R2M00). Sharp cusps are pointy and most of their slopes are straight or concave, whereas the slopes of round cusps are convex. A loph can consist of a single cusp or of several cusps. Structures that had a tip and were equal in height to or exceeded two-thirds of the total crown height were counted as cusps. A similar cutoff point was used for lophs. The crown type scheme is conservative in the recognition of morphological features and underestimates the origin of these features in the phylogeny. For information on crown types in recent mammals, see (*6*).

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Ecological Controls on the Evolutionary Recovery of Post-Paleozoic Crinoids

Mike Foote

Analysis of morphological characters of a global sample of post-Paleozoic crinoid echinoderms shows that this group underwent a rapid diversification after the extinction at the end of the Permian to reach maximal morphological disparity by the Late Triassic, which is essentially the same evolutionary pattern seen during the group's early Paleozoic radiation. The accelerated morphological diversification of a single class implies that, even if clades surviving from the Paleozoic represented ecological incumbents that hindered the origin of new higher taxa, species within individual higher taxa rapidly exploited available ecological opportunities in the Mesozoic.

After the late Paleozoic (Late Permian) mass extinction, the origination of higher taxa (phyla and classes) of marine animals was more subdued than in the early Paleozoic (*1*, *2*). Even though most marine species became extinct in the Late Permian (*3*), most of the major adaptive zones occupied during the Paleozoic were not completely evacuated (*2*, *4*). Thus, Mesozoic taxa may have experienced greater competition than their early Paleozoic counterparts that were diversifying into unoccupied adaptive zones (*4*). Therefore, given a correlation between morphological and ecological diversification (*2*, *5*, *6*), Mesozoic taxa might be expected to have reached peak morphological diversity (disparity) (*7*, *8*) more gradually than did many early Paleozoic clades that rapidly attained maximal disparity (*8*–*10*). Crinoids, a large marine clade, reached a plateau of disparity in the early Paleozoic (*10*) but suffered a great reduction in diversity in the late Paleozoic, apparently to a single lineage (*11*). They then diversified ecologically and morphologically (*12*–*15*). The fossil record of crinoids can thus be used to compare macroevolutionary patterns within the same clade under significantly different ecological circumstances.

The post-Paleozoic radiation of marine animals has been documented mainly with taxonomic data [(*1*, *2*, *5*) but see (*6*)]. Because the correspondence between taxonomic origination and morphological innovation is unclear, it is important to document morphological diversification directly. On the basis of the primary systematic literature, I used data on 69 discrete characters to quantify the major anatomical features (*16*) for a global sample of 355 crinoid species from the Triassic through the Eocene. This sample represents 121 of the $\sim$156 genera known for this $\sim$200-million-year (*17*) period (*18*). This span of time was divided into 11 time intervals (mean duration, 19 million years; SD, 7.1 million years), reflecting a balance between temporal resolution and sample size. Within each interval, species were aggregated into a single statistical sample. Although genealogy is essential in a clade's evolutionary history, disparity concerns net morphological differences rather than branching sequence [(*7*, *8*, *10*) but see (*19*)]. Therefore, disparity was measured as the mean pairwise character difference between species (*9*, *10*, *20*). I compared disparity to genus- and family-level taxonomic diversity [based on several data compilations (*10*, *12*, *15*, *21*, *22*)]. The number of species sampled for each interval is generally proportional to the number of known genera and families.

Disparity among post-Paleozoic crinoids peaked early in the radiation (in the Late Triassic, less than 40 million years into the Mesozoic), well before the time of maximal taxonomic diversity (Fig. 1, A through H) (*23*). This period is similar to the 40 million to 50 million years between the appearance of unquestionable crinoids in the Early Ordovician and the Paleozoic peak of disparity in the Caradocian (*10*, *24*). Disparity declined from the Late Triassic to the Early Jurassic, in part reflecting the extinction of encrinids, holocrinids, and other taxa (*12*, *13*, *15*). Disparity again increased early in the Cretaceous (Neocomian). Much of this increase is attributable to origination within the order Cyrtocrinida, which displays many unusual forms and habits, such as reduced, bilaterally

