

# WHAT REALLY HAPPENED IN THE LATE TRIASSIC?

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Major extinctions occurred both in the sea and on land during the Late Triassic in two major phases, in the middle to late Carnian and, 12–17 Myr later, at the Triassic–Jurassic boundary. Many recent reports have discounted the role of the earlier event, suggesting that it is (1) an artefact of a subsequent gap in the record, (2) a complex turnover phenomenon, or (3) local to Europe. These three views are disputed, with evidence from both the marine and terrestrial realms. New data on terrestrial tetrapods suggests that the late Carnian event was more important than the end-Triassic event. For tetrapods, the end-Triassic extinction was a whimper that was followed by the radiation of five families of dinosaurs and mammal-like reptiles, while the late Carnian event saw the disappearance of nine diverse families, and subsequent radiation of 13 families of turtles, crocodylomorphs, pterosaurs, dinosaurs, lepidosaurs and mammals. Also, for many groups of marine animals, the Carnian event marked a more significant turning point in diversification than did the end-Triassic event.

**KEY WORDS:** Triassic, mass extinction, tetrapod, dinosaur, macroevolution, fauna.

## INTRODUCTION

Most studies of mass extinction identify a major event in the Late Triassic, usually placed at the Triassic–Jurassic boundary. For example, Raup, and Sepkoski (1982) noted the end-Triassic event as one of the five major mass extinctions during the Phanerozoic, equivalent in scale to the Late Ordovician, Late Devonian, and end-Cretaceous events. For marine invertebrates, Sepkoski (1982) estimates a loss of 20% of families, which scales to more than 50% loss of species.

The purpose of this paper is to review previous opinions on what happened, to focus on the question of timing of the event, or events, in the Late Triassic, and to consider briefly the implications for theories of periodicity of extinctions.

## FORMER VIEWS

### *Extinctions*

The Late Triassic event was recognised among terrestrial vertebrates as early as the 1940s. Colbert (1949) described the extinction of a whole range of groups on land, such as the labyrinthodont (i.e. temnospondyl) amphibians, procolophonids, prolacertiforms, rhynchosaurs, thecodontians, and most mammal-like reptiles. In the sea, dominant marine reptiles, such as the nothosaurs and placodonts, also died out during the Late Triassic. The significance of the event for terrestrial vertebrates was emphasised by the replacing animals, a range of new groups, such as the modern amphibians, turtles, sphenodontids (relatives of the lizards), crocodylians, dinosaurs, pterosaurs, mammals, and marine plesiosaurs and

crocodilians. Later publications on the terrestrial vertebrate turnover are reviewed by Benton (1986b).

The Late Triassic event was also recognised among marine invertebrates. Newell (1962, 1963, 1967) and others noted the extinction of ceratite ammonoids, various bivalve groups, major groups of brachiopods, and the last conodonts. At generic and species levels, Hallam (1981) has shown that there were high levels of extinction among ammonoids and bivalves (42% loss of genera, and 92% loss of species of the latter), and Hallam (1991) provides a broader review of terminal Triassic extinctions.

### *Timing*

The timing of the Late Triassic event(s) has always been in dispute. Initially, the extinction was generalised merely as "late Triassic" or "end-Triassic". The marine events, as Hallam (1981) noted, were "either at or very shortly before the end of the period", while the terrestrial vertebrate turnover took place much earlier, in Carnian times, a time difference of 12–17 Myr, depending upon which of several current time scales one accepts (e.g. Cowie and Bassett, 1989; Forster and Warrington, 1985; Harland *et al.*, 1989).

The earlier peak of vertebrate extinction was noted by Bakker (1977), Charig (1979), Benton (1983, 1986a, b, 1987b), Olsen and Sues (1986), and Lucas (1990). In addition, Olsen and Galton (1977, 1984) argued that many of the supposed extinctions of terrestrial vertebrates in the second event, at the end of the period, were imaginary, because a number of supposedly terminal-Triassic horizons were redated as Early and Middle Jurassic.

Benton (1986a) extended the vertebrate evidence, and proposed that there were two Late Triassic events, of which the first was marginally the larger overall. The two events applied to all animals—marine and terrestrial, invertebrate and vertebrate—and not just to terrestrial vertebrates, as has been supposed by some authors (e.g. Hoffman 1989a, p. 204; 1989b, p. 29). Raup and Sepkoski (1984; Sepkoski and Raup, 1986; Sepkoski, 1986, 1989) find these two Late Triassic peaks of extinction in their familial and generic data sets of marine animals, but they suggest that the Carnian peak is not a genuine mass extinction for four reasons:

(1) The Carnian extinction peak is an artefact of a succeeding poor fossil record (Olsen and Sues, 1986, p. 343; Sepkoski and Raup, 1986, p. 11). It is suggested that marine diversity peaked in the early and middle Carnian because of the presence of one or more extremely fossiliferous horizons—particularly the Cassian Beds of Italy—followed by relatively unfossiliferous horizons in the late Carnian and early Norian. In other words, the Carnian decline in diversity is not the result of a mass extinction, but merely a gap in the record.

