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2.13.5 End-Triassic

M. J. BENTON

Introduction

A mass extinction event in the Late Triassic has been recognized for some time. The decline and virtual disappearance of the ammonoids at the Triassic−Jurassic boundary has long been clear to cephalopod workers, while in the nineteen-forties Edwin Colbert described the major extinctions of terrestrial tetrapods at that time.

Recent surveys of mass extinction events in the sea (e.g. Raup & Sepkoski 1982) have identified the end-Triassic event as one of the five major Phanerozoic extinctions, equal in magnitude overall to the end-Ordovician (Section 2.13.2), Late Devonian (Section 2.13.3), and end-Cretaceous (Sections 2.13.6, 2.13.7) events, with a loss of over 20% of approximately 300 families of marine invertebrates and vertebrates. It is also one of the key extinctions in considerations of periodicity (Raup & Sepkoski 1984; Section 2.12.3), occurring as it does about 26−30 million years after the end-Permian event.

Extinction patterns

In the sea, several major lineages of invertebrates and vertebrates went extinct. The main groups to be affected were the cephalopods (58 families became extinct), the gastropods (13), various marine reptiles (13), the brachiopods (12), the bivalves (8), and the sponges (8). 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 as a whole barely survived into the Jurassic. When genera are considered, the Ceratitida reached a peak of *c*. 150 genera in the Carnian, which fell to *c*. 100 in the Norian, and to single figures in the latest Norian, finally disappearing at the Triassic−Jurassic boundary. This corresponds to an extinction rate of 100% at all levels. Only the Phylloceratina passed, at very low diversity, from the Triassic into the Jurassic. The family extinction rate for bivalves was not so marked, but the generic extinction rate was 42%, and the species extinction rate, in Europe at least, was 92% (Hallam 1981). This suggests that both the cephalopods and the bivalves barely scraped through the end-Triassic event into the Jurassic to establish new radiations. The last strophomenid brachiopods, conodonts, conulariids, nothosaurs, and placodonts also disappeared in the Late Triassic.

On land, major extinctions occurred amongst the insects (35 families), 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, procolophonids, prolacertiforms, and rhynchosaurs died out, or were greatly depleted, and new groups, such as the dinosaurs, crocodiles, pterosaurs, turtles, lepidosaurs (lizards and their relatives), lissamphibians (frogs and salamanders), and mammals came on the scene (Benton 1986; Benton; Olson & Sues *in* Padian 1986).

Terrestrial events: competition or mass extinction?

There was a global faunal turnover amongst vertebrates on land in the Late Triassic. In several early papers, E. Colbert drew attention to the loss of a whole range of groups, as noted above. The nature of this massive replacement has been controversial. Initially, Colbert argued that the new groups radiated into effectively empty ecospace after a series of extinctions. Thus, the new lizard-like animals occupied the niches that procolophonids and prolacertiforms had held before, crocodiles filled the niches of the recently-extinct phytosaurs, and so on. However, views changed during the nineteen-sixties and seventies to focus more on competition-based models for the faunal replacement. The idea was that the dinosaurs outcompeted the formerly dominant mammal-like reptiles, rhynchosaurs, and thecodontians. The dinosaurs were said to have advantages in their style of locomotion (upright, instead of sprawling) and/or their thermal physiology. Thus, some authors argued that the dinosaurs must have been fully warm-blooded (endothermic) in order to compete successfully, while others stressed the advantages of cold-bloodedness (the need for less food and water).

However, recent detailed analyses of the fossil data (reviewed in Benton; Olsen & Sues *in* Padian 1986) suggest that the long-term competitive models are not likely. The relative abundances of the major terrestrial tetrapod groups throughout the Triassic show that there was no gradual long-term decline of the earlier groups, and matching radiation of the replacing groups. The dinosaurs were in existence near the beginning of the Late Triassic (in the Carnian), but they were very rare elements in their faunas (1% or less of all individuals) (Fig. 1). Many ecologically important groups then disappeared at the end of the Carnian, as far as the data indicate (rhynchosaurs, various mammal-like reptiles, and thecodontians), and the dinosaurs radiated thereafter in the Early Norian. Further groups of thecodontians and mammal-like reptiles disappeared at the end of the Triassic, and the dinosaurs apparently radiated again.

