Standing, left to right:
Wolfgang Stinnesbeck, Wayne Sousa, Michael Soulé, Jack Sepkoski, Karl Flessa

Seated (center), left to right:
Dave Raup, Tony Hallam, Gerrat Vermeij, Heinz Erben

Seated (front), left to right:
Martin Hüssner, Ken Hsü, David Jablonski

Causes and Consequences of Extinction

Group Report

K. W. Flessa, Rapporteur
H. K. Erben   J. J. Sepkoski, Jr.
A. Hallam   M. E. Soulé
K. J. Hsü   W. Sousa
H. M. Hüssner   W. Stinnesbeck
D. Jablonski   G. J. Vermeij
D. M. Raup

Mass Extinctions, Extinction Events, and Background Extinctions

At the present time the criteria used to distinguish categories of extinction (e.g., mass vs. background) are arbitrary (Sepkoski, this volume). For a variety of reasons, not the least of which are the difficulties associated with the precise resolution of the duration of events in the fossil record, our understanding of the range of variation in extinction intensities is inadequate. Until such time that the durations of episodes of extinction are accurately known, the expression of extinction intensity as a rate (number or proportion/duration), while both possible and desirable, can be misleading. Consider a hypothetical case of two extinction events, each resulting in the extinction of ten species. If one event occurred within a stratigraphic interval of one million years while the other event fell within an interval estimated to be two million years in duration, a twofold variation in calculated rates would result. In any event, extinction intensities calculated as the magnitude of the event divided by the interval's duration will always be underestimates. Instantaneous events are constrained to appear as protracted events if their effect is averaged over a long sample interval.

The possibility remains that the record of Phanerozoic extinctions may be one of a spectrum of extinction intensities ranging from mass extinctions down to background extinction levels; this spectrum may or may not be

continuous. A consensus was reached that the term mass extinction should be set aside for extinctions characterized by substantial magnitude and global extent, broad taxonomic effect, and relatively short temporal duration. We recognize that this definition is not an operational one inasmuch as it fails to specify precisely the magnitude, extent, breadth, and duration needed to qualify. Nevertheless, our failure to provide an operational definition is not likely to retard research into the subject. Research strategies will be governed by the nature of the extinctions themselves, not by our definition.

There is widespread agreement that the five major extinctions of the Phanerozoic – those occurring in the end-Ordovician, Late Devonian, Late Permian, Late Triassic, and end-Cretaceous – were phenomena that stood above and apart from the rest of Phanerozoic extinctions (see Fig. 1).

Episodes of extinction intensity that are intermediate between these five and background levels may be best thought of as "extinction events." Such extinction events may often be taxon- or region-specific and are exemplified by extinctions such as those of Cambrian trilobites at biomere boundaries, Mesozoic ammonites at various horizons, Late Pleistocene mammals of
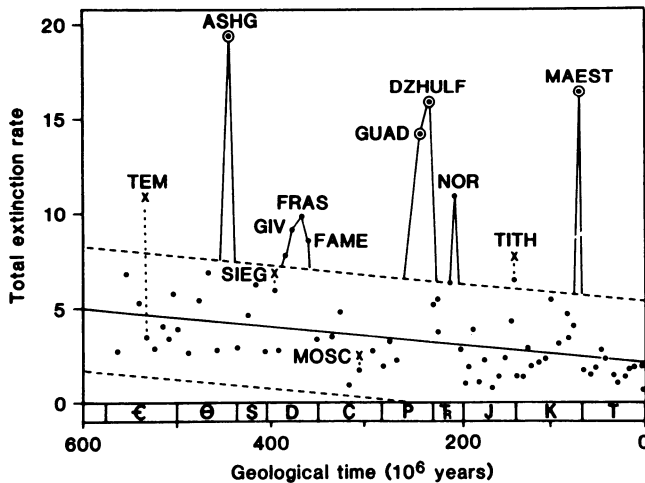

Fig. 1. Extinction rate (families per million years) of marine invertebrates and marine vertebrates through time. Mass extinctions occur in the Late Ordovician (*ASHG*), Late Devonian (*GIV, FRAS, FAME*), Late Permian (*GUAD, DZHULF*), Late Triassic (*NOR*), and Late Cretaceous (*MAEST*). X indicates extinction rate of stage if rarely preserved animals are included. So-called background rates occur within the dashed line on either side of the solid regression line [31]

North America, and Pliocene molluscs of the North Atlantic. Although such extinctions are clearly important events in the history of life, their apparently restricted taxonomic scope, geographic extent, and magnitude set them apart. Some of these taxon-specific extinction events may also be characterized by high origination rates, thus resulting in high evolutionary turnover with little effect on standing diversity. These events may be phenomena that will yield additional insight into those environmental factors that regulate evolutionary rates.

The time span over which extinctions are observed is important at many scales. Even so-called background extinctions, while seemingly continuous when compared to the five mass extinctions of the Phanerozoic, may be episodic if viewed at increasingly finer levels of temporal resolution. Considered on the year-by-year basis available in historic time, the extinctions of the past 300 years may also be episodic.

Less agreement characterized our search for qualitative differences between mass and background extinctions. Although it seems clear that mass extinctions often differ in their effects when compared to background extinctions, such differences could be attributed either to the operation of a threshold effect of to the imposition of causes of a fundamentally different nature. This is an issue to which we return later in this report.

We identified two areas in which future research would be likely to yield insight into the distinctions (if any) between and among mass extinctions, extinction events, and background extinctions.

The Nature of Variation in Extinction Intensity

Is the variation continuous or discontinuous? Critically important for such analyses are data derived from within as detailed a chronostratigraphic context as possible. Particularly useful analytical techniques for the study of the variation in extinction events may be those used in the study of flood and earthquake frequency. In addition, the application of polycohort survivorship techniques (Fig. 2) (for example, see [14, 28]) to taxon-specific analyses of extinctions through time may yield insight into the variation in extinction magnitude.

