

Fig. 2 *a*, Undescribed modern endolithic cyanobacterium freed from Bahamian ooid; view is essentially that seen from the interior of the substrate ($\times 140$; scale bar in *b* = 100 μm). *b*, Two specimens of fossil endolithic microorganisms comparable in morphology, development and inferred ecology to the living population illustrated in *a*; the fossil on the left is seen in longitudinal view, while the smaller individual on the right is viewed from the direction of the pisolith interior ($\times 350$; scale bar, 40 μm).

to have accumulated under sedimentary conditions much like those found today in the Bahamas. Thus, the morphological and reproductive similarity between *H. gigas* and its fossil counterpart is paralleled by a close environmental congruence between the modern and Proterozoic sediments in which the two taxa have been found.

Other fossil populations in the Limestone-Dolomite assemblage also compare closely with extant microorganisms that occur in Bahamian ooids. These include fossils resembling the modern taxa *Plectonema terebrans*, *Cyanosaccus* spp., *Solentia foveolarum* and unnamed coccoidal endoliths described by Harris *et al.*¹³. Perhaps the most interesting population is one composed of densely branched microfossils like that shown in Fig. 2*b*. These fossils have a high cell density, giving the appearance of a hemispherical cell cluster from which many short filaments radiate into the pisolith. Filaments are uniseriate or biseriata, only a few cells long, and often terminated by a pair of end cells. Branches tend to be club shaped, widening towards the pisolith interior. Filaments are 20–47 μm long (mean 33.5 μm , s.d. 8 μm ; $n = 20$) and have a maximum width of 12.5–16 μm (mean 14.5 μm ; s.d. 1.5 μm). Cell dimensions are 8.5–21 by 5–19 μm (mean 12.3 \times 12 μm ; s.d. 3.4 \times 3.7 μm ; $n = 62$). Baeocyte formation has not been demonstrated for this fossil. This taxon is a common constituent of the East Greenland endolith assemblage, but it has no precise counterpart among described species of modern endolithic cyanobacteria. Our comparative studies of Bahamian ooids have revealed the presence of a locally common and hitherto undescribed blue-green (Fig. 2*a*) that is remarkably similar in morphology and development to the fossil population in question. This demonstrates that palaeobiological knowledge of late Proterozoic microfossils has become sufficiently refined to be of use to systematic and ecological studies of modern coastal marine microorganisms.

Equally well-preserved remnants of at least five other intertidal and shallow subtidal communities occur in silicified carbonates and shales of the Limestone-Dolomite Series¹⁴. Although the organisms in these assemblages lived contem-

poraneously with those found in the pisolites, there is essentially no taxonomic overlap between the endolithic and other biotas. Endolithic microfossil assemblages clearly document communities that differed significantly from those of the microbial mat and phytoplankton biotas usually reported from Precambrian rocks; thus, they add significantly to our knowledge of early microbial diversity.

The Limestone-Dolomite fossil endolith assemblage provides new and compelling examples of the close resemblance between Proterozoic prokaryotes and their modern counterparts^{15–17}, in this case a comparison that begins with morphology and extends to reproductive, developmental and ecological similarity. Most important, the comparisons relate several co-occurring fossils from a single Proterozoic assemblage to taxa that occur today as part of a single community in a physically equivalent environment. Collectively, Limestone-Dolomite fossils demonstrate that endolithic cyanobacteria were abundant, diverse and apparently quite modern in shallow marine environments well before the radiation of either grazing or skeletonized metazoans.

This study was funded in part by NSF grants DPP-83-01226 (K.S.), BSR 85-16328 (A.H.K.) and EAR-83-06179 (S.G.). We thank the Commission on Scientific Research in Greenland for permission to do field work in East Greenland, R. Ginsburg for samples of Bahamian ooids and S. Campbell for helpful comments.

Received 13 January; accepted 7 April 1986.

