

Species longevity as a function of niche breadth: Evidence from fossil crinoids

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ABSTRACT

High-resolution stratigraphic and taxonomic data indicate that species longevity among Paleozoic (Mississippian) crinoids (Echinodermata) were affected by differences in niche breadth. A strong positive relationship exists between niche breadth, measured as the number of environments occupied by a species, and stratigraphic range. The robustness of this pattern is verified by a variety of rarefaction and statistical techniques confirming the long-held supposition that among animals ecological "generalists" have greater species longevity than ecological "specialists." The results also support the hypothesis that specialist clades have higher species richness.

INTRODUCTION

Evolutionary processes can be deduced from the study of both living and fossil organisms, the fossil record having the potential to reveal patterns and processes not readily studied on the short time scale of the Holocene. Species longevity is one such example. What determines species longevity? Why do some species persist for longer periods of geologic time than other species? Do they possess traits that increase their chance of survival and, hence, lead to increased species longevity? As natural selection leads to the preservation or extinction of individual species are the differences in mean species longevity between clades merely the result of stochastic processes, or can deterministic factors be identified? We present herein evidence that at least one deterministic factor can be identified in patterns of species longevity between clades. Fossil crinoid clades with greater niche breadth had greater mean species longevity.

Marine rocks from the late Osagean and early Meramecian stages (ca. 340–350 Ma) of the Mississippian in the east-central United States preserve a total of 207 species of crinoids from 63 localities (Ausich and Kammer, 1990, 1991a, 1991b, 1992; Ausich et al., 1997; Kammer and Ausich, 1992, 1993, 1994, 1996). During this time the east-central United States was dominated by the Eastern Interior Seaway bordered on the west by the Burlington-Keokuk carbonate ramp and on the east and southeast by prograding clastic wedges of the Borden deltaic complex and the Fort Payne Formation, respectively. In the north the Borden clastics filled the basin and prograded across the carbonate platform. Crinoids were important faunal elements in numerous environments. They dominated on carbonate platforms and buildups and were very important parts of other paleocommunities (Ausich et al.,

1979; Kammer and Ausich, 1987; Ausich and Meyer, 1990).

The crinoid data set consists of 789 species occurrences (Table 1) represented by a conservative estimate of at least 10 000 specimens in research collections. These 207 species are distributed over ~10 m.y. (± 7 m.y.) (Harland et al., 1990) and can be divided into seven biostratigraphic time intervals (Ausich et al., 1994, Fig. 1). These 207 species are all the crinoid species found in intervals 3–6 (late Osagean–early Meramecian) at the 63 localities. The lowest first occurrence of any species in this study is interval 1 and the highest occurrence is interval 7. Other species living in intervals 1 and 2 (early Osagean) and 7 (middle Meramecian), but not found in intervals 3–6, were not included in the study. The longevity of each species is recorded in terms of these seven time intervals because there is no way to directly measure longevity in years. Furthermore, the environmental (facies) distribution of each species is known.

These Lower Carboniferous crinoids are divided into five, presumably monophyletic, clades that include the camerates (Subclass Camerata) and advanced cladids (Subclass Cladida, poteriocrinids), which are characterized by the possession of pinnules on the arms, and the disparids (Subclass Disparida), primitive cladids (Subclass Cladida, cyathocrinids and dendrocrinids), and flexibles (Subclass Flexibilia), which lack pinnules. These five clades represent distinct body plans among Paleozoic crinoids that are related to differences in feeding ecology (Ausich, 1980; Kammer and Ausich, 1987; Baumiller, 1993). Camerates and advanced cladids with pinnulate arms had the narrowest food grooves, whereas disparids, primitive cladids, and flexibles had wider food grooves. These different crinoids partitioned niches by food size selection during aerosol suspension feeding (Ausich, 1980). Current velocity also played an important role in niche definition; the pinnulate camerate and ad-

