

# 24 The Late Triassic tetrapod extinction events

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## Introduction

The Triassic period (245–208 MYA) is widely recognized as having been crucial in the evolution of the tetrapods. During that period, many of the typical Late Paleozoic tetrapods – labyrinthodonts, procolophonids, and mammal-like reptiles – disappeared, or declined markedly, and new groups – dinosaurs, crocodiles, pterosaurs, lepidosaurs, testudines, and mammals – appeared for the first time. The changeover has been described in terms of a competitively based replacement, a sudden “mass extinction,” or something between these two extremes. Recently, there has been some controversy over both the pattern of the replacement and the mechanisms that may have produced that pattern. Colbert (1958a,b, 1966), Bakker (1977), Olson (1982), Wild (1982), Tucker and Benton (1982), and Benton (1983a,b, 1984a, 1985a) have noted a mass extinction among tetrapods in the Late Triassic, whereas Charig (1979, 1980, 1984), Bonaparte (1982), and others have seen the replacement as having been gradual (i.e., lasting for 25–30 MY). Furthermore, most authors have argued that the replacement was largely competitively based, whether or not they recognized a mass extinction, whereas Benton (1983a,b, 1984a, 1985a,b) has argued strongly that there is no evidence for competition.

In this chapter, I intend to review briefly the evidence that has been presented for and against the competitive models for the radiation of the dinosaurs and other “new” tetrapods in the Late Triassic. I argue that “competition” is a much overused and abused concept in macroevolution. I shall present preliminary data on the changeover as it is recorded in the Keuper sediments of southwestern Germany, and then review other evidence for worldwide tetrapod extinctions in the Late Triassic.

## Mass extinction or competition in the Late Triassic?

The idea of a mass extinction of tetrapods near or at the end of the Triassic is not new. Colbert (1949, 1958a,b, 1966, 1969) described the extinction of a whole range of groups, such as labyrinthodonts, procolophonids, “protorosaurs” (= prolacertiform diapsids), nothosaurs, placodonts, rhynchosaurs, “thecodontians,” and most mammal-like reptiles, at the Triassic–Jurassic boundary. These animals were replaced by new groups, such as the lissamphibians, turtles, ichthyosaurs, plesiosaurs, lepidosaurs, crocodiles, dinosaurs, and mammals. These extinctions and replacements have been noted by many authors. Explanations for these events have recently shifted toward a greater emphasis on competition.

Colbert (1949) initially recognized that the origin or radiation of several of the “new” groups in the Jurassic did not result from competition. The phytosaurs “were a highly successful and very dominant group of reptiles in the final phases of Triassic history” (Colbert 1949), but they died out for unknown reasons. The crocodiles, which were already present as small terrestrial carnivores, radiated into various aquatic niches after the extinction of the phytosaurs; therefore, competition was not responsible. However, in a later account, Colbert (1958a) concluded that some of the groups disappeared at the end of the Triassic because of competition with newly evolved forms. Thus, “eosuchians” (early “lizard-like” forms) “crowded out” the procolophonids, and the thecodontians may have outcompeted the mammal-like reptiles. Colbert had special problems in accounting for the extinction of the thecodontians: “they were well adapted to their environment, and they were widely distributed over several continents in great numbers” (Colbert 1949). He could not explain how the small early dinosaurs

and crocodiles could possibly have "competed" with the thecodontians and the phytosaurs. However, by 1969, Colbert argued that the thecodontians were eliminated by competitive pressure from their descendants, the dinosaurs, and likewise, that the mammal-like reptiles "vanished because of the highly progressive nature of their descendants [the mammals]. They evolved themselves into oblivion" (Colbert 1969, pp. 166-7).

The fact that many tetrapod groups died out at about the same time has suggested to several authors that an environmental change of some kind may have been involved. Colbert (1958b) noted that environments were changing in the Late Triassic to become generally more arid, and he hinted that this might have had something to do with the extinctions. A number of authors accepted this view and sought to link it with the competition-based theories for dinosaur success by arguing that different aspects of the physiology of dinosaurs gave them great advantages over the mammal-like reptiles and thecodontians in the new, more arid conditions. Some of these explanations of dinosaur superiority include: endothermy and nakedness (for heat loss) (Cox 1967; Crompton 1968), uricotelic (for water-retention) and ectothermy (Robinson 1971; Hotton 1980), improved locomotor ability (Bakker 1968, 1971; Charig 1972, 1980, 1984), endothermy (Bakker 1971, 1972, 1975, 1980), or inertial homeothermy (Spotila et al. 1973; Benton 1979; Spotila 1980). The list of "explanations" for the success of the dinosaurs could fill several pages and, if nothing else, it demonstrates the ingenuity of paleontologists (and nonpaleontologists) in making up mechanisms to explain "competitive replacements."

The hypothesis that the origin of the dinosaurs resulted from their successful competition with all comers has been challenged. Tucker and Benton (1982) and Benton (1983a,b, 1984a) presented evidence that several groups of dominant terrestrial reptiles (dicynodonts, diademodonts, rhynchosaurs, as well as most cynodonts and thecodontians) died out at the same time (middle Norian, Late Triassic) and that the dinosaurs radiated only *after* that extinction event. They argued that there was no need for competitive scenarios to explain the success of the dinosaurs: The dinosaurs took their chance and radiated opportunistically into empty ecospace in the Late Triassic, just as the mammals did in the Paleocene.

There are thus two diametrically opposed hypotheses to explain the "success" of the dinosaurs: the competition-based scenarios and the mass-extinction scenario. These should be testable insofar as we can discern different patterns in the fossil record: Benton (1983a) gave sets of criteria that might allow this to be done. However, the mechanisms

underlying the scenarios cannot be tested. Scenario making in paleontology is several steps removed from hard facts – it deals in probabilities, assumptions and guesswork – and it is heavily colored by personal viewpoints. This seems very clear in the attempts that paleontologists make to explain major events in the history of life, such as the Triassic tetrapod replacements. The very terminology that has been used in describing events in the Triassic is based on the assumption that large-scale competition was taking place. For example, Colbert (1958a) distinguished Paleozoic "holdovers," groups such as the labyrinthodonts, procolophonids, and the mammal-like reptiles, from "progressive" forms that arose during the Triassic, such as the lissamphibians, thecodontians, dinosaurs, and mammals. These two kinds of tetrapods have also been termed "palaeotetrapods" and "neotetrapods," respectively by Charig (1979, 1980, 1984). These authors, and many others, have assumed that a progressive group could always beat a holdover group – that the order of appearance of taxa in geological time is directly proportional to their competitive ability. The simple a posteriori observation that group A appears later in time than group B, and seems to have occupied a similar adaptive zone, is taken to prove that group A outcompeted group B. In other words, it is assumed that evolution leads to all round improvement through time in a regular machine-like way; but, who is to say that present-day mammals would "out-compete" their Pleistocene forebears in all conditions? The fact that present-day mammals live 1 MY after Pleistocene mammals does not mean that they are better and much improved creatures.

#### Competition in macroevolution

The role of competition in macroevolution is of particular relevance here. Many evolutionary biologists have assumed that competition is a major force in evolution. However, there is little evidence for this assumption.

A large body of recent research in community ecology has cast doubt on the all-encompassing role of competition. There is no question that competition can be shown to occur between members of the same species or of two similar species. However, it seems far from clear to many ecologists that competition actually shapes the majority of ecological communities or causes long-term evolutionary changes in species distributions or adaptations. Other factors, such as environmental fluctuations, predation, or a combination of several biotic and abiotic aspects of the ecology of a species (individualistic response) may be more important (see Connell 1980; Simberloff 1983; Strong et al. 1984; Price, Slobodkin, and Gaud 1984).