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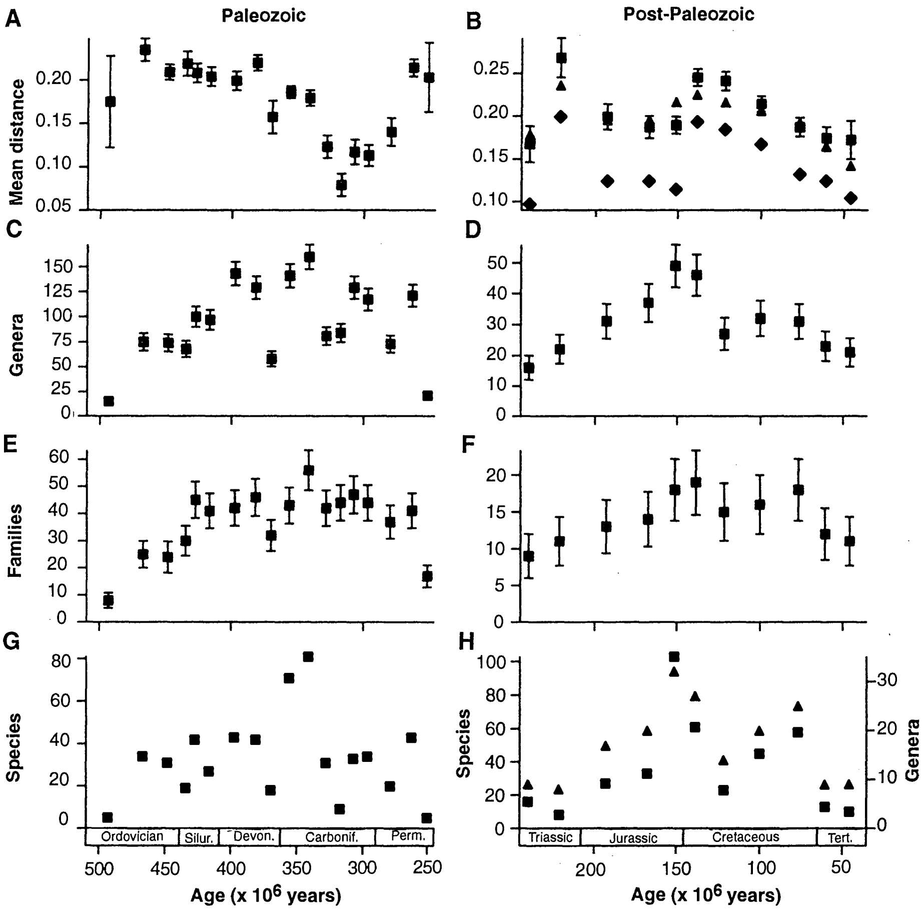

Fig. 1. Temporal pattern of disparity, diversity, and sample size for post-Paleozoic crinoids (right panels). Some earlier results [data from (*10, 12, 15, 22*)] for Paleozoic crinoids are shown for comparison (left panels). Time intervals, from oldest to youngest, are as follows (abbreviations in brackets are used in Fig. 3): Ordovician [Early Ordovician (O1), Llanvirnian through Early Caradocian (O2), Middle Caradocian through Ashgillian (O3)]; Silurian [Llandoverian (S1), Wenlockian (S2), Ludlovian + Pridolian (S3)]; Devonian [Early Devonian (D1), Middle Devonian (D2), Late Devonian (D3)]; Carboniferous [Tournaisian (C1), Visean (C2), Serpukhovian (C3), Bashkirian (C4), Moscovian (C5), Stephanian (C6)]; Permian [Asselian + Sakmarian (P1), Artinskian + Kungurian (P2), Late Permian (P3)]; Triassic [Early and Middle Triassic (T1), Late Triassic (T2)]; Jurassic [Early Jurassic (J1), Middle Jurassic (J2), Late Jurassic (J3)]; Cretaceous [Neocomian (K1), Barremian + Aptian (K2), Albian through Turonian (K3), Senonian (K4)]; Tertiary [Paleocene (P), and Eocene (E)]. (**A** and **B**) Disparity. Squares represent raw data. Error bars show ±1 SE, based on bootstrap resampling (*10*). Because somewhat different characters were used for Paleozoic versus post-Paleozoic crinoids and because each of the two data sets includes only characters that vary within the corresponding span of time, levels of disparity are not comparable between (A) and (B). Triangles in (B) represent data with genus as the sampling unit (that is, only one species sampled per genus per time interval). Diamonds in (B) are data with the morphologically most extreme 40% of species within each interval omitted. The relative sizes of error bars are similar for culled and raw data; for the sake of clarity, these are shown for the raw data only. (**C** and **D**) Genus diversity. (**E** and **F**) Family diversity. Error bars in (C) through (F) show ± $\sqrt{N}$ (N = number of taxa) (*36*). (**G** and **H**) Sample size. Squares represent species. Triangles in (H) designate genera. Genus is the sampling unit for the Paleozoic; the number of species sampled per interval is therefore equal to the number of genera sampled.

