Contributions

from the Museum of Paleontology, University of Michigan

VOL. 34, NO. 9, PP. 123–140 MAY XX, 2022

MORPHOLOGICAL DYNAMICS AND RESPONSE FOLLOWING THE DISPERSAL OF ORDOVICIAN–SILURIAN DIPLOPORAN ECHINODERMS TO LAURENTIA

BY

SARAH L. SHEFFIELD[1], ADRIANE R. LAM[2], STEPHEN F. PHILLIPS[3], AND BRADLEY DELINE[3]

Abstract — The Late Ordovician Mass Extinction (LOME) left vacated niche space and brought about significant changes in echinoderm community structures across Laurentia. New echinoderm communities, having migrated into Laurentia from Baltica, did not fully establish themselves until the middle Silurian. However, the details of the evolutionary dynamics of non-crinoid echinoderms across the Ordovician–Silurian boundary is understudied. Herein, we examine the evolutionary dynamics of a clade of extinct echinoderms, the sphaeronitid diploporans. Using a combination of phylogenetic, morphologic, and biogeographic data, we analyze how sphaeronitids evolved and dispersed across the LOME and filled unoccupied niches during the Silurian in Laurentia. Analyses indicate that one dispersal event occurred from Baltica into Laurentia, during the Middle to Late Ordovician, leading to the enigmatic and well-known *Holocystites* Fauna populating central North America. As the holocystitids filled the unoccupied niches from the LOME, there was no significant expansion of morphological forms, which could be related to the narrow, previously established niches that crinoids vacated during the LOME, or possibly due to developmental constraints within the clade. Although morphological change is constrained during this event, there are some significant changes in community structure (i.e., certain species of diploporans became unusually abundant) and body size (i.e., Laurentian specimens approximately doubled in size compared to Baltic taxa). These changes indicate the importance of competitive release and dispersal events in understanding evolutionary dynamics of fossil taxa.

INTRODUCTION

The faunal composition of filter-feeding echinoderms experienced a dramatic shift across the Late Ordovician Mass Extinction. In crinoids, the fossil record shows a transition from the Ordovician early Paleozoic Crinoid Evolutionary Fauna to the Silurian–middle Mississippian middle Paleozoic Crinoid Evolutionary Fauna (Ausich et al., 1994; Baumiller, 1994; Ausich and Deline, 2012; Deline et al., 2012). This change included crinoid communities being dominated by

[1]School of Geosciences, University of South Florida, NES 107, 4202 E. Fowler Avenue, Tampa, FL, 33620, U.S.A. (ssheffield2@usf.edu).
[2]Department of Geological Sciences and Environmental Studies, Binghamton University SUNY, 165A Science 1, P.O. Box 6000, Binghamton, NY 13902, U.S.A. (alam@binghamton.edu)
[3]Department of Natural Sciences, University of West Georgia, 1601 Maples Street, Carrollton, GA, 30118, U.S.A. (Sfphillips.32@gmail.com; bdeline@westga..edu)

diplobathrid camerate, disparid, and hybocrinid crinoids to communities more dominated by monobathrid camerate, cladid, and flexible crinoids. Crinoids are dominant in Paleozoic echinoderm faunas in terms of abundance and diversity, such that their dynamics are more intensely studied. Whether a similar faunal turnover occurred within blastozoan echinoderms is largely unstudied as are the ramifications of changes in crinoid faunal structures on blastozoan communities.

Although this fundamental shift in echinoderm communities has been largely documented within crinoids, similar patterns in other filter-feeding echinoderms also occurred. These echinoderms were clearly responding to large climatic perturbations throughout the Late Ordovician–Silurian through changes in their biogeographic range, morphological disparity, and community presence. The ability to understand these evolutionary patterns in non-crinoid echinoderms has been negatively influenced by a lack of phylogenetic trees upon which to test hypotheses. In blastozoan echinoderms especially, many of the studies that have preliminarily explored global patterns (e.g., Lefebvre, 2007; Nardin and Lefebvre, 2010; Lefebvre et al., 2013; Zamora et al., 2013), such as responses to global climate changes or biogeography, treated many groups of echinoderms as monophyletic due to an absence of published phylogenetic hypotheses on these taxa. Many of these studies noted the likely non-monophyletic nature of these groups (e.g., Lefebvre et al., 2013). Such is the case with Diploporita (blastozoans with double pore respiratory structures). Many have previously hypothesized that Diploporita is polyphyletic (Paul, 1988; Sumrall, 1997; Lefebvre et al., 2013). A phylogenetic study demonstrated that this group is polyphyletic using quantitative-based methods and therefore, previous understandings of evolutionary patterns must be reassessed in light of this new information (Sheffield and Sumrall, 2019a).

Early echinoderms are excellent models for testing hypotheses of faunal responses to global climatic patterns, as these echinoderms encompass highly complex body morphologies that are disparate across different groups (Deline et al., 2020) and have been shown to be responsive to changing long-term oceanic and climatic patterns (Lefebvre and Fatka, 2003; Clausen, 2004; Dickson, 2002, 2004; Zamora and Smith, 2008; Rahman and Zamora, 2009; Sumrall et al., 2015; Lam et al., 2021). The early Paleozoic is also an excellent time in Earth's history for testing these hypotheses, specifically as the Ordovician and Silurian systems encompass great changes in climatic regimes and biotic interactions (e.g., Jeppson, 1990, 1997; Trotter et al., 2006; Finnegan et al., 2011; Albanesi et al., 2019; Stigall et al., 2019).

Major biodiversity and climatic events across the Ordovician to Silurian, combined with robust phylogenetic hypotheses, allow for the examination of interactions between evolutionary dynamics and external factors for echinoderm groups. This study focuses on an enigmatic group of Paleozoic echinoderms, the sphaeronitid diploporans, a clade of diplopore-bearing taxa. This group was biogeographically limited during the Ordovician but exploded in abundance during the Silurian in Laurentia, which was likely a response to both dispersal events and ecological opportunity following the Late Ordovician extinction and the reconfiguration of echinoderm filter feeding niches. This transition allows for the direct testing, using statistically-informed biogeographic and phylomorphospace methods, of the morphological response to competitive release, ecological opportunity, and dispersal that led to the establishment of the iconic diploporan holocystitid fauna.

BACKGROUND

The Ordovician and Silurian Earth Systems

The Ordovician system was a period of major climatic shifts, beginning with relatively high sea levels and warmer temperatures in the Early Ordovician, with shorter intervals of cooler climates and sea level falls (e.g., Trotter et al., 2008; Albanesi et al., 2019). Into the later Ordovician, a transition from greenhouse-dominated climates to an icehouse occurred, a shift that began in the Floian and grew in intensity into the Late Ordovician (Trotter et al., 2008). These events culminated in the Late Ordovician Mass Extinction (LOME), which was a two-pulsed extinction event. The first pulse, marking the Katian and Hirnantian boundary, has been closely linked to the transition to an icehouse climate and the rapid growth of continental ice sheets on Gondwana (Finnegan et al., 2011), with continental configuration likely playing a role in extinction intensity during this first extinction pulse (Saupe et al., 2020). The second event of the LOME, occurring in the later part of the Hirnantian, is linked to the sudden warming of the oceans and subsequent receding glaciers, which may have caused occurrences of ocean anoxia (Brenchley et al., 1994; Sheehan, 2001; Melchin et al., 2013). How echinoderms responded to these events is uncertain, as the glaciation and subsequent global lowstand that extended from the Late Ordovician throughout the early Silurian, was not conducive to fossil preservation (Smith, 1988; Vennin et al., 1998; Peters and Ausich, 2008).

The Silurian was also characterized by biotic events (e.g., the Ireviken, Mulde, and Lau events; Jeppson, 1990, 1997, 1998; Aldridge et al., 1993; Štorch, 1995), swings in the carbon cycle, temperature oscillations, and second- to third-order sea level changes as a result of tectonic activity (Loydell, 1998; Johnson, 2006, 2010; Haq and Schutter, 2008; Trotter et al., 2016). Such sea level changes led to large disconformities, contemporaneous within the stratigraphic records of Laurentia, Baltica, and Gondwana (Cramer and Saltzman, 2005). Namely, a large disconformity near the Llandovery-Wenlock boundary indicates that the extensive Late Ordovician glaciation continued into the Silurian (Grahn and Caputo, 1992; Finnegan et al., 2011); direct stratigraphic evidence of this glaciation in the Silurian can be found in the Soom Shale, where a record dated to the Hirnantian-Llandovery transition preserves glacial indicators (Gabbott et al., 2010; Gabbott et al., 2017; Vandenbroucke et al., 2009). Such disconformities from the glaciation and lowered

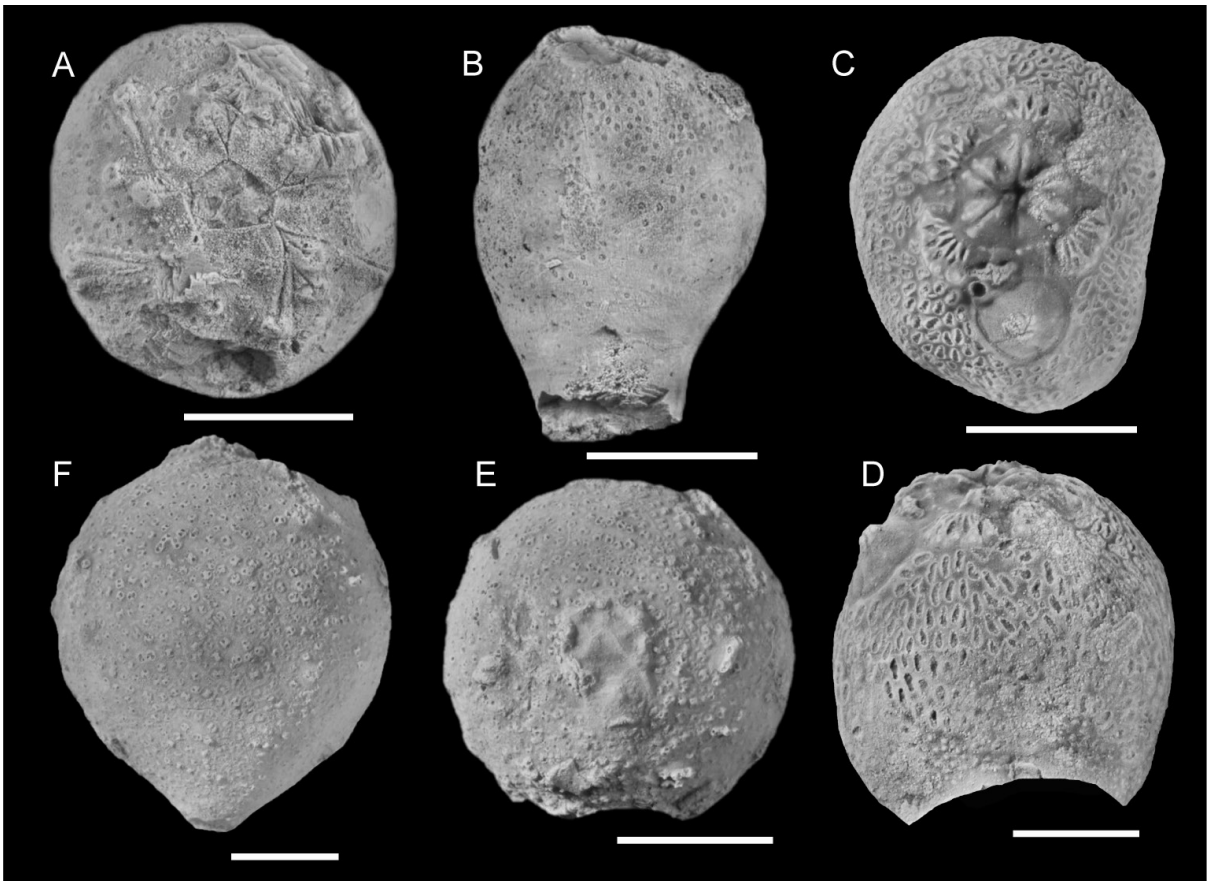

FIGURE 1 — Representative diploporan taxa from Baltica. **A**, Oral view of *Eucystis angelini* (NM-L7695). **B,** Side view of *Eucystis angelini* (NM-L7694). **C**, Oral view of *Haplosphaeronis*. (GIT 540-3). **D,** Side view of *Haplosphaeronis*. (GIT 540-3). **E**, Oral view of *Sphaeronites rossicum globosus* (GIT 540-54). **F**, Side view of *Sphaeronites rossicum globosus* (GIT 540-54). A, B, C, D modified from Sheffield and Sumrall, 2019a. Specimens whitened with ammonium chloride sublimated. Scale bars = 0.5 cm.

