

- Dynamics of extinction*, pp. 183–229. Wiley, New York.
- Jablonski, D. 1986b. Evolutionary consequences of mass extinctions. In: D.M. Raup and D. Jablonski (eds) *Patterns and processes in the history of life*, pp. 313–329. Springer-Verlag, Berlin.
- Officer, C.B., Hallam, A., Drake, C.L. & Devine, J.D. 1987. Late Cretaceous and paroxysmal Cretaceous/Tertiary extinctions. *Nature* **326**, 143–149.
- Prinn, R.G. & Fegley, B., Jr. 1987. Bolide impacts, acid rain, and biospheric traumas at the Cretaceous–Tertiary boundary. *Earth and Planetary Science Letters* **83**, 1–15.
- Raup, D.M. 1987. Mass extinction: a commentary. *Palaeontology* **30**, 1–13.
- Rocchia, R., Boclet, D., Bonte, P., Castellarin, A. & Jehanno, C. 1986. An iridium anomaly in the Middle–Lower Jurassic of the Venetian region, northern Italy. *Journal of Geophysical Research* **91**, E259–E262.
- Shoemaker, E.M. 1984. Large body impacts through geologic time. In: H.D. Holland & A.F. Trendall (eds) *Patterns of change in Earth evolution*, pp. 15–40. Springer-Verlag, Berlin.
- Shoemaker, E.M. & Wolfe, R. 1986. Mass extinctions, crater ages, and comet showers. In: R.S. Smoluchowski, J.N. Bahcall & M.S. Matthews (eds) *The galaxy and the solar system*, pp. 338–386. University of Arizona Press, Tucson.
- Trefil, J.S. & Raup, D.M. 1987. Numerical simulations and the problem of periodicity in the cratering record. *Earth and Planetary Science Letters* **82**, 159–164.
- Wolfe, J.A. 1987. Late Cretaceous–Cenozoic history of deciduousness and the terminal Cretaceous event. *Paleobiology* **13**, 215–226.
- Zachos, J.C. & Arthur, M.A. 1986. Paleocyanography of the Cretaceous/Tertiary boundary event: inferences from stable isotopic and other data. *Paleocyanography* **1**, 5–26.
- Zachos, J.C., Arthur, M.A. & Dean, W.E. 1989. Geochemical evidence for suppression of pelagic productivity at the Cretaceous/Tertiary boundary. *Nature* **337**, 61–64.

2.12.3 Periodicity

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Introduction

Periodicity of extinction is a hypothesis that extinction events (both mass extinctions and their less severe analogues) have occurred at regularly spaced intervals through geological time. It is an empirical claim based upon statistical analyses of the fossil record which indicate that maxima in extinction intensity, recognized in both biostratigraphic studies and taxonomic data compilations, are decidedly non-random with respect to time and seem to fit a regular, periodic time series. This hypothesis was introduced by Fischer & Arthur (1977) for

patterns of diversity in open-ocean pelagic communities and later supported by Raup & Sepkoski (1984), who claimed a 26 million year periodicity in extinction of global marine families. The hypothesis has since proved very controversial largely as a result of association with suggestions of catastrophic, extra-terrestrial forcing agents.

Meaning of periodicity

A perfectly periodic time series has regularly spaced events separated by invariant waiting times (Fig. 1). In most of the debate about periodicity, this pattern has been contrasted with a 'random', or Poisson, time series. A Poisson series can arise when events are independent of one another and determined by a large number of unrelated factors. A classic example is coin flipping, in which the outcome (heads or tails) of each trial results from a multitude of independent forces. The lower time series in Fig. 1 was generated by flipping a pair of coins and recording when both came up heads. The frequency of events (one in four trials) is the same as in the upper, periodic series, but the appearance is very different. The lower series is composed of loose clusters of events with irregular gaps in between; waiting times approach an exponential distribution with the median waiting time shorter than the average frequency.

The relevance of these considerations to the study of extinction events is that traditionally each event has been analysed in isolation from others and independent causal hypotheses have been formulated. Implicit in this is the assumption that extinction events must be randomly spaced in time. Observation of regular spacing, however, implies some organizing principle to extinction events, either some set of factors that governs waiting times so that they appear invariant, or some single ultimate forcing agent that has clock-like properties. Periodicity can also imply that the proximate agent of any one extinction event is the same for all, although this is not a necessary implication if the chain of causation is complex.

The association of periodicity with catastrophism comes from these last considerations. In particular, it has been suggested that: (1) the claimed 26 million year periodicity of extinction events is too long to have been produced by any known terrestrial process with periodic behaviour, leaving some astronomical clock as the likely forcing agent; and (2) the association of the Cretaceous–Tertiary mass extinction with evidence of a large extra-terrestrial



Fig. 1 The contrast between a periodic and a random time series. Both series have the same frequency of 'events', but the random series is characterized by irregular clusters of events with variable gaps between them. (After Sepkoski 1986.)

impact (Section 2.12.2) suggests (as a hypothesis to be tested) that other events in the periodic series might have been similarly caused. Note that these arguments suggest only a possible association, and other, terrestrial mechanisms are still conceivable (Section 2.12.1).

Evidence for periodicity

The hypotheses of periodicity put forward by Fischer & Arthur (1977) and Raup & Sepkoski (1984) were based upon compilations of diversity data and extinction times for taxa in the marine fossil record. Fischer & Arthur were concerned with recurrent fluctuations in the diversity of globigerinid species, ammonoid genera, and large pelagic predators through the Mesozoic and Cenozoic. They argued, without rigorous statistical testing, that these fluctuations were cyclic with a 32 million year waiting time. Using family-level data for the entire marine ecosystem, updated time-scales, and a variety of statistical tests, Raup & Sepkoski corroborated the Fischer–Arthur hypothesis but concluded that the period length was closer to 26 million years. Their statistical tests (which included parametric Fourier and autocorrelation analyses and non-parametric randomization analysis) all indicated a significant non-randomness in the distribution of extinction events and a good, but not perfect, fit to a periodic series.

Raup & Sepkoski's (1984) treatment and testing of familial extinctions were somewhat complex and have led to some confusion. Their analysis was limited to families in the Late Permian through Neogene, where stratigraphic stages are shorter and more accurately dated than in the preceding Palaeozoic. To enhance resolution, only families with extinctions known to the stage level were used

and taxa of soft-bodied and lightly sclerotized animals, or of very uncertain taxonomic position, were rejected. These manipulations left a data set of 567 extinct families ranging over 39 stratigraphic stages. Extinction intensity was measured by percent extinction, the number of extinctions in a stage divided by diversity. This metric (statistical measure) scales extinction to the number of families at risk in any stage but does not incorporate estimates of stage duration, which have limited accuracy. Percent extinction for families exhibits very low values over the Cenozoic, leaving peaks of extinction difficult to discern; Raup & Sepkoski therefore used only the diversity of families extinct before the Recent in the denominator of the metric, inflating its values in the Cenozoic.

The time series constructed by this treatment (Fig. 2) contains 'peaks', or local maxima, that vary considerably in height. Raup & Sepkoski recognized that some of these (e.g. the Guadalupian, Rhaetian, and Maastrichtian) correspond to well documented mass extinctions, but that some of the lower peaks might be spurious. Nevertheless, they chose to analyse all peaks rather than a selected subset, in order to avoid possible subjective bias. Unfortunately, they referred to all 12 peaks as 'mass extinctions'.

A randomization test for periodicity was favoured by Raup & Sepkoski (1984) because it permitted fitting a wide band of period lengths and was not sensitive to unequal spacing of data (imposed by the stratigraphic time-scale) or to variation in magnitudes of extinction peaks (which were presumed to fluctuate freely). The test (which is akin to bootstrap procedures) involved fitting periodicities to the observed extinction peaks and then comparing the goodness of fits to randomized (i.e. shuffled) versions of the data. The peaks were treated as if they all fell at the ends of stages; this, however, was merely a formalization, and equivalent results would have obtained if the peaks were consistently placed at the middles or beginnings. The shuffling procedure converted the data into what was essentially a random walk with the only constraint being that peaks must be separated by at least two stages.

The randomization test showed that periodicity fits the observed data better than 99.99% of random walks at 26 million years, even though the fit to the peaks (especially the smaller peaks) was not perfect (Fig. 2). On this basis, Raup & Sepkoski concluded that there was a 26 million year periodicity to 'mass extinctions' through the Mesozoic and Cenozoic Eras. No periodicity was found in the Palaeozoic, however. Rampino & Stothers (1984) corroborated

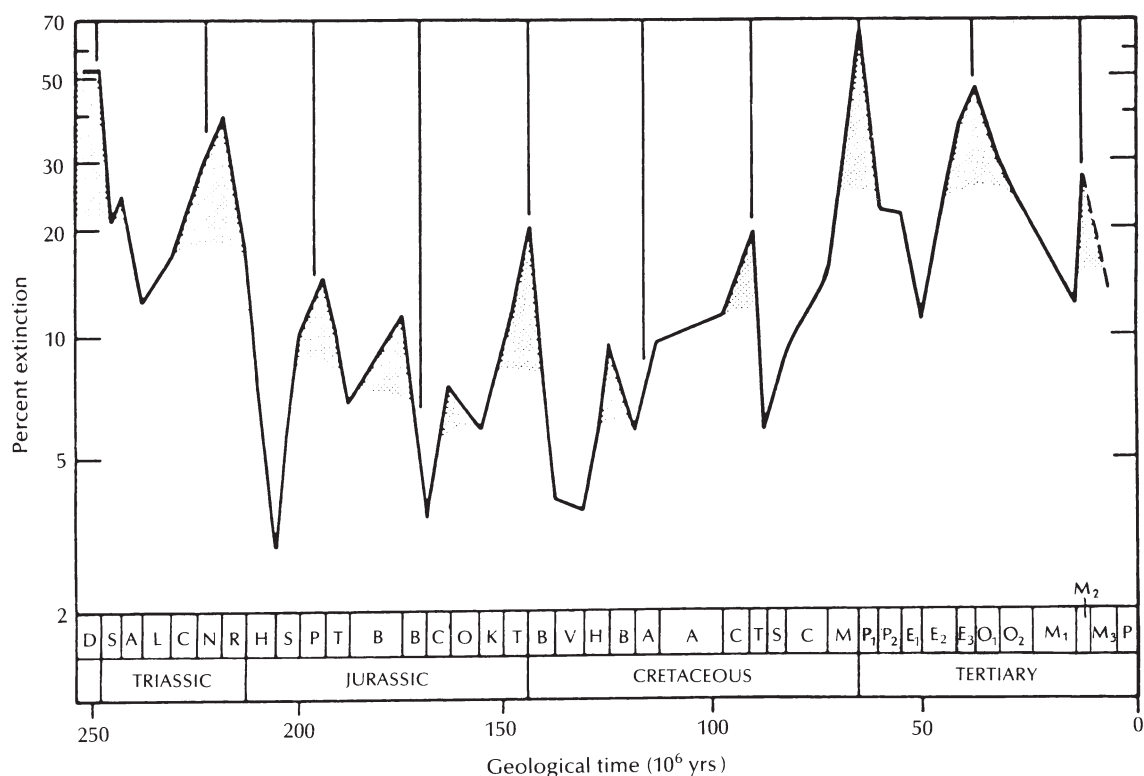


Fig. 2 Raup & Sepkoski's (1984) time series for familial extinction from the Late Permian to Neogene, computed from their highly culled sample of marine animal families. The 12 'peaks' of extinction are highlighted by stippling, and the fit to the 26 million year periodicity is indicated by the vertical lines (note the lack of fit in the Middle Jurassic and Early Cretaceous). Geological systems and stages (small boxes with initial letters of names) are indicated along the bottom of the graph (note the variable stage lengths, especially through the Cretaceous and Tertiary). The y axis is logarithmic. Abbreviations along the time axis: D = Dzhulfian; S = Scythian, A = Anisian, L = Ladinian, C = Carnian, N = Norian, R = Rhaetian; H = Hettangian, S = Sinemurian, P = Pliensbachian, T = Toarcian, B = Bajocian + Aalenian, B = Bathonian, C = Callovian, O = Oxfordian, K = Kimmeridgian, T = Tithonian; B = Berriasian, V = Valangian, H = Hauterivian, B = Barremian, A = Aptian, A = Albian, C = Cenomanian, T = Turonian + Coniacian, S = Santonian, C = Campanian, M = Maastrichtian, P₁ = Danian, P₂ = Upper Palaeocene, E₁ = Lower Eocene, E₂ = Middle Eocene, E₃ = Upper Eocene, O₁ = Lower Oligocene, O₂ = Upper Oligocene, M₁ = Lower Miocene, M₂ = Middle Miocene, M₃ = Upper Miocene, P = Pliocene.

this result, even after eliminating the three smallest peaks in the time series. A similar period-fitting technique applied to the nine remaining peaks gave a 26 million year period. However, a regression-based technique resulted in a 30 million year period, which they favoured on other grounds.

