

1 Introduction

Ecological communities have changed dramatically over the course of geological history as a result of environmental change, biotic interactions, evolution of new higher taxa, and extinction (Vermeij, 1987; Kelley et al., 2003; Bush & Bambach, 2011; Lyons et al. 2019). At the ecosystem scale, a variety of approaches have been used to evaluate broad patterns of resource utilization, functional diversity, and complexity through deep time using theoretical concepts and methodological approaches like tiering, ecospace filling, limiting components, ecosystem engineering, ecological clustering, network analysis, niche modeling, and abundance distributions (e.g., Ausich, 1983; Bambach, 1983; Ausich & Bottjer, 1982; Wagner et al., 2006; Bambach et al., 2007; Novack-Gottshall, 2007; Erwin, 2008; Stigall, 2012; Dineen et al., 2014; Muscente et al., 2018; Novack-Gottshall et al., 2022). Many of these methods have also been successfully applied to community-level investigations to evaluate various aspects of ecology or make comparisons between paleocommunities (e.g., Brame & Stigall, 2014; Darroch et al., 2018; Perera and Stigall, 2018; Whittle et al., 2019; Cole et al., 2020; Nanglu et al., 2020). However, other ecological aspects of paleocommunities relating to niche partitioning, assembly, and structure are not readily captured by these methods and have received far less attention in past studies, particularly for clades of fossil marine invertebrates.

Niches are complex and multidimensional, reflecting a wide range of traits, behaviors, and abiotic factors that dictate the functional position of organisms within their environment, biotic interactions, and resource partitioning within communities (Hutchinson, 1978). Because of their fundamental role in ecology, niches are a necessary component for fully understanding community structure and evolution through deep time. Characterizing species niches is challenging in the fossil record, in part because of difficulties in extracting relevant biological/ecological information from fossils. As a result, many studies have focused on characterizing niches using abiotic data that can be extracted from the rocks associated with specimen occurrences, such as water depth, substrate consistency, turbidity, and temperature (e.g., Meyer et al., 2002; Holland & Zaffos, 2011; Stigall, 2012; Myers et al., 2015; Antell et al., 2021). Others have used one or more ecologically significant traits like body size as proxies for niche partitioning at broad levels, especially for groups like vertebrates where relationships between size and other niche parameters are well understood (e.g., Andrews et al., 1979; Pineda-Munoz et al., 2016; Fraser & Lyons, 2020; Schroeder et al., 2021). Within marine invertebrate faunas, classic work by Bambach (1983) identified three major categories – feeding, motility, and tiering – that could be used to characterize ecospace utilization, and subsequent investigations have expanded upon this

approach to encompass additional ecological components and methods (Novack-Gottshall, 2007, 2016a, 2016b; Villéger et al., 2011). Although these categorical elements have been used to describe functional diversity within groups (e.g., Schumm et al., 2019; Novack-Gottshall et al., 2022), they are typically too broad to capture the range of variation between ecologically similar species and thus do not represent niche concepts at the species level (Bambach et al., 2007; see Hadly et al., 2009). As a result, ecospace approaches have generally focused on patterns of functional diversity of whole ecosystems rather than the structure and dynamics of species niches within communities.

Some fossil organisms readily preserve anatomical features that can be linked back to ecological functions, referred to as ecomorphological traits. When multiple ecomorphological traits are identifiable for a study group, they can be used in multivariate analyses to evaluate the relative position of species in ecomorphospace. They can also function as a proxy for niche occupation if traits are thought to capture major components of niche differentiation (Ricklefs & Miles, 1994; Pianka et al., 2017). Analyses of ecomorphospace occupation have been conducted widely across fossil and living taxa as a means of quantifying ecological variation, typically with continuous and/or discrete characters, and either with or without direct inferences of niche occupation being made (e.g., Van Valkenburg, 1994; Weiser et al., 2006; Anderson, 2009; Fischer et al., 2017; Pianka, 2017; Walton & Korn, 2018; Cole et al., 2019; Mallon, 2019; Cole & Hopkins, 2021). Using ecomorphospace to characterize species niches in multi-dimensional trait space is a powerful approach for community-level studies because it operationalizes complex concepts like niche breadth and permits investigation of a wide range of hypotheses relating to community assembly, biotic interactions, and resource partitioning. This approach is not without its challenges, however, especially when it comes to identifying ecomorphological traits in the fossil record. In both living and fossil organisms, ecomorphological traits typically relate back to aspects of feeding, mobility, behavior, biotic interactions, environmental interactions (e.g., interface with water currents or substrate), life history, and/or tolerance of abiotic conditions – in short, any traits that affect an organism's ecological niche (Wainwright, 1991; Winemiller, 1991; Bock, 1994; Van Valkenburgh, 1994; for examples of ecomorphological trait identification across diverse clades, see Zanno & Makovicky, 2011; Fountain-Jones et al., 2014; Pianka et al., 2017; Barr, 2018; Cole et al., 2019). In some fossils, the ecological importance of certain traits may be unambiguous, such as dental morphology in mammals, which relates directly to dietary ecology (Evans & Pineda-Munoz, 2018). However, the ecological relevance of other ecomorphological traits may be less intuitive. For example, detailed hydrodynamic studies have identified certain features that are ecologically important for feeding

