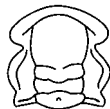


How catastrophic was the end-Triassic mass extinction?

ANTHONY HALLAM

LETHAIA



Hallam, A. 2002 06 14: How catastrophic was the end-Triassic mass extinction? *Lethaia*, Vol. 35, pp. 147–157. Oslo. ISSN 0024-1164.

A review of marine and terrestrial animal and plant fossils fails to reveal convincing evidence of a global catastrophe at the Triassic–Jurassic boundary, although this time marked the final disappearance of ceratite ammonites and conodonts, together with the extinction of most calcareous demosponges; important groups of bivalves and brachiopods went extinct. Because of facies problems, however, there is no stratigraphic section that reveals a clear-cut disappearance over a short distance. Other marine animal groups except perhaps the radiolarians fail to reveal a notable extinction of global extent immediately across the boundary. On the other hand, there was a substantially higher extinction rate among marine animals in the Rhaetian as compared with the previous stage. On the land, the record is equivocal. Dramatic changes across the T–J boundary have been claimed for plants in particular areas, such as eastern North America and East Greenland, but only gradual change has been recognized elsewhere. Similarly, claims of a T–J boundary vertebrate mass extinction have not been supported by others. For the Rhaetian as a whole, however, the turnover rate of reptiles was high. Although much remains to be learned, it seems evident that the fossil record of the latest Triassic is more consistent with a gradual scenario extended over time than a ‘geologically instantaneous’ impact catastrophe. □ *Catastrophe, mass extinction, Triassic–Jurassic boundary*

A. Hallam (A.Hallam@bham.ac.uk), School of Earth Sciences, University of Birmingham, Birmingham B15 2TT, UK; 19th November 2001, revised 21st February 2002.

Since the pioneering studies of Newell (1967), and the statistical work of Raup & Sepkoski (1982), the end of the Triassic has been generally accepted as one of the five big mass extinction events in the Phanerozoic marine fossil record. It remains, however, probably the least studied, for a number of reasons. The number of easily correlated, complete or near-complete richly fossiliferous sections, either in marine or continental facies, is very limited. Many of the fossils belong to groups that are strongly facies-bound, but there has been no comprehensive evaluation of the extent to which biotic changes across the Triassic–Jurassic boundary are influenced by regional rather than global environmental change. Contradictory claims have been made about the extent to which mass extinction in the marine is evident also in the continental record as represented by vertebrates and plants. In consequence of such problems, it is difficult as yet to evaluate the extent to which change at the system boundary was catastrophic or gradual, which clearly has an important bearing on interpretation of the underlying cause or causes.

Despite these shortcomings the time is appropriate for an evaluation of what is known at present, both by reviewing relevant existing data and by presenting

some new information from a study of marine bivalves in southern Europe. This should at least help in pointing the way to future research. For most biotic groups the stratigraphic and taxonomic precision is no more refined than stage and family level, using the database of Benton (1993). This is more comprehensive than that of Sepkoski, on which Raup & Sepkoski (1982) relied, in including data from continental organisms, as well as being more up-to-date and reliable. Despite the restriction in stratigraphic precision, it is helpful to evaluate the respective importance of the Norian and Rhaetian as times when particular groups finally disappeared, though obviously the extent to which they went extinct at the end or within the stages has not been recorded in the Benton compilation. Before the pattern of temporal change in the biota is examined it is necessary to say something about the Rhaetian, as the final stage of the Triassic.

Correlation of the Rhaetian

The Rhaetian as the topmost Triassic stage has had a

Ammonite zones	Lithostratigraphic units
Choristoceras marshi	Eiberg member
Vandaitea sturzenbaumi	Hochalm member
Sagenites reticulatus	Hauptdolomit
Sagenites quinquepunctatus	

Fig. 1. Stratigraphic location of the Kössen Formation, based on Dagens & Dagens (1994) and Golebiowski (1990).

rather chequered history. The term derives from the work of Gümbel in the mid-19th century on the Kössen beds of the Northern Calcareous Alps of Austria and Bavaria. Since they contain the bivalve *Rhaetavicula contorta*, which appears to be confined to what has since been termed the Rhaetian stage, this bivalve has been used for correlation with marine deposits elsewhere in the world which lack ammonites, such as occur in the well-studied deposits of northwest Europe. In the 1970s and 1980s, there arose a tendency to relegate the Rhaetian to a substage of the Norian, following the work of Tozer (1979, 1988), who pointed out that as a stage the Rhaetian could contain no more than one ammonite zone, that of *Choristoceras marshi*. Subsequently, opinion has swung in favour of retaining it as a stage, with more than one ammonite zone, now that more is known about the ammonites in the Zlambach Formation, another terminal Triassic group of deposits in Austria (Krystyn 1987).

While the Rhaetian has now been accepted as a stage, defined by ammonites, three differing opinions have been put forward as to where to locate the type deposits, the Kössen beds, within it. The stage boundary has been placed (1) at the base of the Quinquepunctatus (or Cordilleranus) Zone, (2) at the base of the Reticulatus (or Amoenum) Zone, or (3) the base of the Sturzenbaumi Zone. As indicated in Fig. 1, the first definition places the base of the Rhaetian within the Hauptdolomit, a widely occurring unit in the Northern Calcareous Alps which had hitherto been attributed solely to the Norian, and the third to within the Kössen Formation. Dagens & Dagens (1994) prefer the second definition, for several reasons. It corresponds best to what Gümbel (1859) had originally meant by Rhaetic and with the disappearance of a number of ammonite groups. The base of the Reticulatus Zone also marks the extinction of the important bivalve *Monotis* and the appearance of the conodont *Misikella*, whose range indeed then corresponds with the range of the Rhaetian. For these and other reasons, as presented in that review, the definition of Dagens & Dagens (1994) is accepted here.

For non-marine successions, resort has to be made

to palynology, utilizing information from shallow, nearshore marine deposits to establish correlation with ammonite-containing successions. Schuurmann (1979) proposed a *Rhaetopollis germanicus* Zone, which corresponded with the Rhaetian, identified by a whole group of species. This has been challenged by Fisher & Dunay (1981), on the basis of their researches in western Europe and the Canadian Arctic, who conclude that there is no firm palynological evidence to confine the *R. germanicus* Zone to the Rhaetian. The problem is that there appears to be a gradual turnover of taxa in these regions, as also in central Europe. The most promising genus to use for the T–J boundary is the highly distinctive *Cerebropollenites*, but even here, while it seems to appear at the base of the Jurassic, it increases in abundance through the Hettangian and earliest Sinemurian. Similarly, *Corollina* occurs in great abundance at the base of the Jurassic, but occurs commonly also in the Rhaetian (e.g. Hallam *et al.* 2000).

