

ated or that these forams have been reworked from Paleocene beds on the crater rim that were previously thought to postdate the crater.

Our ^{40}Ar - ^{39}Ar age of 49.15 ± 0.18 Ma implies that the Kamensk structure is early Eocene, not Paleocene or KT boundary age. This isotopic age, recalculated using a reference age of 520.4 Ma for MMhb-1, is 49.84 ± 0.18 Ma, which is identical (within experimental error) to the 50.5 ± 0.8 Ma age reported by Bottomley and York [10] for the 50-km-diameter Montagnais impact structure on the continental shelf off Nova Scotia. This close match in age for the two impact structures may only be fortuitous, but alternatively, it might indicate that both impact structures formed during nearly simultaneous impacts of large fragments of a single disrupted comet.

It is also of interest to try to place Kamensk on the standard paleontologic and magnetostratigraphic timescales. If one uses the Harland et al. [11] or DNAG timescales, an age of 49.84 Ma would fall in chron 21N, and fossil plankton zones P10, CP12, and NP14. However, recent recalibration of the Eocene timescale by Montanari et al. [12] suggests that the standard timescale is off by several million years through most of the Eocene. On the Montanari et al. timescale, the age of the Kamensk structure falls in chron 22R and zones P9, CP11, and NP13. From stepwise alternating field demagnetization measurements of the single specimen of core, we believe that we have recovered the orientation of the specimen and tentatively conclude that the characteristic magnetization is reversed and consistent with an age assignment to chron 22R.

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MASS EXTINCTIONS: PERSISTENT PROBLEMS AND NEW DIRECTIONS. D. Jablonski, Department of the Geophysical Sciences, University of Chicago, 5734 South Ellis Avenue, Chicago IL 60637, USA.

Few contest that mass extinctions have punctuated the history of life, or that those events were so pervasive environmentally, taxonomically, and geographically that physical forcing factors were probably involved. However, consensus remains elusive on the nature of those factors, and on how a given perturbation (impact, volcanism, sea-level change, oceanic anoxic event) could actually generate the observed intensity and selectivity of biotic losses. At least two basic problems underlie these long-standing disagreements: (1) difficulties in resolving the fine details of taxon ranges and abundances immediately prior to and after an extinction boundary and (2) the scarcity of simple, unitary cause-and-effect relations in complex biological systems.

Detailed Stratigraphic Patterns: Local outcrops and cores are the ultimate source of the data used to analyze mass extinctions, but the pitfalls to taking local data at face value are still little

appreciated, resulting in massive overinterpretation of paleontological patterns. The accumulation of sediments and fossils is discontinuous and environmental change is the rule, so that temporal gaps and stepped extinctions are inevitable on some scale in any local sequence. Further, reworking and time-averaging mix fossils from successive intervals; radiocarbon dates on shells collected from surface sediments and forams in core tops indicate a time-averaging window of 10^3 - 10^4 yr in marine shelf and deep-sea sediments alike [1]. Statistical protocols are available to test for artificial extinction steps and to place confidence limits on stratigraphic ranges [2,3], but to date these have seen little use in the mass extinction literature: nearly all workers want to take their data at face value and as virtually devoid of local overprint. Clearly, the answer to this problem is to test patterns against an appropriate null hypothesis.

Inferring Cause from Effect: One fundamental obstacle in linking extinction patterns and hypothesized forcing factors resides in the nature of complex systems: nonlinearities, thresholds, and elaborate feedbacks often rule out the reconstruction of simple cause-and-effect cascades. The same forcing factor might have radically different effects depending on the state of the system at the time of perturbation, and several alternative forcing factors might produce the same biotic response. The survival of an evolutionary lineage during a mass extinction, for example, could be because it (1) lived in a habitat that was not stressed, (2) possessed a physiology or life habit that allowed it to survive in a stressed habitat, (3) was so widespread that its range includes a locality that provided a refuge, and so on. Urgently needed is not another catalog of potential reasons for survival or extinction, but the development of protocols for testing the alternatives. This is partly a matter of constructing large, robust databases amenable to statistical analysis, and coming to grips with the need to integrate local and synoptic databases. With sufficient tuning, the long list of potential KT killing mechanisms can indeed account for virtually any conceivable extinction pattern; therefore, while the mere fact of observed selectivity clearly is no argument against impacts, neither is it an argument in their favor. The time for consistency arguments is past: hypothesized extinction mechanisms need to generate unique predictions on the timing, selectivity (taxonomic, biogeographic, ecologic), or other biotic patterns to advance beyond the status of plausible alternatives.

Selectivity is still a neglected area of study for mass extinctions, and even negative results will be important here. Selectivity is played out, if at all, at lower taxonomic levels (families and genera), biogeographically, or ecologically, and the relevant parameters are largely absent from the synoptic databases [4]. Consider the problem of multiple causation for one general pattern: the apparently higher extinction intensities in the tropics. The question is whether the greater losses of shallow-water late Devonian corals relative to deep-water genera, or of symbiont-bearing KT corals and rudist bivalves relative to nonsymbiotic corals and nonrudist bivalves, occur because (1) tropical biotas in general are fragile, perhaps because their species are adapted to a narrow range of climatic and other conditions; (2) reef communities in particular are such a tightly woven network of biological interactions that the initial removal of the same proportion of species as were lost at high latitudes could be more disruptive; (3) tropical biotas contain a large proportion of extinction-prone endemics, so that losses are high here owing to biogeographic structure; or (4) the favored habitat of reef communities, low-sedimentation, and low-nutrient shallow-water platforms or ramps, is itself easily disrupted [5,6]. Some support exists for