Subsequent analyses performed by Raup & Sepkoski were designed to counter criticisms of their data manipulation and statistical procedures, and to explore the correspondence between global taxonomic data and information from biostratigraphic studies. Sepkoski & Raup (1986) reanalysed the familial data using all extinctions (other than those of soft-bodied animals tied to Konservat-Lagerstätten; Section 3.11) and employing total diversity in the metrics. Fig. 3 illustrates the time

series for percent extinction in this analysis. Three other metrics of extinction were also computed and an attempt was made to assess which extinction peaks could be considered statistically significant. Sepkoski & Raup determined only eight of their previous 12 peaks to be significant and found that the heights of these peaks were generally lower than in the highly culled data set. They argued, however, that seven of the peaks corresponded to extinction events recognized by palaeontologists working at the species level with material collected from outcrops and cores. This indicated to the authors that global familial data could be trusted to reflect important extinction patterns among species in the fossil record.

Sepkoski & Raup (1986) found that the random-

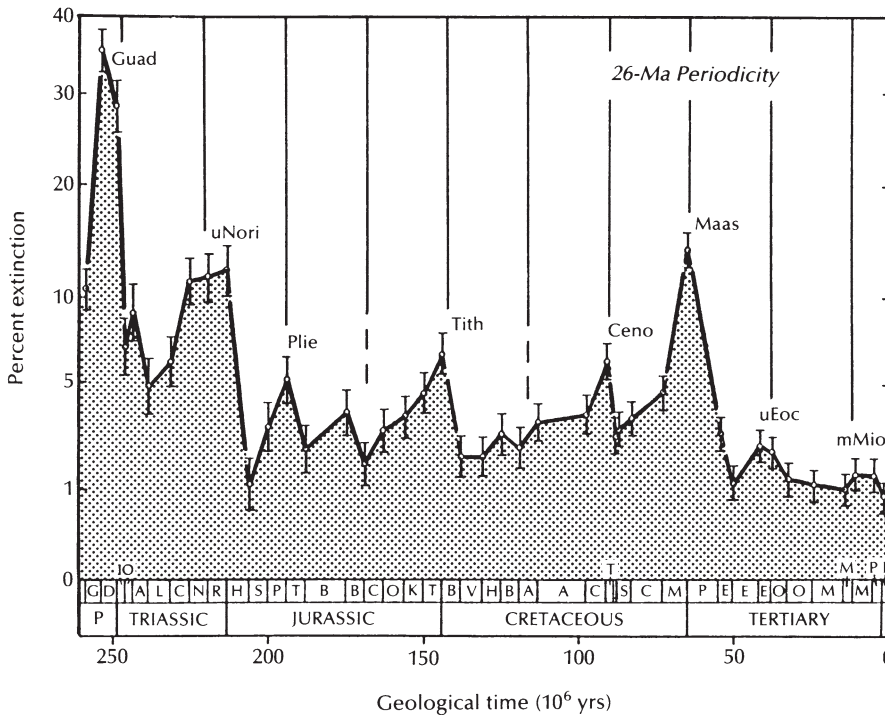


Fig. 3 Percent extinction for all marine animal families based on a data set with 970 extinctions. Peaks that are 'significantly' higher than background are labelled. (Guad = Guadalupian, uNori = Upper Norian or Rhaetian, Plie = Pliensbachian, Tith = Tithonian, Ceno = Cenomanian, Maas = Maastrichtian, uEoc = Upper Eocene, mMio = Middle Miocene, other abbreviations as in Fig. 2). Error bars indicate one estimated standard error on either side of the data points. The y axis is a square root scale. (After Sepkoski & Raup 1986, by permission of the AAAS.)

ization test applied to the eight extinction peaks still indicated a significant periodicity at 26 million years, with the standard error judged to be about ± 1 million years when imprecisions in the time-scale were accommodated. In a companion paper, Raup & Sepkoski (1986) showed that the level of statistical significance of the randomization test varied somewhat if different ages were assigned to the less precisely dated events (end-Permian and end-Triassic). Still, they concluded that most fits of the 26 million year periodicity were significant at or above the 95% level, even after adjustment for the problem of multiple tests (i.e. testing many frequencies in the 12–60 million year band).

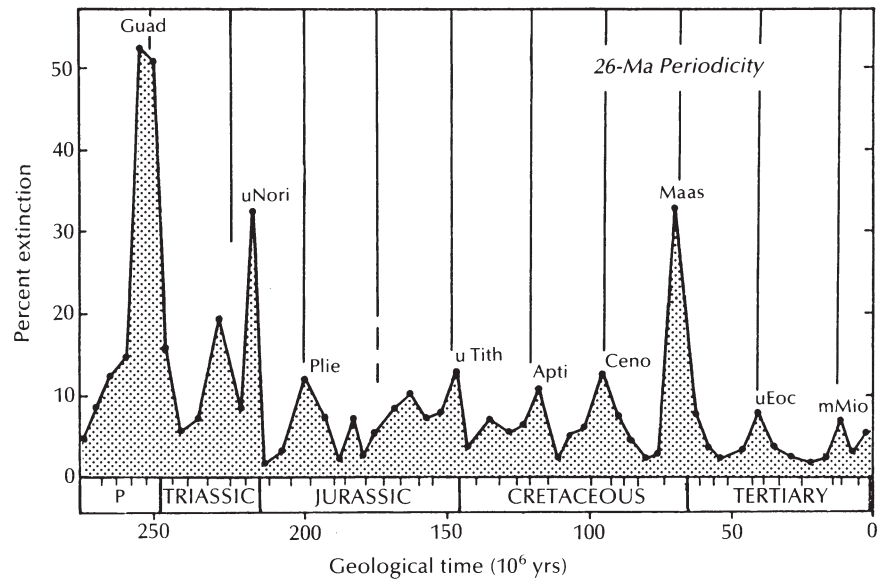
Raup & Sepkoski (1986) and Sepkoski (1986) also conducted analyses at the generic level, using a new compilation for global marine animals. This was done to increase sample size and to obtain a better approximation of species patterns. Higher taxa tend to damp the signal of species extinction since all species within a polytypic taxon must disappear for the taxon to register an extinction event. The new data set contained nearly 10 000 genera in the interval from Upper Permian to Recent. It also incorporated a refined stratigraphic time-scale with 51 intervals (in contrast to the previous 39–43 stages).

Fig. 4 illustrates one of four time series for generic extinction. As expected, the eight peaks of extinction

are more prominent than in the familial data. The peak in the Middle Miocene seems to be confirmed and an extinction event is suggested in the Aptian, which previously appeared as a gap in the periodic sequence (Fig. 3). A gap still exists in the Middle Jurassic despite two questionable peaks (Lower Bajocian and Oxfordian). These two peaks, as well as the Carnian peak (to the left of the Upper Norian peak in Fig. 4), fluctuate erratically with different metrics of extinction, suggesting that they are not robust features of the data.

Raup & Sepkoski (1986) performed the randomization test on these data and concluded that they contained the 26 million year periodicity of extinction. Sepkoski (1986) also performed autocorrelation analyses (i.e. correlating a time series with itself at a given time lag, which assesses amplitude as well as wavelength) and obtained statistically significant results consistent with a 26 million year periodicity. Finally, Fox (1987) performed an elaborate series of Fourier analyses on the generic data and also found a significant 26 million year periodicity. This was true even when he split the time series into two parts: both halves displayed a periodicity with the same wavelength and, very importantly, nearly the same phase. None of these analyses of the generic data showed decisive evidence for a periodicity prior to the Permian, however, although Sepkoski

Fig. 4 Percent extinction for marine genera. (After Sepkoski 1986.) The data illustrated comprise 9773 genera, of which 5594 are extinct. Note that peaks of extinction (labelled as in Fig. 3) are better defined than in the total familial data, and a seemingly periodic Aptian ('Apti') peak appears in the Early Cretaceous. No clearly periodic peak is present in the Middle Jurassic, although low, possibly spurious peaks appear over the Lower Bajocian and Oxfordian; a peak also appears over the Carnian within the Late Triassic.



(1986) did suggest a possible longer (greater than 30 million years) periodicity in the late Palaeozoic.

Critiques of periodicity

The hypothesis of periodicity in extinction engendered immediate attention from scientists as well as the popular press. Not surprisingly, this led to intense scrutiny of both the data and the statistical analyses. The result has been a complex series of critical discussions with various responses by Raup & Sepkoski (see Sepkoski 1989), which can only be briefly summarized here.

Data. The validity of compilations of taxonomic data has been questioned by several authors. Hoffman (1985) argued that familial data are very noisy and that different treatments, including application of alternative time-scales, results in different, seemingly random patterns of extinction peaks. This claim was countered by Sepkoski & Raup's (1986) demonstration of consistency of eight extinction peaks under four different metrics and by Sepkoski's (1986) argument that even Hoffman's composite data display strong periodicity. The presence of the same periodic extinction peaks in the much larger generic data would also seem to indicate signal rather than noise.

Stigler & Wagner (1987), however, argued that periodicity even in the generic data could be an artifact of imperfect sampling of the fossil record. Failure to sample taxa in their last stage of existence will smear the record of extinction backward in time. This will tend to swamp some minor extinction

peaks between major maxima and cause the time series to appear more regular than expected for a Poisson distribution. The counterargument to this claim (Sepkoski & Raup 1986) is simply that detailed biostratigraphic investigations corroborate most of the extinction peaks evident in the generic data, and do not indicate many smaller extinction events in other stages (although some major extinction events may be composites of tightly clustered steps).

Patterson & Smith (1987) questioned the accuracy of any taxonomic compilation that contains paraphyletic taxa (see Section 5.3). They claimed that three-quarters of the families of echinoderms and vertebrates used by Raup & Sepkoski were paraphyletic, monotypic, and/or misdated. When a corrected monophyletic component (equivalent to 10% of Raup & Sepkoski's total data set) was examined, no periodicity was evident. Sepkoski (1987) responded that paraphyly in itself should not be a problem since family extinctions simply represent a sample of species extinctions. He further noted that the monophyletic taxa in Patterson & Smith's analysis failed to show some well documented extinction events (e.g. the Maastrichtian mass extinction) and suggested that this might be due to small sample size, idiosyncracies in the echinoderm and vertebrate records, or biases inherent in the cladistic culling.

