Geographic Variation in the Molluscan Recovery from the End-Cretaceous Extinction

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Biotic recovery patterns after the end-Cretaceous mass extinction differ among the molluscan faunas of the North American Gulf Coast, northern Europe, northern Africa, and Pakistan and northern India. In contrast to the Gulf Coast, the other three regions lack a rapid expansion and decline of "bloom taxa" and have lower proportions of invaders early in the recovery phase. The anomalous Gulf Coast patterns, distinct from extratropical Europe and the tropical regions, provide evidence for the biogeographic and macroevolutionary complexity of biotic recoveries and may have implications for present-day biotas.

Mass extinctions are biologically important not only for the species they eliminate but also for the evolutionary diversification and ecological restructuring that occurs in the aftermath of these events (*1*). The end-Cretaceous (K-T) extinction, one of the five major mass extinctions of the metazoan fossil record, was followed by a rapid recovery of global taxonomic diversity, accompanied in marine and terrestrial communities by the radiation of new or previously minor groups (*1*, *2*). This recovery has generally been analyzed either in local sections (*2*) or in synoptic global databases (*1*). Here, I examine marine molluscan patterns at an intermediate scale, with a comparison among four biogeographic provinces. These regions contain some of the most complete and best preserved macrofaunal sequences and permit comparison of recovery patterns among extratropical and tropical regions: the Gulf Coast of North America [Georgia to Texas (GC)] and northern Europe [Britain to Poland (EU)] compared with northern Africa [Algeria to Egypt (AF)] and the northern margin of the Indian Plate [Pakistan and northern India (PA)], respectively (*3*). Although extinction intensities and selectivities were similar in the molluscan faunas of all four areas (*4*), the regions differ in the dynamics of diversifying clades and in the proportion of local taxa and invaders in the postextinction biotas. Understanding this geographic variation is important for deciphering the ecological and macroevolutionary patterns of recovery episodes and may provide insights on extinction, invasion, and recovery patterns in the present-day biota.

I compared the bivalves and gastropod faunas of Paleocene age (the first epoch of the Cenozoic era) from the four regions using museum collections and an update and synthesis, based on those collections, of the primary literature. Faunas were placed in the global biostratigraphic framework of calcareous nannofossil zones (*5*–*8*) and grouped into five intervals of about 2 million years (My) each (*9*, *10*). Faunas were compiled for the past 5 My of the Cretaceous (the Maastrichtian Stage) [an expanded version of an earlier database (*4*)] as a basis for distinguishing K-T survivors from new Paleocene taxa and for quantifying postextinction biogeographic patterns. This larger preextinction interval was used to reduce sampling artifacts and does not assume abrupt or gradual extinctions at the K-T boundary; restricting the Cretaceous component to latest Maastrichtian macrofaunas where feasible (for example, Stevns Klint, Denmark) did not change the interregional contrasts reported here. The faunas were partitioned into a number of ecologically and phylogenetically important groups to facilitate comparison with Hansen's GC analysis (*11*). Preservation and sampling (and thus sample sizes) inevitably vary among regions and time intervals (Table 1), so to aid interpretation, I show all biotic patterns as both raw numbers and as a percentage of the total number of bivalve and gastropod species within a given fauna; because these metrics respond differently to sampling, patterns will be considered robust only when they involve parallel excursions in both raw and proportional data (*12*). To put the raw numbers in evolutionary context, I used the number of genera and subgenera shared between the latest Cretaceous and earliest Paleocene of a region to provide a minimum estimate of the number of species that crossed the K-T boundary.