In macroevolutionary studies, "competition"

has been used to describe interactions between families, orders, classes, or even phyla. There are numerous problems associated with this view:

1. *Confusion of pattern and mechanism.* Most of the classic examples of long-term "competitive" replacements have been based on a particular kind of pattern that was observed from the fossil record. This has been called the "double-wedge" pattern by Gould and Calloway (1980): One taxon decreases in abundance through time while the other increases – correlated waxing and waning. Of course, such a pattern does not in any way prove that it was produced by competition: the two taxa might not have been interacting at all (e.g., the terrestrial flowering plants were radiating at the same time as the marine ichthyosaurs were declining), or the two taxa might have been responding differently to a new kind of predation or to one or more environmental changes (biotic and/or abiotic). "Competition" describes a mechanism, not a pattern.

2. *Oversimplification.* Competitive scenarios usually boil down to explanations of major faunal replacements in terms of simple key adaptations that supposedly gave their possessors great advantages. One common scenario states that the key adaptation of later archosaurs was their semierect or erect gait, and this is supposed to have been sufficient for them to vanquish the diverse mammal-like reptiles, rhynchosaurs, and the rest. This hypothesis must be a biological oversimplification and, like many such hypotheses, it does not bear close scrutiny. The rhynchosaurs, and many Middle to Late Triassic mammal-like reptiles, had semierect gait, just like many of their supposed betters, the thecodontians. However, erect gait was not the sole preserve of the dinosaurs. Most Late Triassic thecodontians were also erect: Ornithosuchidae, Rauisuchidae, Poposauridae, and Stagonolepididae, as well as some early crocodylomorphs (Saltoposuchidae) and the pterosaurs (Bonaparte 1984; Parrish 1984; Benton 1984b; Padian 1983).

3. *Lack of evidence.* Competition cannot be assumed as the mechanism that has produced most extinctions and mass extinctions in the history of life. The probabilities of other explanations must be assessed in any particular case.

4. *Incorrect scaling of concepts.* There are three points to my critique here. First, it may be wholly inappropriate to apply the terms of individual and species interactions to interactions between larger taxonomic entities. Biologists often try to describe macroevolutionary phenomena that lasted for millions of years ("geological time") in the language of present-day community ecology, which applies to events that take place over days, weeks, or years at most ("ecological time"). It seems likely that major evolutionary events involve mechanisms, such as the

causes of mass extinctions, that are quite distinct from the day-to-day events going on down in the woods.

The second problem of scaling concerns the identification of key adaptations to explain the success of whole groups. Such adaptations (e.g., endothermy or erect gait) might have been selectively advantageous to the first species that possessed them, but it is hard to see how adaptations of these kinds have relevance for higher taxa, which include many and various species. How could a particular key adaptation prove to be advantageous to all of the species within one taxon and in all situations?

The third problem of scaling of competition in macroevolution concerns the duration of selection pressures. Most so-called competitive replacements lasted over millions of generations (typical examples lasted 2–30 MY), and it is hard to see how a differential selection pressure could have been maintained for so long. The advantage, when reduced to the level of the individual organism (because we are considering natural selection), would have been so miniscule as to be indistinguishable from stochastic effects.

#### **A detailed example: the Keuper of southwestern West Germany**

The Late Triassic in the southwest of the Federal Republic of Germany (Baden-Württemberg) is represented by a succession of terrestrial sediments, the Keuper, which has yielded abundant tetrapods at various levels. I studied this succession because the vertebrate-bearing beds are better dated than most other Late Triassic terrestrial sequences. I tried to assess the patterns of faunal replacement in this single case study, and to examine the timing and nature of the radiation of the dinosaurs in particular. The present account is preliminary: some of the results are summarized in Benton (1984c).

#### *The oldest dinosaurs*

Most authors now accept that the first dinosaurs appeared in the Late Triassic. However, many general accounts published in the 1970s draw the different dinosaur lineages well back into the Middle Triassic. The records of Middle Triassic dinosaurs have arisen from three problem areas: (1) thecodontian and indeterminate remains described as those of dinosaurs, (2) imprecise definition of what a "dinosaur" is, and (3) incorrectly dated geological formations that contain dinosaurs.

#### *Doubtful early dinosaurs*

As to the first problem, a large number of remains of doubtful early dinosaurs have been recorded from the Middle, and even the Lower, Triassic of Germany and elsewhere. For example, Huene (1914,

1932) noted ten named dinosaurs from the German Muschelkalk. These have subsequently turned out to be prolacertiforms, unidentifiable archosaurs, or even ?placodonts (Wild 1973; Benton 1984c). One of the key groups of supposed early dinosaurs has been the Teratosauridae from the Middle and Late Triassic of Europe, as well as the Late Triassic and Early Jurassic of South Africa and China. However, these specimens turn out to be an assemblage of skulls and teeth of rauisuchid thecodontians (*Teratosaurus*) or Archosauria inc. sed., together with the skeletons of prosauropods (Walker 1964; Charig, Attridge, and Crompton 1965; Galton 1973; Benton 1984b,c).

#### The Dinosauria

The second factor that may have led to the identification of Middle Triassic dinosaurs concerns the definition of a dinosaur. Until recently, and with only a few exceptions (e.g., Bakker and Galton 1974; Bonaparte 1976), the dinosaurs were thought to have evolved as several separate lineages that derived from ancestors in the Middle Triassic or earlier. However, a remarkable consensus of opinion that the dinosaurs are a monophyletic group has now been reached by several workers who have independently carried out cladistic analyses of the archosaurs (Benton 1984c; Gauthier 1984; Norman 1984; Padian 1984; Parrish 1984; Paul 1984; Sereno 1984; Benton 1984d). The closest sister groups of the Dinosauria are *Lagosuchus*, the Ornithosuchiidae, and, controversially, the Pterosauria (Padian 1984; Gauthier 1984). A monophyletic Dinosauria tends to move the origins of the group upward, possibly to the very top of the Ladinian.

#### Stratigraphy

The third problem that gave rise to extensive records of Middle Triassic dinosaurs was one of stratigraphy. Until the mid 1970s, many authors, especially Romer (e.g., 1970), assigned all beds that contained rhycolosaurs to the Middle Triassic; these included the Santa Maria Formation of Brazil, the Ischigualasto Formation of Argentina, the Maleri Formation of India, and the Lossiemouth Sandstone Formation of Scotland. These are now all firmly dated in the Upper Triassic, either as late Carnian (Bonaparte 1978; Chapter 25), or as early Norian (Anderson and Cruickshank 1978; Tucker and Benton 1982; Benton and Walker 1985).

In this chapter, I accept the stratigraphic assignments given by Anderson and Cruickshank (1978) and Tucker and Benton (1982) for the Early and Middle Triassic reptile beds, and the assignments given by Olsen and Galton (1977, 1984) and Olsen, McCune, and Thomson (1982) for the Late Triassic and Early Jurassic formations. The majority of horizons that Anderson and Cruickshank (1978)

placed in the early-middle Norian are reassigned to the middle-late Carnian (e.g., Santa Maria, Ischigualasto, Maleri, Lossiemouth, Argana, Lockatong, Stockton, Wolfville, Popo Agie). The Chinle and Dockum Formations are assigned wholly to the late Carnian by Olsen et al. (1982) on the basis of stratigraphic evidence from the fossil fish and palynology (Dunay and Fisher 1974, 1979; Gottesfeld 1980). I accept a late Carnian assignment for the lower portions of the Dockum and Chinle. However, some reptile-bearing upper units of both formations may still belong in the early-middle Norian (Chapters 10 and 11), and I assign them there in this chapter.

The oldest dinosaurs, then, are known from the middle to upper Carnian interval (Upper Triassic) from several places around the world: *Staurikosaurus* (Santa Maria Formation, Brazil); *Herrerasaurus*, *Ischisaurus*, and *Pisanosaurus* (Ischigualasto Formation, Argentina); *Saltopus* (Lossiemouth Sandstone Formation, Scotland); unnamed forms (Maleri Formation, India); *Coelophysus* (Chinle Formation, Dockum Formation, western United States); *Azendohsaurus* (Argana Formation, Morocco); and unnamed "fabrosaurids" (Weishampel and Weishampel 1982) from the Wolfville Formation of Nova Scotia, the Chinle Formation of Arizona, the Dockum Formation of Texas, the Chatham Group of North Carolina, and the New Oxford Formation of Pennsylvania. Many of the unnamed "fabrosaurids" are represented only by odd teeth and other fragments, and some may turn out not to be dinosaurs. The earliest dinosaurs from Germany occur in the Unterer Stubensandstein (early to middle Norian): a plateosaurid from Ochsenbach near Heilbronn, and a plateosaurid from Ebersbach a.d. Fils near Stuttgart.

