

## Evolutionary significance of differential species longevity in Osagean–Meramecian (Mississippian) crinoid clades

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**Abstract.**—The pattern of differential species longevity among five Osagean–Meramecian crinoid clades is analyzed for its evolutionary significance. Differences in mean species longevity between clades may have resulted from species sorting based on eurytopy (niche breadth). In order to test the relationship between longevity and eurytopy it was first necessary to recognize generalists (eurytopes) vs. specialists (stenotopes) objectively. Three different approaches were used: (1) the “Eurytopy Index” (EI), which is a measure of mean number of facies per species; (2) analysis of crinoid functional morphology; and (3) use of canonical discriminant analysis to analyze species distributions between facies in order to separate generalists from specialists. Mean species longevity for each clade was evaluated by four different approaches: (1) rarefaction was used to control for differences in sample size, including both species richness and number of occurrences, between clades; (2) potential facies control of species longevity was evaluated by a bootstrap that compared the observed data to a null model where species longevity was limited only by the actual occurrences of each species known facies through time; (3) uniformity of clade species richness through time was evaluated by the “Index of Uniformity for Species Richness” based on the standard deviation of clade species richness across the time intervals; and (4) potential species range truncations were evaluated by a biostratigraphic gap analysis based on the binomial distribution.

The general order of increasing longevity and eurytopy is (from least to most): flexibles, advanced cladids, camerates, disparids, and primitive cladids. In general the pinnulate crinoids (advanced cladids and camerates) were specialists with lower mean species longevity, and the non-pinnulate crinoids (disparids and primitive cladids) were generalists with higher mean species longevity. Pinnulate crinoids were specialized for feeding in high-energy currents and, thus, were limited in their facies distribution and presumably more extinction-prone. The non-pinnulates could feed in both low- and high-energy currents and, thus, were less limited in their facies distribution and presumably less extinction-prone. The flexibles were the exception in that they were non-pinnulate but had the lowest mean species longevity, apparently because they were specialized for deeper-water clastic environments.

On average, generalist clades have mean species longevity that at a minimum are up to 45% ( $\approx 1.0 \pm 0.7$  m.y.) longer than specialist clades. However, greater mean species longevity did not necessarily confer long-term advantages to a clade. The specialist advanced cladids became the dominant crinoid clade of the late Paleozoic and gave rise to the articulate crinoids of the post-Paleozoic. This may have resulted from the more rapid species turnover of stenotopes creating adaptive evolutionary novelties for their clade. Alternatively, it could simply be the result of stochastic processes.

The finer subdivision of niche space by specialists has led previous workers to predict that specialist clades should have higher species richness than generalist clades. The present study supports this prediction.

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### Introduction

Kammer et al. (1997) argued that species longevity in Osagean–Meramecian crinoid clades was a function of niche breadth. We reported a strong positive correlation ( $r = 0.98$ ,  $p < 0.004$ ) between species longevity and niche breadth as measured by the mean number of facies per species. Crinoid clades characterized as ecologic generalists had substan-

tially longer species longevity relative to crinoid clades characterized as ecologic specialists. Could this be an artifact of preservation? Are long stratigraphic ranges merely the result of better preservation, as suggested by some studies (Marshall 1991, 1997; Foote and Raup 1996; Foote 1997), or are there underlying ecologic and evolutionary controls on species extinction rates leading to a pattern of dif-

ferential species longevity between clades? If clade-specific differential species longevities were real, what impact did this have on the evolutionary history of the Crinoidea?

The purpose of the present paper is to provide further background information plus additional data and techniques for analyzing the relationship between species longevity and niche breadth than presented in Kammer et al. (1997). Also, the role of species longevity and niche breadth in the macroevolutionary change from the middle to the late Paleozoic crinoid fauna is considered.

The present study quantifies niche breadth in fossil crinoids using the range of facies occurrences as a proxy for niche breadth. Species with a wide range of facies occurrences are assumed to have had wide niche breadth and, thus, were generalist species. The converse would hold for specialist species. Using this approach it is possible to compare relative species longevities between generalists and specialists. It is then possible to pose the question of whether or not the tempo of evolution is related to niche breadth, at least for Mississippian crinoids.

Mississippian crinoids are divided into five, presumably monophyletic or paraphyletic, clades based on a variety of synapomorphies, predominantly those of the aboral cup and arms (Moore and Teichert 1978). These clades include the camerates (subclass *Camerata*) and advanced cladids (subclass *Cladida*, *poteriocrinids*), which in Mississippian species are characterized by pinnules on the arms, and the disparids (subclass *Disparida*), primitive cladids (subclass *Cladida*, *cyathocrinids* and *dendrocrinids*), and flexibles (subclass *Flexibilia*), which in Mississippian species lack pinnules. The presence or absence of pinnules, density of arm branches, and width of the ambulacral (food) groove are directly related to feeding paleoecology (Ausich 1980; Kammer and Ausich 1987; Baumiller 1993). Unlike most invertebrate groups, crinoids preserve the major features of their feeding apparatus, thus allowing extensive interpretation of their feeding ecology.

#### Data

The data for this study were compiled from taxonomic analysis of all known late Osa-

gean-early Meramecian crinoid species from the east-central United States (Ausich and Kammer 1990, 1991a,b, 1992; Ausich et al. 1997; Kammer and Ausich 1992, 1993, 1994, 1996). More than 10,000 specimens from museum and field collections were studied. Over 600 species names or name combinations have been applied to these crinoids. Prior to 1990 there were 353 valid species names applied to these crinoids, but after substantial taxonomic revisions, Ausich et al. (1994) reduced this to 214 valid species. Because two of these have since been placed in synonymy, and five (*Gaulocrinus robustus*, *G. symmetros*, *G. trautscholdi*, *G. veryi*, and *Onychocrinus grandis*) are restricted to Fort Payne Formation localities still under study, a total of 207 species were included in the present study.

The Osagean and early Meramecian can be finely subdivided into seven biostratigraphic intervals in the Eastern Interior Basin, which includes parts of Missouri, Iowa, Illinois, Indiana, Kentucky, and Tennessee (Ausich et al. 1994; Fig. 1). These seven intervals represent 10 ( $\pm 7$ ) m.y. ranging from approximately 340–350 Ma (Harland et al. 1990). On average each interval is 1.4 ( $\pm 1.0$ ) m.y. in duration. In the Mississippian stratotype region along the Mississippi River valley (Kammer et al. 1990), intervals 1 and 2 are time-equivalent to the lower and upper parts of the Burlington Limestone, respectively; intervals 3 and 4 are time-equivalent to the lower and upper parts of the Keokuk Limestone, respectively; intervals 5 and 6 are time-equivalent to the lower and upper parts of the Warsaw Formation, respectively; and interval 7 is time-equivalent to the Somerset Shale Member at the base of the Salem Limestone in Kentucky and Indiana. The Osagean-Meramecian boundary lies between intervals 5 and 6 (Kammer et al. 1990).

This study includes all crinoids from intervals 3–6 from a total of 60 localities. The only known localities not included in this study are six of the Fort Payne Formation localities in southern Kentucky and northern Tennessee under study by Ausich and Meyer (Meyer et al. 1989; Ausich and Meyer 1990). Species lists for these Fort Payne localities are still incomplete, except for the Order *Flexibilia*, Order *Disparida*, and the camerate *Agaricocrinus* (Ausich

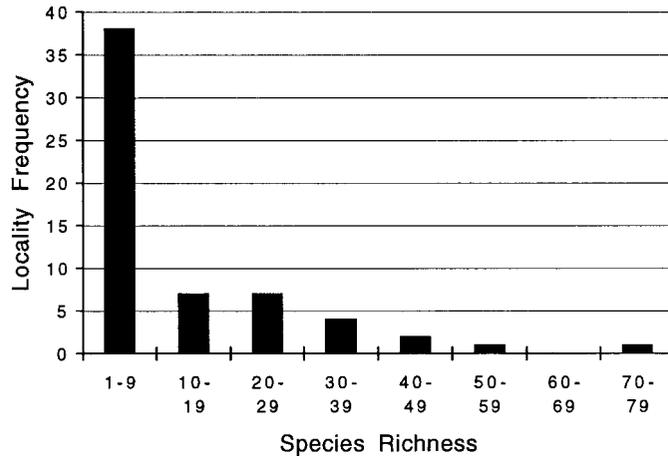


FIGURE 1. Frequency distribution of the 60 localities from intervals 3–6 by species richness. Twenty-two localities contain ten or more species and account for 84% of species occurrences and 97% of species richness. Data in Appendix 1.

and Meyer 1992; Ausich et al. 1997; Meyer and Ausich 1997). The one Fort Payne locality included in this study is the lost Whites Creek Springs locality that was extensively collected in the 19th century and is well represented in museum collections.

TABLE 1. Crinoid species richness of the five clades at the 22 most species-rich localities from time intervals 3–6. Locality codes defined in Appendix 1. The number part of the code equals the time interval from Ausich et al. (1994). Facies: A, low-energy clastics and carbonates; B, carbonate platforms and organic buildups; C, high-energy clastics and carbonates.

Locality	Facies	Camer-ates	Dispar-ids	Primi-tive cladids	Ad-vanced cladids	Flexibles	Total
1. 3A	B	9	0	3	0	1	13
2. 3C	A	8	4	8	5	8	33
3. 3D	A	5	3	8	1	7	24
4. 4B	B	22	2	7	8	1	40
5. 4C	B	16	0	2	7	0	25
6. 4D	B	13	0	6	2	0	21
7. 4E	B	12	2	3	1	3	21
8. 4N	B	10	0	4	0	1	15
9. 4HH	A	8	2	5	3	1	19
10. 4II	C	17	2	8	21	4	52
11. 4JJ	C	9	0	5	14	1	29
12. 4KK	B	16	3	8	4	1	32
13. 4LL	A	12	3	5	3	3	26
14. 4RR	B	18	4	9	1	5	37
15. 5A	C	9	1	1	12	0	23
16. 5C	A	6	1	4	2	1	14
17. 5D	C	24	4	14	29	6	77
18. 6B	C	17	2	6	18	6	49
19. 6C	C	6	0	0	4	0	10
20. 6E	C	6	0	3	4	1	14
21. 6G	C	6	1	1	5	0	13
22. 6H	C	15	2	4	9	1	31

Ranges of crinoid species from intervals 3–6 do not extend below interval 1 or above interval 7. In this study only those species occurring in intervals 1, 2, and 7 that also occur in intervals 3–6 were treated. The total number of occurrences for intervals 3–6 was 738, whereas it increases to 789 for intervals 1–7. A species occurrence is defined as the presence of a species at a single locality regardless of the number of specimens collected.

The localities used in this study, and the occurrences for each species, are given in Appendices 1 and 2. These data are also available in electronic format upon request from T. W. K.