The most striking difference among the four time series is in the behavior of the molluscan families that Hansen (*11*) termed "bloom taxa" on the basis of the evolutionary burst they exhibit in the early Paleocene of the GC. These four families (Ostreidae, Cucullaeidae, Carditidae, and Turritellidae) increase sharply from the latest Cretaceous (interval 1) in species numbers and as a proportion of the GC interval 2 fauna. Such behavior is not seen among these families, singly or as a group, in the other three regions (Fig. 1), nor do other taxa exhibit bloom behavior outside the GC. The EU and AF faunas do show an increase in the number of species within Hansen's bloom taxa later in the Paleocene (interval 3). However, this numerical increase is not accompanied by a proportional increase, so that any true gain in bloom species numbers must have occurred because of better sampling or as part of a general diversification, rather than as the

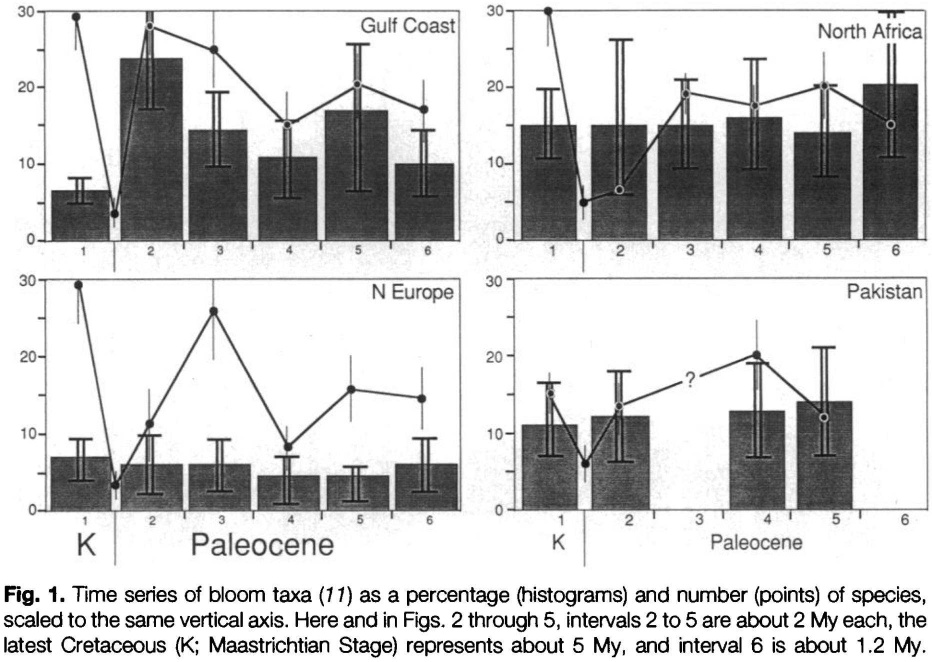

Fig. 1. Time series of bloom taxa (*11*) as a percentage (histograms) and number (points) of species, scaled to the same vertical axis. Here and in Figs. 2 through 5, intervals 2 to 5 are about 2 My each, the latest Cretaceous (K; Maastrichtian Stage) represents about 5 My, and interval 6 is about 1.2 My. Percentages ± 95% confidence intervals, following (*28*); species numbers ± SE, following (*29*).

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anomalous peak seen in GC interval 2.

Recovery patterns differ among regions in other ways. For example: (i) The lucinoidean bivalves diversified in EU but not elsewhere (Fig. 2) (*13*). (ii) Nonsiphonate burrowing bivalves [as defined in (*11*)] dropped sharply across the K-T boundary in species numbers and as a proportion of the fauna in the GC and did not recover fully by the end of the Paleocene (Fig. 3). In the other areas, they remained stable as a proportion of the fauna, and species numbers reattained or approached Late Cretaceous amounts. (iii) Muricoidean gastropods, which constitute most marine predatory snails (*14*), rebounded more abruptly in the GC in terms of species numbers and proportions (Fig. 4).