symmetrical cups directly attached to hardgrounds (*25, 26*). A decline in cyrtocrinid diversity through the Cretaceous effects a drop in disparity, but this drop is partly offset by the proliferation of morphologically and ecologically atypical, planktonic microcrinoids (Roveacrinida) (*26*).

Taxonomic splitting could bias disparity by causing certain forms to be overrepresented. This possibility is especially salient in the Late Jurassic (Fig. 1, D and H), where de Loriol (*27*) described many species on the basis of what may be minor differences. To explore this bias, I calculated disparity for a culled sample containing only one species per genus per time interval (*28*). Culling the data increased disparity estimates in some subsamples and decreased them in others, but the overall pattern was not substantially changed (Fig. 1B).

A few extreme taxa could also bias disparity. To test this, I culled the data within each interval to exclude the 40% of species with the greatest mean distance to contemporaneous species. (This arbitrary proportion reflects an extreme culling; other proportions yield similar results.) The resulting disparity is lower for each interval, but the temporal pattern is the same (Fig. 1B). I also reanalyzed the data several times, each time with a different order omitted (*26*). In each case, the Late Triassic remained the interval with maximal disparity or had disparity equal to that of the Neocomian. Thus, the early radiation to maximal disparity is statistically robust and phylogenetically broad-based (*15*).

Uneven sampling of species could also affect disparity. Because nearly 80% of known genera were sampled, this bias can be circumvented if each genus is represented by its average morphology in each interval within the known stratigraphic range of that genus (*10, 20, 29*). The resulting disparity curve still peaks in the Late Triassic and Neocomian (Fig. 2). Because time intervals are unequal, disparity could also be biased by different degrees of data aggregation. However, there is an

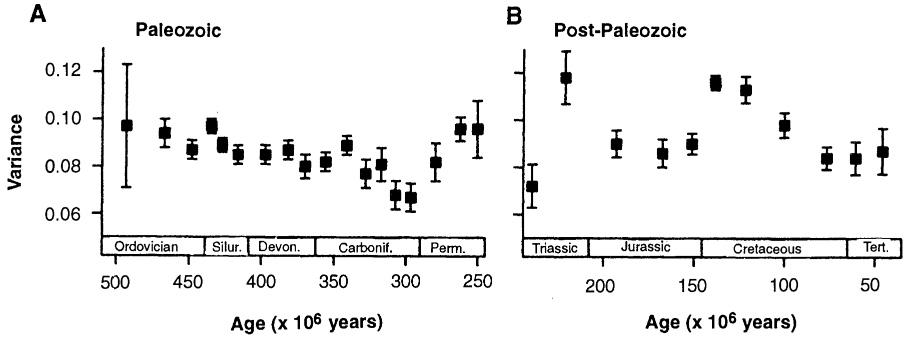

Fig. 2. Temporal pattern of disparity in (**A**) the Paleozoic and (**B**) the post-Paleozoic, allowing average morphology for each genus to span its known stratigraphic range. Disparity is measured as the sum of the sample variances of the first 20 principal coordinates (*10*). Paleozoic data are from (*10*).

insignificant Spearman rank-order correlation coefficient (r_s) between first differences [differences between values at adjacent intervals (*30*)] of disparity and interval length (for genus averages, $r_s = 0.25$, one-tailed $P \approx 0.23$; for raw data, $r_s = 0.37$, one-tailed $P \approx 0.14$). The environmental shift of stalked crinoids into more poorly sampled, deeper waters is also unlikely to bias major patterns of disparity within the Mesozoic, as it occurred mainly in the late Mesozoic and Cenozoic (*6*, *31*).

