

Phylogenetic community paleoecology of one of the earliest complex crinoid faunas (Brechin Lagerstätte, Ordovician)

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ABSTRACT

Integrating phylogenetic biology with paleoecology can provide a valuable context for understanding patterns of community structure and niche partitioning in ancient ecosystems. However, the lack of robust phylogenies for many fossil taxa precludes studies of this nature, particularly among marine invertebrates. Fossil Crinoidea (Echinodermata) comprise an ideal model system for phylogenetic community paleoecology for three reasons: (1) they preserve anatomical features that directly relate to feeding ecology, (2) assemblages of well-preserved specimens represent “ecological snapshots” in time, and (3) recent advances in resolving the crinoid tree of life have produced high-resolution phylogenies for Ordovician lineages. Here, we apply multivariate and phylogenetic comparative methods to investigate patterns of paleocommunity structure, niche partitioning, and ecomorphospace occupation in one of the earliest known complex crinoid paleocommunities, the Brechin Lagerstätte (Upper Ordovician, Katian). Results indicate niche differences among species were determined primarily by characters related to filtration fan morphology. Filtration fan density and body size distributions support phylogenetic niche conservatism, but traits related to the size of the feeding area are more labile and exhibit greater divergence than expected among closely related species. Finally, we compare changes in the shape and phylogenetic structure of niche distributions between the Brechin Lagerstätte and the Edwardsville crinoid fauna, a well-studied Mississippian (Viséan) paleocommunity, to examine patterns of community change across the Early to Middle Paleozoic Crinoid Macroevolutionary Faunas.

1. Introduction

1.1. Overview

Niches are fundamental units in ecology and knowledge of their distributions are integral to understanding the structure, composition, and long-term evolution of communities. The niche is an inherently multivariate concept, representing a complex interplay between environmental conditions, resource distributions, and a suite of biotic interactions favorable for species survival (Hutchinson, 1978; Pianka et al., 2017). To help reduce niche dimensionality, ecologists commonly apply multivariate ordination techniques to summarize the variation among species in one or several axes. Such approaches are powerful because they operationalize elusive concepts (e.g., niche breadth) and facilitate comparison among species within clades and/or communities. For example, ecomorphological analysis uses the positions of species within multivariate morphospace to make ecological inferences and can

be used to test a variety of hypotheses related to patterns of community assembly, niche partitioning, and competition between species (Ricklefs and Miles, 1994; Pianka et al., 2017).

Adding a phylogenetic perspective enhances these approaches in several important ways. First, knowledge of the relatedness among species within the community is necessary for evaluating phylogenetic explanations for adaptation and convergence (Harvey and Pagel, 1991; Miles and Dunham, 1993). It has long been appreciated that traits of closely related species tend to be more similar to one another than more distant relatives (Felsenstein, 1985). For this reason, species within a community (and therefore their niches) should not be compared in a phylogenetic vacuum, because their traits reflect adaptation to local conditions as well as the evolutionary history of their respective lineages. Second, genealogical relationships among species in a community can be used to test hypotheses regarding the underlying processes that shape community composition and trait distributions (Cavender-Bares et al., 2009; Cooper et al., 2010). For example, habitat

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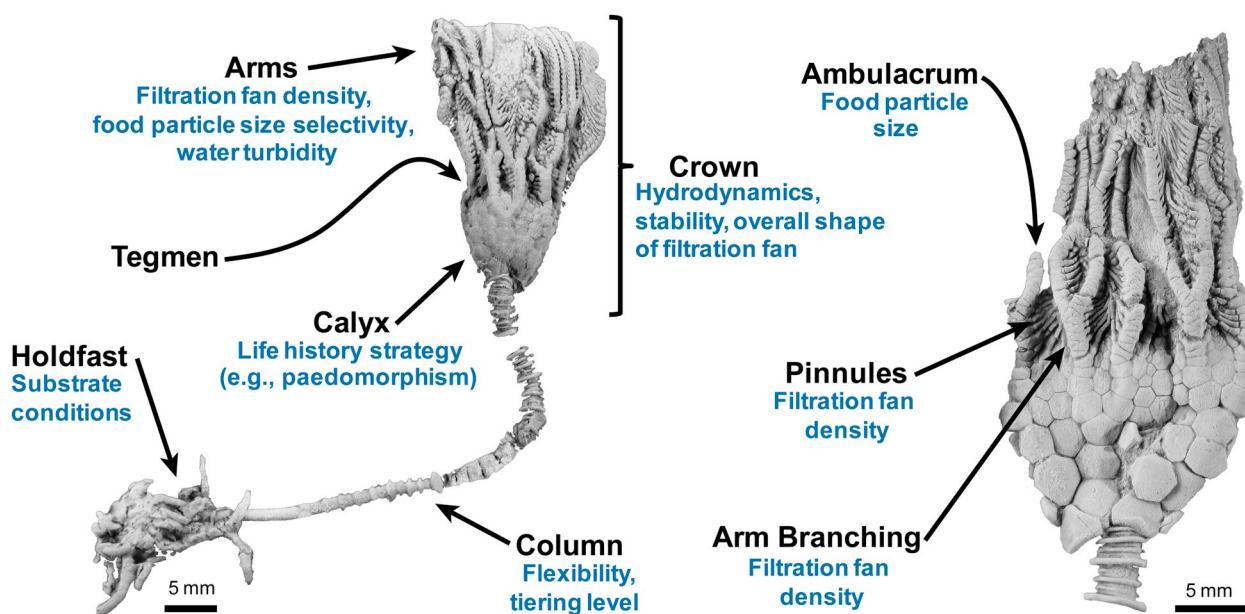


Fig. 1. Relationships between crinoid skeletal morphology and functional ecology. Major skeletal features are labeled in black text, and inferred ecological function (s) are given in blue text. Representative specimens are *Archaeocrinus maraensis* (left) and *Archaeocrinus sundayae* (right) from the Brechin Lagerstätte (Cole et al., 2018). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

filtering is often invoked in cases where communities are comprised of more close relatives than expected under null models (phylogenetic clustering), whereas cases where communities have fewer close relatives than expected (phylogenetic overdispersion) suggest a role for either interspecific competition or phylogenetically widespread convergence (Webb et al., 2002; Cavender-Bares et al., 2009). Finally, the degree of concordance between ecological similarity and phylogenetic relatedness provides insight into the various mechanisms and phylogenetic scales at which patterns of niche conservatism versus niche evolution dominate (Hadly et al., 2009; Webb et al., 2002; Losos, 2008; Smith et al., 2018).

The science of paleoecology has greatly benefited from applying ecomorphological analyses to study niche distributions in extinct communities, especially case studies where there are strong functional links between species ecology and morphology (Ausich, 1980; Van Valkenburgh, 1994; Kitazawa et al., 2007; Curran, 2012). However, few paleoecological studies directly incorporate information on phylogenetic relationships (but see Raia, 2010; Fraser et al., 2015; Polly et al., 2017). In part, this may relate to the relative dearth of available phylogenies for fossil taxa, especially for clades of marine invertebrates. Nevertheless, paleoecologists are increasingly aware of the importance of “tree thinking” (Lamsdell et al., 2017), and the merging of paleoecology with phylogenetic paleobiology represents a promising area of future inquiry and synthesis between disciplines.

In this study, we investigate patterns of paleocommunity structure, niche partitioning, and ecomorphospace occupation in one of the earliest complex paleocommunities of a major clade of marine invertebrates, the Crinoidea (Echinodermata). Crinoids are well suited for investigations of phylogenetic community paleoecology because many aspects of their ecology are linked to well-studied skeletal traits that readily preserve in fossil specimens (Ausich, 1980; Kitazawa et al., 2007). Additionally, intensive systematic investigations in recent years have produced detailed phylogenetic hypotheses and taxonomic revisions of Ordovician crinoids (Ausich et al., 2015; Cole, 2017a, 2018; Wright, 2017a,b; Wright and Toom, 2017; Wright et al., 2017; Ausich, 2018; Cole and Toom, 2018; Cole et al., 2018). Using this robust phylogenetic framework, we apply both multivariate analyses and phylogenetic comparative methods to analyze trait data from 35 fossil crinoid species from the Upper Ordovician (Katian) “Brechin Lagerstätte” (Cole

et al., 2018; Ausich et al., 2018). The Late Ordovician was a particularly important interval in crinoid evolutionary history, as it is associated with the culmination of the Great Ordovician Biodiversification Event (GOBE), which resulted in both taxonomic diversification (Miller and Foote, 1996; Webby et al., 2004) and concomitant increases in ecological complexity of communities (Bambach, 1983; Sepkoski and Sheehan, 1983; Novack-Gottshall and Miller, 2003; Servais et al., 2010; Stigall et al., 2017). Although both taxonomic and morphological components of crinoid diversification during the GOBE have previously been investigated (Sprinkle and Guensburg, 2004; Ausich and Peters, 2005; Deline and Ausich, 2011; Wright and Toom, 2017; Cole, 2018), the ecological components of their diversification are underexplored.

A major goal of this study is to provide a baseline to which other crinoid faunas can be compared to better understand the shifting dynamics of paleocommunity change over the Phanerozoic. Unfortunately, comparable data do not exist in the literature at this time for other early Paleozoic crinoid faunas. Instead, we compare our data with patterns of niche differentiation in a middle Mississippian (Viséan) fauna from the Edwardsville Formation (Indiana, USA), which was previously described in a pioneering paleoecological study by Ausich (1980).

Fossil crinoids have long been considered a model system for paleoecological studies, because their skeletal ecomorphology has been well studied and the unique taphonomic conditions favoring echinoderm Lagerstätten have implications for addressing ecological-time questions in the fossil record (Ausich, 1980, 2016). A brief review of key concepts in crinoid paleoecology and taphonomy are provided below.

1.2. Crinoid ecomorphology

Crinoids are epifaunally tiered, passive suspension feeders that finely partition niches through differences in feeding ecology (Meyer, 1973a,b, 1979, 1982; Macurda Jr. and Meyer, 1974, 1983; Ausich, 1980; Ausich and Bottjer, 1982; Baumiller, 1997, 2008; Messing et al., 2017; and many others). Through both paleontological studies and observations of living crinoids, it is well established that crinoid niche partitioning primarily relates to the differentiation of feeding structures (Ausich, 1980; Kitazawa et al., 2007; Baumiller, 2008) and epifaunal