Other taxonomic studies on the diversity of tetrapod families in the Triassic (Benton 1986; Benton; Olson & Sues *in* Padian 1986) confirm the importance of mass extinction as the triggering factor for the remarkable faunal replacements in the Late Triassic. Indeed, there seems to have been more than one extinction event in the Late Triassic.
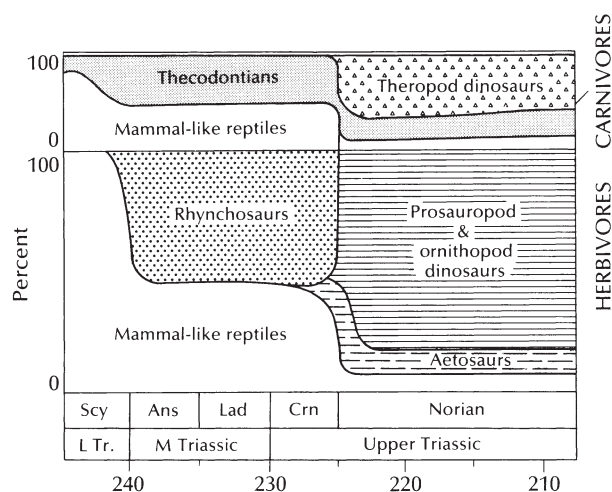
Fig. 1 The pattern of evolution of Triassic non-marine tetrapods, showing the extinction of major groups at the end of the Carnian stage. The dinosaurs, and other replacing groups, appear to have radiated only *after* the extinction event, thus suggesting an opportunistic replacement rather than one involving long-term competition. For abbreviations see the legend to Fig. 2. (After Benton 1988, by permission of Macmillan Magazines Ltd.)

Timing of the extinction events

Was there one mass extinction event in the Late Triassic or several? Many studies (e.g. Raup & Sepkoski 1982, 1984) identify a single event, but a great deal of evidence now appears to disagree with that view. Several authors had already noted that the extinctions in the Late Triassic were either not synchronous in the sea and on land (e.g. Hallam 1981), or that the extinction lasted for much of the Late Triassic, through the Carnian and Norian (the latter including the 'Rhaetian'), a time-span of 18–25 million years (depending on the time-scale used).

The timing of the Late Triassic marine extinction event has not been determined precisely for all groups. The bivalves declined in diversity from a Carnian–Early Norian peak, and were affected by a major extinction event at the end of the Norian (Hallam 1981). Similarly, the ceratite ammonoids reached their peak of diversity in the Carnian, and declined thereafter. The last genera disappeared at the end of the Norian ('Rhaetian'). The mass extinctions of brachiopods and conodonts appear to have occurred at the end of the Norian, while Benton (*in* Padian 1986); Olson & Sues (*in* Padian 1986) identified two extinction events for non-marine tetrapods, one at the end of the Carnian, and another at the end of the Norian.

The timing of the extinction of the marine vertebrates has been disputed. It has generally been assumed (e.g. Raup & Sepkoski 1982) to coincide with the end-Triassic invertebrate extinctions. However, most of the Late Triassic marine reptile families died out in the Carnian (five families), the timing of one is uncertain, and only one died out at the Triassic–Jurassic boundary:

Benton (1986) presented three separate analyses that indicate at least two mass extinction events in the Late Triassic, one probably at the end of the Carnian, and the other 12–17 million years later, at the Triassic–Jurassic boundary:

1 A detailed analysis of ammonoid families suggests that there were several declines in family diversity, the largest two in the Carnian and Late Norian (Fig. 2A). Total extinction rates for ammonoid families vary considerably during the Triassic and Early Jurassic (Fig. 2B), showing high peaks in the Late Scythian, the Late Ladinian, and the Early Carnian, and smaller peaks in the Anisian and in the Middle and Late Norian. Per-taxon extinction rates (Fig. 2C) show high peaks in the Late Scythian, the Late Anisian, the Early Carnian, and the Late Norian. The Late Triassic 'mass extinction' of ammonoid families was not a single event, but at least two — one in the Carnian, and a larger one at the end of the Norian (the 'Rhaetian').