1. Golubic, S., Perkins, D. & Lukas, K. J. in *The Study of Trace Fossils* (ed. Frey, R. W.) 229–259 (Springer, Berlin, 1975).
2. LeCampion-Alsumard, T. *Oceanol. Acta* 2, 143–156 (1979).
3. Campbell, S. E. in *Biomineralization and Biological Metal Accumulation* (eds Westbroek, P. & de Jong, E. W.) 99–104 (Reidel, Amsterdam, 1979).
4. Campbell, S. E. *Phycologia* 19, 25–36 (1980).
5. Campbell, S. E. *Nature* 299, 429–431 (1982).
6. Eha, S. *Meddr. Grönland* 111(2), 1–105 (1953).
7. Katz, H. R. *Meddr. Grönland* 111(1), 1–150 (1952).
8. Haller, J. *Geology of the East Greenland Caledonides* (Wiley-Interscience, New York, 1971).
9. Swett, K. & Knoll, A. H. *J. Sedim. Petrol.* (in the press).
10. Vidal, G. *Grönl. geol. Unders.* 134, 1–40 (1979).
11. LeCampion-Alsumard, T. & Golubic, S. *Arch. Hydrobiol. Suppl.* 71(1/2), 119–148 (1985).
12. Lukas, K. J. & Golubic, S. *J. Phycol.* 19, 129–136 (1983).
13. Harris, P. M., Halley, R. B. & Lukas, K. J. *Geology* 7, 216–220 (1979).
14. Knoll, A. H., Green, J., Swett, K. & Golubic, S. *Geol. Soc. Am. Abstr. Prog.* 17(7), 631 (1985).
15. Golubic, S. & Hofmann, H. J. *J. Paleont.* 50, 1074–1082 (1979).
16. Knoll, A. H., Barghoorn, E. S. & Golubic, S. *Proc. natn. Acad. Sci. U.S.A.* 72, 2488–2492 (1975).
17. Knoll, A. H. & Calder, S. *Palaeontology* 26, 467–493 (1983).

More than one event in the late Triassic mass extinction

Michael J. Benton

Department of Geology, Queen's University of Belfast, Belfast BT7 1NN, UK

The recent hypothesis that mass extinctions are discrete phenomena that have occurred with great regularity during the history of life^{1,2} is testable in several ways. Two essential elements of the hypothesis are (1) that each extinction event represents a significant departure from normal, or 'background', rates of extinction, and (2) that such mass extinction events are spaced equally in time. The analyses of the cyclicity of mass extinctions so far have concentrated on the past 250 Myr, with the first event occurring at the Permian-Triassic boundary, 245 Myr ago^{1–5}. The second event followed 26–33 Myr later^{1–6}, in the late Triassic. Here I present a detailed analysis of the fossil record of marine and non-marine life during the late Triassic which suggests that there were at least two phases of mass extinction during that time, separated by 12–17 Myr.

The late Triassic has long been recognized as an important time of mass extinction^{7–11} (approximately equivalent in magni-