(2) There may have been a backward smearing of the effects of the end-Triassic extinction event (Sepkoski, 1986, p. 286). This is linked to the first argument, but with the allied suggestion that the whole record between the Carnian and the end of the Triassic is so poor that extinctions are pulled back to the start of the gap—the Signor-Lipps effect.

(3) The Carnian peak in extinction was produced mainly by extinctions of ceratite ammonoids and gastropods which were undergoing high turnover at the time (Sepkoski, 1986, p. 286; 1989). The high rates of extinction are simply associated with high origination rates.

(4) Even if there were a Carnian extinction event, it is probably a local Alpine phenomenon, and not global (Hallam, 1991). For example, Newton *et al.* (1987) found no evidence for bivalve extinctions at that time in the western United States, while Olsen *et al.* (1987, 1988) regard the end-Triassic event as the dominant one, at least in the basins of the Newark Supergroup of the eastern United States.

Arguments (1) and (4) are addressed in this paper. Argument (2) is an extreme version of (1), and it is regarded as unlikely to explain much of the Carnian extinction peak since there is a time span of 12–17 Myr involved, and the Norian fossil record is probably not bad enough to allow such a major backwards smearing of the data. The high turnover argument (3) is doubtless true, although it may have something to do with (1) since it is an example of the Lagerstätten Effect, and it is not addressed separately here.

## EVIDENCE FOR A CARNIAN EXTINCTION EVENT

### *Marine Animals*

Simms and Ruffell (1989, 1990) reviewed some of the evidence for extinctions and turnover in the sea during the mid-Carnian, and found significant extinctions in a range of higher taxa. Ceratite ammonoid diversity peaked at about 150 genera in the early Carnian, and fell to 100 or so in the Norian, with peaks in extinction rate in the early to middle Carnian. Although the major extinctions of bivalves occurred at the end of the Triassic (Hallam, 1981), Johnson and Simms (1989) noted high extinction levels among the scallops in the Carnian.

Bryozoans also showed major declines in the Carnian. From a peak in the early Carnian, the group declined from 22 to 13 species in the late Carnian, and only two survived into the Norian (Schäfer and Fois, 1987).

According to Johnson and Simms (1989) and Simms (1991), the major post-Palaeozoic turnover among crinoids took place in the Carnian, not at the end of the Norian. Encrinids and isocrinids, typical of earlier faunas, show a dramatic reduction in diversity between the early and middle Carnian, and in the case of the encrinids, became extinct altogether. Another group, the Somphocrinidae experienced a major decline in abundance and diversity at the end of the late Carnian. The Carnian also witnessed a major decline of echinoids (Smith, 1990; Simms, 1991), and indeed they were unaffected by the end-Triassic event.

Conodonts were also in decline. Although they finally disappeared at the end of the Triassic, the major drops in species and genus origination rates began in the early Carnian (Aldridge, 1988). Only one new genus of conodont arose in the Norian, and the final extinction at the end of the period was a whimper.

Stanley (1988) has documented major turnovers and extinctions among reef organisms. Reefs were absent in the Early Triassic, whereas those of the Middle Triassic to early Carnian resembled Permian reefs, being dominated by *Tubiphytes*, calcisponges, bryozoans, and calcareous algae. Norian reefs, on the other hand, were very different, with scleractinian corals becoming the key framework builders. The changeover in reef type is dated as middle or late Carnian, and it involves marked diversity changes in foraminifera, sponges, corals, bryozoans, algae, and reef-living bivalves and gastropods (Stanley, 1988, p. 177).

For marine and freshwater fishes, Benton (1989) documented a decline of 33%, and there was no detectable extinction event for these groups at the end of the

Triassic (Patterson and Smith, 1987). Four out of six families of marine tetrapods also died out at the end of the Carnian: the Nothosauridae, Simosauridae, Cymatosauridae, and Henodontidae, a 67% drop in their familial diversity (Benton, 1988).

### *Terrestrial Plants and Animals*

Terrestrial plants also show turnovers and extinctions during the Carnian, with a peak in originations in the middle Carnian, and a peak in extinctions at the Carnian-Norian boundary (Boulter *et al.* 1988). Olsen and Sues (1986, p. 345) also find a peak in extinction rate of pollen and spores in the late Carnian that is just as high as the end-Triassic peak.

The extinctions of terrestrial vertebrates in the late Carnian seem to be unequivocal and major in extent. Indeed, Benton (1986a, b), Olsen and Sues (1986), and others have suggested that this earlier event was more significant than the end-Triassic event for two reasons: (1) more taxa apparently died out during the earlier event; and, (2) the new taxa radiating after the earlier event were more significant than those radiating in the earliest Jurassic.

