Other Honors and Achievements

In view of their remarkable achievements, the granting of the Nobel Prize came as the natural culmination of a series of scientific honors and prizes. They had been awarded many different scientific prizes including the Heinrich Weiland Prize, the Pfizer Award, the Passano Award, the Lounsbery Award, the Gairdner Award, the New York Academy of Sciences Award, the Lita Annenberg Hazen Award, the V. D. Mattia award, the distinguished research award of the Association of American Medical Colleges, the research achievement award of the American Heart Association, the Louisa Gross Horvitz Award, the 3-M Life Sciences Award (FASEB), the William Allan Award of the American Society of Human Genetics, and most recently the Lasker award. Both were elected to the National Academy of Sciences in 1980. They have been asked to give many prestigious lectures, were given honorary doctorates (University of Chicago and Rensselaer Polytechnic Institute), and belong to many review committees and editorial boards. Brown is a member of the Board of Scientific Advisers of the James Coffin Clinical Fund and is a senior consultant to the Lucille P. Markey Trust. Goldstein is a member of the Scientific Advisory Board of the Howard Hughes Medical Institute and a nonresident fellow of the Salk Institute. The Nobel Prize therefore came as no surprise to observers of the never-ending stream of Brown and Goldstein's important discoveries. The only question was its timing. Considering their past record, the scientific community is eagerly awaiting their future work.

Background and Mass Extinctions: The Alternation of Macroevolutionary Regimes

DAVID JABLONSKI

Comparison of evolutionary patterns among Late Cretaceous marine bivalves and gastropods during times of normal, background levels of extinction and during the end-Cretaceous mass extinction indicates that mass extinctions are neither an intensification of background patterns nor an entirely random culling of the biota. During background times, traits such as planktotrophic larval development, broad geographic range of constituent species, and high species richness enhanced survivorship of species and genera. In contrast, during the end-Cretaceous and other mass extinctions these factors were ineffectual, but broad geographic deployment of an entire lineage, regardless of the ranges of its constituent species, enhanced survivorship. Large-scale evolutionary patterns are evidently shaped by the alternation of these two macroevolutionary regimes, with rare but important mass extinctions driving shifts in the composition of the biota that have little relation to success during the background regime. Lineages or adaptations can be lost during mass extinctions for reasons unrelated to their survival values for organisms or species during background times, and long-term success would require the chance occurrence within a single lineage of sets of traits conducive to survivorship under both regimes.

THE PAST FEW YEARS HAVE SEEN A BURGEONING OF DATA and hypotheses on mass extinctions (*1, 2*). Most of this work has focused on evidence for or against extraterrestrial impacts as forcing mechanisms, particularly at the Cretaceous-Tertiary boundary, and the evolutionary role of this and other mass extinction events has been relatively neglected. A comparison of extinction patterns among bivalves and gastropods of the Gulf and Atlantic Coastal Plain region over the last 16 million years (m.y.) of the Cretaceous Period with those across the mass extinction boundary, corroborated from the literature on other taxa and extinction events, indicates that mass extinctions are not simply intensifications of processes operating during background times. Current evolutionary theory is formulated almost exclusively in terms of pattern and process during background times (*3, 4*), but if mass and background extinctions are qualitatively as well as quantitatively different in their effects, the alternation of background and mass extinction regimes shapes large-scale evolutionary patterns in the history of life.

Background extinction. For the shallow-water, bottom-dwelling marine organisms that constitute much of the fossil record, three factors affecting survivorship of species and higher taxa during times of normal background extinction are mode of larval development, geographic range (which for some groups is closely tied to larval mode), and the number of species within a taxonomic group (species richness). Each factor will be tested in turn for its effects on background and mass extinction in Late Cretaceous mollusks of the Gulf and Atlantic Coastal Plain of North America (*5*).

Speciation and extinction rates should be relatively high in species having nonplanktotrophic development because characteristically low rates of larval dispersal will be unable to maintain genetic continuity among disjunct populations; isolated populations will tend to become extinct or diverge into new species. Both rates should be lower in planktotrophs, with greater larval dispersal suppressing divergence of populations and imparting colonizing ability and broad geographic ranges that enhance species' ability to survive local extinctions (*6–10*). These predictions were verified in the fossil record for marine gastropods, in which the earliest parts of the shell preserve a record of larval development. In late Cretaceous

David Jablonski is associate professor in the Department of Geophysical Sciences, University of Chicago, Chicago, Illinois 60637.

Table 1. The synergistic effect of geographic range and species richness is lost during the end-Cretaceous extinctions. Pairwise comparisons yield binomial probabilities of 0.24 to 0.55 (see Fig. 2 for definitions).

