The Homology and Phylogeny of the Diploporita (Blastozoa: Echinodermata)

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ABSTRACT

Evolutionary relationships of extinct echinoderms are poorly understood, especially within stem-bearing blastozoans, a large group of echinoderms with unique respiratory structures and feeding brachioles. They were highly experimental in their body plans and very unlike echinoderms today (e.g., sea urchins). Many of the blastozoan subgroups recognized in recent classifications do not represent clades (natural associations of organisms derived from a single ancestor); they are either grades of organization or groups united by superficially similar features. Consequently, these 'traditional' groupings cannot be used to analyze evolutionary questions, such as biogeography or rates of evolution. This problem is highlighted within the diploporitan echinoderms, a blastozoan group united by superficially similar double pore (diplopore) respiratory structures, which appear to encompass multiple independently evolved lineages.

Major diploporitan groups show wide variation in body wall morphology, feeding apparatus, and attachment structures (i.e., stems and holdfasts). Although the diploporitans have been defined by the diplopore structures, recent evidence indicates that they may have evolved in multiple blastozoan groups. Furthermore, other features of the body of diploporitans (e.g., size and shape of the attachment structure) are likely dictated by environmental factors. To date, diploporitans have not been analyzed in a rigorous phylogenetic context and their relationships are uncertain.

To test diploporitan monophyly, taxa were analyzed to identify homologous elements across diploporitans and other closely related blastozoans using the Universal Elemental Homology scheme that has been utilized across multiple early echinoderm clades. This included identifying homologous elements between certain diploporitan blastozoans and early crinoids, echinoderms thought to be rooted within blastozoans.

Morphological data were coded to create a character taxon matrix. Phylogenetic relationships were assessed utilizing maximum parsimony and maximum likelihood; support for the resulting relationships was assessed using bootstrap and Bremer support. Results of the phylogenetic analysis indicate that the diploporitans include at least three distinct lineages rooted within Blastozoa and that crinoids are also rooted within blastozoans. A posteriori testing of elements within the phylogenetic framework supported homology and not homoplasy, which contradicts previous arguments. The reconstructed evolutionary relationships of the diploporitans will provide a framework to explore biogeographic patterns and morphological trends in the future.

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INTRODUCTION

Phylogenetic relationships among echinoderms (relatives of sea stars and crinoids) are poorly understood, especially within the various stalked echinoderms groups. Many of the traditional classes are not monophyletic groupings of organisms (clades), but instead represent grades of organization, or in some cases, groups of unrelated taxa united by convergent features (Sumrall, 1997; Kammer et al., 2013). Such aphyletic groupings are problematic because they are not the product of evolutionary processes, and as such, cannot be used to address evolutionary questions such as the timing of group origination, evolutionary rates, biogeographic patterns, and diversity of life through time.

Diploporitan echinoderms, known from the Ordovician-Devonian, are an excellent example of a potentially aphyletic group, defined as those echinoderms that bear a respiratory system of diplopores that penetrate the skeletal plates of the body wall (Sprinkle, 1973). Historically, Diploporita has comprised three distinct lineages (Glyptosphaeritida, Sphaeronitida, and Asteroblastida). These groups have been considered by many to only be distantly related, thereby not constituting a valid taxonomic grouping (Paul, 1984, 1988; Sumrall et al., 2009). The evidence for this includes fundamentally different constructions of the feeding ambulacral system, differences in the attachment structures, presence or absence of stems, and differences in the physical construction of the class-defining diplopores.

Diploporitans are part of a much larger extinct group of echinoderms, the blastozoans, which are unlike any organisms alive today. Blastozoans from the Ordovician-age were highly experimental in their body plans and respiratory structures (Sprinkle, 1973). These respiratory structures, used for gas exchange, have been used to define the groups, just as diploporitans are defined by diplopore respiratory structures (Kesling, 1967). While most blastozoan groups are understudied, recent research has begun to explain the rich evolutionary history of these animals (Zamora, 2010; Sumrall and Waters, 2012; Kammer et al., 2013; Lefebvre et al., 2013; Zamora et al., 2013).

Previous studies have shown that respiratory features are not always group-specific, but rather have evolved more than once in several blastozoan groups (e.g., Sumrall and Gahn, 2006) and are absent in early members of some clades (e.g., *Macrocystella* Callaway, 1877 and *Cuniculocystis* Sprinkle and Whalman, 1994). It is, therefore, of little surprise that diplopores show convergent evolution, although the evolutionary transitions between respiratory structures remain poorly understood. Unlike other blastozoan groups, diploporitans have never been studied in a rigorous evolutionary context and therefore this research will add vital information to the developing understanding of the evolution of the early echinoderms.

Part I: Homology

The relationships among major echinoderm clades are poorly understood, in no small part because of a fundamental lack of understanding of the

evolutionary fate of homologous elements that originated early in the evolution of the echinoderms (Sumrall and Waters, 2012; Kammer et al., 2013). Recognizing homology, similarity resulting from inheritance from a common ancestor (Hillis, 1994), across Echinodermata can be difficult, as plates are commonly named based on their position rather than their homology with plates of other echinoderm groups (Sumrall, 1997). Often homologous plates are given different names in each major group in which they are found (Smith, 1984; Sumrall, 2010; Sumrall and Waters, 2012), resulting in confusion when attempting to identify alternate character states for phylogenetic inference. This can often lead to polyphyletic assemblages being supported by inferred phylogenetic analyses (Webster and Maples, 2006). This issue is ubiquitous in blastozoan echinoderms, as workers utilize different terminology for plates in the ambulacral and thecal regions for each clade.

The Holocystites Fauna

The *Holocystites* Fauna is an enigmatic group of middle Silurian diploporitans from the midcontinent region of North America. Previous systematic and phylogenetic studies of this clade painted a complicated evolutionary history, requiring major morphological changes to the plating of the oral area (Paul, 1971; Frest et al., 2011). However, upon reexamination of this group of fossils (Sheffield and Sumrall, 2015; Sheffield and Sumrall, 2017), we discovered that the complicated history of the *Holocystites* Fauna was based on an inaccurate understanding of the homologous elements shared between the proposed taxa.

Through analysis of a large collection of museum specimens and new field collections, we determined that all taxa within the *Holocystites* Fauna have a conservative peristomial border-plating pattern that was modified only slightly among taxa, and some taxa were erected based on taphonomic artifacts and not evolutionary differences. This study involving the previously problematic *Holocystites Fauna* indicates that a thorough understanding of homologous elements of diploporitans is necessary for inferring evolutionary relationships within the larger echinoderm tree of life.

A Reinterpretation of Eumorphocystis and the Origin of Crinoids

Recent debates over the evolutionary relationships of early groups of echinoderms have relied on morphological details of the feeding ambulacral systems. *Eumorphocystis* Branson and Peck 1940, a Middle-Late Ordovician diploporitan, has been a focus in these debates because it bears ambulacral features that show strong morphological similarity, here interpreted as homologous, to early crinoid arms. In these taxa, a radial plate supports a composite arm structure formed from uniserial extensions of the thecal wall supporting floor plates of the erect ambulacrum. These plates bound an encased coelomic extension that connects to the thecal interior. To test whether these features of eumorphocystitid arms are truly homologous with early crinoids or are convergent, taxa spanning the echinoderm clade were subjected to a phylogenetic analysis. The analysis found *Eumorphocystis* to be the sister group of the early crinoids included in this analysis, supporting the interpretation that

the groups' similar arm constructions are homologous. This study also suggests that crinoids are nested within blastozoans, a conclusion that is different from previously proposed hypotheses of crinoid origins (Sprinkle and Guensberg, 2007, 2009).

Part II: Phylogenetic Relationships of Diploporita

To unravel the evolutionary relationships of diploporitans, important museum collections were restudied to code species for phylogenetic analyses. All aspects of morphology were examined and coded as phylogenetic characters. However, particular suites of characters were emphasized and reinterpreted in a universal elemental homology framework including the nature of the feeding ambulacral system, morphology of the theca, nature of the diplopore respiratory structures, and the nature of the attachment structure. Taxa were selected to cover the bulk of the morphological diversity present across currently defined Diploporita and concentrated on species that were both well preserved and known from complete specimens. Phylogenetic characters utilized in this analysis were assumed to be hereditable; characters likely driven by ecophenotypic plasticity (e.g., shape of the holdfast structures, which are likely controlled by the shape of the substrate to which it was attached) were not included (Gil Cid and García-Rincón, 2012; Sheffield and Sumrall, 2017).

Taxa from other echinoderm groups (e.g., Rhombifera, Eocrinoidea, Blastoidea) were also coded for analysis in order to better understand where diploporitans fell within the larger echinoderm tree of life. The analysis was

conducted utilizing maximum parsimony; a heuristic search of most optimal trees was performed. The resulting evolutionary relationships uncovered from this analysis will allow for a full taxonomic revision of the diploporitans and place diploporitans into a testable framework for future analysis involving questions rooted in evolutionary theory (e.g., biogeography, trait evolution).

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CHAPTER 1:
GENERIC REVISION OF THE HOLOCYSTITIDAE OF NORTH AMERICA (DIPLOPORITA: ECHINODERMATA) BASED ON UNIVERSAL ELEMENTAL HOMOLOGY

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My major contributions to this paper include: (1) conduction systematic evaluation of fossil taxa included; (2) writing the manuscript; (3) creating figures and photographs; (4) submitting and revising the manuscript. Colin D. Sumrall, co-author, agreed with interpretations of the fossil taxa and made minor revisions of the manuscript before journal submission.

Abstract

The *Holocystites* Fauna is an enigmatic assemblage of North American diploporitans that present a rare window into unusual middle Silurian echinoderm communities. Multiple systematic revisions have subdivided holocystitids based on presumed differences in oral area plating and respiratory structures. However, these differences were based on a fundamental misunderstanding of the homologous elements of the oral area, and the taphonomic process. Taphonomic disarticulation of the oral area formed the basis for the erection of *Pentacystis* and *Osgoodicystis* as separate genera and *Osgoodicystis* is interpreted as the junior synonym of *Pentacystis*. Holocystitids show a conservative peristomial bordering plate pattern that is shared among all described genera. The peristome is bordered by seven interradially positioned oral plates, as is typical for oral plate bearing blastozoans. A second open circlet of facetal plates lies distal to the oral plates; five of these facetal plates bear facets for feeding appendages (lost on the A ambulacrum in some taxa), while two lateral facets (present in all taxa except *Pustulocystis*) do not. Holocystitid taxa show minor modifications to this

basic peristomial bordering plate pattern. As thecal morphologies are highly variable within populations, taxonomic revision of holocystitids is based on modifications of the plating of the oral area.

Introduction

Silurian-age diploporitan echinoderms are relatively scarce in the fossil record (Witzke et al., 1979; Thomka and Brett, 2014). The *Holocystites* Fauna, however, is an important exception and presents a rare window into unusual middle Silurian echinoderm communities. This fauna is an abundant and diverse collection of middle Silurian diploporitan taxa from the midcontinent region of North America (i.e., Wisconsin, Illinois, Indiana, Kentucky, Ohio, Tennessee) (Frest et al., 2011) and possibly Australia (Jell, 2011) that provides a unique opportunity to study paleoecology, taphonomy, and phylogenetics of this enigmatic clade. This study focuses on the generic classification of holocystitids, the dominant component of this fauna.

Understanding the systematics of Holocystitidae has been complicated by a number of issues. First, holocystitids have a plastic thecal morphology that shows wide variation within populations, resulting from irregular plating of the theca, allometric changes, and ecophenotypic variation, making species identification based on thecal morphologies unreliable (Sheffield and Sumrall, 2015a). Some work has been done to identify holocystitids from preserved holdfasts attached to hardgrounds (e.g., Thomka et al., 2016). However, thecae are disassociated from these holdfasts, so the taxonomic affinity is based on

preserved aboral plating and general size of the holdfast. However, when found attached to large bioclasts, holocystitid holdfasts in softground settings can be extremely plastic (Gil Cid and García-Rincón, 2012), taking on the size and morphology of the underlying attachment surfaces, casting some doubt on the reliability of holdfast morphology for discriminating taxa across holocystitid-bearing localities. Second, many holocystitid species are based on extremely poorly preserved internal molds in sugary dolomite that are difficult to reconcile with more pristine specimens preserving external morphologies as original calcite (Sheffield and Sumrall, 2015a). Third, species and genera were described with a poor understanding of the plating of the oral and summit structures, emphasizing presumed differences (often preservational) while overlooking fundamental similarities.

Fossils from the *Holocystites* Fauna were first published over a century and a half ago (e.g., Hall, 1861, 1864, 1870). At that time, *Holocystites* Hall, 1861 was the only proposed genus within the fauna encompassing a wide variety of morphologies; a multitude of later studies (e.g., Miller, 1878, 1879, 1888; Miller and Gurley, 1894, 1895), proposed over 50 species assigned to this genus alone. Frest et al. (2011) noted that the number of species proposed by Miller correlated closely with the number of specimens found within the formations being studied. These initial papers sought to document the wide disparity of morphologies present within holocystitids primarily via describing the differences noted across the thecae. Detailed description of a large majority of these

specimens were complicated by poor preservation that erased important information concerning thecal ornamentation and the oral area morphology.

More recent studies (Tillman, 1967; Paul, 1971; Frest et al., 1977, 2011) recognized the high morphological disparity within the numerous species of *Holocystites* and divided known taxa among multiple genera including: *Holocystites* Hall, 1861, *Trematocystis* Jaekel, 1899, *Triamara* Tillman, 1967, *Pentacystis* Paul, 1971, *Pustulocystis* Paul, 1971, *Brightonicystis* Paul, 1971, *Osgoodicystis* Frest and Strimple, 2011, and *Paulicystis* Frest and Strimple, 2011 (taxa used within this study are listed in Table 1). These genera were based on major variations in the morphology of the pore systems and observed differences within the plating of the oral area (Paul, 1971). However, issues of taphonomy, especially concerning the preservation of the oral area, were interpreted taxonomically in these studies, leading to some species being based on state of preservation rather than phylogeny (Sheffield and Sumrall, 2015a).

The systematics of Holocystitidae has been continuously revised and subdivided based on inferred differences in thecal and oral area morphology, but in the absence of a unifying plating model of the oral area. Although two circlets of plates around the peristome were recognized (periorals, herein interpreted as orals sensu Sumrall, 2010) forming the mouth frame and facetals bearing large facets for feeding appendages (Paul, 1971), it was not realized that each of the holocystitid genera has the same compliment of plates. This paper aims to review the *Holocystites* Fauna in a modern context, by reinterpreting

morphologies of the oral area through Universal Elemental Homology (Sumrall, 2010; Sumrall and Waters, 2012; Kammer et al., 2013) and emending the generic diagnoses.

Holocystitid plate morphologies

Until recently, it was not recognized that a highly conserved set of axial skeletal elements – referred to as Universal Elemental Homology (UEH) – was common to all derived blastozoan echinoderms. These taxa share a peristome that is bordered by seven interradially positioned oral plates (Sumrall, 2010, 2015). The CD interray is divided into three plates O1, O6, and O7; O1 and O6 form the peristomial border, and O7 sutures distally to them and are associated with the hydropore and gonopore (Fig. 1.1[1]). Plates O2 - O5 are positioned clockwise in the remaining four interradii forming the bifurcation points of the proximal ambulacra. In holocystitids, these oral plates were recognized as periorals except for O7, which was thought to belong to the facetal circlet (see below).

Oral plates are present in all holocystitids, but their recognition is complicated by two factors. First, in *Holocystites*, there is a slight clockwise rotation of the ambulacra system with respect to the theca (Fig. 1.1). This results in the ambulacral food grooves being positioned radially on the oral plates rather

[1] All figures and tables placed within Appendix 1-1.

than along the sutures of the ambulacral system as is typical for most pentaradiate echinoderms (Sumrall, 2015). The identity of the oral plates is straightforward because the compound oral plate complex, O1, O6 and O7, is positioned in the CD interray, based on 2-1-2 ambulacral symmetry and the position of the hydropore, gonopore, and anus (Sumrall, 2010). Similar rotations are also seen in other diploporitans such as *Glyptosphaerites* Müller, 1854 and *Eucystis* Angelin, 1878.

Secondly, an open circlet of differentiated plates, called facetals, lies immediately distal to the oral plate circlet (Fig. 1.1). This facetal circlet normally includes seven plates: five are radially positioned and generally bear facets for stout appendages associated with each of the five main ambulacral rays (Paul, 1971; Frest et al., 2011) and labeled here A-E based on which ambulacrum they support (Fig. 1.1). In taxa bearing four ambulacra, the A ambulacrum is undeveloped and consequently the A facetal plate lacks a facet. Two additional lateral facetals (labeled L) do not bear facets for appendages and are positioned between the B and C facetals to the right and the C and E facetals to the left in most taxa (Fig. 1.1). The facetal circlet is open between the C and D facetals because of the placement of O7 (Fig. 1.1). The facetal plate series is not part of the ambulacral system; rather, they are thecal plates that have ambulacra supported upon them epithecally (Sheffield and Sumrall, 2015a). This is a common theme among diploporitans (e.g., *Glyptosphaerites* and *Eucystis*).

The plating of the oral area of *Brightonicystis* is inconsistent with the model presented for Holocystitidae (Paul, 1971; Frest et al., 2011; Fig. 1.2). It was described as having ten periorals (=orals) and it was unclear if it had a defined facetal circlet. The specimen is unavailable for study, but based on the illustrations in Paul (1971), the presence of ten orals cannot be confirmed nor is there any suggestion that this is the case. Indeed, if ten orals are present, it would not only be unique to holocystitids, but to all stemmed echinoderms. It is possible that deep, angular food grooves mimic plate sutures as there are no indentations for three plate junctions on the appendage facets as illustrated (Fig. 1.2). Furthermore, the placement of additional non-facet bearing facetals in between the A and B and D and E ambulacra, coupled with the wide geographic separation of this taxon cast doubt on *Brightonicystis* sharing a close relationship with other holocystitids.

Pustulocystis (Fig. 1.3) also appears to vary from this holocystitid model. Although few specimens were available for analysis, previous authors (Paul, 1971; Frest et al., 2011) indicate that the oral plates bordering the peristome are in the standard configuration, and the lateral facetal plates are absent, leaving only facetals A-E. Additionally, most specimens suggest loss of the A ambulacrum.

Taphonomy

North American holocystitids have two distinct taphonomic trends based on the formation in which they were deposited (Paul, 1971). First, many

holocystitid diploporitans are preserved as internal and external molds in coarsely crystalline dolomite **(**Fig. 2.1, 2.2). Typically in older collections, only the poorly preserved internal mold of the specimen was recovered; the taxonomically important external mold counterparts of the specimens were left behind. On occasion, these internal molds can be used to describe generalized plating of the theca, but the combination of coarse crystallization and the preservation of only the internal morphology make interpretation of the oral area and respiratory pores nearly impossible. Consequently, most of the moldic specimens cannot be confidently diagnosed beyond holocystitid because of the significant loss of thecal morphologies.

The other dominant mode of preservation for holocystitids is preservation as original calcite showing external morphology in easily weathered mudstone (Fig. 2.3, 2.4). Consequently, the preservation is generally quite good and the only problems are that: (1) specimens are most often isolated from their holdfast structures; (2) many of the specimens are slightly compressed; and (3) many of the best-preserved specimens have been aggressively cleaned with air abrasion. Additionally, Thomka et al. (2016) noted that a significant percentage of diploporitan specimens are encrusted to some degree, with some overgrowth of the oral area. Regardless, the plating of the oral area and thecal morphologies are much more readily identifiable in fossils preserved as original calcite than those with moldic preservation. Unfortunately, associated free feeding appendages are not preserved with specimens of either preservation type in

current collections. External morphologies of specimens preserved as original calcite are often difficult to reconcile with internal morphologies of those preserved as molds because of the inability to identify thecal morphologies and oral plating in the latter.

While holocystitid thecae are thick and heavily plated, the oral plates seem to be easily disarticulated and often become disassociated from otherwise well preserved thecae, presumably due to some amounts of reworking after initial burial. This has taphonomically produced a variety of oral–facetal plate configurations described among specimens (Paul, 1971; Frest et al., 2011). When fully articulated, the peristomial opening is bordered by six oral plates, O1-O6. Oral 7 and the seven facetal plates are in contact with this proximal oral circlet and are not in contact with the peristomial opening (Fig. 3.1). In some specimens, O2–O5 have become disarticulated from the peristome making it appear as if the seven facetals, O1, and O6 (but not O7) border the taphonomically enlarged peristomial opening (Fig. 3.2). Still in other cases, O1-O6 have become disassociated with the theca leaving a taphonomically enlarged peristomial border bordered by seven facetals and O7 (Fig. 3.3). Taphonomic effects are often exacerbated by aggressive use of air abrasion during specimen preparation that has worn away oral plates either in part or in whole. This situation formed the basis for the identification of *Osgoodicystis*, which is only distinguishable from *Pentacystis* by the lack of oral plates.

Non-holocystitid Silurian diploporitans from North America

Holocystitids are typified by a number of features that appear to be unique to this clade. The thecae are typically large in size (compared to other diploporitans), with some specimens reaching 15 cm in thecal height. With the possible exception of diplopore-bearing *Triamara* (which may or may not be a holocystitid; see discussion below), holocystitids bear humatipores that lie solely within individual thecal plates and have numerous coelomic canals covered by a bulbous, lightly skeletonized covering. Other diploporitan groups typically have simple, diplopores, composed of a single, uncalcified thecal canal that is rarely preserved. In fossils, these structures are expressed as two pores contained within a depression on the external portion of the thecal plate (for further information regarding diploporitan respiratory structures, please reference Paul, 1972).

The ambulacra of holocystitids are also morphologically different from other diploporitans. They have highly reduced proximally recumbent ambulacral systems that are restricted to the summit on the orals and facetals, and erect appendages (recumbent and epithecally positioned in *Paulicystis*) of unknown affinities; the oral areas of holocystitids do not bear floor plates incorporated into the theca as most blastozoans (Sumrall, 2010, 2015). Erect appendages, either erect ambulacral floor plates presumably bearing brachioles or more likely greatly enlarged terminal brachioles borne on facets that are positioned on the facetal circlet, are unique to holocystitids. Based on the size of the facets and plating

scars on *Paulicystis,* these appendages are biserial and proportionately exceptionally large for a blastozoan.

Other occurrences of diploporitans from the Silurian of North American are morphologically highly dissimilar to holocystidids and until recently, the only described taxon was *Gomphocystites* Hall, 1864 **(**Fig. 4.1**)**. *Gomphocystites* occurs slightly earlier than the holocystitids, with the earliest undoubted occurrence in the Llandovery-age Hopkinton Dolomite of Iowa (Witzke, 1976) and persists as a common faunal component in strata containing the *Holocystites* Fauna (which are largely restricted to Wenlock-age). *Gomphocystites* also has a greater biogeographic range than holocystitids, with fossils known from New York, USA (Brett, 1985a), and the Baltic *Celtacystis* (*Gomphocystites*) *gotlandicus* (Angelin, 1878)*,* which has been proposed to be very closely related to *Gomphocystites* (Bockelie, 1979, 1984). The morphology of *Gomphocystites* deviates strongly from holocystitids. It has a typical oral plate bearing oral area but lacks O7, and plates O2 and O5 are not in contact with the peristomial opening. The recumbent ambulacra are long and spiraling, and wrap around the theca, but bear brachiole facets only on the left side, and seem to be borne on floor plates that are restricted to the left side. They also bear true diplopores instead of the humatipores of holocystitids.

The only other known Silurian diploporitan from North America is a recently discovered and undescribed species of *Eucystis* from Wenlock-age strata of the Bainbridge Group of Missouri (Sheffield and Sumrall, 2015b). These

specimens (Fig. 4.2) share strong morphological similarities with *Eucystis* from the Ordovician Baltican and peri-Gondwanan faunas. Like their Baltican and peri-Gondwanan counterparts, these specimens have five multi-branching ambulacra extending across the orals and proximal thecal plates without underlying floor plates. These food grooves each end in a brachiole facet. The diplopores are simple and the theca bears an unusually large holdfast that flares slightly at the attachment surface (whether this flaring is characteristic of this taxon or if it was formed around an unusually large bioclast is unclear). However, these specimens share a similar, slightly clockwise rotation of the oral plates with respect to the ambulacra with *Holocystites* and *Glyptosphaerites*. It is clear, based on strong morphological deviations that neither *Gomphocystites* nor these recently discovered eucystitid specimens are closely related to members of Holocystitidae. Details of the relationships between these taxa are pending phylogenetic analyses.

Previous phylogenetic analysis

An evolutionary hypothesis of the Holocystitidae was proposed by Frest et al. (2011), based assumed trends in peristomial morphology. A second analysis based on a stratocladistic model is not discussed here. The resulting phylogeny (Fig. 5) shows a complicated evolutionary history with drastic changes in the oral area of the diploporitans from an inferred hypothetical ancestor to the more derived taxa (Table 1). *Holocystites* and *Trematocystis* are depicted as grades of organization at nodes rather than as monophyletic groupings of taxa. Frest et al.

(2011) drew the conclusion that more derived holocystitids trended towards a reduced number of plates within the oral area. As mentioned above, the number of plates observed was affected by taphonomy and specimen preparation and is, therefore, not based on the evolutionary history of the taxa involved. Further, Paul (1971) and Frest et al. (2011) misidentified an oral plate (O7) as a facetal plate, which influenced their interpretations. Some of the characters within their analysis were based on counting the numbers of plates present in proposed taxa. However, characters based on the number of plates present in the absence of a clear understanding of which homologous elements are present and absent among taxa are not properly constructed because the alternate states are not derived from a single character transformation.

Materials and Methods

All taxa studied for this analysis, along with their locality and age information, are listed in Table 2. All specimens are housed in research collections from the following museums or institutions: Cincinnati Museum Center (CMCIP), Field Museum of Natural History (FMNH; UC), The University of Iowa (SUI), Miami University (MUMG), and Yale Peabody Museum (YPM). *Brightonicystis* was not examined for this study based on a lack of available material.