In the absence of ammonites, palynological correlation is important in marine strata of the Southern Alps of Lombardy and the Apennines. Within the Lombardy Basin there is an enormously expanded succession. Overlying the Dolomia Principale, which seems to be an equivalent to the Hauptdolomit of the Northern Calcareous Alps, are two major units, in succession the Riva di Solto Shale and the Zu Limestone (Jadoul *et al.* 1994), which collectively bear a close resemblance to the Kössen Formation. The Italian workers put the Riva di Solto Shale and the basal part of the Zu Limestone in the Upper Norian, but in the absence of ammonites and conodonts the evidence is not convincing and all these rocks could just as well be Lower Rhaetian. The T–J boundary has traditionally been placed directly above or within the overlying Conchodon Dolomite, a unit ranging in thickness from 100 to over 250 m thick, but this interpretation has been challenged on palynological grounds by Cirilli *et al.* (2000). In the top unit of the Zu Limestone (Zu 4) is found *Cerebropollenites macroverrucosus*, which is taken as marking the base of the Jurassic. In northern Europe, however, this

species is taken as making the base of the Sinemurian (J. B. Riding, pers. comm.). Benthic foraminifera are abundant in some of the strata, but their stratigraphic value is limited because of changes in response to varying facies. *Triasina* is generally considered a latest Triassic genus, though it occurs in the Upper Norian as well as the Rhaetian. Its disappearance marks the start of the Jurassic, which is not marked by the introduction of new taxa, either in the Southern Alps or Apennines (G. Ciarapica, pers. comm.).

New research (Palfy *et al.* 2001) suggests that a negative anomaly in the carbon isotope curve may prove a useful marker, as in various regions in Europe, Greenland and North America, but it should be used with caution in the absence of corroborative fossils. Use of magnetostratigraphy for correlation of marine and continental sections is at an early stage and has not yet revealed significant results, except that the T–J boundary in both southwest England and the Newark Basin of eastern North America occurs within a predominantly normal interval (Hounslow *et al.* 2001). The T–J boundary is now dated at 200 m.y. (Palfy *et al.* 2000).

Temporal change in major organic groups

The amount of precision with which information on temporal changes can be presented varies considerably with different groups. Partly this is a result of a dependence on appropriate facies being present in given sections, partly a lack of information. Nowhere can the precision match that which has now been determined for some Cretaceous–Tertiary or Permian–Triassic boundary sections. In a number of cases it is no better than family to the nearest stage, using the Benton (1993) compilation. In this case, it is useful to specify the number of family extinctions in the Rhaetian, compared with those in the Norian, to see if the rate of extinction increased during or at the end of the Rhaetian. The Benton data extend ranges to the end of the stage, so that there is no way of distinguishing between groups that died out early in, as opposed to at the end of the stage. Furthermore, in evaluating the significance of numbers of family extinctions within the two stages, it has to be borne in mind that the Norian is likely to have lasted much longer than the Rhaetian. A recent much quoted radiometric time-scale is that of Gradstein *et al.* (1994), who attribute 11 m.y. to the Norian and 4 to the Rhaetian. Thus the extinction of, say, three families within the Rhaetian is likely to be of greater significance than in the more enduring Norian. On

the basis of cyclostratigraphic studies in the Newark Basin, in the northeastern United States, Palfy (in press) has estimated a duration of only 2 m.y. for the Rhaetian.

Only groups with a relatively good fossil record, together with vertebrates, because of their importance, are considered.

Bivalves

Bivalves are the most abundant and diverse of macroinvertebrates in early Mesozoic shallow marine facies and their stratigraphic distribution across the T–J boundary is relatively well known. At family level they were little affected by the end-Triassic extinction, with only two families out of 52 (the Myophoridae and Mysidiellidae) going extinct (Benton 1993). At generic level, there was a much higher extinction rate, as established by Hallam (1981). This work was based on use of the Treatise on Invertebrate Paleontology, which rarely distinguished Rhaetian from Norian, and it was normal anyway at this time to treat the Rhaetian as a substage of the Norian. Therefore, there was no indication of how sharp the end-Triassic extinction event was. In an attempt to improve on this situation, a study has been made of the Rhaetian bivalve faunas of the Northern Calcareous Alps of Austria and Bavaria and the Southern Alps of Lombardy, which are the richest in diversity not only in Europe but in the rest of the world. Whereas the Rhaetian bivalve faunas of northwest Europe are well known, they are of low diversity because they lived in an epicontinental sea of abnormally low salinity (Hallam & El Shaarawy 1982) and hence are not suitable for this kind of analysis.

The analysis was based on examinations of collections in the Bayerisches Staatsammlung, Munich, the Natural History Museum and University Geological Institute in Vienna, and the Natural History Museum in Bergamo and the Earth Sciences Department of the University of Milan. Formerly there were rich collections, described by Stoppani, in the Natural History Museum in Milan, but these were destroyed during bombing in the Second World War. Fortunately, the Bergamo collection is a good one. The fossils came from the Kössen and Zlambach Formations in Austria and Bavaria and the Zu Limestone in Lombardy. In the collections, the bivalves have been given a variety of species names, dating back to the 19th century, and involve taxonomic splitting to a degree unacceptable today (Hallam 1976). Thus, it is difficult to determine the reliability of many species of common genera such as *Chlamys*, *Plagiostoma*, *Palaocardita* and *Modiolus*. In the absence of modern, statistically based work taking full account of variation, the species attribu-

Table 1. List of the genera found in the Alpine collections referred to in the text, listed in order of major taxonomic groupings within the bivalves. K = Kössen Formation, Zl = Zlambach Formation, Zu = Zu Limestone. Asterisks signify those genera that failed to survive the Triassic.