Species richness	Species geographic range	
	Widespread (%)	Restricted (%)
Rich	59	65
Poor	60	56

(Fig. 1, A and B) (*11*), early Cenozoic (*12*), and late Cenozoic (*9, 10*) faunas, nonplanktotrophic species exhibit significantly higher speciation and extinction rates than planktotrophic species during background times.

Even for taxa in which development types are not known, or are homogeneous throughout, geographic range is closely related to geologic longevity (*12, 13*). This relation is statistically significant in the Coastal Plain Cretaceous bivalves and gastropods (*14*). Taxonomic survivorship analysis (*15*) reveals significant differences in species duration when restricted, intermediate, and broad geographic ranges are compared (Fig. 2A).

One characteristic that reportedly imparts extinction-resistance to higher taxa or clades (monophyletic evolutionary lineages) is species richness: species-poor clades are more likely to be terminated as a result of random extinction of their constituent species than are species-rich clades. Extremely volatile clades may be exceptions to this generalization, but the species-richness effect is commonly observed and is in accord with probabilistic models of background extinction at high taxonomic levels (*4, 16*).

In Late Cretaceous bivalves and gastropods, geologic durations of species-rich genera are significantly greater than those of species-poor genera (Fig. 3, A and B). Because a number of genera range across the Cretaceous-Tertiary boundary, it might be suspected that this result represents an integration of background and mass extinctions rather than the operation of background processes alone. However, the observed pattern is due to differences in survivorship among genera endemic to the Coastal Plain region (median durations for species-rich and species-poor genera are 23 and 10 m.y., respectively). As discussed below, endemic genera suffer such great losses during mass extinctions that their evolutionary patterns are a good index of pure background processes. In contrast, the widespread genera, whose durations reflect the integration of background and mass extinctions, fail to exhibit a significant difference between species-rich and species-poor genera (median durations, 79 and 73 m.y., respectively).

During background times, there is also a synergistic interaction between species richness and the geographic range of the individual species constituting a clade. As might be predicted from the preceding results, species-rich genera composed mainly of widespread species exhibited significantly greater geologic longevities than species-poor genera composed mainly of species with restricted geographic ranges; the other two alternatives are of intermediate duration (Fig. 2B).

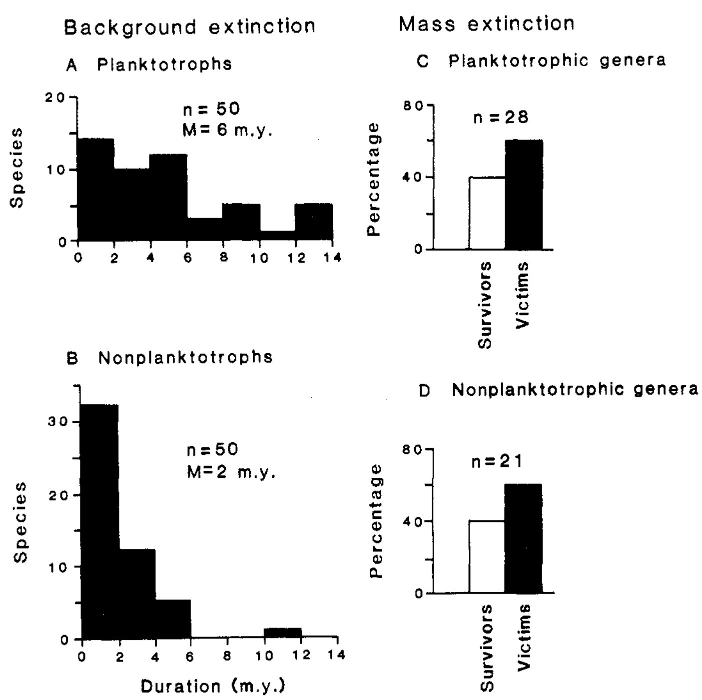

Fig. 1. Effect of larval ecology on taxonomic survivorship of Late Cretaceous gastropods during background and mass extinctions. (A and B) Background extinctions. During background times species with (A) planktotrophic larval development exhibit significantly greater duration than species with (B) nonplanktotrophic development (Kolmogorov-Smirnov test, $P < 0.01$). (B and C) Mass extinction. Mode of larval development had no statistically significant influence on survivorship of gastropod genera during the end-Cretaceous extinction event; 39 percent each of the genera inferred to have (C) planktotrophic and (D) nonplanktotrophic larvae survived. Abbreviations: M, median; m.y., millions of years (binomial probability, 0.50). For sources of data and methods for inferring modes of larval development, see (*11*).

