



THE DYNAMICS OF MARINE STEPWISE MASS EXTINCTION

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ABSTRACT

Mass extinction is characterized by the loss of 50 – 90 + percent of genetically and ecologically diverse species within 1 - 3.5 Myr intervals. Three conflicting theories exist: (1) *Graded Mass Extinction*; (2) *Stepwise Mass Extinction*; and (3) *Catastrophic Mass Extinction*. These can only be adequately tested with high resolution (cm-scale) stratigraphic data spanning the entire mass extinction interval and adjacent strata. Such data are presently available only for the Eocene-Oligocene (E-O), Cretaceous-Tertiary (K-T) and Cenomanian-Turonian (C-T) extinctions. In general, prevalent uniformitarian stratigraphic philosophy and use of the modern Earth/Life system as a model for the Phanerozoic has hindered the search for, and expectations of, high-resolution stratigraphic data critical to mass extinction research. The modern Earth/Life “model” predicts highly variable, environmentally and biologically resilient systems and predominantly autocyclic stratigraphic response to large-scale forcing mechanisms. Yet, present environmental systems are not typical of 90 + percent of Phanerozoic history characterized by more stable and delicately balanced environmental/ecological systems, no permanent polar ice, much higher sealevel, warmer and more equable, maritime-dominated climates, little seasonality, and much broader temperature and habitat gradients. Phanerozoic marine species were largely adapted to widespread warm stable environments, and were predominantly stenotopic and stenothermal. Phanerozoic Earth/Life systems were capable of rapid, widespread response to abrupt environmental fluctuations, including mass extinction. A stratigraphic and biological record dominated by near-isochronous to short-term depositional events is predicted by dominant Phanerozoic environments. Testing of the three mass extinction hypotheses with the best high-resolution data available (C-T, K-T, E-O boundary intervals) demonstrates the following phenomena in common: (1) All are stepwise extinctions, graded ecologically from stenotopic (first) to eurytopic groups, and from Tropical to Temperate taxa, over 1-3.5 Myr intervals. Steps are abrupt (100 Kyr or less) to catastrophic; background extinction rates and patterns separate them. (2) All steps of each mass extinction are contained within an interval of extraordinarily large (2-5 times background), rapid fluctuations in atmospheric/oceanic temperature and chemistry, as depicted from geochemical profiles. These exceeded the adaptive ranges and evolutionary response rates of many marine taxa, causing steps of extinction at major fluctuations. (3) Each interval has diverse evidence for one or more comet/asteroid impacts (“storms”) on Earth, clustered around the extinction interval. Most well-defined impact events are directly associated with major marine geochemical excursions and mass extinction steps. A mass extinction theory based on these case histories suggests that initial impacts by comets/asteroids within a storm were in the sea, causing large-scale disruption of temperature, chemistry, stratification, and circulation dynamics within the marine system, and a dense, solar-screening, water vapor cloud in the atmosphere, collectively initiating long-term dynamic feedback processes represented by large-scale geochemical fluctuations. Many fluctuations were too large and rapid for survival by narrowly adapted, predominantly stenotopic, stenothermal marine taxa; stepwise extinction resulted. Additional impacts exaggerated the oceanic/climatic perturbations, and reset the extinction clock.

Keywords: Mass extinction, Stepwise extinction, Uniformitarianism, Earth/Life system, Extraterrestrial events, Geochemical anomalies.

RESUMEN

La extinción en masa se caracteriza por la pérdida del 50 al 90 %, o más, de especies genética y ecológicamente diferentes en intervalos de 1 a 3,5 Ma. Hay tres teorías diferentes: 1) Extinción en masa gradual; 2) Extinción en masa por etapas y 3) Extinción en masa catastrófica. Sólo pueden probarse con datos estratigráficos de alta resolución (escala centimétrica) que se extiendan durante todo el intervalo de extinción y los estratos adyacentes. Tales datos se tienen sólo para las extinciones del Eoceno-Oligoceno (E-O), Cretácico-Terciario (K-T) y Cenomaniense-Turonense (C-T). En general, la filosofía uniformitarista predominante junto con el uso del sistema Tierra/Vida como modelo para el Fanerozoico han obstruido la búsqueda y la expectativa de datos estratigráficos finos críticos para la investigación de las extinciones en masa. El modelo actual Tierra/Vida predice sistemas biológica y ambientalmente adaptables muy variables, así como principalmente respuestas estratigráficas autocíclicas a los mecanismos de gran escala. Sin embargo, los sistemas ambientales actuales no son típicos del más del 90 % de la historia fanerozoica, caracterizada por sistemas ecológico/ambientales más estables y con un balance ajustado, sin hielos polares perpetuos, nivel del mar más altos, más cálidos y más uniformes, climas marítimos dominantes, escasa estacionalidad y gradientes amplios en la temperatura y en los hábitats. Las especies marinas fanerozoicas estaban adaptadas a ambientes estables cálidos muy extensos y eran en su mayoría estenotópicas y estenotermas. Los sistemas fanerozoicos Tierra/Vida fueron capaces de respuestas rápidas y amplias a cambios ambientales bruscos, incluida la extinción en masa. Los ambientes fanerozoicos predicen un registro estratigráfico, dominado por acontecimientos deposicionales cuasisíncronos o de corta duración temporal. El contraste de las tres hipótesis de extinción en masa con los datos disponibles (límites C-T, K-T y E-O) demuestra los siguientes fenómenos comunes: 1) Todos ellos responden a extinciones por etapas, ecológicamente gradadas desde los estenotópicos (en primer lugar) a los euriópicos y desde los taxones tropicales a los de zonas templadas, a lo largo de intervalos entre 1 y 3,5 Ma. Las etapas son bruscas (100 Ka o menos) a catastróficas; están separadas por extinciones de fondo características. 2) Todas las etapas se dan en intervalos muy amplios (2-5 veces la de fondo) de rápidas fluctuaciones en la temperatura atmosférica/oceánica, como se dibujan en perfiles geoquímicos. Las cuales exceden los rangos adaptativos y los índices evolutivos de respuesta de muchos taxones marinos, dando lugar a las etapas de extinción en las mayores fluctuaciones. 3) Cada intervalo tiene impactos de cometas/asteroides sobre la Tierra, agrupados alrededor de los momentos de extinción. La mayoría de los acontecimientos de impacto bien definidos están directamente asociados con variaciones principales en la geoquímica marina y con las etapas de extinción en masa. Una teoría de extinción en masa basada en esos ejemplos sugiere que los impactos de cometas/asteroides, en forma de lluvia de meteoritos, se dieron en el mar, provocando una disrupción a gran escala a la temperatura, química, estratificación y dinámica de circulación de los sistemas marino, así como una nube de vapor de agua densa y oscura en la atmósfera, iniciando conjuntamente procesos de retroalimentación de largo período representados por fluctuaciones geoquímicas a gran escala. Muchas de esas fluctuaciones fueron demasiado largas y rápidas para la supervivencia de los taxones marinos muy adaptados, predominantemente estenotópicos y estenotermos; de ello resultó una extinción en etapas. Otros impactos adicionales exageraron las perturbaciones oceánicas/climáticas y pusieron en marcha de nuevo el reloj de las extinciones.

Palabras clave: Extinción en masa, extinción por etapas, Uniformitarismo, Sistema Tierra/Vida, Fenómenos extraterrestres, anomalías geoquímicas.

INTRODUCTION

Mass extinction is characterized by the loss of more than half of the ecologically and genetically diverse species on Earth within a very short interval of geological time (50-95 % species loss in 1.0-3.5 Myr in well-documented examples). Rates and ecological patterns of species loss during mass extinctions are distinct from those of background extinction (Jablonski, 1986); taxa with predictably long species life, based on population size, dispersal mechanisms, dispersion and breadth of adaptive range, commonly die out at the same time as those with predictably short species lifespans during mass extinction.

The fact of mass extinction lies in the more than century-old, careful stratigraphic documentation of the fossil record by systematic paleontologists and biostratigraphers who have consistently noted narrow stratigraphic intervals of marked biological change that exceed the predictions of normal envi-

ronmental/habitat changes. Many of these events lie within uniform facies precluding their interpretation as responses to rapid environmental change. These data have been the bases for statistical documentation of the timing and magnitude of mass extinction events, and their relationship to background extinction, by Raup and Sepkoski (1984, 1986); from these analyses has evolved the hypothesis of a 26.2 Myr periodicity of mass extinction events. Subsequently, estimates by diverse authors on mass extinction cyclicity have ranged from 26-33 Myr.

