

FOOD AVAILABILITY AS A TRIGGER FOR THE AGE OF CRINOIDS: EVIDENCE FROM THE PRESENT AND THE PAST

BY

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Abstract — Crinoid and blastoid diversity and abundance peaked during the Late Devonian – early Mississippian (Famennian – Viséan), an interval known as the Age of Crinoids. In North America, localities with maximum crinoid and blastoid diversity and abundance occurred in carbonate ramp and delta platform and slope deposits offshore from the Appalachian tectonic highlands. Living shallow-water crinoids reached maximum species diversity and abundance in more heterotrophic waters of the Indo-West Pacific Coral Triangle, Great Barrier Reef, and Caribbean crinoids are less diverse around coral-rich offshore islands and atolls in more oligotrophic waters. Ancient crinoids and blastoids were suspension feeders, limited by very narrow food grooves to capturing very small food particles. Blastoids in particular had food grooves <300 µm width, but crinoid food grooves were $\leq 100\ \mu\text{m}$ to >1.25 mm, with most species <math><400\ \mu\text{m}</math>. Living crinoids, both unstalked and stalked, also have narrow food grooves in a similar range and ingest a large proportion of detrital particles << food groove diameter. Shallow-water crinoid diversity has been associated with proximity to runoff and increased abundance of plankton and detritus over the entire evolutionary range since the early Paleozoic. Limitation of ingested food particles by narrow food grooves first appeared in Ordovician crinoids, followed by blastoids, and also characterizes present-day crinoids. New data we present here on biogeographic patterns of diversity and food groove width support the proposal of Riding, who included the Age of Crinoids peak with other globally pervasive features of this Late Devonian – early Mississippian interval that he suggested were consequences of a "bloom" of calcareous bacterioplankton in the wake of mass extinction of acritarchs during Late Devonian time coincident with a major drop of atmospheric CO₂. We suggest that the Age of Crinoids was the result of multiple driving factors, including food and nutrient supply, in addition to unique clade dynamics, open circulation free of reef development, and turnover of durophagous vertebrate predators previously proposed.

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INTRODUCTION

For those of us who are fascinated with crinoids, we are living at the wrong time! While there are about 600 living species of crinoids, crinoid biodiversity peaked during the Mississippian Subperiod during an interval known as the "Age of Crinoids" (Kammer and Ausich, 2006; Ausich et al., 2021). Crinoids dominated the global carbonate factory to an extent not seen prior to the Mississippian and not seen after. Although the Mississippian was a time of extreme crinoid biodiversity and abundance, it was also a time in which other marine groups suffered biodiversity nadirs. A comprehensive summary of Paleozoic biodiversity by Fan et al. (2020) showed that ten invertebrate groups had lower biodiversity during the Mississippian than at any time in the

Paleozoic between the beginning of the Great Ordovician Biodiversification Event (GOBE) and the onset of the End Permian Extinction Events. Their high-resolution summary shows a protracted biodiversity decline that began in the Eifelian (Devonian) and continued to the end of the Viséan. Biodiversity increases rather sharply during the Serpukhovian as part of a previously unrecognized Carboniferous – Permian Biodiversification Event that Fan et al. (2020) equated to the GOBE. No echinoderm clades were components of the Fan et al. (2020) study.

The obvious question that arises out of the discussion is why did crinoids enjoy a burst of biodiversification during the Mississippian while many other invertebrate groups suffered significant biodiversity declines? Thanks to extensive systematic reviews and revisions by Ausich and Kammer

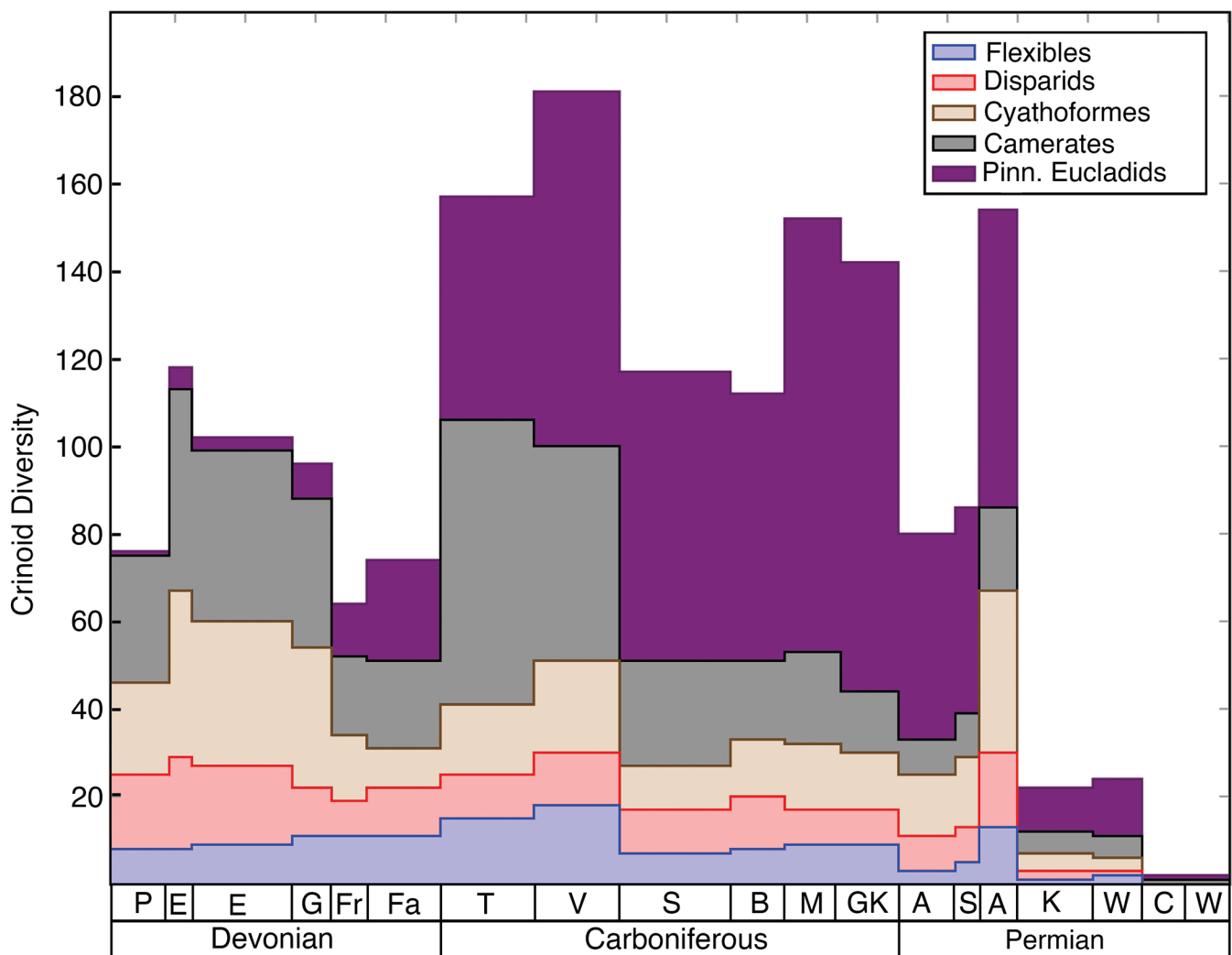


FIGURE 1 — Crinoid generic diversity from the Devonian through Permian. Stage abbreviations: P – Pragian, E – Emsian, E – Eifelian, G – Givetian, Fr – Frasnian, Fa – Famennian, T – Tournaisian, V – Viséan, S – Serpukhovian, B – Bashkirian, M – Moscovian, GK – Gzhelian and Kasimovian, A – Asselian, S – Sakmarian, A – Artinskian, K – Kungurian, W – Wordian and Roadian, C – Capitanian, W – Wuchiapingian. Data from Ausich et al. 2021.

Summary		Scatter plot	Scores
PC	Eigenvalue	% variance	
1	1196.36	71.346	
2	396.657	23.655	
3	72.0578	4.2972	
4	6.33087	0.37754	
5	5.44525	0.32473	