Inaccuracies in the estimated ages of stratigraphic intervals used in the data sets pose numerous problems. As noted above, Hoffman (1985) argued that use of different time-scales causes differences in extinction peaks. Shoemaker & Wolfe (*in* Smoluchowski *et al.* 1986) assessed the estimated

ages of Raup & Sepkoski's (1984) 12 extinction peaks and concluded that only three (the Cenomanian, Maastrichtian, and Upper Eocene) were reliable; this was too small a sample to support periodicity. Raup & Sepkoski (1986), however, showed that their randomization test did give significant results for the last four, best-dated extinction events (including the Middle Miocene event which Shoemaker & Wolfe rejected on the basis of familial data, but which Raup and Sepkoski accepted on the evidence of the generic data).

Stigler & Wagner (1987) questioned the strength of this test, arguing that the 26 million year periodicity might be embedded in the time-scale. This is not surprising, however, since some stratigraphic boundaries are placed at points of major turnover (e.g. the Palaeozoic–Mesozoic and Mesozoic–Cenozoic boundaries). Potential coupling of the stratigraphical and biological records was recognized by Raup & Sepkoski (1984, 1986), who shuffled the time-scale in their tests in order to avoid this problem. It should be noted that the 51-interval time-scale used in the generic data, with longer stages subdivided and shorter stages amalgamated, does not display any embedded 26 million year periodicity.

Statistical analyses. Many technical aspects of the statistical tests conducted by Raup & Sepkoski have been questioned. Hoffman & Ghiold (1985) claimed that the analyses did not properly test for a random walk. They argued that the familial data displayed a mean frequency of one peak in every four stages, which is indistinguishable from the expectation of a random walk. But these authors (and likewise Noma & Glass 1987) failed to recognize that Raup & Sepkoski's randomization procedure in essence converted the extinction data into random walks (although perhaps with less variance than proper, as pointed out by Quinn (1987)). Also, Sepkoski's (1986) autocorrelation analysis with the refined time-scale showed a peak every fifth interval in the generic data, which is not consistent with a random walk.

Noma & Glass (1987) used turning points in the familial data to argue that the hypothesis of randomness could not be rejected. However, their test was very sensitive to variance in stage durations (which range from 1 million years for the Coniacian to 15.5 million years for the Albian), and it is unclear whether Noma & Glass demonstrated anything more than this variance. They also argued that there were flaws in the selection of 'significant' extinction

peaks by Raup & Sepkoski (1986) (as well as Sepkoski & Raup 1986). This argument is valid, and at best Sepkoski & Raup merely eliminated demonstrably insignificant peaks from their familial analyses. However, other evidence presented by Sepkoski & Raup suggests that the remaining eight peaks were not insignificant since: (1) the same peaks appeared even more prominently in the generic time series (Fig. 4); and (2) most of the peaks correspond to independently identified events in biostratigraphic analyses.

Kitchell & Pena (1984) reanalysed the familial data assuming equal durations of stages and applying a series of autoregressive models (i.e. regression equations in which values in each time interval are predicted from values in preceding intervals). They rejected a simple model with periodic impulses but found adequate fits with a model incorporating five-stage memory, which they concluded demonstrated only pseudoperiodicity in the data. However, the rejected simple periodic model imposed a regular amplitude as well as wavelength, and required equal numbers of stages between extinction peaks. (The number of stages between Raup & Sepkoski's periodic peaks varied from two to six; see Fig. 2). Again, Sepkoski's (1986) autocorrelation analysis of the generic data suggested that a simple periodic impulse model could provide a statistically significant fit when the stratigraphic intervals were adjusted to be more equal in length.

Quinn (1987) criticized Raup & Sepkoski's (1984) randomization test for ignoring the autocorrelation in the data (although Stigler & Wagner (1987) did not consider this to be a problem). Quinn failed to note that Raup and Sepkoski had recognized this problem and used only randomizations that had the same number of peaks as observed in the data. Quinn offered an alternative test that compared waiting times between peaks to the expectation of random events (a broken-stick distribution). This test, he claimed, failed to demonstrate any evidence of periodicity in either the familial or the generic data. Unfortunately, he used an arbitrary definition of 'mass extinction' (either all stages with extinction intensities in the upper quartile of the data, or all peaks exceeding the mean intensity after log–linear adjustment for temporal trends). His test appears to be sensitive to the number of points selected and could reject a moderately noisy sine curve if the number of points exceeded the number of cycles.

Running Quinn's test for different numbers of cycles or points would have presented difficulty in assessing the significance level for multiple tests.

Quinn (1987) complained that Raup & Sepkoski (1984) did not calculate the joint significance level for the 49 independent tests that were conducted in assessing all periodicities between 12 and 60 million years (although Raup & Sepkoski did attempt to tackle this, albeit incorrectly). Quinn claimed the joint significance level was only 39%, given a significance of 99% for the fit of the 26 million year period. Tremaine (*in Smoluchowski et al.* 1986) calculated the joint significance level to be 95.4%, using a recomputed significance of 99.74% for the 26 million year period. Tremaine went on to argue, however, that random simulations run over the 12–60 million year band indicated a joint significance level of less than 90% for the 12 peaks of Raup & Sepkoski (1984) and less than 50% for the eight peaks of Sepkoski & Raup (1986). But these results may have been sensitive to his assumption that variance in fit was directly proportional to period length in his tests. Raup & Sepkoski (1986) used Tremaine's procedure without this assumption and obtained joint significance levels greater than 95%.

All of these tests and arguments have used a Poisson model of randomness as a basis of comparison. Lutz (1987) argued that this is not the only alternative in testing for periodicity. He tested Raup & Sepkoski's (1984) familial time series against models for Poisson distributions, 'noisy' periodicities, and constrained episodicities (i.e. γ distributions in which the standard deviation in waiting times is less than the mean waiting time). He found that the Poisson model could be rejected at the 95% significance level, but he could not distinguish between fits of noisy periodicities and of episodicities with variances less than 30% of mean waiting time (although it is not clear how sensitive these results are to selection of events and to errors in the time-scale).

Lutz (1987) concluded that an exogenous forcing agent with clock-like behaviour was not necessary to explain the data. Stanley (1987) proffered a similar argument on qualitative grounds. He suggested that extinction events eliminate particularly vulnerable taxa and that there is a lag time after each event during which few vulnerable taxa are available for extinction. Thus, palaeontologically recognizable perturbations should be spaced more widely than expected from a Poisson distribution. The counter to this argument is that recovery times observed for most extinction events in the Mesozoic and Cenozoic are only one or two stages, which is within the lag time built into Raup & Sepkoski's randomization procedure.

It cannot be claimed that any of these arguments and counterarguments is decisive, and it is doubtful whether new, more accurate data could settle the matter (although more precise data would certainly promote better understanding of extinction in the fossil record). A definitive settlement will be reached only if a clear agent of periodic extinction is discovered.

Possible causes of periodicity

Both terrestrial and extra-terrestrial mechanisms have been suggested as ultimate causes of periodicity in extinction. The terrestrial mechanisms involve hypothetical quasiperiodic processes in the deep Earth that lead to episodes of intense volcanism. The extra-terrestrial mechanisms involve a variety of observed and hypothesized astronomical clocks that might induce periodic cometary bombardments of the Earth.

Evidence that extra-terrestrial impacts might be important in periodic extinction come from two sets of observations (see also Section 2.12.2):

- 1 Materials presumed to be of impact origin (excess iridium, microtektites, and/or shocked mineral grains) are associated with several periodic extinction events, including the Cenomanian, Maastrichtian, Upper Eocene, and Middle Miocene.
- 2 Ages of terrestrial craters seem to exhibit a weak periodicity, involving 25–50% of impacts, that has a phase and period length (variously estimated at 27–32 million years) that are roughly congruent with the extinction periodicity (see Shoemaker & Wolfe *in Smoluchowski et al.* 1986).

The periodic impactors are presumed to be comets derived from the Oort Cloud at the outer fringes of the Solar System. It has been hypothesized that a gravitational perturbation from a body as small as four times Jupiter's mass could induce a comet shower that would bring up to 10^9 comets into the inner Solar System; about 25 of these on average would strike the Earth over a 1 million year interval. Four mechanisms, all of which are flawed, have been suggested to produce such comet showers periodically (reviewed by Sepkoski & Raup 1986; Shoemaker & Wolfe *in Smoluchowski et al.* 1986):

- 1 A dim binary companion to the Sun, dubbed 'Nemesis'. This small star is hypothesized to have a highly eccentric orbit with a mean revolution time of 26–28 million years. At aphelion, it would pass through the Oort Cloud and induce a comet shower. However, a distant companion has never been ob-

served, and simulations indicate it would be unstable and easily stripped from its orbit by passing field stars and molecular clouds.

2 An unobserved tenth planet, usually called 'Planet X'. If it had a slightly eccentric orbit inclined to the plane of the Solar System, orbital precession could bring the perihelion into the solar plane twice every 52–56 million years, at which time the planet would scatter comets from the inner edge of the Oort Cloud. However, a tenth planet has never been observed, and it is not clear whether it would have sufficient mass to scatter enough comets to leave a recognizable periodic signature on Earth.

3 Oscillation of the Solar System perpendicular to the Galactic plane. This well known behaviour moves the Solar System every 31–33 million years through the dense plane of the Galaxy, where gravitational encounters with molecular clouds might perturb the Oort Cloud. However, the oscillation is out of phase with the extinction periodicity, and it has been argued that the mass of the Galaxy is not sufficiently concentrated in the plane to affect any distinct periodicity over a 270 million year interval.

4 Quasiperiodic transit of the Solar System through the spiral arms of the Galaxy. During its galactic orbit, the Solar System passes through either two or four arms, where concentrated mass may perturb the Oort Cloud. However, the intervals between transits are either about 60 or 125 million years, which is much longer than the observed periodicity of extinction.

Alternative hypotheses that deep-Earth processes could induce periodic extinction are based on two lines of evidence (see also Section 2.12.1): (1) there is an arguable periodicity of around 30 million years in the frequency of reversals of the Earth's magnetic field, suggesting some kind of regularity in deep-Earth dynamics (Loper *et al.* 1988); and (2) several periodic extinction events are associated with immense volcanic deposits (e.g. the Siberian traps, Deccan traps, and Columbia River basalts), which were produced during major episodes of basaltic volcanism. Such episodes could release large quantities of particulates, sulphates, and carbon dioxide into the atmosphere, perturbing climate and inducing extinction.

Loper *et al.* (1988) argued that major volcanic episodes would be quasiperiodic if they were caused by variation in the thickness of the thermal layer at the base of the mantle. Thickening of this layer through time could lead to dynamical insta-

bilities that would spawn mantle plumes and cause widespread basaltic volcanism. Release of the plumes would draw material from the thermal layer, re-establishing stability and thus limiting the duration of the volcanic episode.

This hypothesis of terrestrial forcing challenges, but does not negate, a role for extra-terrestrial impacts in producing the observed distribution of extinction events: coincidental impact during a volcanic episode could greatly amplify a biotic crisis. Both sets of hypotheses are consistent with the implication from periodicity that most Mesozoic–Cenozoic extinction events share a common ultimate cause. But, as Lutz (1987) noted, the deep-Earth mechanism is not strictly clocklike but would operate by constraining waiting times between events to generate the non-random distribution that is seen in the fossil record of extinction.

