

25

Correlation of continental Late Triassic and Early Jurassic sediments, and patterns of the Triassic–Jurassic tetrapod transition

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Introduction

The Late Triassic–Early Jurassic boundary is frequently cited as one of the thirteen or so episodes of major extinctions that punctuate Phanerozoic history (Colbert 1958; Newell 1967; Hallam 1981; Raup and Sepkoski 1982, 1984). These times of apparent decimation stand out as one class of the great events in the history of life.

Renewed interest in the pattern of mass extinctions through time has stimulated novel and comprehensive attempts to relate these patterns to other terrestrial and extraterrestrial phenomena (see Chapter 24). The Triassic–Jurassic boundary takes on special significance in this light. First, the faunal transitions have been cited as even greater in magnitude than those of the Cretaceous or the Permian (Colbert 1958; Hallam 1981; see also Chapter 24). Second, like the Cretaceous–Tertiary boundary, the Triassic–Jurassic boundary heralded a new, long-lasting regime of dominant animals, the dinosaurs. Third, but unlike the Cretaceous, a definite bolide impact structure is known in the Late Triassic. The 70 km Manicouagan crater in Québec, Canada has been dated at 210 ± 4 MY (Grieve 1982), which is within the margin of error of the currently accepted dates for the Triassic–Jurassic boundary. Despite considerable uncertainty, scenarios of asteroid impact have already been proposed to explain the Triassic–Jurassic extinctions, much as they have been for the Cretaceous–Tertiary extinctions (Raup and Sepkoski 1984; Rampino and Stothers 1984); but as such attempts at explanation proceed, the pattern itself must be continually examined. Experts on the patterns of each of the supposed mass extinction events must define the terms and taxa involved, and ask whether each “event” is real or artificial.

Olsen and Galton (1977) previously asked this question of the Triassic–Jurassic extinctions. The ap-

parent answer was that the supposed mass extinctions in the tetrapod record were largely an artifact of incorrect or questionable biostratigraphic correlations. On reexamining the problem, we have come to realize that the kinds of patterns revealed by looking at the change in taxonomic composition through time also profoundly depend on the taxonomic levels and the sampling intervals examined. We address those problems in this chapter. We have now found that there does indeed appear to be some sort of extinction event, but it cannot be examined at the usual coarse levels of resolution. It requires new fine-scaled documentation of specific faunal and floral transitions.

Stratigraphic correlation of geographically disjunct rocks and assemblages predetermines our perception of patterns of diversity, extinctions, and originations. This poses an especially difficult problem for the Early Mesozoic because there are virtually no unquestioned Early Jurassic continental vertebrate assemblages. Correlations are of such paramount importance to any study of change during the Early Mesozoic that we devote the first part of this chapter to a summary description of the rationale for correlating various continental sequences with those of the Late Triassic and Early Jurassic type areas of Europe.

The second part of this chapter details the taxonomic changes through the Early Mesozoic based on these correlations. We examine the skeletal record of continental tetrapods by looking at the global record at the family and stage levels. Unfortunately, the family and stage levels are too coarse a level of analysis for these kinds of questions. We try to circumvent this problem by examining two subsets of the world data, data from the Newark Supergroup (Froelich and Olsen 1984) and data from the European Early Mesozoic.

The unique periodic lacustrine cycles of the

Newark allow us to look at chronometric sampling intervals of two million years as well as the individual stage lengths. Although the data are reliable at the generic level, we use these data at the level of the family rather than the genus or species because too many species are from single localities for the compilations of generic distributions to be meaningful. In addition, it can be argued that when looking at one geographic area, sampling can exert a severe bias, especially in the Newark, where osseous remains are not common and there is a bias toward lacustrine taxa. Therefore, we also look at vertebrate ichnotaxa because they are sampled in the same kind of depositional environment through the Newark, and they are extremely abundant and therefore not as subject to the problems of small sample size that plague bony remains. Pollen and spore taxa are examined as an independent check on the diversity patterns. They are reliable at a much finer taxonomic level than bones or ichnotaxa, and they do not suffer from small sample size.

We examine the European Early Mesozoic only at a stage level, because there is as yet no way to calibrate the section independently at a finer stratigraphic level. Relative dates are not reliable, and chronostratigraphic measures are elusive. For the most part, absolute dating has not been done. As we do for the global data, we also restrict our analysis of the European fossil vertebrates to the family level because we are unsure of potential synonymies at lower taxonomic levels within the assemblages themselves. Finally, we compare taxonomic rates from the global record of tetrapods to those of the marine invertebrate record of the Early Mesozoic, at the stage and family level. Of interest here is the comparison among the different patterns. We treat all of these data, including the global data, with consistent methods of calculating the average number of taxa, normalized origination and extinction rates per million years, and probabilities of extinction and origination.

In the third section of this chapter, we identify which taxa in particular are responsible for the observed patterns. We go on to examine physical and biological changes through the Early Mesozoic and comment on events that might be synchronous with (and therefore perhaps related to) faunal changes that stand above background levels.