Three existing hypotheses of mass extinction (Kauffman, 1986, 1988; Hut *et al.*, 1987) are shown in Figure 1; these are much debated. Historically, systematic paleontologists and ecologists have favored an hypothesis of **GRADED MASS EXTINCTION** (Kauffman, 1984a, 1986)-an acceleration of background rates of extinction reflecting acceleration of biological stress brought on by relatively rapid Earth-bound environmental changes (i.e. rapid thermal, chemical, climatic, oceanographic and/or sedimentologic fluctuations). Rapid climate changes associated

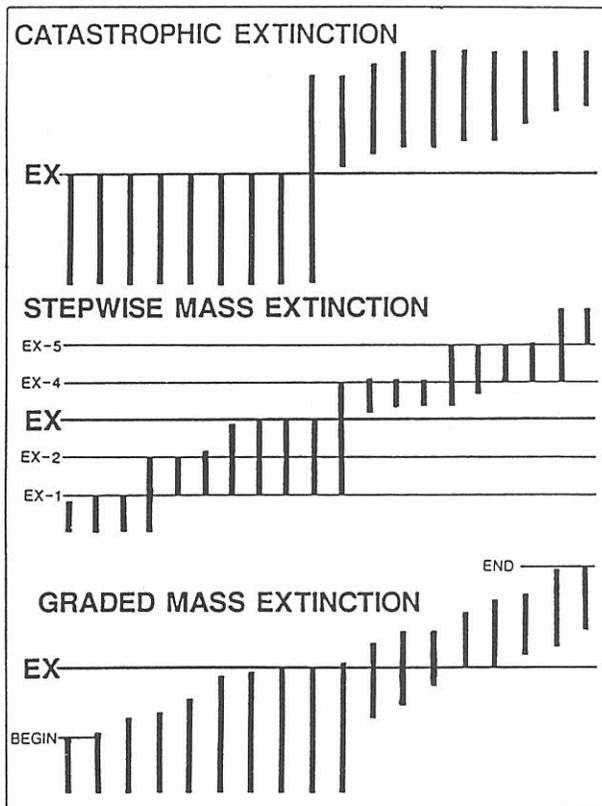


Figure 1. Models for the three major Mass Extinction hypotheses (Kauffman, 1986, 1988). *Graded Mass Extinction* infers acceleration of background extinction rates correlative with increased biological stress from rapidly deteriorating global environments related to, e.g., eustatic fall, greenhousing, glaciation and cooling, etc. Extinction is graded from, first, more sensitive (Tropical, shallow water, stenotopic) organisms to, last, more adaptive (eurytopic, Temperate, deeper water) taxa. The interval spans 1-3.5 Myr. *Stepwise Mass Extinction* infers a series of ecologically graded (stenotopic first, eurytopic last), short-term (100 Kyr or less) to catastrophic steps (EX-1-5), each eliminating a major, ecologically linked portion of the global biota over 1-3.5 Myr. Rates and patterns of stepped extinctions are notably different from background extinction separating steps. Proposed causes are the integrated effects of multiple comet/meteorite impacts, mostly in the oceans, disrupting oceanic temperature, chemistry, and circulation, and initiating a series of large-scale, short-term oceanic fluctuations in these parameters—a dynamic feedback process—that exceed the adaptive ranges and evolutionary response rate of diverse taxa. *Catastrophic Mass Extinction* infers a single global extinction event among ecologically and genetically diverse taxa within days to years, caused by an extraordinary perturbation to the Earth environment, usually taken to be a large asteroid or comet impact event.

with intervals of intense volcanism, major glaciation or greenhousing, eustatic sealevel fall, large-scale regression of epicontinental seas and associated loss

or rapid modification of ecospace etc., are typical mechanisms for extinction cited by those favoring the graded mass extinction hypothesis (e.g. Hallam, 1987). The great ecological range of the modern global biota, and the inference that ancient biotas were similarly resilient (a uniformitarian argument which is subject to strong criticism), is further cited as favoring graded mass extinction theory. Ideally, extinction is ecologically graded in this hypothesis from (first) ecological specialists (stenotopic taxa) to (finally) ecological generalists (eurytopic taxa), and from taxa in more exposed habitats to those in more protected habitats.

STEPWISE MASS EXTINCTION (Kauffman, 1984a, b; 1986, 1988; Kauffman and Hansen, 1985; Keller, 1986) is a new hypothesis suggesting that mass extinction proceeds through a series of discrete steps, each a near-simultaneous (“catastrophic”) to short-term (100 Kyr or less) interval of highly accelerated extinction rates, between which extinctions return to background levels. Cumulatively, these steps may span up to 3.5 Myr or more. Only a portion of the global biota is affected by each step, and the steps show a general ecological gradient through time. Early steps in a marine system mainly affect Tropical-Subtropical and/or otherwise stenotopic shallow water taxa (e.g. reef ecosystems); intermediate steps affect warm water plankton and shallow water, moderately stenotopic taxa; and later steps mainly affect more Temperate, deeper water, and/or more eurytopic taxa. The data presented in favor of stepwise mass extinction theory are the extinction patterns documented for the three global biotic crises with the most detailed stratigraphic resolution—the middle Cretaceous Cenomanian-Turonian (C-T), the Cretaceous-Tertiary (K-T), and the Eocene–Oligocene (E-O) mass extinctions (reviewed in Kauffman, 1986, 1988). Mechanisms cited for stepwise mass extinctions include multiple meteorite/comet impacts and/or extraordinarily rapid, large-scale shifts in climatic and oceanic parameters (temperature, chemistry, circulation patterns, etc.), possibly related to multiple impacting.

CATASTROPHIC MASS EXTINCTION theory (Alvarez *et al.*, 1980) proposes that world-wide extinction of ecologically and genetically diverse taxa occurs simultaneously, within days, months, or tens of years at the most, as a result of some catastrophic perturbation to the global ecosystem. No ecological or evolutionary gradient exists. The most common cited causes are large and/or multiple extraterrestrial impacts by meteorites and comets (Alvarez *et al.*, 1980, 1984; Hut *et al.*, 1987) and deep-seated explosive volcanism (Officer & Drake, 1985; Officer *et al.*, 1987; references therein). Both hypotheses have the potential for development of dense atmospheric debris/ash/smoke clouds, rapid global cooling (anti-greenhousing) and warming (greenhousing) pulses, consumption of the ozone layer and the subsequent potential for increased radiation, and chemical poisoning from fallout (acid rain, etc). The effects of

very close supernovae, close-passing stars, solar explosions, or other extraterrestrial phenomena are more remote possible causes cited in the literature. The large meteorite impact(s) proposed for the K-T (Alvarez *et al.*, 1980, 1984) and late Devonian (Frasnian-Famennian) mass extinction boundaries (McLaren, 1985) are the most cited examples of catastrophic processes.

THE DATA BASE: QUALITY AND CONSTRAINTS

Detailed data suitable for the testing of these three hypotheses are lacking for nearly all mass extinction events cited by Raup and Sepkoski (1984, 1986). Only data for the C-T, K-T, and E-O events are partially adequate for this purpose (Kauffman, 1986, 1988). Similar data are being developed for several other mass extinctions but are not yet available.

The problem with most published data on biotic and environmental changes through mass extinction intervals is its scale of resolution. Fine-grained, marine shelf and basinal facies (those preserving the most complete record) represent 1,000 years in 1-2 cm of rock (average). Thus, sampling resolution to test conflicting mass extinction theories must be at the cm-scale instead of the more normal 10 cm (5-10 Kyr) to 1 m (50-100 Kyr) scales of sampling for fossil biotas across mass extinction intervals. The reasons are: (1) the evidence for a catastrophic mass extinction will be contained within 1-2 cm of fine-grained rock, at the most. In most cases we don't yet know where, if at all, such events occur in a given rock column; entire 1-3.5 Myr extinction sequences must therefore be tested cm by cm; (2) the same argument as (1) can be made for stepwise mass extinction, where individual steps, in theory, will be contained within 1 to 100 cm of strata; (3) the proof of graded mass extinction lies in the precise documentation of the last and first occurrences of taxa, again at the cm-scale; (4) our search for causes, whether catastrophic, short-term, or graded over millions of years, also requires cm-scale physical and geochemical analyses of strata spanning a mass extinction interval in a search for causal mechanisms. Even graded mass extinction may be driven by short-term events. Thus, **all** hypotheses for mass extinction require cm-scale collecting of data over the 1-3.5 Myr extinction interval for adequate testing.