sea levels have made the evolutionary history of diploporan echinoderms, as well as their paleobiogeographic patterns through the early Paleozoic, extremely difficult to infer.

Sphaeronitid Diploporans and the *Holocystites* Fauna

Diploporan blastozoans encompass broad morphological diversity and disparity (Paul, 1988; Sheffield and Sumrall, 2019a; Deline et al., 2020). Phylogenetic analyses (Sheffield and Sumrall, 2019a, 2019b) showed that Diploporita is a polyphyletic group, and because of that, analyses of evolutionary patterns cannot rely on treating Diploporita as a monophyletic entity (Lam et al., 2021). Of the traditional groups named within Diploporita, only one has been recovered as a clade, the Sphaeronitida (Paul, 1988; Sheffield and Sumrall, 2019a), the clade of focus in this study (Figs. 1, 2). The sphaeronitids are united by several synapomorphic traits; namely, short ambulacral grooves that are restricted to the oral area, and a lack of floor plating associated with the ambulacral grooves (Sheffield and Sumrall, 2019a). Within the sphaeronitids, there are two smaller clades. The first clade comprises diploporans that have branching ambulacral grooves each ending in single brachiole facets (e.g., *Eucystis* (Figs. 1A–B), *Haplosphaeronis* (Figs. 1C–D), and *Sphaeronites* (Figs. 1E–F)), and the second comprises diploporans that have unbranching ambulacra ending in a single, terminal brachiole facet (e.g., *Pentacystis* (Figs. 2A–B), *Trematocystis* (Figs. 2C–D), *Holocystites* (Figs. 2E–F), and *Paulicystis* (Figs. 2G–H)).

Diploporans are first known from Lower Ordovician rocks and reached relatively high species diversity throughout the Ordovician (Lefebvre et al., 2013; Sheffield and Sumrall, 2019a). While these species reached a global distribution, there were few Ordovician occurrences of diploporans in Laurentia, with some exceptions such as *Eumorphocystis* of the Bromide Fauna (Branson and Peck, 1940; Sprinkle, 1980) and some more recent finds from the Late Ordovician, such as a diploporan from Anticosti Island (Sheffield et al., 2017). The majority of diploporan taxa did not survive across the LOME, but of those taxa that did survive, they primarily belonged to

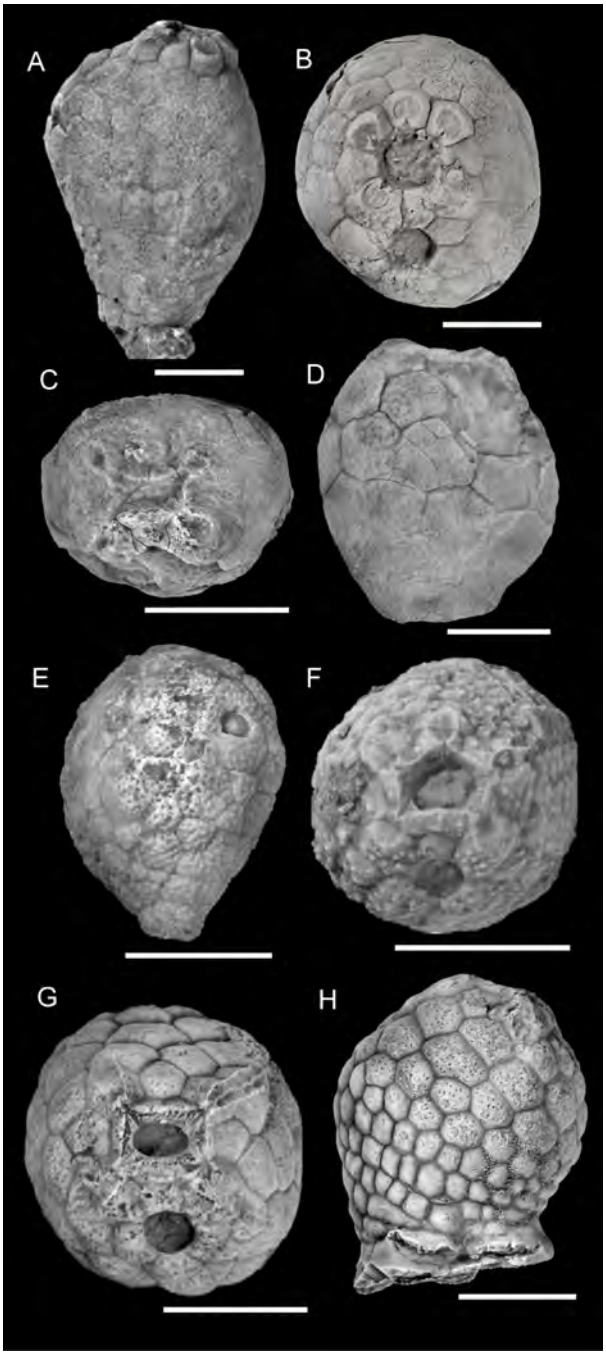

FIGURE 2 — Representative diploporan taxa from Laurentia. **A**, Side view of *Pentacystis gibsoni* (SUI 46316). **B**, Oral view of *Pentacystis gibsoni* (SUI 46316). **C**, Oral view of *Trematocystis magniporatus* (SUI 48198). **D**, Side view of *Trematocystis magniporatus* (SUI 48198). **E**, Side view of *Holocystites scutellatus* (SUI 48183). **F**, Oral view of *Holocystites scutellatus* (SUI 48183). **G**, Oral view of *Paulicystis sparsus* (SUI 48164). **H**, Side view of *Paulicystis sparsus* (SUI 48164). All modified from Sheffield and Sumrall, 2017. Specimens whitened with ammonium chloride sublimated. Scale bars = 1 cm.

the sphaeronitid clade. Similar to their taxonomic contraction, diploporans also saw a reduction in their biogeographic range and were less common globally, but they did become far more common in Laurentian strata. Sphaeronitids proliferated across central North America in the Silurian (Fig. 2), predominantly as a group informally known as the *Holocystites* Fauna (Paul, 1971; Frest et al., 2011; Sheffield and Sumrall, 2017).

The *Holocystites* Fauna is an enigmatic group that has been the focus of great scientific discussion due to their taphonomic patterns, evolutionary relationships, and their biogeographic history (Paul, 1971; Frest et al., 2011; Thomka et al., 2016; Sheffield and Sumrall, 2017, 2019a; Lam et al., 2021). Holocystitids are morphologically distinct from other diploporans and even other sphaeronitids, with a specialized type of respiratory structure (calcified, buried dipore structures called humatipores, as opposed to non-calcified, surficial diplopores), unusually large brachiole facets, a holdfast as opposed to a stem, and an enlarged mouth (Sheffield and Sumrall, 2019a). The *Holocystites* Fauna is also iconic for the sheer numbers in which they are found. Unlike the majority of other diploporan species, these holocystitids are ubiquitous in middle Silurian echinoderm deposits, with an extremely high number of fossilized specimens. Until recently, it was thought that the group existed exclusively within the middle Silurian, until a Late Ordovician representative was found (Sheffield et al., 2017).

Crinoid Faunal Dynamics Across the Ordovician–Silurian

Early Paleozoic echinoderms showed a steady morphological expansion away from the forms found in the Cambrian (Deline et al., 2020). Subsequent extinctions of transitional forms and increased stereotypy within body plans established fairly discrete and distinctive clusters by the Middle Ordovician. However, an increase in convergent evolution and continual evolutionary flexibility dampened the distinctiveness of higher order taxonomic body plans during the Late Ordovician (Deline et al., 2020). This pattern through the early Paleozoic resulted in the sustained ability within echinoderms for taxonomic, morphologic, and ecological turnover events.

These ecological turnover events have been most explored within crinoids, which experienced a dramatic shift throughout the Ordovician, including the LOME, which is known as the transition from the early to the middle Paleozoic Crinoid Evolutionary Faunas (Ausich et al., 1994; Ausich and Deline, 2012; Cole and Wright, 2021). During the LOME crinoid communities changed from being dominated by diplobathrid camerate, disparid, and hybocrinid crinoids to those dominated by monobathrid camerate, cladid, and flexible crinoids. Crinoid ecology and niche occupation are often closely tied to broad taxonomy (e.g., subclass), such that the transition between crinoid evolutionary faunas can be seen as an ecologic as well as a taxonomic event (Kammer and Ausich, 1987; Cole et al., 2019; also see Wright et al., 2017 for detailed analysis of Paleozoic crinoid systematics). These ecological differences

can also appear at lower taxonomic levels (e.g., family); in particular, lower tier crinoids with simple, unbranching, stout arms either went extinct (Porocrinidae) or suffered higher extinction rates (Hybocrinidae) during the transition between crinoid evolutionary faunas (Ausich and Deline, 2012). The ecological effect of the loss of this crinoid body plan (simple, unbranching, stout arms) was exaggerated with a significant reduction in blastozoan diversity into the Silurian (Nardin and Lefebvre, 2010). This transition likely left open niche space within the fairly structured filter-feeder community, thus enabling the establishment of broad-armed lower-tiered blastozoans such as sphaeronitid diploporitans.

INSTITUTIONAL ABBREVIATION

All taxa studied for this analysis are listed in Table 1. The specimens examined were largely limited to type specimens to ensure that the specimen data corresponded to the named species within the analyses. All specimens are housed in research collections from the following museums or institutions:

CMCIP	—	Cincinnati Museum Center, Cincinnati, Ohio, United States of America.
FMNH/UC	—	Field Museum of Natural History, Chicago, Illinois, United States of America.
GIT	—	Geological Institute of Tallinn, Tallinn, Estonia.
GSC	—	Geological Survey of Canada, Ottawa, Canada.
SUI	—	The University of Iowa, Iowa City, Iowa, United States of America.