Mass extinctions. In strong contrast to patterns during background times, extinction and survival among Coastal Plain mollusks during the end-Cretaceous mass extinction was influenced by neither larval development nor species richness. Instead, geographic range at the clade level, but not at the species level, appears to have been among the most favorable traits.

Gastropod genera were classified as planktotrophic or nonplanktotrophic according to the larval shell morphology of their constituent species; genera in which both modes of development were present were excluded from the analysis. Planktotrophs and nonplanktotrophs showed identical levels of extinction during the end-Cretaceous event (61 percent of 28 and 23 genera, respectively) (Fig. 1, C and D). Hansen's analyses of the early Tertiary gastropods of the Coastal Plain region (*11*) demonstrates, however, that the larval mode soon regained its prominent role in determining evolutionary patterns within the postextinction biota.

Geographic range at the species level had little influence on the survival of genera during the end-Cretaceous extinction. The frequency distributions of geographic ranges of the component species within both victims and survivors of the mass extinction are not significantly different (Fig. 2, E and F). Moving up another level in the taxonomic hierarchy reveals an unexpected difference in survivorship, however. Although species-level patterns are not influential, clades with species outside the Coastal Plain Province exhibit significantly higher survivorship than clades restricted to this biogeographic province. For bivalves (Fig. 2C), 33 percent of the extinct genera were restricted to that province, but only 3 percent of the genera that survived were endemic; viewed another way, 55 percent of the widespread genera survived, but only 9 percent of the endemics. For gastropods (Fig. 2D), 48 percent of the extinct genera were endemic, but only 11 percent of the survivors were restricted to the province; thus, 50 percent of the widespread genera survived, but only 14 percent of the endemics. This is a selectivity manifested at a different hierarchical level from those characteristic of background times.

Again in contrast to background times, species richness did not improve a genus's chances of survival, nor did species-poor genera suffer disproportionate extinction (Fig. 3, C and D). For bivalves, about 40 percent of the victims of the mass extinction were species-rich, as were 40 percent of the survivors; thus, 47 percent of the species-rich genera and 45 percent of the species-poor genera survived. Among the gastropods, about 50 percent of the victims, but only about 33 percent of the survivors were species-rich; this yields a rather surprising reversal of the background pattern: 29 percent of the species-rich genera survived, but a significantly greater 47 percent of the species-poor genera survived.

The synergistic effect of species richness and species' geographic ranges is also lost during the mass extinction. Species-rich taxa containing mainly widespread species show no higher survivorship (59 percent) than do species-poor taxa with geographically restricted species (56 percent).

Comparison to other extinctions. Patterns of extinction and survival during the end-Cretaceous extinction are discordant with the patterns of clade expansion and contraction during the times of background extinction preceding and succeeding the event. Not only did extinction rates soar during this time interval, but different kinds of taxa were vulnerable to extinction. After the mass extinction, there was a return to normal background levels and to a different constellation of traits favoring taxonomic survivorship. Comparative data for other extinctions are sparse, but the available studies are consistent with the end-Cretaceous patterns.

Among Ordovician-Jurassic bivalves (*17*), endemic genera diversified during background times but underwent preferential extinction relative to widespread and cosmopolitan genera during all four mass extinctions within the interval: end-Ordovician, late Devonian, late Permian, and end-Triassic events. Recovery of the bilvalve fauna after these extinctions derived mainly from cosmopolitan survivors. During the Pliocene molluscan extinction in the North Atlantic, species survivorship was also unrelated to traits that enhanced background survivorship (*18*). Again in common with the end-Cretaceous extinction, endemic taxa became disproportionately extinct relative to widespread taxa, regardless of species richness (*19*).

Anstey (*20*) also detected qualitative differences between background and mass extinctions in Paleozoic Bryozoa. Morphologically simple genera (interpreted as ecological generalists) had fairly steady extinction rates throughout the Paleozoic, but losses among morphologically complex genera (inferred specialists) are concentrated at mass extinctions. When the effects of mass extinctions are removed, complex taxa actually had lower background extinction rates than simple taxa did. Furthermore, because the complex genera tend to be richer in species and more geographically restricted than the simple genera (*21*), this shift in survivorship patterns during mass extinctions coincided with the one observed for end-Cretaceous mollusks.

The ammonites are such a volatile group that it is difficult to separate the effects of background and mass extinction over the course of their boom-and-bust history. In keeping with the bivalve and gastropod pattern, however, ammonite clades consisting of few, long-lived taxa tended to survive or be the last to vanish at mass extinction boundaries (*22*); these same clades tended to be geographically widespread rather than endemic (*23*).