Systematic Paleontology

Subphylum Blastozoa Sprinkle, 1973

Class Diploporita Müller, 1854

Superfamily Sphaeronitida Neumayr, 1889

Family Holocystitidae Miller, 1889

Type genus: *Holocystites* Hall, 1861

Other Genera: *Trematocystis* Jaekel, 1899; *Pentacystis* Paul, 1971; *Pustulocystis* Paul, 1971; *Brightonicystis* Paul, 1971; *Paulicystis* Frest and Strimple, 2011.

Emended diagnosis: Large diploporitans with peristomial border plating pattern comprising two distinct circlets of plates, oral plate series and facetal series. O1-O6 surround peristome; O1 and O6 preclude O7 from the peristomial border. O7 is in contact with the periproct. Facetal plate series distal to oral plate series. Five facetal plates lie radially and bear large facets for feeding appendages (some facets missing in taxa bearing fewer than five ambulacra). Two lateral facetal plates positioned between B and C and the D and E ambulacra lack facets; these lateral facetal plates are lacking in *Pustulocystis*. Facetal plate series open, being interrupted by O7. Floor plates not incorporated into oral surface, either absent or restricted to unknown erect ambulacra. Stem absent. Holdfast present at distal end of theca.

Remarks*:* The plating of the oral area with the orals bordered by facetals is unique to Holocystitidae and is the primary distinguishing feature of the clade. The large facets on the facetal series connect to food grooves extending from the peristome without underlying floor plates. The nature of the appendages that arise from these facets remains unknown. Two scenarios are thought to be possible. First, erect ambulacra in the form of biserial ambulacral floor plates likely bearing biserial brachioles arise from the facets. Their biserial nature is supported by the facet having scars for two perradially positioned plates. Further, the scars on *Paulicystis* where the appendages are not preserved but recumbent show them to be biserial. The second option is that these facets are for extremely stout terminal brachioles. If these are brachioles, they would be among the most robust brachioles known being an order of magnitude larger in diameter than those typically found in blastozoans. Only material preserving these appendages will elucidate the nature of these appendages and add more data to the diagnosis.

Previously proposed subfamilies within Holocystitidae include: Holocystitinae Miller, 1889 (comprising *Holocystites* and *Brightonicystis*), Trematocystinae Frest and Strimple, 2011 (comprising *Trematocystis, Pustulocystis*, and *Paulicystis*), and Pentacystinae Frest and Strimple, 2011 (comprising *Pentacystis* and *Osgoodicystis*). These subfamilies were identified by the previous phylogenetic analysis and differentiated from one another largely on the basis of numbers of facetal and oral plates. Frest et al. (2011) interprets

Holocystitinae as being a paraphyletic grade with respect to Trematocystinae and Pentacystinae (Fig. 5). Furthermore, the Pentacystinae were partially designated on taphonomic features (Sheffield and Sumrall, 2015a). These subfamilies are not discussed here further pending phylogenetic analysis of the taxa in question.

Triamara was separated from Holocystitidae and placed within Aristocystitidae Neumayr, 1889, based on *Triamara* having simple diplopores and not humatipores (Tillman, 1967). As blastozoan respiratory structures have been shown to appear more than once in evolutionary history (Sumrall and Gahn, 2006), it is not clear that using respiratory structures is valid for defining higher level taxonomy. *Triamara* shares some similar features concerning the peristomial border plating system, but there are also some strong deviations (see discussion of *Triamara* below for further details); unfortunately, the oral areas of the studied specimens of *Triamara* were insufficiently preserved to be interpreted in detail. Pending better material, we retain Aristocystitidae for species of *Triamara*.

Genus *Holocystites* Hall, 1861

Figures 6.1, 6.2, 7.1, 7.6, 7.7, 7.8

Type species. — *Caryocystites cylindricum* Hall, 1861

Emended diagnosis.– Five ambulacra present, extending from peristome to facet scars that straddle distal edges of oral plate series and facetal plates, typically positioned on more than one facetal plate (Fig. 6.1, 6.2). Oral plate series slightly rotated clockwise with respect to ambulacra. Thecal plates tumid with sunken sutures (Fig. 7.1).

Remarks.– This diagnosis is based on preserved oral areas of multiple *Holocystites* species. *Holocystites* bears the stereotypical peristomial plate arrangement of holocystitids. All five ambulacra lead to facetal scars that are partly positioned between the oral plate series and the facetal circlet (Fig. 6.1, 6.2). The positioning of the facets is looser than other taxa spread across the edges of more than one facetal.

Holocystites species show wide morphological variability suggesting that more than one clade may be represented (Fig. 7.6, 7.7, 7.8). Proposed species show wide variation in the organization of the theca, ranging from moderately well organized plate circlets to disorganized, irregularly plated thecae and species with large plates and relatively small plates. *Holocystites* species also encompass a wide range of thecal body shapes, ranging from long and elongate to very globose. Further, ontogenetic sequences for most holocystitids are not understood; therefore, changes in plating patterns and thecal shape that occurred during ontogeny of species are likely adding to confusion concerning holocystitid systematics. Holdfasts can range from tapering to an almost stem-

like projection to robust forms that lack noticeable narrowing. Unfortunately, many of the species currently assigned to *Holocystites* do not have oral areas preserved. Because the features of the theca and holdfast are so highly variable, they cannot be used to determine genus-level placement of species.

Genus *Trematocystis* Jaekel, 1899

Figures 6.7, 6.8, 7.2

Type species.— *Holocystites subglobosus* Miller, 1889 (*H. globosus* Miller, 1878)

Emended diagnosis.— Four ambulacra, B, C, D, and E, extend from peristome to facet scars that lie on top of facetal plates (Fig. 6.7, 6.8); A ambulacrum not developed. B-E facets centered on facet-bearing facetal plates. Lateral facetals and A facetal plate depressed. O7 proportionally small. Thecal plates large and flat without sunken sutures (Fig. 7.2) Theca globular and squat, with relatively wide cementation disk.

Remarks.— *Trematocystis* bears the stereotypical holocystitid peristomial border plating (Fig. 6.7, 6.8). It is unusual because the A ambulacrum is not developed, likely resulting from paedomorphic reduction, a phenomenon seen in other blastozoan groups (Sumrall and Wray, 2007). Among holocystitids, this reduction is also seen in *Paulicystis*, but there the appendages are recumbent, as

evidenced by biserial scars extending a short way down the thecal plating near the summit. Large facets for the B-E ambulacra are centered on the facetal-bearing plates and the presence of facets that do not cross the facetal plate boundaries serve to separate this taxon from *Holocystites*. The lateral, non-facet bearing facetal plates and the A facetal plate are depressed with respect to others within the facetal plate series as seen in *Pentacystis*.

Genus *Paulicystis* Frest and Strimple, 2011

Figures 6.9, 6.10, 7.3

Type Species .— *Paulicystis densus* Frest and Strimple, 2011

Emended diagnosis.— Four ambulacra, B, C, D, and E, extend from peristome to facet scars that lie on top of facetal plates. A ambulacrum not developed. Ambulacra epithecally recumbent upon theca (Fig. 6.9, 6.10). Lateral facetals and A facetal plate depressed. Periproct relatively large. Theca squat and globular (Fig. 7.3). Plates small, tumescent, with deeply depressed sutures. Relatively wide cementation disk.

Remarks .— *Paulicystis* bears the stereotypical plate arrangement for the peristomial border (Fig. 6.9, 6.10). As with *Trematocystis,* the A ambulacrum is absent, likely resulting from paedomorphic ambulacral reduction as seen

commonly among blastozoans (Sumrall and Wray, 2007). The B-E ambulacra are not erect, as in the other genera, but instead lie recumbently on the thecal surface, beginning with the facet scars on the facetal plates. This shows the appendages to be biserial (Fig 6.9), but adds little information about whether they are floor plates or brachiolar plates. Large facets for the B-E ambulacra are centered on facetal-bearing plates and the presence of facets that do not cross plate boundaries serve to separate this taxon from *Holocystites*. The non-facet bearing facetal plates and the A facetal plates are depressed with respect to others within the facetal plate series.

Genus *Pentacystis* Paul, 1971

Figures 6.2, 6.3, 7.4

Type species.— *Pentacystis simplex* Paul, 1971

Emended diagnosis.—Five ambulacra extend from peristome to very large facet scars that lie on top of facetal plates. Facetal plates large and elevated to form a low spout-like protuberant summit structure (Fig 6.3, 6.4). Plates of the oral series narrow and confined to peristomial depression, except for relatively large O7. Theca elongate, narrows slightly toward the base without a constricted distal portion. Plates large and flat, without depressed sutures (Fig 7.4).

Remarks.—Pentacystis bears the stereotypical holocystitid peristomial border plating. All five ambulacra extend to very large facets that bear erect feeding appendages. These facets are wholly supported on the facet-bearing plates and do not cross facetal plate boundaries. This serves to separate this taxon from *Holocystites*; the presence of a facet on the A facetal serves to separate *Pentacystis* from *Trematocystis* and *Paulicystis*. The oral plates within the oral plate circlet are proportionally narrow compared to O7. The facetals form a spout-like protuberant summit structure unlike the rounded summits of other holocystitids. The non-facet bearing lateral plates are not depressed with respect to other plates within the facetal series adding to the spout-like appearance of the summit area. Humatipores are present on the thecal plates.

Pentacystis was proposed as a separate genus within Holocystitidae based on the oral plates being greatly reduced or absent (Paul, 1971). Species within this genus were delineated by the presence or complete absence of oral plates; specimens with present or reduced (herein interpreted as partially disarticulated) oral plates were used to describe *P. wykoffi* (Miller, 1891), whereas specimens with absent oral plates were assigned to *P. simplex* and *P. sphaeroidalis* **(**Miller and Gurley, 1895; Fig. 8).

Osgoodicystis Frest and Strimple, 2011 (Figs. 6.5, 6.6, 7.5) was erected within the same subfamily as *Pentacystis* (Pentacystinae) based on the presence of the oral plates observed in some specimens. Species of *Pentacystis* with preserved oral plates, like *P. wykoffi,* were reassigned to *Osgoodicystis* to reflect

this. *Osgoodicystis* closely resembles *Pentacystis* in thecal shape and outside of the differences in size and number of the oral plates, are nearly identical in terms of major morphological features **(**Figs. 6.3, 6.4, 6.5, 6.6, 7.4, 7.5).

Reinvestigation of these specimens shows that the differences previously noted in the oral areas are based on taphonomy and preparation. Attachment scars from O1-O6 are clearly visible upon all the specimens in question, though in many cases obscured by aggressive preparation with air abrasion. Oral 7 is contained within the CD interray, as is typical for all holocystitid specimens. As the only major difference between *Pentacystis* and *Osgoodicystis* is taphonomic, *Osgoodicystis* Frest and Strimple, 2011 is reassigned as a junior synonym of *Pentacystis* Paul, 1971.

Genus *Brightonicystis* Paul, 1971

Figure 1.2

Type Species.— *Brightonicystis gregarius* Paul, 1971

Remarks.—The oral area plating of *Brightonicystis* (Paul, 1971; Frest et al., 2011) is inconsistent with the model presented for Holocystitidae. It was described as bearing ten periorals (=orals) and it was unclear if it had a defined facetal circlet. Plates consistent with the facetal series suggest the presence of additional plates between the A and B, and E and A ambulacra, unlike any other

holocystitid (Fig. 1.2). Furthermore, the illustrations in Paul (1971) do not adequately document the presence of ten orals (Fig. 1.2), which seems highly unlikely as this condition is unknown in any other echinoderm. It may be that each of the oral plates is being interpreted as a pair of plates and the food grooves interpreted as sutures based on rotation of the oral plates. However, based on a lack of available material, *Brightonicystis* will not be rediagnosed in this study.

Pustulocystis Paul, 1971

Figure 1.2, 9.1, 9.2

Type Species.— *Holocystites ornatissimus* (Miller, 1891)

Remarks.— One specimen of *Pustulocystis,* Paul 1971 was examined as part of this study. This taxon has the normal holocystitid oral area with seven oral plates in the standard configuration bordered by a facetal series. The primary difference is the absence of the lateral facetal plates, leaving only facetals A-E (Figs. 1.2, 9.1). The lateral facetal plate absence serves to diagnose this taxon. Species within *Pustulocystis* are largely differentiated by the number of ambulacra present; some proposed species within this taxon are diagnosed by the absence of the A ambulacrum, whereas others have no reduction of ambulacra. Based on a lack of available material, the diagnosis for this taxon is not herein emended.

Superfamily Aristocystitidae Neumayer, 1889

Remarks.— Members of Aristocystitidae are characterized by very short and unbranched ambulacra (Kesling, 1967). All other genera within Aristocystitidae are placed within subfamilies, except for *Triamara,* due to uncertainty about its placement (Paul, 1971).

Genus *Triamara* Tillman, 1967

Figures 9.3, 9.4

Type Species.— *Triamara cutleri* Tillman, 1967

Emended diagnosis.— Three ambulacra, likely shared BC, D, and E based on their relative positions with respect to oral plates, extend from peristome to facet scars that lie on top of a facetal plate (Fig. 9.1). D ambulacrum bifurcates and leads to two distinct facets on the D facetal plates. Facetal plates not clearly diagnosable from other plates in summit area, slightly elevated to form a moderately high spout-like protuberant summit. Oral plates relatively large. Theca narrows into constricted distal holdfast (Fig. 9.2). Diplopores present on thecal plates.

Remarks.—Triamara appears to bear most aspects of the stereotypical holocystitid peristomial border plating pattern. Unfortunately, heavy taphonomic disarticulation has affected the oral areas of the majority of curated specimens

and details concerning the number and placement of the facetals cannot be determined at this time. Oral 1-6 surround the ovate peristome. Oral 1, O6, and O7 are within the CD interray, with O1 and O6 precluding O7 from the peristome. Facetal D and E are in the expected position, but the position of the facetal in association with shared B and C ambulacrum is unclear due to taphonomic overprinting (i.e. disarticulation and breakage of plates in the oral area, along with noticeable thecal compaction). In some specimens of *Triamara* (e.g., *Triamara ventricosa* Paul, 1971), a plate appears to separate O7 from the periproct, unlike holocystitids (Fig. 9.3). It is unclear whether this is common to *Triamara* or unique to *T. ventricosa.* Both oral plates and facetal plates are extremely large, even when considering that *Triamara* is relatively larger than most holocystitids. Theca plates are relatively large and appear to have two generations of plates, primary and secondary (Fig. 9.4). Diplopores, as opposed to humatipores, are densely and evenly spread across the thecal plates.

The peristomial border plating pattern of *Triamara* bears strong similarities to Holocystitidae, as does the makeup of the theca. However, due to dissimilarities in the sizing of the oral and facetal plates, the presence of diplopores, the different positioning of the periproct with respect to O7, and the poor preservational detail of the oral area that pervades curated specimens, it is unclear if *Triamara* is a member of the holocystitid clade. As such, it will not be reassigned until new data can be collected.

Conclusions

Previous studies of the *Holocystites* Fauna were problematic because of over-splitting of poorly preserved species and a misinterpretation of the peristomial border plate system resulting in a complicated and unparsimonious evolutionary history. Careful analysis of numerous well-preserved specimens shows that the peristomial border plate system among holocystitid taxa is much more conservative than previously described. Many of the ascribed differences proposed by previous authors were based on taphonomic differences or because of a lack of understanding of the homologous elements of the oral plating system. Consequently, *Osgoodicystis* Frest and Strimple, 2011 is a junior synonym of *Pentacystis,* Paul, 1971. The systematic placement of *Triamara* Tillman, 1967 is unclear, based on poor preservation. While it bears many peristomial border similarities to holocystitids, there are also a number of differences in the size and placement of these oral area plates. Numerous examples of blastozoan respiratory structures re-evolving suggests that delineating higher-level systematics based solely on the presence of humatipores or diplopores is likely not valid. However, these other differences in *Triamara*, in combination with the presence of simple diplopores, suggest the possibility that it is not a member of the holocystitid clade. Pending new data, we retain Aristocystitidae for species of *Triamara*.

The oral area of blastozoan echinoderms is the key to delineating systematic relationships, as evidenced by the plastic nature of the theca in the

holocystitids. While it is very likely that a number of species proposed within the remaining genera of the *Holocystites* Fauna should be synonymized or reassigned to other genera, a lack of preserved oral areas that pervades a significant number of type specimens makes it is impossible to assess the systematic placement of many species.

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Appendix 1-1

Figure 1.1. Typical peristomial border plating of holocystitids. **(1)** The peristome (M) is bordered by seven oral plates (gray). The facetal circlet (white) lies distal to the oral plates and comprises seven plates; five generally bear facets for stout appendages and are associated with ambulacral rays (labeled A-E) and two lateral facet plates do not bear lateral scars (labeled L). The gonopore (black circle) is typically situated on O7. O7 is situated in the CD interray, in contact with the periproct (P) and is precluded from the peristome by O1 and O6. Modifications to this basic pattern are the basis for the identification of different taxa within the holocystitids. Modified from Sheffield and Sumrall, 2015a; **(2)** *Brightonicystis* has been described as having ten oral plates, which is inconsistent with the model presented for Holocystitidae. It is unclear whether this taxon bears a defined facetal circlet. Illustrations in Paul (1971) do not unequivocally document the presence of ten oral plates, which has not been observed in any other echinoderm; more likely, each oral plate has been interpreted as two separate plates due to ambiguous plate sutures. Modified from Paul, 1971; **(3)** *Pustulocystis* was previously described as having six facetal plates, although the plate in contact with O1 and O6 is here interpreted as O7, and not a facetal. This taxon has five facetal plates and seven oral plates; the lateral facet plates that do not bear facets are not present, leaving only facetal plates A-E. Note the loss of A ambulacrum. Line drawing of *Pustulocystis pentax* Paul, 1971 (MUMG-T 226).

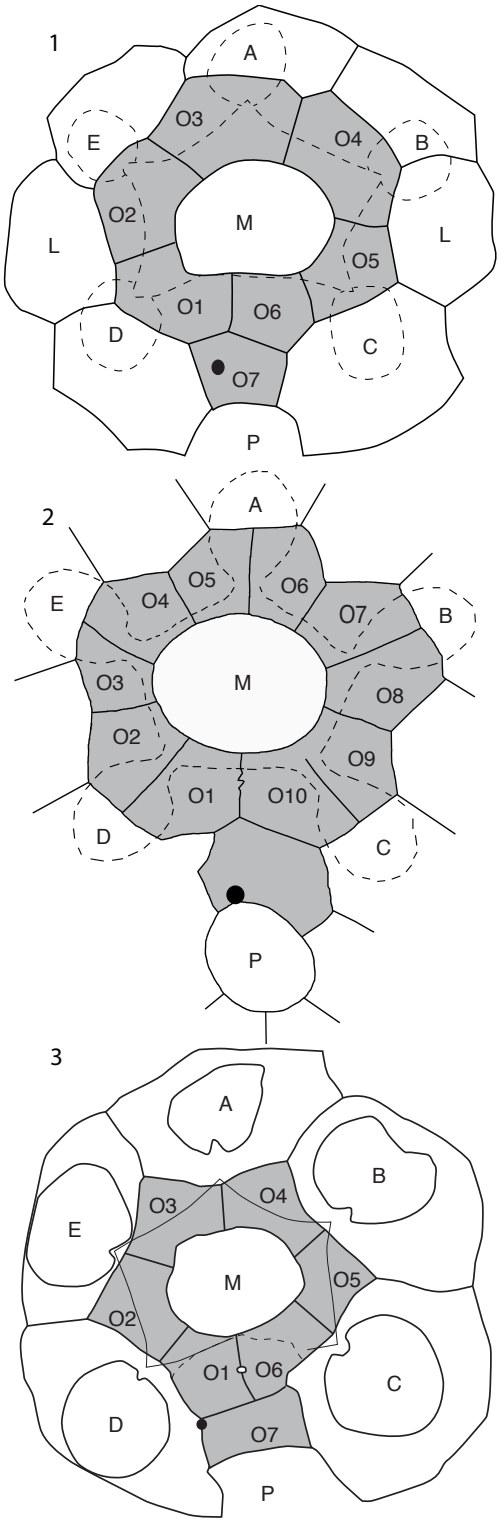


Figure 1.1 continued.

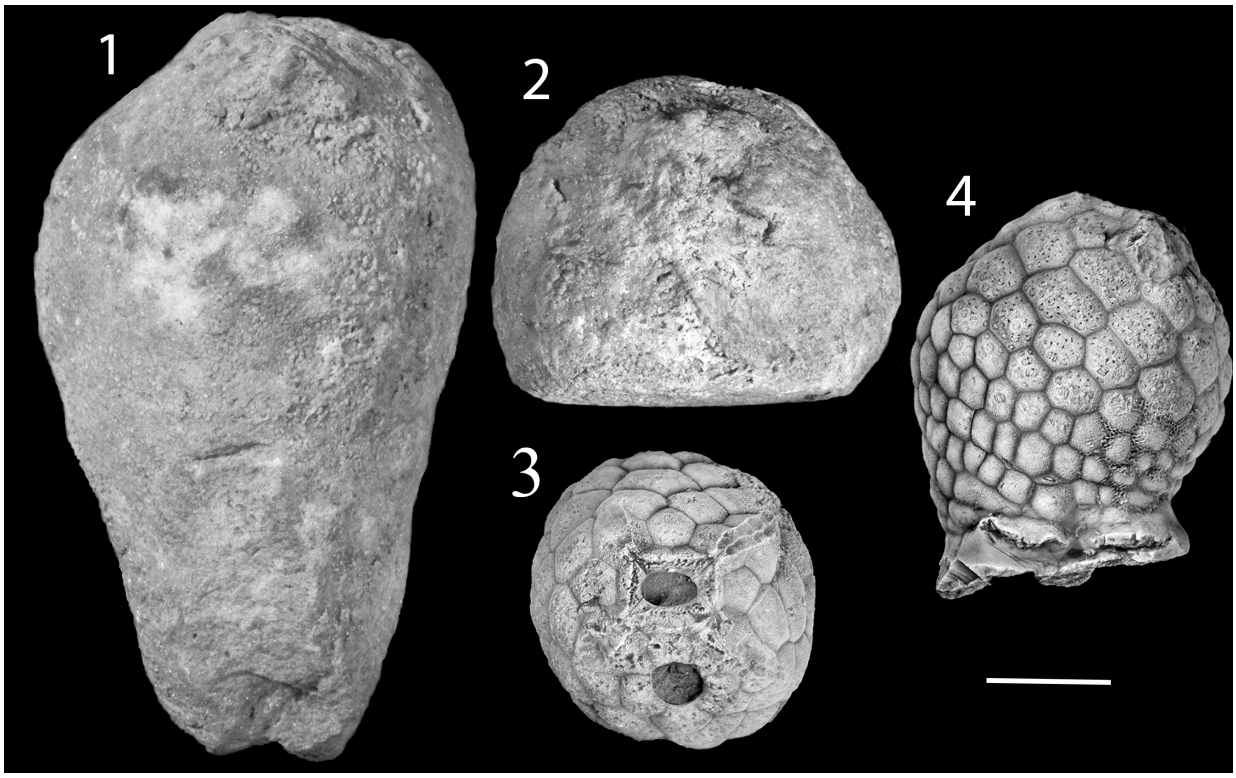


Figure 1.2. Two common taphonomic preservation types found in holocystitids. **(1)** lateral view of typical holocystitid mold ("Racine Formation", Wisconsin); **(2)** The internal mold preserved as coarse crystalline dolomite does not usually preserve plating of the oral area, and often of the theca, in enough detail to study (*Holocystites winchelli* Hall, 1868; CMCIP 26438); **(3)** Oral view of specimen preserved as original calcite; thecal plates are typically well preserved (Massie Formation, Indiana); **(4)** Lateral view of well preserved specimen (*Paulicystis sparsus*; SUI 48164). These two very dissimilar preservational types make it difficult to reconcile the systematics of specimens found across holocystitid-bearing localities. Scale bar=1cm

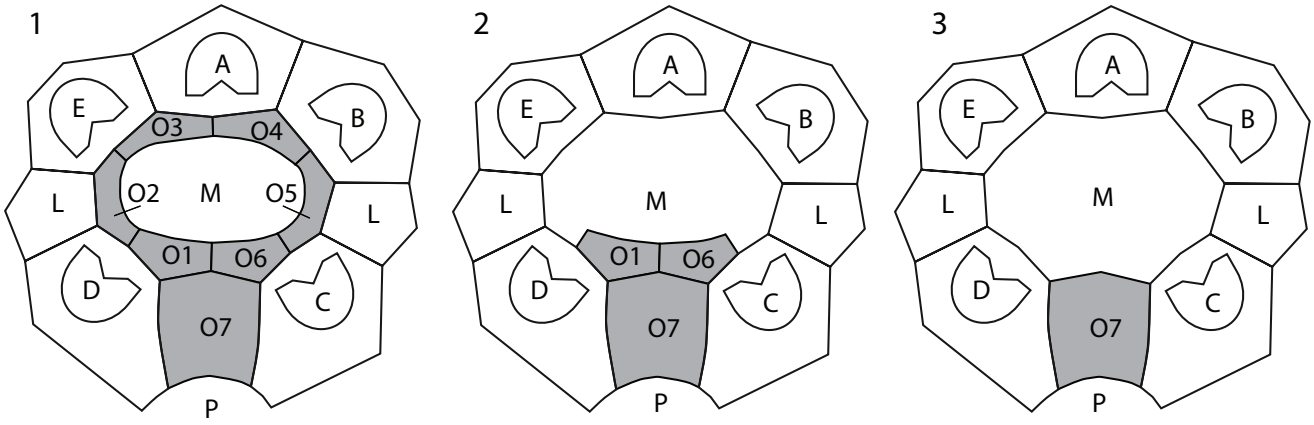


Figure 1.3. Common disarticulation patterns of holocystitid oral plating. **(1)** All seven oral plates associated with the theca, bordering the peristome. Schematic line drawing of *Holocystites scutellatus* (SUI 48183); **(2)** O2-O5 become disarticulated from the peristome, giving the appearance of an enlarged peristome being bordered by the facetal circlet and O6 and O7. Schematic line drawing representative of the oral area of *Holocystites spangleri* Miller, 1891 (SUI 48197); **(3)** O1-O6 have been disarticulated, giving the appearance of a greatly enlarged peristomial opening being bordered by the facetal plate circlet. This plating pattern has been used to separate *Pentacystis* Paul, 1971 (those without most oral plates) and *Osgoodicystis* Frest and Strimple, 2011 (those with oral plates); because the only significant difference between these two proposed genera is taphonomic, *Osgoodicystis* is rejected as a junior synonym of *Pentacystis*. Schematic line drawing of *Pentacystis gibsoni* Frest and Strimple, 2011 (SUI 46316). M=mouth, P=periproct, L=lateral facet.