Palaeonucula	K, Zu
Nuculana	K, Zu
Parallelodon	K, Zu
Modiolus	K, Zu
Pinna	K, Zu
* Rhaetavicula	K, Zu
Gervillea	K, Zu
Bakevellia	K
* Hoernesia	K
* Cassianella	K, Zu, Zl
* Pseudomyoconcha	Zu
Oxytoma	K
Chlamys	K, Zu
Entolium	Zu
Atreta	K, Zu
Lopha	K, Zu, Zl
Liostrea	K, Zu
Inoperna	K, Zu
Placunopsis	K, Zu
Plagiostoma	K, Zu
Trigonia	Zl
* Myophoria	K, Zu
* Neoschizodus	Zu
* Unionites	Zu
Isocyprina	K, Zu
* Palaeocardita	K, Zu
Protocardia	K, Zu
* Myophoriopsis	K, Zu
* Megalodon	K, Zu
* Triamegalodon	Zu
* Conchodon	K, Zu
Pleuromya	K, Zu
Homomya	K, Zu
Pholadomya	K
? Cercomya	Zu

tions are not considered useable, either for determining diversity levels within the Triassic or for comparing species across the T–J boundary. Field observations in the Kendelbach graben in Austria and the Albenza region of Lombardy support what has been reported in the literature, that the distribution of bivalves is not uniform throughout either the Kössen or the Zu (the Zlambach Formation has only relatively sparse bivalves and is poorly exposed today). In the Kössen Formation, bivalves are commoner in the lower part, what has been traditionally termed Swabian facies, following the pioneer work of Suess and Mojsisovics (1868), which is succeeded by the relatively brachiopod-rich and bivalve-poor Carpathian facies (Golebiowski 1990). The facies distinction is based on fossils rather than on rocks, which are uniformly thin microsparitic limestone and shale alternations. Similarly, it is only in the lower and middle parts of the Zu Limestone that abundant bivalves occur. This point is made both by Allasinaz (1992) and McRoberts *et al.* (1995), who attribute the overlying Conchodon Dolomite to the topmost

Triassic. However, despite its name this last formation is now attributed on palynological grounds to the basal Jurassic, as noted earlier, and the name is based on an old misattribution of megalodontids to it (Lakew 1990).

With regard to bivalves, the Alpine sections are unsuitable for analysing change across the T–J boundary because the basal Jurassic is generally poor in this group as a result of significant facies changes reflecting considerable tectonic subsidence (Allasinaz 1992). The only Hettangian bivalve fauna of any quality is the silicified one from the Sedrina Limestone of Lombardy (Gaetani 1970). This, however, only contains 15 species belonging to 12 genera, a much less diverse fauna than known in northwest Europe.

Table 1 presents a list of genera found during examination of the collections. It can only be considered as representative of the commoner taxa, because a slightly greater diversity has been recorded in the literature. However, this is not necessarily to be regarded as a handicap, because the collections can be considered to be representative of forms that were still surviving abundantly into the Rhaetian. Their disappearance by the end of the period is therefore a biologically significant event. The Kössen and Zu faunas are extremely similar to each other, and collectively they must be considered a good sample of Rhaetian full marine faunas. The proportion going extinct by the end of the Triassic is 31%, a figure which is identical to that determined for the Norian globally by Hallam (1981), once corrections have been made to Table 5 in that paper, which wrongly restricts a small number of genera to the Triassic rather than extending them into the Jurassic. This striking result strongly suggests that those Triassic bivalve genera that survived into the Norian persisted also into the Rhaetian, which is consistent with but does not firmly establish a catastrophic scenario. As mentioned earlier, this is because no sharp change at the system boundary is observed because of progressive disappearance through the facies change.

It is noteworthy that no very large bivalves survived the end-Triassic extinction. This is most evident for the megalodontids, dicerocarditids and wallowaconchids. The largest of these seen in the collections examined was *Conchodon*, with a maximum dimension of 34 cm. The largest *Megalodon* seen was 17 cm. The distinctive and common *Gervillea inflata*, unusually large for early Mesozoic representatives of the genus, measured 13 cm. In marked contrast, all the Hettangian bivalves described by Gaetani (1970) are small in size, even for their genus. The largest *Liostrea* in the Kössen and Zu collections was 8.6 cm in maximum dimension, much larger than the abundant Lower Hettangian oysters of northwest Europe.

Brachiopods

According to Benton (1993), of 19 families 5 went extinct by the end of the Rhaetian, which all belong to the Spiriferida (Diplospirellidae, Nucleospiridae, Neoretziidae, Thecospiridae and Bactrynidae). In comparison, only two families (Athyrisinidae and Thecospirellidae) went extinct by the end of the longer-lasting Norian.

Pearson (1977) has made a detailed study of the Rhaetian brachiopods of Europe, all of which are confined to the fully marine deposits of the Alpine–Carpathian region. Of 13 genera, only 5 extend into the Jurassic but only *Metzeliopsis* and *Piarorhynchia* are widespread. Such characteristic Alpine Rhaetian genera as the terebratulid *Rhaetina*, the spiriferid *Zugmayerella* and rhynchonellid *Fissirhynchia* are uncommon and only very localized in the Liassic. *Oxycolpella*, a striking and not uncommon form in the Alps, is one of the youngest athyrid genera, and failed to survive the boundary. The T–J boundary marks the effective end of the Athyriidae, Retziidae and the terebratulid family Dielasmatidae.

Brachiopods, although subordinate in abundance and diversity to the bivalves, are among the commonest macroinvertebrates in the Kössen and Zu, though only in the so-called Carpathian facies. As with the bivalves, although no sharp cut-off can be observed in particular sections, their distribution is consistent with a catastrophic mass extinction of important groups at the T–J boundary. Among those species that disappeared, some are very large for brachiopods, e.g. *Oxycolpella oxycolpos*, maximum dimension 4.7 cm, *Rhaetina pyriformis* 3.7 cm. In contrast, the Hettangian brachiopods described by Gaetani (1970) are all small, with a maximum dimension (*Lobothyris ovattissimaeformis*) of 2 cm; the two rhynchonellid species are much smaller. Similarly, Hettangian brachiopods in the fully marine Hettangian of northwest Europe are all small.

Ammonites

The T–J boundary has been generally accepted as marking the most important extinction event within ammonite history, with a major group, the Ceratitina, disappearing and hardly any genera surviving (Tozer 1981). According to the Benton (1993) compilation, 17 families went extinct at the end of the Rhaetian, compared with 8 at the end of the Norian. A closer examination of Rhaetian ammonite faunas rather complicates the picture, however. Unlike what might be expected from the above, diversity is quite low in the Rhaetian, and ammonites not generally common. The most obvious change across the T–J boundary is

the replacement of the last Triassic survivor *Choristoceras* by the earliest Jurassic ammonite genus *Psiloceras*. It should be noted, however, that a newly proposed definition of the boundary in Nevada lowers it slightly to the first appearance of *Psiloceras pacificum*, which occurs slightly below the last *Choristoceras* (Taylor *et al.* 2000). Many notable extinctions took place either late in, or at the end of, the Norian, such as before the Quinquepunctatus Zone (disappearance of Distichitidae, Clydonitidae, Thetidae, etc.) and Reticulatus Zone (Metasibiridae, Tibetidae, Arpaditidae, etc.) (Dagys & Dagys 1994). Other ceratites that survived into the Rhaetian did so neither in great numbers nor diversity. This picture is confirmed by a close scrutiny of Fig. 2 of Tozer (1981). The impression given by the literature is of a greatly increased extinction rate starting in the middle or late Norian, with the T–J event making only a final demise. As regards size, giant ammonites such as *Pinacoceras* (maximum dimension in a specimen displayed in the Vienna Natural History Museum 60 cm), which had disappeared before the Rhaetian, are not matched until the Sinemurian with *Coroniceras*.