Benton (1986b, p. 315) documented the extinction of seven out of 23 families of terrestrial tetrapods (30% drop) both at the end of the Carnian, and at the end of the Triassic. Olsen and Sues (1986, p. 328) found similar figures from their independently compiled data set: a loss of 10 out of 26 families (38% drop) during the Carnian, and a loss of 13 out of 30 families (43% drop) during the Norian. Olsen *et al.* (1987) modified these figures to a loss of 10 out of 24 families (42% drop) during the Carnian, and 14 out of 31 families (45% drop) during the Norian. Note, however, that the figures presented by Olsen and colleagues cover extinctions during the whole of the Carnian and the whole of the Norian, not just their final parts: the comparable all-Carnian and all-Norian figures from Benton's (1986b) data are 7 out of 23 families (30% drop) and 13 out of 29 families (45% drop) respectively. Hence, it is not clear from the global data of Olsen and Sues (1986) and Olsen *et al.* (1987) whether the late Carnian or the end-Triassic event is the larger. Scaled to time, the late Carnian extinction peak is by far the greater, as Benton (1986a, b) found, simply because the Carnian stage is regarded as shorter (5–12 Myr) than the Norian (12–17 Myr), according to recent time scales.

At species level, however, Benton (1986b, pp. 313–6) found a drop of 66% in species diversity from the late Carnian to the early Norian, and 12% from the end-Norian ("Rhaetian") to the Hettangian (earliest Jurassic). Part of the large drop in species diversity from the late Carnian to the early Norian could reflect a more incomplete fossil record of the latter substage (but see below).

More detailed analyses of Triassic tetrapod diversity are possible at present only for local basins because of problems of stratigraphic correlation. Olsen and Sues (1986) found that, for the Newark Group successions of the eastern United States, there were similar levels of extinctions concentrated in the late Carnian and in the latest Norian, based on skeletal and footprint evidence sampled at 2 Myr intervals. This broadly confirms the equivalent role of both extinction events, although sampling may again have been a problem (see below).

### *New Evidence on Terrestrial Vertebrates*

The distributions of fossil reptile families in the Late Triassic and Early Jurassic have been revised considerably since publication of the data bases by Benton

(1983b, 1986a, b, 1987), Olsen and Sues (1986), and Olsen *et al.* (1987, 1988). A new data set is presented here (Figure 1) in which all generally accepted families are listed and their stratigraphic distributions noted. The families listed are based on the latest cladistic reassessments available, and stratigraphic assignments are based on the latest finds (some new ones since 1986) and on the latest views on stratigraphy. Full details of the amphibian, reptile, and mammal familial data are given in Milner (1992), Benton, (1992), and Stucky (1992) respectively.

An important issue that was not fully tackled by Benton (1986b), Olsen and Sues (1986), and other authors is the significance of singleton families. These contain only one species, often based on a single specimen from a single locality, and they make up an appreciable proportion of the families listed for the Late Triassic (12 out of 58, i.e. 21%, according to Figure 1). It is clearly unacceptable to accord such 'families' the same status as diverse families for two reasons:

(1) they have a point distribution in time, and clearly cannot be used in rate calculations, since their temporal distribution is infinitesimally small and could give infinitely high rate measures; and,

(2) it is hard to draw a limit to the multiplication of such families: if one scoured the literature assiduously, dozens of singleton families could be found, many based on uncertain material, that might be used to bolster the apparent magnitude of a particular extinction event.

Hence, the data are presented here (Figures 1, 2) in two forms, both with and without singleton taxa.

As for stratigraphy, this is based upon recent publications by Olsen and Galton (1977, 1984), Olsen *et al.* (1982, 1987), Lucas and Hunt (1989), Hunt and Lucas (1991a, b), and papers cited therein. Olsen and colleagues re-dated many formations from the latest Triassic up to the Early Jurassic, and from the Norian down to the late Carnian, on the basis of radiometric dating, palynology, fishes, and comparisons of tetrapod skeletal and footprint evidence. Lucas and Hunt have further refined late Carnian stratigraphy by proposing the existence of two distinctive types of faunas, based upon a comparison of the phytosaurs: the *Paleorhinus* Biochron (early late Carnian) and the *Rutiodon* Biochron (late late Carnian). These divisions are accepted here in Figures 1 and 2.

The key conclusion from the new data compilation is that the late Carnian "event" for tetrapods was considerably more dramatic than was the end-Triassic. Thirteen families died out (nine, excluding singletons) during the former, compared to six during the latter. Peaks of extinction rate are about equal for both events because of the higher global familial diversity in the late Carnian (Figure 2b). The late Carnian episode is marked by two high extinction rate values, while the end-Triassic episode appears to be marked by three, in the "Late Norian", "Rhaetian", and in the Hettangian (Figure 2b). Oddly, the last is marginally higher than the "Rhaetian" extinction rate, the one of most interest to proponents of a terminal-Triassic extinction event. Both broad pulses of extinction are matched by high origination rates, so that both could be interpreted equally to record either episodes of high turnover, or episodes of unusually good fossil preservation.