References

- Fischer, A.G. & Arthur, M.A. 1977. Secular variations in the pelagic realm. In: H.E. Cook & P. Enos (eds) *Deep-water carbonate environments*. Special Publication of the Society of Economic Paleontologists and Mineralogists No. 25, pp. 19–50.
- Fox, W.T. 1987. Harmonic analysis of periodic extinctions. *Paleobiology* **13**, 257–271.
- Hoffman, A. 1985. Patterns of family extinction: dependence on definition and geologic time scale. *Nature* **315**, 659–662.
- Hoffman, A. & Ghiold, J. 1985. Randomness in the pattern of 'mass extinctions' and 'waves of originations'. *Geological Magazine* **122**, 1–4.
- Kitchell, J.A. & Pena, D. 1984. Periodicity of extinctions in the geologic past: deterministic versus stochastic explanations. *Science* **226**, 689–692.
- Loper, D.E., McCartney, K. & Buzyna, G. 1988. A model of correlated episodicity in magnetic-field reversals, climate, and mass extinctions. *Journal of Geology* **96**, 1–16.
- Lutz, T.M. 1987. Limitations to the statistical analysis of episodic and periodic models of geologic time series. *Geology* **15**, 1115–1117.
- Noma, E. & Glass, A.L. 1987. Mass extinction pattern: result of chance. *Geological Magazine* **124**, 319–322.
- Patterson, C. & Smith, A.B. 1987. Is the periodicity of extinctions a taxonomic artefact? *Nature* **330**, 248–251.
- Quinn, J.F. 1987. On the statistical detection of cycles in extinctions in the marine fossil record. *Paleobiology* **13**, 465–478.
- Rampino, M.R. & Stothers, R.B. 1984. Terrestrial mass extinctions, cometary impacts and the Sun's motion perpendicular to the galactic plane. *Nature* **308**, 709–712.
- Raup, D.M. & Sepkoski, J.J., Jr. 1984. Periodicity of extinctions in the geologic past. *Proceedings of the National Academy of Sciences, U.S.A.* **81**, 801–805.
- Raup, D.M. & Sepkoski, J.J., Jr. 1986. Periodic extinction of

- families and genera. *Science* **231**, 833–836.
- Sepkoski, J.J., Jr. 1986. Global bioevents and the question of periodicity. In: O. Walliser (ed.) *Global bio-events*, pp. 47–61. Springer-Verlag, Berlin.
- Sepkoski, J.J., Jr. 1987. Is the periodicity of extinction a taxonomic artefact? Response. *Nature* **330**, 251–252.
- Sepkoski, J.J., Jr. 1989. Periodicity in extinction and the problem of catastrophism in the history of life. *Journal of the Geological Society of London* **146**, 7–19.
- Sepkoski, J.J., Jr. & Raup, D.M. 1986. Periodicity in marine extinction events. In: D.K. Elliott (ed.) *Dynamics of extinction*, pp. 3–36. Wiley, New York.
- Smoluchowski, R.S., Bahcall, J.N. & Matthews, M.S. (eds) 1986. *The galaxy and the solar system*. University of Arizona Press, Tucson.
- Stanley, S.M. 1987. *Extinction*. Scientific American Books, New York.
- Stigler, S.M. & Wagner, M.J. 1987. A substantial bias in non-parametric tests for periodicity in geophysical data. *Science* **238**, 940–945.

2.13 Mass Extinction: Events

2.13.1 Vendian

M. A. S. McMENAMIN

Introduction

The earliest known, reasonably well documented mass extinction is of Vendian age, and seems to have occurred in the middle part of the Vendian, about 650 Ma. The severity and timing of this extinction is somewhat obscured by the difficulty of obtaining precise dates for Vendian sediments. Also, some losses of Vendian diversity appear to be the continuation of declines that began before the beginning of the Vendian, such as the loss of many different types of stromatolites.

Micro-organisms

Stromatolites reached a peak in diversity (nearly 100 recognized taxa) in the Late Riphean (c. 850 Ma). Following this acme, stromatolites underwent a precipitous decline (see also Section 1.5) starting in the second half of the Late Riphean and continuing through the Vendian. Stromatolite diversity bottomed out at less than 30 taxa by the beginning of the Cambrian. Although this decline does not necessarily represent the extinction of any of the individual microbial species that participated in the formation of stromatolites, it does indicate that the conditions became much less favourable for many formerly successful types of benthic microbial communities. For example, well formed specimens of the conical Proterozoic stromatolite *Conophyton*

are unknown after the Vendian. The advent of burrowing and grazing metazoans, and disturbance to microbial mats as a result of their activities, has been hypothesized as the factor responsible for the decline of stromatolites.

Individual taxa of benthic microbial organisms (Section 1.2), represented by delicate unicells and filamentous chains of cells preserved in chert, seem to have been largely unaffected by extinction during the Vendian, although it is difficult to recognize taxonomic turnover in floras consisting primarily of morphologically simple coccoidal and filamentous microbes. This problem is further compounded by the fact that fossilized benthic microbiotas are rare after the beginning of the Cambrian; apparently the conditions necessary for fossilization of microbes in chert became much less common after the end of the Vendian.

A different situation exists with acritarchs, a heterogeneous group of organic-walled microfossils recovered from sediment by acid maceration. By comparison with modern dinoflagellate cysts, most acritarchs are thought to represent the resting stages of planktic, eukaryotic marine algae (Section 1.7.2). Both within-flora and total taxonomic diversity of these planktic microfossils underwent a severe decline during the Middle to Late Vendian, which Vidal & Knoll (1982) regarded as indicative of major extinctions in the eukaryotic phytoplankton. Diagnostic acritarch taxa such as *Trachysphaeridium laufeldi* and the distinctively striate *Kildinella lophostriata* (Vidal & Knoll 1982) disappeared by the Middle Vendian.

These distinctive Late Riphean–Early Vendian acritarchs were succeeded by a depauperate flora typified by *Bavlinella faveolata* (an acritarch that

resembles the existing colonies of spherical cyanobacteria called chroococcaleans) and the ribbon-shaped vendotaenid algae. The sediments containing this depauperate flora also have curiously large amounts of organic matter (sapropel) derived from the burial of acritarchs and other organic-walled objects. The re-radiation of the plankton from this low-diversity interlude was slow. Acritarch diversity in most stratigraphic sections did not recover to Early Vendian levels until well into the Lower Cambrian, when very spiny forms such as *Skiagia* became abundant (but see Zang & Walter 1989).

Metazoans

The soft-bodied fossils of the Ediacaran fauna are generally thought to be metazoans (Section 1.3). Frondose or leaf-like Ediacaran forms such as *Charnia* and *Charniodiscus* are known throughout the world in sediments of Vendian age. Some of these organisms attained sizes of up to one metre in length. The second half of the Vendian (the Kotlin Horizon) is marked by local extinction on the Russian Platform of many of these large, distinctive soft-bodied creatures. Possibly coincident with the decline in phytoplankton diversity, Late Vendian metazoan faunas of the Russian Platform were reduced to rare problematic forms of medusoids and small trace fossils (Fedonkin 1987; Sections 1.3, 1.5).

The Ediacaran fauna seems to have died off by the end of the Vendian (the top of the Rovno Horizon of the Siberian Platform), although a few of these soft-bodied forms may have survived into the Early Cambrian. Seilacher (1984) argued that the end of the Vendian witnessed a mass extinction of the soft-bodied Ediacaran forms, and that these extinctions were real and were not an artifact of preservation. It must be noted, however, that the intensity of burrowing increased greatly in the terminal Vendian. The trace fossils at this time became more complicated, deeper and larger, indicating an increase in the dimensions of infaunal animals. This development may have reduced the potential for preservation of soft-bodied animals.

The Late Vendian increase in burrowing intensity was accompanied by an explosion in the diversity of trace fossils. Numerous new ichnotaxa appeared that have ranges continuing through most or all of Phanerozoic time. Of the dozens of new ichnogenera that first appeared in the Vendian, only six became extinct by the end. Of these, *Neonoxites*, and *Palaeopascichnus* were horizontal grazing or very shallow

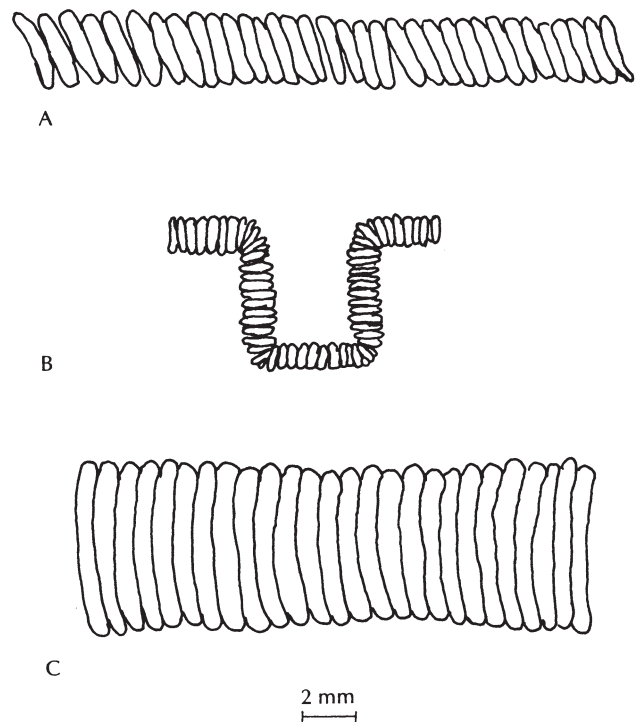


Fig. 1 Three ichnogenera known from the late Vendian. A, *Harlaniella*. B, *Neonoxites*. C, *Palaeopascichnus*. All three are shallow deposit feeding or grazing, horizontal bedding plane trace fossils.

deposit feeding traces (Fig. 1). If there was indeed a mass extinction at the end of the Vendian, it was overshadowed by the metazoan diversification occurring at this time.

The study of Vendian extinctions is hampered by a paucity of well preserved macrofossils. Nevertheless, the disappearance of acritarchs suggest that the Middle Vendian was marked by a mass extinction event that rivalled in magnitude the better known mass extinctions occurring later in the Phanerozoic. This Middle Vendian acritarch extinction event was linked to the Varangian glaciation by Vidal & Knoll (1982), who invoked climatic cooling as a causal mechanism. More evidence is needed to clarify the timing, severity, and possible climatic control of these extinction events. Of particular interest is the unresolved question of whether global metazoan mass extinctions occurred in the Vendian, and whether or not they were coincident with the phytoplankton extinctions.

References

- Fedonkin, M.A. 1987. *The non-skeletal fauna of the Vendian and its place in the evolution of metazoans*. Nauka, Moscow (in Russian).

- Seilacher, A. 1984. Late Precambrian and Early Cambrian Metazoa: preservational or real extinctions? In: H.D. Holland & A.F. Trendall (eds) *Patterns of change in Earth evolution*, pp. 159–168. Springer-Verlag, Berlin.
- Vidal, G. & Knoll, A.H. 1982. Radiations and extinctions of plankton in the late Proterozoic and early Cambrian. *Nature* **297**, 57–60.
- Zang, W.L. & Walter, M.R. 1989. Late Proterozoic plankton from the Amadeus Basin in central Australia. *Nature* **337**, 642–645.

2.13.2 End-Ordovician

P. J. BRENCHLEY

Introduction

About 22% of all families became extinct in the Late Ordovician, which makes this one of the largest episodes of mass extinction (Raup & Sepkoski 1982). Although there were some extinctions throughout the Ashgill, the main phase of extinction was in the Late Ashgill. The Late Ordovician extinctions cannot be related to a single stratigraphic level, but occurred in at least two steps. One phase coincided with the start of a major regression at the end of the Rawtheyan (the penultimate stage in the Ashgill) and a second phase coincided with a transgression at the end of the Hirnantian (the last Ashgill stage), about 1–2 million years later (Brenchley 1984). There may in addition have been some extinctions throughout Hirnantian times. The two major phases of extinction have been best documented from clastic sequences in Europe. Upper Ordovician extinctions of comparable magnitude are known from carbonate sequences in North America but have not been clearly differentiated into two phases.

