

PERMIAN AND EARLY TRIASSIC EXTINCTION OF NON-MARINE TETRAPODS

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ABSTRACT. The non-marine tetrapods of the Permian and Early Triassic experienced four significant episodes of extinction during a time of relatively high turnover at the family level. The Artinskian, Ufimian, and Scythian extinctions appear genuine, but the Tatarian extinction is compromised by spurious data. The quality of the Tatarian data is considered in the light of the poor stratigraphical record for the Late Permian and Permian-Triassic boundary. Various extinction mechanisms are considered, bearing in mind that the radiation of the mammal-like reptiles forms a large portion of the diversity data. The most likely hypothesis is that non-marine tetrapods were subjected to environmental stress as climates fluctuated, at first in association with glaciation, and then with continental warming.

THE end-Permian extinction devastated marine invertebrate faunas. All too often the corresponding, but not necessarily correlated, elimination of non-marine tetrapods is overlooked. Reasons for this may include an insufficiency of Permian-Triassic (P-Tr) terrestrial sections, difficulties in correlating continental deposits, a taxonomic inflation of Permian and Triassic tetrapods, and less analysis of vertebrate extinctions because there are fewer vertebrate than invertebrate palaeontologists.

The Late Permian sequence of marine sediments is incomplete, punctuated by regressions of the Late Permian seas, but the terrestrial rock record is even more incomplete. There are no complete terrestrial P-Tr boundary sections, with the possible exception of Rio Grande du Sol, Brazil (Barberena *et al.* 1985), and there are no complete marine sections, with the possible exception of some seemingly conformable sequences in South China (Teichert 1990). The most complete terrestrial sections are found in the Karoo Basin of South Africa (Kitching 1977) and Sinkiang Province, China (Cheng 1980). The lack of complete sequences causes problems with the collection and correlation of data, and the interpretation of diversity patterns, but there is no justification for ignoring the available data.

The taxonomy of the relevant tetrapod groups has been thoroughly revised in recent years, but there is a need for constant revision. Accordingly, the main concern with the type of analysis attempted here is the validity of the taxonomic and stratigraphic data. All the conclusions presented here regarding the timing of origination and extinction, and the diversity of families, are derived from a study of Benton's (1987) database for families of non-marine tetrapods. The validity of the taxonomy and stratigraphy used in Benton's database has been examined: comparison with several other compilations revealed that it is most accurate (Maxwell and Benton 1990) and, therefore, most suitable for use here. Minor alterations made to the data base subsequent to publication (Benton pers. comm. 1991) have been incorporated.

Analyses of P-Tr vertebrate extinctions invariably conclude that there were four major episodes of non-marine tetrapod extinction, one each at the end of the Early Permian (Artinskian), Late Permian (Tatarian), Early Triassic (Scythian) and Late Triassic (Carnian) (see, for example, Olson 1982; Benton 1989*a*). The Late Triassic event has been split into two separate events, Carnian and Rhaetian (Benton 1986; Olsen and Sues 1986), but those events are not considered here. A third Permian event occurred during the Ufimian (earliest Late Permian) and was of the same magnitude as the Artinskian event. The character of the Permian and Scythian extinctions and possible causal mechanisms are considered here.

PATTERN OF EXTINCTION AND TAXA AFFECTED

The pattern of extinction of amphibians and reptiles throughout the Permian and Early Triassic is detailed in Table 1. All range data were calculated using the Palmer (1983) timescale. For those families whose stratigraphic range does not exceed a single stratigraphic stage, the range, in time, is taken as half the length of that stage. For those families whose range extends beyond a single stratigraphic stage, the range in time is taken as the interval between the mid-points of the first and last stages.

TABLE 1. Extinction and origination data for amphibian and reptile families during four stage extinctions. Number of stages spanned and duration in millions of years (Myr) are average figures for all amphibian or reptile families suffering extinction in that stage. Abbreviations: A, Amphibia; Art, Artinskian; Kas, Kasimovian; Kaz, Kazanian; Kun, Kungurian; Mos, Moscovian; R, Reptilia; Sak, Sakmarian; Scy, Scythian; Serp, Serpukhovian; Tat, Tatarian; Ufi, Ufimian.