METHODS

Time Calibrated Phylogenetic Hypothesis

We used a phylogenetic hypothesis of blastozoan echinoderms published in Sheffield and Sumrall (2019a), which tested the hypothesis that Diploporita was not a monophyletic group. Sheffield and Sumrall (2019a) chose representative species for each genus used in the analysis (with one exception where more than one species per genus was included, *Holocystites*). In Lam et al. (2021), this same phylogenetic hypothesis was used to determine biogeographic pathways of the taxa used in the study. Stratigraphic and geographic occurrence data for species in the phylogeny was collected from published literature searches and paleontological databases (i.e., The Paleobiology Database, FossilID.info), and stratigraphic occurrence information was updated to the Geologic Time Scale 2016 ages (Ogg et al., 2016) using graptolite and conodont zones to time calibrate the phylogeny. For further details on the time-calibrated phylogenetic tree, please refer to Lam et al. (2021).

For this analysis, we were most interested in the sphaeronitids' evolutionary adaptations in terms of disparity and biogeography. Therefore, we culled non-sphaeronitid taxa from the phylogenetic analysis in Sheffield and Sumrall (2019a), leaving members of the sphaeronitid clade. It should be noted that one of the taxa used in this analysis was not identical to that in Sheffield and Sumrall (2019a); we used *Haplosphaeronis* sp. instead of *Haplosphaeronis oblonga*. This substitution was necessary, as non-compacted and relatively taphonomically complete specimens were central to performing the morphological analyses discussed below. The tree in Sheffield and Sumrall (2019a) uses a singular species of *Eucystis, E. angelini*. In the current study, we also included *E. quadrangularis* in the analyses given the morphological differences between species (i.e., differing in the number of ambulacra; *E. quadrangularis* exhibits a reduction of ambulacra from five to four). However, we are confident that both of these species clearly represent *Eucystis*, as they share the same eucystitid traits (e.g., *E. quadrangularis* also bears a 36˚ rotation of the ambulacral grooves such that the grooves lie on the center of the oral plates, as opposed to along the sutures, a feature of eucystitids, as well as short, branched ambulacra that each end in single brachiole facets that do not extend past the oral summit (Sumrall, 2017; Sheffield and Sumrall, 2019a).

Geographic Framework

To infer biogeographic patterns of sphaeronitid echinoderms, we used the same basins from the BioGeoBEARS analysis of Lam et al. (2021: https://doi.org/10.5061/dryad.4tmpg4f6j). From the aforementioned study, eight areas were defined: Baltica, Gondwana, and six basins within Laurentia (Southern Appalachian Basin, Northern Appalachian Basin, Cincinnati Basin, Southern Laurentia, North of the Transcontinental Arch, and Western Midcontinent; Figs. 3, 4). The R package BioGeoBEARS (Matzke, 2013) uses a common likelihood framework to implement three programs and their key assumptions in biogeography: the dispersal-extinction-cladogenesis (DEC) of Lagrange (Ree and Smith, 2008), dispersal-vicariance-analysis (DIVA; Ronquist, 1997), and BayArea (Landis et al., 2013). Within BioGeoBEARS, DIVA and BayArea were converted into a likelihood framework, so they are referred to as DIVALIKE and BAYAREALIKE. Each of the three models allows for dispersal or range expansion, and range loss or extirpation, which are modeled within the program through the parameters *d* and *e*, respectively. Each model within the program includes a *+j* parameter, which models the relative probability of founder-event speciation, more commonly termed 'jump dispersal', during cladogenesis (Matzke, 2014).

From the Lam et al. (2021) study, BioGeoBEARS results indicated the best-fit model for the blastozoan phylogeny was DIVALIKE+*j*. In all cases within the original analysis, the addition of the *+j* parameter improved model fit. This

TABLE 1 — Diploporan taxa included in the current study.

Genus	Species	Number of Specimens	Period	Stage	Locality	Basin
Aristocystites	*bohemicus*‡	NA	Ordovician	Darriwilian to Katian	Morocco; Prague Basin, Czech Republic	Gondwana
Eucystis	*angelini*	1	Ordovician	Katian	Pskov District, Russia	Baltica
Eucystis	*quadrangularis**	1	Ordovician	Katian	Pskov District, Russia	Baltica
Haplosphaeronis	*oblonga*	1	Ordovician	Katian	Põlva County, Estonia	Baltica
Sphaeronites	*rossicum*	2	Ordovician	Sandbian	Pskov District, Russia	Baltica
Pentacystis	*gibsoni*	3	Silurian	Homerian	Indiana, USA	Cincinnati
Holocystites	*cylindricus*‡	NA	Silurian	Wenlock	Indiana, USA; Tennessee, USA; Illinois, USA	Cincinnati; Southern Appalachian
Holocystites	*salmoensis*	1	Ordovician	Hirnantian	Anticosti Island, Canada	Southern Laurentia
Holocystites	*scutellatus*	7	Silurian	Homerian	Indiana, USA; Tennessee, USA; Illinois, USA	Cincinnati; Southern Appalachian
Trematocystis	*magniporatus*	2	Silurian	Homerian	Indiana, USA	Cincinnati
Triamara	*ventricosa*‡	NA	Silurian	Wenlock	Indiana, USA; Tennessee, USA	Cincinnati; Southern Appalachian
Tristomiacystis	*globosus*‡	NA	Devonian	Givetian	Kentucky, USA	Cincinnati
Paulicystis	*densus*	4	Silurian	Homerian	Indiana, USA	Cincinnati
Pustulocystis	*pentax*‡	NA	Silurian	Wenlock	Tennessee, USA	Southern Appalachian

* Taxa included in the morphospace study only, not the biogeographic analysis
‡ Taxa included in this study but not the focus of the morphospace nor biogeographic analyses
NA= Not applicable

finding indicated that within-area speciation (sympatry) and range expansion (anagenetic dispersal) were not sufficient enough to explain the biogeographic patterns within the phylogeny, a finding that was also discovered for early Paleozoic brachiopods, trilobites, and other echinoderm groups (Lam and Stigall, 2015; Lam et al., 2018; Congreve et al., 2019; Bauer, 2021). Importantly, Lam et al. (2021) did not focus on reconstructed Silurian dispersal patterns from

TABLE 2 — Properties of the character suites used to explore sphaeronitid morphological patterns. The modified character suite was constructed by combining and binning measurements into ratio and removing characters with over 30% missing data and characters that didn't vary within the specimens being examined. The culled character suite is identical to the modified suite but removing any characters with over 10% missing data.

Character suite	Number of characters	Binary	Multistate	Measurement/Ratio	% Missing	% Non-applicable
Original	145	70	22	53	15.16%	26.68%
Modified	52	29	6	17	7.42%	17.93%
Culled	37	23	4	9	1.62%	19.85%

their BioGeoBEARS analysis. In this study, we used the DIVALIKE+*j* model of Lam et al. (2021) to infer dispersal patterns for the sphaeronitids from the Middle to Late Ordovician and into the Silurian.

Morphological Patterns and Phylomorphospace

To explore morphological trends during this biogeographic transition within diploporans, we constructed a novel character suite (Table 2). The initial character suite was constructed to exhaustively characterize any aspect of morphology based on literature sources (e.g., Kesling, 1967) and museum specimens. The characters included direct measurements of features (e.g., length of particular ambulacra or height of the theca), binary characters (e.g., presence or absence of the A ambulacrum), or multistate characters (e.g., the number of brachiole facets on a particular ambulacra). The character suite focused on characters associated with the oral system given the consistency of plating in that region compared with the rest of the organism. We utilized the Universal Elemental Homology model in the characterization of the oral system (Sumrall and Waters, 2012; Kammer et al., 2013), which has been extensively applied to understanding diploporan morphology (Sheffield and Sumrall, 2015, 2017; Sheffield and Sumrall, 2019a, 2019b; Sumrall, 2017). A total of 22 specimens from 8 genera (10 species) were then coded using this dataset following the methods outlined in Deline and Ausich (2011). Supplementary File 1 contains the characters used for this analysis; Supplementary File 2 contains the specific codings for each taxon.

The resulting dataset was then culled to eliminate any characters that did not vary across the specimens analyzed (the exclusion of invariant characters had no effect on the resulting morphospace) or included significant proportions of missing data. Missing data is unavoidable and non-random with variably preserved specimens, which can result in distorting the observed morphological patterns (Lloyd, 2016; Gerber, 2019; Deline, 2021). Even though taphonomic effects of character loss has been shown to be minimal within blastozoan echinoderms related to number of morphological features that can be coded from disarticulated material (Deline and Thomka, 2017), we still eliminated characters with significant missing unpreserved data (i.e., characters with either 30% or 10% of the states coded as missing because of incomplete preservation). We utilized thresholds for eliminating characters given the clear and non-random distribution of missing data that results from taphonomic degradation. Finally, we transformed all of the direct measurements to ratios (e.g., length/width of the peristome) to eliminate effects of specimen size, which varies extensively across the dataset. The ratios were then broadly binned to easily compare to the binary or multistate characters. This process significantly reduced the overall size of the character suites (Table 2), but also significantly reduced the amount of missing data. Morphospaces were then built using Gower similarity (Gower, 1971) and principal coordinate analysis.

To explore changes in morphology within a phylogenetic context, we then constructed a phylomorphospace using the culled tree from Sheffield and Sumrall (2019a) and the morphological character suite. There are multiple techniques that have been used to reconstruct the positions of ancestral nodes, which can broadly be broken into pre- and post-ordination methods (Lloyd, 2018). Pre-ordination ancestral character reconstruction is based on the tree, tip data, and a model of evolution using maximum likelihood or Bayesian methods such as stochastic character mapping (Huelsenbeck et al., 2003). These methods often provide more accurate placement of ancestors within the resulting morphospace as well as additional quantitative information regarding phylogenetic signals and evolutionary rates (Lloyd, 2018). In addition, Bayesian methods provide posterior probabilities of ancestral character states to assess the degree of certainty. For the current study, we first employed stochastic character mapping analyses to reconstruct ancestral character states. However, because of the tree structure or the distribution of tip data many of the ancestral character states were poorly resolved (i.e., fairly equitable posterior probabilities for all character states), thus the modeled character states and the location of ancestral taxa within morphospace were unreliable. Therefore, we used post-ordination methods

to construct the phylomorphospace. This method uses a phylogenetic tree and positions of taxa within morphospace to estimate ancestral positions using maximum likelihood (Sidlauskas, 2008). This method forces ancestral positions to be limited to the space already explored by tip data; it places ancestral data into positions that may not reflect a realistic combination of characters and imposes a strong phylogenetic signal into the position of the ancestral nodes (Lloyd, 2018; Deline, 2021). However, these methods allow a visualization of morphological evolution that has been previously utilized to understand trends in echinoderm disparity (Hopkins and Smith, 2015; Wright, 2017); thus, these methods were applied herein. All of the morphological analyses were conducted in R version 4.1.0 (R Core Team, 2021) utilizing the cluster (Maechler, 2019), ape (Paradis et al., 2004), vegan (Oksanen et al. 2020), and phytools (Revell, 2012) packages.