A second failing of much existing data pertaining to mass extinctions is the extent of stratigraphic coverage. Most available biological and environmental extinction data are focused around the 1-2 meters on either side of the paleontologically designated main extinction boundaries (usually stage boundaries). This, in effect, is a test for only a single step or catastrophe. However, the Raup-Sepkoski data (1984, 1986) initially defining mass extinction events, are only resolved to the stage level (6-8 Myr on the average) and do not pinpoint thin strati-

graphic intervals or horizons, nor stage boundaries. It is further significant that most extinction events carefully documented for the C-T and E-O "boundaries", and certain important K-T extinctions, actually took place **below** these explicit stage boundaries. Data from well-documented extinctions of the C-T, K-T, and E-O boundary intervals (Kauffman, 1986, 1988) demonstrate that cm-scale sampling must span 3.5 Myr to adequately test various mass extinction hypotheses. Significantly, Hut (Hut *et al.*, 1987) independently calculated that a single comet shower derived from perturbation of the Oort Comet Cloud (a primary candidate for impact-related mass extinctions) would cause an increase in the rate of Earth impacts over a 3 Myr time span, and that crater ages clustered around mass extinction intervals (Grieve, 1982; Alvarez & Muller, 1984) also span a few million years.

STRATIGRAPHIC AND ENVIRONMENTAL CONCEPTS

Fine-scale sampling of paleontological, geochemical and physical data for mass extinction intervals has also been seriously hampered by prevalent stratigraphic philosophies derived from Uniformitarianism (Kauffman, 1987b). Uniformitarian concepts in biology and geology are still largely based on the modern Earth-Life system model which, when compared to that characterizing the bulk of geological time, is ecologically atypical, environmentally more variable and resilient, generally cooler, and still strongly influenced by the Pleistocene Ice Age, remnant polar glaciation, and unusually low sealevel. Process models based on today's environmentally unstable Earth predict a dominance of localized autocyclic forcing and response in shaping the stratigraphic and paleontologic record. They do not predict, nor encourage the search for short-term, event-stratigraphic/bio-event phenomena of regional and global extent. Yet, these would predictably be developed in response to widespread Earthbound and extraterrestrial, allocyclic processes, to major point perturbations such as meteorite impacts, and/or to rapid large-scale shifts in Earth environments acting on a more uniform, stable, and less resilient Earth-Life system.

Approximately 90% of the Phanerozoic was, in contrast, characterized by a lack of permanent polar ice, by significantly higher eustatic sea level (Haq, *et al.*, 1987) covering up to 85% of the globe, and as a result, by predominantly warm, equable, widespread maritime climates, low seasonality, more sluggish, stratified, oxygen-deficient oceans, and by extensive epicontinental seas. Such environmental regimes had much broader thermal gradients, more widely distributed Tropical-Temperate climate zones, more extensive and continuous watermasses, and as a result, more widespread, temporally stable marine and terrestrial habitats than today. These were predictably more delicately perched on the Earth's surface, and

highly sensitive to even small-scale cyclic changes or perturbations (e.g. Milankovitch climate cycles, giant storm events, extraterrestrial impacts, etc). Consequently, widespread allocyclic forcing of Phanerozoic sedimentary and biological phenomena should have been more important, even dominant, in shaping the stratigraphic record than today. Through most of the stratigraphic record, short-term event deposits and abrupt biotic changes should be common, readily observed, and useful in refined regional correlation as chronostratigraphic (isochronous to short-term) units. The emergence of high-resolution event stratigraphy (HIRES), and detailed studies in event stratification, including extinction events (e.g. Einsele & Seilacher, 1982; Kauffman, 1986, 1987, 1988) reflect the realization that short-term deposits and biological events are much more predominant in ancient strata than predicted from the modern Earth/Life system model by uniformitarian philosophy.

The search for, and development of cm-scale, high-resolution stratigraphic data within mass extinction intervals has been contemporaneous with the rapid rise of HIRES as a modern tool of regional/global correlation. Mass mortalities, mass extinction steps and catastrophes; explosive volcanism; impact-related deposits and their geochemical signals; and rapid, large-scale geochemical fluctuations in the ocean-climate system commonly associated with mass extinction intervals (Kauffman, 1986, 1988) are also common and important components of high-resolution chronostratigraphy. Punctuational and allocyclically forced physico-chemical events of exceptional rate and magnitude may reflect, in part, causal mechanisms for mass extinction (Kauffman, 1986, 1988).

It is equally important to mass extinction theory to consider probable biological response to the warm, equable maritime-dominated environments that characterized high sealevel stands of the Phanerozoic. Characteristic Phanerozoic global biotas were adapted to a world characterized by much more widespread, stable habitats with relatively more predictable, narrower year to year thermal and environmental fluctuations than found today over most of the Earth. Stenotopic, stenothermal taxa would have dominated most ecosystems after long time-stable intervals of evolution. These biotas would have been "extinction-prone" in the face of the extraordinarily large scale, unpredictable, rapid environmental perturbations that characterized most well-documented mass extinction events, as determined by geochemical and paleoecological analyses (Kauffman, 1984a, b; 1986, 1988). Rapid to catastrophic mass extinction events among ecologically diverse taxa would clearly be much more probable in typical Phanerozoic environments than today, and could be caused by relatively smaller-scale perturbations than those that would result in widespread mortality among the modern biota. Catastrophic and stepwise extinction theories find logical support in the predictions of predominantly more stable, delicately balanced Phanerozoic environments associated with warmer, more equable climates and higher global sea level.

Proof of this hypothesis comes from high-resolution stratigraphic analysis of the three best-studied mass extinction boundaries (C-T, K-T, E-O), each of which is characterized by a series of short-term to near-catastrophic stepwise extinction events. These extinctions are ecologically graded in a general way, with the loss of Tropical stenotopic taxa first, to Temperate, more eurytopic taxa last. In each of these mass extinctions, individual extinction steps can be clearly related to widespread, large-scale, geochemically and physically defined perturbations imposed on broadly equable, warm, maritime-dominated global environments. No examples of graded mass extinction emerged from this research. A summary of each of these mass extinction intervals is given below, with references to detailed data sources.

Kauffman (1986, 1988) has most recently summarized these events.

CASE HISTORIES FOR STEPWISE MASS EXTINCTION

Cenomanian-Turonian (C-T) Mass Extinction (Fig. 2)

Raup and Sepkoski (1984, 1986) documented the C-T boundary interval, long regarded as one of the biologically best-defined stage boundaries of the Mesozoic, as a moderate-scale mass extinction within their 26.2 Myr extinction cycle. Koch (1977, 1980) and Kauffman (1984a-c) first collated North American Interior data for this boundary interval. They noted that it consisted of a series of short-term, ecologically graded extinction events associated with abrupt major marine paleobiogeographic changes, and environmental perturbations of unusual magnitude and character (e.g., a global oceanic anoxic event, The Bonarelli Event: rapid changes in temperature, marine chemistry, etc.), occurring at an unusual time. The C-T extinction occurred near peak eustatic highstand, global climate amelioration, and normalization of marine epicontinental environments. Jefferies (1963) had documented similar biotic patterns in England and France within this interval.

Subsequently Pratt (1985) and Zelt (1985) did highly detailed geochemical analyses across the boundary interval in North America, defining extraordinarily large, rapid (50-150 Kyr) stable isotope ($\delta^{18}\text{O}$; $\delta^{13}\text{C}$) perturbations, Mn, Corg and Uranium-Thorium fluctuations over a 1.5-2 Myr interval which also encompassed the C-T mass extinction. Collectively, these data reflect dynamic changes in temperature (2-5.0 °C estimated), and salinity (normalization followed by an unusual 0.2 Myr freshening event crossing the C-T boundary in North America) in shallow seas, and widespread changes in the marine carbon cycle ($\delta^{13}\text{C}$ spike) associated with the Bonarelli global oceanic anoxic event (OAE) and a major Mn spike (Orth *et al.*, 1988).