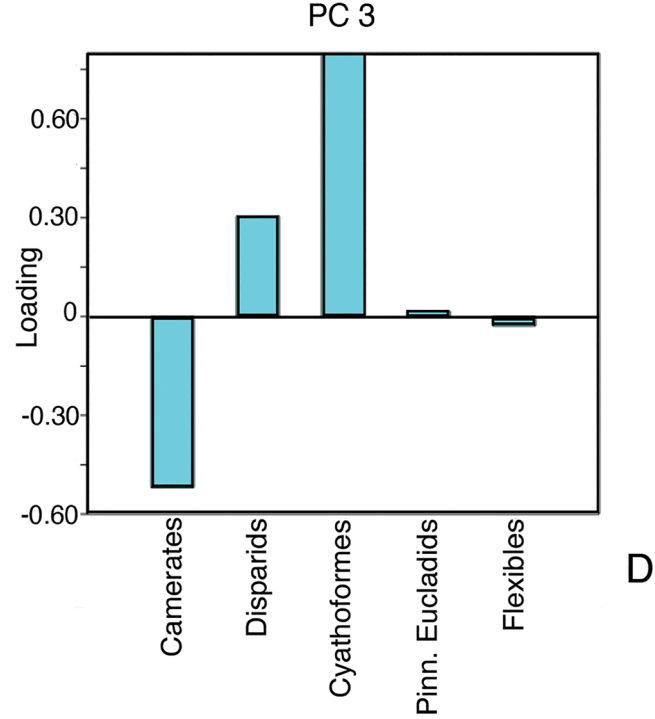
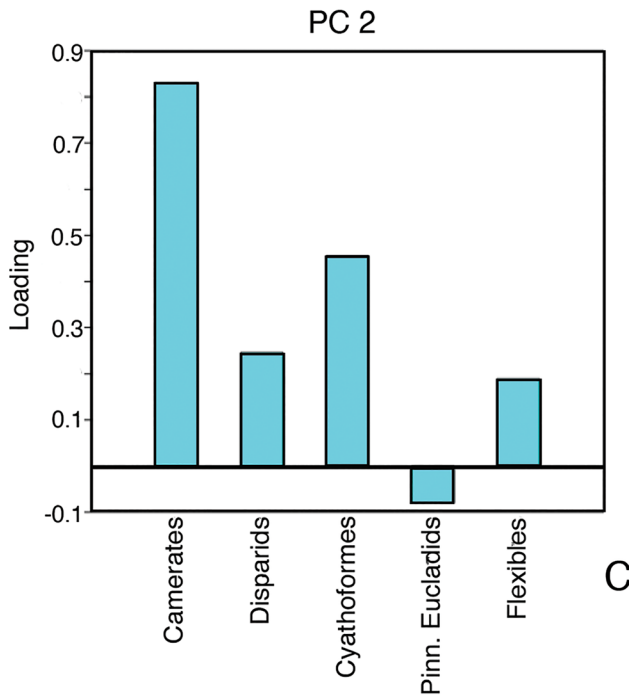
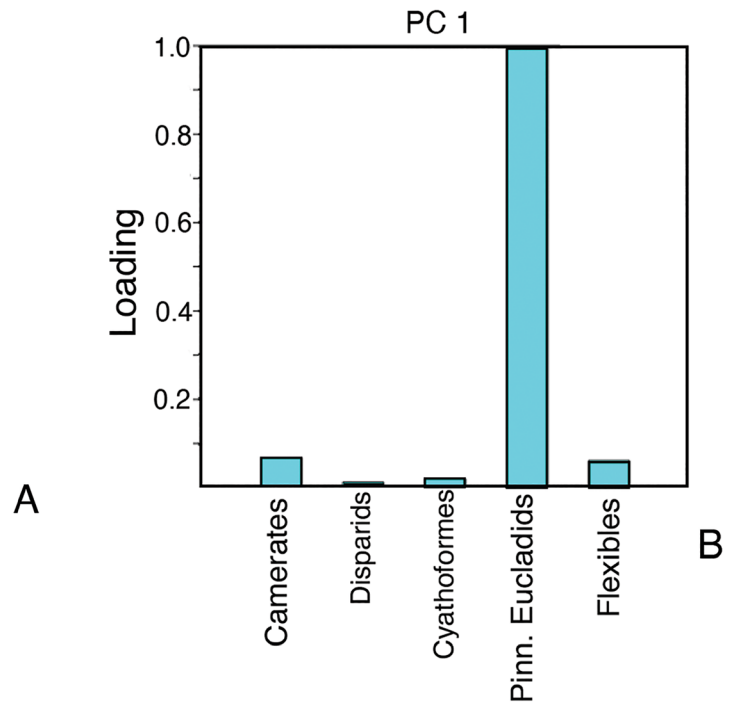


FIGURE 2 — PCA analysis of crinoid diversity data from the Devonian through the Permian. **A**, Summary of eigenvalues and % variance. **B**, pinnulate eucladids primarily responsible for PC 1 loading. **C**, Camerates, disparids and cyathoformes responsible for PC2 loading. **D**, PC 3 loading positively impacted by disparids and cyathoformes, negatively impacted by camerates.

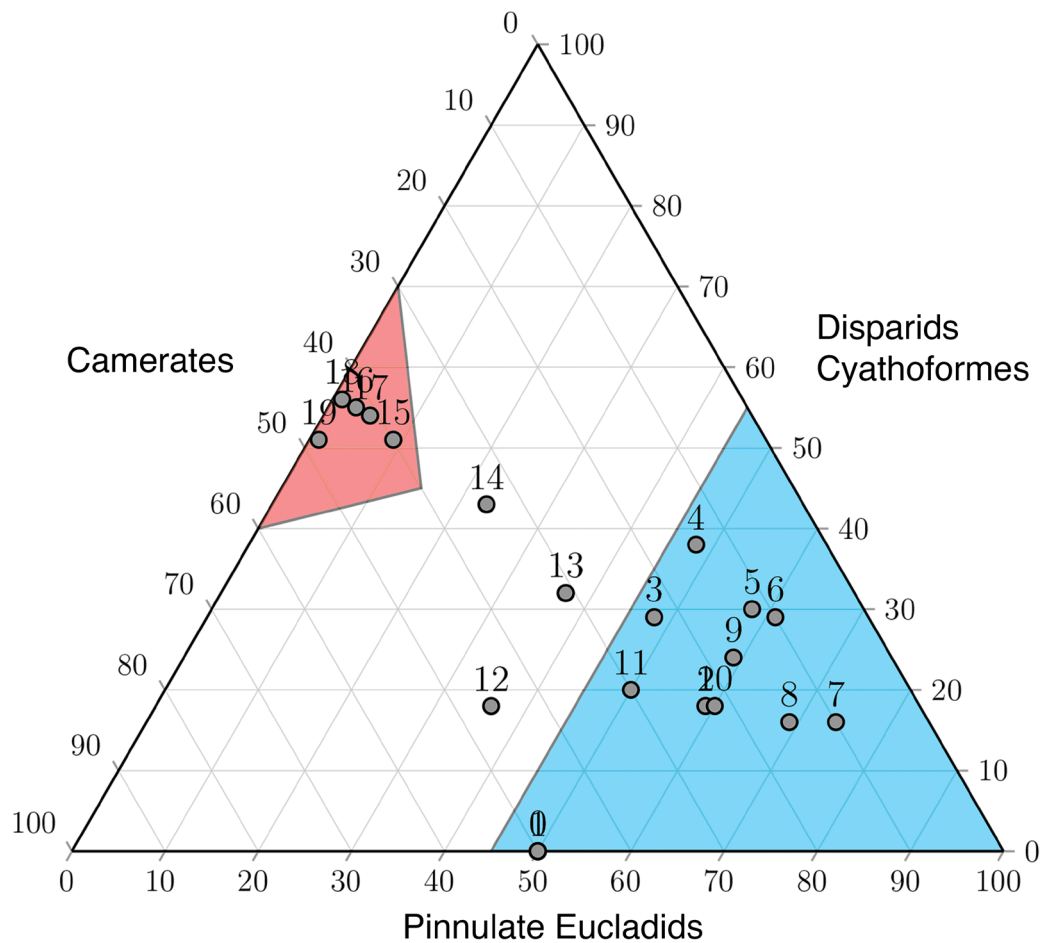


FIGURE 3 — Ternary diagram of stage-level crinoid communities. Communities segregate into MPCEF (red) with communities from the Lochkovian – Givetian, and LPCEF in Cyan (Viséan – end Permian). Frasnian, Famennian, and Tournaisian faunas plot between two groupings. Viséan is #11. The plot suggests the transition between the MPCEF and the LPCEF encompassed the Famennian through Tournaisian.

(2013), Segessenman and Kammer (2018) and Ausich et al. (2021), the Phanerozoic peak of crinoid biodiversity occurred in the Mississippian Subperiod with 157 genera in the Tournaisian and 181 genera in the Viséan. In addition, another pelmatozoan clade, the extinct blastoids, also peaked at more than 40 genera (Waters, 1988) during this time. Not only was the Mississippian the peak of pelmatozoan biodiversity, it was also a unique time of great abundance, yielding carbonate sediments dominated by echinoderm skeletal fragments as thick limestones covering vast areas of shallow seas as carbonate ramps or regional encrinites (Ausich, 1997). Crinoid-dominated sediments are nowhere to be found in modern seas and encrinites are a "vanished lithofacies" since the Jurassic (Ausich, 1997).

Paleozoic crinoid communities were organized into evolutionary faunas by Baumiller (1993). The transition from the Middle Paleozoic Crinoid Evolutionary Fauna

(MPCEF) to the Late Paleozoic Crinoid Evolutionary Fauna (LPCEF) began in the early Viséan (Kammer and Ausich 1987; Baumiller 1993; Ausich et al. 1994; Kammer et al. 1998; Ausich et al. 2021). Ausich et al. (2021) concluded that the elevated crinoid biodiversity in the Tournaisian and Viséan was the result of transition between these two CEFs. Monobathrid camerates, pinnulate eucladid crinoids, and flexibles dominated the Middle Paleozoic CEF while the Late Paleozoic CEF was dominated by advanced, pinnulate cladid crinoids by the end of the Viséan. Biodiversity was high in the Mississippian because the Tournaisian primarily contains elements of the Middle Paleozoic CEF, and the early Viséan contained significant elements of both the Middle and Late Paleozoic Paleozoic CEFs (Kammer and Ausich 2006; Ausich et al. 2021).