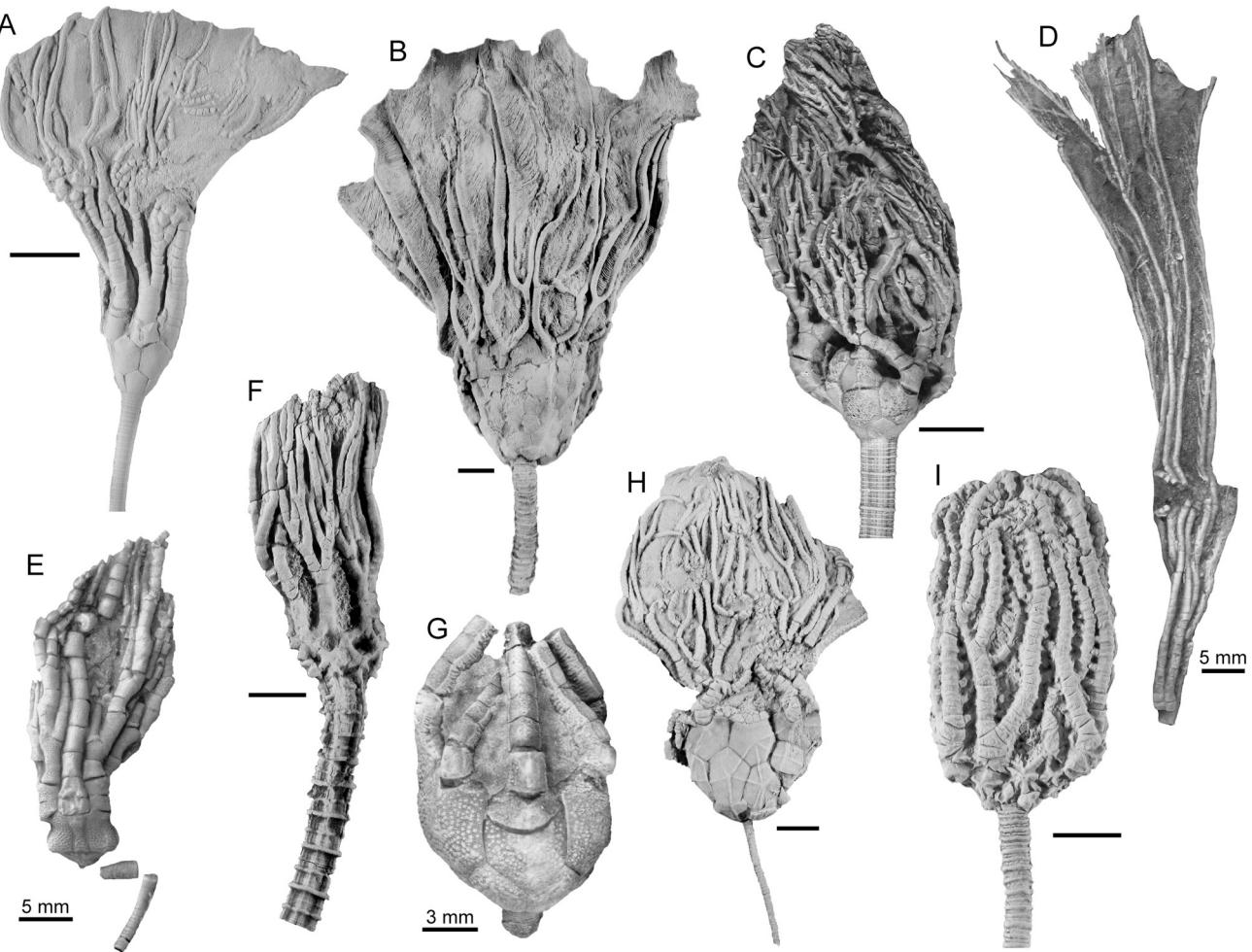


Fig. 2. Examples of exceptionally preserved crinoids from the Brechin Lagerstätte. (A) *Cupulocrinus humilis*, (B) *Glyptocrinus ramulosus*, (C), *Anomalocrinus astrictus*, (D), *Eustenocrinus springeri*, (E) *Cremacrinus guttenbergensis*, (F) *Reteocrinus alveolatus*, (G) *Hyboocrinus tumidus*, (H) *Carabocrinus vancortlandti*, (I) undescribed penta-crinoid “Pentacrinoidea sp. A.” All scale bars 1 cm unless otherwise indicated.

tiering (Ausich and Bottjer, 1982) (Fig. 1). The former can affect feeding ecology through differences in size selectivity of food particles and/or density of the filtration fan. Although other structures like the holdfast and column morphology also contribute to niche partitioning, the roles of these features are less pronounced because they are influenced primarily by environmental parameters like substrate conditions rather than feeding ecology.

Because crinoids are suspension feeders, they position their feeding apparatus (arms, pinnules, tube feet) within the water column and extract suspended particulates carried by currents (Meyer, 1973a,b, 1979, 1982; Macurda Jr. and Meyer, 1974; Ausich, 1980; Ausich and Bottjer, 1982; Messing et al., 2017). Like most other suspension feeders, crinoids extract food from the water in accordance with the principles of aerosol particle capture (Rubenstein and Koehl, 1977; LaBarbera, 1978), which means that captured particles are able to pass through the filter meshwork. Crinoid food size consumption (which may contrast with capture) is limited by the width of the ambulacrual grooves of the feeding appendages (pinnule, ramule, or arm), so large food particles that do not fit into the ambulacrual groove of the feeding appendage will be rejected. Ambulacrual groove width can vary by more than an order of magnitude (Ausich, 1980), and previous studies have indicated size of the food particles captured were clade-specific in at least Mississippian and Ordovician faunas (Ausich, 1980; Brower, 2007).

Optimum particle size capture in an aerosol suspension-feeding system is also a function of the density of the food-capturing branches, i.e., filtration fan density. Structures that increase the overall number of

terminal feeding appendages will result in filtration fans with higher density. The density of the filtration fan will ultimately control the rate of water and particulate flow through the fan and affect the ability of the crinoid to capture food particles. The total number of feeding structures can be increased in several different, non-mutually exclusive ways, including branching of the arms, addition of ramules, and/or addition of pinnules. Because filtration fan density is linked to the rate of water flow through the filtration fan, it is also expected that filtration fans of different densities will have different corresponding optimal microenvironmental conditions for feeding (Kammer, 1985; Holterhoff, 1997; Brower, 2007). These conditions may be met by adjusting the height of the filtration fan above the substrate through changes in the length of the column or by preference for certain habitats or environments (e.g., higher energy carbonate ramps versus lower energy siliciclastic settings) (Kammer and Ausich, 1987).

Finally, crinoids differentiate niches through epifaunal tiering. From an organism's standpoint in a unidirectional current regime, food moves horizontally through the water column. Thus, organisms at consistently different heights above the substratum feed from largely different parcels of seawater, which allows them to exploit different food sources (Lane, 1963, 1973; Ausich, 1980; Ausich and Bottjer, 1982). The relationship between stem length and niche partitioning has been studied in a variety of both fossil and extant communities (Ausich, 1980; Ausich and Bottjer, 1982; Kitazawa et al., 2007; Baumiller, 2008) and is supported by modeling studies using computational fluid dynamics (Dynowski et al., 2016).

1.3. Taphonomy: crinoid paleocommunities as ecological snapshots

The way in which crinoid fossils can be exceptionally preserved further suits crinoids to paleoecological studies. Following previous taphonomic studies of living and fossil crinoids (e.g., Meyer, 1971; Liddell, 1975; Meyer and Ausich, 1983; Donovan, 1991; Brett et al., 1997; Taylor and Brett, 1996; Ausich, 2001), Ausich (2016) argued that the unique conditions leading to the formation of abundant, exceptionally preserved crinoid specimens facilitates the study of ecological-time questions in the fossil record. Because crinoids rapidly disarticulate upon death, fossil assemblages preserving an abundance of complete skeletons represent deposits with little to no time-averaging (Brett et al., 1997). Thus, beds containing multiple individuals and/or species record the composition of once living communities with high fidelity and represent “ecological snapshots” of ancient ecosystems. Here, we utilize the exceptionally preserved crinoids from the Brechin Lagerstätte to build upon the quantitative model for crinoid niche differentiation first described by Ausich (1980). The taphonomic setting of the Brechin Lagerstätte supports its recognition as an ecological snapshot (Brett and Liddell, 1978; Cole et al., 2018) and therefore makes it an ideal fauna for detailed investigations of community paleoecology.

2. Materials and methods

2.1. The Brechin Lagerstätte

The Upper Ordovician (lower Katian) Bobcaygeon and Verulam formations from the Lake Simcoe region of Ontario contain a diverse echinoderm assemblage, which has been named the Brechin Lagerstätte (Cole et al., 2018) after the nearby town of Brechin, Ontario. Recent and ongoing efforts have aimed to conduct a comprehensive re-evaluation and description of the crinoids from the fauna, which has resulted in the identification of 37 crinoid species and 26 genera (Fig. 2); of these, 14 species and 3 genera were previously undescribed. As a result, the Brechin Lagerstätte has been recognized as the most diverse crinoid fauna known from the Katian (Cole et al., 2018; Ausich et al., 2018). Crinoids from the Brechin Lagerstätte are exceptionally preserved with arms, stems, and attachment structures intact in many specimens. Complete stems are known for nearly half of the species in the fauna, and all but two species preserved at least one representative with a complete crown.

To date, taxonomic revisions have been conducted for diplobathrid crinoids (Cole et al., 2018) as well as disparid and hyboocrinid crinoids (Ausich et al., 2018). Forthcoming research will complete evaluation of the fauna by addressing the monobathrids, porocrinids, flexibles, and eucladids. Because we are using recent and ongoing revisions, all new species awaiting formal description are referred to in this study with placeholder names (e.g., “*Periglyptocrinus* sp. A”, “*Eucladid* sp. B”).

Crinoids from the Brechin Lagerstätte are from a stratigraphic interval spanning the Bobcaygeon–Verulam contact, which is gradational and indistinct in outcrop (Armstrong, 2000). The section contains approximately 15 m of the upper Bobcaygeon Formation and 5 m of the lower Verulam Formation (Cole et al., 2018). In this interval, the Bobcaygeon and Verulam formations are predominantly comprised of bioclastic wackestones with interbedded calcareous shales and siltstones. The paleoenvironment is interpreted as a shallow shelf setting with a slight deepening upwards trend. Specimens were preserved in situ on either hardground surfaces or in high-density clusters in shale-filled topographic lows (Brett and Liddell, 1978; Cole et al., 2018). As described above, preservation of delicate, articulated skeletal material requires rapid burial and minimal post-depositional disturbance. Both sedimentological and taphonomic evidence suggests these horizons represent a series of ecological snapshots with minimal to no time averaging (Cole et al., 2018). A comparison of slabs from different horizons and quarries reveals remarkable similarity in taxonomic composition and relative abundance, indicating a relatively

homogenous fauna throughout the sampled interval. Additional details regarding the stratigraphic context, sedimentology, geologic setting, and taphonomy of the Brechin Lagerstätte are in Cole et al. (2018).

2.2. Data collection

We collected trait data for ten quantitative and three composite characters. We refer to these as ecomorphologic characters, because each is a morphological feature inferred to have either direct ecological functionality or is otherwise hypothesized to be strongly correlated with species ecology. Consequently, we emphasize traits relating to the structure of the filtration fan.

Quantitative traits measured for Brechin Lagerstätte crinoids include (1) calyx width at its maximum point at or below where the arms become free; (2) calyx height, from the base of the calyx to the top, defined as the position where the arms become free; (3) arm length, measured from where the arms become free from the calyx to their tips; (4) arm number, counted at the upper margin of the calyx where the arms become free (i.e., number of arm openings); (5) arm branching, counted as the maximum number of in line bifurcations that occur within a free arm; (6) terminal feeding appendages (Ω), defined as the total number of feeding structures including pinnules, ramules and/or apinnulate/aramulate arms; (7) brachial width, measured at the midpoint of the arms; (8) brachial height, measured at the midpoint of the arms; (9) pinnule/ramule density, measured as the number of structures per 5 mm of an arm at the midpoint of the arms; and (10) pinnule/ramule width, measured on a pinnule/ramule from the midpoint of the arms. In addition, we also gathered data for three composite characters. The first of these was body size (V), measured here as calyx volume. We calculated body size using the standard equation for a cone:

$$V = \frac{1}{3}\pi r^2 h \quad (1)$$

where r is the radius of calyx at its maximum width (quantitative trait 1), and h is the height of the calyx from the base to the place where the arms become free (quantitative trait 2). Filtration fan area (f_A) was calculated using the Ausich (1980) equation with modifications by Cole (2017b) to account for the area of the tegmen:

$$f_A = \pi(L + r)^2 - \pi r^2 \quad (2)$$

where L is the total length of the arms (quantitative trait 3). Filtration fan density (F_D) was calculated by dividing the total number of terminal feeding appendages (Ω , quantitative trait 6) by the total area of the filtration fan (f_A):

$$F_D = \frac{\Omega}{f_A} \quad (3)$$

to give the number of feeding structures within a given area of the filtration fan, where higher numbers indicate denser filtration fans and lower numbers reflect more open filtration fans (Ausich, 1980). Units for filtration fan density are given as number of feeding structures (Ω) per area of the filtration fan; here we use feeding structures per cm^2 (Ω/cm^2).

Morphological data were collected for 165 specimens across 36 of 37 taxonomically valid species recognized in the fauna. Data for *Cleioocrinus regius* were unavailable for study, and *Plicodendrocrinus proboscidiatus* was excluded because no specimens preserved a complete crown, so a total of 35 species were used in all subsequent analyses. Measurements were primarily taken from specimens from the collection of J.M. Koniecki, which includes both private collections and material deposited at the University of Michigan Museum of Paleontology. Additional measurements were taken from specimens from the National Museum of Natural History and in uncommon instances for rare taxa, supplemented from published literature (e.g., *Illemocrinus amphiatus* [Eckert, 1987]). During data collection, it was noted whether structures like arms were preserved incompletely, so that analyses could be

conducted using only complete measurements. Following collection of specimen data, species averages were calculated for each of the ten measured morphological traits and the three calculated variables.