The species richness values for the 60 localities from intervals 3–6 are highly variable, ranging from 1 to 77, and are not normally distributed (Fig. 1). A few localities have high species richness and are considered Lagerstätten, such as Indian Creek with 77 species (Table 1, number 17), whereas many localities have low species richness. Twenty-two localities preserve 10 or more species (Table 1). These 22 localities contain 84% (617/738) of the species occurrences and 97% (200/207) of species richness. Thus, these 22 localities are a close approximation of the paleoecologic data preserved in the larger data set of 60 localities. These 22 localities, rather than all 60, were used in the canonical discriminant analysis described later.

A frequency distribution plot of localities by

TABLE 2. Time and facies distribution of the 60 localities and the 22 most species-rich localities (in parentheses) from intervals 3–6.

Facies	Time interval			
	3	4	5	6
Facies A: low-energy clastics and carbonates	5 (2)	3 (2)	1 (1)	
Facies B: carbonate platforms and buildups	2 (1)	34 (7)		
Facies C: high-energy clastics and carbonates		2 (2)	3 (2)	10 (5)

species richness exhibits a pattern of geometric decline (Fig. 1). This pattern may simply reflect random taphonomic processes. Alternatively, it may reflect a primary ecologic signal in the data. The Gleasonian community concept holds that “the community was an opportunistic collection of species” (Brown 1995: p. 36). Each species has unique requirements that determine its distribution and abundance, hence many localities will have only a few species of a given group, whereas a few localities will have many species of the same group (Brown 1995: Fig. 3.2a).

### Specialists vs. Generalists

For the purposes of this study we define ecologic specialists as those species found in fewer environments, or facies, than ecologic generalists. A sliding scale termed the Eurytopy Index (EI) (Kammer et al. 1997) represents the number of recorded facies for each species. The EI of a clade is the mean number of facies occupied by the species in the clade.

*Osagean–Meramecian Facies.*—A variety of clastic and carbonate facies are present in intervals 3–6 of the study area (Kammer and Ausich 1987; Ausich and Meyer 1990; Kammer et al. 1990). In order to increase the reproducibility of this study, only three major facies are recognized because subdividing the localities into more than three major facies, which is possible, would be more open to subjective interpretation of original depositional environments. Also, recognizing only three facies is a conservative strategy and is less likely to unduly inflate the eurytopy index for any given clade.

The three major facies recognized are (A)

TABLE 3. Eurytopy index (mean number of facies per species) for intervals 3–6. The eurytopy index does not increase for any clade when intervals 1, 2, and 7 are included. See Figure 7 for standard errors of eurytopy index.

Clade	Eurytopy index
Primitive cladids	1.92
Disparids	1.78
Camerates	1.59
Flexibles	1.33
Advanced cladids	1.27

lower-energy clastic mudstones and minor carbonates; (B) carbonate platforms and organic buildups; and (C) higher-energy clastics, siltstones and sandstones, and carbonates (Table 2). Environments are arranged from lowest current velocity (A) to highest current velocity (C) based on sedimentary structures, mean sediment grain size, sorting, and basin topography.

*Eurytopy Index.*—Specialists have lower values on EI and are thus assumed to have had narrower niches, whereas generalists have higher values on the EI and are assumed to have had broader niches. The five crinoid clades can be arranged from specialist to generalist, lowest EI to highest EI, in the following order: advanced cladids, flexibles, camerates, disparids, and primitive cladids (Table 3). Of course, within clades the EI is variable, and it is possible to have generalist species in a specialist clade and vice versa. Although crinoid niche parameters are difficult to determine for long-extinct species, crinoids are rheophilic suspension feeders, and we may assume that at a minimum, niche parameters included relative current velocity, food size and type, stem length, and substrate preference. Previous studies dealing with these aspects of crinoid niche parameters are briefly summarized below.

*Crinoid Paleocology.*—Classification of Mississippian crinoids reflects, among other features, major aspects of arm morphology. Crinoid arms form the filtration fan used for suspension feeding, so it is possible to generalize feeding behaviors for the various crinoid clades.

Camerates and advanced cladids are characterized by the possession of pinnules on the

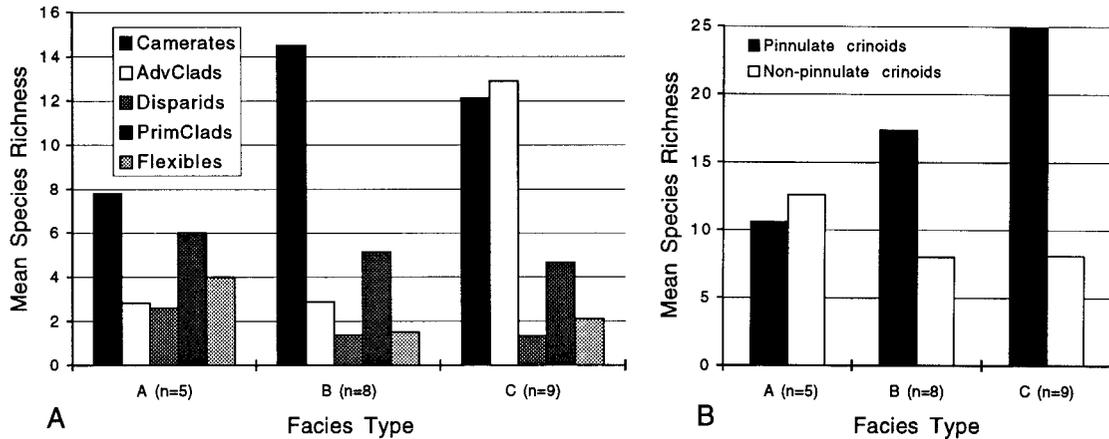


FIGURE 2. A, Mean clade species richness for the 22 most species-rich localities; B, Mean species richness for pinnulate (camerates and advanced cladids) and non-pinnulate (disparids, primitive cladids, and flexibles) crinoids from the 22 most species-rich localities. Total mean species richness by facies: A = 23.20; B = 25.39; C = 33.11.

arms. During the Osagean–Meramecian camerates had biserially pinnulate arms, whereas advanced cladids had uniserially pinnulate arms. Disparids, primitive cladids, and flexibles lacked pinnules. Also, camerates and advanced cladids, with pinnulate arms, had the narrowest food grooves, whereas disparids, primitive cladids, and flexibles had wider food grooves. Ausich (1980) inferred that these differences in morphology allowed crinoids to partition food particles by size. The pinnulate/non-pinnulate dichotomy is also thought to have played a major role in determining crinoid niches, especially with regard to current velocity. Baumiller (1993) argued that because pinnulate crinoids had dense filters that formed a resistant barrier to flow, they would require higher current velocities to force fluid and nutrients through their arms. Alternatively, non-pinnulate crinoids had low-resistance filters and would not be confined to high current-velocity settings. This argument is supported by the distribution of Osagean–Meramecian taxa: pinnulate camerate and advanced cladid crinoids showed clear preferences for benthic environments with strong current velocities, whereas the non-pinnulate disparids and primitive cladid crinoids showed few preferences for current velocities (Kammer and Ausich 1987; Baumiller 1993) (Fig. 2). Flexible crinoids showed a preference for clastic sedimentary environments, particularly those in deeper water, rea-

sons for which are not fully understood. Webster (1989) noted a similar environmental distribution for flexibles from the Lower Mississippian of western North America.

*Canonical Discriminant Analysis (CDA).*—CDA is a multivariate statistical technique that defines the contribution of each variable in discriminating between groups defined a priori (Dillon and Goldstein 1984). The SAS software for CDA computes squared Mahalanobis distances between objects of the groups, as well as univariate and multivariate one-way analysis of variance (ANOVA) (SAS Institute, Inc. 1990). In this study, the defined groups are the three major facies distributed among the 22 most species-rich localities, and the variables are the species counts for each of the five crinoid clades (Table 1). A plot of the 22 localities in canonical variate space defined by Mahalanobis distances clearly separates the three major facies on the basis of species counts for each of the five clades (Fig. 3). This demonstrates that crinoid species distributions are environmentally linked because the facies are clearly separated on the plot. It also demonstrates that the taxonomic signal for each site has been accurately sampled.

CDA was also used to test whether the multivariate group means are statistically distinguishable. The probability that the multivariate group means are equal, based on pairwise comparisons of facies groups, is less than 0.0001, and thus, the groups are statistically

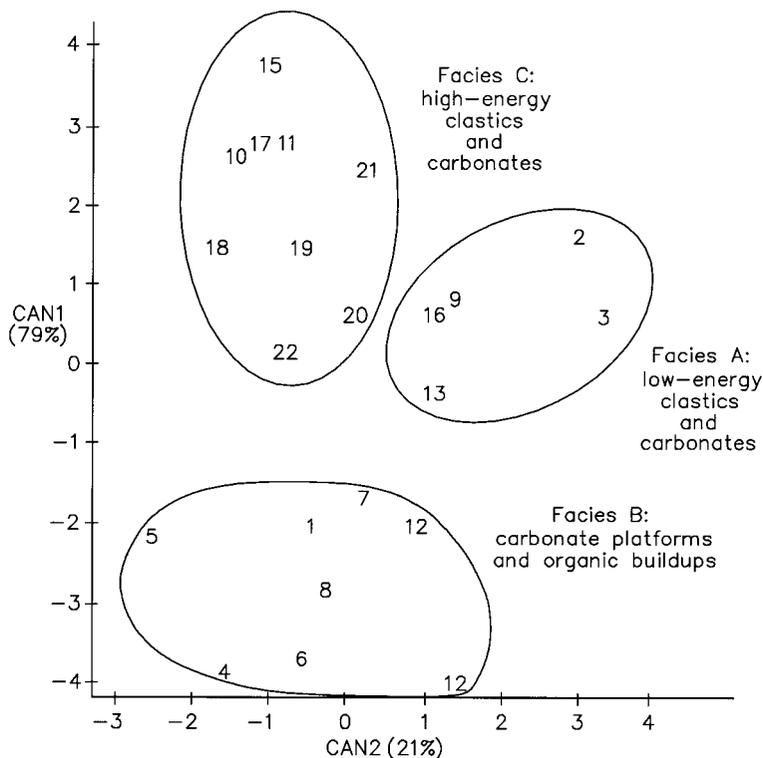


FIGURE 3. Canonical discriminant analysis of the 22 most species-rich localities grouped by the three major facies; numbers are keyed to Table 1. Discriminant variables are the species richness for each of the five crinoid clades (Table 4). Canonical variate space is defined by Mahalanobis distances between localities. The two canonical variates, CAN1 and CAN2, account for 79% and 21% of the variance between groups, respectively. CAN1 is correlated with advanced cladids and camerates; 0.58 and  $-0.29$ , respectively. CAN2 is correlated with disparids, flexibles, camerates, and advanced cladids; 0.48, 0.45,  $-0.50$ , and  $-0.52$ , respectively.

distinct. However, some variables provide more power in discriminating between groups than do other variables. The more powerful discriminating variables have significantly different group means, whereas the less discriminating variables have more simi-

lar group means. Univariate ANOVA was used to test the statistical significance of the group means for each variable (Table 4).

