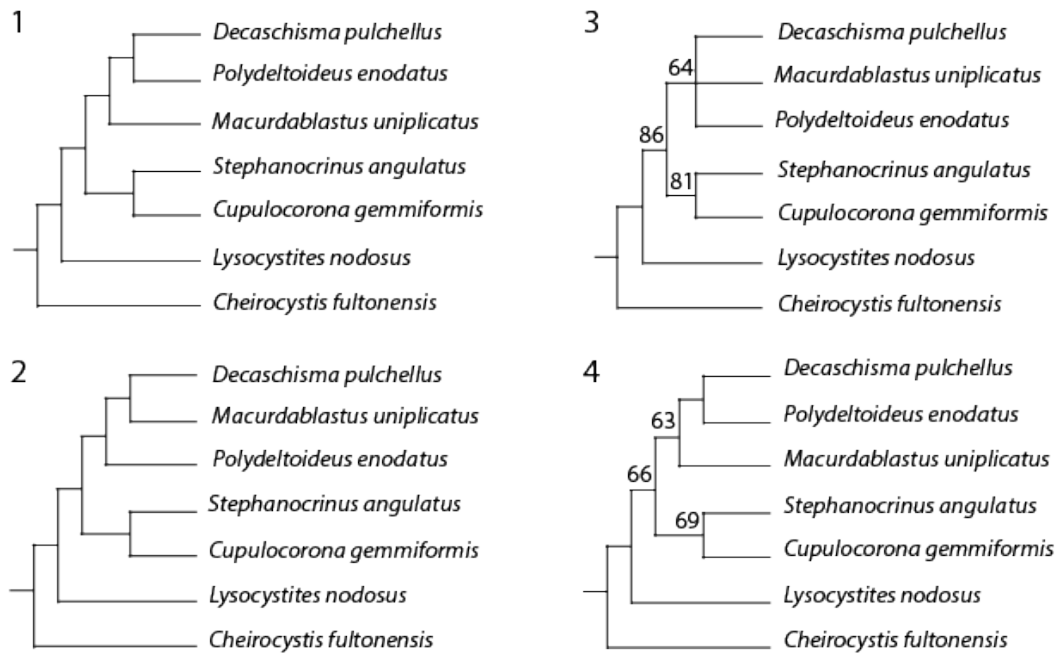


Figure 2.5. Resulting tree topology from both maximum parsimony and maximum likelihood analyses. Bootstrap values are represented at nodes with maximum likelihood bootstrap values on the left and maximum parsimony bootstrap values on the right. **(1)** Tree 1 inferred from maximum parsimony analysis. **(2)** Tree 2 inferred from maximum parsimony analysis. **(3)** Strict consensus of two most parsimonious trees with 46 steps, CI = 0.848, RI = 0.696, RC = 0.590; HI = 0.152; **(4)** Single tree recovered from maximum likelihood analysis, lnL = 195.992, AIC = 481.985, AICc = 654.485, BIC = 583.168.

Appendix 2-2

[Link to reconstructed *Macurdablastus uniplicatus* holotype specimen \(USNM 359645\)](#)

[Link to reconstructed *Macurdablastus uniplicatus* paratype specimen \(USNM 359646\)](#)

Appendix 2-3

Character descriptions and character states.

Primary Peristomial Cover Plates

1. Peristomial Cover plates sutured to theca: (0) Absent; (1) Present
2. PPCP size and differentiation: (0) Small and undifferentiated; (1) Large and differentiated
3. PPCP arrangement on the summit: (0) Plates are flat/flush with summit surface; (1) Plates are elevated above the summit surface

Ambulacra

4. Distal ambulacra length to width relationship: (0) Length is greater than width; (1) Length is much greater than width (more than double); (2) Width is subequal to length
5. Proximal ambulacral length: (0) Short and restricted adorally; (1) Elongate - a thin extension that the food groove sits on prior to reaching the floor plates and lancet
6. Main food groove placement: (0) Oral-oral suture to floor plates; (1) Oral-oral suture to lancet; (2) Oral-oral suture to lancet and floor plates
7. Ambulacral outline: (0) Parallel sided; (1) Lanceolate; (2) Oblanceolate; (3) Rhombiform
8. Shape of the ambulacral, proximal to distal in lateral view: (0) Straight; (1) Convex

9. Abaxial surface of ambulacra, perpendicular to primary body axis: (0) Flat; (1) Concave; (2) Convex
10. Interambulacral shape in summit view: (0) Flat; (1) Concave; (2) Convex
11. Ambulacral position with respect to surrounding thecal plates: (0) Below; (1) In-line; (2) Above
12. Reduced D ambulacrum: (0) Absent; (1) Present
13. Ambulacra recumbent: (0) Absent; (1) Present
14. Lateral food grooves curve: (0) Straight; (1) Adorally; (2) Aborally
15. Ratio of plates surrounding the ambulacra: (0) Radial > Oral; (1) Radial = Oral; (2) Radial < Oral

Lancet Plate

16. Lancet shape: (0) Button, circular; (1) Restricted, elongate; (2) Extends for entire ambulacrum
17. Lancet interaction with ambulacral floor plates (often referred to as side plates in blastoid taxa): (0) Side plates overlap lancet completely; (1) Partial exposure; (2) Lancet exposed for length of ambulacra
18. Lancet plate is a facet plate for erect ambulacra: (0) Absent; (1) Present

Oral + Radial Plate Interactions

19. Oral (referred to deltoid in blastoid text) and radial plate overlap: (0) Oral plates overlap radial plate; (1) Oral plates abut radial plates; (2) Radial plates overlap oral plates
20. Relative size comparison of oral and radial plates: (0) Oral plates are larger than radial plates; (1) Oral plates are approximately equal in size to radial plates; (2) Oral plates are smaller than radial plates
21. Oral and radial suture shape: (0) Flat; (1) V-shaped; (2) Lobate

Oral Plates

22. Oral plate body: (0) Absent; (1) Present
23. Oral plate crest: (0) Absent; (1) Present
24. Oral plate septum: (0) Absent; (1) Present
25. Oral plate growth lines: (0) Straight-fine growth lines; (1) Straight-coarse growth lines; (2) Wavy growth lines
26. Oral plate ornamentation, surface modification: (0) None present; (1) Nodes in linear arrays; (2) Nodes in random orientation, no clear pattern; (3) Large protrusions along ambulacra
27. Oral plates project above the summit/oral surface: (0) Flat on the surface; (1) Raised above the surface
28. Spiracles penetrate the oral plate body: (0) Absent; (1) Present

Anal Area Oral Plating

29. Oral plate 1 (O1; commonly referred to as epideltoid): (0) Absent; (1) Present
30. Oral plate 1 borders anus: (0) Absent; (1) Present
31. Oral plate 7 (O7; commonly referred to as hypodeltoid): (0) Absent; (1) Present
32. Oral plate 7 possesses a hood or extension away from the surface created by surrounding thecal plates: (0) Absent; (1) Present
33. Oral plate 6 (O6; commonly referred to as cryptodeltoids): (0) Absent; (1) Present and fused (previously called subdeltoid); (2) Present and split (cryptodeltoids).
34. Oral plate 6 exposure in anal area: (0) Hidden, not exposed; (1) Exposed in anal area; (2) Exposed and elongate (down theca)
35. Anus bordered by: (0) O1 and O7; (1) O1, O7, and O6; (2) O1, O6, O7, and ambulacral plating, (3) O1, O7, and ambulacral plating

Radial Plate Circlet

36. Radial-oral plate sutures: (0) Flat suture; (1) Recessed suture
37. Radial sinus development, the sinus holds the ambulacra and often has a defined end at the aboral most end of the sinus: (0) No development at aboral most end; (1) Development of lip or extension of radial plate; (2) Sinus extends far from thecal axis and has a projection at the aboral end of sinus
38. Radial plate growth lines: (0) Straight-fine growth lines; (1) Straight-coarse growth lines; (2) Wavy
39. Radial plate ornamentation, surface modification: (0) None present; (1) Nodes in linear arrays; (2) Nodes in random orientation, no clear pattern

40. Radial prongs, extensions of the radial sinus that protrude from the summit and body axis: (0) Absent; (1) Present
41. Radial plates project above the summit/oral surface: (0) Absent; (1) Present
42. The widest portion of the radial plate: (0) Limbs; (1) Ambulacral sinus end; (2) Middle of plate
43. Radial plates project below the basal plate circlet: (0) Absent; (1) Present
44. Secondary thickening on radial plates: (0) Absent; (1) Present

Basal Plate Circlet

45. Position of azygous basal plate: (0) AB; (1) DE
46. Secondary thickening around stem facet: (0) Absent; (1) Present
47. Basal-radial plate suture: (0) Flat; (1) Recessed
48. Basal-radial relative size: (0) $B > R$; (1) $B = R$; (2) $B < R$
49. Basal circlet orientation: (0) Flat; (1) Invaginated/concave; (2) In line with thecal plates (3) Small angle (4) large angle
50. Basal plate ornamentation, surface modification: (0) None present; (1) Nodes in linear arrays; (2) Nodes in random orientation, no clear pattern
51. Distal basal shape from basal view: (0) Circular; (1) Triangular; (2) Pentagonal

Respiratory Structures

52. Endothecal respiratory structures: (0) Absent; (1) Present
53. Exothecal respiratory structures: (0) Absent; (1) Present

54. Number of respiratory fields: (0) 8 fields; (1) 9 fields; (2) 10 fields
55. Respiratory structures exposed above ambulacral floor plates: (0) Absent; (1) Present
56. Hydrospire slits: (0) Absent; (1) Present
57. Hydrospire pores: (0) Absent; (1) Poorly developed; (2) Well-developed
58. Coronal canals: (0) Absent; (1) Present
59. Spiracle development: (0) None; (1) Underdeveloped; (2) Well-developed
60. Non-anal side spiracle manifestation: (0) Single; (1) Paired
61. Anus position with spiracles: (0) Separate; (1) Confluent
62. Spiracle shape: (0) Tear drop; (1) Bean-shaped; (2) Circular; (3) Elliptical
63. Hydrospire pore location: (0) Between floor plates and radial or oral plate; (1) Pore punctures radial or oral plate
64. Hydrospire pores extend for the duration of the ambulacra: (0) Absent; (1) Present
65. Number of hydrospire pores per floor plate set: (0) One; (1) Two; (2) Three+
66. Hydrospire slit length in comparison to ambulacral length: (0) Slit(s) extend for 50% or more of ambulacral length; (1) Slit(s) extend for approximately 50% of ambulacral length; (2) Slit(s) extend for less than 50% of ambulacral length
67. Placement of hydrospire slit: (0) Slit(s) are situated on oral and radial plates subequally; (1) Slit(s) are situated primarily on oral plates (>50%); (2) Slit(s) are situated primarily on radial plates (>50%)
68. Hydrospire slit exposure: (0) Concealed by floor plates; (1) Partially exposed; (2) Completely exposed

69. Number of hydrospire slits per field: (0) 1-2; (1) 3-5; (2) 6+
70. Number of hydrospire folds per field: (0) 1; (1) 2-3; (2) 3+ folds
71. Change in hydrospire folds per field depending on location in theca: (0) Absent; (1) Present
72. Anal area hydrospires differ from other fields: (0) No hydrospires (1) No difference; (2) Reduction of hydrospires
73. Hydrospire occupation of thecal space: (0) Little; (1) Moderate; (2) Full
74. Hydrospire cleft enlargement: (0) Absent; (1) Present
75. Hydrospire fold to spiracle transitions through theca: (0) No shifts; (1) 1 shift; (2) 2 or more shifts
76. Individual folds reach the exterior of the theca: (0) Absent; (1) Present

Miscellaneous Characters

77. Stem sutured to basals: (0) Absent; (1) Present
78. Columnal type: (0) Holomeric; (1) Polymeric
79. Widest part of theca: (0) Summit; (1) Middle; (2) Base
80. Ridges that extend from ambulacral sinus across radials and basals: (0) Absent; (1) Present

Appendix 2-4

Character matrix used for phylogenetic analysis.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Decaschisma pulcellus</i>	?	?	?	0	0	0	0	0&1	0&2	0	0	0	1	1	0
<i>Macurdablastus uniplicatus</i>	?	?	?	0	0	?	?	0	0	1	1	0	1	?	0
<i>Polydeltoideus enodatus</i>	?	?	?	0	0	0	0	1	0	1	0	0	1	0	1
<i>Stephanocrinus angulatus</i>	1	1	0	?	1	?	0	0	0	0	?	0	0	1	?
<i>Cupulocorona gemmiformis</i>	?	?	0	0	?	?	0	?	0	2	0	0	0	?	?
<i>Lysocystites nodosus</i>	?	?	?	?	?	?	0	?	2	2	1	0	0	?	?
<i>Cheirocystis fultonensis</i>	0	0	0	0	?	?	1	1	2	?	?	0	0	1	?
	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>Decaschisma pulcellus</i>	2	0	0	?	2	0&1	1	1	1	?	0	0&1	0	1	1
<i>Macurdablastus uniplicatus</i>	1	?	0	2	2	?	1	1	1	?	?	0	0	1	1
<i>Polydeltoideus enodatus</i>	2	0	0	2	2	1	1	1	1	?	?	1	?	1	?
<i>Stephanocrinus angulatus</i>	0	?	1	2	2	0	1	0	0	?	0	1	0	1	1
<i>Cupulocorona gemmiformis</i>	0	?	1	2	2	?	1	1	?	?	?	1	?	1	0
<i>Lysocystites nodosus</i>	1	?	?	?	2	?	1	1	?	0	1	0	?	?	?
<i>Cheirocystis fultonensis</i>	?	?	0	?	?	?	?	?	?	0	0	0	?	1	0
	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
<i>Decaschisma pulcellus</i>	0&1	0	1	1	1	0	1	0	0	0	0	1	0	0	0
<i>Macurdablastus uniplicatus</i>	?	?	?	?	?	0	?	0	0	0	0	1	0	?	0
<i>Polydeltoideus enodatus</i>	1	0	2	1	?	0	1	0	0	0	1	1	0	?	0
<i>Stephanocrinus angulatus</i>	1	?	?	?	0	0	0	?	1	0	1	2	0	0	0
<i>Cupulocorona gemmiformis</i>	1	0	?	?	?	?	?	0	?	0	1	2	0	0	0
<i>Lysocystites nodosus</i>	?	?	?	?	?	?	?	?	1	0	0	2	0	0	0
<i>Cheirocystis fultonensis</i>	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
<i>Decaschisma pulcellus</i>	0	0	2	2	0	0&1	1	?	2	0&1	1	0	0	1	0

<i>Macurdablastus uniplicatus</i>	?	0	2	2	?	?	1	?	2	?	1	?	0	1	?
<i>Polydeltoideus enodatus</i>	?	0	0	2	?	1	1	?	2	1	1	0	0	0	?
<i>Stephanocrinus angulatus</i>	0	0	2	2	1	1	0	1	?	?	0	0	1	0	?
<i>Cupulocorona gemmiformis</i>	0	?	?	2	?	1	?	1	?	?	?	?	1	?	?
<i>Lysocystites nodosus</i>	0	?	?	?	?	0	?	1	?	?	?	?	0	?	?
<i>Cheirocystis fultonensis</i>	?	?	?	?	?	0	1	0	?	?	?	?	0	?	?
	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
<i>Decaschisma pulcellus</i>	0&1	1	?	?	?	0	0&2	0&2	1&2	?	?	?	?	?	?
<i>Macurdablastus uniplicatus</i>	?	?	?	?	?	0	2	?	0	?	?	?	?	?	?
<i>Polydeltoideus enodatus</i>	?	?	?	?	?	0	2	1	2	?	?	2	?	?	?
<i>Stephanocrinus angulatus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cupulocorona gemmiformis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Lysocystites nodosus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cheirocystis fultonensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	76	77	78	79	80										
<i>Decaschisma pulcellus</i>	?	0	?	0	0										
<i>Macurdablastus uniplicatus</i>	?	?	?	0	0										
<i>Polydeltoideus enodatus</i>	?	?	?	0	0										
<i>Stephanocrinus angulatus</i>	?	0	?	1	1										
<i>Cupulocorona gemmiformis</i>	?	?	?	1	?										
<i>Lysocystites nodosus</i>	?	?	?	1	?										
<i>Cheirocystis fultonensis</i>	?	?	?	1	?										