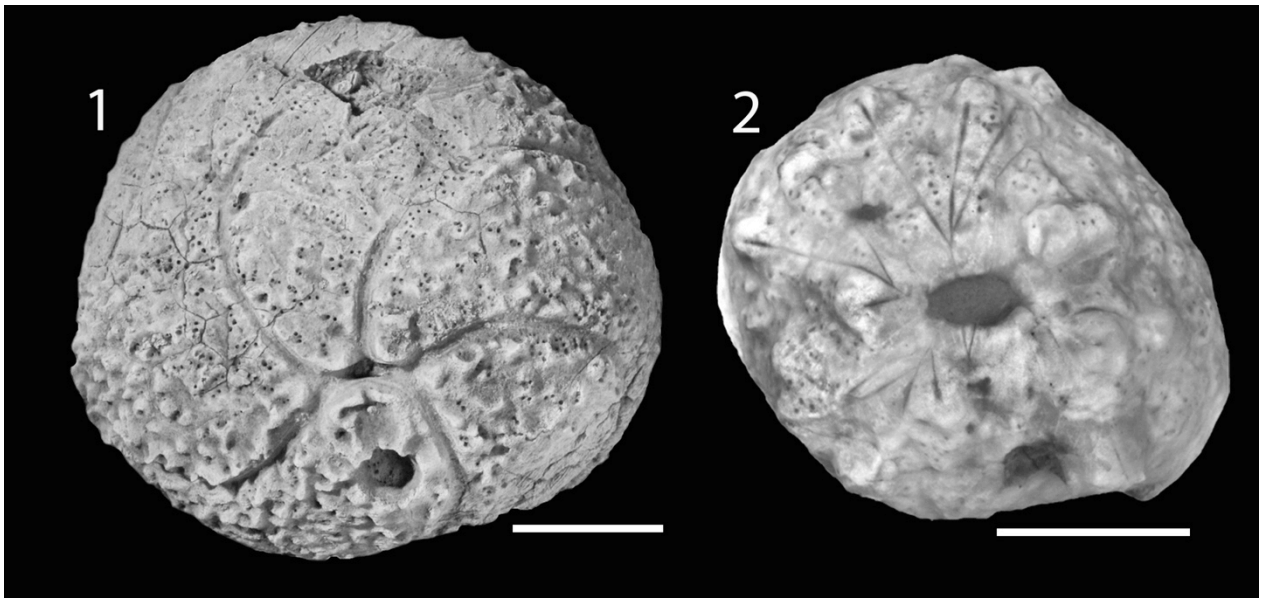


Figure 1.4. Non-holocystitid Silurian diploporitans from Laurentia. **(1)** *Gomphocystites indianensis* Miller, 1889*,* a non-holocystitid diploporitan from the Silurian of North America. Note the long, spiraling ambulacra. Brachiole facets are borne from the left side of the ambulacra only. True diplopores situated within shallow, elliptical peripores are clearly seen in this image (FMNH 19708); **(2)** Middle Silurian *Eucystis* specimen from the Bainbridge Formation of Missouri. Oral area pictured shows five multi-branching ambulacra extending across the orals and proximal thecal plates and ending in various numbers of large brachiole facets (CMCIP 53630). Scale bars=1 cm

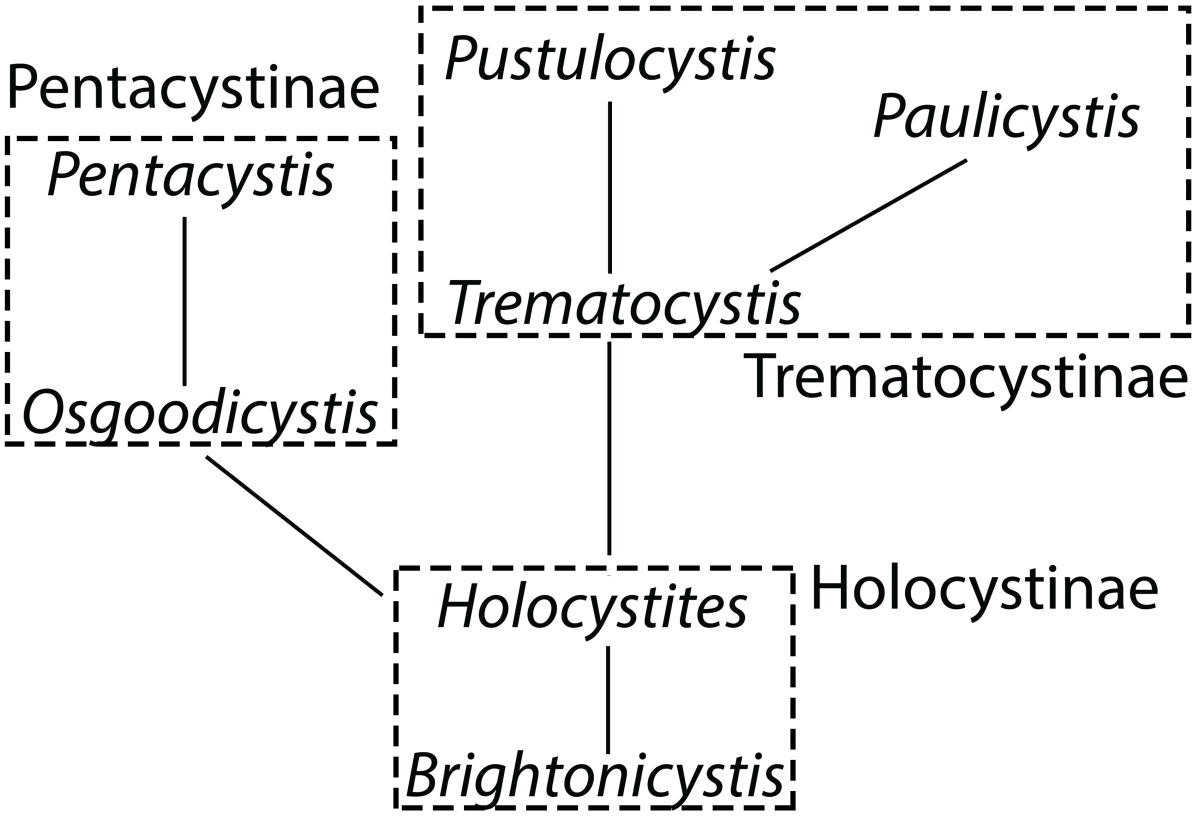


Figure 1.5. A proposed evolutionary hypothesis of the *Holocystites* Fauna, proposed by Frest et al. (2011), based on changes within peristomial morphology; note that Holocystitinae, *Holocystites* and *Trematocystis* are all paraphyletic. This analysis interpreted a trend towards a reduction in oral plates in advanced holocystitids, such as *Pentacystis*, whose species were described as having vestigial or absent oral plates. Figure modified from Frest et al., 2011.

Figure 1.6. Oral area interpretations of holocystitid taxa. **(1)** *Holocystites scutellatus* (SUI 48183) oral view; **(2)** Interpretation of oral area of *Holocystites scutellatus;* note that facet bearing facetal plates are loosely positioned on more than one facetal; **(3)** *Pentacystis gibsoni* (SUI 46316) oral view; **(4)** Interpretation of oral area of *Pentacystis gibsoni*; note five facetal scars lying atop facet-bearing plates and semi-protuberant summit. Attachment scars on the oral area of *Pentacystis* (SUI 46316) clearly show where O1-O6 were attached before they were disarticulated; **(5)** *Osgoodicystis bissetti* Frest and Strimple, 2011 (SUI 48166) oral view; **(6)** Interpretation of oral area of *Osgoodicystis bissetti* shows an identical plating pattern to *Pentacystis*, with the exception that the oral plates are still intact; **(7)** *Trematocystis magniporatus* (SUI 48198) oral view; **(8)** Interpretation of oral area of *Trematocystis*; note absence of A ambulacrum and firm positioning of facets on one facetal plate; **(9)** *Paulicystis sparsus* (48164) oral view; **(10)** Interpretation of oral area of *Paulicystis sparsus*; note absence of A ambulacrum and presence of recumbent ambulacral scars on the theca. OO indicates disarticulated oral plates of this specimen. Open circles on O7 indicate position of gonopore. O=Oral plate; P=Periproct. M=Mouth. Scale bars=1 cm. Modified from Sheffield and Sumrall, 2015**.**

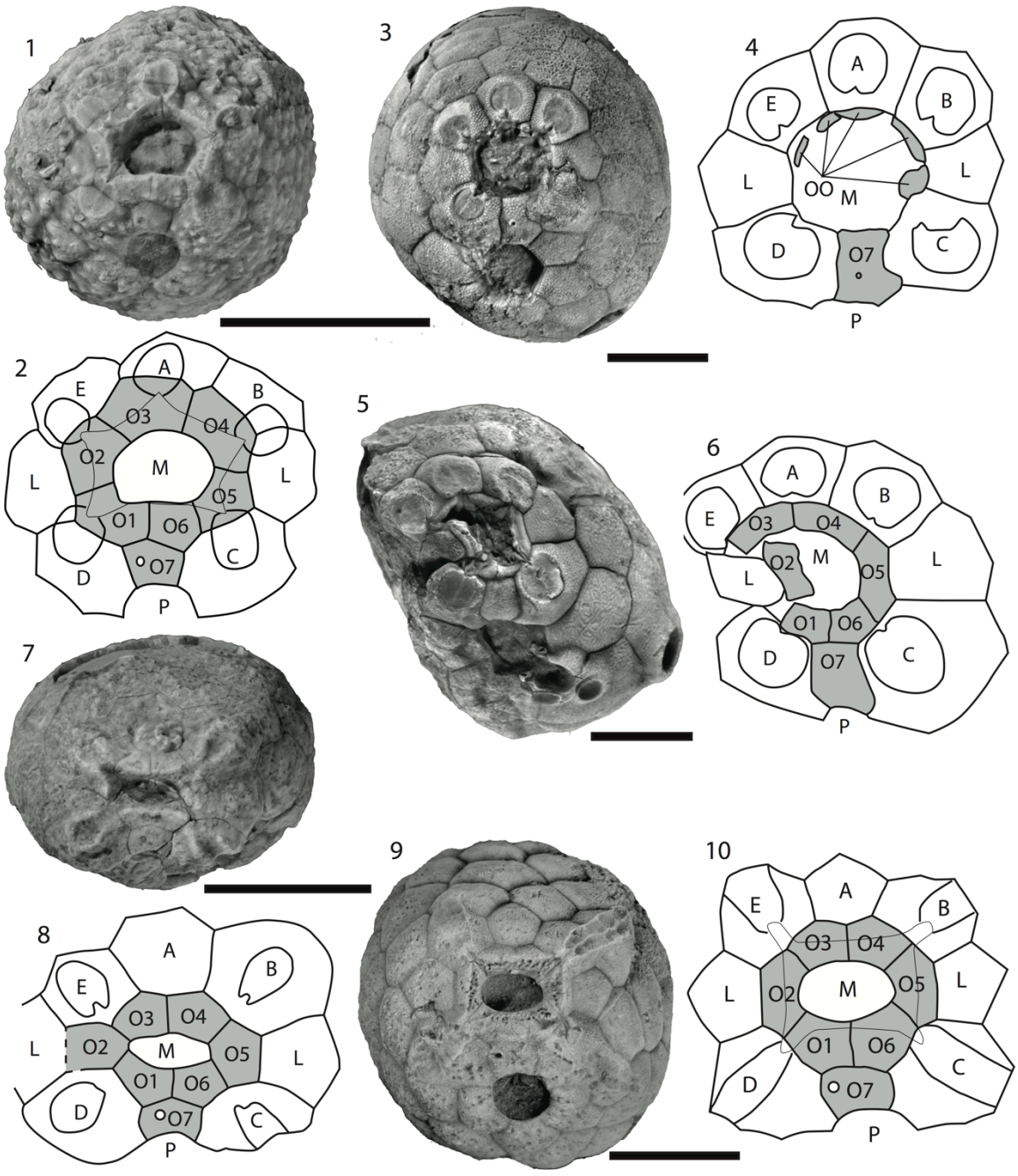


Figure 1.6 continued.

Figure 1.7. Thecal views of representative holocystitid taxa. **(1)** *Holocystites scutellatus* (SUI 48183). Theca squat, globular with numerous, tumid plates with moderately impressed sutures. Distal end tapers considerably into holdfast; **(2)** *Trematocystis magniporatus* (SUI 48198). Theca squat, with large and flat plates, without impressed sutures. Theca narrows slightly into holdfast; **(3)** *Paulicystis sparsus* (SUI 48164). Theca squat, globular with numerous small, tumid plates with deeply impressed sutures. Theca widens distally into holdfast; **(4)** *Pentacystis gibsoni* (SUI 46316). Theca elongate to globular with relatively large, flat plates without impressed sutures. Theca narrows moderately into holdfast; **(5)** *Osgoodicystis bissetti* (SUI 48166) is highly morphologically similar to *Pentacystis*; theca elongate with relatively large, flat plates without impressed sutures. Theca narrows moderately into holdfast. Note that circular depressions on theca are attributed to parasitic embedment structures, *Oichnus* Bromley (*Tremichnus* sensu Brett, 1985b); **(6)** *H. sp.* (YPM 34764). Theca is relatively large, and narrows considerably distally. Plates are highly disorganized and of multiple generations; **(7)** *H. cylindricus* (YPM 19175). Theca is elongated and cylindrical without distal constriction. Plates are organized and of one generation; **(8**) *H. sp.* (YPM 519465). Theca is squat and globular and narrows distally into holdfast. Plates are disorganized and of multiple generations. Scale bar=1 cm.

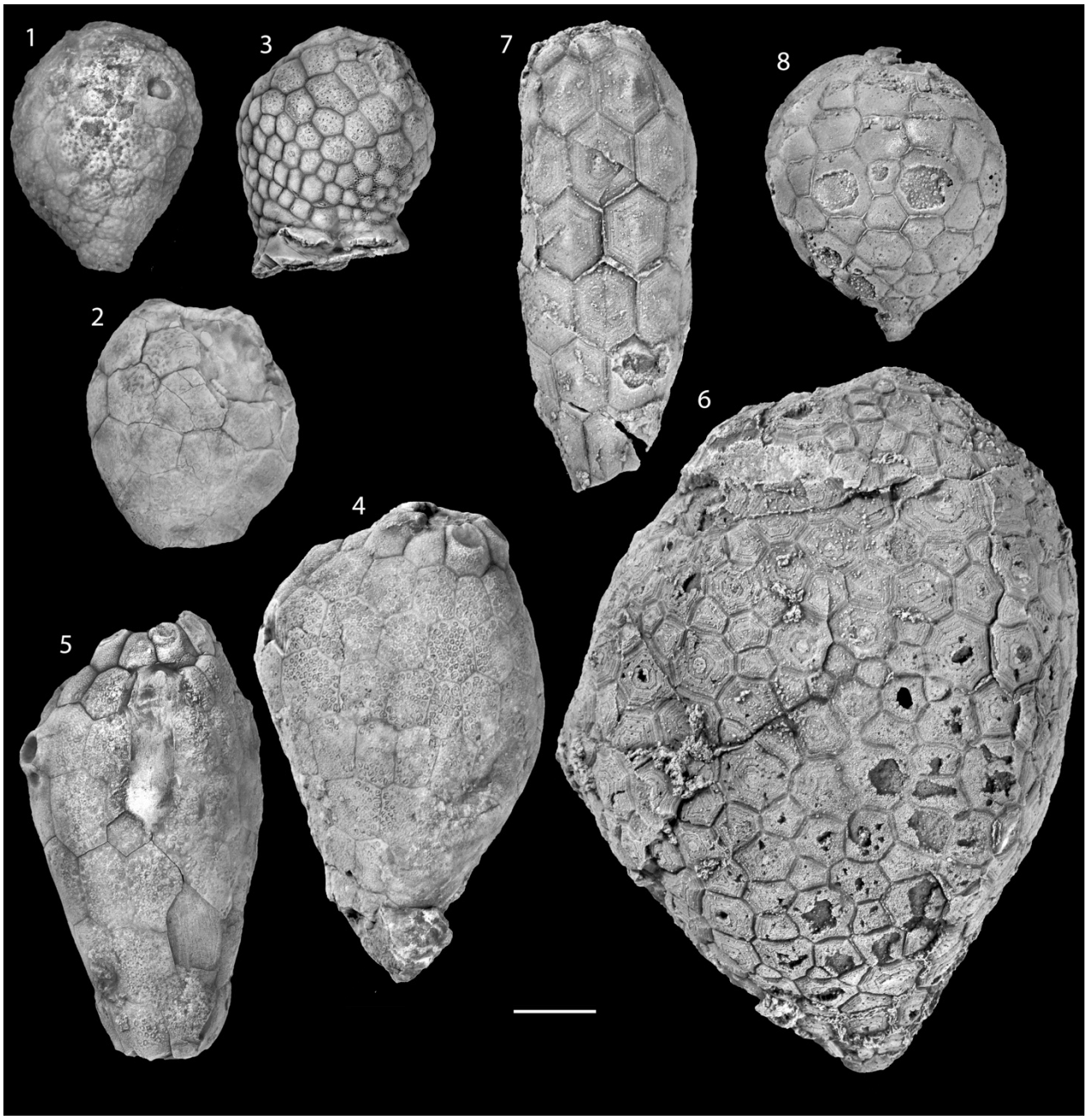


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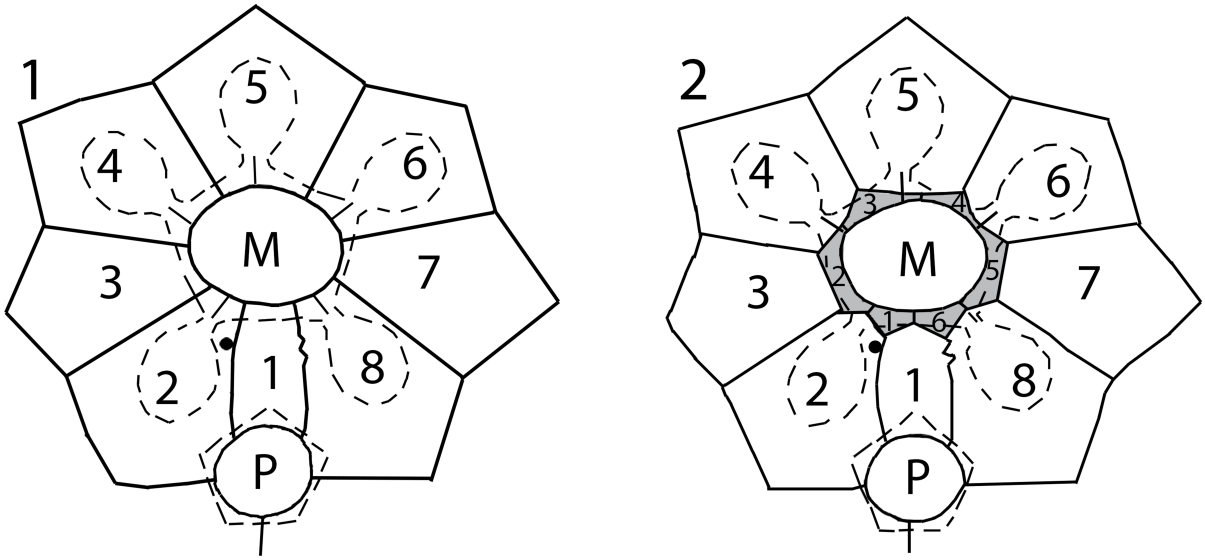


Figure 1.8. Species of *Pentacystis* were previously proposed based on whether oral plates were present, reduced, or absent. **(1)** *P. simplex* Paul, 1971 was described as having no oral plates; **(2)** *P. wykoffi* (Miller 1891) was described as having six oral plates (O7 was misidentified as a facetal plate). *P. wykoffi* was later reassigned to *Osgoodicystis* to reflect the presumed systematic differences of those without oral plates (*Pentacystis*) and those with oral plates (*Osgoodicystis*). Oral plates of *P. wykoffi* are outlined in gray. Gonopore position indicated as black circles. P=Periproct. M=Mouth. Modified from Paul, 1971.

Figure 1.9. *Pustulocystis* and *Triamara*. **(1)***Pustulocystis pentax* (MUMG-T 266). Oral area shows the normal holocystitid oral area, with O1-O7 in the standard configuration. However, the lateral non-facet bearing facetal plates are absent leaving only facetals A-E. Gonopore visible on O7, hydropore slit straddles the suture between O1 and O6. **(2)** Side view. Theca elongate. Plates numerous and flat without depressed sutures. Theca narrows into holdfast. **(3)** *Triamara ventricosa* (UC5997). Oral area potentially shows a similar peristomial border plating pattern to holocystitids, but due to poor preservation, this cannot be confirmed. A ambulacrum absent; shared ambulacrum BC present, as well as D and E. D ambulacrum food grove bifurcates distally and terminates in two separate facets on top of facetal bearing plates. The position and number of the facets cannot be determined from this specimen. A crinoid holdfast is growing around the border of the periproct, which is separated from O7 by a thecal plate; **(4)** Side view. Theca proportionally large and elongate. Plates numerous and appear to represent two generations. Plates flat without impressed sutures. Theca narrows considerably into holdfast. Scale bar=1 cm.

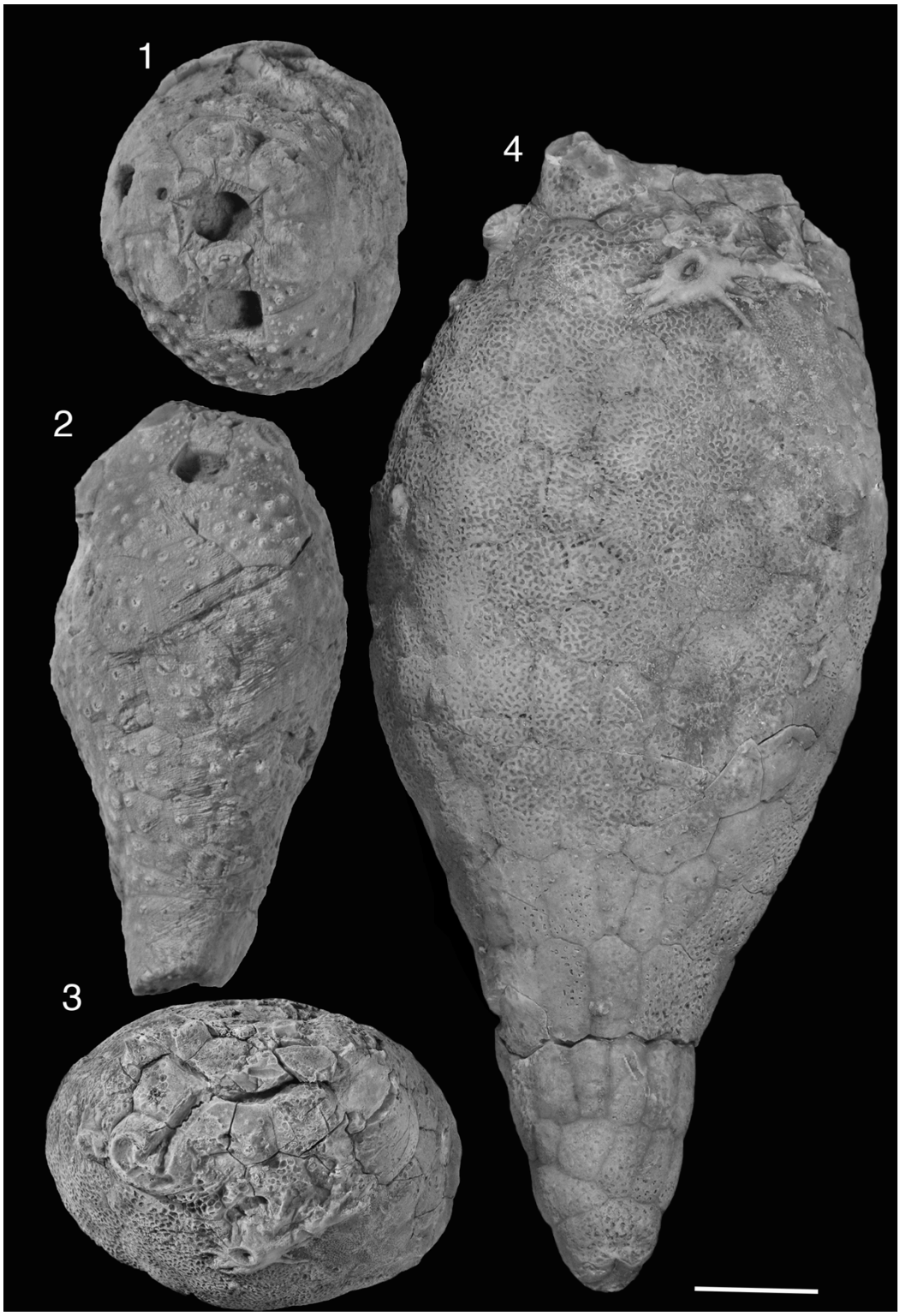


Figure 1.9 continued.

Table 1.1. Holocystitid taxa were delineated largely based on the inferred numbers of plates within each of the two circlets. The number of oral plates ranged from zero in *Pentacystis* to six in *Holocystites.* A revised analysis asserts that the changes in plate numbers are solely a taphonomic artifact. *Brightonicystis* was excluded from this study based on a lack of available material.