My analysis of Alekseyev's (*24*) global compilation of 586 families and 1816 genera from marine, terrestrial, and freshwater habitats at the end of the Cretaceous shows no significant difference between the frequency distribution of genera within families for victims and survivors (contrary to Alekseyev's proposition) (Kolmogorov-Smirnov test, $0.20 < P < 0.40$). Again, taxonomic structure, albeit at a higher level, evidently had little bearing on clade survivorship during the end-Cretaceous extinction.

Macroevolutionary regimes. The fossil record near the end-

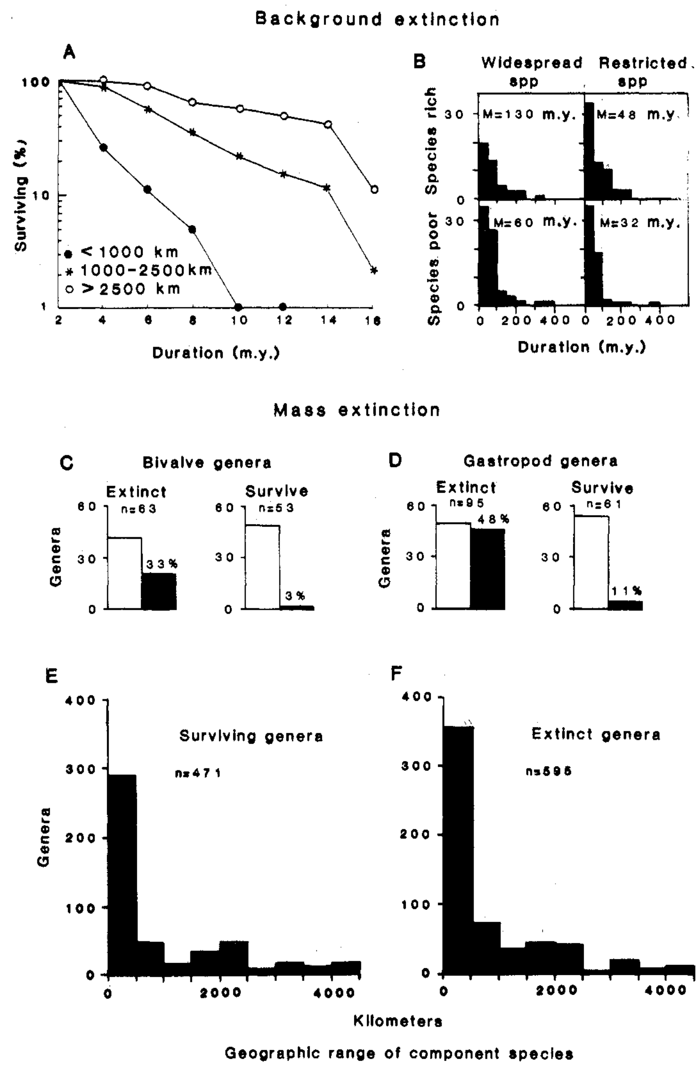

Fig. 2. Effect of geographic range on taxonomic survivorship of Late Cretaceous bivalves and gastropods during background and mass extinctions. (A) During background times, taxonomic survivorship curves are significantly different for species having narrow ranges (<1000 km), intermediate ranges (1000 to 2500 km), and broad ranges (>2500 km) (Kolmogorov-Smirnov test on original frequency distributions of durations among categories, $P < 0.01$ with Bonferroni-type correction). Taxonomic survivorship curves reflect the probability of extinction with respect to age for a given assemblage of taxa: the steeper the slope, the higher the extinction rate (*15*). (B) Also during background times, geographic ranges of constituent species influence duration of genera, in a synergistic interaction with species richness. Species-rich clades with predominantly widespread species are significantly longer lived than species-poor clades with predominantly restricted species ($P < 0.05$, Kolmogorov-Smirnov test). Species-rich, those having three or more species in the last, best known, 6 m.y. of the Late Cretaceous strata in the study region; widespread species, clades having 50 percent species with geographic ranges > 500 km along the Late Cretaceous outcrop belt of the Coastal Plain. Other cutoff limits for either trait had little effect on the calculations (see Table 1 for mass extinction pattern). During mass extinctions (C to F), geographic ranges of constituent species had no significant effect on clade survival, but geographic range of clades did have a significant effect. Frequency distribution of geographic ranges of species within genera are not significantly different for survivors (E) and victims (F) on the mass extinction ($0.50 > P > 0.40$, Kolmogorov-Smirnov test). However, endemic genera (genera restricted to the Coastal Plain province) were overrepresented among victims of the end-Cretaceous mass extinction among both bivalves (C) and gastropods (D). For bivalves, 55 percent of the widespread genera and only 9 percent of the endemic genera survived (a statistically significant difference; binomial probability = 0.00004); for gastropods, 51 percent of the widespread genera and 14 percent of the endemic genera survived (binomial probability = 0.0000005).

