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Late Triassic to Middle Jurassic extinctions among continental tetrapods: testing the pattern

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Introduction

Several attempts have been made to document patterns of diversity change and postulated extinctions of amphibians and reptiles through the Triassic and Early Jurassic interval, both on a global scale (e.g., Benton, 1983, 1986a,b, 1991, 1993a; Olsen and Sues, 1986; Zawiskie, 1986; Lucas, 1990; Hunt, 1991) and based on localized sequences of faunas in Germany (e.g., Benton, 1986b, 1993a; Olsen and Sues, 1986) and North America (e.g., Olsen and Sues, 1986; Olsen, Shubin, and Anders, 1987, 1988; Olsen, Fowell, and Cornet, 1990; Hunt, 1991). The results have been equivocal, with strong arguments being presented both for the existence of two extinction events (one in the late Carnian, and one at the Triassic–Jurassic boundary) and in favor of a single event (at the end of the Triassic). In the record of tetrapods, little evidence has been found for mass extinctions during the Early and Middle Jurassic, although such extinctions have been predicted based on analyses of the marine record by Sepkoski (1989, 1990) at the Pliensbachian–Toarcian boundary and in the Bajocian and/or Callovian.

The debate about tetrapod extinctions has ramifications for the wider question of whether there was a Carnian extinction event among marine life (Stanley, 1988; Sepkoski, 1989; Simms and Ruffell, 1989, 1990; Simms et al., Chapter 21) or merely a single mass extinction at the end of the Triassic period, as well as the question whether or not there is any significance to the (admittedly low) peaks of extinction reported by Sepkoski (1989,1990) in the Early and Middle Jurassic. In addition, there is considerable relevance to the debate over the suggestion of impact-produced mass extinctions and the postulated periodicity of extinction crises.

The evidence in these debates has been reviewed by Hallam (1990), who favors a single terminal-Triassic extinction event, and by Benton (1991) and Simms et al. (Chapter 21), who favor two, of which the late Carnian one, they argue, was critical in wiping out terrestrial and marine life. Olsen et al. (1990), on the other hand, focused on the role of the end-Triassic event as it relates to the diversity of terrestrial tetrapods. As for the postulated Early and Middle Jurassic events, Hallam (1986) argued that the Pliensbachian extinction was merely a European affair, and Benton (1987b) noted the rather incomplete nature of the tetrapod fossil record during much of the Jurassic, and hence the difficulty of identifying extinction events during that time interval. The debates no doubt have a great deal of running in them yet, and the purpose of this chapter is not to reiterate previous arguments.

The data on extinctions

Stratigraphy

The rationale behind the stratigraphic scheme used here is based on several independent approaches that give relatively confident age assignments for some tetrapod-bearing units. The biostratigraphy of the Late Triassic is founded on the temporal distribution of ammonoids from the Alpine region (Figure 22.1). Detailed correlations are possible with marine sequences in other parts of the world, such as western Canada (Tozer, 1974, 1979). Attempts are being made to correlate the palynological zonation of the Late Triassic with this marine standard, by studies of the marginal and terrestrial sequences around the Alpine marine area, but the temporal acuity of the palynological biostratigraphic zones is poorer than that of the marine ammonoid zones: 6 palynological zones, compared with 13 ammonoid zones in the Carnian and Norian (including Rhaetian), giving mean durations for the

Stage	Substage	Ammonoid zones	Palynological zones	Tetrapod zones	Chinle pollen zones	Newark pollen zones	Phytosaur biochrons	Aetosaur biochrons
(Rhaetian)		Crickmayi	(Rhaetian)	NOR L2				
NORIAN	U.	Amoenum	Sevatian			'Upper Balls Bluff-Upper Passaic' Palynofloral zone		?
		Cordilleranus		NOR L1				
		Columbianus	Upper Norian (Alaunian)	NOR M2	?			
	M.	Rutherfordi						*Redondasuchus* Biochron
		Magnus		NOR M1	III			
		Dawsoni	Lower Norian (Lacian)			'Lower Passaic-Heidlersburg' Palynofloral zone		
	L.	Kerri		NOR E			*Pseudopalatus* Biochron	*Typothorax* Biochron
CARNIAN		Macrolobatus		CRN L2	II	'New Oxford-Lockatong' Palynofloral zone	*Rutiodon* Biochron	*Stagonolepis* Biochron
	U.	Welleri	Tuvalian					
		Dilleri		CRN L1	I	'Chatham-Richmond-Taylorsville' Palynofloral zone	*Paleorhinus* Biochron	*Longosuchus* Biochron
	L.	Nanseni	Julian	CRN M	?	?		
		Obesum	Cordevolian	CRN E				
LADINIAN		Sutherlandi						
	U.	Maclearni	Langobardian	LAD				
		Meginae						

Figure 22.1. Zonation of the Late Triassic, by means of ammonoids, palynomorphs, and tetrapods. Based on data from Tozer (1974, 1979), Visscher and Brugman (1981), Litwin et al. (1991), and Hunt and Lucas (1990, 1991a, b, c, 1992).

zones of 4.2–5.0 and 1.9–2.3 million years, respectively, depending upon the accepted total duration of the Late Triassic – 25 million years (Forster and Warrington, 1985; Cowie and Bassett, 1989), 27 million years (Harland et al., 1990), or 30 million years (Olsen, Schlische, and Gore, 1989).

Lithostratigraphic techniques have allowed a relative correlation of the Middle and Late Triassic sediments of the Germanic Basin (Figure 22.2), extending from Bavaria and Thuringia in eastern Germany to Baden-Württemberg in southwestern Germany, as well as northwestern Switzerland, Luxembourg, and Lorraine, France (e.g., Brenner, 1973, 1979; Gwinner, 1980; Brenner and Villinger, 1981). These terrestrial sediments are geographically close to the marine rocks of the Alps, and attempts have been made to establish detailed unit-by-unit correlations between the two using ostracods, bivalves, gastropods, fish, amphibians, palynomorphs, and charophytes (Kozur, 1975; Dockter et al., 1980; Blendinger, 1988). In addition, attempts are being made to establish standard palynological zones for the Alpine succession that will correlate with the ammonoid zones (e.g., Klaus, 1960; Mädler, 1964; Schulz, 1967; Scheuring, 1970; Morbey, 1975; Dunay and Fisher, 1978; Schuurman, 1979; Visscher, Schuurman, and Van Erve, 1980; Visscher and Brugman, 1981; Van der Eem, 1983; Blendinger, 1988; Weiss, 1989). The results have been reasonably good for the Late Triassic (Figures 22.1 and 22.2), in which a number of direct tie points between palynomorphs and ammonoids have been possible, but Weiss (1989) was unable to extend this kind of scheme into the Early Jurassic.

There currently are two ways of interpreting the position of the Carnian–Norian boundary in the German Keuper (Figure 22.2). According to what we shall call interpretation A, the Rote Wand and Kieselsandstein are early Norian in age (Geiger and Hopping, 1968; Fisher, 1972; Fisher and Bujak, 1975; Dunay and Fisher, 1979; Dockter et al., 1980; Anderson, 1981; Schröder, 1982), whereas according to interpretation B, those two horizons are late Carnian (Kozur, 1975; Gall, Durand, and Muller, 1977; Olsen, McCune, and Thomson, 1982). Paleoclimatic evidence tends to favor interpretation B, according to Dockter et al. (1980, p. 960). The oberer Gipskeuper (= Rote Wand + Kieselsandstein, or Rote Wand + Blasensandstein) contains numerous evaporitic horizons, some of which carry gypsum, which is true also of the southern Alpine Torrer Schichten, Opponitzer Schichten, and

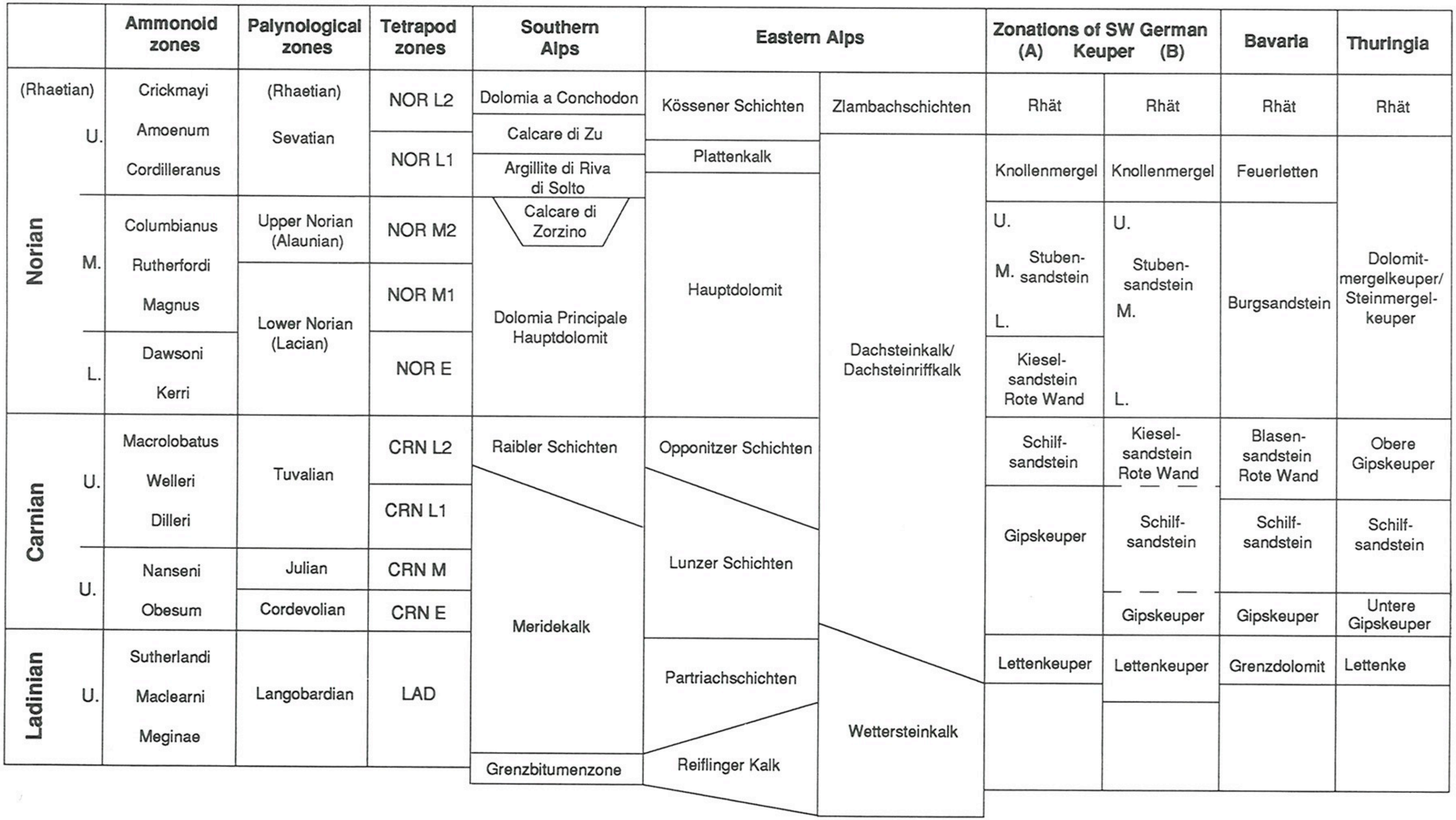

Figure 22.2. Stratigraphic chart of the major Late Triassic formations of the terrestrial Germanic Basin and marine Alpine areas. The Alpine ammonoid zones (after Tozer, 1974, 1979) and palynological zones (after Visscher and Brugman, 1981) are indicated as standards. Two schemes for the relative placing of the divisions of the Keuper in southwestern Germany are noted, and scheme B is preferred here. The sequences in Bavaria and Thuringia are indicated in line with scheme B. Based on data from Brenner (1973), Zapfe (1974), Kozur (1975), Gwinner (1978, 1980), Dockter et al. (1980), Brenner and Villinger (1981), and Benton (1993a).

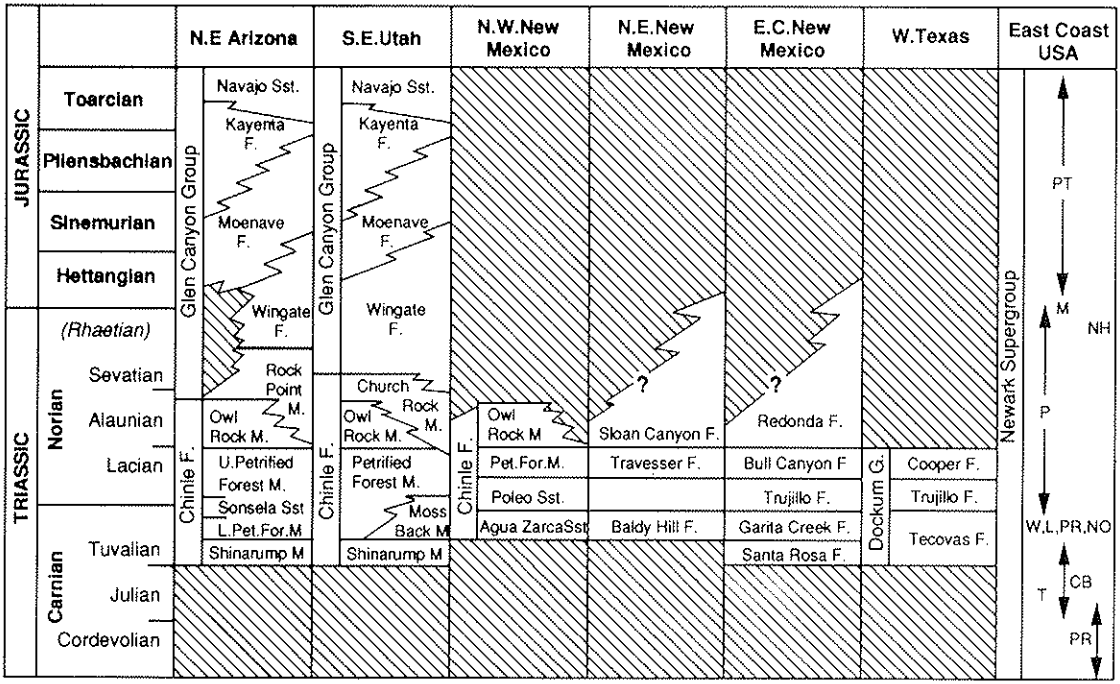

Figure 22.3. Stratigraphy of some Late Triassic and Early Jurassic vertebrate-bearing sequences in North America. The expansion of the Chinle Formation and the Dockum Group through the late Carnian and much of the Norian is based on comparisons of tetrapods with the German sequence by Olsen and Sues (1986), Hunt and Lucas (1990, 1991a, b, c, 1992), and others, and on palynological work by Litwin et al. (1991). Abbreviations: CB, Cow Branch Formation; L, Lockatong Formation; M, McCoy Brook Formation; NH, New Haven Arkose; NO, New Oxford Formation; P, Passaic Formation; PK, Pekin Formation; PT, Portland Formation; T, Turkey Branch Formation; W, Wolfville Formation.

Raibler Gips of Austria. The Opponitzer Schichten are dated as uppermost Carnian (Tuvalian) by their brackish-water fauna, via ammonoids and palynomorphs, and the oberer Gipskeuper is given the same date by its rich ostracod fauna, including *Costatoria vestita* (Dockter et al., 1980). The remaining gypsiferous horizons of the Alpine and Germanic basins are then correlated on paleoclimatic grounds. Magnetostratigraphic evidence, on the other hand, indicates that the Schilfsandstein is latest Carnian in age (Hahn, 1982), and this favors interpretation A. In addition, Wild (1989) implied support for scheme A because he dated both the Untere and Mittlere Stubensandstein as middle Norian on the basis of the shared presence of *Aetosaurus* in these units and in the Calcare de Zorzino of northern Italy, dated by ammonoids as Alaunian (Figure 22.2). In this chapter interpretation B is followed; if A had been selected, the results would have been little changed. Other aspects of the dating in detail of the Keuper are still unclear; for example, the lower boundary of the Gipskeuper, in north Württemberg at least, falls in the uppermost Ladinian (Bachmann and Gwinner, 1971).

Litwin, Traverse, and Ash (1991) have extended the palynological scheme to the Chinle Formation and Dockum Group of the southwestern United States (Figures 22.1 and 22.3). These units, in New Mexico, Arizona, and Utah, include palynomorphs of three zones, termed I, II, and III, which correspond to the early part of the Tuvalian, the later Tuvalian (both late Carnian), and the Lacian (?early Norian, pre-Rhaetian). Litwin et al. (1991) correlate these palynological zones with those of the eastern United States: They regard the "Chatham-Richmond-Taylorsville Palynofloral Zone" of Cornet (1977, 1989; Cornet and Olsen, 1985) as partially equivalent to their zone I, but the Newark zone extends lower, into the Julian, and possibly into the Cordevolian (early Carnian). Litwin et al. (1991) equate their zone II with Cornet's (1977) "New Oxford–Lockatong Palynofloral Zone," and their zone III with Cornet's "Lower Passaic–Heidlersburg Palynofloral Zone." Cornet's (1977) youngest zone, renamed by Litwin et al. (1991) the "Upper Balls Bluff–Upper Passaic Palynofloral Zone," is not represented by an equivalent in the southwestern United States (Figure 22.1). These palynological zones are tied to European, and other, schemes. It is interesting to note that the palynological work of Litwin et al. (1991) confirms the expansion of the Triassic formations of the American Southwest from a limited late Carnian duration (e.g., Dunay and Fisher, 1979; Olsen and Sues, 1986) to a

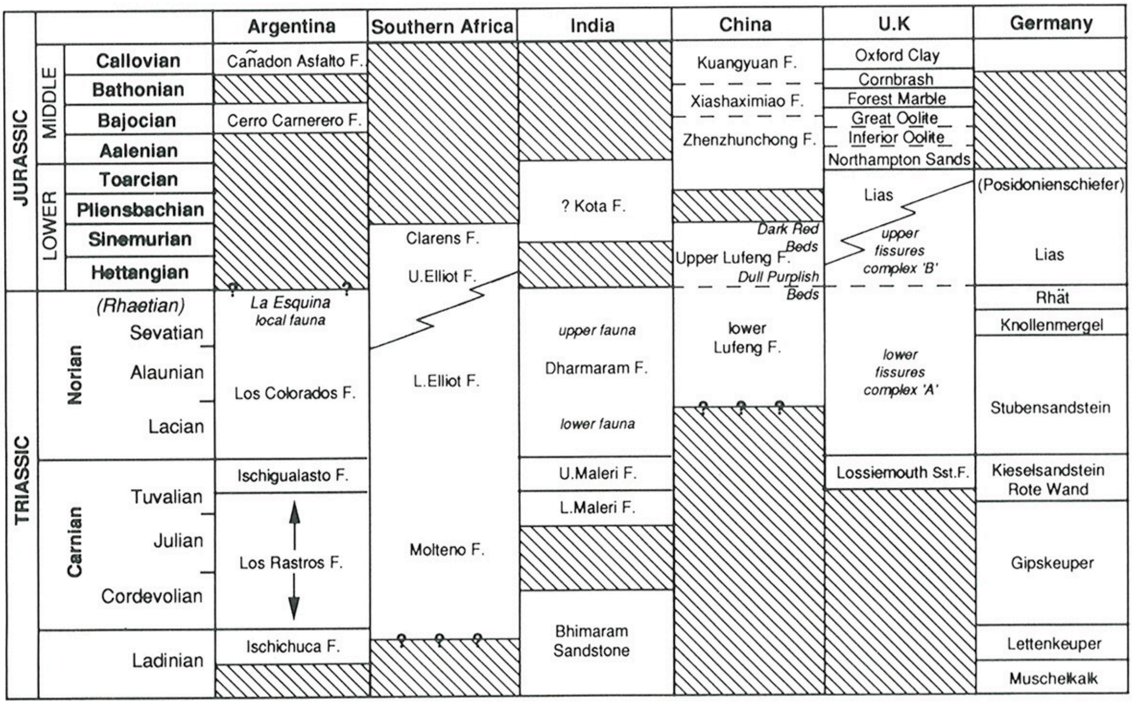

Figure 22.4. Stratigraphy of vertebrate-bearing sequences from the Late Triassic to Middle Jurassic for various parts of Gondwana and Europe. The dates are based largely on comparisons of tetrapods with the German sequence by Olsen and Sues (1986) and others, with some sporadic information from palynology, invertebrates, and absolute age dates. Based on data from Anderson and Cruickshank (1978), Benton (1983, 1993a), Olsen and Galton (1984), Kutty and Sengupta (1989), Olsen et al. (1989), Weishampel (1990), and Hunt and Lucas (1990, 1991a,b,c, 1992).

potential span from late Carnian to the latest Triassic; the latter view was indicated independently by studies of the tetrapods.