CHAPTER 3
A COMPREHENSIVE PHYLOGENY OF EUBLASTOIDEA
(ECHINODERMATA): UTILITY OF RESPIRATORY STRUCTURES
IN BLASTOZOAN CLASSIFICATION

Abstract

Understanding the evolution of Paleozoic invertebrates is limited to assessing the external morphology of the organisms. These similarities and differences in external morphology form the basis of classification. Blastozoan echinoderms have been separated into higher taxa based primarily on the external expression of respiratory structures. Unfortunately, these structures are convergent in their external expression (e.g., pore rhombs, diplopores). Here we use Eublastoidea, a temporally expansive, geographically widespread, and conservatively plated clade, to examine the validity of subclade separation based on variation in respiratory structures. This work focused on reducing ambiguous external and internal character data and examined individual elements to develop a comprehensive character list to infer evolutionary relationships. Results suggest higher taxonomic groupings may be retained, but the family level separation needs to be revisited. Digitally reconstructed internal respiratory structures appear to provide additional resolution in the inferred tree topology, and this work should serve as a baseline for future systematic revision of other blastozoan clades. Comprehensive systematic revision of other blastozoan clades can use this work as a baseline for exploring character data and incorporating internal anatomy into analyses.

Introduction

Quantitatively assessing clade-defining characters in Paleozoic groups is becoming increasingly common as statistical methods are adapted to morphological data (e.g., Heath et al., 2014; Hunt et al., 2016; Wright et al., 2016). Testing complex questions such

as rate of character change and biogeographic patterns requires an understanding of the evolutionary relationships within the clade to use as a framework to quantitatively assess these questions. Relatively few phylogenetic studies have been conducted on Blastozoa, stemmed echinoderms possessing brachioles and complex respiratory structures (Sprinkle, 1973).

At present, blastozoans are separated into major groups (e.g., classes, orders, etc.) based on the presence of specific respiratory structures (Paul, 1968, 1972; Sprinkle, 1973), but recent work suggests that the evolution of specific respiratory structures (e.g., rhombs and diplopores) may be convergent within these taxa (Paul, 1968, 1972; Sumrall, 1997; Sheffield and Sumrall, in review; Qualls et al., 2017a, b). This study aims to reassess the importance of character data derived from the external expression of respiratory structures within a large group of blastozoans: the Eublastoidea.

Eublastoidea as a focus group

Taxa within Eublastoidea have a wide variation in gross body (thecal) morphology but have a stable arrangement of major thecal plates unlike many other echinoderm groups, where thecal plates are added in a semi-random manner. This allows individual plates to be recognized on every species regardless of morphological variation. Detailed studies can be conducted by examining the 18–21 stable thecal plates within a well-defined set of homologous elements (e.g., Waters et al., 1985; Foote, 1991). Additionally, eublastoids have upwards of a 200-million-year temporal range from the middle Silurian (Wenlock) to the end Permian extinction event and are found on every continent with the exception of Antarctica (likely present but unsampled), mainly in limestones and limey

shales (Fay, 1967; Waters, 1990). The long temporal range, global distribution of species, and stable body plan make the eublastoids an ideal focus group for testing evolutionary questions such as biogeographic trends and gross body plan changes related to climatic events in the Paleozoic.

Eublastoid classification

Eublastoidea Bather 1899 has recently been resurrected (Bauer et al., in prep.). This clade includes all those possessing recumbent ambulacra on an elongate lancet plate and hydrospire respiratory structures, the “blastoids” of contemporary usage. Blastoidea includes eublastoids, coronates, *Lysocystites*, and *Macrurablastus* (following Donovan and Paul, 1985; Bauer et al., in prep.).

Eublastoids have been separated into two orders, Fissiculata and Spiraculata. These groupings are based on external details of the respiratory structures called hydrospires (Jaekel, 1918; Wanner, 1940; Fay, 1967; Waters and Horowitz, 1993), which are thin, elongate folds of stereom on the thecal interior through which ambient seawater flows for gas exchange (Macurda, 1967; Beaver 1996). In fissiculates, the external expression of the respiratory structures is exposed hydrospire slits associated with a gap along the abradial edge of the side plates for water flow. Conversely, in spiraculates, the hydrospire slit is covered by lateral extensions of the side plates forming hydrospire pores that line the edge of the floor plates and terminate in round openings near the summit called spiracles (Fig. 1; Waters, 1988). In practice, the separation of these groups has been primarily on the basis of presence or absence of spiracles and hydrospire pores (Fay, 1967; Breimer and Macurda, 1972; Macurda, 1983; Waters and Horowitz, 1993). Critical

examination of hydrospire slits and pores suggests that binary separation it is not so simple. For example, *Troosticrinus reinwardti*, a recognized spiraculate, has poorly developed hydrospire pores and spiracles, but also bears slits covered by side plates. For this reason, these morphological features should be treated as separate characters. If treated as a single character, then species, such as *Troosticrinus reinwardti*, violates the conjunction test of homology, where if a species possesses both structures they cannot be homologous transformation of a character sequence (Patterson, 1988).

The taxonomy and classification of fissiculates and spiraculates have been examined separately over the last 50 years (Breimer and Macurda, 1972; Macurda, 1983; Breimer, 1988a, b; Waters and Horowitz, 1993) but few studies have utilized rigorous methodology to evaluate evolutionary relationships between the two groups (Atwood, 2013; Bodenbender and Fisher, 2001). Previous studies have concluded that the spiraculates are polyphyletic, occurring many times and nested within a larger fissiculate clade (Waters, 1990; Waters and Horowitz, 1993). This hypothesis was supported by a recent phylogenetic analysis by Atwood (2013) and previous work on assessing eublastoid phylogeny by Bodenbender (1995) and Bodenbender and Fisher (2001). Atwood (2013) generated a phylogenetic framework to determine clade supporting characters and sub-clade origination among eublastoids relying on external morphological characters. Results of Atwood (2013) suggested that the higher-level eublastoid classification scheme need to be reevaluated as the resulting tree topology of 24 species included a polyphyletic Spiraculata nested within a larger Fissiculata and family relationships not retained. These previous studies utilized external thecal

morphology to construct character matrices and largely ignored the complex internal morphology (Bodenbender, 1995; Bodenbender and Fisher, 2001; Sumrall and Brochu, 2003; Atwood, 2013).

Here we present a new phylogeny for Eublastoidea based on revised external morphological character data and digitally reconstructed internal anatomy. The inclusion of additional taxa in the current study has resulted in the inference of a more robust and comprehensive evolutionary hypothesis for Eublastoidea.

Materials and methods

Materials

Character data were recorded directly from museum specimens rather than the primary literature to avoid the introduction of errors or alternate interpretations of morphology made by earlier workers. Specimens were examined from a number of institutions including: National Museum of Natural History (USNM), Cincinnati Museum Center (CMC), Yale Peabody Museum (YPM), Field Museum of Natural History (FMNH), Sam Noble Museum of Natural History (SNMNH), and the personal collection of J.A.W. Of all the species initially examined (approximately 88), fifty-five were included for the phylogenetic analysis (see Appendix 3-2). Species were removed if they lacked specific identification or incompleteness or poor preservation resulted in a high proportion of character data not coded. If a species was one of many in a genus, the species with the most complete coding scheme was included.

Building a comprehensive character matrix

The most common method to understand the internal structures was to create serial sections of specimens. Breimer and van Egmond (1968) produced acetate peel data sets for approximately forty eublastoid species. Much of this data was never published, but recent efforts have been made to digitally reconstruct the complete hydrospire structures from these legacy acetate peels (Waters et al., 2014, 2015, 2017; Bauer et al., 2015, 2017; Qualls et al., 2017a, b). Internal character data were reconstructed from serially sectioned specimens reposted at the Naturalis Biodiversity Center in Leiden, Netherlands. This collection of acetate peels was produced by Breimer and van Egmond (1968) and contains approximately 40 blastoid species. The acetate peels were digitized and used to create digital three-dimensional anatomical models of the hydrospires. For details on the methodology used to construct these structures see Waters et al. (2015, 2017).

Ideally, all of the taxa used to infer eublastoid phylogeny would be represented by species for which there are both specimens to code external morphology and internal data derived from acetate peels to code internal morphology. Constructing hydrospire models from acetate peels is time consuming and computationally costly but provides critical data for inferring eublastoid phylogeny (Bauer et al., 2015, 2017). This study incorporates the complete internal datasets for nine eublastoid taxa (Qualls et al., 2017b). The nine taxa include two fissiculate and seven spiraculate taxa.

External characters

External character sets for eublastoids, were originally defined by A.S. Horowitz, A. Breimer, and D.B. Macurda Jr. in the 1960s. Additional character data has been accumulating over the past decades resulting in a variety of morphometric and phylogenetic based analyses creating a robust understanding of eublastoid morphology (Foote, 1991; Bodenbender, 1995; Bodenbender and Fisher, 2001; Sumrall and Waters, 2012; Atwood, 2013). Previously utilized characters were reassessed considering recent advances in understanding blastozoan homology. This allowed for a comprehensive character matrix rooted in shared ancestry. Additional work was conducted to assess individual plate elements in order to reduce ambiguous characters.

This methodology allows us to create a character matrix independent of poorly developed characters such as thecal shape. For example, previous character matrices created categories of different eublastoid thecal shapes as defining ‘characters’ (e.g., pyriform, globose, godoniform, vase-shaped). However, the distributions of individual thecal plates can vary widely between species with the same overall shape (Fig. 2). Both *Globoblastus* and *Nucleocrinus* (Fig. 2) are globose in shape, but the former has small deltoids with the bulk of the theca formed from radial plates whereas the latter had the vast majority of theca formed from deltoids but with very small radials. Rather than utilizing a single, ambiguous term to delineate thecal shape in eublastoids, character suites were developed in the current study for specific plate circlets to incorporate the individual character transformations, which results in overall gross morphology.

Oral plates in the CD interray: The plating of the anal area of eublastoids has also been utilized as an important taxonomic character in familial level classification (Fay, 1967). Anal plating in eublastoids has not been entirely reconciled with other blastozoan clades and needs further investigation. In most blastozoans, three plates from the anal side oral plate complex (Sumrall, 2010; Sumrall and Waters, 2012) but at least six different plates associated with the anal opening have been recognized within blastoids (Fig. 3.1–5; Beaver et al., 1967).

The character suite developed for the anal area incorporates these changes in anal area plating for better assessment of taxa. In UEH, the epideltoid (Fig. 3) is recognized as O1 and is always bordering the oral opening and in some taxa, it also borders the anal opening. The hypodeltoid is recognized as O7 and is always bordering the anus. The remaining oral plate (O6), has been considered problematic in eublastoids and was not defined within UEH (Sumrall and Waters, 2012). Cryptodeltoids are located on opposite sides of the anal opening adjacent to O1 and O7 and can either be exposed at the summit or concealed by other plates (Beaver, 1967). The subdeltoid has been previously suggested to be fused cryptodeltoids, which share a congruent position strengthening this argument (Beaver et al., 1967).

Here we agree with the assessment that the subdeltoid is likely fused cryptodeltoids and this plate likely represents O6. The position of O6 in other blastozoans is recognized as having variable position related to other oral plates. The position of the subdeltoid as surrounding the aboral half of the anal opening is situated in the same position as the two cryptodeltoids. In some cases, the cryptodeltoids are not exposed at the surface and

extend for the entire theca in other species. This variability has led to confusion with these plates. In some cases, the external anal opening is only bordered by O1 and O7 but in other instances ambulacral floor plating also borders the anal opening. Other differences in the Beaver (1967) anal plate arrangements are simply the relative proportion of each plate surrounding the anal opening. The term superdeltoid is rejected as a homolog of the epideltoid in cases where O1 borders the oral opening alone and not the anal opening. Anideltoid is also rejected as the examples of possessing a single plate are often attributable to preservational bias. Paradeltoids have been recognized in *Polydeltoideus enodatus* alone and appear to rest atop the hypodeltoid plate with no inferable homolog in other taxa.

Lancet plate: Additionally, the lancet plate, which is incorporated into ambulacral structure, can be entirely exposed, entirely covered, or exposed for a portion of the ambulacral length. The exposure, shape, and position of the lancet plate are significant as this plate is in direct contact with the respiratory and feeding structures. Additionally, this plate has been suggested to be a synapomorphy of the Eublastoidea within the larger Blastoidea clade.

Internal characters

Internal characters, specifically the number of hydrospire folds, have been utilized to delineate eublastoid species in the past. Here, internal characters are based on the complete reconstructions of the respiratory structures and characters that have been previously used to delineate species (Bauer et al., 2015, 2017; Qualls et al., 2017a, b). Internal characters include: (1) the number of hydrospire folds in each hydrospire field;

(2) any change in number of hydrospire folds depending on the location in the theca; (3) differences in anal area hydrospires in comparison to hydrospires in other fields, in some cases there are none or they are reduced in hydrospire fold number; (4) hydrospire fold occupation of internal thecal space; (5) hydrospire cleft enlargement, an extension that accommodates multiple fold originations along its length; (6) hydrospire fold to spiracle transitions or how many steps seawater would undergo before leaving the theca; and (7) whether individual hydrospire folds reach the exterior of the theca as they do with some fissiculate species.