A further conclusion is that, at species level, the late Carnian event *far* exceeded the terminal-Triassic event in its magnitude. As shown by Table 1, the relative diversities of the families affected by both extinction events were very different. Of the nine non-singleton tetrapod families that died out during the late Carnian,

	LAD.	CARNIAN				NORIAN				RHT	HET	SIN.
		Cor.	Jul.	Tuvanian		Lacian		Ala.	Sevatian			
		E	M	L1	L2	E	M1	M2	L	RHT		
<b>AMPHIBIA</b>												
Capitosauridae												
Mastodontosauridae												
Trematosauridae												
Laticosauridae									?			
Metoposauridae												
Chigutisauridae												
Plagiosauridae												
Gymnophiona indet. (s)												
Anura fam. indet. (s)												---
<b>REPTILIA</b>												
Procolophonidae												
Proganochelyidae												
Proterochersidae (s)												---
Kaentachelyidae (s)												---
Kuehneosauridae										?		
Thalattosauridae												
Clazziidae												
Trilophosauridae												
Rhynchosauridae												
Proleceratidae												
Tanystropheidae												
Proterochampsidae												
Phytosauridae												
Stagonolepididae												
Rauisuchidae												
Poposauridae												
Ornithosuchidae												
Lagosuchidae												
Scleromochlidae (s)												
Erpetosuchidae (s)												
Trialestidae (s)												
Saltoposuchidae												?
Sphenosuchidae												?
Protosuchidae												?
Orthosuchidae (s)												?
Dimorphodontidae												?
Eudimorphodontidae (s)												?
Staurikosauridae (s)												
Herrerasauridae												
'Ceratosauridae'												
Thecodontosauridae												
Massospondylidae												
Yunnanosauridae												
Plateosauridae												
Melanorosauridae												
Vulcanodontidae (s)												?
'Fabrosauridae'												---
'Scelidosauridae'												---
Heterodontosauridae												---
Sphenodontidae												---
Gephyrosauridae (s)												---
Kannemeyeriidae												?
Traversodontidae												---
Chiniquodontidae												---
Tritylodontidae												---
Trithelodontidae												---
<b>MAMMALIA</b>												
Haramiyidae												?
Morganucodontidae										?		---
Kuehneotheriidae												?

Figure 1

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**Table 1** The species-level diversity of families of tetrapods that went extinct in the late Carnian and in the "Rhaetian" (=latest Norian, or late Sevatian). The numbers represent global totals of named species and unnamed records of members of the family that are yet to be described. Data are from Benton (1983b, 1986b), Olsen and Sues (1986), Olsen *et al.* (1987), Weishampel (1990), and other sources. Abbreviation: (s), singleton family.

Families extinct	Species numbers		
	Late Carnian	Norian (excl. Rhaetian)	Rhaetian
<b>LATE CARNIAN 1</b>			
1. Mastodonsauridae	1	0	0
2. Trematosauridae	1	0	0
3. Prolacertidae	2	0	0
4. Staurikosauridae (s)	1	0	0
5. Chiniquodontidae	4	0	0
<b>LATE CARNIAN 2</b>			
1. Rhynchosauridae	6	0	0
2. Proterochampsidae	3	0	0
3. Scleromochlidae (s)	1	0	0
4. Erpetosuchidae (s)	1	0	0
5. Trialestidae (s)	1	0	0
6. Herrerasauridae	2	0	0
7. Traversodontidae	10	0	0
8. Kannemeyeriidae	7	0	0
<b>"RHAETIAN"</b>			
1. Procolophonidae	5	0	2
2. Phytosauridae	11	7	1
3. Ornithosuchidae	2	0	1
4. Stagonolepididae	14	3	2
5. Rausuchidae	6	2	1
6. Thecodontosauridae	1	1	1

four were represented by four or more species each in the late Carnian: the Traversodontidae by ten, the Kannemeyeriidae by seven, the Rhynchosauridae by six, and the Chiniquodontidae by four (Table 1). The mean terminal diversity of these nine families is four species (36 in all).

The six families that disappeared during the end-Triassic event tell a very different story. Their mean terminal diversity was only 1.3 species (with a maximum of two). The total species-level loss for these families was only eight globally. Indeed, three of the six families that died out at this time (Ornithosuchidae, Rausuchidae, Stagonolepididae) are known in the latest Triassic only from the Los Colorados Formation of Argentina, despite the availability of numerous other "Rhaetian"-age reptile-bearing formations

**Figure 1** Known temporal distributions of all families of amphibians, reptiles, and mammals that existed in the Late Triassic, spanning from the Ladinian (late Middle Triassic) to the Sinemurian (Early Jurassic). Uncertainties in the distributions are shown by dashed lines. The stratigraphic division are stages (upper case), palynological zones (lower case), and estimated tetrapod substages. L1 and L2 are divisions of the late Carnian proposed by Lucas (1990), and the other tetrapod substages are explained in (Benton, 1986b). Data are based on Benton (1992), Milner, (1992), and Stucky (1992). Singleton families are indicated by "(s)". Abbreviations: Ala, Alaluanian; Cor, Cordevolian; E, Early; HET, Hettangian; Jul, Julian; L, Late; LAD, Ladinian; M, Middle; RHT, "Rhaetian"; SIN, Sinemurian.

elsewhere (see Table 2). These same six families all survived through the end-Carnian event, but their species-level loss was much more dramatic than at their final demise (Table 1): 39 species belonging to these six families existed in the late Carnian, and this fell to nine during the Norian. Hence, the end-Carnian event was apparently the major determinant in reducing the dominance of these six families. They survived through the Norian at low diversity, and many only in restricted areas (refugia), until they finally disappeared at the end of the Triassic. So much for the emphasis given by some palaeontologists to the end-Triassic event in mediating tetrapod replacements on land!

