

1 Introduction

Echinodermata is a diverse group of morphologically disparate, temporally expansive, and geographically widespread animals with nearly unparalleled levels of diversity (Smith, 1992, 2005; Mooi et al., 1994; Sumrall and Waters, 2012; Deline et al., 2018, 2020). Echinoderms have been a critical component of ecosystems for over 500 million years and have been shown to respond to changes in ocean temperatures, salinity, and oxygen content (Clausen, 2004; Dickson, 2004; Clausen and Smith, 2005, 2008; Zamora and Smith, 2008; Rahman and Zamora, 2009). As such, they are a valuable group in assessing broad macroevolutionary patterns and change through time, from the Cambrian to modern times. A considerable effort to elucidate the echinoderm evolutionary tree of life has been undertaken in the past few decades, specifically with establishing evolutionary relationships with both extinct and extant taxa (e.g., Smith, 1992; Bodenbender and Fisher, 2001; Janies, 2001; Ausich et al., 2015; O'Malley et al., 2016; Bauer et al., 2017, 2019; Cole, 2017; Thompson et al., 2017; Wright et al., 2017; Sheffield and Sumrall, 2019a, b; Kroh, 2020). However, there are many unresolved questions about how many echinoderm groups are related to one another, especially those in the Paleozoic.

Echinodermata is linked as a phylum by a number of synapomorphic traits: a radial symmetry superimposed over bilateral symmetry, a skeleton of stereom calcite, and a water vascular system (Ubaghs, 1968a; Bottjer et al., 2006; Rahman and Zamora, 2009). While the water vascular system (WVS) varies broadly in the different echinoderm groups and has been suggested to have multiple functions, including feeding, locomotion, and/or respiration (Briggs et al., 2017), the vast majority of our knowledge of the WVS is limited to extant echinoderms, which all possess tube feet. In extinct forms, most of our knowledge of the WVS comes from calcified structures and rare instances of soft-tissue preservation. Some examples of this fossil evidence include asteroids from Upper Ordovician rocks of Kentucky, USA and Shropshire, UK (Spencer, 1916; Gale, 1987; Glass, 2006). Other examples include edrioasteroids from Silurian rocks of the United Kingdom (Briggs et al., 2017) and a stylophoran from Lower Ordovician rocks of Morocco (Lefebvre et al., 2019).

It is easier to envision the tube feet of extinct groupings with modern equivalents (e.g., asteroids, echinoids), but for extinct echinoderms that have no modern-day equivalents, such as blastozoans, it is less clear how tube feet would have looked and functioned, and it is likely they may not have had them at all. Breimer and Macurda (1972) suggested additional respiratory function may have occurred in blastoids, as it does in extant crinozoans, through epithelial cells of the podia and the ambulacral epidermis. However, blastoids may not be an appropriate

model of comparison to other blastozoans, as other brachiole-bearing blastozoans lack the ambulacral groove system of blastoids. As of yet, tube feet have not been documented in blastozoan respiratory structures, nor have they been identified in concert with the ambulacral feeding structures (Sprinkle, 1973). Further clarification is required in the form of exceptionally preserved fossils, which may show rare soft-tissue preservation (such as those discussed previously), and a rigorous phylogenetic framework; this is a key area of future research.

Blastozoan echinoderms, a large group that encompasses broad diversity and high disparity of extinct echinoderms, waxed and waned in presence throughout the Paleozoic (Sprinkle, 1973; Nardin and Lefebvre, 2010; Lefebvre et al., 2013). Blastozoa has a combined temporal distribution from the early Cambrian to the late Permian, with several classes within it (Fig. 1) (Sprinkle, 1973; Broadhead, 1980; Sumrall and Waters, 2012). Other groups have been included in and removed from Blastozoa over the past few decades (e.g., Brett et al., 1983; David et al., 2000); while a consensus of which groups phylogenetically belong in Blastozoa is still unclear, in this Element we present the groups as outlined by Sprinkle (1973) and Sumrall and Waters (2012), including Blastoidea, Eocrinoidea, Diploporita, Rhombifera, Paracrinoidea, and Parablastoidea.