The GC also differs from the other regions in the biogeographic affinities of faunal constituents in the first postextinction interval. Recovery faunas for any region consist of three components: local survivors (extant in the region before the extinction), immigrant survivors (extant elsewhere before the extinction, "invaders"), and newly evolved taxa. With genera and subgenera as the units of analysis, the GC has a greater proportion of invaders in interval 2 than the other regions (Fig. 5A). The GC outlier is unexpected given the similar extinction intensities in all four regions, because variation in the susceptibility of living and fossil biotas to invasion often appears to be mediated by disparities in preinterchange extinction (*15*, *16*).

These interregional differences are unlikely to be due entirely to differences in depositional environments or preservation. The earliest Paleocene comprises a range of lithologies and thus depositional environments for each region (*17*). Furthermore, the fact that only one set of GC taxa exhibits postextinction excursions indicates that the behavior of the bloom taxa is not some inevitable by-product of the GC fossil record. Finally, the greater proportion of postextinction invasions in the GC is opposite to the expectation based on interregional differences in the quality of the fossil record. Because the GC has the best preserved and best sampled latest Cretaceous molluscan faunas in the world (*4*) and its Paleocene record is at least equal to that of EU and superior to that of AF and PA, local survivors rare in preextinction faunas are more likely to be recognized in the GC than in other regions; this difference should reduce perceived immigration relative to other regions, but the opposite trend is found. Interprovincial differences are thus likely to carry a biogeographic and evolutionary signal rather than simply to reflect environmental or preservational artifacts.

The contrasts between the GC recovery and those of the other regions are striking in light of the close geographic and climatic affinities of EU and the GC at this time and the geographic separation and climatic contrasts between EU and the two tropical regions (*18*). Tropical faunas have generally been thought to suffer more heavily during mass extinctions (*19*) and thus might have been expected to show more dramatic faunal changes during recovery; EU and the GC, lying outside the tropical belt, might be expected to show more modest changes. Not only do the tropical regions fail to show the most extreme recovery patterns, but many participants in the GC recovery were invaders from tropical Maastrichtian fau-

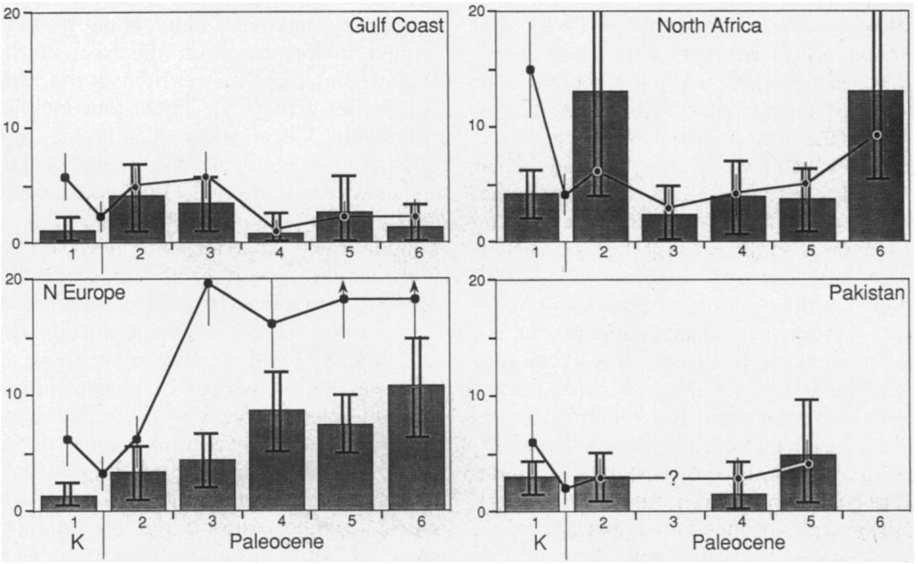

Fig. 2. Percentage and number of species of lucinoid bivalves from the latest Cretaceous to the end of the Paleocene, scaled to the same vertical axis. Abbreviations and confidence limits are as in Fig. 1.