Phylogenetic analysis

Phylogenetic analysis was performed via heuristic searches through maximum parsimony and maximum likelihood in PAUP*4.0b10 (Swofford, 2003; see Appendix 3-4). Maximum parsimony analysis was conducted utilizing TBR for branch swapping, ACCTRAN optimization, and characters were treated as unordered and were equally weighted. Maximum likelihood analysis was conducted utilizing the Mk model for discrete characters (Lewis, 2001) to assess variation between methods. Similar to the parsimony analysis, the characters were unweighted and unordered. Further analysis was conducted to assess the topology differences with and without the hydrospire character data. This involved removing the seven internal characters and reanalyzing the matrix. Outgroup taxon is *Cheirocystis fultonensis*.

Tree stability was assessed via bootstrap analysis of randomly generated matrices through resampling all characters with 100 replicates (Felsenstein, 1978). Tree stability

was assessed by various indices and measures for each method and additional bootstrap analyses were conducted in PAUP*4.0b10 to further assess sub-clade support.

Results

Maximum parsimony analysis recovered 18,600 most parsimonious trees with tree length of 436 steps, indices include CI = 0.401, RI = 0.576, RC = 0.231, HI = 0.741. Autapomorphies and characters that do not change the overall tree topology were excluded as uninformative characters but were retained for the maximum likelihood analysis. Consequently, this analysis had 14 uninformative characters, leaving 66 characters influencing tree topology. The strict consensus of the set of equally most parsimonious trees retains several well supported subclades (Fig. 4.1). These subclades include: (1) clade A (Fig. 4.1) with wide petaloid ambulacra supported by the relative size of the oral and radial plates, the absence of hydrospire slits, and well-developed hydrospire pores; (2) clade B (Fig. 4.1) that includes 10 species united by the elongated proximal ambulacral length, ambulacral position being in line with surrounding thecal plates, the anus being bordered by O1, O7, and O6, hydrospire slits being completely exposed, and the anal area lacking hydrospire structures. This later clade includes a polytomy of several taxa and an additional subclade supported by oral plates overlapping radial plates, oral plates being raised above the oral surface, nodes in linear arrays on the radial plates, the widest portion of the radial plate being in the middle of the plate, and the lack of spiracle development (see Table 1 for detailed list of species and character support and Appendix 3-5 for all node support).

Maximum likelihood analysis resulted in 12 trees (Fig. 4.2) with a best score of 1574.142, AIC = 3428.285, AICc = 42908.285, BIC = 3761.769. All 80 characters were included in the maximum likelihood analysis. This tree topology has retention of major clades seen in the maximum parsimony analysis but there is some variation. Characters that supported clade A (Fig. 4.1) on the maximum parsimony tree support the closest ancestral node in the maximum likelihood group rather than the combination of the larger pentremiid+schizoblastid group. This large clade has a grade of pentremiids leading to two clades. One of the granatocrinids+orbitremiids (Fig. 4.2 clade D) and then granatocrinid leading to a phaenosphimatid clade (Fig. 4.2 clade C).

Discussion

Trees and clade support

The maximum parsimony tree topology suggests an early separation of pentremiids+schizoblastids (Fig. 4.1 clade A) and codasterids+orophocrinids (Fig. 4.1 clade A). There is one large clade that includes 35 species with a few subclades with a nearly pectinate base containing a grade of phaenosphimatids (Fig. 4.1 grade C) to a large grouping of the more globular and elongate globular forms (Fig. 4.1 clade D). Finally, a large terminal clade of granatocrinids+orbitremiids (Fig. 4.1 clade F).

In the maximum likelihood tree, the clade of codasterids+orophocrinids (Fig. 4.2 clade B) diverged prior to the pentremiids+schizoblastids (Fig. 4.2 clade A, A'), unlike the maximum parsimony reconstruction. In the maximum likelihood topology there is not a single grouping of pentremiids+schizoblastids but two smaller clades (Fig. 4.2 clade A,

A'), both in an ambiguous relationship with the largest subclade (includes clades C-F). The codasterids+orophocrinid group (Fig. 4.2 clade B) is further resolved and has additional character support. The clade of granatocrinids+orbitremiids (Fig. 4.2 clade F) also has increased resolution and different arrangement of species. The major difference is the sister clade to the larger nucleocrinid+granatocrinid+orbitremiid clade (Fig. 4.2 clade D). Thus, additional subclade includes a granatocrinid grade, troosticrinid clade, and a phaenoschismatid clade. This large group formed the pectinate base of the large clade in the maximum parsimony analysis.

Removal of internal character data

The removal of the seven internal hydrospire characters caused disruption in several locations on the maximum parsimony tree. *Lophoblastus* was removed from the pentremiid+schizoblastid clade (Fig. 4.1 clade A) and the codasterid+orophocrinid clade (Fig. 4.1 clade B) was split in half. Taxa from both clade A and B lost support and resulted in increased ambiguous relationships. The granatocrinid+orbitremiid clade was split and the nucleocrinids appear within a derived position in a granatocrinid clade. The impact of removal of characters on the maximum likelihood analysis was only apparent in the granatocrinid+orbitremiid clade (Fig. 4.2 clade F). This clade contains three of the nine species with models included in this analysis and different relationships are inferred with the lack of internal character data.

Comparison to previous classification

Much of the comprehensive previous work (e.g., Fay, 1967; Breimer and Macurda, 1972) separates the taxa included into the analysis into fissiculates and spiraculates prior to examining evolutionary relationships. Examination of fissiculates and spiraculates separately operates with the assumption that these groups are natural evolutionary clades.

Spiraculate classification was revised by Waters and Horowitz (1993) and the fissiculate classification was reassessed by Breimer and Macurda (1972) and Macurda (1983) but these two groups have not been analyzed together to assess the monophyly of the classification scheme and the utility of respiratory structures as synapomorphies. It has been suggested that spiraculates evolved multiple times within a larger fissiculate clade (Waters and Horowitz, 1993; Atwood, 2013). Under both inference methods, neither Fissiculata or Spiraculata are monophyletic groups. Both methods place *Phaenoblastus caryophyllatus* as being sister taxon to the rest of Eublastoidea, retain several subclades, and suggest that the possession of slits, pores, and spiracles are not clade defining. In some cases, species possess slits, underdeveloped or developed pores, and underdeveloped spiracles (e.g., *Troosticrinus*, *Hyperoblastus*, *Cryptoschisma*; see Fig. 5).

Although maximum parsimony and likelihood produce different evolutionary histories, they provide a basis from which to assess the diagnostic characteristics of the stable clades, to reassess relationships within those subgroups, and to provide identification for the next digital reconstruction of hydrospires. Phaenoschismatids have

been previously proposed to be the ancestral group (Fay, 1967), which is supported by the maximum parsimony inferred topology. Alternatively, the inferred topology via maximum likelihood suggests the phaenoschismatids arose from a grade of granatocrinids and troosticrinids

A previous phylogenetic study by Bodenbender and Fisher (2001) provided a large dataset of external blastoid characters but also incorporated stratigraphic and crystallographic information into the analysis. Incorporating non-character-based data into the analysis did not provide accurate phylogenetic inference because the stratigraphic distribution of fossil taxa is non-random and may not correlate with evolutionary relationships (Sumrall and Brochu, 2003). Although their work included stratigraphy and crystallographic data into phylogenetic hypotheses, they provided a comprehensive discussion and analysis on the variation and resolution between datasets. Tree inference produced solely by morphological character data (Bodenbender and Fisher, 2001, see Figure 7) produced a grade of Permian fissiculatids and *Codaster* leading to a large clade that was largely unresolved. Unsurprisingly, the well supported nucleocrinid clade was resolved with several smaller grantocrinid clades. The addition of crystallographic and stratigraphic data, however, significantly confounds the evolutionary trends within Eublastoidea. Sumrall and Brochu (2003) reran the character matrix from Bodenbender and Fisher (2001) and produced an Adams consensus tree that pull taxa that are pairing with many taxa to their lowest common node (Adams, 1972). This allows for the retention of clades in a strict consensus that are inferred by all most parsimonious trees when rogue taxa are removed. The revised tree structure (Sumrall and Brochu, 2003)

based on the dataset of Bodenbender and Fisher (2001) infers a basal grade rather than a clade of codasterids inferred herein (Fig. 4 clade B). The large granatocrinid clade is retained with several subclades, including the nucleocrinids, much like the trees inferred in this study. Major differences in topology include the pentremiid clade being in an ambiguous relationship with the large granatocrinid clade in a more derived position than on the trees presented here (Fig. 4 clade D).

Bather (1899) described several groupings of eublastoids, which were referred to as series. Here the Granatoblastida series of Bather (1899) is retained as the largest subclade on the inferred tree topology. This includes the nucleocrinids, which were removed during the last revision of spiraculate classification (Waters and Horowitz, 1993). This large clade includes species of several other families including Schizoblastidae and Orbitremiidae. Additionally, Codonoblastida series of Bather (1899) is partially retained with the clade of orophocrinids, neoschismatids, and codasterids. The revised Pentremiida of Waters and Horowitz (1993) is separated into three clades in the maximum parsimony analysis and two clades and a grade in the maximum likelihood analysis. The phaenochismatids are represented as a grade in the maximum parsimony analysis and a clade in the maximum likelihood analysis. Results thus indicate that higher taxonomic groupings are generally retained, but the family level separation needs to be revisited.

Implications and future directions

Blastozoan higher taxa have been separated out largely based on the possession of specific respiratory structures (Paul, 1968, 1972; Sprinkle, 1973). While it is true that the

hydrospire respiratory structures in eublastoids are clade diagnostic, they are poorly understood despite the fact that details of their construction form the basis of older classifications. Utilizing revised character suites to better capture minute changes in morphology, including internal morphological characters, and excluding stratigraphic position from the analyses provides a more comprehensive and robust understanding of eublastoid evolution. The results presented in this study and other recent work (e.g., Sheffield and Sumrall, in review) suggest that the other blastozoan clades require phylogenetic revision and reclassification.

The morphological character data gained from reassessing characters following the Universal Elemental Homology scheme, and reconstructing the respiratory structures added in increased resolution in this work and rejects clade separation based on the external expression of hydrospires. This suggests that reexamination of homologous elements and better understanding of the respiratory structures for other blastozoan echinoderms is extremely important and will likely provide further details on clade evolution within Blastozoa.

Additional phylogenetic analyses were conducted removing the seven hydrospire characters assembled from examination of the ten digitally reconstructed models. Nine of the ten species with all seven internal characters were incorporated into the analysis. The tenth species was unable to be included due to poor preservation on loaned specimens. Four out of the nine species fall within the granatocrinid+orbitremid clade (Fig. 4 clade D) and an additional three within clade A of pentremidids+schizoblastids. In both analyses the removal of hydrospire character data results in either reduced resolution or

different inferred evolutionary relationships, suggesting that the data is providing important support within the tree structure. The addition of taxa and generation of more hydrospire models will likely provide increased resolution and help to resolve these topological differences.

Future studies will add eublastoid species into this phylogenetic framework. These additional taxa will aid in inferring other stable groupings of eublastoids providing a more complete understanding of their evolutionary history. This will be accompanied by the generation of additional internal models to the data set to fill out this framework. The additional models will also increase the amount of character information we are able to gain from the internal anatomy. There are several species that have been identified as being ancestral to others, specifically in relation to the transition from the fissiculate to spiraculate morphotype. Future work will include testing the utility of placing species at ancestral nodes rather than all as terminal taxa. The classification of Eublastoidea will need to be revised and incorporate a more comprehensive phylogenetic framework to begin to assess evolutionary changes.

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Appendix 3-1

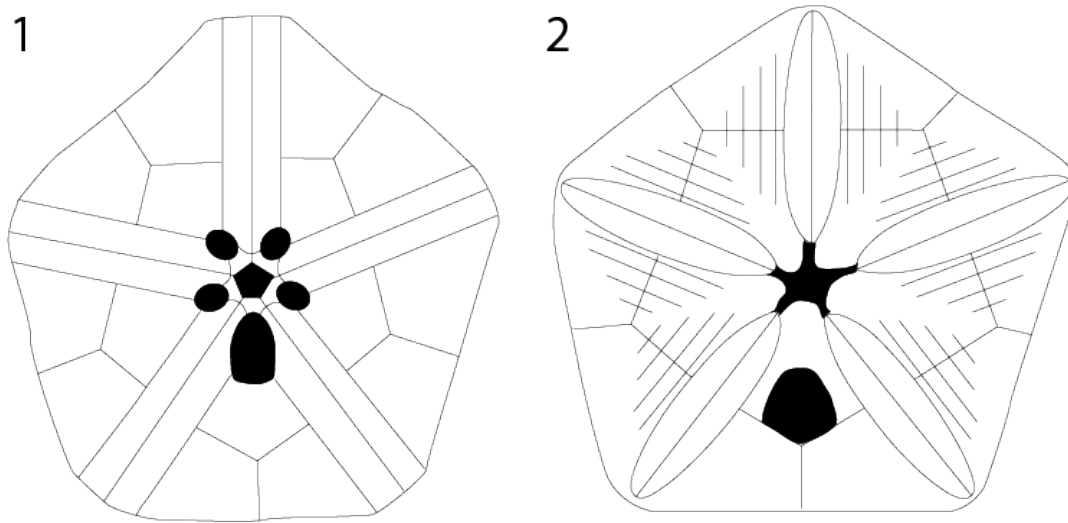


Figure 3-1. Generalized diagram of the two external expressions of eublastoid respiratory structures. **(1)** Spiraculata possess large circular openings on the summit and pores that line the ambulacra; **(2)** Fissiculata possess slits that run parallel to the ambulacra and cross the deltoid radial suture. Modified from Beaver (1967).