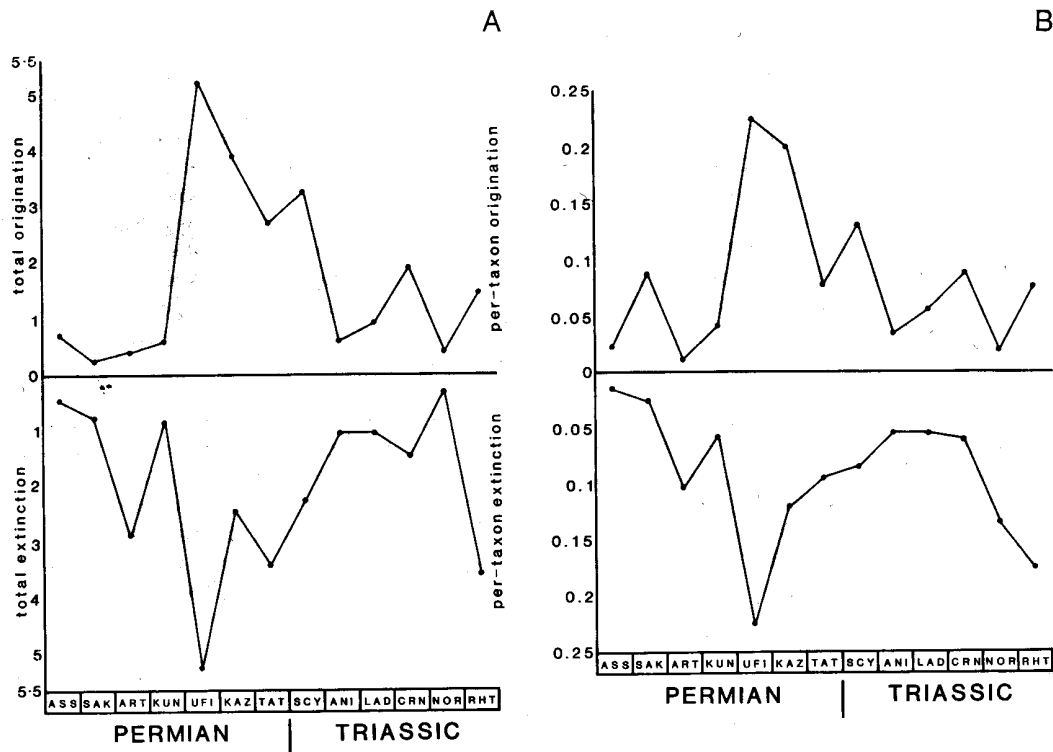
	ART		UFI		TAT		SCY	
	A	R	A	R	A	R	A	R
Number of families becoming extinct	7 (46%)	7 (70%)	11 (55%)	7 (58%)	6 (67%)	21 (78%)	4 (44%)	7 (41%)
Number of families originating	1	1	5	8	4	18	6	11
Overall decline in diversity	6 (14%)	1 (60%)	1 (9%)	-1 (-8%)	2 (22%)	3 (11%)	-2 (22%)	-4 (-24%)
Range of extinct families	Serp-Art	Mos-Art	Kas-Ufi	Kun-Ufi	Ufi-Tat	Sak-Tat	Tat-Scy	Kaz-Scy
Number of stages spanned	5.7	4.7	4.8	1.4	2.5	1.6	1.5	2
Duration in Myr	37.1	27.5	23.8	2.3	7.4	5.5	4.5	6.7

Taxa affected

The majority of reptile families eliminated during the Permian were therapsids, the mammal-like reptiles, which underwent a spectacular radiation throughout the second half of the period. The highly successful Early Permian pelycosaurs gave way to therapsids in the Late Permian: dinocephalians, theriodonts, and the abundant widespread dicynodonts. The relatively high levels of total and per-taxon origination and extinction during most of the Late Permian (Text-fig. 1) can be taken, in part, as a reflection of the radiation of the therapsids during this time.

Padian and Clemens (1985) raised the possibility that changes in therapsid diversity throughout the late Early Permian and Late Permian could be related to ecological, rather than to evolutionary changes, as differential preservation and sampling of environments may give a misleading picture of faunal variation through time. The similarity in patterns of faunal replacement in the Permian beds of the former USSR and the USA may represent evidence of a genuine evolutionary trend, but there is no certainty that this is the case, as worldwide ecological trends are possible (Padian and Clemens 1985). The complexities of ecological and faunal change during the Permian cannot be resolved easily at present and the difficulties of correlating the deposits and faunas of the former USSR, USA, and South Africa will hinder further work.

The therapsid predecessors, the pelycosaurs, were dominant in the Early Permian. Their success may be related to the development of the adductor jaw musculature in the carnivorous forms, enabling them to become the first truly carnivorous as opposed to insectivorous reptiles (Barghusen 1973; Carroll 1986), and the adaptation of edaphosaurids and caseids to a herbivorous mode of life, becoming the first tetrapods to invade this particular adaptive zone in any abundance (Kemp 1982,



TEXT-FIG. 1. Total and per-taxon origination and extinction rate for all tetrapods during the Permian and Triassic. Abbreviations: ANI, Anisian; ASS, Asselian; CRN, Carnian; LAD, Ladinian; NOR, Norian; RHT, Rhaetian; others given in Table 1 explanation.

p. 37). Four of six pelycosaur families became extinct in the Artinskian. The remaining two families were eliminated in the Kungurian.