The probability that the advanced cladids have equal facies group means, on the basis of pairwise comparisons of facies groups, is less than 1%; for camerates it is less than 10%. This indicates that these two taxa are environmental specialists because they are very uneven in their environmental distribution (Fig. 2). In fact, 67% of the variance between facies groups is explained by the advanced cladids and camerates alone. The flexibles and disparids are less specialized and the probability that they have equal facies group means for any two facies groups is approximately 22% and 24%, respectively; they account for only 29% of the variance between the facies groups. The primitive cladids are clearly generalists as the probability that the facies group means are equal is 78%, indicating a very even distribu-

TABLE 4. Amount of variance ( $r$ -squared) between the three facies groups (distributed over the 22 most species-rich localities) explained by each crinoid clade, and the probability (one-way ANOVA) that the group means of each of the five crinoid clades are equal using pairwise comparisons of facies groups. Calculations are from Discriminant Canonical Analysis in SAS.

Clade	$r$ -squared	Probability of equal group means
Advanced cladids	0.4459	0.0037
Camerates	0.2202	0.0941
Flexibles	0.1475	0.2195
Disparids	0.1396	0.2397
Primitive cladids	0.0255	0.7828
	0.9787	

TABLE 5. Mean species longevity based on biostratigraphic intervals. Longevity for 188 scaled occurrences is from the rarefied data for intervals 1–7 (Figure 6). Note that at 188 scaled occurrences, disparids have the greatest longevity of the clades. Data for intervals 3–6 are presented because they were used in the bootstrap test for autocorrelation between longevity and eurytopy (Figure 7). Also see Figure 7 for standard errors of longevity for intervals 3–6.

Clade	Longevity		
	Intervals 1–7	188 scaled occurrences	Intervals 3–6
Primitive cladids	2.72	2.02	2.28
Disparids	2.33	2.10	2.11
Camerates	2.01	1.66	1.86
Advanced cladids	1.58	1.58	1.57
Flexibles	1.46	1.44	1.38

tion; they account for only 3% of the variance between the facies groups.

The results of univariate ANOVA ranks the crinoid clades in the following order from specialists to generalists: advanced cladids, camerates, flexibles, disparids, and primitive cladids. This order is similar to the order based on the EI (Table 3), the only difference being that the order of the camerates and flexibles is reversed.

**Summary.**—The EI, data from crinoid paleoecology, and CDA all indicate that the five crinoid clades, each as a whole, can be ranked on a sliding scale of specialist to generalist. The general order is advanced cladids, camerates, flexibles, disparids, and primitive cladids.

### Measuring Longevity

The most direct way to measure mean species longevity for each clade is to calculate the average number of biostratigraphic intervals per species in each clade for intervals 1–7 (Table 5). Using this metric, the clades can be arranged in order of increasing longevity as follows: flexibles, advanced cladids, camerates, disparids, and primitive cladids.

There are at least four potential problems with using mean species longevity directly: (1) the sample sizes of clades are not the same because of differences in species richness and number of occurrences (both total occurrences and occurrences per species) between clades, (2) the distribution of the three facies among biostratigraphic intervals is uneven, (3) the biostratigraphic intervals are of unequal du-

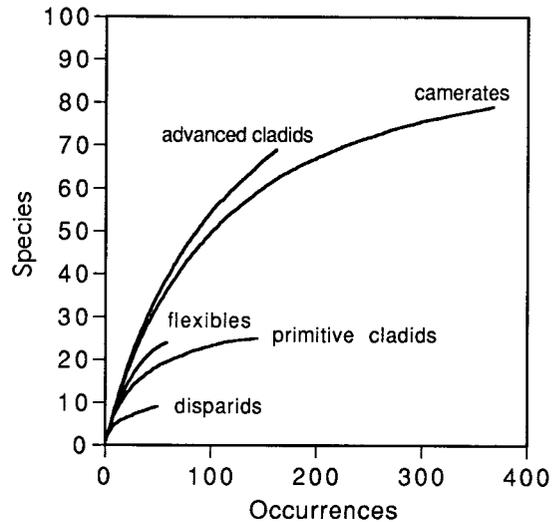


FIGURE 4. Species richness rarefaction curves for each of the five crinoid clades in intervals 1–7. Total species richness by clade: disparids = 9; flexibles = 24; primitive cladids = 25; advanced cladids = 69; camerates = 80. Data listed in Appendix 2.

ration, (4) the relative completeness of species ranges may be systematically biased. Each of these four problems will be addressed below.

**Differences in Sample Size.**—To remove the influence of differences in sample size, we used rarefaction curves. These were calculated to determine if the observed differences in species longevity are representative of the underlying longevity structure. Rarefaction is a resampling method that compensates for differences in sample size (Sanders 1968; Raup 1975; Foote 1992). The available samples provide only an estimate of true species longevity, but rarefaction allows the relative differences in species longevity to be normalized for sample size.

The database for each clade was randomly resampled (without replacement) 100 times, and iterative calculations of both species richness and longevity were recorded from sample size 1 to sample size *n*. The mean values of species richness and longevity were then plotted for each clade (Figs. 4–6).

The rarefaction curves of species richness (Fig. 4) allow qualitative evaluation of how thoroughly each clade has been sampled. If the slope of a curve levels off and approaches zero, then it is safe to assume that the most common species have been found, although

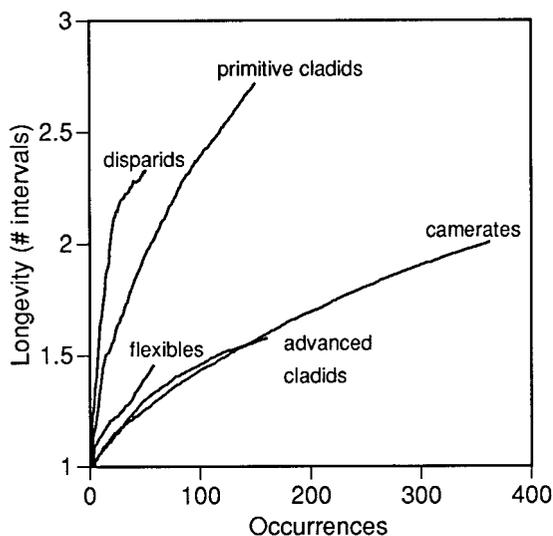


FIGURE 5. Longevity rarefaction curves for actual occurrences for the five crinoid clades in intervals 1–7. Total occurrences by clade: disparids = 51; flexibles = 59; primitive cladids = 151; advanced cladids = 162; camerates = 366. Data listed in Appendix 2.

an unknown number of rare species might still be found with continued sampling. In this case the primitive cladids and disparids appear to be the best sampled clades, followed by camerates and the flexibles, which appear close to leveling off, but the advanced cladids are the most poorly sampled as their curve is still climbing. The pattern of sampling completeness shown by the rarefaction curves does mimic the pattern of longevity values (Table 5). This may indicate that shorter longevity values are the result of poorer sampling, but it may also reflect the possibility that shorter-lived species had fewer occurrences per species in each time interval.

The rarefaction curves for longevity (Fig. 5) cannot be directly compared because of differences in clade species richness. Smaller clades may be expected to exhibit steeper curves than the larger clades simply because on average small clades have fewer total species occurrences, thus reaching their maximum longevity values with fewer occurrences. For the same number of occurrences sampled, the observed ranges of a small clade may be fully sampled, whereas only partial ranges of the more species-rich larger clades will be sampled. This will result in smaller clades having greater average longevity per

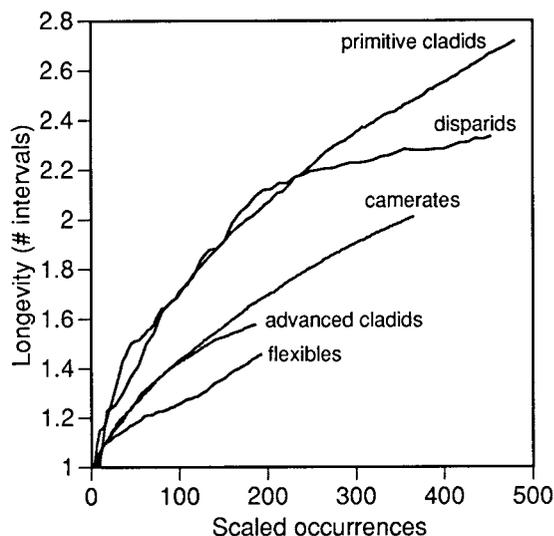


FIGURE 6. Longevity rarefaction curves with occurrences scaled for equal species richness in intervals 1–7. The following scaling factors were used (all clades scaled to a hypothetical 80 spp.): camerates ( $\times 1.0$ ), advanced cladids ( $\times 1.16$ ), primitive cladids ( $\times 3.20$ ), flexibles ( $\times 3.33$ ), disparids ( $\times 8.89$ ).

occurrence. To reduce this source of bias it is necessary to standardize for species richness. This was done by scaling the number of occurrences for each clade as if all clades had 80 species, the maximum species richness (camerates) found among the five clades (Fig. 6). For example, to compare disparid longevity (9 species) to that of the camerates (80 species), each disparid occurrence sampled equals 8.89 camerate occurrences. Of course, this approach is only an approximation because true values of clade species richness are unknown (Fig. 4).

After scaling occurrences using the above strategy, longevity can be compared for all five clades. Longevity can be directly compared at 188 scaled occurrences, which is the maximum value for the clade (advanced cladids) with the fewest scaled occurrences (Table 5, Fig. 6). Note that the order of increasing longevity (flexibles, advanced cladids, camerates, primitive cladids, and disparids) is similar to the order of increasing EI (Table 3), as well as to the order of discriminating power in canonical discriminant analysis (Table 4). The flexibles, pinnulate advanced cladids, and camerates are ecologic specialists and have the shortest species longevity values and lowest EI val-

TABLE 6. Percentage increases in mean longevity between clades at 188 scaled occurrences for intervals 1–7 (Table 5).

	To: Disparids	Primitive cladids	Camerates	Advanced cladids
From:				
Primitive cladids	4			
Camerates	27	22		
Advanced cladids	33	28	5	
Flexibles	45	39	14	9

ues, whereas the non-pinnulate primitive cladids and disparids are ecologic generalists and have the greatest species longevity and EI values.

Comparing the percentage increases in longevity from the shorter-longevity to the higher-longevity clades at 188 scaled occurrences produces a range of 4–45%, with the greatest difference between flexibles and disparids (Table 6). A 45% increase in longevity from flexibles to disparids, where the mean duration of an interval is 1.4 m.y., corresponds to 0.9 m.y. ( $\approx 1.0$  m.y.). This is a minimum value as longevity at 188 scaled occurrences do not represent the maximal values of longevity, but rather the maximum values for equally scaled occurrences set by the minimum number of occurrences present for all five clades.