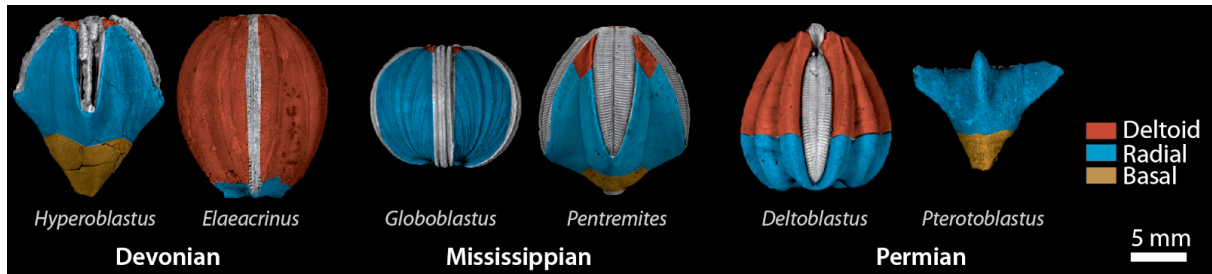


Figure 3-2. Major plate circlets outlined on lateral views of different species. The oral (deltoid) plate circlet is in red, radials in blue, and basals in orange. In *Hyperoblastus*, *Globoblastus*, and *Pterotoblastus* the oral plates are small and restricted to the summit. In *Elaeacrinus*, *Globoblastus*, and *Deltoblastus* the basals are invaginated and hidden from lateral view. Both *Elaeacrinus* and *Globoblastus* are considered to be ‘globose’ and *Pentremites* and *Deltoblastus* are considered ‘godoniform’. Although these broadly defined shapes are similar the individual elements that create the shape are quite different.

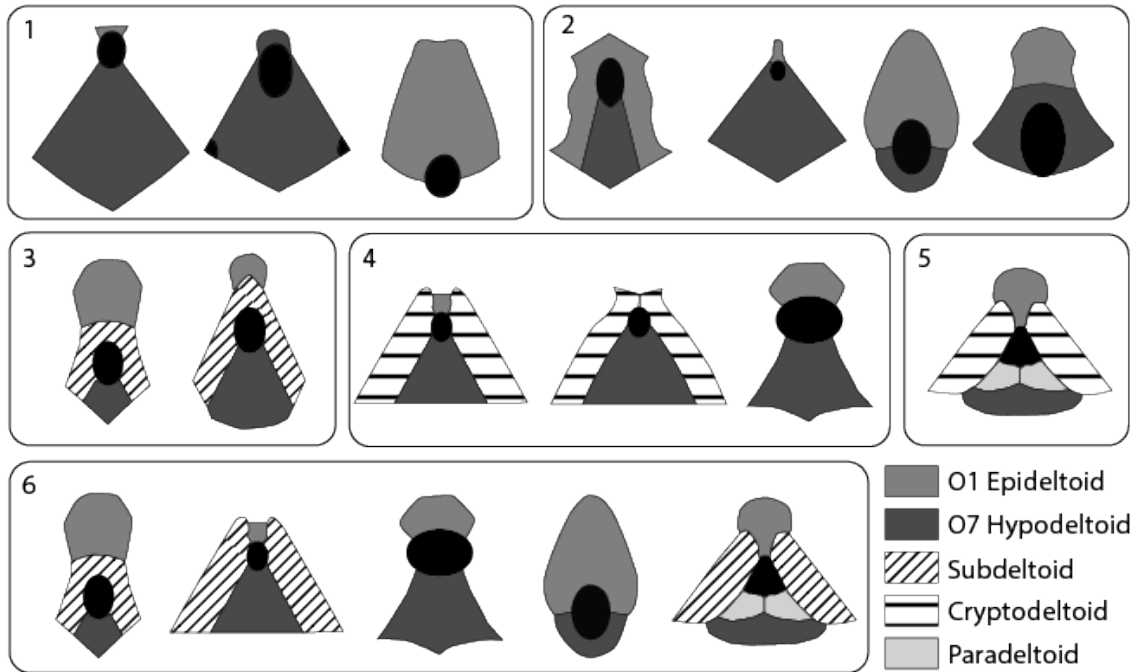
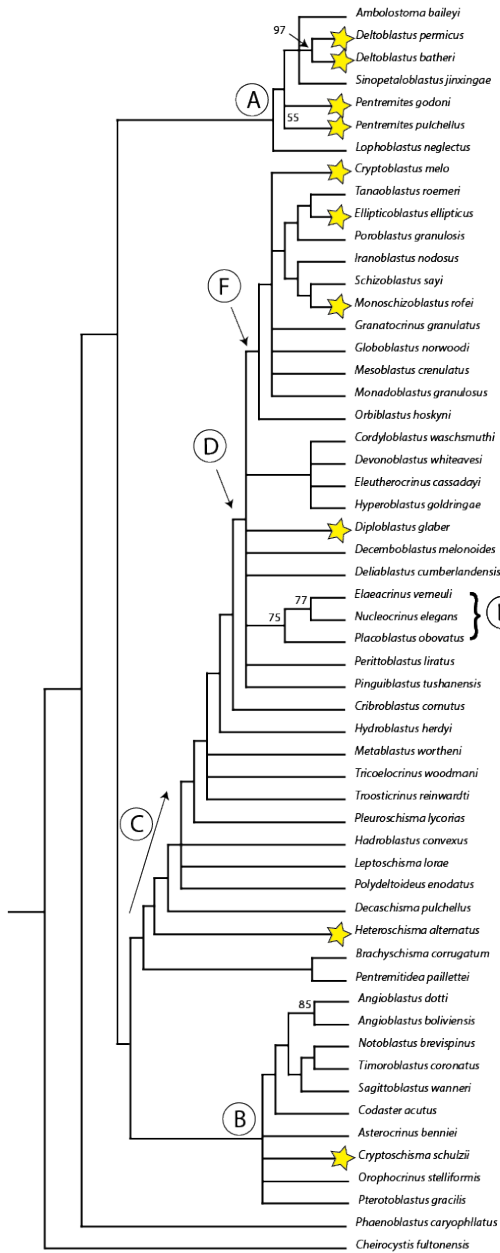


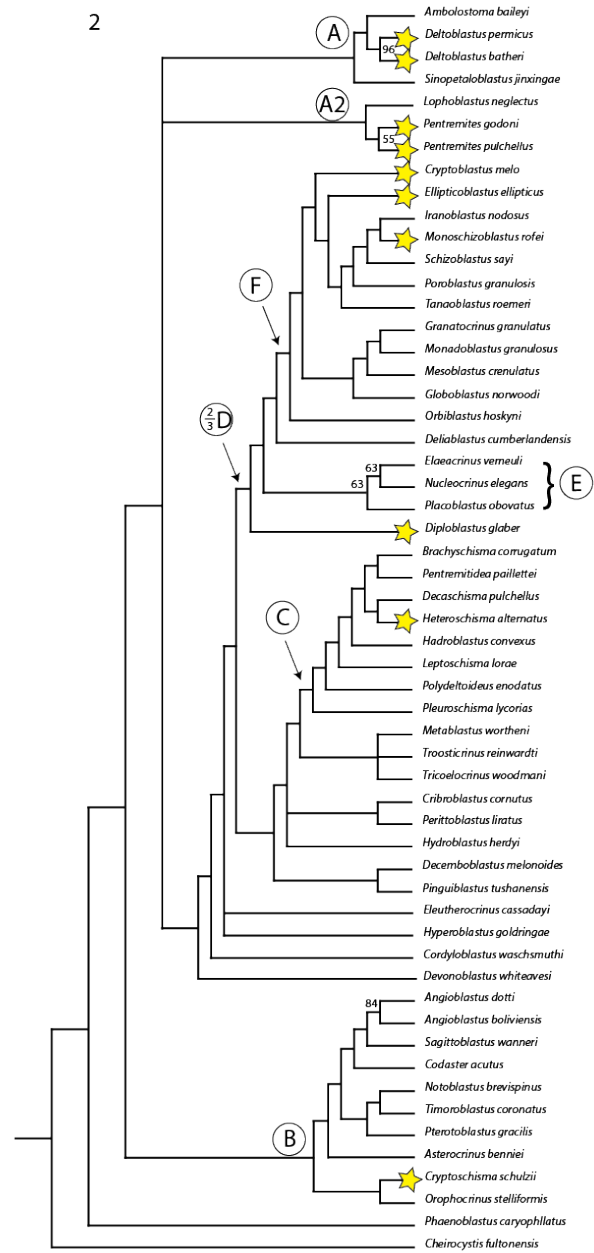
Figure 3-3. Previously proposed types of anal-deltoid relationships in eublastoids. **(1)** Group one was suggested to possess only one anal deltoid; **(2)** Group two possessed two anal deltoids; **(3)** Group 3 possessed three anal deltoids; **(4)** Group four possessed four anal deltoids; **(5)** Group five possessed five anal deltoids. **(6)** Revised anal plating. The epideltoid (O1) always appears present and bordering the mouth but is not always in contact with the anal opening. Cryptodeltoid and subdeltoid are synonymized as representing O6. Modified from Beaver (1967).

Figure 3-4. Results of phylogenetic inference, species with complete digitally reconstructed hydrosphere structures denoted by stars. **(1)** Tree search conducted under maximum parsimony. Clade A includes pentrematids+schizoblastids, Clade B includes codasterids+orophocrinids, Grade C includes phaenoschismatids, Clade D includes nucleocrinids+granatocrinids+orbitrematids, Clade E includes nucleocrinids, Clade F includes granatocrinids+orbitrematids. **(2)** Tree search conducted under maximum likelihood analysis. Letters indicate same groupings, but differences lie in C forming a clade rather than a grade, seven species that formed D in the maximum parsimony analysis are not included in the maximum likelihood clade.

1



2



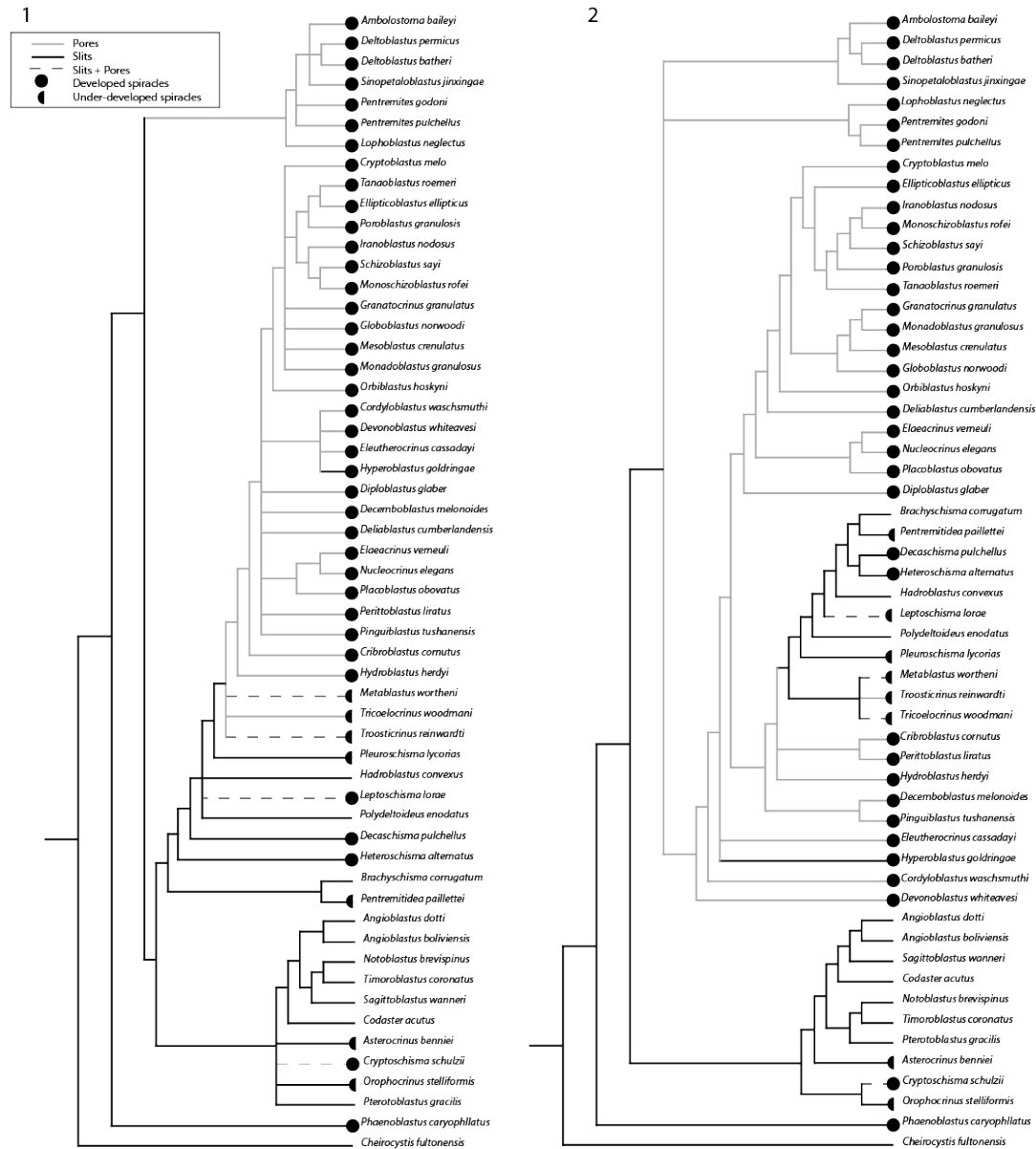


Figure 3-5. Tree topologies with respiratory structures mapped onto the branches and terminal tips. (1) Maximum parsimony analysis; (2) Maximum likelihood analysis. Gray bars indicate hydrospire pores, black bars indicate hydrospire slits, full circles indicate well-developed spiracles, and half-circles indicate underdeveloped spiracles.