The Geographic Extent of Extinction

Several extinction events can be considered as "candidates" for mass extinction, yet their geographic extent is poorly documented (see Sepkoski, this volume). Attention should be directed toward such extinction events as the Late Cambrian biomere events, the Fammenian Tournasian, the Pliensba-
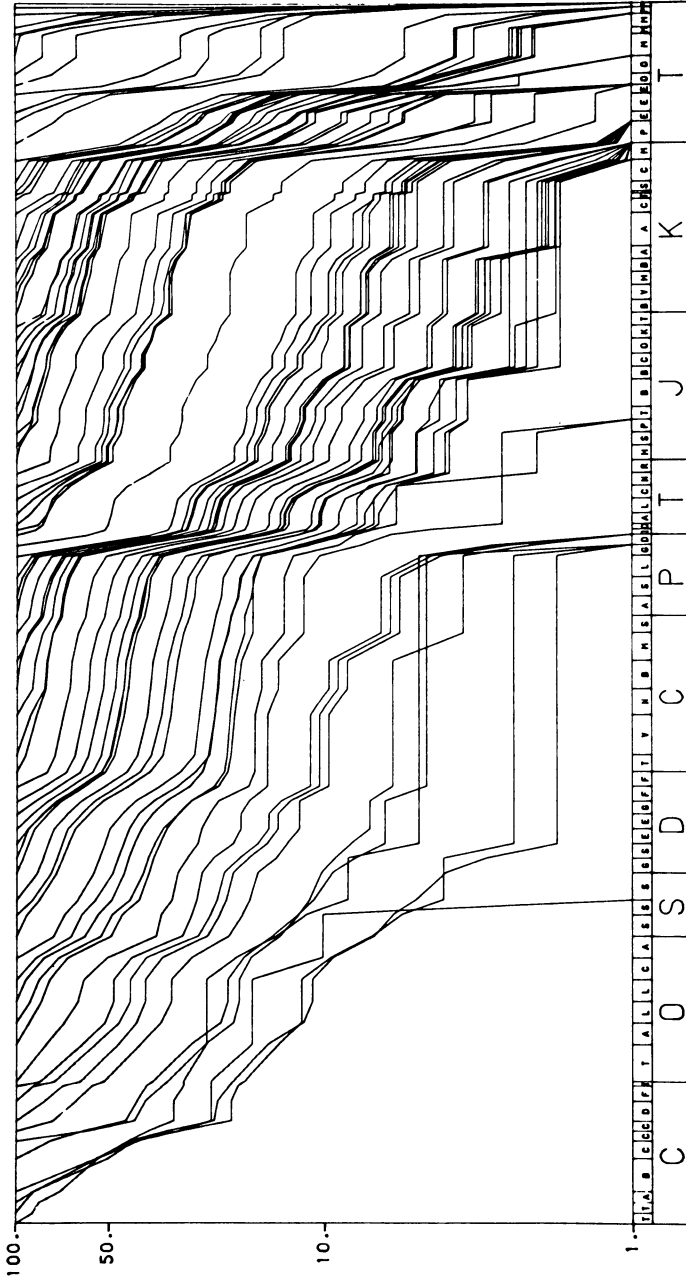
Fig. 2. Polycohort survivorship of 2316 extinct marine families during the Phanerozoic. Each curve traces the survivorship of families that were extant (the polycohort) during a geologic stage. Steep portions of the curve represent intervals of elevated extinction rates. Low slopes record intervals of low extinction rates. Because the same family may belong to several polycohorts (for example, a family present in both the Middle and Upper Devonian will belong to both polycohorts), the extinction of a single family may be reflected in more than one survivorship curve. This tends to exaggerate the intensity of episodes of mass extinction

chian-Toarcian, the Tithonian, and the Cenomannian-Turonian in an effort to assess their importance. Knowledge of the geographic extent of an extinction event may provide important clues as to its cause.

Extinctions During Historic Time

We have no knowledge of recent "natural" extinctions of entire species, at least those on continents and in the marine environment. Patterns and levels of extinction on contemporary islands can be instructive, but the extrapolation of the extinction of local populations to the global extinctions of species must be done with great care. The demise of species during historic time results almost exclusively from the direct and indirect consequences of human activities. The destructiveness of *Homo sapiens* may parallel some of the environmental catastrophes of the geologic past – estimates of the extinction of species resulting from the cutting of the South American rain forests approach values typical of the mass extinctions of the Phanerozoic. If the destructiveness of humans is comparable to the destructiveness and effects of purported meteorite impacts or other events that precipitate mass extinctions, we might be able to generalize about or predict the relative vulnerability of species of biotas to such prehistoric events.

Among contemporary species, there are certain life-history traits and extrinsic factors that appear to alter or affect the probability of extinction. These factors, endogenous or exogenous, deterministic or random, have been reviewed by many authors, including Simberloff (this volume). Many of these characteristics tend to occur as constellations within species, i.e., they are inter-correlated (see LaBarbera, this volume, for a review of those factors related to body size). To summarize these studies briefly, the best predictors of susceptibility to extinction based on our very limited knowledge of contemporary, anthropogenic extinctions of animals are a) large body size; b) low r (intrinsic rate of population increase); c) low N (population size); d) high variance of r or N; e) dependence on rare, dispersed, or ephemeral resources; f) poor or low vagility; and g) local endemism.

Exacerbating these factors would be a reduction in geographic range or effective population size. Should a species or one of its popuplations be reduced in numbers to the range 10^1 to 10^3 individuals, this will lead to inbreeding and a loss of genetic variation.

Recent reviews of the subject [1, 22] are approaching a consensus on the issue of heterozygosity: a significant loss of genetic variation by a population is frequently associated with a loss of immediate or short-term fitness

of its individuals, expressed as decreased growth rate, metabolic efficiency, developmental homeostasis (e.g., bilateral symmetry), viability, and longevity. Inbreeding in species that do not normally undergo selfing or inbreeding is virtually always deleterious. The relevance of such consequences of reduced population size to understanding the causes of fossil extinction is not clear. The processes that result in the extinction of species having but 10^1 to 10^3 individuals (such species might be virtually "invisible" in the fossil record) may be quite different than the processes that initiate the decline in population size to such a precarious level.

Extinctions during historic time can be attributed to a) competition, b) predation, c) random population fluctuation, and d) habitat change. With the exception of island settings and direct competition with *Homo sapiens,* competition does not appear to play a major role in contemporary extinctions. Again, with the possible exceptions of islands and the hunting activities of historic and prehistoric humans, predation seems to be an uncommon cause of species extinctions. Random population fluctuations, while often the most proximal causes of species extinctions, probably play but a minor role in continent and continental shelf settings. Habitat alteration, either directly or indirectly induced by humans, seems to be the major cause of extinctions during historic time. In addition, the extinction of a key species within a community can lead to damaging effects on other species, perhaps resulting in an ecologically generated cascade of species extinctions.