(3) and (4). First, among-province variation in mass extinction intensities within latitudinal belts tends to be positively related to the proportion of endemic genera in the preextinction biota [7]. Second, a global analysis of end-Cretaceous extinction in marine bivalves found that tropical settings outside the carbonate platforms suffered no greater losses than did extratropical faunas [8]; the reported latitudinal gradient in plankton extinction intensities may have a similar basis. The statistical dissection of alternative mechanisms offers considerable promise for improving our understanding of extinction mechanisms and biological consequences, both for the Big Five mass extinctions and for the smaller extinction maxima that occur throughout the Phanerozoic.

The initial physical and biological conditions must play a role in the biotic response to a perturbation. Perhaps, for example, impacts or volcanism at times of low relative sea level yield greater taxonomic losses than the same event at times of high sea level when the thermal inertia and other ameliorating effects of shallow seas are prominent. This frequent suggestion has yet to be modeled rigorously, let alone tested empirically, but may help to explain why some geologically detectable impacts evidently had negligible biotic effects. The global biota or even individual taxa may vary in relative extinction vulnerability through time. For example, it may take time to accumulate a new crop of extinction-prone taxa after a major extinction event has removed all but the hardiest lineages. Conversely, lineages may evolve in directions that make them less vulnerable to successive perturbations. Such biotic lags and long-term shifts might explain waiting times between extinction events [9, but see 10], and the differential responses of individual taxa to successive extinctions [7].

The evolutionary impact of mass extinctions is another active area of research. Many of the biotic replacements once thought to represent competitive victories over inferior lineages now appear to have been mediated by major extinction events, even though most species extinctions in the fossil record, probably >90%, occur outside the five major extinction events [11]. Mass extinctions have such profound biological consequences because they bite deep into standing diversity and disrupt background selection regimes, not because they account for most species terminations. Traits that favor survival during mass extinctions need have little correlation with those that enhance survival and diversification during background times, so mass extinctions can have unpredictable and lasting evolutionary effects [5,7]. Not only do mass extinctions remove taxa and adaptations well-suited to the background regimes that represent the great bulk of geologic time, they create ecological and evolutionary opportunities by removing incumbent, dominant taxa and enabling other taxa to diversify in the aftermath of the extinction event. On the other hand, mass extinctions do not completely reset the evolutionary clock: many major evolutionary and ecological trends transcend even the Big Five events (e.g., the modernization of marine communities, the rise of flowering plants, and of predatory neogastropods). We need to understand survivors and rebounds as well as victims and ecosystem collapse.

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GLOBAL BIOTIC EFFECTS OF THE KT BOUNDARY EVENT: MASS EXTINCTION RESTRICTED TO LOW LATITUDES? G. Keller, Department of Geological and Geophysical Sciences, Princeton University, Princeton NJ 08544, USA.

One of the most important recent developments in KT boundary studies is the growing awareness that (1) the mass extinction associated with this event is not the result of a single catastrophe, (2) that extinctions occurred over an extended time period and were selective rather than random within organismal groups as well as between different groups, and (3) that the biotic effects were most severe and sometimes limited to tropical-subtropical regions while high-latitude faunas and floras escaped virtually unscathed. The growing global body of high-resolution faunal and floral data upon which these observations are based now provides the empirical database and the opportunity to test various KT catastrophe scenarios whether volcanic or bolide-impact based. Moreover, specific details of these scenarios can now be tested, including the dust cloud-darkness and shutoff of photosynthesis, acid rain, nuclear winter, and global greenhouse scenarios all presumably leading to global mass extinctions. Unfortunately, there has been no serious test of these scenarios based on empirical data, largely because (1) many catastrophists ignore paleontologists' data and interpretations that widely disagree with their theories, (2) many paleontologists ridicule catastrophists' theories for which they see no basis in the fossil record, and (3) experts disagree among themselves depending on which side of this scientific chasm their sympathies lie. Despite these seemingly insurmountable differences, there is hope for a growing interdisciplinary discourse as both sides accumulate and synthesize more observational data. All scientists agree that a major environmental change occurred across the KT boundary; they disagree on the cause, whether impact or volcanism, and on the biotic effects of this environmental change. Here I will address the latter. Ultimately it is the biotic data that must determine how significant a bolide impact or massive volcanism at KT boundary time was for life on Earth.

The planktic foraminiferal record has played a unique role in the KT boundary controversy. Near the base of the food chain, these single-celled marine plankton are both sensitive to environmental changes and a critical food source for higher, more complex organisms. Moreover, they have long been known to undergo a virtually complete faunal turnover between the end of the Cretaceous and early Tertiary with deep-sea studies documenting a sudden mass extinction at the boundary [1–3]. This prior interpretation cannot be supported by subsequent studies for three major reasons. First, this conclusion was originally based on deep-sea sections that have been subsequently shown to contain major hiatuses spanning from 60 k.y. to 500 k.y. of the basal Tertiary [4,5]. In these sections extinctions and originations, spanning as much as 0.5 m.y. across the KT transition, are artificially concentrated at one horizon giving the appearance of a sudden catastrophic mass extinction. In contrast, shallow