TABLE 1. SPECIES RICHNESS, OCCURRENCES, EURYTOPY INDEX, AND MEAN LONGEVITIES FOR THE FIVE CRINOID CLADES

Clade	Species richness	Occurrences* intervals		Eurytopy index † intervals		Mean longevity § intervals		
		2-6	1-7	2-6	1-7	2-6	1-7	2.35 occur./sp.#
Primitive cladids	25	144	151	1.92	1.92	2.48	2.72	2.05
Disparids	9	50	51	1.78	1.78	2.22	2.33	1.95
Camerates	80	359	366	1.59	1.59	1.95	2.01	1.64
Advanced cladids	69	162	162	1.27	1.27	1.58	1.58	1.58
Flexibles	24	58	59	1.33	1.33	1.41	1.46	1.44

* An occurrence is the presence of a single species at a single locality. Intervals are biostratigraphic time intervals (Ausich et al., 1994). All crinoid species (n = 207) found in intervals 3-6 were treated; the maximum ranges of some of these species extended as low as interval 1 or as high as interval 7.

† Eurytopy index defined as mean number of facies per species.

§ Longevity measured in biostratigraphic time intervals. Numerical analyses (Figs. 1-3) were done on intervals 2-6 (98% of occurrences), rather than 1-7, in order to decrease the effect of data outliers. Longevity differences between clades would be even greater by including intervals 1 and 7.

Longevity if all clades were limited to only 2.35 occurrences/species, the lowest of any clade.

vanced cladid crinoids showed clear preferences for benthic environments with strong current velocities, whereas the nonpinnulate disparids and primitive cladid crinoids showed no clear preferences for current velocities (Kammer and Ausich, 1987; Baumiller, 1993). These four clades were common in both clastic and carbonate facies. Flexible crinoids were the most restricted in their environmental distribution. They showed a preference for clastic facies with their greatest species richness in deeper water environments. They were relatively rare in shallow water carbonate environments at this time (Kammer and Ausich, 1987).

For the eurytopy indices and longevities discussed below, two sets of analyses were completed, one for intervals 1–7 and the other for intervals 2–6. Intervals 2–6 include 98% of the occurrences. The 2% of occurrences in intervals 1 and 7 have a disproportionate impact on mean species longevities increasing longevity as much as 10% for the primitive cladids. Both analyses produced similar results (Table 1), but only those for intervals 2–6, which provide more conservative estimates of longevity, are graphically presented (Figs. 1–3).

EURYTOPY INDEX

We propose a simple standard for measuring niche breadth: the eurytopy index, which is the mean number of facies occupied by the species in a clade. This eurytopy index can be readily calculated for each of the five crinoid clades based on known occurrences (Table 1). Generalists (eurytopes), by definition, occur in a greater number of environments than specialists (stenotopes).

In order to increase the reproducibility of this study, only three major facies are recognized; subdividing the localities into more than three major facies, which is possible (Kammer and Ausich, 1987; Kammer et al., 1990), would be more open to subjective interpretation of original depositional environments. The three major facies are (1) lower energy clastic mudstones and minor carbonates ($n = 9$ localities); (2) carbonate platforms and organic buildups ($n = 38$); and (3) higher energy clastics, siltstones and sandstones, and carbonates ($n = 16$). Environments are arranged from lowest current velocity (1) to highest current velocity (3) on the basis of sedimentary structures, mean sediment grain size, sorting, and basin topography. Eurytopy values in this study range from 1.27 to 1.92 for the crinoid clades and are the same for intervals 2–6 and 1–7 (Table 1).

SPECIES LONGEVITY

Mean species longevity per clade is measured by tabulating the number of biostratigraphic zones per species (Ausich et al., 1994) (Table 1). However, this approach does not account for differences in number of occurrences per species between clades; i.e., species with a greater num-