Researchers originally linked Blastozoa as a subphylum by some combination of unifying traits (though not all blastozoans have all of these traits): multiple small, biserial food-gathering appendages (i.e., brachioles), the presence of respiratory structures, which exist as either external or internal features in the form of pores or fold-like slits, plates exhibiting holoperipheral growth, and a holdfast or columnar-bearing stem (Sprinkle, 1973). The respiratory structures, especially, have been used to separate the subgroups within Blastozoa (e.g., Diploporita, Blastoidea). However, the array of diversity present in these respiratory structures does not fall easily into these groupings; there is significant convergence in the respiratory structures that requires close analysis to better understand evolutionary patterns.

This Element aims to provide a comprehensive review of the morphology of the respiratory structures within each of the main blastozoan groups, along with a review of the ontogeny, paleoecology, and functional morphology literature that has been previously published. We consider where these respiratory structures are convergent and do not appear to accurately define major evolutionary groupings. Finally, we identify areas of future study within these groups.

2 Assessing Blastozoan Echinoderm Evolutionary Relationships

Some of the difficulties with understanding the evolutionary relationships of extinct echinoderms comes from (1) the role that taphonomic, geographic, and

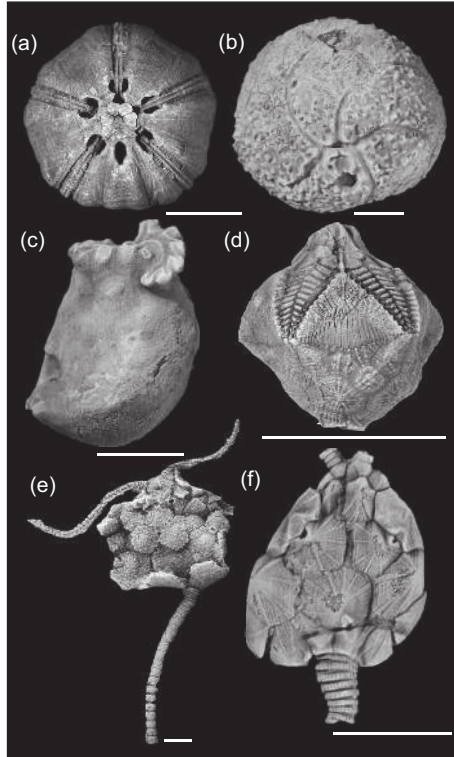


Figure 1 Traditional blastozoan groupings. a. Oral view of blastoid *Nucleocrinus* sp. Conrad, 1842 (USNM 455893). b. Oral view of diploporan *Gomphocystites indianensis* Miller, 1889 (FMNH 19708; modified from Sheffield and Sumrall, 2017). c. Lateral view of paracrinoïd *Canadocystis tennesseensis* Parsley and Mintz, 1975 (USNM 241272). d. Lateral view of parablasteroid *Eurekablasterus ninemilensis* Sprinkle and Sumrall, 2008 (TMM 1778TX14; modified from Sprinkle and Sumrall, 2008). e. Lateral view of eocrinoid *Ubaghsicystis segurae* Gil Cid and Domínguez Alonso, 2002 (MNCN-I-30849; modified from Zamora, 2010). f. Lateral view of rhombiferan *Pleurocystites squamosus* Billings, 1854 (CMC-IP 39537; modified from Zamora et al., 2017), anterior-posteriorly flattened. Scale bars a, c, d= 10 mm. b, e, f= 5mm. Specimens whitened with ammonium chloride sublimated.

temporal biases play in the understanding of fossil diversity; (2) the broad morphological disparity that is exhibited in Echinodermata and within Blastozoa; and (3) the difficulty in reconciling homologous elements between different disparate taxa.

Many of the limitations of our knowledge of extinct echinoderms are ultimately derived from biases in the fossil record. While many echinoderms have lower preservation potential than other fossil groups due to their skeletons with numerous, easily disarticulated plates (Lewis, 1980; Brett et al., 1997), and while delicate brachiole plates and oral area plates often are not preserved with the thecal body (Sheffield and Sumrall, 2017), the lack of preservation of blastozoans extends beyond preservation bias with significant temporal and geographic biases. Geographically, an unbalanced effort to discover new echinoderm fossils has been concentrated in Laurentian, Baltic, and Avalonian deposits, while other areas (i.e., South China, Gondwana) have remained comparatively much less documented until recently (Miller, 2000; Tarver et al., 2007; Sumrall and Zamora, 2011; Lefebvre et al., 2013; Sumrall et al., 2013; Lam et al., 2021) and many areas remain poorly explored for fossils, a phenomenon that is also seen in other fossil groups as well. Single or limited fossil finds of blastozoan fossils in either previously unexplored areas or rare preservational types have been able to drastically alter what was once thought to be known of blastozoan evolutionary trends (Zamora et al., 2013b, 2017; Sumrall et al., 2015); as an example, recent finds of a holocystitid diploporan in Australia (Jell, 2010) extended the biogeographic range of a group that was largely contained to the Laurentian Cincinnati Basin (Paul, 1971; Lam et al., 2021; Sheffield et al., 2022).