Predictably, the magnitude of these changes, and their rapid shifts within 50-150 Kyr intervals,

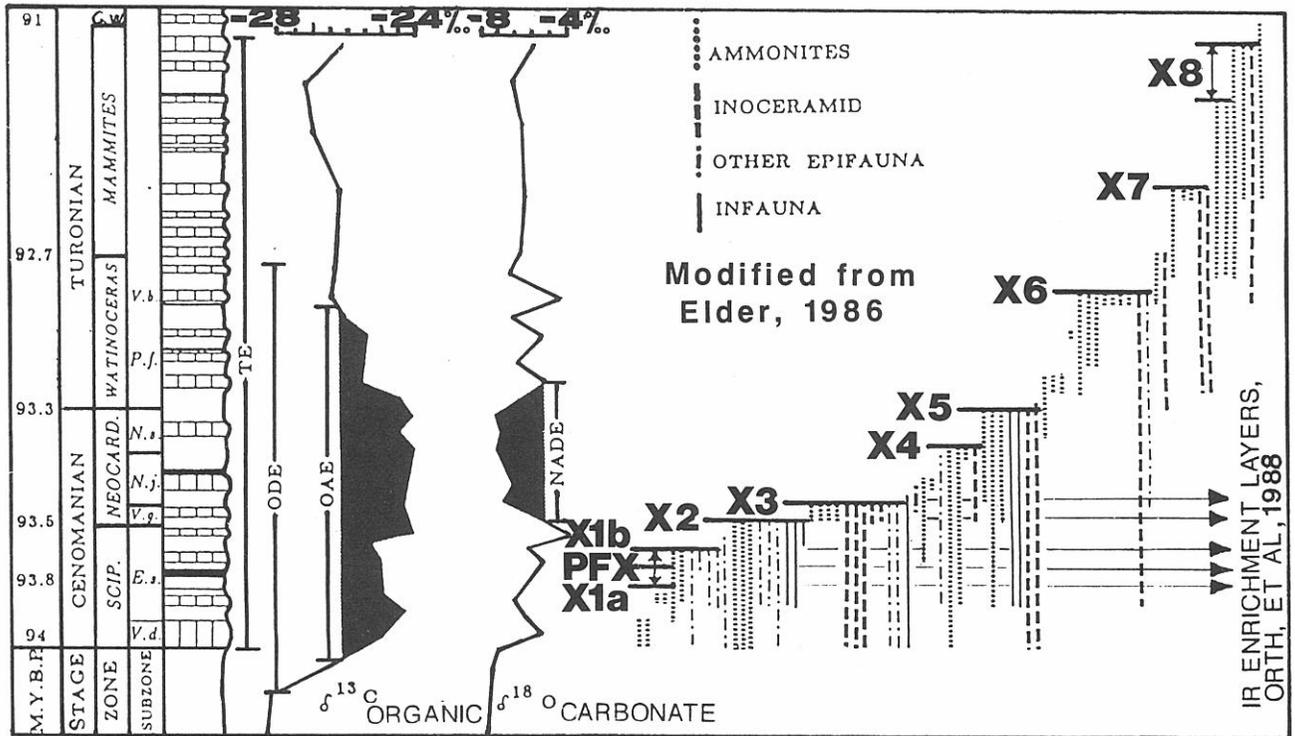


Figure 2. The stratigraphic, geochemical, and biological record of the Cenomanian-Turonian (C-T) stepwise mass extinction as shown by molluscan and foraminiferal species data from the Western Interior Basin of the United States (modified from Elder, 1986, 1987; in Kauffman, 1986, 1988; and in Hut *et al.*, 1987). Stratigraphic section and geochemical data are taken from the Pueblo, Colorado reference section (Elder and Kirkland, 1985; Pratt, 1985). Biological range data (molluscan species) are composited from detailed cm-scale sampling of 14 sections between Utah and Kansas, and Montana to New Mexico (Elder, 1986, 1987), integrated through standard and graphic correlation techniques utilizing bentonites and Milankovitch cycle chronostratigraphic horizons (see Kauffman, 1986, 1988). Iridium enrichment layers (arrows and lines) from Orth *et al.* (1988). Note that Ir enrichment levels precisely correlate, within cms, to the first four molluscan extinction steps (1a-3) and the major planktonic foraminifer extinction (PFX) (*Rotalipora* extinction). Key to symbols: X1 - X8 are successive short-term molluscan or mollusc-foraminifer extinction steps; ODE—Oceanic and climatic destabilization interval characterized by extraordinarily rapid, large-scale fluctuations in marine temperature and chemistry, compared to background; note that ODE encompasses most of the mass extinction interval; OAE—Bonarelli global oceanic anoxic event, characterized by incursion of oxygen minima zones into world epicontinental and shelf seas, producing anoxic benthic conditions and laminated dark organic-rich shales. NADE—North American desalination event, possibly representing an exaggerated monsoonal interval near peak eustatic highstand of the Cenomanian transgression (Greenhorn Cycle). TE—major thermal event in Western Interior Seaway, represented by extensive short-term immigration of Tropical and Subtropical taxa into normally Warm-Mild-Temperate portions of the seaway (Kauffman, 1984c).

should have exceeded the adaptive ranges of many "extinction prone" marine taxa that had become adapted to broadly equable, warm marine environments associated with eustatic highstand. Subsequently, high-resolution stratigraphic sampling and geochemical analysis across the 2-3 Myr boundary interval (Orth *et al.*, 1988) revealed an interval of iridium enrichment containing two moderate size and possibly three minor spikes just below the C-T boundary at Pueblo, Colorado (Fig. 2); each Ir spike correlates precisely or very closely with one of the first five extinction steps comprising the C-T mass extinction interval (Elder, 1986, 1987; Elder & Kirkland, 1986; Kauffman, 1984a-c, 1986, 1988). The lower four Ir spikes have elemental associations suggesting a mantle (degassing) origin, whereas the high-

est and most pronounced Ir spike may represent an extraterrestrial impact below the C-T stage boundary. Two broadly dated impact craters (Grieve, 1982; Alvarez & Muller, 1984) are known near the C-T boundary. Major regional volcanic ash layers occur within the C-T extinction and stage boundary interval (Fig. 2) but have no correlation to either extinction steps or iridium enrichment horizons; in fact, these ashes yield lower than background iridium levels (Orth *et al.*, 1988). Volcanism seems to have had no direct relationship to mass extinction or C-T boundary events in North America. Within this well-studied, 1.5-2 Myr interval of extraordinary perturbations in temperature and marine chemistry, Elder (1986, 1987; Elder & Kirkland, 1986; and in Kauffman, 1986, 1988) has carefully documented the ex-

tion history of Mollusca in the Western Interior of North America through high-resolution stratigraphic analysis and graphic event correlation of faunas from 14 widely spaced boundary sections (Fig. 2). These have subsequently been integrated with equally detailed physical and geochemical data. Elder's data (1986, 1987) show eight major, abrupt mollusc extinction steps spanning the C-T boundary interval in North America, with low background extinction levels between them (Fig. 2). Eicher and Diner (1985) and Leckie (1985) documented, for North America, an abrupt planktonic foraminifer extinction (*Rotalipora* extinction) between Elder's steps 1a and 1b (Fig. 2). Nearly all extinction steps lie below or at the C-T stage boundary, within the interval of initiation and peak development of $\delta^{18}\text{O}$, $\delta^{13}\text{C}$, Mn, and Corg fluctuations, and of iridium enrichment.

Integration of all physical, chemical, and biological data across the C-T boundary interval in North America suggest the following series of events: (1) Initiation of an interval of major stable isotope disruption ($\delta^{13}\text{C}$) at about 94.25 Myr associated with onset of the Bonarelli OAE and a major interval of Mn enrichment (Pratt, 1985; Orth *et al.*, 1988). Disruption of the $\delta^{18}\text{O}$ signal follows shortly at 94 Myr (Fig. 2), just prior to initial iridium enrichment and the first mollusc extinction step in the Western Interior of North America. The cause of these abrupt perturbations is unknown, but is best explained by an aquatic impact. Here or earlier in the Late Cenomanian, data on Tropical reef-building rudistid bivalve extinction recently compiled by the author and C.C. Johnson (in manuscript) for all Caribbean Province species show a major extinction event for Tropical reef communities. (2) The first small steps of North American (mainly Subtropical) mollusc extinction consist of two discrete levels between which lies the major C-T planktonic foraminifer extinction level (*Rotalipora* extinction; Eicher & Diner, 1985; Leckie, 1985). The first of two major iridium enrichment layers and subsequent two minor Ir spikes of probable mantle degassing origin (Orth *et al.*, 1988) are associated precisely with the lower step 1a mollusc extinction, the *Rotalipora* extinction, and the upper step 1b mollusc extinction of Elder (1986, 1987; Elder & Kirkland, 1986), as are major positive and negative excursions of the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ isotope curves (Fig. 2), respectively. This interval also incorporates a major portion of the Bonarelli global oceanic anoxic event and the global Mn excursion. A general relationship between an early oceanic impact, resultant mantle degassing and iridium enrichment, major oceanic (stable isotope) temperature/chemistry disruptions, and ecologically selective stepwise extinction is implied. The most diverse Warm Temperate to Subtropical marine biotas of North America are broadly decimated at this time, and probably follow an earlier Tropical reef extinction.