Gastropods

Though one of the commoner macroinvertebrate groups, they nevertheless occur only sparsely and sporadically in the Alpine, as in other contemporary Rhaetian deposits. Recourse must therefore be had to the Benton (1993) compilation. Whereas 35 families continue into the Jurassic, none went extinct by the end of the Rhaetian, whereas 7 did so by the end of the Norian, including the notable Palaeozoic survivors – the Murchisoniidae. Thus a broad brush scrutiny at the gastropod record does not support a mass extinction at the T–J boundary.

Echinoderms

Echinoderms only occur very sporadically in the Alpine Rhaetian and nothing can be said about their extinction. The Benton (1993) compilation shows that one crinoid family, the Somphocrinidae, becomes extinct at the end of the Rhaetian, one at the end of the Norian and one, the Pentacrinitidae, persists into the Jurassic. Four families of asteroids go through and none go extinct, while among the echinoids, 34 families continue into the Jurassic and none go extinct.

Corals and sponges

There was a substantial diversity increase of scleractinian corals in the Norian of the Northern Calcareous

Alps, following the establishment of this group as major reef components in the Carnian, a phenomenon quite possibly bound up with the establishment of a symbiotic relationship with zooxanthellae (Stanley & Swart 1995). At the end of the Triassic, however, there was a dramatic disappearance of reef corals and sponges in the Northern Calcareous Alps, which appears to reflect mass extinction on a global scale. No clear distinction has been made in the field between Norian and Rhaetian reef limestones, so no data are available on possible Norian extinctions. Nowhere else in the world is there known such a rich Upper Triassic reef fauna (Stanley 1988). The sudden disappearance of many reef-building corals and sponges in other parts of the world, such as Asia, North and South America, suggests a global phenomenon (G.D. Stanley, pers. comm.). A compilation of Phanerozoic global reef data indicates a clear restriction of reef development after the close of the Triassic, to a zone about 30°N (Kiessling 2001). According to the Benton (1993) compilation, 12 families of corals survived the extinction while 3 went extinct in the Rhaetian. At generic level the extinction was much more pronounced for, according to Beauvais (1984), of 50 scleractinian genera recognized globally in the Upper Triassic, only 11 survived into the Jurassic. The extinction had a much more severe effect on the calcareous demosponges known as sphinctozooids, with only 2 families surviving the Rhaetian while 16 went extinct (Benton 1993). The Sphinctozoa are essentially a Permian holdover group, like the conodonts. The spongiomorph hydrozoans are another reef-associated group that went extinct at the end of the Triassic.

Foraminifera, ostracods and radiolaria

Apart from *Triasina* and some related taxa, there appear to be no notable disappearances at the T–J boundary among the Foraminifera. According to Benton (1993), 38 families survive the boundary and only 3 go extinct (Milioliporidae, Duostaminidae and Asymmetrinidae), whereas 2 go extinct by the end of the Norian. A major episode of mass extinction was claimed for the ostracods by Whatley (1988), characterized by the virtual disappearance of the Palaeocopida and severe reductions in the Cytheracea and Bairdacea. However, consultation of Whatley's contribution to the Benton (1993) volume indicates that all 12 Rhaetian families continue into the Jurassic, and that only one palaeocopid family survives the Palaeozoic, going extinct after the Lower Triassic. Furthermore, the changes at family level among the Bairdacea and Cytheracea seem insignificant. This throws into

serious doubt Whatley's earlier claims of mass extinction.

El Shaarawy (1981) undertook an interesting study comparing the foraminiferal and ostracod faunas of the Rhaetian of the Northern Calcareous Alps (Kössen and Zlambach Formations) and Rhaetian and Lower Liassic of England and Wales. Rich and diverse faunas occur only in the Rhaetian of the former and Liassic of the latter region. He found that many of the species in the Kössen and Zlambach Formations occur also in the Hettangian of England and Wales, but not in the latest Triassic marginal marine Penarth Group, having evidently migrated with the marine transgression into northwest Europe. Taking account of data from both regions, he estimated an end-Triassic species extinction of 21% for the forams and 23% for the ostracods.

As regards radiolarians, the work of Carter, in Tipper *et al.* (1994), on the faunas in the Queen Charlotte Islands of British Columbia indicates a diverse assemblage within the topmost Triassic, with 35 genera recognized, being followed by a low diversity Hettangian assemblage with only a few genera. That this major end-Triassic extinction event is truly global is strongly suggested by comparable patterns in the western Pacific (Hori 1992) and the Tethys (Tekin 1999).

Vertebrates including conodonts

With regard to marine vertebrates, no claims have been made for an extinction event among the fish, and indeed consultation of Benton (1993) shows that of 12 osteichthyan families living at the end of the Triassic, none went extinct at the system boundary. In contrast, conodonts finally went extinct, but the event cannot be regarded as dramatic, because there had been a progressive decline in diversity through the Triassic, with four families at the start of the period, two in the middle and only one family, the Gondolellidae, in the late Triassic. While Mostler *et al.* (1978) claim no fewer than 10 genera in the early part of the Kössen Formation, only 5 survived until the marshi zone and only one, *Misikella*, lasted until the end of the period. The diversity at this time in British Columbia was only slightly higher. The conodonts can hardly, therefore, be considered to have suffered a mass extinction at the T–J boundary.

Continental vertebrates in the form of reptiles present a rather confused picture at present, which no doubt reflects at least in part the poor quality of the record. Whereas Olsen *et al.* (1987, 1990), on the basis of data from a study of both skeletons and footprints in the Newark Supergroup, have made a strong claim for an end-Triassic mass extinction event, this has been challenged by Benton (1994), Weems (1992),

Lucas (1994) and Cuny (1995). Benton and Lucas point out that Norian–Rhaetian tetrapod skeletal remains are almost absent from the Newark deposits, and Lucas also remarks that there is no place where Rhaetian and Hettangian tetrapod faunas are clearly superposed. Cuny (1995) argues that the main changes recognized in France are a consequence of the Rhaetian transgression. On the other hand, the Benton (1993) compilation indicates a high T–J turnover of reptiles at family level: 12 families survived, but 10 went extinct within the Rhaetian, compared with 4 within the Norian. The within- or end-Rhaetian extinction affected both terrestrial and aquatic forms, and include such important groups as phytosaurs, ornithosuchids and thecodontosaurs. Further advances in this field of research are most likely to come from the study of microvertebrate remains, e.g. Curtis & Padian (1999).