Much of our data on prehistoric extinctions comes from the stratigraphic record of marine habitats, but we know virtually nothing about contemporary extinctions in such environments. Therefore, a major challenge to paleobiology lies in the prediction of the vulnerability of fossil marine taxa to changes in habitat size, temperature, oxygen tension, turbidity, seawater chemistry, and light. The characteristics of organisms that determine their susceptibility to those exogenous changes are metabolic rates, capacity to become dormant, resistance to sudden, variable, or prolonged changes in temperature, the ability to tolerate prolonged periods of starvation and to find and exploit isolated patches of resources, and the production of resistant and persistent dispersing offspring.

As Sousa's [39] review of the role of natural disturbance in extant communities shows, organisms have evolved mechanisms for coping with a wide variety of natural physical disturbances. Indeed, some species (i.e., fugitives, *sensu* Hutchinson [17]) have come to depend on them for their very persistence. However, the scales of disturbance that result in species extinction appear to be quite distinct from those to which these species have evolved.

Insight into the processes of extinction among fossil species might be gained from study of contemporary examples of large-scale habitat alteration, e.g., the ambitious experiments of the World Wildlife Fund in Brazil [23]. In addition, we expect that much can be gained from a systematic review of the literature concerning large-scale habitat alteration in such marine settings as the Baltic and the Mediterranean Seas.

The Record of Extinctions:
Issues of Quality and Temporal Pattern

The past few years have seen considerable progress in our understanding of the character of extinctions, and the plausibility and persuasiveness of many extinction models is now considerable. We should not lose sight of the fact that our evidence on the precise timing, duration, and faunal effects of many extinctions is still remarkably limited. Consider, for example, that our knowledge of changes in the marine macrofossil record in the immediate vicinity of the Cretaceous-Tertiary boundary is based on very few sections. In addition to this limited degree of geographic documentation we should recognize that the stratigraphic and chronostratigraphic resolution of our data is very uneven. While the range terminations of many taxa are known with confidence, other precise age assignments are precarious, ambiguous, and almost always disputable. For example, the precise stratigraphic level of the final extinction of the ammonites remains a controversial issue. This situation requires an intensification of our empirical work, with detailed work on new as well as previously studied stratigraphic sections that contain important extinction horizons. Such careful stratigraphic work may provide important constraints and tests for many extinction models.

Our ability to discern the abruptness of an extinction in the fossil record is dependent on stratigraphic and paleontologic resolution. Stratigraphic incompleteness, diagenesis, facies changes, and biogeographic changes can cause gradual extinctions to appear as if they were sudden events of great magnitude. Two factors can conspire to *reduce* the observed magnitude of an event: reworking of fossils up a stratigraphic section and "backward smearing." Bioturbation, especially in deep-sea sediments sampled in cores, tends to cause the diffusion of fossils upward over scales of centimeters to decimeters, and together with resedimentation can cause microfossils to occur at horizons slightly above their actual level of extinction. Geochemical

signatures within the tests of these microfossils may provide a means for the recognition of such upward mixing. More serious is the backward smearing of observed extinction resulting from incomplete sampling of the fossil record. In most paleontologic analyses, extinction events are assessed from the observed stratigraphic ranges of species or higher taxa; these ranges are simply the time range between the first and last observations of a taxon either in a local stratigraphic section or in a compilation based on the correlation of numerous sections. However, observed ranges are always minimum estimates of actual ranges, and the failure to sample a taxon over all of its true range will cause truncation at both the bottom and top of the actual range. Signor and Lipps [37] have shown by means of statistical models that the failure to sample taxa at the precise time of their last appearance can quickly alter the appearance of an abrupt extinction event in stratigraphic range charts, causing observed numbers of extinctions to increase gradually well before (sometimes several stages before, in the case of very large extinction events) and then accelerate just before the actual horizon of the mass extinction. This pattern will be further exacerbated if there are any facies changes below the extinction horizon. Jablonski [18] and Waterhouse and Bonham-Carter [48] have shown empirically that this backward smearing does indeed occur in the fossil record. In Jablonski's analysis of the "Lazarus effect," he showed that taxa that actually survived an extinction event "disappeared" well below the extinction event, only to "reappear" above it. The artificial last occurrences were smeared backward in the record as predicted (see also Jablonski, this volume). Once recognized, such artificial extinctions can be used to place confidence limits on the observed pattern of final extinction in critical time intervals [18].

Because an important current issue in the study of extinctions involves their temporal distribution, the quality of the geologic time scale will affect our effort to detect any periodic pattern in the record of extinctions. Inasmuch as the search for periodicity in the record of extinctions has focused on the record of the past 250 myr, the quality of the time scale for the Cenozoic and Mesozoic is especially important. Although the Cenozoic time scale seems well established, the Mesozoic time scale prior to the mid-Cretaceous is currently rather poor. This is because of an insufficient number of biostratigraphically well located, reliable radiometric dates and a lack of correlation with seafloor magnetic anomalies. In consequence, the range in age of some stages among several recently proposed time scales is on the order of five million years and is as much as 14 million years for the Jurassic-Cretaceous boundary. It is clear that there is an urgent need to obtain many more radiometric dates and to refine methods of establishing

time scales through the use of ammonite chrons as the minimum unit of stratigraphic subdivision.

Taking into account reasonable estimates of sedimentation rates in deep-sea cores, the age of the Cretaceous-Tertiary Boundary event perhaps can be estimated on the basis of sedimentation rates to within a few thousand years or even less. But nowhere else in the Phanerozoic has a major extinction event been dated to such a degree of precision. Magnetic stratigraphy has proven useful, especially for correlation between marine and continental sections, but here the time resolution is commonly on the order of 0.5 myr. Thus, it remains an article of faith that the dinosaur and calcareous plankton extinctions of the Cretaceous-Tertiary were precisely synchronous, as required by certain extinction scenarios.