2.3. Statistical methods

2.3.1. Multivariate analyses

To assess differences in the occupation of ecomorphospace, we first constructed a dissimilarity matrix of all 10 quantitative traits using Gower's coefficient (Gower, 1971) and then conducted a Principal Coordinate Analysis (PCO) on the resulting dissimilarity matrix. To help identify the dominant morphological features associated with each major axis of variation, we used Spearman's rank correlation to statistically compare the relationship between PCO scores and the three composite characters: body size (V), filtration fan area (f_A), and filtration fan density (F_D). These three characters were not included in the dissimilarity matrix to avoid any potential circularity in interpreting PCO axes (see below). In addition to these three composite characters, we also performed Spearman's rank correlation tests between all individual quantitative traits and the recovered PCO axes to help interpret the first three principal components and determine morphological features contributing to variation along the first three principal components (Supplemental information). Finally, the species-level phylogeny of Brechin crinoids was overlain on the recovered morphospace to permit visualization of phylogenetic relationships in morphospace (Revell, 2012) (see below).

To identify phenetic groupings of ecologically similar taxa and facilitate comparisons with patterns of phylogenetic relationships, we also conducted a cluster analysis on the dissimilarity matrix using Ward's method (Ward, 1963).

2.3.2. Tree-based analyses

Applying phylogenetic comparative approaches to community paleoecology requires time-calibrated phylogenetic hypothesis of fossil species occurring within a paleocommunity. Recent phylogenetic studies on Ordovician crinoids are comprehensive at high taxonomic scales and are nearly complete at the genus level (Ausich et al., 2015; Cole, 2017a; Wright, 2017a,b; Wright and Toom, 2017; Wright et al., 2017; Cole and Toom, 2018; Ausich, 2018; Cole et al., 2018). Based on this existing framework, we assembled a phylogenetic tree of 36 crinoid species occurring in the Brechin Lagerstätte. The backbone of the tree comprises relationships among genera unambiguously recovered by character data in previous studies (e.g., Ausich et al., 2015; Cole, 2017a; Wright, 2017a). Ambiguous relationships were resolved by collapsing branches into polytomies at the least inclusive clade supported by previous computational analyses, and species were then appended to the genus-level tree as unresolved polytomies within their respective genera (Fig. 3). Rather than condition our results on a single phylogeny, we randomly resolved polytomies and applied *cal3* (Bapst, 2012, 2013), an a posteriori probabilistic approach to time-scaling paleontological trees, to draw node ages from a probability distribution consistent with best-fit parameter estimates of diversification and sampling rates (Foote, 1997). We repeated this procedure 100 times to generate a distribution of time-scaled phylogenies reflecting uncertainty in both phylogenetic relationships and branching times (see Supplemental information for additional details and sensitivity tests). To visualize differences between ecological and phylogenetic relationships among species, we constructed a tanglegram using the *cophylo()* function from the R package *phytools* (Revell, 2012) and compared the dendrogram from the cluster analysis with the Brechin crinoid phylogeny. To assess whether mismatches between the phylogeny and the ecophenetic clusters were significantly different from random expectation, the recovered ecological relationships were compared to a null distribution by using a Monte Carlo procedure comparing the Robinson-Foulds distance (Robinson and Foulds, 1981) between the dendrogram and 10,000 random tree topologies.

To determine the degree to which ecological similarity is predicted by phylogeny, we calculated phylogenetic signal for three ecomorphologic characters: body size, filtration fan density, and filtration fan area. As a measure of phylogenetic autocorrelation in traits, phylogenetic signal can provide insight into understanding the process(es) driving trait evolution, and in some cases can be used to identify niche conservatism (Losos, 2008; Cooper et al., 2010). For example, Pagel's lambda (λ) ranges from 0 to 1, where $\lambda = 1$ indicates a model of evolution consistent with expectations from Brownian motion, and $\lambda = 0$ indicates no correlation between traits and phylogeny (Pagel, 1999). Blomberg's K is another metric to quantify phylogenetic signal (Blomberg et al., 2003). Blomberg's K is also bounded by zero, but unlike Pagel's λ it can take values greater than one (Blomberg et al., 2003). A value of $K = 1$ is consistent with Brownian evolution with a similar interpretation to $\lambda = 1$. However, $K > 1$ are consistent with niche retention, a form of niche conservatism where traits of the sampled species are more similar to those of their ancestors than expected given a Brownian motion model of evolution. We calculated phylogenetic signal using Pagel's λ and Blomberg's K over a distribution of 100 time-scaled phylogenies. Because traits vary over several orders of magnitude, all were log-transformed prior to analysis. Over all phylogenies, we used likelihood ratio tests to compare the estimated phylogenetic signal to a null model assuming no signal (Revell, 2012). To summarize the degree to which the statistical significance of phylogenetic signal varied across multiple time-scaled trees, we calculated both the mean *p*-value and the percentage of trees for which *p*-values were < 0.05 .

3. Results

3.1. Trait variation among clades

Mean body size of all crinoid species from the Brechin Lagerstätte is 1.67 cm^3 but varies by four orders of magnitude across species (Table 1, Fig. S1, Supplemental data). The smallest calyces measured belonged to the disparid *Eustenocrinus springeri*, which averaged 0.01 cm^3 , whereas the largest were from the porocrinoid *Carabocrinus vancortlandti*, which had a mean volume of 14.46 cm^3 . On average, camerates tend to have larger calyces (mean = 2.86 cm^3) than pentacrinoinds (mean = 0.99 cm^3), although the large size of *C. vancortlandti* is a notable exception (Table 1, Fig. S1). The next largest species after *C. vancortlandti* is *Glyptocrinus ramosus* with an average calyx volume of 6.56 cm^3 . Monobathrid and diplobathrid camerates have calyces of comparable sizes, although stem eucamerates are somewhat smaller (Table 1, Fig. S1). Disparids have the smallest mean body size out of all crinoid groups from the Brechin Lagerstätte. Euclidids are somewhat larger than disparids, but smaller than flexibles (Table 1, Fig. S1). Porocrinoids have the largest mean body size among pentacrinoinds, although this is skewed by the large size of *C. vancortlandti*. The remaining species of porocrinoid have calyces ranging from about 0.42 to 0.84 cm^3 .

Area of the filtration fan ranges from 9.65 cm^2 in *Hybocystites problematicus* to 241.7 cm^2 in *Carabocrinus vancortlandti*. Although body size is positively correlated with filtration fan area (Spearman's $Rho = 0.410$, $p = 0.014$, Fig. S2), there are several notable exceptions. For example, stem eucamerates have the smallest filtration fans on average despite moderately large calyces, and flexibles have the largest filtration fans on average despite relatively small calyces (Table 1, Fig. S1). The large-bodied monobathrids have large filtration fans, and the relatively small-bodied euclidids have relatively smaller filtration fan areas (Table 1, Fig. S1).

Filtration fan density is not significantly correlated with filtration fan area (Spearman's $Rho = 0.236$, $p = 0.172$, Fig. S2). The most open filtration fan is found in *Carabocrinus vancortlandti* ($0.17 \Omega/\text{cm}^2$), and *Pararchaeocrinus* "sp. A" has the highest filtration fan density ($90.23 \Omega/\text{cm}^2$). Filtration fans of camerata crinoids (mean = $28.43 \Omega/\text{cm}^2$) are

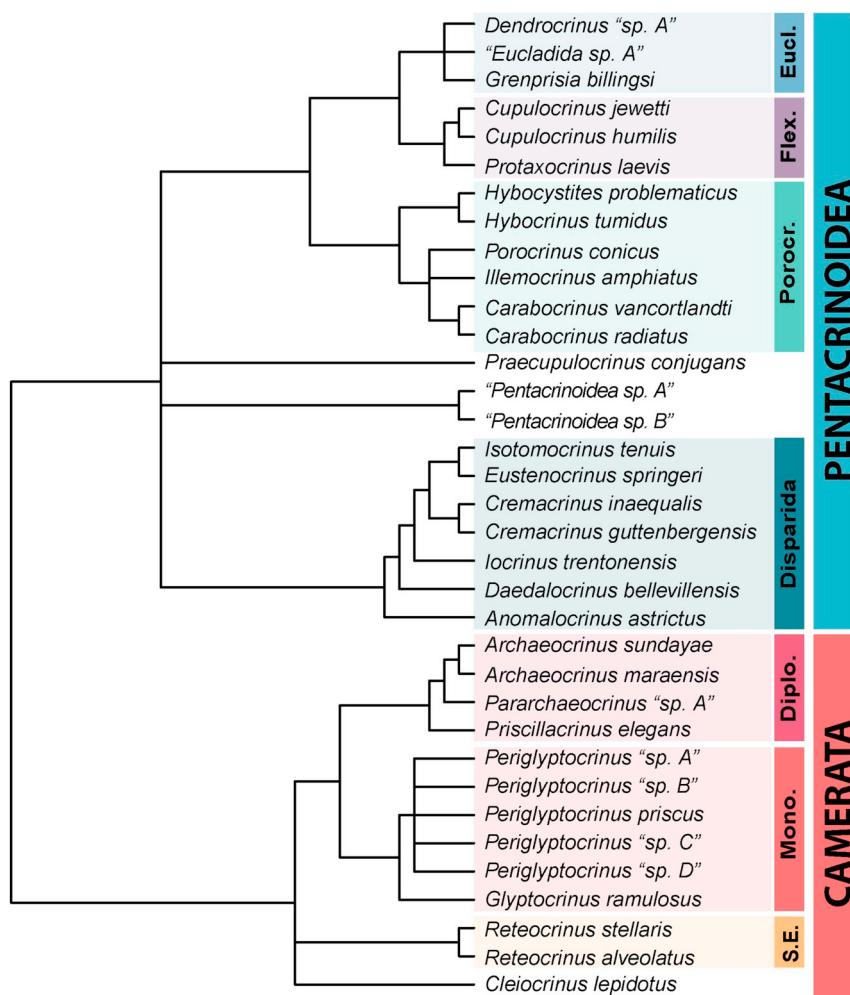


Fig. 3. Phylogeny of crinoids from the Brechin Lagerstätte with major groups identified. S.E. = stem eucamerates; Mono. = Monobathrida; Diplo. = Diplobathrida; Porocr. = Porocrinidea; Flex. = Flexibilia; Eucl. = Euclidida.

significantly denser than those of pentacrinoidea (mean = $5.62 \Omega/\text{cm}^2$; t -test, $p = 0.007$), with diplobathrid crinoids having filtration fans that are much denser than any other group, although there is overlap between means for the two groups (Table 1, Fig. S1). Notably, stem eucamerates have filtration fans that are far more open than other eucamerates, and disparid crinoids have filtration fans that are intermediate in density between stem eucamerates and monobathrids. The higher average density of disparids is driven by *Anomalocrinus astrictus*, which has a density of $72.75 \Omega/\text{cm}^2$; other disparid filtration fans range in density from 0.84 to $2.56 \Omega/\text{cm}^2$.

3.2. Results of multivariate analyses

In the principal coordinates analysis, PCO's 1–3 account for 41.12%, 16.63%, and 12.66% of variance, respectively, for a total of 70.41%. Spearman's rank correlation tests indicate PCO1 is significantly correlated with the density of the filtration fan (Spearman's $\rho = -0.73$, $p = 7.78 \times 10^{-7}$) as well as other individual traits related to the overall fan shape and structure (e.g., pinnule density) (Table S1). Similarly, PCO2 was significantly correlated with the size of the feeding structures and areal extent of the fan (Spearman's $\rho = 0.72$, $p = 3.02 \times 10^{-6}$), whereas PCO3 was significantly correlated with calyx volume (Spearman's $\rho = 0.54$, $p = 8.73 \times 10^{-4}$). Based on the combination of quantitative and composite traits found to significantly correlate with each of the PCO axes (Table S1), we interpret the first three principal coordinate axes as filtration fan density, filtration fan area,

Table 1

Mean calyx volume, filtration fan area, and filtration fan density of crinoid species from the Brechin Lagerstätte, grouped by subclasses Camerata and Pentacrinoidea and their respective subgroups.

	Mean calyx volume (cm^3)	Mean filtration fan area (cm^2)	Mean filtration fan density (Ω/cm^2)	Species per group
Camerata	2.86	89.40	28.43	13
Monobathrida	3.05	111.20	26.14	6
Diplobathrida	3.39	86.49	40.17	5
Stem eucamerates	0.97	31.19	5.92	2
Pentacrinoidea	0.99	75.52	5.62	22
Disparida	0.21	80.93	13.34	6
Porocrinidea	2.98	55.67	1.00	6
Flexibilia	0.56	114.32	1.74	3
Euclidida	0.32	71.28	4.62	7

and body size, respectively (Fig. 4, Table S1). Interestingly, several traits previously identified as important components of crinoid niche differentiation (Ausich, 1980; Kammer, 1985; Kammer and Ausich, 1987), such as food size selectivity (i.e., pinnule width, brachial width) were not recovered as being solely responsible for variation along any one PCO axis.