Extinction patterns

The Late Ordovician extinctions involved significant changes to a number of groups:

Trilobites. Only about 14 of the 38 families of Middle Ashgillian trilobites survived into the Silurian. The main decline in diversity occurred at the end of the Rawtheyan when about 15 families disappeared. Generic diversity which had been fairly constant throughout the Ashgill declined by 45–75% at the top of the Rawtheyan (Fig. 1) and species diversity was possibly reduced even more.

Brachiopods. Thirteen families of brachiopods became extinct at or near the Ordovician–Silurian boundary. Of the 27 families which crossed the boundary, nine showed a marked decline in abundance (Sheehan 1982). Amongst the rich brachiopod faunas of the Ashgill of northwest Europe, 25% of genera disappeared at the top of the Rawtheyan and another 40% at the top of the Hirnantian (Fig. 1).

Graptolites. The diversity of graptolite species decreased from a high point in the Late Caradoc to a nadir in the *Climacograptus extraordinarius* and *Glyptograptus persculptus* zones, when the total world graptolite fauna consisted of only a few genera.

Primitive echinoderms. The diversity of cystoid, edriasteroid, and cyclocystoid families declined sharply in the Late Ashgill. The sharpest drop in numbers of cystoid genera in the families Diploporita and Dichoporita was at the Rawtheyan–Hirnantian boundary, when the rich and varied Rawtheyan fauna with 26 genera was reduced to a small but distinctive Hirnantian fauna with only eight. Most of the latter fauna apparently disappeared at the end of the Hirnantian.

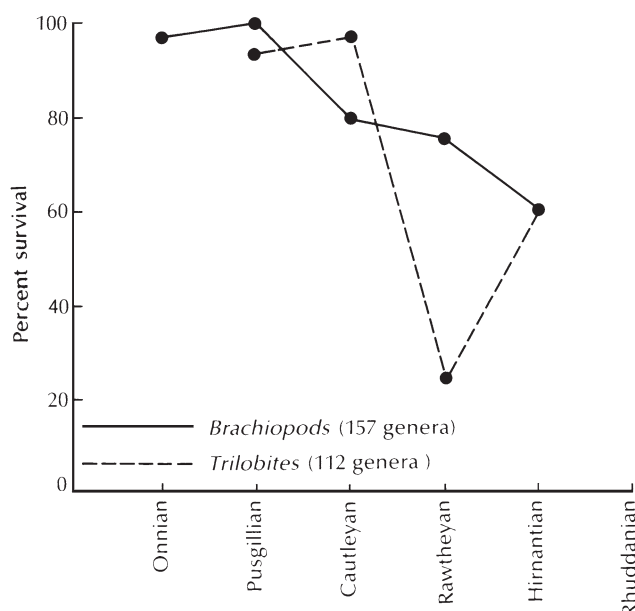


Fig. 1 Percentage survival of genera from stage to stage in the Upper Ordovician, e.g. 98% of Cautleyan trilobite genera survived into the Rawtheyan and 25% of Rawtheyan genera survived into the Hirnantian. The graphs are based on genera found in sequences with good stratigraphical control mainly in Europe. (After Brenchley 1984, by permission of John Wiley & Sons Ltd.)

Conodonts. The mainly clastic Hirnantian sequences of Europe have yielded very few species of conodonts, even where collecting has concentrated on the more promising limestone horizons. In the carbonate sequences of North America diverse conodont faunas declined a little in the Gamachian and disappeared almost completely at the Ordovician–Silurian boundary.

Chitinozoa, acritarchs, and ostracodes. All three groups show major decreases in diversity and changes in taxonomic composition at or near the Ordovician–Silurian boundary.

Corals. The best data for the Late Ordovician show that *c.* 50 of the 70 tabulate and heliolitoid genera became extinct in Late Ordovician times. It is not clear whether this was an end-Rawtheyan or Hirnantian extinction.

Following the first wave of extinction at the end of the Rawtheyan there was a residual fauna, dominated by brachiopods, which is usually referred to as the *Hirnantia* fauna. This fauna is unusually cosmopolitan and appears to have ranged from circumpolar to sub-tropical latitudes, though it was not well developed in the carbonate environments of tropical regions. The *Hirnantia* fauna is commonly considered to have been a relatively cool water fauna.

The second wave of extinction at the top of the Hirnantian (top Gamachian in Canada) was relatively modest in the clastic sequences of Europe. Several elements of the *Hirnantia* fauna disappeared at this level, and coral and ostracode faunas may have been heavily depleted. Coral-stromatoporoid reefs which occur at the top of the Hirnantian are rare or absent in the lower levels of the succeeding Silurian.

In North America the diversity of brachiopods, trilobites, conodonts, acritarchs, and ostracodes greatly diminished at the end of the Ordovician (Lespérance 1985), but because the detailed stratigraphy is uncertain the extinctions could be Early or Late Hirnantian.

Environmental changes

In most shelf sequences there is a change of facies at the Rawtheyan–Hirnantian boundary, reflecting the start of the regression which reached its maximum in the Middle or Upper Hirnantian. The regression partially drained many clastic shelves leaving a variety of shallow-marine sandy deposits.

A major part of the world's carbonate platforms became exposed with widespread development of karst surfaces and unconformities.

At the top of the Hirnantian there is generally a sharp change in facies indicating a rapid transgression. In many clastic sequences the shallow-marine rocks of the Upper Hirnantian are overlain by black graptolitic shales. In carbonate regions there is a progressive return to more offshore carbonate facies.

It has been estimated that the regression involved a fall in sea-level of 50–100 m (Fig. 2). In several Hirnantian sequences there is some evidence of fluctuations of sea-level (two to four regressions) but the pattern is not clear on a global scale.

Causes

The cause or causes of the extinctions are debatable. The stepped nature of the extinctions makes an extra-terrestrial cause, such as meteorite impact, unlikely. Furthermore no iridium anomaly was discovered in detailed investigations of the Ordovician–Silurian stratotype at Dob's Linn or in the carbonate sequence of Anticosti Island. The very precise correlation between the disappearance of faunas in many sections and the first evidence of regression makes it likely that the extinctions were related to contemporaneous environmental changes such as the following:

1 Sea-level changes. The fall in sea-level during the Hirnantian would have drastically reduced the size of continental shelves and platforms and hence the habitable area for shelf benthos. Many very extensive platforms (N. America, Baltica and the Russian Platform) were covered by shallow seas during most of the Ordovician so a sea-level fall of tens of metres would have had a profound effect.

The main argument against a major role for sea-level change in causing extinctions is that the faunal changes were concentrated at the Rawtheyan–Hirnantian boundary while the regression appears to have continued throughout the early part of the Hirnantian. The second phase of extinction at the top of the Hirnantian coincides with a rise in sea-level, and consequently a potential increase in habitable area. However, following the transgression, black shales were deposited on many clastic shelves, indicating widespread anoxic or dysaerobic conditions hostile to benthic faunas (see also Section 2.12.1).

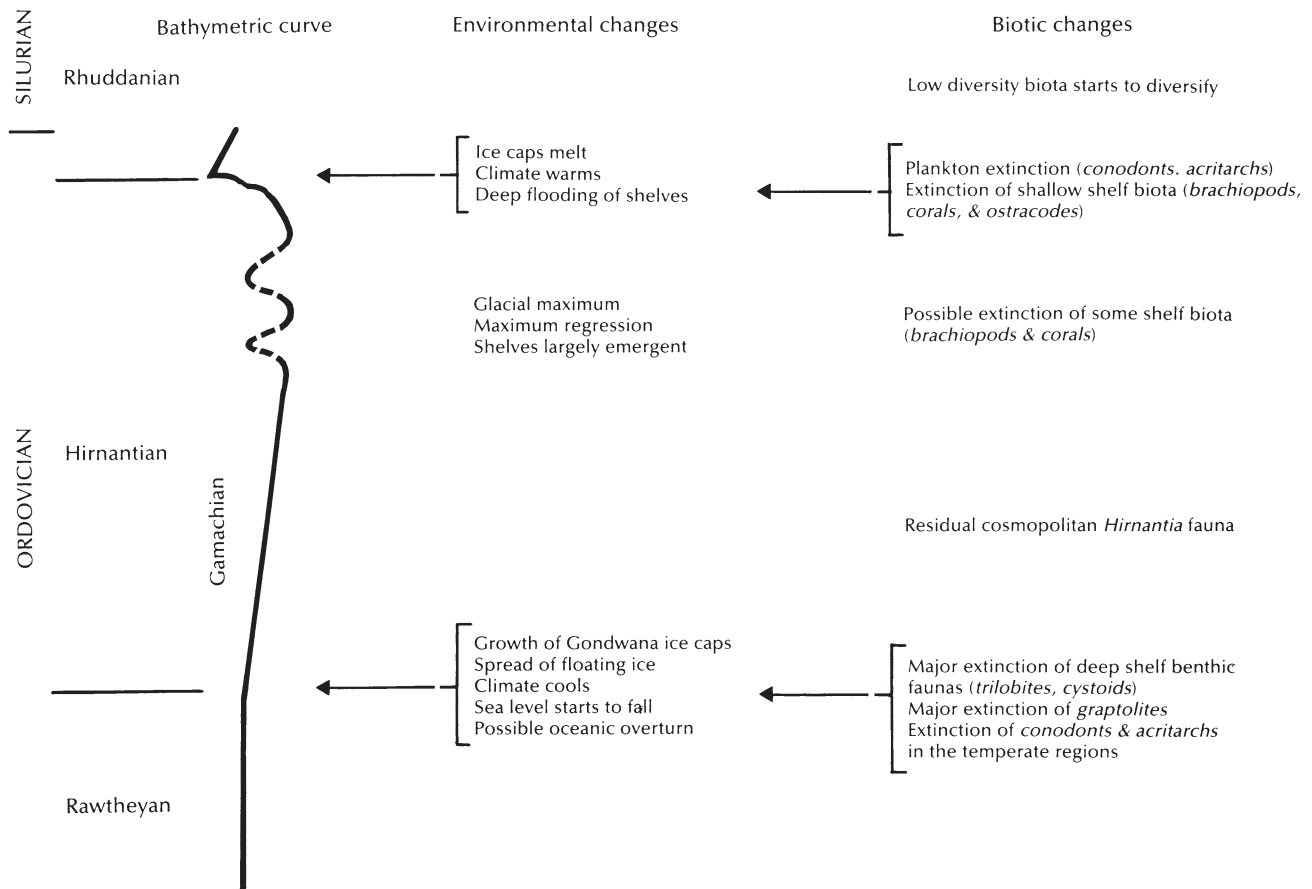


Fig. 2 Summary diagram showing the Late Ordovician–Early Silurian bathymetric curve and associated environmental and biotic changes.

Although changes in sea-level may have had some effect on the shelf benthos they do not satisfactorily account for the major extinctions amongst the plankton.

2 Temperature. There is evidence from the wide extent of upper Ordovician continental glaciation on Gondwanaland, and the occurrence of marine tilloids peripherally, for a very substantial extension of arctic and subarctic conditions in the Hirnantian. On the other hand, tropical carbonate environments survived at the same time in equatorial latitudes. There might well have been a substantial reduction in the area of temperate seas and some restriction of tropical regions which could account for the reduction in diversity of microplankton and graptolites. The widespread distribution of the *Hirnantia* fauna might be related to the spread of cool water, which could even have impinged on formerly tropical areas during major phases of glaciation.