In addition to differences between species, morphological diversity can be quantified as the range of morphology (*8*), which, because it depends on sample size (*32*), should be compared to the number of species sampled (Fig. 3). As in the Paleozoic, the range of morphology of post-Paleozoic crinoids continued to increase after the early peak in disparity, but this increase is consistent with the expectation of increasing sample size. Even if sample size reflects true species diversity, the post-Triassic proliferation of crinoid species involved no net increase in variance. This result contrasts with the expectation of unconstrained morphological evolution, in which diversification would yield an increase in variance (that is, an increase in range beyond the expectation of sample size differences) (*20*, *33*).

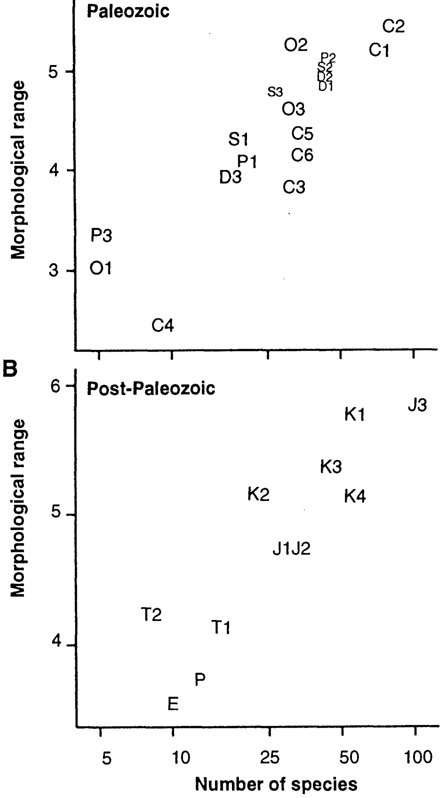

Fig. 3. Sample size (logarithmic scale) and morphological range in (**A**) the Paleozoic and (**B**) the post-Paleozoic. Range is the sum of ranges of the first 20 principal coordinates. Abbreviations are for the time intervals given in the legend to Fig. 1. Paleozoic data are from (*10*).

These analyses of crinoid morphology show that peak disparities in the Paleozoic and post-Paleozoic were attained at comparable rates. Thus, morphological diversification of crinoids was evidently not more strongly hindered in the ostensibly more crowded marine ecosystems of the Mesozoic (*2*). At least three explanations can be offered for these results. First, the anatomical characters studied may not be ecologically significant. However, the close correspondence between soft and hard anatomy and the extensive coverage of structural and functional characters over the entire crinoid skeleton suggest that important autecological factors are captured (*10*, *14*, *25*; *34*). Second, perhaps the early Mesozoic world really was as empty ecologically as the early Paleozoic world. Although the number of ecological guilds absent in the early Paleozoic, but represented in the earliest Mesozoic as holdovers from the late Paleozoic, seems to provide prima facie evidence for a greater degree of ecological saturation in the early Mesozoic (*2*, *4*), diversity and abundance within guilds also need to be considered. This issue remains to be explored with fine-scale ecological data.

Finally, if ecological crowding was important, it may have influenced evolutionary patterns mainly at larger scales than those studied here. Although taxonomic rank is subjective, the origin of higher taxa (classes and phyla) is commonly thought to reflect major morphological transitions (*2*, *5*, *6*). If such transitions require the crossing of thresholds between adaptive zones and if ecological incumbency was important as a competitive force because most adaptive zones were already partially occupied by Paleozoic holdovers, then incumbency could have retarded higher taxonomic origination (*1*, *2*, *5*, *35*). (For example, outside the Crinoidea, no new clades of stalked echinoderms originated in the Mesozoic. The origin of new taxa of attached suspension-feeding echinoderms could have been hindered by suspension feeders in the unstalked echinoderm classes or in other phyla.) However, the incomplete occupation of a particular adaptive zone (for example, that occupied by a single class such as crinoids) could still leave numerous opportunities for a clade to diversify and explore ecological and morphological themes within that zone.