The mean longevity for all 207 species is 1.82 biostratigraphic intervals, which corresponds to 2.6 ( $\pm 1.8$ ) m.y. This longevity is of similar magnitude to that reported for other fossil groups (Stanley 1979: Figs. 9.1, 9.2); mammals, trilobites, insects, and ammonites all have species durations less than 2 m.y., whereas birds, graptoloids, and freshwater fishes have durations of approximately 2–3 m.y. Groups with substantially longer species durations ranging from 5 to 25 m.y. include (in order of increasing longevity) echinoids, marine ostracods, marine gastropods, marine bivalves, reef corals, and planktonic forams. Stanley (1990) suggested that the order of increasing longevity is inversely related to complex stereotypic behavior, which is a form of ecological specialization. The more complex the behavior, the shorter the average species duration.

Baumiller (1993), using survivorship analysis at the substage level for Paleozoic crinoid

genera, reported mean species durations of 1.2 m.y. for camerates, 2.4 m.y. for inadunates (disparids and primitive and advanced cladids), and 2.3 m.y. for flexibles. Given the much coarser level of stratigraphic and taxonomic resolution and the longer time interval used in that study, it is encouraging that Baumiller's results are of similar magnitude to those of the present study.

*Potential Facies Control.*—To determine whether the temporal distribution of facies could generate the eurytopy-longevity correlation, we compared the relationship between eurytopy and longevity of the observed data with that of a null model (Fig. 7). In the null model all species were initially assigned equal durations of 4.00 intervals (intervals 3–6), but their observed facies distributions were retained; thus each species could be found only in those time intervals where its known facies occurred (Table 2). As for observed data, longevity for the null model were calculated as the difference between the highest and lowest stratigraphic occurrence. If the distribution of facies exerted no control on observed longevity, then in the null model all clades should have identical species longevity equal to the assigned duration (4 intervals) and the slope for the eurytopy-longevity line should be indistinguishable from zero. If the temporal distribution of facies does exert an influence on longevity because some facies are not found in all time intervals, species longevity should be lower than assigned, and longevity of stenotopes should be more affected (shorter) than those of eurytopes, producing a positive correlation between eurytopy and longevity. The results of testing the null model are consistent with the latter scenario as the slope of the eurytopy-longevity line was positive (0.45).

Although the above result demonstrates that the distribution of facies does generate noise that can produce an artifactual relationship between eurytopy and longevity, there may still be a sufficient signal in the observed data to support a causal relationship between eurytopy and longevity. Because the slope for the actual data (slope = 1.31) is significantly higher ( $p < 0.001$ ) than for the null model (slope = 0.45), the signal of a causal relation-

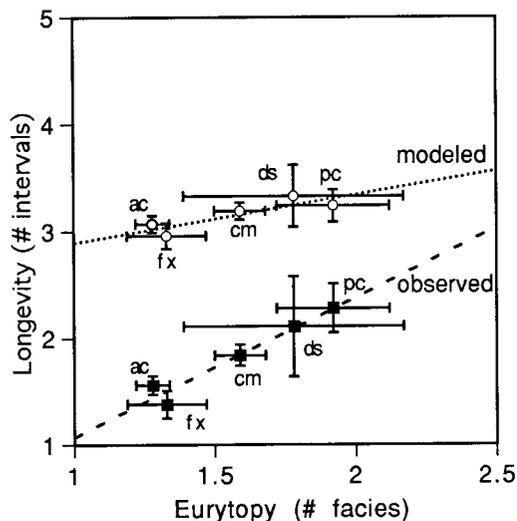


FIGURE 7. Eurytopy-longevity plots for the modeled data and the observed data for intervals 3–6, the only intervals where all crinoid species were included. Modeled data assumes the occurrence of each species in every time interval its preferred facies are known to occur, regardless of the actual time distribution of the species. The line of best fit for the observed data has a steeper slope (1.31) than the line for the modeled data (0.45). To test for statistical significance of the eurytopy-longevity pattern, a bootstrap technique was used in which 100 simulations were derived from the observed data set. In each simulation species were randomly selected, with replacement, up to the actual number of species of each clade in the data set. The longevitys and eurytopies for the five clades were then calculated for each simulation, and the slope of the fitted line was compared with the slope for the same simulated data under the null model expectation, i.e., with longevitys of all species, which had identical durations, calculated by assuming that they occurred only in the appropriate facies (gaps between lowest and highest stratigraphic occurrences were included when calculating longevity for each species). Of 100 simulations randomly chosen, with replacement, from the observed data set, all 100 simulations had slopes greater than the modeled data. Thus the null model, that longevitys are merely a function of facies distribution in time, can be rejected at  $p < 0.01$ . Error bars are standard errors. ac = advanced cladids; fx = flexibles; cm = camerates; ds = disparids; pc = primitive cladids.

ship may indeed be strong enough. To verify that a non-artifactual signal is discernible in the eurytopy-longevity pattern, a bootstrap technique was developed (Kammer et al. 1997) (Fig. 7). In the bootstrap technique 100 simulations were derived from the observed data set. In each simulation (1) species were randomly selected, with replacement, up to the actual number of species of each clade in the data set. (2) observed longevitys and eurytopy-

pies for each selected species were calculated, (3) the average EI and longevity were calculated for each of the five clades, and (4) the slope of the best-fit line to the EI-longevity data for the 5 clades was obtained. On each simulated data set a second analysis was then performed: (2b) longevitys and eurytopies for each species were calculated under the assumptions of the null model, i.e., assuming that species occurred in all those stratigraphic intervals in which their appropriate facies existed; (3b) the average EI and longevity under the null model was calculated for each of the five clades; and (4b) the slope of the best-fit line to the EI-longevity null-model data for the five clades was obtained. For each simulation the null-model EI values of each clade could not differ from the observed EI values, whereas the null-model longevity values were always higher because a longevity of 4.0 intervals was theoretically possible for all species under the null model. For each simulation the observed and null-model slopes were compared. In all 100 simulations the slope of the observed data was higher than that of the null model. Thus, the bootstrap result allows us to reject ( $p < 0.01$ ) the hypothesis that longevity differences for crinoid clades of different EI are merely a function of facies distributions; we conclude that there is a causal relationship between eurytopy and longevity. When interval 2 is included similar, but less robust ( $p < 0.05$ ), results are obtained (Kammer et al. 1997: Fig. 3). The higher probability that the null model is correct when interval 2 is included is caused by there being only one facies (B) present in interval 2. This tends to make the modeled data more similar to the observed data so that the slopes of the EI-longevity best fit lines are more similar. The results for intervals 3–6 are judged as best because a greater diversity of facies are represented (mean = 2.0 facies/interval) than in intervals 2–6 (mean = 1.8 facies/interval).

Another approach to the problem of uneven facies distribution is to perform rarefaction of longevitys assuming only one facies was preserved, instead of three. Only facies C (intervals 4–7) has enough data to attempt this approach. When this was done and occurrences for each clade were scaled for species richness

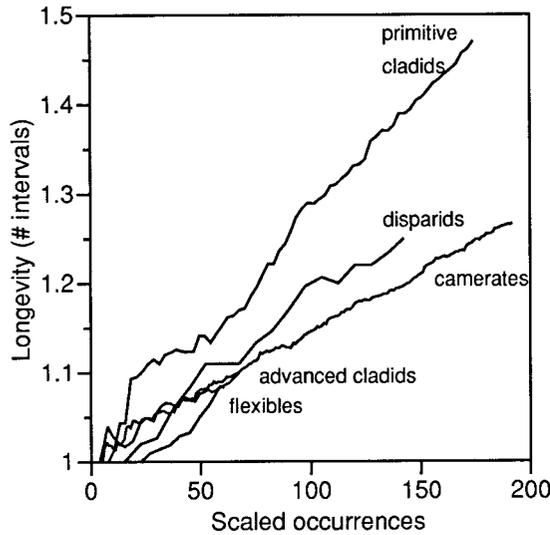


FIGURE 8. Longevity rarefaction curves for facies C (intervals 4–7 only). Occurrences scaled for clade species richness, based on those species that occur in facies C (Appendices 1 and 2).

(many species have no occurrences in facies C), the results are qualitatively similar to longevities for the entire data set (Fig. 8). Once again, the order of longevity differences between clades is preserved, demonstrating the strength of the underlying ecologic signal in the data.

*Uniformity of Species Temporal Distribution.*—There are no presently available methods to determine the absolute time duration of each biostratigraphic interval dealt with in this study. Available data (Harland et al. 1990) suggest that the seven intervals span 10 million years ( $\pm 7$  m.y.), and thus, on average each interval was 1.4 m.y. ( $\pm 1$  m.y.). However, the intervals may have been substantially unequal in duration. If clade species richness were not evenly distributed through the biostratigraphic intervals, longevity values could be biased, whereas an even distribution through the biostratigraphic intervals would not bias longevity values.

When species richness data per interval are tabulated for each clade (Table 7), there do not appear to be substantial differences in temporal distribution between clades, except for the advanced cladids. As shown in Table 7, maximum species richness for all clades was reached during interval 4. This may indicate

TABLE 7. Index of uniformity for crinoid species richness during intervals 3–6. Counts are based on Appendix 2. Biostratigraphic gaps were counted in reconstructing species richness for each time interval. The index of uniformity is the standard deviation (SD) of the percentage maximum values of species richness for each clade. Use of the percentage maximum values adjusts for difference in species richness between clades. The lower the value of the standard deviation, the more uniform is the temporal distribution for a given clade.

	Species richness: time interval				Index of uniformity for species richness
	3	4	5	6	
Camerates	21	53	36	37	
% maximum value	40	100	68	70	SD = 24.52
Disparids	4	7	5	3	
% maximum value	57	100	71	43	SD = 24.35
Primitive cladids	14	20	15	9	
% maximum value	70	100	75	45	SD = 22.55
Advanced cladids	7	41	36	24	
% maximum value	17	100	88	59	SD = 36.92
Flexibles	9	13	6	6	
% maximum value	69	100	46	46	SD = 25.58
Total species richness	55	134	98	79	
% maximum value	41	100	73	59	SD = 24.89
% of 100	15	37	27	22	

that interval 4 was the longest, or simply that it preserved the most localities (Table 2). If species richness per clade is converted into percent maximum value, then the temporal distribution of species richness can be directly compared between clades. Calculating the standard deviation of the percent maximum species richness for each clade over intervals 3–6 yields the index of uniformity for species richness (Table 7).

The index of uniformity for species richness is remarkably similar for four of the five clades, the exception being the advanced cladids. The camerates, disparids, primitive cladids, and flexibles have similar distributions of relative species richness over intervals 3–6. The advanced cladids have a less even temporal distribution than the other four clades because of their low species richness in interval 3. This most likely reflects the absence of facies C in interval 3 (Table 2), the facies most preferred by advanced cladids (Fig. 2). This could suggest that the lowermost ranges of some of the advanced cladids were artificially truncated because the appropriate facies were not available in interval 3. Were this the case, some of the advanced cladids should appear below interval 3, in the Burlington Limestone.