Critical transitions in invertebrate evolution, and echinoderm evolution specifically, such as the transitions across the Cambrian–Ordovician boundary and the Ordovician–Silurian boundary, are underrepresented in the rock record due to global lowstands of the seas (Smith, 1988; Vennin et al., 1998; Peters and Ausich, 2008; Zamora, 2012; Sheffield et al., 2018). With taphonomic, geographic, and temporal bias compounded, it often means that critical data points are lost. Many groups of blastozoans are present in the Cambrian, but the poor fossil record, with an extremely low number of echinoderm-bearing formations from the late Cambrian, limits our understanding of diversity and evolutionary change through this time (Zamora et al., 2013b, c). Exceptions exist, such as Cambrian-age fossil discoveries of *Macrocystella* Callaway, 1877, and *Sanducystis* Zamora et al., 2017, which illuminate the evolutionary pathway of respiratory structure evolution in glyptocystitid rhombiferans (Aceñolaza, 1986, 1999; Zamora et al., 2017).

While many critical pieces of fossil evidence have not yet been discovered, we know that early echinoderms diversified rapidly across the Cambrian Explosion and continued this expansion through the Great Ordovician Biodiversification Event of the Darriwilian (Stigall et al., 2019), which resulted

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in high morphological disparity and high diversity (Sprinkle, 1980; Sumrall and Waters, 2012; Sheffield and Sumrall, 2019b; Deline et al., 2020). This high disparity and diversity is reflected in the erection of approximately 21 classes assigned to Echinodermata that have evolved over the past 500 million years (though many of these groups are likely polyphyletic or paraphyletic; Bodenbender and Hiemstra, 2004; Lefebvre et al., 2013). A recent study of echinoderm disparity by Deline et al. (2020) indicated that throughout the Cambrian and the Ordovician extinction events, the differences between echinoderm groups were heightened and multiple events of convergent evolution throughout this time blurred what can be easily learned about broad evolutionary patterns.

While blastozoans have traditionally been subdivided primarily based on the presence of types of respiratory structures (Sprinkle, 1973; Brett et al., 1983), a number of studies have indicated that many of the respiratory structure types of blastozoans are likely convergent and, therefore, are not appropriate features to define natural groups (Paul, 1968, 1988; Sumrall and Sprinkle, 1995; Sumrall and Gahn, 2006; Sumrall, 2010; Sumrall and Waters, 2012; Sheffield and Sumrall, 2019a). Paul (1968b) hypothesized that many different respiratory structures developed in the Paleozoic independently from one another and that grouping organisms together would obscure their true evolutionary relationships. To better estimate these relationships and determine whether respiratory structures can be accurately used to define large taxonomic relationships, it is critical to understand and evaluate the homologous elements between taxa through phylogenetic analysis (Sumrall, 1997).

Previous work to develop homology schemes has been subgroup specific (e.g., eublastoids or crinoids), making it difficult to reconcile homologies and separate out convergent characters across these groups. The universal elemental homology (UEH) model (Sumrall, 2010, 2017; Sumrall and Waters, 2012) was constructed to clarify terminology across derived blastozoan groups and classify homologous elements of the oral and ambulacral areas. This hypothesis was later expanded to include plesiomorphic blastozoans, edrioasteroids, and crinoids (Kammer et al., 2013). Universal elemental homology uses the Carpenter system (Carpenter, 1884) to identify plates bordering the peristome and ambulacra of blastozoan echinoderms. The extraxial-axial theory (EAT) model, another echinoderm homology scheme that was originally based on echinoid echinoderms, subdivided the echinoderm skeletons into either axial (i.e., associated with the mouth and ambulacra) or extraxial (i.e., associated with the body wall; Mooi et al., 1994; Mooi and David, 1997, 1998, 2008; David et al., 2000; Paul, 2017).