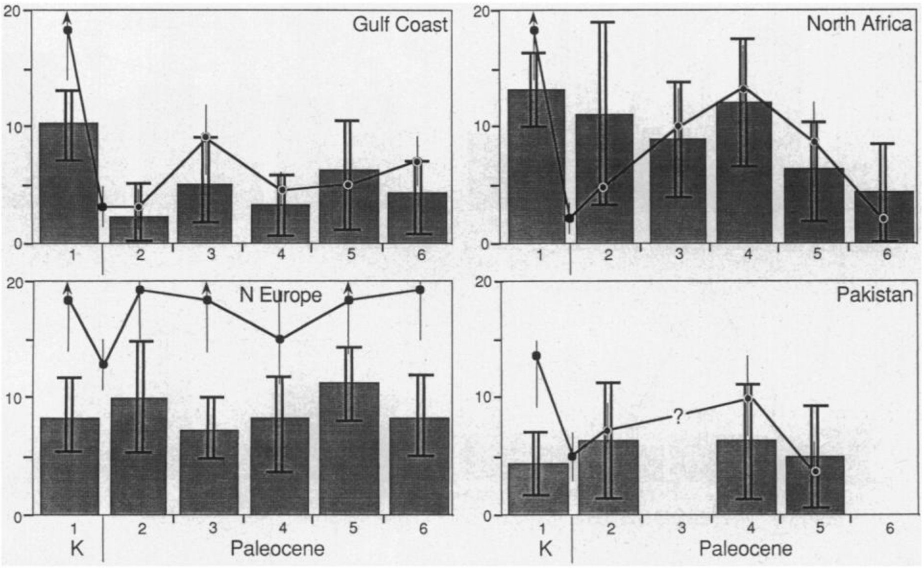

Fig. 3. Percentage and number of species of nonsiphonate bivalves other than bloom taxa from the latest Cretaceous to the end of the Paleocene, scaled to the same vertical axis. Abbreviations and confidence limits are as in Fig. 1.

Table 1. Number of bivalve and gastropod species recorded in each interval. Abbreviations are as in text; interval 1, latest Cretaceous, intervals 2 to 6, Paleocene. A dash indicates that there are no known faunas this age.

Interval	GC	EU	AF	PA
1	542	464	363	295
2	123	184	46	105
3	177	462*	128	–
4	136	185	106	147
5	80	372	139	85
6	166	245	71	–

*Reflects exceptional sampling and preservation, for example, Calcaire de Mons.

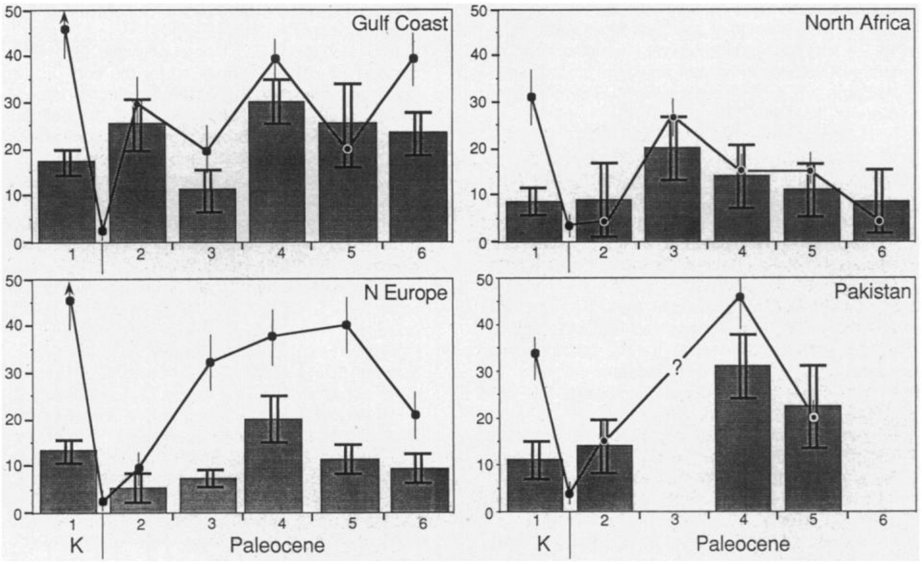

Fig. 4. Percentage and number of species of muricoid gastropods from the latest Cretaceous to the end of the Paleocene, scaled to the same vertical axis. Abbreviations and confidence limits are as in Fig. 1.

nas, including *Calyptraphorus*, *Baluchicardia*, *Venericor*, and *Sigmesalia* (*20*); the last three are members of Hansen's bloom taxa.