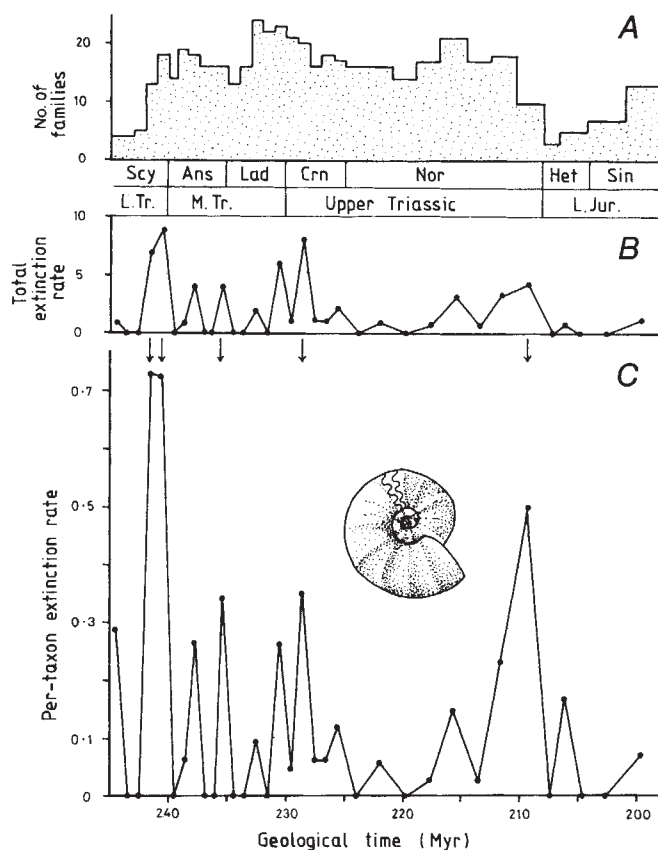


Fig. 1 Total diversity (A), total extinction rates (B) and per-taxon extinction rates (C) of families of Triassic ammonoids. The total extinction rates were calculated as the numbers of families dying out per Myr, and the per-taxon extinction rates were calculated according to the Van Valen metric²³, that is, the total extinction rate divided by the number of taxa at risk. (The latter was estimated as the number of taxa at the beginning of the interval, minus half the extinctions, plus half the originations in the interval.) The five highest per-taxon extinction rates (possible mass extinctions) are indicated by arrows. Data on ammonoid distributions taken from refs 12 and 22, and the timescale from ref. 21. The Triassic and earliest Jurassic subseries and stages are indicated. Diversity and extinction rate data were calculated by substages (Scythian, Hettangian, Sinemurian) and by zones (Anisian–Norian). The 'Rhaetian' stage is included in the late Norian¹². The fossil shown is *Ceratites*. Ans, Anisian; Crn, Carnian; Het, Hettangian; Lad, Ladinian; L. Jur., Lower Jurassic; L. Tr., Lower Triassic; M. Tr., Middle Triassic; Nor, Norian; Scy, Scythian; Sin, Sinemurian.

tude to the famous event at the end of the Cretaceous¹⁰, when the dinosaurs died out), and involved an overall reduction in the diversity of families in the sea of ~23% (ref. 10) with a similar reduction in diversity of families on the land. The main groups that were affected in the sea were the sponges (loss of 8 families), the gastropods (13 families lost), the bivalves (8), the cephalopods (58), the brachiopods (12) and various marine reptiles (13). The effects on the ceratitid cephalopods, which were abundant and widespread in the Triassic, were dramatic (all 46 late Triassic families died out) and the ammonoids barely survived into the Jurassic¹². When genera are considered, the *Ceratitida* reached a peak of ~150 genera in the Carnian, falling to ~100 genera in the Norian, and to single figures in the latest Norian¹³. The extinction rate for bivalve families was not so marked, but the extinction rate for genera was 42%, and the species extinction rate, in Europe at least, was 92% (ref. 11). The last strophomenid brachiopods, conodonts, conulariids,

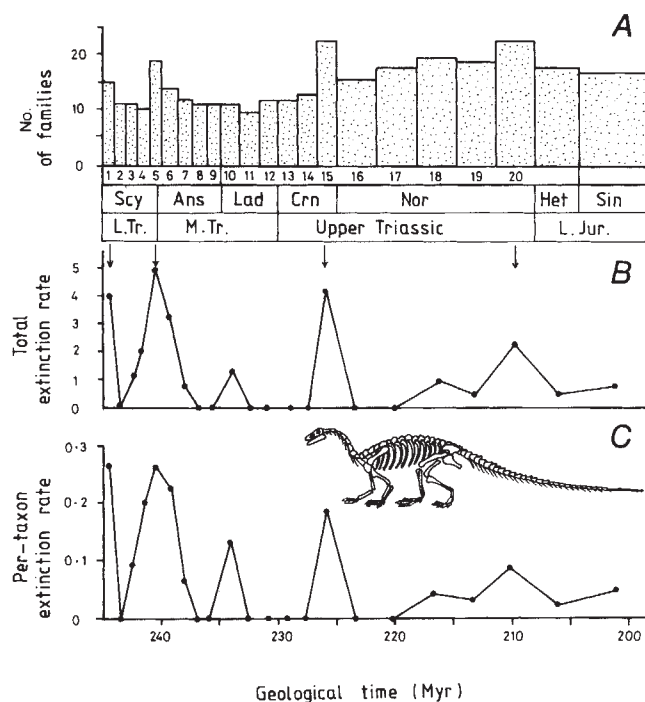


Fig. 2 Total diversity (A), total extinction rates (B) and per-taxon extinction rates (C) of families of Triassic and earliest Jurassic non-marine tetrapods. The four highest total extinction rates (possible mass extinctions) are indicated by arrows. The timescale is subdivided into informal 'substages', numbered 1–20 in the Triassic according to ref. 24. Data on tetrapod distributions are taken from refs 17, 18 and 24, with biostratigraphic zonations revised according to refs 25 and 26.

nothosaurs and placodonts also disappeared in the late Triassic.