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The Clementine Bistatic Radar Experiment

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E. Malaret, M. Robinson, E. M. Shoemaker

During the Clementine 1 mission, a bistatic radar experiment measured the magnitude and polarization of the radar echo versus bistatic angle, β, for selected lunar areas. Observations of the lunar south pole yield a same-sense polarization enhancement around β = 0. Analysis shows that the observed enhancement is localized to the permanently shadowed regions of the lunar south pole. Radar observations of periodically solar-illuminated lunar surfaces, including the north pole, yielded no such enhancement. A probable explanation for these differences is the presence of low-loss volume scatterers, such as water ice, in the permanently shadowed region at the south pole.

The possibility of ice on the moon was suggested in 1961 (*1*). Volatiles degassed from the primitive moon or deposited on the lunar surface by cometary and asteroidal impacts might migrate to and collect in permanently shadowed cold traps near the lunar poles, where they could be stable over geologic time (*1–5*). Because these cold traps receive no direct solar illumination, and emit little radiation, they are difficult to observe from the Earth. Radar can identify deposits of frozen volatiles because, under certain conditions, they produce a unique radar signature (*6*). However, such radar observations may not be conclusive depending on the quantity of volatiles present, the nature of the surface, and the sensitivity of the measurements. Frozen volatiles have much lower transmission loss than silicate rocks, producing a higher average radar reflectivity than silicate rocks. Total internal reflection also preserves the transmitted circular polarization sense in the scattered signal. An opposition surge or coherent backscatter opposition effect (CBOE) (*7–12*) may also be observed as the phase, or bistatic angle β (Fig. 1), approaches 0. The CBOE requires scattering centers (cracks or inhomogeneities) imbedded in a low loss matrix such as ice (*7–9*). The preservation of the sense of polarization for CBOE has been observed in the laboratory using laser illumination of a particle suspension (*13*, *14*). A high ratio of same sense to opposite sense polarization and high reflectivity has been detected by radar observations of the Galilean satellites of Jupiter (*15*, *16*, *17*), the residual south polar ice cap of Mars (*18*), portions of the Greenland ice sheet (*19*, *20*), and the permanently shadowed polar craters of Mercury (*21–23*). These results are generally attributed to total internal reflection and/or CBOE produced by low loss frozen volatiles (*6*), although other mechanisms have been proposed (*24*). High-resolution ground-based synthetic aperture (monostatic) radar observations, from Arecibo, of the lunar south pole revealed some small anomalous same-sense polarization bright patches that are permanently shadowed (*25*). Brightening and enhancement of same sense polarization can be caused by double bounce reflections from large blocks or surface roughness. The presence of CBOE could distinguish brightening and polarization reversal produced by a low loss target from other scattering mechanisms. Bistatic radar measurements, using a spacecraft in orbit acting as the transmitter, can be used as a test for CBOE (*13*, *14*, *20*) by measuring the echo magnitude and polarization sense as a function of β.

The Clementine 1 mission (*26*) provided data on the environment and geology of the polar regions of the moon (*27*, *28*). In the northern hemisphere, no large basin overlaps the polar area. The south pole, however, is located within the South Pole–Aitken basin (SPA), an impact crater over 2500 km in diameter and averaging 12 km deep near the center of the basin (*29*). The pole is about 200 km inside the rim crest of

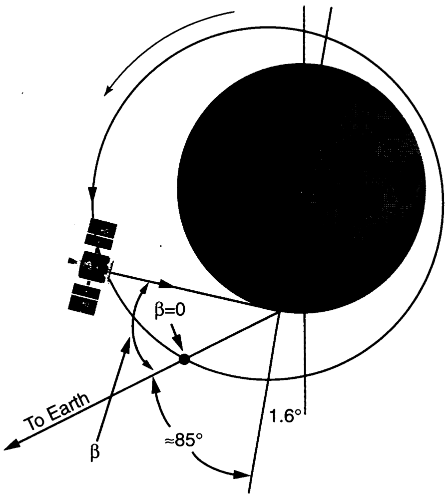

Fig. 1. Orbital geometry of the Clementine bistatic radar experiment. The lunar polar tilt relative to the ecliptic (1.6°), the lunar tilt toward Earth (~5°), and the bistatic angle β between spacecraft, lunar surface, and Earth receiver are shown.

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