The second phase of extinction at the top of the

Hirnantian should have been at a time of rising temperature so it is unlikely that this phase of extinction was the result of changing climate.

3 Oceanic overturn. It has been suggested that during periods of climatic change the stability of weakly stratified ocean waters might be disturbed, and that they could overturn bringing 'unconditioned' biologically-toxic bottom water to the surface (Wilde & Berry 1984). Such overturns might occur either during a period of climatic deterioration, when cold water from high latitudes intruded below weakly stratified ocean waters, or during times of climatic amelioration.

The model of oceanic overturn has several attractions, as it can account for the coincidence of the two phases of extinction with times of maximum climatic change, and for extinction of both plankton and shelf benthos. Furthermore, the effects of overturn would have been rapid, which accords with the disappearance of faunas at precise levels in

many sections. Unfortunately no evidence of oceanic overturn has yet been detected in the sedimentary record.

In summary, changes in both temperature and sea-level, for which there is good evidence, might have played a significant role in the faunal extinctions. A related oceanic overturn could have been important, but remains hypothetical.

References

- Brenchley, P.J. 1984. Late Ordovician extinctions and their relationship to the Gondwana glaciation. In : P.J. Brenchley (ed.) *Fossils and climate*, pp. 291–315. John Wiley & Sons, Chichester.
- Lespérance, P.J. 1985. Faunal distributions across the Ordovician–Silurian boundary, Anticosti Island and Percé, Quebec, Canada. *Canadian Journal of Earth Sciences* **22**, 838–849.
- Raup, D.M. & Sepkoski, J.J., Jr 1982. Mass extinctions in the marine fossil record. *Science* **215**, 1501–1503.
- Sheehan, P.M. 1982. Brachiopod macroevolution at the Ordovician–Silurian boundary. *Proceedings of the Third North American Paleontological Convention* **2**, 477–481.
- Wilde, P. & Berry, W.B.N. 1984. Destabilisation of the oceanic density structure and its significance to marine ‘extinction’ events. *Palaeogeography, Palaeoclimatology, Palaeoecology* **48**, 143–162.

2.13.3 Frasnian–Famennian

G. R. McGHEE, Jr

Extinction patterns

The massive deterioration in ecosystems which occurred throughout the world during the Frasnian–Famennian event can be described correctly as catastrophic in effect (McLaren 1982). Frasnian ecosystems were ecologically very diverse and equitable in structure. Early Famennian ecosystems, in contrast, were impoverished in ecological diversity and in overall species richness. The effect of the biotic crisis can easily be seen in the ‘bottleneck’ constriction of ecological complexity which occurred in the Appalachian region of eastern North America. There the diverse Frasnian ecosystem is replaced by an ecologically depauperate Famennian ecosystem proportionately over-dominated by reduced species numbers of brachiopods, bivalves, and glass sponges (McGhee 1982).

The analysis of the fossil remains of organisms around the globe which perished during the extinction event, as well as those which survived, reveals the following ecological patterns:

Latitudinal effect. Tropical reefal and perireefal marine ecosystems were particularly hard hit. The low-latitude, geographically widespread and massive stromatoporoid-tabulate reefal ecosystems vanished, and perireefal rugose coral-tabular stromatoporoid bioherms were decimated. The stromatoporoids suffered a severe reduction in biomass, but they did not become extinct nor did they totally lose their reef-building potential (Stearn 1987). Post-Frasnian stromatoporoid structures are of small dimensions, and are generally found in the warm water equatorial region of the Palaeotethys. Famennian stromatoporoids found outside this area are generally labechiids, which are believed to have been better adapted to cool water than the majority of Frasnian species, which were tropical and low-latitude in distribution.

Differential survival of high-latitude, cool-water adapted species is also exhibited by the brachiopods, which were the dominant form of shelly animal in Frasnian benthic ecosystems (Copper 1986). Of the total brachiopod fauna, approximately 86% of Frasnian genera did not survive into the Famennian. However, 91% of brachiopod families whose species were generally confined to low-latitude, tropical regions perished in the extinction event, in contrast to a loss of 27% of those families with species which ranged into high-latitude, cool-water regions.

Other elements of the marine benthos which exhibit latitudinal patterns of survival include the foraminifera. They suffered major losses in species diversity with the substantial reduction which occurred in the area of the global belt of carbonate sedimentation. Species of the high-latitude regions differentially survived the event; species of the cool-water Siberian realm expanded their geographical ranges into low-latitude regions with the latitudinal contraction in the range of Palaeotethys species.

Bathymetric effect. In general, shallow-water marine ecosystems were much more severely affected during the Frasnian–Famennian interval than deeper-water systems. The bathymetric selectivity in extinction is seen most dramatically within the rugose corals, a group which suffered a massive loss in biomass. Only 4% of the shallow-water species

survived. Deeper-water species suffered a 60% extinction in their numbers, and while this reduction was severe it pales in comparison with the 96% loss of species in the shallow waters. The decimation of the shallow-water corals was actually more severe than that of the stromatoporoids (Stearn 1987).

A particularly intriguing bathymetric pattern of selective extinction and diversification occurs across the Frasnian–Famennian boundary in the Appalachian marine ecosystems of eastern North America. Simultaneously with the extinction of many shallow-water benthic species, the hyalosponges (glass sponges) migrated from deeper water into the shallows and underwent a burst of diversification in species numbers. Modern glass sponges are generally found in water depths in excess of 200 m, and are considered to be better adapted to colder waters than most other invertebrate species. Blooms in other siliceous organisms, most notably the radiolarians, are also reported during the Frasnian–Famennian interval.

Habitat effect. A marked habitat effect in selective survival can be observed in the Devonian fish groups which included both marine and freshwater species. Only 35% of marine placoderm species survived, in contrast to 77% of those which lived in freshwater. A similar pattern occurs in the acanthodian fishes: only 12% of marine species survived, in contrast to 70% of freshwater species.

A key environmental parameter which differentiates the two habitat regions (other than salinity) is temperature. In general, freshwater species are adapted to seasonal and diurnal fluctuations in temperature, in contrast to those species in temperature-buffered shallow-water marine regions. The differential survival of freshwater fish may reflect their greater tolerance to temperature changes. Other elements of the terrestrial ecosystem appear to have been unaffected by the event. Floras exhibit no major disruptions, and plant biomass productivity appears to have been unchanged, or even perhaps enhanced, during the Frasnian–Famennian interval.

Within the shallow-water marine benthos, epifaunal filter-feeding organisms appear to have been most affected by the extinction event; infauna and detritus feeders were relatively unaffected.

In common with other extinction events, the upper oceanic water habitat of the marine plankton was massively disrupted. Approximately 90% of the preservable phytoplankton was affected, and

massive biomass reductions also occurred among the zooplankton.

Summary. The ecological signature preserved in the fossil record of the Frasnian–Famennian extinction event appears to indicate a significant drop in global temperatures during the crisis interval. The decimation of low-latitude tropical reef ecosystems and of warm-water shallow marine faunas, combined with the relatively higher survival of high-latitude faunas, deep-water faunas, and terrestrial fauna and flora, seems most compatible with lethal temperature decline at a global level. At the local and regional level the extinction event doubtless records additional local environmental factors.

Evolutionary dynamics

The precise timing of the Frasnian–Famennian extinction event is still uncertain. Present evidence, however, indicates that extinction rates were elevated above average during a geologically significant span of time during the latter half of the Frasnian, for a period of perhaps 3–4 million years (Fig. 1). There appears to have been no single synchronous extinction peak shared by all species, but a series of stepwise extinctions of different species groups. It has been consistently observed, however, that a marked drop in standing species diversity occurred at the very end of the Frasnian. The fact that extinction rates were elevated above average for a significant period of time before the terminal Frasnian suggests that the drop in species diversity at the Frasnian–Famennian boundary was not a simple function of extinction rate magnitudes (McGhee 1982).

In the analysis of ecosystem evolution it is often misleading to consider the pattern and timing of extinction rates alone. Species diversity is a function of the relationship of two evolutionary variables: the rate at which species were lost from the system (extinction rate), and the rate at which new species were added (origination rate). While either rate alone is of considerable interest, the evolutionary behaviour of the total ecosystem can best be characterized by the sign and magnitude of species diversity changes (the turnover rate, i.e. origination rate minus the extinction rate). If origination and extinction rates were of equal magnitude, the ecosystem was in a state of dynamic equilibrium with no diversity change. Where origination exceeded extinction (positive turnover rates), the system was

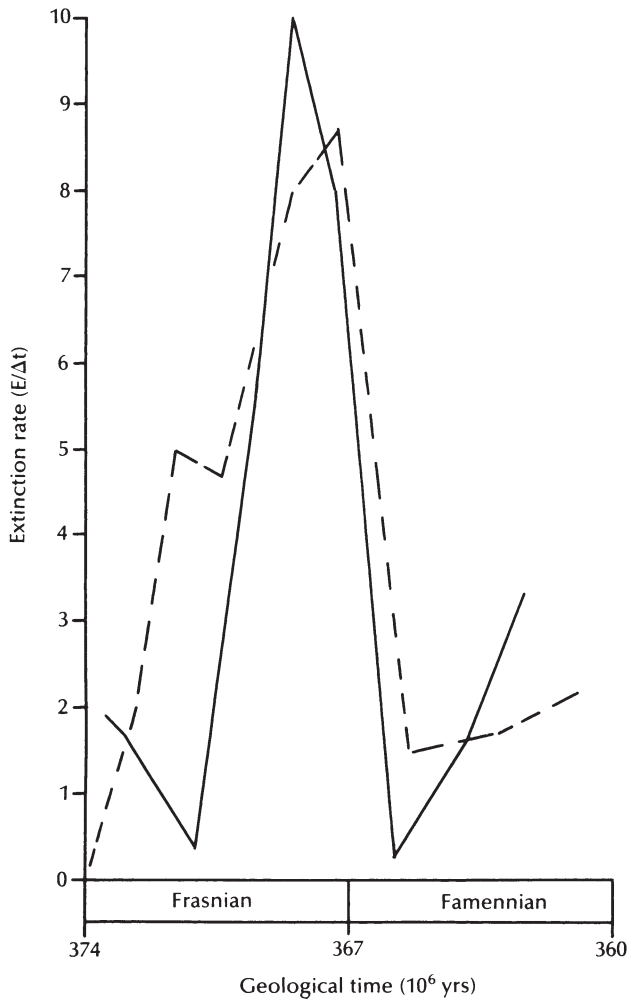


Fig. 1 Elevated extinction rates during the Middle and Late Frasnian exhibited by brachiopods from the Appalachians, U.S.A. (solid line) contrasted with the Urals, U.S.S.R. (dashed line). Extinction rate metric is the number of species extinctions (E) per million years (Δt).

diversifying, whereas if extinction exceeded origination (negative turnover rates) the system was losing species diversity.

Marine ecosystems appear to have been flourishing (in terms of standing species diversity) during the interval of time characterized by some of the highest extinction rates which occurred in the latter half of the Frasnian. This phenomenon is due to the fact that species origination rates were even higher per time interval than the corresponding extinction rates.