Taxa fall into two primary regions of morphospace along PCO axes 1–2 (Fig. 4). The first group is entirely composed of eucamerate taxa, whereas the second group is entirely composed of pentacrinoidea. The two stem eucamerates, *Reteocrinus stellaris* and *R. alveolatus*, are

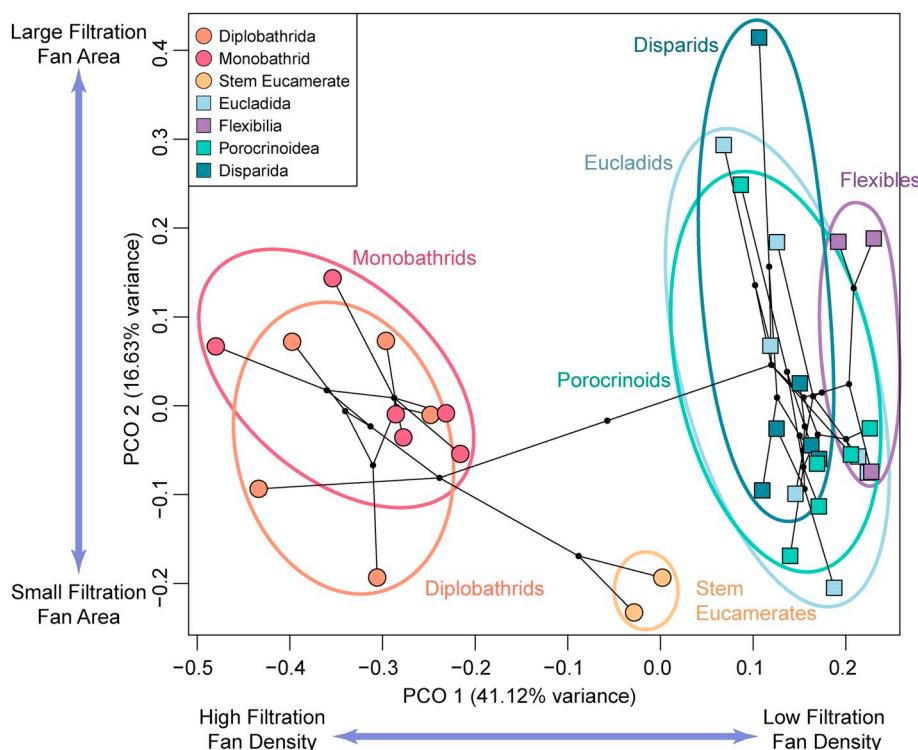


Fig. 4. Ecomorphospace plot of the first two PCO axes with major crinoid groups circled. Squares = pentacrinoidea, circles = eucamerata. See Fig. S3 for species labels.

positioned between the clusters formed by these two larger clades. The region of morphospace occupied by the eucamerate group has roughly equivalent ranges in variation for the first three PCO's. There is extensive overlap between the monobathrids and diplobathrids within this group, although diplobathrids have a greater range of variation along PCO2 than do monobathrids. The pentacrinoidea occupy a much larger region of morphospace than do the eucamerata. Most of their variation occurs along PCO2 and PCO3, whereas the range of variation along PCO1 is relatively small. Subclades within the pentacrinoidea region of morphospace overlap extensively along PCO1 and PCO2, although more distinct and non-overlapping groups form along PCO3. For example, porocrinoids and flexibles occupy one endmember of PCO3, whereas eucladids and disparids occupy the other (Figs. 4, S3).

The cluster analysis recovered a dendrogram with two major groups (Fig. 5). One group contains only pentacrinoidea taxa with the exception of the stem eucamerate, *Reteocrinus stellaris*. The other group is dominated by the remaining eucamerate taxa but also includes eight pentacrinoidea. Pentacrinoidea included in the eucamerate-dominated cluster are *Grenprisia billingsi*, *Anomalocrinus astrictus*, *Eustenocrinus springeri*, *Dendrocrinus* "sp. A", *Daedalocrinus bellevillensis*, *Cupulocrinus humilis*, and both undescribed species of a new pentacrinoidea genus, "Pentacrinoidea sp. A" and "Pentacrinoidea sp. B." At lower taxonomic levels, there is even less concordance between clusters and phylogenetic relationships, but there are nevertheless some similarities. For example, three of the four porocrinids group together, and three of the five diplobathrids are clustered. However, other subclades, such as members of Disparida and Flexibilia, are widely distributed across the dendrogram.

3.3. Results of tree-based analyses

Comparisons of the dendrogram to the phylogenetic tree reveal that the Robinson-Foulds distance between the dendrogram and the phylogeny was significantly shorter ($p = 0.008$) than the distances calculated between the dendrogram and a distribution of 10,000 random trees (Fig. S5). This indicates that the dendrogram resulting from the cluster analysis is more similar to the phylogeny than would be expected by

random.

Phylogenetic signal calculated over a distribution of 100 times-scaled trees recovered significant phylogenetic signal for some, but not all characters considered. Filtration fan density and body size expressed significant phylogenetic signal for both Pagel's λ and Blomberg's K , with significant p -values recovered for 100% of trees used (Fig. 6, Table 2). Filtration fan area was the only character that did not show significant phylogenetic signal, with a mean Pagel's λ of 0.12 (mean $p = 0.8$, % $p < 0.05 = 0$) and mean Blomberg's K of 0.63 (mean $p = 0.3$, % $p < 0.05 = 15$).

4. Discussion

4.1. Niche differentiation in the Brechin Lagerstätte

Evaluating patterns of niche partitioning first requires identifying the most important traits contributing toward niche separation. In this study, we find niche differences among crinoids from the Brechin Lagerstätte are associated primarily with variation in three characters: filtration fan density, filtration fan area, and body size.

The primary niche axis corresponds to filtration fan density and has a bimodal distribution. Fan density reflects many aspects of food particle capture, such as particle size and rate of capture (Ausich, 1980; Kitazawa et al., 2007). This distribution among Brechin crinoids exhibits strong concordance with taxonomic membership, with two highly separated regions comprising the infraclass Eucamerata and subclass Pentacrinoidea (Fig. 4). The importance of phylogenetic structure to filtration fan density is further evidenced by significant phylogenetic signal for this trait (Table 2). In addition, estimated values of Blomberg's K are consistent with niche retention between the two subclasses (Blomberg's $K > 1$ in 84% of phylogenies), which is a form of phylogenetic niche conservatism where closely related species are more similar than expected by models assuming simple diffusion through morphospace. Thus, our results suggest that modes of food capture among Brechin crinoids exhibit significant phylogenetic structure.

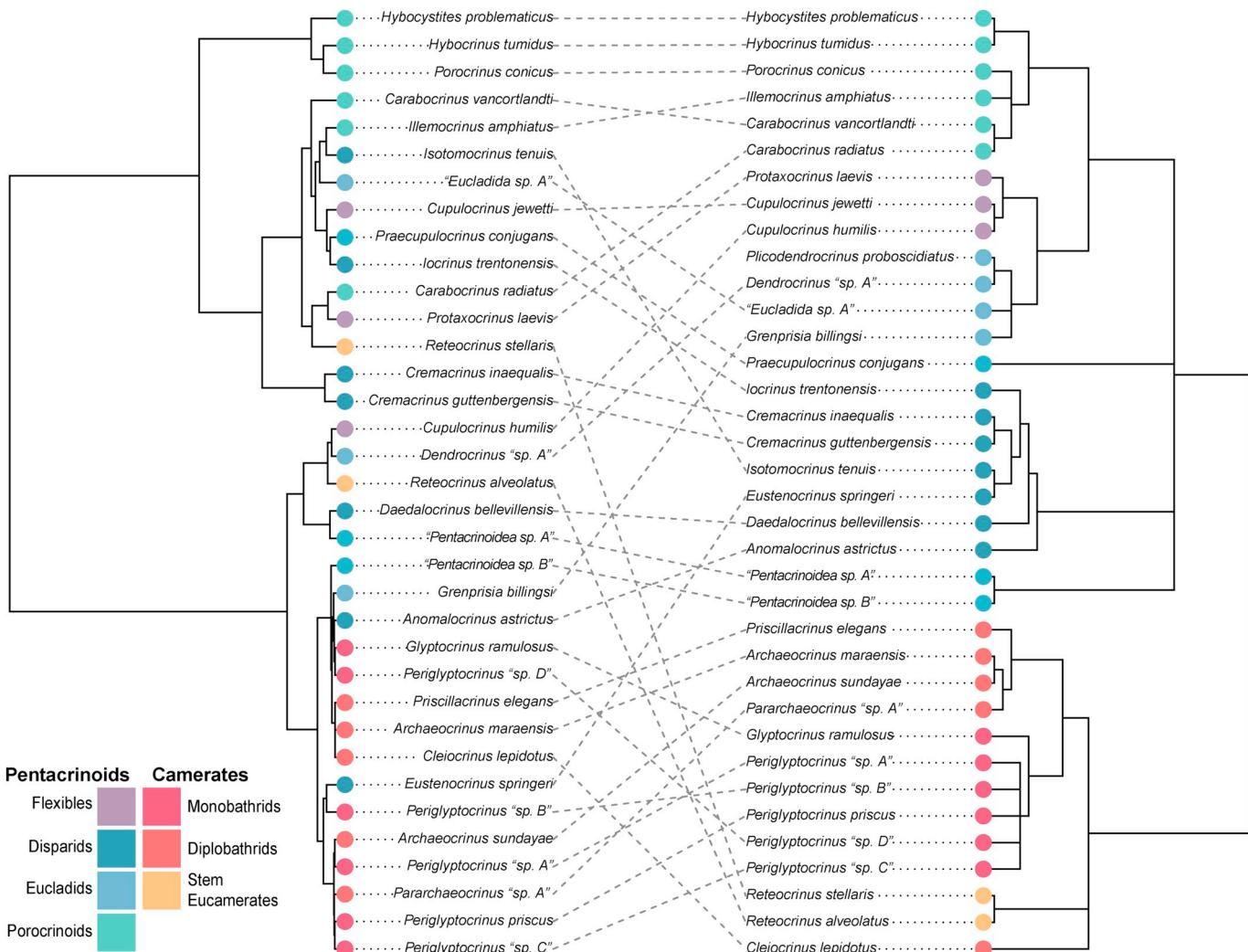


Fig. 5. Tanglegram with the correspondence between ecological groupings recovered from the cluster analysis (left) and the phylogeny (right). Taxa are connected by dashed lines between the two trees.

The striking separation in ecomorphospace between the Eucamerata and Pentacrinoidea warrants further consideration regarding anatomical features related to fan density morphology and their distributions among Ordovician clades. Although there are several different morphometric features that contribute to fan density (e.g., brachial height, pinnule density, arm openings, branching number), separation between eucamerates and pentacrinooids along the fan density axis is primarily determined by the presence or absence of pinnules. All the eucamerate crinoids from the Brechin Lagerstätte possess pinnules but pentacrinooids do not. “Stem eucamerates” (e.g., *Reteocrinus*) lack pinnules but have many arms, resulting in filtration fans of intermediate density, which is reflected by their position in ecomorphospace that is intermediate between the eucamerate and pentacrinoidean regions (Fig. 4). Because pinnules add additional feeding structures to the arms, resulting in higher fan densities, eucamerates from the Brechin Lagerstätte are characterized by fan densities that typically exceed those of pentacrinooids by at least an order of magnitude. Despite lacking pinnules, pentacrinooids can nevertheless increase filtration fan density through numerous branching of the arms and/or the presence of rami. However, these structures are typically not sufficient for the pentacrinoidean filtration fan to reach the density of pinnulate cameratae fans (although the disparid *Anomalocrinus astrictus* is an exception). The importance of fan density to niche partitioning is consistent with a previous study by Brower (2007) on Upper Ordovician crinoids, which

summarized extensive variation in filtration fan structure across multiple taxa and paleocommunities.

The size of the filtration fan was identified as the second major trait influencing niche partitioning (Table S1). Interestingly, the magnitude of variation within subclades is greater along PCO2 than along PCO1. For example, in pentacrinooids, the variance of PCO2 scores is more than three times greater than that along PCO1. The niche axis corresponding to filtration fan area is the only ecomorphologic character not found to exhibit significant phylogenetic signal for either Pagel's λ or Blomberg's K (Table 2). Thus, trait evolution concerning the size of the filtration fan area may have fewer phylogenetic or developmental constraints than other ecomorphologic characters. Given that filtration fan size is a major contributor to niche differences in Brechin crinoids, it is possible that competition among closely related species may have led to increased phenotypic divergence, which over time can contribute to the erosion of phylogenetic signal.