Appendix 3-2

Specimen list of all species coded for phylogenetic analysis. NMNH = National Museum of Natural History; SNMNH = Sam Noble Museum of Natural History; YPM = Yale Peabody Museum; FMNH = Field Museum of Natural History

<i>Species</i>	Specimen number	Museum
<i>Ambolostoma baileyi</i>	PAL 111762	NMNH
<i>Angioblastus boliviensis</i>	PAL 160591	NMNH
<i>Angioblastus dotti</i>	PAL 111249	NMNH
<i>Brachyschisma corrugatum</i>	PAL 387783	NMNH
<i>Brachyschisma corrugatum</i>	OU Topotype	SNMNH
<i>Cryptoblastus melo</i>	YPM 36131	YPM
<i>Cryptoblastus melo</i>	YPM 6541	YPM
<i>Codaster acutus</i>	S 6137	NMNH
<i>Cordyloblastus waschsmuthi</i>	S 6147	NMNH
<i>Crioblastus cornutus</i>	USNM 160641	NMNH
<i>Cryptoschisma schulzii</i>	OU strat	SNMNH
<i>Diploblastus glaber</i>	YPM strat	YPM
<i>Diploblastus glaber</i>	FMNH PE 54423	FMNH
<i>Diploblastus glaber</i>	FMNH 26804	FMNH
<i>Diploblastus kirkwoodensis</i>	OU 18517	SNMNH
<i>Diploblastus kirkwoodensis</i>	FMNH P31840	FMNH
<i>Decaschisma pulchellum</i>	S 3212	NMNH
<i>Decaschisma pulchellum</i>	USNM 248323	NMNH
<i>Decaschisma pulchellus</i>	UC 2810	FMNH
<i>Decaschisma pulchellus</i>	OU 18509	SNMNH
<i>Decemboblastus melonoides</i>	USNM S5360	NMNH
<i>Decemboblastus melonoides</i>	USNM S5359	NMNH
<i>Deliablastus cumberlandensis</i>	USNM 416252	NMNH
<i>Deltoblastus permicus</i> var. <i>elliptica</i>	OU 18532	SNMNH

Species	Specimen number	Museum
<i>Deltoblastus batheri</i>	OU 28439	SNMNH
<i>Devonoblastus whiteavesi</i>	USNM S4144	NMNH
<i>Eleutheroocrinus cassadayi</i>	YPM 36128	YPM
<i>Eleutheroocrinus cassadayi</i>	YPM 6514	YPM
<i>Elaeocrinus verneuili</i>	UC 9956	FMNH
<i>Elaeocrinus verneuili</i>	OU 28432	SNMNH
<i>Elaeocrinus verneuili</i>	YPM 82121	YPM
<i>Elaeocrinus verneuili</i>	YPM 82115	YPM
<i>Elaeocrinus verneuili</i>	YPM 82109	YPM
<i>Elaeocrinus venustus</i>	OU 18485	SNMNH
<i>Ellipticoblastus orbicularis</i>	UC 13877	FMNH
<i>Hadroblastus convexus</i>	USNM 160762	NMNH
<i>Hadroblastus convexus</i>	USNM 160763	NMNH
<i>Hadroblastus convexus</i>	OU 18484	SNMNH
<i>Heteroschisma pyramidatus</i>	OU 18507	SNMNH
<i>Heteroschisma canadensis</i>	YPM 82129	YPM
<i>Heteroschisma canadensis</i>	YPM 390529	YPM
<i>Heteroschisma alatus</i>	YPM 82130	YPM
<i>Heteroschisma alatus</i>	YPM 390526	YPM
<i>Heteroschisma alternatus</i>	YPM 82131	YPM
<i>Heteroschisma alternatus</i>	YPM 390530	YPM
<i>Heteroschisma</i> sp.	YPM 390514	YPM
<i>Heteroschisma</i> sp.	YPM 7074	YPM
<i>Heteroschisma</i> sp.	YPM 390511	YPM
<i>Hyperoblastus goldringae</i>	YPM 82135	YPM
<i>Hyperoblastus goldringae</i>	YPM 390483	YPM
<i>Hyperoblastus goldringae</i>	YPM 390482	YPM
<i>Hyperoblastus goldringae</i>	YPM 390478	YPM
<i>Hyperoblastus goldringae</i>	YPM 390479	YPM

<i>Species</i>	Specimen number	Museum
<i>Hyperoblastus filosa</i>	PAL 455889	NMNH
<i>Hyperoblastus filosa</i>	YPM 7077	YPM
<i>Hyperoblastus filosa</i>	YPM 390464	YPM
<i>Hyperoblastus filosa</i>	YPM 82137	YPM
<i>Hyperoblastus filosa</i>	YPM 390480	YPM
<i>Hyperoblastus</i> sp.	PAL 455890	NMNH
<i>Hyperoblastus americana</i>	FMNH Hall #321a	FMNH
<i>Hyperoblastus reimanni</i>	OU 18505	SNMNH
<i>Hyperoblastus reimanni</i>	OU 18457	SNMNH
<i>Granatocrinus granulosus</i>	YPM 006510.A	YPM
<i>Globoblastus norwoodi</i>	YPM 82140	YPM
<i>Globoblastus norwoodi</i>	YPM 8467	YPM
<i>Globoblastus norwoodi</i>	YPM 390541	YPM
<i>Globoblastus norwoodi</i>	YPM 34765	YPM
<i>Lophoblastus neglectus</i>	S 6155	NMNH
<i>Leptoschisma lora</i>	USNM 160713	NMNH
<i>Macurda blastus uniplicatus</i>	USNM 359646	NMNH
<i>Mesoblastus crenulatus</i>	YPM 33561	YPM
<i>Mesoblastus crenulatus</i>	S 3775b	NMNH
<i>Mesoblastus sphaeroidalis</i>	FMNH P31879	FMNH
<i>Metablastus wortheni</i>	FMNH P31882	FMNH
<i>Metablastus wortheni</i>	S6145	NMNH
<i>Metablastus lineatus</i>	FMNH 13597	FMNH
<i>Metablastus bipyramidalis</i>	OU 48045	SNMNH
<i>Monadoblastus granulosus</i>	OU strat	SNMNH
<i>Nucleocrinus cucullatus</i>	YPM 82114	YPM
<i>Nucleocrinus elegans</i>	YPM 7076	YPM
<i>Notoblastus brevispinus</i>	OU 18496	SNMNH
<i>Orbiblastus hoskyni</i>	USNM 158779	NMNH

Species	Specimen number	Museum
<i>Orophocrinus stelliformis</i>	YPM 8464	YPM
<i>Orophocrinus stelliformis</i>	YPM 6540	YPM
<i>Orophocrinus stelliformis</i>	OU18464	SNMNH
<i>Orophocrinus</i> sp.	YPM 8536	YPM
<i>Orophocrinus catactus</i>	USNM 162415	NMNH
<i>Orophocrinus conicus</i>	USNM 162402	NMNH
<i>Deltoschisma archiaci</i>	UC 51678	FMNH
<i>Pentremitidea pailletia</i>	YPM 19181	YPM
<i>Pentremitidea paillettei</i>	FMNH 19088	FMNH
<i>Pentremitidea palletti</i>	OU strat	SNMNH
<i>Perittoblastus liratus</i>	USNM 416245	NMNH
<i>Phaenoblastus caryophyllatus</i>	S 6148	NMNH
<i>Phaenoblastus caryophyllatus</i>	FMNH UC 19082	FMNH
<i>Phaenoblastus pecki</i>	OU strat	SNMNH
<i>Placoblastus obovatus</i>	FMNH P19678	FMNH
<i>Pleuroschisma lycorias</i>	USNM 160718	NMNH
<i>Pleuroschisma ontario</i>	USNM 114491	NMNH
<i>Polydeltoideus enodatus</i>	USNM 160706	NMNH
<i>Poroblastus granulosus</i>	S 3717	NMNH
<i>Poroblastus</i> sp.	OU 18465	SNMNH
<i>Pterotoblastus gracilis</i>	USNM 248336	NMNH
<i>Pentremites abruptus</i>	S 3244	NMNH
<i>Pentremites angularis</i>	S 3250a	NMNH
<i>Penremites angustus</i>	YPM 502326	YPM
<i>Pentremites angustus</i>	S 3254a	NMNH
<i>Pentremites angustus</i>	OU 267	SNMNH
<i>Pentremites angustus</i>	OU strat	SNMNH
<i>Pentremites angustus</i>	OU 48359	SNMNH
<i>Pentremites conoideus</i>	YPM 8491	YPM

<i>Species</i>	Specimen number	Museum
<i>Pentremites conoideus</i>	OU18479	SNMNH
<i>Pentremites conoideus</i> var. <i>amplus</i>	YPM 6535	YPM
<i>Pentremites elongatus</i>	YPM 82053	YPM
<i>Pentremites florealis</i>	YPM 226859	YPM
<i>Pentremites godoni</i>	YPM 226915	YPM
<i>Pentremites godoni</i>	YPM 226883	YPM
<i>Pentremites godoni</i>	OU 4350	SNMNH
<i>Pentremites godoni-florealis</i>	YPM 6572	YPM
<i>Pentremites laminatus</i>	OU 47202	SNMNH
<i>Pentremites prematurus</i>	YPM 226926	YPM
<i>Pentremites pulchellus</i>	YPM 226878	YPM
<i>Pentremites pyriformis</i>	YPM 226869	YPM
<i>Pentremites rusticus</i>	YPM 512388	YPM
<i>Pentremites rusticus</i>	OU 4458	SNMNH
<i>Pentremites rusticus</i>	OU 264	SNMNH
<i>Pentremites rusticus</i>	OU strat	SNMNH
<i>Pentremites rusticus</i>	OU 48363	SNMNH
<i>Pentremites sulcatus</i>	YPM 82101	YPM
<i>Pentremites</i> sp.	OU 5049	SNMNH
<i>Pentremites</i> sp.	OU 18500	SNMNH
<i>Pentremites</i> sp.	OU 48261	SNMNH
<i>Sagittoblastus wanneri</i>	USNM 102187	NMNH
<i>Schizoblastus</i> sp.	YPM 36126	YPM
<i>Schizoblastus</i> sp.	YPM 390539	YPM
<i>Schizoblastus</i> sp.	YPM 390540	YPM
<i>Schizoblastus</i> sp.	YPM 6542	YPM
<i>Schizoblastus sayi</i>	FMNH 12341	FMNH
<i>Timoroblastus coronatus constrictus</i>	OU 18503	SNMNH

Appendix 3-3

Character definitions and coding used for the phylogenetic analysis

Primary Peristomial Cover Plates

1. Peristomial Cover plates sutured to theca: (0) Absent; (1) Present
2. PPCP size and differentiation: (0) Small and undifferentiated; (1) Large and differentiated
3. PPCP arrangement on the summit: (0) Plates are flat/flush with summit surface; (1) Plates are elevated above the summit surface

Ambulacra

4. Distal ambulacra length to width relationship: (0) Length is greater than width; (1) Length is much greater than width (more than double); (2) Width is subequal to length
5. Proximal ambulacral length: (0) Short and restricted adorally; (1) Elongate - a thin extension that the food groove sits on prior to reaching the floor plates and lancet
6. Main food groove placement: (0) Oral-oral suture to floor plates; (1) Oral-oral suture to lancet; (2) Oral-oral suture to lancet and floor plates
7. Ambulacral outline: (0) Parallel sided; (1) Lanceolate; (2) Oblanceolate; (3) Rhombiform
8. Shape of the ambulacral, proximal to distal in lateral view: (0) Straight; (1) Convex
9. Abaxial surface of ambulacra, perpendicular to primary body axis: (0) Flat; (1) Concave; (2) Convex

10. Interambulacral shape in summit view: (0) Flat; (1) Concave; (2) Convex
11. Ambulacral position with respect to surrounding thecal plates: (0) Below; (1) In-line; (2) Above
12. Reduced D ambulacrum: (0) Absent; (1) Present
13. Ambulacra recumbent: (0) Absent; (1) Present
14. Lateral food grooves curve: (0) Straight; (1) Adorally; (2) Aborally
15. Ratio of plates surrounding the ambulacra: (0) Radial > Oral; (1) Radial = Oral; (2) Radial < Oral

Lancet Plate

16. Lancet shape: (0) Button, circular; (1) Restricted, elongate; (2) Extends for entire ambulacrum
17. Lancet interaction with ambulacral floor plates (often referred to as side plates in blastoid taxa): (0) Side plates overlap lancet completely; (1) Partial exposure; (2) Lancet exposed for length of ambulacra
18. Lancet plate is a facet plate for erect ambulacra: (0) Absent; (1) Present

Oral + Radial Plate Interactions

19. Oral (referred to deltoid in blastoid text) and radial plate overlap: (0) Oral plates overlap radial plate; (1) Oral plates abut radial plates; (2) Radial plates overlap oral plates

20. Relative size comparison of oral and radial plates: (0) Oral plates are larger than radial plates; (1) Oral plates are approximately equal in size to radial plates; (2) Oral plates are smaller than radial plates
21. Oral and radial suture shape: (0) Flat; (1) V-shaped; (2) Lobate

Oral Plates

22. Oral plate body: (0) Absent; (1) Present
23. Oral plate crest: (0) Absent; (1) Present
24. Oral plate septum: (0) Absent; (1) Present
25. Oral plate growth lines: (0) Straight-fine growth lines; (1) Straight-coarse growth lines; (2) Wavy growth lines
26. Oral plate ornamentation, surface modification: (0) None present; (1) Nodes in linear arrays; (2) Nodes in random orientation, no clear pattern; (3) Large protrusions along ambulacra
27. Oral plates project above the summit/oral surface: (0) Flat on the surface; (1) Raised above the surface
28. Spiracles penetrate the oral plate body: (0) Absent; (1) Present

Anal Area Oral Plating

29. Oral plate 1 (O1; commonly referred to as epideltoid): (0) Absent; (1) Present
30. Oral plate 1 borders anus: (0) Absent; (1) Present
31. Oral plate 7 (O7; commonly referred to as hypodeltoid): (0) Absent; (1) Present

32. Oral plate 7 possesses a hood or extension away from the surface created by surrounding thecal plates: (0) Absent; (1) Present
33. Oral plate 6 (O6; commonly referred to as cryptodeltoids): (0) Absent; (1) Present and fused (previously called subdeltoid); (2) Present and split (cryptodeltoids).
34. Oral plate 6 exposure in anal area: (0) Hidden, not exposed; (1) Exposed in anal area; (2) Exposed and elongate (down theca)
35. Anus bordered by: (0) O1 and O7; (1) O1, O7, and O6; (2) O1, O6, O7, and ambulacral plating, (3) O1, O7, and ambulacral plating

Radial Plate Circlet

36. Radial-oral plate sutures: (0) Flat suture; (1) Recessed suture
37. Radial sinus development, the sinus holds the ambulacra and often has a defined end at the aboral most end of the sinus: (0) No development at aboral most end; (1) Development of lip or extension of radial plate; (2) Sinus extends far from thecal axis and has a projection at the aboral end of sinus
38. Radial plate growth lines: (0) Straight-fine growth lines; (1) Straight-coarse growth lines; (2) Wavy
39. Radial plate ornamentation, surface modification: (0) None present; (1) Nodes in linear arrays; (2) Nodes in random orientation, no clear pattern
40. Radial prongs, extensions of the radial sinus that protrude from the summit and body axis: (0) Absent; (1) Present
41. Radial plates project above the summit/oral surface: (0) Absent; (1) Present

42. The widest portion of the radial plate: (0) Limbs; (1) Ambulacral sinus end; (2) Middle of plate
43. Radial plates project below the basal plate circlet: (0) Absent; (1) Present
44. Secondary thickening on radial plates: (0) Absent; (1) Present