However, there is only one advanced cladid species that extends below interval 3 into the Burlington Limestone. This could imply that the Burlington Limestone was not an appropriate setting for advanced cladids, but this is not likely because Bassler and Moodey (1943) recorded 48 species of advanced cladids from the Burlington Limestone. One of us (T. W. K.) has studied specimens of these Burlington advanced cladids, and none of these species, with the exception of *Springericrinus doris*, occurs within intervals 3–6. This provides further evidence of the rapid evolutionary turnover for the advanced cladids relative to other clades.

In summary, the overall pattern of longevity differences does not appear to have been caused by clades being restricted in their temporal distribution relative to other clades. There is no correlation between longevity and the index of uniformity for species richness ( $r = -0.59$ ,  $p < 0.30$ ). The longevity differences must reflect different rates of evolutionary turnover rather than biases in temporal distribution of clades and facies.

**Biostratigraphic Gap Analysis.**—One measure of the completeness of species stratigraphic ranges is the number and distribution of biostratigraphic gaps (Marshall 1991, 1997). The greater the frequency and duration of gaps, the less confidence there is that the observed ranges are representative of the true stratigraphic ranges. The stratigraphic ranges of the 207 crinoid species are listed in Appendix 2. There are only 14 biostratigraphic gaps in the data set of 207 species and not a single gap is greater than one biostratigraphic interval. The time intervals are finely subdivided as shown by the fact that intervals 3–7 are equivalent to a single conodont range zone, the *Gnathodus texanus* Roundy zone (Collinson et al. 1971). This suggests that the species ranges are highly representative of the true ranges. If true ranges were substantially longer than recorded, more gaps would be expected.

Of the 207 species in intervals 1–7, 94 are known from only 1 time interval. When a species occurs in only 1 time interval, gap analysis cannot be used to determine the accuracy of the range because there is no way to estimate if the observed range is truncated.

However, once there are multiple time occurrences, as there are for the remaining 113 species, it is then possible to estimate the relative accuracy of the species ranges by a gap analysis technique. This technique is derived from the binomial distribution because there are only two possible outcomes, a species range with no gap, or one with a gap. For example, if the true range of a species is 3 intervals, but the species is observed in only 2 intervals, there are three possible combinations: occurrence in intervals 1 and 2, 2 and 3, or 1 and 3. Two-thirds of these combinations have no gap, whereas one-third have a gap. If  $q$  is the probability of finding no gap, and  $p$  is the probability of finding a gap, then

$$p = 1 - q$$

and

$$q = \frac{(s - r) + 1}{\binom{s}{r}}$$

rearranging gives

$$p = 1 - [(s - r) + 1](r!)(s - r)!/s!$$

where  $s$  is the true range, and  $r$  is the observed number of intervals. This fact allows us to evaluate the percentage of taxa that would be expected to possess gaps in their ranges (Fig. 9). If the mean observed number of observed intervals ( $r$ ) for a group of taxa is 2 time intervals and the true mean duration was 3 time intervals, we would expect 33% of the taxa to have gaps in their ranges; if the true mean duration was 4 time intervals, 50% should have gaps, if it was 5 time intervals, 60% should have gaps, if it was 6 time intervals, 67% should have gaps. As the number of missing time intervals ( $s - r$ ) increases, so should the percentage of taxa with gaps (Fig. 9).

In this study, of the 113 multiple-time-occurrence species only 14 have gaps in their ranges, representing 12% of the total. The average longevity of the 113 species is 2.65 time units and we would like to know how confident we can be that this is accurate. Because we can evaluate the expected gapiness ( $p$ ) as a function of actual to observed range only for integer values, we will evaluate this function

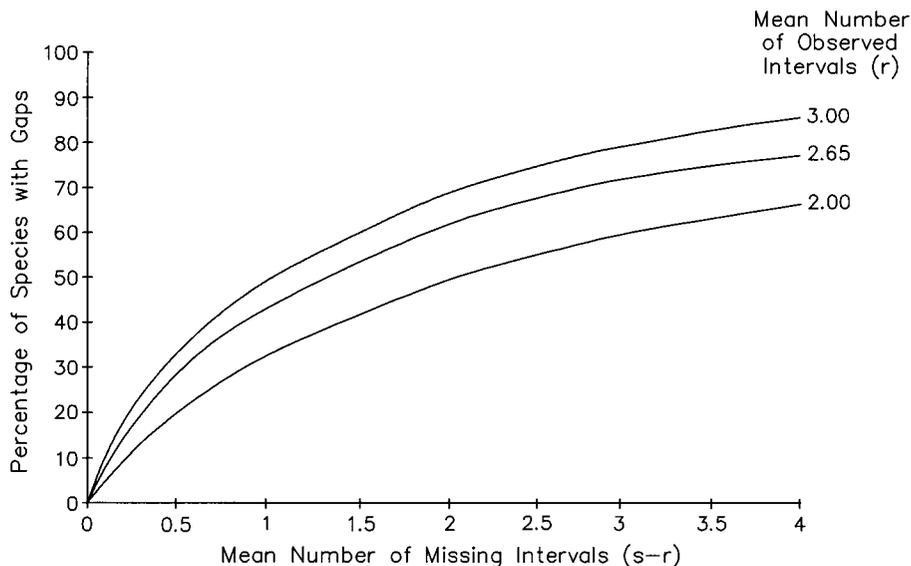


FIGURE 9. Curves showing the percentage of species (expected or observed) with biostratigraphic gaps for a given mean number of observed intervals ( $r$ ) and mean number of missing intervals ( $s - r$ ). The mean longevity of the 113 species ranging through two or more intervals is 2.65. The curve for 2.65 intervals is a linear interpolation between the values for 2.00 and 3.00 intervals. Values for the curves between 0 and 1 on the abscissa are interpolated.

for average durations of 2 and 3 time units and use linear interpolation to get an estimate for an average duration of 2.65 time units. The middle curve in Figure 9 represents such an interpolation and it shows that when 12% of the taxa possess gaps, the error on the average duration is very small, only 0.18 or 18% of a time interval. Thus, the discrepancy between true range and observed range must be about 18% of a time interval, otherwise the percentage of taxa with gaps in their ranges would be greater than 12%, assuming that preservation is random through time. However, such an assumption of randomness is, for a variety of reasons, probably untestable, so the results of this gap analysis are at best only an estimate of the amount of missing time.

We can also use the above approach to ask how likely it would be that of the 113 species only 14 would have gaps if the average observed duration was in error by 1, 2, or 3 time units. We do this by calculating

$$P(x) = \frac{n!}{x!(n-x)!} p^x q^{n-x}$$

where  $n$  is the number of multiple time occurrence species (113),  $x$  is the number of species with gaps in their ranges (14),  $p$  is the

probability of a species having a gap, and  $q$  is the probability that the species range has no gap. The probability that there would be 14 or fewer species with gaps,  $\Sigma (P(x))$ , is the sum of the binomial evaluated for values of  $x$  from 0 to  $n$  (14). This calculation could be made using the interpolated values for an average duration of 2.65 time units, but here we chose to use a conservative average duration of 2 time units. The probability that there would be no more than 14 species with gaps if the average range was in error by 1 unit is  $4 \times 10^{-7}$ , that it was in error by 2 units is  $3 \times 10^{-17}$ , that it was in error by 3 units is 0; these values suggest that there is very little chance that the average longevity can be very much in error.

The true mean number of missing time intervals is unknown, although it is assumed to be small based on the above analysis. Because of evolutionary turnover, not all 113 species with multiple time intervals would be expected to have originally occurred in all four time intervals from 3–6. But if they had, then the mean number of missing time intervals would be 1.35 ( $2.65 + 1.35 = 4.00$ ), and there would be approximately 50% biostratigraphic gaps in their ranges (Fig. 9). The fact that there are so few gaps (14/113 or 12%) strongly sup-

ports the assertion that the recorded species ranges are representative and can be used to evaluate relative differences in clade longevity.

Of course the argument can be made that the small number of biostratigraphic gaps is an artifact created by taxonomic practice where there was a conscious, or unconscious, effort to restrict stratigraphic ranges. However, our taxonomic practice has had the effect of doing just the opposite. As previously pointed out, our taxonomic papers (Ausich and Kammer 1990, 1991a,b, 1992; Ausich et al. 1997; Kammer and Ausich 1992, 1993, 1994, 1996) reduced through synonymy the number of valid species names from 353 to 207. We also found new localities and new specimens in both the field and museums that extended the ranges of many species. Some colleagues have wondered if we are rampant “lumpers,” but our papers provide ample evidence of the taxonomic splitting common among the 19th century paleontologists who named most of the 353 species. In the process of taxonomic revision, the ranges of many species were extended, creating more, not fewer, opportunities for biostratigraphic gaps.

*Summary.*—The relative differences in mean species longevity between clades are judged to be real in spite of potential biases from differences in sample size, uneven facies distribution, uneven species temporal distribution, and truncated species ranges. These potential biases were evaluated by rarefaction analysis, bootstrap analysis of facies control, the index of uniformity for species richness, and biostratigraphic gap analysis, respectively.

### Discussion

Is there autocorrelation between longevity and eurytopy? Does increased longevity merely reflect better preservation in a wider variety of facies? An independent test of the eurytopy index exists in the canonical discriminant analysis (Table 4, Fig. 3), which is neither time-dependent nor species-specific. The data are at the clade level with no specific information on individual species and their time distribution. Because the rankings of specialist to generalist are nearly identical for both the eurytopy index and discriminant

TABLE 8. Species-level analysis of longevity versus eurytopy for the 207 species of crinoids from intervals 3–6. Species longevity increases regularly with increasing eurytopy as does eurytopy with increasing longevity. A chi-square contingency table analysis indicates this pattern is significant at the  $p = 0.0001$  level.

Number of time intervals	Species counts			Eurytopy index
	1 facies	2 facies	3 facies	
1	98	3	3	1.09
2	26	20	11	1.74
3	10	13	15	2.13
4	0	0	8	3.00
Mean longevity	1.35	2.28	2.76	

analysis, the eurytopy index is judged to be independent of longevity. The bootstrap technique also shows eurytopy and longevity to be independent of each other (Fig. 7). Even when accounting for uneven distribution of facies through time, the correlation between longevity and eurytopy is still robust.

Is it possible that a “phylogenetic artifact,” rather than eurytopy, influenced longevity? In other words, might the generalist-specialist ordering of clades actually reflect underlying differences in evolutionary rates between clades (Stanley 1979: Fig. 9-1)? If this were the case, we would expect that the longevity-eurytopy correlation based on clade comparisons would break down on a species-level comparison of all 207 species. A tabulation of longevity versus eurytopy for all 207 species from intervals 3–6 indicates that the longevity-eurytopy correlation is robust ( $p = 0.0001$ ) at the species level (Table 8).