2 Triassic and Early Jurassic families of non-marine tetrapods (Fig. 3A) show 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 total extinction rate (Fig. 3B) and in per-taxon extinction rate (Fig. 3C). The end-Carnian mass extinction of non-marine tetrapods was apparently the larger of the two Late Triassic events, according to Benton (1986), while the analysis by Olsen & Sues (*in* Padian 1986) suggested that the end-Norian event was larger than the end-Carnian one. These differences arise from the use of slightly different data sets.

3 Diversity and extinction rate data for all marine and non-marine animals in the Late Triassic (Benton 1986) indicate average marine diversity of about 340 families, and non-marine diversity of about 190 families. The numbers of family extinctions in marine taxa per time unit ranged from 3 to 54 (mean: 23.0), and in non-marine taxa from 4 to 45 (mean: 18.1). The plots of marine and non-marine family diversity (Fig. 4A) showed declines at the end of the Carnian, and smaller ones at the Triassic–Jurassic boundary. In all cases, both the total extinction rates (Fig. 4B), and the per-taxon extinction rates
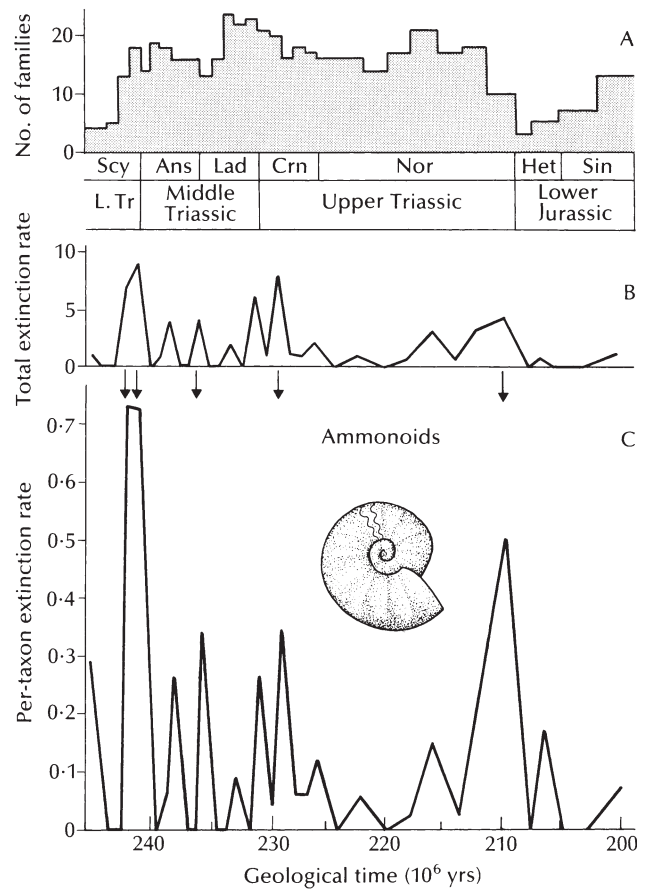
Fig. 2 Triassic ammonoid families. A, Total diversity. B, Total extinction rates. C, Per-taxon extinction rates. The total extinction rates were calculated as the numbers of families dying out per million years, and the per-taxon extinction rates as the total extinction rate divided by the number of taxa at risk. The five highest per-taxon extinction rates (possible mass extinctions) are indicated with arrows. Diversity and extinction rate data were calculated by Triassic and earliest Jurassic substages (Scythian, Hettangian, Sinemurian), and by zones (Anisian–Norian). The 'Rhaetian' stage is included in the Late Norian. Abbreviations: Ans = Anisian, Crn = Carnian, Het = Hettangian, Lad = Ladinian, L. Tr = Lower Triassic, Nor = Norian, Scy = Scythian, Sin = Sinemurian. The fossil is *Ceratites*. (After Benton 1986.)

(Fig. 4C) showed two similar peaks, with a slightly higher one in the Late Norian, and a lower one in the Carnian.