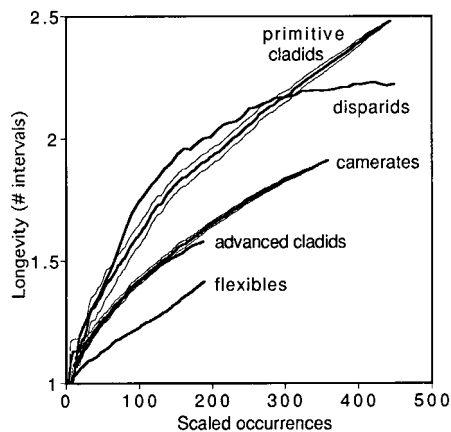


Figure 1. Rarefaction curves of species longevities for five crinoid clades. Longevity units based on biostratigraphic intervals 2–6 of late Osagean–early Meramecian (Ausich et al., 1994). In this rarefaction technique, data of occurrences linked to biostratigraphic zones for each species were used. Occurrences for each clade were randomly resampled (without replacement) 100 times, and iterative calculations of longevity were recorded from sample size 1 to n occurrences. Mean values of longevity for 100 runs are plotted for each clade (thick lines) together with ± 2 standard errors (thin lines) for camerates and primitive cladids demonstrating that even at moderate sample sizes clade longevities differ from each other significantly. Occurrences for each clade are scaled relative to the largest clade (camerates) to account for differences in species richness between clades (see Table 1) so that rarefaction curves could be compared between clades because, other factors being equal, a more species-rich clade should, on average, have more total occurrences than a less species-rich clade simply because it has more species. Scaling occurrences corrects for this bias. The following scaling factors were used (all clades scaled to a hypothetical 80 species): camerates ($\times 1.0$), advanced cladids ($\times 1.16$), primitive cladids ($\times 3.20$), flexibles ($\times 3.33$), disparids ($\times 8.89$).

ber of occurrences could have longer recorded time ranges simply because they were better sampled. To account for this potential bias in calculating longevities, we used the rarefaction method which is a resampling technique that permits direct comparison of a given variable between samples of different sizes (Raup, 1975; Foote, 1992). Initial rarefaction curves of longevity versus occurrences for each clade cannot be directly compared because numbers of species and occurrences are different for each clade. To address these problems we have taken three approaches to rarefaction analysis of longevity (Figs. 1 and 2; Table 1).

The first approach adjusts for differences in clade size by scaling the number of occurrences for each clade as if it had 80 species, the size of the largest clade. If the number of occurrences are not scaled upward, smaller clades will have steeper curves and seemingly greater longevities.

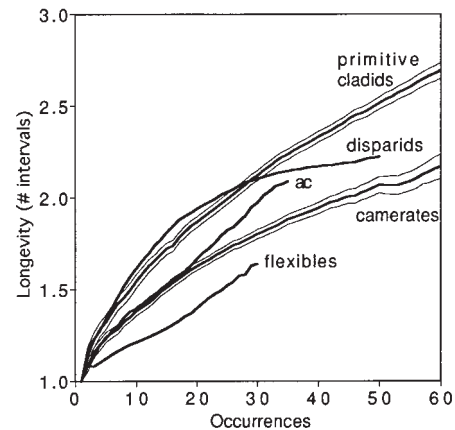


Figure 2. Rarefaction curves of species longevities for five crinoid clades normalized for clade size. Only nine species, the size of the smallest clade (disparids), were sampled at random from each clade. The occurrences were then sampled at random without replacement for each nine-species sample and longevities were calculated as a function of the number of occurrences sampled. The process of selecting nine species, sampling occurrences, and calculating longevities was repeated 100 times. The average longevities based on the 100 runs are plotted as a function of occurrences sampled for each clade (thick line) together with ± 2 standard errors for the camerates and the primitive cladids. Standard errors for the other clades are comparable in size and there is no overlap between longevities for clades at large number of occurrences. At small number of occurrences the longevities of camerates and advanced cladids cannot be distinguished; the same is true for disparid and primitive cladid longevities. ac = advanced cladids

At 188 scaled occurrences, the highest number of occurrences obtained by all five clades, differences in longevity between clades are apparent (Fig. 1). The second approach adjusts clade size to nine species, the size of the smallest clade. In this approach only nine species are randomly sampled from each clade. The rarefaction curves are similar to the first approach but not identical because only a subset of species are used for each clade, except the disparids (Fig. 2). The third approach standardizes occurrences by limiting each clade to a mean of 2.35 occurrences per species, the lowest rate of occurrences for any clade (Table 1). This approach also yields less than maximum longevity values because only a subset of occurrences are used.