(3) Mollusc extinction step 2 (93.48 My) (Fig. 2) is associated precisely with a slight iridium enrichment level (mantle degassing signal), initiation

of the major negative excursion of $\delta^{18}\text{O}$, depicting the start of a regional desalination event (giant storm and/or monsoon interval?) in the Western Interior Seaway of North America, and initiation of the largest positive excursion of global $\delta^{13}\text{C}$, recording a major change in the marine carbon cycle. (4) Mollusc extinction step 3 (93.45 My), the largest of the sequence, is precisely correlated with the last and strongest iridium spike of Orth *et al.*, (1988), possibly reflecting an impact, and near maximum development of the North American desalination event and the global Bonarelli OAE; (5) Mollusc extinction step 4 is moderately developed, spread out over about 50 Kyr, and occurs in close association with peak development of the global $\delta^{13}\text{C}$ positive excursion and $\delta^{18}\text{O}$ negative excursion (North American desalination event), but not with Ir-enrichment, just below the C-T boundary at 93.4 Myr. This is the first C-T extinction step without Ir enrichment, but is precisely correlative to stable isotope peaks representing extraordinary ocean perturbation; (6) Extinction step 5, of moderate proportions, lies at the C-T boundary (93.3 Myr) and is characterized by final loss of surviving cosmopolitan, warm water Cenomanian ecological generalists and great reduction in the magnitude of the major $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopic excursions marking the end of the North American Desalination Event. Very low diversity among Temperate ecological generalists results from this extinction event. Peak eustatic highstand and the final wave of immigration and diversification of Subtropical mollusc taxa into the Western Interior of North America follows this 100-150 Kyr low diversity interval. (7) Extinction 6 (92.8 Myr) (Fig. 2) is the last major sharp step of the C-T mass extinction interval, affecting mainly new stenotopic Subtropical and Warm Temperate immigrant molluscs, and correlates precisely with the last abrupt positive $\delta^{18}\text{O}$ excursion, return of $\delta^{13}\text{C}$ values to background levels, and final low-level phases of the Bonarelli OAE before return to stable background levels. (8) A small extinction Step 7 occurs abruptly at eustatic highstand, about 92.3 Myr, among Warm-Temperate to Subtropical Mollusca but is not associated with any lithologic or geochemical signal suggesting a cause. (9) Extinction 8 is not a clear step but rather spread out over 91-91.2 Myr and is associated with the last isolated, moderate stable isotope excursions of the C-T boundary sequence. It marks the final demise of surviving Tropical/Subtropical mollusc faunas and loss of some Warm Temperate elements in the Western Interior Seaway of North America, immediately following eustatic highstand.

Major features of the C-T mass extinction, as defined by high-resolution stratigraphic data in North America and the Caribbean, are as follows: at least nine major, short-term (100 Kyr) to subcatastrophic, ecologically graded extinction steps, starting with decimation of Tropical Caribbean reef communities and terminating with extinction of remaining Warm Temperate and Subtropical Mollusca, comprise the mass extinction; low background rates separate the-

se steps. An interval of extraordinarily large, rapid temperature and marine chemistry changes encompasses at least the middle seven extinction steps (the main C-T boundary interval) including a global anoxic event, a positive global $\delta^{13}\text{C}$ (carbon cycle) and Mn excursion, and a regional desalination event marked by a very negative $\delta^{18}\text{O}$ excursion in the North American Interior Seaway. A zone of Iridium enrichment, comprising two major iridium enrichment horizons separated by three minor spikes, is known from Pueblo, Colorado (Orth *et al.*, 1988) each of the five Ir levels closely (within 10 cm) or precisely correlates with an extinction step (1-3 and the main plankton extinction between molluscan steps 1a and 1b, Fig. 2). Most steps correlate closely with major spikes in the stable isotope disruption curves, suggesting direct cause and effect. The Ir is largely of deep-seated mantle origin but the largest enrichment level (5) may bear an extraterrestrial signal. Two known impact crater ages roughly correlate with the C-T boundary interval. No explosive volcanic events near the C-T boundary in North America bear significant iridium or are correlative with extinction steps. The mass extinction interval spans 2.5-3 Myr or possibly more (depending upon the exact age of the Tropical reef extinction event), with the main events spanning 1.5 Myr around (mainly below) the C-T boundary in North America. At present, the C-T boundary mass extinction is the best known and most completely preserved of all Phanerozoic biotic crises.

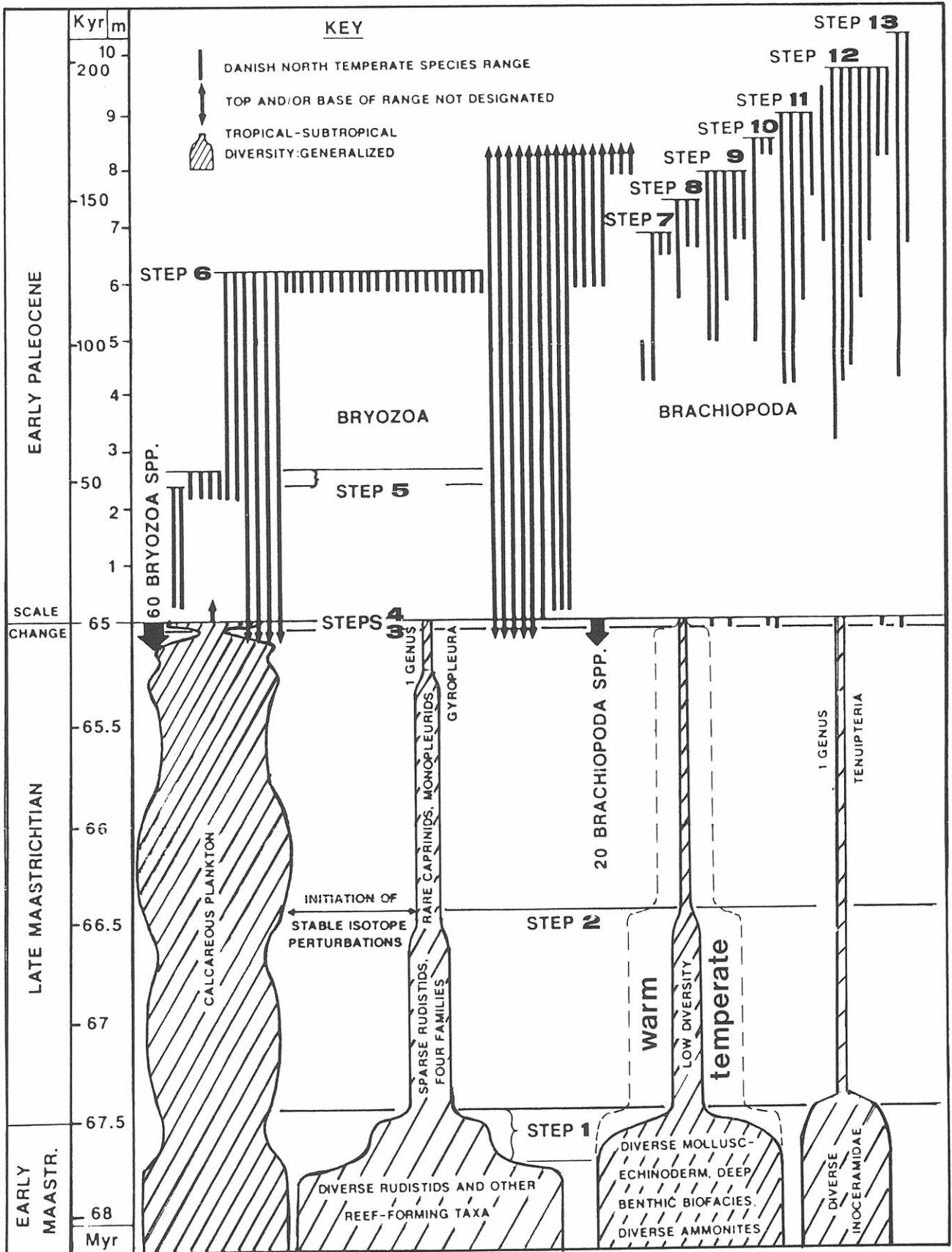
Cretaceous-Tertiary (K-T) Mass Extinction (Fig. 3)

