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CRINOID DISTRIBUTION AND FEEDING MORPHOLOGY THROUGH A DEPOSITIONAL SEQUENCE: KOPE AND FAIRVIEW FORMATIONS, UPPER ORDOVICIAN, CINCINNATI ARCH REGION

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ABSTRACT—Crinoid columnals are major faunal components of interbedded shales and carbonates of the Upper Ordovician Kope to Fairview formations (Edenian-Maysvillian) of the Cincinnati Arch region. Six species can be identified on the basis of distinctive morphological characters of the columnals. Crinoid distribution was plotted from point-counted carbonate samples taken through a 68-m thick composite section of the Kope to Fairview formations in Campbell County, Kentucky. This section spans a shallowing-upward, third-order depositional sequence (C1), part of C2, and the Edenian-Maysvillian Stage boundary. The slender cladid crinoid *Merocrinus* occurs in the lowermost Kope below the base of this section. The slender disparids *Cincinnaticrinus* and *Ectenocrinus* occur throughout the section but are most abundant in the lower 25 m where the shale percentage is 60–90 percent. The larger, more robust disparid *Iocrinus* appears within the carbonate-rich Grand Avenue member of the Kope at 40–50 m, and the large, plated camerate *Glyptocrinus* first appears just above the Grand Avenue and becomes the dominant crinoid above the C1–C2 sequence boundary that lies just above the Kope-Fairview contact. The largest and most robust crinoid in this sequence, *Anomalocrinus*, occurs at the top of the Grand Avenue Member. Siliciclastic ratio and biofacies composition indicate that the occurrence of larger, more robust crinoid taxa is correlated with shallowing depth. Crinoid trophic niche differentiation is also correlated with decreasing depth and the concomitant increase in water movement caused by waves and currents. The deeper water disparids have a nonpinnulate filtration fan with low branch density and wider ambulacral grooves. The shallower water camerate *Glyptocrinus* has a pinnulate filtration fan with high branch density and narrower ambulacral grooves. These relationships are consistent with the predictions of aerosol filtration theory.

INTRODUCTION

ALTHOUGH CRINOIDS are among the most common macrofossils in Paleozoic epicontinental marine environments, their use in environmental interpretation has been relatively limited because identifiable specimens are usually rare and the far more common disarticulated material, dominated by columnals, is usually considered to be unidentifiable. In this paper we demonstrate that crinoid taxa (names based on crowns) can be identified on the basis of disarticulated columnals and used to track crinoid distribution through a depositional sequence of interbedded shales and carbonates of the Upper Ordovician Kope to Fairview formations (Endenian–Maysvillian) of the Cincinnati Arch region. This information provides a quantitative test of the predicted environmental distribution of crinoids based on studies of Recent crinoids (Meyer, 1973), theoretical considerations (Baumiller, 1993) and facies relationships found in much younger Paleozoic settings (Ausich, 1980; Kammer, 1985; Kammer and Ausich, 1987; Holterhoff, 1997b). Our study reveals trophic niche differentiation among co-occurring taxa very similar to those described by Brower (1992a, 1992b, 1994), in his exhaustive morphometric analysis of crinoids from the Middle Ordovician Galena Group of the upper Mississippi Valley. The present study also demonstrates a correlation between crinoid feeding morphology and water depth changes controlled by sequence stratigraphic architecture.

STRATIGRAPHIC SETTING

The Kope and Fairview formations are the lowermost formations of the type Cincinnatian Series (Upper Ordovician). Both units consist of interbedded terrigenous mudstone, calcisiltite, skeletal packstone, and grainstone deposited on a shallow, northward-dipping ramp. Bedding characteristics, sedimentary structures, and taphonomic evidence indicate the pervasive influence of storm depositional processes in these units as well as throughout the entire Cincinnatian Series (Kreisa, 1981; Tobin, 1982; Jennette and Pryor, 1993). The Kope and lower Fairview formations span two (C1 and part of C2) of the six third-order depositional sequences recognized within the Cincinnatian Series (Holland, 1993; Holland and Patzkowsky, 1996). The Kope has a high shale-to-limestone ratio (80 percent) and is interpreted as an offshore facies, deposited below wave base of all but severe storms (Tobin, 1982; Holland, 1993; Jennette and Pryor, 1993). The Fairview has a lower shale-to-limestone ratio (50 percent) and is interpreted as shallower, transition zone or deep subtidal facies, deposited between fair-weather and storm wave base (Tobin, 1982; Holland, 1993; Jennette and Pryor, 1993).