Niche Evolution and Phylogenetic Community Paleocology 3

and stability of both fossil cinctan echinoderms (Rahman et al., 2020) and Ediacaran organisms (Rahman et al. 2015; Gibson et al., 2021). Similarly, the ecological roles of many other traits in fossil organisms have only been confidently identified through a variety of creative approaches, such as biomechanical and other experimental studies (e.g., Kammer 1985; Baumiller & Ausich, 1996; Carrano, 1997; Peterman et al., 2021), evidence of interactions between co-occurring organisms (e.g., Baumiller & Gahn, 2003; Taylor, 2016; Feng et al., 2017), or study of modern analogues (Stanley, 1970; Macurda & Meyer, 1974; Meyer & Ausich, 1983). As a result, extensive expertise in the morphology, taxonomy, biomechanics, biotic interactions, and/or behavior of the study group is often required in order to diagnose a robust suite of ecomorphological traits.

Incorporating phylogenetic perspectives into studies of species niches can provide further insight into community ecology and niche evolution. When integrated with community-level data, phylogenies can be used to recognize evolutionary changes in patterns of assembly, structure, and trait distributions within communities, in addition to the underlying processes responsible for generating observed patterns. Further, combining phylogenies with data on niche occupation can allow identification of phenomena like niche convergence, divergence, and niche conservatism. Although phylogenetic community ecology has been applied widely to studies of modern systems (for reviews see Webb et al., 2002; Cavender-Bares et al., 2009; Qian & Jiang, 2014), it is challenging to obtain both robust phylogenetic hypotheses and detailed ecomorphological data for many fossil taxa. Nevertheless, the merging of phylogenetic and paleoecological perspectives represents a promising area of paleontological research (Lamsdell et al., 2017; Cole et al., 2019), and case studies using these approaches are becoming increasingly widespread, especially for terrestrial vertebrate communities (Raia, 2010; Fraser et al., 2015; Polly et al., 2017, Fraser & Lyons, 2017, 2020). Although these methods have been less commonly applied to invertebrate fossil groups (e.g., Cole et al., 2019; Chang & Skipwith, 2020), fossil crinoids are a particularly promising system because they preserve extensive ecological data and have a robust phylogenetic framework (Wright et al., 2017; Cole et al., 2019). As a result, they are the only fossil invertebrate group for which community-level niche dynamics have been studied in a phylogenetic context (Cole et al., 2019; Cole et al., 2020) and have the potential to provide deep-time perspectives on niche evolution, niche dynamics, and community ecology.

1.1 Crinoid Paleocology and Niche Partitioning

Among fossil marine invertebrates, it is often challenging to identify characters with unambiguous ecological functions, which can hinder quantitative

investigations of niche evolution in deep time. Crinoids are ideally suited for questions that require knowledge of species ecology in deep time, because their skeletons preserve many features that directly correspond to ecological functions. This allows fossil crinoid niches to be quantitatively reconstructed with a high degree of fidelity. Notably, the ecology of both fossil and living crinoids has been studied extensively and cross-compared (Meyer, 1973, 1979; Macurda & Meyer, 1974; Ausich, 1980; Ausich & Bottjer, 1982; Baumiller, 1997; Brower, 2007, 2013; Kitazawa et al., 2007; Meyer et al., 2021; Messing et al., 2017). As passive suspension feeders, crinoids primarily partition niches through differences in feeding ecology, such as the differentiation of feeding structures (for example, the number, arrangement, and structure of arms and pinnules [Meyer, 1979; Ausich, 1980; Kitazawa et al., 2007]) and tiering (the height of the crinoid crown and feeding apparatus above the substrate, most commonly controlled by stem length [Ausich & Bottjer, 1982]). The role these traits play in crinoid feeding ecology and niche partitioning has been extensively reviewed elsewhere (e.g., Baumiller, 2008; Cole et al., 2019: Figure 1).