Table 2. Faunal replacements previously regarded as competitive that now seem to have been mediated by mass extinctions (*28*).

Taxa	Reference
End-Ordovician brachiopods	(*29*)
Late Paleozoic mammal-like reptiles	(*30*)
Post-Paleozoic benthos	(*31*)
End-Triassic tetrapods	(*32*)
End-Cretaceous tetrapods	(*33*)
End-Cretaceous reef-builders	(*34*)
Mid-Tertiary carnivorous mammals	(*35*)

Cretaceous and other extinction events suggest that large-scale revolutionary patterns are shaped by two macroevolutionary regimes. Microevolutionary and macroevolutionary processes of the background regime are occasionally disrupted, presumably by external abiotic forcing factors (*25*), and replaced by the mass extinction regime. Many traits of individuals and species that had enhanced the survival and proliferation of species and clades during background times become ineffective during mass extinctions, and other traits that were not closely correlated with survivorship differences become influential. The mass extinction regime is apparently relatively short-lived—1 or 2 m.y. at most for the end-Cretaceous event, and perhaps considerably less.

During these mass extinction events, evolution is channeled in directions that could not have been predicted on the basis of patterns that prevailed during background times. As indicated by the observed selectivity with respect to clade-level deployment, mass extinction is not a regime of complete randomness, but this selectivity will be indifferent to many adaptations that had been valuable during the much more prolonged background regime—a process resembling what Raup (*26*) has called "nonconstructive selectivity." Particular traits captured during background times can be lost not because they are in themselves maladaptive but because they occur in clades that lack the environmental tolerances or geographic distribution necessary to survive the mass extinction regime. Thus, a broader range of hypotheses must be considered in analyzing the histories of higher taxa and major adaptations, hypotheses that recognize the potential role of extinction processes that will not be congruent during mass and background regimes, or across levels in the biological hierarchy.