#### Stratigraphy of the Upper Triassic in Germany

Fossil tetrapods have been collected from at least seventy localities in the Keuper of Baden-Württemberg in a strip that runs from Heilbronn and Schwäbisch Hall in the northeast to Donaueschingen in the southwest (Fig. 24.1). The most abundant finds come from the general areas of Stuttgart and Tübingen, and the most important museum collections are housed in those two cities. The Keuper deposits continue northeast into Franconia and Thuringia, and southwest into Switzerland and into Lorraine and Luxembourg, where further similar reptile finds have been made, but are less abundant than in Baden-Württemberg.

The lithostratigraphy of the Keuper of Baden-Württemberg is well established on the basis of detailed field observations throughout the whole region (Brenner 1973, 1978a,b), and standard sections have been drawn up (Brenner and Villinger 1981; Gwinner 1981). A typical section (Fig. 24.2) shows a se-

quence of largely terrestrial sediments. The marine Muschelkalk (Middle Triassic, not shown) passes up through the transitional marine and brackish Lettenkeuper (Unterer Keuper) into the terrestrial Mittlerer Keuper (Oberer Keuper) into the terrestrial Mittlerer Keuper. The Rät (Oberer Keuper) represents a return to marine conditions. During the critical Mittlerer Keuper episode, and especially in the Stubensandstein, when dinosaurs appeared in Germany, there were no major environmental changes (Brenner 1973, 1979).

It has proved difficult so far to correlate the almost entirely terrestrial German Keuper with standard marine ammonite zones of the southern Alps. The ammonite zones of the Late Triassic (Tozer 1967, 1974, 1979) have been tentatively correlated with provisional standard palynological zones for terrestrial sediments (Visscher, Schuur-

man, and Van Erve 1980; Visscher and Brugman 1981; Anderson 1981) (see Fig. 24.3). Palynomorphs are well known from several horizons in the Keuper, but until a worldwide standard is agreed, it will be hard to date individual beds precisely. There appear to be two ways of interpreting the German Keuper, and these are shown in Figure 24.3. According to interpretation (A), the Rote Wand and Kieselsandstein are early Norian (Geiger and Hopping 1968; Fisher 1972; Fisher and Bujak 1975; Dunay and Fisher 1979; Dockter et al. 1980; Anderson 1981; Schröder 1982), while according to interpretation (B), those two horizons are late Carnian (Kozur

Figure 24.1. Localities in southwestern West Germany that have yielded Late Triassic tetrapods. Main rivers and towns are marked for orientation, and each fossil locality is coded by the stratigraphic horizon that yielded the tetrapod(s) (see explanatory box on the figure). The data came from the collections of Keuper tetrapods in Stuttgart and Tübingen, and from the paleontological and geological literature. A base map of central Europe is also given. Abbreviations: AUS, Austria; BRD, West Germany; CZ, Czechoslovakia; DDR, East Germany; FR, France; N, Netherlands; SW, Switzerland.

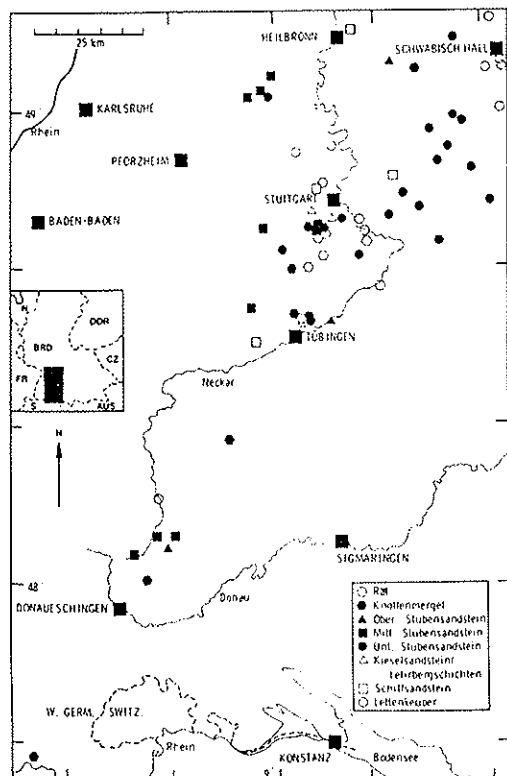


Figure 24.2. A summary lithostratigraphic section through the Keuper of southwestern West Germany. The rock units are named on the left, and the current stratigraphic terms are given on the right, with the standard abbreviations. Tetrapods have come from numerous horizons within this sequence (shown by arrows). Based on Brenner and Villinger (1981).

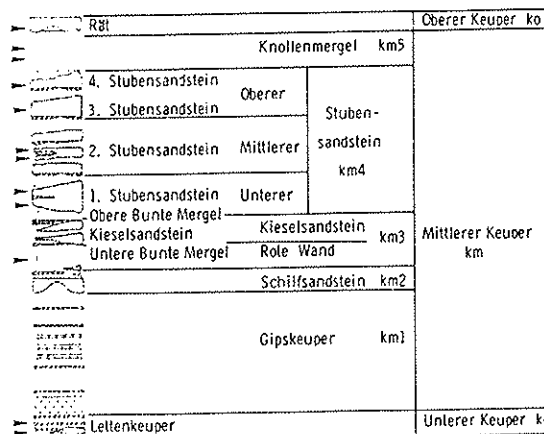


Figure 24.3. Biostratigraphy of the Upper Triassic. The ammonite zones (\* = Tozer 1979, 1974, 1979) are tentatively correlated with provisional palynological zones (\*\* = Visscher et al. 1980, Visscher and Brugman 1981, Anderson 1981). See the text for explanations of the alternative stratigraphic and chronometric assignments.

	Ammonite zones*	Palynological zones**	Zonations of German Keuper (A)	Zonations of German Keuper (B)	Dates (Ma)
					(1) (2) (3)
Rhaetian	Erickhaysi Amoenus Cordilleranus	Rhaetian Sevastian	Rät Knollenmergel	Rät Knollenmergel	213 204 208
Norian	Columbianus Rutherfordi Mannus	U. Norian Altagian	Stubensandstein	Stubensandstein	
	Dawsoni Kera	L. Norian Raciani	Kieselsandstein Rote Wand	Kieselsandstein Rote Wand	225 220 225
Carnian	Macrolonatus Welleri	Tovallian	Schiffsandstein	Schiffsandstein	
	Bilieri Norseum Obesum	Julian Corvillian	Gipskeuper	Schiffsandstein Gipskeuper	
Ladinian	Sulzerlandi Macleari Nigunae	Langobardian	Lettenkeuper	Lettenkeuper	231 229 230

1975; Gall, Durand, and Muller 1977; Olsen et al. 1982). Magnetostratigraphic evidence indicates that the Schilfsandstein is latest Carnian in age (Hahn 1984), and this favors interpretation (A). For the purposes of the rest of this study, interpretation (A) is followed: If (B) had been selected, my conclusions would be little changed.

A final problem with the stratigraphy concerns the numerical ages of the various formations. Three recently published time scales (Odin 1982; Harland et al. 1982; Palmer 1983) offer different age dates for the stage boundaries (1, 2, and 3, respectively, in Fig. 24.3). I have arbitrarily selected Palmer's (1983) dates, as the more recent compilation. Again, my conclusions would not be materially affected by the use of either of the other two time scales.