All three rarefaction approaches yield parallel results demonstrating the robust pattern of longevity differences between clades. Generalists, primitive cladids and disparids, have distinctly greater longevities than specialists, camerates, advanced cladids, and flexibles. Although longevity differences between clades are real and distinct, absolute longevities are indeterminate.

Among the crinoid clades, eurytopy and longevity have a strong positive correlation (correla-

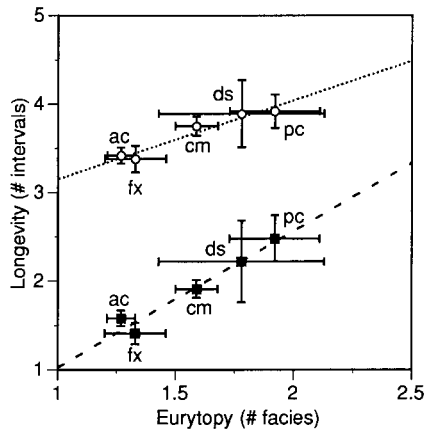


Figure 3. Eurytopy-longevity plots for modeled data (white circles) and observed data (black squares) for intervals 2–6 (Ausich et al., 1994). Modeled data assume occurrence of each species in every time interval its preferred facies are known to occur regardless of actual time distribution of species. Line of best fit for observed data has steeper slope than line for modeled data. To test for statistical significance of eurytopy-longevity pattern, bootstrap technique was used in which 100 simulations were derived from observed data set. In each simulation actual number of species for each clade were randomly selected individually, with replacement. Longevities and eurytopies for five clades were then calculated for each simulation, and slope of fitted line was compared to slope for same simulated data under the null model expectation, i.e., with longevities of all species, which had identical durations, calculated by assuming that they occurred only in appropriate facies (gaps between lowest and highest stratigraphic occurrences were included when calculating longevity for each species). If in more than 95% of simulations slope of actual data was higher than that for null model, null model would be rejected at $P < 0.05$. Of 100 simulations randomly chosen, with replacement, from observed data set, 96 simulations had slopes greater than modeled data. Thus null model, that longevities are merely function of facies distribution in time, can be rejected at $P < 0.05$. Error bars are standard errors. ac = advanced cladids; fx = flexibles; cm = camerates; ds = disparids; pc = primitive cladids.

tion coefficient, $r = 0.98$; probability of randomness, $P < 0.004$) for time intervals 2–6 (Table 1). Niche generalists, primitive cladids and disparids, had greater mean longevities than niche specialists, camerates, advanced cladids, and flexibles. However, this relationship could be an artifact of facies distribution across intervals 2–6: if a given species is restricted to a particular facies and if that facies has a limited temporal distribution, then observed species longevity may systematically underestimate true longevity (Marshall, 1991).

TEST OF EURYTOPY-LONGEVITY PATTERN

To determine whether the facies distribution generated the eurytopy-longevity correlation, we

compared the relationship between eurytopy and longevity of observed data to a null model (Fig. 3). In the null model all species were initially assigned equal durations of 5.00, but their facies distributions were retained; thus each species could occur only in those time zones where its known facies occurred. If facies distribution exerted no control on observed longevities, then all clades should have identical mean species longevities equal to the assigned duration, and the slope for the eurytopy-longevity line should be indistinguishable from zero. This was not the case. The slope of the fitted line for the null model was positive (0.89), demonstrating that facies distribution can generate noise and produce an artifactual relationship between eurytopy and longevity. The noise, however, could not overwhelm the signal of the actual data, because the slope of the data (1.54) is significantly higher than for the null model ($P < 0.001$). To verify the statistical significance of the eurytopy-longevity pattern, a bootstrap technique was developed (Fig. 3). The results of the bootstrap produced a higher slope for the actual data than the null model, i.e., species longevities controlled only by facies distribution, is rejected at $P < 0.05$, indicating that longevity differences between clades are real.