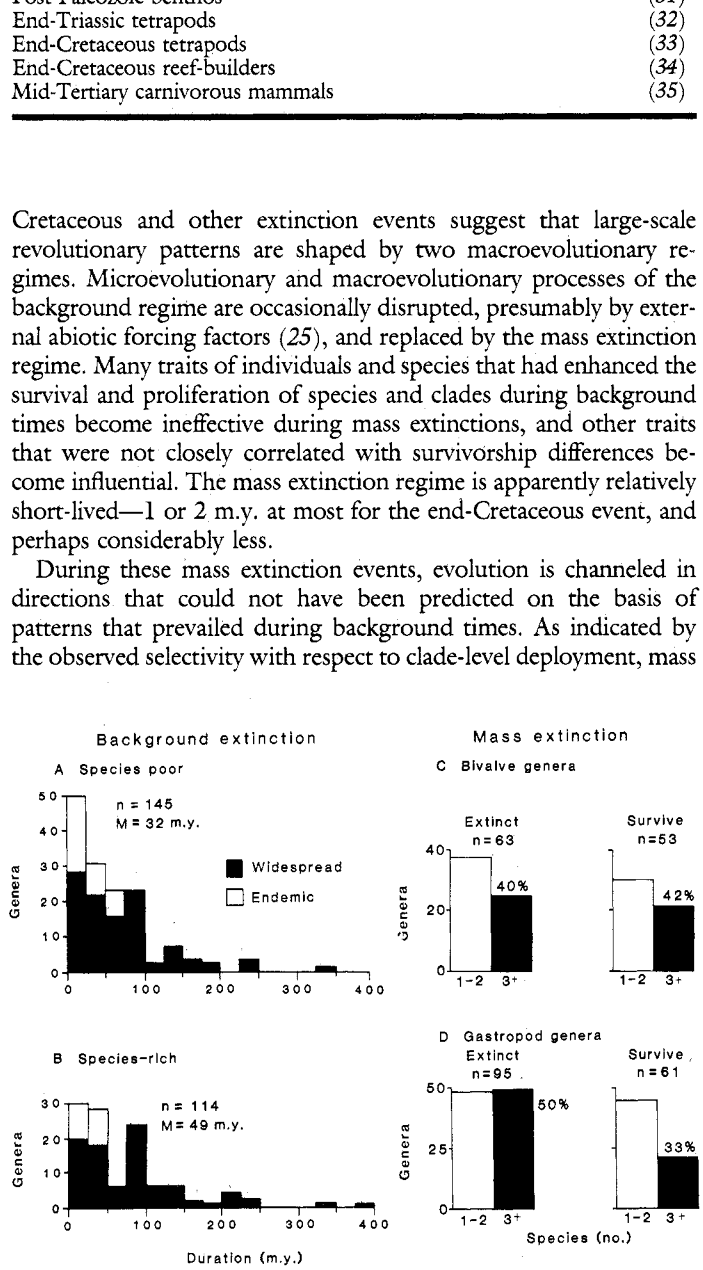

Fig. 3. Effect of species richness on taxonomic survivorship of Late Cretaceous bivalves and gastropods during background and mass extinctions. During background times, median geologic durations of species-rich bivalve and gastropod genera are greater than those of species-poor genera. The basis for this difference lies in the endemic genera, which suffer so severely during mass extinctions that their patterns of survivorship are a good index of purely background processes (Kolmogorov-Smirnov test, $P < 0.05$); there is no significant difference between species-rich and species-poor widespread genera ($0.40 > P > 0.20$). During the end-Cretaceous mass extinction, species-rich bivalve genera are equally represented among the victims and survivors (C); 47 percent of species-rich genera and 45 percent of the species-poor genera survive (binomial probability, 0.60). Among the gastropods (D), species-rich genera are disproportionately represented among the victims of the mass extinction; 29 percent of species-rich genera and 47 percent of species-poor genera survive (binomial probability, 0.0018).

At the same time, these results imply that mass extinctions play a larger role than is generally appreciated in creating opportunities for faunal change, removing dominant taxa and thereby enabling other groups—previously unimportant but with traits enhancing survivorship during mass extinctions—to undergo adaptive radiations. In recent years a number of major faunal replacements have been interpreted in this way (Table 2). The most persistent and diverse clades may therefore be those in which major new adaptations and other traits favored during background times happen to be associated with traits that favor survival under the mass extinction regime. Such an association may underlie the steady success of post-Paleozoic extratropical bivalves and gastropods relative to other marine clades.

Comparative analyses among mass extinctions are needed to test this view of macroevolution. Pairwise comparisons of survivorship patterns across a spectrum of extinction magnitudes can determine whether there is a true threshold or a gradual changeover between the background and mass extinction regimes. Some similarities in biotic patterns certainly exist among the mass extinctions (*2*), but some differences remain, such as the apparent selectivity in favor of nonplanktotrophic clades during the end-Permian event (*27*) and the lack of any larval pattern at the end of the Cretaceous. Such differences may be due to contrasts in biogeographic and other factors immediately before the various extinction events, but each particular mass extinction may prove to be an isolated excursion away from the background regime.

The patterns reported here support a hierarchical view of evolution, in which selection, drift, and other evolutionary processes operate at a variety of focal levels, with consequences both upward and downward within a genealogical hierarchy from gene to clade (*4*). Taxonomic survivorship during the end-Cretaceous extinction is a function of clade geographic range per se, rather than a direct consequence of the environmental tolerance or other features of individual organisms (as indicated by the lack of effect of individual species' ranges on clade survivorship); clade geographic range behaved in this instance as an emergent property that influenced evolutionary fates at other levels. Evolutionary processes at these other levels did not cease, but selectivity at a higher focal level became more important and had cascading effects through the biological hierarchy. However, this selectivity at the clade level cannot yet be inferred to indicate an ongoing process of evolution by clade selection. An important component of such a process—heritability of geographic range at the clade level—has not been demonstrated.

Rather than simply accelerating or emphasizing trends already manifest during background times, the end-Cretaceous mass extinction was characterized by qualitative as well as quantitative changes in patterns of extinction and survival. The few comparable data available from other mass extinctions suggest that these events, too, imposed survivorship patterns having little correspondence with those of background times. Because the traits that enhance survival during mass extinctions (for example, broad geographic range at the clade level) tend to be poorly correlated with traits that enhance survival and diversification during background times, mass extinctions will not promote the long-term adaptation of the biota. In fact, mass extinctions can break the hegemony of species-rich clades honed by millions of years of selection and thereby permit radiation of taxa little favored during the interval preceding the extinction event. The alternation of these macroevolutionary regimes disrupts any smooth extrapolation of microevolutionary or macroevolutionary processes across the sweep of geological time; a complete theory of evolution must incorporate the different sets of selective and random processes that characterize the background and mass extinction regimes.