Our discussions of patterns in the record of extinctions focused almost exclusively on the detection and significance of patterns in the timing of mass extinctions and extinction events during the past 250 million years. Little attention was paid to potential patterns in the variation of extinction intensity through time. In part this may be due to the difficulty in providing confident estimates of the intensities of extinctions, in part to the allure of the issue of periodicity.

Are extinction events uniformly spaced (periodic) in geologic time? Claims of regular periodicity in the marine fossil record have been published by Fischer and Arthur [6], Raup and Sepkoski [32], Rampino and Stothers [27], and Kitchell and Pena [21] (a pseudo-periodicity, in their analysis) with periods of 32, 26, 30, and 31 myr, respectively. Discussion of these claims raises complex questions of statistical procedure and of uncertainties in the empirical data [13]. The more fundamental question, however, is whether the distribution of extinctions in time is a consequence of a) many independent causes operating in an unpredictable fashion, or b) a single driving mechanism or ultimate cause. If the former is true, and this has been the conventional wisdom, one can predict that the extinction events should show a random spacing in time; but it can be shown that the major extinctions have a distinctly nonrandom distribution. That is, they are more evenly spaced than is typical of random distributions. For extinctions from Permian time to Present, the nonrandomness appears statistically highly significant. Furthermore, stationary periodicity yields excellent fits to the extinction data at both generic and family levels for fossil marine animals. This does not prove that the simple periodicity is the best description of the extinction pattern because it is logically impossible to test all nonrandom patterns that could describe the actual distribution. However, given a choice between randomness and periodicity, tests of the data sug-

gest periodicity, and periodicity thus emerges as the hypothesis to investigate.

As discussed above, the quality and temporal precision of the data base is a persistent issue. In the face of uncertainties over the data, two approaches are possible: a) the use of all available data in the hope that if the pattern of periodicity is strong enough, the signal will be apparent, even in the degraded data at hand, and b) the use of high-quality subset of the whole data base, culled so as to remove the most untrustworthy data. It is impressive that both approaches reveal a more or less uniform spacing between extinctions [35]. Uncertainties in the timing of extinctions persist, but errors in their age assignments would tend to decrease the chances of detecting a periodic signal and are not likely to generate or enhance a periodic signal. By the very nature of statistical tests, it is an easier task to reject the null hypothesis of randomness than it is to accept the conclusion of periodicity. Considering the work on this issue to date, either the patterns detected in the record of extinctions of the past 250 myr are robust or the statistical tests are not very sensitive (see Connor, this volume, for a review of analytical techniques useful for time-series data).

The periodicity issue is very important. This is not because it favors one causal hypothesis or another. Rather, it is important because it would suggest that most extinctions have similar causes and that the causes of one extinction, if discovered, would inform us about the causes of other extinctions.

Three research programs are likely to prove especially important in the study of temporal patterns of extinction.

Refinement of Taxonomic and Stratigraphic Data

Detailed local studies in the vicinity of extinction events and careful global compilations of such local studies will reveal crucial data on the timing and intensity of extinction. The need for such study is especially acute in the Paleozoic, where a periodic signal has yet to be detected.

Detailed Examination of the Fabric of Periodicity in the Marine Record

Efforts to detect periodicity within subsets of the marine fossil record may prove instructive. If the periodic pattern is particularly characteristic of certain clades or groups of clades, the paleobiology of those groups may suggest a cause of the pattern.

Extinctions in the Terrestrial Realm

The record of extinctions of terrestial plants and animals should be examined for evidence of synchronicity with the marine record and for periodicity. The presence or absence of periodicity in the terrestrial realm will have profound consequences for our understanding of the causes of global extinctions.

Victims and Survivors:
The Selectivity of Extinction

Why do some groups survive extinction events while others perish? As suggested in studies of contemporary extinctions, the biological properties of species may affect their probability of extinction. The fossil record also provides some information on this issue. Inasmuch as we can document the occurrence (if not often the cause) of more extinctions in the fossil record than have been documented in historic time, the fossil record may also provide information on the susceptibility of living species to extinction.

Some fossil groups, such as the ammonites and some Cambrian trilobites, show a "boom and bust" pattern of diversity. In these volatile clades high extinction rates are accompanied by high origination rates at most times. The paleobiology of these groups might suggest characteristics that result in high extinction rates.

The features that we identify below seem important in determining a taxon's probability of extinction. Few of these features can be said to be well established predictors of evolutionary survival. Nevertheless, each has some evidence in its favor, and while all deserve greater scrutiny and additional study, all support the proposition that extinction is not random with respect to a species' biology.

Geographic Range

It does seem well established that the geographic range of a taxon is correlated with its geologic duration (e.g., [3, 4]). Widespread taxa tend to be geologically long-lived, while geographically restricted, endemic taxa have relatively brief geologic durations. Recent evidence suggests, and it is reasonable to assume, that geographically restricted species (species on islands are good examples) tend to be more susceptible to the ravages of disease, accidents, predation, competition, and regional environmental change.

Among the factors that tend to result in a broad geographic distribution is dispersal ability. Because the larval shell morphology of bivalves and gastropods is often preserved on the hard parts of the adult, dispersal abilities can often be inferred directly from the fossil specimens themselves [19]. That dispersal ability, as expressed by larval shell type, is correlated with geographic range among extinct species of Cretaceous and Tertiary molluscs [12, 18] suggests that dispersal ability limits geographic range in evolutionary as well as ecological time. Yet a broad geographic distribution does not invariably result in a low probability of extinction. Mesozoic ammonites and bivalves such as *Monotis* and the inoceramids typically have broad geographic ranges, yet these groups are characterized by high extinction and high origination rates [9, 10].

Although a broad geographic distribution appears to confer extinction resistance on species during times of background extinction, analysis of species longevities and geographic distributions of Cretaceous-Tertiary bivalves and gastropods of the southern U.S. fails to reveal any correlation (Jablonski, this volume). In this case, the role of geographic distribution may express itself at a higher taxonomic level. Bivalve and gastropod genera with representatives in more than one province tend to survive the end-Cretaceous event, whereas those genera with species restricted to but one province tend to perish. This suggests that selection during mass extinction regimes may differ and may be expressed at higher hierarchical levels than selection during background times (Jablonski, this volume).