Body size, as measured by calyx volume, was recovered as the third major trait contributing to niche differences. Similar to filtration fan density, body size was also found to have significant phylogenetic signal, including values of Blomberg's K consistent with niche retention (Blomberg's $K > 1$ in 75% of phylogenies) (Table 2). Differences in body size may be related to different metabolic levels and/or energetic needs of species, and these differences are phylogenetically structured at high taxonomic scales. For example, cameratae crinoids tend to have

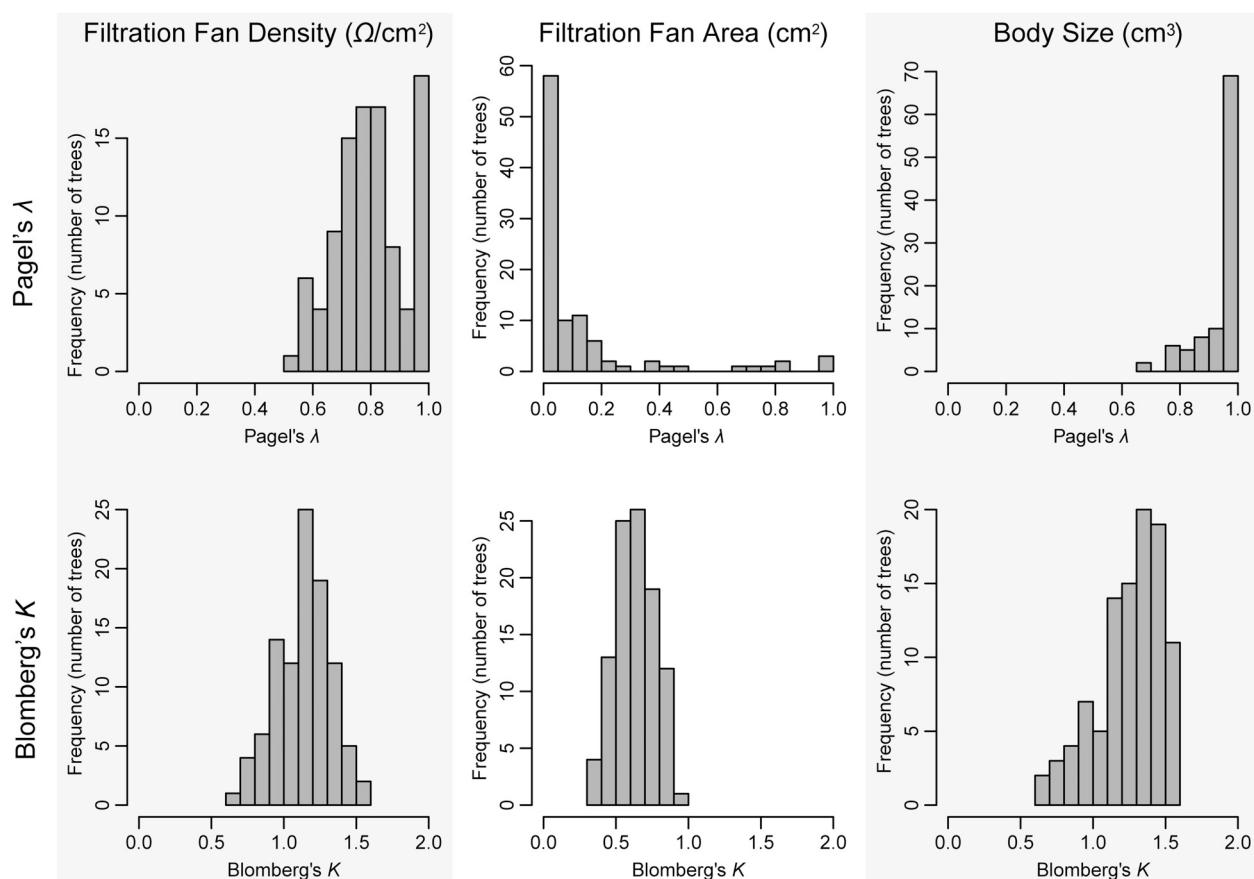


Fig. 6. Histograms of two metrics of phylogenetic signal, Pagel's λ and Blomberg's K , calculated for major ecomorphologic traits over a distribution of 100 time-scaled trees. Frequency is given as the number of trees recovered per bin.

Table 2
Summary statistics for phylogenetic signal of major ecomorphologic characters.

	Filtration fan density (Ω/cm^2)	Filtration fan area (cm^2)	Body size (cm^3)
Pagel's λ			
Mean λ	0.80	0.12	0.95
Mean p -value	1.2×10^{-4}	0.80	4.9×10^{-5}
Percent p -value < 0.05	100%	0%	100%
Blomberg's K			
Mean K	1.14	0.63	1.25
Mean p -value	0.002	0.30	0.001
Percent p -value < 0.05	100%	15%	100%

larger body sizes than pentacrinoidea (Table 1), which may reflect higher metabolic needs and greater requirements for nutrient uptake. The higher density of camerate filtration fans may correspond to increased food capture to support larger body size. Although there are other potential ecological consequences of body size in crinoids (e.g., fecundity, hydrodynamic stability, ontogeny, life history), links between these ecological traits and body size are poorly understood and difficult to confidently identify.

Although we establish filtration fan density, fan area, and body size as the dominant characters structuring niche distributions in the Brechin Lagerstätte, other features not included in our study may have also been important for structuring niche differences within the community. For example, epifaunal tiering is a well-documented strategy that allows taxa with similarities in feeding structures and/or food size

selectivity to differentiate niches by feeding from different portions of the water column (Lane, 1963, 1973; Ausich, 1980; Ausich and Bottjer, 1982; Kitazawa et al., 2007; Baumiller, 2008). Although data for stem length were not included in the analyses for this study, the height of the crinoid crown above the substrate almost certainly plays a major role in niche differentiation among Brechin Lagerstätte crinoids. Of the specimens measured for this study, 22% had complete stems, which were represented by 16 of the 36 species. Complete stems ranged in length from 1.5 cm in *Hybocystites problematicus* to over 40 cm in "Pentacrinoidea sp. B." In many cases, taxa that overlapped extensively in ecomorphospace were found to have very different stem lengths. For example, most species of *Pararchaeocrinus* and *Archaeocrinus* are closely clustered in ecomorphospace (Figs. 4, S3), but species of *Archaeocrinus* have much longer stems than do species of *Pararchaeocrinus*. In the former, maximum column lengths range from 25 to 30 cm between the two species, whereas stems reach maximum lengths of only 7 to 18 cm in species of *Pararchaeocrinus*. This differentiation in feeding height would allow species with similar filtration fan densities and/or food size selectivity to coexist by exploiting food sources from different parcels of seawater (Lane, 1963, 1973; Ausich, 1980; Ausich and Bottjer, 1982).

Finally, this study only considered crinoids from the Brechin Lagerstätte but a variety of other pelmatozoans are known from the fauna (Springer, 1911; Brett and Liddell, 1978; Cole et al., 2018). Future comparative studies may consider investigating patterns of niche distributions within non-crinoid echinoderm lineages and/or how other suspension feeding taxa may have influenced patterns of niche partitioning in crinoids.

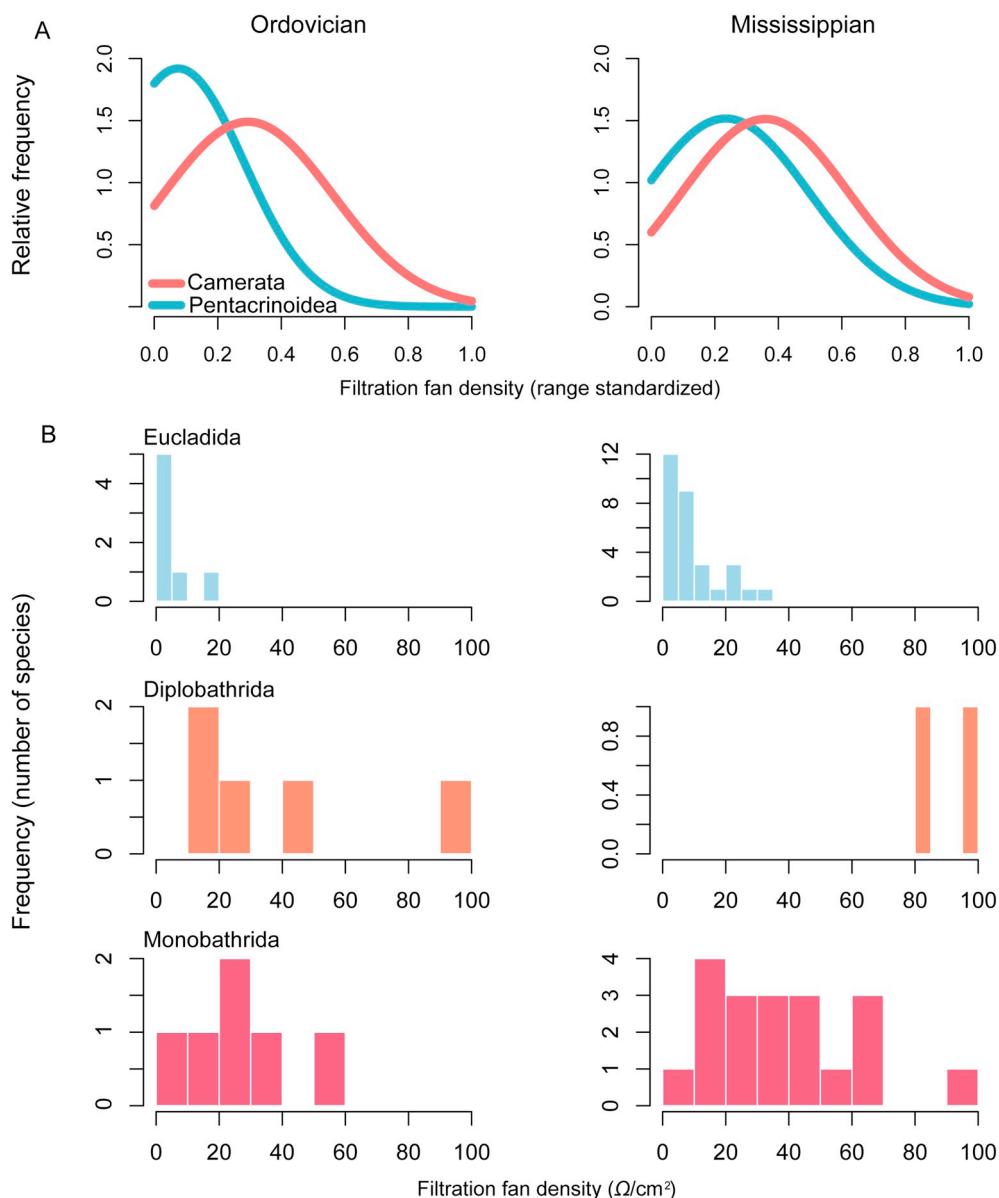


Fig. 7. Comparison of filtration fan densities (f_D) of crinoid clades from Ordovician vs. Mississippian communities. (A) Camerates increase in mean f_D but retain a similar distribution between the Ordovician and Mississippian. Although pentacrinooids also increased in mean f_D between the Ordovician and Mississippian, the shape of their distribution changed markedly between intervals. Relative frequency distributions were obtained by a curve fitting procedure after range standardizing the data. (B) Histograms for three major subclades occurring in both intervals: Eucladida (Pentacrinoidea), Diplobathrida (Camerata), and Monobathrida (Camerata).

4.2. Community structure through time: comparing niche distributions between early and middle Paleozoic Crinoid Macroevolutionary Faunas

In this study, we have focused on quantifying the relative contribution of ecomorphologic characters influencing niche differentiation in crinoids from the Brechin Lagerstätte. An obvious next step would be to ask how paleocommunities change along spatial gradients or have evolved through time. Unfortunately, few studies can be directly compared to the present study because they do not include comparable data on the major characters contributing to niche differences (e.g., Brower, 2007). A study by Ausich (1980) on crinoids from Edwardsville Formation (Mississippian, Viséan) is one of the only previous investigations with comparable paleocommunity data for filtration fan density. Below, we compare niche distributions between major

crinoid clades of the Brechin Lagerstätte and the Mississippian fauna described by Ausich (1980) to examine patterns of paleocommunity change over time. Although these paleocommunities are separated widely in space and time, differences between them may highlight major changes in community structure and environments that occurred between the Early and Middle Paleozoic Crinoid Macroevolutionary Faunas (Ausich et al., 1994; Sallan et al., 2011; Thompson and Ausich, 2015; Ausich and Kammer, 2013).