This pattern of relative origination–extinction rate magnitudes reversed abruptly during the latest Frasnian, precipitating a rapid loss of species diversity (Fig. 2). Extinction rates in many cases remained the same, or actually declined in some, but species

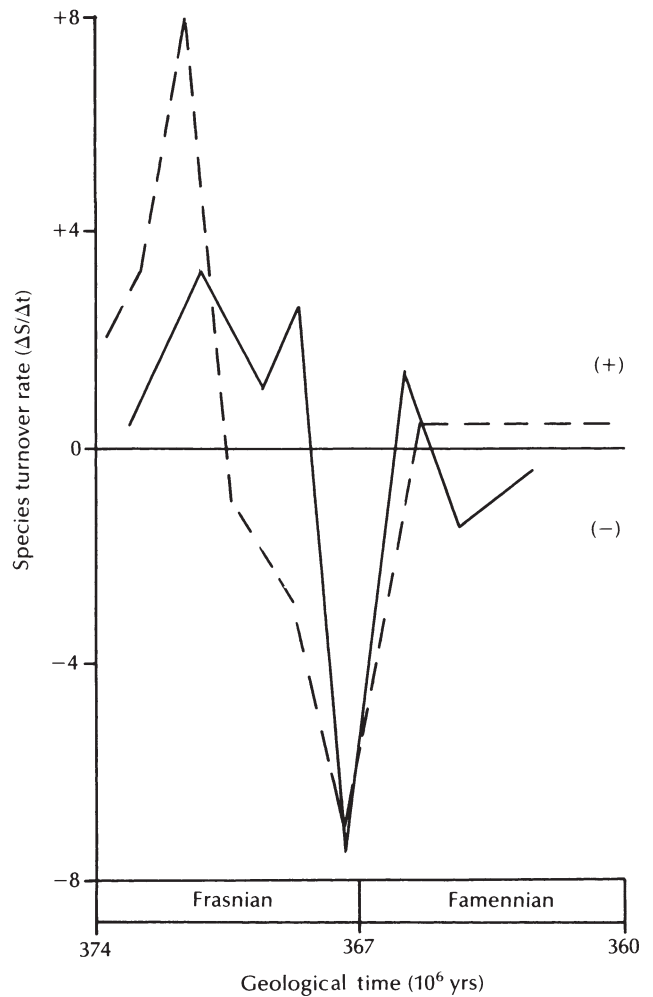


Fig. 2 Species turnover rates for brachiopods from the Appalachians, U.S.A. (solid line) and the Urals, U.S.S.R. (dashed line) during the Frasnian–Famennian interval. A sharp negative pulse in turnover rates occurs in both regions at the very end of the Frasnian, signalling a severe and rapid loss of species diversity in this interval of time. Turnover rate metric is the change in the number of species (ΔS) per million years (Δt).

turnover rates became sharply negative (Fig. 2). Whether extinction rates were rising or falling, it was the decline in species originations which drove species turnover rates sharply negative at the very end of the Frasnian.

Thus, while there was no single synchronous extinction rate pulse during the Frasnian, the ecosystem did exhibit a rather abrupt and massive drop in species diversity in the terminal Frasnian. In understanding the ultimate cause of the extinction event the most important question may not be what triggered the elevated extinction rates, but what was the inhibiting factor that caused the cessation of new species originations.

References

- Copper, P. 1986. Frasnian/Famennian mass extinction and cold-water oceans. *Geology* **14**, 835–839.
- McGhee, G.R., Jr. 1982. The Frasnian–Famennian extinction event: a preliminary analysis of Appalachian marine ecosystems. *Special Paper of the Geological Society of America* **190**, 491–500.
- McLaren, D.J. 1982. Frasnian-Famennian extinctions. *Special Paper of the Geological Society of America* **190**, 447–484.
- Stearn, C.W. 1987. Effect of the Frasnian–Famennian extinction event on the stromatoporoids. *Geology* **15**, 677–679.

2.13.4 End-Permian

D. H. ERWIN

Introduction

During the latest Permian 54% of all marine families became extinct (Table 1), as did 83% of all marine genera (Sepkoski 1986). Several authors have estimated that as many as 90–96% of all durably-skeletonized marine invertebrate species became extinct (e.g. Sepkoski 1986). This extinction was the most severe of the Phanerozoic and eliminated twice as many families as the second largest, the end-Ordovician mass extinction (Section 2.13.2). Many major taxa were eradicated or declined drastically in diversity, eliminating the shallow-water, sessile, epifaunal, brachiopod–bryozoan–pelmatazoan echinoderm communities which dominated the Palaeozoic. This permitted the expansion of the mobile, infaunal, molluscan-dominated communities which dominated the post-Palaeozoic. The effects of the extinction on land are less clear, but extinctions and changes in faunal dominance occurred in both terrestrial vertebrates and plants throughout the Permian.

Despite its magnitude and significance, analysis of the patterns and causes of the extinction has been hampered by the restricted number of marine sections of latest Permian age. The number of well-studied sections has increased recently, particularly in South China and elsewhere in the Tethyan region. However, facies changes at the boundary indicate that no continuous Late Permian–Early Triassic sections have been discovered.

The assembly of the supercontinent Pangaea was largely completed with the collision of the

Table 1 Extinction percentages for 17 major groups of marine families during each series of the Permian. Families not resolved to series were not used in the analysis. A = Asselian, S = Sakmarian, L = Leonardian, G = Guadalupian, D = Dzulfian. (Data from Sepkoski 1982.)

Marine family	Percentage extinction				
	A	S	L	G	D
Foraminifera	0	0	3	6	38
Porifera	0	0	18	24	10
Tabulata	0	14	15	42	100
Rugosa	0	6	38	62	100
Gastropoda	0	0	15	25	11
Bivalvia	0	3	2	12	11
Cephalopoda	17	0	20	43	47
Other Mollusca	0	17	40	33	0
Other Arthropoda	0	0	21	33	25
Ostracodes	4	8	8	35	29
Bryozoa	10	4	4	23	65
Brachiopoda	0	3	12	34	71
Crinoidea	0	16	5	93	0
Other Echinodermata	5	5	5	37	8
Conodonts	0	20	0	20	25
Other taxa	0	0	0	9	3
Marine vertebrates	0	0	0	39	0

Kazakhstan, Tarim, and Siberian blocks in the Late Carboniferous and the accretion of this unit to the Russian platform by the end of the Artinskian Stage (Fig. 1). The North China block collided with Kazakhstan in the latest Permian. The South China block closely approached the North China block in the latest Permian but rotation and accretion of the two blocks was not completed until the Late Triassic or Early Jurassic. (Considerable movement and rotation occurred between tectonic blocks during the Permian. Consequently, palaeocontinental reconstructions are poorly constrained until the Late Triassic.)

The Late Carboniferous–Early Permian glaciation in Gondwanaland ended during the Asselian–Sakmarian as the South Pole moved off the continent and the formation of Pangaea led to increased temperatures and seasonality (see Fig. 2 for time-scale). Continuing climatic oscillations into the Late Permian are suggested by sea-level fluctuations on a 2–2.5 million year cycle. Scattered reports of Late Middle to Late Permian glaciation, however, involve only restricted mountain glaciations. Global warming continued into the Triassic and there is no evidence for widespread cooling or glaciation during the Late Permian.

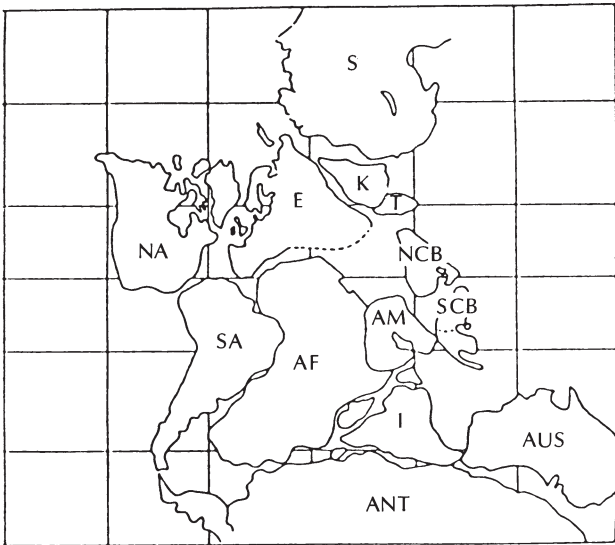


Fig. 1 Palaeocontinental reconstruction for the Late Permian. AF = Africa, AM = Asia Minor, ANT = Antarctica, AUS = Australia, E = Europe, I = India, K = Kazakhstan, NA = North America, NCB = North China block, S = Siberia, SCB = South China block, T = Tarim. (From Lin *et al.* 1985. Reprinted by permission from *Nature* vol. 313 pp. 444–449. Copyright © 1985 Macmillan Magazines Ltd.

The increased temperatures and seasonality associated with the formation of Pangaea are indicated by evaporites and red beds. As continents become more exposed during a regression, the ameliorating effects of the ocean (due to the high heat capacity of water) decline, climates become more severe, and seasonality increases, a condition described as increased continentality or inequability (Valentine & Moores *in* Logan & Hills 1973; Jablonski 1986). The concentration of land area in one unit exacerbated the trend, leading to high seasonality in continental interiors. The effects were not limited to continental interiors. Storm activity, particularly monsoons in the Tethyan realm, and consequent disturbances in shallow-marine ecosystems, increased. The largest Permian evaporite deposits are of Kungurian age, coinciding with the initial formation of Pangaea, although these are dwarfed by later Triassic deposits. Finally, a sharp marine regression occurred at the end of the Permian.

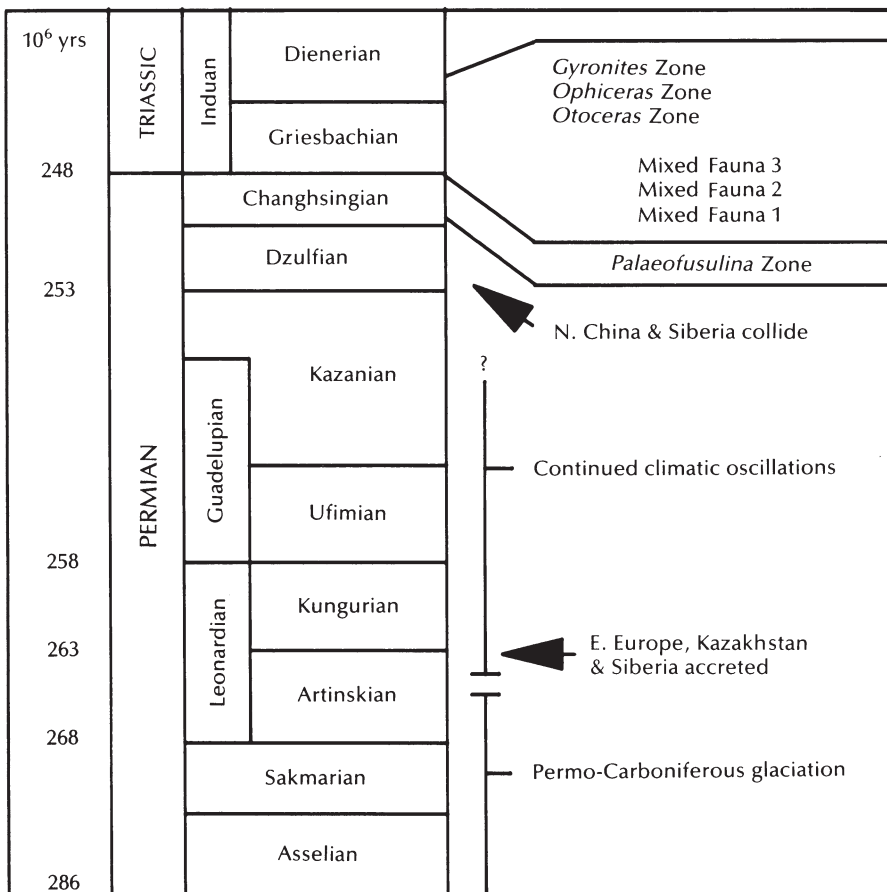


Fig. 2 Permian and lowest Triassic geological stages, Permo-Triassic boundary biostratigraphic zones, and major tectonic and climatic events. Most workers consider the *Palaeofusulina* Zone the final zone of the Changhsingian Stage, and the mixed faunas the lower-most units of the Triassic. The *Gyronites* Zone marks the Griesbachian–Dienerian boundary. (Geological dates from Harland *et al.* 1982.)