The K-T biotic crisis is the most intensively studied mass extinction. Yet the marine record of it is very sparse, especially in regard to macrofaunas, and completely preserved in only a few continuous boundary sections worldwide. This reflects widespread epicontinental erosion associated with terminal Cretaceous to Lower Paleocene eustatic draw-down (Haq, *et al.*, 1987). Reviews of existing data and pertinent references have recently been provided by Kauffman (1984a, 1986), based on the detailed work of many paleontologists. Figure 3 summarizes these events as follows; most data suggest a stepwise mass extinction pattern.

(1) The mass extinction event initiates (Step 1) with global demise of Tropical reef ecosystems and the most diverse Tropical to Warm Temperate, shallow benthic community elements, near the Early-Late Maastrichtian boundary ("Middle"-Late of some authors) (Fig. 3; 67.5-67.75 Myr). The exact timing and duration of this step world-wide is difficult to define from scattered carbonate platform sequences. In Jamaica it lies in the basal part of the *A. maya-roensis* planktonic foraminifer biozone (67.4-67.5 Myr) and occurs within a meter of rock within a continuous carbonate platform limestone-marl sequence. The extinction of most true inoceramids, dominant Cretaceous Bivalvia, takes place at this level (Ward, 1988). (2) A second abrupt extinction step (2; Fig. 3) occurs in the middle Late Maastrichtian, about 66.5 Myr, and is marked by loss of the last scattered paucispecific rudistid frameworks, and by depletion of diverse mollusc-echinoderm-dominated, Tropical-Subtropical benthic communities. A major interval of extraordinarily large, stable isotope excursions reflecting rapid marine temperature and chemistry fluctuations begins at this point. (3) Just prior to the K-T boundary ($\pm 100-150$ Kyr), calcareous nannoplankton data suggest a major short-term depletion in populations (e.g. Thierstein, 1981), especially among specialized Tropical-Subtropical groups, followed by recovery to near-normal levels. Specialized planktonic foraminifers show a moderate decline at this level (e.g. Herm, 1965). Initiation of significant species losses among remaining Tropical-Subtropical shelf molluscs (Hansen *et al.*, 1984, 1987) and North Temperate brachiopods (Surlyk & Johansen, 1984), Bryozoa (Birkelund & Hakansson, 1982) and Mollusca (Alvarez *et al.*, 1984, Fig. 4; also see papers in Birkelund & Bromley, 1979, etc.) generally correspond to this level (Step 3; Fig. 3), the data for which are still being precisely correlated to determine the duration and magnitude of this extinction step (Hansen & Kauffman, in ms.).

(4) The K-T boundary extinction (Step 4; Fig. 3) is the major catastrophe of this sequence, broadly decimating remaining Tropical-Subtropical groups of corals, larger foraminifera, molluscs and echinoderms, Temperate mollusc, brachiopod and bryozoan species, and the great bulk of calcareous plankton and

Figure 3. Stepwise extinction across the Cretaceous-Tertiary boundary interval, compiling various global data against planktonic foraminifer biostratigraphy and a standard time scale. Rudistid reef data from Jamaica, Puerto Rico, Mexico, Spain, Middle East (Kauffman, 1984a; Kauffman and Johnson, in prep.); molluscan and calcareous plankton data from diverse sources; Brachiopod data (Danish) from Surlyk and Johansen (1984 and personal communication, 1987); Bryozoan data (Danish) from Birkelund and Hakansson (1982). Note: collapse of Tropical reef systems near base of Late Maastrichtian (Step 1); a poorly defined molluscan step (2) (two scenarios for Tropical-Subtropical, and Warm Temperate settings; dashed line) leading up to the K-T boundary; a distinct microplankton step (3) expressed by rapid population collapse among many taxa and loss of some stenotopic, specialized planktonic foraminifera about 100 Kyr below the K-T boundary; the massive K-T boundary event (Step 4) (Alvarez, *et al.*, 1984; Kauffman, 1984a, and references cited); and several species-level steps (5-13) among Lower Paleocene Temperate brachiopod and Bryozoa species. The total mass extinction interval spans nearly 3 Myr with the biggest event at the K-T boundary associated with a large meteorite or comet impact.



Radiolaria at or near a peak in their evolutionary diversification. This extinction event simultaneously affected groups of diverse evolutionary and ecological character and with decimation of a large portion of the oceanic plankton, must have caused a significant disruption or temporary collapse of the marine food chain (Kauffman, 1977). Of equal importance, this event also marks extinction of the last remaining cosmopolitan taxa and ecological generalists among once-dominant Cretaceous groups such as marine and flying reptiles, ammonites, belemnites, rudistid and inoceramid bivalves (papers in Birkelund & Bromley, 1979; Christensen & Birkelund, 1979; review and references in Kauffman, 1984a, 1986; Alvarez *et al.*, 1984). This event coincides with diverse evidence for a major bolide impact on Earth (papers in Silver & Schultz, 1982), including large-scale iridium enrichment (Alvarez *et al.*, 1980), shock-metamorphic mineral grains (Bohor *et al.*, 1984), a global smectitic boundary clay, microtektite-sized and shaped, mineralized spheres (Montanari *et al.*, 1983), and a crater in Iowa (Manson structure, Hartung *et al.*, 1986) of K/T boundary age. A giant tsunami deposit (Bourgeois, *et al.*, 1988 a, b) recorded at the K-T boundary in Texas and elsewhere in the Caribbean Province suggests a water impact of a large bolide (Hildebrand and Boynton, 1988), and thus multiple K-T boundary impacting events. The K-T boundary event is further marked by the most profound $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ isotopic (temperature, carbon cycle) excursions of the mass extinction interval (e.g. Boersma, 1984; Perch-Nielsen *et al.*, 1982), depicting rapid cooling (antigreenhousing) followed by rapid warming (greenhousing?) (Perch-Nielsen *et al.*, 1982, Fig. 8). (5) A series of very abrupt extinction steps among North Temperate bryozoans and brachiopods are suggested by published Danish data (Birkelund & Hakansson, 1982; Surlyk & Johansen, 1984) during the 200-250 Kyr following the K-T boundary (steps 5-13, Fig. 3) within uniform carbonate shelf facies containing abundant bryozoan mounds.

In the Gulf Coast region of North America (Hansen and Kauffman, in prep.) this same Early Paleocene interval includes the final abrupt extinction of Cretaceous style nannoplankton and eurytopic molluscan generalists (Hansen, *et al.*, 1987; Hansen, 1988; Upshaw & Hansen, 1988), and possibly 1-2 iridium spikes suggesting additional impacts (Ganapathy *et al.*, 1981; Asaro *et al.*, 1982; Hansen *et al.*,

1984, 1987). Details and regional correlation of these events between Denmark and the Gulf Coast are still under investigation so that no definitive global sequencing is now possible. This series of extinctions is totally contained within the last half of a global interval of extraordinary stable isotope disruption (e.g. Perch-Nielsen *et al.*, 1982; Fig. 8).