Distribution of tetrapods in the southwestern West German Keuper

Tetrapod remains have been collected from numerous localities (Fig. 24.1) and horizons (Fig. 24.2) in the Baden-Württemberg Keuper. The largest collections of these are preserved in the Staatliches Museum für Naturkunde Stuttgart and the Institut für Geologie und Paläontologie der Universität Tübingen, with smaller collections in the museums in München, Erlangen, Göttingen, Berlin, and London. I examined the specimens in all of these collections, and took notes of locality, stratigraphic horizon, material present, and collecting data for each specimen. I attempted to track down each locality precisely with the help of topographic and geological maps and to establish the precise stratigraphic horizon that had yielded reptiles by the use of the collecting data, the general literature, and geological maps and memoirs. This work was done in the excellent libraries attached to the museums in Stuttgart and Tübingen. I then made up a sheet for each locality, listing all of the tetrapod specimens that had been collected, and estimated the minimum numbers of individual animals present at each. For this, I attempted to count only skulls, or only left femora of a particular species. Full details of localities, stratigraphy and species counts will be published elsewhere.

For the present general study, I wanted to assess the approximate changes in the relative composition of the faunas through time. I added up the numbers of individuals from each locality that had come from a particular horizon, such as the Schilfsandstein or the Unterer Stubensandstein, and converted these to percentages of the totals. To my knowledge, no tetrapods have been found in the Gipskeuper or the Rote Wand, and only very few specimens are known from the Kieselsandstein or Bunte Mergel (Lehrbergsschichten). I did not make

estimates of tetrapod distributions in the Rät bonebeds. Furthermore, the figures for the Lettenkeuper were based on data for the Kupferzell excavation (Wild 1980). Both the Lettenkeuper and the Rät represent very different environments of deposition from the remaining Mittlerer Keuper – both show clear marine-brackish water influence. The significant faunal changes that are of interest here occurred in the more typical floodplain sandstone deposits of the Mittlerer Keuper, and the faunal changes are not associated with any obvious environmental change.

The results of the preliminary study (Table 24.1 and Fig. 24.4) show that the earlier faunas were heavily dominated by amphibians (Lettenkeuper, Schilfsandstein). The gap in the record between the Schilfsandstein and the Stubensandstein is unfortunate, because by early Stubensandstein times, the amphibians were much rarer (ca. 10 percent of the fauna). The commonest animals were early turtles (*Proganochelys* and *Proterochersis*). Thecodontians (rauisuchids and phytosaurs) were present, as well as a couple of plateosaurid dinosaurs, the first dinosaurs from Germany (ca. 7 percent of the fauna).

By middle Stubensandstein times, the proportion of dinosaurs had risen to 21 percent, and several genera are known: the prosauropods *Plateosaurus*, *Sellosaurus*, *Thecodontosaurus*, and *Efraa-*

Figure 24.4. Faunal changes through southwestern German Keuper (Late Triassic). The time scale for stage boundaries is from Palmer (1983), and the Keuper formations are spaced arbitrarily through the whole time span. Nonmarine tetrapod faunas are known from several horizons, but only those from the Lettenkeuper, Schilfsandstein, Stubensandstein, and Knollenmergel were abundant enough to give data on proportional composition. The total number of specimens of each genus that had been found in each formation was assessed (see text for details), and approximate percentages were calculated for each (Table 24.1). Labyrinthodonts dominated early faunas, but the dinosaurs radiated rapidly in Stubensandstein times. Abbreviations: DINO, dinosaurs; LABY, labyrinthodonts; PHYT, phytosaurs; TEST, testudines; THEC, thecodontians; VAR, various (odd diapsids, ?cynodonts).

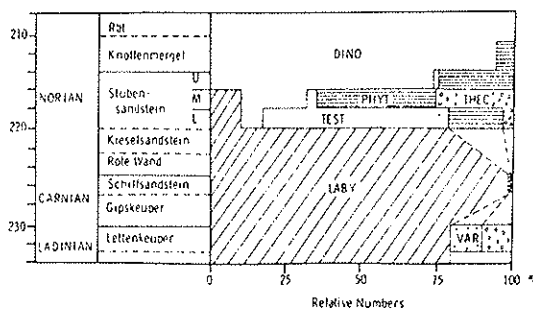


Table 24.1 Typical nonmarine tetrapod faunas from the Keuper southwestern West Germany (FRG).

		No.	%
Lettenkeuper (Wild 1980)*			
LABY	<i>Plagiosternum</i>		70
	<i>Mastodonsaurus</i> , etc.		10
DIAP	<i>Tanystropheus</i> , etc.		6
THEC	rauisuchid; indet.		10
THER	? cynodonts		4
Schilfsandstein			
LABY	<i>Metoposaurus</i>	8	12
	<i>Cyclotosaurus</i>	50+	785
THEC	<i>Belodon</i>	1	3
	<i>Dyoplax</i>	1	
	indet.	2	
Unterer Stubensandstein			
LABY	<i>Cyclotosaurus</i>	2	10
	<i>Plagiosaurus</i>	1	
TEST	<i>Proganochelys/Proterochersis</i>	18	60
THEC	<i>Teratosaurus</i>	1	3
	phytosaur	6	20
PROS	"plateosaurid"	2	7
Mittlerer Stubensandstein			
LABY	<i>Cyclotosaurus</i>	10	10
	<i>Plagiosternum</i>	4	
	<i>Metoposaurus</i>	3	
TEST	<i>Proganochelys</i>	3	2
THEC	<i>Aetosaurus</i>	31	19
	<i>Teratosaurus</i>	14	8
	phytosaur	65	39
PROS	<i>Plateosaurus/Sellosaurus</i>	22	18
	<i>Thecodontosaurus</i>	4	
	<i>Efraasia</i>	3	
COEL	<i>Procompsognathus</i>	2	3
	<i>Halticosaurus</i>	3	
CROC	<i>Saltoposuchus</i>	2	1"
Oberer Stubensandstein			
TEST	<i>Proganochelys</i>	3	6
THEC	phytosaur	9	17
PROS	<i>Plateosaurus</i>	41	77
Knollenmergel†			
THEC	phytosaur	1	5
PROS	<i>Plateosaurus</i>	19	95

Note: The data are based mainly on the collections in Stuttgart and Tübingen. Abbreviations: COEL, Coelurosauria; CROC, Crocodylia; DIAP, Diapsida (odd groups); LABY, Labyrinthodontia; PROS, Prosauropoda; TEST, Testudines; THEC, "thecodontians"; THER, Theropoda.  
 Note: "Estimated percentages.

sia, and the theropods *Procompsognathus* and *Halticosaurus*. Phytosaurs, rauisuchids, and aetosaurs were also fairly abundant. The late Stubensandstein faunas consist almost entirely of the dinosaur *Plateosaurus* (ca. 77 percent of the fauna) with rarer turtles and phytosaurs. By Knollenmergel times, the proportion of dinosaurs had risen to 95 percent.

These data from the German Keuper show an increase in the proportion of dinosaurs present in typical terrestrial faunas from 7 to 95 percent in a time span of 8 MY or so, and the main increase, from 21 to 77 percent, occurred in as little as 2–4 MY (Mittlerer–Oberer Stubensandstein, Middle Norian). However, the data cannot simply be taken as defining the shape of the adaptive radiation of the dinosaurs. As mentioned earlier, there are clearly collection and preservation biases that cannot be precisely assessed, but the changes in proportions (7–95 percent) are probably large enough to have some biological meaning. More important is the fact that the generic diversity of dinosaurs declined from the Mittlerer Stubensandstein to the Knollenmergel; there were five or six genera of dinosaurs in the former, and probably only one in the latter. The “radiation” from 21 to 95 percent was all *Plateosaurus*. A second problem is that *Plateosaurus* is already quite an advanced dinosaur, and dinosaurs had appeared earlier in other parts of the world (see above). The timing of events suggests that what we are seeing in Germany is the result of an immigration of dinosaurs from elsewhere, and the sample of dinosaurs from the Knollenmergel is probably restricted by preservation bias.

The absence of mammal-like reptiles and rhynchosaurs in Germany makes it hard to compare events there with the typical Gondwana pattern. The oldest known dinosaurs are middle or late Carnian in age (see above) – the dinosaurs in North and South America arose at least 8–10 MY before they reached Germany. The oldest European dinosaur, *Saltopus* (if it is a dinosaur), also dates from the late Carnian. The earliest clearly identifiable true dinosaurs were podokesaurids (e.g., *Coelophysis*), and this group is known from the Mittlerer Stubensandstein (*Halticosaurus*, *Procompsognathus*). A first for Germany, however, was the appearance of prosauropods, which were diverse in the Mittlerer Stubensandstein (*Plateosaurus*, *Sellosaurus*, *Efraasia*, *Thecodontosaurus*), and then spread to other parts of Europe and to South America in the late Norian, and to South Africa, North America, and Southeast Asia in the Early Jurassic.