Hunt and Lucas (1990, 1991a,b,c, 1992) have been developing global correlation schemes for Late Triassic terrestrial units based on phytosaurs and aetosaurs, arguing that certain genera of both groups are sufficiently restricted in temporal duration, sufficiently identifiable, and sufficiently widespread to permit their use as index fossils. The phytosaur *Paleorhinus* (synonyms: "*Mesorhinus*," *Promystriosuchus*, *Francosuchus*, *Ebrachosuchus*, *Parasuchus*) is represented in several parts of the world (Germany, Austria, Morocco, India, North America), and Hunt and Lucas (1991a) use it to define the *Paleorhinus* Biochron (Figure 22.1). This is tied to the marine ammonoid sequences by a specimen from the lower part of the Opponitzer Schichten of southern Austria, which are dated as Tuvalian (Zapfe, 1974), and lower Tuvalian for the phytosaur horizon. This is then used by Hunt and Lucas (1991a) to assign an early Tuvalian age to all other beds containing *Paleorhinus*, namely the Popo Agie Formation of Wyoming, the lower part of the Petrified Forest Member of Arizona, the Camp Springs Member of the Tecovas Formation of Texas, the lower Dockum Group of Texas, the Blasensandstein of Bavaria, the Argana Formation of Morocco, and the Maleri Formation of India (Figures 22.3 and 22.4). The *Paleorhinus* Biochron is followed by the *Rutiodon* Biochron (latest Carnian) and the *Pseudopalatus* Biochron (early Norian) (Hunt, 1991; Hunt and Lucas, 1991b).

The aetosaurs give less datable zones, but Hunt and Lucas (1990, 1992) established a sequence, the *Longosuchus* Biochron (middle to late Carnian), the *Stagonolepis* Biochron (latest Carnian), the *Typothorax* Biochron (early to middle Norian), and the *Redondasuchus* Biochron (middle to late Norian). Hence, the *Longosuchus* Biochron is partly equivalent to the *Paleorhinus* Biochron, the *Stagonolepis* Biochron is broadly equivalent to the *Rutiodon*, and the *Typothorax* broadly to the *Pseudopalatus* (Figure 22.1). This scheme has not yet been fully developed, nor has it been tested, but it offers some promise.

The zones used here for terrestrial tetrapod-bearing units during the Late Triassic (Figure 22.1) take advantage of the new palynological work, especially that tied to ammonoid zonations, and the new tetrapod-based schemes. The zones are based on the broad palynological divisions of the Carnian and Norian, where early, middle, and late time slices are recognized; further, the late Carnian, middle Norian, and late Norian are each divided into two subunits, reflecting the suggestions of various authors, based on ammonoids, palynomorphs, and tetrapods. The tetrapod-based time units are not formally named, but are coded CRN E, CRN M, CRN L1, and CRN L2 for early Carnian, middle Carnian, early part of the late Carnian, and later part of the late Carnian, respectively, and similarly for the Norian. Note, in particular, that the Rhaetian stage is not used here, following recommendations by Tozer (1974) and others, because it is applicable only to the marine Rhaetic facies of Britain and central Europe. The later part of the Sevatian substage (NOR L2) is essentially equivalent to the "Rhaetian" of older usage.

The stratigraphic assignments of tetrapod-bearing formations from all parts of the world in the interval from the end of the Middle Triassic to the end of the Middle Jurassic are listed in Appendix 22.1 and summarized in Figures 22.2–22.4. The age assignments are based on numerous references, including Anderson and Cruickshank (1978), Benton (1983, 1993a), Olsen and Galton (1984), Kutty and Sengupta (1989), Olsen et al. (1989), Weishampel (1990), Hunt and Lucas (1990, 1991a,b,c, 1992), and Hunt (1991).

Taxonomy

For the present compilation, the familial assignments of Late Triassic to Middle Jurassic tetrapods are based, so far as possible, on current cladistic studies, such as Milner (1988, 1993b) on amphibians, Gauthier, Kluge, and Rowe (1988) on basal reptiles, Gaffney and Meylan (1988) on turtles, Benton (1985) and Evans (1988) on basal diapsids, Benton and Clark (1988) on Triassic archosaurs and crocodylomorphs, Gauthier (1986) and Weishampel, Dodson, and Osmólska (1990) on dinosaurs, Wellnhofer (1978) and Unwin (1991) on pterosaurs, Estes (1983) and Estes, de Queiroz, and Gauthier (1988) on lizards, Kemp (1982), Hopson and Barghusen (1986), and King (1988) on therapsids, and Hahn, Sigogneau-Russell, and Wouters (1989) and Stucky and McKenna (1993) on mammals. Exclusively marine groups, such as the Sauropterygia (Pachypleurosauria, Placodontia, "Nothosauria," Plesiosauria), Ichthyosauria, Askeptosauridae, Claraziidae, Thalattosauridae, and Pleurosauridae are omitted. The stratigraphic distribution data for each family are based on information from Milner (1993a), Benton (1993b), and Stucky and McKenna (1993) for amphibians, reptiles, and mammals, respectively, as well as numerous comments by contributors to this volume. The ranges are plotted in Figure 22.5, and the firsts and lasts for each family are summarized in Appendix 22.2.

Patterns

The diversity of terrestrial tetrapod families through the Middle Triassic–Middle Jurassic interval is shown in Figure 22.6a, with calculated metrics of origination and extinction for families shown in Figures 22.6B and 22.6C, respectively. In all cases, two curves are shown, one for all families documented in Figure 22.5, and one for the nonsingleton families only (i.e., those families based on more than a single genus – often a single species, or even a single specimen).

The graphs of diversity change show significant drops at the end of the Carnian and in the Early Jurassic. The magnitudes of these decreases are greater than it may seem from the graphs, because they are masked to some extent by the origin of new families in the succeeding stages; for example, the diversity drop at the Triassic–Jurassic boundary does not appear clearly in Figure 22.6A because an equivalent number of new families apparently originated during the Hettangian time interval. High rates of origination and extinction occur in the two late Carnian substages and in the "Rhaetian." High origination rates also occur in the Hettangian, Sinemurian, and Bathonian, but these may be partly *Lagerstätten* effects, in that these stages follow gaps in the record during the Sinemurian and the Toarcian–Bajocian interval. High extinction rates in the Sinemurian, Pliensbachian, and Toarcian may be connected with these same gaps.

Quality of the data

Stratigraphy

Accuracy of dating. The assignment of precise ages to Triassic and Jurassic terrestrial faunas is very difficult. Indeed, recent reviews of the stratigraphy of these faunas (e.g., Olsen and Galton, 1977, 1984; Olsen and Sues, 1986) introduced dramatic reappraisals of ages, with many units previously dated as "Late Triassic" being reassigned to the Early and even Middle Jurassic (a jump of four to seven stages, or 10–35 million years) on the basis of exact age dates from associated volcanic horizons, fossil fish, palynomorphs, footprints, and comparisons of tetrapod faunas.

Other stratigraphic approaches that may be of assistance in the future include chronostratigraphy and magnetostratigraphy. Exact ages have been reported for volcanic horizons in earliest Jurassic rocks in several basins in the Newark Supergroup and later in the Early Jurassic in southern Africa. Other data points are needed within the Late Triassic, associated with tetrapod-bearing sediments, to supplement the poorly documented ?Carnian date from Argentina (Forster and Warrington, 1985, p. 107). Outline magnetostratigraphic schemes are available for the Germanic Basin Late Triassic (Hahn, 1982) and the Newark Supergroup

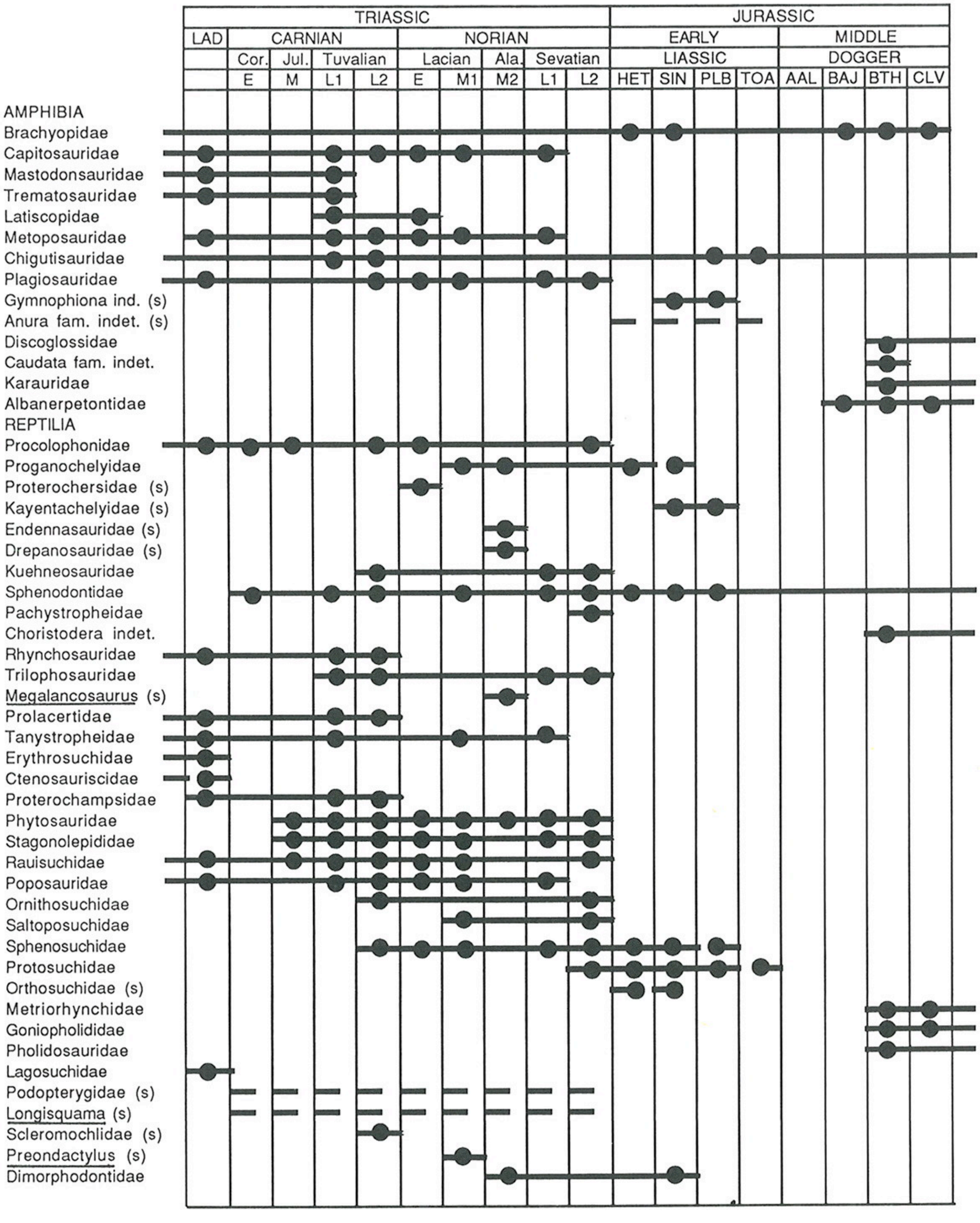

Figure 22.5. Ranges of families of nonmarine tetrapods during the Middle Triassic–Middle Jurassic interval. Ranges are shown based on data in Appendix 22.2. Black dots indicate that fossil material of the family in question is known from the stratigraphic unit indicated. Singleton taxa are denoted by (s).

(Olsen et al., 1989, p. 7; Witte, Kent, and Olsen, 1991). Current work in the Newark Supergroup should greatly enhance the usefulness of the latter.

Dramatic as many of the recent revisions of Late Triassic and Early Jurassic terrestrial biostratigraphy have been, the different approaches are tending to confirm the new schemes (Figures 22.1–22.4). Hence, it seems unlikely that these will be heavily revised in the future, at least not to the extent of the changes set in train by Olsen and Galton (1977). Recent revisions have concerned fine-scale stratigraphic reassignments, generally from one substage to another, involving

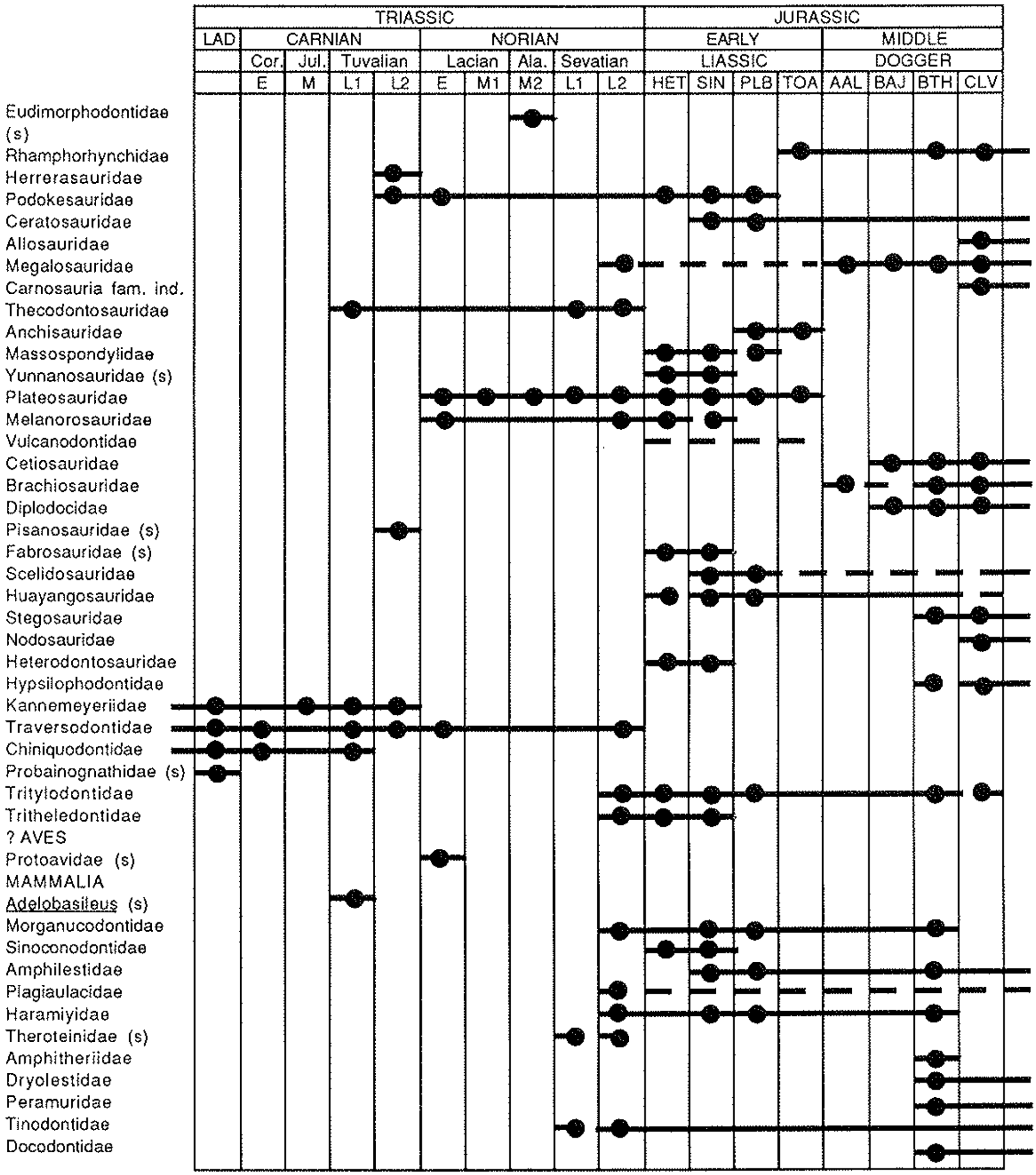

Figure 22.5 (*Continued*)

timespans estimated at 2–5 million years. Nevertheless, such revisions are crucial, and we await further confirmations of the marine–terrestrial biostratigraphic link in Europe and in North America and the proper integration of southern-continent sequences into such schemes.