RESULTS

Biogeographic Patterns of Sphaeronitids

Results and discussions surrounding interpretations of biogeographic patterns are limited to the sphaeronitids (see bolded taxa names, Fig. 3). Biogeographic dispersal patterns among the sphaeronitids were inferred by taking into account the geographic areas occupied by the descendants and ancestors; dispersal events and directions from the phylogeny (Fig. 3B) were inferred using most likely areas reconstructed using the DIVALIKE+*j* analysis (Fig. 3B; Lam et al., 2021). For example, we infer a dispersal event when a descendant occupies a different or additional area than its ancestor. This inference does not take into account rare or uncertain events and does not produce an estimate of uncertainty. However, as our goal is to generally reconstruct events among a small group of species, this approach is sufficient. Below, we summarize the dispersal events (no vicariance events were inferred) that took place within our focal taxa (Table 1).

Within the Middle to Late Ordovician (470.0–443.8 Ma), it is clear from reconstructed area relationships that *Sphaeronites rossicum*, *Haplosphaeronis oblonga*, and *Eucystis angelini* were a group restricted to Baltica (Fig. 3B), the probability of which is rather high, as seen in the ancestral node reconstructions (Fig. 3A). The shared ancestor between this group and the rest of the species likely resided in Baltica, with a descendant dispersing into Laurentia, specifically into the Cincinnati Basin (Figs. 3B, 4) and establishing a population there. During the Late Ordovician, ancestors of *Holocystites salmoensis* dispersed from the Cincinnati Basin eastward into Southern Laurentia. However, it should be noted that from the BioGeoBEARS analysis, there is also a high probability that ancestors of *H. salmoensis* may have resided in Southern Laurentia (Fig. 3A), in which case *H. salmoensis* would have evolved through sympatric speciation.

Dispersal patterns within the Silurian (443.8–419.2 Ma) are mainly restricted to within Laurentian basins (Figs. 3, 4). Specifically, five dispersal events occurred into the Appalachian Basin from the Cincinnati Basin (ancestors of *Holocystites cylindricus*, *Holocystites scutellus*, *Trematocystis magniporatus*, *Triamara ventricosa*, and *Pustulocystis pentax*), with two of these events taking place among the sphaeronitids (*H. scutellus* and *T. magniporatus*), indicating a strong connection between these basins through the Silurian.

Morphological Patterns of Sphaeronitids

The resulting morphospace shows notable phylogenetic and biogeographic structure with the Baltic specimens largely clustering negatively on the first and second axes (Fig. 5A). The primary axis (PCO1) captures differences in thecal plating, shape, and ornamentation, number of brachiole facets, ambulacral width, and the overall shape of the theca. The primary axis also strongly correlates with characters associated with oral side plates (extra plates inserted within the oral frame), which only occur within *Holocystites salmoensis* resulting in its outlier position. The second axis (PCO2) captures differences in the presence and features of the A ambulacra (e.g., curvature, width, and length), which is often developmentally lost within blastozoan echinoderms (Sumrall and Wray, 2007). The first two and five axes represent 34.65% and 62.6% of the eigenvectors, respectively. Within species or genera, morphological variability is minor (Fig. 5B) with most taxa covering limited and non-overlapping areas within morphospace. The only exception to this is the large range of morphologies shown between the two included species of *Eucystis* that differ with *E. quadrangularis* reducing the number of ambulacra (loss of A). Overall, the Baltic and Laurentian taxa cover comparable regions of morphospace as shown in similar sum of ranges and sum of variation measured across the first five axes (Table 3). In addition, the Baltic and Laurentian taxa occupy distinctive and adjacent, but non-overlapping areas of morphospace (NPMANOVA, first five axes, $p=0.001$).

To test how taphonomy and the missing data alter perceived morphological patterns, we further reduced the threshold for culling characters from 30% missing data to 10% (Table 2). This reduction in the number of characters (culling 15 characters reducing the overall character number by 29%) had little effect on the resulting morphospaces (Fig. 5C, D). The taphonomically culled dataset differs in two primary ways: first, *Pentacystis* and *Paulicystis* switch positions within morphospace. Second, the distance between the two species of *Eucystis* is diminished. Both differences, shown primarily in the second axis, are the result of culling multiple characters associated with the A ambulacrum which distinguishes these taxa. In addition, there is a minor increase of within genus variation with the taphonomically culled dataset. However, the taphonomically reduced dataset retained the key aspects in terms of the hypotheses being examined in the current study such as the morphological variation within taxa from different basins as well as the strong phylogenetic structure.

Incorporating the tree structure onto the morphospace (i.e., constructing a phylomorphospace), allows us to consider the morphological structure in an evolutionary and biogeographic framework. The intercontinental dispersal from Baltica to

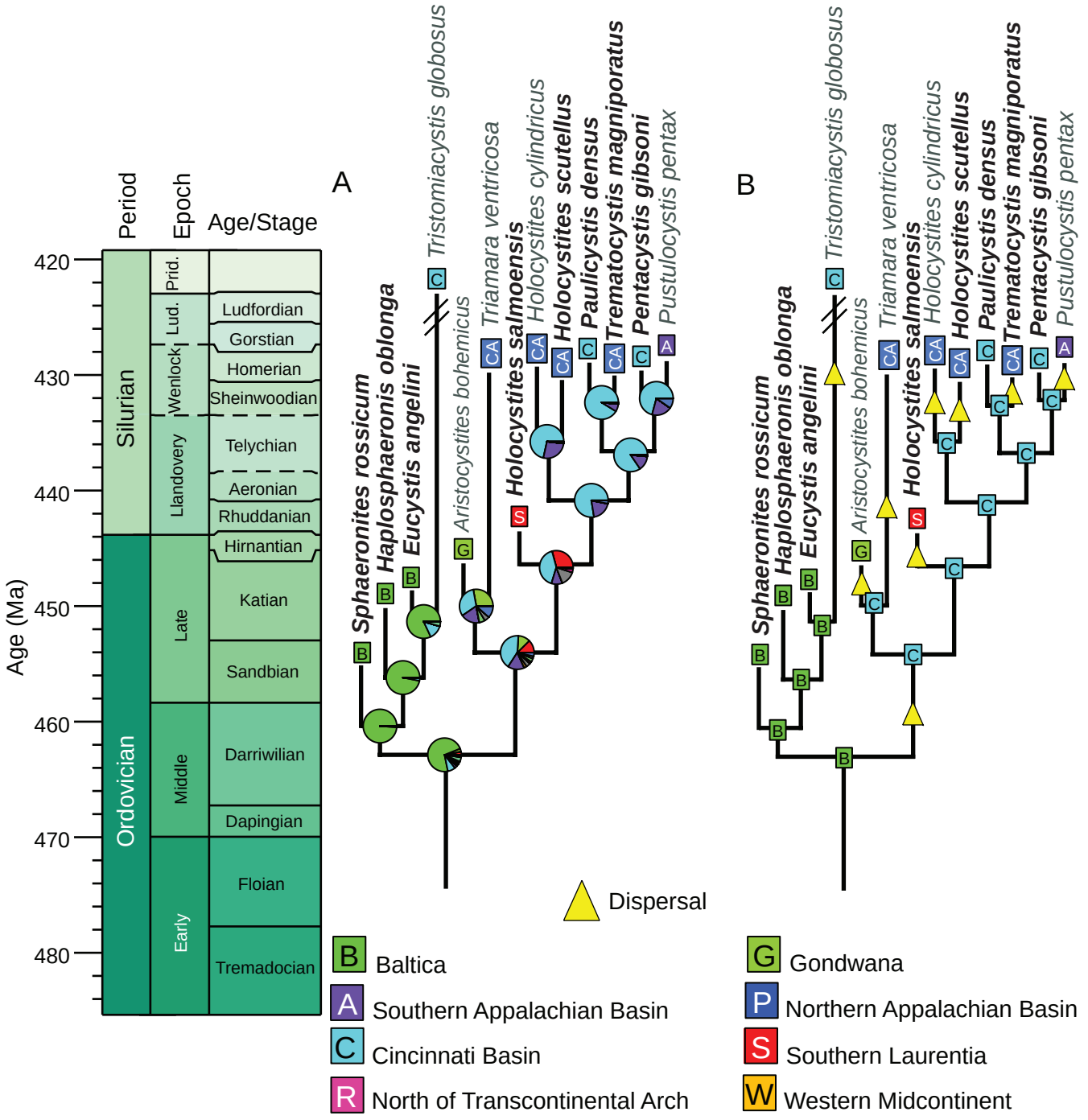

FIGURE 3 — Maximum-likelihood ancestral range estimation of the diploporan blastozoan phylogeny as modified from Lam et al. (2021) to focus on sphaeronitid taxa examined in this study (bolded genus and species names). **A**, Phylogeny with pie charts at nodes that indicate the probability of ancestral ranges from the DIVALIKE+*j* model. **B**, Most likely areas occupied by ancestors as inferred from the pie charts in A. Hatch marks on *T. globusus* range indicate this species ranges into the Devonian. Chronostratigraphy and age from the Geologic Time Scale 2016 (Ogg et al., 2016).

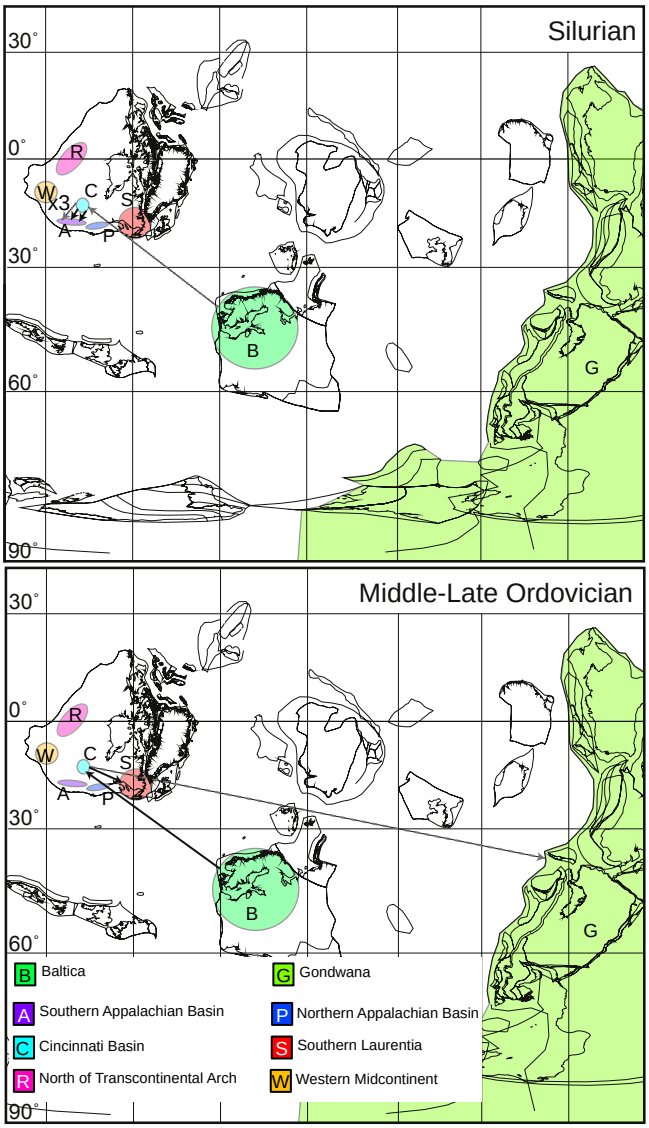

FIGURE 4 — Dispersal maps of sphaeronitid echinoderms (bolded) for two time slices: the Middle to Late Ordovician (470.0–443.8 Ma), and the Silurian (443.8–419.2 Ma). Solid black lines indicate dispersal events that took place for sphaeronitid species that are the focus of this study (Table 1), whereas dashed grey lines indicate a dispersal event that occurred for a species that is not the focus of this study. Duplicate lines (e.g., two bolded lines from the Cincinnati Basin to the Southern Appalachian Basin on the Silurian map) indicate multiple dispersal events (i.e., one line per dispersal). In the Silurian panel, the 'x3' beside the dispersal event from the Cincinnati Basin to the Southern Appalachian Basin indicates dispersal occurred three times for non-sphaeronitid species. Dispersal directions and types are inferred from the DIVALIKE+*j* analysis (FIGURE 3). Basin colors on the maps match those in Figure 3 as indicated in the key located in the bottom left corner of the Middle to Late Ordovician panel. Paleogeographic map modified from Torsvik and Cocks (2013).