The early evolution of dinosaurs is still obscure in many respects, but there is evidence now that the small- to medium-sized podokesaurids and others radiated (i.e., became diverse and widespread) to some extent in the middle and late Carnian (225–8

MY), and then much more so in the middle Norian (215–21 MY). The prosauropods became established and radiated in the middle Norian, as seen in Germany, and then spread worldwide in the late Norian, and especially in the Early Jurassic. The middle Norian radiation of podokesaurids and of prosauropods occurred some 4–5 MY after the extinction of a range of thecodontian and mammal-like reptile groups at the end of the Carnian, and the Early Jurassic radiations again occurred after the extinction of the last thecodontians (see below).

#### Evidence for mass extinctions of nonmarine tetrapods in the Late Triassic

Several authors (e.g., Colbert 1949, 1958b; Bakker 1977; Olson 1982; Tucker and Benton 1982; Wild 1982; Benton 1983a,b, 1984a) have noted a mass extinction of nonmarine tetrapods in the Late Triassic, or at the Triassic–Jurassic boundary. There are many problems associated with identifying mass extinctions among fossil vertebrates (the patchy record and stratigraphic uncertainty), but several kinds of evidence point to the occurrence of two such events in the Late Triassic.

The term “mass extinction” can have different meanings. In this chapter, I use the term only as a descriptor of a pattern that may be observed in the fossil record, and I define a mass extinction as a genuine fall in diversity that occurred during a stratigraphic stage. This definition calls for the observation of a drop in the number of taxa present when one stratigraphic stage is compared with its forerunner, and the strong belief that the drop is not simply the result of a gap in the fossil record (produced by preservation failure or collection failure). The restriction of time to a stratigraphic stage is simply a pragmatic measure of the maximum resolution that is possible for most terrestrial vertebrate deposits – we may believe that the mass extinction occurred “overnight,” but usually proof of that is lacking. I do not imply that a mass extinction need be caused by an excessively high extinction rate [cf. Raup and Sepkoski’s (1982) statistical test] because a marked fall in diversity may equally be caused by a low origination rate. In other words, the definition of a mass extinction in terms of rates would imply the assumption of one kind of mechanism as having been involved. I believe that the study of rates, and of other aspects of mass extinctions, such as biological and physical causes, must be secondary to the observation of a mass extinction pattern.

#### Family diversity analysis

A plot of the numbers of families of nonmarine tetrapods present through time was produced (Fig. 24.5). This study is concerned with the fossil record of nonmarine tetrapods: this is taken to include ter-



restrial, freshwater and flying forms, but excludes fully marine families. A listing of all of the families of terrestrial tetrapods was made using the most recent taxonomic reviews, as well as secondary literature, to the end of 1984 [details of the main sources of data are given in Benton (1985a)]. A small number of extinct families was excluded from the analysis because they were based on single, often incomplete, specimens. This left a total of 730 families, of which 469 are extinct. The range in geological time for each family was determined from the most recent available literature, and this was resolved to the level of the stratigraphic stage (duration, 2–19 MY; mean duration, 6 MY). The time scale selected was that of Palmer (1983), which is based on several recent compilations, including Harland et al. (1982), Odin (1982), and Snelling (in press). The term "Rhaetian" refers to a stage at the very top of the Triassic that is often included in the Norian now (Tozer 1979; Hallam 1981).

The graph of tetrapod family diversity versus time shows several declines, including one in the Late Triassic (Fig. 24.5). Total family diversity fell from 25 in the Norian to 22 in the "Rhaetian" and

17 in the Hettangian. The Norian–"Rhaetian" drop in diversity represents a loss of 28 percent of families that were present at the start (cf. the Maastrichtian drop of 14 percent).

Extinction, origination, and diversification rates were then calculated from the data on non-marine tetrapod family diversity. Total extinction ( $R_e$ ) and total origination ( $R_o$ ) rates were calculated as the number of families that disappeared or appeared, respectively, during a stratigraphic stage, divided by the estimated duration of that stage ( $\Delta t$ ):

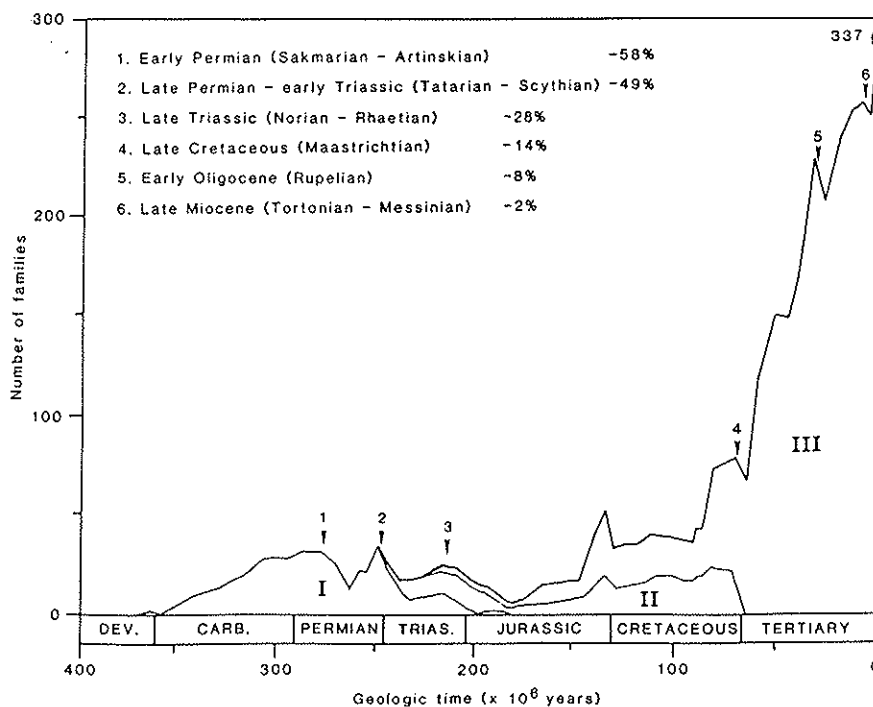
$$R_e = \frac{E}{\Delta t} \quad \text{and} \quad R_o = \frac{S}{\Delta t}$$

where  $E$  is the number of extinctions and  $S$  is the number of originations. Per taxon extinction ( $r_e$ ) and origination ( $r_o$ ) rates were calculated by dividing the total rates by the end-of-stage family diversity  $D$  (Sepkoski 1978):

$$r_e = \frac{1}{D} \cdot \frac{E}{\Delta t} \quad \text{and} \quad r_o = \frac{1}{D} \cdot \frac{S}{\Delta t}$$

The per taxon rates can be seen as the "probability of origin" or the "risk of extinction." The diversi-

Figure 24.5. Diversity (total number of families recorded in a stage) through time for families of terrestrial tetrapods. The upper curve shows total diversity through time, and six apparent mass extinctions are indicated by drops in diversity (see the text for explanations). These are numbered 1–6, and the relative magnitude of each drop is given in terms of the percentage of families that disappeared. Three assemblages of families succeeded each other through time; I, labyrinthodont amphibians, anapsids, mammal-like reptiles; II, early diapsids, dinosaurs, pterosaurs; III, the "modern groups": frogs, salamanders, lizards, snakes, turtles, crocodiles, birds, and mammals. These assemblages (I–III) are shown for illustrative purposes only: the data are not robust enough for a factor analysis (cf. Sepkoski 1981). Abbreviations: CARB., Carboniferous; DEV., Devonian; TRIAS., Triassic.



fication rate ( $r_d$ ) was calculated as the difference between the per taxon origination and the per taxon extinction rate (Sepkoski 1978):