Niche distributions based on filtration fan densities reveal major differences among subclades between Upper Ordovician and Lower Mississippian communities (Fig. 7). Ordovician pentacrinooids, which are apinnulate, have more open filtration fans with densities of $< 20 \Omega/cm^2$. The only exception to this pattern is a single disparid, *Anomalocrinus astrictus*. By contrast, Ordovician camerates—both

pinnulate eucamerates and the apinnulate stem eucamerates—have denser filtration fans that all exceed $20\Omega/\text{cm}^2$. Notably, there are substantial differences in the shape of fan density distributions between the two subclasses during the Ordovician. By the Mississippian, mean filtration fan density had increased for both subclasses, although the magnitude of this increase was greater in pentacrinoïds than in camerates. This resulted in increased overlap between pentacrinoïd and camerate fan density during the Mississippian compared to the Ordovician (Fig. 7a). Within subclades during the Mississippian, both maximum fan density and variance increased for eucladids and monobathrids, whereas diplobathrids exhibited a decrease in variance and persistence of only forms with high-density fans (Fig. 7b).

The increased overlap between pentacrinoïd and camerate fan density during the Mississippian suggests pentacrinoïds converged on camerate ecomorphospace during this interval. This pattern was primarily driven by the evolution of pinnules in eucladid pentacrinoïds. Pinnulate articuliform eucladids evolved by at least the Devonian (Wright, 2017b) and allowed pentacrinoïd filtration fans to become more similar to those of camerates. It is possible the convergence of eucladid pentacrinoïds on camerate-like filtration fans led to increased competition with camerate crinoids, which may have had macroevolutionary consequences. For example, diplobathrid crinoids began to sharply decline during the Devonian, and went extinct by the end of the Serpukhovian (late Mississippian) (Cole, 2018). The cause of the decline and ultimate extinction of diplobathrids remains unexplained, but it is possible that increased competitive interactions with pentacrinoïds played a role (sensu Jablonski, 2008). Similarly, a transition between the Middle and Late Paleozoic Crinoid Macroevolutionary Faunas occurred during the Viséan (middle Mississippian) (Ausich et al., 1994; Ausich and Kammer, 2013) when eucladid crinoids replaced camerates as the dominant faunal constituents. The evolution of pinnules in eucladid pentacrinoïds, coupled with retention of apinnulate forms in other lineages, would have increased the number of functional groups occupied by pentacrinoïds and therefore expanded their ability to exploit diverse resources and occupy a variety of habitats, setting the stage for the major transition between Crinoid Macroevolutionary Faunas.

4.3. Future directions

We believe the data, results, and general framework outlined in this study provide a paleoecological baseline to further explore key issues in crinoid evolutionary history, including (but not limited to) the relationship between ecological diversity and species richness, patterns of niche occupation and evolution at multiple hierarchical scales, and relating changes in paleocommunity structure and composition with other macroevolutionary currencies. One particularly fruitful direction of future research concerns patterns of ecological diversification during the Great Ordovician Biodiversification Event. Such studies would complement previous work on patterns of taxonomic and morphologic diversification and therefore produce a more comprehensive view of life during this significant interval of evolutionary history. Finally, it is our hope that the case-study presented here will encourage other paleontologists to apply similar approaches to other faunas and taxonomic

groups, particularly marine invertebrates, which have received comparatively little attention at the community scale in the field of phylogenetic paleobiology.

5. Conclusions

We combined phylogenetic approaches with community paleoecology to study niche partitioning and ecomorphospace occupation in crinoids from the Brechin Lagerstätte, a taxonomically diverse fauna representing one of the earliest complex crinoid paleocommunities. We identified three primary controls on ecomorphospace occupation, each corresponding to a major axis of niche differentiation: filtration fan density, filtration fan area, and body size. Niches were strongly partitioned at the subclass level, particularly along the axis of filtration fan density, where camerates had denser filtration fans and pentacrinoïds were characterized by more open filtration fans. Estimates of phylogenetic signal for filtration fan density and body size are consistent with phylogenetic niche conservatism. In contrast, traits related to the size of feeding area are more labile at lower taxonomic scales. Finally, comparison with a Lower Mississippian crinoid community reveals shifts in the niche space of pentacrinoïds and camerates through time. Notably, the evolution of pinnules in eucladid pentacrinoïd lineages resulted in an expansion to regions of ecomorphospace previously occupied only by camerates, which may have led to increased competitive interactions and influenced turnover between the Early and Middle Paleozoic Crinoid Macroevolutionary Faunas.

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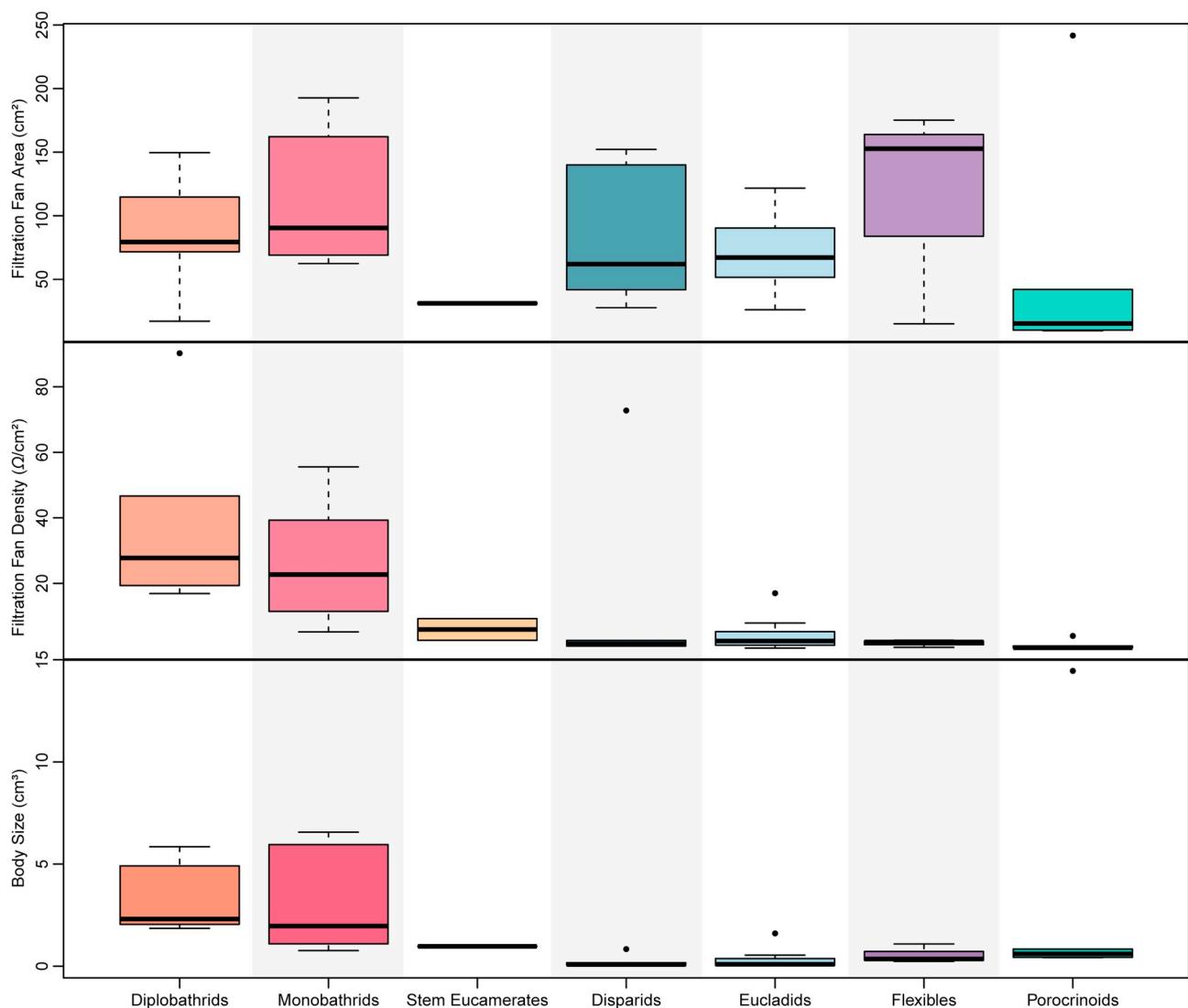


Fig. S1. Boxplots of filtration fan area, filtration fan density, and body size for crinoids from the Brechin Lagerstätte. Taxa are divided by clade/paraclade to highlight morphological differences between groups. Black points represent outliers and horizontal black lines represent median values.

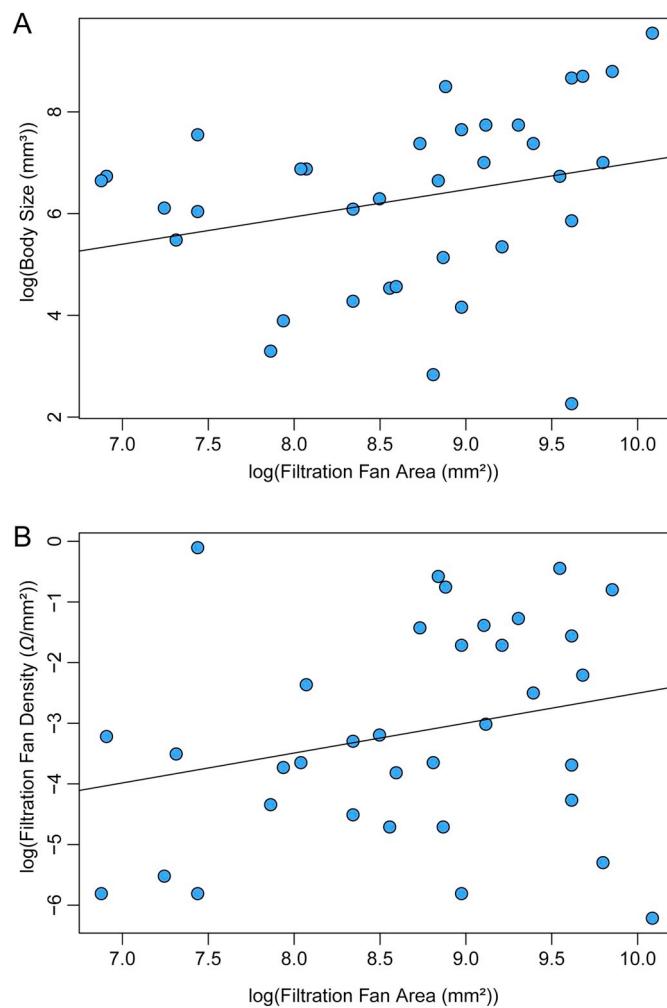


Fig. S2. Positive but non-significant correlations between (A) filtration fan area and body size (Spearman's Rho = 0.410, p = 0.014) and between (B) filtration fan area and filtration fan density (Spearman's Rho = 0.236, p = 0.172).