Using data on crinoid diversity from the Devonian through the Permian from Segessenman and Kammer (2018) and

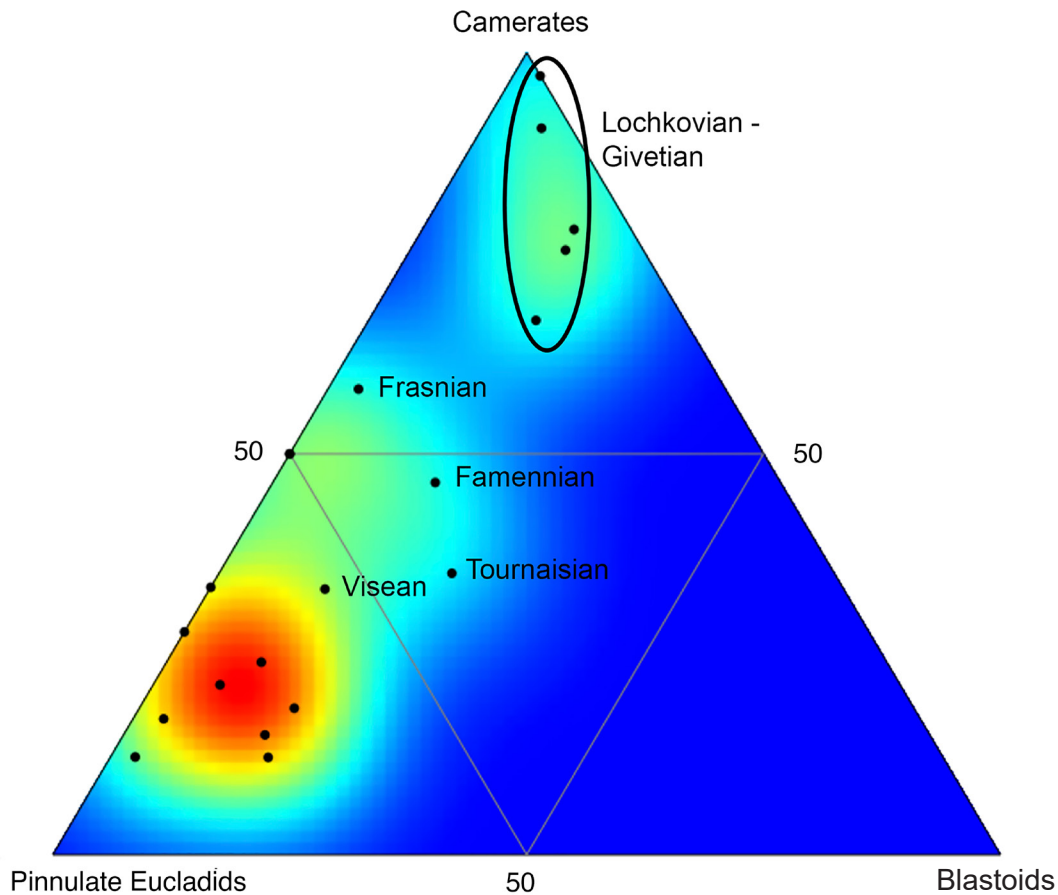


FIGURE 4 — Ternary diagram of stage level biodiversity of camerates, pinnulate eucladids, and blastoids. The Lochkovian – Givetian communities dominated by camerates and blastoids segregate as do the Viséan – Permian communities dominated by pinnulate eucladids. Frasnian, Famennian, and Tournaisian communities are intermediate in nature. Compare to Figure 3. Blastoid data from Waters (unpublished).

Ausich et al. (2021), we have investigated the transition between these two crinoid evolutionary faunas. Figure 1 shows crinoid diversity through time divided into the primary clades. Figure 1 compares favorably to figure 3 from Ausich et al., (2021), showing patterns of crinoid richness throughout the Paleozoic. Our Figure 1 shows peaks of crinoid diversity in the Emsian (MPCEF), the Tournaisian and Viséan (transition between the MPCEF and the LPCEF), Serpukhovian and Artinskian (LPCEF). Table 1 is the Correlation Matrix for biodiversity among the major crinoid groups and blastoids. Biodiversity of pinnulate eucladids is not correlated with other crinoid groups or blastoids. Biodiversity of blastoids is correlated with that of camerates and flexibles but not the other crinoid clades.

Figure 2 shows the results of a PCA analysis of the crinoid diversity data. PC1 accounts for 71% of the variance and primarily reflects the variation in the diversity of pinnulate eucladids. PC 2 accounts for 23% of the variance and reflects

the diversity of camerates, cyathiformes and disparids. PC 3 accounts for 4% of the variation and has positive contributions from the cyathiformes and disparids and negative contribution from the camerates.

Figure 3 is a ternary plot of stage level crinoid diversity. The grouping outlined in red reflects the MPCEF with communities from the Lochkovian through the Givetian. The grouping outlined in blue reflects the LPCEF and ranges in age from the Viséan (11) through the end of the Permian. Data between these two groupings are Frasnian (14), Famennian (13) and Tournaisian (12). This analysis suggests that the transition from the Middle Paleozoic CEF to the Late Paleozoic CEF began in the Frasnian and continued through the Tournaisian, a time interval of some 37 million years. Figure 4 shows the crinoid biodiversity with the addition of blastoid biodiversity.

The demise of the MPCEF coincides with the collapse of reef ecosystems which began during the Eifelian extending through the Frasnian / Famennian boundary. The impact of

TABLE 1 — Correlation Matrix for biodiversity among the major crinoid groups and blastoids. Asterisk (*) indicates $p > 0.05$. Biodiversity of Advanced Cladids is not correlated with other crinoid groups or blastoids. Biodiversity of blastoids is correlated with that of camerates and flexibles, but not the other crinoid clades. Blastoid data from Waters (unpublished).

	Camerates	Disparids	Primitive Cladids	Advanced Cladids	Flexibles	Blastoids
Camerates	—	—	—	—	—	—
Disparids	0.68*	—	—	—	—	—
Primitive Cladids	0.62*	0.88*	—	—	—	—
Advanced Cladids	0.09	0.04	0.03	—	—	—
Flexibles	0.79*	0.64*	0.60*	0.39	—	—
Blastoids	0.65*	0.43	0.44	0.41	0.66*	—

the crinoid extinction event can clearly be seen in the changes in the composition of crinoid communities. The Givetian – Tournaisian interval was a time of climatic instability, a significant drop in CO_2 and global oceanic instability recorded in anoxia events and massive carbon isotopic excursions.

Several causative factors have been proposed for the Age of Crinoids, including prevalence of widespread areas of carbonate shelves and ramps during the Tournaisian and Viséan, along with changes in circulation across shelf seas following the extinction of reefs during the Late Devonian (Kammer and Ausich, 2006), plus turnover in the composition of durophagous fish predators (Sallan et al., 2011).

For a long time, we have been intrigued by the question raised initially by N.G. Lane (1973) in his work on the world-renowned Mississippian crinoid fauna from Crawfordsville, Indiana: *What were all these suspension feeders eating?* After noting that the phytoplankton food web of the Mississippian may have been depleted in diversity and abundance, Lane stated: "Regardless of its taxonomic composition, there must have been a sufficient quantity of small organic material in the water to sustain all suspension-feeding types found at this site." We and others (Ausich and Kammer, 2013) have considered that the food supply during that part of the Mississippian could have somehow played a role in the diversification that produced the peak in crinoid and blastoid diversification, in addition to factors previously proposed. In 2009, Robert Riding brilliantly connected several key geological, biogeochemical, and paleontological events that occurred during the Late Devonian – early Mississippian interval, coinciding with the Age of Crinoids, that could be causally related to a global drawdown in atmospheric carbon dioxide. These events included: increased burial of organic carbon as

black shales, worldwide extinction of coral-stromatoporoid reefs, extinction of microfossil acritarchs leading to a "phytoplankton gap", worldwide occurrence of carbonate mud mounds, and *the peak in diversity of pelmatozoan echinoderms - the Age of Crinoids itself* (Riding, 2009). Riding suggested that the drop in dissolved CO_2 in the oceans induced a carbon-concentrating mechanism in nano- or pico-bacterioplankton that "bloomed" in the seas to become the dominant marine phytoplankton following the acritarch extinction. He linked this bloom of calcareous bacterioplankton to the production of carbonate muds by cyanobacterial calcification and the abundance and diversification of marine suspension feeders including echinoderms that were well adapted for this new abundant food source. Although Riding's suggestions about relationships between the key events he listed could be debated and tested, we were especially intrigued by his recognition that the worldwide, all-time maximum of species diversity and abundance of suspension-feeding crinoids and blastoids with narrow food grooves could have been nourished by the expansion of a new component of the marine phytoplankton. Could this potentially new food source have fueled the Age of Crinoids, and acted in concert with other factors noted above as multiple drivers for this largely overlooked episode of Paleozoic marine diversity?

In this paper we present evidence from both living and fossil crinoids and blastoids of the relationship between biodiversity, abundance, and productivity of potential food sources. We will offer more information in support of Riding's suggestion that the crinoid peak was fueled by a worldwide turnover in the nature and abundance of marine phytoplankton during the early Mississippian that was particularly advantageous to benthic suspension feeders that