Taxon	Facetals (Frest et al. 2011)	Orals (Frest et al. 2011)	Facetals (Revised Interpretation)	Orals (Revised Interpretation)
Brightonicystis	10	10	Not included	Not included
Holocystites	8	6	7	7
Osgoodicystis	8	2-6?	7	7
Paulicystis	8	6	7	7
Pentacystis	8	0	7	7
Pustulocystis	6	6	Not included	Not included
Trematocystis	8	6	7	7
Triamara	Not included	Not included	Likely 7	7

Table 1.2. Specimens utilized in this study. SUI=University of Iowa; YPM=Yale Peabody Museum; CMCIP=Cincinnati Museum Center; AMNH=American Museum of Natural History; FMNH=Field Museum; UC=University of Chicago (note: all University of Chicago specimens are now reposited at The Field Museum); MUMG=Miami University Museum of Geology. Age and locality information are provided.

Taxon	Specimen Number	Age	Formation	Type
***Holocystites* Hall 1861**				
H. scutellus	SUI 48183	Middle Silurian	Osgood Formation	–
H. cylindricus	YPM 19175	Middle Silurian	Osgood Formation	–
H. winchelli	CMCIP 26438	Middle Silurian	Racine Formation	–
H. spangleri	SUI 48197	Middle Silurian	Osgood Formation	–
H. sp.	YPM 34764	Middle Silurian	Osgood Formation	–
H. sp.	YPM 526736	Middle Silurian	Osgood Formation	–
***Triamara* Tillman 1967**				
Triamara ventricosa	UC 5997	Middle Silurian	Osgood Formation	Holotype
***Paulicystis* Paul 1971**				
P. sparsus	SUI 48164	Middle Silurian	Osgood Formation	Holotype
***Trematocystis* Miller 1878**				
T. mangiporatus	SUI 48198	Middle Silurian	Osgood Formation	Holotype
***Pentacystis* Paul 1971**				
P. gibsoni	SUI 46316	Middle Silurian	Osgood Formation	Holotype
P. simplex	AMNH 020271A	Middle Silurian	Osgood Formation	Holotype

Table 1.2 continued.

Taxon	Specimen Number	Age	Formation	Type
***Osgoodicystis* Frest and Strimple 2011**				
O. bisetti	SUI 48166	Middle Silurian	Osgood Formation	Holotype
***Gomphocystites* Hall 1864**				
G. indianensis	FMNH 19708	Middle Silurian	Niagaran	–
***Eucystis* Angelin 1878**				
E. sp.	CMCIP 766	Middle Silurian	Bainbridge Formation	–

CHAPTER 2:
A REINTERPRETATION OF THE AMBULACRAL SYSTEM OF *EUMORPHOCYSIS* AND ITS BEARING ON THE EVOLUTION OF EARLY CRINOIDS

Abstract

Recent debates over the evolutionary relationships of early echinoderms have relied on evidence concerning morphological details of the feeding ambulacral systems. *Eumorphocystis*, a Late Ordovician diploporitan, has been a focus in these debates because it bears ambulacral features that show strong morphological similarity to early crinoid arms. Undescribed and well-preserved specimens of *Eumorphocystis* from the Bromide Formation (Oklahoma, USA) provide new data illustrating that composite arms supported by a radial plate and bearing a triserial arrangement of axial and extraxial components encasing a coelomic extension are not unique to crinoids, as previously reported. These features have not been previously observed in blastozoan echinoderms, although there is some similarity with middle Cambrian *Dibrachicystis*. Phylogenetic analysis indicates that shared features of *Eumorphocystis* and early crinoids are sister taxa, making these shared features homologous. This evidence suggests that crinoid arms were derived from a specialized blastozoan ambulacral system that lost feeding brachioles and strongly suggests that crinoids are nested within blastozoans.

Introduction

The evolutionary relationships of early Paleozoic echinoderms are poorly understood. This is especially apparent when considering the phylogenetic relationships of stemmed echinoderms, where arguments have not been resolved concerning whether the presence of a stem in these taxa suggests a

homology or homoplasy (Ausich et al., 2015). Early echinoderms diversified rapidly through both the Cambrian Explosion and the Ordovician Radiation, which resulted in high morphological disparity (Sprinkle, 1980; Sumrall and Waters, 2012). This high disparity is reflected by approximately 21 named taxonomic classes, but the true diversity of Echinodermata cannot be understood until phylogenetic relationships of the major groups are resolved.

The phylogenetic relationships of crinozoans to other echinoderm clades have been widely debated and many hypotheses have been proposed (e.g., Paul and Smith, 1984; Sumrall, 1997; Ausich, 1998; David et al., 2000; Guensburg and Sprinkle, 2007, 2009; Guensburg et al., 2010; Guensburg, 2012; Kammer et al., 2013; Ausich et al., 2015; Guensberg et al., 2016; O'Malley et al., 2016). A number of arguments against crinozoans and blastozoans sharing common ancestry have been made based on *a priori* assumptions of evolutionary morphological trends and the presence of "key" features having stronger significance in determining ancestry without quantifiable justification. Further, the majority of these arguments have not been presented within a rigorous phylogenetic context to test proposed relationships (Guensburg and Sprinkle, 1997, 2007, 2009; Guensburg et al., 2010).

Eumorphocystis Branson and Peck, 1940, a Late Ordovician glyptosphaeritid diploporitan, has been at the center of many recent debates concerning the evolutionary relationships of stemmed echinoderms. The unusual structure of the exothecal extensions of the feeding ambulacra of this taxon

bears striking resemblance to the arm structures of early crinoids (Parsley, 1982; Paul, 1988; Sumrall, 2010). Features shared by *Eumorphocystis* and early crinoids include: a triserial plate arrangement of the arms, a uniserial arrangement of the thecally derived plates on the outer portion of the arm, a single supporting thecal plate for the extension of the arm (herein referred to as a radial plate), and the presence of a coelomic canal. *A posteriori* testing of these features through rigorous phylogenetic analysis indicates that these features are homologous and do not represent homoplasy. In these analyses, *Eumorphocystis* shares a sister group relationship with early crinoids. Further analysis utilizing constrained trees indicates that early crinoids sharing a sister group relationship with edrioasteroids (Guensberg and Sprinkle, 2007, 2009; Guensberg et al., 2016) is less parsimonious and is therefore rejected.

Universal Elemental Homology

A common problem in echinoderm paleontology is that skeletal elements are often named based on location or function rather than evolutionary lineage. Such naming schemes often result in individual names being used for a variety of unrelated plate types across echinoderm groups; this is highlighted within the stemmed echinoderm group (see Sumrall and Waters, 2012 for a comprehensive list of problematic names for homologous skeletal elements across Paleozoic echinoderms). These issues act as a barrier when determining which skeletal elements are homologous to all echinoderms. As morphological characters for phylogenetic analysis are constructed as hypotheses of homology (Patterson,

1982; Sumrall, 1997), understanding homologous elements is of critical importance when trying to infer accurate evolutionary relationships.

Universal Elemental Homology (UEH) focuses on the ambulacral homology of the Carpenter system (Carpenter, 1884) with the homology of the plate types bordering the peristome and the ambulacral system (Sumrall, 2010; Sumrall and Waters, 2012; Kammer et al., 2013). This homology scheme is useful when identifying deep homologies within Echinodermata. The other leading homology scheme that is used for echinoderm phylogenetics, the Extraxial-Axial Theory (Mooi et al., 1994; Mooi and David, 1997, 1998, 2008; David et al., 2000) differentiates the echinoderm skeleton into two large categories: axial (skeletal parts associated with the mouth and ambulacral system) and extraxial (the body wall); UEH only refers to elements within the axial system (Sumrall, 2017).

For the purposes of this study, certain morphological terms are defined here. True arms are defined following Zamora and Smith (2011): those arms with a central lumen, or coelomic canal, which are directly connected to the theca. Guensberg et al. (2016) add to this definition, suggesting that arms also have both axial and extraxial skeletal components along with the coelomic canal. An erect ambulacrum is one that is not attached to the surface of the theca distally; this erect ambulacrum may or may not have an extension of the extraxial skeleton or brachioles.

Testing for Homology

Three tests can be performed to determine homology when describing scientifically valid characters (Patterson, 1982): similarity, conjunction, and congruence. Similarity and conjunction are performed *a priori*, whereas congruence is performed *a posteriori.* Similarity states that if two structures are similar in their fine details, then the hypothesis that the structures are homologous is not rejected. Conjunction states that if two structures in question are homologous, they cannot simultaneously appear in the same organism; if the organism possesses both, the structures are clearly not homologous and the hypothesis is rejected (Williams, 1993).

Congruence is tested after the analysis has been conducted; if the tree structure requires the evolution of the feature more than once in the resolved phylogenetic tree, it is not homologous and the hypothesis can be rejected (see Sumrall, 1997 for a thorough review of these homology tests and examples concerning echinoderm morphology).

Previous Arguments Concerning Blastozoan-Crinozoan Ancestry

Morphological arguments

Arguments against shared blastozoan and crinozoan ancestry have primarily focused on emphasizing differences between crinozoan and blastozoan morphology (e.g., Guensberg and Sprinkle, 2001, 2009; Guensberg et al., 2016).

However, these arguments were not made phylogenetically and were instead made by highlighting “key” features that drove the separation between the blastozoan and crinozoan groups. Guensberg et al. (2016) also asserts that superficial similarities between blastozoans and crinozoans are likely related to plesiomorphic pentaradial patterns of stemmed echinoderms, an argument that is not rooted in phylogenetic understanding, as it confuses the definitions of homology and homoplasy (Sumrall, 2017). In contrast, phylogenetic arguments are rooted in the discovery of suites of synapomorphies providing support for nodes within proposed evolutionary trees.

Previous arguments posit that crinozoans are likely derived from a Cambrian edrioasteroid ancestor (Fig. 1[2]; Guensberg and Sprinkle, 2001; Guensberg et al., 2016). Morphological evidence for this ancestry focuses on shared biserial floor plates lacking through-going pores and branched ambulacra in both edrioasteroids and crinoids. Further, Guensberg and Sprinkle (2001, 2009) argue that blastozoans have no extraxial components of the arms and lack coelomic canals, and emphasize differences in stem and thecal plating between crinozoans and blastozoans. However, these arguments mean little without rigorous phylogenetic analysis. *A priori* assumptions of evolutionary relationships

[2] All figures and tables are placed in Appendix II-I.

based on the presence or absence of features contradicts the nature of science and testing falsifiable hypotheses.

Stratigraphic Timing

The earliest crinoids appear in the Early Ordovician (the problematic Cambrian genus *Echmatocrinus* is not considered a crinoid in this analysis; Ausich and Babcock, 1998. See Sprinkle and Collins, 1998 for an alternative view), later than the first groups of blastozoans, which appeared in the middle Cambrian (Zamora et al., 2013). This difference in timing has been used as an argument against crinoids being nested within blastozoans. However, this argument is poorly constructed, as timing is consistent, and further, stratigraphy is not hereditable. The timing of crinoid origins is fully consistent with their placement within the blastozoan tree; numerous groups of blastozoans appear at the same time as the crinoids (e.g., all major groups of diploporitans; Kesling, 1967; Lefebvre et al., 2013) and new glyptocystitoid rhombiferans appear in the latest parts of the Cambrian (Zamora et al., 2016).

Further, it has been argued that because *Eumorphocystis* is a derived Late Ordovician taxon, it cannot possibly share ancestry with early crinoids (Guensberg et al., 2016). This argument ignores that Late Ordovician crinoids and *Eumorphocystis* are both derived from an earlier ancestor, which does not negate the possibility of a sister group relationship for eumorphocystitids and crinoids.

Materials and Methods

Repositories and institutional abbreviations

All specimens for this analysis are reposited in museum collections; a list of the taxa studied, specimen numbers, and museum repositories is located in Table 1. All studied specimens came from the following museum collections: University of Iowa Paleontology Repository (SUI); Paleontology Museum of Guizhou, China (GM); University of Oklahoma (OU); Cincinnati Museum Center (CMCIP).

Methods

To perform a phylogenetic analysis, a character matrix was constructed to include ten taxa and sixty-nine characters, of which 25 were parsimony-informative (character list located in Appendix II-II). Taxa selected included *Eumorphocystis* and a range of early crinoid, blastozoan, and edrioasteroids taxa; *Kalidiscus* was defined as the outgroup to polarize character state transformations (refer to Table 1). The matrix was analyzed utilizing PAUP* v. 4.0a147 (Swofford, 2003) utilizing both parsimony and maximum likelihood algorithms. A branch and bound search algorithm was used to uncover optimal trees and was computed via a stepwise function. All characters were unordered and equally weighted. Tree support was determined using bootstrap analysis and Bremer support (Felsenstein, 1985; Bremer, 1988).

A further constrained topology analysis was performed to test the veracity of the edrioasteroid origin of crinoids on the present matrix. The constrained tree topology forced crinoids (*Hybocrinus, Gaurocrinus,* and *Carabocrinus*) and edrioasteroids (*Edriophus*) to form a clade. All other taxa were reduced to a polytomy and *Kalidiscus* was used as the outgroup to polarize the matrix; code to perform this function in PAUP* v. 4.0a147 was added to the original nexus file (Appendix II-IV). This tree topology was explored in PAUP* v. 4.0a147 using the same analytical techniques as above.

Results

Phylogenetic Analysis

Both the parsimony and the likelihood analysis resulted a single most optimal tree with 83 steps .Two major clades were recovered; the first clade contains all crinoids (*Carabocrinus, Hybocrinus,* and *Gaurocrinus*) with *Eumorphocystis* as its sister taxon. This is well supported by bootstrap analysis, with the relationship of *Eumorphocystis* to crinoids having bootstrap support of 94%. The sister group relationship of *Gaurocrinus* to *Hybocrinus* and *Carabocrinus,* and the sister group relationship of *Hybocrinus* to *Carabocrinus* is also well supported, with bootstrap support values of 98% and 79%, respectively. The second clade contains rhombiferans *Hemicosmites* and *Cheirocrinus* sharing a most recent common ancestor with coronoid *Stephanocrinus* (with bootstrap support values of 74%). Eocrinoid *Gogia* and edrioasteroid *Edriophus* are most

distantly related to taxa within these two clades (Fig. 2). Synapomorphies for the recovered clade containing *Eumorphocystis* and crinoids are: (1) ambulacral system erect as composite structure; (2) presence of coelomic canal; and (3) presence of arm generating plate (radial plate).

Constraint Analysis

To test whether crinoids are closely related to edrioasteroids, an analysis was conducted that constrained tree topologies only to those that recovered a crinoid clade (*Carabocrinus, Hybocrinus,* and *Gaurocrinus*) as sister taxon to *Edriophus* (Fig. 3.1). One optimal tree was recovered with a tree length of 90 and a consistency index of 0.833 (Fig. 3.2). Other relationships (i.e., *Stephanocrinus* was sister taxon to rhombiferans) were retained.

Systematic Paleontology

Class DIPLOPORITA Müller, 1854

Order SPHAERONITIDA Neumayer, 1889

Family EUMORPHOCYSTIDAE Branson and Peck, 1940

Genus *Eumorphocystis* Branson and Peck, 1940

Eumorphocystis multiporata Branson and Peck, 1940

Figures 4.1, 4.2, 6.1, 7.1, 7.2, 7.3

Type.— *Eumorphocystis multiporata* Branson and Peck, 1940; 6757 University of Missouri.

Eumorphocystis multiporata Branson and Peck, 1940, p. 88-92, pl. 13

Regnellicystis typicalis Bassler, 1950, p. 276-277, p. 275, fig. 6-8

Strimplecystis oklahomensis Bassler, 1950, p. 277, p. 265, fig. 19

Description.— Theca, approximately 16mm in height and 13mm at the widest point, slightly globular to elongate oval shape with large number of irregularly arranged, polygonally-shaped plates (Fig. 7.1, 7.2); ambulacra arranged in 2-1-2 symmetry and oral plates each bear a high spine border the peristome; CD interray contains O1, with no evidence of O6 or O7; oral plates are non-diplopore bearing (Fig. 7.3). Primary peristomial cover plates are undifferentiated from the cover plate series; presence of either hydropore or gonopore is not discernable. Periproct located in CD interray, 0.25mm in diameter, in contact with oral plate in the CD interray, appears to be composed of numerous small plates; high taphonomic disarticulation prevents further detailed descriptions. Ambulacra divided into proximal recumbent portion and distal erect portion. Proximally, ambulacral floor plates are highly differentiated from cover plate series, wedge shaped, singly biserial and alternate with primary food groove along periradial suture; periradial suture follows a zigzag pattern across the theca. Floor plates non-diplopore bearing; brachioles are mounted in the center of each ambulacral

flood plate. Proximal food groove is covered by doubly biserial ambulacral cover plates; distal food groove is formed into erect, triserially-arranged arms (Fig. 7.3). Portion of arms are exothecally derived from a uniserial extension of the extraxial skeleton; entire arm is supported from a single non-diplopore bearing thecal plate at the base of the arm connecting with the uniserial extraxial plates (Fig. 7.1). Uniserial plates are overlain by singly biserial ambulacral floor plates. The union of biserial ambulacral floor plates and uniserial exothecally-derived plates is pierced by lumen that runs throughout the appendage and pierces the theca. Brachiole plates articulate directly to short, equant ambulacral floor plates; brachioles extend from the main food groove and attach to the center of a single floor plate via a short, narrow groove. Uniserial brachioles alternate from left and right along main food groove; first brachiole extending from each ambulacrum is on the left side. Total length of distal ambulacra unknown (Fig. 7.3).

Thecal plates irregularly shaped, typically five or six-sided with roughly equal suture lengths, though the plates vary widely with respect to size. The largest thecal plates, presumably primary generation of plates, are typically between 1.0-1.5 mm in diameter, whereas presumably secondary generation plates are typically between 0.25-0.5 mm in diameter; smaller plates typically roughly quadrangular. The surfaces of the plates are not marked with pits or granulose textures and without evident growth lines; new plates are irregularly added anywhere within the thecal plating. Ridges running horizontally, vertically, and diagonally radiate from each arm (three from each arm) across the theca

(Fig. 7.1). Ridges run from plate center to plate edge and are much higher towards center of the plate than at the edge. The thecal plates are noticeably convex and are arched towards the center of the plate; the sutures between the plates are clearly defined and deeply depressed in all places not marked by taphonomic overprint. Diplopores are simple paired perpendicular canals within very shallow elliptical peripore; average distance between the perpendicular canals is 0.5 mm; average diameter of the pores is 0.2 mm. Each pair of perpendicular canals enters the coelom separately. The diplopores are irregularly clustered, generally within the plate center; some diplopores cross plate sutures, most commonly in conjunction with smaller plates.

Basals, 4, large, equal-sized, non-diplopore bearing; average basal height is 1.5 mm, average width is 3mm. Basals have thickened ridge around base of attachment structure (Fig. 7.2). Only proximal portion of stem is known, preserved length 4.2 mm, circular in cross section with proportionally small circular lumen piercing the center (approximately 0.2 mm in diameter). No crenulae present. Holomeric stem comprises two distinct alternating columnal sizes, one that is approximately twice as tall as the other (Fig. 7.1).

Occurrence-Upper Ordovician; Bromide Formation of Oklahoma.

Discussion

Ambulacral Systems of Eumorphocystis and Early Crinoids

The arms of early crinoids and *Eumorphocystis* are here interpreted as homologous structures based on the three tests of homology presented by Patterson (1988): similarity, conjunction, and congruence. *Eumorphocystis* arms (Fig. 4.1, 4.2) comprise a triserial plate arrangement: (1) a uniserial, extraxial component of brachial plates on the outer edge of the arm, composed solely of non-pore bearing plates derived from the theca; this plate series is supported on all five arms by a single non-pore bearing thecal plate, which is homologous to the radial plate of a crinoid; (2) singly biserial, axial floor plates that form the food grove and provides mounting facets for food gathering brachioles; and (3) axial ambulacral cover plates that overlay the floor plates and protect the food groove. The biserial floor plates and the uniserial brachial plates encapsulate a coelomic canal that extends from the end of the erect arm and pierce the theca.

This triserial arrangement of *Eumorphocystis* described above is nearly identical to that of a protocrinoid's (Fig. 5.1, 5.2). The triserial arrangement of a protocrinoid arm is as follows: (1) extraxial brachial plates derived from the theca, supported by a radial plate; (2) biserial, axial ambulacral floor plates; and (3) axial ambulacral cover plates. As is with *Eumorphocystis,* the coelomic canal of a protocrinoid is encapsulated between the brachial plates and the ambulacral floor plates. While Guensberg et al. (2016) interpret blastozoans as lacking extraxial

brachial plates, it is clear that *Eumorphocystis* does indeed have a triserial arrangement with thecally derived (extraxial) brachial plates (Fig. 4.1, 4.2).

There are some notable construction differences between the ambulacral systems of early crinoids and eumorphocystitids; this analysis does not take the position that every element of the axial skeleton is entirely similar. The proximal food grooves of *Eumorphocystis* are developed on alternating biserial plates (Fig. 6.1). In *Carabocrinus*, the proximal food grooves are confined to the oral plate sutures and presumed soft anatomical structures that extend over the coelomic canal (Fig. 6.2). The coelomic canal of *Eumorphocystis* perforates the thecal wall at the junction between the proximal ambulacral floor plates and plating of the thecal wall (Fig. 4.1, 4.2), whereas in early crinoids, such as *Carabocrinus,* the coelomic canal perforates the thecal wall at the junction between the oral plates and the thecal wall (Fig. 6.2). This is effectively the same place because most crinoids lack calcified floor plates and those taxa that bear them, such as protocrinoids (Guensberg and Sprinkle, 2009; Guensberg, 2012; Guensberg et al., 2016), the position of the coelomic canal is identical to that seen in *Eumorphocystis*. Furthermore, the presence of a small plate series on the proximalmost arm between the floor plates and the brachial plates is consistent among these taxa.

The most significant difference between eumorphocystitid and the early crinoid ambulacral systems is that *Eumorphocystis*, like all non-crinozoan blastozoans, have brachioles for feeding. However, it is not unreasonable to

consider that early crinozoans lost brachioles much the same way that crinozoans also lost their ambulacral floor plating series in more derived forms (Guensberg et al., 2016). Further, crinoids have also re-evolved biserial pinnules for feeding more than once, within the cladid, disparid, and camerate clades (Ausich, 1988).

Phylogenetic Analysis

The phylogenetic analysis presented in this study is an *a posteriori* test of the hypothesis that arm features of early crinoids and eumorphocystitid arms are homologous structures. As is indicated by the resulting optimal tree, the most parsimonious explanation of the arm features present in both groups of taxa is that the structures are homologous. This analysis corroborates a growing number of phylogenetic analyses that place crinozoans within the larger blastozoan clade utilizing solely morphological data (Paul and Smith, 1984; Sumrall, 1997), as well as an analysis utilizing preserved organic molecules (O'Malley et al., 2016). Arguments that have been previously made against crinozoans being nested within blastozoans are not made utilizing a phylogenetic analysis to test the assertions being made and are not supported by morphological or molecular evidence (David et al., 2000; Guensberg and Sprinkle, 2001, 2009; Guensberg et al., 2016).

The constraint analysis further tests this model by determining whether the crinoids derived from edrioasteroid model (Guensberg and Sprinkle, 2001, 2009;

Guensberg et al., 2016) is viable on the current matrix (Appendix II-II) Constraining the tree morphologies to only those consistent with the edrioasteroid model resulted in a tree that was considerably less parsimonious by an extra seven steps, which indicates that crinozoans being rooted within edrioasteroid ancestry is not well-supported by current data; other relationships, such as *Stephanocrinus'* sister group relationship to rhombiferans, is still supported in the constraint analysis. Based on these results, we reject the edrioasteroid origins of crinoids model.

Conclusions

This study demonstrates that understanding the homologous elements of echinoderm skeletons is critical towards understanding evolutionary relationships. *Eumorphocystis*, a Late Ordovician diploporitan echinoderm, shares homologous arm structures with early crinoids; both have a triplate arm comprising both extraxial and axial skeletal components, a coelomic canal, and a radial plate that supports the arm. *A posteriori* testing of whether these features are homologous indicate that they are, indeed, homologous.

Results presented here strongly suggest that crinozoans are rooted within blastozoans; this hypothesis is supported by rigorous phylogenetic analyses and adds to the growing number of published phylogenetic studies that have reached similar conclusions (e.g., Sumrall, 1997; Ausich et al., 2015; O'Malley et al., 2016). Further, the other leading hypothesis, that crinoids and edrioasteroids

share common ancestry (e.g., Guensberg and Sprinkle 2007, 2009; Guensberg et al., 2016), is not supported by the data, as a constraint tree indicates that this is much less parsimonious than blastozoans and crinozoans sharing common ancestry.

This study is part on an ongoing effort to place early Paleozoic echinoderms within an evolutionary framework. Many groups of these echinoderms are likely not monophyletic and the homologies of taxa within them need to be reinterpreted in order to place them within a phylogenetic analysis. In particular, the validity of diploporitan monophyly has been questioned by several authors (e.g., Paul, 1988; Sumrall, 1997; Lefebvre et al., 2013; Sheffield and Sumrall, 2015) because of wide morphological disparity present in the feeding ambulacral systems, theca, and attachment structures of taxa. By placing the diploporitans within a testable evolutionary framework, it can be determined if they represent one, natural group, or if they should be dispersed throughout the larger echinoderm tree of life.