There are several outstanding stratigraphic problems. For example, there is debate over the dating of the "fissure Complex-A" of southwest Britain (see Fraser, Chapter 11, and Evans and Kermack, Chapter 15). In addition, as mentioned earlier, the faunas in the Late Triassic and Early Jurassic of South America, India, and China, require clearer definitions and firmer correlations with the European and North American formations. New data are still revealing how poorly defined many such units are, as illustrated, for example, by the splitting of the fauna of the Santa Maria Formation of Brazil into two (Barberena, Araújo, and Lavina, 1985), and of the faunas of the Maleri Formation and the Dharmaram Formation of the Pranhita-

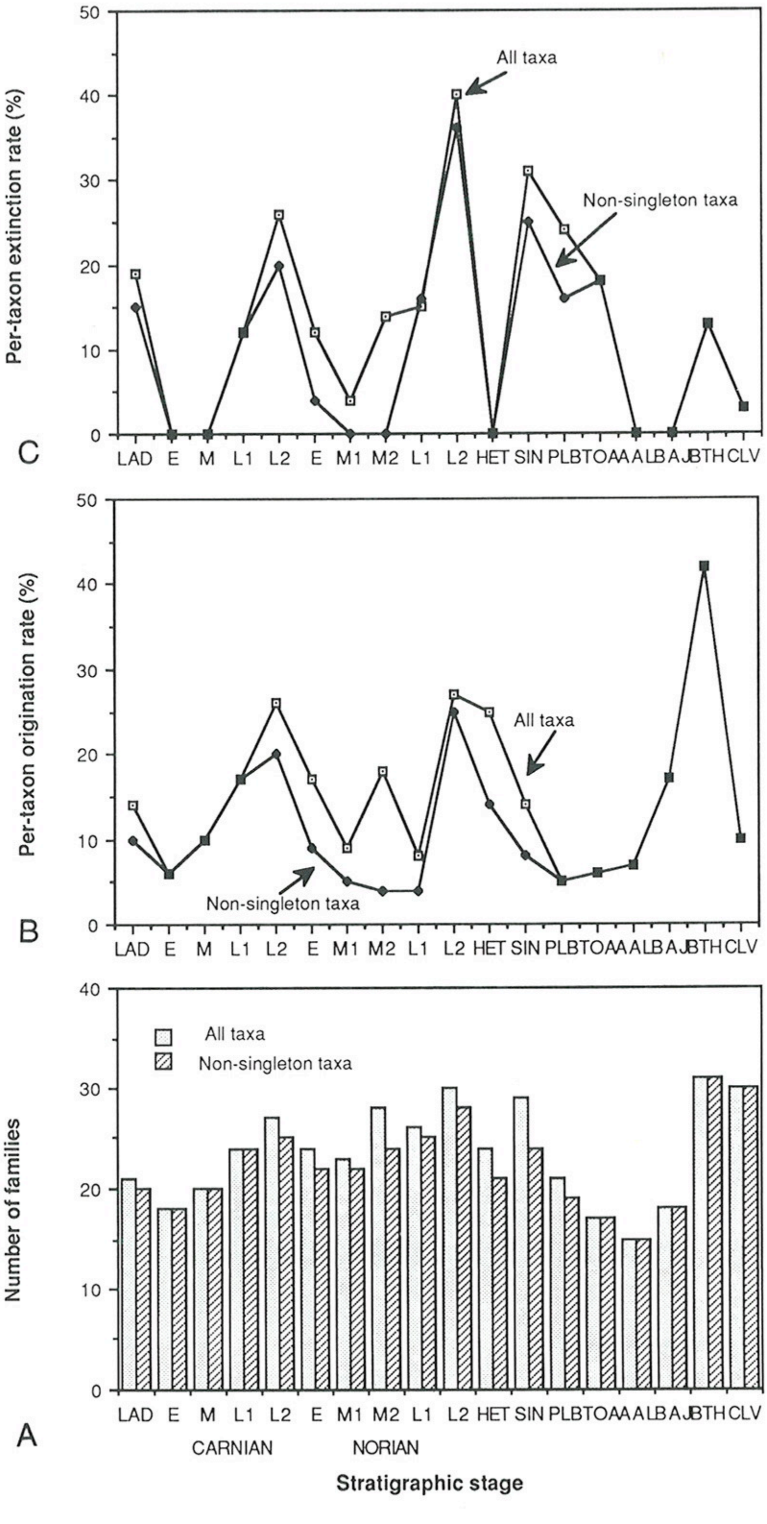

Figure 22.6. Diversity and evolutionary rates for Middle Triassic–Middle Jurassic nonmarine tetrapods, indicated by stratigraphic stage or substage. Measures are given separately for nonsingleton taxa and for all taxa (including singleton families). Where a particular formation is assigned tentatively to two stratigraphic stages, the families are counted as if present in both. For less well-dated formations that span more than two time units, the families are ignored altogether (this applies only to four families here: the Anura fam. indet., Podopterygidae, *Longisquama*, and Vulcanodontidae). Questionable extensions to familial ranges, indicated by dashed lines (for the Megalosauridae, Scelidosauridae, Plagiaulacidae) are counted as confirmed. Rates are percentages, scaled to the total numbers of taxa present in a time unit. They are not scaled to time because the stratigraphic stages and substages are of rather variable durations, depending on the time scale employed; in any case, the durations are roughly comparable, ranging from 3–11 million years (mean: 4.6 million years), according to dates by Cowie and Bassett (1989). (A) Total diversity. (B) Per-taxon origination rate. (C) Per-taxon extinction rate.

Godavari Valley in India into two each (Kutty and Sengupta, 1989). It is astonishing how little we know of such seemingly fundamental matters.

Continuity of sections. Adequate tests of patterns of diversity change through time, including mass extinctions, will require fossiliferous sections that span the interval in question as completely as possible. There are many such sequences of Late Triassic and Early Jurassic terrestrial rocks in various parts of the world that would seem to be suitable on superficial inspection. However, many of them are not so good when examined in detail. This issue is explored by Benton (1993a) and is summarized here.

The sequences in the Germanic Basin are thick, up to 1,750 m (Schröder, 1982), and relatively well dated by palynology and comparisons with the marine Alpine sequences. Fossil tetrapods have been found throughout the sequences (Brenner 1973; Benton 1986a, 1993a), but are rare in the Carnian. Hence, those sequences are barely adequate to test any postulated late Carnian extinction event. They are of no use for testing the end-Triassic event because the relatively rich "Rhaetian" faunas (mixed marine and derived terrestrial material) are followed by a major facies change to fully marine conditions, and hence the terrestrial faunas of the time are very poorly sampled.

The Late Triassic and Early Jurassic sequences in the southwestern United States (Figure 22.3) seem to hold more promise, for analysis of the postulated late Carnian event at least. The Chinle Formation, Dockum Group, and equivalents in Texas, Arizona, New Mexico, and Utah are now know to span from late Carnian times well into the Norian, possibly to the top (Hunt and Lucas, 1990, 1991a,b,c; Litwin et al., 1991; Lucas, 1991), and many diverse tetrapod faunas are known from all levels of the succession. However, the total thicknesses of these successions are not great, about 300–550 m, and more information is needed regarding possible unconformities. The transition from the Chinle Formation to the Glen Canyon Group seems to continue the succession fairly conformably across the Triassic–Jurassic boundary, but better biostratigraphic control will be required for these upper units in order to determine the value of such sequences for testing the nature of the postulated end-Triassic extinction event.

The Newark Supergroup of the eastern United States and Canada covers a time span from the middle Carnian, or earlier, to the Pliensbachian (Figure 22.3), within a thickness of over 6,000 m of lacustrine and fluviatile sediments (Olsen et al., 1989, 1990). It has been argued that this represents the best succession for testing the nature of tetrapod extinctions during the Late Triassic–Early Jurassic interval (Olsen and Sues, 1986; Olsen et al., 1987, 1990; Hallam, 1990). However, skeletal fossils from the various basins within the Newark Supergroup offer little hope of testing such events. Faunas in the middle and late Carnian are relatively diverse, as are those in the earliest Jurassic. Indeed, Olsen et al. (1987, 1988) and Shubin et al. (1991) have argued that the basal Jurassic fauna of the McCoy Brook Formation of Nova Scotia provides a crucial test of the effects of the postulated end-Triassic extinction event. However, the Norian interval in the Newark Supergroup is nearly devoid of tetrapod skeletal fossils, having yielded only about ten specimens in all from the extensive Passaic Formation and the New Haven Arkose. The near absence of Norian fossils makes it impossible to test either the after effects of the postulated late Carnian event or the nature of pre-extinction faunas for the postulated end-Triassic event. Footprint faunas are richer during the Norian interval in the Newark Supergroup, and they may offer some possibility of assessing extinction events (Olsen and Sues, 1986; Olsen et al., 1990), but there is always the serious problem of assigning tracks to the correct trackmakers, as noted by Olsen et al. (1990). For example, tracks of the ichnogenus *Rhynchosauroides* extend into the Norian, well beyond the disappearance of the rhynchosaurs at the end of the Carnian as documented by skeletal fossils. However, it is likely that *Rhynchosauroides*-type tracks were made by a wide range of terrestrial diapsids; indeed, probably rather few, such as those from the Middle Triassic of England (Benton et al., Chapter 7), were actually made by rhynchosaurs. Hence the documented stratigraphic range of *Rhynchosauroides* prints is difficult to interpret in terms of the appearance and disappearance of particular animal groups.

In Britain, the fissures of the Bristol region and South Wales (Figure 22.4) may offer hope for testing such events. They are classified into those of Complex A, dated broadly as "Late Triassic," and those of Complex B, dated more securely by associated palynomorphs as Sinemurian (Fraser 1986, and Chapter 11; Evans and Kermack, Chapter 15). One Complex-A fissure in Tytherington Quarry has been assigned a Rhaetian (late Sevatian) age on the basis of palynomorphs (Marshall and Whiteside, 1980), and Whiteside (1986) suggested that all fissure Complex-A sites were late Sevatian in age. However, as Fraser (Chapter 11) notes, this is not a necessary conclusion. It is not even demonstrated that all the fissures at Tytherington are late Sevatian in age; indeed, fieldwork suggests that many quarries in Carboniferous limestone in South Wales and around Bristol contain fissure fills of varying ages. Simms (1990a) has argued that many of the fissures could extend back in age to the middle or late Carnian, based on the assumption of their formation during an early to middle Carnian pluvial episode. Benton (1993a) concurred on the basis of the tetrapod faunas, some elements of which are closely comparable with animals from the geographically isolated Lossiemouth Sandstone Formation (late Carnian), and others with animals from the German Stubensandstein (early to middle Norian). If these dates are confirmed, and if the fissures can be arranged in a stratigraphic sequence, they may offer detailed samples of the smaller elements of Carnian to Sinemurian tetrapod faunas and hence be of tremendous potential for testing the nature of Late Triassic events.

The Late Triassic sequence in the Ischigualasto basin in the province of La Rioja, Argentina (Figure 22.4), may offer potential for testing at least the postulated late Carnian event. The 1,500-m-thick, seemingly conformable succession through the Ischichuca, Ischigualasto, and Los Colorados formations has yielded rich tetrapod faunas at several levels. In particular, the late Carnian Ischigualasto Formation passes continuously into the base of the Los Colorados Formation, but tetrapod fossils are rare in the latter. The La Esquina fauna of dinosaurs and other reptiles comes from the top 100 m of the Los Colorados Formation and is dated as late to latest Norian. It is not followed by Early Jurassic faunas, so the postulated end-Triassic event cannot be studied. Independent palynological dating of this succession is urgently needed.

Independent dating is also needed for the Late Triassic sequence of the Pranhita-Godavari Valley in India (Figure 22.4). Here, the Bhimaram, Maleri, Dharmaram, and Kota formations make up a 1,230-m-thick sequence spanning in age from the Ladinian to the Sinemurian/Toarcian. The Maleri Formation has yielded two faunas, of late and latest Carnian age (Kutty and Sengupta, 1989), and the Dharmaram Formation has a lower fauna of early Norian age. These might be used to constrain aspects of the postulated late Carnian event. The upper Dharmaram fauna appears to be late, or latest, Norian in age, but it is followed by a considerable unconformity before the Kota Formation, which is often dated as Sinemurian, but might be Toarcian, or younger, in age. Palynological evidence is limited at present, and more detailed studies will be required to firm up the age assignments of the tetrapod-bearing formations.

In southern Africa, the Stormberg succession (i.e., the Elliot and Clarens formations) (Figure 22.4) forms a sequence only 250 m thick that spans in age from the early Norian to the Sinemurian. Both formations have yielded a sequence of faunas (Kitching and Raath, 1984) that may provide evidence of the nature of the postulated end-Triassic event. However, vertebrate fossils are absent from the underlying Carnian-age Molteno Formation, and hence nothing can be said of the postulated late Carnian event. Again, more palynological control is needed on the ages of the Elliot and Clarens formations.

The Lower Lufeng Formation of Yunnan, China (Figure 22.4), also appears to straddle the Triassic–Jurassic boundary and could therefore be used to test the nature of the postulated end-Triassic event. The sequence is 750 m thick and has yielded separate faunas in the Dull Purplish Beds and the Dark Red Beds. The former may be latest Norian or earliest Jurassic in age (Zhen et al., 1985), and the latter appear to be Hettangian or Sinemurian in age (Sun and Cui, 1986). The ages are confirmed to some extent by ostracods and molluscs, but more refined biostratigraphic work is required.

In conclusion of this section, the terrestrial sequences of the Germanic basin, possibly the British fissures, the sequences of the American Southwest, and possibly those from the Ischigualasto basin of Argentina and the Pranhita-Godavari Valley of India may allow testing of the nature of the postulated late Carnian event. Further, the terrestrial sequences of the British fissures, and possibly the Stormberg sequence of southern Africa and the Lower Lufeng Formation of China, may allow testing of the nature of the postulated end-Triassic event. Other sequences cannot allow study of the latter event because terminal-Triassic faunas are followed by marine Jurassic sequences (the Germanic Basin, the British, French, and Swedish "Rhaetic") or by an apparent gap (India, Argentina), or else the terminal-Triassic record is lacking or inadequate (?American Southwest, Newark Supergroup, and possibly also southern Africa and China).

Gaps and collection failure

Qualitative arguments. The key question to be tackled in any study that purports to identify extinction events is, are they real, or merely the result of gaps in the record? This criticism has been leveled by Olsen and Sues (1986, p. 343), Sepkoski (1986, p. 286), Sepkoski and Raup (1986, p. 11), and others at the postulated late Carnian peak of extinction for both marine and terrestrial organisms. A qualitative counterargument is simply to assert that it is more parsimonious to read the fossil record literally, to accept the appearance of a sharp drop in diversity as real, than to argue for special cases of variable preservation conditions. Olsen et al. (1987, 1988) took such a literal view in arguing that the McCoy Brook Formation of Nova Scotia, dated as earliest Jurassic, could be used to constrain the nature of the postulated end-Triassic event. Because certain Triassic tetrapods, such as tanystropheids, procolophonids, rhynchosaurids, and traversodontids, were not found in the McCoy Brook Formation, Olsen et al. (1988) argued plausibly that they had died out previously.

Benton (1991) has argued similarly that the absence from the early Norian of groups of readily fossilizable tetrapods that had been abundant in the late Carnian, such as mastodonsaurids, trematosaurids, rhynchosaurids, proterochampsids, kannemeyeriids, and chiniquodontids, actually proves that they had already

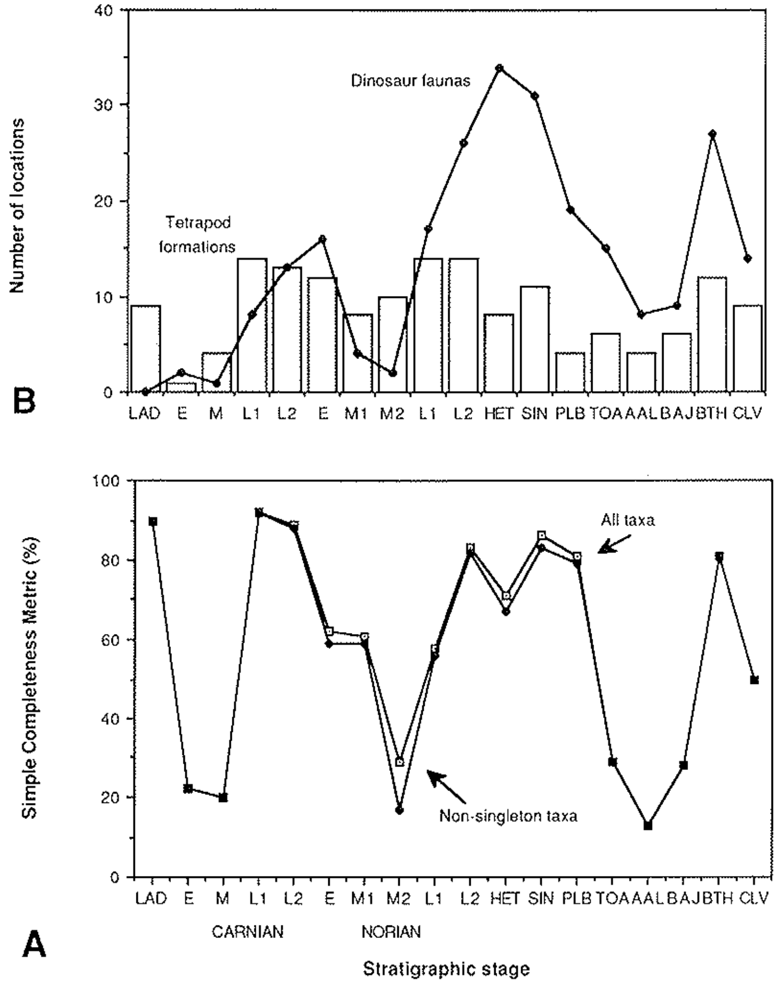

Figure 22.7. Measures of the possible effects of completeness of the fossil record on the patterns of diversification, origination, and extinction recorded. (A) The SCM (a measure of relative completeness; see Table 22.1) measured by time units for nonmarine tetrapod families for the Middle Triassic–Middle Jurassic time interval. High values indicate a good record, low values a poorer one. (B) The availability of rocks containing nonmarine tetrapods during the same time interval. Two measures are shown, a count of the geological formations enumerated in Appendix 22.1, and counts of dinosaur skeleton and footprint localities listed in Table 22.2. The peaks and troughs in dinosaur formations, in particular, roughly mimic the SCM values in part A.

died out. Olsen and Sues (1986, p. 343), on the other hand, state that "early Norian vertebrate assemblages are very poorly known, and, therefore, it is difficult to place much faith in the peak of Carnian extinctions." Such diverging assertions require a more precise test of whether the late Carnian extinction peak truly represents a mass extinction or is merely an artifact of a subsequent gap.

Measuring relative completeness: finding gaps. A first approach is to attempt to quantify completeness. The relative completeness of a fossil record may be estimated by calculating the proportions of "actual" and "assumed" fossil groups represented within each time unit. Actual groups represented are those for which fossils have been found in rocks of the age in question, and the assumed groups are the actual groups plus those that are known to span the time interval under study. Hence the difference between assumed and actual numbers represents the number of Lazarus taxa. The ratio, as a percentage, has been termed the simple completeness metric (SCM) by Benton (1987b), and it ranges from zero (i.e., no fossils found) to 100 percent (all groups assumed to be present are represented by actual fossil finds). The SCM does not take account of taxa that arise, die out, or have their duration within a gap, and the effectiveness of the SCM as an estimator of completeness diminishes as the gap size increases (Benton, 1987b). Such problems can be partially overcome by probabilistic modifications to the SCM, based on measures of the general spottiness of the record of a particular clade and on aspects of the relevant rock record (Strauss and Sadler, 1989).

SCM values for the stages and substages employed in this tabulation of taxa (Figure 22.5) are listed in Table 22.1 and shown in Figure 22.7A. These show high SCM values in the Ladinian, late Carnian (both substages), early Norian, middle Norian (1), late Norian to Pliensbachian, Bathonian, and Callovian,

Table 22.1. *Simple completeness metric (SCM) values for nonmarine tetrapods from the Middle Triassic to the Middle Jurassic*[a]

Time unit	No. of families Apparent	Recorded	SCM (%)	SCM from Benton (1986a)
Callovian	30	15	50	
Bathonian	31	25	81	
Bajocian	18	5	28	
Aalenian	15	2	13	
Toarcian	17	5	29	
Pliensbachian	21	17	81	
Sinemurian	29	25	86	
Hettangian	24	17	71	67
Late Norian 2	30	25	83	78
Late Norian 1	26	15	58	37
Middle Norian 2	28	8	29	75
Middle Norian 1	23	14	61	22
Early Norian	24	15	62	25
Late Carnian 2	27	24	89	(96)
Late Carnian 1	24	22	92	(96)
Middle Carnian	20	4	20	54
Early Carnian	18	4	22	0
Ladinian	21	19	90	

[a]The data are derived from Figure 22.5, based on all taxa, and the SCM is calculated as the percentage of recorded fossils to apparent family presences during each time unit. Treatment of uncertain records is as explained in the legend to Figure 22.6. High values indicate a good-quality record, and low values indicate a poor record. For comparison, the SCM values from Benton (1986a) are shown.

and low values in the early to middle Carnian, middle Norian, and Toarcian to Bajocian. Hence, it is clear that there was no "gap" during the early Norian, as had been stated (e.g., Olsen and Sues, 1986), despite earlier SCM figures that seemed to indicate such a gap (Benton, 1986a, 1991). Redating of the Chinle and Dockum sequences (e.g., Litwin et al., 1991) and restudy of the Germanic Basin early Norian have filled the early Norian "gap." There is, however, an apparent gap in the middle Norian record of nonmarine tetrapods, when groups that are known to have spanned that interval are rather poorly represented by fossils. This does not prove that the late Carnian extinction peak is an artifact of a poor fossil record.