Regardless of the homology scheme(s) employed, it is critical to test these hypotheses of homology with a phylogenetic framework, as opposed to traditional systematic studies that elevate certain characters as holding more weight in determining taxonomic groupings (see Sumrall, 1997, for a thorough analysis of the three tests of homology developed in Patterson, 1982, and examples using echinoderm fossils). To determine whether or not specific types of respiratory structures are synapomorphic features for blastozoan groups (e.g., epispires of eocrinoids, diplopores of diploporans), it is necessary to perform phylogenetic analyses with careful consideration of homology. While evaluating the phylogenetic legitimacy of blastozoan groupings is outside the scope of this review, we address the advances in respiratory structure research and consider the convergence seen in the respiratory structures across the blastozoan groupings.

3 Respiratory Structures

Blastozoan respiratory structures have been classified in a number of ways (Table 1), which have been used to delineate large taxonomic groupings in the past, though phylogenetic data from more recent studies do not support these respiratory structures as being group-defining traits (e.g., Nardin and Bohatý, 2012; Sheffield and Sumrall, 2019a). Sprinkle (1973) categorized respiratory structures in the following manner: sutural pores/epispires (such as those found in eocrinoids), fold-like respiratory structures (such as cataspores found in parablastoids), crinozoan respiratory structures (those found in some crinoids), and diploporan respiratory structures (those found in diploporans). Paul (1968b, 1972) introduced another method of categorizing these pores as “endothecal” (i.e., gas exchange occurring inside the theca, with external pores connecting to internal folds through which seawater circulates) or “exothecal” (i.e., gas exchange occurring outside the theca, via internal pores connecting canals within the thecal plate, through which body fluids circulate). Endothecal respiratory structures are lightly calcified infoldings of the body wall and commonly well preserved in specimens with complete thecae (Paul, 1968b; Sprinkle, 1973; Sprinkle and Sumrall, 2008; Sumrall and Waters, 2012); however, they can be difficult to examine in a comprehensive manner because well-preserved thecae are tightly sutured. These internal structures can be examined in greater detail through serial sectioning of specimens (destructive in nature) or through more advanced nondestructive techniques such as X-ray computed tomography (see Bauer and Rahman, this volume, for a detailed discussion on virtual paleontology). Examples of endothecal respiratory structures include hydrospires in eublastoids and cataspores of parablastoids, both of which are also classified as fold-like structures.

Table 1 Blastozoan subgroupings and their associated respiratory structures. Locations of descriptions (e.g., Beaver et al., 1968 and Sprinkle, 1973), and figures within this Element also included. T

	Respiratory Structure	Type	Location	Invertebrate Treatise
Eocrinoidea	Epispires (sutural pores)	Exothecal, single pores	Thecal plate sutures, random or adoral	Part S, Volume S455–4
Rhombifera	Pectinirhombs	Endothecal folds	Thecal plates, random or 3 fixed positions	Part S, Volume S85–26
	Cryptorhombs	Endothecal folds	Thecal plates, multiple identified arrangements	Part S, Volume S85–26
	Humatirhombs	Exothecal, tubes and canals	Internal surface of thecal plates	Part S, Volume S85–26
Parablastoidea	Cataspikes	Endothecal folds	Under deltoids, from radials to ambulacra	Part S, Volume S293–2
Eublastoidea	Hydrospires	Endothecal folds	Inside theca with external openings (slits, pores) adjacent to ambulacra	Part S, Volume S398–4
Coronoidea	Coelomic (coronal) canals	Exothecal, canals	Coronal crests, radial plates	Part S, Volume S389–3

Table 1 (cont.)

	Respiratory Structure	Type	Location	Invertebrate Treatise
<i>Lysoecystites</i>	Unnamed	Exothecal, covered pores with internal canals	Thecal plates and sutures	Part S, Volume 1, S487–490
<i>Macurdablastus</i>	Unnamed	Endothecal fold	Inside theca, external openings unknown but span ambulacral length	N/A
Diploporita	Diplopores	Exothecal, double pores	Through thecal plates, often random	Part S, Volume 1, S85–266
	Humatipores	Exothecal, double pores	Through thecal plates, often random	Part S, Volume 1, S85–266
Paracrinoidea	Epispires (sutural pores)	Exothecal, single pores	Thecal plate sutures	Part S, Volume 1, S268–269

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Exothecal respiratory structures are generally characterized by external surfaces where gaseous exchange occurred, which can be found in groups such as eocrinoids, paracrinoids, some rhombiferans, and diploporans. It is presumed that soft tissue covered exothecal pore structures. There are some taxa within all of these groups, but particularly paracrinoids and eocrinoids, that do not possess any form of specialized respiratory structures (Parsley and Mintz, 1975; Broadhead, 1980; Nardin, 2007; Sheffield and Sumrall, 2019a). Those lacking respiratory structures still likely respired exothecally, as respiration is assumed to have occurred across thecal plate surfaces (Broadhead, 1980).