Body Size

Species of large-bodied individuals appear to become extinct with greater frequency than species characterized by small-bodied individuals. This pattern has been suggested in studies of both terrestrial vertebrates [44] and marine invertebrates [8]. Explanations for this pattern are varied, but the lower population densities, lower birth rates, and/or greater nutritional requirements of larger organisms are the most likely proximal reasons for greater susceptibility to extinction. That large body size could tend to increase the probability of extinction is an especially interesting hypothesis inasmuch as the prevalence of Cope's Rule (see LaBarbera, this volume) has suggested to many that there are advantages to the evolution of large body size. If Cope's Rule is generated through selective pressures for a larger body size (however, see [40] for a cogent, nonadaptive explanation for Cope's Rule), a correlation between body size and the probability of extinction would suggest that what may benefit individuals (size increase) may be

harmful to the species. Thus, selection could be seen as operating in opposing directions at different hierarchical levels. Another apparent paradox that presents itself in this regard is the correlation between body size and geographic range among terrestrial mammals of North America [5]. It would appear that whatever extinction resistance is conferred by a broad geographic range, it is outweighed by the disadvantages of lower population densities associated with large size.

Tropical Setting

Although little systematic work has been done, it often appears that species inhabiting tropical habitats (especially those in reefs) are more extinction-prone than those in extratropical habitats. This effect is most apparent during times of mass extinction [36] but has not been well documented for intervals of background extinction. It is not clear if this association of high extinction rates with tropical habitats is due to a) the sensitivity of reef-building organisms to environmental change (with the species dependent on the reef-builders for their habitat becoming extinct as a cascading effect), b) the sensitivity of tropical species in general, c) the smaller geographic ranges of tropical species (McCoy and Connor [24] document smaller geographic ranges among tropical species of North American mammals), or d) is a simple consequence of the greater number of species in the tropics (i.e., the "selectivity" may be more apparent than real).

Productivity

Areas of low productivity might contain biotas that would be prone to environmental crises that affect primary productivity. Vermeij [46] and Vermeij and Petuch [47] note different extinction susceptibilities among Tertiary molluscs on the west and east sides of the Isthmus of Panama. They find that those species that inhabit high productivity waters are the ones most likely to persist, perhaps because their high fecundity enabled them to recover quickly.

Species-Richness within Clades

All other things being equal, clades characterized by many species will tend to persist for longer intervals of geologic time than will clades having only few species. This pattern is apparent at long time scales with more diverse classes persisting longer than less diverse ones [34] and at shorter time scales among genera of Gulf Coast (USA) bivalves and gastropods during times characterized by background extinction rates (though not during the Cre-

taceous-Tertiary mass extinction) (Jablonski, this volume). Increasing species richness within families through geologic time has also been offered as an explanation [7] for the decline in familial extinction rates noted by Raup and Sepkoski [31] and Van Valen [45] (but see also Sepkoski, this volume).

In the group discussions Bambach reported on some preliminary results of a study he is conducting with Gilinsky. Early results suggest that among clades of Phanerozoic marine invertebrates, the probability of family extinction is higher during mass extinctions that occur late in the history of the clade than during mass extinctions that occur early in the history of the clade. These results deserve far greater scrutiny and study, especially because they suggest that a family's probability of extinction during mass extinction times is dependent on how long its clade has been in existence.

Two research programs for exploring the issue of selectivity of extinctions were suggested.

Comparison of Extinction Intensities in Marine and Terrestrial Habitats

Terrestial habitats may be characterized by higher extinction rates than marine habitats because of the greater likelihood of restricted geographic distributions in the terrestrial realm. Marine habitats, because of their greater absolute extent and because of the interconnection of the oceans, may house species with greater geographic ranges. Furthermore, the terrestrial realm may be more frequently disturbed by global environmental changes whose effects are buffered in the aquatic environment.

Comparison of the Victims and Survivors of Both Background and Mass Extinctions

In light of the patterns discussed above, how do victims and survivors differ with respect to their geographic distribution, body size, feeding adaptations, trophic positions, substrate adaptations, biogeographic affinities, species richness, and other features? Is there any systematic variation in the intensity of extinction with respect to these categories? Are the patterns of selection different during background and mass extinction times? Are the patterns of selectivity different at different mass extinctions?

Causes of Mass Extinction in the Geologic Past

Physical factors, even though they can provoke a series of biotic changes in the environment, seem the most likely proximate causes for extinction.

The biotic changes that are associated with extinctions in the fossil record, with the possible exception of some floral changes (Niklas, this volume), are difficult to attribute to the direct effects of competition.

Changes in the physical environment must have global consequences if they are to precipitate a mass extinction. Raup [29] has shown that extinctions of the magnitude seen during mass extinctions could not be produced through the extirpation of one or a few provincial biotas.

It is important to note here that our review of the mechanisms of extinction focuses not on the ultimate causes (companion stars disturbing the paths of comets, variation in rates of seafloor spreading, and so forth) but rather on the more proximate causes of extinction, for at least two reasons: a) the same proximate cause may have different ultimate causes [25], and b) it is the proximate causes that are most likely to leave independent physical or geochemical evidence of their effect. We also note that we recognize that each mass extinction could, in principle, be caused by a different set of environmental changes, and that a particular extinction event could be the result of the interplay of several of the potential causes that we enumerate here.

Impact of Extraterrestrial Objects

While offered as an explanation for many Phanerozoic extinctions, this hypothesis has received the greatest attention (and the most supporting evidence) with regard to the terminal Cretaceous extinctions. Recent hypotheses of the impact of extraterrestial objects for the terminal Cretaceous extinctions were proposed on the basis of two lines of non-biotic evidence: sedimentological indicators (shocked quartz, boundary clays) of environmental disturbances, and enrichment of heavy metals such as iridium in deposits at the Cretaceous-Tertiary Boundary. These anomalies took on added significance because high-precision stratigraphic studies suggested a very short duration (less than 4.7×10^5 years, perhaps on the order of 10^4 years for many taxa [15]), and because an important component of marine life, the calcareous plankton, were almost completely wiped out. The mass extinctions constituted the corpse, the geochemical anomalies provided the circumstantial evidence, and the iridium anomaly in sediments around the world is the "smoking gun" that indicated an extraterrestrial bolide. The Snowbird Conference [38] presented several computer-based scenarios of the effects of the impact of a large body on the Earth. Assuming the impact of a 10 km diameter meteorite (an asteroid or a comet), the resulting disturbance of the physical environment would be sufficient to cause large-scale and profound environmental change and mass mortality among many

groups. The theoretically predicted and partially confirmed (or at least not contradicted) scenarios entail a) global darkness (10^{-1} to 10^0 years duration); b) atmospheric pollution (10^{-1} to 10^0 years duration); c) destruction of stratospheric ozone (10^0 to 10^1 years duration); and d) chemical pollution of the ocean, in particular a lowering of the pH of seawater (10^2 to 10^4 years duration) (see Hsü, this volume). The biological consequences of such environmental changes include massive reduction in population sizes, temporary suppression of primary production on land (10^{-1} to 10^0 years duration), and drastic suppression of primary productivity in the sea (10^2 to 10^4 years duration). These predicted changes (as well as others similar to many produced in nuclear winter scenarios) could account for the extinctions at the Cretaceous-Tertiary Boundary.