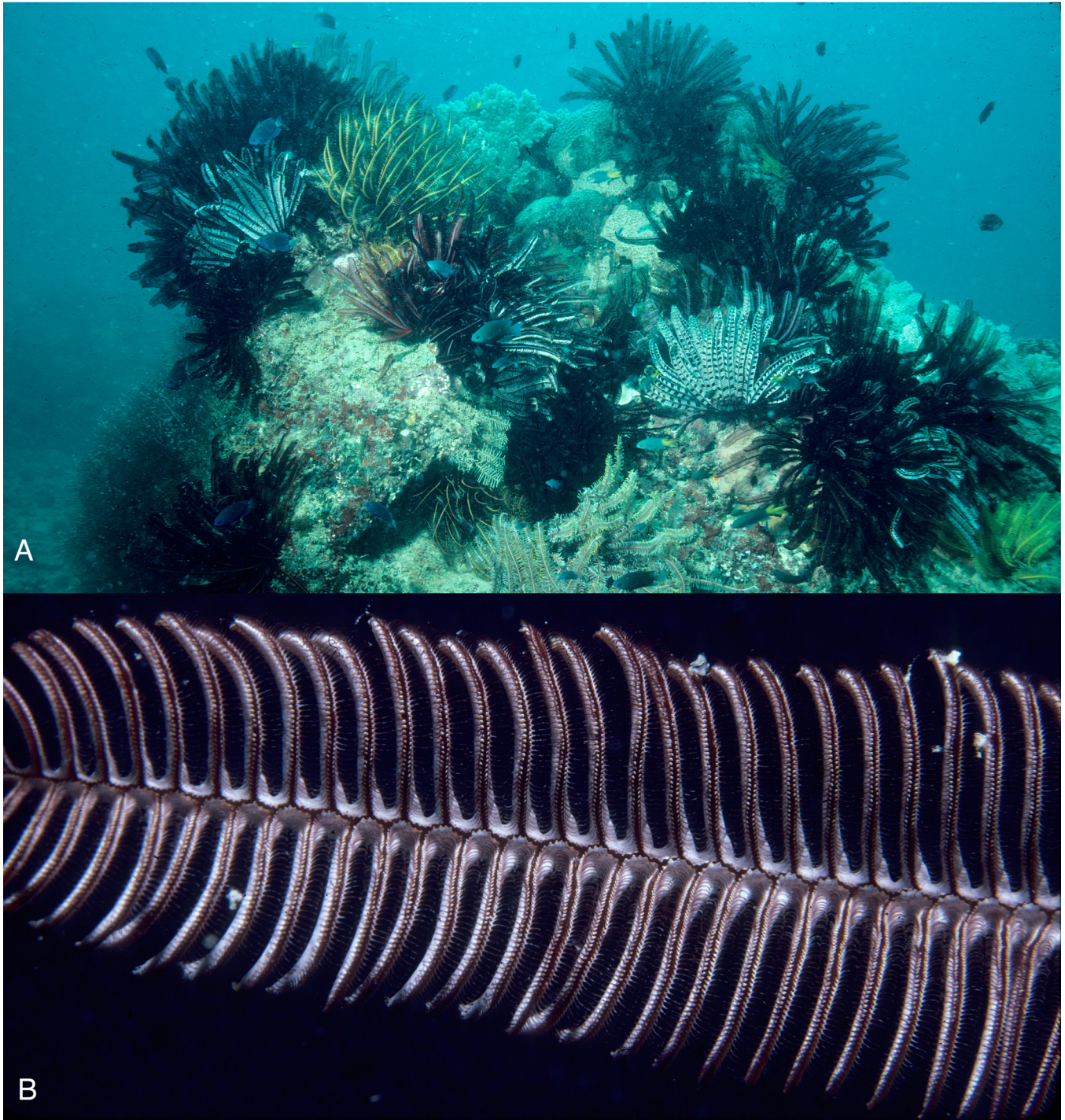


FIGURE 5 — **A**, North Reef, Lizard Island, Great Barrier Reef, depth 8 m, with ~14 crinoid spp visible by day. **B**, Arm and pinnules of Recent comatulid crinoid in life showing open food grooves and tube feet. Pinnule length ~ 1 cm. Photos by D. Meyer.

TABLE 2 — Mean density and species richness of crinoids (feather stars) of the Central Great Barrier Reef (data from Fabricius, 1994). For Davies Reef, mean crinoid density ranged from 0.7/m² (lagoon) to 7.8/m² (windward) and mean species number from 3.4 (lagoon) to 11.4 (windward).

Location (sites)	Mean density, m ⁻²	Mean species richness
Outer shelf (12)	2.6	7.2
Mid-shelf (10) *	8.1	9.1
Nearshore (2)	0.7	2.5

*Excluding Davies Reef

could capture very minute suspended food particles. As a kind of test of Riding's proposal, we can evaluate its underpinnings by addressing weaknesses as well as additional supporting evidence. It is very important for this analysis that we will look at the diversity and biogeographic distribution of both Recent crinoids and their feeding habits and preferences, as well as the extensive fossil record of crinoids and blastoids to determine the connections between their paleobiodiversity and their ancient environments. We find that there is considerable information in the large published literature on these groups both living and extinct that has never been collated and brought to bear on many major questions about their evolutionary history. Therefore, this paper is a review and compilation of available information, presentation of new data, and application to understanding major aspects of the half-billion-year-old evolutionary record of these echinoderms.

DIVERSITY AND ZOOGEOGRAPHY OF RECENT SHALLOW-WATER CRINOIDS

Until SCUBA diving became widely available in the years following World War II, very little was known about crinoids living in shallow marine waters (<100 m). Crinoids were described from trawling and dredging in deep waters since the 19th Century, and stalked crinoids in particular were regarded as deep-sea animals. H. L. Clark (1915) studied diverse shallow-water unstalked crinoids (feather stars) collected by a surface-supported diver on the Great Barrier Reef. The first SCUBA diving studies of reef-dwelling feather stars in the Red Sea were made by Magnus (1963, 1964) and later by Rutman and Fishelson (1969). The first reports of crinoids from similar reef environments in the tropical Western Atlantic were feather stars on shallow reefs at Dominica in the Windward Islands (Kier, 1966; pers. comm. to DM; Breimer, 1978a, fig. 210). Subsequently, Meyer (1973a, b) studied reef-dwelling crinoids found abundantly at several sites across the Caribbean such as Jamaica, Curaçao, Bonaire, Antillean islands, Colombia, and Panama. Extensive collections from deep water over the entire tropical Western Atlantic region

by R/V *Pillsbury* and R/V *Gerda* were identified by Messing, Macurda, and Meyer (Meyer et al., 1978). Crinoid occurrences at many shallower reef sites across the region were recorded by Meyer and Macurda using SCUBA diving. Data from these shallow and deeper water studies were combined by Meyer et al., (1978).

Shallow Water Crinoid Diversity in the Tropical Western Atlantic

The maximum crinoid diversity at a single shallow-water site in the tropical Western Atlantic is 7 species (San Blas, Panama), and at typical well-developed coral reef sites it is 4-5 species (Meyer, 1973a; Macurda and Meyer, 1977). Despite the low diversity for the entire region compared to much higher regional diversity in the Indo-West Pacific for shallow-water invertebrates and vertebrates, including crinoids (see below), diversity in the Western Atlantic suggested an interesting pattern. The localities where shallow-water crinoids are most diverse and abundant, Panama and Colombia, are both nearshore, close to high coastal topography with nearby river outflows. In both areas, there are diverse fringing coral reefs but water clarity is often lower than that at more offshore sites such as Curaçao or Jamaica, sites known for the best-developed and most diverse reefs (also including Bonaire, Barbados, the Antillean Arc). Crinoids reach their peak diversity closer to the S. American coastline or Isthmus of Panama with sediment influx and freshwater runoff, both factors known to limit maximum reef development. A recent survey of well-developed reefs in the Jardines de la Reina, offshore of the south-central coast of Cuba by about 30 miles, yielded 3 reef-dwelling crinoid species, although more extensive study of the Cuba coast is still lacking (Meyer, pers. obs., 2016). Meyer (1973a) cited studies available at the time indicating that plankton productivity increases from the more offshore waters of the Caribbean and equatorial Atlantic toward the South American coast and that runoff from discharge of major rivers such as the Magdalena and coastal upwelling also introduced higher nutrient input and productivity for nearshore zones and islands (such as the San Blas Islands of Panama and Santa

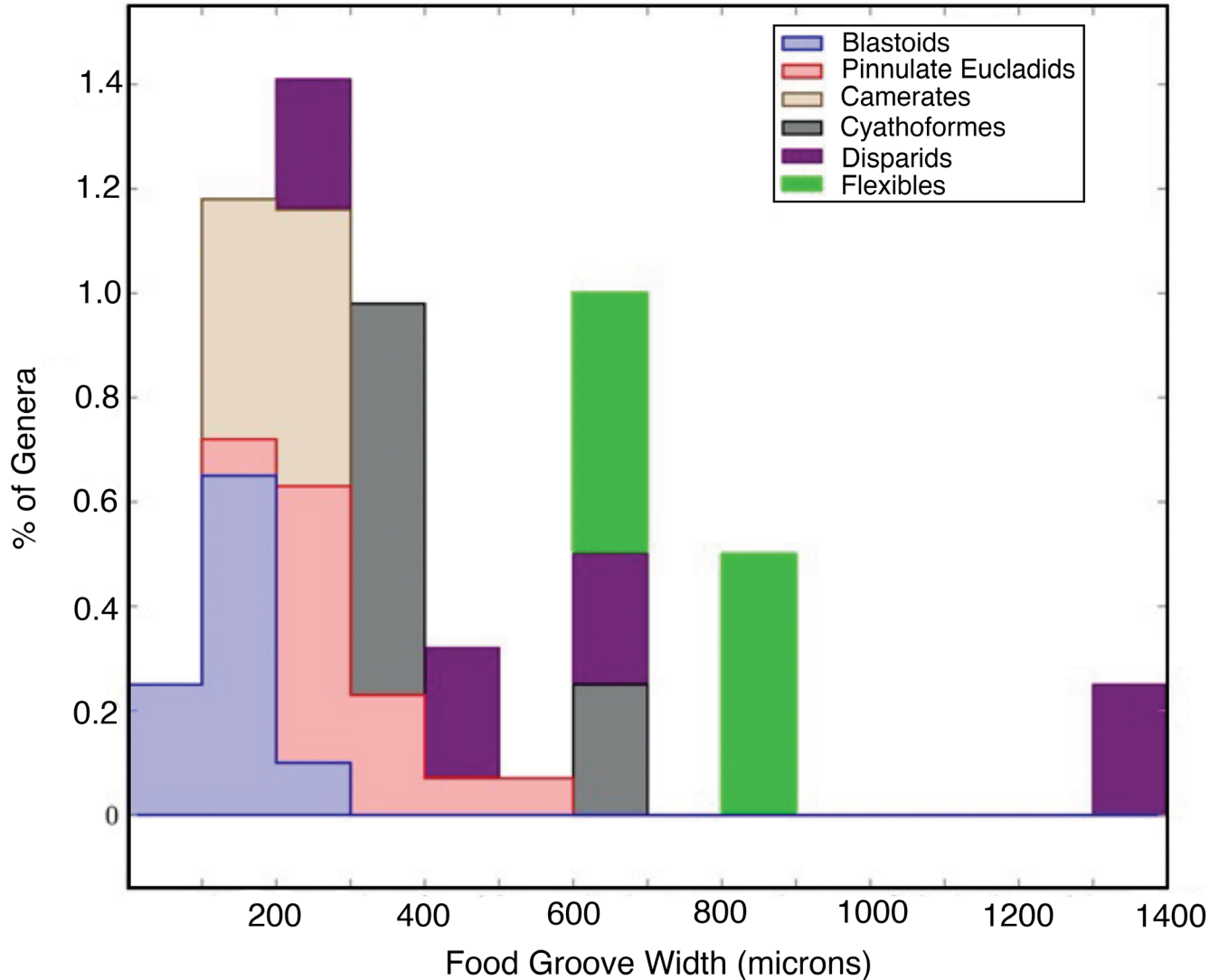


FIGURE 6 — Stacked plot of the food groove widths (microns) for blastoids and crinoid clades. Crinoid data from Ausich (1980). Blastoid data from Table 3 herein. Data for each clade normalized and reported as percent in each bin. Blastoids have very narrow food grooves in the brachioles. Camerate crinoids also have narrow food grooves even though branching arms with pinnules are the primary feeding structures. Advanced eucladids have a wider range of food groove widths but overlap blastoids and camerates. Cyathoformes have wider food grooves than camerates and most blastoids. Flexibles have significantly wider food grooves than the other clades. Disparids exhibit a very wide range of food groove widths.