METHODS

Samples of fossiliferous limestones were recovered from a 68-m composite section near the Ohio River, just upriver from Cincinnati. This section, known as K445, includes most of the Kope Formation except for the basal 10 m, and continues into the lower 8 m of the Fairview Formation (Fig. 1). Holland et al. (1997) provided a locality map and detailed stratigraphic section.

As part of the high-resolution description of this section, a field census was taken of the fossil assemblage on every fossiliferous bed encountered, and 102 slab samples were taken of major fossiliferous horizons at approximately half-meter intervals. Abundance of crinoids was determined by counting all columnals within a 5 × 5 cm quadrat placed on each slab in the laboratory. Each data point for columnal abundance plotted in Figure 1 is an average of four such quadrats per sample.

Although very few crinoid calyxes were encountered in the samples, columnals were ubiquitous and provided the basis for identification of crinoid genera. Columnals have distinctive morphology when viewed either as articulated sections or as isolated columnals displaying the articular surface. Morphological characteristics of Kope and Fairview crinoid columnals are shown in Table 1 and examples are shown in Figure 2. Columnal abundance can be considered only as a rough measure of actual relative abundance of the crinoid taxa that produced them because species differ greatly in length of the stalk. Furthermore, information is lacking as to the rate of formation of new columnals during the life of the crinoid.