Most would agree that a good case, though perhaps not an overwhelming one, has been made for the impact of an extraterrestial body at the Cretaceous-Tertiary Boundary. This is a remarkable state of affairs considering that ten years ago such a hypothesis would not have been tolerated in scientific circles. This acceptability is due in no small measure to the value of independent, physical evidence for this particular hypothesis. Without the geochemical and sedimentological evidence, it would be just another wild idea. Of course problems persist, especially with regard to scenarios that predict environmental changes that seem to call for total extinction rather than the substantial (but obviously less than total) and selective extinctions that are recorded in the rocks. The paleontological evidence for selectivity at this boundary needs to constrain the models and scenarios that the impact hypothesis has generated. Further constraints on such extinction scenarios can be provided by a consideration of the role of primary productivity in the Recent ocean. Survival of even detritus-feeding benthos would be unlikely if primary productivity had indeed ceased for 10^4 years (J. S. Levinton, personal communication).

Reduction of Available Marine Habitat as a Result of Change in Sea Level

That this is such a long-standing hypothesis [26] is testimony to at least circumstantial evidence in its favor. Many extinctions of marine organisms occurred at times of relative low stand of sea level (see Fig. 3 for the timing and extent of Phanerozoic sea level changes). Despite this association in timing of extinctions and marine regressions, problems plague this hypothesis as well. Not every regression is accompanied by an extinction, Pleistocene sea level fluctuations did not cause substantial extinctions of marine organisms, and the existence of island as possible refuges for families of the
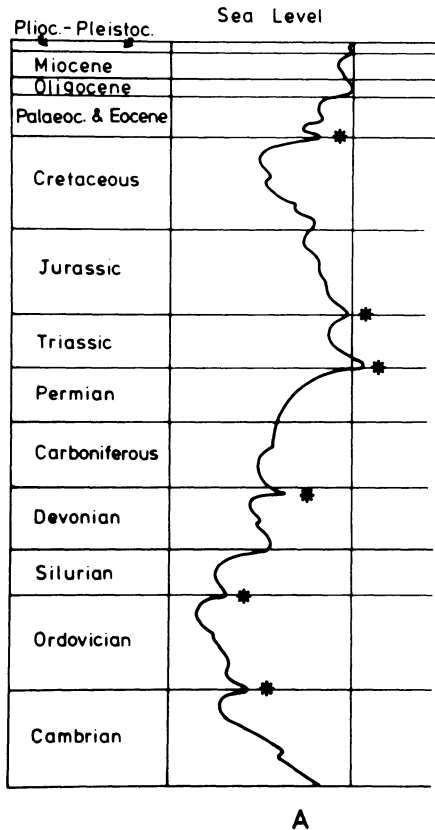
Fig. 3. Record of Phanerozoic sea level change. Relative low stands of sea level are shown as excursions of the curve to the right, high stands to the left. Times of mass extinctions are shown by * [11]

marine benthos could have served to repopulate the continental shelves during the following transgression [18]. These criticisms might suggest that, first, paleogeographic setting is important. A sea level change on the relatively emergent continents of the Pleistocence would not result in as large a change in area of shallow sea per meter of sea level change as would a change in sea level during times of low continental relief and low continental freeboard. Under paleogeographic conditions more typical of the Earth's history marine organisms might have become "perched" [20] – stenotopic and restricted to epeiric seas and thus prone to extinction during rapid regressions. Second, the duration of a sea level low stand may be important; the relatively brief Pleistocene low stands may have been insufficient for an equilibration of marine diversity to some lower value. Third, distinctive habitats, found only on continental shelves or in the broad, shal-

low inland seas characteristic of much of the Paleozoic might have harbored many of the faunas that suffered extinction. Finally, the withdrawal of the seas might prompt significant changes in patterns of nutrient cycling, entraining environmental changes far from the continents themselves.

Climatic Change

Climatic change, especially the effects of "refrigeration," has been recently championed as a significant agent of mass extinction by Stanley [41]. Global cooling is indeed associated with the extinctions of the late Eocene and the late Ordovician, and some evidence for a change in climate can be found at the Cretaceous-Tertiary Boundary. Climatic cooling is a plausible agent of extinction given the often narrow thermal tolerances of many marine species and the effect of climate on oceanic circulation. Nevertheless, the lack of precise chronological correlation of many major extinctions (the Permo-Triassic, the Late Triassic, the Late Devonian) with major episodes of climatic cooling and the lack of major extinctions associated with major episodes of climatic cooling (the Pleistocene, the Permo-Carboniferous) tends to reduce the attractiveness of climatic cooling as an agent of mass extinction.

Oceanic Anoxia

Episodes of oceanic bottom water stagnation can be recorded in the stratigraphic record by the widespread deposition of such organic-rich sediments as black shales. Such anoxic events may be prompted by sea level change [10, 11] and their onset appears to be sudden. The extinctions of the Cenomanian-Turonian (Middle Cretaceous), Toarcian (Early Jurassic), and Frasnian-Famennian (Late Devonian) occur at the same time as episodses of oceanic anoxia. Less convincing evidence for oceanic anoxia is seen at the Cretaceous-Tertiary Boundary, the Late Triassic, the Permo-Triassic, and the basal Silurian (shortly after the Late Ordovician extinctions). While anoxia might be implicated in some marine extinctions, it is clear that anoxia are not invariably associated with every Phanerozoic extinction, but a link between marine and terrestrial events leading to oceanic anoxia is not clear. Furthermore, the global extent of many episodes of oceanic anoxia is questionable – the Toarcian anoxic event, for example, appears limited in its geographic extent.