On land, major extinctions occurred among the insects (35 families lost), the freshwater bony fishes (8) and the thecodontians (8). There was a major faunal turnover amongst non-marine tetrapods in the late Triassic, during which the formerly dominant labyrinthodonts, mammal-like reptiles, thecodontians and rhynchosaurs died out, or were greatly depleted, and new groups, such as the dinosaurs, crocodiles, pterosaurs, turtles, lepidosaurs and mammals, arrived on the scene^{14–18}.

Several authors have already noted that the extinctions in the late Triassic were either not synchronous in the sea and on land^{11,15}, or that the extinction lasted for much of the late Triassic, through the Carnian, Norian and Rhaetian stages⁵ (the 'Rhaetian' is included here in the late Norian stage^{11,12}). A more detailed study of events during this timespan of 18–25 Myr is therefore required.

Here I present data on the rates of extinction of families of marine and non-marine organisms during the late Triassic. Some groups of organisms whose fossil records are relatively well known are examined first, in order to establish the kinds of patterns of mass extinction that occurred in the late Triassic. Then a broader analysis of the fossil record of all plants and animals during that time is attempted.

The ammonoids—cephalopod molluscs with coiled shells—have a relatively good Triassic fossil record¹²; 35 ammonoid zones are recognized in the Triassic, which lasted for 35–41 Myr^{19–21}. Tozer¹² has summarized the stratigraphic ranges of the 75 families of Triassic ammonoids accurate to the level of zones. The numbers of families present in each zone (or substage, in the Scythian) are plotted as a simple histogram in Fig. 1A; the diagram has been extended into the early Jurassic²² in order

Table 1 Total numbers of families of marine and non-marine animals and plants present in each stratigraphic stage from the middle Triassic (Ladinian) to the early Jurassic (Sinemurian)

	Ladinian	Carnian	Lower Norian	Middle Norian	Upper Norian	Hettangian	Sinemurian
Marine families							
Protozoa	43	46	45*	45*	50*	49*	52*
Porifera	33	36	28*	28*	30*	30	30
Coelenterata	19	20	20*	21*	20*	20	21
Ctenophora	1	1	1	1	1	1	1
Priapulida	1	1	1	1	1	1	1
Nematoda	1	1	1	1	1	1	1
Mollusca							
Gastropoda	53*	51*	48*	49*	46*	47*	49*
Bivalvia	49	56	57	57	58	58	57
Cephalopoda	34	37*	23*	29*	22*	13	18
Others	6	6	6	6	6	6	6
Sipunculida	1	1	1	1	1	1	1
Annelida	21	20	20	20	21	21	21
Arthropoda	21	22†	23†	23†	20†	20*	23*
Bryozoa	4	4	5	5	6	6	6
Brachiopoda	17	18	17*	17*	18*	12	14
Chaetognatha	1	1	1	1	1	1	1
Echinodermata	16*	18	19*	19*	21*	31	33
Pogonophora	1	1	1	1	1	1	1
Conodonts	2	2	2	2	2	—	—
Chordata	18	14	8*	9*	11*	13	17
Total:	342*	356*	327*	338*	337*	332*	353*
Non-marine families							
'Thallophyta' (genera/orders)	33	33	33	33	35	39	37
Bryophyta (orders)	4	4	4	4	5	5	5
Charophyta	2	2	2	2	2	2	2
Pteridophyta	11	13	13	13	14	15	15
Gymnospermophyta	6	11	10	10	16	17	15
Mollusca							
Gastropoda	8	8	8	8	8	8	8
Bivalvia	3	4	4†	4†	3†	4†	3†
Onychophora	1	1	1	1	1	1	1
Arthropoda							
Insecta	30	35†	36†	37†	63†	55†	63†
Others	21	20	20‡	21‡	22‡	21	21
Chordata							
'Fish'	24	16*	13‡	13‡	13‡	11	11
Tetrapoda	12	23	16	21	25	18	16
Total:	155	170*	160‡	167‡	207‡	206*	197*
Overall no. of families	497*	526*	487*	505*	544*	538*	550*