Present evidence points to as many as three Triassic extinction events: at the end of the Scythian, in the Middle to Late Carnian, and at the Triassic–Jurassic boundary; none of these is clearly larger than either of the other two. The temporal spacings of the three events are as follows:
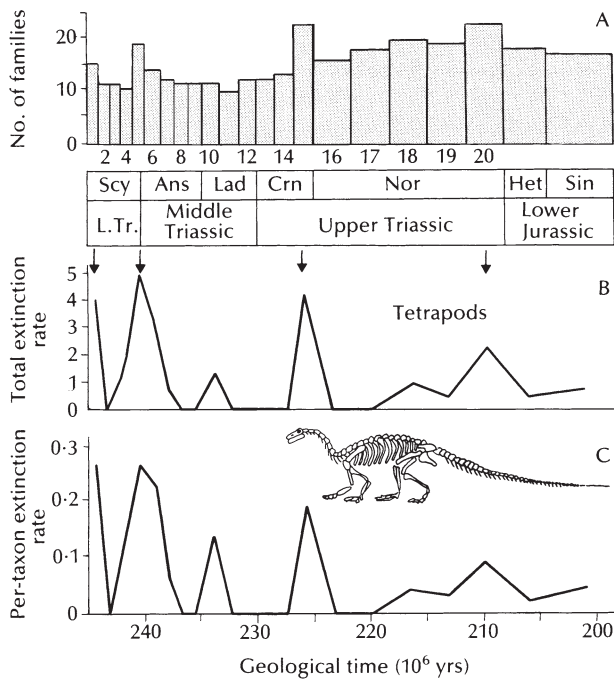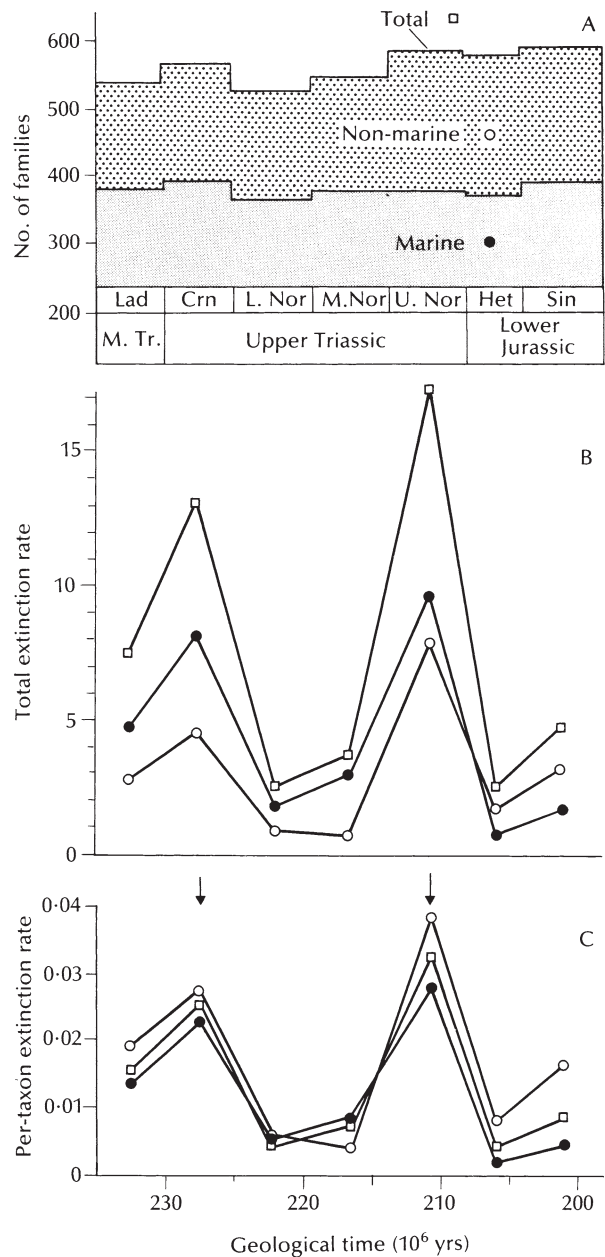
Fig. 3 Triassic and earliest Jurassic non-marine tetrapod families. A , Total diversity. B, Total extinction rates. C, Per-taxon extinction rates. The four highest total extinction rates (possible mass extinctions) are indicated with arrows. The time-scale is subdivided into informal 'substages', numbered 1–20 in the Triassic. For abbreviations see the legend to Fig. 2. The fossil is *Thecodontosaurus*. (After Benton 1986 by permission from Macmillan Magazines Ltd.)

end-Permian to end-Scythian:	5–6 Myr
end-Scythian to end-Carnian:	15–19 Myr
end-Carnian to end-Norian:	12–17 Myr

If the periodicity theory of mass extinctions (Raup & Sepkoski 1984) is to be valid (Section 2.12.3), there should have been a single event 26–30 million years after the end-Permian event, thus 219–222 Ma, in the Early Norian, according to current time-scales. Present evidence on the Late Triassic record of marine and non-marine animals strongly contra-dicts this prediction.