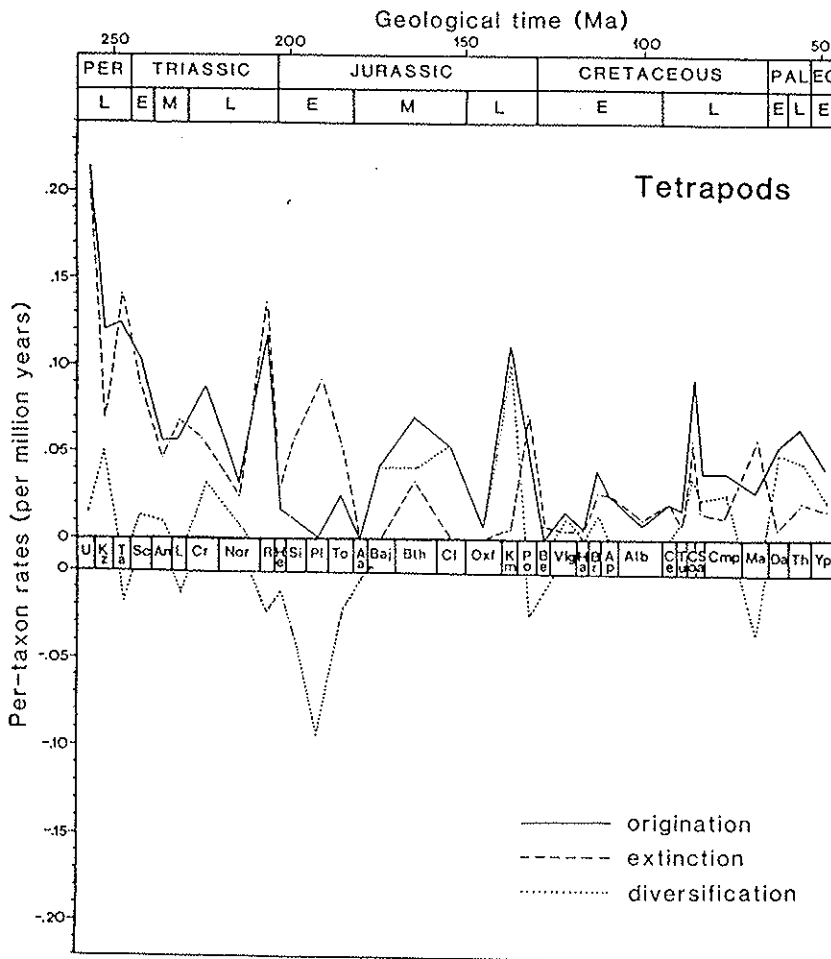
$$r_d = r_s - r_e$$

In this example, the per taxon family extinction and origination rates were not very high in the Norian, but they were high in the "Rhaetian" (Fig. 24.6). The diversification rate was negative in the "Rhaetian," although not quite as low as in the terminal Cretaceous (Maastrichtian) (Fig. 24.6) (Benton 1985a). The very low diversification rate in the

Pliensbachian, and the high rates from the Bajocian to the Kimmeridgian, may be an artifact of the poor fossil record of terrestrial tetrapods during parts of the Early and Middle Jurassic.

The record of turnover of nonmarine tetrapod families may be studied in more detail. Many of the important tetrapod-bearing formations have been tentatively assigned to particular parts of the five (or six) standard Triassic stages. For example, Anderson and Cruickshank (1978) were able to determine twenty tetrapod "substages" in the Triassic. I have modified their compilation of data for the Late Trias-

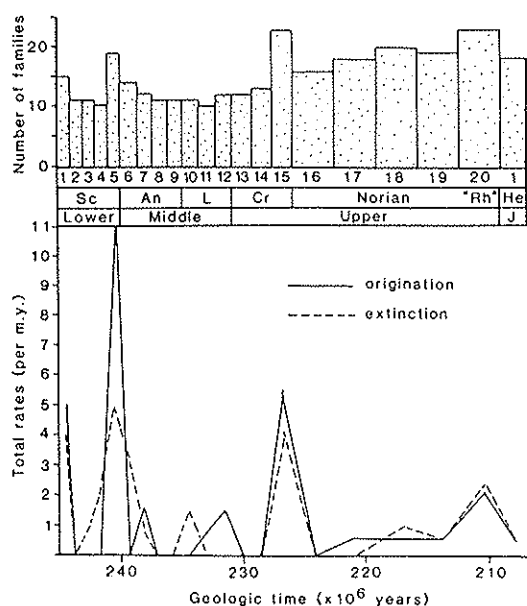
Figure 24.6. The pattern of origination, extinction, and diversification of terrestrial tetrapod families between the Late Permian and the Early Eocene. Per taxon rates are plotted on the vertical axis, and time (in millions of years) on the horizontal axis. The time scale is from Palmer (1983). The high extinction rate and low diversification rate in the Early Jurassic are probably the result of the poor fossil record of parts of the Early and Middle Jurassic, rather than being true rates. Abbreviations of stratigraphic stages: Aa, Aalenian; Alb, Albian; An, Anisian; Ap, Aptian; Baj, Bajocian; Be, Berriasian; Br, Barremian; Bth, Bathonian; Ce, Cenomanian; Cl, Callovian; Cmp, Campanian; Co, Coniacian; Cr, Carnian; Da, Danian; Ha, Hauterivian; He, Hettangian; Km, Kimmeridgian; Kz, Kazanian; L, Ladinian; Ma, Maastrichtian; Nor, Norian; Oxf, Oxfordian; Pl, Pliensbachian; Po, Portlandian; R, Rhaetian; Sa, Santonian; Sc, Scythian; Si, Sinemurian; Ta, Tatarian; Th, Thanetian; To, Toarcian; Tu, Turonian; U, Ufnian; Vlg, Valanginian; Yp, Ypresian.



sis according to the new dating scheme of Olsen and Galton (1977, 1984). I plotted family diversity and total origination and extinction rates for families of Triassic nonmarine tetrapods (Fig. 24.7). Family diversity fluctuated throughout the Triassic, with particularly noticeable drops at the end of the Scythian (cf. "substages" 5 and 6) and in the Late Triassic (substages 15-16 and 20-Jurassic 1). Extinction rates were high in the early and late Scythian (substages 1 and 5), the early Anisian (substage 6), the late Carnian (substage 15), and the "Rhaetian" (substage 20). The high Scythian and Anisian rates may be partly explained as artifacts of a subsequent poor fossil record (i.e., some of the recorded extinctions might have occurred later, during the gap in the record). The high rate in the late Carnian, which was associated with a marked drop in diversity, however, cannot be explained in that way, although the "Rhaetian" extinction might be partly an artifact of a poorer Hettangian record (cf. Table 24.3 and Fig. 24.9 below).

It must be noted that, although the extinction rates in the Late Triassic, in general, and in the late Carnian and "Rhaetian" in particular, are high, they are not detected as excessively high outliers from a linear regression analysis, using the techniques of Raup and Sepkoski (1982). There are, however, statistical and theoretical problems with this technique (Quinn 1983; Raup, Sepkoski, and Stigler 1983), and one further problem is that it takes no account of the effects of a depressed origination rate that can mimic the effects of a mass extinction by reducing overall taxonomic diversity. Total origination rates were low in the "substages" following the late Carnian and the "Rhaetian" (Fig. 24.7). It should be noted, in this context, that the marked drop in the diversity of nonmarine tetrapods at the end of the Cretaceous period (Fig. 24.5) is not associated with a statistically high total extinction rate (using the methods of Raup and Sepkoski 1982). Several key groups had their last known representatives then (e.g., dinosaurs and pterosaurs), but most of the fall in diversity was caused by a low origination rate (Fig. 24.6) (Benton 1985a).

Figure 24.7. The turnover of nonmarine tetrapod families in the Triassic. The data on family distributions, and the tetrapod "substages" 1-20 are taken from Anderson and Cruickshank (1978), with stratigraphic modifications according to Olsen and Galton (1977, 1984, see the text). Family diversity and total extinction and origination rates are shown from the early Scythian to the early Hettangian (lowermost Jurassic). The time scale is from Palmer (1983). Abbreviations: J, Jurassic; Sc, Scythian; An, Anisian; L, Ladinian; Cr, Carnian; "Rh," "Rhaetian"; He, Hettangian; J, Jurassic.