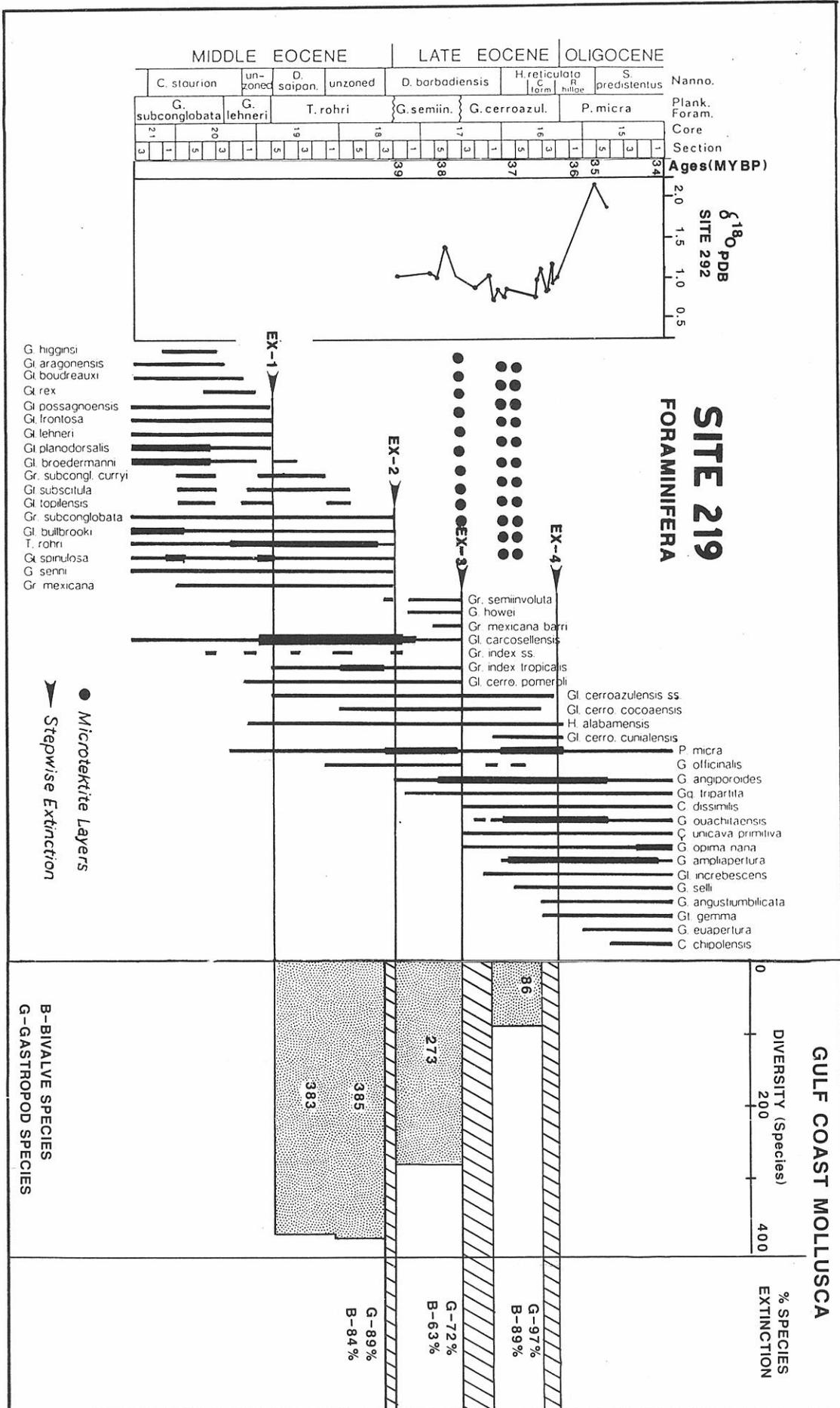
In summary (Fig. 3), the 2.75-3 Myr long K-T boundary interval is characterized by 4-13 discrete steps of highly accelerated to catastrophic extinction, ecologically graded from Tropical reef ecosystems (first), through Warm Temperate-Subtropical plankton and benthic macrofaunas (below and at the K-T boundary), and terminates with decimation of outer shelf Temperate macrofaunas and ecological/trophic generalists. All but the earliest steps lie within a zone of extraordinary climatic and oceanic perturbations as indicated by rapid, large-scale stable isotope fluctuations and a giant K/T boundary tsunami bed in the Caribbean Province. The tsunami bed, a continental crater, one or more levels of iridium enrichment, shock metamorphism, altered microtektites etc, depict multiple extraterrestrial impacts during this mass extinction interval.

Eocene-Oligocene (E-O) Mass Extinction (Fig. 4)

Though less detailed data are available for this boundary than for the C-T and K-T events, very similar relationships exist. Hansen (1988b) studied molluscan extinction patterns of the Gulf Coast of North America (summary in Kauffman, 1986, Fig. 18), and Keller (1986) provided very detailed data for the global record of planktonic foraminifer extinction and microtektite stratigraphy. A stepwise pattern of mass extinction predominates, and is summarized on Figure 4, and in Hut *et al.* (1987) over a 3.5 Myr or less interval (Keller, 1986). The species-level extinction consists of four major steps; Keller (1986) has shown additional levels of severe foraminifer population depletion during the Late Eocene.

(1) Step 1 (41-42 Myr) occurs at the top of the Middle Eocene *G. lehneri* foraminifer zone; it abruptly eliminates 4 of 13 planktonic foraminifer species and causes severe population decline in others. No molluscan extinction, microtektites or stable isotope disruptions are recorded for this level; (2) Step 2 (39 Myr) is a major extinction and/or population crisis

Figure 4. Summary of Eocene-Oligocene mass extinction events, showing stepwise pattern among data for Mollusca (Hansen, in Hut *et al.*, 1986; Hansen, 1988) and Foraminifera (from Keller, 1986). EX1 - EX4 represent integrated molluscan-foraminiferal species extinction steps. Note correlation of extinction steps 2-4 with main interval of rapidly fluctuating, large-scale stable isotope disruptions (left column; Keller, 1986) and with one of three well defined microtektite horizons in oceanic sediments (dark round circles; Keller, 1986). G-% indicates percent of existing gastropod species becoming extinct in the Gulf Coast area at each extinction step; B-% indicates similar data for Bivalvia. Numbers in shaded blocks indicate standing molluscan species diversity for each interval (Modified from Kauffman, 1986, 1988).



of planktonic foraminifera (Keller, 1986), eliminating 6 of 15 species. Among molluscs, Hansen (1988b, and Fig. 4, herein) reports 89% loss of existing gastropod species and 84% loss of bivalve species among 385 molluscan taxa; this is coincident with the foraminifer extinction and initiation of a major positive excursion in the $\delta^{18}\text{O}$ isotope record at the Middle-Late Eocene boundary. Subsequent mollusc origination rates are high.

(3) Step 3 (37.75 Myr) is the most dramatic event of the sequence (Fig. 4), and is marked by loss of 6 of 13 planktonic foraminifer species, great population depletion of others (Keller, 1986), and loss of 72% and 63% of existing gastropod and bivalve species ($N = 273$) respectively, without high origination levels. This is associated with the lowest widespread microtektite layer and a strong negative $\delta^{18}\text{O}$ isotope excursion. Two microtektite layers succeed this level but are not associated with major extinctions; they do mark major foraminifer popula-

tion changes (Keller, 1986). (4) The final extinction step (4) occurs just below and/or at the E-O boundary associated with the largest negative $\delta^{18}\text{O}$ excursion of the interval; 3 of 15 planktonic foraminifer species and 89% (bivalve) to 97% (gastropod) of the 86 extant Upper Eocene molluscan species become extinct near this level over a ± 100 Kyr interval (Hansen, 1988; Fig 4, herein).