REFERENCES AND NOTES

1. D. M. Raup, *Science*, in press; K. W. Flessa *et al.*, in *Patterns and Processes in the History of Life*, D. M. Raup and D. Jablonski, Eds. (Springer-Verlag, Berlin, in press).
2. D. Jablonski, in *Patterns and Processes in the History of Life*, D. M. Raup and D. Jablonski, Eds. (Springer-Verlag, Berlin, in press); in *Dynamics of Extinction*, D. K. Elliott, Ed. (Wiley, New York, in press).
3. G. G. Simpson, *Tempo and Mode in Evolution* (Columbia Univ. Press, New York, 1944); *Major Features of Evolution* (Columbia Univ. Press, New York, 1953).
4. S. M. Stanley, *Macroevolution* (Freeman, San Francisco, 1979); S. J. Gould, *Science* **216**, 380 (1982); in *Perspectives on Evolution*, R. Milkman, Ed. (Sinauer, Sunderland, MA, 1982), pp. 83–104; N. Eldredge, *Syst. Zool.* **31**, 338 (1982); E. S. Vrba and N. Eldredge, *Paleobiology* **10**, 146 (1984).
5. Species durations were estimated with eight stratigraphic intervals of approximately 2 m.y. each. Geographic ranges were mapped on the discontinuous, 5000-km outcrop belt to an accuracy of ± 20 km. This degree of temporal and geographic resolution permitted a standardized comparison among sedimentary basins and time intervals throughout the study area [see Jablonski (*11*) for details]. During the Late Cretaceous, the Gulf and Atlantic Coastal Plain constituted a single cohesive biogeographic province [N. F. Sohl, *Proc. First N. Am. Paleontol. Conv.* **2**, 1610 (1971)]; E. G. Kauffman, in *Atlas of Palaeobiogeography*, A. Hallam, Ed. (Elsevier, Amsterdam, 1973), pp. 353–383], so that appearance and disappearance of species within the study area are likely to represent global rather than local invasion or extinction. Although the last 1 m.y. of the Cretaceous Period is unrecorded in the Coastal Plain region, prohibiting detailed analysis of the timing of the end-Cretaceous event, the excellent preservation of the diverse molluscan faunas permits comparison of survivorship across the boundary with patterns of background extinction in the immediately preceding 16 m.y. to a degree unparalleled by other stratigraphic sections in shallow-marine sediments.
6. D. Jablonski and R. A. Lutz, *Biol. Rev.* **58**, 21 (1983).
7. J. A. Pechenik, R. S. Scheltema, L. E. Eyster, *Science* **224**, 1097 (1984); C. S. Gallardo and F. E. Perron, *Malacologia* **22**, 109 (1982).
8. G. J. Vermeij, *Biogeography and Adaptation* (Harvard Univ. Press, Cambridge, 1978).
9. R. S. Scheltema, in *Concepts and Methods of Biostratigraphy*, E. G. Kauffman and J. E. Hazel, Eds. (Dowden, Hutichinson & Ross, Stroudsburg, PA, 1977), pp. 73–108; in *Marine Organisms: Genetics, Ecology and Evolution*, B. Battaglia and J. A. Beardmore, Eds. (Plenum, New York, 1978), pp. 303–332; in *Historical Biogeography, Plate Tectonics and the Changing Environment* (Oregon State Univ. Press, Corvallis, 1979), pp. 391–397.
10. T. Shuto, *Lethaia* **7**, 239 (1974); *Bull. Mar. Sci.* **33**, 536 (1983).
11. D. Jablonski, *Proc. Third N. Am. Paleontol. Conv.* **1**, 257 (1982); *Bull. Mar. Sci.*, in press.
12. T. A. Hansen, *Science* **199**, 885 (1978); *Paleobiology* **6**, 193 (1980).
13. J. B. C. Jackson, *Am. Nat.* **108**, 541 (1974); A. J. Boucot, *Evolution and Extinction Rate Controls* (Elsevier, Amsterdam, 1975); A. Hoffman and B. Szubdzda-Studencka, *Neues Jahrb. Palaeontol. Abh.* **163**, 122 (1982).
14. Simple linear regression reveals a significant linear relation between geographic range and species duration [$n = 1066$ species, slope $= 2.00 \pm 0.07$ (million years per 10^3 km); $P < 0.0005$; *t*-test]. When species that originated in the last 2 m.y. preceding the end-Cretaceous mass extinction (and thus are most likely to suffer truncation of durations by mass extinction rather than background processes) are omitted from the analysis, n drops to 848 and 95 percent confidence limits fail to overlap [slope $= 2.19 \pm 0.08$ (million years per 10^3 km)]. The fact that even these truncated species frequently attained broad geographic ranges before becoming extinct suggests that during background times geologic duration is a function of geographic range and not vice versa.