Before turning to the terrestrial plant record, it is worth recording summary data from Benton (1993) for all animal groups considered, including, besides those mentioned above, the coleoids and nautiloids. The total number of families passing from the Triassic to the Jurassic is 257, 61 of which became extinct within or at the end of the Rhaetian, the corresponding figure for the Norian being 32. Allowing for the relative durations of the two stages, this suggests a much increased rate of extinction for the Rhaetian.

Plants

The terrestrial record is one of macroplants on the one hand and pollen and spores on the other. The best known macroplant record is that of East Greenland, where it has been established for many years that the Rhaetian Lepidopteris and Hettangian Thaumatopteris macrofloral zones are quite distinct from each other, with very few taxa in common (Pedersen & Lund 1980). These zones are also distinguishable in northern Europe (Scania), but the situation in central Europe is apparently different. Frankonia, in north-eastern Bavaria, is one of the few European regions in which both terrestrial and marine facies continue from the Upper Triassic into the basal Jurassic. According to Kelber (1998), it is correct to refer to the contained flora as a Rhaeto-Liassic flora, with no indication of a mass extinction event. A similar conclusion is drawn for North America by Ash (1986).

There is similar conflicting evidence from palynology. Unlike the macroplants, the pollen and spores across the T–J boundary in Greenland have many species in common, suggesting to Pedersen & Lund (1980) that some indistinguishable palynomorphs have been produced by different macrofossil plants, which implies that palynologists are likely to under-

estimate the degree of floral turnover at a given boundary. It is therefore noteworthy that although the change in pollen and spores through the Late Triassic to Early Jurassic interval in Europe is not especially marked (Lund 1977; Fisher & Dunay 1981; Karle 1984), the biggest ‘species’ turnover takes place exactly at the T–J boundary (Visscher & Brugman 1981; Traverse 1988). No mass extinction is evident, however, but such an event is claimed by Fowell & Olson (1993) in the Newark Supergroup of eastern North America, with a diverse assemblage of monosulcates and bisaccates being sharply replaced by *Corollina*-dominated palynofloras. A pronounced palynofloral turnover is also recorded from the Sverdrup Basin of Arctic Canada (Embry & Suneby 1994). On the other hand, the Arctic record of northern Siberia appears to show no abrupt change across the T–J boundary (Sarjeant *et al.* 1992: table 13.5). The only other part of the world where there is a well-described record is Australia, where the greatest change in the whole Mesozoic record takes place in what the authors consider without ammonite control as middle Hettangian (Helby *et al.* 1987). This is marked by a massive increase, to dominance, of *Corollina*. However, *Corollina* is also the dominant pollen in what are undoubtedly Rhaetian deposits in southern Tibet, which in early Mesozoic times was located much closer to Australia (Hallam *et al.* 2000). Therefore Helby *et al.*’s Hettangian event could easily mark the T–J boundary, or even a slightly older horizon.

There thus remains considerable uncertainty about the amount and geographic extent of any mass extinction among terrestrial plants, and the evidence cannot be said at present to support an event of global extent. Any suggestion that the extinction appears most pronounced in high palaeolatitudes (Greenland, Arctic Canada, Australia) is not supported by the data from northern Siberia, nor from the claims for a major extinction event in the lower latitude Newark Basin of the eastern USA.

Dinoflagellates

This planktonic group of marine unicellular algae has a fossil record confined to resistant resting cysts. The European record, at least, indicates a marked increase in extinctions at the T–J boundary, with 6 of the 8 recorded taxa having range tops at that boundary (Riding, *in* Hallam 1995). Because the cysts are benthic in occurrence, this change need not signify any change in the plankton.

Table 2 presents in summary form what is currently known about the fossil groups discussed above. It should be apparent from this that there remains a great deal of uncertainty about the global extent and

Table 2. Mode of mass extinction in various groups.

Group	Mass extinction	
	C	E
Bivalves	Probably	
Brachiopods	Probably	
Ammonites		✓
Gastropods		Not recognized
Echinoderms		Not recognized
Reef biota	Probably	
Corals		
Sponges	Probably	
Foraminifera		Not recognised
Ostracods		Not recognised
Radiolaria	Probably	
Conodonts		✓
Land vertebrates		✓
Land plants	Regional	
Dinoflagellates	Regional	

C = confined to Triassic–Jurassic boundary. E = extended through Rhaetian.

duration of the end-Triassic mass extinction event, for those groups that seem to have been affected. Thus the claim by Palfy *et al.* (2000), that the end-Triassic biotic crisis on land preceded that in the sea by at least several hundred thousand years, is over optimistic. The evidence at present is not good enough to justify such a statement. It is generally apparent in a broader context, however, that the Rhaetian was a time of increased extinction rate relative to the preceding Triassic stage.

Relationship of biotic to environmental change

Even amongst those groups for which T–J boundary mass extinction is cited in Table 2 as probable, namely the bivalves, brachiopods, radiolarians and reef biota, facies changes related to regional tectonics obscure the recognition of global events. McRoberts *et al.* (1995) acknowledged this problem for the Lombardy Alps, attributing the progressive disappearance of bivalves up the Triassic succession to shallowing culminating in the Conchodon Dolomite, which however is now considered to be early Hettangian rather than enveloping the T–J boundary, as noted earlier. More generally in the Alps, the severe reduction in diversity of bivalves in the early Hettangian is primarily related to the advent of deeper water facies (in the Lombardy Alps post-Conchodon Dolomite) related partly to a pronounced eustatic sea-level rise and partly to tectonic collapse anticipating the formation of ocean nearby, a phenomenon bound up with the creation of the proto-Mediterranean and Atlantic oceans. The striking disappearance of reef biota in the Northern Calcareous Alps is probably attributable to the same phenomenon. Smith *et al.* (2001), in a sceptical paper

devoted primarily to the Cenomanian–Turonian boundary mass extinction, speculated that the disappearance of many taxa at the end of the Triassic could also perhaps be attributed to deepening of the sea. This, however, can be ruled out for the bivalves, which exhibit a high diversity in the Hettangian shelf sea of northwest Europe. Furthermore, an extensive shallow carbonate platform persisted at this time in parts of the Southern Alps and Apennines, as indicated by the Calcare Masiccio, yet it lacks megalodontids, which could have been expected to occur if they had not gone extinct.