Although the anomalous molluscan recovery in the GC—with its excursion of bloom taxa and invader-rich biota—is consistent with the hypothesized oblique trajectory for the K-T impact at Chicxulub, Yucatan (*21*), more definitive tests are required. The hypothesized directional effects could be tested by determining whether recovery patterns in eastern Mexico are more similar to those of the GC to the north or to those of the tropical faunas to the east; patterns in northern South America can test whether those of the GC simply reflect proximity to the impact site.

The anomalous GC recovery is problematic in light of the similar K-T extinction intensities among the study areas. Two alternatives should be explored:

1) More severe GC losses could be masked by rapid reinvasion by taxa that had been present in the region before the K-T event. This hypothesis could be tested by detailed phylogenetic and biogeographic analysis of widespread taxa present in the GC both before and after the extinction (*22*).

2) Similar K-T extinction intensities might yield different long-term consequences among regions depending on the ecological roles of the victims or the invaders. This hypothesis would require, for example, that extinction-prone endemics (*1*, *4*) or other K-T victims in the GC were arrayed ecologically so that their disappearance was especially disruptive, for example, of competitive and trophic interactions (*23*). Keystone species are well understood in relatively few present-day communities, but this hypothesis could be at least partially tested by interregional analyses of the ecological roles, including the relative abundances, of local victims and survivors. Invaders of the GC are not enriched in predators or other feeding types relative to the other regions, so that the simplest hypothesis of community disruption is not supported. However, taken as a group, the invaders of the four regions tended to be more widespread than the rest of the K-T survivors before the event (Fig. 5B), lending support to the general view that invaders are not a random sample of the biota.

The geographic variation in patterns of biotic recovery, including differences among provinces as donors and recipients of invading taxa, provides additional evidence for the macroevolutionary complexity of post-extinction intervals (*1*). Recoveries do not necessarily unfold simultaneously and in coordinated fashion among regions; instead, clade expansion or stability may be region-specific rather than depending simply on clade-specific diversification rates or competitive ability. These results add a geographical dimension to the contingencies imposed by major mass extinctions, the "evolutionary founder effect" hypothesized by Raup (*24*).

These results may also have implications for present-day biotas, which appear to be increasingly subject to anthropogenic extinctions and to invasions involving global networks of interchanges. Asymmetries in such interchanges are the rule today as in the geologic past, with properties of invaders, recipient communities, and the physical environment each implicated by theory or data in determining invasion success for different situations (*15*, *16*, *25*, *26*). The Cretaceous data show that extinction intensity in the recipient region is not a universal predictor of such imbalances; potential explanations range from a threshold in extinction magnitude above which such predictions fail to an ecological trauma unique to North America. The fact that successful invaders of post–K-T faunas were widespread before the event suggests a line of research that could contribute to a more complete, general theory of donor-recipient dynamics for biotic invasions.