Gaps do not necessarily indicate poor preservation. Gaps in the fossil record can suggest either poor sampling of a diverse fauna or excellent sampling of a depauperate fauna. The gap could indicate genuinely depauperate faunas in the middle Norian (and in the Toarcian–Bajocian interval), following the trauma of a preceding mass extinction. Is it possible to distinguish between the literal reading of a gap as a time of low biotic diversity and the less parsimonious reading of such as the result of poor sampling of a fully diverse biota? Benton (1991) and Smith (1990) have explored some possible tests.

Interpreting gaps: preservation failure or post-extinction biotas? The first approach, applied by both Benton (1991) and Smith (1990), was to test the assertion that the diversity decline from late Carnian to early Norian times simply mirrored the decline in fossiliferous deposits. This is seemingly partially true for the marine case, but not so for the terrestrial situation. A crude impression can be obtained by examination of a histogram of numbers of tetrapod-yielding formations recorded in Appendix 22.1 (Figure 22.7B). This shows similar numbers of formations dated as late Carnian 2 and early Norian (13 and 12, respectively), although it takes no account of the available areas of outcrop, the available rock volume, nor the proportion of potentially fossiliferous sedimentary facies in rocks of different ages. It is not, however, evident that any of these factors vary significantly between the late Carnian 2 and the early Norian occurrences.

Benton (1991) provided a similar test based on the independent data compilation by Weishampel (1990) in which he listed major basins that have yielded

Table 22.2. *Numbers of sedimentary rocks of different ages, from Middle Triassic to Middle Jurassic, that have produced dinosaur skeletal fossils or dinosaur footprints*[a]

Time unit	N. America	Europe	Asia	S. America	Africa	Australasia	Total
Callovian	0	8	2	3	1	0	14
Bathonian	0	21	2	0	4	0	27
Bajocian	0	6	1	1	0	1	9
Aalenian	0	7	1	0	0	0	8
Toarcian	7	2	2	3	1	0	15
Pliensbachian	9	1	3	3	3	0	19
Sinemurian	6	5	4	3	13	0	31
Hettangian	9	8	5	3	9	0	34
Late Norian 2	2	19	2	3	0	0	26
Late Norian 1	0	16	1	0	0	0	17
Middle Norian 2	1	1	0	0	0	0	2
Middle Norian 1	2	2	0	0	0	0	4
Early Norian	5	2	1	0	8	0	16
Late Carnian 2	7	2	1	3	0	0	13
Late Carnian 1	3	2	2	0	1	0	8
Middle Carnian	?1	0	0	0	0	0	?1
Early Carnian	1	?2	0	0	0	0	?3
Ladinian	0	0	0	0	0	0	0

[a]These figures are taken from Weishampel's (1990) state-by-state listing and include all formations dated certainly, or tentatively, by him. Tentatively dated units are assigned to precise time units by counting them twice (if dated across two of the time divisions used here). Some very poorly dated formations are excluded. Note that dinosaur fossils are not known clearly before the late Carnian, and hence the low numbers of faunas during that early time do not correspond to the overall number of nonmarine tetrapod-bearing formations.
Source: Data from Weishampel (1990).

remains of dinosaurs, both skeletal and ichnological. A histogram of the numbers of basins per time unit through the Late Triassic and Early to Middle Jurassic (Table 22.2; Figure 22.7B) confirms that there was no major drop in numbers of fossiliferous basins between the late Carnian and the early Norian: The totals fall from 21 to 16 (or rise from 13 to 16 if one counts only the late Carnian 2 substage formations), hardly a significant change. Across the postulated end-Triassic event, the totals rise from 26 latest Triassic ("Rhaetian") fossiliferous basins to 34 Hettangian, which is of significance for those attempting to chart the apparent diversity decline through that time interval.

Smith's (1990) other tests provided convincing evidence that the late Carnian diversity decline among marine echinoids was real. Some of these tests might be applicable to the tetrapod record, and should be so applied in the future. These tests are as follows:

1. Does the pattern of decline continue through several time units after the supposedly most highly fossiliferous horizons (*Lagerstätten*)? If there is no such longer-term decline, the highly fossiliferous interval may truly be followed by an episode of preservation failure. This is hard to determine for the tetrapod record because of the coarseness of stratigraphic acuity. Smith (1990) found such a pattern of decline in echinoid species diversity after the time of the highly fossiliferous Cassian Beds.

2. How many Lazarus taxa are there in the interval where a gap is postulated? If there are many taxa that apparently disappear and then reappear after the postulated gap, then preservation failure is implicated. If Lazarus taxa are not abundant, then the interval may truly represent a depauperate postextinction fauna. Smith (1990) found that many major echinoid lineages disappeared in the late Carnian, never to reappear, and he concluded from the low number of Lazarus taxa that the early Norian was not a time of serious preservation failure. For the terrestrial tetrapod record, the early Norian interval includes 12 Lazarus family-level taxa, compared with only 4 actually represented by fossils, and 7 extinctions at the end of the Carnian, all at the family level, according to Benton (1986a, p. 315). However, the new data set (Figure 22.4) indicates 7 Lazarus taxa in the early Norian time

interval, compared with 16 families actually represented by fossils, the change being the result of more precise dating of the Chinle and Dockum groups. Note, however, as stressed before, that Lazarus taxa may represent either preservation or collection failure, as is usually assumed, or they may indicate times of depauperate faunas when individuals were so rare that we hardly ever find them.

3. Are there any indications of poorer-quality preservation during the gap interval? Smith (1990) argued that if diversity levels were actually high during the gap interval, but fossils were rare, one would expect to find a higher proportion of incomplete or poorly preserved fossils. He found that that was not the case for the early Norian interval and that the proportion of disarticulated echinoid remains compared with complete remains did not increase. This test could be applied to the tetrapod record by comparing the proportions of complete and incomplete skeletons recovered from different time intervals.

4. Do different indicators of diversity reveal the same patterns? Smith (1990) found that graphs of diversity based on whole echinoid tests and those based on isolated spines showed the same patterns, and therefore he assumed, on the reasoning of Sepkoski et al. (1981), that these were close to the true patterns. It may be possible to apply such a test to the terrestrial tetrapod record by comparing the data from skeletal fossils and trace fossils. However, much more work on the patterns of the global appearances and disappearances of tetrapod footprint types is needed, more importantly, clear cases for equating particular footprint types with particular animal groups are required. It is likely that certain footprint types, having been produced by an array of taxonomic groups, would have to be omitted from such compilations.

Taxonomy

The assignment of fossil tetrapod specimens to species, genera, and families is a process fraught with problems at various levels. Certain groups in the Triassic and Jurassic appear to be well-defined cohesive clades, but many others are somewhat less tangible. For these latter taxa there may be only scattered fossil material available; in some cases such material may be difficult to study or poorly described, the material may indicate an assortment of taxonomic characters that defy clear-cut identification of the taxon, or the attributes of the beast may defy phylogenetic analysis. Problems of these sorts at all levels of systematic study are typical and they make the job of assessing biotic diversity in the past (as well as the present) quite difficult. One approach is to ignore such problems, because they introduce nonsystematic errors to any macroevolutionary analysis; that is, they will introduce a certain amount of background noise to the data set, but will not necessarily distort it in any particular direction, a point made by Sepkoski (1989). The errors will be stochastic, nondirectional; that is, in popular terms, they may cancel each other out.

In the compilations of tetrapod data presented here, three measures have been taken in an attempt to improve the taxonomic quality of the information:

1. The families are all based on recent cladistic phylogenetic analyses and, so far as possible, are all monophyletic clades. Interestingly, this produces little change at the family level when one compares these family lists with older, pre-cladistic lists (Maxwell and Benton, 1990). For a long time, most tetrapod families have been defined by sharply indicated unique characters that are now called synapomorphies. The revolution wrought by the application of cladistic techniques to fossil and living tetrapods has generally affected our understanding of relationships at suprafamilial levels: the refinement of our views of early amphibian relationships (including the abolition of the "labyrinthodonts" and "lepospondyls"), the recognition that prolacertiforms are archosauromorph diapsids, the shift of rhynchosaurs from the lepidosaurs to the archosauromorphs (including the abolition of the "Rhynchocephalia" and the "Eosuchia"), the refinement of classifications of Triassic archosaurs (including the recognition of the monophyly of Dinosauria and the postulated sister-group relationship of Dinosauria and Pterosauria), the clarification of relationships within Cynodontia (including recognition of a monophyletic taxon Mammalia), and many more. These changes have not generally affected our interpretation of the boundaries of the families, but other taxonomic revisions have.

2. The contents of most families of Triassic and Jurassic tetrapods have been reassessed at the alpha-taxonomic level. In other words, paleontologists have examined much of the original material on which species, genera, and families were founded, and they have been obliged to synonymize many such taxa, or to declare them nomina dubia. This has been particularly true for the Permo-Triassic "mammal-like reptiles," for which many new taxa were erected with great enthusiasm earlier this century, but also for Triassic dinosaurs and for other groups to a lesser extent. The results of alpha-taxonomic revisions of these groups have had dramatic effects on the shape of current data bases, even when compared with those of the 1960s (Maxwell and Benton, 1990).

3. Singleton taxa are identified and treated in two ways, in order to highlight their existence. Many families of Triassic and Jurassic tetrapods have been erected on the basis of single genera, even single species or single specimens from single localities. Many such families have been synonymized with others, but others remain, and these are probably largely valid and distinct. Some day they may acquire new bedfellows, and hence cease

to be singletons. For the present, however, singleton families can be argued to distort macroevolutionary data bases, for four main reasons: (a) They are not equivalent, in ecological terms, to nonsingleton families, many of which were diverse, were abundant in individual faunas, and had global distributions. (b) They are commonly associated with fossil *Lagerstätten*, times of exceptional preservation, and hence distort the background signal coming from more typically fossilized groups. (c) They have point distributions in time, so that they do not have a true duration, and hence cannot strictly contribute to calculations of rates of change. (d) Many of them may be dubious and will disappear on further taxonomic revision.

None of these arguments against the inclusion of singleton taxa is devastating. In the first case (a), of course, singleton taxa are just one end of a continuum of family diversities, ranging from families containing a single species, families with two, three, or four, up to families with, say, 50 species. There is therefore no reason to draw a qualitative distinction between all singleton families and all nonsingleton families. In the second case (b), fossil *Lagerstätten* actually give us a more nearly true picture of the life of the past than do normal kinds of fossil deposits (Briggs, 1991), and they should really be used exclusively in attempts to plot past biotic diversities, while the data from non-*Lagerstätten* intervals should be corrected upward to take account of preservation loss. In the third case (c), this is a semantic quibble: Singleton families probably are singletons only because of our limited knowledge of the fossil record. It is unlikely that the Archaeopterygidae were really an isolated family of six or seven individual birds existing for an instant of time in the Tithonian of southern Germany, and having no forebears, contemporaries, or descendants. Finally, in the fourth case (d), it is true that many singleton families of tetrapods have already been discarded, because they were based on hopelessly inadequate or ill-defined material, but most of the singleton families in current lists are based on good, complete specimens of bizarre creatures (e.g., Kayentachelyidae, Drepanosauridae, Podopterygidae, Eudimorphodontidae, Protoavidae, Theroteinidae), and their families doubtless will continue to be deemed distinct from all others.

Therefore, for the purposes of my analyses, I have identified the singleton families and carried out the analyses both with and without them. Their inclusion tends to raise the rates of both origination and extinction during times of peaks, as would be expected, but in no case do the singletons alone generate such a peak.

Data bases and the future

Changing data bases. Comparison of the changing shapes of mass-extinction peaks through the years indicates no clear trend (Maxwell and Benton, 1990). The main conclusion seems to be that the data bases may change fundamentally, by 50 percent or more over the past two decades for tetrapods, and yet the extinction events and their magnitudes remain fairly static. Sepkoski (1990) reports similar findings from analyses of his evolving family-level and generic-level data bases on marine animals.

Two opposite kinds of predictions can be made about the effects of future collecting on the nature of extinction peaks. At a detailed stratigraphic level, it might be expected that more collecting will sharpen up the shape of extinction peaks. Certainly, the studies by Ward (1990) on ammonite species distributions before the Cretaceous–Tertiary boundary show that as more collecting is done, the sharper the extinction becomes, because the Signor-Lipps effect (backward smearing of an instantaneous mass-extinction event) is being diminished. An opposite prediction might be that, in some cases, increasing knowledge will tend to broaden out the peaks of extinction intensity, on the assumption that "firsts" will be extended back in time, and "lasts" will be extended forward in time. So far, it is not yet clear which way we are heading with the Late Triassic extinction peaks.

Nevertheless, our views on the systematics and biostratigraphy of Triassic and Jurassic tetrapods have changed fundamentally in the past two decades, and many new fossil finds have been made. Surely there have been changes in the identification and the nature of the mass extinctions revealed? Surely, comparisons may also indicate the main reasons for such changes in our understanding and may hint at avenues for future research. An attempt is made here (Figure 22.8) to compare the results from data bases over the past two decades, starting with Olsen's (1982) paper, which is essentially based on Romer (1966).

The results show that the most dramatic cause of change in the patterns discovered over the past two decades has been rather prosaic: It is simply that the stratigraphic divisions in use have been refined from the rather crude "Middle Triassic" and "Upper Triassic" used by Olsen (1982) to the smaller substage revisions used in more recent analyses. Other changes have resulted from the discovery of new taxa during the past decade (e.g., Gymnophiona indet., Kayentachelyidae, Endennasauridae, Drepanosauridae, *Megalancosaurus*, Protoavidae, *Adelobasileus*, Theroteinidae), nearly all in "known" tetrapod-bearing sedimentary basins, however. Ranges have also been extended by new finds (e.g., Jurassic temnospondyls, Discoglossidae, Caudata fam. indet., Albanerpetontidae, Choristodera indet., Traversodontidae, Plagiaulacidae), again largely from "known" localities. New localities have been discovered recently, but they have yet to yield taxa that are entirely new or that will dramatically alter known ranges. Other recent changes in the ranges are results of alpha-level taxonomy, the familial reassignment of

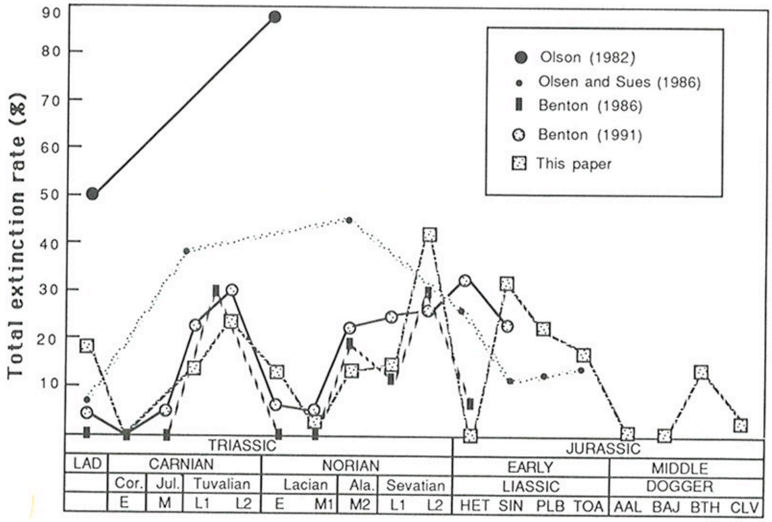

Figure 22.8. Changing perceptions of the nonmarine tetrapod extinction events during the Late Triassic and Early to Middle Jurassic. Earlier works did not clearly discriminate time intervals. Post-1985 results show improving time precision and reveal two peaks of high extinction rates in the Late Triassic, and possibly one in the Early Jurassic.

individual specimens, and small-scale stratigraphic reshuffling. The sample of data used here is too small to quantify usefully the roles of such factors in effecting changes in our ideas of macroevolutionary patterns among Late Triassic–Middle Jurassic tetrapods.

The major changes resulting from cladistic revisions, confirmed also by the findings of Patterson and Smith (1987) on data bases of echinoderms and fish, may be restricted to the current phase in the history of our science. Large-scale cladistic reviews of most tetrapod groups have now been carried out and will no doubt continue. It may be that the major revolution has passed, for the vertebrates at least, and future cladistic work will be restricted to minor adjustments that will not feed through to the data bases in such a radical way. In 50 years' time, it will be interesting to see whether we have experienced a short intense phase of major phylogenetic revision of higher-level tetrapod relationships (1975–90) or whether the rate of discovery of new phylogenetically deep nodes will continue. For eutherian mammals, at least, Novacek (1992) notes a growing concordance of phylogenetic trees produced from molecular data, morphological traits, and the fossil record. Of course, as he also notes, the congruence of several independently produced phylogenetic trees does not indicate that systematists are close to the truth: All of the analyses may be incorrect.

Future research directions. I predict that information on the Triassic and Jurassic extinctions of terrestrial tetrapods will improve along a number of lines:

1. A great deal remains to be learned by further discoveries of fossils, in the Jurassic interval in particular. New collection techniques, and the new focus on smaller tetrapod fossils, often sampled by screen-washing techniques, will doubtless continue to reveal many taxa.

2. A major desideratum is refined knowledge of the stratigraphy of sequences in Europe and North America, and the closer association of the southern-continent sequences with the new biostratigraphic schemes. This will require a closer link between the refined marine stratigraphic standards and the terrestrial palynological (and ostracod, conchostracan, fish, footprint, and other) schemes. New work in magnetostratigraphy and chronometric data may also contribute, but the ammonoid zonal scheme is considerably more refined in terms of stratigraphic acuity (units of about 1 million years in the Late Triassic, and less than 1 million years in the Jurassic), and such precision hardly seems likely in the foreseeable future from either magnetostratigraphy or chronometry.

3. Continuing alpha-taxonomy and higher-level cladistic revisions of existing collections will greatly assist in resolving difficulties over family definitions.

These avenues of research may permit vertebrate paleontologists to attempt serious studies of the Triassic and Jurassic events based on genera, or even species, in the future. At present, this is not possible, because too many genera and species have only point distributions in time. As Padian and Clemens (1985) noted (and it is true for most Mesozoic vertebrates), the dinosaurs actually went extinct globally at the generic level dozens of times: so few genera span from one stratigraphic stage to the next. This problem of the mismatch of our taxonomic acuity and our stratigraphic acuity can be overcome only by a great improvement in the precision of dating faunas. At present, the time intervals in use are too crude, and their durations are greater than the mean generic durations for most vertebrates (1–5 million years) (Stanley, 1979).

Causation of Late Triassic extinctions. There are, broadly, three views on the causes of the major faunal changes that took place among tetrapods during the Late Triassic. One, a firming-up of the "classical" view of Romer (1970), is that the replacement of mammal-like reptiles and rhynchosaurs by thecodontians, and then by dinosaurs, was a long-term competitive process (e.g., Bonaparte, 1982; Charig, 1984).

That viewpoint has been refuted by Benton (1983, 1986a,b, 1987a,b, 1991), who has argued for a second model: that the dominant mammal-like reptiles and rhynchosaurs died out during a late Carnian extinction event, possibly related to a major floral change, and possibly to climatic stresses (Simms et al., Chapter 21, this volume), and that the dinosaurs (and turtles, sphenodontians, crocodylomorphs, pterosaurs, and mammals) radiated opportunistically during the Norian to fill the ecological void.