Basal Plate Circlet

45. Position of azygous basal plate: (0) AB; (1) DE
46. Secondary thickening around stem facet: (0) Absent; (1) Present
47. Basal-radial plate suture: (0) Flat; (1) Recessed
48. Basal-radial relative size: (0) $B > R$; (1) $B = R$; (2) $B < R$
49. Basal circlet orientation: (0) Flat; (1) Invaginated/concave; (2) In line with thecal plates (3) Small angle (4) large angle
50. Basal plate ornamentation, surface modification: (0) None present; (1) Nodes in linear arrays; (2) Nodes in random orientation, no clear pattern
51. Distal basal shape from basal view: (0) Circular; (1) Triangular; (2) Pentagonal

Respiratory Structures

52. Endothecal respiratory structures: (0) Absent; (1) Present
53. Exothecal respiratory structures: (0) Absent; (1) Present
54. Number of respiratory fields: (0) 8 fields; (1) 9 fields; (2) 10 fields
55. Respiratory structures exposed above ambulacral floor plates: (0) Absent; (1) Present

56. Hydrosfire slits: (0) Absent; (1) Present
57. Hydrosfire pores: (0) Absent; (1) Poorly developed; (2) Well-developed
58. Coronal canals: (0) Absent; (1) Present
59. Spiracle development: (0) None; (1) Underdeveloped; (2) Well-developed
60. Non-anal side spiracle manifestation: (0) Single; (1) Paired
61. Anus position with spiracles: (0) Separate; (1) Confluent
62. Spiracle shape: (0) Tear drop; (1) Bean-shaped; (2) Circular; (3) Elliptical
63. Hydrosfire pore location: (0) Between floor plates and radial or oral plate; (1) Pore punctures radial or oral plate
64. Hydrosfire pores extend for the duration of the ambulacra: (0) Absent; (1) Present
65. Number of hydrosfire pores per floor plate set: (0) One; (1) Two; (2) Three+
66. Hydrosfire slit length in comparison to ambulacral length: (0) Slit(s) extend for 50% or more of ambulacral length; (1) Slit(s) extend for approximately 50% of ambulacral length; (2) Slit(s) extend for less than 50% of ambulacral length
67. Placement of hydrosfire slit: (0) Slit(s) are situated on oral and radial plates subequally; (1) Slit(s) are situated primarily on oral plates (>50%); (2) Slit(s) are situated primarily on radial plates (>50%)
68. Hydrosfire slit exposure: (0) Concealed by floor plates; (1) Partially exposed; (2) Completely exposed
69. Number of hydrosfire slits per field: (0) 1-2; (1) 3-5; (2) 6+
70. Number of hydrosfire folds per field: (0) 1; (1) 2-3; (2) 3+ folds

71. Change in hydrospire folds per field depending on location in theca: (0) Absent; (1) Present
72. Anal area hydrospires differ from other fields: (0) No hydrospires (1) No difference; (2) Reduction of hydrospires
73. Hydrospire occupation of thecal space: (0) Little; (1) Moderate; (2) Full
74. Hydrospire cleft enlargement: (0) Absent; (1) Present
75. Hydrospire fold to spiracle transitions through theca: (0) No shifts; (1) 1 shift; (2) 2 or more shifts
76. Individual folds reach the exterior of the theca: (0) Absent; (1) Present

Miscellaneous Characters

77. Stem sutured to basals: (0) Absent; (1) Present
78. Columnal type: (0) Holomeric; (1) Polymeric
79. Widest part of theca: (0) Summit; (1) Middle; (2) Base
80. Ridges that extend from ambulacral sinus across radials and basals: (0) Absent; (1) Present

Appendix 3-4

Character matrix used to infer tree topologies

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
<i>Amblostoma baileyi</i>	?	?	?	1	0	1	2	0&1	2	2	0	0	1	0&1	1	2	2	0	2	1	1	1	1	?	?
<i>Angioblastus boliviensis</i>	?	?	?	0	1	0	1	1	2	2	1	0	1	1	1	2	0	0	?	2	1	1	0	0	?
<i>Angioblastus dotti</i>	?	?	?	0	1	0	1	0	0	2	1	0	1	1	2	2	0	0	0	2	1	1	0	0	?
<i>Asterocrinus benniei</i>	?	?	?	0	0&1	0	2	1	2	2	0	1	1	1	0	2	0	0	?	2	1	1	1	1	?
<i>Brachyschisma corrugatum</i>	?	?	?	0	0	0	1	1	2	1	2	0	1	1	0	2	0&2	0	0&2	2	0&1	1	1	1	1
<i>Cryptoblastus melo</i>	?	?	?	1	0	0	0	0	2	1	0	0	1	1	0	2	1	0	2	2	1	1	1	1	?
<i>Codaster acutus</i>	?	?	?	0	1	0	2	1	0	0	1	0	1	1	1	2	0	0	?	2	1	1	1	1	?
<i>Cordyloblastus waschmuthi</i>	?	?	?	0	0	0	0	0	2	1	1	0	1	0	0	2	0	0	?	2	1	1	?	?	0
<i>Crioblastus cornutus</i>	?	?	?	1	0	0	0	0	2	1	0	0	1	1	0	2	0	0	2	2	1	1	1	1	?
<i>Cryptoschisma schulzii</i>	?	?	?	2	1	1	3	1	0	1	1	0	1	1	0	2	2	0	1	2	1	1	1	1	?
<i>Diploblastus glaber</i>	?	?	?	1	0	0	0	0	2	1&2	1	0	1	1	0	2	0	0	2	2	1&2	1	1	1	0
<i>Decaschisma pulchellus</i>	?	?	?	0	0	0	0	0&1	0&2	0	0	0	1	1	0	2	0	0	?	2	0&1	1	1	1	?
<i>Decemboblastus melonoides</i>	?	?	?	1	0	0	0	0	2	2	2	0	1	1	?	2	0	0	0	2	1	1	1	1	0
<i>Deliablastus cumberlandensis</i>	?	?	?	1	0	0	0	0	2	2	1	0	1	1	0	2	0	0	2	2	1	1	?	?	?
<i>Deltoblastus permicus</i>	1	1	1	1	0	1	1	1	2	1	0	0	1	1	2	2	2	0	2	0	1&2	1	1	1	?

<i>Deltoblastus batheri</i>	1	1	1	1	0	1	1	1	2	1	0	0	1	1	2	2	1	0	2	0	1	1	1	1	?
<i>Devonoblastus whiteavesi</i>	?	?	?	1	0	2	0	0	2	0	2	0	1	1	0	2	0	0	2	0	1	1	?	1	0
<i>Eleutheroocrinus cassadayi</i>	?	?	?	1	0	0	0	0	2	2	1	1	1	1	0	2	0	0	2	2	1	1	1	1	?
<i>Elaeocrinus verneuili</i>	1	1	0	1	0	0	0	0	2	2	1	0	1	1	2	2	0	0	0	0	2	1	1	1	2
<i>Ellipticoblastus ellipticus</i>	?	?	?	1	0	2	0	0	2	0	1	0	1	1	0	2	1	0	2	2	1	1	1	1	0
<i>Granatocrinus granulosus</i>	?	?	?	1	?	?	0	0	2	?	2	0	1	?	1	2	?	0	?	2	2	1	?	?	0
<i>Globoblastus norwoodi</i>	?	?	?	1	0	0	0	0	2	2	2	0	1	1	0	2	0	0	2	2	1	1	1	1	?
<i>Hadroblastus convexus</i>	?	?	?	0	0	0	0&1	0&1	2	0	2	0	1	1	1	2	0	0	?	1&2	1	1	1	1	?
<i>Heteroschisma alternatus</i>	?	?	?	0	0	0	0	0	2	0	1	0	1	1	0	2	0	0	0	2	?	1	1	1	?
<i>Hydroblastus herdyi</i>	?	?	?	1	0	0	2	0	0	1	0	0	1	1	0	2	0	0	2	2	1	1	1	1	0
<i>Hyperoblastus goldringae</i>	?	?	?	1	0	0	0	0	2	1&2	1	0	1	1	0	2	0	0	2	2	1	1	1	1	0
<i>Iranoblastus nodosus</i>	?	?	?	1	0	0	0	0	0	1	0	0	1	1	2	2	0	0	0	0	2	1	1	1	0
<i>Lophoblastus neglectus</i>	?	?	?	0	0	0	2	1	2	2	1	0	1	1	0	2	0	0	0	1	1	1	1	1	?
<i>Leptoschisma lorae</i>	?	?	?	0	0	0	1	1	2	0	0	0	1	1	0	2	0	0	2	2	?	1	1	1	?
<i>Mesoblastus crenulatus</i>	?	?	?	1	0	0	0	0	2	0&2	1&2	0	1	1	0	2	0	0	2	2	2	1	1	1	0
<i>Metablastus wortheni</i>	?	?	?	0	0	0	0	0	0	0&1	0	0	1	1	0	2	0	0	2	2	1	1	1	1	?
<i>Monadoblastus granulosus</i>	?	?	?	1	0	1	0	0	2	1	2	0	1	?	0	2	0	0	2	2	2	1	1	1	0
<i>Monoschizoblastus rofei</i>	?	?	?	1	0	0	0	0	2	0	1	0	1	1	2	2	0	0	0	0	1	1	1	1	?
<i>Nucleocrinus elegans</i>	1	1	0	1	0	0	0	0	2	2	1	0	1	1	2	2	0	0	0	0	2	1	1	1	2
<i>Notoblastus brevispinus</i>	?	?	?	0	1	0	1	1	0	2	2	0	1	1	1	2	?	0	?	2	?	1	1	1	?
<i>Orbiblastus hoskyni</i>	?	?	?	1	0	0	0	0	2	2	1	0	1	1	0	2	0	0	2	1	1	1	1	1	0

<i>Orophocrinus stelliformis</i>	?	?	?	1	1	2	2	0	2	1	1	0	1	1	0	2	2	0	2	2	1	1	1	1	?
<i>Pentremitidea paillettei</i>	?	?	?	0	0	0	2	1	2	1	0	0	1	1	0	2	0	0	1&2	2	?	1	1	1	?
<i>Perittoblastus liratus</i>	?	?	?	1	0	0	0	0	2	1	1	0	1	1	0	2	0	0	2	2	1	1	1	1	1
<i>Phaenoblastus caryophyllatus</i>	?	?	?	0	0	2	1	1	2	2	0	0	1	1	2	2	2	0	2	2	0	1	1	1	?
<i>Placoblastus obovatus</i>	?	?	?	1	0	0	0	0	2	1	2	0	1	1	2	2	0	0	0	0	2	1	?	1	0
<i>Pleuroschisma lycorias</i>	?	?	?	1	0	0	0	0	2	1	0	0	1	1	0	2	0	0	2	2	1	1	1	1	?
<i>Polydeltoideus enodatus</i>	?	?	?	0	0	0	0	1	0	1	0	0	1	0	1	2	0	0	2	2	1	1	1	1	?
<i>Poroblastus granulosis</i>	?	?	?	1	0	2	0	0	2	0	1	0	1	1	1	2	1	0	2	2	1	1	1	1	0
<i>Pterotoblastus gracilis</i>	?	?	?	0	1	0	2	1	1	1	2	0	1	1	0	2	0	0	?	2	1	1	1	1	?
<i>Pentremites godoni</i>	?	?	?	1	0	2	2	1	2	1	0	0	1	1	1	2	2	0	2	1	1	1	1	1	0
<i>Pentremites pulchellus</i>	?	?	?	1	0	2	2	1	2	2	0	0	1	1	0	2	2	0	2	1	1	1	1	?	0
<i>Pinguiblastus tushanensis</i>	?	?	?	0	0	0	0	0	2	2	?	0	1	1	0	2	0	0	0	2	1	1	1	1	?
<i>Sagittoblastus wanneri</i>	?	?	?	2	1	0	1	1	0	2	0	0	1	1	2	2	0	0	?	2	1	1	1	1	?
<i>Schizoblastus sayi</i>	?	?	?	1	0	2	0	0	2	1	1	0	1	1	2	2	0	0	?	0	1	1	1	1	0
<i>Sinopetaloblastus jinjingae</i>	?	?	?	1	0	1	2	1	?	2	1	0	1	1	0	2	2	0	?	2	1	1	1	1	?
<i>Tanaoblastus roemeri</i>	?	?	?	1	0	2	0	0	2	0	1	0	1	1	0	2	1	0	2	2	1	1	1	1	?
<i>Timoroblastus coronatus constrictus</i>	?	?	?	0	1	0	0	0	2	1	0	0	1	1	0	2	0	0	0	2	0	1	1	1	?
<i>Tricoelocrinus woodmani</i>	?	?	?	1	0	0	0	0	0	1	0	0	1	1	0	2	0	0	2	2	0	1	1	1	0
<i>Troosticrinus reinwardti</i>	?	?	?	1	0	0	0	0	0	0	0	0	1	1	0	2	0	0	2	2	1	1	1	1	?
<i>Cheirocystis fultonensis</i>	0	0	0	0	?	?	1	1	2	?	?	0	0	1	?	?	?	0	?	?	?	?	?	?	0

Characters 26–50

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
<i>Ambolostoma baileyi</i>	0	1	0	1	1	1	1	?	?	2	0&1	0	?	0	0	0	1	0	0	?	?	?	?	?	?
<i>Angioblastus boliviensis</i>	0	1	0	1	1	?	?	0	?	0	0	1	?	1	0	0	2	0	0	0	?	1	2	2	?
<i>Angioblastus dotti</i>	0	1	0	1	1	?	?	0	?	0	0	1	?	1	0	0	2	0	0	0	?	1	2	2	?
<i>Asterocrinus benniei</i>	0	0	0	1	1	?	?	?	?	0	0	?	?	2	0	0	1	0	0	?	?	0	2	2	2
<i>Brachyschisma corrugatum</i>	0	0	?	1	0&1	1	0	1	1	1	0	2	1	0	0	0	1	0	?	0	?	1	2	3	?
<i>Cryptoblastus melo</i>	0	0	0	1	1	1	0	2	0	2	1	0	?	1	0	0	0	1	0	0	0	1	2	1	0
<i>Codaster acutus</i>	?	0	0	1	1	?	0	0	?	?	0	0	?	?	0	0	2	0	?	0	?	0	2	2	?
<i>Cordyloblastus waschsmuthi</i>	0	0	0	?	?	1	0	2	0	2	0	1	0	0	0	0	1	0	?	0	?	0	2	4	?
<i>Crioblastus cornutus</i>	0	1	0	1	1	1	1	?	?	0	0	?	0	0	0	0	1	0	?	?	?	?	2	0	?
<i>Cryptoschisma schulzii</i>	?	0	0	?	?	?	0	0	?	2	0	1	0	0	0	0	1	0	0	0	0	0	2	2	?
<i>Diploblastus glaber</i>	2	0	0	1	1	1	1	2	0	1	?	1	0	0	0	0	1	0	0	0	0	0	?	3	0
<i>Decaschisma pulchellus</i>	0	0&1	0	1	1	0&1	0	1	1	1	0	1	0	0	0	0	1	0	0	0	0	0	2	2	0
<i>Decemboblastus melonoides</i>	0	1	0	1	1	1	1	?	?	?	0	1	0	2	0	?	?	0	?	?	?	?	?	?	?
<i>Deliablastus cumberlandensis</i>	?	0	0	?	?	?	1	1	1	1	1	0	?	1	0	0	0	?	?	?	?	?	2	0	?
<i>Deltoblastus permicus</i>	0	1	0	1	1	1	1	0	?	0	0&1	0	?	0	0	0	1	1	0	?	?	0	2	1	?
<i>Deltoblastus batheri</i>	0	1	0	1	1	1	1	0	?	0	0	0	?	0	0	0	1	1	0	?	?	0	2	1	?
<i>Devonoblastus whiteavesi</i>	0	0	0	1	1	1	?	2	0	2	0	1	0	0	0	0	1	0	?	0	?	0	2	4	?
<i>Eleutherocrinus cassadayi</i>	0	0	0	1	1	1	0	2	0	2	0	1	0	0	0	0	1	0	0	0	0	0	?	3	0
<i>Elaeocrinus verneuili</i>	0	0&1	0	1	1	1	1	2	2	1	1	1	2	0	0	0	0&1	1	0	0	0	0	1&2	1	?