Further, are the longevity values biased by the temporal distribution of species and the relative length of the biostratigraphic intervals? The distribution of clade species richness is variable between time intervals, but the relative distribution of species richness is uniform for four of the five clades as shown by the index of uniformity for species richness (Table 7). Thus, there does not appear to be any systematic skewing of species distributions in time that would generate the differences in longevity between clades.

Many studies on species longevity or duration count an occurrence in a single time unit as half a time unit, and for multiple time occurrences first and last occurrences are counted as half a time unit each (e.g., three

time intervals would reduce to two, four time intervals reduce to three, etc.) (Baumiller 1993 and references therein). This is an appropriate approach when estimating the absolute time of species longevity because it averages together species that may have lived for only a very short part of a time period with species that lived through most of the time period. Single occurrences most likely do not represent all the time represented by a biostratigraphic interval. We have not taken this approach, which would actually increase the relative differences in longevity between the five clades by increasing the weighting of species occurring in three or more time intervals, because the intervals between first and last occurrence count more. Consider the difference in longevity between species A, which occurs in only one time interval, and species B, which occurs in three time intervals. Our method would indicate that species B lived 200% longer than species A, whereas the other method would indicate that species B lived 300% longer. Thus, by counting all time occurrences as whole time units, we may actually be underestimating the relative differences in longevity between clades.

*Taphonomy.*—Could differences in mean species longevity between clades be an artifact of taphonomic processes? In other words, are species ranges truncated because disarticulated specimens were not included? Among fossil crinoids there is a wide range of preservation style ranging from completely articulated crowns to completely disarticulated specimens represented by isolated ossicles (Meyer et al. 1989). Completeness of preservation is usually a function of rapidity of burial after death. The best preserved specimens were probably buried alive, whereas disarticulated specimens lay on the seafloor long enough for muscles and ligaments to decay. Some clades were more resistant to complete disarticulation, particularly the camerates, disparids, and primitive cladids whose aboral cups tended to remain articulated longer. In compiling the crinoid occurrence data (Appendix 2), we used all available specimens that could be identified, including crowns, cups, isolated cup plates, and even brachials for some species. By comparing disarticulated materials to

articulated crowns in museum collections it is usually possible to identify these loose plates. Kammer (1984) used this approach to identify 36 species included in the present study. So although there is always the possibility of taphonomic bias, we have tried to minimize this bias by identifying partial and disarticulated specimens whenever possible. Furthermore, several of the localities have preservation of complete specimens. Such rapid burial preserves all specimens and taphonomic biases are not a factor.

*Species Sorting.*—Species sorting is defined “as the differential origin and extinction of species within monophyletic taxa regardless of cause(s)” (Eldredge 1996: p. 50). A classic example of species sorting is Vrba’s (1980, 1984) study of African antelope clades including the stenotopic wildebeest clade and the eurytopic implala clade. Differential rates of speciation and extinction, and associated species longevities, were related to the niche breadth of these two clades.

The results of the present study support the idea of species sorting. Among Osagean–Meramecian crinoids, clades with niche generalists have increased mean species longevities relative to niche specialists. Although this is a logical relationship, few data have previously been developed to rigorously test this relationship. Similar patterns of increased longevity in generalists have been reported for other fossil organisms including foraminifers (Buzas and Culver 1984; Norris 1991, 1992), marine gastropods (Hansen 1978, 1980; Jablonski 1986; Gili and Martinell 1994), marine bivalves (Stanley 1986), crinoids (Baumiller 1993), shrews (Novacek 1984), and antelopes (Vrba 1980, 1984, 1987).

Stanley (1990) provided several examples of how niche breadth is related to rates of speciation and extinction and, ultimately, species longevity. Stenotopic species have high rates of speciation and extinction because they are especially vulnerable to environmental change. Combining high rates of speciation and extinction leads to short species longevity.

Eldredge (1979) theorized that eurytopes should be more extinction-resistant because they are less affected by fluctuating environments, whereas stenotopes should evolve

more rapidly in response to fluctuating environments. Thus eurytopes will have greater species longevities. A corollary prediction he made is that stenotopes should have higher clade species richness because of division of niche resources during the process of accommodation. Vrba (1980, 1984, 1987), in her work on late Cenozoic African antelopes, reported that generalist clades have lower rates of both speciation and extinction leading to greater species longevity. She also suggested that generalist species with overlapping resource bases will tend to exclude each other and have species-poor clades. Specialists accommodate each other and have species-rich clades.

The results of this study are in agreement with both Eldredge's (1979) and Vrba's (1980, 1984, 1987) conclusions on eurytopy-longevity and species richness. The stenotopic camerates and advanced cladids have the shortest longevities and the highest species richness, whereas the eurytopic disparids and primitive cladids have the highest longevities and the lowest species richness (Table 1). The flexibles are an exception, probably because they are the most environmentally limited of the five clades.

### **Evolutionary History of the Crinoidea**

The late Osagean-early Meramecian interval was a critical time during the history of the Crinoidea. As argued by Baumiller (1994) and Ausich et al. (1994), Paleozoic crinoid history is divisible into three evolutionary faunas, with the late Osagean-early Meramecian the interval of transition from the middle to the late Paleozoic fauna. Whereas the middle Paleozoic evolutionary fauna was co-dominated by monobathrid camerates, primitive cladids, and advanced cladids, the late Paleozoic evolutionary fauna was dominated only by advanced cladids. Traditionally, the macroevolutionary transition to the late Paleozoic evolutionary fauna was considered the result of mass extinction (Laudon 1948); however, Ausich et al. (1994) demonstrated that this change resulted from rapid faunal turnover. Ultimately, this transition dictated crinoid history for the remainder of the Phanerozoic, because advanced cladids were the ancestors of all post-Paleozoic crinoids (Simms and Sevas-

topulo 1993). If mass extinction did not bring about this change, what processes did? What role, if any, did paleoecology, eurytopy/stenotopy, and species longevities during the late Osagean-early Meramecian play in the macroevolutionary change from the middle to the late Paleozoic evolutionary fauna?

As discussed above, advanced cladids and camerates were pinnulate crinoids. Pinnulation produces a more dense filtration fan than the ramulate or nonbranching arms of other crinoids; and between camerates and advanced cladids, camerates had much denser fans because their arms were biserially pinnulate. Advanced cladids were unique among all Osagean-Meramecian crinoids because these crinoids were the only Paleozoic crinoids that evolved muscular articulations between brachials and pinnules (Moore and Laudon 1943; Van Sant 1964; Ubaghs 1978; Ausich and Baumiller 1993). Other crinoids had only ligamentary articulations and had either only passive or weak, slow movement capabilities of the arms. Muscular articulations on advanced, pinnulate cladids conferred on these crinoids the capability of rapid, directed movement of the arms, pinnules, and crown. We can only speculate on the advantages or disadvantages that this adaptation offered to advanced cladids. Crinoids without muscular arm articulations had been very successful since the Ordovician, so the lack of muscular articulations did not hinder crinoid success on a grand scale.

One potentially important advantage may be pinnule flicking, although the evidence is, admittedly, anecdotal. Pinnule flicking may be analogous to the arm waving reported by Young and Emson (1994). Observations on living crinoids during submersible dives indicates that pinnule flicking may be a behavior for eliminating excess coarse particulates captured by the filtration fan. W. I. A. and T. K. B. observed this behavior during submersible dives of the Johnson Sea Link with Charles G. Messing in the Straits of Florida. When normally feeding isocrinids were subjected to a heavy load of particulates from the wash of the submersible propeller, there was an immediate burst of rapid and continuous pinnule flicking across the entire fan. This was

observed in several individuals. Both flow velocity and the amount of particulates increased as the submersible turned and subjected the crinoids to propeller wash. Because increased current velocity does not induce pinnule flicking in other situations, we inferred that this behavior is for elimination of nonpalatable particulates from the fan. The rapid motion required for pinnule flicking is only possible where muscular articulations occur between brachials and pinnules. So, presumably, advanced cladids were capable of pinnule flicking, but other Lower Mississippian crinoids were not.

If pinnule flicking behavior for ridding the fan of particulates can be inferred for advanced cladids, the only muscled Osgoetian–Meramecian crinoids, then this may explain why advanced cladids were specialized for moderate to high turbulence siliciclastic settings where the frequency of filtration fan clogging would be high. Lane (1971) was the first to show quantitative data demonstrating the preference of pinnulate cladids for siliciclastic facies. Their initial principal success was in siliciclastic facies during the Devonian and Early Mississippian, and they dominated in all facies in the late Paleozoic crinoid fauna (Lane 1971, 1972). Perhaps the combined effects of the following may be largely responsible for the rapid faunal turnover that characterized the transition to the late Paleozoic evolutionary fauna: (1) advanced cladids specialized for siliciclastic habitats; (2) these specialists had short species durations and were evolving rapidly; and (3) a major paleoenvironmental shift from carbonate or mixed carbonate-siliciclastic habitats to siliciclastic-dominated habitats occurred in most low-latitude areas due to the prograding clastics resulting from middle to late Paleozoic mountain building associated with the assembly of Pangea (Windley 1977). In essence, crinoids adapted to the newly dominant siliciclastic facies were rapidly evolving specialists. While these crinoids evolved rapidly, other clades specialized for other habitats declined as their habitats were eliminated and generalists evolved slowly. The net result was a rapid, substantial faunal turnover to faunas dominated by advanced cladids. Beginning in the

Chesterian (Serpukhovian) nearly all late Paleozoic crinoid assemblages were dominated, both in diversity and abundance, by advanced cladids. Ecological adaptations in a dynamic interval of habitat change resulted in a macroevolutionary change in crinoid faunas.

### Conclusions

Conclusions drawn from the present study include (1) niche generalists have greater species longevity than niche specialists, at a minimum up to 45% greater ( $\approx 1.0 \pm 0.7$  m.y.); (2) the more rapid evolutionary turnover of niche specialists may have contributed to the evolutionary success of the advanced cladids in the late Paleozoic; and (3) niche generalists tend to have fewer species per clade than niche specialists.

The longevity-eurytopy correlation may be robust only during times of background extinction when Darwinian natural selection is strongest. The example studied here is from a time of rapid species turnover, and there is no evidence of mass extinction (Ausich et al. 1994). Mass extinctions, because of their universal and catastrophic nature, often undo the cumulative effects of natural selection (Gould 1985). Whereas niche generalists, such as the opossum or cockroach, are famous as survivors of mass extinctions (Newell 1963), there is no guarantee that among various clades only the generalists will survive mass extinctions. Fortuitous events, best modeled as stochastic processes, probably dictate the survivors of mass extinctions in most cases. The survival of the advanced cladids as the Articulata (Simms and Sevastopulo 1993) appears to make sense in light of the Discussion presented above; however, if they had not survived the Permian extinctions we would accept crinoids as just another extinct class of echinoderms, such as the blastoids, the other major group of pelmatozoans.