Fan morphology.—Morphological parameters were measured

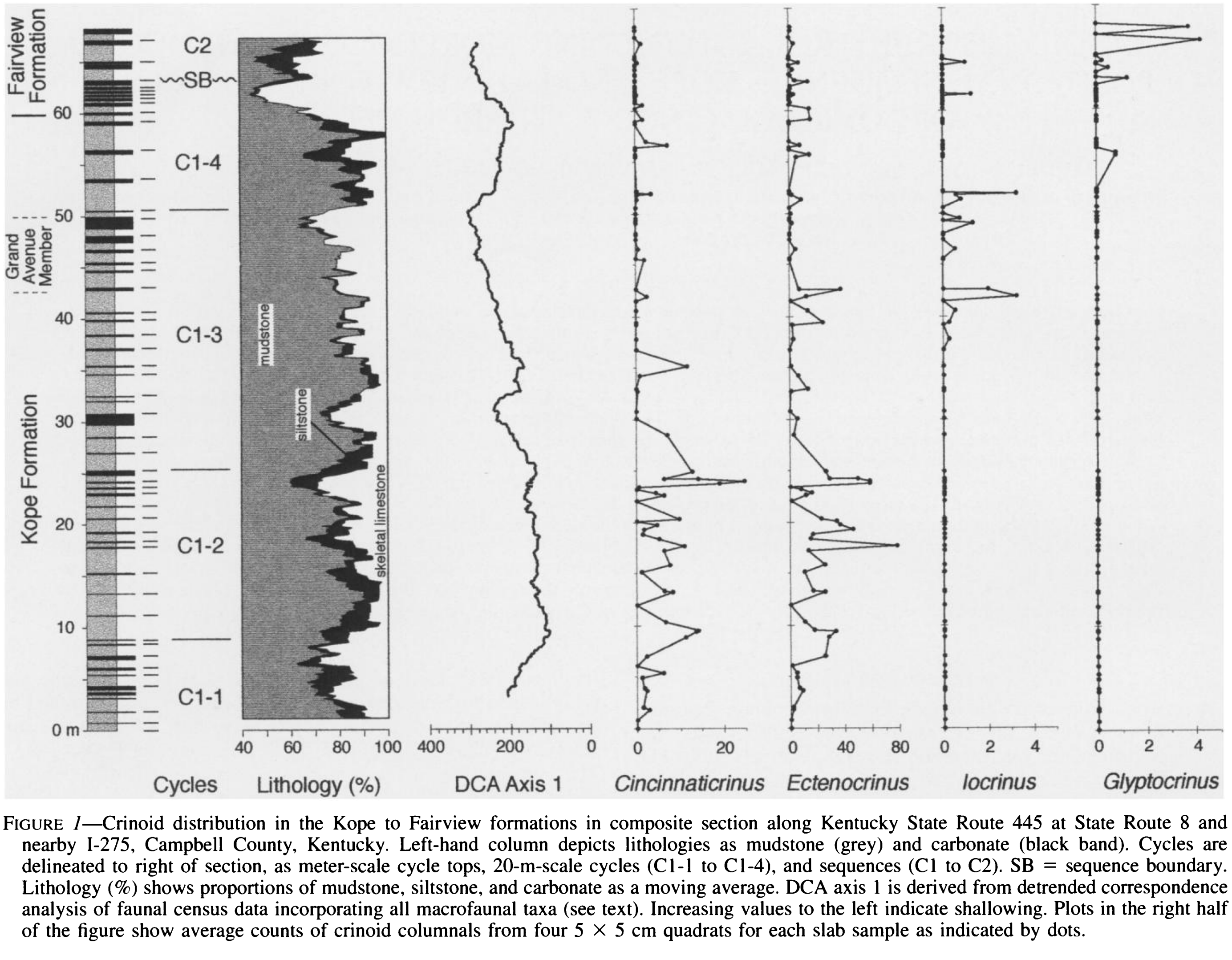

FIGURE 1—Crinoid distribution in the Kope to Fairview formations in composite section along Kentucky State Route 445 at State Route 8 and nearby I-275, Campbell County, Kentucky. Left-hand column depicts lithologies as mudstone (grey) and carbonate (black band). Cycles are delineated to right of section, as meter-scale cycle tops, 20-m-scale cycles (C1-1 to C1-4), and sequences (C1 to C2). SB = sequence boundary. Lithology (%) shows proportions of mudstone, siltstone, and carbonate as a moving average. DCA axis 1 is derived from detrended correspondence analysis of faunal census data incorporating all macrofaunal taxa (see text). Increasing values to the left indicate shallowing. Plots in the right half of the figure show average counts of crinoid columnals from four 5 × 5 cm quadrats for each slab sample as indicated by dots.

TABLE 1—Morphological characters of Cincinnatian crinoid columnals from the Kope-Fairview sequence. Modified from Donovan (1986, Table 2). Explanation of all characters can be found in Donovan (1986), except *canted latus*, which refers to asymmetrical appearance of nodal latus shown in Fig. 2.9.

	Subclass	Disparida				Cladida	Camerata
Morphology	Genus	*Anomalocrinus*	*Cincinnaticrinus*	*Ectenocrinus*	*Iocrinus*	*Merocrinus*	*Glyptocrinus*
Merism	Holomeric				X	X	X
	Pentameric	X	X				
	Trimeric			X			
Column outline	Circular	X	X	X		X	X
	Pentastellate				X		
	Pentagonal		X		X		
	Pentalobate	X					
Latus	Planar					X	X
	Convex	X	X		X		
	Canted			X			
Column form	Holomorphic					X	
	Heteromorphic	X		X	X		X
	Xenomorphic	X	X				
Lumen outline	Circular				X	X	X
	Pentagonal		X				
	Pentalobate	X		X			X
Articulation	Symplexial			X	X	X	X
	Tuberculate	X					
	Petaloid		X				

on a series of well-preserved specimens to characterize the filtration fan morphology of the taxa occurring in the Kope to Fairview interval. Specimens used were not necessarily collected from the Kope or Fairview formations but represented the same species occurring in the Kope to Fairview interval. Measurements were made using calipers and an ocular micrometer for cup height, proximal cup width, distal cup width, arm length, and ambulacral groove width, following Ausich (1980). The number of branches was determined by counting pinnules or ramules along one ray and multiplying by the total number of rays. Using these parameters, filtration fan area was calculated as the area of a cone expanded at 45 degrees from the oral-aboral axis, following Brower (1992b). Branch density was then calculated as the number of branches per unit area of the conical filtration fan.

RESULTS

Crinoid distribution.—Point counts of slabs are used to reconstruct the distribution of four crinoid genera through the Kope and Fairview formations at the K445 section (Fig. 1). The disparids *Cincinnaticrinus varibrachialus* Warn and Strimple and *Ectenocrinus simplex* (Hall) occur together throughout the section but are most common in the lower 25 m of the Kope at K445. *Ectenocrinus* columnals exceed those of *Cincinnaticrinus* in abundance. The disparid *Iocrinus subcrassus* (Meek and Worthen) and the camerate *Glyptocrinus decadactylus* Hall columnals are much less common. *Iocrinus* appears just below the carbonate-rich Grand Avenue Member, within the Grand Avenue, and again in the lower Fairview. *Glyptocrinus* appears rarely in the Kope above the Grand Avenue but commonly in the Fairview.