The third view, argued by Olsen et al. (1987, 1988, 1990) and Hallam (1990), is that the Carnian event was nonexistent, or at least is difficult to detect, and that the end-Triassic event was the key one. This has been linked explicitly to extraterrestrial causation by Olsen et al. (1987, 1988, 1990) and Sepkoski (1989), among others, specifically to the impact of the asteroid that produced the giant Manicouagan crater in Canada. However, this crater dates, if anything, closer to the Carnian–Norian than to the Triassic–Jurassic boundary (Olsen et al., 1987; Hodych and Dunning, 1992), and the Triassic–Jurassic boundary sections have not yielded up the expected impact indicators (e.g., shocked quartz, glass spherules) found in such abundance at the Cretaceous–Tertiary boundary. The recent report (Bice et al.,1992) of shocked quartz from a Triassic–Jurassic boundary section in the Il Fiume gorge in northern Italy is not such strong evidence for impact as might at first be thought. The "shocked" quartz grains occur in the putative Triassic–Jurassic boundary layer, but also in two layers 1–3 m below. In addition, the grains do not have more than four sets of planar deformation features (indeed, most have only single sets), and the angular distribution of the planar deformation features is rather diffuse. As Bice et al. (1992, p. 445) note, "these differences [from classic K-T shocked quartz] make it impossible to demonstrate unambiguously that the grains at the T-J [*sic*] boundary have a shock-metamorphic origin. . . . An alternative hypothesis would be that these grains contain highly unusual Böhm lamellae" presumably produced by normal earthbound tectonism.

Hence, I find little in favor of the impact-induced extinction model, and I adhere firmly to the reality of the late Carnian extinction as being ecologically the key event for terrestrial tetrapods, and as having real significance in the sea as well (e.g., Stanley, 1988; Simms and Ruffell, 1989, 1990; Simms, 1990b; Smith, 1990; Simms et al., Chapter 21). In recent reviews, both Sepkoski (1990) and Hallam (1992) accept the significance of the late Carnian extinction event. This is not to deny the reality of the end-Triassic event: It was a great catastrophe for marine life, but ecologically seemingly less significant for tetrapods.

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References

Anderson, J. M. 1981. World Permo-Triassic correlations: their biostratigraphic basis. Pp. 3–10 in M. M. Cresswell and P. Vella (eds.), *Gondwana Five*. Rotterdam: A. A. Balkema.

Anderson, J. M., and A. R. I. Cruickshank. 1978. The biostratigraphy of the Permian and Triassic. Part 5. A review of the classification and distribution of Permo-Triassic tetrapods. *Palaeontologia Africana* 21: 15–44.

Bachmann, G. J., and M. P. Gwinner. 1971. *Nordwürttemberg. Sammlung Geologischer Führer*. Berlin: Borntraeger.

Barberena, M. C., D. C. Araújo, and E. L. Lavina. 1985. Late Permian and Triassic tetrapods of southern Brazil. *National Geographic Research* 1: 5–20.

Benton, M. J. 1983. Dinosaur success in the Triassic: a noncompetitive ecological model. *Quarterly Review of Biology* 58: 29–55.

1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society* 84: 97–164.

1986a. More than one event in the Late Triassic mass extinction. *Nature* 321: 857–861.

1986b. The Late Triassic tetrapod extinction events. Pp. 303–320 in K. Padian (ed.), *The Beginning of the Age of Dinosaurs: Faunal Change across the Triassic–Jurassic Boundary*. Cambridge University Press.

1987a. Progress and competition in macroevolution. *Biological Reviews* 62: 305–338.

1987b. Mass extinctions among families of non-marine tetrapods: the data. *Mémoires de la Société Géologique de France* 150: 21–32.

1991. What really happened in the Late Triassic? *Historical Biology* 5: 263–278.

1993a. Late Triassic terrestrial vertebrate extinctions: stratigraphic aspects and the record of the Germanic Basin. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*.

1993b. Reptilia. In M. J. Benton (ed.), *The Fossil Record*, Vol. 2. London: Chapman & Hall.

Benton, M. J., and J. M. Clark. 1988. Archosaur phylogeny and the relationships of the Crocodylia. Pp. 289–332 in M. J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods. Vol. 1: Amphibians, Reptiles, Birds.* Oxford: Clarendon Press.

Bice, D. M., C. R. Newton, S. McCauley, P. W. Reiners, and C. A. McRoberts. 1992. Shocked quartz at the Triassic–Jurassic boundary in Italy. *Science* 255: 443–446.

Blendinger, E. 1988. Palynostratigraphy of the late Ladinian and Carnian in the southeastern Dolomites. *Review of Palaeobotany and Palynology* 53: 329–348.

Bonaparte, J. F. 1982. Faunal replacement in the Triassic of South America. *Journal of Vertebrate Paleontology* 21: 362–371.

Brenner, K. 1973. Stratigraphie und Paläogeographie des Oberen Mittelkeupers in Südwest-Deutschland. *Arbeiten aus dem Institut für Geologie und Paläontologie an der Universität Stuttgart* 68: 101–222.

1979. Paläogeographische Raumbilder Südwestdeutschlands für die Ablagerungszeit von Kiesel- und Stubensandstein. *Jahresbericht des oberrheinischen geologischen Vereins, Neue Folge* 61: 331–335.

Brenner, K., and E. Villinger. 1981. Stratigraphie und Nomenklatur des südwestdeutschen Sandsteinkeupers. *Jahreshefte des geologischen Landesamts von Baden-Württemberg* 23: 45–86.

Briggs, D. E. 1991. Extraordinary fossils. *American Scientist* 79: 130–141.

Charig, A. J. 1984. Competition between therapsids and archosaurs during the Triassic period: a review and synthesis of current theories. *Symposia of the Zoological Society of London* 52: 597–628.

Clemens, W. A. 1980. Rhaeto-Liassic mammals from Switzerland and West Germany. *Zitteliana* 5: 51–92.

Cornet, B. 1977. The palynostratigraphy and age of the Newark Supergroup. Ph.D. dissertation, Pennsylvania State University.

1989. Richmond basin lithostratigraphy and paleoenvironments. Pp. 47–53 in P. E. Olsen, R. W. Schlische, and P. J. W. Gore (eds.), *Tectonic, Depositional, and Paleoecological History of Early Mesozoic Rift Basins.* 28th International Geological Congress, Field Trip Guidebook T351. Washington, D. C.: American Geophysical Union.

Cornet, B., and P. E. Olsen. 1985. A summary of the biostratigraphy of the Newark Supergroup of eastern North America with comments on early Mesozoic provinciality. Pp. 67–81 in R. Weber (ed.), *Simposio sobre Floras del Triasico Tardio, su Fitogeografia y Paleoecologia.* III Congresso Latinoamericano de Paleontologia, Mexico.

Cowie, J. W., and M. G. Bassett. 1989. *International Union of Geological Sciences, 1989 Global Stratigraphic Chart, Episodes 22, Supplement.*

Cuny, G. 1991. Nouvelles données sur la faune et l'age de Saint Nicolas de Port. *Revue de Paléobiologie* 10: 69–78.

Dockter, J., P. Puff, G. Seidel, and H. Kozur. 1980. Zur Triasgliederung und Symbolgebung in der DDR. *Zeitschrift für Geologische Wissenschaften* 8: 951–963.

Dunay, R. E., and M. J. Fisher. 1978. The Karnian palynofloral succession in the northern Calcareous Alps, Lunz-am-See, Austria. *Pollen et Spores* 20: 177–187.

1979. Palynology of the Dockum Group (Upper Triassic), Texas, U. S. A. *Review of Palaeobotany and Palynology* 28: 61–92.

Estes, R. 1983. *Sauria terrestria, Amphisbaenia. Handbuch der Paläoherpetologie* 10A: 1–249.

Estes, R., K. de Queiroz, and J. Gauthier. 1988. Phylogenetic relationships within Squamata. Pp. 119–281 in R. Estes and G. Pregill (eds.), *Phylogenetic Relationships of the Lizard Families.* Stanford University Press.

Evans, S. E. 1988. The early history and relationships of the Diapsida. Pp. 221–260 in M. J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods. Vol. 1: Amphibians, Reptiles, Birds.* Oxford: Clarendon Press.

Fisher, M. J. 1972. The Triassic palynofloral succession in England. *Geoscience and Man* 4: 101–109.

Fisher, M. J., and J. Bujak. 1975. Upper Triassic palynofloras from Arctic Canada. *Geoscience and Man* 11: 87–94.

Forster, S. C., and G. Warrington. 1985. Geochronology of the Carboniferous, Permian and Triassic. Pp. 99–113 in N. J. Snelling (ed.), *The Chronology of the Geological Record.* London: The Geological Society.

Fraser, N. C. 1986. Terrestrial vertebrates at the Triassic–Jurassic boundary in south west Britain. *Modern Geology* 10: 147–157.

Gaffney, E. S., and P. A. Meylan. 1988. A phylogeny of turtles. Pp. 157–219 in M. J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods. Vol. 1: Amphibians, Reptiles, Birds.* Oxford: Clarendon Press.

Gall, J.-C., M. Durand, and E. Muller. 1977. Le Trias de part et d'autre du Rhin. Corrélations entre les marges et le centre du bassin germanique. *Bulletin du Bureau de Recherches Géologiques et Minières, sér. 2,* 3: 193–204.

Gauthier, J. A. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences* 8: 1–55.

Gauthier, J. A., A. G. Kluge, and T. Rowe. 1988. The early evolution of the Amniota. Pp. 103–155 in M. J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods. Vol. 1: Amphibians, Reptiles, Birds.* Oxford: Clarendon Press.

Geiger, M. E., and C. A. Hopping. 1968. Triassic stratigraphy of the southern North Sea Basin. *Philosophical Transactions of the Royal Society of London* B254: 1–36.

Gwinner, M. P. 1978. *Geologie der Alpen.* Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung.

1980. Eine einheitliche Gliederung des Keupers (Germanische Trias) in Süddeutschland. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1980: 229–234.

Hahn, G. G. 1982. Paläomagnetische Untersuchungen im Schilfsandstein (Trias, Km2) Westeuropas. *Geologische Rundschau* 73: 499–516.

Hahn, G., D. Sigogneau-Russell, and G. Wouters. 1989. New data on Theroteinidae. Their relations with Paulchoffatiidae and Haramiyidae. *Geologica et Palaeontologica* 23: 205–215.

Hahn, G., R. Wild, and G. Wouters. 1987. Cynodontier-Zähne aus der Ober-Trias von Gaume (S-Belgien). *Mémoires pour servir à l'Explication des Cartes Géologiques et Minières de la Belgique* 24: 1–33.

Hallam, A. 1986. The Pliensbachian and Tithonian extinction events. *Nature* 319: 765–768.

1990. The end-Triassic mass extinction event. *Geological Society of America Special Paper* 247: 577–583.

1992. Major bio-events in the Triassic and Jurassic. In O. H. Walliser (ed.), *Patterns and Causes of Global Bio-Events in the Phanerozoic.* Berlin: Springer-Verlag.

Harland, W. B., R. L. Armstrong, A. V. Cox, L. E. Craig, A. G. Smith, and D. G. Smith. 1990. *A Geologic Time Scale 1989.* Cambridge University Press.

Hodych, J. P., and G. R. Dunning. 1992. Did the Manicouagan impact trigger end-of-Triassic mass extinction? *Geology* 20: 51–54.

Hopson, J. A., and H. R. Barghusen. 1986. An analysis of therapsid relationships. Pp. 83–106 in N. Hotton III, P. D. MacLean, J. J. Roth, and E. C. Roth (eds.), *The Ecology and Biology of Mammal-like Reptiles.* Washington, D. C.: Smithsonian Institution Press.

Hunt, A. P. 1991. The early diversification pattern of dinosaurs in the Late Triassic. *Modern Geology* 16: 43–60.

Hunt, A. P., and S. G. Lucas. 1989. Late Triassic vertebrate localities in New Mexico. Pp. 72–101 in S. G. Lucas and A. P. Hunt (eds.), *The Dawn of the Age of Dinosaurs in the American Southwest.* Albuquerque: New Mexico Museum of Natural History.

1990. Re-evaluation of "*Typothorax*" *meadei*, a Late Triassic aetosaur from the United States. *Paläontologische Zeitschrift* 64: 317–328.

1991a. The *Paleorhinus* biochron and the correlation of the nonmarine Upper Triassic of Pangaea. *Palaeontology* 34: 487–501.

1991b. A new rhynchosaur from the Upper Triassic of West Texas, and the biochronology of Late Triassic rhynchosaurs. *Palaeontology* 34: 927–938.

1991c. A new aetosaur from the Redonda Formation (Late Triassic: middle Norian) of east-central New Mexico, USA. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1991: 728–736.

1992. The first occurrence of the aetosaur *Paratypothorax andressi* (Reptilia, Aetosauria) in the western United States and its biochronological significance. *Paläontologische Zeitschrift* 66: 147–157.

Kemp, T. S. 1982. *Mammal-like Reptiles and the Origin of Mammals.* London: Academic Press.

King, G. M. 1988. *Anomodontia. Handbuch der Paläoherpetologie* 17C: 1–174.

Kitching, J. W., and M. A. Raath. 1984. Fossils from the Elliot and Clarens formations (Karoo sequence) of the northeastern Cape, Orange Free State and Lesotho, and a suggested biozonation based on tetrapods. *Palaeontologia Africana* 25: 111–125.

Klaus, W. 1960. Sporen der Karnischen Stufe der ostalpinen Trias. *Jahrbuch der Geologischen Bundesanstalt, Sonderbericht* 5: 107–182.

Kozur, H. 1975. Probleme der Triasgliederung und Parallelisierung der germanischen und tethyalen Trias. Teil II. Anschluss der germanischen Trias an die internationale Triasgliederung. *Freiberger Forschungshefte* C304: 51–77.

Kutty, T. S., and D. P. Sengupta. 1989. The Late Triassic formations of the Pranhita-Godavari Valley and their vertebrate faunal succession – a reappraisal. *Indian Journal of Earth Sciences* 16: 189–206.

Litwin, R. J., A. Traverse, and S. R. Ash. 1991. Preliminary palynological zonation of the Chinle Formation, southwestern U. S. A., and its correlation to the Newark Supergroup (eastern U. S. A.). *Review of Palaeobotany and Palynology* 68: 269–287.

Lucas, S. G. 1990. The rise of the dinosaur dynasty. *New Scientist* 127: 44–46.

1991. Sequence stratigraphic correlation of nonmarine and marine Late Triassic biochronologies, western United States. *Albertiana* 9: 11–18.

Lucas, S. G., and A. P. Hunt (eds.). 1989. *The Dawn of the Age of Dinosaurs in the American Southwest.* Albuquerque: New Mexico Museum of Natural History.

Mädler, K. 1964. Bemerkenswerte Sporenformen aus dem Keuper und Lias. *Fortschritte der Geologie von Rheinland und Westfalen* 12: 169–200.

Marshall, J. E. A., and D. I. Whiteside. 1980. Marine influences in the Triassic "uplands." *Nature* 287: 627–628.

Maxwell, W. D., and M. J. Benton. 1990. Historical tests of the absolute completeness of the fossil record of tetrapods. *Paleobiology* 16: 322–335.

Milner, A. R. 1988. The relationships and origin of living amphibians. Pp. 59–102 in M. J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods. Vol. 1: Amphibians, Reptiles, Birds.* Oxford: Clarendon Press.

1993a. Amphibia. In M. J. Benton (ed.), *The Fossil Record*, Vol. 2. London: Chapman & Hall.

1993b. *Temnospondyli. Handbuch der Paläoherpetologie.*

Molnar, R. E., S. M. Kurzanoy, and Z. Dong. 1990. Carnosauria. Pp. 169–209 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria.* Berkeley: University of California Press.

Morbey, S. J. 1975. The palynostratigraphy of the Rhaetian stage, Upper Triassic in the Kendelbachgraben. *Palaeontographica* B152: 1–75.

Novacek, M. J. 1992. Mammalian phylogeny: shaking the tree. *Nature* 356:121–125.

Olsen, P. E., S. J. Fowell, and B. Cornet. 1990. The Triassic/Jurassic boundary in continental rocks of eastern North America: a progress report. *Geological Society of America Special Paper* 247: 585–593.

Olsen, P. E., and P. M. Galton. 1977. Triassic–Jurassic extinctions: are they real? *Science* 197: 983–986.

1984. A review of the reptile and amphibian assemblages from the Stormberg of southern Africa, with special emphasis on the footprints and the age of the Stormberg. *Palaeontologia Africana* 25: 87–110.

Olsen, P. E., A. R. McCune, and K. S. Thomson. 1982. Correlation of the early Mesozoic Newark Supergroup by vertebrates, principally fishes. *American Journal of Science* 282: 1–44.

Olsen, P. E., R. W. Schlische, and P. J. W. Gore. 1989. *Tectonic, Depositional, and Paleoecological History of Early Mesozoic Rift Basins, Eastern North America.* Washington, D. C.: American Geophysical Union.

Olsen, P. E., N. H. Shubin, and M. H. Anders. 1987. New Early Jurassic tetrapod assemblages constrain Triassic–Jurassic tetrapod extinction event. *Science* 237: 1025–1029.

1988. Triassic–Jurassic extinctions [reply to comment by Padian]. *Science* 241: 1359–1360.

Olsen, P. E., and H.-D. Sues. 1986. Correlation of continental Late Triassic and Early Jurassic sediments, and patterns of the Triassic–Jurassic tetrapod transition. Pp. 321–351 in K. Padian (ed.), *The Beginning of the Age of Dinosaurs: Faunal Change across the Triassic–Jurassic Boundary.* Cambridge University Press.

Olson, E. C. 1982. Extinctions of Permian and Triassic non-marine vertebrates. *Geological Society of America Special Paper* 190: 501–511.

Padian, K., and W. A. Clemens. 1985. Terrestrial vertebrate diversity: episodes and insights. Pp. 41–96 in J. W. Valentine (ed.), *Phanerozoic Diversity Patterns: Profiles in Macroevolution.* Princeton University Press.

Patterson, C., and A. B. Smith. 1987. Is periodicity of mass extinctions a taxonomic artefact? *Nature* 330: 248–252.

Romer, A. S. 1966. *Vertebrate Paleontology*, 3rd ed. University of Chicago Press.

1970. The Triassic faunal succession and the Gondwanaland problem. Pp. 375–400 in *Gondwana Stratigraphy.* IUGS Symposium Buenos Aires 1967. Paris: UNESCO.

Scheuring, B. W. 1970. Palynologische und palynostratigraphische Untersuchungen des Keupers im Bolchentunnel (Solothurner Jura). *Schweizerische Paläontologische Abhandlungen* 88: 1–119.

Schröder, B. 1982. Entwicklung des Sedimentbeckens und Stratigraphie der klassischen Germanischen Trias. *Geologische Rundschau* 71: 783–794.

Schulz, E. 1967. Sporenpaläontologische Untersuchungen rätoliassischer Schichten im Zentralteil des Germanischen Beckens. *Paläontologische Abhandlungen* B2: 544–633.

Schuurman, W. M. L. 1979. Aspects of Late Triassic palynology. 3. Palynology of latest Triassic and earliest Jurassic deposits of the Northern Limestone Alps in Austria and southern Germany, with special reference to a palynological characterization of the Rhaetian Stage in Europe. *Review of Palaeobotany and Palynology* 27: 53–75.

Sepkoski, J. J., Jr. 1986. Phanerozoic overview of mass extinctions. Pp. 277–296 in D. M. Raup and D. Jablonski (eds.), *Patterns and Process in the History of Life.* Berlin: Springer-Verlag.

1989. Periodicity in extinction and the problem of catastrophism in the history of life. *Journal of the Geological Society, London* 146: 7–19.