Recent work established a series of continuous ecomorphological traits that could be used to capture niche differentiation in crinoids through variation in feeding structures and body size (Cole, 2017a, 2019). In a subsequent study,

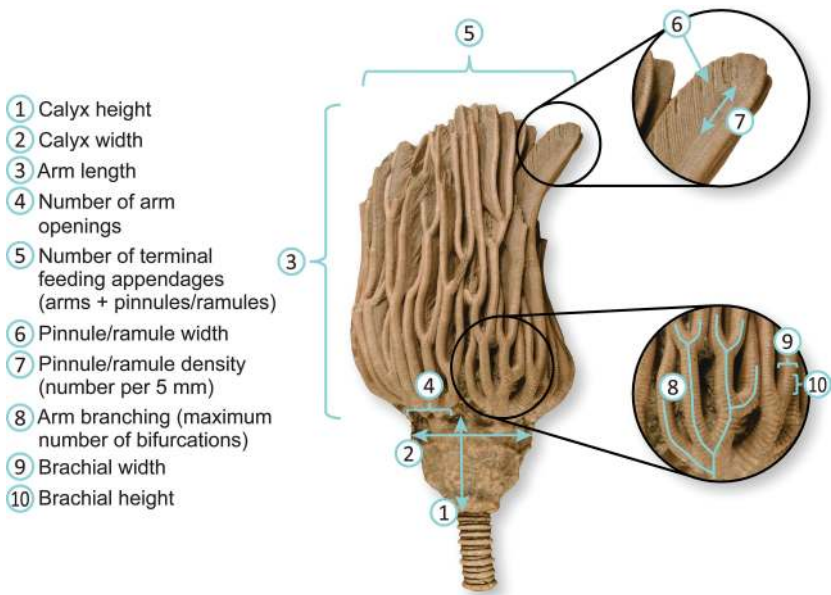


Figure 1 Collected measurements of ecomorphologic traits. Representative specimen shown is *Actinocrinites gibsoni* (Mississippian, Cincinnati Museum Center, CMCIP 71449; photo courtesy of W. I. Ausich).

Niche Evolution and Phylogenetic Community Paleocology 5

ecomorphological traits were combined with phylogenetic data to investigate niche occupation and community paleocology of crinoids from the Upper Ordovician (Katian) Brechin Lagerstätte and to test a wide range of hypotheses relating to community structure, niche partitioning, and niche conservatism within the fauna (Cole et al., 2019). Although this investigation primarily focused on a single fauna, it also looked at differences in filtration fan density between crinoids from the Ordovician-age Brechin Lagerstätte and the Mississippian-age Edwardsville Fauna and found that substantial shifts occurred through time, especially within subclass Pentacrinoidea (Cole et al., 2019). Notably, this study also provided a methodological proof of concept for phylogenetic investigations into the long-term evolution of crinoid niches and the structure of ecological communities through deep time.

In this Element, we apply a series of trait- and phylogeny-based analyses to crinoids from the Upper Ordovician (Sandbian) Bromide Formation of Oklahoma in order to characterize patterns of community assembly and niche space occupation. In addition, we compare the paleocology of crinoids from the Bromide fauna to that of crinoids from the geologically younger Brechin Lagerstätte (Upper Ordovician, Katian), which was investigated in a previous study (Cole et al., 2019). We further characterize and compare aspects of crinoid functional ecology between the two faunas via application of disparity analyses to community-wide ecomorphological trait data. Through these comparisons, we evaluate niche partitioning, niche evolution, phylogenetic structure of niches, and changes in community structure over a ~5 million-year period. This work highlights the utility of integrating phylogenetic and trait-based methods for application to paleocommunities and provides a robust framework for future investigations of crinoid community evolution and changes in niche space through time.