Marta coast of Colombia). Meyer suggested that suspended food supply, along with favorable current flow, supported the higher diversity and abundance of suspension feeders like crinoids in shallow waters less favorable to more extensive coral reef development.

Shallow Water Crinoid Diversity in the Indo-West Pacific

In 1975 Meyer had a unique opportunity to take part in the *Rumphius II* research cruise in the Molucca Islands of Indonesia, in the heart of the famed "Coral Triangle" known for high diversity of shallow marine invertebrates and

vertebrates. Although it turned out that SCUBA diving could not be supported onboard the research vessel, collection of crinoids was made using snorkel diving, aided by specimens brought to the vessel by local people at every place we stopped during a two-week cruise. Identification based on available taxonomic references resulted in a total of about 27 species (Meyer, 1976), and specimens were deposited at a university at Ambon and at the National Museum of Natural History of the Smithsonian Institution.

Since that time, many studies on Indo-West Pacific shallow-water crinoids and their symbionts have been published, extending from the Red Sea, across the Indian Ocean, Coral

Triangle, and into the Central Pacific. Messing (1998) presented a critical summary of available records of shallow-water crinoid distribution in the region. Messing pointed out several factors that should be taken into consideration when consulting records from particular localities, such as methods of collection, collecting effort, and use of updated taxonomic resources. A recent paper on the crinoids and their symbionts at Sulawesi (Virgili et al., 2020) provided an excellent summary of current knowledge of crinoid biodiversity across this vast region. These authors pointed out that many studies on the symbionts associated with shallow water crinoids have not provided comprehensive data on crinoid host species diversity or were based on now-outdated taxonomic determinations. Therefore, we will mention only those studies that are based on the latest revisions of crinoid taxonomy for the most complete sampling of crinoids at a given locality, as well as those based on personal field experience.

In the 1970s Meyer and Macurda (1980) studied reef-dwelling crinoids from the Palau Islands in Micronesia, reporting 21 species from depths <50 m. Messing (2007), using updated taxonomy, identified 22 species from the same area. Subsequently, several comprehensive studies were reported from localities closer to the Coral Triangle. From Papua New Guinea, 25 species were reported at Hansa Bay (Deheyn et al., 2006) and 40 species at Madang (Messing, 1994). Kogo et al. (2019) reported 31 species from the Indonesian islands of Ambon and Lombok. Virgili et al. (2020) reported 39 species from Bangka Island, North Sulawesi. Messing and Tay (2016) reported 39 species from waters around Singapore, based on a new survey conducted in 2013, plus previously recorded taxa.

Although outside the limits of the Coral Triangle, the Australian Great Barrier Reef has a highly diverse and abundant crinoid fauna and has received a considerable amount of attention from researchers. Beginning in 1975, Meyer and Macurda visited the Lizard Island reefs and other GBR reefs several times through 2000. Lyle Vail and Anne Hoggett, both crinoid specialists, have worked at Lizard Island Research Station as resident co-directors since 1990. Based on their longtime observations, they organized the Lizard Island Field Guide, an online illustrated guide to the reef fauna at Lizard Island (<http://lifg.australian.museum/Hierarchy.html?hierarchyId=PVWrQCLG>, accessed Oct. 20, 2020). This guide lists 51 shallow water crinoid species, a total comparable to that obtained during the work of Meyer and Macurda and also to the total of 57 species reported by Messing (1998) (Fig. 5A). These figures probably reflect to some degree the intensive study of the Lizard Island crinoids by specialists for nearly 50 years but suggest that similar totals might be obtained by more extensive study at other high-diversity sites mentioned above.

Another major research program was established by the Australian Institute of Marine Sciences (AIMS), to document marine diversity along a transect from the Outer Barrier Reef bordering the Coral Sea, across mid-shelf reefs to nearshore reefs close to the mainland in the Central Great Barrier Reef region. Crinoids were an invertebrate group selected for

sampling using a standard protocol at designated reefs. In 1983 Meyer participated in the effort to identify the many crinoids that were sampled and also was able to visit Outer Barrier reefs such as Myrmidon and mid-shelf reefs such as Brewer and Davies. At Davies Reef a total of 27 species-level taxa were identified (Bradbury et al., 1987).

A later sampling of crinoids at <12 m depth in the Central GBR was conducted in 1988 (Fabricius and Dale, 1993; Fabricius, 1994) at 46 sites on 12 reefs, including Davies Reef. This survey is significant for the purposes of this review in being the only quantitative assessment of crinoid diversity comparing reefs across the Central GBR from the continental mainland to reefs of the mid-shelf and outer barrier. With the benefit of revised and updated taxonomy (Rowe et al., 1986), the total of approximately 44 species from Davies increased the known taxa from 27 reported by Bradbury et al. (1987). The entire dataset was analyzed using a variety of multivariate techniques. Data in Table 2 indicate that mid-shelf reefs and Davies Reef in particular have higher crinoid densities and higher number of species compared to outer shelf reefs and nearshore reefs.

A similar pattern was suggested by crinoid richness at Lizard Island, a high island on the mid-shelf, that contrasted with apparent lower crinoid diversity and abundance on outer barrier reefs (Carter-Yonge) at the same latitude (Meyer, pers. observations). On these outer barrier reefs, qualitative observations suggested maximum coral cover and richness, with exceptional water clarity (highly oligotrophic). The waters around Lizard Island, while highly diverse in all reef life, including crinoids (Fig. 5A), often seemed to have lower water clarity despite being quite far offshore (~20 miles) from mainland runoff. Was it possible that increased turbidity resulted from greater primary productivity of plankton and particulate organic matter (more heterotrophic conditions) over the mid-shelf region? Higher productivity could, in turn, provide enhanced food supply for suspension feeding reef dwellers like crinoids.

A 1982 paper published by AIMS biological oceanographers Andrews and Gentien documented nutrient enrichment and enhanced phytoplankton productivity of mid-shelf reefs from upwelling that originates along the outer shelf break that might account for the greater richness of suspension feeding crinoids around mid-shelf reefs where there is also localized upwelling. According to Fabricius (pers. comm., 2017), upwelling along the GBR is still not well understood and additional factors such as current patterns, structural complexity, and patterns of sedimentation play a role.

FOOD COMPOSITION OF LIVING CRINOIDS

The foregoing summary of the diversity and biogeography of living shallow water crinoids suggests that the highest diversity and abundance of crinoids in both the tropical Western Atlantic and Indo-West Pacific realms occurs where plankton productivity is increased in proximity to large landmasses such as islands and continents. However, this

leaves open the question: *exactly what suspended particles ingested by crinoids supply their main nutritional source?*

Suspension Feeding by Modern Crinoids

Crinoids are regarded as non-selective passive suspension feeders, capturing any particles striking the mucus-coated tube feet that flick to transfer them to the food grooves where they are entrained as a mucus string by ciliary currents leading to the mouth (Meyer, 1982b). Because the tube feet act as a "sticky filter", particles smaller than the minute gap between extended tube feet can be captured, as well as larger particles (LaBarbera, 1978). Large aggregates of suspended material can be carried along the food grooves but are usually discarded before reaching the mouth (Holland et al., 1991; video by A. Stevenson, in Meyer et al., 2021). Overall, relative nutritive value of identifiable items as well as the detrital component and DOM remain to be determined. The main limiting factor for capture of suspended particles is maximum width of the pinnular food groove (75–~300 microns, according to several studies cited below).

Studies of the gut and fecal contents of both stalked and unstalked crinoids from shallow as well as deep water have been reported for a number of species. A wide variety of particles have been identified from these samples, including phytoplankton, Protozoa (Foraminifera), Crustacea, fecal pellets, and sediment grains, and in most cases detritus that makes up a large proportion of the material (shallow water feather stars (LaTouche and West, 1980; Liddell, 1982; Meyer, 1982a; deep water stalked crinoid, Featherstone et al., 1998). The maximum width of most identifiable items is usually less than about 200 microns, within the width of the pinnular food grooves. However, some items can range to about 300–400 microns in width. [It should be noted that some living suspension feeders are known to ingest particles larger than microplankton normally assumed, for example, several bivalves (Lehane and Davenport, 2002)]. Detrital material appears as a mass in the samples, and single particles are unresolvable in light microscopy. Therefore, size data for the detritus are not available in size-frequency plots for identifiable items. LaTouche and West (1980) suggested that the detrital particles may have microbial material adhering that could have nutritive value for the crinoid. Actual caloric content of all food items has not been determined. Uptake by absorption of dissolved organic matter (DOM) across the body wall has been demonstrated for crinoids and may provide nutrition for a crinoid during regeneration after loss of the visceral mass from autotomy or predation (Smith et al., 1981).