Species diversity analysis

A more detailed study of the distribution in time of all Late Triassic nonmarine tetrapods was carried out. A list of all species of amphibians and reptiles from the Carnian, Norian, and Rhaetian was compiled from the most recent available sources. Where possible, a monographic review of a whole family was used, and more recently described taxa were appended from other sources. Species that are based on single fragmentary and questionable specimens were omitted. The main references for the species data are given in Table 24.2.

Stratigraphic assignments were taken from Olsen and Galton (1977, 1984), as explained above. The data are shown in Figure 24.8, which takes the form of a spindle diagram of families in which the width of the spindle is directly related to the number of species present in each time interval. The time scale is that of Palmer (1983).

This more detailed overview of the occurrence of tetrapod species in the Late Triassic shows that there was not a single time during which an overall and decimating mass extinction occurred. However, there are several intervals during which species diversity levels fell markedly. These may be further elucidated by studying the data in Figure 24.8.

It is evident from Figure 24.8 that the fossil record is incomplete in places: Every dashed line represents a time interval during which fossils have not been found. However, the group is assumed to have been present because it is known from below and above that particular time interval. Thus, for example, family No. 1 (the Capitosauridae) is not

recorded from the early or middle Carnian or the lower middle Norian, but it is known from above and below each of these time intervals. Furthermore, it is evident that certain time intervals (e.g., the early Carnian and the early Norian) have poorer fossil records overall than the others. A measure of the completeness of the record of nonmarine tetrapods was calculated by taking the ratio of families recorded to the families apparently present for each of the time intervals used in the Late Triassic (Table 24.3). The apparent number of species per time interval was then divided by the completeness ratio in order to give an indication of the probable number of species that would have been collected if the fossil record were equally complete (or incomplete) throughout the Late Triassic.

The unadjusted species counts and the adjusted species counts (Table 24.3 and Figure 24.9) show three drops against an overall rising trend through time. These drops, in order of magnitude, represent losses of 66 percent (late Carnian to early

Norian), 43 percent (early middle to late middle Norian), and 38 percent (late middle to late Norian) of all species present (from the adjusted species counts). The small drop from the "Rhaetian" to the Hettangian, seen in the unadjusted species counts, is removed when the completeness ratio is applied. These figures are high and the first one certainly approaches the figures calculated for marine species in the major terminal Permian extinction event [77–96 percent loss of species (Sepkoski 1982)].

The analysis of family diversity in the Late Triassic suggests that there were two main extinction events, one at the end of the late Carnian, and one at the end of the "Rhaetian," thus at the Triassic–Jurassic boundary. In terms of magnitude, the first of these was the greater. The analysis of species diversity confirms the first event, and its impact, but there is no clear drop in species numbers at the Triassic–Jurassic boundary. In fact, two possible declines are identified in the middle and late Norian.

Table 24.2 Main sources of data on the species of Late Triassic nonmarine tetrapods

	Taxon	Source
1–5	Labyrinthodontia	Carroll and Winer 1977
6	Procolophonidae	Colbert 1960
7	Proganochelyidae	Gaffney and Meeker 1983
8–11	Various diapsids	Benton 1985b
12	Proterochampsidae	Sues 1976
13	Aetosauridae	Krebs 1976
14	Rauisuchidae	Bonaparte 1981
15	Poposauridae	Chatterjee 1985
16	Phytosauridae	Westphal 1976, Buffetaut and Ingavat 1982
17	Ornithosuchidae	Bonaparte 1975
18	Scleromochlidae	Benton and Walker 1985
19	Eudimorphodontidae	Wild 1978
20	Dimorphodontidae	Wild 1978
21	Saltoposuchidae	Bonaparte 1978
22	Sphenosuchidae	Bonaparte 1978
23	Protosuchidae	Nash 1975
24	Podokesauridae	Steel 1970
25	Anchisauridae	Galton 1976
26	Plateosauridae	Huene 1932, Galton 1976
27	Melanorosauridae	Bonaparte 1978
28	Fabrosauridae	Colbert 1981
29	Heterodontosauridae	Hopson 1975
30	Sphenodontidae	Benton 1985b
31	Kannemeyeriidae	Keyser and Cruickshank 1979
32	Traversodontidae	Bonaparte 1978, Chatterjee 1982
33	Chiniquodontidae	Bonaparte 1978
34	Tritylodontidae	Kermack 1982
35	Trithelodontidae	Chatterjee 1983
36–38	Mammals	Lillegraven et al 1979

Note: See Figure 24.8. Many more references were used, but they could not all be listed.

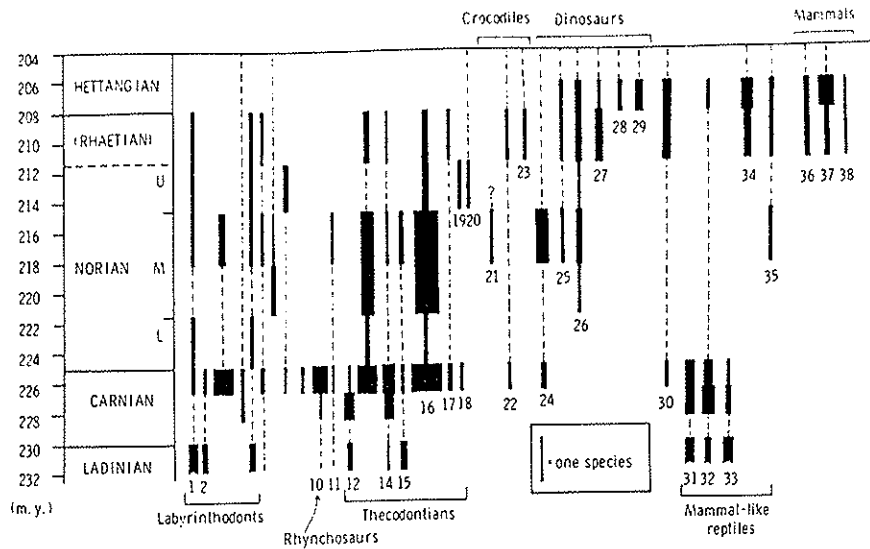


Figure 24.8. The pattern of species distributions of Late Triassic nonmarine tetrapods, arranged by families. The time scale is based on Palmer (1983). Each vertical shape represents one tetrapod family, and the width of the shape shows the number of species present worldwide through time. Certain families that have been based on single, or indeterminate, specimens are omitted, as are marine forms. The main sources of data are given in Table 24.2; stratigraphic distributions are mainly from Olsen and Galton (1977, 1984). The families are: 1, Capitosauridae; 2, Mastodonsauridae; 3, Metoposauridae; 4, Chigutisauridae; 5, Plagiosauridae; 6, Procolophonidae; 7, Proganochelyidae; 8, Kuehnesauridae; 9, Trilophosauridae; 10, Rhynchosauridae; 11, Tanystropheidae; 12, Proterochampsidae; 13, Aetosauridae; 14, Rauisuchidae; 15, Popsauridae; 16, Phytosauridae; 17, Ornithosuchidae; 18, Scleromochlidae; 19, Eudimorphodontidae; 20, Dimorphodontidae; 21, Saltoposuchidae; 22, Sphenosuchidae; 23, Protosuchidae; 24, Podokesauridae; 25, Anchisauridae; 26, Plateosauridae; 27, Melanorosauridae; 28, Fabrosauridae; 29, Heterodontosauridae; 30, Sphenodontidae; 31, Kannemeyeriidae; 32, Traversodontidae; 33, Chiniquodontidae; 34, Tritylodontidae; 35, Tritheledontidae; 36, Haramiyidae; 37, Morganucodontidae; 38, Kuehneotheriidae.