2 Characteristics of the Bromide and Brechin Crinoid Faunas

The Upper Ordovician was a key interval in the early evolutionary history of crinoids. The earliest known crinoids are from the Lower Ordovician (Tremadocian) of Utah (Guensburg & Sprinkle, 2003), but crinoid taxonomic diversity remained relatively low until the Middle Ordovician (Peters & Ausich, 2008). During the Middle–Late Ordovician, rapid diversification of crinoids occurred as part of the Great Ordovician Biodiversification of marine invertebrate life (Webby et al., 2004; Wright & Toom, 2017). Peak genus-level diversity was reached during the Katian stage of the Upper Ordovician before it dropped precipitously during the Late Ordovician mass extinction across the Katian–Hirnantian boundary (Peters & Ausich, 2008; Wright & Toom, 2017; Cole, 2018). In crinoids,

this rapid diversification occurred at both the genus and species levels and led to greater morphological and ecological variation (Foote, 1994, 1999; Deline & Ausich, 2011; Wright, 2017a; Deline et al., 2018, 2020; Cole & Hopkins, 2021) and increases in community complexity (Cole et al., 2020) during the Upper Ordovician. As a result, the Upper Ordovician is a dynamic interval of time in crinoid evolutionary history that is ideal for evaluating the evolution of niche occupation and community assembly in early crinoid communities. In terms of taxonomic richness, the two faunas compared here – the Bromide and the Brechin – have the highest known crinoid diversities from the Sandbian and Katian, respectively. As a result, both paleocommunities should be broadly representative of Laurentian crinoid faunas during these stages of the Upper Ordovician. For example, the relative proportions of major groups that make up the Brechin fauna are comparable to those of other Katian-age crinoid assemblages (Cole et al., 2017; Cole et al., 2020).

When making comparisons between fossil communities, it is important to account for potential biases that could generate spurious results, such as those relating to differences in taphonomy, depositional environment, and sampling intensity. The following sections summarize these aspects of the Bromide and Brechin crinoid faunas to highlight both strengths and limitations of the comparative study of these two crinoid paleocommunities.

2.1 Taxonomic Diversity

The Bromide Formation is the most diverse echinoderm fauna known throughout the entire fossil record from a single formation and is the most species-rich assemblage of Ordovician crinoids. As of 1982, more than 11,000 echinoderm specimens had been recovered from the Bromide Formation, representing more than 60 genera across 13 classes (Sprinkle, 1982a). Echinoderms from the Bromide fauna, including a diverse crinoid assemblage, were described in detail in a 1982 monograph (Sprinkle, 1982a) that remains the most comprehensive treatment of Bromide echinoderms to date. Including subsequent studies describing new taxa, crinoid diversity from the Bromide Formation currently stands at 28 genera and 38 valid named species. However, specimens representing at least nine additional taxa have been figured in published literature but left indeterminate or questionably assigned because of poor preservation (e.g., Sprinkle 1982a), and other specimens representing new species or higher taxa are still awaiting formal description (e.g., Sprinkle et al., 2015, 2018). As a result, the total diversity of crinoids from the Bromide Formation is likely closer to 50 species.

Niche Evolution and Phylogenetic Community Paleocology 7

The Brechin Lagerstätte is the second most diverse Ordovician crinoid fauna known. A description of the Brechin fauna, historically referred to as the “Kirkfield,” was first published by Frank Springer in 1911, but the faunal list was incomplete. Subsequent collecting produced a large number of exceptionally preserved specimens that were used as the basis for a reevaluation of the diversity of the fauna. These revisions of the fauna were covered in a series of recent publications that resulted in the recognition and description of 15 new species and three new genera, bringing the known diversity of Brechin crinoids to 27 genera and 39 nominal species (Cole et al., 2018, 2020; Ausich et al., 2018; Wright et al., 2019). Similar to the Bromide fauna, the Brechin also preserves a number of species belonging to other echinoderm classes (e.g., Sumrall & Gahn, 2006; Blake & Koniecki 2019, 2020), although most have not received comprehensive taxonomic assessment. In addition to echinoderms, both the Brechin and the Bromide preserve abundant faunas that are typical constituents of benthic Ordovician communities, such as trilobites, bryozoans, and brachiopods (Brett & Liddell, 1978).