15. L. Van Valen, *Evol. Theory* **1**, 1 (1973); D. M. Raup, *Paleobiology* **1**, 82 (1975).
16. D. M. Raup, *ibid.* **4**, 1 (1978); *Acta Geol. Hispanica* **16**, 25 (1981); S. J. Gould *et al.*, *Paleobiology* **3**, 23 (1977); R. R. Strathmann and M. Slatkin, *ibid.* **9**, 97 (1983).
17. P. W. Bretsky, *Geol. Soc. Am. Bull.* **84**, 2079 (1973).
18. S. M. Stanley, *Proc. Third N. Am. Paleontol. Conv.* **2**, 505 (1982). It is surprising that this much smaller extinction also disrupted survival patterns relative to background times. Shifts in selective pressures owing to climatic changes, rather than a switch to the extinction regime characterizing the major mass extinctions, may have been involved.
19. G. J. Vermeij, in *Dynamics of Extinction*, D. K. Elliott, Ed. (Wiley, New York, in press).
20. R. L. Anstey, *Paleobiology* **4**, 407 (1978).
21. Of the genera for which biogeographic data were available, 23 percent of the simple genera ($n = 44$) are present on four or more paleocontinental blocks, but only 9 percent of the complex genera ($n = 36$) are so widespread (binomial probability, 0.044) [G. G. Astrova, *Akad. Nauk SSSR Paleontol. Inst. Trudy* **169**, 1 (1978); J. R. P. Ross, *Palaeontology* **21**, 341 (1978); *ibid.* **24**, 313 (1981); R. A. Robison, Ed., *Treatise on Invertebrate Paleontology*, vol. 1 part G, *Bryozoa* (Geological Society of America, Boulder, CO, revised edition, 1983).
22. P. D. Ward and P. W. Signor, III, *Paleobiology* **9**, 183 (1983).
23. J. Wiedmann, quoted by E. G. Kaufmann, in *Catastrophes and Earth History*, W. A. Berggren and J. A. Van Couvering, Eds. (Princeton Univ. Press, Princeton, NJ, 1984), pp. 151–246.
24. A. S. Alekseyev, *Int. Geol. Rev.* **26**, 1006 (1984).
25. Of course, this change in macroevolutionary regime does not necessarily confirm the hypothesis that an extraterrestrial impact triggered the end-Cretaceous mass extinction. It does indicate that a major perturbation took place, crossing a threshold beyond which normal background processes were of secondary importance. Nor does the crossing of this threshold during other extinction events necessarily require an identical forcing factor.
26. D. M. Raup, *Science* **206**, 217 (1979); in *Patterns of Change in Earth Evolution*, H. D. Holland and A. F. Trendall, Eds. (Springer-Verlag, Berlin, 1984), pp. 5–14.
27. R. R. Strathmann, *Evolution* **32**, 894 (1978); J. W. Valentine, *Bull. Mar. Sci.*, in press.
28. M. J. Benton, *Nature (London)* **302**, 16 (1983).
29. Orthacians and strophomenids replaced by spiriferids and other brachipod groups; P. M. Sheehan, *Proc. Third N. Am. Paleont. Conv.* **2**, 477 (1982).
30. Synapsids replaced by therapsids; T. S. Kemp,, *Mammal-Like Reptile and the Origin of Mammals* (Academic Press, London, 1982).
31. Articulate brachiopods replaced by bivalves; S. J. Gould and C. B. Calloway, *Paleobiology* **6**, 383 (1980); see (*27*).
32. Mammal-like reptiles replaced by dinosaurs; M. J. Benton, *Q. Rev. Biol.* **58**, 29 (1983).
33. Dinosaurs replaced by placental mammals; D. A. Russell, *Annu. Rev. Earth Planet Sci.* **7**, 163 (1979).
34. Rudist bivalves replaced by scleractinian corals; N. D. Newell, *Am. Mus. Novit. No. 2465* (1971), p. 1; P. M. Sheehan, *Geology* **13**, 46 (1985).
35. Archaic carnivores, Orders Creodonta and Condylartha, replaced by Order Carnivora; L. B. Radinsky, *Paleobiology* **8**, 177 (1982).

36. I thank A. J. Boucot, J. H. Brown, K. W. Flessa, E. G. Kauffman, S. M. Kidwell, D. M. Raup, M. L. Rosenzweig, J. J. Sepkoski, Jr., S. Suter, J. W. Valentine, and G. J. Vermeij for valuable discussions and reviews. Supported by NSF grants EAR 81-21212 and EAR 84-17011.

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