Finally, we offer a variety of approaches for evaluating the relationship between longevity and eurytopy-stenotopy, and accounting for potential biases. These approaches may be suitable for evaluating large-scale longevity patterns for other clades in the search for causes of macroevolutionary patterns.

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## Appendix 1

Register of localities used in this study. The number part of the code equals the time interval (Ausich et al., 1994). Facies defined in Table 2. Localities not referenced are from museum labels and are mostly listed in Bassler and Moodey (1943). References are as follows: 1, Ausich and Kammer 1990; 2, Ausich and Kammer 1991b; 3, Ausich and Kammer 1992; 4, Feldman 1989; 5, Kammer 1984; 6, Kammer and Ausich 1987; 7, Lane 1972; 8, Welch and Lane 1977. Occurrences are number of species recorded at each locality.

Code	Facies	Ref.	Occurrences	Horizon and location
1	B		5	lower part, Burlington Ls., Iowa
2	B		14	upper part, Burlington Ls., Iowa
3A	B		13	Montrose Chert Mbr., Keokuk Ls., Keokuk, Iowa
3B	B		4	Montrose Chert Mbr., Keokuk Ls., Pleasant Grove, Iowa
3C	A	5	33	New Providence Shale, Button Mold Knob, Kentucky
3D	A	5	24	New Providence Shale, Kentucky Solite Quarry, Kentucky
3E	A		1	New Providence Shale, Kings Tunnel, Kentucky
3F	A		1	New Providence Shale, Lincoln Co., Kentucky
3G	A	5	4	New Providence Shale, Clark Co., Indiana
4A	A		1	Borden Group, Edwardsville, Indiana
4B	B	3	40	Keokuk Ls., Keokuk, Iowa
4C	B	1	25	Keokuk Ls., Hamilton, Illinois
4D	B	1	21	Keokuk Ls., Warsaw, Illinois
4E	B	2	21	Keokuk Ls., Nauvoo, Illinois
4F	B		7	Keokuk Ls., Niota, Illinois
4G	B		2	Keokuk Ls., Augusta, Iowa
4H	B		2	Keokuk Ls., Nashville, Iowa
4I	B		2	Keokuk Ls., Monroe Co., Illinois
4J	B	1	1	Keokuk Ls., Bonaparte, Iowa
4K	B		1	Keokuk Ls., Denmark, Iowa
4L	B		2	Keokuk Ls., Curryville, Missouri
4M	B		7	Keokuk Ls., Jersey Co., Illinois
4N	B	6	15	Keokuk Ls., Clark Co., Missouri
4O	B		5	Keokuk Ls., Green Co., Illinois
4P	B		2	Keokuk Ls., near Alton, Illinois
4Q	B		1	Keokuk Ls., Biggsville, Illinois
4R	B		1	Keokuk Ls., Hancock Co., Illinois
4S	B		6	Keokuk Ls., Otterville, Illinois
4T	B		1	Keokuk Ls., Appanoose, Illinois
4U	B	1	2	Keokuk Ls., Fox River, Kahoka, Missouri
4V	B		4	Keokuk Ls., Wayland, Missouri
4W	B		1	Keokuk Ls., Joplin, Missouri
4X	B	1	6	Keokuk Ls., Boonville East, Missouri
4Y	B	1	1	Keokuk Ls., Geode Glen, Illinois
4Z	B	1	6	Keokuk Ls., Iowa Gateway Terminal, Iowa
4AA	B	1	2	Keokuk Ls., Gray's Quarry, Illinois
4BB	B	1	5	Keokuk Ls., Troy, Missouri
4CC	B	1	6	Keokuk Ls., Highways 61 and V, Missouri
4DD	B	1	4	Keokuk Ls., David's Chamber, Illinois
4EE	B		2	Keokuk Ls., LaGrange, Missouri
4FF	B	2	1	Keokuk Ls., Sandusky, Iowa
4GG	B	1	9	Keokuk Ls., Interstate 55, Missouri
4HH	A	6	19	Edwardsville Fm., lower quarry, Crawfordsville, Indiana
4II	C	6	52	Edwardsville Fm., upper quarry, Crawfordsville, Indiana
4JJ	C	6	29	Edwardsville Fm., Waldrip site, Monroe Reservoir, Indiana
4KK	B	6	32	Edwardsville Fm., Allens Creek bank, Monroe Reservoir, Indiana
4LL	A	6	26	Edwardsville Fm., Boy Scout camp, Monroe Reservoir, Indiana
4RR	B	6	37	Fort Payne Fm., Whites Creek Springs, Tennessee
5A	C	3	23	lower part, Warsaw Fm., Keokuk, Iowa
5B	C	1	2	lower part, Warsaw Fm., Hamilton, Illinois
5C	A	1	14	lower part, Warsaw Fm., Cragwold Rd.-Meramec River, Missouri
5D	C	6	77	Edwardsville Fm., Indian Creek, Indiana
6A	C		2	Harrodsburg Ls., Washington Co., Indiana
6B	C	7	49	Harrodsburg Ls., Canton, Indiana
6C	C	7	10	Harrodsburg Ls., Bono, Indiana
6D	C		1	Harrodsburg Ls., Harrison Co., Indiana
6E	C	8	14	Harrodsburg Ls., Judah Branch, Indiana
6F	C		3	Harrodsburg Ls., Edwardsville, Indiana
6G	C	1	13	upper part, Warsaw Fm., Warsaw, Illinois
6H	C	1	31	upper part, Warsaw Fm., Boonville West, Missouri
6I	C	1	3	upper part, Warsaw Fm., Cragwold Rd.-Meramec River, Missouri
6J	C	1	8	upper part, Warsaw Fm., Lisbon, Missouri
7	C	4	11	Somerset Shale Mbr. of Salem Ls., central Kentucky

## Appendix 2

Crinoid species occurrence data. Locality codes defined in Appendix 1.

## Camerate species

*Abatocrinus clavigerus* 4B  
*Abatocrinus grandis* 4II, 4KK, 4RR  
*Abatocrinus stereopes* 4C, 4RR  
*Actinocrinites benedicti* 6B  
*Actinocrinites gibsoni* 4B, 4HH, 4II, 4KK, 4LL, 5D, 6A, 6B, 7  
*Actinocrinites grandissimus* 4KK, 6B  
*Actinocrinites jugosus* 4B, 4C, 4D, 4O  
*Actinocrinites lowei* 3A, 3B, 4C, 4D, 4E, 4F, 4G, 4M, 4N, 4P, 4V, 4X, 4BB, 4KK, 5C, 6B  
*Actinocrinites magnificus* 4RR, 5D  
*Actinocrinites pernodosus* 4B, 4C, 4D, 4N, 4RR, 5A, 6B, 6H  
*Actinocrinites probolus* 2, 3B  
*Agaricocrinus americanus* 4B, 4C, 4D, 4E, 4F, 4N, 4P, 4V, 4HH, 4KK, 4LL, 4RR, 5D  
*Agaricocrinus crassus* 4B, 4C, 4RR, 6A  
*Agaricocrinus excavatus* 2, 3A  
*Agaricocrinus macadamsi* 4B, 4C, 4M, 4N, 5D, 6B  
*Agaricocrinus nodulosus* 4B, 4C, 4D, 4M, 4N, 4RR, 6B  
*Agaricocrinus whitfieldi* 4B, 4M, 4N, 4O, 5D  
*Agaricocrinus wortheni* 4B, 4C, 4D, 4N, 4V, 4HH, 5A, 5B, 5D, 6B  
*Alloprosallocrinus conicus* 4HH, 4KK, 4RR, 5D  
*Amphorocrinus* sp. 3C, 3D, 4KK  
*Aorocrinus kelloggi* 4B, 4C, 4D  
*Aorocrinus strenuus* 6H  
*Arballocrinus whitei* 2, 3A  
*Camptocrinus crawfordsvillensis* 4II  
*Camptocrinus myelodactylus* 5D  
*Camptocrinus parvulus* 4II, 6H  
*Camptocrinus pleniccirrus* 4II, 4JJ  
*Cribanocrinus benedicti* 6C, 6E  
*Cribanocrinus coxanus* 4JJ, 5A, 5D, 6H  
*Dichocrinus blairi* 6H  
*Dichocrinus dichotomus* 5A, 6G  
*Dichocrinus ficus* 4II, 6H, 7  
*Dichocrinus gracilis* 2, 4E  
*Dichocrinus simplex* 6E, 7  
*Dichocrinus ulrichi* 4II, 4JJ, 4LL, 6C, 6E, 6H  
*Dizygocrinus biturbinatus* 4B, 4C, 4E, 4L, 4N, 4X, 4Z, 4GG, 5A  
*Dizygocrinus cantonensis* 6B, 6E  
*Dizygocrinus caroli* 5A, 5B, 5C, 6G, 6H  
*Dizygocrinus gorbyi* 5A, 6C, 6H, 6J  
*Dizygocrinus indianensis* 4II, 5D  
*Dizygocrinus montgomeryensis* 4II, 5D, 6F  
*Dizygocrinus mutabilis* 5D  
*Dizygocrinus originarius* 6B, 6C, 6F, 6G  
*Dizygocrinus peculiaris* 6H  
*Dizygocrinus venustus* 6H, 6J, 7  
*Dizygocrinus whitei* 6B, 6C, 6E, 6F, 7  
*Dorycrinus mississippiensis* 4B, 4C, 4D, 4E, 4U, 4Z, 4DD, 4RR, 6J  
*Dorycrinus gouldi* 4B, 4C, 4D, 4L, 4U, 4X, 4EE, 4FF, 4KK, 4LL, 4RR, 5C, 5D, 6B, 6J  
*Eretmocrinus granuliferus* 4HH, 4II, 5D  
*Eretmocrinus magnificus* 4II, 4JJ, 4KK, 4LL, 4RR, 5D  
*Eretmocrinus praegravus* 4RR  
*Eretmocrinus ramulosus* 3A, 4E, 4G, 4RR, 5D  
*Eretmocrinus yandelli* 3C  
*Eucladocrinus millebrachiatus* 3A, 3C, 4B, 4D, 4E, 4F, 4H, 4N, 4GG, 4KK, 4LL  
*Eutrochocrinus planodiscus* 4B, 4E  
*Eutrochocrinus trochiscus* 3A  
*Gilbertsocrinus faberi* 4W  
*Gilbertsocrinus lyonanus* 5D, 6B