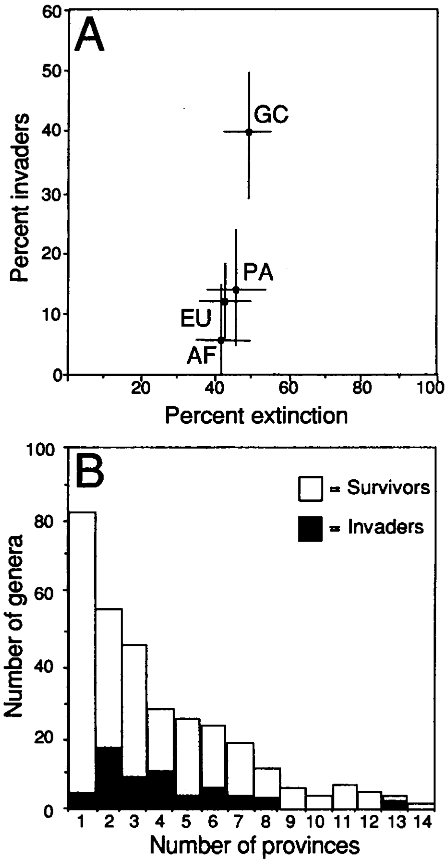

Fig. 5. (**A**) Relation between extinction intensity and proportion of invader genera in the first post-extinction time interval; extinction intensity in the GC fauna of North America is similar to those of other regions, but invasion intensity is not. The rank order of the two variables does match, but the extinction intensities form a tight cluster. (**B**) Geographic range of invaders and other K-T survivors. Distributions are significantly different ($P < 0.05$; Kolmogorov-Smirnov test).

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10. Nannofossil zones are grouped into the following intervals: 1, Maastrichtian nannofossil zones upper NC20 to NC23; 2, lower Danian zones NP1 to lower NP3; 3, upper Danian–lower Selandian zones upper NP3 to lower NP4; 4, upper Selandian zones upper NP4 to lower NP5; 5, lower Thanetian zones NP6 to NP8; and 6, upper Thanetian zone NP9. The last Paleocene interval is briefer than the others [1.2 My according to (*27*)], but as this disparity produces no anomalous diversity peaks or valleys, no attempt was made to expand the interval to include the earliest Eocene.
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Geomagnetic Modulation of the ^{36}Cl Flux in the GRIP Ice Core, Greenland

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Geomagnetic field strength is expected to affect the production rate of cosmogenic isotopes such as beryllium-10, carbon-14, or chlorine-36. Chlorine-36 data from the Greenland Ice Core Project (GRIP) ice core agree well with a production rate calculation based on a paleomagnetic reconstruction for the past 100,000 years over both long- and short-term variations. A chlorine-36 peak at 38,000 years ago previously found in the beryllium-10 record from the Vostok ice core can be explained by a period of low geomagnetic field intensity.

The geomagnetic dipole field shields the Earth from low-energy cosmic ray particles (*1*); this shielding effect is strongest at the magnetic equator and virtually absent at the magnetic poles. Hence, variation of the field strength affects the production rate of cosmogenic isotopes such as ^{14}C, ^{10}Be, or ^{36}Cl. The ^{14}C calibration curve is short, and so a definite interpretation of its long-term variability as a geomagnetic field effect is difficult (*2*). Longer time series, such as a comparison of the Vostok ^{10}Be data with geomagnetic profiles (*3*) and a comparison of geomagnetic paleointensity and ^{10}Be in the same core (*4*), support the correlation for the past 100,000 years, but it has been difficult to demonstrate a correlation on short time scales. Here, we present a high-resolution investigation into the correlation between a radioisotope flux curve and a geomagnetic field reconstruction using data from the GRIP ice core.

The abundance of ^{36}Cl and ^{10}Be for the past 100,000 years has been measured in the Summit GRIP ice core (*5*, *6*). Similar data are available in the Summit Greenland Ice Sheet Project 2 (GISP2) ice core (*7*), but at a somewhat lower resolution. We assume that the flux of ^{36}Cl and ^{10}Be over southern and central Greenland is directly related to the global average production of these isotopes. Greenland receives a considerable part of its precipitation from lower latitudes, and this pattern persisted during the last ice age (*8*). Therefore, it is unlikely that the flux of ^{36}Cl and ^{10}Be is dominated by local radioisotope production, which is not very

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