Suspension Feeding by Extinct Crinoids

It is generally assumed that ancient crinoids had suspension feeding habits similar to living crinoids - passive suspension feeders utilizing tube feet for particle capture and ambulacral grooves by which particles were carried to the mouth. Detailed

research on the morphology of ancient crinoid feeding structures (arms, pinnules, food grooves, column length) has revealed a wide range of variation within and among major groups of crinoids and blastoids that probably had consequences for the size-range of food particles captured.

Most significant are studies on variation within ancient communities with excellent preservation of in situ assemblages that permit comparisons between taxa with differing morphologic features of the feeding apparatus. Lane (1963) first documented the existence of co-occurring crinoid species preserved with many specimens with articulated calyces, arms, pinnules, and columns complete to a holdfast that were "stratified" (later termed "tiered") at different heights above the sea floor. These assemblages are among the best preserved fossil crinoids ever known on large slabs of specimens from classic localities near Crawfordsville, Indiana in the Lower Mississippian Edwardsville Formation (Lane, 1963, 1973). Study of crinoid communities from distinct facies of the Edwardsville Formation, around Monroe Reservoir, Indiana, by Ausich (1980) introduced the concept of niche differentiation based on several morphologic parameters including height above substratum (column length), filtration fan density (branches/fan area), and ambulacral groove width. Ausich demonstrated that co-occurring crinoids in different facies of the Edwardsville were distributed along a niche differentiation spectrum that dictated differential capture of particles based on particle size. Furthermore, his analysis showed that the probable size range of captured particles is similar to that for living crinoids, ranging from about ≤ 0.1 mm to >1.25 mm (his fig. 4 and our Fig. 6 that includes blastoids). The most common crinoids in the assemblage studied by Ausich had pinnular food grooves in the range $\leq 0.1 - 0.4$ mm in width (implying a similar size range of particles). Fewer taxa having wider food grooves occupied the tail of a right-skewed distribution of width.

Ausich stated that his data and conclusions were dictated by principles of aerosol filtration theory as applied to suspension feeding by Rubenstein and Kohl (1977) and LaBarbera (1978). Despite the fact that soft-part structures such as exact food groove width and tube feet are not preserved, the preservable morphology of the arms and pinnules permits application of these principles to a close approximation. In living crinoids the food groove width is measured from soft tissue located slightly above the pinnular ossicles (Fig. 5B; also see Breimer, 1978b: fig. 2). We would add that in many of these Mississippian crinoids, the food groove was deeply embedded in the preservable skeleton of the pinnules, sometimes with covering plates in place. [Examples are illustrated in the *Treatise on Invertebrate Paleontology*, Part T: Ubaghs, 1978, figs. 131-1d, 136-7, 160 (fossil crinoids); Breimer, 1978b fig. 29-3 (for Recent *Neocrinus decorus*).] Thus, the width as measured by Ausich should be very close to that in the living animal. Aerosol filtration predicts that the parameters of a biological filter determine the size range of particles captured and that filters having different mesh sizes will have differing optimal size ranges. Further research by Ausich and Kammer

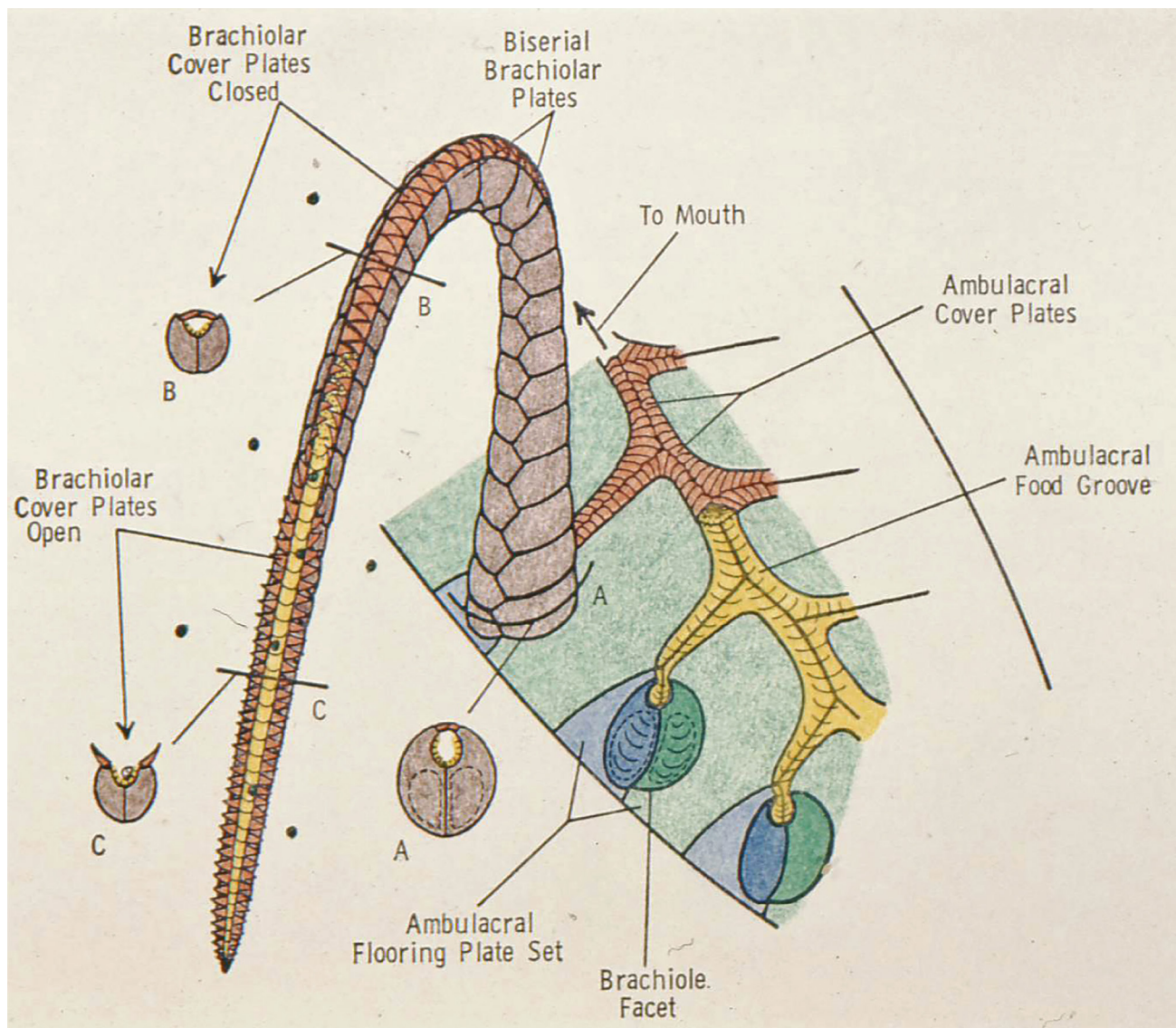


FIGURE 7 — Schematic detail of blastoid brachiole and ambulacral tract. Modified from Sprinkle, 1973, used courtesy of J. Sprinkle.

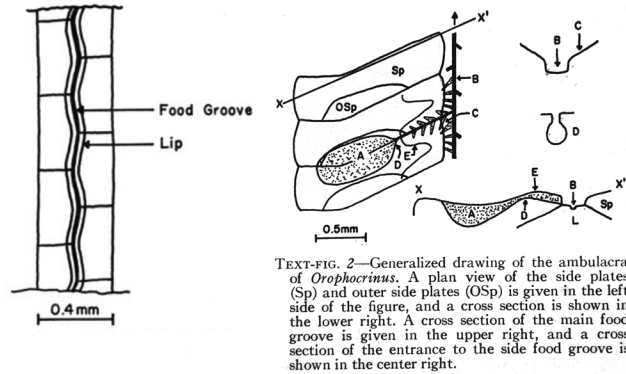
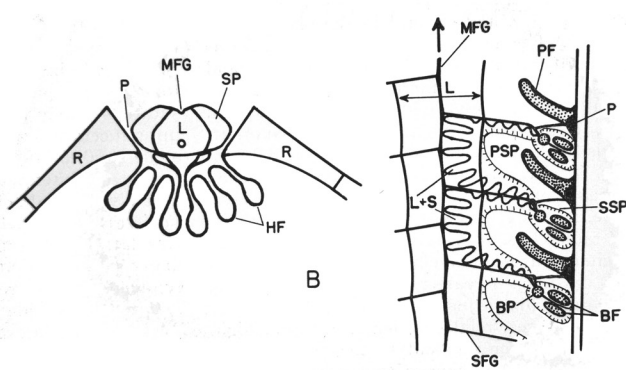
(Kammer, 1985; Kammer and Ausich, 1987) explained faunal differences among Lower Mississippian crinoid communities on the basis of aerosol filtration and current velocities.

There are no known cases of fossil preservation of stomach or fecal contents of crinoids by which direct comparisons to studies of living crinoids as described above can be made. Therefore, it is necessary to infer the size range of particles that could be entrained in the food grooves by both crinoids and blastoids (see below).

FUNCTIONAL MORPHOLOGY AND FEEDING BEHAVIOR OF BLASTOIDS

Blastoids are members of an extinct echinoderm class ranging from the Upper Ordovician to the Upper Permian.

Like crinoids, blastoids were attached to the seafloor by a slender column comprised of disc-like columnals. Unlike crinoids, the blastoid column held up a regularly plated theca that encased internal structures and included five ambulacral tracts that converged on the "summit" of the theca. In crinoids, the ambulacra are termed exothecal as they elevated the arms away from the plated calyx, enabling the formation of the filtration fan discussed earlier. Blastoids lacked the arms and pinnules present in crinoids; instead, very slender, elongate, unbranched structures called brachioles lined the ambulacral tracts and extended radially, perhaps like bristles. A blastoid with a full array of brachioles might have resembled a "bottle brush". Breimer and Macurda (1972: figs. 101, 102) illustrated reconstructions of fissiculate blastoids with extended brachioles forming filtration fans oriented to filter a horizontal



TEXT-FIG. 2.—Generalized drawing of the ambulacra of *Orophocrinus*. A plan view of the side plates (Sp) and outer side plates (OSp) is given in the left side of the figure, and a cross section is shown in the lower right. A cross section of the main food groove is given in the upper right, and a cross section of the entrance to the side food groove is shown in the center right.