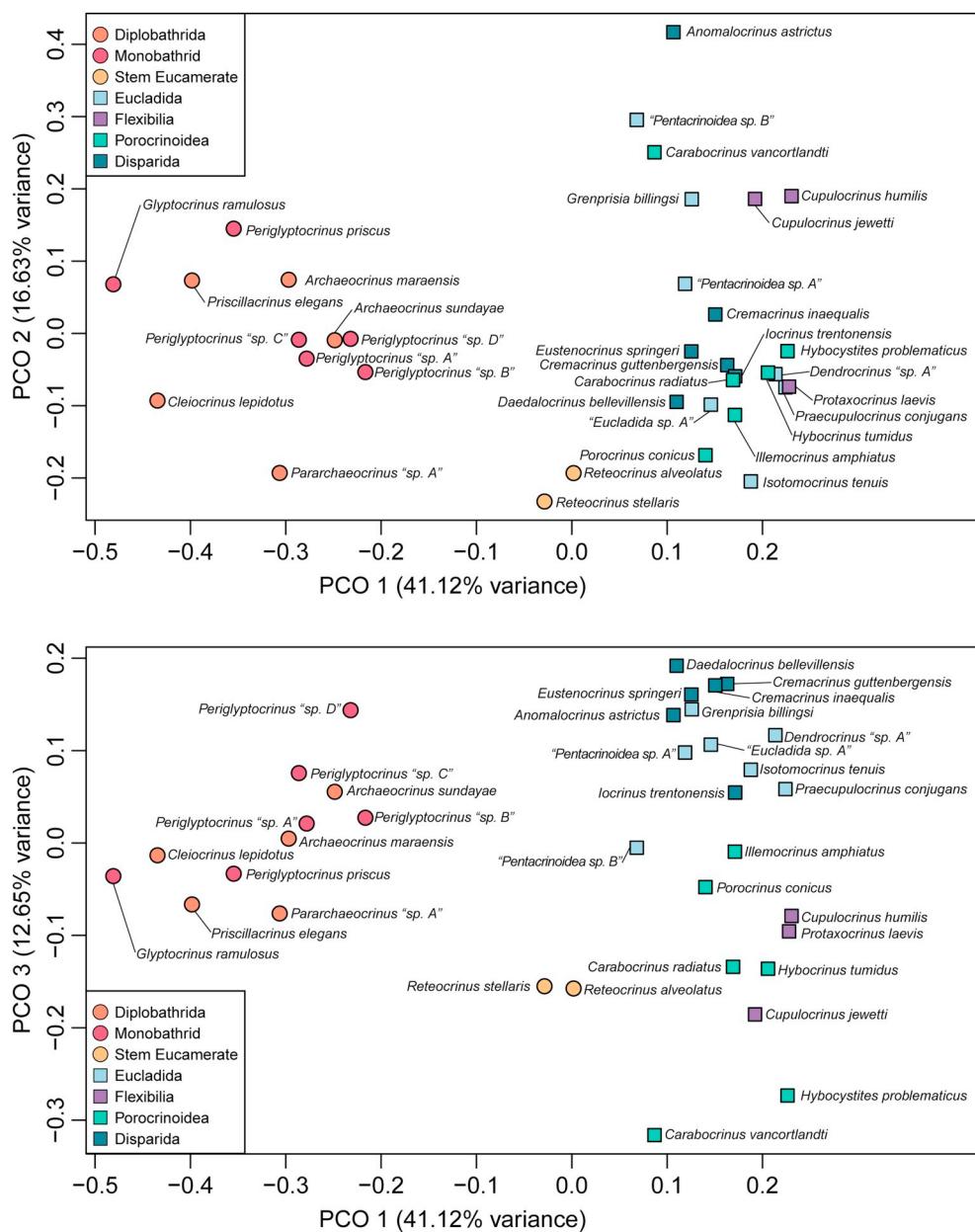


Fig. S3. Ecomorphospace occupation of Brechin Lagerstätte crinoids along the first three principal coordinates with species labeled.

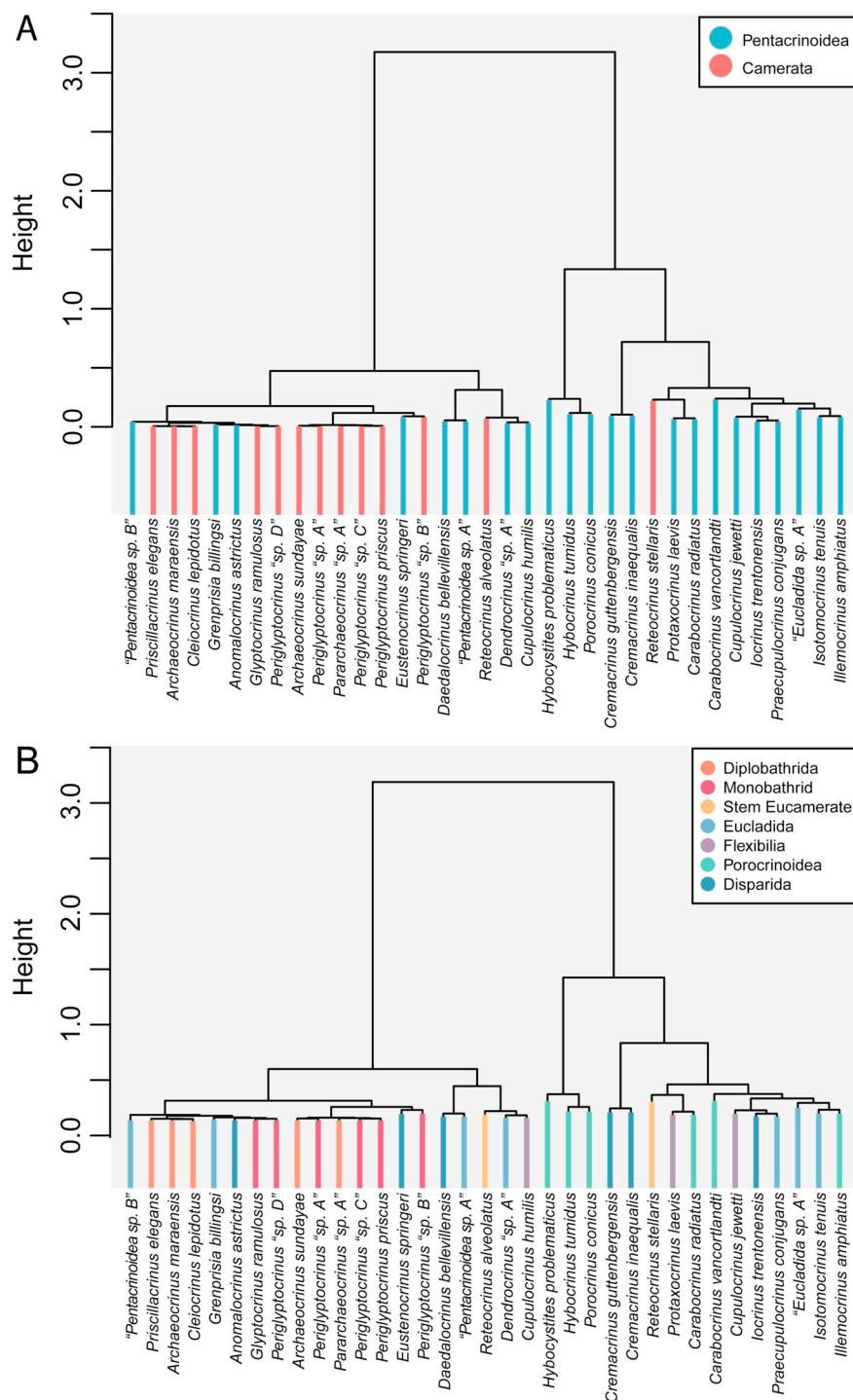


Fig. S4. Results of cluster analysis with species color-coded by (A) subclass and (B) subclade.

Data availability

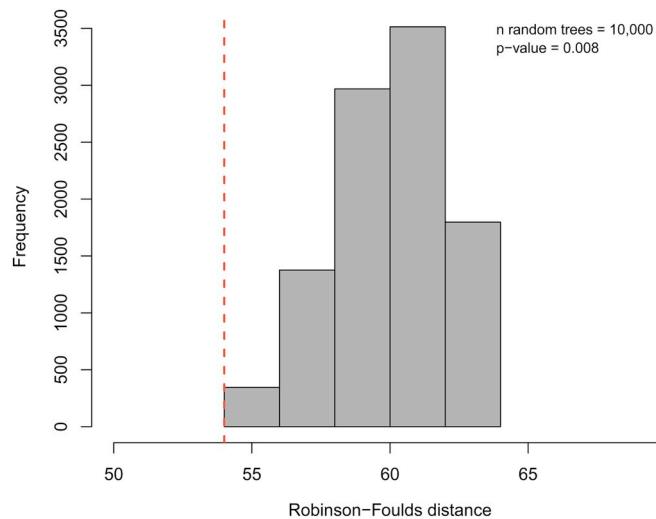


Fig. S5. Histogram of Robinson-Foulds distances between cluster analysis results and 10,000 random tree topologies. Red dashed line indicates RF distance between the cluster analysis and the inferred phylogenetic tree, which is significantly shorter than RF for random trees ($p=0.008$).

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2019.02.006>. Additional supplementary tables and data files can be accessed through Mendeley at <http://dx.doi.org/10.17632/h665kchhng.1>.