There is a large diversity reduction among bivalve and other benthic groups from the fully marine Rhaetian of the Alps to the abnormally low-salinity sea of northwest Europe (Hallam & El Shaarawy 1982), a phenomenon consistent with what is known today in seas such as the Baltic. The proportion of Rhaetian genera going extinct at the T–J boundary is less than half that in the Alps (Hallam & Wignall 1997), suggesting that more stenotopic genera were more vulnerable to extinction, which is indeed what would be expected. Stenotopic taxa tend to have a K-selected adaptation strategy, one of the consequences of which is growth to large size for the group. Extinction survivors tend to be opportunists, and mature relatively early at a small size. The bivalves, ammonites and brachiopods across the T–J boundary accord with this pattern (see the data presented earlier). As already noted, those taxa that went extinct include representatives that grew to large size, whereas all the early Hettangian taxa are small (Hallam 1998).

The foraminiferal and ostracod record also indicates a strong facies relationship. As already outlined, the change from marginal to fully marine salinity across the T–J boundary in northwest Europe is marked by a strong increase in diversity as a result of the migration of taxa that in Rhaetian times had been confined to the Alps. *Triasina* is confined to the Alps, characteristically in limestone facies and, in the Austrian Alps, is associated with reef facies.

As regards terrestrial plants, pollen and spore distribution is likely to have been strongly facies-bound, which compromises their value in biostratigraphy (Fisher & Dunay 1980). The precise relationship between facies and particular taxa has not yet been worked out. Among the macroplants, the extinction across the T–J boundary in Greeland and Scania has been related, on the basis of stomatal index studies of the leaves, to a marked increase in atmospheric CO₂ causing temperature rise, associated with flood basalt eruptions in the Central Atlantic Magmatic Province (McElwain *et al.* 1999). The conclusion, however, has been disputed by Tanner *et al.* (2001) on the basis of analysis of the carbon isotope

compositions of pedogenic calcite, which suggests relative stability of atmosphere CO₂ across the boundary (but see discussion in *Nature* 415, pp. 386–8 (2002)). Neither is it in accord with the oxygen isotope work in Austria suggesting no change in temperature across the boundary (Hallam & Goodfellow 1990), nor the research of Kelber (1998) indicating no significant extinction event among plants in Central Europe. Clearly, the potentially fascinating area of stomatal density (or index) studies requires more research to establish confirmation of the results of McElwain *et al.* (1999).

Conclusions

Though the current evidence cannot decisively exclude it, the foregoing review does not favour a major T–J boundary catastrophe. The best evidence for a significant increase in extinction rate in marine habitats comes from the bivalves and brachiopods, but facies problems restrict indications of clear-cut change over a short distance in any given stratigraphic section. It is consistent also with the final disappearance of ceratite ammonites, and conodonts, but the dramatic disappearance of reef biota at the very end of the Triassic in the Northern Calcareous Alps is most evidently bound up with regional tectonics. Its probable global extent is indicated, however, in Fig. 1 of Kiessling (2001). Similarly, although a sharp increase in T–J boundary extinction rate has been noted in different regions among the radiolarians and dinoflagellates, more work is needed to establish their global significance if any. For other groups, a mass extinction is not recognizable, although important and distinctive individual taxa such as the foraminifer *Triasina* disappeared.

The continental picture is equivocal. As regards plants, a catastrophic change has only been claimed in the eastern United States, and the striking changes from the Lepidopteris to the Thaumatopteris zones in East Greenland are also consistent with catastrophe, although in both these cases precise correlation with the marine T–J boundary has not yet been, and perhaps never will be, established; as has been mentioned earlier, however, carbon isotopes offer some promise in this respect. The same problem arises in the case of Australia, where a striking change consistent with catastrophe has been dated on dubious grounds as middle Hettangian. Elsewhere there are no indications of other than a gradual, though probably accelerated, transition. The one claim of a catastrophic extinction among vertebrates has been disputed by others.

On the other hand, there is strong evidence of a succession of important changes extended through the Rhaetian, so that Hettangian biota are generally very different from those of the Norian, and the extinction rate in the Rhaetian was substantially greater than that in the Norian. The beginning is marked in the marine realm by the sharp disappearance of the hitherto abundant bivalve *Monotis*, as well as a number of ammonite families. Dagys & Dagys (1994) report some notable end-Norian extinctions among brachiopods, while Palaeozoic survivors such as the murchisonacean gastropods also apparently disappeared at this time. Though the evidence is far from conclusive, it appears to favour a non-catastrophic extinction extending through the Rhaetian, culminating in a final coup de grâce.

While this paper is not concerned with possible causal factors, it should be pointed out that the extinction patterns are not consistent with an end-Triassic bolide impact scenario, as proposed by Olsen *et al.* (1987) and more tentatively by McRoberts *et al.* (1995). No convincing evidence has been put forward for either a significant iridium anomaly or shocked quartz at the T–J boundary. A claim for shocked quartz in a section in the northern Apennines is open to serious doubt (Hallam & Wignall 1997) and has not been confirmed by others despite intensive search. It is more plausible to invoke terrestrially-bound phenomena, such as associated with the Central Atlantic Magmatic Province, which has been dated at ~200 m.y., approximately coeval with the T–J boundary (Marzoli *et al.* 1999). Extensive epeirogenic or even eustatic movements of the sea, associated with plume activity, leading to a regression–transgression couplet, could have provoked the sorts of major environmental changes that caused increased extinction in the marine realm (Hallam & Wignall 1999).

Acknowledgements – I thank Drs. A. Paganoni, S. Renesto, G. Schairer and H. Summersberger for granting me access to collections under their charge, and Professors G. Ciarapica, S. Cirilli, M. Gaetani and F. Jadoul for helpful discussions and guidance in the field. Drs. G.D. Stanley and P.B. Wignall provided helpful suggestions as referees. The field and museum research in Austria, Bavaria and Italy was supported by a research fellowship from the Leverhulme Trust.

References

- Allasinaz, A. 1992: The Late Triassic–Hettangian bivalve turnover in Lombardy (Southern Alps). *Rivista Italiana di Paleontologia e Stratigrafia* 97, 431–454.
- Ash, S. 1986: Fossil plants and the Triassic–Jurassic boundary. In Padian, K. (ed.): *The Beginning of the Age of Dinosaurs*, 21–29. Cambridge University Press, Cambridge.
- Beauvais, L. 1984: Evolution and diversification of Jurassic Scleractinia. *Paleontographica Americana* 54, 219–224.