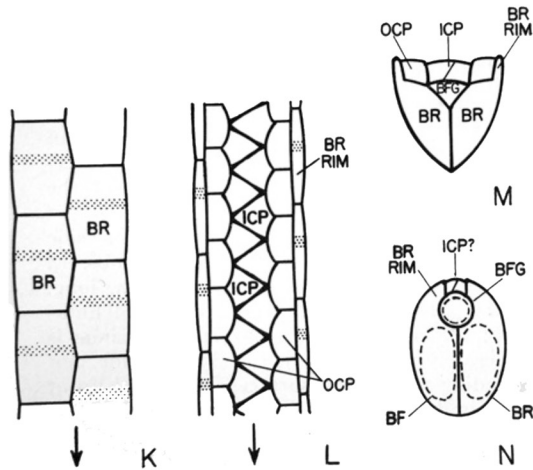


FIGURE 9 — Brachiole (left) and details of ambulacra of *Orophocrinus conicus* (right), from Macurda, 1965, used with permission.

FIGURE 8 — Thecal ambulacra (upper 2 diagrams) and brachioles (lower diagrams, K-N) of *Costatoblastus*, Dev. — Miss., Montana (from Sprinkle and Gutschick, 1990, used with permission).

current or to capture particles settling from above,

James Sprinkle's (1973) reconstruction of the morphology of the brachiole attached to the theca in feeding position shows how brachioles are fundamentally distinct from arms arising from a crinoid calyx (Fig. 7). The biserial brachioles are comprised of solid, wedge-shaped ossicles (brachiolar) that bear a brachiolar groove that was covered by biserial covering plates that could be opened to expose the ambulacral groove. Sprinkle's reconstruction shows minute food particles suspended in the surrounding water and in the groove on their way to the mouth, located at the thecal summit. Sprinkle hypothesized that the food groove was lined with tissue bearing cilia that beat synchronously to create a feeding current, drawing flow around the brachioles and through the array of extended cilia. This feeding current presumably conveyed suspended particles to the exposed food groove where they were entrained by ciliary flow towards the theca.

Although Sprinkle (1973) postulated that, unlike crinoids, blastoids did not have tube feet, Breimer and Macurda (1973) suggested that tube feet could have been housed within

minor grooves radiating toward the side and main ambulacral grooves, as part of the side plates. It follows from Sprinkle's reconstruction that the width of exposed food groove would be a primary limiting factor for the size of particles that could be entrained (Fig. 7). At the point where the brachiolar food groove joined the theca, particles must have entered the ambulacral food groove through the brachiolar pit (Fig. 8, BP in detail at upper right). If the diameter of the brachiolar pit was \leq the width of brachiolar food groove, entrained particles would have encountered a secondary size limiting factor. Note that in Sprinkle's reconstruction, the ambulacral groove of the thecal plates was equipped with cover plates, whereby the feeding current would have become subtheal from that point onward toward the mouth. In 1973, Sprinkle concluded that blastoids were limited to feeding on very small particles. In 2006, Sprinkle stated that "blastozoan (including blastoids) brachioles almost always had narrow food grooves, implying that they fed on small food particles."

Given that Sprinkle's 1973 reconstruction is schematic and without a scale, it is necessary to examine preserved morphology of blastoids to see if this morphology is present throughout the class and how the actual size limitations would have constrained food particle size. Blastoids preserved with attached stem and brachioles are exceedingly rare. However, several well-documented cases of exceptionally well-preserved blastoids provide data on feeding morphology. Table 3 lists sixteen taxa, both fissulates and spiraculates, for which detailed descriptions of brachiolar and ambulacral morphology are available.

Macurda (1965) provided detailed drawings with scale from which we could determine the width of the brachiolar and thecal ambulacral food groove and the brachiolar pit in the Mississippian fissiculate *Orophocrinus conicus*. In Macurda's Text-figure 1 (our Fig. 9), the width of the entire brachiole is 0.4 mm, therefore the width of the brachiolar food groove is 0.0246 mm or 24.6 microns, the narrowest width reported. In our Fig. 9 (his Text-fig. 2, plan view at left) point D marks the

TABLE 3 — Brachiolar food groove width or brachiolar pit width (bp) in some blastoids. F = fissiculate, S = spiraculate. Data obtained from published figures with scale except as indicated.

<i>Orophocrinus conicus</i> , F, Miss.: 24.6 μm (Macurda, 1965)
<i>Orophocrinus</i> cf. <i>O. gracilis</i> , F, Miss.: 195 μm (bp) (Sprinkle and Gutschick, 1990)
<i>Pyramblastus fusiformis</i> , S, L. Miss.: 127 μm (Fay and Reimann, 1962)
<i>Koryschisma elegans</i> , F, Miss.: 167 μm (Sprinkle and Gutschick, 1990)
<i>Montanablastus baldyensis</i> , S, Miss.: 163 μm (Sprinkle and Gutschick, 1990)
<i>Costatoblastus sappingtonensis</i> , S, Devonian: 89-94 μm (Sprinkle and Gutschick, 1967)
<i>Hyperoblastus nuciformis</i> , S, M. Dev.: 171 μm (Fay and Reimann, 1962)
<i>Monoschizoblastus rofei</i> , S, Miss. 85 μm (bp) (New, SEM photo)
<i>Monoschizoblastus rofei</i> , S, Miss. 75 μm (bp) (New, SEM photo)
<i>Strongyloblastus laudoni</i> , S, Miss.: 271 μm . (Sprinkle and Gutschick, 1990)
<i>Pentremites godoni</i> , S, (juvenile) Miss. 55 μm (bp) (New, SEM photo)
<i>Pentremites robustus</i> , S, Miss. 130 μm (bp) (New, SEM photo)
<i>Pentremites robustus</i> , S, Miss. 136 μm (bp) (New, SEM photo)
<i>Deltoblastus</i> sp., S, Permian. 145 μm (bp) (New, SEM photo)
<i>Heteroschisma alatum</i> , F, Devonian, 94 μm (bp) (New, SEM photo)
<i>Cryptoschisma schultzi</i> , F, Devonian, 169 μm (bp) (New, SEM photo)

location of the brachiolar pit (BP) that must be the same width as that of the BFG, 24.6 μm . The enlarged cross sections at the right in our Fig. 9 (his Text-fig. 2) lack a scale, but it is apparent that the BP at point D must be exceedingly small. Cross section D shows the BP to have a keyhole shape, with a pore that restricts the entrance to 24.6 μm , widening below. The main food groove at B is wider, as it is a collector for all BFG feeding into the ambulacrum.

In the description of a Mississippian spiraculate blastoid, *Costatoblastus*, Sprinkle and Gutschick (1967: fig. 9, left) illustrated a cross section of the entire ambulacrum (our Fig. 8, left) with a plan view of the half-ambulacrum at the right. In the full cross section, point P marks the pore leading into the blastoid's hydrospire folds. The brachiolar pit (BP) in the plan view is circular in section and feeds into the main food groove (MFG). From the scale provided for their figure, the width of

the BFG is 89-94 μm (insets M, N). M is a cross section of the brachiolar showing covering plates and BFG, and N is a cross section of the brachiolar facet, where it attached to the side plates (SP) of the ambulacrum.

Fay and Reimann (1962) illustrated a fragment of a brachiolar of a Devonian blastoid *Hyperoblastus nuciformis* with a cross section with cover plates in place over the BFG. Using the scale, we determined the width of the BFG to be 171 μm . Table 3 shows other determinations of BFG widths from published illustrations in Fay and Reimann 1962) and in Sprinkle and Gutschick (1990), plus brachiolar pit width from SEM images of specimens in the collection of J. Waters.

As noted by Waters (1988), blastoids were components of echinoderm communities along with crinoids and peaked during the early Mississippian. In particular, blastoid generic diversity is highly correlated with that of monobathrid

camerate crinoids ($r=0.65$, $P<0.02$, Waters, 1988). Later during the Mississippian, blastoid diversity was not significantly correlated with that of eucladid crinoids, a group that attained a peak in diversity in the Pennsylvanian before declining toward the end of the Paleozoic. Blastoids became extinct with the end-Permian mass extinction, after regaining diversity during the Late Permian before the extinction.

Waters (1988) also pointed out that blastoids had not been successfully placed within the niche partitioning model introduced by Ausich (1980) for crinoids, because of limited information then available on the stem lengths and brachiole morphology of blastoids. This was also hindered by the contrast between crinoid filtration fans of arms and pinnules with tube feet and the blastoid brachioles that apparently lacked tube feet and could not form filtration fans like those of crinoids. Waters conjectured that blastoids might have been utilizing a specific food particle size range or even a wider particle size range than crinoids. In the present study we have presented limited data on the morphology of the brachiolar and ambulacral grooves that indicate a limitation of particle size range toward the lower end of the size spectrum (Table 3, Fig. 6). Although more data are needed for these parameters in blastoids, we can begin to assess the position of blastoids in the benthic food web of the Mississippian Age of Crinoids.

DISCUSSION

We have presented information derived from the published literature and new information that bear on the role of food availability as an additional causative factor for the all-time peak in diversity and abundance of crinoids and blastoids during the "Age of Crinoids" in Early Mississippian time. One set of information (secondary heading below) pertains to the connection between diversity of crinoids and food supply and productivity of suspended particulate food materials for both living crinoids and also extinct crinoids during the critical interval. The other set of information (next secondary heading) reviews existing knowledge of the makeup of material found in the gut and feces of living crinoids and its contribution to crinoid nutrition. We also consider the possible composition of the food of extinct crinoids in light of what is known about marine plankton at that time, particularly in terms of the available suspended particles in the size range crinoids and blastoids could ingest. We will summarize the information in both areas below and integrate it with previously published research on the relationship between species diversity and food supply, productivity, and nutrition of crinoids and shallow marine benthos over time.