References

- Armstrong, D.K., 2000. Paleozoic geology of the northern Lake Simcoe area, south-central Ontario. In: Ontario Geological Survey, Open File Report 6011, (34 pp.).
- Ausich, W.I., 1980. A model for niche differentiation in Lower Mississippian crinoid communities. *J. Paleontol.* 64, 273–288.
- Ausich, W.I., 2001. Echinoderm taphonomy. In: Jangoux, M., Lawrence, J.M. (Eds.), *Echinoderm Studies. vol. 6*. A.A. Balkema, Rotterdam, pp. 171–227.
- Ausich, W.I., 2016. Fossil species as data: a perspective from echinoderms. In: Allmon, W.D., Yacobucci, M.M. (Eds.), *Species and Speciation in the Fossil Record*. University of Chicago Press, pp. 301–311.
- Ausich, W.I., 2018. Morphological paradox of disparid crinoids (Echinodermata): phylogenetic analysis of a Paleozoic clade. *Swiss J. Palaeontol.* <https://doi.org/10.1007/s13358-018-0147-z>.
- Ausich, W.I., Bottjer, D.J., 1982. Tiering in suspension-feeding communities on soft substrate throughout the Phanerozoic. *Science* 216, 173–174.
- Ausich, W.I., Kammer, T.W., 2013. Mississippian crinoid biodiversity, biogeography and macroevolution. *Palaeontology* 56, 727–740.
- Ausich, W.I., Peters, S.E., 2005. A revised macroevolutionary history for Ordovician-Early Silurian crinoids. *Paleobiology* 31, 538–551.
- Ausich, W.I., Kammer, T.W., Baumiller, T.K., 1994. Demise of the middle Paleozoic crinoid fauna: a single extinction event or rapid faunal turnover? *Paleobiology* 20, 345–361.
- Ausich, W.I., Kammer, T.W., Rhenberg, E.C., Wright, D.F., 2015. Early phylogeny of crinoids within the pelmatozoa clade. *Palaeontology* 58, 937–952.
- Ausich, W.I., Wright, D.F., Cole, S.R., Koniecki, J.M., 2018. Disparid and hyocrinid crinoids (Echinodermata) from the Upper Ordovician (lower Katian) Brechin Lagerstätte of Ontario. *J. Paleontol.* 92, 850–871.
- Bambach, R.K., 1983. Ecospace utilization and guilds in marine communities through the Phanerozoic. In: Tevesz, M.J., McCall, P.L. (Eds.), *Biotic Interactions in Recent and Fossil Benthic Communities*. Springer, Boston, pp. 719–746.
- Bapst, D.W., 2012. paleotree: an R package for paleontological and phylogenetic analyses of evolution. *Methods Ecol. Evol.* 3, 803–807.
- Bapst, D.W., 2013. A stochastic rate-calibrated method for time-scaling phylogenies of fossil taxa. *Methods Ecol. Evol.* 4, 724–733.
- Baumiller, T.K., 1997. Crinoid functional morphology. *Paleontol. Soc. Pap.* 3, 45–68.
- Baumiller, T.K., 2008. Crinoid ecological morphology. *Annu. Rev. Earth Planet. Sci.* 36, 221–249.
- Blomberg, S.P., Garland Jr., T., Ives, A.R., 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57, 717–745.
- Brett, C.E., Liddell, W.D., 1978. Preservation and paleoecology of a Middle Ordovician hardground community. *Paleobiology* 4, 329–348.
- Brett, C.E., Moffat, H.A., Taylor, W.L., 1997. Echinoderm taphonomy, taphofacies, and Lagerstätten. *Paleontol. Soc. Pap.* 3, 147–190.
- Brower, J.C., 2007. The application of filtration theory to food gathering in Ordovician crinoids. *J. Paleontol.* 81, 1284–3000.
- Cavender-Bares, J., Kozak, K.H., Fine, P.V., Kembel, S.W., 2009. The merging of community ecology and phylogenetic biology. *Ecol. Lett.* 12, 693–715.
- Cole, S.R., 2017a. Phylogeny and morphologic evolution of the Ordovician Camerate (Class Crinoidea, Phylum Echinodermata). *J. Paleontol.* 91, 815–828.
- Cole, S.R., 2017b. *Phylogeny, Diversification, and Extinction Selectivity in Camerate Crinoids* (Ph.D. thesis). The Ohio State University, Columbus (355 pp.).
- Cole, S.R., 2018. Phylogeny and evolutionary history of diplobathrid crinoids (Echinodermata). *Palaeontology*. <https://doi.org/10.1111/pala.12401>.
- Cole, S.R., Toom, U., 2018. New camerate crinoid genera from the Upper Ordovician (Katian) of Estonia: evolutionary origin of family Opsocrinidae and a phylogenetic assessment of Ordovician Monobathrida. *J. Syst. Palaeontol.* <https://doi.org/10.1080/14772019.2018.1447519>.
- Cole, S.R., Ausich, W.I., Wright, D.F., Koniecki, J.M., 2018. An echinoderm Lagerstätte from the Upper Ordovician (Katian), Ontario: taxonomic re-evaluation and description of new cycylic camerate crinoids. *J. Paleontol.* 92, 488–505.
- Cooper, N., Jetz, W., Freckleton, R.P., 2010. Phylogenetic comparative approaches for studying niche conservatism. *J. Evol. Biol.* 23, 2529–2539.
- Curran, S.C., 2012. Expanding ecomorphological methods: geometric morphometric analysis of *Cervidiae post-crania*. *J. Archaeol. Sci.* 39, 1172–1182.
- Deline, B., Ausich, W.I., 2011. Testing the plateau: a reexamination of disparity and morphologic constraints in early Paleozoic crinoids. *Paleobiology* 37, 214–236.
- Donovan, S.K., 1991. The taphonomy of echinoderms: calcareous multi-element skeletons in the marine environment. In: Donovan, S.K. (Ed.), *The Processes of Fossilization*. Belhaven Press, London, pp. 241–269.
- Dynowski, J.F., Nebelsick, J.H., Klein, A., Roth-Nebelsick, A., 2016. Computational fluid dynamics of the fossil crinoid *Enocrinus lilliformis* (Echinodermata, Crinoidea). *PLoS One* 11, e0156408. <https://doi.org/10.1371/journal.pone.0156408>.
- Eckert, J.D., 1987. *Illemocrinus amphiatua*, a new cladid inadunate crinoid from the Middle Ordovician of Ontario. *Can. J. Earth Sci.* 24, 860–865.
- Felsenstein, J., 1985. Phylogenies and the comparative method. *Am. Nat.* 125, 1–15.
- Foote, M., 1997. Estimating taxonomic durations and preservation probability. *Paleobiology* 23, 278–300.
- Fraser, D., Gorelick, R., Rybczynski, N., 2015. Macroevolution and climate change influence phylogenetic community assembly of North American hooved mammals. *Biol. J. Linn. Soc.* 114, 485–494.
- Gower, J.C., 1971. A general coefficient of similarity and some of its properties. *Biometrics* 27, 857–871.
- Hadly, E.A., Spaeth, P.A., Li, C., 2009. Niche conservatism above the species level. *Proc. Natl. Acad. Sci.* 106, 19707–19714.
- Harvey, P.H., Pagel, M.D., 1991. *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford (239 pp.).
- Holterhoff, P.F., 1997. Filtration models, guilds, and biofacies: crinoid paleoecology of the Stanton Formation (Upper Pennsylvanian), midcontinent, North America. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 130, 177–208.
- Hutchinson, G.E., 1978. *An Introduction to Population Biology*. Yale University Press, New Haven and London (256 pp.).
- Jablonski, D., 2008. Biotic interactions and macroevolution: extensions and mismatches across scales and levels. *Evolution* 62, 715–739.
- Kammer, T.W., 1985. Aerosol filtration theory applied to Mississippian deltaic crinoids. *Paleobiology* 59, 551–560.
- Kammer, T.W., Ausich, W.I., 1987. Aerosol suspension feeding and current velocities: distributional controls for late Osagean crinoids. *Paleobiology* 13, 379–395.
- Kitazawa, K., Oji, T., Sunamura, M., 2007. Food composition of crinoids (Crinoidea: Echinodermata) in relation to stalk length and fan density: their paleoecological implications. *Mar. Biol.* 152, 959–968.
- LaBarbera, M., 1978. Particle capture by a Pacific brittle star: experimental test of the aerosol suspension feeding model. *Science* 201, 1147–1149.
- Lamsdell, J.C., Congreve, C.R., Hopkins, M.J., Krug, A.Z., Patzkowsky, M.E., 2017. Phylogenetic paleoecology: tree-thinking and ecology in deep time. *Trends Ecol. Evol.* 32, 452–463.
- Lane, N.G., 1963. The Berkeley crinoid collection from Crawfordsville, Indiana. *J. Paleontol.* 27, 1001–1008.
- Lane, N.G., 1973. Paleontology and paleoecology of the Crawfordsville fossil site (upper Osagean, Indiana). *Geol. Sci. Univ. Calif. Publ.* 99 (141 pp.).
- Liddell, D.W., 1975. Recent crinoid biostratinomy. *Geol. Soc. Am. Abstr. Programs* 7, 1169.
- Losos, J.B., 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.* 11, 995–1003.
- Macurda Jr., D.B., Meyer, D.L., 1974. Feeding posture of Modern stalked crinoids. *Nature* 247, 394–396.
- Macurda Jr., D.B., Meyer, D.L., 1983. Sea lilies and feather stars. *Am. Sci.* 71, 354–365.
- Messing, C.G., Hoggett, A.K., Vail, L.L., Rouse, G.W., Rowe, F.W.E., 2017. 7: class Crinoidea. In: O'Hara, T., Byrne, M. (Eds.), *Australian Echinoderms: Biology, Ecology and Evolution*. CSIRO Publishing, pp. 167–225.
- Meyer, D.L., 1971. Post-mortem disintegration of recent crinoids and ophiuroids under natural conditions. *Geol. Soc. Am. Abstr. Programs* 3, 645–646.
- Meyer, D.L., 1973a. Feeding behavior and ecology of shallow-water unstalked crinoids (Echinodermata) in the Caribbean Sea. *Mar. Biol.* 22, 105–129.
- Meyer, D.L., 1973b. Distribution and living habits of comatulid crinoids near Discovery Bay, Jamaica. *Bull. Mar. Sci.* 23, 24–259.
- Meyer, D.L., 1979. Length and spacing of the tube feet in crinoids (Echinodermata) and their role in suspension-feeding. *Mar. Biol.* 51, 361–369.
- Meyer, D.L., 1982. Food and feeding mechanisms. In: Jangoux, M., Lawrence, J.M. (Eds.), *Echinoderm Nutrition*. A.A. Balkema Press, Rotterdam, pp. 25–42.
- Meyer, D.L., Ausich, W.I., 1983. Biotic interactions among Recent and among fossil

- crinoids. In: Tevesz, M.J.S., McCall, P.L. (Eds.), *Biotic Interactions in Recent and Fossil Benthic Communities*. Springer, Boston, pp. 377–427.
- Miles, D.B., Dunham, A.E., 1993. Historical perspectives in ecology and evolutionary biology: the use of phylogenetic comparative analyses. *Annu. Rev. Ecol. Syst.* 24, 587–619.
- Miller, A.I., Foote, M., 1996. Calibrating the Ordovician radiation of marine life: implications for Phanerozoic diversity trends. *Paleobiology* 22, 304–309.
- Novack-Gottshall, P.M., Miller, A.I., 2003. Comparative geographic and environmental diversity dynamics of gastropods and bivalves during the Ordovician Radiation. *Paleobiology* 29, 576–604.
- Pagel, M., 1999. Inferring the historical patterns of biological evolution. *Nature* 401, 877–884.
- Pianka, E.R., Vitt, L.J., Pelegri, N., Fitzgerald, D.B., Winemiller, K.O., 2017. Toward a periodic table of niches, or exploring the lizard niche hypervolume. *Am. Nat.* 190, 601–616.
- Polly, P.D., Fuentes-Gonzalez, J., Lawing, A.M., Bormet, A.K., Dundas, R.G., 2017. Clade sorting has a greater effect than local adaptation on ecometric patterns in Carnivora. *Evol. Ecol. Res.* 18, 61–95.
- Raia, P., 2010. Phylogenetic community assembly over time in Eurasian Plio-Pleistocene mammals. *Palaios* 25, 327–338.
- Revell, L.J., 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* 3, 217–223.
- Ricklefs, R.E., Miles, D.B., 1994. Ecological and evolutionary inferences from morphology: an ecological perspective. In: Wainwright, P.C., Reilly, S.M. (Eds.), *Ecological Morphology: Integrative Organismal Biology*. University of Chicago Press, pp. 13–41.
- Robinson, D.F., Foulds, L.R., 1981. Comparison of phylogenetic trees. *Math. Biosci.* 53, 131–147.
- Rubenstein, D.I., Koehl, M.A.R., 1977. The mechanisms of filter feeding: some theoretical considerations. *Am. Nat.* 111, 981–994.
- Sallan, L.C., Kammer, T.W., Ausich, W.I., Cook, L.A., 2011. Persistent predator-prey dynamics revealed by mass extinction. *Proc. Natl. Acad. Sci.* 108, 8335–8338.
- Sepkoski, J.J., Sheehan, P.M., 1983. Diversification, faunal change, and community replacement during the Ordovician radiations. In: Tevesz, M.J.S., McCall, P.L. (Eds.), *Biotic Interactions in Recent and Fossil Benthic Communities*. Springer, Boston, pp. 673–717.
- Servais, T., Owen, A.W., Harper, D.A., Kröger, B., Munnecke, A., 2010. The Great Ordovician Biodiversification Event (GOBE): the palaeoecological dimension. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 295, 99–119.
- Smith, A.B., Godsoe, W., Rodríguez-Sánchez, F., Wang, H.H., Warren, D., 2018. Niche estimation above and below the species level. *Trends Ecol. Evol.* <https://doi.org/10.1016/j.tree.2018.10.012>.
- Springer, F., 1911. On a Trenton echinoderm fauna at Kirkfield, Ontario. Canada Department Mines, Memoir 15-P, pp. 1–70.
- Sprinkle, J., Guensburg, T.E., 2004. Crinozoan, Blastozoan, Echinozoan, Asterozoan, and Homalozoan echinoderms. In: Webby, D.B., Paris, R., Droser, M.L., Percival, I.G. (Eds.), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, pp. 266–280.
- Stigall, A.L., Bauer, J.E., Lam, A.R., Wright, D.F., 2017. Biotic immigration events, speciation, and the accumulation of biodiversity in the fossil record. *Glob. Planet. Chang.* 148, 242–257.
- Taylor, W.L., Brett, C.E., 1996. Taphonomy and paleoecology of echinoderm Lagerstätten from the Silurian (Wenlockian) Rochester Shale. *Palaios* 11, 111–140.
- Thompson, J.R., Ausich, W.I., 2015. Testing for escalation in Lower Mississippian camarate crinoids. *Paleobiology* 41, 89–107.
- Van Valkenburgh, B., 1994. Ecomorphological analysis of fossil vertebrates and their paleocommunities. In: Wainwright, P.C., Reilly, S.M. (Eds.), *Ecological Morphology: Integrative Organismal Biology*. University of Chicago Press, pp. 140–166.
- Ward, J.H., 1963. Hierarchical grouping to optimize an objective function. *J. Am. Stat. Assoc.* 58, 236–244.
- Webb, C.O., Ackerly, D.D., McPeek, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* 33, 475–505.
- Webby, B.D., Paris, F., Droser, M.L., Percival, I.G. (Eds.), 2004. *The Great Ordovician Biodiversification Event*. Columbia University Press, New York (484 pp.).
- Wright, D.F., 2017a. Bayesian estimation of fossil phylogenies and the evolution of early to middle Paleozoic crinoids (Echinodermata). *J. Paleontol.* 91, 799–814.
- Wright, D.F., 2017b. Phenotypic innovation and adaptive constraints in the evolutionary radiation of Palaeozoic crinoids. *Sci. Rep.* 7, 13745. <https://doi.org/10.1038/s41598-017-13979-9>.
- Wright, D.F., Toom, U., 2017. New crinoids from the Baltic region (Estonia): fossil tip-dating phylogenetics constrains the origin and Ordovician–Silurian diversification of the Flexibilia (Echinodermata). *Palaeontology* 60, 893–910.
- Wright, D.F., Ausich, W.I., Cole, S.R., Rhenberg, E.C., Peter, M.E., 2017. Phylogenetic taxonomy and classification of the Crinoidea (Echinodermata). *J. Paleontol.* 91, 829–846.