Declining Provinciality

Global diversity is a function not only of the degree of species packing within habitats but of the degree of biotic provinciality. Valentine and Moores [42] suggested that the changing geographies resulting from plate tectonic processes contributed to the regulation of Phanerozoic faunal diversity in the marine realm. And both Schopf [33] and Valentine and others [43] argue that changing patterns and levels of marine provinciality could explain much of the variation in familial diversity during Phanerozic time. The Late Permian extinction event seems to be the best candidate for a biogeographically induced extinction. In addition, origination rates might be lowered as a consequence of the paleogeographic setting of the Late Permian [16], thus exacerbating the environmental and biogeographic effects of continental assembly. The role of declining provinciality in other Phanerozoic extinction events is less clear.

Increased Volcanic Activity

The association in time between extensive outpouring of plateau basalts and the terminal Cretaceous extinctions should direct our attention to this hypothesis. This is particularly because extensive volcanism can produce not only geochemical anomalies much like those at the Cretaceous-Tertiary Boundary but environmental conditions much like those found in many nuclear winter and impact scenarios.

Magnetic Reversals

The weak but intriguing correlation between reversal frequency and extinction rate [30] suggests further inquiry into the possible links between magnetic reversals and extinctions. We simply know too little about the direct effects of zero magnetic fields on organisms. Our ignorance on this matter should promote rather than preclude research on the topic.

Two research programs that are directed towards understanding the causes of mass extinction were suggested.

Fine-scale Studies of Extinctions and Environmental Changes

Detailed examinations of changes in species occurrence and abundance in the vicinity of extinction events should be undertaken. Detailed environmental analyses, including geochemical studies, should accompany the paleontological work in an effort to relate changes in local environmental changes to the magnitudes and timing of extinction seen in the local stratigraphic sections.

Integration of the Physical and Paleobiological Record of Extinction

Efforts should be made to match the timing, duration, and magnitude of extinctions to independent (physical and geochemical) evidence for the timing, duration, and magnitude of environmental changes such as those recorded by iridium anomalies, isotopic fluctuations, sea level change, climatic cooling, oceanic anoxia, bursts of volcanism, and others. The pattern of extinction and survival in the face of each of these environmental changes may be predictable, given knowledge of the paleobiology of the species involved. We may be able not only to match the timing, duration, and magnitude of an environmental change with an extinction event, but also to compare the predicted outcome with the actual effect.

Evolutionary Effects of Mass Extinctions

To a large degree the immediate, and perhaps the subsequent, effects of mass extinctions depend on the selectivity and cause(s) of the extinction itself. For example, if extinctions selectively remove large-bodied species, perhaps we should not be too surprised at the prevalence of small-bodied forms as ancestors. We expect that the species that are likely to survive mass extinctions are probably opportunistic, "weedy" species – ones that are capable of survival in disturbed habitats. Such opportunistic species are often the most vagile forms and may have been present in refugia during the extinction episodes. We note that opportunistic species can often be morphologically simple species – the typical stock from which many groups diversify.

The proposition that clade-level properties, such as the distribution of genera among several provinces, are subject to selection during mass extinctions suggests the possibility that some species-level characteristics may persist simply by virtue of their fortuitous association with a higher level trait (Jablonski, this volume). Such properties, "carried through" the extinction by other traits, may affect the range of morphologies and adaptations seen in post-diversification biotas.

Mass extinctions may have biogeographic effects. If mass extinctions selectively remove geographically restricted taxa, the post-extinction biota will contain a smaller porportion of endemics than the initial fauna. The surviving biota will be characterized by geographically widespread forms, and global provinciality will be low. This line of reasoning suggests that the decline in provinciality that has often associated with mass extinctions may actually be an effect of rather than a cause or a contributing agent to the extinction event.

Of related biogeographic interest is the notion of refugia and their roles as "extinction shelters" and as source areas for rediversification. The geographic extent of the environmental catastrophe that precipitates a mass extinction may determine whether refugia are actually particular geographic areas (the high latitudes, for example) or somewhat species-specific or habitat-specific (nearshore settings, for example), and thus different for different species.

A common feature of post-extinction time is rediversification. Such rediversification is often concentrated in particular clades and may represent the replacement of previously dominant groups by species derived from heretofore subordinate forms. The replacement of the dinosaurs by the mammals following the Cretaceous-Tertiary extinctions is the most often cited example. There is little evidence to suggest that such replacements represent competitive displacement. Rather, the patterns of diversity change through time of potentially competing groups seems more consistent with the phenomenon of a preemptive occupation of adaptive zones. It appears that whichever clade first diversifies within an adaptive zone is the clade most likely to persist and dominate that zone (see [2] for an example of this among therapsids and dinosaurs). Thus, high speciation rates may be as important as "adaptive superiority" in determining which clade fills the newly vacated adaptive space.

The following research program on the evolutionary effects of mass extinctions was identified.

Detailed Examination of Instances of Ecological Replacements after Mass Extinctions

More examples with greater temporal precision are needed of this phenomenon. Studies which integrate our knowledge of the paleoecology, functional morphology, and temporal variation in diversity among clades should shed light on those features most important in shaping the course of post-extinction evolution. Particular attention should be paid to the marine fossil record, where few well documented examples of replacement exist, yet where the data are most amenable to such study.