The Norian is subdivided into three units which correspond to the Lower, Middle and Upper substages¹². Data are listed by phyla or other major groups from refs 27–32. Families that have both marine and non-marine representatives are counted once only as 'marine'. In some cases, the precise stage of origination or termination of a family has not been established, and estimates have been calculated on the basis of stratigraphic stage durations and an assumption of equal probabilities through time. Thus, for 'Middle Triassic' originations and terminations, half are assumed to have occurred in the Ladinian. For 'Upper Triassic' originations and terminations, one-quarter are assumed to have occurred in each of the Carnian, Lower Norian, Middle Norian and Upper Norian. For 'Lower Jurassic' originations and terminations, one-quarter are assumed to have occurred in the Hettangian and in the Sinemurian (the remainder of the Lower Jurassic is approximately equal in duration to the Hettangian plus Sinemurian). These uncertain assignments represent ~5% of the total number of families. In addition, certain family extinctions in the Norian stage have not been assigned to the Lower, Middle or Upper Norian divisions. One-third of all such extinctions are assumed to have occurred in each division. In cases where these calculations have been applied, an error estimate is indicated as follows: * < ±5%; ‡ < ±10%; † > ±10%.

to compare the late Triassic events with those that followed. Several declines in family diversity are evident, the largest occurring in the Carnian and late Norian.

Extinction rates for ammonoid families vary considerably during the Triassic and early Jurassic. Total extinction rates (Fig. 1B) show peaks in the late Scythian, the late Ladinian and the early Carnian, with smaller peaks in the Anisian and in the middle and late Norian. The plot of per-taxon extinction rates (Fig. 1C), which take account of the numbers of families present and give a measure of the probability of extinction²³, reveals peaks in the late Scythian, the late Anisian, the early Carnian and the late Norian. Thus, the late Triassic 'mass extinction' of ammonoid families was not a single event, but consisted of at least two—one in the Carnian, and a larger one 17–20 Myr later at the end of the Norian (the 'Rhaetian'). The timing and relative sizes of these two peaks are the same when different current timescales are used^{19–21}.

The fossil record of non-marine tetrapods also lends itself to this type of analysis. The ranges of tetrapod families have been compiled^{7,18,24–26} accurate to a number of informal 'substages'²⁴ that range in length from 1 to 3.4 Myr (mean ~2 Myr). The

histogram of Triassic and early Jurassic families of non-marine tetrapods (Fig. 2A) shows declines in diversity in the early and late Scythian, at the end of the Carnian, and at the end of the Norian. These declines are matched by peaks in the total extinction rate (Fig. 2B) and per-taxon extinction rate (Fig. 2C). The mass extinction of non-marine tetrapods at the end of the Carnian was apparently the larger of the two late Triassic events, the extinction rates being approximately twice those associated with the event at the end of the Norian.

The fossil records of non-marine tetrapods and of ammonoids show that at least three mass extinction events occurred in the late Triassic: at the end of the early Carnian (ammonoids: smaller event), at the end of the Carnian (tetrapods: larger event) and at the end of the Norian, at the Triassic–Jurassic boundary (ammonoids: larger event; tetrapods: smaller event).

Below, I attempt to generalize the study to include all families of late Triassic plants and animals. The stratigraphic distributions of families of marine invertebrates and vertebrates²⁷ and non-marine tetrapods^{28,29} have already been compiled. Data on families of non-marine invertebrates and fish were extracted from various sources^{30–32}, and from an unpublished compilation