Laurentia coincides with a large shift across morphospace within the Middle to Late Ordovician (Figs. 4, 5). However, the smaller intracontinental dispersals within holocystidids between Laurentian basins in the early Silurian correspond to minor shifts across morphospace. This pattern within the phylomorphospace is also retained within the taphonomically reduced dataset. Overall, the portions of the phylomorphospace representing dispersal events are not distinctive compared to the rest of the analysis. However, the relationship between morphological evolution and mode of speciation needs to be further explored in a more expansive study.

DISCUSSION

While there were some instances of dispersal between Laurentian basins during the Silurian (e.g., multiple events took place from the Cincinnati Basin to the Southern Appalachian Basin; Fig. 3), there was only one dispersal event

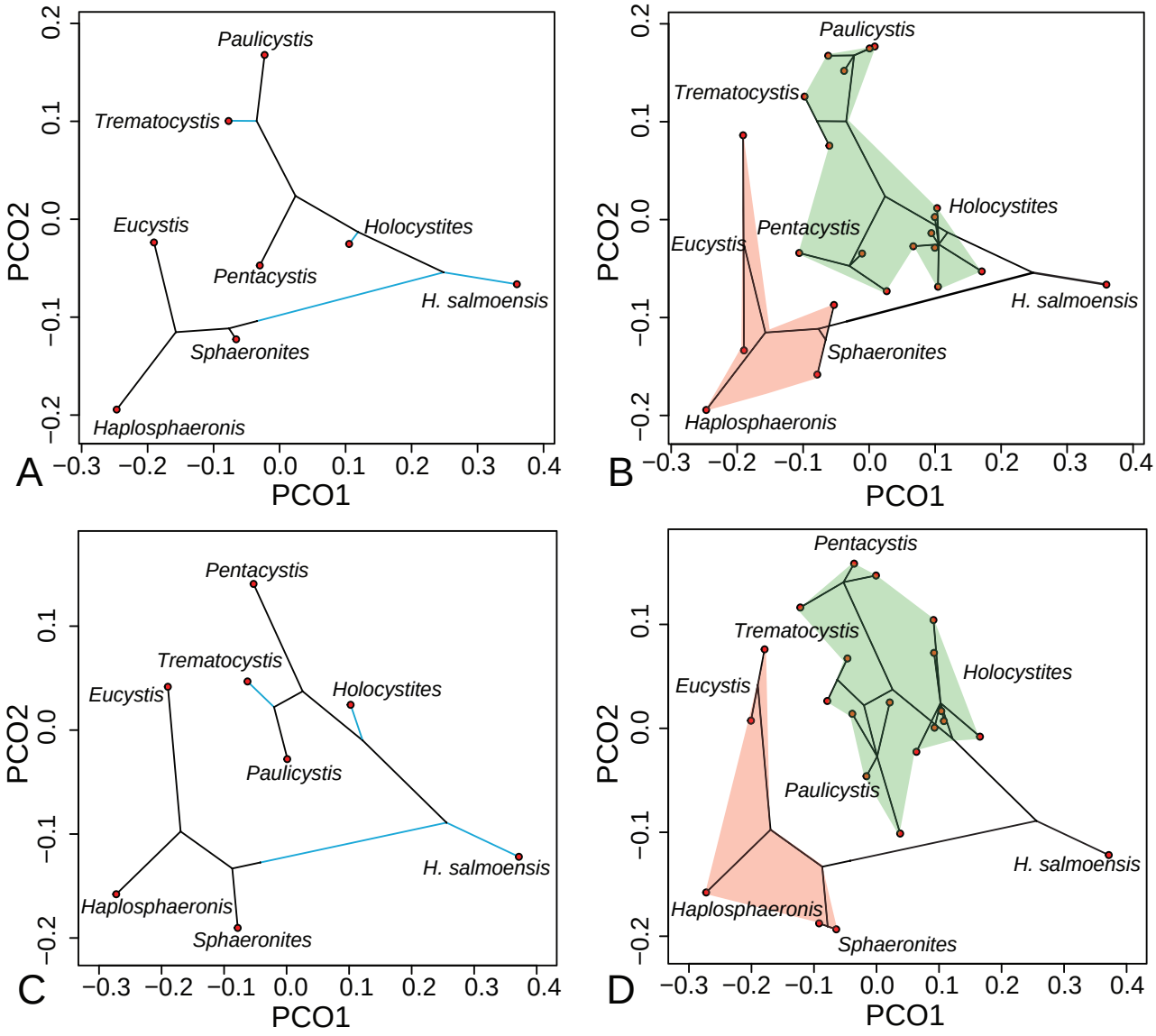

FIGURE 5 — Phylomorphospace of sphaeronitid diploporans. Ancestral positions based on post-ordination maximum likelihood. The phylomorphospaces are displayed in two ways, first, the position of the individual genera is plotted based on the ancestral node to show overall trends (A, C). Alternatively, all individual specimens are plotted in the phylomorphospace (B, D). Individual specimens within a genus are placed into a polytomy with short branch lengths. *Holocystites salmoensis* is separated from *H. scutellatus* based on its geographic position and unique morphology. **A**, **B**, phylomorphospace constructed from the modified character suite (Table 2). **C**, **D**, phylomorphospaces constructed from the culled character suite (Table 2). Specimens from Baltica are denoted in pink while those from Laurentia are in green. The portions of the phylomorphospace that represent dispersal events are shown in blue (A, C).

between Laurentia and other paleocontinents, specifically from Baltica to Laurentia (Fig. 4). This signal may indicate that as Baltica moved closer to Laurentia through the Ordovician and into the Silurian, dispersal became limited to occurring between these two paleocontinents within the sphaeronitids. Additional dispersal events between Laurentia and Gondwana may have decreased due to tectonically induced geographic barriers (e.g., the Taconic highlands from the Ordovician-early Silurian Taconic Orogeny; Van Staal et al., 2009; Torsvik and Cocks, 2013), and/or sea level fluctuations that could have limited dispersal. However, as our dataset is rather small, it is hard to infer such patterns and processes from this analysis alone.

Sphaeronitid dispersal events that occurred across ocean basins were likely controlled by wind-driven surface currents and gyre systems that operated between paleocontinents.

TABLE 3 — A comparison of European and North American sphaeronitids within morphospace (See FIGURE 5).

Region	N	Sum of Ranges	Sum of Ranges (Culled)	Sum of Variance	Sum of Variance (Culled)
Europe	5	1.170±0.20	1.215±0.19	0.050±0.011	0.054±.012
North America	17	1.223±0.15	1.108±0.14	0.029±0.008	0.026±0.007

From previous analyses of blastozoan echinoderms, it was hypothesized that dispersal between Baltica and Laurentia through the Ordovician was likely facilitated by the Iapetus Current and coastal upwelling (Pohl et al., 2016; Pohl et al., 2018; Lam et al., 2021). We invoke the same processes here to explain how species traveled, likely in their larval stages (Lam et al., 2018), between Baltica and Laurentia. Laurentian dispersal dynamics for marine invertebrates was likely facilitated by strong storm and hurricane activity, potentially sweeping species across physical and thermal barriers into new areas (Lam et al., 2018). As the Silurian is not well-preserved in Laurentian sections, it is difficult to assess the abiotic drivers of dispersal during this period. However, it is clear from our biogeographic analysis, specifically the five dispersal events from the Cincinnati Basin into the Southern Appalachian basins, that some abiotic factor(s) may have pushed species from the Cincinnati Basin to the south.

Bauer (2021) conducted a paleobiogeographic analysis for eublastoids, ranging from the Silurian through the late Permian. Through the study interval, there were limited dispersal events among paleocontinents, especially during the Silurian. However, dispersal among basins of Laurussia (i.e., the paleocontinent formed from the collision of Laurentia and Baltica) dominated during this time. Beginning in the Devonian, Bauer (2021) found that intercontinental dispersal began to increase for the eublastoids, a pattern that may be explained by reduced distances among paleocontinents (Torsvik and Cocks, 2013). Too few diploporans crossed the Devonian boundary to be able to thoroughly assess if this pattern holds true in other blastozoan groups. Bauer's (2021) finding of increased dispersal among Laurentian/Laurussian basins into and through the Silurian matches with the patterns recovered from this analysis. However, additional analyses are required to fully assess the causes of increased intracontinental dispersal more fully for blastozoans from the Late Ordovician to Silurian and increased intercontinental dispersal into the Devonian. Specifically, such additional analyses should ideally be performed in a robust phylogenetically informed and statistical framework, as patterns and processes for the Silurian are complicated for Baltica, Gondwana, and especially Laurentia due to large disconformities in the stratigraphic record that may be obscuring species' ranges (Cramer and Saltzman, 2005).

Taphonomic preservation has the potential to significantly bias morphologic interpretation and, therefore, also alter phylogenetic and morphologic conclusions, a phenomenon noted across multiple fossil groups (Sheffield and Sumrall, 2015, 2017; Murdock et al., 2016; Sansom, 2016; Deline and Thomka, 2017). However, the inclusion of taphonomic data can indicate the degree of bias and potentially increase the resolution of evolutionary studies (Murdock et al., 2016, Deline and Thomka, 2017). While diploporans are not the most susceptible echinoderms in terms of complete disarticulation (Brett et al., 1997), it is still uncommon for individuals to show complete preservation. Most often, we find that the stems or holdfasts of the specimens are disarticulated from the theca (Thomka et al., 2016) and the delicate brachiole plates are almost never found articulated (Paul, 1971; Frest et al., 2011). Furthermore, the intricate plates of the oral area, which often contain significant phylogenetic information in many blastozoans (Sumrall and Waters, 2012; Kammer et al., 2013), are often disarticulated from the theca. However, the theca itself is sutured tightly together, which presents another taphonomic difficulty in that the sutures and features of the thecal plates become significantly abraded even in articulated specimens. This taphonomic overprinting in diploporans has resulted in new taxa being erected based solely on taphonomic differences rather than morphologic differences (Sheffield and Sumrall, 2015, 2017).