1990. The taxonomic structure of periodic extinction. *Geological Society of America Special Paper* 247: 33–44.

Sepkoski, J. J., Jr., R. K. Bambach, D. M. Raup, and J. W. Valentine. 1981. Phanerozoic marine diversity and the fossil record. *Nature* 293: 435–437.

Sepkoski, J. J., Jr., and D. M. Raup. 1986. Periodicity in marine extinction events. Pp. 3–36 in D. K. Elliott (ed.), *Dynamics of Extinction.* New York: Wiley.

Shishkin, M. A. 1991. [A labyrinthodont from the Jurassic of Mongolia.] *Paleontologischeskiy Zhurnal* 1991(1): 81–95. [in Russian]

Shubin, N. H., A. W. Crompton, H.-D. Sues, and P. E. Olsen. 1991. New fossil evidence on the sister-group of mammals and early Mesozoic faunal distributions. *Science* 251: 1063–1065.

Simms, M. J. 1990a. Triassic palaeokarst in Britain. *Cave Science* 17: 93–101.

1990b. Crinoid diversity and the Triassic/Jurassic boundary. *Cahiers de l'Université Catholique de Lyon, Séries Scientifique* 3: 67–77.

Simms, M. J., and A. H. Ruffell. 1989. Synchroneity of climatic change and extinctions in the late Triassic. *Geology* 17: 265–268.

1990. Climatic and biotic change in the late Triassic. *Journal of the Geological Society, London* 147: 321–327.

Smith, A. B. 1990. Echinoid evolution from the Triassic to Lower Liassic. *Cahiers de l'Université Catholique de Lyon, Séries Scientifique* 3: 79–117.

Stanley, G. D., Jr. 1988. The history of early Mesozoic reef communities: a three-step process. *Palaios* 3: 170–183.

Stanley, S. M. 1979. *Macroevolution.* San Francisco: Freeman.

Strauss, D., and P. M. Sadler. 1989. Classical confidence intervals and bayesian probability estimates for ends of local taxon ranges. *Mathematical Geology* 21: 411–427.

Stucky, R. K., and M. C. McKenna. 1993. Mammalia. In M. J. Benton (ed.), *The Fossil Record*, Vol. 2. London: Chapman & Hall.

Sun, A. L., and K. H. Cui. 1986. A brief introduction to the Lower Lufeng saurischian fauna (Lower Jurassic: Lufeng, Yunnan, People's Republic of China). Pp. 275–278 in K. Padian (ed.), *The Beginning of the Age of Dinosaurs: Faunal Change across the Triassic–Jurassic Boundary.* Cambridge University Press.

Tozer, E. T. 1974. Definitions and limits of Triassic stages and substages: suggestions prompted by comparisons between North America and the Alpine-Mediterranean region. Pp. 195–206 in H. Zapfe (ed.), *Die Stratigraphie der alpin-mediterranen Trias.* Wien: Springer-Verlag.

1979. Latest Triassic ammonoid faunas and biochronology, western Canada. *Geological Survey of Canada Paper* 79–1B: 127–135.
Unwin, D. M. 1991. The morphology, systematics, and evolutionary history of pterosaurs from the Cretaceous Cambridge Greensand of England. Ph.D. thesis, University of Reading.
Van der Eem, J. G. L. A. 1983. Aspects of Middle and Late Triassic palynology. 6. Palynological investigations in the Ladinian and Lower Karnian of the western Dolomites. *Review of Palaeobotany and Palynology* 39: 189–300.
Visscher, H., and W. A. Brugman. 1981. Ranges of selected palynomorphs in the Alpine Triassic of Europe. *Review of Palaeobotany and Palynology* 34: 115–128.
Visscher, H., W. M. L. Schuurman, and A. W. Van Erve. 1980. Aspects of a palynological characterisation of Late Triassic and Early Jurassic "standard" units of chronostratigraphical classification in Europe. *Proceedings of the Fourth International Palynological Conference, Lucknow* (*1976–77*) 2: 281–287.
Ward, P. D. 1990. The Cretaceous/Tertiary extinctions in the marine realm; a 1990 perspective. *Geological Society of America Special Paper* 247: 425–432.
Weishampel, D. B. 1990. Dinosaurian distribution. Pp. 63–139 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*. Berkeley: University of California Press.
Weishampel, D. B., P. Dodson, and H. Osmólska (eds.) 1990. *The Dinosauria*. Berkeley: University of California Press.
Weiss, M. 1989. Die Sporenfloren aus Rät und Jura Südwest-Deutschlands und ihre Beziehung zur Ammoniten-Stratigraphie. *Palaeontographica* B215: 1–168.
Wellnhofer, P. 1978. *Pterosauria. Handbuch der Paläoherpetologie* 19: 1–82.
Whiteside, D. I. 1986. The head skeleton of the Rhaetian sphenodontid *Diphydontosaurus avonis* gen. et sp. nov. and the modernizing of a living fossil. *Philosophical Transactions of the Royal Society of London* B312: 379–430.
Wild, R. 1989. *Aetosaurus* (Reptilia: Thecodontia) from the Upper Triassic (Norian) of Cene near Bergamo, Italy, with a revision of the genus. *Rivista del Museo Civico di Scienze Naturali "Enrico Caffi," Bergamo* 14: 1–24.
Witte, W. K., D. V. Kent, and P. E. Olsen. 1991. Magnetostratigraphy and paleomagnetic poles from Late Triassic–earliest Jurassic strata of the Newark basin. *Geological Society of America Bulletin* 103: 1648–1662.
Zapfe, H. 1974. Trias in Oesterreich. Pp. 245–251 in H. Zapfe (ed.), *Die Stratigraphie der alpin-mediterranen Trias*. Wien: Springer-Verlag.
Zawiskie, J. M. 1986. Terrestrial vertebrate faunal succession during the Triassic. Pp. 353–362 in K. Padian (ed.), *The Beginning of the Age of Dinosaurs: Faunal Change across the Triassic–Jurassic Boundary*. Cambridge University Press.
Zhen, S., B. Zhen, N. J. Mateer, and S. G. Lucas. 1985. The Mesozoic reptiles of China. *Bulletin of the Geological Institute of the University of Uppsala* 11: 133–150.

Appendix 22.1

Assignments of terrestrial tetrapod-bearing formations to stages and "substages" of the Middle and Late Triassic and the earliest Jurassic, based on data from Anderson and Cruickshank (1978), Benton (1983,1993a), Olsen and Galton (1984), Kutty and Sengupta (1989), Olsen et al. (1989), Weishampel (1990), and Hunt and Lucas (1990, 1991a,b,c, 1992). The dating of the Complex-A fissure fills from southwest Britain is problematic; they are assigned here a conservative late Norian (Sevatian) age.

Ladinian

Lettenkeuper, SW Germany
Grenzdolomit, SE Germany
Oberer Muschelkalk, Germany
Grenzbitumenzone, Switzerland (ANS/LAD)
Tschermakfjellet Member, Spitsbergen
Sol'lletsk Series (Zone VII), Russian Platform
Ischichuca (Chañares) Formation, Argentina
Bhimaram Sandstone, India
?Karamay Formation, Junggar, Xinjiang, China
?Batung Formation, Hunan, China

Early Carnian (Cordevolian)

Turkey Branch Formation, Virginia, USA

Middle Carnian (Julian)

Unterer Schilfsandstein, Germany
Hosselkus Limestone, California, USA
Pekin Formation, North Carolina, USA
Cumnock Formation, North Carolina, USA

Late Carnian 1 (early Tuvalian)

Oberer Schilfsandstein, Germany
Blasensandstein (lower part), SW Germany
Opponitzer Schichten (lower part), Austria
Cow Branch Formation, Virginia, USA
Wolfville Formation, Nova Scotia, Canada
Popo Agie Formation, Wyoming, USA
Chinle Formation (Shinarump Member), Arizona, USA
Santa Rosa Formation, New Mexico, USA
Tecovas Formation (Camp Springs Member), Texas, USA
Lower Dockum Group, Texas, USA
Santa Maria Formation (*Dinodontosaurus* Assemblage Zone), Brazil
Argana Formation, Morocco
Maleri Formation (lower fauna), India
Tiki Formation, India

Late Carnian 2 (late Tuvalian)

Blasensandstein (upper part), Germany
Kieselsandstein, SW Germany
Rote Wand, Lehrbergschichten, untere Bunte Mergel, Germany
Lossiemouth Sandstone Formation, Scotland, UK
New Oxford Formation, Pennsylvania, USA
Lockatong Formation, Pennsylvania, USA
Chinle Formation (Petrified Forest Member, lower part, and Moss Back Member), Arizona, USA
Garita Creek Formation, New Mexico, USA
Tecovas Formation (post-Camp Springs Member), Texas, USA
Santa Maria Formation (*Scaphonyx* Assemblage Zone), Brazil
Caturrita Formation, Brazil
Ischigualasto Formation, Argentina
Maleri Formation (upper fauna), India

Early Norian (early Lacian)

Unterer Stubensandstein, SW Germany
Unterer Burgsandstein, Germany
Unterer Dolomitmergelkeuper, E Germany
Passaic Formation (lower part), Pennsylvania and New Jersey, USA
Chinle Formation (Petrified Forest Member, upper part, above the Sonsela Sandstone), Arizona, USA
Trujillo Formation, Texas and New Mexico, USA
Bull Canyon Formation, New Mexico, USA
Cooper Formation, West Texas, USA
Lower Elliott Formation, Lesotho, South Africa
Mpandi Formation, Zimbabwe
Bushveld Sandstone Formation (Springbok Flats Member), South Africa
Dharmaram Formation (lower fauna), India

Middle Norian 1 (late Lacian)

Mittlerer Stubensandstein, SW Germany
Mittlerer Burgsandstein, SE Germany
Mittlerer Dolomitmergelkeuper, E Germany
Passaic Formation (lower and middle parts), Pennsylvania and New Jersey, USA
New Haven Arkose (?lower and middle parts), Connecticut, USA
Chinle Formation (Owl Rock Member), Arizona, Utah, and New Mexico, USA
Redonda Formation (lower part), New Mexico, USA
Sloan Canyon Formation (lower part), New Mexico, USA

Middle Norian 2 (Alaunian)

Oberer Stubensandstein, SW Germany
Oberer Burgsandstein, SE Germany
Oberer Dolomitmergelkeuper, E Germany
Calcare di Zorzino, N. Italy
Dolomia di Forni, N. Italy
Passaic Formation (middle part), Pennsylvania and New Jersey, USA
New Haven Arkose (middle part), Connecticut, USA
Chinle Formation (Rock Point Member), New Mexico, USA
Chinle Formation (Church Rock Member), Utah, USA
Redonda Formation (middle part), New Mexico, USA
Sloan Canyon Formation (middle part), New Mexico, USA

Late Norian 1 (early Sevatian)

Fissure fills, SW England, South Wales, UK (Complex A) (late NOR–RHT?)
Knollenmergel, Germany, Switzerland
Lehrbergstufe, SW Germany
Feuerletten, SE Germany
Obere Bunte Mergel, Switzerland
Argillite di Riva di Solto, Italy
Magnesian Conglomerate, England, UK
Grès à *Avicula contorta*, France
Marnes irisées supérieures, France (= Steinmergelkeuper, Germany)
Passaic Formation (upper part), Pennsylvania and New Jersey, USA
New Haven Arkose (middle and upper parts), Connecticut, USA
Redonda Formation (upper part), New Mexico, USA
Sloan Canyon Formation (upper part), New Mexico, USA
Dharmaram Formation (upper fauna), India

Late Norian 2 (late Sevatian; Rhaetian)

Rhaetic, England, Wales, UK
Fissure fills, SW England, South Wales, UK (Complex A) (late NOR–RHT?)
Westbury Formation, England, UK
Rhätsandstein, Germany, Switzerland
Rhétien, France
Saint-Nicolas-de-Port, France
Rhaetic, Scania, Sweden
Passaic Formation (upper part), Pennsylvania and New Jersey, USA
New Haven Arkose (upper part), Connecticut, USA
Wingate Formation, Arizona and Utah, USA
Los Colorados Formation (La Esquina local fauna), Argentina
Quebrada del Barro Formation, Argentina
El Tranquilo Formation, Argentina
Dull Purplish Beds, Lower Lufeng Formation, Yunnan, China

Hettangian

McCoy Brook Formation, Nova Scotia, Canada
Wingate Formation, Arizona, USA
Vulcanodon Beds, Zimbabwe

Hettangian/Sinemurian

"Fissure complex B," South Wales, UK
Lower Portland Formation, Connecticut, USA
Upper Elliott Formation, Lesotho, South Africa
Forest Sandstone, Zimbabwe
Dark Red Beds, Lower Lufeng Series, Yunnan, China

Sinemurian

Lower Lias, Dorset, Warwickshire, Leicestershire, England, UK

Unnamed unit, Beiro Litoral, Portugal
Bushveld Sandstone Formation (Zoutpansberg Member), South Africa
Clarens Formation, South Africa

Sinemurian/Pliensbachian

Moenave Formation, Arizona, USA
Kayenta Formation, Arizona, USA

Pliensbachian/Toarcian

Navajo Sandstone, Arizona, USA
Portland Formation (upper part), Connecticut, USA

Toarcian

Lias epsilon, Germany
Posidonienschiefer, SW Germany
Kota Formation, India

Toarcian/Bajocian

Zhenzhunchong Formation, Sichuan, China

Aalenian

Northampton Sands Formation, Northamptonshire, England

Aalenian/Bajocian

Inferior Oolite, Northamptonshire, Gloucestershire, Dorset, and Wiltshire, England

Aalenian–Callovian

Dapuka Group, Xizang Zizhqu, China

Bajocian

Inferior Oolite, Yorkshire and Oxfordshire, England
Cerro Carnerero Formation, Chubut, Argentina
Injune Creek Beds, Queensland, Australia

Bathonian

Sharp's Hill Formation, Oxfordshire, England (early Bathonian)
Chipping Norton Formation, Gloucestershire and Oxfordshire, England (early Bathonian)
Stonesfield Slate, Oxfordshire, England (middle Bathonian)
Great Oolite, Nottinghamshire, Northamptonshire, Buckinghamshire, and Wiltshire, England (late Bathonian)
Forest Marble, Northamptonshire, Gloucestershire, Oxfordshire, Wiltshire, and Dorset, England (late Bathonian)
Cornbrash Formation, Oxfordshire, England (late Bathonian)
Calcaire de Caen, Normandy, France (early Bathonian)
Guettioua Sandstone, Morocco
Isalo Formation, Madagascar

Bathonian/Callovian

Xiashaximiao Formation, Sichuan, China
Kuangyuan Series, Sichuan, China

Callovian

Lower Oxford Clay, Northamptonshire and Dorset, England (middle Callovian)
Oxford Clay, Cambridgeshire and Oxfordshire, England (middle–late Callovian)
Middle Oxford Clay, Buckinghamshire, England (late Callovian)
Marnes d'Argences, Calvados, France (middle Callovian)
Marnes de Dives, Calvados, France (late Callovian)
Cañadon Asfalto Formation, Chubut, Argentina

Appendix 22.2

Documentation of firsts and lasts for all families of terrestrial tetrapods recorded during the Middle Triassic–Middle Jurassic interval. The amphibian data are authored by Andrew R. Milner; for greater detail, see Milner (1993a). The reptile data are based on Benton (1993b), and the mammalian data on Stucky and McKenna (1993). For further details, the reader should consult these compilations. Paraphyletic taxa are indicated by (p).

Amphibia

Temnospondyli Zittel, 1888

Family Brachyopidae Lydekker, 1885
P.(KAZ/TAT)–J. (CLV)

First: *Bothriceps major* Woodward, 1909, Lithgow Coal Measures, Airly, New South Wales, Australia.
Last: *Ferganobatrachus riabinini* Nessov, 1990, Balabansay Formation, Kirghizia.
Comment: *Ferganobatrachus* was described as a "capitosauroid," but the holotype clavicle appears to be brachyopid (Shishkin, 1991). A brachyopid, *Gobiops desertus*, has been described from the Upper Jurassic (stage uncertain) of Shara Teg, Mongolia (Shishkin, 1991).

Family Capitosauridae Watson, 1919
Tr.(GRI/DIE–NOR)

First: *Parotosuchus rewanensis* Warren, 1980, *P. gunganj* Warren, 1980, and *P. aliciae* Warren and Hutchinson, 1988, Arcadia Formation, Queensland, Australia; and *P. madagascariensis* (Lehman, 1961), Sakamena Formation, Madagascar.
Last: *Cyclotosaurus carinidens* (Jaekel, 1914), Knollenmergel, Halberstadt, Germany.

Family Mastodonsauridae Lydekker, 1885
Tr.(SPA/ANS–CRN)

First: *Mastodonsaurus cappelensis* Wepfer, 1923, oberer Buntsandstein, Kappel, Baden-Württemberg, Germany.

Last: *Mastodonsaurus keuperinus* Fraas, 1889, Schilfsandstein, Stuttgart, Baden-Württemberg, Germany.

Family Trematosauridae Watson, 1919 Tr.(GRI–CRN)

First: *Gonioglyptus longirostris* Huxley, 1865, *Glyptognathus fragilis* Lydekker, 1882, and *Panchetosaurus panchetensis* Tripathi, 1969, Panchet Formation, Bengal, India.

Last: *Hyperokynodon keuperinus* Plieninger, 1852, Schilfsandstein, Baden-Württemberg, Germany.

Family Latiscopidae Wilson, 1948 Tr.(CRN–NOR)

First: *Almasaurus habbazi* Dutuit, 1972, Argana Formation, Argana Valley, Morocco.

Last: *Latiscopus disjunctus* Wilson, 1948, Cooper Formation, upper Dockum Group, Texas, USA.

Family Metoposauridae Watson, 1919 Tr.(LAD–NOR)

First: *Trigonosternum latum* Schmidt, 1931, Lettenkeuper, Germany, and an undescribed skull, Baden-Württemberg, Germany.

Last: "new, small metoposaurid," upper Redonda Formation, New Mexico, USA (Hunt and Lucas, 1989).

Comment: Slightly older material includes unnamed metoposaurids from lower in the Redonda Formation and from the Sloan Canyon Formation of New Mexico, USA (Hunt and Lucas, 1989), as well as species of *Metoposaurus*, *Anaschisma*, and *Kalamoiketer*, upper Petrified Forest Member, Arizona, Bull Canyon Formation, New Mexico, and Cooper Formation, Texas, USA (all early Norian). The youngest European material is *Metoposaurus stuttgartensis* Fraas, 1913, Lehrbergstufe, late Carnian, Baden-Württemberg, Germany.

Family Chigutisauridae Rusconi, 1951 Tr.(GRI/DIE)–K.(BER/ALB)

First: *Keratobrachyops australis* Warren, 1981, Arcadia Formation, Queensland, Australia.

Last: Unnamed material, Strzelecki Formation, Victoria, Australia.

Family Plagiosauridae Jaekel, 1914 Tr.(GRI/DIE–RHT)

First: *Plagiobatrachus australis* Warren, 1985, Arcadia Formation, Queensland, Australia.

Last: *Gerrothorax rhaeticus* Nilsson, 1934, Rhaetic, Scania, Sweden.

Lissamphibia Haeckel, 1866

Family unnamed J.(SIN/PLB)

First and last: Undescribed gymnophionan, Kayenta Formation, Arizona, USA.

Family Unnamed J.(HET/TOA)

First and last: *Vieraella herbstii* Reig, 1961, Roca Blanca Formation, Santa Cruz Province, Argentina.