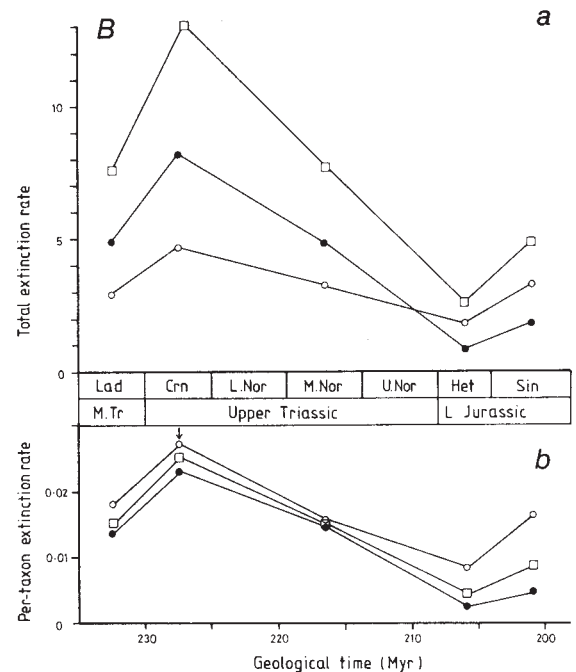
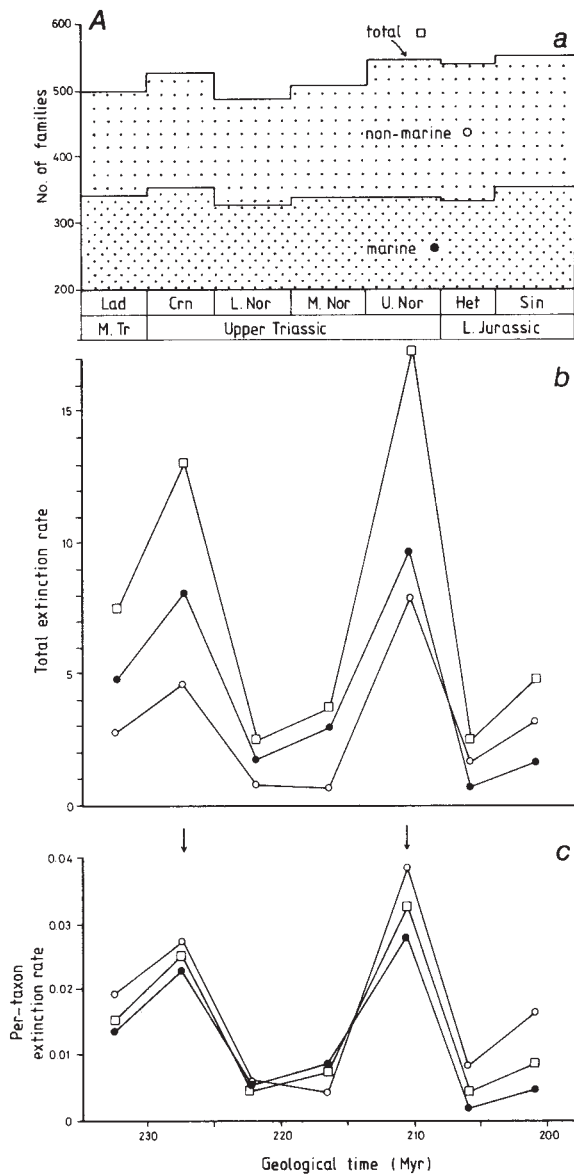


Fig. 3 **A**, Total diversity (**a**), total extinction rates (**b**) and per-taxon extinction rates (**c**) of families of late Triassic and earliest Jurassic plants and animals. The data are plotted separately for marine (●), non-marine (○) and total (□) families. The two mass extinctions (end-Carnian and end-Norian) are indicated by arrows. Data on family distributions from refs 27–32, Sepkoski's unpublished listing of non-marine families, and other sources cited therein. The data were calculated by stratigraphic stage, except for the Norian which was subdivided into Lower, Middle and Upper substages. Each Norian substage was assumed to have the same duration. **B**, Total extinction rates (**a**) and per-taxon extinction rates (**b**) of families of late Triassic and earliest Jurassic plants and animals. When the Norian data are combined, the terminal Triassic extinction event is 'smoothed out' and there appears to have been a single event in the Carnian (arrowed).

by J. J. Sepkoski Jr. Note that, because of the nature of the fossil record, the data on some groups such as insects and plants are rather poor. The time period under study spans from the Ladinian (middle Triassic) to the Sinemurian (early Jurassic), an interval of ~38 Myr²¹, and family extinctions have been noted to the level of the stratigraphic stage. The Norian stage is much longer (~17 Myr) than all the other stages (4–6 Myr), and was subdivided into Lower, Middle and Upper units, according to the standard scheme¹². The stages, and substages, used in this analysis range in duration from 4 to 6 Myr (mean 5.4 Myr).

Table 1 summarizes the diversities of families of plants and animals during the late Triassic; Table 2 summarizes the family extinctions. The present data indicate an average marine diversity of ~340 families, and non-marine diversity of ~190 families. The numbers of family extinctions per time unit range from 3 to 54 (marine; mean 23.0), and from 4 to 45 (non-marine; mean 18.1). Plots of marine and non-marine family diversity (Fig. 3Aa) show declines at the end of the Carnian, and smaller ones at the Triassic–Jurassic boundary. In all cases, both the total (Fig. 3Ab) and per-taxon (Fig. 3Ac) extinction rates show two similar peaks, a slightly higher one in the late Norian, and a lower one in the Carnian.

The two (or more) mass extinctions in the late Triassic have been identified as a single event in most previous studies^{1–4,6–10,15–17,23,28,29}. Indeed, when all the extinctions in the Norian are summed, the two mass extinction peaks are 'smoothed out' to give a single broad peak (Fig. 3B). Raup and Sepkoski^{2,33} have recently noted an extinction peak in the late Carnian in their analysis of fossil marine animal genera, but they regard it as "an artefact of sampling".