The first three therapsid families, the Brithopodidae (dinocephalians), the Phthinosuchidae (eotheriodonts), and the Venjukoviidae (anomodonts) originated during the Kungurian. The therapsids radiated to become dominant during the Late Permian, co-existing with a variety of captorhinomorphs, procolophonids, and early diapsids.

The pattern of therapsid extinction and radiation has been studied in detail, revealing no less than ten separate extinction events, each of which removed the largest animals of the time and those with the fewest mammalian characters (Sloan 1985). Turnover was particularly high in the Tatarian. Sloan records six extinctions and estimates that more than 50 per cent of morphological change from the earliest reptiles to the earliest mammals took place during this time. This sequential radiation and rapid turnover of groups accounts for much of the diversity data recorded for the Permian, but this alone cannot explain the high level of extinction observed among amphibians and reptiles throughout the late Early Permian and Late Permian.

The first stage of the Early Triassic, the Scythian, is characterized by high total and per-taxon origination rates (Text-fig. 1) and faunas of low diversity. The low diversity of the faunas, a consequence of the preceding Tatarian extinction, is best illustrated by the dominance of one dicynodont genus, *Lystrosaurus*, which comprises approximately 90 per cent of all the individual tetrapod specimens collected in Antarctica and South Africa (Benton 1983).

CONSIDERATIONS OF THE DATA AND ITS VALIDITY

The largest single stage extinction of amphibians and reptiles is recorded for the Tatarian, regardless of whether the classes are considered separately or together. The data must be examined to determine whether the perceived increased level of extinction is a result of increased extinction rates coupled with reduced origination rates, bias in either the fossil or rock record, or a combination of the two. As noted earlier, the completeness of the Tatarian marine sedimentary sequence is compromised by gaps that resulted from regressions. Restriction or withdrawal of the normal depositional environment resulted in a hiatus. Subsequent aerial erosion removed sediment that had been deposited immediately prior to regression, effectively increasing the perceived duration of the gap. Even the most conformable P-Tr marine sequences show evidence of emergence and erosion (Teichert 1990). The terrestrial sedimentary sequence is usually much worse than the corresponding marine sequence for any given time, such is the unlikelihood of conformable terrestrial deposition, so a certain amount of speculation will always be involved when considering terrestrial extinctions.

The extinction data appear more convincing for the Tatarian, compared with the other three stages considered in detail here, simply by weight of numbers. A 50 per cent rate of extinction stands up to scrutiny much better if it represents, for example, an elimination of thirty families from a sample of sixty compared with the elimination of two families from a total sample of four. The figure of twenty-seven families eliminated from a total of thirty-six during the Tatarian is credible, from a simple statistical point of view, because of the larger total sample (a total diversity of thirty-six families for the Tatarian compared with twenty-five for the Artinskian, twenty-three for the Ufimian, and twenty-six for the Scythian). The fact that more tetrapod families are preserved in the Tatarian than in the three other stages considered here may lead to an assumption that the preservational biases common in the terrestrial rock record are manifested in the Late Permian and Early Triassic rock record. This is discussed below.

TABLE 2. Simple Completeness Metric (SCM) for non-marine tetrapod families in each stage from Artinskian to Ladinian (from Benton 1987).