Deline and Thomka (2017) explored the effects of differential taphonomic processes on blastozoan echinoderm disparity. This study found the resulting structure of the morphospace and patterns of disparity through time were stable even when taphonomic biases were significantly exaggerated. This is because many blastozoan morphological features can be observed in disarticulated specimens (e.g., respiratory structures) compared with other echinoderms, such as crinoids, that require articulated theca to discern the major features (Deline and Thomka, 2017). The current analysis of sphaeronitid diploporans is consistent with the suggestion that most blastozoans are not taphonomically sensitive regarding studies of morphologic disparity. As stricter taphonomic criteria were used to characterize morphologic patterns the overall structure of the morphospace was retained. Any difference in the resulting morphospaces with the varied taphonomic criteria are largely the result of shifting emphasis

on different body regions as characters are non-randomly removed (e.g., reducing the number of characters associated with the A ambulacrum), which is similar to patterns shown in the disparity of crinoids (Deline and Ausich, 2017). Overall, the relevant morphological patterns in the current analysis are retained even with stricter criteria for taphonomically missing data, thus these results are unlikely to be significantly biased by preservational differences between taxa.

The Late Ordovician Mass Extinction propelled ecological changes amongst filter feeding echinoderms (Ausich and Deline, 2012; Cole et al., 2019; Cole and Wright, 2021). The mass extinction paired with ecological restructuring opened potential niches and eased competitive pressures. The loss of lower-tiered Porocrinoidea (e.g., *Hybocrinus* and *Porocrinus*) and a reduction in blastozoan diversity enabled the successful establishment of holocystitids that filled the same broad ecological niche following their dispersal from Baltica to Laurentia. The morphological response to this type of biogeographic and ecological shift is understudied, but we hypothesized that the permissive ecology within niche space would result in increased disparity within the invasive taxa. This pattern of rapid morphological change often occurs following mass extinctions or the evolution of key innovations leading toward the establishment of a new niche (Hughes et al., 2013). Even though the transcontinental dispersal coincided with a large shift across regions of morphospace (i.e., the distance between centroids of the two groups ~36.4% of the range of values across PCO1), the area occupied by holocystitids was comparable to that of the Baltic diploporans (Table 3). Thus, even with the permissive ecology related to lower competition within their niche, morphology both within and between holocystitid taxa was constrained.

The reasons for this perceived lack of morphological response to the release of competitive pressure following the faunal migration could be related to the nature of a niche being filled or developmental constraints. Competition and niche partitioning has been extensively studied in late Paleozoic echinoderm communities in terms of elevation above the sea floor (Ausich and Bottjer, 1982; Bottjer and Ausich, 1986), filter density (Kammer and Ausich, 1987), and size of food particles (Meyer et al., 2002; Brower, 2006). The early Paleozoic establishment of these patterns has been recently explored in a phylogenetic context (Cole et al., 2019; Cole and Wright, 2021). Examinations of the ecomorphology of crinoid Lagerstätte in the Late Ordovician indicates a steady divergence of feeding ecologies with niches becoming more discrete and distinctive (Cole and Wright, 2021). Extensive niche partitioning would in turn lead to increasingly narrowly defined ecological niches, such that the dispersal and establishment of diploporans into one of these niches would have a stabilizing effect and prevent extensive morphological diversification. This interpretation is strengthened by the nature of many of the characters included in the current study that have ecological significance (e.g., width of ambulacra, facet shape, and number of facets per ambulacrum).

Alternatively (or in addition), the lack of morphological expansion in sphaeronitids could be related to developmental constraint. It has been hypothesized that as large-scale morphological features become more complex through time, they become increasingly evolutionarily rigid and unable to change (Riedl, 1977). This pattern has also been proposed for gene regulatory networks becoming more elaborate and static through time (Congreve et al., 2018; Erwin, 2020). Deline et al. (2020) explored early Paleozoic echinoderm morphological disparity and found that the phylogenetic signal was similar regardless of the scale of the character, which indicates a prolonged flexibility within echinoderm anatomy through time. However, observing this pattern broadly across the phylum may not necessarily translate into the evolutionary dynamics of a specific, small clade. In addition, given the focus on sphaeronitids, the characters used in the current study are smaller in scale and specific such that developmental constraints might play a larger role in the lack of morphological expansion.

The competitive release and permissive ecology following establishment in Laurentia may not have had an extensive effect in terms of characteristics and overall shape, but this ecological change might have been expressed in other manners. Foremost are changes in population ecology, wherein a decrease in competition results in high abundance of specific taxa along with uneven community structure. Baltic sphaeronitids can be locally abundant (Bockelie, 1984), but overall Ordovician diploporans, like many blastozoans, are often minor components in marine ecosystems. However, *Holocystites scutellus*, which likely filled niches vacated by crinoids, is the most common echinoderm by far within the lower Silurian Massie Formation (Frest et al., 2011; Thomka et al., 2016). In addition, there is a significant shift in body size during this transition from Baltica to Laurentia, which can be seen with the limited scale of this study with the Laurentian specimens (theca height 37.91 ± 5.53 mm, theca width 24.69 ± 2.22 mm) over double the thecal size of those from Baltica (theca height 15.04 ± 1.75 mm, theca width 13.91 ± 1.71 mm).

One particularly intriguing result of the current analyses is the shifts in phylomorphospace relative to the recognized dispersal event. The intercontinental dispersal event from Baltica to the Cincinnati Basin corresponds to a large shift across morphospace (Figs. 4, 5). The morphological shift during this transition represents roughly 48% of the range shown on the primary axis but is likely exaggerated by the aberrant morphology of *Holocystites salmoensis*. If the outlier status of *H. salmoensis* is excluded, the morphological shift corresponding to the dispersal is still robust (34.6% of the range shown on the primary axis). However, the following intracontinental dispersal events from the Cincinnati Basin to the Southern Appalachian Basin reflect minor changes in morphospace position. Dispersal events between geographically adjacent basins likely had significant gene flow and could potentially mute morphological shifts relative to migrations across wide ocean basins. However, to explore the relationship between mode of speciation (vicariance vs dispersal), dispersal distance, and morphological evolution in the future would require a more expansive study using rate-based comparative phylogenetic methods.

CONCLUSIONS

This study uses phylogenetically-informed paleobiogeography combined with a phylomorphospace analysis to infer dispersal patterns and morphological changes across the Ordovician–Silurian boundary. To date, the majority of research related to echinoderm evolutionary responses across the LOME have been focused on crinoids, leaving questions about how other groups of echinoderms may have responded to extinction dynamics. In the sphaeronitid diploporans, very little morphological change was detected across the Ordovician–Silurian boundary as these taxa dispersed in one major event from Baltica to Laurentia during the Middle–Late Ordovician; these dispersals led to the establishment of new echinoderm communities in the middle Silurian. This lack of morphological change could indicate that these diploporans filled a narrow and previously defined niche structure that was vacated by crinoids during the LOME, but it could also indicate that diploporans were under developmental constraints preventing new morphological innovation. These sphaeronitid diploporans do exhibit some changes, particularly in their body size and in their community structure. As diploporans migrated from Baltica to Laurentia, they approximately doubled their body size. In terms of community structure, some sphaeronitids became increasingly more abundant. While some sphaeronitids were locally abundant in the Ordovician, taxa such as *Holocystites scutellus* became one of the most abundant echinoderm taxa in the Silurian of Laurentia, which could be due to a decrease in competition from the vacated niches following the LOME.

We also uncover several dispersal events throughout the studied time range of the Ordovician– Silurian and increasing levels of morphospace change correlating positively with dispersal distance. Dispersal among paleocontinents virtually stopped during the Silurian and there were few intracontinental dispersal events constrained from the Cincinnati Basin to the Southern Appalachian Basin. While further studies and a larger dataset would be necessary to explore this pattern more fully, it is possible that the lack of intercontinental dispersal could have been related to a number of factors, such as tectonically-induced geographic barriers that formed during the Late Ordovician–Silurian or sea level fluctuations that would have caused further isolation of basins. Future work to better understand both the patterns of morphological shifts in relation to dispersal distance and the patterns of increased and decreased dispersal throughout this time in the early Paleozoic can be explored by weaving together datasets from multiple clades using rate-based comparative phylogenetic methods in combination with an expanded biogeographic dataset.

ACKNOWLEDGEMENTS

We are honored to submit this work to the special volume recognizing the career of Tomasz Baumiller. B. Deline volunteered at the University of Michigan Museum of Paleontology under Dr. Baumiller's supervision while he was in high school and then studied with him as an undergraduate. Dr. Baumiller provided valuable professional guidance, mentorship, encouragement, and opportunities that formed a solid foundation for his career in paleontology. S. Sheffield was supported by the Paleontological Society's Arthur James Bocout Early Career Grant. The University of South Florida's School of Geosciences provided funding to B. Deline to facilitate data collection. We thank J. Bauer, and reviewers J. Lamsdell and E. Nardin for their comments and suggestions that greatly improved this manuscript. We thank U. Toom, Geological Institute of Tallinn; G. Baranov, Geological Institute of Tallinn; B. Hunda, Cincinnati Museum Center; T. Adrain, The University of Iowa; Paul Mayer, The Field Museum; and Jean Dougherty, the Geological Survey of Canada for access to specimens. M. McCoy assisted in constructing the morphological character suite. Supplementary File 1 contains the characters used for this analysis. Supplementary File 2 contains the character codings. B. Deline and S. Sheffield designed the study, all authors collected and analyzed the data, and B. Deline, S. Sheffield, and A. Lam wrote the paper.

Supplemental Online Material:
https://dx.doi.org/10.7302/4375

LITERATURE CITED

ALBANESI, G. L., C. R. BARNES, J. A. TROTTER, I. S. WILLIAMS, and S. M. BERGSTRÖM. 2019. Comparative Lower–Middle Ordovician conodont oxygen isotope palaeothermometry of the Argentine Precordillera and Laurentian margins. Palaeogeography, Palaeoclimatology, Palaeoecology, 549: 109115. doi: 10.1016/j.palaeo.2019.03.016

ALDRIDGE, R. J., L. JEPPSSON, and K. J. DORNING. 1993. Early Silurian oceanic episodes and events. Journal of the Geological Society of London, 150, 501–513.

AUSICH, W. I., and D. J. BOTTJER. 1982. Tiering in suspension-feeding communities on soft substrata throughout the Phanerozoic. Science, 216: 173–174.

AUSICH, W. I., and B. DELINE. 2012. Macroevolutionary transition in crinoids following the Late Ordovician extinction event (Ordovician to early Silurian). Palaeogeography, Palaeoclimatology, Palaeoecology, 361: 38–48.