Both endothecal and exothecal respiratory structures are found in single classes of blastozoans (e.g., Rhombifera includes taxa that possess endothecal and exothecal respiratory structures). In some special cases, both endothecal and exothecal structures can be found in the same organism. For example, the eublastoid species *Troosticrinus reinwardti* Shumard, 1866, possesses endothecal hydrospires and exothecal coronal/coelomic canals (Sumrall and Waters, 2012). These complexities have made it difficult to reconcile homology, determine synapomorphies, and understand Blastozoa as a subphylum.

3.1 Functionality and Efficiency

Inferring functional morphology of the respiratory structures of blastozoans has been challenging. While it is now accepted that the structures themselves are, in fact, for respiration, other hypotheses have been suggested. Other proposed functions for these structures included nutrient intake (Hyman, 1955), balancing organs (Delpey, 1941), and reproduction (Katz and Sprinkle, 1976). Paul (1968b) refuted the idea that the respiratory structures could be used for balance, as the structures are often not evenly distributed across the body, something that is particularly true for taxa with exothecal structures. Some blastozoans lack respiratory structures altogether, indicating that they would certainly need other processes to facilitate nutrient intake and reproduction, which renders it unlikely that these structures functioned for other vital purposes. In the past, these inferences of functional morphology were based heavily on expert systematic opinions and the discussions were based on visible morphologic structures and comparisons to other living organisms. Now, with the advancement of virtual paleontological techniques to generate digital fossils (see Bauer and Rahman, this volume) in concert with computational fluid dynamics (e.g., Rahman et al., 2015, 2020; Rahman, this volume) the functionality, efficiency, and life mode can be more quantitatively addressed.

The hydrospires of eublastoids have received the most attention due to the complexity and well-preserved nature of these endothecal structures (Macurda,

1965; Beaver, 1968; Katz and Sprinkle, 1976; Schmidting and Marshall, 2010; Huynh et al., 2015; Waters et al., 2017). Waters et al. (2017) suggested active flow through the structures, likely driven by cilia, and determined that the functionality of hydrospires is far more complex than previous interpretations suggested. However, as hydrospires are already considered to be the most advanced blastozoan respiratory structures, making comparisons to other types of respiratory structures is difficult. Huynh et al. (2015) constructed both digital and physical hydrospire models based on the same sections used in Schmidting and Marshall (2010) with the goal of examining how incurrent seawater enters the pores and moves through the hydrospire structures.

Determining functional efficacy of non-eublastoid blastozoans has been more straightforward due to the generally simpler structure allowing for an understanding of functionality (e.g., Paul, 1972; Paul and Bockelie, 1983; Huynh et al., 2015). However, there have been considerably fewer studies examining functionality in non-eublastoid blastozoans.

Hypotheses of efficiency have been proposed for some exothecal respiratory structures, such as diplopores, under the assumption that respiratory capacity is directly related to the area of respiratory surfaces present on the theca. The essential controls governing the understanding of efficiency presented in these studies are as follows: (1) the area of exchange surface (i.e., the larger the surface area, the greater amount of potential gas exchange for respiration); (2) the resistance to exchange (i.e., the thinness and thickness of thecal plates; thinner plates have less resistance to gas exchange); and (3) the concentration gradient across the exchange surface (Paul, 1972, 1973). Most studies on functionality of respiratory structures have posited that exothecal pore structures are overall less efficient than endothecal respiratory structures (e.g., Paul, 1972; Bockelie, 1984), which is an idea that is supported by fossil data. Taxa with exothecal respiratory structures generally have a much higher density of the respiratory structures than those with endothecal structures (e.g., diploporeans compared with eublastoids). Many fossil taxa that do not have respiratory structures have noticeably thinner plates (e.g., eocrinoids), further supporting hypotheses of respiratory structure efficiency presented in Paul (1972, 1973). Nardin (2007) hypothesized that the thinner plates without respiratory structures were likely more efficient than if they had had respiratory structures.

4 Materials

All photographed specimens are housed in research collections from the following museums or institutions: The University of Iowa (SUI), Miami University (MUGM), Prague National Museum (NM), Museo de Ciencias