### *Impact of the Late Triassic Events on New Radiations*

The impact of a mass extinction may be assessed by its killing effects, but also by the radiations of new groups that follow after. In the case of the two Late Triassic events, there are clear differences in scale and significance in terms of the groups that radiated within the succeeding 10 Myr.

The Carnian event had a profound effect on marine biotas. In general, Norian marine invertebrates have been said to have closer affinities with the Jurassic than with the preceding part of the Triassic (Stanley, 1988; Simms, 1991). The Carnian and end-Triassic events are equal in terms of recovery rates of the marine biota: Van Valen (1985) counted, from Sepkoski's data set, 49 new families of marine animals in the Norian and Rhaetian, and 50 new families in the Hettangian and Sinemurian (earliest Jurassic), two approximately equal time spans, according to most time scales.

Stanley (1988) documents the diversification of various reef-living organisms after both the Carnian and the end-Triassic events, and he shows similar rates of recovery among the corals and other groups. The diversification of corals seems to have been rapid in the Norian.

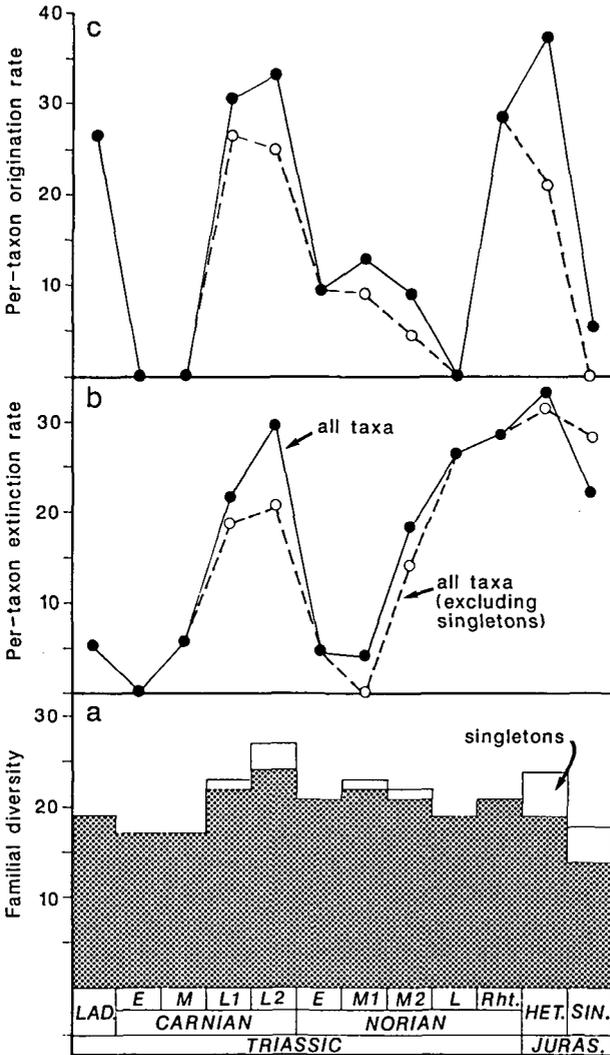
Other marine invertebrates show slower rates of recovery after both events, but again the Carnian event usually turns out to have been as important as the end-Triassic event. Indeed, for echinoderms, the Carnian event was more significant. Smith (1990) shows a steady recovery in diversity of echinoids after their crash during the Carnian, with no significant change in the rate of recovery during the Norian and earliest Jurassic. Simms (1991), similarly, records sluggish diversification rates for crinoids throughout the Norian to Sinemurian interval, but with a slight upturn in the earliest Jurassic.

The Carnian event unequivocally had greater impact than the end-Triassic event among terrestrial vertebrates. In the early and middle Norian (c.10 Myr), the following groups of terrestrial tetrapods radiated, presumably as a consequence of the late Carnian extinction event (Figure 1): turtles (Proganochelyidae, Proterochersidae), crocodylomorphs (Saltoposuchidae), pterosaurs (Eudimorphodontidae, Dimorphodontidae), dinosaurs ("Ceratosauridae", Thecodontosauridae, Plateosauridae, Melanorosauridae), lepidosaurs (Sphenodontidae), and mammals (Kuehneotheriidae, Haramiyidae, Morganucodontidae).