Comment: *Vieraella* has been placed in the Leiopelmatidae (= Ascaphidae), but it is more likely a stem-anuran with no immediate relationship to any living family (Milner, Chapter 1).

Family Discoglossidae Guenther, 1859 J.(BTH)–Rec.

First: *Eodiscoglossus oxoniensis* Evans, Milner, and Mussett, 1990, Forest Marble Formation, Oxfordshire, England.

Family Unnamed J.(BTH)

First and last: *Marmorerpeton kermacki* and *M. freemani* Evans, Milner, and Mussett, 1988, Forest Marble Formation, Oxfordshire, England.

Family Karauridae Ivakhnenko, 1978 J.(BTH–KIM)

First: *Kokartus honorarius* Nessov, 1988, black and red shales, Kizylsu River, Kirghizia.

Last: *Karaurus sharovi* Ivakhnenko, 1978, Karabastau Formation, Kazakhstan.

Family Albanerpetontidae Fox and Naylor, 1982 J.(BAJ)–T.(BUR/LAN)

First: Atlas centrum referred to *Albanerpeton megacephalus*, Aveyron, France.

Last: *Albanerpeton inexpectatum* Estes and Hoffstetter, 1976, Miocene fissures, La Grive St. Alban, France.

Reptilia Laurenti, 1768

Family Procolophonidae Cope, 1889 P.(KAZ)–Tr.(NOR)

First: *Owenetta rubidgei* Broom, 1939, *Aulacephalodon-Cistecephalus* Assemblage Zone, South Africa.

Last: *Hypsognathus fenneri* Gilmore, 1928, upper Passaic Formation, New Jersey and Pennsylvania, USA.

Comment: *Sphodrosaurus pennsylvanicus* Colbert, 1960, Hammer Mill Formation, Pennsylvania, USA, seems to be a diapsid (H.-D. Sues and D. Baird, pers. commun.), while the Rhaetian or latest Norian "procolophonoid" described by Cuny (1991) from the Saint-Nicolas-de-Port locality in France is incorrectly identified (P. S. Spencer, pers. commun., 1992).

Testudines Batsch, 1788

Family Proganochelyidae Baur, 1888 Tr.(NOR)–J.(HET)

First: *Proganochelys quenstedtii* Baur, 1887, mittlerer and oberer Stubensandstein, Germany.

Last: Unnamed proganochelyid, upper Elliot Formation (Red Beds), Orange Free State, South Africa.

Comment: The age of *P. ruchae* is assumed to be equivalent to the German formations, but that is not certain.

Family Proterochersidae Nopcsa, 1928 Tr.(NOR)

First and last: *Proterochersis robusta* E. Fraas, 1913, unterer Stubensandstein, Baden-Württemberg, Germany.

Family Kayentachelyidae Gaffney, Hutchison, Jenkins, and Meeker, 1987 J.(SIN/PLB)

First and last: *Kayentachelys aprix* Gaffney, Hutchison, Jenkins, and Meeker, 1987, Kayenta Formation, Arizona, USA.

Diapsida Osborn, 1903

Diapsida incertae sedis

Family Endennasauridae Carroll, 1987 Tr.(NOR)

First and last: *Endennasaurus acutirostris* Renesto, 1984, Calcare di Zorzino, Bergamo, Italy.

Family Drepanosauridae Carroll, 1987 Tr.(NOR)

First and last: *Drepanosaurus unguicaudatus* Pinna, 1980, Calcare di Zorzino, Bergamo, Italy.

Lepidosauromorpha Benton, 1983

Family Kuehneosauridae Romer, 1966 Tr.(CRN–RHT)

First: *Icarosaurus siefkeri* Colbert, 1966, Lockatong Formation, New Jersey, USA; and "?kuehneosaur jaw fragments," lower unit of Petrified Forest Member, Chinle Formation, Arizona, USA.

Last: *Kuehneosaurus latus* Robinson, 1962, Pant-y-ffynon Quarry, Glamorgan, Wales.

Comment: Pant-y-ffynon Quarry is dated as Rhaetian. The type material of *K. latus* comes from Emborough Quarry, Somerset, England, whose age is probably Norian, but this is not certain. Later supposed kuehneosaurs, or close relatives, such as *Cteniogenys antiquus* Gilmore, 1928 from the Upper Jurassic and *Litakis gilmorei* Estes, 1964 from the Upper Cretaceous are very doubtful. *Cteniogenys* has been reclassified as a choristodere.

Family Sphenodontidae Cope 1870 (p) Tr.(CRN)–Rec.

First: "sphenodontian," Turkey Branch Formation, Virginia, USA; *Brachyrhinodon taylori* Huene, 1912, Lossiemouth Sandstone Formation, Elgin, Scotland. Extant.

Comment: Other "late" late Carnian sphenodontids have been reported from Arizona, New Mexico, and Texas. Older supposed sphenodontids, such as *Palacrodon* from the Early Triassic of South Africa, and *Anisodontosaurus* from the Middle Triassic of Arizona, may be procolophonids. *Elachistosuchus* is an archosauromorph. The family Sphenodontidae, as presented here, is paraphyletic because of the exclusion of the Pleurosauridae. *Sapheosaurus* and *Gephyrosaurus* are included here within the Sphenodontidae and are not given separate families.

Archosauromorpha Huene, 1946

Choristodera Cope, 1876

Family Pachystropheidae Kuhn, 1961 Tr.(RHT)

First and last: *Pachystropheus rhaeticus* E. von Huene, 1935, Rhaetic bonebed, southern England, Germany.

Family Unnamed J.(BTH–KIM)

First: *Cteniogenys antiquus* Gilmore, 1928, Chipping Norton Formation, lower Bathonian, Gloucestershire, England; Forest Marble Formation, upper Bathonian, Oxfordshire, England.

Last: *Cteniogenys antiquus* Gilmore, 1928, Morrison Formation, Wyoming, USA.

Comment: The familial assignment of these early choristoderes has not been confirmed, and relationships to the pachystropheids and to later champsosaurs are unclear at present. Earlier choristoderes, perhaps belonging to this group, have been noted from the Kayenta Formation (J. Clark, pers. commun., 1991).

Rhynchosauria Osborn, 1903

Family Rhynchosauridae Huxley, 1887 (Cope, 1870) Tr.(SCY–CRN)

First: *Howesia browni* Broom, 1905, and *Mesosuchus browni* Watson, 1912, *Cynognathus-Diademodon* Assemblage Zone, Karoo Basin, South Africa.

Last: *Hyperodapedon gordoni* Huxley, 1859, Lossiemouth Sandstone Formation, Scotland; *Scaphonyx sanjuanensis* Sill, 1970, Ischigualasto Formation, San Juan, Argentina; *Scaphonyx sulcognathus* Azevedo and Schultz, 1988, Caturrita Formation, Rio Grande do Sul, Brazil; *Otischalkia elderae* Hunt and Lucas, 1991, lower Dockum Group, Texas, USA; undescribed rhynchosaur, Wolfville Formation, Nova Scotia, Canada.

Comment: *Noteosuchus colletti* (Watson, 1912) from the *Lystrosaurus-Procolophon* Assemblage Zone of South Africa has been called the oldest rhynchosaur, but it lacks diagnostic characters of the group. Other late Carnian rhynchosaurs are known, but these are dated as "early" late Carnian by Hunt and Lucas (1991b), while the "Lasts" listed earlier are given as "late" late Carnian.

Family Trilophosauridae Gregory, 1945 Tr.(CRN–RHT)

First: *Trilophosaurus buettneri* Case, 1928, lower Dockum Group, Crosby County, Texas, USA.

Last: *Tricuspisaurus thomasi* Robinson, 1957, Late Triassic (Norian?), Ruthin Quarry fissure, Glamorgan, Wales.

Comment: Earlier supposed trilophosaurids, such as the Triassic taxa *Doniceps* and *Anisodontosaurus*, as well as

Toxolophosaurus from the Lower Cretaceous, probably are not trilophosaurids. It is unclear whether or not *Tricuspisaurus* and *Variodens*, both from the English-Welsh fissures, are trilophosaurids.

Family Unnamed Tr.(NOR)

First and last: *Megalancosaurus preonensis* Calzavara, Muscio, and Wild, 1980, Dolomia di Forni, Udine, Italy.

Prolacertiformes Camp, 1945

Family Prolacertidae Parrington, 1935 Tr.(SCY–CRN)

First: *Prolacerta broomi* Parrington, 1935, *Lystrosaurus-Procolophon* Assemblage Zone, Karoo Basin, South Africa, and Fremouw Formation, Antarctica.

Last: *Malerisaurus robinsonae* Chatterjee, 1980, Maleri Formation, Andhra Pradesh, India; and *M. langstoni* Chatterjee, 1986, Tecovas Formation, lower Dockum Group, Howard County, Texas, USA.

Family Tanystropheidae Romer, 1945 Tr.(ANS–NOR)

First: "*Tanystropheus*" *conspicuus* Huene, 1931, oberer Buntsandstein, southern Germany.

Last: *Tanystropheus fossai* Wild, 1980, Argillite di Riva di Solto, Val Brembana, Itlay.

Archosauria Cope, 1869

Family Erythrosuchidae Watson 1917 Tr.(SCY–LAD)

First: *Fugusuchus hejiapensis* Cheng, 1980, He Shanggou Formation, Shanxi Province, North China, and *Garjainia prima* Ochev, 1958, Yarenskian Horizon, upper part of Zone V, Orenburg region, Russia, both middle to late Scythian.

Last: *Cuyosuchus huenei* Reig, 1961, Cacheuta Formation, Mendoza Province, Argentina.

Family Ctenosauriscidae Kuhn, 1964 Tr.(SCY–ANS/LAD)

First: *Ctenosauriscus koeneni* (Huene, 1902), mittlerer Buntsandstein, Germany.

Last: *Lotosaurus adentus* Zhang, 1975, Batung Formation, Hunan, China.

Comment: These two taxa of archosaurs share long dorsal neural spines, but their systematic position is uncertain. It is not clear whether they are related to each other or not.

Family Proterochampsidae Sill, 1967 Tr.(LAD–CRN)

First: *Chanaresuchus bonapartei* Romer, 1971, and *Gualosuchus reigi* Romer, 1971, Chañares Formation, La Rioja Province, Argentina.

Last: *Proterochampsa barrionuevoi* Reig, 1959, Ischigualasto Formation, San Juan Province, Argentina.

Family Phytosauridae Lydekker, 1888 Tr.(CRN–RHT)

First: "*Rutiodon* sp.," Pekin Formation, middle Carnian, North Carolina, USA (Olsen et al., 1989).

Last: *Rutiodon* sp., Rhät, Switzerland, North Germany; "phytosaurs," upper Passaic Formation, New Jersey, upper New Haven Arkose, Connecticut, USA.

Comment: Apparently older phytosaurs, *Mesorhinosuchus fraasi* (Jaekel, 1910) from the mittlerer Buntsandstein (Scythian) of Bernburg, Germany, and others from the Muschelkalk of Germany (Anisian–Ladinian) are all doubtful records. There are numerous late Carnian phytosaurs, *Paleorhinus bransoni* Williston, 1904, Popo Agie Formation, Fremont County, Wyoming, USA, and other species of *Paleorhinus* from Arizona and Texas, USA, Morocco, West Germany, Austria, and India (Hunt and Lucas, 1991a).

Family Stagonolepididae Lydekker, 1887 Tr.(CRN–RHT)

First: *Longosuchus*, Pekin Formation, North Carolina, USA (Olsen et al. 1989); *Longosuchus meadei* (Sawin, 1947), lower Dockum Group, Howard County, Texas; Salitral Member, Chinle Formation, Rio Arriba County, New Mexico, USA (Hunt and Lucas, 1990).

Last: *Neoaetosauroides engaeus* Bonaparte, 1969, upper Los Colorados Formation, La Rioja, Argentina; aetosaur elements, Penarth Group ("Rhaetian"), SW England.

Comment: There are numerous late Carnian stagonolepidids: *Stagonolepis robertsoni* Agassiz, 1844, Lossiemouth Sandstone Formation, Scotland; *Aetosauroides scagliai* Casamiquela, 1960, and *Argentinosuchus bonapartei* Casamiquela, 1960, Ischigualasto Formation, San Juan, Argentina; *Desmatosuchus haplocerus* (Cope, 1892), lower units of the Chinle Formation and Dockum Group, New Mexico and Texas, USA; unnamed stagonolepidid, Wolfville Formation, Nova Scotia, Canada.

Family Rauisuchidae Huene, 1942 Tr.(ANS–RHT)

First: *Wangisuchus tzeyii* Young, 1964, and *Fenhosuchus cristatus* Young, 1964, Er-Ma-Ying Series, Shansi, China; *Vjushkovisaurus berdjanensis* Ochev, 1982, Donguz Series, Orenburg region, Russia; *Stagonosuchus major* (Haughton, 1932) and "*Mandasuchus*," upper bonebed of the Manda Formation, Ruhuhu region, Tanzania; "rauisuchid," Yerrapalli Formation, India.

Last: *Fasolasuchus tenax* Bonaparte, 1978, upper Los Colorados Formation, La Rioja, Argentina.

Family Poposauridae Nopcsa, 1928 Tr.(ANS–NOR)

First: *Bromsgroveia walkeri* Galton, 1985, Bromsgrove Sandstone Formation, Warwick, England.

Last: Poposaurid, upper Redonda Formation, New Mexico, USA.

Comment: If the "last" record is not confirmed, there are several early and middle Norian poposaurids: *Teratosaurus suevicus* Meyer, 1861, mittlerer Stubensandstein, Baden-Württemberg, Germany; *Postosuchus kirkpatricki* Chatterjee, 1985, upper Dockum Group, Texas, USA.

Family Ornithosuchidae Huene, 1908 Tr.(CRN–RHT)

First: *Ornithosuchus longidens* Newton, 1894, Lossiemouth Sandstone Formation, Scotland, and *Venaticosuchus rusconii* Bonaparte, 1971, Ischigualasto Formation, La Rioja, Argentina.

Last: *Riojasuchus tenuiceps* Bonaparte, 1969, upper Los Colorados Formation, La Rioja, Argentina.

Crocodylomorpha Walker, 1968

Family Saltoposuchidae Crush, 1984 Tr.(NOR–RHT)

First: *Saltoposuchus connectens* Huene, 1921, mittlerer Stubensandstein, Wüttemberg, Germany.

Last: *Terrestrisuchus gracilis* Crush, 1984, Ruthin Quarry, Glamorgan, Wales.

Family Sphenosuchidae Huene, 1922 Tr.(CRN)–J.(SIN/PLB) (p)

First: *Hesperosuchus agilis* Colbert, 1952, lower Petrified Forest Member, Chinle Formation, Arizona, USA.

Last: Unnamed form, Kayenta Formation, Arizona, USA (Sues et al., Chapter 16).

Comment: *Hallopus victor* (Marsh, 1877) is a crocodylomorph that may belong to this clade (Clark, in Benton and Clark, 1988). It is probably from the lower Ralston Creek Formation (Callovian) of Freemont County, Colorado.

Family Protosuchidae Brown, 1934 Tr.(RHT)–J.(PLB/TOA)

First: *Hemiprotosuchus leali* Bonaparte, 1969, upper Los Colorados Formation, La Rioja, Argentina.

Last: Unnamed forms, Kayenta Formation, Arizona, USA (Clark, in Benton and Clark, 1988); *Stegomosuchus longipes* Lull, 1953, upper Portland Group, Connecticut, USA.

Comment: The range of Protosuchidae could be much greater if one includes *Dyoplax arenaceus Fraas*, 1867, Schilfsandstein, Germany, as Walker (1961) suggests, and *Edentosuchus tienshanensis* Young, 1973, Wuerho, China, (Early Cretaceous), as Clark (in Benton and Clark, 1988) suggests.

Family Orthosuchidae Whetstone and Whybrow, 1983 J.(HET/SIN)

First and last: *Orthosuchus stormbergi* Nash, 1968, upper Elliot Formation, Lesotho, South Africa.

Family Metriorhynchidae Fitzinger, 1843 J.(BTH)–K.(HAU)

First: *Teleidosaurus calvadosi* (J. A. Eudes-Deslongchamps, 1866), *T. gaudryi* Collot, 1905, and *T. bathonicus* (Mercier, 1933), Bathonian, Normandy and Burgundy, France.

Last: *Dakosaurus maximus* (Plieninger, 1846), Hauterivian, Provence, France.

Family Goniopholididae Cope, 1875 J.(BTH)–K.(MAA)

First: "Goniopholids," Ostracod Limestone, Skye, Scotland (Savage, 1984), Chipping Norton, White Limestone, and Forest Marble formations, Gloucestershire and Oxfordshire, England.

Last: "*Goniopholis*" *kirtlandicus* Wiman, 1931, Maastrichtian, New Mexico, USA.

Family Pholidosauridae Eastman, 1902 J.(BTH)–K.(CEN)

First: *Anglosuchus geoffroyi* (Owen, 1884), *A. laticeps* (Owen, 1884), White Limestone Formation, Oxfordshire, England.

Last: *Teleorhinus mesabiensis* Erickson, 1969, Cenomanian, Iron Range, Minnesota, USA.

Ornithodira Gauthier, 1986

Family Lagosuchidae Arcucci, 1987 Tr.(LAD)

First and last: *Lagosuchus talampayensis* Romer, 1971, *Lagerpeton chanarensis* Romer, 1971, and *Pseudolagosuchus major* Arcucci, 1987, all Chañares Formation, La Rioja, Argentina.

Family Podopterygidae Sharov, 1971 Tr.(CRN/NOR)

First and last: *Sharovipteryx mirabilis* (Sharov, 1971), Madyigenskaya Svita, Fergana, Kirghizia.

Family unnamed Tr.(CRN/NOR)

First and last: *Longisquama insignis* Sharov, 1970, Madyigenskaya Svita, Fergana, Kirghizia.

Family Scleromochlidae Huene, 1914 Tr.(CRN)

First and last: *Scleromochlus taylori* Woodward, 1907, Lossiemouth Sandstone Formation, Morayshire, Scotland.

Pterosauria Owen, 1840 (Kaup, 1834)

Family Unnamed Tr.(NOR)

First and last: *Preondactylus buffarini* Wild, 1983, lower middle part of the "Dolomia Principale," Udine, Italy.

Family Dimorphodontidae Seeley, 1870 Tr.(NOR)–J.(SIN)

First: *Peteinosaurus zambellii* Wild, 1978, upper half of the Calcare di Zorzino, Bergamo, Italy.

Last: *Dimorphodon macronyx* (Buckland, 1829), upper Blue Lias, Dorset, England.

Family Eudimorphodontidae Wellnhofer, 1978 Tr.(NOR)

First and last: *Eudimorphodon ranzii* Zambelli, 1973, upper half of the Calcare di Zorzino, Bergamo, Italy.

Family Rhamphorhynchidae Seeley, 1870 J.(TOA–TTH)

First: *Parapsicephalus purdoni* (Newton, 1888), upper Lias, Yorkshire, England; *Dorygnathus banthensis* (Theodori, 1930), upper Lias, Germany.

Last: *Rhamphorhynchus longicaudus* (Münster, 1839), *R. intermedius* Koh, 1937, *R. muensteri* (Goldfuss, 1831), *R. gemmingi* Meyer, 1846, *R. longiceps* Woodward, 1902, *Scaphognathus crassirostris* (Goldfuss, 1831), and *Odontorhynchus aculeatus* Stolley, 1936 (?nom. nud.), Solnhofener Schichten, Bavaria, Germany.