*Gilbertsocrinus tuberosus* 3C, 4B, 4HH, 4II, 4JJ, 4KK, 4LL, 6B  
*Gilbertsocrinus typus* 2, 3A, 3B  
*Macrocrinus cantonensis* 6B  
*Macrocrinus mundulus* 4B, 4D, 4E, 4X, 4Z, 4AA, 4BB, 4CC, 4GG, 4HH, 4II, 4JJ, 5C, 5D, 6B, 6H  
*Macrocrinus strotobasilaris* 4JJ, 4KK, 4LL  
*Paradichocrinus polydactylus* 3C, 3D, 4II  
*Paradichocrinus planus* 3C, 3D, 4GG, 4KK, 4LL, 4RR, 5D  
*Paradichocrinus* sp. 6G  
*Platycrinites brevinodus* 2, 3A, 4B, 4BB, 5D  
*Platycrinites georgii* 4B, 4X, 4Y, 5C, 5D, 6B, 6C, 6E, 6G, 6H, 6I, 6J, 7  
*Platycrinites hemisphaericus* 3C, 3D, 4HH, 4II, 4JJ, 4KK, 4LL, 4RR  
*Platycrinites nototensis* 4C, 4E, 4F, 6H  
*Platycrinites nodostriatus* 2, 4KK, 4LL  
*Platycrinites pumilus* 6G  
*Platycrinites recurvibrachiatus* 4II  
*Platycrinites saffordi* 3A, 3B, 3C, 3D, 4B, 4C, 4D, 4E, 4F, 4M, 4N, 4V, 4X, 4Z, 4AA, 4CC, 4DD, 4EE, 4KK, 4LL, 4RR, 5A, 5C, 5D  
*Strimplecrinus coxanus* 5A, 5D, 7  
*Uperocrinus apheles* 4JJ  
*Uperocrinus heteroclitus* 6H  
*Uperocrinus marinus* 4II, 5D  
*Uperocrinus nashvillae* 4B, 4C, 4D, 4E, 4RR  
*Uperocrinus robustus* 4RR

## Disparid species

*Catillocrinus tennesseae* 2, 3C, 3D, 4KK, 4LL, 4RR, 5D  
*Eucatillocrinus bradleyi* 4II, 5D  
*Halysiocrinus bradleyi* 4HH  
*Halysiocrinus springeri* 3C, 3G  
*Halysiocrinus tunicatus* 3C, 3D, 4B, 4E, 4CC, 4DD, 4GG, 4II, 4KK, 4LL, 4RR, 5A, 5D, 6H  
*Halysiocrinus* sp. 6B  
*Synbathocrinus blairi* 4B, 5D, 6B, 6G, 6H, 6I, 6J, 7  
*Synbathocrinus swallowi* 3C, 3D, 3E, 4B, 4E, 4O, 4R, 4Z, 4GG, 4HH, 4KK, 4LL, 4RR, 5C, 5D  
*Synbathocrinus troosti* 4RR

## Primitive (non-pinnulate) cladid species

*Atelestocrinus robustus* 3A, 4RR  
*Barycrinus crassibrachiatus* 1, 2, 4D, 4HH, 5D  
*Barycrinus magister* 4B, 4D, 4F, 4N, 4Q  
*Barycrinus punctus* 6H, 7  
*Barycrinus rhombiferus* 1, 2, 3A, 3C, 3D, 4D, 4E, 4F, 4M, 4S, 4Z, 4BB, 4CC, 4GG, 4HH, 4II, 4KK, 4LL, 4RR, 5A, 5C, 5D, 6B, 6C, 6H, 6J  
*Barycrinus spurius* 3C, 3D, 4B, 4C, 4D, 4N, 4S, 4II, 5C, 6B  
*Barycrinus stellatus* 4B, 4D, 4E, 4N, 4O, 4CC, 4DD, 4GG, 4HH, 4JJ, 4KK, 4LL, 4RR, 5D  
“*Barycrinus*” *stellifer* 6D, 6E  
*Barycrinus* ? *stenobrachiium* 4JJ, 4KK, 4LL  
*Cestocrinus signatus* 5D, 6B  
*Costalocrinus cornutus* 1, 2, 3C, 3G, 4KK, 4RR  
*Cyathocrinites asperrimus* 3D, 4KK, 4RR  
*Cyathocrinites glenni* 4KK, 4RR  
*Cyathocrinites harrodi* 3C, 3D, 4BB, 5C, 5D, 6B, 6E, 6H, 6I  
*Cyathocrinites iowensis* 1, 2, 3C, 3D, 4B, 4C, 4I, 4CC, 4GG, 4II, 4JJ, 4KK, 4LL, 4RR, 5C, 5D, 6B, 6E, 7  
*Cyathocrinites farleyi* 3C, 4B, 4D, 4E, 4N  
*Cyathocrinites kelloggi* 1, 2, 3C, 3D, 4O, 4RR, 5D  
*Cyathocrinites multibrachiatus* 3C, 3D, 4HH, 4II, 4JJ, 4KK, 4LL, 4RR, 5D, 6B  
*Goniocrinus harrisi* 4II, 5D  
*Meniscocrinus magnitubus* 5D  
*Nuxocrinus intermedius* 3A, 4B, 4HH  
*Parisocrinus crawfordsvillensis* 4II, 5D  
*Parisocrinus labyrinthicus* 5D, 6H

*Pellecrinus hexadactylus* 3D, 4B, 4HH, 4II, 5D  
*Saccosomopsis insperatus* 4II, 4JJ, 5D

#### Advanced (pinnulate) cladid species

*Abrotocrinus coreyi* 4II, 4JJ, 4LL, 5A, 5D, 6B, 6E, 6H  
*Abrotocrinus cymosus* 6B  
*Abrotocrinus granulatus* 3C  
*Abrotocrinus occidentalis* 4C, 5D  
*Abrotocrinus manus* 5D  
*Abrotocrinus unicus* 4II, 4JJ, 4KK, 5A, 5D  
*Adinocrinus nodosus* 3C, 4KK, 4RR  
*Armenocrinus neglectus* 4HH  
*Armenocrinus tenuidactylus* 5A, 5D  
*Aulocrinus bellus* 5D, 6B, 6C, 6E  
*Bollandocrinus?* sp. 4D  
*Corythocrinus fragilis* 4II, 5D  
*Corythocrinus gracilis* 4II  
*Corythocrinus insculptus* 5D  
*Cosmetocrinus gracilis* 5D  
*Cromyocrinus orbicularis* 4B  
*Culmicrinus? mammaeformis* 6G  
*Culmicrinus verus* 5D  
*Cydrocrinus concinnus* 4C, 4II, 5D  
*Cydrocrinus subramulosus* 4B  
*Decadocrinus penicilliformis* 4C  
*Decadocrinus tumidulus* 4II, 5D  
*Dinotocrinus latidactylus* 4C  
*Eratocrinus commaticus* 6H  
*Eratocrinus coxanus* 4C, 4K, 5A  
*Eratocrinus salemensis* 4JJ, 5D, 6B  
*Histocrinus coreyi* 4II, 4JJ, 4LL  
*Histocrinus graphicus* 4II, 4JJ  
*Histocrinus? stellatus* 5D, 6B  
*Holcocrinus nodobrachiatus* 4II, 4JJ  
*Hylodecrinus asper* 5D, 6E  
*Hylodecrinus bonoensis* 6C, 6H  
*Hylodecrinus briareus* 4JJ, 5A, 5C, 5D, 6B, 6C, 6H  
*Hylodecrinus gibsoni* 4E, 4II, 4JJ, 5D  
*Hylodecrinus robustus* 3C, 3F  
*Hylodecrinus sculptus* 4JJ, 4KK, 5D, 6B  
*Hylodecrinus? validus* 6G  
*Hypselocrinus arcanus* 6B, 6H  
*Hypselocrinus hoveyi* 4B, 4II, 4JJ, 5D, 6B, 6E  
*Hypselocrinus vansanti* 4II  
*Lanecrinus depressus* 4B, 4HH, 4II, 4JJ, 5D, 6B  
*Lanecrinus repertus* 5D, 6B, 6C, 6H  
*Lanecrinus? otterensis* 4S  
*Lebetocrinus grandis* 4II, 4JJ, 5D, 6B  
*Lekocrinus divaricatus* 6G

*Lekocrinus planobrachiatus* 4I, 5A  
*Linocrinus praemorsus* 6B, 6H  
*Ophiurocrinus* sp. 4B  
*Pachylocrinus aequalis* 4B, 4II, 5A  
*Pachylocrinus asper* 5A  
*Parascytolecrinus validus* 5D, 6B  
*Parascytolecrinus hamiltonensis* 4C, 4S, 5A  
*Poteriocrinites arachnaeformis* 4D  
*Poteriocrinites amplus* 5D  
*Sarocrinus asperatus* 5A  
*Sarocrinus kirki* 4B, 4C  
*Sarocrinus varsoviensis* 4II, 4JJ, 5A, 5D, 6B, 6G, 6H  
*Scytolecrinus cantonensis* 6B  
*Scytolecrinus decadactylus* 4S, 4T, 4II, 5C, 5D  
*Scytolecrinus disparilis* 4II  
*Scytolecrinus robustus* 4II, 4JJ, 5D, 6B  
*Springericrinus doris* 2, 4KK  
*Springericrinus magniventrus* 3C, 4HH, 4II, 4LL  
*Springericrinus sacculus* 5D  
*Stinocrinus granulatus* 3C, 3D  
*Ulrichicrinus agnatus* 4II, 5D, 6B, 6H  
*Ulrichicrinus? illinoisensis* 6G  
*Ulrichicrinus? keokuk* 4B, 4M  
*Worthenocrinus paterus* 5A

#### Flexible species

*Euryocrinus tennesseensis* 3C, 3D  
*Forebesiocrinus greenei* 4A  
*Forbesiocrinus pyriformis* 4RR  
*Forbesiocrinus saffordi* 4RR  
*Forbesiocrinus washingtonensis* 6B, 6E  
*Forbesiocrinus wortheni* 4B, 4E, 4N, 4II, 4LL, 5C, 5D, 6B, 7  
*Gaulocrinus bordeni* 3C, 3D  
*Lecocrinus? springeri* 3C, 3D  
*Mespilocrinus romingeri* 3C  
*Metichthyocrinus clarkensis* 3C, 3D, 3G, 4RR  
*Metichthyocrinus tiaraeformis* 3C, 3D, 4RR  
*Nipterocrinus monroensis* 4KK, 4LL  
*Onychocrinus exsculptus* 4E, 4I, 4II  
*Onychocrinus ramulosus* 4II  
*Onychocrinus ulrichi* 5D, 6B  
*Parichthyocrinus meeki* 4E, 4H  
*Parichthyocrinus nobilis* 2, 3A  
*Parichthyocrinus subovatus* 5D, 6B  
*Taxocrinus colletti* 4HH, 4II, 4LL, 4RR, 5D  
*Taxocrinus giddingsi* 6B, 6H  
*Taxocrinus praestans* 5D, 6B  
*Taxocrinus pustulosus* 3C, 3D  
*Taxocrinus ungula* 4JJ, 5D  
*Wachsmuthicrinus spinosulus* 3C, 3D, 3G