- Benton, M.J. (ed.) 1993: *The Fossil Record 2*. 845 pp. Chapman & Hall, London.
- Benton, M.J. 1994: Late Triassic to Middle Jurassic extinctions among continental tetrapods: testing the pattern. In Fraser, N.C. & Sues, H.-D. (eds): *In the Shadow of Dinosaurs*, 366–397. Cambridge University Press, Cambridge.
- Cirilli, S., Galli, M.T., Jadoul, F., Rettori, R. & Spina, A. 2000: Implicazioni stratigrafico-paleoclimatiche ed evoluzione paleogeografica della successione Retico-Hettangiano del M. Albenza (Prealpi Bergamasche). *Accademia Nazionale di Scienze e Lettere Arti di Modena: Collana di Studi* 21, 79–85.
- Cuny, G. 1995: French vertebrate faunas and the Triassic–Jurassic boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* 119, 343–358.
- Curtis, K. & Padian, K. 1999: An early Jurassic microvertebrate fauna from the Kayenta Formation of northeastern Arizona: microfaunal change across the Triassic–Jurassic boundary. *Paleobios* 19, 19–34.
- Dagys, A.S. & Dagys, A.A. 1994: Global correlation of the terminal Triassic. *Mémoires de Géologie (Lausanne)* 22, 25–34.
- El Shaarawy, Z. 1981: Foraminifera and ostracods of the topmost Triassic and basal Jurassic of England, Wales and Austria. Unpublished PhD thesis. University of Birmingham.
- Embry, A.F. & Suney, L.B. 1994: The Triassic–Jurassic boundary in the Sverdrup Basin, Arctic Canada. *Canadian Society of Petroleum Geologists Memoir* 17, 857–868.
- Fisher, M.J. & Dunay, R.E. 1981: Palynology and the Triassic/Jurassic boundary. *Reviews of Palaeobotany and Palynology* 34, 129–135.
- Fowell, S.J. & Olsen, P.E. 1993: Time calibration of Triassic–Jurassic microfloral turnover, eastern North America. *Tectonophysics* 222, 361–369.
- Gaetani, M. 1970: Faune hettangiane della parte orientale della provincia di Bergamo. *Rivista Italiana di Paleontologia e Stratigrafia* 76, 355–442.
- Golebiewski, R. 1990: The alpine Kössen Formation, a key for European topmost Triassic correlations. *Albertiana* 8, 25–35.
- Gradstein, F.M., Agterberg, F.P., Ogg, J.G., Hardenbol, J., van Veen, P., Thierry, J. & Huang, Z. 1994: A Mesozoic time-scale. *Journal of Geophysical Research* 99, 24051–24074.
- Gümbel, C.W. 1859: Über die Gleichstellung der Gesteinsmassen in den nordöstlichen Alpen mit ausseralpinen Flötzschichten. *Amt Berichten Versammlungen deutschen Naturforschung und Ärzte* 34, 80–88.
- Hallam, A. 1976: Stratigraphic distribution and ecology of European Jurassic bivalves. *Lethaia* 9, 245–259.
- Hallam, A. 1981: The end-Triassic bivalve extinction event. *Palaeogeography, Palaeoclimatology, Palaeoecology* 35, 1–44.
- Hallam, A. 1995: Major bio-events in the Triassic and Jurassic. In Walliser, O.H. (ed.): *Global Events and Event Stratigraphy*, 265–283. Springer-Verlag, Berlin.
- Hallam, A. 1998: Speciation patterns and trends in the fossil record. *Géobios* 30, 421–430.
- Hallam, A. & El Shaarawy, Z. 1982: Salinity reduction of the end-Triassic sea from the Alpine region into northwestern Europe. *Lethaia* 15, 169–178.
- Hallam, A. & Goodfellow, ?? 1990: Facies and geochemical evidence bearing on the end-Triassic disappearance of the Alpine reef ecosystem. *Historical Biology* 4, 131–138.
- Hallam, A. & Wignall, P.B. 1997: *Mass Extinctions and Their Aftermath*. 320 pp. Oxford University Press, Oxford.
- Hallam, A. & Wignall, P.B. 1999: Mass extinctions and sea-level changes. *Earth Science Reviews* 48, 217–258.
- Hallam, A., Wignall, P.B., Yin, J. & Riding, J.B. 2000: An investigation into possible facies changes across the Triassic–Jurassic boundary in southern Tibet. *Sedimentary Geology* 137, 101–106.
- Helby, R., Morgan, R. & Partridge, A.D. 1987: A palynological zonation of the Australian Mesozoic. In Jell, P.A. (ed.): *Studies in Australian palynology. Memoir of the Association of Australian Palynology* 4, 1–94.
- Hori, R. 1992: Radiolarian biostratigraphy at the Triassic/Jurassic period boundary in bedded cherts from the Inuyama area, central Japan. *Journal of Geosciences, Osaka City University* 35, 53–65.
- Hounslow, M.W., Warrington, G. & Posen, P.E. 2001: Magnetostratigraphic correlation of marine (UK) and non-marine (eastern USA) Triassic/Jurassic boundary successions. *Abstract for Poster Presentation, Earth Systems Processes Meeting* (Geological Society of London and Geological Society of America), Edinburgh.
- Jadoul, F., Masetti, D., Cirilli, S., Berra, F., Claps, M. & Frisa, S. 1994: Norian–Rhaetian stratigraphy and paleogeographic evolution of the Lombardy Basin (Bergamasc Alps). *Excursion B1, 15th IAS Regional Meeting, April 1994*, 38 pp. Ischia, Italy.
- Karle, U. 1984: Palynostratigraphische Untersuchung eines Rhät/Lias–Profils am Fonsjoch, Achensee (Nördliche Kalkalpen, Österreich). *Mitteilungen der Österreich geologische Gesellschaft* 77, 331–353.
- Kelber, K.-P. 1998: Phytostratigraphische Aspekte der Makroflora des süddeutschen Keupers. *Documenta naturae* 117, 89–115.
- Kiessling, W. 2001: Paleoclimatic significance of Phanerozoic reefs. *Geology* 29, 751–754.
- Krystyn, L. 1987: Zur Rhaet-stratigraphie in den Zlambach-Schichten (vorläufiger Bericht). *Sitzungsber. Österreichische Akademie der Wissenschaft, Mathematische Naturwissenschaftliche Klasse* 1/196, 21–36.
- Lakew, T. 1990: Microfacies and cyclic sedimentation of the Upper Triassic (Rhaetian) Calcare di Zu (Southern Alps). *Facies* 22, 187–232.
- Lucas, S.G. 1994: Triassic tetrapod extinctions and the compiled correlation effect. *Canadian Society of Petroleum Geologists Memoir* 17, 869–875.
- Lund, J.J. 1977: Rhaetic to Lower Liassic palynology of the onshore south-eastern North Sea Basin. *Danmarks Geologiske Undersøgelse, II. Rk., 109*, Copenhagen.
- Marzoli, A., Renne, P.R., Piccirillo, E.M., Ernesto, M., Bellieni, G. & De Min, A. 1999: Extensive 200-million-year-old continental flood basalts of the Central Atlantic Magmatic Province. *Science* 284, 616–618.
- McElwain, J.C., Beerling, D.J. & Woodward, F.I. 1999: Fossil plants and global warming at the Triassic–Jurassic boundary. *Science* 285, 1386–1390.
- McRoberts, C.A., Newton, C.R. & Allasinaz, A. 1995: End-Triassic extinction; Lombardian Alps, Italy. *Historical Biology* 9, 287–317.
- Mostler, H., Scheuring, B. & Urlichs, M. 1978: Zur Mega-, Mikrofauna und Mikroflora der Koessener Schichten (alpine Obertrias): von Weissloferbach in Tirol unter besonderer Berücksichtigung in der suessi- und marshi-Zone auftretender conodonten. *Österreichische Akademie der Wissenschaft, Schriftenreihe Erdwissenschaftlichen Kommunikationen* 4, 141–174.
- Newell, N.D. 1967: Revolutions in the history of life. *Geological Society of America Special Paper* 89, 63–91.
- Olsen, P.E., Shubin, N.H. & Anders, M.H. 1987: New Early Jurassic tetrapod assemblages constrain Triassic–Jurassic tetrapod extinction event. *Science* 237, 1025–1029.
- Olsen, P.E., Fowell, S.J. & Cornet, B. 1990: The Triassic/Jurassic boundary in continental rocks of eastern North America; a progress report. *Geological Society of America Special Paper* 247, 585–594.
- Palfy, J. in press: Volcanism of the Central Atlantic Magmatic Province as a potential driving force in the end-Triassic mass extinction. In: *The Central Atlantic Magmatic Province. Memoir of the American Geophysical Union*.
- Palfy, J., Mortensen, J.K., Carter, E.S., Smith, P.L., Friedman, R.M. & Tipper, H.W. 2000: Timing the end-Triassic mass extinction: first on land, then in the sea? *Geology* 28, 39–42.
- Palfy, J., Demeny, A., Haas, J., Hetenyi, M., Orchard, M.J. & Veto, I. 2001: Carbon isotope anomaly and other geochemical changes at the Triassic–Jurassic boundary from a marine section in Hungary. *Geology* 29, 1047–1050.
- Pearson, D.A.B. 1977: Rhaetian brachiopods of Europe. *Denkschriften der naturhistorisches Museum Wien* 1, 1–70.
- Pedersen, K.R. & Lund, J.J. 1980: Palynology of the plant-bearing