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Appendix 2-1

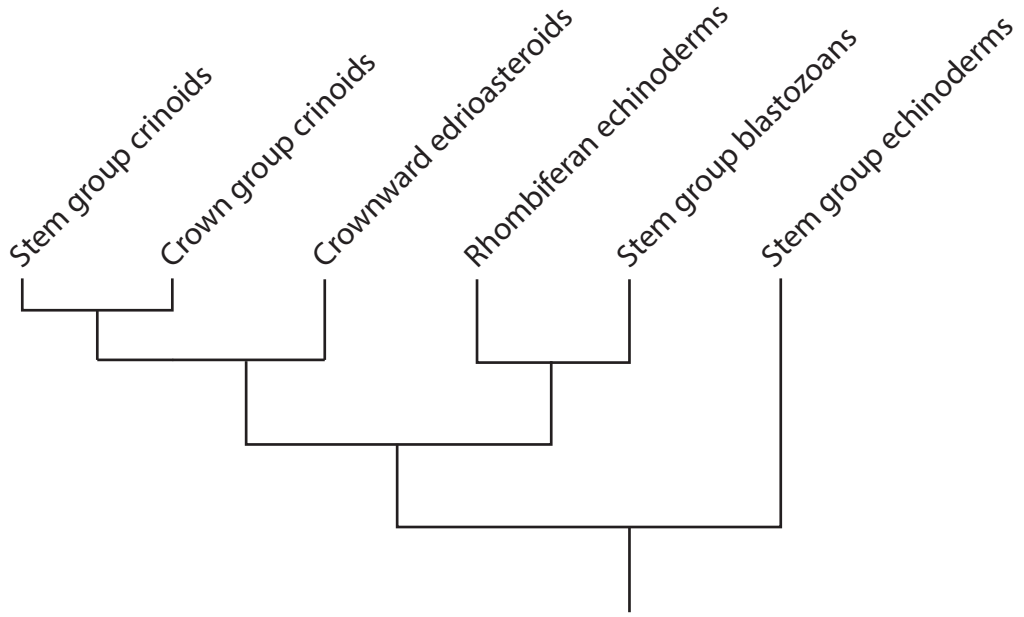


Figure 2.1. Proposed evolutionary relationships of crinoids and edrioasteroids. Previous arguments place edrioasteroids as sister taxa to crinoids, based on presumed shared branched ambulacra and shared biserial floor plates lacking through-going pores (modified from Guensberg and Sprinkle, 2001).

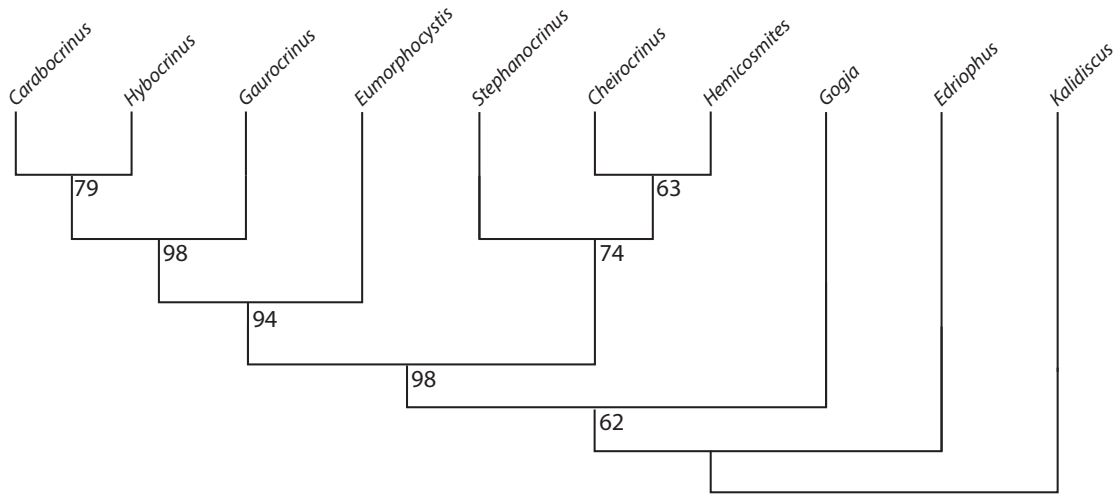


Figure 2.2. Optimal tree recovered from this study; *Eumorphocystis* is sister taxon to crinoids; well-supported by bootstrap analysis (support value of 94); *Stephanocrinus* is sister taxon to rhombiferans, *Hemicosmites* and *Cheirocystis* (support value of 74). Tree length=83, CI=0.914.

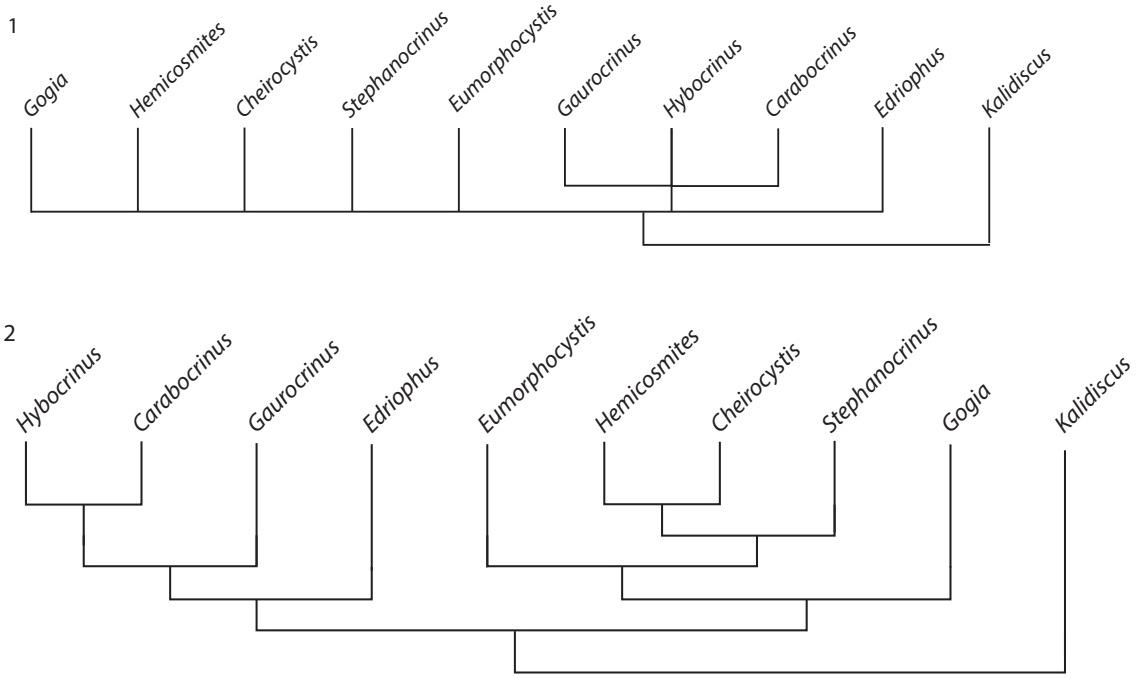


Figure 2.3. Constraint tree topology, forcing edrioasteroids and crinoids to be sister taxa. **(1)** Constraint topology, forcing crinoids and *Edriophus* to be a clade. All other taxa were reduced to a polytomy and the matrix was polarized using *Kalidiscus* as the outgroup. **(2)** Most optimal tree within the topological constraints enforced. This phylogenetic hypothesis, proposed by Guensberg and Sprinkle (2001, 2009) is significantly less parsimonious than the one presented in this study. Tree length=90; CI= 0.833.

Figure 2.4. Arm morphology of *Eumorphocystis multiporata.* **(1)** Radial view of erect arms of *E. multiporata*. **(2)** Radial view of erect arms of *E. multiporata* with triserial arm arrangement interpretation. Blue= uniserial, extraxial brachial plates derived from thecal plates, with supporting radial plate initiating the series. Green= singly biserial, axial ambulacral floor plates. Tan= axial ambulacral cover plates. Red= oral plates. Note the coelomic canal that is encompassed between the brachial plates and the ambulacral floor plates. Scale= 0.5cm.

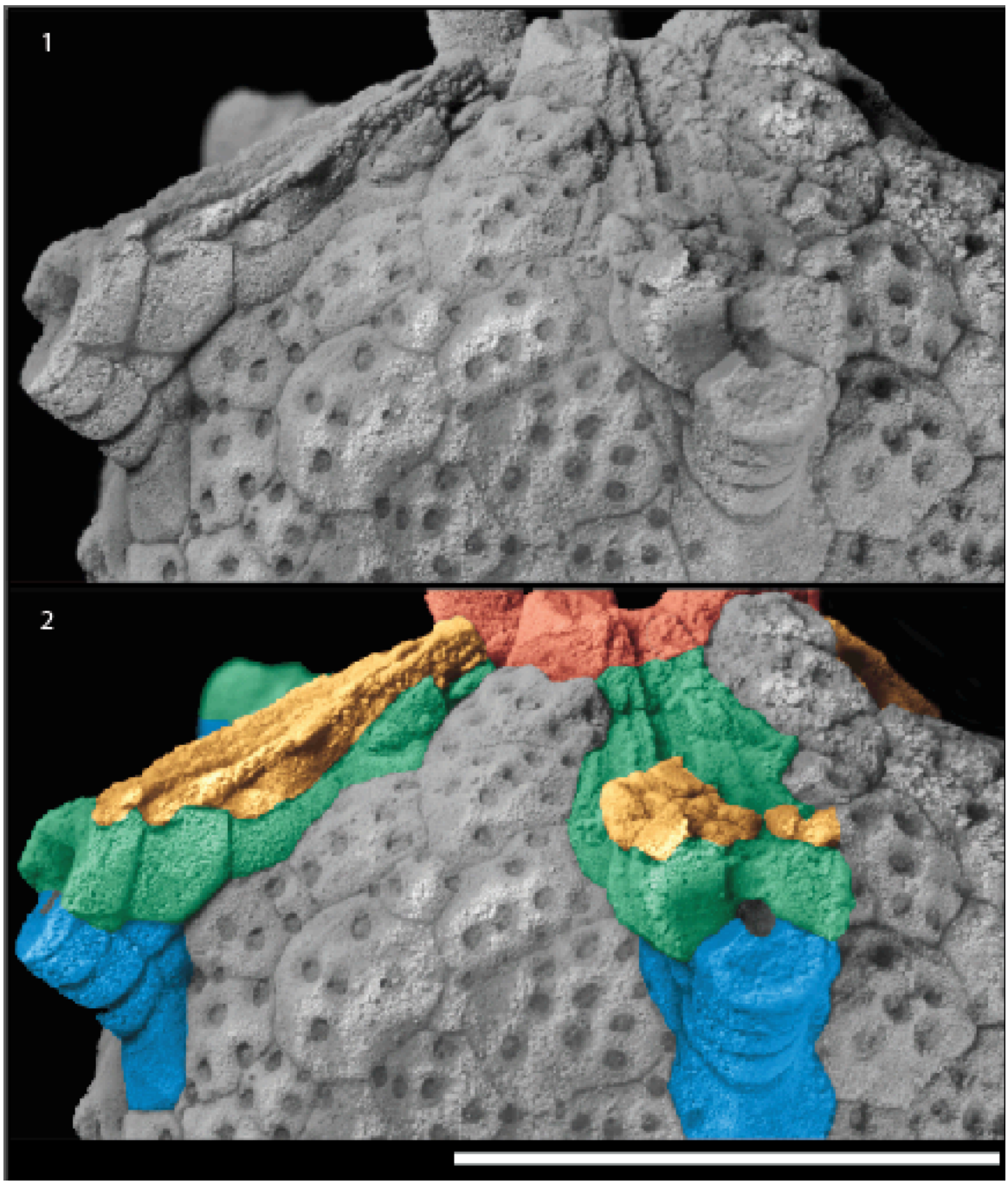


Figure 2.4 continued.

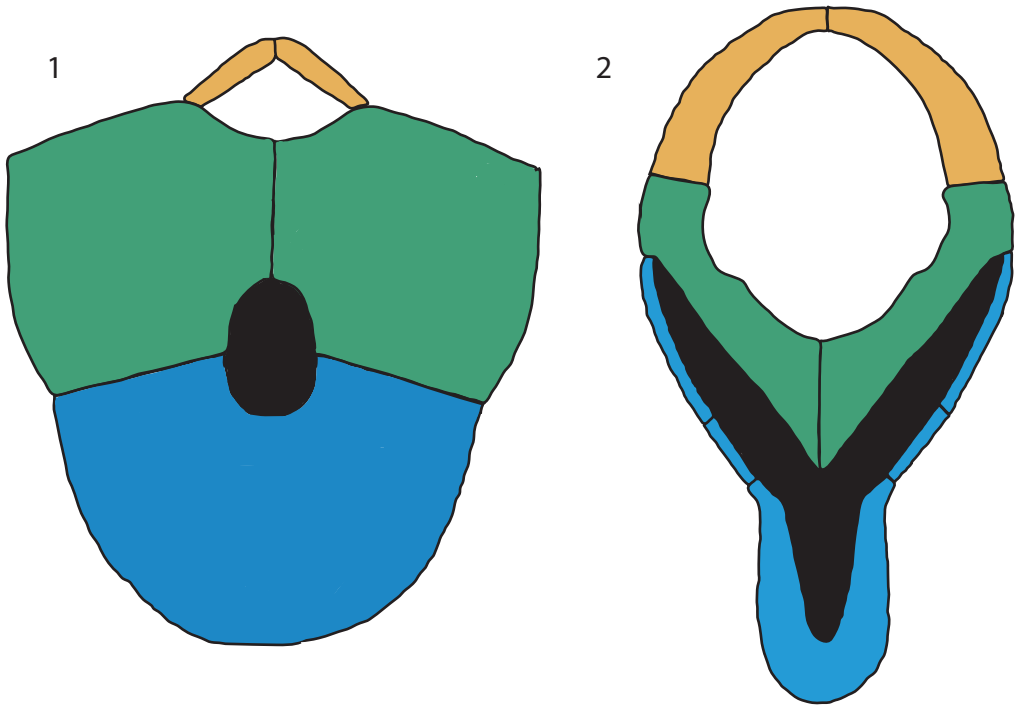


Figure 2.5. Triplate arm arrangements of *Eumorphocystis* and an early crinoid are homologous with one another; these cross sections show extraxial thecally-derived brachial plate (blue), axial, biserial ambulacral floor plates (green), and axial ambulacral cover plates (tan). Coelomic canal colored black. **(1)** Cross section of *Eumorphocystis* arm. **(2)** Cross section of early crinoid arm (modified from Guensberg et al., 2016).

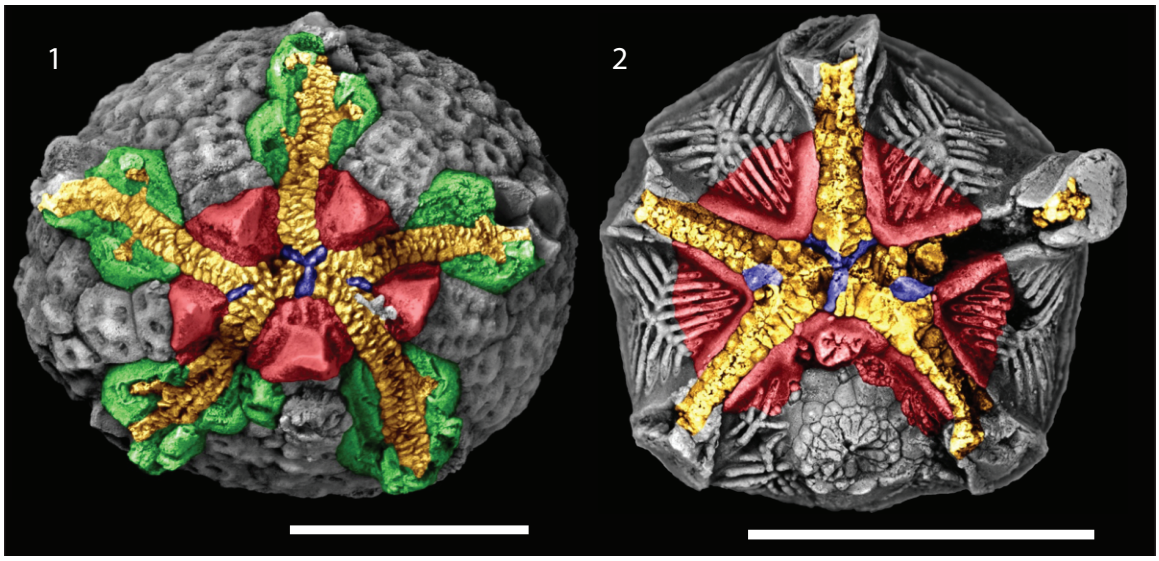


Figure 2.6. Constructional differences between *Eumorphocystis* and early crinoids **(1)** The proximal food grooves of *Eumorphocystis* are developed on alternating biserial plates (SUI 97598). **(2)** The proximal food grooves of *Carabocrinus* are confined to the oral plate sutures (OU 9127). Note that the coelomic canal perforates the body at the edge of the oral summit at the edge of the oral plate series. Red= oral plates. Blue= primary peristomial cover plates. Tan= ambulacral cover plates. Green= ambulacral floor plates. Scale= 5mm (Modified from Kammer et al., 2013).

Figure 2.7. *Eumorphocystis multiporata* (SUI ea74). **(1)** Radial side view; Theca globular to elongate with numerous, irregular plates. Plates are convex and raised ridges run across the center of many of the plates. Distal arms branch exothecally and are supported by single non-diplopore bearing thecal plate. Distal end narrows into four equal-sized basal plates that form around stem. Stem holomeric, with two distinct columnal sizes, one being twice as high as the other. **(2)** View of stem; stem has a circular and proportionally small lumen. Stem lacking crenulae. **(3)** Oral view; five ambulacra branch from the mouth. Primary food grove lies down on periradial suture; short grooves leading from the primary food groove end in brachiole facets that are attached in the center of single ambulacral floor plates, alternating from the left and right side of the primary food groove, with the first brachiole facet branching on the left. Total length of ambulacra unknown. Scale bar= 1cm.

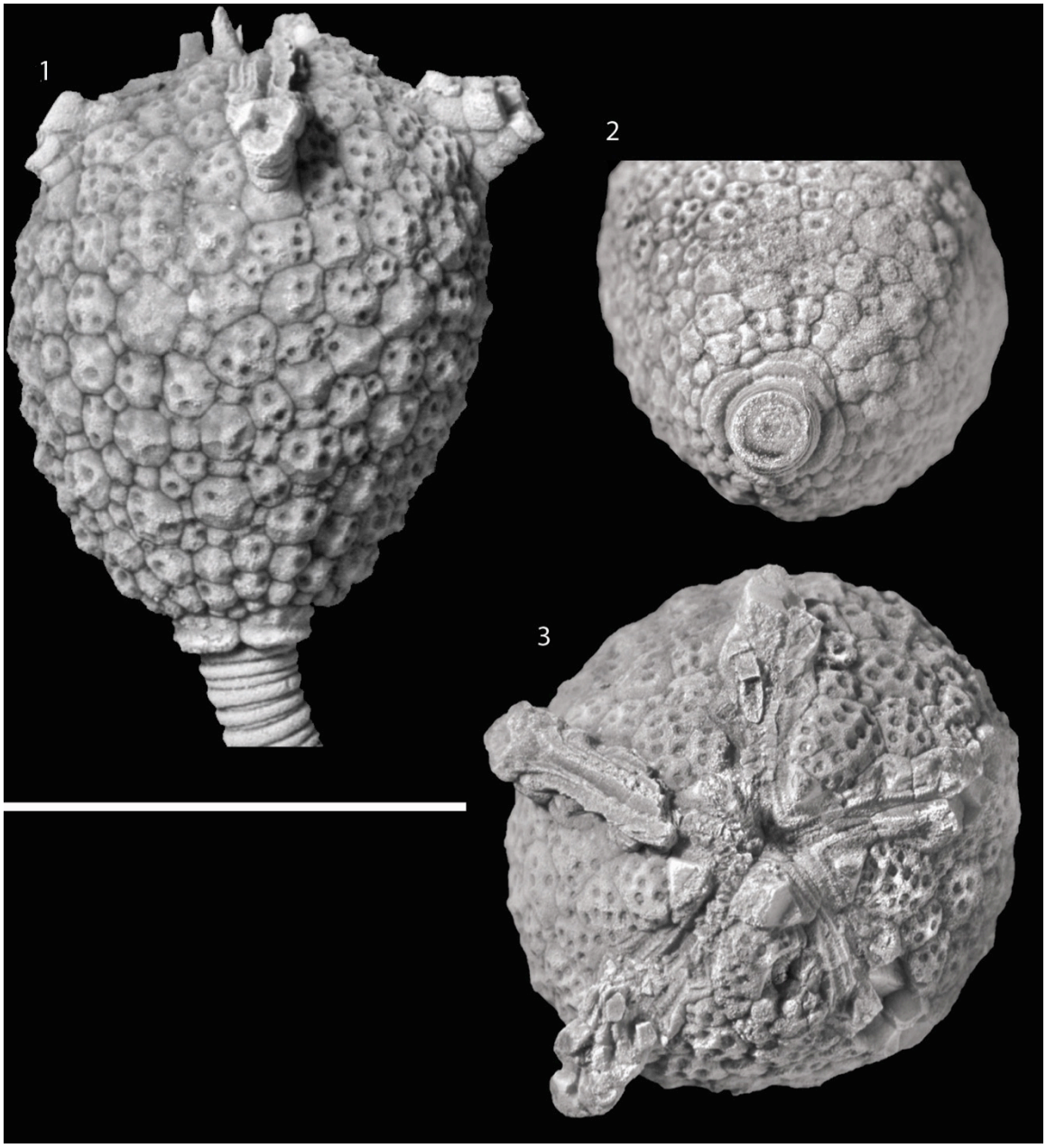


Figure 2.7 continued.

Table 2.1.Specimens utilized in this study. SUI=University of Iowa; USNM= United States National Museum; OU= University of Oklahoma; CMCIP=Cincinnati Museum Center; PMO= Natural History Museum, University of Oslo; GM= Paleontology Museum of Guizhou University, China; SUI= University of Iowa; NHMUK= Natural History Museum, London, United Kingdom

Taxa	Specimen Number
Eumorphocystis multiporata Branson and Peck, 1940	SUI 97598
Gogia sp.	USNM 553409
Cheirocystis fultonensis Sumrall and Schumacher, 2002	CMCIP 50403
Hybocrinus nitidus Sinclair, 1945	OU 9179
Gaurocrinus nealli (Hall, 1866)	NHMUK E14942
Stephanocrinus gemmiformis Conrad, 1842	SUI 134869
Kalidiscus chinensis Zhao et al., 2010	GM 2103
Edriophus levis Bather, 1914	CMCIP 40480
Rhopalocystis destombesi Ubaughs, 1963	PMO A29122
Carabocrinus treadwelli Sinclair, 1945	OU 9127

Appendix 2-2

Explanation of Characters

1. 0: Oral frame plates proximal to the peristome and separate the peristome from the oral plates absent. 1: Oral frame plates present.
2. 0: Shape of the theca near the stem facet is circular. 1: Triangular in shape. 2: Square in shape.
3. 0: Interambulacral plating (plate series between ambulacra on the oral surface) present. 1: Interambulacral plating absent.
4. 0: Absence of stem (plated columnal with plates stacked on top of one another) from theca. 1: Presence of stem.
5. 0: Region surrounding the periproct (anus) not elevated. 1: Periproctal region elevated.
6. 0: Nature of interambulacral plating is imbricate (following a certain directionality). 1: Tessellate (multiplated without directionality)
7. 0: Ambulacra do not branch on the oral surface. 1: Ambulacra do branch on the oral surface.
8. 0: Stem is attached to holdfast as an adult. 1: Stem is automized from holdfast as an adult.
9. 0: Plating of the holdfast is multielemental. 1: Plating of the holdfast is a single element. 2: Holdfast is cemented. 3: Thecal base is cemented
10. 0: Sessile (unable to change locations as an adult). 1: Vagrant (able to change locations as an adult).
11. 0: Oral plates absent. 1: Oral plates present

12. 0: Plate series proximal to mouth is oral plate series. 1: Plate series proximal to mouth is oral frame plate series. 2: Plate series proximal to mouth is adradial floor plate series.
13. 0: Posterior oral plates (oral plates within CD interray) O1, O6, and O7 present. 1: Only O1 and O6 present. 2: Only O1 and O7 present. 3: Only O1 present.
14. 0: Oral plates are flush with the oral surface. 1: Oral plates are spinous and rise above oral surface. 2: Oral plates are blade-shaped and rise above oral surface.
15. 0: Oral plates relatively small. 1: Oral plates relatively large.
16. 0: O2 and O5 from oral plate series are missing. 1: O2 and O5 from oral plate series are present.
17. 0: Peristome bordered by O2 and O5 (i.e., in contact with O2 and O5). 1: Peristome not bordered by O2 and O5 (i.e., not in contact with O2 and O5).
18. 0: Brachiole facets are located on oral plates. 1: Brachiole facets are not on oral plates.
19. 0: Peristome exposed on the oral surface of the theca. 1: Peristome is subtegmenal, and not exposed at the surface.
20. 0: Primary peristomial cover plates are differentiated from other cover plates in the ambulacral area. 1: Primary peristomial cover plates are

absent. 2: Primary peristomial cover plates are undifferentiated from other cover plates in the ambulacral area.

21. 0: Adambulacral floor plates present. 1: Adambulacral floor plates absent.
22. 0: Suturing of adambulacral floor plates to one another is biserial. 1: Suturing of adambulacral floor plates to one another is uniserial.
23. 0: Biserially arranged transverse ridges in food grooves absent. 1: Biserially arranged transverse ridges in food grooves present.
24. 0: Main food grooves extend on outer floor plates. 1: Main food groves extend extend on inner floor plates. 2: Main food grooves extend on thecal plates without floor plates. 3: Main food grooves extend onto thecal plate interiors without floor plates.
25. 0: Adambulacral pores absent in the food groove. 1: Present. 2: Present as podial ba-sins.
26. 0: Absence of secondary abradial floor plates. Presence of secondary abdradial floor plates.
27. 0: Ambulacral floor plates structurally forming part of the thecal wall. 1: Ambulacral floor plates are lying epithecally on theca and do not form part of the wall.
28. 0: Brachioles present. 1: Brachioles absent.
29. 0: Brachiole facets born on center of abambulacral plates. 1: Brachiole facets born from between abambulacral floor plates. 2: Brachiole facets born from abambulacral primary and secondary floor plate pairs. 3:

Brachiole facets born from thecal plates without floor plates. 4: Brachiole facets born from oral frame plate sutures. 5: Brachiole facets born from oral plates. 6: Brachiole facets arise from adambulacral floor plates.

30. 0: Brachioles are not coiled. 1: Brachioles are coiled.