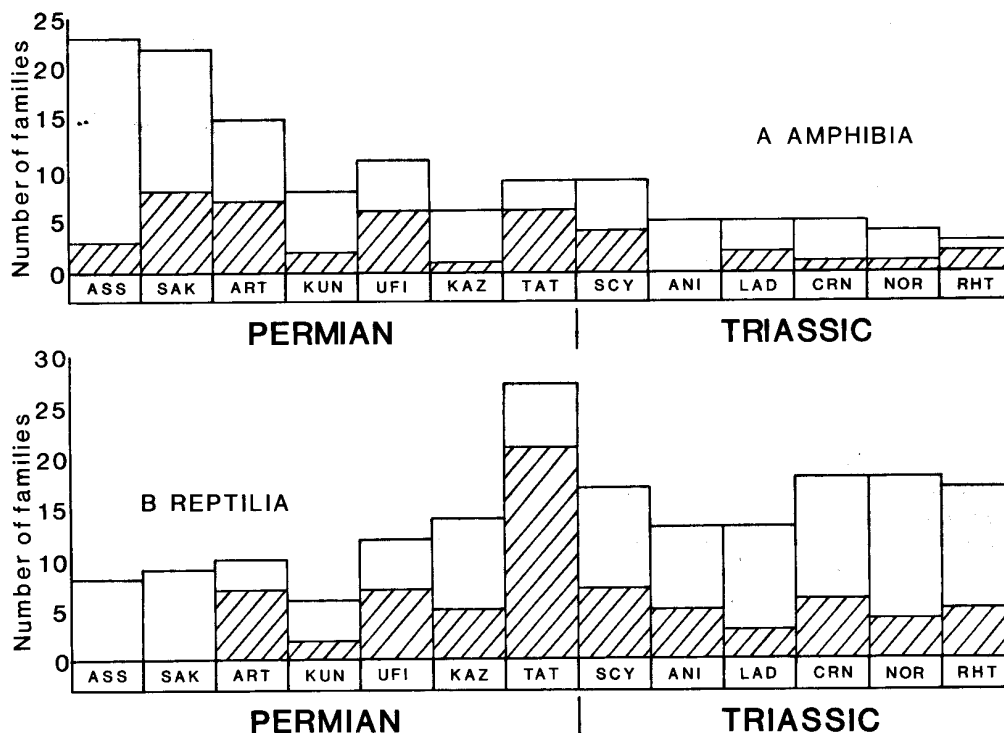
Period	Epoch	Stage	SCM
Triassic	Middle	Ladinian	94.1
		Anisian	94.1
	Early	Scythian	100
Permian	Late	Tatarian	100
		Kazanian	80
		Ufimian	100
	Early	Kungurian	64.3
		Artinskian	96

The Simple Completeness Metric (SCM: Benton 1987) for each stage (Table 2) shows that three of the four stages with a high level of extinction are 100 per cent complete, while the fourth, the Artinskian, is 96 per cent complete. The two stages which make up the remainder of the Late Permian, the Kungurian and Kazanian, have lower SCMs and a reduced level of extinction. The extinction level in the Tatarian, therefore, is apparently not biased at family level by the effect of Lazarus taxa.

CAUSES OF THE EXTINCTION

Any common links between marine and terrestrial extinctions may help reveal a shared extinction mechanism. The poor terrestrial record and the punctuated marine record make any kind of correlation of marine and terrestrial faunas unfeasible, but the information regarding the period of

most severe extinction in each community may be real, despite preservational biases. It would, therefore, be reasonable to compare the timing of the peaks of extinction in each realm. The peak of tetrapod extinction occurred in the Tatarian (Text-fig. 2) compared with a peak of invertebrate extinction in the Kazanian (Sepkoski 1986). The peaks most likely reflect the most severe period of extinction in each realm, such is the difference in magnitude between them and the other stage extinctions, and they are separated in time by approximately 8 Myr, so it is unlikely that the same causal mechanism accounted for the extinctions in both realms. Erwin (1990) provides an excellent review of marine invertebrate extinction patterns and proposed mechanisms.



TEXT-FIG. 2. Bar-graph of the number of families of A, amphibians and B, reptiles for the Permian and Triassic. The full bar shows the number of families for each stage. The hatched portion shows the number of families that became extinct during the stage. Abbreviations given in explanations to Text-figure 1 and Table 1.

The pattern of tetrapod extinctions throughout the Permian and Triassic shows a gradual change in the families eliminated, stage by stage, from predominantly amphibians to predominantly reptiles (Text-fig. 2). It is tempting to try to link this change to some plausible extinction mechanism, such as steady climatic deterioration which affected terrestrial reptiles more than aquatic or semi-aquatic amphibians, but the reason for the change is probably much more simple. Reptile diversity was low throughout the Carboniferous and Early Permian, but amphibian diversity was at its highest level for the entire Palaeozoic. Simple evolutionary turnover of the large amphibian population would explain the Late Carboniferous extinctions and the greater level of Early Permian amphibian extinction, relative to the extinction levels of the much less diverse reptiles. After the Artinskian (late Early Permian) amphibian diversity remains steady, averaging nine families per Late Permian stage, while reptile diversity increases, principally as a result of the radiation of the therapsids, from six families in the Kungurian to twenty-seven in the Tatarian (Text-fig. 2). This change is also reflected

in the relative proportions of amphibian and reptile families eliminated per stage in the Late Permian (Text-fig. 2). During the Early Triassic, amphibian diversity is still lower than reptile diversity and reptile families make up the bulk of those families eliminated in each stage, but not to the same extent as in the Late Permian stages.