DISCUSSION AND CONCLUSIONS

Results of this study indicate that among Mississippian crinoids niche generalists had greater species longevities than niche specialists. Although logical, 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), Paleozoic crinoids (Baumiller, 1993), and Cenozoic mammals (Vrba, 1987).

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. A variety of factors are at work here. Eurytopes, because of their ability to live in a wider array of habitats, should be less affected by fluctuating environments. They also will, on average, have a larger overall population size than stenotopes simply because they have a broader geographic range by living in a greater number of environments (Lawton et al., 1994). In general, large and geographically widespread populations are more extinction resistant (Pimm et al., 1988; Brown, 1995, p. 212). The capacity to live in a wide variety of environments also gives eurytopes an advantage when a specific type of environment critical to stenotopes is degraded or eliminated

drastically reducing the stenotopes population size and increasing the probability of extinction (Soulé, 1991). Thus eurytopes should have greater species longevities. Alternatively, stenotopes, more specifically adapted to a particular habitat, should evolve in response to environmental fluctuations and, therefore, undergo more rapid evolution. With increased rates of speciation morphological change should accumulate more rapidly in stenotopic clades (Eldredge, 1979). Also, for stenotopes to maintain constant clade size they must evolve more rapidly than eurytopes (Stanley, 1990).

A corollary prediction Eldredge (1979) made is that stenotopes should have higher clade species richness because of division of niche resources during the process of accommodation. Accommodation encompasses a variety of processes that leads to subdivision of niches as species “make room for one another.” Such processes may include character displacement between two similar species or development of unique feeding behaviors and food preferences in individual species. Stenotopic clades, because of the tendency of their species to specialize, will occupy a greater variety of niches than will eurytopic clades. Vrba (1987), in her work on late Cenozoic African mammals, reported that generalist clades have lower rates of both speciation and extinction leading to greater species longevity. Vrba 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.

Results of this study are in agreement with both Eldredge’s (1979) and Vrba’s (1987) conclusions on eurytopy-longevity and species richness. The stenotopic camerates and advanced cladids have shorter longevities and higher species richness, whereas the eurytopic disparids and primitive cladids have greater longevities and lower species richness (Table 1). The flexibles having both short longevity and low species richness are an exception, probably because they are the most environmentally limited of the five clades as previously explained.

The more rapid evolution of niche specialists may produce evolutionary innovations that confer long-term advantages to their clade. This may be why the advanced cladids, with their uniquely muscular arms, came to dominate crinoid faunas during the late Paleozoic (Baumiller, 1994) and were the ancestors of modern crinoids, the Articulata (Simms and Sevastopulo, 1993).

Two major conclusions are drawn from this study. (1) On average, niche generalists have greater species longevities than niche specialists. (2) Niche generalists tend to have fewer species per clade than niche specialists. These conclusions are probably robust only during times of background extinction when Darwinian natural selection prevails. The example studied here is from a time of rapid species turnover with no ev-

idence 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 generalists will survive mass extinctions. Fortuitous events probably dictate the survivors of mass extinctions in many cases. The crinoid descendants of Mississippian niche generalists were in decline by the end of the Paleozoic and did not survive Permian extinctions. The oldest Triassic crinoid, *Holocrinus*, is either the youngest advanced cladid or the oldest articulate (Hagdorn, 1995) and was derived from one of the specialist Mississippian clades.

Ecologic theory predicts that niche generalists should survive longer because they have more habitat options than specialists (Brown, 1995). Habitat fluctuations over geologic time are assumed to have been a major engine for evolutionary change as organisms were forced to adapt to a variety of physical changes as tectonic plates moved, epicontinental seas expanded and contracted, climates varied, etc. The current global extinctions caused by human-induced reductions, or disturbance, of terrestrial habitats have the greatest influence on niche specialists due to negative impacts on habitats (Soulé, 1991). Earth's biota is becoming more cosmopolitan, species poor, and increasingly dominated by niche generalists adapted to environments impacted by humans (Wilson, 1988; Brown, 1995).

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