Crinoid Diversity has been Closely Associated with Food Availability and Productivity Since the Paleozoic and at Present

For living shallow-water crinoids we argue that available knowledge of biogeographic distribution indicates that crinoids, chiefly feather stars, reach maximum richness and

abundance in both tropical Western Atlantic and Indo-West Pacific realms where there is enhanced plankton productivity caused by influx of nutrients from terrestrial sources via river outfalls and possibly regional upwelling. These conditions occur mainly close to continental margins (South America, Central America, Australia) or high islands (Coral Triangle of the IWP).

Species diversity in the broad sense of both species richness and population size (γ diversity), for living and extinct crinoids especially during the early Mississippian, peaked 347 – 331 mya during the Viséan, ranging from the Tournaisian through the Serpukhovian and attained a secondary peak during the Pennsylvanian (Moscovian). Blastoids also reached an all-time diversity peak during the Viséan but not during the Pennsylvanian. Significant events during the Mississippian and Pennsylvanian included the plate tectonic closure of the Iapetus Sea, resulting in the orogenic uplift of the Appalachian belt and especially major clastic runoff into the epicontinental sea from the Catskill and Borden Deltaic complexes. In addition, the Age of Crinoids coincided with the drawdown of global atmospheric CO_2 that Riding (2009) inferred to have triggered a major turnover or "bloom" of marine phytoplankton following the drastic decline of planktonic acritarchs in the Late Devonian, initiating the so-called "phytoplankton blackout" (Riegel, 2008).

In his comprehensive study of species richness in marine benthic habitats through the Phanerozoic, Bambach (1977) suggested that the evolution of land plants in the Silurian initiated an increase in supply of organic nutrients that might have affected species richness in the Paleozoic. He also noted that the crinoid community at Crawfordsville, Indiana studied by Lane (1973) had the highest diversity for level-bottom communities of the entire Paleozoic. However, Ausich et al. (1979) pointed out that the total diversity for the Crawfordsville community of 73 species reported by Bambach greatly understated the actual diversity there of more than 150 invertebrate species. Later, Algeo et al. (1995) emphasized the role of land plant evolution in the middle to late Paleozoic as it affected soil weathering and introduction of nutrients into the seas.

The high species diversity of level bottom communities dominated by suspension feeders (including sponges, bryozoans, and brachiopods in addition to crinoids and blastoids) associated with the Mississippian Borden Delta (Ausich et al., 1979) suggests a parallel to the relationship discussed earlier between increased diversity of living crinoids and higher productivity closer to continental margins. Indeed, in this case, the past may well provide the key to the present.

Even though the Age of Crinoids during the Mississippian does not stand out within studies of Phanerozoic marine diversity fluctuations at taxonomic levels of family and genus, crinoids and blastoids are a significant contribution to Sepkoski's (1981) Paleozoic Evolutionary Fauna (PEF) as indicated above. The assertions we are making of the connections between pelmatozoan diversity and food supply, nutrients and productivity are fully in concert with

several large-scale analyses of the role of these factors as primary controls over diversity in Phanerozoic time by Bambach (1993), Vermeij (1995), Martin (2003), Bush and Bambach (2011), Allmon and Martin (2014) and the recent comprehensive review by Martin and Servais (2020). Closer examination of how these and other factors contributed to the diversity trends of particular component taxa of the PEF is overdue.

Suspension-Feeding by Crinoids and Blastoids was Limited to Capture of Very Small Food Items by the Narrow Width of Food Grooves

The narrow width of pinnular food grooves in crinoids and brachiolar food grooves in blastoids has been recognized for quite some time. The width of particles in gut and fecal samples from living crinoids, both unstalked and stalked, plot as right-skewed frequency distributions, with the bulk of the material in the range of about 100 – 200 μm . The presence in samples of a considerable volume of "detritus" with unresolvable particles indicates that the size distributions may be more heavily right-skewed than those drawn from resolvable, identifiable items such as plankton, fecal pellets, and even sediment grains. Detrital particles in the size range less than the minimum spacing of crinoid tube feet can be captured and retained because the tube feet are "sticky filters" coated with mucus (LaBarbera, 1978). Although blastoids lacked tube feet, the ciliated brachioles likely were also mucus coated. Fossil crinoids and blastoids had narrow food grooves in a range similar to that in living crinoids but were probably incapable of capturing larger particles because of skeletal restrictions not present in living forms in which the food grooves are in stretchable soft tissues.

We have no direct evidence of any fossilized gut contents, so that the taxonomic identification of their gut contents is not known. However, we can state with confidence that ancient crinoids and blastoids were collecting very small particles from the water mass. The immense volume of pelmatozoan-rich limestones (encrinites) of early Mississippian age from all over the world *requires* that these marine suspension feeders and others like bryozoans and sponges were supported by an abundant supply of nutritious particles from the near-bottom waters of the Paleozoic shallow seas, including phytoplankton, zooplankton, and also organic detritus and microbial pico- or nanoplankton.

Paradoxically, when we consider the fossil record of the marine plankton, we find that the Age of Crinoids coincides with a long interval from the Late Devonian through the early Mesozoic for which the fossil record is exceptionally poor (Tappan, 1968: fig. 1; Martin, 2003: fig. 2B; Riding, 2009: fig. 8; Martin and Servais, 2020: fig.1C; others). In all these records, the only component of the marine plankton present in the microfossil record during the Age of Crinoids is acritarchs with a possible trace of early dinoflagellates in some (Tappan, 1968: fig. 1) plus a trace of coccolithophorids (Martin and Servais, 2020: fig.1C). Major components

of Recent phytoplankton, such as the dinoflagellates, coccolithophorids, and diatoms, do not have major increases in their abundances until the Mesozoic and Cenozoic (Knoll and Fellows, 2016). Among the zooplankton, foraminiferans and radiolarians are certainly present in Paleozoic, and diverse larvae must have been present but usually unpreservable (with possible exception of microfossils, such as from the Ediacaran Doushantuo Formation of China, 635–551 Ma). Ironically, the Age of Crinoids interval is extraordinarily rich in benthic suspension feeders with a good fossil record (crinoids, blastoids, sponges, conulariids, corals, mollusks, and especially bryozoans). The question "What were all these suspension feeders eating?" becomes all the more significant in view of the richness and abundance of the entire marine benthic suspension feeder guild.

It must be considered that the marked lack of preserved marine phytoplankton during the Age of Crinoids reflects a taphonomic artifact as a consequence of an abundance of either nonskeletonized or poorly preservable components of the microplankton at that time, a potential problem that has been discussed at length by Martin and Servais (2020). Riding (2009) discussed the possibility that the phytoplankton blackout could be "more apparent than real". As Riding suggested, it may have been the result of a major shift in plankton composition from acritarch dominance to abundance of "relatively invisible picophytoplankton" including cyanobacteria and other groups such as prasinophyte green algae (Riding, 2009). As further pointed out by Riding, as well as Martin and Servais (2020), the modern marine plankton contains bacterioplankton ($< 1 \mu\text{m}$) and picoplankton ($\sim 1\text{--}2 \mu\text{m}$), and we also suggest that non-skeletonized protozoans such as flagellates and ciliates would have been part of the non-fossilizable Paleozoic plankton. There may be limitations on our ability to fully characterize the makeup of the Paleozoic marine plankton biota, but it is the main assertion of this paper that the richness and abundance of the Mississippian suspension feeding guild of crinoids and blastoids and other groups, like bryozoans, demonstrates that the primary producers of that time were dominated by very small organisms as suspended particles.

CONCLUSIONS

In a single paragraph Riding (2009) succinctly summarized the evidence from the Mississippian fossil record that crinoids and blastoids at their all-time peak in richness and abundance in the Age of Crinoids possessed narrow food grooves well-suited for gathering very small food particles, suggesting "both a shift and increase in food supply toward smaller particles, such as picoplankton or the microplankton that feed on them".

In the present paper we have argued that food supply, nutrients, and productivity are *among* the chief factors controlling diversity of Recent and Mississippian crinoids. We have presented an analysis of the feeding mechanism of Recent and fossil crinoids and blastoids that explains why

Mississippian crinoids and blastoids were preferentially capturing very small suspended particles. For both groups, the range of food groove width dictates that most particles were smaller than about 400 μm . For the crinoids studied by Ausich (1980) some taxa had food grooves capable of capturing larger particles, but most blastoids were more closely constrained toward the smaller end of the size spectrum. We postulate that blastoids were actually specialists at gathering very small suspended food particles. Of sixteen taxa with well-preserved brachiolar food grooves or pores, the maximum width is 271 μm . Thanks to the mechanisms of aerosol filtration, blastoid cilia and larger crinoid tube feet probably acted as sticky filters (LaBarbera, 1978) that could trap particles finer than the mesh size of the filter. Both groups evolved their feeding morphologies millions of years before the Early Mississippian acme (Brower, 2007, 2011; Cole et al., 2019). When circumstances of the global atmosphere changed so as to shift primary production in the seas to the most minute bacterio- and picoplankton proposed by Riding (2009), crinoids, blastoids, and perhaps other suspension feeders could take advantage of the new food source. They were, in a sense "preadapted", to hazard an old, perhaps disfavored view. In the sense of Gould and Vrba (1982) the suspension feeding abilities of crinoids and blastoids became "exaptations" that enabled these groups to diversify opportunistically and become enormously productive. The abundance of thick regional encrinites (Ausich, 1997) became some of the most extensive limestones known, an enduring testimony to this unique phase of the Paleozoic oceans known as the Age of Crinoids.

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