In addition to the four genera encountered in the K445 section, two other crinoid genera were found in the Kope during this study. The cladid *Merocrinus curtus* Ulrich occurs in the lowermost Kope, such as along the AA Highway (Kentucky Route 9) at Holst Creek Road in Bracken County and along Duck Creek 3 km southeast of the K445 section (Algeo and Brett, 1999). Large columnals of *Anomalocrinus incurvus* (Meek and Worthen) were collected by G. Schumacher (personal commun., 1996) at the K445 section about 8 m below the Kope–Fairview contact, at a horizon very close to the top of the Grand Avenue Member (Fig. 1).

Functional morphology.—Both *Cincinnaticrinus* and *Ectenocrinus* are characterized by very small, slender crowns and long, thin stalks. Both genera are illustrated by Ausich (1996, fig. 17-3). The maximum stalk length of cincinnaticrinids was "probably about one meter" (Warn and Strimple, 1977). *Ectenocrinus simplex* also possessed a very long stalk. A complete small adult specimen (cup height 2.5 mm) of *E. simplex* from the Galena Group of Minnesota has a stalk 25.5 cm long (Brower, 1992b). A larger specimen (cup height 8.5 mm) from the Cincinnatian also has 25 cm of stalk attached with no evidence of a distal termination. *Cincinnaticrinus* has ten nonpinnulate arms with ramules that branch heterotomously. *Ectenocrinus* also has ten arms bearing slender ramules from opposite sides every second brachial. The ramules are unbranched and become shorter distally (Brower, 1992b). Brower (1992b, fig. 13) reconstructed the feeding posture and filtration fan of *E. simplex.*

Iocrinus subcrassus is similar to *Cincinnaticrinus* and *Ectenocrinus* in cup shape, but crown size can be greater and the overall construction is more robust. For illustrations see Ausich (1996, fig. 17-3). Kelly (1978) illustrated a complete crown about 6 cm long. Stalk length for *I. subcrassus* crowns of 5 cm length was estimated at greater than 40 cm (Kelly, 1978). The ten main rami of *Iocrinus* are nonpinnulate and branch isotomously three to eight times, but usually not more than three or four times (Kelly, 1978). The total number of terminal branches can range from 40–400, with 100–150 as a typical upper range (Kelly, 1978). The specimen used in calculations for Figures 3 and 4 had 60 branches, yielding a low branch density based on a conical filtration fan.

Merocrinus curtus is a cladid with a slender, narrow cup and nonpinnulate arms that branch isotomously (Moore and Teichert, 1978, fig. 409). Cup width does not greatly exceed that of the stalk. Total stalk length is unknown, although a stalk measuring more than 60 cm without crown or termination was found in the lower Kope Formation at Duck Creek near the K445 section. Although no complete crowns were available for calculation of filtration fan morphology, *Merocrinus* is probably comparable to the disparids in having a low filtration fan density.

Anomalocrinus is the largest of all Cincinnatian crinoids in crown size and stalk length. Data for a small and a larger specimen are shown in Figures 3 and 4. Unlike the other disparids, *Anomalocrinus* has a large, globose cup. See Moore and Teichert (1978, fig. 349) for an illustration of the crown. A very large, complete specimen (CMNH P171) preserves the entire length of stalk of one meter from crown to the massive, encrusting holdfast. *Anomalocrinus* is similar to much younger, Mississippian crinoids in having a thick stalk, at least 1 cm in diameter in the middle part, reaching 2 cm near the base. The arms have a massive character and branch several times. Ramules arise from the same side of successive brachials, beginning with the tertibrachs. On the two branches of a pair, ramules arise from opposite sides of the brachials, so that ramules do not overlap within a fork. In this manner, *Anomalocrinus* developed a high density of branches, efficiently covering gaps within the filtration fan. In one specimen, 112 branches were counted in a single ray. Thus the total number of branches in a larger specimen could be at least 500. Nevertheless, branch density based on a conical fan was low and comparable to other nonpinnulate crinoids (Fig. 4).

Glyptocrinus differs from the disparids and cladids in having a large, plated calyx and 20 densely pinnulate arms. See Ausich (1996, fig. 17-2) for an illustration. Total stalk length for *G. decadactylus* from the Fairview Formation is unknown, but a complete crown of 5 cm length from the Corryville Formation (Maysvillian, C3 sequence) has 5.6 cm of stalk attached without the characteristic coiled termination. Crown length of the specimen used for Figures 3 and 4 is 8.5 cm, suggesting a greater stalk length. In Figures 3 and 4, two specimens of *Pycnocrinus dyeri* [Corryville and "Arnheim Formation" (Richmondian, C4 sequence)] are plotted because of their close similarity to *G. decadactylus.* Both taxa have 20 pinnulate arms and a similar spacing of pinnules along the arms. *Glyptocrinus decadactylus* has a lower filtration fan density by virtue of greater arm length and conical fan area. The fan density for *G. decadactylus* exceeds that for all other taxa shown in Figure 4.