The end-Triassic event seems to have passed almost unnoticed. It triggered, or permitted, the radiation of four small dinosaur families (Massospondylidae, Yunnanosauridae, Heterodontosauridae, "Scelidosauridae"), two families of mammal-like reptiles (Tritheledontidae, Tritylodontidae), and four singleton families (Kayentachelyidae, Orthosuchidae, Vulcanodontidae, Gephyrasauridae) during the first 10 Myr of the Jurassic (Figure 1).

In other words, the great tetrapod turnover, and radiation of modern groups

(turtles, sphenodontids, crocodylians, pterosaurs, dinosaurs, mammals) appears to have been mediated by the Carnian event, rather than by the end-Triassic extinction, as was noted by Colbert (1949, 1958), Bakker (1977), Charig (1979), Bonaparte (1982), Benton (1983, 1986a, b, 1987, 1988), Olsen and Sues (1986), Lucas (1990), and numerous others. Interestingly, there has been a tendency recently for some authors to focus more on the end-Triassic event rather than the Carnian because it is more tractable to stratigraphic testing, because it relates



**Figure 2** Global diversity (a), extinction (b), and origination (c) "rates" (measured as percentages) of terrestrial tetrapods during the Late Triassic, based upon the data in Figure 1. Per-taxon percentages are shown (i.e., rates are scaled to total diversity in each substage), but they are not scaled to time, since there is no way of assessing the real time differences between substages. Percentages are plotted separately for all families, and for all non-singleton families. Abbreviations as in Figure 1.

clearly to a major marine event, and because of possible catastrophic explanations of extinction (e.g. Olsen *et al.*, 1987, 1988).

## TESTING THE REALITY OF THE EXTINCTION

There are clearly sampling problems in all studies of extinction events. In particular, there is the problem of gaps in the fossil record that create apparent extinction events. This has been suggested as a specific explanation for the Carnian extinction peak: that the peak in extinction is an artefact of a poor fossil record in the subsequent early and middle Norian (e.g. Sepkoski and Raup, 1986, p. 11).

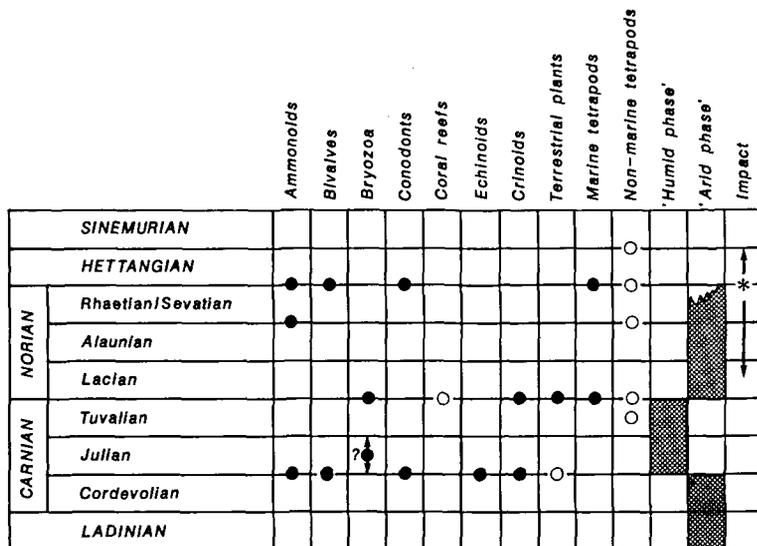
The same could be said for the Carnian tetrapod extinction peak (e.g. Olsen and Sues, 1986, p. 343), since there appears to be a gap in the record during the early Norian (e.g. Benton, 1986b, Figure 24.8). The early Norian was estimated as being only 25% complete by Benton (1986b, p. 315), according to the Simple Completeness Metric (SCM), compared to a figure of 96% complete for the late Carnian. However, the SCM is not an ideal measure of completeness since it refers only to the numbers of higher taxa represented by fossils compared to those known to span a particular time interval. It does not address the question of whether a gap is the result of poor knowledge (the usual assumption), or truly reflects an episode of low diversity globally and locally.

A low SCM could demonstrate the existence of a gap following a spurious high extinction peak, or it could document the opposite: a genuinely depauperate fauna in the aftermath of a major extinction event. Fossils could be hard to find because the animals were genuinely rare, rather than simply poorly preserved. Can one test between these two hypotheses for gaps?

Olsen and Sues (1986, p. 343) state that "early Norian vertebrate assemblages are very poorly known, and, therefore, it is difficult to place much faith in the peak of Carnian extinctions". One could attempt to counter this view by arguing that some of the families supposedly going extinct in the late Carnian (e.g. Rhynchosauridae, Kannemeyeriidae, Chiniquodontidae, Traversodontidae) contained abundant and readily fossilizable medium- to large-sized animals, which would be expected to occur as fossils if they had survived. Hence, their absence in the early Norian truly reflects their earlier extinction. However, this is not an entirely satisfactory argument.