2.2 Geology and Paleoenvironmental Setting

The Bromide Formation extends throughout a large portion of the Arbuckle Mountains and Criner Hills regions of south-central Oklahoma. Although the Bromide is over 100 m thick, echinoderm fossils have primarily been recovered from two zones in the middle Mountain Lake Member and a cluster of horizons in the overlying Pooleville Member. These fossil-bearing horizons are distributed over a ~75 m section of the Bromide Formation, and crinoids have been collected from numerous localities for each of these zones (Sprinkle, 1982b). Similar to the crinoid occurrences in the Brechin fauna (the Bobcaygeon and Verulam formations; see the discussion in the following paragraph), crinoid-bearing horizons in the Bromide Formation are predominantly shale beds interbedded with grainstones, packstones, and wackestones (Sprinkle, 1982b; Carlucci et al., 2014). During the interval of interest for this Element, deposition of the Bromide Formation occurred along a carbonate-dominant ramp in a NW-SE trending trough (Carlucci et al., 2014). The fossiliferous horizons from which crinoids have been recovered are interpreted to have been deposited in shallow-to deep-shelf paleoenvironments (Longman, 1982; Carlucci et al., 2014). The Bromide Formation is thought to span the majority of the Sandbian stage (Carlucci et al., 2014), which is approximately 5.4 myr in length, concluding around 453 Ma (Goldman et al., 2020). However, fossil crinoids do not occur in the lower sandstone member (Sprinkle, 1982b), so the total age range spanned by crinoids from the Bromide is much shorter.

Crinoids from the Brechin Lagerstätte have been recovered from multiple quarries in the Lake Simcoe region of southern Ontario, Canada (Cole et al., 2018). These quarries are all located within ~6 km of the town of Brechin, Ontario, for which the fauna is named. Crinoid-bearing horizons are present throughout a ~20 m thick interval that spans the uppermost ~15 m of the Bobcaygeon Formation and ~5 m of the lowermost Verulam Formation (for further discussions of stratigraphic divisions, correlations, and nomenclature for the Upper Ordovician of southern Ontario, see Armstrong [2000], Cole et al. [2018], and Paton & Brett [2019]). The Bobcaygeon and overlying Verulam formations are composed of bioclastic grainstones, packstones, and wackestones that are interbedded with calcareous shales and siltstones. These strata are interpreted to have been deposited in a proximal carbonate shelf environment that varied in depth from shallow shelf in the Bobcaygeon to deep shelf in the Verulam (Armstrong, 2000), with gradual deepening moving upward through the Bobcaygeon to Verulam (Liberty, 1969). Fossil horizons that make up the Brechin Lagerstätte span the lower portion of the Katian within the middle-upper Bobcaygeon and lower Verulam Formations. Although numerical ages for this interval are not tightly constrained, the Verulam–Bobcaygeon boundary should be approximately 451 Ma and the fauna should span an interval of roughly 2 million years or less (Sproat et al., 2015; Paton & Brett, 2019; Goldman et al., 2020). Thus, the estimated time between the latest fossiliferous horizons of the Bromide and the earliest fossiliferous horizons comprising the Brechin fauna is relatively short (~2 myr), and the time elapsed between median ages for the faunas is <5 million years.

2.3 Taphonomy and “Paleocommunities”

The Bromide and Brechin faunas are similar taphonomically, although there is greater taphonomic heterogeneity between fossil-bearing horizons in the Bromide Formation. A greater proportion of articulated cups and crowns are recovered from the Brechin than from the Bromide, but the sheer number of specimens recovered from the Bromide has resulted in a large sample of well-preserved specimens with arms intact. As a result, the two faunas are broadly comparable in terms of taphonomy and specimen-level sampling intensity of their constituent species.

Because crinoids disarticulate rapidly upon death, preservation of specimens with arms and/or stems intact signals rapid burial and little to no time-averaging or transport (Donovan, 1991; Brett et al., 1997; Ausich, 2001, 2021; Ausich & Baumiller, 1993). As a result, horizons of well-preserved crinoids, such as those recovered from the Bromide and Brechin faunas,

Niche Evolution and Phylogenetic Community Paleocology 9

should not be subject to spatial or temporal averaging (Kidwell & Behrensmeyer, 1993). Individual horizons of well-preserved crinoids can be treated as ecological snapshots (Ausich, 2016), and this approach has been applied to hardground surfaces in the Brechin fauna (Taylor & Brett, 1996; Paton et al., 2019). However, here we combine all crinoid-bearing horizons from the Bromide and Brechin faunas in order to provide reasonable sample sizes. As a result, as they have been assembled here, the Bromide and Brechin datasets do not represent ecological snapshots per se. Instead, they reflect recurring species assemblages that are both temporally and spatially restricted (e.g., within a single basin), which is consistent with the traditional use of the term “paleocommunity” in paleoecological literature (e.g., Walker and Laporte, 1970; Ausich, 1980; Bennington & Bambach, 1996; Wagner et al., 2006; Perera & Stigall, 2018; Lyons et al., 2019).