DISCUSSION

Crinoid distribution in relation to paleobathymetry.—Crinoid distribution through the Kope and Fairview formations can be compared to a measure of biofacies change related to paleobathymetry. One of the curves in Figure 1 represents the first axis of a detrended correspondence analysis (DCA) of fossil census data taken from every fossiliferous bed in the section. Although crinoids are included in the census data, this analysis provides a different measure of faunal composition taken at more closely spaced points through the section. We have argued in two separate papers that the DCA ordinates samples collected throughout the region along the first axis according to relative water depth (Holland et al., 2001; Miller et al., 2001). Increasing values to the left indicate shallowing. The DCA axis suggests that the peak abundance of the small, slender disparids (*Ectenocrinus* and *Cincinnaticrinus*) in the lower 25 m of the section occurs in the deepest

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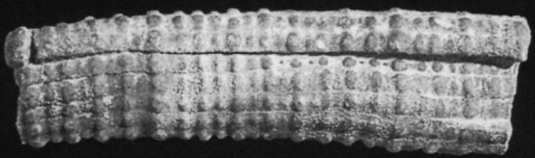

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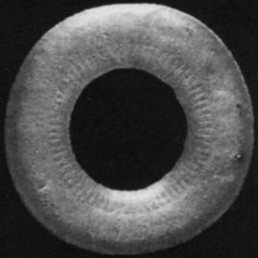

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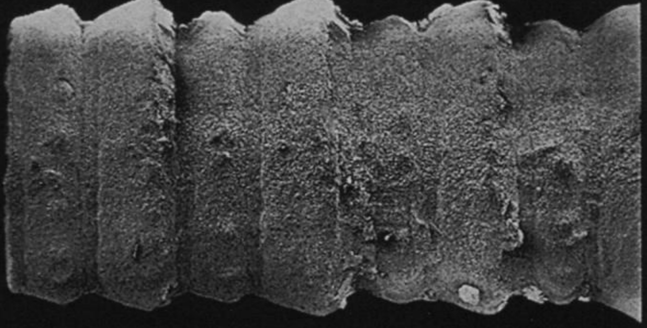

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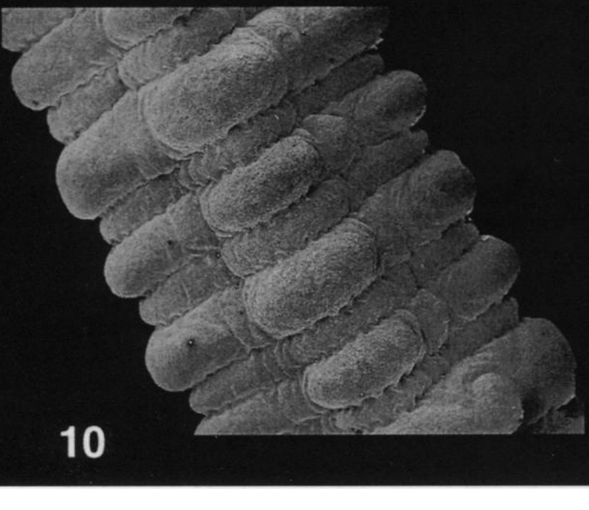

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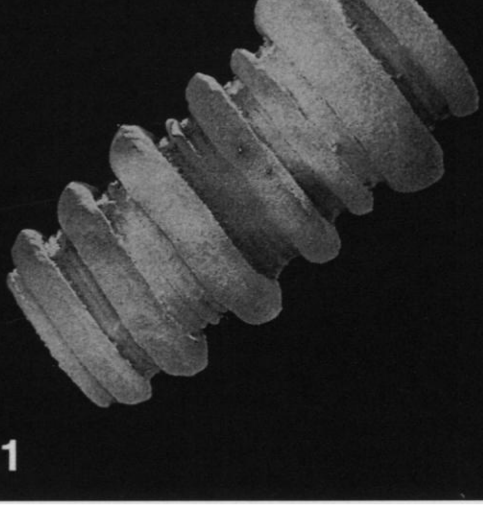

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part of the C1 sequence. The appearance of *Iocrinus* and *Anomalocrinus* in the Grand Avenue Member corresponds to a shallowing indicated by the DCA. Finally, the appearance of *Glyptocrinus* coincides with shallowing.