<i>Ellipticoblastus ellipticus</i>	1	0	1	1	1	1	0	2	0	2	0	0	?	1	0	0	0	1	0	?	0	?	2	1	?
<i>Granatocrinus granulosus</i>	1	0	?	?	?	1	0	?	?	?	?	1	?	1	0	0	1	1	0	?	?	?	2	1	?
<i>Globoblastus norwoodi</i>	0	0	1	1	1	1	0	2	0	?	1	1	?	1	0	0	1	1	0	?	0	0	2	1	0
<i>Hadroblastus convexus</i>	0	0	0	1	1	1	1	?	?	?	0&1	0	0	0	0	0	1	0	0	0	0	0	2	2	?
<i>Heteroschisma alternatus</i>	0	0	0	1	1	?	?	?	?	1	0	1	0	0	0	0	1	0	0	0	0	0	2	2	0
<i>Hydroblastus herdyi</i>	0	1	0	1	1	1	1	2	1	2	0	1	0	0	0	0	1	0	0	0	0	0	2	2	0
<i>Hyperoblastus goldringae</i>	0	0	0	1	1	1	?	?	?	2	0	1	0	0	0	0	1	0	0	?	0	0	2	3	?
<i>Iranoblastus nodosus</i>	3	?	0	1	1	1	?	0	?	0	1	?	0	0	0	0	0	1	0	?	0	?	2	1	?
<i>Lophoblastus neglectus</i>	1	0	0	1	1	1	1	0	?	?	1	1	0	?	0	0	1	0	?	0	?	0	2	4	?
<i>Leptoschisma lorae</i>	?	1	0	1	0	1	0	1	1	1	?	1	?	0	0	0	1	1	?	0	?	0	1	2	?
<i>Mesoblastus crenulatus</i>	1	0	0	1	1	?	?	2	0	?	0	1	0	1	0	0	1	0&1	0	0	0	0&1	2	0	?
<i>Metablastus wortheni</i>	?	1	0	1	1	1	0	2	1	1	0	1	0	0	0	0	1	0	0	0	0	0	2	0	0
<i>Monadoblastus granulosus</i>	1	0	?	1	1	1	?	0	?	0	1	1	0	1	1	0	0	1	0	?	?	?	2	?	?
<i>Monoschizoblastus rofei</i>	1	0	0	1	1	1	1	0	?	0	1	0	?	1	0	0	0	1	0	0	0	?	2	1	?
<i>Nucleocrinus elegans</i>	0	0	0	1	1	1	0	2	2	1	1	1	2	0	0	0	1	1	0	?	0	0	2	1	0
<i>Notoblastus brevispinus</i>	?	0	0	1	1	1	0	0	?	0	?	0	?	?	1	0	1	0	?	0	?	0	2	0	?
<i>Orbiblastus hoskyni</i>	0	0	0	1	1	1	0	?	?	0	0	1	0	1	0	0	0	1	?	?	?	0	2	1	?
<i>Orophocrinus stelliformis</i>	0	0	0	1	1	1	0&1	0	?	0	0	1	?	0	0	0	1	0	0	0	0	0	2	2&3	0
<i>Pentremitidea paillettei</i>	0	0&1	0	1	1	1	?	1	1	1	0	1	0	0	0	0	1	0&1	0	0	0	0	0	3	?
<i>Perittoblastus liratus</i>	0	1	0	1	1	1	?	2	1	1	1	1	1	?	0	0	1	0	?	0	?	1	2	0	?
<i>Phaenoblastus caryophyllatus</i>	?	0&1	0	1	1	1	0	?	?	0	0	1	0	0	0	0	1	0	0	0	0	0	0&2	2	?

<i>Placoblastus obovatus</i>	0	0	0	?	?	1	?	2	2	1	1	1	2	0	0	0	1	1	0	?	?	?	2	1	?
<i>Pleuroschisma lycorias</i>	?	1	?	1	1	?	?	2	1	1	0	1	0	0	0	0	1	0	?	?	?	?	?	2	?
<i>Polydeltoideus enodatus</i>	?	1	?	1	?	1	0	2	1	?	0	1	0	0	0	1	1	0	?	0	?	0	0	2	?
<i>Poroblastus granulosis</i>	1	0	0	1	1	1	1	0	?	0	1	1	0	1	0	0	0	1	?	0	?	?	2	0	?
<i>Pterotoblastus gracilis</i>	?	1	0	1	1	?	?	0	?	0	0	1	0	1	1	1	1	0	?	0	?	0	2	2	?
<i>Pentremites godoni</i>	0	0	0	1	1	1	0	0	?	2	0	2	0	0	0	0	1	0	0	0	0&1	0	2	4	0
<i>Pentremites pulchellus</i>	0	0	0	1	1	1	0	?	?	2	0	1	0	0	0	0	1	0	0	0	1	0	2	2	0
<i>Pinguiblastus tushanensis</i>	0	0	0	1	1	?	?	2	0	1	0	1	1	2	0	0	1	0	0	0	1	0	2	3	2
<i>Sagittoblastus wanneri</i>	0	1	0	1	1	?	?	0	?	0	1	0	0	1	0	0	2	0	?	0	?	0	2	1	?
<i>Schizoblastus sayi</i>	1	0	0	1	1	1	1	0	?	0	0	1	0	1	0	0	1	1	0	?	0	?	2	0	?
<i>Sinopetaloblastus jinxingae</i>	?	0	0	1	1	1	0	?	?	2	0	0	1	0	0	0	1	0	0	0	?	?	2	1	?
<i>Tanaoblastus roemeri</i>	1	0	0	1	1	1	1	2	0	1	0	1	0	1	0	0	0	0	0	0	?	1	2	0	1
<i>Timoroblastus coronatus constrictus</i>	1	1	0	1	1	1	1	0	?	0	0	0	0	1	1	0	2	0	0	0	0	0	2	0	?
<i>Tricoelocrinus woodmani</i>	0	?	0	1	1	1	0	2	1	1	0	2	0	0	0	0	1	0	0	0	0	?	2	2	0
<i>Troosticrinus reinwardti</i>	?	0	0	1	1	1	0	2	0	1	0	0	0	0	0	0	1	0	0	0	0	0	2	2	0
<i>Cheirocystis fultonensis</i>	0	0	?	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Characters 51–80

	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	
<i>Ambolostoma baileyi</i>	?	1	?	2	0	0	2	0	2	0	1	3	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	
<i>Angioblastus boliviensis</i>	0	1	?	0	1	1	0	0	0	?	?	?	?	?	?	0	0	2	1	?	?	?	?	?	?	?	?	?	1	0	
<i>Angioblastus dotti</i>	0	1	?	?	?	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	
<i>Asterocrinus benniei</i>	?	1	?	0	?	1	0	?	1	1	?	3	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0
<i>Brachyschisma corrugatum</i>	1	1	?	0	0	1	0	0	0	?	?	?	?	?	?	0	2	1	1	?	?	2	?	?	?	?	?	?	?	0	0
<i>Cryptoblastus melo</i>	?	1	?	2	0	0	2	0	2	1	1	3	0	0	1	?	?	?	?	1	0	1	0	0	1	0	0	?	1	0	
<i>Codaster acutus</i>	1	1	?	0	0	1	0	0	0	?	?	?	?	?	?	0	0	2	2	?	?	?	?	?	?	?	?	?	?	0	0
<i>Cordyloblastus waschmuthi</i>	1	1	?	2	0	0	2	0	2	0	1	3	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	
<i>Crioblastus cornutus</i>	?	1	?	2	0	0	2	0	2	1	1	3	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	
<i>Cryptoschisma schulzii</i>	0	1	?	0	0	1	1	0	1	0	?	3	?	?	?	?	?	0	?	2	1	0	2	1	2	1	1	?	0	0	
<i>Diploblastus glaber</i>	0	1	?	2	0	0	2	0	2	0&1	0	0&1	0	1	0	?	?	?	?	1	0	1	1	0	1	0	0	?	1	0	
<i>Decaschisma pulchellus</i>	0&1	1	?	2	0&1	1	0	0	1	0	0&1	1	?	?	?	0	0&2	0&2	1&2	?	?	?	?	?	?	?	?	0	?	0	0
<i>Decemboblastus melonoides</i>	?	1	?	2	0	0	2	0	2	1	0	3	0	1	0	?	?	?	?	?	?	?	?	?	?	?	1	?	1	0	
<i>Deliablastus cumberlandensis</i>	?	1	?	?	?	0	2	0	2	?	?	?	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	
<i>Deltoblastus permicus</i>	0	1	?	2	0	0	2	0	2	?	0	0	0	0	0	?	?	?	?	1	0	2	0	0	1	0	?	?	2	0	
<i>Deltoblastus batheri</i>	0	1	?	?	0	0	2	0	2	?	0	?	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	
<i>Devonoblastus whiteavesi</i>	1	1	?	2	0	0	2	0	2	0	1	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	
<i>Eleutheroocrinus cassadayi</i>	1	1	?	2	0	0	2	0	2	0	1	2	0	1	0	?	?	?	?	?	?	?	?	?	?	?	0	?	1	0	
<i>Elaeocrinus verneuili</i>	0	1	?	2	0	0	2	0	2	1	0&1	0&3	0	1	0	?	?	?	?	?	?	?	?	?	?	?	0	?	0&1	0	

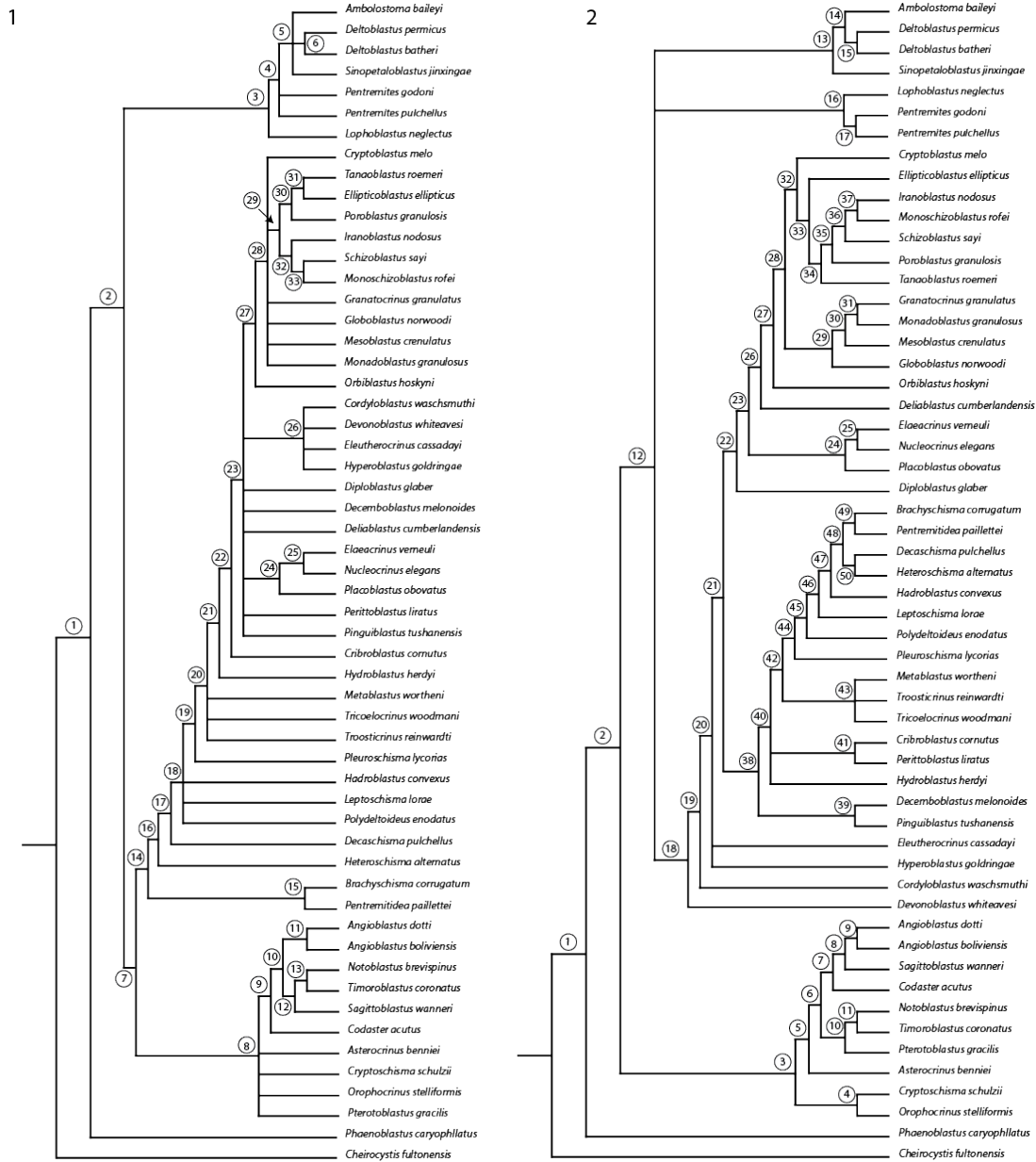
<i>Ellipticoblastus ellipticus</i>	0	1	?	2	0	0	2	?	2	0	1	2	1	1	0	?	?	?	?	0	0	1	1	0	0	0	?	?	1	0		
<i>Granatocrinus granulosus</i>	0	1	?	?	?	0	2	0	2	?	?	?	0	1	0	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0		
<i>Globoblastus norwoodi</i>	0	1	?	2	0	0	2	0	2	0	1	2	1	0	1	?	?	?	?	?	?	?	?	?	?	?	0	?	1	0		
<i>Hadroblastus convexus</i>	1	1	?	0&2	0&1	1	0	0	0	?	?	?	?	?	?	0	0&2	1&2	2	?	?	2	?	?	?	?	?	0	?	1	0	
<i>Heteroschisma alternatus</i>	0	1	?	0	1	1	0	0	1	?	?	?	?	?	?	0	0	?	1&2	?	?	?	?	?	?	?	?	0	?	0	0	
<i>Hydroblastus herdyi</i>	1	1	?	2	0	0	2	?	2	1	0	3	0	1	0	?	?	?	?	2	?	?	?	1	1	0	0	?	1	0		
<i>Hyperoblastus goldringae</i>	0&1	1	?	2	0	1	2	0	2	0	1	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	0	?	1	0	
<i>Iranoblastus nodosus</i>	0	1	?	2	0	0	2	?	2	1	1	2	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	
<i>Lophoblastus neglectus</i>	0	1	?	2	0	0	2	0	2	1	0	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	
<i>Leptoschisma loraie</i>	1	1	?	2	1	1	1	0	1	?	?	?	?	?	?	0	2	1	2	?	?	?	?	?	?	?	?	?	?	?	1	0
<i>Mesoblastus crenulatus</i>	0	1	?	2	0	0	2	0	2	1	1	3	0	0	2	?	?	?	?	?	?	?	?	?	?	?	0	?	2	0		
<i>Metablastus wortheni</i>	1	1	1	2	0	1	2	1	1	1	0	1&3	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	0	?	1	1	
<i>Monadoblastus granulosus</i>	?	1	?	?	0	0	2	0	2	?	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	
<i>Monoschizoblastus rofei</i>	0	1	?	2	0	0	2	?	2	1	1	3	0	1	0	?	?	?	?	0	0	1	0	0	0	0	0	?	?	1	0	
<i>Nucleocrinus elegans</i>	0	1	?	2	0	0	2	0	2	1	0	3	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	
<i>Notoblastus brevispinus</i>	0	1	?	2	?	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	0	
<i>Orbiblastus hoskyni</i>	0	1	?	2	0	0	2	0	2	1	0	3	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	
<i>Orophocrinus stelliformis</i>	0	1	?	2	0	1	0	0	1	1	0	3	?	?	?	1&2	0&2	2	?	2	?	?	?	?	?	?	?	0	?	0&1	0	
<i>Pentremitidea paillettei</i>	0	1	?	0	0&1	1	2	0	1	0	?	1	0	1	0	0	0&2	1	1&2	?	?	?	?	?	?	?	?	0	?	0	0	
<i>Perittoblastus liratus</i>	0	1	?	2	0	0	2	0	2	1	?	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	