31. 0: Brachiole plating is gracile (small). 1: Brachiole plating is robust (larger).

32.0: Shared ambulacra (BC, DE) do not bear brachiole facets. 1: Shared ambulacra do bear brachiole facets.

33. 0: First brachiole of the distal ambulacra branches on the left. 1: First brachiole of the distal ambulacra branches on the right.

34. 0: Brachioles found on both sides of ambulacra. 1: Brachioles restricted solely to the left side of ambulacra.

35. 0: Brachioles are plated biserially. 1: Brachioles are uniserial.

36. 0: Periproct is located between C and D ambulacra (within CD interray). 1: Periproct located between B and C ambulacra (within BC interray). 2: Periproct located at aboral pole.

37. 0: Periproctal membrane absent. 1: Periproctal membrane present.

38. 0: Stem present. 1: Stem absent.

39. 0: Proximal stem width is not greatly expanded with respect to distal stem. 1: Proximal stem width is greatly expanded with respect to distal stem.

40: 0: Plating of the proximal stem is irregular. 1: Plating of the proximal stem is polymeric. 2: Plating of the proximal stem is holomeric.

41. 0: Proximal stem does not have alternating inner and outer columnals. 1: Proximal stem does have alternating inner and outer columnals.

42. 0: Spiraling pivot points on proximal stem are absent. 1: Spiraling pivot points on proximal stem are present.

43. 0: The base of the theca and the stem are not clearly delineated (demarked) from one another. 1: The base of the theca and the stem are clearly delineated from one another.

44. 0: Stem facet is located at the aboral pole (opposite the oral area). 1: Stem facet is located in the area between the B and C ambulacra.

45. 0: Lumen of the stem is relatively large (meaning, mostly hollow) and comprises more than 75% of the total stem diameter. 1: Lumen of the stem is relatively small (not hollow) and comprises less than 75%

46. 0: Stem lumen is circular. 1: Stem lumen is Pentagonal. Stem lumen is triangular.

47. 0: Distal columnals of the stem are of relatively similar thickness (which are thin). 1: Distal columnals are thick and barrel shaped, longer than wide.

48. 0: Oral plates border the periproct on one side. 1: Only interambulacral plates border the periproct. 2: Only thecal plates border the periproct. 3: Both interambulacral and thecal plates border the periproct. 4: Tegmanal plates border the periproct.

49. 0: Distal ambulacra are recumbent against the theca. 1: Distal ambulacra are erect as floor plates. 2: Distal ambulacra are erect as composite structures of multiple plate types.

50. 0: Distal ambulacra do not branch. 1: Distal ambulacra do branch.

51: 0: Coelomic canal absent. 1: Coelomic canal present.

52. 0: Coelomic canal pierces the edge of oral plates. 1: Coelomic canal pierces theca subtegmenally. 2: Coelomic canal pierces the theca.

53. 0: Plates of the theca are irregular. 1: Plates are arranged in blastoid configuration. 2: Plates are arranged in glyptocystitid condition. 3: Plates are arranged in hemicosmitoid condition.

54. 0: Lateral ambulacra (B, C, D, and E) branch. 1: Lateral ambulacra do not branch.

55. 0: Primary peristomial cover plates are undifferentiated with respect to other cover plates and are the same size. 1: Primary peristomial cover plates are larger than other cover plates.

56. 0: Shared cover plates (between lateral ambulacra) present. 1: Shared cover plates present.

57. 0: Cover plates present. 1: Cover plates absent.

58. 0: Cover plate plating is multi-tiered. 1: Cover plate plating is biserial.

59. 0: Hydropore absent. 1: Hydropore located in oral plates. 2: Hydropore located in interambulacral plates.

60. 0: Gonopore absent. 1: Gonopore located in oral plates. 2: Gonopore located in interambulacral plating. 3: Gonopore located in thecal plating.

61. 0: Hydropore and gonopore have separate openings and are not combined. 1: Hydropore and gonopore have confluient openings and are combined.

62. 0: Basals absent or undifferentiated from other thecal plates. 1: One basal plate. 2: Three basals with paracrinoid configuration. 3: Three basals with blastoid configuration. 4: Three equally sized basals. 5: Four basals in glyptocystitid condition. 6. Four basals in hemicosmitoid condition. 7. Four equally sized basals. 8. Five equally sized basals.

63. 0: Arm generating plate (radial plate) absent. 1: Arm generating plate present.

64. 0: Exothecal portion of the composite arm structure (axial and extraxial components) is not incorporated into the wall of the theca. 1: Exothecal portion of the composite arm structure is incorporated into the wall of the theca.

65. 0: No line of radially positioned thecal plates below or along each ambulacrum. 1: Line of radially positioned thecal plates below or along each ambulacrum present.

66. 0: Epispires (exothecal respiration structures, comprising a single pore) are absent. 1: Epispires are present.

67. 0: Epispires are not covered. 1: Epispires are covered with platelets. 2: Epispires are covered with a layer of stereom.

68. 0: Diplopores (exothecal respiration structures, comprising a double pore system) absent. 1: Diplopores present.

69. 0: Endothecal respiratory structures absent. 1: Catispires (parablastoid condition) present. 2: Hydrospires (blastoid condition) present. 3: Pectinirhombs (glyptocystitoid condition) present. 4: Cryptorhombs (hemicosmitoid condition) present. 5: Goniospires present. 6. Corrugated plate margins present. 7. *Carabocrinus*-like condition.

Appendix 2-3

Character Codings

1. *Carabocrinus*: 0 1 0 0 – 0 0 ? 0 ? 1 0 ? 0 0 ? 0 0 1 - - 0 - - 0 - - - - - - 0 1 0 0 0 0 1 0 1 0 1 1 0 0 0 0 1 1 – 1 0 1 0 – 0

2. *Hybocrinus*: 0 1 0 0 – 0 0 ? 0 ? 1 0 ? 0 0 ? 0 0 1 - - 0 - - 0 - - - - - - - 0 1 0 0 0 0 1 0 1 0 0 1 0 0 0 0 1 1 – 1 0 1 0 – 0

3. *Gaurocrinus*: 0 1 0 0 – 1 1 – 0 ? ? ? ? ? ? – 1 ? 1 - - 0 - - 0 - - - - - - - 0 0 0 0 0 0 1 0 1 ? 1 1 0 0 ? 0 ? ? – 1 1 1 0 – 0

4. *Eumorphocystis*: 0 1 0 0 – 0 ? ? 0 ? 1 0 ? 0 0 1 0 0 1 – 0 0 0 0 1 0 0 0 0 0 0 1 0 0 0 0 0 0 1 0 1 0 0 1 0 0 0 0 1 ? ? 0 0 0 0 - 1

5. *Hemicosmites*: 0 1 0 0 – 0 ? ? 0 ? 1 0 ? 1 – 0 0 0 1 - ? 0 1 – 1 2 0 0 1 0 0 ? 0 0 0 0 0 0 1 0 1 0 0 0 1 0 0 0 1 1 0 0 ? 0 0 - 0

6. *Stephanocrinus*: 0 1 0 0 – 0 0 ? 0 ? 1 0 ? 0 0 0 0 0 1 - ? 0 1 – 1 2 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 ? 0 0 0 1 1 0 1 1 ? 0 ? 0 0 - 0

7. *Cheirocrinus*: 0 1 0 0 – 0 1 – 1 ? 1 0 ? 0 1 0 0 0 1 – 1 0 1 0 1 2 0 0 1 0 0 0 1 1 0 1 1 1 1 0 0 1 0 0 0 0 0 0 1 1 0 0 ? 0 0 - 0

8. *Gogia:* 1 0 0 0 1 0 0 0 0 ? 0 1 ? - - - 0 0 0 ? ? 0 - - 1 ? ? 0 0 ? 0 0 0 0 0 0 - - 0 0 1 – 0 0 0 0 0 0 1 2 ? 0 ? 0 1 1 0

9. *Kalidiscus*: 1 0 1 0 1 0 – 0 0 – 1 1 ? 0 - - 0 2 0 0 0 1 0 0 0 - - - - - - - 0 0 1 - - - - - - - 0 0 0 – 0 0 0 2 0 0 ? – 0 – 0

10. *Edriophus*: 1 0 1 0 1 0 – 0 0 ? 1 1 ? 0 - - 0 0 1 – 0 1 0 0 0 - - - - - - - 0 0 1 - - - - - - - 0 0 0 0 0 0 1 1 1 0 ? – 0 - 0

Appendix 2-4

Code for constraint analysis in PAUP*

```
TREE Default_symmetrical = (((1,2),(3,(4,5))),((6,7),(8,(9,10))));
        TREE Default_bush = (1,2,3,4,5,6,7,8,9,10);
        TREE Default_ladder = (1,(2,(3,(4,(5,(6,(7,(8,(9,10)))))))));
```

CHAPTER 3:
THE PHYLOGENY OF DIPLOPORITA (BLASTOZOA: ECHINODERMATA)

Abstract

The phylogenetic relationships of Paleozoic blastozoan echinoderms are poorly understood and many of the traditionally ascribed groups are likely polyphyletic. The diploporitan blastozoans, those echinoderms with double pore (diplopore) respiratory structures, have never been placed within a rigorous phylogenetic framework and their highly variable morphologies suggest that they do not represent a natural clade. The phylogenetic analysis utilizing maximum parsimony presented here, spanning a wide range of morphologies present in Diploporita, indicated a polyphyletic grouping for diplopore-bearing blastozoans and suggests that diplopore respiratory structures have likely evolved more than once within the echinoderm tree of life. A constraint analysis was performed to compare the original groupings of diplopore-bearing taxa against the results in this study; results of the constraint analysis indicate that a single diplopore-bearing clade is less parsimonious than multiple diplopore-bearing clades. These results further refine understanding the echinoderm tree of life.

Introduction

Blastozoans, a highly diverse group of Paleozoic echinoderms, are an integral component of marine communities during critical times of Earth's history (Foote, 1992). Blastozoans lived through times of dramatic climate change, such as the Ordovician, and their diverse morphologies are likely reflecting responses to changing environments (Lefebvre et al., 2013). However, the phylogenetic

relationships of blastozoans are poorly understood (Paul, 1988; Sumrall, 1997; Kammer et al., 2013) because of their complex morphologies, lack of well-understood skeletal homologies, and a paucity of well-preserved specimens for many taxa. Blastozoans previously have been subdivided into class-level groupings based on the types of respiratory structures present in previously ascribed taxa (Sprinkle, 1973). A growing body of evidence indicates that at least some of these respiratory structures are likely homoplastic and, consequently, circumscribe groups of species that are not united by the evolutionary process (Paul, 1988; Sumrall and Gahn, 2006). To date, a number of blastozoan groups are thought to be polyphyletic (e.g., edrioasteroids, rhombiferans, diploporitans; Sprinkle and Bell, 1978; Lefebvre and Fatka, 2003; Zamora and Rahman, 2014). Aphyletic groupings represent an obstacle to addressing basic paleobiological questions about blastozoan echinoderms, as no questions rooted in evolutionary theory can be answered in the absence of a phylogeny.

Diploporitans have long been considered one of the most problematic groups of blastozoans, as multiple authors have considered them to be polyphyletic (Paul, 1988; Sumrall, 2010; Lefebvre et al., 2013; Sheffield and Sumrall, 2015). These taxa, which ranged from the Ordovician through the Devonian, have been traditionally diagnosed as those blastozoans with diplopore (double pore) respiratory structures that pierce the skeletal plates of the body wall (Sprinkle, 1973). However, diplopores are constructed differently across Diploporita, suggesting multiple origins (Paul, 1988; Sheffield and Sumrall, 2015),

non-diploporitan echinoderms have been discovered to have diplopores (Sumrall and Gahn, 2006), and some traditionally ascribed diploporitans do not have diplopores (Haeckel, 1896). Consequently, diplopores are likely not a reliable synapomorphy for all taxa presently assigned to diploporitans. Further, diploporitans encompass wide morphological variation across the three previously ascribed groups, which suggests that they are only distantly related and do not constitute a valid phylogeny-based grouping (Fig. 1).

To date, Diploporita has not been analyzed in a phylogenetic context. Here we test diploporitan monophyly by analyzing taxa that encompass the wide morphological variation currently assigned to the group and closely related non-diploporitan taxa. Furthermore, this experimental design tests the monophyly of the various named subgroups of Diploporita (Glyptosphaeritida, Sphaeronitida, Asteroblastida). The results of this study suggest that a major revision of this group is necessary. Placing diplopore-bearing taxa within a phylogenetic framework is the first step towards being able to assess evolutionary trends (e.g., trait evolution, biogeography) within these taxa.

Previous Phylogenetic Investigations of Blastozoa and Diploporita

Although blastozoan echinoderms are a large and globally distributed component of the Paleozoic marine fauna, there are relatively few phylogenetic studies performed on this group and its monophyly has not been assessed.

Previous studies have focused on analyzing small subsets of blastozoan groups or have focused only on a few representative taxa to encompass a vast amount of morphology (Breimer and Macurda, 1972; Paul, 1988; Sumrall, 1997; Frest et al., 2011; Sumrall and Waters, 2012; Sumrall et al., 2012; Ausich et al., 2015). Regardless of advances in understanding these evolutionary relationships, a number of blastozoan groups are almost certainly polyphyletic (e.g., rhombiferans, diploporitans, eocrinoids), masking the true diversity of Paleozoic echinoderms (Sumrall, 1997; Nardin et al., 2009).

Very few studies have investigated the phylogenetic relationships of the diploporitans within a rigorous quantitative framework. Paul (1988) included sphaeronitid diploporitans in a high-level taxonomy phylogenetic analysis that placed sphaeronitids (those diploporitans described as being spherical to ovoid in shape, with short ambulacra and a small or absent column; Kesling, 1967) as sister taxon to eocrinoid *Lichenoides* Barrande, 1846. Other diploporitan taxa were excluded from this analysis because of their confusing morphology. The only other phylogenetic analysis involving diploporitans was performed by Frest et al. (2011) and was limited to members of the Silurian *Holocystites* Fauna (see Paul, 1971; Frest et al., 2011; Sheffield and Sumrall, 2017 for a comprehensive review). The relationships presented by Frest et al. (2011), however, were derived from an analysis that included several inaccurate character codings, several non-independent characters, and some characters that did not represent logical morphological transitions of homologous elements (e.g., numbers of oral

plates as characters; Sheffield and Sumrall, 2017). Neither of these analyses were performed using rigorous phylogenetic methods or with a full understanding of shared homologous features and therefore do not inform of the relationships of the diplopore-bearing taxa within the larger blastozoan echinoderm group.

Currently Defined Diploporitan Relationships

Diploporita Müller, 1854, as most recently established in Kesling (1967), is divided into three major groups: Glyptosphaeritida Bernard, 1895, Sphaeronitida Neumayr, 1889, and Asteroblastida Bather, 1900. Glyptosphaeritids include diplopore-bearing blastozoans with globular, ovate, pear-shaped, or saclike thecae, with ambulacra extending across the theca, ending in one or multiple brachiole facets, and with diplopores present on both thecal plates and plates bearing ambulacral grooves. This group includes a variety of taxa that either bear or have lost floor plates, have different configurations of the positioning of the food grooves on the oral plates and have either aboral holomeric stems or holdfasts.

Sphaeronitids include diplopore-bearing blastozoans with ovate to elongate thecae that are constricted distally as well as short and unbranched ambulacra (Paul, 1988). This group includes taxa with and without floor plates, different configurations of proximal food grooves with respect to the oral plates, different configurations of brachial facets on the ambulacral systems, presence or

absence of facetal plates, and different types of diplopores borne on the thecal plates.

Asteroblastids include diplopore-bearing blastozoans with bud or bullet shaped thecae, with recumbent ambulacra lying directly on the theca, and diplopores that are restricted to ambulacral floor plates. Taxa within this group show a variety of thecal plate configurations and constructional differences of the ambulacra with respect to the underlying thecal plates. All bear holomeric stems.

These differences suggest that these three groups likely represent more distant evolutionary relationships than is currently suggested and that these groupings do not uniquely capture the high morphological disparity present in proposed taxa of Diploporita. A number of features used to diagnose the different higher-level groups (e.g., theca shape, presence of stems or holdfasts) likely either re-evolved during the course of the groups' evolution, limiting their usefulness in determining systematic relationships, or the features are clade-diagnostic, but the classification of the clade is incorrect. Further, construction of the diplopores, the morphological feature that defines Diploporita, varies across these three groups as well suggesting multiple originations of these features (Kesling, 1967). This suggests that these groupings are polyphyletic and in need of phylogenetic revision, a central goal of this study.

Diplopores as a Synapomorphy

Classical Linnaean systematics diagnoses groups of organisms based on the presence or absence of key diagnostic features. Blastozoan echinoderms traditionally have been subdivided into groups arbitrarily placed at the class rank, primarily based on the presence of different types of respiratory structures found in their constituent species (Sprinkle, 1973). This classification scheme assumes that respiratory features are complex and, therefore, unlikely to evolve independently in numerous lineages. However, recent evidence has shown that complex respiratory structures do evolve independently in many lineages, suggesting that basing classification on respiratory structures alone is an oversimplification (Sumrall and Gahn, 2006).

The only morphological feature that currently groups species into Diploporita is the presence of diplopore respiratory structures. Diplopore-bearing blastozoans show wide variation in nearly every other major morphological feature, including the makeup of the body wall, feeding apparati, and attachment structure (Fig. 1[3]). However, even within the group-defining diplopores, there is wide variety across taxa. Simple diplopores are defined as a double pore system, connected by a single, uncalcified thecal canal. The pores are contained within the peripore, a depression contained on the thecal plate. Presumably, this

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[3] All figures and tables placed within Appendix III-I

formed an attachment point where a fluid-filled, fleshy bulb through-attached for respiration. A number of diplopore-bearing blastozoans have a modified version of simple diplopores, humatipores (restricted to taxa within the *Holocystites* Fauna), which are buried under the surface of the thecal plate with multiple calcified canals connecting the two pores (Paul, 1971; Frest et al., 2011; Sheffield and Sumrall, 2017). There have been reports of 'unbranched' diplopores in *Pachycalix* Chauvel 1936, haplopores, which consist of a single pore contained within a depression (for a thorough discussion of the variety of diplopore morphotypes, see Paul (1972)). Specimens of *Pachycalix* were not available for study, so these observations cannot be confirmed. Further, there are diplopore-bearing blastozoans without any discovered respiratory structures, such as *Amphoracystis* Haeckel, 1896 (Fig. 2), a taxon from Lower Ordovician strata of the Prague Basin.

Increasing evidence has indicated that blastozoan respiratory structures are not appropriate characters on which to base evolutionary groupings (Paul, 1988; Sumrall, 1997; Sumrall and Gahn, 2006). Phylogenetic analyses of other blastozoan echinoderms, such as rhombiferans, indicate that the presence or absence of rhomb respiratory structures has no bearing on whether taxa are or are not included within a monophyletic group (Brochu and Sumrall, 2001; Zamora et al., 2016). Some early taxa like *Macrocystella* Callaway 1877 and *Cuniculocystis* Sprinkle and Wahlman, 1994 predate the evolution of

pectinirhombs and other taxa, such as *Amecystis* Ulrich and Kirk, 1921 lost rhombs secondarily (Sumrall and Sprinkle, 1995).

Further, *Thresherodiscus*, a Late Ordovician isorophid edrioasteroid, has numerous diplopores connected by a raised, thin-walled bulb of stereo within the interambulacral plating series (Sumrall and Gahn, 2006). The presence of diplopores in taxa not closely related to Diploporita suggests that respiratory structures are likely convergent.

Materials and methods

Repositories and institutional abbreviations

All taxa studied for this analysis are listed in Table 1. All specimens are housed in research collections from the following museums or institutions: Cincinnati Museum Center (CMCIP), Field Museum of Natural History (FMNH; UC), The University of Iowa (SUI), Miami University (MUMG), Yale Peabody Museum (YPM), Prague National Museum (NM), and the Geological Institute of Tallinn (GIT).

Methods

Characters were developed to reflect homology across echinoderm taxa utilizing tests for determining potential homology in morphological characters proposed in Patterson (1982); an explanation of characters utilized in this analysis is placed within Appendix III-II. Characters in the analysis are presumed

to be hereditary; characters concerning the shape of the theca and holdfast were not emphasized in this analysis, as these are likely driven by environmental factors, shown by the highly variable morphologies present across specimens within specimens of a single species (Gil Cid and García-Rincón, 2012; Sheffield and Sumrall, 2017). Taxa used in this analysis were coded at the species level, primarily utilizing physical specimens examined by the authors and supplemented by the primary literature; if absolutely necessary, in the case of difficult to obtain specimens, primary literature comprised the majority of the dataset for certain taxa (e.g., *Asteroblastus stellatus*).

The character matrix for this analysis (Appendix III-III) was analyzed in phylogenetic program PAUP* v. 4.0a147 (Swofford, 2003) utilizing parsimony. The analysis included 61 characters, of which 41 were parsimony-informative and 28 taxa spanning traditionally ascribed Diploporita and representatives of other Paleozoic stemmed echinoderm groups. A heuristic search of most optimal trees was run utilizing a tree-bisection-reconnection (TBR) branch-swapping algorithm (reconnection limit of eight). Tree support was measured via bootstrap analysis.

A constrained topology analysis was performed to test the monophyly of the three traditionally proposed groups of diploporitans (Glyptosphaeritida, Sphaeronitida, and Asteroblastida). The constrained tree topology forced taxa from the three groups to form three individual clades. All other taxa were reduced to a polytomy and eocrinoid *Gogia* was used as the outgroup to polarize the

matrix; code to perform this function in PAUP* v. 4.0a147 was added to the original nexus file (Appendix III-IV). This tree topology was explored in PAUP* v. 4.0a147 using the same analytical techniques as above.

Selection of Taxa

Taxa were selected to cover a breadth of morphological diversity spanning Diploporita. Excluded from the analysis were taxa that likely represent junior synonyms of taxa included in the analysis. Also excluded from the analysis are taxa without preserved oral and stem areas to prevent an excessive amount of missing data and taxa that were unable to be examined by the authors.

Synonymies.— *Regnellicystis typicalis* Bassler 1950, a diplopore-bearing taxon found in deposits of the Ordovician Benboldt Formation of Virginia, is considered by both Parsley (1982) and here to be a junior synonym of *Eumorphocystis multiporata*, based on identical plating of the oral area, makeup of the theca, and plating of the stem (Fig. 3.1, 3.2).

Celtacystis gotlandicus (Angelin, 1878), an Ordovician Baltican diplopore-bearing taxon, was proposed by Bockelie (1979), as *Celtacystis* was described as having a reduced oral area of four oral plates, instead of the seven that *Gomphocystites* has. This interpretation is rejected here based on drawings and photographs of the specimens that show *Celtacystis* has having seven oral plates that were misinterpreted by Bockelie (1979). *Celtacystis gotlandicus*

(Angelin, 1878) is rejected as a junior synonym of *Gomphocystites gotlandicus* Angelin, 1878. The physical specimen was not available for study.

Osgoodicystis Frest and Strimple, 2011, a Silurian diplopore-bearing taxon from Laurentia was proposed as a separate genus from *Pentacystis* Paul, 1971 based on the presence of oral plates within the ambulacral system, whereas *Pentacystis* was described as having no oral plates (Paul, 1971; Frest et al., 2011). However, once reexamined, this genus was erected solely on taphonomic disarticulation of the oral plates (Sheffield and Sumrall, 2015; Sheffield and Sumrall, 2017); therefore, *Osgoodicystis* Frest and Strimple, 2011 is rejected as a junior synonym of *Pentacystis* Paul, 1971 and is not utilized as a separate taxon in this analysis.

Incomplete or Unobtainable Taxa

A number of taxa are only known from a small number of very incomplete specimens. The large majority of these taxa were not utilized in this study, to prevent the analysis from being overwhelmed by missing data. Specimens of note that were excluded: *Archegocystis* Jaekel, 1899 (known only from incomplete oral areas; Fig. 4.1); *Tholocystis* Chauvel, 1941 (known from incomplete oral and thecal areas; information concerning the majority of the plating of the ambulacral system undeterminable from preserved specimens (Fig. 4.2) and *Amphoracystis* Haeckel, 1896 (only known from incomplete specimens of the theca, without oral or stem area; Fig. 2). *Protocrinites* (most specimens

incomplete; interpretations of morphology of this taxon, especially those concerning the stem, are highly varied and inconclusive at this time; Fig. 4.3).

Specimens that were unobtainable for this analysis were largely excluded to prevent incorrect conclusions concerning morphological characters being drawn from previous interpretations. *Brightonicystis* Paul, 1971 was not available for study; previous interpretations consider this taxon to have ten oral plates; this interpretation is highly unlikely, as it would prove to be the only echinoderm taxon known with more than seven oral plates; (Sheffield and Sumrall, 2017). Specimens of Asteroblastida were not available for analysis either; however, in an effort to encompass as much morphological diversity as possible, *Asteroblastus stellatus* was coded utilizing primary literature (Kesling, 1967), with the understanding that some of the interpretations may change once specimens are available for study. *Calix segwicki* Roualt, 1851 was also not included in this analysis, due to poor preservation of specimens and diverse interpretations of its morphology.

Results

Phylogenetic Analysis

The parsimony analysis identified twelve optimal trees of 129 steps excluding uninformative characters. The strict consensus tree (Fig. 5) inferred a clade that aligns with the relationships currently described as Sphaeronitida, indicating that the original classification of these diplopore-bearing blastozoans

represents a monophyletic group, supported by the presence of food grooves that are restricted to the oral summit and a lack of floor plates. Contained within the sphaeronitids is a large clade comprising the *Holocystites* Fauna (bootstrap support of 74) supported by the presence of short food grooves that end in single brachiole facets and proximal thecal plates modified into brachiole-bearing plates. Sister group to the *Holocystites* Fauna is a clade comprising *Haplosphaeronis oblonga* and *Eucystis angelini* supported by the multiterminal ambulacral grooves and a rotation of the grooves to lie on oral plates, instead of the sutures.