In a study of fossil assemblages of the Fairview at a locality 6 km to the southwest of our section, Diekmeyer (1998) found that crinoid columnals reached a maximum of more than 50 percent of fossil fragments in samples taken 16 m above the base of the Fairview. *Glyptocrinus* is known to occur in the upper Fairview (Davis, 1992), and we have found articulated specimens at the locality studied by Diekmeyer. Our results quantitatively confirm the pattern of crinoid distribution presented by Holterhoff (1997b) for the same stratigraphic interval.

Morphology and environment.—The association of small, slender crinoid morphotypes (*Ectenocrinus* and *Cincinnaticrinus*) with deeper and relatively calm-water environments and larger, more robust forms (*Iocrinus*, *Glyptocrinus*, *Anomalocrinus*) with shallower, more wave and current swept settings has been observed among Recent as well as other fossil crinoids. In Recent coral reefs, larger, more robust comatulid (stemless) crinoids prefer microhabitats and bathymetric zones exposed to stronger currents and waves than smaller, more delicate forms (Meyer, 1973).

Relationships between morphological features such as stalk length, calyx construction, and feeding structures in these Late Ordovician crinoids match very closely the same aspects of related crinoid taxa from the Middle Ordovician Galena Group of the Upper Mississippi Valley (Brower, 1992b, 1994) as well as younger Paleozoic crinoid faunas. Ausich (1980) characterized trophic niche differentiation among diverse assemblages of Early Mississippian crinoids using the parameters of stalk length, branch density of the filtration fan, and ambulacral groove width. Although data on stalk lengths are incomplete for the Ordovician crinoids, it is very likely that the slender disparids (*Ectenocrinus* and *Cincinnaticrinus*) possessed stalks up to one meter in length. The more robust disparid, *Iocrinus*, appears to have had an intermediate length of around 40 cm, but the camerate *Glyptocrinus* had a much shorter stalk, perhaps no more than 10 cm. The large and robust *Anomalocrinus* also had a stalk up to one meter in length. With the exception of *Anomalocrinus*, stalk length is inversely correlated with presumed level of water movement energy and positively correlated with preferred depth. The relationship between ambulacral groove width and filtration fan branch density for the Ordovician taxa reported here (Fig. 4) is very similar to that shown by Ausich (1980) for crinoids from the Early Mississippian and by Brower (1994) for the Middle Ordovician. Pinnule-bearing camerates in the present study and in the analyses of Ausich and Brower have higher fan density and narrower ambulacral width than disparids. In Brower's study, camerates were substantially different from disparids (including *Ectenocrinus simplex*) and cladids, based on a cluster analysis of branch density, tube foot spacing, and ambulacral groove width as variables.

Furthermore, Kammer and Ausich (Kammer, 1985; Kammer and Ausich, 1987) found that camerates were dominant in wave and current dominated carbonate settings, whereas disparids characterized calmer water clastic facies. Similar relationships have also been reported for Pennsylvanian crinoids (Holterhoff, 1997a, 1997b). Among recent crinoids, species preferring microhabitats characterized by strong waves and currents also use filtration fans with more closely spaced pinnules and tube feet, while species in calmer water settings have multidirectional feeding postures with longer, more widely spaced tube feet (Meyer, 1979).