AUSICH, W. I., T. W. KAMMER, and T. K. BAUMILLER. 1994. Demise of the middle Paleozoic crinoid fauna: a single extinction event or rapid faunal turnover? Paleobiology, 20: 345–361.

BAUER, J. E. 2021. Paleobiogeography, paleoecology, diversity, and speciation patterns in the Eublastoidea (Blastozoa: Echinodermata), Paleobiology, 47: 221–235. doi: 10.1017/pab.2020.27.

BAUMILLER, T.K. 1994. Patterns of dominance and extinction in the record of Paleozoic crinoids. In B. David, A. Guille, J.P. Feral, and M. Roux (eds.), Echinoderms Through Time, Balkema: Rotterdam, pp. 193–198.

BOCKELIE, J. F. 1984. The Diploporita of the Oslo region, Norway. Palaeontology, 27: 1–68.

BOTTJER, D. J., and W. I. AUSICH. 1986. Phanerozoic development of tiering in soft substrata suspension-feeding communities. Paleobiology, 12: 400–420.

BRANSON, E. R., and R.E. PECK. 1940. A new cystoid from the Ordovician of Oklahoma. Journal of Paleontology, 14: 89–92.

BRENCHLEY, P. J., J. D. MARSHALL, G. A. F. CARDEN, D. B. R. ROBERTSON, D. G. F. LONG, T. MEIDLA, L. HINTS, and T. F. ANDERSON. 1994. Bathymetric and isotopic evidence for a short-lived Late Ordovician glaciation in a greenhouse period. Geology, 22: 295–298.

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

BROWER, J. C. 2006. Ontogeny of the food-gathering system in Ordovician crinoids. Journal of Paleontology, 80: 430–446.

CLAUSEN, S. 2004. New early Cambrian eocrinoids from the Iberian Chains (NE Spain) and their role in nonreefal benthic communities. Eclogae Geologicae Helvetiae, 97: 371–379.

COLE, S. R., and D. F. WRIGHT. 2021, September 27. Niche evolution and phylogenetic community paleoecology of Late Ordovician Crinoids. https://doi.org/10.32942/osf.io/r6jta

COLE, S. R., D.F. WRIGHT, and W.I. Ausich. 2019. Phylogenetic community paleoecology of one of the earliest complex crinoid faunas (Brechin Lagerstätte, Ordovician). Palaeogeography, Palaeoclimatology, Palaeoecology, 521: 82–98.

CONGREVE, C. R., A. Z. KRUG, and M. E. PATZKOWSKY. 2019. Evolutionary and biogeographical shifts in response to the Late Ordovician mass extinction. Palaeontology, 62: 267–285.

CONGREVE, C. R., A.R. FALK, and J.C. LAMSDELL. 2018. Biological hierarchies and the nature of extinction. Biological Reviews, 93: 811–826.

CRAMER, B. D., and M. R. SALTZMAN. 2005. Sequestration of ^{12}C in the deep ocean during the early Wenlock (Silurian) positive carbon isotope excursion. Palaeogeography, Palaeoclimatology, Palaeoecology, 219: 333–349.

DELINE, B. 2021. *Echinoderm morphological disparity: Methods, patterns, and possibilities*. Cambridge University Press.

DELINE, B., and W.I. AUSICH. 2011. Testing the plateau: a reexamination of disparity and morphologic constraints in early Paleozoic crinoids. Paleobiology, 37: 214–236.

_____. 2017. Character selection and the quantification of morphological disparity. Paleobiology, 43: 68–84

DELINE, B. and J. R. THOMKA. 2017. The role of preservation on the quantification of morphology and patterns of disparity within Paleozoic echinoderms. Journal of Paleontology, 91: 618–632.

DELINE, B., W. I. AUSICH, and C. E. Brett. 2012. Comparing taxonomic and geographic scales in the morphologic disparity of Ordovician through Early Silurian Laurentian crinoids. Paleobiology, 38: 538–553.

DELINE, B., J. R. THOMPSON, N. S. SMITH, S. ZAMORA, I. A. RAHMAN, S. L. SHEFFIELD, W. I. AUSICH, T. W. KAMMER, and C. D. SUMRALL. 2020. Evolution and development at the origin of a phylum. Current Biology, 30: 1–8. doi: 10.1016/j.cub.2020.02.054.

DICKSON, J. A. D. 2002. Fossil echinoderms as a monitor of the Mg/Ca ratio of Phanerozoic oceans. Science, 298: 1222–1224.

_____. 2004. Echinoderm skeletal preservation: calcite-aragonite seas and the Mg/Ca ratio of Phanerozoic oceans. Journal of Sedimentary Research, 74: 355–365.

ERWIN, D.H. 2020. The origin of animal body plans: a view from fossil evidence and the regulatory genome. Development, 147: dev182899.

FINNEGAN, S., K. BERGMANN, J. M. EILER, D. S. JONES, D. A. FIKE, I. EISENMAN, N. C. HUGHES, A. K. TRIPATI, and W. W. FISCHER. 2011. The magnitude and duration of Late Ordovician–Early Silurian glaciation. Science, 331: 903–906.

FREST, T. J., H. L. STRIMPLE, and C. R. C. PAUL. 2011. The North American *Holocystites* fauna (Echinodermata: Blastozoa: Diploporita): paleobiology and systematics. Bulletins of American Paleontology, 380: 1–141.

GABBOTT, S. E., J. ZALASIEWICZ, R.J. ALDRIDGE, and J.N. THERON. (2010). Eolian input into the Late Ordovician postglacial Soom Shale, South Africa. Geology, 38: 1103–1106.

GABBOTT, S. E., C. BROWNING, J.N. THERON, and R.J. WHITTLE. 2017. The late Ordovician Soom Shale Lagerstätte: an extraordinary post-glacial fossil and sedimentary record. Journal of the Geological Society, 174: 1–9.

GERBER, S. 2019. Use and misuse of discrete character data for morphospace and disparity analysis. Palaeontology, 62: 305–319.

GOWER, J. C. 1971. A general coefficient of similarity and some of its properties. Biometrics, 27, 857–871.

GRAHN, Y. G., and M.V. CAPUTO. 1992. Early Silurian glaciation in Brazil. Palaeogeography, Palaeoclimatology, Palaeoecology, 99: 9–15.

HAQ, B. U., and S.R. SCHUTTER. 2008. A chronology of Paleozoic sea-level changes. Science, 322: 64–68.

HOPKINS, M. J., and A. B. SMITH. 2015. Dynamics evolutionary change in post-Paleozoic echinoids and the importance of scale when interpreting changes in rates of evolution. Proceedings of the National Academy of Sciences, 112: 3758–3763.

HUELSENBECK, J. P., R. NIELSEN, and J.P. BOLLBACK. 2003. Stochastic mapping of morphological characters. Systematic biology, 52: 131–158.

HUGHES, M., S. GERBER, and M.A. WILLS. 2013. Clades reach highest morphological disparity early in their

evolution. Proceedings of the National Academy of Sciences, 110: 13875–13879.

JEPPSON, L. 1990. An oceanic model for lithological and faunal changes tested on the Silurian record. Journal of the Geological Society of London, 147: 663–674.

_____.1997. Recognition of a probable secondo-primo event in the Early Silurian. Lethaia, 29: 311–315.

_____.1998. Silurian oceanic events: summary of general characteristics. In E. Landing and M.E. Johnson (eds.), New York State Museum Bulletin, 491, 239–257.

JOHNSON, M. E. 2006. Relationship of Silurian sea-level fluctuations to oceanic episodes and events. GFF, 128: 115–121.

_____. 2010. Tracking Silurian eustasy: alignment of empirical evidence or pursuit of deductive reasoning? Palaeogeography, Palaeoclimatology, Palaeoecology, 296: 276–284.

KAMMER, T. W., and W. I. AUSICH. 1987. Aerosol suspension feeding and current velocities: distributional controls for late Osagean crinoids. Paleobiology, 13: 379–395.

_____, C. D. SUMRALL, S. ZAMORA, W. I. AUSICH, and B. DELINE. 2013. Oral region homologies in Paleozoic crinoids and other plesiomorphic pentaradial echinoderms. PLoS One, 8. doi: 10.1371/journal.pone.0077989

KESLING, R.V. 1967. Cystoidea. In R. C. Moore (ed.), *Tre*atise on Invertebrate Paleontology, Part S, Echinodermata 1, University of Kansas Press and Geological Society of America: Lawrence, Kansas, and Boulder, Colorado, pp. S85–S262.

LAM, A. R., and A. L. STIGALL. 2015. Pathways and mechanisms of Late Ordovician (Katian) faunal migrations of Laurentia and Baltica. Estonian Journal of Earth Sciences, 64: 62–67.

_____ _____, and N. J. MATZKE. 2018. Dispersal in the Ordovician: speciation patterns and paleobiogeographic analyses of brachiopods and trilobites. Palaeogeography, Palaeoclimatology, Palaeoecology, 489: 147–165.

_____, S. L. SHEFFIELD, and N. J. MATZKE. 2021. Estimating dispersal and evolutionary dynamics in diploporan blastozoans (Echinodermata) across the Great Ordovician biodiversification event. Paleobiology, 47: 198–220.

LANDIS, M., N. J. MATZKE, B. R. MOORE, and J. P. HUELSENBECK. 2013. Bayesian analysis of biogeography when the number of areas is large. Systematic Biology, 62: 789–804.

LEFEBVRE, B. 2007. Early Palaeozoic palaeobiogeography and palaeoecology of stylophoran echinoderms. Palaeogeography, Palaeoclimatology, Palaeoecology, 245: 156–199.

_____, and O. FATKA. 2003. Palaeogeographical and palaeoecological aspects of the Cambro–Ordovician radiation of echinoderms in Gondwanan Africa and peri-Gondwanan Europe. Palaeogeography, Palaeoclimatology, Palaeoecology, 195: 73–97.

_____, C. D. SUMRALL, R. A. SHROAT-LEWIS, M. REICH, G. D. WEBSTER, A. W. HUNTER, E. NARDIN, S. V. ROZHNOV, T. E. GUENSBERG, A. TOUZEAU. 2013. Palaeobiogeography of Ordovician echinoderms. Geological Society, London, Memoirs, 38: 173–198.

LLOYD, G. T. 2016. Estimating morphological diversity and tempo with discrete character-taxon matrices: implementation, challenges, progress, and future directions. Biological Journal of the Linnean Society, 118: 131–151.

_____. 2018. Journeys through discrete-character morphospace: synthesizing phylogeny, tempo, and disparity. Palaeontology, 61: 637–646.

LOYDELL, D. K. 1998. Early Silurian sea level changes. Geology, 135: 447–471.

MAECHLER, M. 2019. Finding groups in data: cluster analysis extended Rousseau et. *R package version*, *2*(0).

MATZKE, N. J. 2013. Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. Frontiers in Biogeography, 5: 242–248.

_____. 2014. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. Systematic Biology, 63: 951–970.

MELCHIN, M. J., C. E. MITCHELL, C. HOLMDEN, and P. ŠTORCH. 2013. Environmental changes in the Late Ordovician–early Silurian: review and new insights from black shales and nitrogen isotopes. GSA Bulletin, 125:1635–1670.