Table 24.3 Completeness of the Late Triassic nonmarine tetrapod fossil record

	No. of families		Completeness ratio ( $\frac{\text{recorded}}{\text{apparent}}$ )	No. of species	
	Apparent	Recorded		Recorded	Actual
Hettangian	18	12	0.667	22	33
"Rhaetian"	23	18	0.783	26	33
Late Norian	19	7	0.368	9	24
Middle Norian (L.)	20	15	0.750	29	39
Middle Norian (E.)	18	4	0.222	15	68
Early Norian	16	4	0.250	5	20
Late Carnian	23	22	0.957	56	59
Middle Carnian	13	7	0.538	17	32
Early Carnian	12	0	0	0	?

Note: The number of families recorded per stratigraphic unit (see Fig. 24.8) is compared with the apparent number of families (i.e., those that are recorded, plus those that occur below and above the unit in question). The ratio of recorded to apparent numbers gives a measure of how complete the record is for each stratigraphic unit. This completeness ratio was used to establish the approximate numbers of tetrapod species that would have been recorded per stratigraphic unit, assuming that the fossil record was equally complete (or incomplete) throughout.

Relative abundances

Benton (1983a) presented a study of the relative abundances of the major groups of nonmarine tetrapods through the Late Permian and the Triassic. This analysis was done mainly to test the commonly held view that the dinosaurs arose and radiated as the culmination of a series of drawn-out "competitive" processes in which the thecodontians gradually took over from the mammal-like reptiles, and the dinosaurs then successfully competed with the thecodontians. In fact, it became clear that the thecodontians never convincingly "beat" the carnivorous mammal-like reptiles, the cynognathoid cynodonts. Various mammal-like reptiles, thecodontians, rhynchosaurs, and other groups, died out at the end of the Carnian. The dinosaurs, which were already present as rare faunal elements, apparently radiated in the early and middle Norian. Several thecodontian lineages lived on right to the end of the Triassic, and the dinosaurs (especially the prosauropods) spread worldwide in the Early Jurassic. Benton (1983a) regarded the late Carnian extinction event (mistakenly dated there as middle Norian) as crucial to the "opportunistic" radiation of the dinosaurs, and thus the central event in shaping terrestrial vertebrate faunas for the rest of the Mesozoic.

Studies of changes in relative abundance through time are, of course, prone to various sources of error. [The assumption is made that the diversity of specimens in museums represents, in some way, the diversity of the living assemblage, and allowance has to be made for collection and preservation bias

(see Benton 1983a)]. However these sources of bias can give a general impression of an extra dimension that is missing from simple taxonomic plots. They add a measure of the relative importance of different groups in typical ecosystems through time. Thus, for example, the rhynchosaurs were never represented by more than a couple of species worldwide at any one time, and yet where they occur, they regularly make up 40–70 percent of all tetrapods collected in a fauna. In contrast, the various groups of thecodontians may be represented by fifteen to twenty species at any one time (ca. 40 percent of all species of tetrapods worldwide), and yet each species could be based on only a handful of specimens (ca. 5–10 percent of all individual tetrapods). Both approaches are worthwhile. In the present example, both the taxic and the relative abundance studies suggest that the end-Carnian event was more significant in its impact on communities.

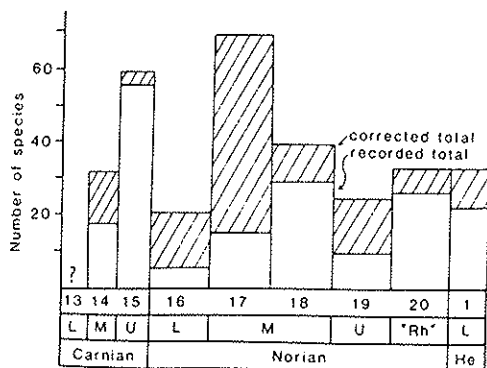
Discussion

The Late Triassic tetrapod extinctions have been linked to an increasing aridity that was observed in reptile-bearing beds in various parts of the world (e.g., Colbert 1958b; Cox 1967; Robinson 1971). Tucker and Benton (1982) and Benton (1983a,b) elaborated this hypothesis, noting an increase in hot subtropical arid to semiarid conditions, as indicated by tetrapod-bearing sediments, in the latest Triassic of most parts of the world. Linked with these climatic changes, they noted that there were also major floral replacements, in the Norian and "Rhaetian." The *Dicroidium* flora of Gondwanaland was replaced by a worldwide conifer-bennettitalean flora in the "Rhaetian" and Early Jurassic. Tucker and Benton (1982) suggested that the climatic and floral changes could have led to the extinction of various tetrapod groups.

Bakker (1977) presented an alternative theory, linking the Late Triassic (and other) tetrapod extinctions to marine regressions and reduced orogenic activity. According to this theory, the Late Triassic marine regression exposed great areas of lowlands around all continents, and the low level of mountain building reduced the geographic-topographic diversity. This meant that fewer habitats were available on land, reproductive barriers to speciation were removed, and speciation rates fell. The overall effect was a reduction in terrestrial tetrapod diversity. In support of this view is the fact that the Late Triassic extinction event was associated with a reduced family origination rate as much as with an elevated extinction rate.

There were mass extinctions among other groups in the Late Triassic. The marine extinction events were particularly severe: It is thought that nearly all species of ammonites and bivalves died out

Figure 24.9. The diversity of species of nonmarine tetrapods in the Late Triassic. The recorded totals are taken from Figure 24.8, and the "corrected" totals include a supplement to take account of the different levels of incompleteness of the fossil record in each "substage" (data from Table 24.3). Declines in diversity occurred after the Upper Carnian, the lower Middle Norian, and the upper Middle Norian.



at the end of the Triassic, and only a few scraped through into the Jurassic to establish new radiations (Hallam 1981). Several major groups of brachiopods, nautiloids, and gastropods, and the last of the conodonts also disappeared at the end of the Triassic. The Norian marine extinction event was comparable in magnitude overall to the Maastrichtian, Frasnian, and Ashgillian events (Raup and Sepkoski 1982, 1984; Sepkoski 1982) – over 20 percent of approximately 300 extant families of marine invertebrates and vertebrates were eliminated.

The timing of the Late Triassic marine extinction event has not been given precisely for all groups. The bivalves declined in diversity from a Carnian–early Norian peak, and they were affected by a major extinction event at the end of the “Rhaetian”–Sevastian (Hallam 1981). Similarly, the main group of Triassic ammonites, the ceratites, reached their peak of diversity in the Carnian and declined thereafter. The last genera disappeared at the end of the “Rhaetian,” but it is not clear how extreme this event was (Kennedy 1977; Hallam 1981). The mass extinctions of brachiopods and conodonts appear to have occurred at the end of the “Rhaetian” (Hallam 1981). Bakker (1977) and Benton (1983a) placed the extinction event of nonmarine tetrapods rather earlier, in the middle Norian; however, it seems, from the evidence given in this chapter, that there were two events, the earlier or major one at the end of the Carnian, and the later or lesser one at the end of the Triassic (“Rhaetian”).

One final comment concerning the extinctions of marine vertebrates: These have been tied in with the terminal Triassic invertebrate extinctions (e.g., Raup and Sepkoski 1982; Sepkoski 1982). However, as far as we know, most of the Late Triassic marine reptile families died out in the Carnian (Thalattosauridae, Nothosauridae, Cymatosauridae, Henodontidae, Shastasauridae); others are uncertain (Simosauridae), and only one died out at the Triassic–Jurassic boundary (Placochelyidae) (Anderson and Cruickshank 1978).

The precise dating and nature of the Late Triassic extinction event(s) are uncertain, then. Several kinds of explanations have been given for the extinctions of all groups at the end of the Triassic: widespread marine regression followed by an anoxic event (Hallam 1981, 1984), temperature changes (Stanley 1984), extraterrestrial impact, or other extraterrestrial event (McLaren 1983; Raup and Sepkoski 1984). Most of these hypotheses are tied to the idea that major extinctions, of which the Late Triassic event was one, have occurred in regular cycles through time. Much more information is needed on the pattern of the Late Triassic extinction (and most of the others) before the proposed mechanisms can be adequately considered.

### Acknowledgments

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