Diplopore-bearing taxa traditionally comprising the group Glyptosphaeritida are spread across the tree, representing a polyphyletic group; paracrinoid *Canadocystis barrandei* is rooted within a cluster of glyptosphaeritids and other traditionally defined glyptosphaeritids are nested within other clades.

Eumorphocystis and *Hybocrinus* are united as a clade (bootstrap support of 71), supported by the presence of a radial plate, coelomic canal, and arms comprising extraxial and axial components. Parablastoid *Eurekablastus* and asteroblastid diploporitan *Asteroblastus stellatus* are sister taxa to *Eumorphocystis* and *Hybocrinus*. These two clades are sister taxa to *Stephanocrinus*, *Hemicosmites*, and *Cheirocystis* (nodal support of 63) supported by the presence of brachiole facets being attached to the center of primary and secondary floor plates. This analysis indicates that rhombiferans are polyphyletic,

as *Stephanocrinus* is more closely related to *Hemicosmites* than *Cheirocystis.* Eocrinoid *Rhopalocystis* is sister taxa to all of these taxa discussed above.

Constraint Analysis

A secondary analysis was performed constraining the original systematic placement of diplopore-bearing taxa to form a monophyletic group (i.e., Glyptosphaeritida, Sphaeronitida, Asteroblastida, and non-diploporitan taxa) is as parsimonious as the phylogenetic hypothesis presented in this study (Fig. 6). The most parsimonious tree within the provided constraints was 143 steps.

Discussion

Diploporita

The most optimal tree uncovered from the constraint analysis is 14 steps longer than the most parsimonious tree uncovered in this study. This suggests that it is far less parsimonious to treat Diploporita as monophyletic than it is to treat diplopore-bearing taxa as multiple groups spread throughout the blastozoan tree of life.

Sphaeronitids

Only the sphaeronitids have been argued to represent a monophyletic group (Paul, 1988); this analysis supports the Sphaeronitida as a natural evolutionary group. The sphaeronitids share short ambulacral grooves restricted to the oral area and a lack of floor plating associated with the ambulacral

grooves. Two major groups within the sphaeronitids are inferred: those that end in multiple terminal brachiole facets (*Haplosphaeronis, Eucystis,* and *Sphaeronites*; Fig. 7.1, 7.2,, 7.3, 7.4) and those with ambulacra ending in a single terminal brachiole facet (those diplopore-bearing blastozoans called the *Holocystites* Fauna; Fig. 7.5, 7.6)

Haplosphaeronis and *Eucystis* are linked by a feature that appears to re-evolve more than once within diplopore-bearing blastozoans. In both taxa, there is a rotation of approximately 36˚ degrees (Sumrall, 2015), so that the ambulacral grooves are not lying on the sutures of the oral plates (the plesiomorphic condition), but they are centered on the oral plates (Fig. 7.1, 7.3). This feature also appears in *Glyptosphaerites,* as well as in *Holocystites*. The poorly documented Ordovician taxon *Tholocystis* (Fig. 4.2) from peri-Gondwana, likely belongs within the *Eucystis* and *Haplosphaeronis* clade, potentially as sister taxon to *Haplosphaeronis.* Both taxa are united by the first primary peristomial cover plate being split into two, a feature not seen in any other diplopore-bearing echinoderm taxa. However, due to incomplete preservation of the theca, respiratory structures, and a large portion of the oral area, the relationships of *Tholocystis* were not assessed in this analysis.

The *Holocystites* Fauna, a group of diplopore-bearing taxa restricted to the North American continent, represent a clade within the sphaeronitids. The group is united by a number of synapomorphies: floor plate-less food grooves that end in a single brachiole facet; and extremely large brachiole facets; proximal thecal

plates that are differentiated into facetal plates upon which brachiole facets are born (Fig. 1.2, 7.5). While it has been suggested by multiple authors that this fauna does represent a monophyletic group (Paul, 1971; Frest et al., 2011; Sheffield and Sumrall, 2017), it was not understood if *Triamara*, found in many of the same middle Silurian deposits as the *Holocystites* Fauna, was a member. The simple diplopores found in *Triamara* differ fundamentally in the construction when compared to the humatipores found in the rest of the *Holocystites* Fauna (Sheffield and Sumrall, 2017). However, *Triamara* and *Aristocystites* (known from Early Ordovician deposits of the Prague Basin) are found to be sister taxa (nodal support of 68) to the humatipore-bearing members of the *Holocystites* Fauna in this analysis.

Asteroblastids

Asteroblastus stellatus is sister taxon to parablastoid *Eurekablastus* (parablastoids are diagnosed as blastozoans with endothecal cataspire respiratory structures) in this analysis, indicating that the placement of this group within Diploporita is not supported by current data. It also further indicates that diplopore respiratory structures have re-evolved multiple times throughout the course of echinoderm evolution in the most parsimonious optimization of this character. The two taxa share a unique combination of characters (squat plates (refer to Appendix 3-2 for an explanation of characters), ridges along basal plates, presence of stem, presence of O6, straight, extended ambulacra, floor plates that form the thecal wall). The sister group to the *Eurekablastus*-

Asteroblastus clade contains crinoid *Hybocrinus* and *Eumorphocystis.* The most parsimonious explanation for the evolution of diplopore respiratory structures within this clade is that diplopores were evolved independently in both *Eumorphocystis* and *Asteroblastus*. However, it is also possible that diplopores appeared earlier in the tree and was lost on four separate occasions. While this is a less parsimonious explanation, it is difficult to fully ascertain trait history with the limited sampling present in eumorphocystitid and asteroblastid-type taxa. Further sampling of these groups will likely refine the results of this analysis and better constrain the history of diplopore respiratory structure evolution.

It is possible that the asteroblastid group (comprising *Asteroblastus, Asterocystis*, and *Metasterocystis*) could represent a monophyletic group; lack of available samples prevented full phylogenetic analysis; however, the phylogenetic analysis indicates that *Asteroblastus* does not belong within the traditional Diploporita group.

Glyptosphaeritids

The glyptosphaeritids, as previously described, represent a polyphyletic group, as *Eumorphocystis* (Fig. 1.3, 3.1, 3.2) is contained within a clade of non-diploporitan taxa, including crinoids. The group that does appear rooted within diplopore-bearing taxa (excluding *Eumorphocystis*) is paraphyletic, as non-diplopore bearing paracrinoid *Canadocystis* is contained within it (Fig. 5). These blastozoans are united by ambulacra that extend down the theca and end in alternating brachiole facets (e.g., *Estonocystis*; Fig. 7.7, 7.8). Ambulacral floor

plates are present in the majority of the taxa, including *Canadocystis*, but they are lost in *Gomphocystites indianensis* (Fig. 1.1).

Crinoids with a blastozoan origin

The origin of crinoids has been debated in many studies; the two major hypotheses posit crinoids being derived either from Cambrian edrioasteroids (Guensberg and Sprinkle, 2007, 2009; Guensberg et al., 2016) or from within blastozoans (Sumrall, 1997; Ausich et al., 2015; O'Malley et al., 2016). This analysis supports crinoids being rooted within blastozoans, with *Eumorphocystis multiporata* as their sister taxon. This relationship is supported in the analysis by multiple shared features: 1) presence of a coelomic canal; 2) arms comprising a composite of extraxial and axial skeletal components; 3) and an extraxial thecal plate (radial plate) supporting the exothecal arm. This analysis corroborates a growing number of phylogenetic studies that place crinozoans within the blastozoans.

Rhombiferans

Rhombiferan blastozoans previously have been described as polyphyletic (Paul, 1988; Sumrall, 1997; Nardin et al., 2009). This analysis supports this idea, as hemicosmitoid rhombiferan *Hemicosmites* and *Stephanocrinus* are most closely related to one another, and glyptocystitoid rhombiferan *Cheirocrinus* is sister taxa to them. This indicates that rhomb-type endothecal respiratory structures may have evolved more than once in the echinoderm tree, and is

further evidence that respiratory structure types are likely not clade-defining features. *Hemicosmites* and *Stephanocrinus* share: 1) erect ambulacra without extraxial components; 2) large peristome; 3) and brachiole facets on the oral plates. *Cheirocystis*, *Hemicosmites,* and *Stephanorinus* share the presence of brachiole facets being attached to the center of primary and secondary floor plates.

Increased Sampling

While this is the first wide-scale phylogenetic analysis of diplopore-bearing echinoderms, further sampling of critical taxa is necessary to more fully document the evolutionary transitions of diplopore-bearing blastozoans. In order to understand how many times in echinoderm evolution diplopore respiratory structures evolved, better sampling of eumorphocystitid-type and asteroblastid-type taxa is necessary. Further, sampling of diplopore-bearing blastozoans from under sampled times in Earth's history (e.g., late Cambrian) and under sampled areas of Earth (e.g., Gondwana, South China) has the potential to change much of what is currently understood about the evolution of these taxa.

Conclusions

This analysis indicates that diplopore-bearing blastozoan echinoderms do not represent a monophyletic group, but rather a polyphyletic grade. Diplopores

have evolved as respiratory structures multiple times within Paleozoic blastozoan echinoderms and, as such, are not a synapomorphy, as previously used to erect Diploporita. This finding adds to the growing body of evidence that respiratory structures in blastozoans are convergent and are not clade defining. Sphaeronitids do represent a natural group of diplopore-bearing blastozoans, characterized by short, floor plate-less food grooves that are restricted to the oral surface. The *Holocystites* Fauna is a clade within the sphaeronitids, united by proximal thecal plates modified into facetal plates for bearing single brachiole facets. The proposed glyptosphaeritids are a polyphyletic clade of diplopore-bearing blastozoans. The Asteroblastids are sister taxon to parablastoids and are not contained within the traditionally ascribed Diploporita. *Eumorphocystis* is sister taxon to crinoids and adds support to the hypothesis that crinoids are rooted within blastozoans. A constraint analysis to test the monophyly of Diploporita indicates that it is far less parsimonious than the phylogenetic hypothesis presented in this analysis.

Future Implications

Echinoderms, with their complex and highly disparate morphologies, have been shown to respond to long-term oceanic environmental patterns such as: oxygenation levels and seawater ion ratios (Paul, 1968; Clausen, 2004; Dickson, 2002, 2004; Clausen and Smith, 2005, 2008; Zamora and Smith, 2008; Rahman and Zamora, 2009). Blastozoan echinoderms during the early Paleozoic would have been responding to significant global climate changes during the Ordovician

(Lefebvre et al., 2013); these responses to climate change are likely driving the convergence of respiratory structures and other morphological features. Previous studies have focused on attempting to understand how global climate change affected the biodiversity and biogeography of Paleozoic echinoderms (e.g., Lefebvre and Fatka, 2003; Lefebvre, 2007; Lefebvre et al., 2013; Zamora et al., 2013; Sumrall et al., 2015). However, without a full understanding of the phylogenetic relationships of blastozoans, it is impossible to assess how these taxa are responding.

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Appendix 3-1

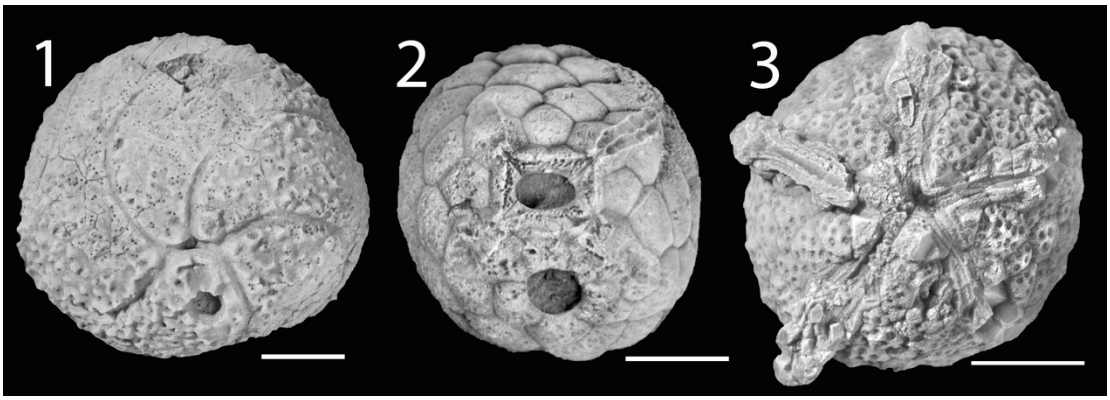


Figure 3.1. Diploporita encompasses wide morphological variability, likely indicating that the group is polyphyletic. **(1)** *Gomphocystites indianensis* (Glyptosphaeritida), characterized by a reduced mouth, diplopores and long, spiraling ambulacra without floor plates (FMNH 19708). **(2)** *Paulicystis densus* (Sphaeronitida), characterized by a large mouth, proximal thecal plates modified into comparatively large brachiole facets, and humatipore respiratory structures (SUI 48164). **(3)** *Eumorphocystis multiporata* (Glyptosphaeritida), characterized by ambulacra that are erect distally and lie on biserial floor plates (SUI ea74). Scale bar=1cm.



Figure 3.2. *Amphoracystis irregularis* Barrande, 1887; taxon within proposed group Sphaeronitida, characterized by irregular thecal plating, globular theca, presence of a holdfast, and lack of respiratory structures (NM-L 13063). Known specimens of *Amphoracystis* do not have preserved oral areas. Scale bar=1cm.

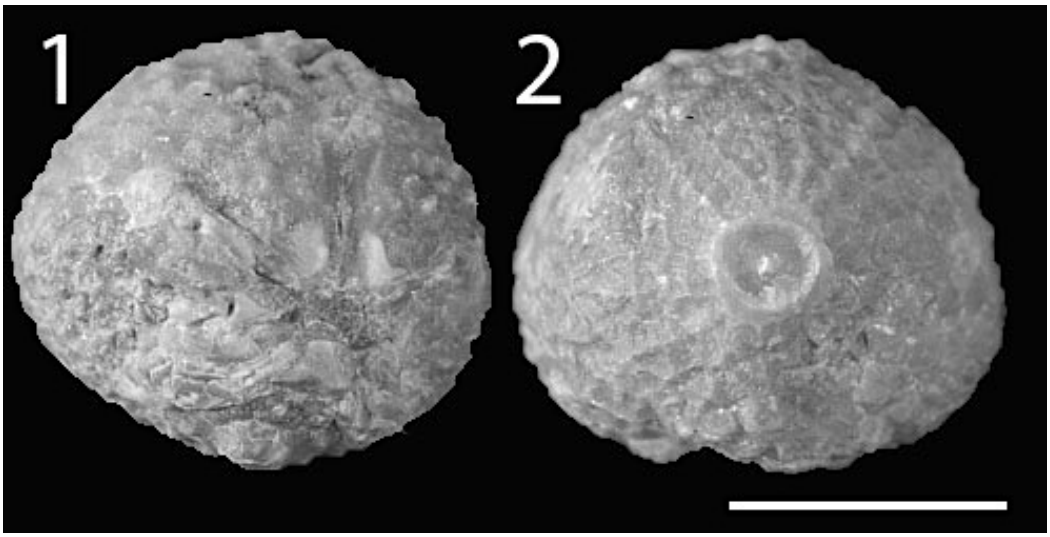


Figure 3.3. *Regnellicystis typicalis* is rejected as a junior synonym of *Eumorphocystis multiporata.* **(1)** Oral view of holotype of *Regnellicystis typicalis*, showing ambulacra bordered by biserial floor plates that are erect distally. **(2)** Stem view, showing holomeric stem, pierced by a small, circular lumen. Stem encloses around four equally-sized basal plates. (USNM PAL113308; images provided by Department of Paleobiology, Smithsonian Institution). Scale bar=1cm.

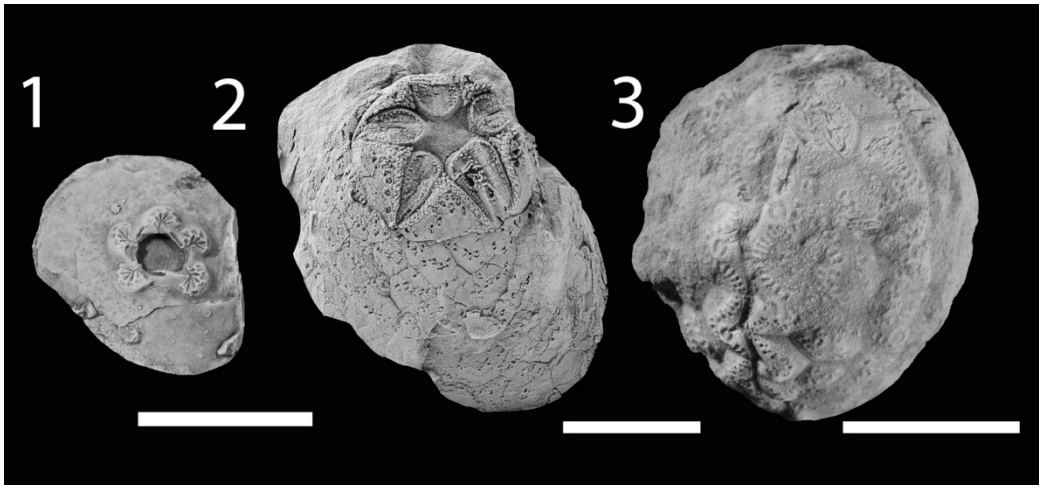


Figure 3.4. Representative taxa excluded from this analysis for incompleteness. **(1)** Oral view of *Archegocystis desiderata* (NM-L). This taxon is only known from incomplete oral area; information about the theca, attachment structure, and respiratory structures were largely unavailable. **(2)** Oral view of *Tholocystis sp.* *Tholocystis* is only known form incomplete oral areas. Information concerning the presence and number of oral plates, ambulacral floor plates, hydropore, and gonopore are unavailable. **(3)** Side view of *Protocrinites oviformis* (GIT 540-57). While some oral areas of this taxon have been found, it was not able to be examined during this study. Due to conflicting ideas about the morphology of the stem (whether it detaches as an adult or not), as well as different interpretations of the oral area, this taxon was excluded from the analysis.

Figure 3.5. Strict consensus of the most parsimonious reconstruction with a tree length of 129 steps. Bootstrap values of supported relationships above 50% are indicated by the appropriate node. This tree indicates that the original classification of Sphaeronitida is a natural evolutionary group, whereas Glyptosphaeritida is polyphyletic, as paracrinoid *Canadocystis* is rooted within taxa traditionally grouped with the glyptosphaeritids and *Eumorphocystis* shares a sister taxon relationship with crinoid *Hybocrinus*. It is unclear from this analysis if Asteroblastida constitutes a monophyletic clade, but it is clear that diplopore-bearing taxa are polyphyletic, as asteroblastids are contained within another clade of echinoderm taxa and sister group to parablastoid *Eurekablastus.* Further, this analysis indicates that rhombiferans may be polyphyletic, as evidenced by the relationships of coronoid *Stephanocrinus* to rhombiferans *Cheirocystis* and *Hemicosmites* and further supports the hypothesis that crinoids were derived from blastozoans, as evidenced by the most parsimonious placement of *Hybocrinus.* CI= 0.654; RI= 0.726.

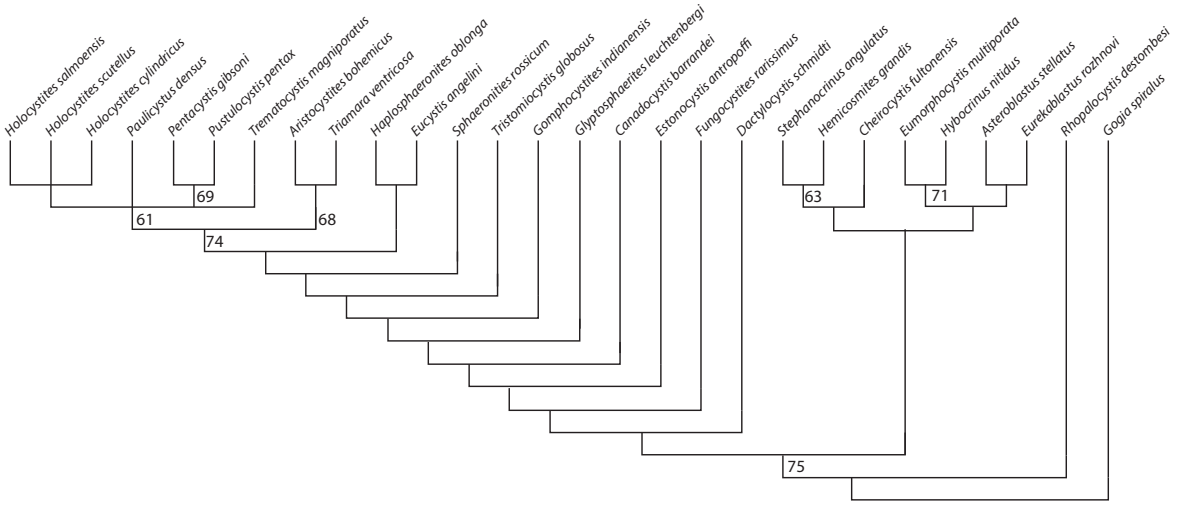


Figure 3.5 continued.

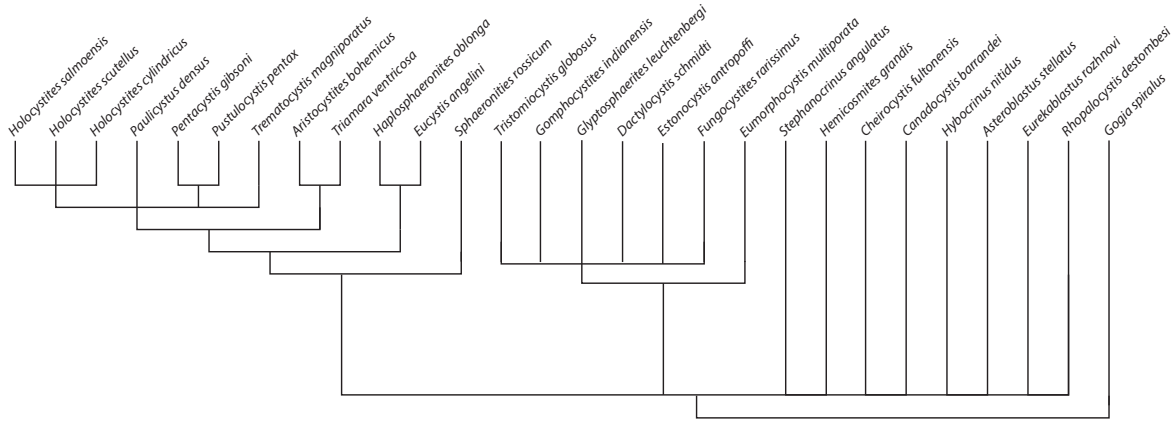


Figure 3.6. Strict consensus tree of the most parsimonious arrangement of taxa, if the three traditionally ascribed classifications of Diploporita (Sphaeronitida, Glyptosphaeritida, Asteroblastida) were forced to be monophyletic clades. The resulting tree had a tree length of 143, 14 steps longer than the most parsimonious tree without topological constraints of diplopore-bearing taxa. CI=0.608; RI= 0.667.

Figure 3.7. Representative diploporitan taxa used in this analysis. **(1)** Oral view of *Eucystis angelini* (NM-L7695). Ambulacral grooves are short and restricted to the summit; grooves are multiterminal and end in a varying number of brachiole facets without underlying floor plates. Grooves are positioned on the oral plates, as opposed to lying on the oral plate sutures. **(2)** Side view of *E. angelini* (NM-L7694). Diplopores randomly arranged on irregularly plated theca and narrows distally into a holdfast. **(3)** Oral view of *Haplosphaeronis* sp. (GIT 540-3). Ambulacral grooves are extremely short, restricted to the summit, and multiterminal; grooves are positioned on the oral plates, instead of lying on the sutures between the oral plates. Note that first primary peristomial cover plate is split into two. **(4)** Side view of *H.* sp. (GIT 540-3). Note that the diplopores are aligned vertically on the thecal plates. Holdfast is approximately the same width of the theca. **(5)** Oral view of *Pustulocystis pentax* (MUMG-T 266). Extremely short ambulacral grooves that lie on oral plate sutures end on thecal plates modified with large, single brachiole facets. **(6)** Side view of *P. pentax* (MUMG-T-266)**.** Humatipores distributed randomly across thecal plates; theca narrows distally into holdfast. **(7)** Oral view of *Estonocystis antropoffi* (GIT 540-80). Ambulacral grooves that lie on the oral plate sutures anastomose down the theca. **(8)** Side view of *E. antropoffi* (GIT 540-80). Short grooves extending from the main food groove connect to brachioles that are situated in the center of single ambulacral floor plates. Diplopores align horizontally along the floor plates. Basals, 4, form around circular stem.