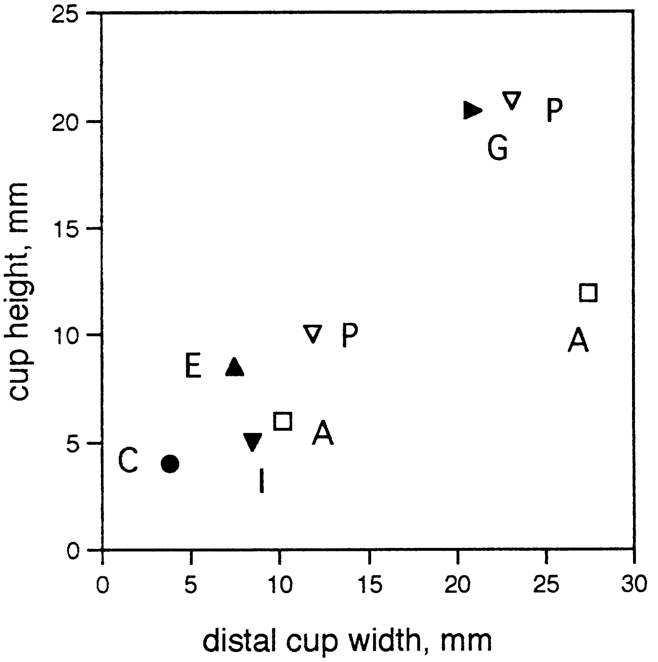

FIGURE 3—Relationship between distal cup width and cup height for Cincinnatian crinoids. A = *Anomalocrinus incurvus*, C = *Cincinnaticrinus varibrachialus*, E = *Ectenocrinus simplex*, G = *Glyptocrinus decadactylus*, I = *Iocrinus subcrassus*, P = *Pycnocrinus dyeri*. Specimens used are listed in Appendix 1.

Baumiller (1993, 1997) has experimentally and theoretically investigated the relationships between crinoid filtration fan density, flow velocity, and feeding efficiency. He demonstrated that crinoids having more densely branched filtration fans capture food particles more efficiently in higher velocity flow regimes than those having less densely branched filtration fans. Furthermore, there is an optimal range of water flow in which a particular filtration fan morphology will function with maximum efficiency in capturing food particles. (See Holterhoff, 1997a, fig. 2, for a graphical depiction of this concept.) Below and above this optimal flow velocity range, a filtration fan will be unable to capture enough food for survival, defining a minimum velocity threshold (MinVT) and a maximum velocity threshold (MaxVT) for a given fan density (Baumiller, 1993, 1997). The MinVT for crinoids with densely branched fans is higher than that for less densely branched fans, and the MaxVT is lower for crinoids with less densely branched fans than that for more densely branched fans.

These considerations can be applied to interpretation of the patterns of crinoid distribution in the Kope and Fairview formations. Small disparids with low fan density were best adapted for deeper water settings where normally low velocity bottom currents prevailed, punctuated by storms that account for occasional catastrophic burial and preservation of articulated crinoids. The

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FIGURE 2—Crinoid columnals from Kope to Fairview sequence. *1, 8, Cincinnaticrinus varibrachialus* Warn and Strimple; *1,* articular surface ×17; *8,* lateral view of mature section ×10. *2, 9, Ectenocrinus simplex* (Hall); *2,* articular surface ×16; *9,* lateral view ×21. *3, 10, Iocrinus subcrassus* (Meek and Worthen); *3,* articular surface ×9; *10,* lateral view ×8. *4, 7, 11, Glyptocrinus decadactylus* Hall; *4, 7,* articular surfaces of internodal, nodal, respectively, ×7; *11,* lateral view ×10; note three cycles of internodals. *5, Merocrinus curtus* Ulrich, articular surface ×9. *6, Anomalocrinus incurvus* (Meek and Worthen), lateral view of compressed section with fracture separating meres, ×1.2.

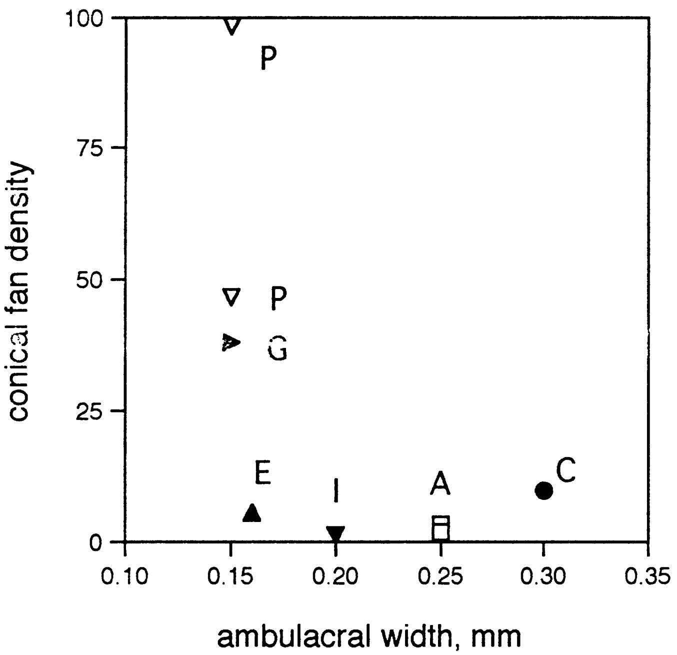

FIGURE *4*—Relationship between ambulacral width and branch density of a conical filtration fan for crinoids as indicated in Figure 3. Data and calculations are shown in the Appendix.

transition to shallower waters brought higher flow velocities associated with wind-driven circulation and increasing effects of waves, favoring both more robustly constructed morphotypes (*Iocrinus*, *Anomalocrinus*) as well as more densely branched filtration fans (*Glyptocrinus*). Overall crinoid diversity increased because morphotypes having lower density filtrations fans were still able to exist during intervals of deepening or within sheltered microhabitats. The occasional co-occurrence of *Iocrinus* with the smaller disparids suggests that their optimal flow velocity ranges overlapped, but the fact that *Glyptocrinus* is usually not associated with other taxa suggests that its MinVT exceeded the MaxVT threshold for the smaller disparids.