Dinosauria Owen, 1842 (p)

Family Herrerasauridae Benedetto, 1973 Tr.(CRN)

First and last: *Staurikosaurus pricei* Colbert, 1970, *Scaphonyx* Assemblage Zone, Santa Maria Formation, Rio Grande do Sul, Argentina; *Herrerasaurus ischigualastensis* Reig, 1983, Ischigualasto Formation, San Juan, Aregentina.

Family Podokesauridae Huene, 1914 Tr(CRN)–J.(PLB)

First: *Coelophysis bauri* (Cope, 1889), lower part of Petrified Forest Member, Chinle Formation, Arizona, USA.

Last: *Syntarsus kayentakatae* Rown, 1989, Kayenta Formation, Arizona, USA.

Comment: The famous *Coelophysis* quarry at Ghost Ranch, New Mexico, USA, is in the upper part of the Petrified Forest Member, dated lower Norian.

Family Ceratosauridae Marsh, 1884 (p) J.(SIN–KIM/TTH)

First: *Sarcosaurus woodi* Andrews, 1921, Lias, Leicestershire, England.

Last: *Ceratosaurus nasicornis* Marsh, 1884, Morrison Formation, Colorado, USA.

Family Allosauridae Marsh, 1879 J. (CLV)–K.(ALB)

First: *Piatnitzkysaurus floresi* Bonaparte, 1979, Cañadon Asfalto Formation, Chubut, Argentina.

Last: *Chilantaisaurus marotuensis* Hu, 1964, unnamed unit, Nei Mongol Zizhiqu, China.

Family Megalosauridae Huxley, 1869 Tr.(RHT)?–K.(VLG/ALB)Terr.

First: *Megalosaurus cambrensis* (Newton, 1899), Rhaetic, Glamorgan, Wales.

Last: *Kelmayisaurus petrolicus* Dong, 1973, Lianmugin Formation, Xinjiang Uygur Zizhiqu, China.

Comment: The family Megalosauridae is not accepted by Molnar et al. (1990), although they suggest that *Megalosaurus*, *Magnosaurus*, and *Kelmayisaurus* may be related. There is little evidence that *M. cambrensis* is a true megalosaur. If not, the earliest records of *Megalosaurus* are Aalenian and Bajocian.

Family Unnamed J.(CLV–KIM/TTH)

First: *Eustreptospondylus oxoniensis* Walker, 1964, Oxford Clay, Oxfordshire and Buckinghamshire, England.

Last: *Torvosaurus tanneri* Galton and Jensen, 1979, Morrison Formation, Colorado, USA.

Comment: This family is hinted at by Molnar et al. (1990, p. 209), in suggesting a phyletic link among *Eustreptospondylus*, *Torvosaurus*, and *Yangchuanosaurus*.

Family Thecodontosauridae Huene, 1908 Tr.(CRN–RHT)

First: *Azendohsaurus laaroussi* Dutuit, 1972, Argana Formation, Argana Valley, Morocco.

Last: *Thecodontosaurus antiquus* Riley and Stutchbury, 1836, Magnesian Conglomerate, Avon, England; fissure, fillings, Glamorgan, Wales.

Family Anchisauridae Marsh, 1885 J.(PLB/YOA)

First and last: *Anchisaurus polyzelus* (Hitchcock, 1865), upper Portland Formation, Connecticut and Massachusetts, USA.

Family Massospondylidae Huene, 1914 J.(HET–SIN/PLB)

First: *Massospondylus carinatus* Owen, 1854, upper Elliot Formation, Clarens Formation, and Bushveld Sandstone, South Africa; Forest Sandstone, Zimbabwe; upper Elliot Formation, Lesotho.

Last: *Massospondylus* sp., Kayenta Formation, Arizona, USA.

Family Yunnanosauridae Young, 1942 J.(HET/SIN)

First and last: *Yunnanosaurus huangi* Young, 1942, upper Lower Lufeng Series, Yunnan, China.

Family Plateosauridae Marsh, 1895 Tr.(NOR)–J.(PLB/TOA)Terr.

First: *Sellosaurus gracilis* Huene, 1907–8, unterer and mittlerer Stubensandstein, Baden-Württemberg, Germany.

Last: *Ammosaurus major* (Marsh, 1891), upper Portland Formation, Connecticut; Navajo Sandstone, Arizona, USA.

Family Melanorosauridae Huene, 1929 Tr.(NOR–HET/SIN)

First: *Euskelosaurus browni* Huxley, 1866, lower Elliot Formation and Bushveld Sandstone, South Africa;

lower Elliot Formation, Lesotho; Mpandi Formation, Zimbabwe; *Melanorosaurus readi* Haughton, 1924, lower Elliot Formation, South Africa.

Last: *Lufengosaurus huenei* Young, 1941, upper Lower Lufeng Series, Yunnan, China.

Comment: cf. *Lufengosaurus* is noted from the Zhenzhunchong Formation, Sichuan, China, dated as Toarcian/Bajocian (Weishampel, 1990).

Family Vulcanodontidae Cooper, 1984 (p?) J.(HET–TOA)

First: *Vulcanodon karibaensis* Raath, 1972, *Vulcanodon* Beds, Mashonaland North, Zimbabwe.

Last: *Ohmdenosaurus liasicus* Wild, 1978, Posidonienschiefer, Baden-Württemberg, Germany.

Family Cetiosauridae Lydekker, 1888 (p) J.(BAJ–KIM/TTH)

First: *Cetiosaurus medius* Owen, 1842, Inferior Oolite, West Yorkshire, England; *Amygdalodon patagonicus* Cabrera, 1947, Cerro Carnerero Formation, Chubut, Argentina; ?*Rhoetosaurus brownei* Longman, 1925, ?Injune Creek Beds, Queensland, Australia.

Last: *Haplocanthosaurus priscus* (Hatcher, 1903) and *H. delfsi* McIntosh and Williams, 1988, Morrison Formation, Colorado and Wyoming, USA.

Family Brachiosauridae Riggs, 1904 J.(?AAL/BTH)–K.(ALB)

First: "brachiosaurid," Northamptonshire Sand Formation, Northamptonshire, England.

Last: *Brachiosaurus nougaredi* Lapparent, 1960, "Continental Intercalaire," Wargla, Algeria; *Chubutisaurus insignis* Corro, 1974, Gorro Frigio Formation, Chubut, Argentina.

Comment: If the Northamptonshire brachiosaurid is not confirmed, definite Bathonian examples include the following: *Bothriospondylus robustus* Owen, 1875, Forest Marble, Wiltshire, England; *B. madagascariensis* Lydekker, 1895 and *Lapparentosaurus madagascariensis* Bonaparte, 1986, Isalo Formation, Madagascar.

Family Diplodocidae Marsh, 1884 J.(BAJ)–K.(CMP/MAA)

First: *Cetiosauriscus longus* (Owen, 1842), Inferior Oolite, West Yorkshire, England.

Last: *Nemegtosaurus mongoliensis* Nowinski, 1971, Nemegt Formation, Omnogov, Mongolia.

Family Pisanosauridae Casamiquela, 1967 Tr.(CRN)

First and last: *Pisanosaurus mertii* Casamiquela, 1967, Ischigualasto Formation, La Rioja Province, Argentina.

Family Fabrosauridae Galton, 1972 J.(HET/SIN)

First and last: *Lesothosaurus diagnosticus* Galton, 1978, upper Elliot Formation, Mafeting District, Lesotho.

Comment: Other supposed fabrosaurids such as *Technosaurus* and *Revueltosaurus* (CRN), *Scutellosaurus* (HET), *Fabrosaurus*, *Tawasaurus*, and *Fulengia* (HET/HIN), *Xiaosaurus* (BTH), *Alocodon* and *Trimucrodon* (OXF), *Nanosaurus* (KIM), and *Echinodon* (BER) are not regarded as fabrosaurids, but merely Ornithischia incertae sedis, or thyreophorans (e.g., *Scutellosaurus*), or prosauropods (e.g., *Fulengia*, *Tawasaurus*, *Technosaurus* in part).

Family Scelidosauridae Huxley, 1869 (p?) J.(SIN–TTH?)

First: *Scelidosaurus harrissoni* Owen, 1861, lower Lias, Dorset, England.

Last: *Echinodon becklesi* Owen, 1861, middle Purbeck Beds, Dorset, England.

Comment: The family Scelidosauridae is equated here with the "basal Thyreophora." If *Echinodon* is not a "basal thyreophoran," the family range becomes SIN–PLB?, with *Scutellosaurus lawleri* Colbert, 1981, as the youngest member.

Family Huayangosauridae Dong, Tang, and Zhou, 1982 J.(HET/PLB–BTH/CLV)

First: *Tatisaurus oehleri* Simmons, 1965, Dark Red Beds of the Lower Lufeng Group, Yunnan, China.

Last: *Huayangosaurus taibaii* Dong, Tang, and Zhou, 1982, Xiashaximiao Formation, Sichuan, China.

Family Stegosauridae Marsh, 1880 J.(BTH)–K.(CON)

First: Unnamed stegosaur, Chipping Norton Formation, lower Bathonian, Gloucestershire, England, and from other Bathonian localities in Gloucestershire and Oxfordshire.

Last: *Dravidosaurus blanfordi* Yadagiri and Ayyasami, 1979, Trichinopoly Group, Tamil Nadu, India.

Family Nodosauridae Marsh 1890 J.(CLV)–K.(MAA)

First: *Sarcolestes leedsi* Lydekker, 1893, lower Oxford Clay, Cambridgeshire, England.

Last: "*Struthiosaurus transilvanicus*" Nopcsa, 1915, Sinpetru Beds, Hunedoara, Romania; Gosau Formation, Niederösterreich, Austria; "*Denversaurus schlessmani*" Bakker, 1988, Lance Formation, South Dakota, USA.

Family Heterodontosauridae Romer, 1966 J.(HET/SIN–SIN)

First: *Lycorhinus angustidens* Haughton, 1924, *Lanasaurus scalpridens* Gow, 1975, and *Abrictosaurus consors* (Thulborn, 1975), upper Elliot Formation, South Africa and/or Lesotho.

Last: *Heterodontosaurus tucki* Crompton and Charig, 1962, Clarens Formation, Cape Province, South Africa.

Family Hypsilophodontidae Dollo, 1882
J.(BTH/CLV)–K.(MAA)

First: *Yandusaurus honheensis* He, 1979, Xiashaximiao Formation, Sichuan, China.

Last: *Thescelosaurus neglectus* Gilmore, 1913, Lance Formation, Wyoming, USA; Hell Creek Formation, Montana and South Dakota, USA; Scollard Formation, Alberta, Canada; ?*T. garbanii* Morris, 1976, Hell Creek Formation, Montana, USA.

Synapsida Osborn, 1903

Therapsida Broom, 1905 (p)

Anomodontia Owen, 1859

Family Kannemeyeriidae Huene, 1948
Tr (SCY = CRN)

First: *Kannemeyeria simocephalus* (Weithofer, 1888), lower Etjo Beds, southwest Africa; *K. wilsoni* Broom, 1937, *Cynognathus-Diademodon* Assemblage Zone, South Africa; *K. argentinensis* Bonaparte, 1966, Puesto Viejo Formation, Mendoza Province, Argentina; *Vinceria andina* Bonaparte, 1967, Cerro de Las Cabras Formation, Mendoza Province, Argentina.

Last: *Jachaleria colorata* Bonaparte, 1971, boundary between Ischigualasto Formation and lower Los Colorados Formation, La Rioja Province, Argentina.

Cynodontia Owen, 1860

Family Traversodontidae Huene, 1936
Tr.(SCY–RHT)

First: *Pascualgnathus polanskii* Bonaparte, 1966, Puesto Viejo Formation, and *Andescynodon mendozensis* Bonaparte, 1967, and *Rusconiodon mignonei* Bonaparte, 1972, Rio Mendoza Formation, Mendoza Province, Argentina (Bonaparte, 1982).

Last: *Microscalenodon nanus* Hahn et al. 1988, lower "Rhaetian" bonebed, Gaume, Belgium.

Family Chiniquodontidae Huene, 1948
Tr.(?ANS–CRN)

First: *Aleodon brachyramphus* Crompton, 1955, Manda Formation, Ruhuhu Valley, Tanzania. If this is not a chiniquodontid, the oldest representatives are *Probelesodon lewisi* Romer, 1969, and *Chiniquodon* sp. from the Chañares Formation, La Rioja Province, Argentina (Ladinian).

Last: *Chiniquodon theotonicus* Huene, 1936, *Dinodontosaurus* Assemblage Zone, Santa Maria Formation, Rio Grande do Sul, Brazil.

Comment: A chiniquodontid tooth, *Lepagia gaumensis* Hahn, Wild, and Wouters, 1987, has been reported from the lower Rhaetian bonebed of Gaume, southern Belgium (Hahn, Wild, and Wouters, 1987).

Family Probainognathidae Romer, 1973 Tr.(LAD)

First and last: *Probainognathus jenseni* Romer, 1970, lower beds of Chañares Formation, La Rioja Province, Argentina.

Family Tritylodontidae Cope, 1884
Tr.(RHT)–J.(BTH/CLV)

First: "cf. *Tritylodon*," upper beds of Los Colorados Formation, La Rioja Province, Argentina.

Last: *Bienotheroides wanhsienensis* Young, 1982, upper Xiashaximiao Formation, Sichuan, China.

Family Tritheledontidae Broom, 1912
Tr.(RHT)–J.(SIN)

First: *Chaliminia musteloides* Bonaparte, 1980, Los Colorados Formation, La Rioja Province, Argentina.

Last: *Pachygenelus monus* Watson, 1913, Clarens Formation, South Africa, Lesotho.

Comment: *Therioherpeton cargnini* Bonaparte and Barberena, 1975, Santa Maria Formation, Parana basin, Brazil (Carnian), is sometimes classified as the oldest tritheledontid, but Shubin et al. (1991) show that this assignment is incorrect.

?Aves

Family Protoavidae Chatterjee, 1991 Tr.(NOR)

First and last: *Protoavis texensis* Chatterjee, 1991, Cooper Formation, Texas, USA.

Comment: Whether or not *Protoavis* is a bird, it may well prove to represent a unique family-level taxon.

Mammalia Linnaeus, 1758

Triconodonta Osborn, 1888

Family Morganucodontidae Kühne, 1958
Tr.(RHT)–J.(BTH)

First: *Eozostrodon parvus* Parrington, 1941, and other species, fissure fillings, Somerset, England; *Morganucodon watsoni* Kühne, 1949, fissure fillings, Glamorgan, Wales; *M. peyeri* Clemens, 1980, and *Helvetiodon schuetzi* Clemens, 1980, Rhaetic bonebed, Hallau, Switzerland; *Brachyzostrodon coupatezi* Sigogneau-Russell, 1983, Saint-Nicolas-de-Port, France.

Last: *Wareolestes rex* Freeman, 1979, Forest Marble Formation, Oxfordshire, England.

Comment: Other species of *Eozostrodon* and *Morganucodon*, as well as *Erythrotherium*, from southern Africa and China, are all probably Early Jurassic in age.

Family Sinoconodontidae Mills, 1971
J.(HET/SIN–SIN)

First: *Sinoconodon rigneyi* Patterson and Olson, 1961, *Lufengoconodon changchiawaensis* Young, 1982, and other species, Dark Red Beds, Lower Lufeng Formation, Yunnan, China.

Last: *Megazostrodon rudnerae* Crompton and Jenkins, 1968, Clarens Formation, Lesotho.

Family Amphilestidae Osborn, 1888
J.(SIN/PLB)–K.(?CMP)

First: *Dinnetherium nezorum* Jenkins, Crompton, and Downs, 1983, Kayenta Formation, Arizona, USA.

Last: *Guchinodon hoburensis* Trofimov, 1978 and *Gobiconodon borissiaki* Trofimov, 1978, both Khovboor locality, Mongolia.

Multituberculata Cope, 1884

Family Plagiaulacidae Gill, 1872
?Tr.(RHT)/J.(OXF)–K.(BER/APT/ALB)

First: *Pseudobolodon oreas* Hahn, 1977, *Paulchoffatia delgadoi* Kühne, 1961, *Guimarotodon leiiensis* Hahn, 1977, all Guimarota, Portugal.

Last: *Paulchoffatia* sp. and *Bolodon* sp., Galve local fauna, Spain; plagiaulacid, Trinity Sands, Texas, USA.

Comment: A possible paulchoffatiid (= plagiaulacid), *Mojo usuratus* Hahn, Lepage, and Wouters, 1987, has been described from the lower Rhaetian bonebed of Gaume, Belgium (Hahn et al., 1987).

Haramiyoidea Hahn, 1973

Family Haramiyidae Simpson, 1947
Tr.(RHT)–J.(BTH)

First: *Haramiya moorei* (Owen, 1871), *H. fissurae* (Simpson, 1928), and *Thomasia anglica* Simpson, 1928, Holwell Quarry, Somerset, England; *Haramiya* and *Thomasia* species, Rhaetic bonebeds, Stuttgart area, Germany, and Hallau Bonebed, Switzerland (Clemens, 1980).

Last: Haramiyid, Forest Marble Formation, Oxfordshire, England.

Allotheria incertae sedis

Family Theroteinidae Sigogneau-Russell, Frank, and Hemmerlé, 1986 Tr.(NOR/RHT)

First and last: *Theroteinus nikolai* Sigogneau-Russell, Frank, and Hemmerlé, 1986, Saint-Nicolas-de-Port, Lorraine, France.

Comment: The age of this locality has been disputed, being assigned to the lower Rhaetian, or to the late Norian, as an equivalent of the Knollenmergel.

Dryolestoidea Butler, 1939

Family Amphitheriidae Owen, 1846 J.(BTH)

First and last: *Amphitherium prevostii* (von Meyer, 1832), Stonesfield Slate, Oxfordshire, England.

Family Dryolestidae Marsh, 1879
J.(BTH)–K.(CMP/MAA)

First: Dryolestid, Forest Marble Formation, Oxfordshire, England.

Last: *Leonardus cuspidatus* Bonaparte, 1990, *Groeberitherium stipanicici* Bonaparte, 1986, and *G. novasi* Bonaparte, 1986, all Los Alamitos Formation, Neuquén Province, Argentina; dryolestid, Mesa Verde Formation, Wyoming, USA.

Incertae sedis

Family Peramuridae Kretzoi, 1946
J.(BTH)–K.(?ALB)

First: *Palaeoxonodon ooliticus* Freeman, 1976, Forest Marble Formation, Oxfordshire, England.

Last: *Arguimus khosbajari* Dashzeveg, 1979, Mongolia.

Family Tinodontidae Marsh, 1887
Tr.(NOR)–K.(CMP)

First: *Kuehneotherium praecursoris* Kermack, and Mussett, 1968, Bridgend, Glamorgan, Wales; *Kuehneotherium* sp., Emborough Quarry, Somerset, England.

Last: *Bondesius ferox* Bonaparte, 1990, El Molino Formation, Neuquén Province, Argentina; *Mictodon simpsoni* Fox, 1984, Milk River Formation, Alberta, Canada.

Comment: Emborough Quarry is dated as pre-Rhaetian on topographic evidence by Fraser (1986, and Chapter 11).

Family Docodontidae Simpson, 1947 J.(BTH–KIM)

First: *Borealestes serendipitus* Waldman and Savage, 1972, Ostracod Limestone, Isle of Skye, Scotland; *Simpsonodon oxfordensis* Kermack, Lee, Lees, and Mussett, 1987, Forest Marble Formation, Oxfordshire, England.

Last: *Docodon victor* (Marsh, 1890), and other species, Morrison Formation, Colorado and Wyoming, USA.