Alterations in global climate

The development of the Permian climate has been detailed by Erwin (1990). Although Permo-Carboniferous glaciation had come to an end in the Sakmarian, glacial centres continued to migrate across Gondwana to reach India and the western margin of Australia by Artinskian times (Caputo and Crowell 1985). This was not a time of exceptionally high invertebrate extinction, although some families were eliminated and most Artinskian brachiopod genera failed to survive the stage (Dagis and Ustritsky 1973). The co-incidental decline in tetrapod families during the Artinskian was the first major Permian extinction of terrestrial tetrapods, primarily affecting members of the Permo-Carboniferous chronofauna which was widespread within the tropics of the time (Kemp 1982, p. 66). Gondwana and Laurasia were moving toward final union in the Artinskian and global climates were soon to become warmer and drier, with high seasonality, as temperature gradients became established across the supercontinent of Pangaea (Dickins 1983; Parrish *et al.* 1986).

During the Artinskian, the Permo-Carboniferous chronofauna was abundant in Texas, and other parts of North America, where many lakes, streams and swamps existed in a warm and humid climate (Kemp 1982, p. 65). An alteration to a drier climate and eventually very arid conditions in this equatorial region is indicated by the evaporite deposits of the Clear Fork in Texas (Kemp 1982, p. 66). The aridity may have resulted from an increase in temperature, presaging the warming of global climates, or regressions of the mid-continent sea associated with glaciation in the southern hemisphere. Increased aridity may have contributed to the extinction of water-dependent members of the Permo-Carboniferous chronofauna such as the pelycosaurs *Ophiacodon* and *Edaphosaurus*. Warming in the tropics, therefore, may have influenced the development of arid conditions that led to Artinskian extinctions. As there were significant rises in sea level every 2.5 Myr throughout the Artinskian, which were presumably under glacioeustatic control, the development of aridity may have been linked to regression rather than warming.

Patterns of floral change and the deposition of extensive evaporites are consistent with, and reflect a period of, global warming following the Early Permian glaciation (Erwin 1989). The Late Permian–Early Triassic interval was a time of global warming with increasingly inequable climates, high seasonality, and high temperatures, briefly interrupted by bipolar cooling near the end of the Permian (Erwin 1990). The Ufimian (early Late Permian) would, therefore, appear to have been a time of gradual warming with no readily discernible violent fluctuations in climate or temperature within any one geographical region. The development of seasonality and increasing inequability may have disrupted species' biotic environment, playing a role in the tetrapod extinctions, but there is no certainty that this was the case.

Global cooling at the end of the Kazanian continued into the Tatarian, but de-glaciation and warming began in the southern hemisphere as Pangaea continued to move northward (Jablonski 1986). The possibility of a link between this period of cooling and Tatarian tetrapod extinctions is discussed below.

Catastrophism

Geochemical and invertebrate faunal data provide good reasons for concluding that Late Permian invertebrate extinctions were gradual and not initiated or influenced by the impact of an extraterrestrial body (Maxwell 1989, pp. 154–159). The pattern of tetrapod extinction evident from Text-figure 2 does not provide any reason for invoking a catastrophic extinction mechanism. The effects of catastrophic vulcanism have been considered by some workers, largely because analyses of boundary sediments have uncovered trace elements and elemental ratios that suggest the presence of ash which originated in massive volcanic eruptions (Clark *et al.* 1986; Zhou and Kyte 1988). The expulsion of extensive ash clouds into the upper reaches of the Earth's atmosphere would result in

climatic variations and a reduction in the intensity of light incident upon the surface. This may be sufficient to eliminate one or more critical elements of the biota and, through an ecological chain reaction, eliminate taxa higher in the food chain (Olson 1989). Such an hypothesis may be applied to the data with some success, but the timing of the extinctions and the taxa affected do not allow serious consideration of this mechanism.

Reduced speciation

There is an observed synchronicity throughout the geological record of large-scale tetrapod extinctions and widespread regressions that are thought to coincide with periods of reduced orogenic activity. This has been termed the Haug Effect (Johnson 1971). It links maximum transgression with maximum orogeny and hence a high topographic-geographic diversity of species with high speciation rates and standing diversity. It has been proposed that a diminution of orogenic activity, especially when accompanied by regression, would reduce the number of continental habitats, resulting in a decline in the speciation rate below the extinction rate, and hence, a significant decrease in species numbers and diversity (Bakker 1977).

Total and per-taxon extinction rates soared in the Late Permian (Text-fig. 1). The elimination of such a large number of families in such a relatively short space of time cannot be attributed solely to a very low origination rate coupled with normal background extinction or slightly increased extinction rates. Reduction of speciation rates in the Late Permian may have contributed to the overall loss of families, but the increased extinction rates more likely reflect the pressure of one or more external physical forces.