Causes

The Late Triassic tetrapod extinctions have been linked to an increasing aridity observed in reptile-bearing beds in various parts of the world (Benton *in* Padian 1986). Associated with these climatic changes were abrupt floral replacements in the Norian. The *Dicroidium* flora of Gondwanaland was replaced by a world-wide conifer-bennettitalean flora at the end of the Norian ('Rhaetian') and in the Early Jurassic. It has been suggested that these

Fig. 4 Late Triassic and earliest Jurassic plant and animal families. A, Total diversity. B, Total extinction rates. C, Per-taxon extinction rates. The data are plotted separately for marine (closed circles), non-marine (open circles), and total (open squares) families. The two mass extinctions (end-Carnian; end-Norian) are indicated with arrows. 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. For abbreviations see the legend to Fig. 2. (After Benton 1986, by permission from Macmillan Magazines Ltd.)

climatic and floral changes could have led to the extinction of various tetrapod groups. Another view links the extinctions with marine regressions and

reduced orogenic activity. These would have resulted in lower habitat diversity on land as new lowlands appeared, removal of reproductive barriers, and lower speciation rates. Indeed, much of the decline in diversity of tetrapods at this time is linked to depressed origination rates.

Several kinds of explanations have also been given for extinctions in the marine realm: widespread marine regression followed by an anoxic event (Hallam 1981; see also Section 2.12.1), temperature changes, or extraterrestrial impact (Section 2.12.2). Indeed, the last proposal is supported by the Manicougan crater in Canada (70 km in diameter) which is dated at 206–213 Ma. However, to date, no iridium anomaly or shocked quartz occurrence has been reported that coincides with either of the possible Late Triassic extinction events.

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2.13.6 Cretaceous–Tertiary (Marine)

F. SURLYK

Introduction

The alleged mass extinction at the end of the Mesozoic Era has been one of the most intensively debated subjects within geology and palaeontology (see also sections 2.12.1, 2.12.2). In the forefront of the discussion has been the meteorite impact hypothesis (see Alvarez *et al.* 1984). The Mesozoic–Cenozoic Era boundary is placed at the boundary between the Maastrichtian and Danian Stages. The Danian was, however, originally considered the end-Cretaceous Stage.

Discussions about the stratigraphic position of the Danian first started with Bramlette & Martini's (1964) observation that a major turnover of calcareous marine plankton took place at the Maastrichtian–Danian boundary. The broad pattern of marine extinctions is now known for both microfauna and flora, and macrofauna (see reviews by Kauffman 1984; Stanley 1987). The detailed extinction pattern, however, is known only for planktic foraminifera and calcareous nannoplankton, although new data are continually appearing for other microfossil groups. High-resolution stratigraphic information on the extinction across the boundary is virtually non-existent for marine invertebrates. Only a few groups have been studied and lend themselves to investigation on the basis of closely spaced sample series.

While the broad extinction patterns at the stage level can be relatively easily assessed on the basis of the literature, all discussions on the detailed patterns across the boundary come down to the question of sampling. It is well known that sampling effects can modify diversity patterns on both regional and local scales. Signor & Lipps (1982) particularly emphasized the effect of reduced sample size and artificial range truncation in the top Maastrichtian. Although this may seem trivial, it is overlooked in most reviews of the end-Maastrichtian extinction. Oceanic micro- and nannoplankton have a more complete record because the sediment itself is commonly composed of their skeletal remains. This is particularly true of biogenic sediments deposited above the carbonate compensation depth. Data based on randomly collected macroinvertebrate fossils, however, are poorly suited to illuminate the detailed nature of the extinction, and the existing data-base for invertebrates is totally inadequate to illustrate the short term nature and rate of extinction and diversification across the boundary.

A standard boundary sequence

A major breakthrough in high-resolution stratigraphy across the boundary was reached with the recognition that the same lithological and faunal succession could be traced over all major ocean basins (Smit & Romein 1985). This 'standard K–T boundary event sequence' contains a succession of five lithological units (1–5) which reflect the sequence of events across the boundary. The sequence