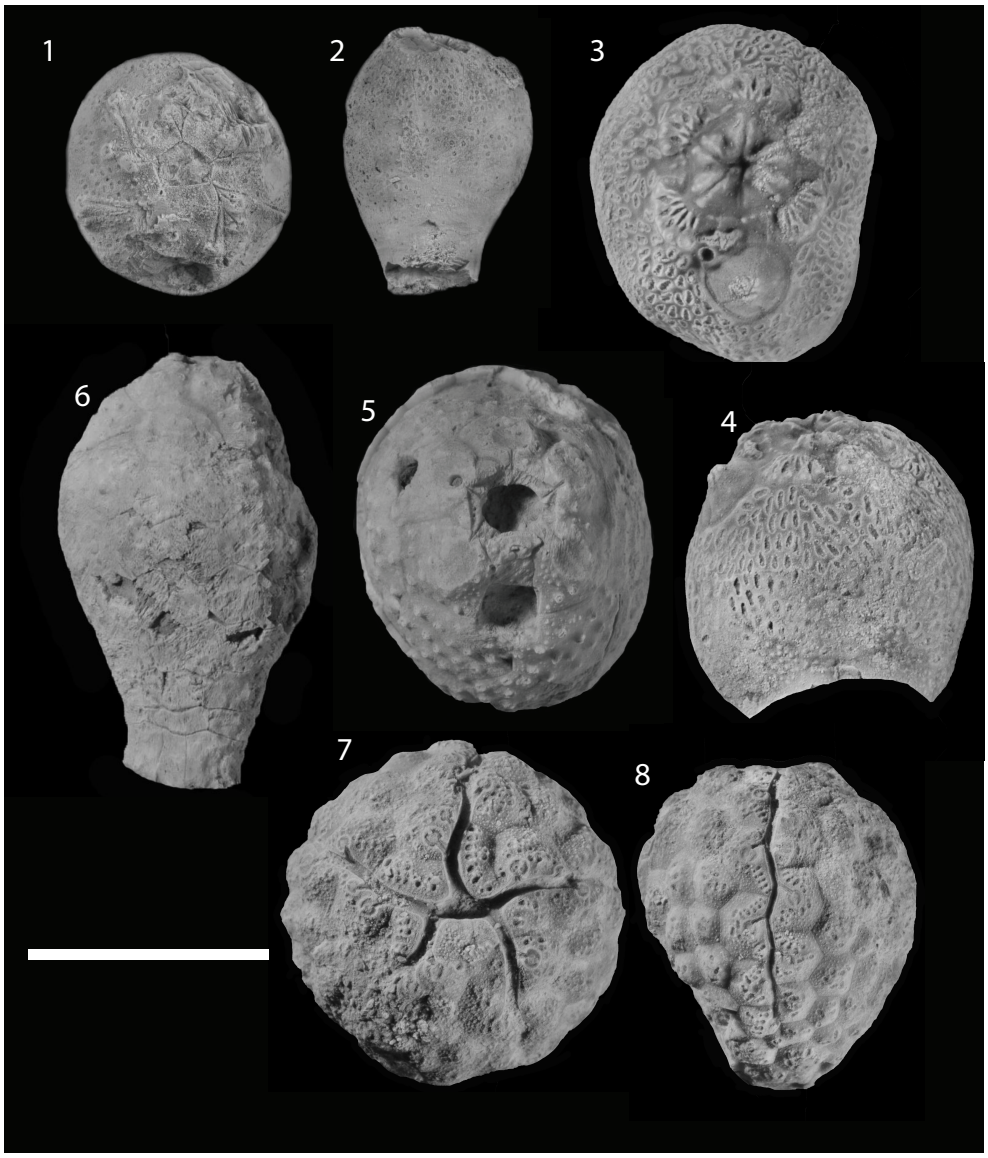


Figure 3.7 continued.

Table 3.1. Diplopore-bearing taxa utilized within this phylogenetic analysis. The original classifications of taxa (i.e., Glyptosphaeritida, Sphaeronitida, and Asteroblastida) are indicated.

Species name	Author	Original Taxonomic Classification within Diploporita
Aristocystites bohemicus	Barrande, 1887	Sphaeronitida
Asteroblastus stellatus	Eichwald, 1862	Asteroblastida
Dactylocystis schmidti	Jaeckel, 1899	Glyptosphaeritida
Estonocystis antropoffi	Jaekel, 1918	Glyptosphaeritida
Eucystis angelini	Angelin, 1878	Glyptosphaeritida
Eumorphocystis multiporata	Branson and Peck, 1940	Glyptosphaeritida
Fungocystites rarissimus	Barrande, 1887	Glyptosphaeritida
Glyptosphaerites leuchtenbergi	Volborth, 1846	Glyptosphaeritida
Gomphocystites indianensis	Miller, 1889	Glyptosphaeritida
Haplosphaeronis oblonga	Angelin, 1878	Sphaeronitida
Holocystites cylindricus	Hall, 1861	Sphaeronitida

Table 3.1 continued.

Species name	Author	Original Taxonomic Classification within Diploporita
Holocystites sp.	Hall, 1861	Sphaeronitida
Holocystites scutellus	Hall, 1861	Sphaeronitida
Paulicystis sparsus	Paul, 1971	Sphaeronitida
Pentacystis gibsoni	Paul, 1971	Sphaeronitida
Pustulocystis pentax	Paul, 1971	Sphaeronitida
Sphaeronites pomum	Gyllenhaal, 1772	Sphaeronitida
Trematocystis magniporatus	Frest and Strimple, 2011	Sphaeronitida
Triamara ventricosa	Paul, 1971	Sphaeronitida

Appendix 3-2

Explanation of Characters

Theca

1. 0: Irregular; no standardized, organized plate circlets. 1: Plates organized into glyptocystitid condition. 2: Plates organized into blastoid condition. 3: Irregularly plated into discrete circlets.
2. 0: Plates elongated, or taller than wide. 1: Plates squat, or wider than tall or equal in both dimensions.
3. 0: No raised ridges connecting thecal plate centers. 1: Raised ridges running connecting plate centers.
4. 0: Basal plates undifferentiated from proximal thecal plates. 1: Differentiated in paracrinoid condition (i.e., two zygous (large) and one azygous (small) basal plate, with the small basal contained within BC interray). 2: Differentiated in blastoid condition (i.e., two zygous and one azygous basal plate, with small basal contained within AB interray. 3: Differentiated in eumorphocystitid condition (i.e. four basals of equal size) 4: Differentiated in estonocystitid condition (i.e., 4 small basals and one large; large in BC interray). 5: Differentiated in hemicosmitoid condition. 6: Hybocrinid condition (i.e., 5 basals of equal size). 7: Differentiated in glyptocystitoid condition (i.e., two zygous and one azygous basal plate, with small basal plate contained within AE interray)). 8: One single basal plate. 9: Differentiated in parablastoid condition.

5. 0: Ridges running laterally across differentiated basal plates absent. 1: Ridges running laterally across differentiated basal plates present
6. 0: Theca is widest proximally (top). 1: Theca is widest around the middle and narrower at the top and bottom. 2: Theca is widest distally (bottom).

Respiratory Structures

7. 0: Endothecal respiratory structures absent. 1: Hydrospires present. 2: Cryptorhombs. 3: Pectinirhombs. 4: Cataspires
8. 0: Exothecal respiratory structures absent. 1: diplopores (double pores in a single depression). 2: epispire (single pore in a depression). 3: Coronal canal (U-shaped canal with slits, present in coronoids and blastoid *Troosticrinus*).
9. 0: Diplopores simple with a single thecal canal connecting the two pores. 1: Humatipores, with multiple buried and calcitic canals connecting the two pores.
10. 0: Peripore containing diplopores elliptically shaped. 1: Diplopores both oval and horseshoe shape. 2: circular in shape.
11. 0: Diplopore pairs are situated in the center of the peripore. 1: Diplopores situated at each edge of the peripore.
12. 0: Diplopore pairs are absent from edges of plates or across sutures. 1: present in small quantities. 2: Diplopore line plate sutures with high frequency.

13. 0: Diplopores are present on extraxial plates (i.e., plates not of the ambulacral system). 1: Diplopores are not present on extraxial plates.
14. 0: Diplopores have no clear directionality or orientation (randomly oriented). 1: Diplopores are aligned horizontally (perpendicular to thecal height). 2: Diplopores aligned vertically (parallel to thecal height).
15. 0: Diplopores are absent from ambulacral floor plates. 1: Diplopores are present on ambulacral floor plates.

Stem and Holdfast

16. 0: No stem present. 1: Stem present.
17. 0: Each stem columnal comprises a single plate (holomeric). 1: Each stem columnal comprises multiple, regular plates (polymeric). 2: Stem is polymeric, but irregularly plated.
18. 0: Lumen that pierces the center of the stem is circular in shape. 1: Lumen is pentagonal. 2: Lumen is triangular.
19. 0: The diameter of the lumen as compared to the diameter of the stem is proportionally large (greater than ~25% of the stem diameter). 1: The diameter of the lumen as compared to the diameter of the stem is proportionally small (less than ~25% of the stem diameter).
20. 0: Holdfast is approximately the same width as the theca. 1: Holdfast narrows distally from the theca. 2: Holdfast widens distally from the theca.
21. 0: Holdfast is located directly under the proximal theca. 1: Holdfast is positioned laterally on the side of theca.

Oral Area

22. 0: Oral plates present. 1: oral plates absent.
23. 0: Oral frame plates absent. 1: Oral frame plates present.
24. 0: Oral plate 7 present in oral plating series. 1: Oral plate 7 is absent.
25. 0 Oral plate 6 present in oral plating series. 1: Oral plate 6 absent in oral plating series.
26. 0: Oral plates 2 and 5 are not in contact with the peristome, marking true 2-1-2 symmetry. 1: Oral plates 2 and 5 are in contact with the peristome, marking derived 2-1-2 symmetry.
27. 0: Oral plates have proportionally wide shelf, measured proximally to distally from the peristome. 1: Oral plates have proportionally narrow shelf, measured proximally to distally from the peristome.
28. 0: Oral plates are flush with the peristome and not elevated. 1: Oral plates are not flush with the peristome and are elevated in the form of spines. 2: Oral plates are elevated in the form of blades (as seen in coronoids).
29. 0: Diplopores are not present on oral plates. 1: Diplopores are present on oral plates.
30. 0: Brachial facets branching from food grooves are located on oral plate series. 1: Brachial facets branching from food grooves are not located on oral plate series.
31. 0: There are no shared cover plates between lateral ambulacra. 1: There are shared cover plates between lateral ambulacra.

32. 0: Primary peristomial cover plates are flush with the peristome and are not elevated. 1: Primary peristomial cover plates are not flush with the peristome and are elevated above it.
33. 0: Primary peristomial cover plates are not differentiated from ambulacral cover plate series. 1: Primary peristomial cover plates are differentiated from ambulacral cover plate series.
34. 0: Primary peristomial cover plate 1 (in CD interray) is not split into two. 1: Primary peristomial cover plate 1 is split into two.
35. 0: Single peristomial opening in oral area. 1: Two peristomial openings present in oral area. 2: Three peristomial openings present in oral area.
36. 0: Oral summit is not elevated from the top of the theca. 1: Oral summit is elevated from the top of the theca.
37. 0: Peristome is relatively small with respect to surrounding oral plates and oral area. 1: Peristome is relatively large with respect to surrounding oral plates and oral area.
38. 0: Periproct located in the area between the C and D ambulacra (CD interray). 1: Periproct is located in the BC interray.
39. 0: The hydropore straddles O1 and O6 plate boundaries. 1: The hydropore sits squarely on O1. 2: The hydropore sits squarely on O7.
40. 0:Hydropore not rugose (i.e., wrinkled). 1: Hydropore rugose.
41. 0: Gonopore is located on O7. 1: Gonopore straddles O1 and O7. 2: Gonopore is located on O1.

42. 0: Ambulacra restricted to the oral summit. 1: Ambulacra extend distally down the theca.
43. 0: Ambulacral grooves are straight for the entirety of their duration. 1: Ambulacral grooves spiral around theca in a horizontal pattern. 2: Ambulacral grooves anastomose down theca vertically.
44. 0: Ambulacral grooves lying on oral sutures. 1: Ambulacral grooves have been rotated to lie on oral plates, instead of the sutures.
45. 0: Floor plate-less food grooves are restricted to the summit. 1: Floor plate-less food grooves extend down theca.
46. 0: Floor plate-less food grooves alternate brachiole facets down the length of the ambulacra. 1: Food grooves end in multiple terminals. 2: Food grooves end in single terminal.
47. 0: Exothecal arms (those that branch off the surface of the theca) are not supported by a single thecal plate (radial plate). 1: Exothecal arms are supported by a single thecal plate.
48. 0: Coelomic canal absent. 1: Coelomic canal present.
49. 0: Ambulacra are not erect. 1: Ambulacra are erect, without extraxial (thecally derived) components. 2: Ambulacra are erect with extra axial components.
50. 0: Branches off of main food groove of multiterminal ambulacra are of the same length. 1: Branches off of main food groove are of differentiated lengths.

51. 0: Ambulacral floor plates do not form the thecal wall. 1: Ambulacral floor plates do form the thecal wall.
52. 0: A ambulacrum is present in the oral series. 1: A ambulacrum is missing from the oral series.
53. 0: Laterally shared ambulacra split into distal B, C, D, and E ambulacra. 1: Laterally shared ambulacra do not split.
54. 0: Ambulacral floor plates, the plates distal to the oral plates perradially or radially positioned that bear food grooves and facets for brachioles, are absent. 1: Ambulacral floor plates are present.
55. 0: Adambulacral plates that form a single row along ambulacral grooves absent. 1: Adambulacral grooves present.
56. 0: Brachiole facet scars relatively small (blastoid-like). 1: Brachiole facet scares relatively large.
57. 0: Brachiole attachment scar situated in the middle of two floor plates, straddling the suture. 1: Brachiole attachment scar situated solely on one floor plate. 2: Multiple brachiole attachment scars situated solely on one floor plate. 3: Brachiole facets are shared between primary and secondary floor plates.
58. 0: Brachioles are not recumbent, or lying down, against the theca. 1: Brachioles are epithecally recumbent upon the theca.

59. 0: Proximal thecal plates surrounding the oral plate series are not differentiated into facetal plates for brachiole facets. 1: Proximal thecal plates are differentiated into facetal plates.
60. 0: BC, DE facetal plates are present for a total of seven facetal plates. 1: BC, DE facetal plates are not present.
61. 0: Facetal scars are solely positioned on one facetal plate and one oral plate. 1: Facetal scars are positioned across two facetal and oral plates.

Appendix 3-3

Character Codings

1. *H.* sp.: 0 1 0 ? ? 1 0 1 1 - - 0 0 0 – 0 - - - ? ? 0 0 0 0 1 1 0 0 0 0 ? 1 ? 0 0 1 0 ? ? 0 0 0 (0 1) 0 2 0 0 0 - - 0 0 0 0 1 – 0 1 0 1
2. *H. scutellus*: 0 1 0 0 – 1 0 1 1 - - 0 0 0 – 0 - - - 1 0 0 0 0 0 1 1 0 0 0 0 ? 1 ? 0 0 1 0 ? ? 0 0 0 (0 1) 0 2 0 0 0 - - 0 0 0 0 1 – 0 1 0 1
3. *H. cylindricus*: 3 0 1 0 – 3 0 1 1 - - 0 0 0 – 0 - - - 0 0 0 0 0 0 1 1 0 0 0 0 ? 1 ? 0 0 1 0 ? ? 0 0 0 (0 1) 0 2 0 0 0 - - 0 0 0 0 1 – 0 1 0 1
4. *Paulicystis densus*: 0 1 0 0 – 1 0 1 1 - - 0 0 0 – 0 - - - 2 0 0 0 0 0 1 1 0 0 0 0 ? 1 ? 0 0 1 0 0 ? 0 0 0 0 0 2 0 0 0 - - 1 0 0 0 1 – 1 1 0 0
5. *Pustulocystis pentax*: 0 1 0 0 – 1 0 1 1 - - 0 0 0 – 0 - - - 1 0 0 0 0 0 1 1 0 0 0 0 ? 1 ? 0 1 1 0 1 0 0 0 0 0 0 2 0 0 0 - - 0 0 0 0 1 – 0 1 1 0
6. *Trematocystis magniporatus*: 0 1 0 0 – 1 0 1 1 - - 0 0 0 – 0 - - - 1 0 0 0 0 0 1 1 0 0 0 0 ? 1 ? 0 0 1 0 0 0 0 0 0 0 0 0 2 0 0 0 - - 1 0 0 0 1 – 0 1 0 0
7. *Pentacystis gibsoni*: 0 1 0 0 – 1 0 1 1 - - 0 0 0 – 0 - - - 1 0 0 0 0 0 1 1 0 0 0 0 ? 1 ? 0 1 1 0 ? ? 0 0 0 0 0 2 0 0 0 - - 0 0 0 0 1 – 0 1 0 0
8. *Triamara ventricosa*: 0 0 0 0 – 1 0 1 0 1 1 2 0 0 – 0 - - - 1 0 0 0 0 0 1 0 0 0 0 ? ? 1 ? 0 0 1 0 ? 0 ? 0 0 0 0 2 0 0 0 - - 1 1 0 0 1 – 0 1 0 0
9. *Gomphocystites indianensis*: 0 1 0 ? – 0 0 1 0 0 1 0 0 0 – 0 - - - 0 0 0 0 0 0 0 0 0 1 0 0 ? ? ? 0 0 0 0 0 0 0 1 1 0 1 0 0 0 0 - - 0 0 0 1 0 – 0 0 - -
10. *Eucystis angelini*: 0 1 0 0 – 1 0 1 0 0 1 0 0 0 – 0 - - - 1 0 0 0 0 0 1 0 0 0 1 0 ? ? ? 0 0 1 0 ? ? ? 1 0 1 0 1 0 0 0 1 – 0 0 0 0 0 – 0 0 - -

11. *Sphaeronites rossum*: 0 1 0 0 – 1 0 1 0 0 ? 0 0 0 – 0 - - - 1 0 0 0 ? ? 0 ? 0 0 1 0 0 1 ? 0 0 0 0 ? ? 0 0 0 0 0 1 0 0 0 0 – 0 0 0 0 0 – 0 0 - -
12. *Haplosphaeronites oblonga*: 0 1 0 0 – 1 0 1 0 0 1 0 0 2 – 0 - - - 0 0 0 0 0 0 1 0 0 0 1 0 0 1 1 0 0 ? 0 ? ? 1 0 0 1 0 1 0 0 0 0 – 0 0 0 0 0 – 0 0 - -
13. *Eumorphocystis multiporata*: 0 1 1 3 1 1 0 1 0 0 0 1 0 0 0 1 0 0 1 - - 0 0 1 1 1 0 1 0 0 1 0 0 0 0 0 0 0 0 ? ? ? 0 0 0 - - 1 1 2 – 1 0 0 1 0 0 1 0 0 - -
14. *Glyptosphaerites leuchtenbergi*: 0 1 0 0 ? 1 0 1 0 0 ? 0 0 0 - ? ? ? ? ? ? 0 0 0 0 0 0 ? 1 1 0 1 0 0 0 0 0 0 1 1 1 2 1 1 0 0 0 0 - - 0 0 0 0 0 – 0 0 - -
15. *Estonocystis antropoffi*: 0 1 0 4 0 1 0 1 0 0 1 0 0 1 1 1 ? 0 1 - - 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 ? 1 2 0 - - 0 0 0 – 1 0 0 1 0 0 2 0 0 - -
16. *Aristocystites bohemicus*: 0 1 0 0 – 0 0 1 0 1 1 2 0 0 – 0 - - - 0 1 0 0 ? ? 1 0 0 1 ? ? ? ? ? 0 0 1 0 ? 0 ? 0 0 ? 0 2 0 0 0 - - 1 1 0 0 1 – 0 1 - -
17. *Tristomiocystis*: 0 1 0 0 – 1 0 1 0 0 1 0 0 0 1 0 - - - 1 0 0 0 1 0 ? 0 0 1 1 ? 0 1 ? 2 0 ? 0 0 0 2 1 0 0 - - 0 0 0 – 1 0 0 1 0 0 1 0 0 - -
18. *Dactylocystis scmidti*: 0 ? 0 ? ? 1 0 1 0 0 0 0 1 1 1 1 ? ? ? - - 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? ? ? ? ? ? 1 0 ? - - 0 0 0 – 1 ? ? 1 0 0 1 0 0 - -
19. *Fungocystites rarissiumus*: 0 1 0 0 – 1 0 1 0 0 1 0 0 0 1 0 - - - 0 0 0 0 ? 0 1 ? 0 1 0 ? 0 ? ? 0 0 0 0 0 ? ? 1 2 0 - - 0 0 0 – 1 0 0 1 0 0 ? 0 0 - -
20. *Asteroblastus stellatus*: 0 1 ? 0 1 1 0 1 0 0 0 0 0 2 0 1 ? ? ? - - 0 0 1 1 1 1 0 0 0 0 ? ? ? 0 0 0 ? ? ? ? 1 0 0 - - 0 0 0 – 1 0 0 1 0 0 1 0 0 - -
21. *Stephanocrinus*: 2 0 1 2 1 1 0 3 - - - - - - - 1 0 0 1 - - 0 0 0 1 1 0 2 – 1 0 ? 1 0 0 0 1 0 2 ? ? 0 0 0 - - 0 0 1 - - 0 0 1 0 0 3 0 0 - -

22. *Cheirocrinus*: 1 0 1 7 1 3 3 0 - - - - - - - 1 0 0 0 - - 0 0 0 0 0 0 0 – 0 1 ? 0 0 0 0 0 1 2 0 1 0 0 0 - - 0 0 0 – 1 0 0 1 0 0 3 0 0 - -
23. *Hemicosmites*: 4 0 1 5 1 1 2 0 - - - - - - - 1 0 2 1 - - 0 0 0 0 – 0 0 – 1 1 ? 0 0 0 0 1 0 ? 0 0 0 0 0 - - 0 0 1 – 1 0 1 1 0 0 3 0 0 - -
24. *Gogia*: 0 ? 0 0 – 0 0 2 - - - - - - - 1 2 0 1 - - 1 1 - - - - ? - - 1 ? 0 0 0 0 0 0 – 0 ? 0 0 0 - - 0 0 0 – 1 0 0 1 0 0 ? 0 0 - -
25. *Rhopalocystis*: 0 1 0 8 0 0 0 2 - - - - - - - 1 0 0 1 - - 0 0 0 0 1 0 0 – 0 1 ? 0 0 0 0 0 ? 0 ? 0 0 0 - - 0 0 0 – 1 0 0 1 0 0 1 0 0 - -
26. *Hybocrinus*: 0 0 0 6 ? 1 0 0 - - - - - - - 1 1 1 1 - - 0 0 1 1 1 0 0 - ? 1 ? 0 0 0 0 0 0 ? 0 ? 0 0 0 ? – 1 1 2 - - 0 0 0 0 0 - - 0 - -
27. *Eurekablastus*: 0 1 1 9 1 1 4 0 - - - - - - - 1 0 0 1 - - 0 0 1 1 ? 0 0 – 0 0 0 1 0 0 1 0 0 ? ? ? 1 0 0 - - 0 0 0 – 1 0 0 1 0 0 1 0 0 - -
28. *Canadocystis*: 0 1 0 1 0 1 ? ? ? - - - - - - 1 ? 0 1 - - 0 0 0 0 ? ? 0 – 1 ? ? 0 0 0 0 0 1 ? ? ? 1 1 ? - - 0 0 0 – 1 0 1 0 0 0 1 0 0 - -

Appendix 3-4

Constraint Text Placed within PAUP*

constraint = (Gogia, ((H._salmoensis, H._scutellus, H._cylindricus, Pentacystis_gibsoni, Haplosphaeronites_oblonga, Pustulocystis_pentax, Paulicystis_densus, Trematocystis_magniporatus, Eucystis_angelini, Aristocystites_bohemicus, Triamara_ventricosa, Sphaeronites_rossicum), Asteroblastus_stellatus, Cheirocystis, Eurekablastus, Stephanocrinus, Rhopalocystis, Canadocystis, Hemicosmites, Hybocrinus, (Glyptosphaerites_leuchtenbergi, Fungocystites, Dactylocystis, Estonocystis_antropoffi, Tristomiacystis, Gomphocystites_indianensis, Eumorphocystis_multiporata)));

CONCLUSIONS

The poor understanding of the evolutionary relationships of diplopore-bearing blastozoan taxa to each other, and to other blastozoan groups, has hampered our ability to assess biogeographic patterns, trait evolution, and other questions rooted in evolutionary theory.

Without a thorough understanding of the shared homologies between echinoderms, however, it is not possible to properly infer evolutionary relationships. Reinterpretations of homology have drastically changed long-held ideas of echinoderm evolution. The *Holocystites* Fauna, which has been heavily studied for over a century, was previously interpreted to have a very complicated evolutionary history, with multiple changes occurring in the ambulacral area over time. However, once a reinterpretation of the homologous elements shared between these enigmatic taxa, it became clear that the oral plating patterns of these diplopore-bearing taxa are conservative and bear the plesiomorphic plating shared among blastozoan echinoderms.

The reinterpretation of the homologous elements shared between *Eumorphocystis* and early crinoids has the potential to reshape our understanding of the origin of crinoids. *Eumorphocystis* shares a number of features with early crinoids: arms comprising extraxial and axial components, a radial plate, and the presence of a coelomic canal running throughout the arm. A phylogenetic analysis utilizing this understanding of homology places *Eumorphocystis* as sister taxon to crinoids. The other leading hypothesis

concerning crinoid origins, that edrioasteroids are sister taxa to crinoids, was tested utilizing a constraint analysis. The tree inferred suggests that the most parsimonious explanation of crinoid origins lies within the Blastozoa, and not edrioasteroids.

The results of these analyses were used in the final chapter of this dissertation, which focused on testing the monophyly of the traditionally ascribed Diploporita. The reinterpretations of homology were used to construct a character matrix for phylogenetic analysis. A wide variety of diplopore-bearing taxa was included, as well as a number of non-diplopore bearing echinoderms. The analysis inferred suggests that the Diploporita is polyphyletic and that diplopores likely evolved multiple times within blastozoan history. This analysis adds to a growing body of evidence that the respiratory structures typically used to delineate blastozoan groups are likely not appropriate clade-defining features, as respiratory structures are convergent. These analyses strongly suggest that the traditionally ascribed Diploporita is not a monophyletic group and a major taxonomic revision of this group is necessary.

This body of work is the first step towards better understanding the evolution of the diplopore-bearing blastozoans. As blastozoan echinoderms likely evolved in response to times of intense climate change in the early Paleozoic (e.g., Ordovician), having a phylogenetic framework for these taxa will allow for future studies of biogeography and trait evolution during these periods of climate change.

VITA

Sarah Sheffield was born in Torrington, CT in 1989 and later moved to Fayetteville, North Carolina, where she attended elementary, middle, and high school. She attended The University of North Carolina as a Carolina Covenant Scholar, where she pursued her B.S. in Geological Sciences. She attended Auburn University for her M.S., where her research focused on understanding crinoid growth and ontogeny; her research was recognized by Auburn University's College of Arts and Sciences. Upon graduation, she moved to Knoxville, TN to begin her doctoral studies at The University of Tennessee in the Earth and Planetary Sciences Department. Apart from her studies, she has been active in science education outreach through local school programs, The University of Tennesseee,'s Darwin Day program, and the McClung Museum of Natural History. Her research has been funded through numerous external grants and has been presented at multiple national and international scientific meetings.