Endothermy and competition

The spectacular radiation of the therapsids into a wide variety of terrestrial herbivorous and carnivorous niches during the Late Permian has been explained by the idea that they were warm-blooded (Bakker 1986, p. 413). The development of endothermy might be used to explain the change from local faunas of low diversity in the Early Permian, a time of ectothermic reptiles, to faunas of much increased diversity in the Late Permian, populated primarily by supposed endothermic reptiles, but there are a number of problems associated with this kind of macroevolutionary concept. These include the difficulty in proving whether the therapsids had made such an evolutionary advance, the impossibility of proving the exact timing of such a development, and the numerous problems associated with simplistic interclade competitive replacement models (Benton 1983, 1986).

Histological studies show no conclusive evidence for endothermy in Late Permian therapsids (Reid 1984) and, even if they did, the acquisition of one key adaptation, such as endothermy, by a particular group is unlikely to trigger an adaptive radiation within the group (Kemp 1985). Overall the data from the fossil record do not support the idea of a competitive replacement by therapsids.

TATARIAN DATA: REAL OR BIASED?

The geological record is incomplete throughout the Late Permian and close to the P-Tr boundary. It is possible that many tetrapods that supposedly went extinct during the Tatarian actually spanned the P-Tr boundary, but were not preserved. The first stage of the Triassic, the Scythian, has an SCM of 100 per cent. The next two stages, the Anisian and Ladinian, both have an SCM of 94.1 per cent (Table 2) so it appears that any Lazarus genera or species do not manifest themselves at family level. It is also assumed that those families whose genera may have spanned the P-Tr boundary were eliminated within a few million years during the early Scythian.

The survivors of the Tatarian extinction are of particular relevance in light of the latter assumption. Of the three amphibian and six reptile families that spanned the P-Tr boundary, all but one failed to survive the Scythian: the temnospondyl family Brachyopidae continued through the Triassic, and much of the Jurassic. In addition, no less than seven of the eight families that failed to survive the Scythian originated in the Tatarian.

Fifteen of twenty-seven families that suffered extinction in the Tatarian also originated in that stage. When combined with the seven families that range from Tatarian to Scythian we have, from a total diversity in the Tatarian and Scythian of fifty-three families, a total of twenty-one amphibian and reptile families originating in the Tatarian and becoming extinct later in that stage or during the Scythian. Amphibian families were then removed from the analysis in accordance with the notion that reptiles make a much greater contribution to the biomass and, therefore, are more accurate indicators of environmental change. This resulted in a figure of eighteen reptile families, from a total diversity of thirty-eight reptile families in the Tatarian and Scythian, whose stratigraphic range was Tatarian or Tatarian to Scythian.

These figures could be interpreted as indicating a period of environmental upheaval, resulting in the extinction of families possessing restricted scope for adaptation, or the presence of a severe preservational bias in the latest Tatarian and Scythian. Families originating in the Tatarian were either unable to survive the environmental and evolutionary pressures of the Tatarian and Scythian, or were not preserved in the Scythian rock record. Is it reasonable to assume that some of the families recorded as being confined to the Tatarian survived into the Triassic but were not preserved, with the implication that the Tatarian extinction was not so extreme as to eliminate the majority of Palaeozoic amphibians and reptiles at that time?

The elimination of a large number of families that originated in the Tatarian may be linked to the bipolar cooling episode that interrupted the global warming trend. Throughout the global warming of the late Early Permian and early Late Permian, evolutionary adaptations may have resulted in the origination of reptiles adapted to increased temperatures. The cooling of the global climate that accompanied bipolar glaciation late in the Kazanian may have placed reptile genera adapted to warmer conditions under environmental stress throughout the succeeding stage, the Tatarian.

TABLE 3. Reptile families confined to the Tatarian or Tatarian and Scythian stages. Abbreviations: Scy, Scythian; Tat, Tatarian.

Family	Suborder	Range	Family	Suborder	Range
Younginidae	Younginiformes	Tat	Cistecephalidae	Anomodontia	Tat
Tangasauridae	Younginiformes	Tat	Kingoriidae	Anomodontia	Tat-Scy
Proterosuchidae	Proterosuchia	Tat-Scy	Moschorinidae	Therocephalia	Tat
Endothiodontidae	Anomodontia	Tat	Whaitsiidae	Therocephalia	Tat
Cryptodontidae	Anomodontia	Tat	Scaloposauridae	Therocephalia	Tat-Scy
Aulacocephalodontidae	Anomodontia	Tat	Silphestidae	Cynodontia	Tat
Dicynodontidae	Anomodontia	Tat	Procynosuchidae	Cynodontia	Tat
Pristerodontidae	Anomodontia	Tat	Dviniidae	Cynodontia	Tat
Emydopidae	Anomodontia	Tat-Scy	Galesauridae	Cynodontia	Tat-Scy

The eighteen reptile families confined to the Tatarian and Scythian are detailed in Table 3. Fifteen families are therapsids and eight of these are anomodonts. There are currently fourteen families of anomodonts recognized, not including the monospecific family Otsheriidae. Only one family, the Kannemeyeriidae, extends beyond the Scythian before suffering extinction in the Carnian. All others become extinct in the Late Permian or Scythian. Three of the eighteen families listed in Table 3 are therocephalians and four are cynodonts. There are six recognized families of therocephalians and all but one died out in the Late Permian or Scythian; the Bauriidae ranged from the Scythian to the Anisian. Of the eleven families of cynodonts recognized, only those four shown in Table 3 originated before the Scythian. The remaining seven cynodont families are Mesozoic forms.