Extinction patterns

Taxa which became extinct include tabulate and rugose corals, conularids, eurypterids, leperditiid ostracodes, several gastropod groups, goniatitic ammonites, orthid and productid brachiopods, blastoids, inadunate, flexible, and camerate crinoids, and the few remaining trilobites (Table 1; Fig. 3). A number of other groups suffered sharp drops in diversity, including the cryptostomate and trepostomate bryozoans, foraminifera, ammonoids and fish. Reefs were eliminated and tropical ecosystems in general were severely affected. Jablonski (1986) analysed survival patterns of articulate brachiopods and noted that 75% of the families confined to the tropics became extinct, while only 56% of extra-tropical families died out. All fusulinid foraminifera and 54% of all foraminiferan families became extinct, including both planktic and benthic taxa. In general the zooplankton, sessile filter feeders, and the high-level carnivores (ammonoids and fish) were the most strongly influenced trophic groups.

The diversity history of marine vertebrates parallels that of invertebrates, with the decline beginning in the Guadalupian and accelerating in the Dzulifian. Elasmobranchs, Holocephali and marine Chondrostei and Holostei follow this pattern. Freshwater and euryhaline fish and amphibians, however, reach a diversity low in the Leonardian and appear to be diversifying across the boundary.

Sepkoski identified three distinct assemblages of taxa during the Phanerozoic, each with characteristic diversity maxima (Section 1.6). His Palaeozoic evolutionary fauna includes the groups which dominated the Palaeozoic: articulate brachiopods, crinoids and other pelmatozoan echinoderms, and bryozoans. These taxa suffered disproportionate extinction during the end-Permian, with a 79% familial extinction, while bivalves, gastropods, some arthropod taxa, and others which constitute the Mesozoic–Cenozoic evolutionary fauna declined 27%. This differential extinction pattern contributed to the development of burrowing, infaunal, molluscan-dominated communities in the post-Palaeozoic.

The Permian extinction produced a large number of 'Lazarus taxa': taxa which disappear from the record during the Late Permian, only to reappear in the Triassic (Jablonski 1986). As Batten (*in* Logan & Hills 1973) noted, 'Palaeozoic'-aspect gastropods are better represented in the Triassic than in the latest Permian. The number of Lazarus taxa indicates that the record across the boundary is too fragmentary

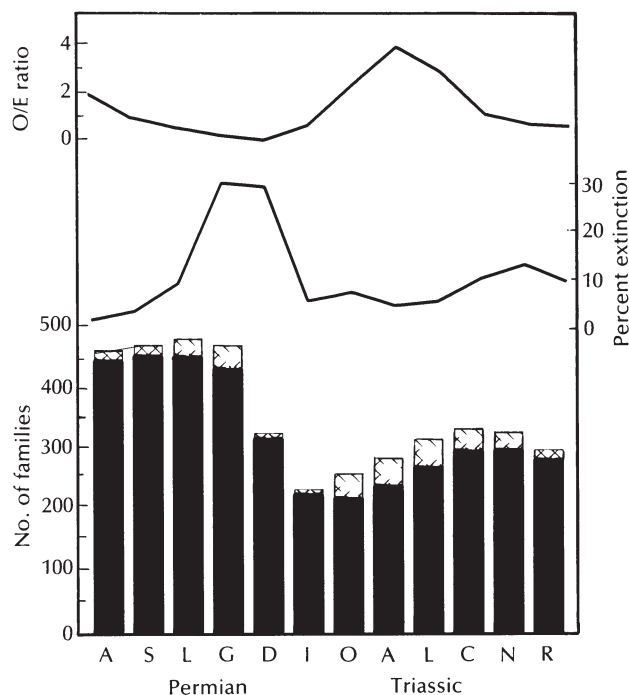


Fig. 3 Permian and Triassic data for marine families. The histogram shows the total number of families in each series, with the new families indicated by the cross-hatched symbol. The percentage extinction [calculated as percentage (total extinctions)/(initial diversity + total originations)] is shown above. Families whose originations or extinctions could not be resolved to series are not included. The graph at the top shows the ratio of originations to extinctions (O/E). The ratio falls below 1.0 during the Leonardian, begins to rise in the Induan, but does not climb above 1.0 until the Olenekian. A = Asselian, S = Sakmarian, L = Leonardian, G = Guadalupian, D = Dzulifian, I = Induan, O = Olenekian, A = Anisian, L = Ladinian, C = Carnian, N = Norian, R = Rhaetian. (Data from Sepkoski 1982.)

and sparse to accurately reflect the rate and duration of the extinction. Furthermore, many groups which first appear in the Triassic, including zygopleurid gastropods and scleractinian corals, are clearly descended from Palaeozoic ancestors but with a significant gap between ancestor and descendant. The restricted number of sections, the paucity of the fossil record, and the obvious sampling problems make it difficult to determine whether the extinction began in the Guadalupian or was restricted to the Dzulifian–Changhsingian (see also Jablonski 1986). Preliminary generic diversity data (Fig. 4) show the extinction peak in the Guadalupian, although this may be a preservational artifact (Sepkoski 1986).

An indirect method of determining the duration of an extinction event is to analyse the replacement ratio, or the ratio of originations to extinctions (O/E

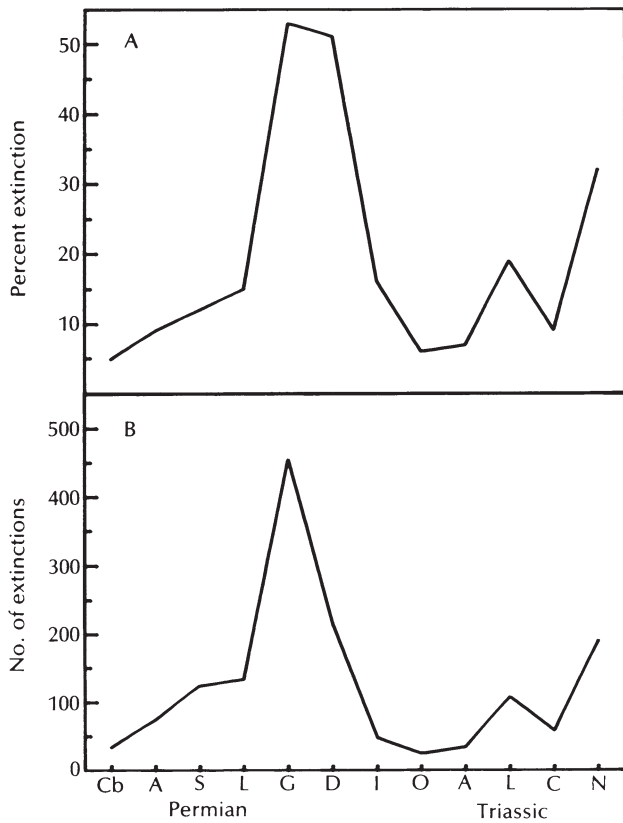


Fig. 4 Permian and Triassic extinctions in marine genera. A, Percentage extinction (calculated as in Fig. 3). B, Total number of generic extinctions. Cb = Carboniferous. Other abbreviations as in Fig. 3. (Data from Sepkoski 1986.)

Fig. 3). This ratio is 2.0 in the Asselian, but falls below 1.0 in the Leonardian and reaches a minimum of 0.1 in the Dzulfian. Extinctions exceed originations from the Leonardian onward. Note that originations continue, with 38 new families in the Guadalupian or a 9% origination rate for the stage; however, extinctions total 152 (32%), and 100 (31%) in the Dzulfian. Several authors have even argued that an 'extinction' never occurred but origination rates were severely depressed. While originations did decline, this cannot explain a drop in familial diversity of 54%.

Terrestrial vertebrates and plants experienced a series of extinctions and ecological replacements from the Early Permian through the Triassic (Fig. 5). Eighty-one per cent of amphibian families became extinct near the end of the Leonardian; interestingly, most of these families first appeared during the preceding glaciation. A second extinction pulse at the close of the Permian primarily affected therapsids, and was followed closely by a third extinction episode at the close of the Lower Triassic.

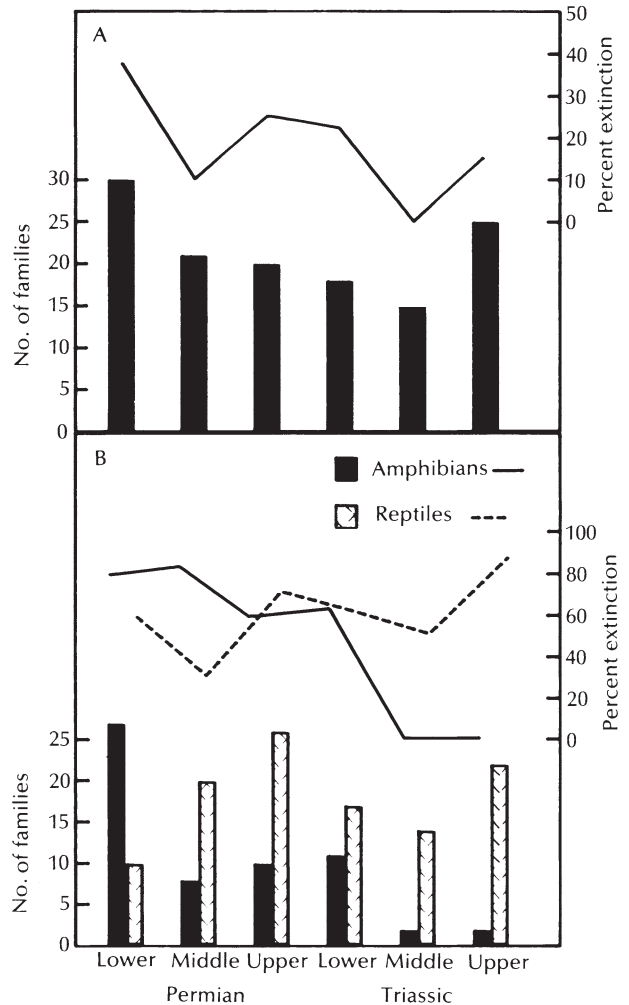


Fig. 5 Number of families and percentage extinction (calculated as in Fig. 3) per stage of the Permian and Triassic. A, Terrestrial plants. (Data from Knoll 1984.) B, Terrestrial amphibians (lepospondyli and labyrinthodonts) and reptiles (captorhinomorphs, pelycosaur, therapsids, and archosaurs). (Data from Olson *in* Silver & Schultz 1982.)

The fourth occurred at the end of the Triassic (Section 2.13.5) and removed archosaurian reptiles (Olson *in* Silver & Schultz 1982). R. Sloan distinguished a more complex pattern of vertebrate extinction episodes: two in the Sakmarian–Leonardian, two in the Guadalupian, and six in the Dzulfian. His analysis showed that the survivors of each extinction had a higher percentage of mammalian characters and smaller body size than those which became extinct. Sloan suggested that the regular cycle of extinction and replacement was caused by post-glacial climatic oscillations. Preservation quirks are apparent as well, for the magnitude of the Late Permian–Early Triassic extinction is accentuated by an unusual upland fauna from the