References

1. Allendorf F, Leary RF (1986) Heterozygosity and fitness in natural populations of animals. In: Conservation biology: Science of diversity, ed Soulé ME. Sunderland, MA: Sinauer

2. Benton MJ (1983) Dinosaur success in the Triassic: a noncompetitive ecological model. Q Rev Biol 58:29–55
3. Boucot AJ (1975) Evolution and extinction rate controls. Amsterdam: Elsevier
4. Bretsky PW (1973) Evolutionary patterns in the Paleozoic bivalvia: documentation and some theoretical consideration. Geol Soc Am Bull 84:2079–2096
5. Brown JH (1981) Two decades of homage to Santa Rosalia: toward a general theory of diversity. Am Zool 21:877–888
6. Fischer AG, Arthur MA (1977) Secular variations in the pelagic realm. SEPM Spec Pub 25:19–50
7. Flessa KW, Jablonski D (1985) Declining Phanerozoic background extinction rates: effect of taxonomic structure? Nature 313:216–218
8. Hallam A (1975) Evolutionary size increase and longevity in Jurassic bivalves and ammonites. Nature 258:439–496
9. Hallam A (1976) Stratigraphic distribution and ecology of European Jurassic bivalves. Lethaia 9:245–260
10. Hallam A (1981) The end-Triassic bivalve extinction event. Palaeogeog Palaeoclimatol Palaeoecol 35:1–44
11. Hallam A (1984) Pre-Quaternary sea-level changes. Ann Rev Earth Planet Sci 12:205–244
12. Hansen TA (1980) Influence of larval dispersal and geographic distribution on species longevity in neogastropods. Paleobiology 6:193–207
13. Hoffman A (1985) Patterns of family extinction depend on definition and geological timescale. Nature 315:659–662
14. Hoffman A, Kitchell JA (1984) Evolution in a pelagic system: a paleobiologic test of models of multispecies evolution. Paleobiology 10:9–33
15. Hsü KJ, He Q, McKenzie JA, Weissert H, Perch-Nielsen K, Oberhänsli H, Kelts K, LaBrecque J, Tauxe L, Kränenbühl U, Percival SF Jr, Wright R, Karpoff AM, Petersen N, Tucker P, Poore NZ, Gombos AM, Pisciotto K, Carman MF Jr, Schreiber E (1982) Mass mortality and its environmental and evolutionary consequences. Science 216:249–256
16. Hüssner H (1983) Die Faunenwende Perm/Trias. Geologische Rundschau 72:1–22
17. Hutchinson GE (1951) Copepodology for the ornithologist. Ecology 32:571–577
18. Jablonski D (1986) Causes and consequences of mass extinctions: a comparative approach. In: Dynamics of extinction, ed Elliott EK. New York: Wiley, pp 183–229
19. Jablonski D, Lutz RA (1980) Molluscan larval shell morphology: ecological and paleontological applications. In: Skeletal growth of aquatic organics, eds Rhoads DC, Lutz RA, pp 323–378. New York: Plenum Press
20. Johnson JG (1974) Extinction of perched faunas. Geology 2:479–482
21. Kitchell JA, Pena D (1984) Periodicity of extinctions in the geologic past: deterministic versus stochastic explanations. Science 226:689–692
22. Ledig FT (1986) Heterozygosity, heterosis, and fitness in outcrossed plants. In: Conservation biology: Science of diversity, ed Soulé ME. Sunderland, MA: Sinauer
23. Lovejoy TE, Bierregaard RO, Rankin JM, Schubart HOR (1983) Ecological dynamics of forest fragments. In: Tropical rainforest: Ecology and management, eds Sutton SL, Whitmore TC, Chadwick AC. London: Blackwell
24. McCoy ED, Connor EF (1980) Latitudinal gradients in the species diversity of North American mammals. Evolution 34:193–203
25. McLaren DJ (1983) Bolides and biostratigraphy. Geol Soc Am Bull 94:313–324

26. Newell ND (1967) Revolutions in the history of life. Geol Soc Am Spec Paper 89:63–91
27. Rampino MR, Stothers RB (1984) Terrestrial mass extinctions, cometary impacts and the Sun's motion perpendicular to the galactic plane. Nature 308:709–712
28. Raup DM (1978) Cohort analysis of generic survivorship. Paleobiology 4:1–15
29. Raup DM (1982) Biogeographic extinction: a feasibility test. Geol Soc Am Spec Paper 190:277–282
30. Raup DM (1985) Magnetic reversals and mass extinctions. Nature 314:341–343
31. Raup DM, Sepkoski JJ Jr (1982) Mass extinctions in the marine fossil record. Science 215:1501–1503
32. Raup DM, Sepkoski JJ Jr (1984) Periodicity of extinctions in the geologic past. Proc Natl Acad Sci USA 81:801–805
33. Schopf TJM (1976) The role of biogeographic provinces in regulating marine faunal diversity through geologic time. In: Historical biogeography, plate tectonics, and the changing environment, eds Gray J, Boucot AJ, pp 449–458. Corvallis, OR: Oregon State University Press
34. Sepkoski JJ Jr (1981) A factor analytic description of the Phanerozoic marine fossil record. Paleobiology 7:36–53
35. Sepkoski JJ Jr, Raup DM (1985) Periodicity in marine mass extinctions. In: Dynamics of extinction, ed Elliott DK. New York: Wiley
36. Sheehan PM (1985) Reefs are not so different – they follow the evolutionary pattern of level-bottom communities. Geology 13:46–49
37. Signor PW III, Lipps JH (1982) Sampling bias, gradual extinction patterns and catastrophes in the fossil record. Geol Soc Am Spec Paper 190:291–296
38. Silver LT, Schultz PH (eds) (1982) Geological implications of impacts of large asteroids and comets on the earth. Geol Soc Am Spec Paper 190
39. Sousa WP (1984) The role of disturbance in natural communities. Ann Rev Ecol Syst 15:353–391
40. Stanley SM (1973) An explanation for Cope's Rule. Evolution 27:1–26
41. Stanley SM (1984) Marine mass extinctions: a dominant role for temperature. In: Extinctions, ed Nitecki MH, pp 69–118. Chicago: University of Chicago Press
42. Valentine JW, Moores EM (1972) Global tectonics and the fossil record. J Geol 80:167–184
43. Valentine JW, Foin TC, Peart D (1978) A provincial model of Phanerozoic diversity. Paleobiology 4:55–66
44. Van Valen LM (1975) Group selection, sex, and fossils. Evolution 29:87–94
45. Van Valen LM (1984) A resetting of Phanerozoic community evolution. Nature 307:50–52
46. Vermeij GJ (1986) Survival during biotic crises: the properties and evolutionary significance of refuges. In: Dynamics of extinction, ed Elliott DK. New York: Wiley, pp 231–246
47. Vermeij GJ, Petuch EJ (1986) Differential extinction in tropical American molluscs: endemism, architecture, and the Panama Land Bridge. Malacologia 27:29–42
48. Waterhouse JB, Bonham-Carter G (81976) Range, proportionate representation, and demise of brachiopod families through Permian Period. Geol Mag 113:401–428