- Rhaetian to Hettangian Kap Stewart Formation, Scoresby Sund, East Greenland. *Reviews of Palaeobotany and Palynology* 31, 1–69.
- Raup, D.M. & Sepkoski, J.J. 1982: Mass extinction in the fossil record. *Science* 215, 1501–1503.
- Sarjeant, W.A.S., Volkheimer, W. & Zhang, W. 1992: Jurassic palynomorphs of the circum-Pacific region. In Westermann, G.E.G. (ed.): *The Jurassic of the Circum-Pacific*, 273–292. Cambridge University Press, Cambridge.
- Schuermann, W.M.L. 1979: Aspects of Late Triassic palynology. 3. Palynology of latest Triassic and earliest Jurassic deposits of the Northern Limestone Alps in Austria and southern Germany, with special reference to a palynological characterisation of the Rhaetian stage in Europe. *Reviews of Palaeobotany and Palynology* 27, 53–75.
- Smith, A.B., Gale, A.S. & Monks, N.E.A. 2001: Sea-level change and rock record bias in the Cretaceous: a problem for extinction and biodiversity studies. *Paleobiology* 27, 241–253.
- Stanley, G.D. 1988: The history of early Mesozoic reef communities, a three step process. *Palaos* 3, 170–183.
- Stanley, G.D. & Swart, P.K. 1995: Evolution of the coral-zooxanthellae symbiosis during the Triassic: a geochemical approach. *Paleobiology* 21, 179–199.
- Suess, E. & Mojsisovics, E. 1868: Studien über die Gliederung der Trias und Jurabildungen in der östlichen Alpen. 2. Die Gebirgsgruppe des Osterhorns. *Jahrbuch der geologische Reichsanstalt Wien* 18, 167–200.
- Tanner, L.H., Hubert, J.F., Coffey, B.P. & McInerney, D.P. 2001: Stability of atmospheric CO₂ levels across the Triassic/Jurassic boundary. *Nature* 411, 675–677.
- Taylor, D.G., Boelling, K. & Guex, J. 2000: The Triassic/Jurassic system boundary in the Gabbs Formation, Nevada. *GeoResearch Forum* 6, 225–236.
- Tekin, U.K. 1999: Biostratigraphy and systematics of late Middle and late Triassic radiolarians from the Taurus Mountains and Ankara region, Turkey. *Geologisch-Paläontologisch Mitteilungen, Sonderband* 5, 1–296.
- Tipper, H.W., Carter, E.S., Orchard, M.J. & Tozer, E.T. 1994: The Triassic–Jurassic (T–J) boundary in Queen Charlotte Islands, British Columbia defined by ammonites, conodonts and radiolarians. *Geobios* 17, 485–492.
- Tozer, E.T. 1979: Latest Triassic ammonoid faunas and biochronology, western Canada. *Geological Survey of Canada Paper* 79, 127–135.
- Tozer, E.T. 1981: Triassic Ammonoidea: classification, evolution and relationship with Permian and Jurassic forms. In House, M.R. & Senior, J.R. (eds): *The Ammonoidea*, 65–100. Academic Press, London.
- Tozer, E.T. 1988: Rhaetian: a substage, not a stage. *Albertiana* 7, 9–15.
- Traverse, A. 1988: Plant evolution dances to a different beat: plant and animal evolutionary mechanisms compared. *Historical Biology* 1, 277–302.
- Visscher, H. & Brugman, W.A. 1981: Ranges of selected palynomorphs in the Alpine Triassic of Europe. *Reviews of Palaeobotany and Palynology* 34, 115–128.
- Weems, R.E. 1992: The ‘terminal Triassic catastrophic event’ in perspective: a review of Carboniferous through Early Jurassic vertebrate extinction patterns. *Palaeogeography, Palaeoclimatology, Palaeoecology* 94, 1–29.
- Whatley, R.C. 1988: Patterns and rates of evolution among Mesozoic Ostracoda. In Hanai, T., Ikeya, N. & Ishizaki, K. (eds): *Evolutionary Biology of Ostracoda*, 1021–1040, Kodausha, Tokyo.