The eighteen reptilian families detailed above are predominantly members of the earliest groups within the mammal-like reptiles. It is possible that these early synapsids, many of which had developed into large forms, had little tolerance to changes in their environment, and were

subsequently eliminated within a timespan of a few million years around the P-Tr boundary, such as the intensity of climatic variation at that time. Large forms tend to be specialized to particular habitats and are consequently restricted in their niches and scope for adaptation (Benton 1989*b*). Minor environmental fluctuations were abundant throughout the Phanerozoic (Pearson 1978) and it is envisaged that only very small changes are required to reduce the adaptation of a species. Such changes may not affect a particular species directly, but can have profound effects on the species' biotic environment (Kemp 1982, p. 322). It has been claimed that the large size of the major tetrapods would have placed them in jeopardy if there were any radical changes in the climate, drastically altering the *Glossopteris* flora which, together with small vertebrates and insects, provided the trophic base (Olson 1989). Therefore, it is perhaps significant that post-glacial climatic oscillations are envisaged for the Tatarian and that terrestrial tetrapods surviving the Late Palaeozoic extinctions tended to be of small body size (Parrington 1948; Bakker 1977; Kemp 1982, p. 322; Sloan 1985), although the contention of large forms being less adaptable to change has been questioned by Vrba (1980).

If this was not the case and many forms survived into the Scythian, why are they not preserved? Global warming began again after the Kazanian/Tatarian cooling episode. An increase in temperature, and hence aridity, could only serve to reduce terrestrial deposition, and this may be reflected in the continental red beds of the Triassic. The likelihood of preservation of terrestrial vertebrates is normally poor and a further reduction in the volume of sediment deposited and subsequently preserved in the Early Triassic could be utilized to explain the absence of Permian survivors from the fossil record. However, the continental red beds of the Triassic may represent the large land areas in tropical and sub-tropical latitudes rather than reflecting a global trend toward aridity. Much of the data on Permo-Triassic tetrapods relates to forms from the Karoo Basin of South Africa which was situated approximately 60° south of the equator during the Tatarian and Early Triassic and showed no sign of drying up (Hiller and Stavakis 1984).

It has also been suggested that many large herbivores and carnivores crossed the P-Tr boundary in South Africa, but were not preserved because they were confined to restricted upland regions after the Early Triassic (Parrington 1948; Cox 1967; Pitrat 1973). The occurrence of global marine transgressions throughout the Early Triassic led to flooding of low-lying terrestrial environments, such as those described for the Karoo, and resulted in the formation of predominantly semi-aquatic habitats. The low-lying swamps and estuaries of the Early Triassic may have been unsuitable for large animals requiring extensive habitats and preservation of remains is more likely in low-lying, semi-aquatic areas. This may explain why small temnospondyls, cynodonts, and dicynodonts were preserved, but larger dicynodonts and other therapsids that may have survived into the Triassic were not, because of the relative unlikelihood of deposition in upland areas (Cox 1967). This could account for a large bias in the tetrapod diversity data, but the idea of upland faunas may be open to question. The upland fauna of Clear Fork therapsids noted by Kemp (1982, p. 74), and referred to earlier, consisted of small, and not large, animals. More work is required to establish if such an upland component was present in Tatarian faunas and if its absence from Scythian faunas has a biasing affect on the data.

DISCUSSION

The analysis of databases without recourse to the constituent fossils, a practice sometimes labelled 'taxon counting', has been criticised, mainly because all taxa at the same level are given equal weight. For example, a family containing many genera is given the same statistical importance as a family containing, say, two genera, or one genus is given the same credibility as another, regardless of the number of constituent species (King 1990; Teichert 1990). This is a valid criticism. All too often taxa are counted, diversity patterns are determined, and conclusions are arrived at without consideration of the quality of the data. Criticisms are also levelled at the use of families, rather than genera or species, in determining diversity patterns.