If the cyclical models of mass extinction are correct, there should have been a single event in the late Triassic, within the Norian. According to the Harland timescale¹⁹, and a 26-Myr cyclicity pattern^{1,2}, this event should have occurred at 222 Myr and, according to the Odin timescale²⁰, at 219 Myr, both in the early Norian. If it is assumed that the mass extinctions occurred at the ends of stages, the late Triassic events documented here occurred at ~225 Myr and ~213 Myr, according to the Harland timescale, at ~220 Myr and ~204 Myr, according to the Odin timescale, and at ~225 Myr and ~208 Myr, according to the 'DNAG' timescale²¹. If the preceding extinction events, at the end of the Permian and at the end of the Scythian^{1,2,5,6,16,28,29,34} (see also Figs 1, 2), are considered, the spacings between these events are highly variable, according to each of the present timescales (Table 3).

Table 2 Total numbers of extinctions of marine and non-marine families in each stratigraphic stage from the middle Triassic (Ladinian) to the early Jurassic (Sinemurian)

	Ladinian	Carnian	Lower Norian	Middle Norian	Upper Norian	Hettangian	Sinemurian
Marine families							
Protozoa	—	1	1†	—†	5†	—	—
Porifera	—	8	—	—	—	—	—
Coelenterata	—	1	—†	2†	4†	—	—
Mollusca							
Gastropoda	4	4†	2†	1†	2†	—†	1†
Bivalvia	—	1	—†	1†	6†	1	1
Cephalopoda	8	14	5†	10†	21‡	1	4
Annelida	1	—	—	—	—	—	—
Arthropoda	2†	1†	1†	2†	2†	—	—
Brachiopoda	—	2	1†	1†	8†	—	1
Echinodermata	1	2	—	—	1	1	1
Conodonts	—	—	—	—	2	—	—
Chordata	8	7	—	—	3	—	2
Total:	24*	41‡	10†	17†	54‡	3†	10‡
Non-marine families							
Pteridophyta	—	—	—	—	2	—	1
Gymnospermophyta	1	—	—	—	2	2†	1†
Mollusca	—	—†	—†	1†	—†	1†	—†
Arthropoda	1	7†	5†	3†	23†	1†	5†
Chordata							
'Fish'	8	4†	—†	—†	4†	1	3
Tetrapoda	4	12	—	—	14	2	9
Total:	14	23‡	5†	4†	45‡	7†	19†
Overall no. of families	38*	66‡	15†	21†	99‡	10†	29‡

The data are listed by phyla, or other major groups, from refs 12, 18, 27–32. Stratigraphic terms and error estimates are explained in Table 1.

Table 3 Gaps (Myr) between consecutive mass extinction events in the late Permian, early Triassic and late Triassic, according to three current timescales

	Harland ¹⁹	Odin ²⁰	Palmer ²¹
Late Permian	5	6	5
Late Scythian	18	19	15
Late Carnian	12	16	17

These results indicate that the record of mass extinctions is not as straightforward as has been assumed by some authors: the choice of timescale may be crucial⁵, and closer analysis of the fossil data may reveal quite different patterns from those presented so far^{1–10,23,28,29}. For example, in a recent study of the two mass extinctions in the Jurassic required by the 26-Myr cyclicity theory (end-Pliensbachian, end-Tithonian), Hallam³⁵

found that the extinctions were regional, not global, in extent, being restricted largely to Europe.

The record of mass extinctions is not yet well known. It should be possible to obtain more precise data on the stratigraphic and geographical ranges of different taxa, to refine geological timescales, and to revise the systematics of various groups. Many authors have hitherto identified a single late Triassic mass extinction but more detailed studies of particular groups (for example, ammonoids and non-marine tetrapods) and of the whole marine and non-marine fossil record have indicated that there were two quite separate mass extinction events. This conclusion suggests that recent models of bolide-mediated cyclicity of mass extinctions may be incorrect. Cladistic analyses are essential for such studies²⁹.

I thank A. Hallam and P. E. S. Whalley for information on molluscs and insects respectively, J. J. Sepkoski Jr for supplying unpublished data on marine and non-marine families, and Ms E. A. Lawson for drawing the diagrams.