A more precise test may be possible. Were there really so few early and middle Norian tetrapod faunas? Certainly, according to many current views (e.g. papers in Lucas and Hunt, 1989), the Chinle and Dockum Groups of the south-western United States provide extensive and detailed coverage of this time interval, as do the Stubensandstein and Burgsandstein of Germany, and possibly the Lower Elliott Formation of southern Africa. These five major formations compare with ten or so major late Carnian faunas (see, e.g., Benton, 1983b, 1986b; Olsen and Sues, 1986). That could partially account for the gap, but probably not for a decline from 96% to 25% in completeness.

A more quantified estimate was based on the data on sedimentary basins that have yielded dinosaur bones and footprints listed by Weishampel (1990). These show (Table 2) that there were 17 late Carnian faunas and 14 early Norian ones, a decline of 18%. These 14 early Norian faunas have produced fewer bones and fewer taxa than the 17 late Carnian ones, but the explanation could well be that the faunas were depauperate, rather than just badly sampled. Certainly, there is no



**Figure 3** Overview of extinction events (solid circles) and major phases of turnover (i.e. high extinction and high origination rates; open circles) of various marine and non-marine groups, based on data in Simms and Ruffell (1990) and other sources. Generalised climatic data are noted, as is the range of dates for the Manicouagan impact structure (from Olsen *et al.*, 1987).

evidence at global level for a massive decline in the number of reptile-bearing formations. This idea should be tested with more local studies on the abundance and diversity of taxa through the Carnian-Norian interval.

**Table 2** The numbers of sedimentary formations of different ages that have produced dinosaur bones or dinosaur footprints, based on Weishampel (1990). These figures are taken from his state by state listing, and include all formations dated certainly, or tentatively, by him, and by other recent authors cited in the text. "Rhaetian" faunas include those noted as "Rhaetian" or "latest Norian".

	N. America	Europe	Asia	S. America	Africa	Totals
Late Carnian	10	2	1	3	1	17
Early Norian	5	2	0	0	7	14
"Rhaetian"	2	19	1	3	0	25
Hettangian	9	8	5	3	9	34

Olsen *et al.* (1987, 1988) are carrying out such a test for the end-Triassic event. The Hettangian has never been assessed as having such a low SCM as the early Norian. Benton (1986b, p. 315) found a value of 67%, compared to 78% in the "Rhaetian" (latest Norian). Indeed, the range of well-known faunas is similar on both sides of the Triassic-Jurassic boundary: four below (British fissures, European marine Rhaetic, Los Colorados Formation, New Haven Arkose), and four above (British fissures, Upper Elliott Formation, Forest Sandstone, McCoy Brook Formation). From Weishampel's (1990) fuller listing for dinosaur skeletons and footprints, the numbers of reptiliferous formations rose from 25 globally in the latest Triassic ("Rhaetian") to 34 in the Hettangian, a rise of 36%.

Olsen *et al.* (1987, 1988) use the evidence of the absence of thecodontians and

procolophonids in the earliest Jurassic faunas to argue for the true disappearance of these groups at the end of the Triassic. An analogous argument now seems valid for the late Carnian event. If it was so unimportant, why do we not find in any of the early Norian faunas evidence of the nine non-singleton families that apparently disappeared? Does the sparseness of these early Norian faunas actually give positive evidence of a depauperate tetrapod world following a major extinction event—indeed, more depauperate than the post-“Rhaetian” world?

Smith (1990) has carried out analogous studies for the fossil record of echinoids. These suffered a massive decline during the Carnian, but this superficially matches the loss of lagerstätten deposits, and the drop could be explained by the near absence of echinoid-bearing deposits in the early and middle Norian. Smith provides four tests that suggest that much of the decline is real:

(1) The decline in diversity continues after the highly fossiliferous Cassian Beds, and does not fall to zero immediately.

(2) Lazarus taxa (those that span an interval, but are unknown within that interval) are less common than would be expected if the low-diversity interval were simply poorly sampled.

(3) Echinoid taxa represented only by spines are rarer in the low-diversity interval than would be expected if it were a time of high echinoid diversity, but poor preservation.

(4) The patterns of diversification and extinction of echinoids based on spine data and whole-test data are comparable, and do not suggest dramatically different levels of sampling (spines only should dominate in intervals of poor preservation).

These studies on gaps in the record and the apparent vs. real magnitudes of the Late Triassic events require further work for both the tetrapods and the marine invertebrate record as a whole.

## GEOGRAPHIC EXTENT OF THE END-CARNIAN EVENT

It has been suggested that the Carnian extinctions may only have been a European phenomenon, without clear parallels elsewhere. Stanley (1988) and Simms and Ruffell (1989, 1990) have argued, on the other hand, that most of the marine extinctions appear to have been global in extent. In addition, there appear to have been major physical changes on the Earth at this time which supply possible mechanisms for extinction.