CONCLUSIONS

1) Six crinoid species can be identified on the basis of distinctive columnals occurring in the Upper Ordovician Kope to Fairview Formations (Edenian–Maysvillian) in the Cincinnati Arch region.

2) The cladid *Merocrinus* is restricted to the lowermost few meters of the Kope Formation. The small, slender disparid crinoids (*Cincinnaticrinus* and *Ectenocrinus*) are dominant above this basal interval for about 25 m. Crinoid diversity increases upward with the appearance of the larger disparid *Iocrinus* around 40 m and the monobathrid camerate *Glyptocrinus* near the top of the Kope and especially within the Fairview above the C1–C2 sequence boundary. The large disparid *Anomalocrinus* occurs in the upper Kope near the top of the Grand Avenue Member.

3) These changes in the crinoid assemblage are paralleled by macrofaunal transitions and a decrease in the siliciclastic ratio related to an overall shallowing-upward trend.

4) The disparids and cladids have a nonpinnulate filtration fan with low branch density and relatively wider ambulacral grooves compared to the camerate *Glyptocrinus* that has a pinnulate filtration fan with higher branch density and narrower ambulacral grooves.

5) In accordance with aerosol filtration theory, crinoids with more open mesh filtration fans and wider ambulacral grooves are associated with deeper waters and lower intensity,of water movement from waves and currents. Crinoids with more densely branched filtration fans and narrower ambulacral grooves characterize shallower waters with higher intensity of water movement.

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APPENDIX

Morphometric data and formulas used in Figures 3 and 4. Morphologic parameters shown in accompanying diagram.

Taxon	Cup height, mm	Proximal cup width	Distal cup width	Arm length	Branch number	Ambulacral width	R_2	Conical fan area, cm^2	R_3	Planar fan area, cm^2	Conical fan density	Planar fan density	Species	Museum number	Horizon	Comments
Cincinnaticrinus	4	1.8	3.8	12.7	50	0.3	10.9	5.098	14.6	6.58	9.81	7.6	*C. varibrachialus*	CMNH P3871	Kope	Holotype
Ectenocrinus	8.5	3.5	7.5	40	250	0.16	32	44.95	43.8	59.69	5.56	4.19	*E. simplex*	CMNH P42679	Cincinnatian	Amb width from Brower, 1992
Iocrinus	5	4	8.5	41.2	60	0.2	33.4	48.69	45.5	63.76	1.23	0.94	*I. subcrassus*	CMNH P44362	Corryville	
Anomalocrinus	6	4.5	10.2	40.6	168	0.25	33.8	49.61	45.7	64.79	3.39	2.59	*A.* sp.	CMNH P170	Corryville	
Anomalocrinus	11.9	8.7	27.4	92.7	500	0.25	79.2	270.6	106	349.76	1.85	1.43	*A.* sp.	CMNH P7341	Maysvillian	
Glyptocrinus	20.5	5.5	20.9	65	5206	0.15	56.4	136.5	75.5	175.41	38.1	29.7	*G. decadactylus*	Uncatalogued	Fairview	
Pycnocrinus	20.9	4.5	23.1	41	3120	0.15	40.5	67.08	52.6	82.56	46.5	37.8	*P. dyeri*	CMNH P37880	Arnheim	
Pycnocrinus	10	3.8	11.9	21.5	1800		21.1	18.3	27.5	22.56	98.3	79.8	*P. dyeri*	Uncatalogued	Corryville	

R_2 = arm length × sin45 + (distal cup width)/2.
conical fan area = pi[(distal cup width)/2 + R_2] × arm length.
R_3 = arm length + (distal cup width)/2.
planar fan area = pi$(R_3)^2$ − pi(distal cup width/2)^2.
conical fan density = (conical fan area)/branch number.
planar fan density = (planar fan area)/branch number.
CMNH = Cincinnati Museum of Natural History.