Received 24 February; accepted 10 April 1986.

- Raup, D. M. & Sepkoski, J. J. Jr *Proc. natn. Acad. Sci. U.S.A.* **81**, 801–805 (1984).
- Raup, D. M. & Sepkoski, J. J. Jr *Science* **231**, 833–836 (1986).
- Rampino, M. R. & Stothers, R. B. *Nature* **308**, 709–712 (1984).
- Kitchell, J. A. & Pena, D. *Science* **226**, 689–692 (1984).
- Hoffman, A. *Nature* **315**, 659–662 (1985).
- Hoffman, A. & Ghiold, J. *Geol. Mag.* **122**, 1–4 (1985).
- Colbert, E. H. *Proc. natn. Acad. Sci. U.S.A.* **44**, 973–977 (1958).
- Newell, N. D. *J. Paleont.* **36**, 592–610 (1962); *Spec. Pap. geol. Soc. Am.* **89**, 63–91 (1967).
- Raup, D. M. & Sepkoski, J. J. Jr *Science* **215**, 1501–1503 (1982).
- Sepkoski, J. J. Jr *Spec. Pap. geol. Soc. Am.* **190**, 283–289 (1982); *Paleobiology* **10**, 246–267 (1984).
- Hallam, A. *Palaogeogr. Palaeoclimatol. Palaeoecol.* **35**, 1–44 (1981).
- Tozer, E. T. in *The Ammonoidea* (eds House, M. R. & Senior, J. R.) 66–100, 397–431 (Academic, London, 1980).
- Kennedy, W. J. in *Patterns of Evolution as Illustrated by the Fossil Record* (ed. Hallam, A.) 251–304 (Elsevier, Amsterdam, 1977).
- Charig, A. J. in *Studies in Vertebrate Evolution* (eds Joysey, K. A. & Kemp, T. S.) 121–155 (Oliver & Boyd, Edinburgh, 1972).
- Bakker, R. in *Patterns of Evolution as Illustrated by the Fossil Record* (ed. Hallam, A.) 439–468 (Elsevier, Amsterdam, 1977).
- Olson, E. C. *Spec. Pap. geol. Soc. Am.* **190**, 501–511 (1982).
- Benton, M. J. *Q. Rev. Biol.* **58**, 29–55 (1983).

- Benton, M. J. in *The Beginning of the Age of Dinosaurs* (ed. Padian, K.) (Cambridge University Press, New York, in the press).
- Harland, W. B. *et al. A Geologic Time Scale* (Cambridge University Press, 1982).
- Odin, G. S. (ed.) *Numerical Dating in Stratigraphy* (Wiley, New York, 1982).
- Palmer, A. R. *Geology* **11**, 503–504 (1983).
- Donovan, B. T., Callomon, J. H. & Howarth, M. K. in *The Ammonoidea* (eds House, M. K. & Senior, J. R.) 101–155 (Academic, London, 1980).
- Van Valen, L. M. *Nature* **307**, 50–52 (1984).
- Anderson, J. M. & Cruickshank, A. R. I. *Palaent. afr.* **21**, 15–44 (1978).
- Olsen, P. E. & Galton, P. M. *Science* **197**, 983–986 (1977).
- Olsen, P. E. & Galton, P. M. *Palaent. afr.* **25**, 87–110 (1984).
- Sepkoski, J. J. Jr *Milwaukee publ. Mus. Contr. Geol. Biol.* **51**, 1–125 (1982) (with revision sheets dated August 1985).
- Benton, M. J. *Nature* **316**, 811–814 (1985); *Bull. Soc. géol. Fr.* (in the press).
- Benton, M. J. *Spec. Pap. Palaent.* **33**, 185–202 (1985).
- Moore, R. C. *et al. Treatise on Invertebrate Paleontology* (Geological Society of America and University of Kansas Press, Lawrence, 1953–1985).
- Harland, W. B. *et al. The Fossil Record* (Geological Society of London, 1967).
- Whalley, P. E. S. *Bull. Br. Mus. nat. Hist. (Geol.)* **39**, 107–187 (1985).
- Sepkoski, J. J. Jr & Raup, D. M. in *Dynamics of Extinction* (ed. Elliott, D.) 3–36 (Wiley, Somerset, New Jersey, 1986).
- Bray, A. A. *Mod. Geol.* **9**, 397–409 (1985).
- Hallam, A. *Nature* **319**, 765–768 (1986).