In summary, the E-O mass extinction interval is comprised of four major steps, three of which are abrupt; one of these is directly associated with a microtektite layer reflecting impact. Major population decrease in surviving warm water foraminifer species is associated with each extinction step and with some intervening intervals containing microtektite layers. At least the last three extinction steps are contained within an interval of large-scale, rapid, stable isotope fluctuations; at least three levels of microtektites and 2-3 impact crater ages (Grieve, 1982; Alvarez & Muller, 1984) are contained within

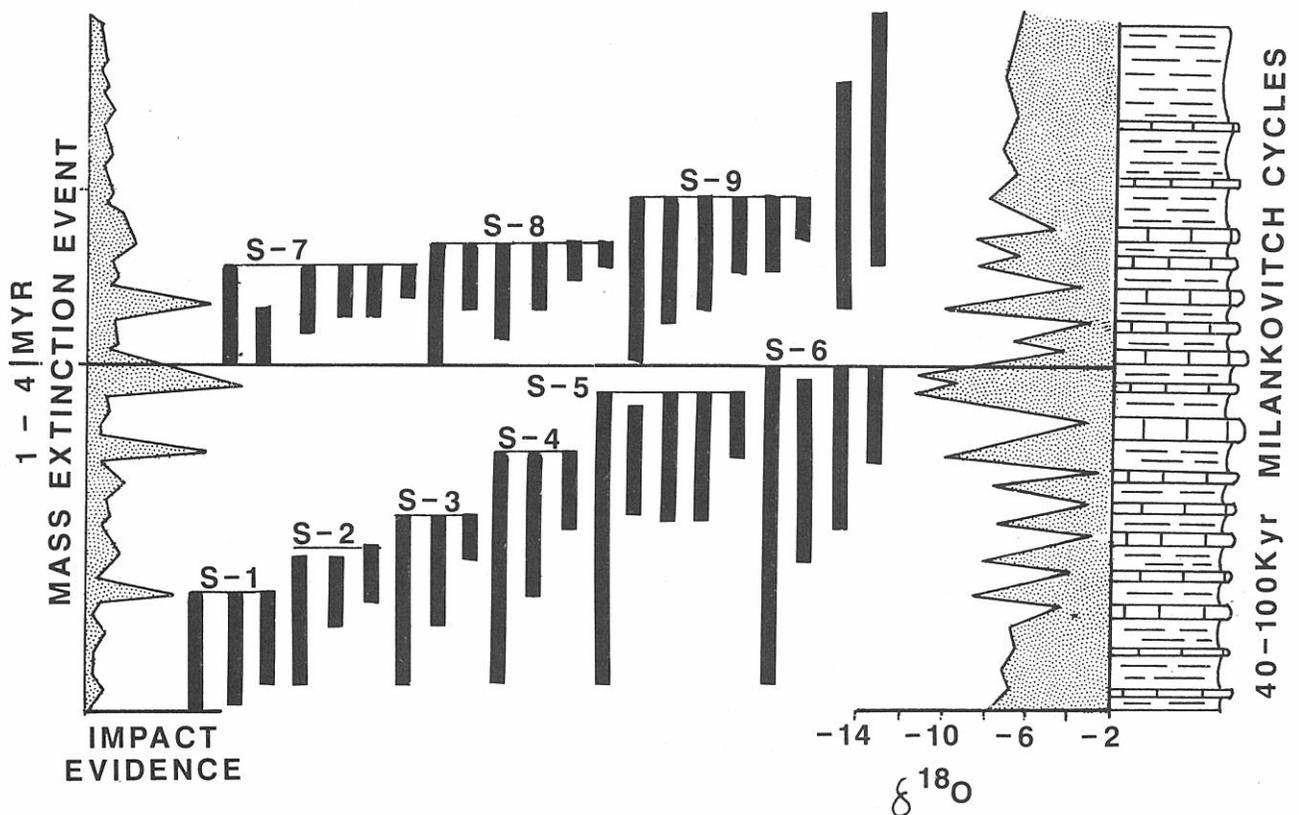


Figure 5. Hypothetical model of mass extinction theory indicated by detailed data from the Cenomanian-Turonian, Cretaceous-Tertiary, and Eocene-Oligocene mass extinction intervals. Vertical dark lines are individual taxonomic groups showing predominant stepwise extinction pattern (S-1 through S-9), ecologically graded from Tropical, stenotopic taxa at S-1 toward more Temperate, eurytopic taxa at S-9. Spikes to left indicate diverse evidence (Ir-spikes, craters, microtektite layers, etc.) for multiple impacts (showers) which initiate and span the mass extinction interval, but which do not necessarily correlate with each mass extinction. To right are shown extraordinarily rapid, large-scale, stable isotope fluctuations associated with all studied mass extinctions, reflecting major shifts in temperature, stratification and ocean chemistry as a result of impact perturbation and dynamic oceanic feedback mechanisms following impact. The scale of 100 Kyr Milankovitch cycles indicated by limestone-shale bedding rhythms to the right is based on Cenomanian-Turonian boundary observations that many stable isotope perturbations seem to be independently driven by climate cycles acting as a catalyst on a stressed ocean chemistry system.

the interval. In a general way, both Foraminifera and Mollusca show ecological grading in successive extinction steps, from a greater effect on stenotopic Warm-Temperate to Tropical taxa early, to elimination of more Temperate or eurytopic taxa later in the extinction.

CONCLUSIONS

The three best documented mass extinction events (C-T, K-T, E-O) of the Phanerozoic share several things in common. They are all stepwise in nature over 3-4 Myr intervals. Each step is characterized by highly accelerated to catastrophic loss of discrete, ecologically compatible species sets. Background rates of extinction separate these steps and are of comparatively low level. In general, the steps are ecologically graded, initially affecting ecological specialists (stenotopes), especially among Tropical reef and platform communities, and ultimately affecting more eurytopic and more Temperate taxa through successive steps to the end of the mass extinction episode. An interval of exceptionally large-scale, rapid geochemical fluctuations envelopes most or all of each mass extinction interval; fluctuations significantly exceed background levels between mass extinctions and larger fluctuations in $\delta^{18}\text{O}$, $\delta^{13}\text{C}$, Mn, Corg etc., are commonly associated with individual extinction steps. These fluctuations depict severe atmospheric, climatic, and/or oceanographic perturbations that probably exceeded the adaptive range and evolutionary rates of many taxa within very short time intervals. Evidence for one or (commonly) more meteorite/comet impacts are associated with and selectively clustered around mass extinction intervals. These shared characteristics suggest the following hypothesis (Fig. 5) for mass extinction to be tested with additional high-resolution stratigraphic data at these and other extinction intervals.

During roughly periodic (26-33 Myr) Phanerozoic intervals of predominantly warm, equable, maritime-dominated climates and higher sea level, climate and ocean systems where more delicately balanced than today, and easily driven to widespread (regional to global) sedimentologic, oceanographic and biologic response by abrupt, large-scale, predictable events/cycles and/or by major perturbations. Marine biotas that evolved within this environmental setting had narrow adaptive ranges, especially for temperature fluctuations (stenotopic, stenothermal taxa) and were thus extinction-prone. Whether by random or periodic disturbance of the Oort Comet Cloud surrounding the solar system (Hut *et al.*, 1987), the Earth was episodically bombarded by comet and associated meteorite showers. Initial and most other impacts into the ocean were predictable during high sea level stand. Such objects would have sharply disrupted the atmosphere for a short time during entry, and would have rapidly disrupted oceanic stratification, thermal and chemical balance upon impact. Mantle degassing could be associated with some impacts. Initial extraterrestrial disruptions

of the ocean would, in turn, have initiated a series of rapid temperature and chemical fluctuations that would predictably exceed the adaptive ranges of at least the most stenotopic taxa (Tropical shallow water species). Whereas rapid "healing" of the atmosphere within a few hundred years is predictable, modern ocean models suggest that such large-scale oceanic perturbations would lead to a longer-term series of dynamic fluctuations in temperature, water mass distribution and movement, density stratification and chemical cycling-intrinsic feedback processes seeking a new oceanic equilibrium. These could be enhanced or even independently driven, in part, by predictable cyclic Earthbound phenomena (e.g. by Milankovitch climate cycles) or additional perturbations (e.g. subsequent impacts, even small impactors). Each additional large oceanic impact would reset the cycle of longer-term oceanic feedback processes. Whether due to individual impacts or the long-term oceanic fluctuations following impact perturbations, each rapid change in ocean temperature and/or chemical cycling would exceed the adaptive ranges and evolutionary response rates of diverse taxa, driving a certain portion of the global biota to rapid extinction, and producing a stepwise pattern. Initial large rapid fluctuations in marine temperature and chemistry, working on an extinction-prone global biota characterized by narrow adaptive ranges, would naturally eliminate the most sensitive stenothermal/stenotopic taxa within the first set of perturbations. Subsequent extinction of more eurytopic Temperate taxa and surviving ecological generalists of once-dominant forms in later extinction steps might reflect the long-term effect of repeated environmental perturbations that eventually would deplete the species, by successive population crises, to numbers too low to guarantee survival under even normal environmental conditions. Within the stepwise extinction process (Fig. 5), large-scale impacts, and/or those producing suspended, long-term debris clouds in the atmosphere through terrestrial impact, would logically account for catastrophic extinction steps of exceptional magnitude, as at the K-T boundary. This hypothesis best accommodates existing data on well-studied mass extinction intervals, but a great deal more data are needed, for different extinction events, to provide discriminating tests.

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