Simms and Ruffell (1989, 1990) relate the extinctions to a middle and late Carnian humid phase for which evidence has been found in Europe, the Middle East, and in the eastern and southwestern United States. They argue that the humid phase affected the subtropical arid belt of Triassic times to 50° north of the Equator, and this area returned to more arid conditions at the Carnian-Norian boundary. Further, Veevers (1989) has pointed out a major stratigraphic and magmatic episode at this time (230±5 Myr ago) when the continental fragments that made up Pangaea finally coalesced, and were then subjected to major rifting prior to their subsequent dispersal. Veevers (1989) also argued that increased levels of vulcanism at this time led to a build-up of CO<sub>2</sub> in the atmosphere, and the development of a greenhouse climate. These physical changes could clearly have had global effects.

Stanley (1988) argued that there was a major faunal turnover in reefs in the

middle and late Carnian, and that this was worldwide in extent: his main examples come from Alpine Europe and Nevada, U.S.A., but he used data from coral localities spanning the whole of the Late Triassic equatorial Tethys, lying in present-day Europe (from England to Greece), Asia (from Turkey to China), Malaysia, and the west coast of North and South America. The replacement of essentially Permian-style reefs of the Anisian to early Carnian by new scleractinian coral-dominated reefs occurred worldwide, and is detectable at familial level, but particularly at generic and specific levels. Detailed studies of Triassic bryozoans (Schäfer and Fois, 1987) also confirm that the greatest loss of species occurred in the Carnian, and that the losses were worldwide in extent.

Some findings point to Carnian extinctions that may have been restricted to Europe. For example, extinctions among scallops and crinoids have so far been documented mainly in Europe (e.g. Johnson and Simms, 1989), while Newton *et al.* (1987) found that some of the bivalves that supposedly disappeared during the Carnian in Europe survived into the Norian of Oregon, U.S.A. However, these results reflect areas where sampling has been done, and such efforts must be extended worldwide in order to achieve a fuller picture.

Terrestrial events, at least, seem to have been global in extent: the late Carnian faunas span from North America and South America to Europe, North Africa, and India (Table 2). Many of their typical faunal elements disappeared during the late Carnian, and are not seen in the early Norian faunas of North America, Europe, and southern Africa. Early Norian tetrapods are not yet known from South America or India.

The balance of evidence for the marine and terrestrial realms suggests an extinction event in the middle to late Carnian of global extent, but with some local effects. It would be incorrect to associate the Carnian event with those in the Pliensbachian and Tithonian, which appear to have affected European marine invertebrate faunas only (Hallam, 1986).

## CONCLUSIONS

There seems to be little question now about the crucial role of the global extinction event during the late Carnian in reorganising terrestrial vertebrate faunas. New data, presented here, point to a loss of nine diverse families of tetrapods (13, including singletons) during the late Carnian, compared to six in the latest Triassic. Per-taxon extinction percentages are 38% (or 48%, including singletons) for the late Carnian, and 29% for the end-Triassic. At species level, the global impact of the late Carnian event seems to have been even more striking: many of those families of tetrapods disappearing were relatively diverse, averaging four species each, while the six families that disappeared at the end of the Triassic had a mean terminal diversity of 1.3 species each. Indeed, these six last families suffered more dramatic species-level declines in the late Carnian, and their final disappearance was very much a whimper.

It has been suggested that the Carnian events were not real extinctions, but the result of a patchy fossil record. In the marine realm, the diversity of taxa affected suggests a real extinction event, and studies of echinoid species distributions support the reality of the event. The evidence for terrestrial faunas suggests that post-Carnian diversity was certainly less, but probably the result of depauperate faunas, not entirely poor preservation or poor collecting. There are nearly as many

early Norian reptile-bearing formations worldwide as in the late Carnian: each simply yields a low-diversity fauna when compared to late Carnian examples.

Another critical suggestion has been that the Carnian event was merely a local, possibly Alpine, phenomenon. However, again, it was clearly global for the vertebrates, and for many marine groups, too. In particular, a revolution in reef structure took place worldwide at this time, and the event had a more significant effect on echinoderms than did the end-Triassic event.

The question of the timing of the Carnian event is intriguing. It appears to have occurred in the mid Carnian for most marine invertebrates, including ammonoids, bryozoans (?), conodonts, echinoids, and certain crinoids (Figure 3; Benton, 1986a; Stanley, 1988; Johnson and Simms, 1989; Simms and Ruffell, 1989, 1990; Smith, 1990; Simms, 1991), but possibly in the late Carnian for reef organisms (Stanley, 1988). Initially, Benton (1983) dated the earlier tetrapod event as mid-Norian on the basis of then-accepted correlations of the relevant deposits. Redating of these led to the view that the correct date was late Carnian (Olsen and Sues, 1986). Lucas (1990) and Hunt and Lucas (1991a, b) now argue for a split in timing of the event, with part occurring in the early part of the late Carnian, and part at the end of the Carnian. These assertions test the limits of our current stratigraphic knowledge.

Further work must focus on (1) documenting extinction rates throughout the Late Triassic at various taxic levels; (2) further assessing the reality of the Carnian event(s); (3) testing the sampling argument; (4) testing the geographic extent of the event; and, (5) testing its timing.

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