3 Methods

3.1 Collection and Vetting of Ecomorphologic Trait Data

We use the term “ecomorphologic traits” to describe morphological characters that directly correspond to or strongly correlate with ecological functions. Following the model of crinoid niche differentiation outlined by Ausich (1980), Cole (2017a), and later expanded upon by Cole et al. (2019), we collected data for ten ecomorphological traits and calculated an additional three composite characters (Figure 1). Measured characters include (1) calyx height, (2) calyx width, (3) arm length, (4) number of arm openings, (5) arm branching, quantified as the maximum number of in-line bifurcations, (6) number of terminal feeding appendages (Ω), (7) brachial width, (8) brachial height, measured at the midpoint of the arms, (9) pinnule/ramule density, and (10) pinnule/ramule width. In addition, we calculated three composite characters that represent important aspects of crinoid morphology and ecology: (1) calyx volume (V), calculated using the standard equation for a cone, (2) filtration fan area (f_A), calculated using the Ausich (1980) equation with modifications by Cole (2017a), and (3) filtration fan density (F_D), calculated by dividing the total number of terminal feeding appendages (Ω , quantitative trait 6) by the total area of the filtration fan (f_A). These traits have been identified as having ecological functions based on a large number of previous studies that include investigations of crinoid biomechanics, functional morphology, feeding in modern crinoids, and biotic interactions (e.g., Meyer 1973, 1979; Macurda & Meyer, 1974; Ausich, 1980; Kammer, 1985; Baumiller & Ausich, 1996; Meyer & Ausich, 1996; Baumiller, 1997, 2008; Brower, 2007, 2013; Meyer et al., 2021). More detailed descriptions of crinoid ecology, trait measurements, and

calculation of composite characters are given in Cole et al. (2019: Figure 1) and the Supplemental Materials.

We collected ecomorphologic data from 95 specimens representing 37 species from the Bromide fauna. Specimens representing juveniles were not included in the study. *Cleiocrinus ornatus* Kolata 1982 was the only named species from the fauna for which data were not collected because it is known only from fragmentary material where fundamental measurements like calyx height and width could not be collected. Of the 37 species for which data were collected, 36 are currently valid named species, and one is represented by an unidentified specimen belonging to the disparid family Cincinnaticrinidae (Sprinkle, 1982a). This specimen has not been assigned a genus or species name because it does not preserve the posterior interray, which is necessary for classification at finer taxonomic scales. However, it was suitable for inclusion in this Element because it preserves a complete calyx and partial arms and unquestionably represents a unique taxon from the Bromide fauna.

Ecomorphological data were collected from Brechin Lagerstätte crinoids in a previous study by Cole et al. (2019) using the same methods that were here applied to the Bromide fauna. For this Element, we added trait data for three additional Brechin species so that all known taxa were included. These species were *Grenprisia springeri*, based on a new, well-preserved specimen (Wright et al., 2019), *Abludoglyptocrinus steinheimeriae*, which was only recently described from the fauna (Cole et al., 2020), and *Cleiocrinus regius*, which did not have any specimens available for study in the original paleoecological investigation. The three composite characters – fan area, fan density, and calyx volume – were also calculated for each species from the Brechin Lagerstätte. In total, the Brechin dataset was compiled from measurements of 168 specimens across all 39 species. For both the Bromide and Brechin datasets, mean values for measured and composite ecomorphological traits were calculated for each species and used for all subsequent analyses.

Some crinoid species from the Bromide and Brechin are known only from poorly preserved specimens and have extensive missing data. In addition, the methods used here would ideally be applicable to crinoid assemblages that are not as well preserved as the Bromide and Brechin, so it is necessary to understand the effect that missing data has on the loss of ecological information. Previous work established the significant effect that taphonomic degradation can have on reconstructing morphological disparity in crinoids and other echinoderms (Deline & Thomka, 2017) based on known patterns of disarticulation at different taphonomic grades (Brett et al., 1997). Here, we conducted a series of sensitivity tests using four