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 extant species (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 partitioned into a number of ecologically and phylogenetically important groups to facilitate comparison with Hansen’s GC analysis (11). Preservation and sampling 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...
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-

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**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.

<table>
<thead>
<tr>
<th>Interval</th>
<th>GC</th>
<th>EU</th>
<th>AF</th>
<th>PA</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>542</td>
<td>464</td>
<td>363</td>
<td>295</td>
</tr>
<tr>
<td>2</td>
<td>123</td>
<td>184</td>
<td>46</td>
<td>105</td>
</tr>
<tr>
<td>3</td>
<td>177</td>
<td>462*</td>
<td>128</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>136</td>
<td>185</td>
<td>106</td>
<td>147</td>
</tr>
<tr>
<td>5</td>
<td>80</td>
<td>372</td>
<td>139</td>
<td>85</td>
</tr>
<tr>
<td>6</td>
<td>166</td>
<td>245</td>
<td>71</td>
<td>-</td>
</tr>
</tbody>
</table>

*Reflects exceptional sampling and preservation, for example, Calcaire de Mons.
actions (example, of competitive and trophic inter-
appearance was especially disruptive, for
were arrayed ecologically so that their dis-
Venericor
-Calyptraphorus
-nas, including Calyptraphorus, Baluchicardia,
Venericor, and Sigmesalia (20); the last three
are members of Hansen’s bloom taxa.

Although the anomalous molluscan re-
covery in the GC—with its excursion of
bloom taxa and invader-rich biota—is con-
sistent with the hypothesized oblique tra-
jectory for the K-T impact at Chicxulub,
Yucatan (21), more definitive tests are re-
quired. 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 Amer-
ica can test whether those of the GC simply
reflect proximity to the impact site.

The anomalous GC recovery is problem-
atic in light of the similar K-T extinction
intensities among the study areas. Two al-
ternatives 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 conse-
quences among regions depending on the
ecological roles of the victims or the in-
vaders. 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 dis-
appearance was especially disruptive, for
example, of competitive and trophic inter-
actions (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 dis-
ruption 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 sam-
ple of the biota.

The geographic variation in patterns of
biotic recovery, including differences among
provinces as donors and recipients of invad-
ing taxa, provides additional evidence for
the macroevolutionary complexity of post-
extinction intervals (1). Recoveries do not
necessarily unfold simultaneously and in co-
ordinated fashion among regions; instead,
clade expansion or stability may be region-
specific rather than depending simply on
clade-specific diversification rates or com-
petitive ability. These results add a geo-
ographical 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 ex-
tinctions and to invasions involving global
networks of interchanges. Asymmetries in
such interchanges are the rule today as in
the geologic past, with properties of invad-
ers, 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 in-
tensity in the recipient region is not a uni-
versal predictor of such imbalances; poten-
tial 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.

REFERENCES AND NOTES

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U.S.A. 91, 6758 (1994); D. Jablonski, in Extinction
Univ. Press, New York, 1995), pp. 25–44; M. J.

2. T. A. Hansen et al., Paleobiology 19, 251 (1993);
3. The Pakistan–India outcrop area was on the northern shelf of the Indian Plate, which was close to or straddling the equator at this time; see, for example, A. G. Smith et al. (Atlas of Mesozoic and Cenozoic Coastlines, Cambridge, 1994).


9. In contrast, N. MacLeod and G. Keller [Paleobiology 20, 143 (1994)] have suggested that high-latitude regions served as a refuge at the K-T boundary and as a postextinction source for oceanic plankton.

10. The NCuca perciformes lineage is lost at the K-T boundary even though the genus NCuca survives to participate in the GC rebound [G. L. Wingard and N. F. Sohl, U.S. Geol. Surv. Bull. 1881, D1 (1991)].

11. For example, the GC’s NCuca perciformes lineage is lost at the K-T boundary even though the genus NCuca survives to participate in the GC rebound [G. L. Wingard and N. F. Sohl, U.S. Geol. Surv. Bull. 1881, D1 (1991)].

12. For review, see M. E. Power et al. [ Bioscience 46, 609 (1996)].


15. Of the basis of the time scale of Berggren et al. (27). This time scale differs from that used by Hansen et al. (2), so GC faunal units used here do not coincide exactly with that study. For the Mesozoic time scale used here, see F. M. Gradstein et al. [ Science 260, 196 (1993); T. J. Case, Biol. Conserv. 78 (1996).]

16. Comparison of the Vostok 10Be data with related data from the GRIP ice core (6) suggests that high-latitude regions served as a postextinction source for oceanic plankton. Greenland receives a considerable fraction of its radiocarbon from the GRIP ice core.

17. The magnetic 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 14C, 10Be, or 36Cl. The 14C 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 10Be data with geomagnetic profiles (3) and a comparison of geomagnetic paleointensity and 10Be 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.

18. The abundance of 36Cl and 10Be for the beryllium-10, 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.

Geomagnetic field strength is expected to affect the production rate of cosmogenic isotopes such as beryllium-10, 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.

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The abundance of 36Cl and 10Be 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 36Cl and 10Be 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 36Cl and 10Be is dominated by local radioisotope production, which is not very geographical.