MEYER, D. L., A. I., MILLER, S. M. HOLLAND, and B. F. DATTILO. 2002. Crinoid distribution and feeding morphology through a depositional sequence: Kope and Fairview Formations, Upper Ordovician, Cincinnati Arch region. Journal of Paleontology, 76: 725–732.

MURDOCK, D. J., S. E. GABBOTT, and M. A. PURNELL. 2016. The impact of taphonomic data on phylogenetic resolution: *Helenodora inopinata* (Carboniferous, Mazon Creek Lagerstätte) and the onychophoran stem lineage. BMC Evolutionary Biology, 16: 1–14.

NARDIN, E., and B. LEFEBVRE. 2010. Unravelling extrinsic and intrinsic factors of the early Palaeozoic diversification of blastozoan echinoderms. Palaeogeography, Palaeoclimatology, Palaeoecology, 294: 142–160.

OGG, J. G., G. OGG, and F. M. GRADSTEIN. 2016. A concise geologic time scale: 2016, Elsevier: Amsterdam.

OKSANEN, J., F. G. BLANCHET, M. FRIENDLY, R. KINDT, P. LEGENDRE, D. MCGLINN, P. R. MINCHIN, R. B. O'HARA, G. L. SIMPSON, P. SOLYMOS, M. HENRY H. STEVENS, E. SZOECS and H. WAGNER. 2020. vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan.

PARADIS, E., J. CLAUDE, and K. STRIMMER. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics, 20: 289–290.

PAUL, C. R. C. 1971. Revision of the *Holocystites* Fauna (Diploporita) of North America. Fieldiana Geology, 24: 1–166.

_____. 1988. The phylogeny of the cystoids. In C. R. C. Paul, and A. B. Smith, (eds). Echinoderm Phylogeny and Evolutionary Biology, Clarendon Press: Oxford, pp. 199–213.

PETERS, S.E., and W. I. AUSICH. 2008. A sampling-adjusted macroevolutionary history for Ordovician–Early Silurian crinoids. Paleobiology, 34: 104–116. doi:10.1666/07035.1.

POHL, A., E. NARDIN, T. R. A. VANDENBROUCKE, and Y. DONNADIEU. 2016. High dependence of Ordovician ocean surface circulation on atmospheric CO_2 levels. Palaeogeography, Palaeoclimatology, Palaeoecology, 458: 39–51.

POHL, A., D. A. T. HARPER, Y. DONNADIEU, G. LE HIR, E. NARDIN, and T. SERVAIS. 2018. Possible patterns of marine primary productivity during the Great Ordovician Biodiversification Event. Lethaia, 51: 187–197.

RAHMAN, I. A., and S. ZAMORA. 2009. The oldest cinctan carpoid (stem-group Echinodermata), and the evolution of the water vascular system. Zoological Journal of the Linnean Society, 157: 420–432.

REE, R. H., and S. A. SMITH. 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. Systematic Biology, 57: 4–14.

REVELL, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution, 3: 217–223.

RIEDL, R. 1977. A systems-analytical approach to macro-evolutionary phenomena. The Quarterly Review of Biology, 52: 351–370.

RONQUIST, F. 1997. Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. Systematic Biology, 46: 195–203.

SANSOM, R. 2016. Preservation and phylogeny of Cambrian ecdysozoans tested by experimental decay of *Priapulus*. Scientific Reports, 6: 32817. doi: 10.1038/srep32817

SAUPE, E. E., H. QIAO, Y. DONNADIEU, A. FARNSWORTH, A. T. KENNEDY-ASSER, J.-B. LADANT, D. J. LUNT, A. POHL, P. VALDES, and S. FINNEGAN. 2020. Extinction intensity during Ordovician and Cenozoic glaciations explained by cooling and palaeogeography. Nature Geoscience, 13: 65–70.

SHEEHAN, P. M. 2001. The late Ordovician mass extinction. Annual Review of Earth and Planetary Sciences, 29: 331–364.

SHEFFIELD, S. L. 2017. Generic revision of the Holocystitidae of North America (Diploporita, Echinodermata) based on universal elemental homology. Journal of Paleontology, 91: 755–766.

_____. 2019a. The phylogeny of the Diploporita: a polyphyletic assemblage of blastozoan echinoderms. Journal of Paleontology, 93: 740–752.

____. 2019b. A re-interpretation of the ambulacral system of *Eumorphocystis* (Blastozoa: Echinodermata) and its bearing on the evolution of early crinoids. Palaeontology, 62: 163–173. doi: 10.1111/ pala.12396.

____, and C. D. SUMRALL. 2015. A new interpretation of the oral plating patterns of the *Holocystites* Fauna. In S. Zamora, and I. Rábano (eds.), Progress in Echinoderm Palaeobiology: Cuademos del Museo Geominero, Instituto Geológico y Minero de España, Madrid, 19, pp. 159–162.

_____, W.I. AUSICH, and C.D. SUMRALL. 2017. Late Ordovician (Hirnantian) diploporitan fauna of Anticosti Island, Quebec, Canada: implications for evolutionary and biogeographic patterns. Canadian Journal of Earth Sciences, 55: 1–7. DOI: 10.1139/cjes-2017-0160

SIDLAUSKAS, B. 2008. Continuous and arrested morphological diversification in sister clades of characiform fishes: a phylomorphospace approach. Evolution, 62: 3135–3156.

SMITH, A.B. 1988. Fossil evidence for the relationships of extant echinoderm classes and their times of divergence. In C.R.C. Paul and A.B. Smith (eds.), Echinoderm phylogeny and evolutionary biology: Clarendon Press, Oxford, pp. 85–106.

SPRINKLE, J. 1980. An overview of the fossil record. Studies in Geology, Notes for a short course, 3: 15–26.

STIGALL, A. L., C. T. EDWARDS, R. L. FREEMAN, and C. M. Ø. RASMUSSEN. 2019. Coordinated biotic and abiotic change during the Great Ordovician Biodiversification Event: Darriwilian assembly of early Paleozoic building blocks. Palaeoceanography, Palaeoclimatology, Palaeoecology, 530: 249–270.

ŠTORCH, P. 1995. Biotic crises and post-crisis recoveries recorded by Silurian planktonic graptolite faunas of the Barrandian area (Czech Republic). Geolines, 3: 59–70.

SUMRALL, C. D. 1997. The role of fossils in the phylogenetic reconstruction of Echinodermata. The Paleontological Society Papers, 3: 267–288.

____. 2017. New insights concerning homology of the oral region and ambulacral system plating of pentaradial echinoderms. Journal of Paleontology, 91: 604–617.

____, and J. A. WATERS. 2012. Universal elemental homology in glyptocystitoids, hemicosmitoids, coronoids and blastoids: steps toward echinoderm phylogenetic reconstruction in derived Blastozoa. Journal of Paleontology, 86: 956–972.

____, and G.A. WRAY. 2007. Ontogeny in the fossil record: diversification of body plans and the evolution of "aberrant" symmetry in Paleozoic echinoderms. Paleobiology, 33: 149–163.

____, B. DELINE, J. COLMENAR, S.L. SHEFFIELD, and S. ZAMORA. 2015. New data on late Ordovician (Katian) echinoderms from Sardinia, Italy. In S. Zamora, and I. Rábano (eds). Progress in Echinoderm Palaeobiology: Cuademos del Museo Geominero, Instituto Geológico y Minero de España, 19: Madrid, pp. 159–162.

THOMKA, J. R., C. E. BRETT, T. E. BANTEL, A. L. YOUNG, and D. L. BISSETT. 2016. Taphonomy of 'cystoids'

(Echinodermata: Diploporita) from the Napoleon quarry of southeastern Indiana, USA: The lower Silurian Massie Formation as an atypical Lagerstätte. Palaeogeography, Palaeoclimatology, Palaeoecology, 443: 263–277.

TORSVIK, T. H., and L. R. M. COCKS. 2013. New global palaeogeographical reconstructions for the Early Palaeozoic and their generation. Geological Society of London Memoir, 38: 5–24.

TROTTER, J. A., I. S. WILLIAMS, C. R. BARNES, C. LEÉCUYER, and R. S. NICOLL. 2008. Did cooling oceans trigger Ordovician biodiversification? Evidence from conodont thermometry. Science, 25: 550–554.

____, ____, ____, P. MAENNIK, and A. SIMPSON. 2016. New conodont δ18O records of Silurian climate change: Implications for environmental and biological events. Palaeogeography, Palaeoclimatology, Palaeoecology, 443: 34–48.

VAN STAAL, C. R., WHALEN, J. B., VALVERDE-VAQUERO, P., ZAGOREVSKI, A., and N. ROGERS. 2009. Pre-Carboniferous, episodic accretion-related, orogenesis along the Laurentian margin of the northern Appalachians. In J. B. Murphy, J. D. Keppie, and A. J. Hynes (eds.) Ancient Orogens and Modern Analogues, Geological Society Special Publications 327, London, pp. 271–316.

VANDENBROUCKE, T. R., S.E.GABBOTT, F. PARIS, R.J. ALDRIDGE, and J.N. THERON. 2009. Chitinozoans and the age of the Soom Shale, an Ordovician black shale Lagerstätte, South Africa. Journal of Micropalaeontology, 28: 53–66.

VENNIN, E., J.J. ÁLVARO, and E. VILLAS. 1998. High-latitude pelmatozoan-bryozoan mud- mounds from the late Ordovician northern Gondwana platform. Geological Journal, 33: 121–140. doi:10.1002/(SICI)1099-1034(1998040)33:2<121:: AID-GJ780>3.0.CO;2-D.

WRIGHT, D. F. 2017. Phenotypic innovation and adaptive constraints in the evolutionary radiation of Palaeozoic crinoids. Scientific Reports, 7: 1–10.

____, W. I. AUSICH, S. R. COLE, M. E. PETER, and E. C. RHENBERG. 2017. Phylogenetic taxonomy and classification of the Crinoidea (Echinodermata). Journal of Paleontology, 91: 829–846.

ZAMORA, S., and A.B. SMITH. 2008. A new Middle Cambrian stem-group echinoderm from Spain: paleobiological implications of a highly asymmetric cinctan. Acta Palaeontologica Polonica, 53: 207–221.

____, B. LEFEBVRE, J.J. ÁLVARO, S. CLAUSEN, O. ELICKI, O. FATKA, P. JELL, A. KOUCHINSKY, J.P. LIN, E. NARDIN, and R. PARSLEY. 2013. Cambrian echinoderm diversity and palaeobiogeography. Geological Society, London, Memoirs, 38: 157–171.

Museum of Paleontology, The University of Michigan
1105 North University Avenue, Ann Arbor, Michigan 48109-1085
Matt Friedman, Director

Contributions from the Museum of Paleontology, University of Michigan is a medium for publication of reports based chiefly on museum collections and field research sponsored by the museum. Jennifer Bauer and William Ausich, Guest Editors;
Jeffrey Wilson Mantilla, Editor.

Publications of the Museum of Paleontology are accessible online at: http://deepblue.lib.umich.edu/handle/2027.42/41251

Print (ISSN 0097-3556), Online (ISSN 2771-2192)