<i>Phaenoblastus caryophyllatus</i>	0&1	1	?	2	1	1	0	0	2	0	?	0	?	?	?	0	2	1	1	?	?	?	?	?	?	?	0	?	1	0	
<i>Placoblastus obovatus</i>	0	1	?	?	0	0	2	0	2	?	?	?	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	
<i>Pleuroschisma lycorias</i>	?	1	?	2	1	1	0	0	1	?	?	?	?	?	?	0	2	1	2	?	?	?	?	?	?	?	?	?	1	0	
<i>Polydeltoideus enodatus</i>	1	1	?	2	1	1	0	0	0	?	?	?	?	?	?	0	2	1	2	?	?	2	?	?	?	?	?	?	?	0	0
<i>Poroblastus granulosis</i>	0	1	?	2	0	0	2	0	2	1	?	3	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	
<i>Pterotoblastus gracilis</i>	0	1	?	0	0	1	0	0	0	?	?	?	?	?	?	2	0	2	1	?	?	0	?	?	?	?	?	?	?	0	0
<i>Pentremites godoni</i>	0	1	?	2	0	0	2	0	2	0	1	0	0	1	0	?	?	?	?	2	?	2	1	1	2	0	0	1	2	0	
<i>Pentremites pulchellus</i>	0	1	?	2	0	0	2	0	2	0	1	0	0	1	0	?	?	?	?	1	1	2	2	1	2	0	0	?	2	0	
<i>Pinguiblastus tushanensis</i>	1	1	?	2	0	?	2	?	2	1	0	3	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	
<i>Sagittoblastus wanneri</i>	0	1	?	0	0	0	0	0	0	1	1	3	?	?	?	2	1	2	?	?	?	?	?	?	?	?	?	?	1	0	
<i>Schizoblastus sayi</i>	0	1	?	2	0	0	2	0	2	1	1	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	0	?	1	0	
<i>Sinopetaloblastus jinxingae</i>	?	1	?	2	0	?	2	?	2	1	1	3	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	
<i>Tanaoblastus roemeri</i>	0	1	?	2	0	0	2	?	2	1	1	3	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	
<i>Timoroblastus coronatus constrictus</i>	?	1	?	2	1	1	0	0	0	?	0	?	?	?	?	1	1	2	0	?	?	?	?	?	?	?	?	?	0	0	
<i>Tricoelocrinus woodmani</i>	1	1	?	?	0	?	2	?	1	0	?	?	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	2	1	
<i>Troosticrinus reinwardti</i>	1	1	1	2	0	1	2	1	1	1	1	3	0	?	0	0	2	0	?	?	?	?	?	?	?	?	0	?	0	1	
<i>Cheirocystis fultonensis</i>	0	1	0	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	

Appendix 3-5

Tree topology with full character support described. Numbers indicate node on corresponding image followed by character number with character state in parentheses.

For example, at node 1 character 4 is at state 1.



(1) Maximum Parsimony Reconstruction

1. 5(0), 11(0), 13(1), 16(2), 19(2), 20(2), 22(1), 23(1), 24(1), 32(0), 36(0), 37(1),
42(1), 43(0), 49(2), 54(1), 56(1), 59(2), 60(0), 68(1)
2. 7(2), 17(0), 21(1), 26(0), 27(0), 33(0), 55(0), 61(0), 65(0), 72(2), 74(1), 75(2)
3. 20(1), 56(0), 57(2)
4. 4(1), 6(2), 17(2), 35(2), 61(1)
5. 6(1), 37(0), 49(1)
6. 1(1), 2(1), 3(1), 7(1), 15(2), 20(0), 27(1), 32(1), 35(0), 43(1), 61(0), 64(0), 79(2)
7. 54(0), 56(1), 57(0), 59(1), 69(1), 79(0)
8. 5(1), 11(1), 35(1), 60(1), 68(2), 72(0)
9. 9(0), 15(1), 19(0), 27(1), 39(1), 42(2), 59(0)
10. 7(1), 10(2), 27(1), 39(1)
11. 23(0), 24(0), 47(1)
12. 37(0), 67(1)
13. 40(1), 49(0), 54(1)
14. 6(0), 33(1), 34(1), 35(1), 68(1)
15. 49(4)
16. 7(0), 55(1)
17. 54(1)
18. 27(0), 51(1), 69(2), 79(1)
19. 4(1), 8(0), 33(2)
20. 9(0), 55(0), 57(2), 60(1), 62(4)

21. 32(1), 56(0), 59(2), 75(1)
22. 9(2)
23. 11(1), 27(0), 51(0), 72(1), 74(0)
24. 15(2), 19(0), 20(0), 21(2), 34(2), 36(6), 38(2), 43(1), 49(1)
25. 1(1), 2(1), 3(0), 10(2), 25(2)
26. 35(2), 51(1), 60(0), 61(1)
27. 32(0), 39(1), 43(1), 49(1)
28. 26(1), 34(0), 35(0), 36(1), 61(1), 65(1), 71(0)
29. 11(1), 32(1), 42(0), 70(0), 75(0)
30. 6(2), 10(0), 17(1), 37(0)
31. 63(1), 36(0)
32. 15(2), 19(0), 20(0), 33(0)
33. 65(0)

(2) Maximum Likelihood Reconstruction

1. 5(0), 6(2), 10(2), 13(1), 16(2), 17(2), 19(2), 20(2), 23(1), 24(1), 30(1), 32(1),
35(0), 36(0), 37(1), 42(1), 43(0), 47(0), 49(2), 54(1), 56(1), 57(0), 59(2), 79(1)
2. 4(0), 7(2), 10(1), 11(1), 15(0), 21(1), 33(0), 51(0), 74(1)
3. 5(1), 54(0), 62(3), 68(2), 72(0), 79(0)
4. 10(1), 59(1), 70(1),
5. 4(0), 6(0), 17(0), 60(1)
6. 19(0), 39(1), 59(0), 67(0)
7. 9(0), 42(2)

8. 7(1), 27(1), 79(1)
9. 23(0), 24(0), 47(1)
10. 11(2), 40(1)
11. 37(0), 49(0), 54(1)
12. 4(1), 35(2), 49(5), 56(0), 57(2), 61(1), 64(1), 65(0), 72(2)
13. 6(1), 37(0), 49(1)
14. 11(0), 27(1), 32(1)
15. 1(1), 2(1), 3(1), 7(1), 10(1), 15(2), 20(0), 35(0), 43(1), 61(0), 64(0), 74(0), 79(2)
16. 20(1)
17. 6(2), 11(0), 75(2), 79(2)
18. 7(0), 8(0), 17(0), 33(2), 34(0), 51(1)
19. 6(0)
20. 49(4)
21. 32(1), 35(1), 60(1), 61(0), 75(1)
22. 51(0), 70(1), 71(0), 72(1), 74(0)
23. 36(1), 43(1), 49(1)
24. 15(2), 19(0), 20(0), 21(2), 34(2), 38(2)
25. 1(1), 2(1), 3(0)
26. 39(2), 42(0)
27. 32(0), 35(0)
28. 61(1), 65(1)
29. 11(2), 21(2), 42(1)

- 30. 26(1)
- 31. 65(0)
- 32. 17(1), 47(0)
- 33. 6(2), 10(0), 26(1), 75(0)
- 34. 32(2), 49(0)
- 35. 33(0)
- 36. 15(2), 17(0), 20(0)
- 37. 6(0), 19(0), 49(1)
- 38. 62(4)
- 39. 19(0), 39(2)
- 40. 10(1), 11(0), 27(1), 34(1), 49(2)
- 41. 49(0)
- 42. 32(0), 56(1), 59(1), 66(0), 67(2)
- 43. 9(0), 53(1), 58(1), 80(1)
- 44. 55(1), 57(0), 68(1), 69(20)
- 45. 4(0), 8(1)
- 46. 10(1), 33(1)
- 47. 27(0)
- 48. 60(0), 62(1), 79(0)
- 49. 49(4), 54(0)
- 50. 8(0), 10(1)

CONCLUSIONS

Separation of eublastoid taxa into Spiraculata and Fissiculata strictly by the external expression of their internal respiratory structures has hindered our understanding of evolutionary trends within Eublastoidea. Morphological characters describing eublastoid external morphology have been assembled over the past fifty years, but the internal anatomy of the respiratory structures (hydrospires) has been largely ignored. Digitally reconstructed hydrospire models allow these complex structures to be critically examined in three-dimensions providing a thorough understanding of form and function. This comprehensive examination highlights novel morphological characters that when incorporated with the external character data provided increased resolution in tree topology. The methodology used to reconstruct the internal anatomy can be easily applied to other invertebrate groups.

Reassessment of *Macurdablastus uniplicatus* through examination of morphological features and digital internal models provided new insights into the history of Blastoidea. *Macurdablastus uniplicatus* shares a conservatively plated body and plate arrangement with eublastoids but bears a small elliptical lancet plate instead of an elongate lancet plate to support the length of the ambulacra characteristic of eublastoids. Rather, *M. uniplicatus* possesses an extension of the radial plate that supports the recumbent ambulacra. Through synchrotron tomography, we were able to digitally reconstruct the respiratory structures. This allowed for further examination of their internal expression, showing that these structures do not cross plate boundaries, as the hydrospires consistently do in eublastoids. These differences are critical characters in

clade separation and based on ensuing phylogenetic analysis, *M. uniplicatus* is rejected as being within Eublastoidea but falls within the larger Blastoidea, which includes coronoids, *Lysocystites*, and eublastoids.

Eublastoidea has been subdivided into groups primarily based on the external expression of the hydrospire structures. Spiraculata possess hydrospire pores that terminate in spiracles on the summit and Fissiculata possess hydrospire slits that cross plate boundaries and run parallel to the ambulacra. Eublastoid species ascribed to Spiraculata and Fissiculata were critically examined to assess the validity of group separation by these characters. Additionally, the digital hydrospire models and data generated in Chapter 1 were incorporated into a character matrix of reevaluated external morphological characters. The reassessment of previously ascribed synapomorphies, applying the Universal Elemental Homology scheme, and the digitally reconstructed hydrospire models contributed to a more complete understanding of eublastoid species relationships. Results reject clade separation based on the external expression of hydrospires. This work provides evidence that the classification and understanding of blastozoan echinoderms is enhanced by this multifaceted approach.

This body of work provides insights on examining internal anatomy and the utility of internal character data when reconstructing fossil phylogenies. As many groups of blastozoan echinoderms are classified by the external morphology of their respiratory structures, this provides reason to explore advancing technologies to gain better insight into the internal anatomy of these extinct forms. Now that a quantitative framework has been assembled, we can add taxa to the analysis and begin to test more complex

questions regarding trait evolution, macroevolutionary processes, and biogeographic patterns.

VITA

Jennifer E. Bauer was born in Darien, IL in 1989, and she attended elementary, middle, and high school in the Downers Grove Township. She attended the University of Illinois at Chicago where she pursued her B.S. in Biological Sciences with a minor in Earth and Environmental Studies. She attended Ohio University for her M.S., where her research focused on understanding brachiopod evolutionary patterns and biogeographic trends; her teaching was recognized by Ohio University and she was a recipient of the Graduate Associate Outstanding Teaching Award. Upon graduation, she moved to Knoxville, TN to begin her doctoral studies at The University of Tennessee, Knoxville (UT) in the Department of Earth and Planetary Sciences. The last year of her dissertation was funded in part by the Yates Dissertation Fellowship through UT. Apart from her studies, she has been active in science education outreach through local school programs, UT's Darwin Day program, the McClung Museum of Natural History, the creation of an educational blog (Time Scavengers), and her work with K-12 teachers on developing lesson plans utilizing fossils. Her research has been funded through numerous external grants and has been presented at multiple national and international scientific meetings.