The family, the taxonomic unit employed in Benton's (1987) database, is most likely the best

measure of the general patterns of change in non-marine tetrapod diversity through the Permian and Early Triassic. Ideally the number of species, and numbers of individuals in a species would be used in any study of changes in taxic diversity, but this is impractical. Sources of error affecting our interpretation of the fossil record, reviewed by King (1990), are of less importance at the family level than at the genus or species level (Raup 1979). The incomplete stratigraphical record for the Late Permian prevents accurate determination of the times of origination and extinction of tetrapod genera and species in many cases. Such sampling errors and inadequacies are perhaps best countered by considering data at the family level. In other words, families correspond in coarseness to the stratigraphic precision available at present.

The radiation of the therapsids to dominate terrestrial faunas during the Late Permian forms a large portion of the faunal replacement and diversity data for that time, but clearly there were external factors increasing the rate of extinction. The most credible factor appears to be alterations of climate related to the waning of Permo-Carboniferous glaciation, subsequent global warming throughout the late Early Permian and Late Permian, and a brief period of bipolar glaciation. Reasonably, resulting climatic fluctuations and associated environmental perturbations may have had significant effects on large animals that were restricted in their niches and scope for adaptation.

There is evidence that increased aridity was a factor in the Artinskian extinctions. There is no immediately apparent explanation for the Ufimian event other than a response to increasingly inequable climates. The Tatarian extinctions may have resulted from the climatic fluctuations that occurred when the late Kazanian bipolar glaciation interrupted a global warming trend. Sloan (1985) recorded six Tatarian therapsid extinctions with a regular cyclic character that suggests response to post-glacial climatic oscillations. Unfortunately the detailed chronostratigraphical and faunal evidence, doubtless necessary to produce this sort of explicit observation, has not been published.

It would be desirable to test the facts, such as their relevance to the debate on the validity of Tatarian data, and to learn the timing of the six extinctions and the location of the fossil localities that contributed data to the analysis. It would then be possible to lend weight to each proposed extinction, depending upon whether it is based on the elimination of all genera from one particular horizon or section, or from a variety of locations, preferably from different continents.

The Scythian extinction appears to reflect the adaptive radiation of amphibians and reptiles. Global marine transgressions in the Scythian, following the extensive regressions of the Late Permian, flooded low-lying littoral plains and resulted in the development of new habitats in and around estuaries and swamps (Anderson and Cruickshank 1978). Subsequent radiation of Scythian tetrapods, mainly temnospondyl amphibians and thecodontian and cynodont reptiles, is reflected by the high total and per-taxon origination rates (Text-fig. 1) and resulted in an overall increase in diversity of six families despite the extinction of eleven families.

The development of endothermy in the therapsids cannot be proved and there is little or no evidence for the decline of 'anapsids' and diapsids at the expense of competitively superior therapsids. It may be more credible to attribute the radiation of therapsids, and the expansion of their geographical range, to the opportunistic utilization of recently vacated ecospace, rather than a dominance over their contemporaries.

The invertebrate and vertebrate extinctions are difficult to correlate because of the various geochronological schemes employed, the poor terrestrial record, and the punctuated marine record. However, data on the period of most severe extinction in each realm may be real, despite preservational biases, and should be compared.

The peak of invertebrate extinction in the Kazanian may be related to bipolar glaciation with attendant regressions and frigid global temperatures. The peak of vertebrate extinction has been related to the climatic fluctuations throughout the Tatarian that followed the Kazanian cooling interval (see above). It appears that the most significant extinction in each realm resulted from the response to the drop in temperature that briefly interrupted the global warming trend.

CONCLUSIONS

1. The Artinskian, Ufimian, Tatarian, and Scythian extinctions are distinct events affecting non-marine tetrapods during a period of high evolutionary turnover and adaptation. The data seem to be valid for all but the Tatarian event, a large part of which appears confused and biased by an incomplete rock record and possibly by ecological trends.
2. The high turnover from Artinskian to Scythian times is, in part, a consequence of the radiation of the mammal-like reptiles, but upheavals in the environment and frequent climatic fluctuations associated with warming and cooling trends played a significant, if not dominant, role.
3. Throughout the Permian, most especially the Late Permian, the mammal-like reptiles radiated. Much evidence is available to counter claims of competitively superior, endothermic therapsids displacing ectothermic reptiles. The pattern of faunal replacement does not support the role of competition as a macroevolutionary mechanism, and therapsids and undoubted ectotherms co-existed throughout the Late Permian.
4. The timing and pattern of extinction, combined with the results from several geochemical studies, effectively rules out the possibility of a catastrophic cause. There is some evidence of massive volcanic explosions during the Tatarian, but their size and nature was insufficient to cause the high level of terrestrial extinctions.
5. The extinctions in the marine realm during the Late Permian are most readily credited to the effects of global cooling accompanied by regressions of shallow seas. These factors probably influenced the extinctions of non-marine tetrapods during this time.

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