The rationale for correlation of continental Early Mesozoic tetrapod assemblages

A dramatic change in facies marks the transition between Triassic and Jurassic systems in the Germanic Basin of Central Europe. The continental and paralic Germanic facies of the Upper Triassic, the Keuper, give way to the fully marine Lias of the

Lower Jurassic (Gall, Durand, and Muller 1977; Chapter 1). Terrestrial tetrapod remains are fairly common in the Keuper, but are all but absent in the Lias. As a consequence, it is impossible to compare Triassic and Jurassic tetrapod assemblages directly in the type area of the Early Mesozoic. The main goal of this chapter is to make just such a comparison, and thus it is necessary to correlate, by whatever means available, other continental beds with those of the European Early Mesozoic. Unfortunately, correlation of principally continental beds with the marine Jurassic beds has proved very difficult. Obviously, whatever sections we choose as correlative with those of the European Lias determine our view of the transition in tetrapods. This view is necessarily indirect, and therefore our conclusions based on cumulative faunal lists of the world are somewhat uncertain (as stressed by Colbert in Chapter 1).

Correlation problems within the type areas in Europe

Colbert (Chapter 1) reviews the origins of the main divisions of the Triassic and Jurassic within Europe. For our purposes, it is necessary to say a little more about these divisions and outline the crucial problems of correlating the type areas of the Triassic and Jurassic systems with the type areas of the standard marine stages.

The type area of the Triassic is the Germanic Basin of Central Europe. The earliest Mesozoic in the Germanic Basin consists of three vertically segregated facies: (1) a lower continental and paralic sequence, the Buntsandstein; (2) a middle marine sequence, the Muschelkalk; and (3) an upper continental and paralic sequence, the Keuper. These are lithological divisions.

The wholly marine sequences of the Alps provide the type areas for the stages of the Late Triassic; their history is reviewed by J. T. Gregory (in prep.). The stages in the Alpine Triassic are recognized principally by marine invertebrate zones, especially ammonites. These stages are time-stratigraphic, not lithological, units, and there are problems in correlating the type areas of the stages of the Late Triassic. Specifically, the youngest of the stages of the Triassic, the Rhaetian, contains only one ammonite zone and is now generally included as the uppermost division of the Norian (Tozer 1974, 1979; Hallam 1981; Pearson 1970). Accordingly, we do not recognize the Rhaetian as a separate stage. On the other hand, correlation of the Alpine zones with the Muschelkalk of the Germanic Basin has been fairly straightforward, with the Anisian and Ladinian stages mostly represented by the Muschelkalk. However, the upper and lower boundaries of the Muschelkalk have proved diachronous, as might be

expected. The upper part of the Middle and the Upper Buntsandstein and the Lower Keuper are included in the Early Anisian and Late Ladinian, respectively. The rest of the Buntsandstein is apparently equivalent to the Scythian of the Alpine section (Gall et al. 1977).

Correlation of the different lithostratigraphic divisions of the Keuper with the Alpine stages is weak. At present, there are two different correlation schemes for the Keuper and Alpine Triassic (reviewed by Benton, Chapter 24). The main difficulties with the correlation center on the Upper Gipskeuper [the Kieselsandstein, Bunte Mergel, and Rote Wand = km3 of the standard stratigraphic scheme (Laemmlen 1958; Gwinner, 1980)]. Perhaps because the data are scarce, palynologists and invertebrate paleontologists differ on the correlation. The paleomagnetic data of Hahn (1984) probably demonstrate that at least some Keuper units (such as the Schilfsandstein = km2) are time-transgressive. However, these data cannot yet bear on stage level correlations because the magnetic stratigraphy of the Triassic is known at far too coarse a level; alternative stage level correlations to other magnetozones cannot be excluded. For the purposes of this chapter we accept the correlations of Kozur (1975) and Brinkmann (1960) (see Fig. 25.1) that place the km3 beds within the Carnian, because this agrees with placement of the Haupt Unconformity at the basal Norian and at the base of km4 beds (Steinmergelkeuper) in the Keuper (Schroeder 1982).

The type intervals of the Jurassic System are exposed in the Jura Mountains of southeastern France, the rocks of which are marine and highly fossiliferous. The type areas of the various stages of the Jurassic occur widely through much of Europe. Even correlation of stage boundaries outside the type areas has been reasonably straightforward and was worked out by the middle of the nineteenth century. Correlation is principally by Opel ammonite zones, and the main works on the detailed correlation stand as classics in biostratigraphy (Opel 1856–8; Arkell 1933). In marine rocks, the stage boundaries of the Jurassic have been successfully extended essentially worldwide (Tozer 1979).

Correlation of the European Early Mesozoic outside the type areas

Lithostratigraphic correlation

Because the type Triassic of the Germanic Basin consists of roughly two-thirds continental rocks, correlation to other continental areas is aided by the shared suites of continental fossils. Unfortunately, the exposed continental sequences of the Germanic Basin are very thin compared to the total amount of time they must represent. This is especially true for the Keuper, which has an exposed

thickness of around 500 m (Rutte 1957; Brinkmann 1960). When correlated with the Alpine section, the sequence covers the interval from late Ladinian to the Triassic–Jurassic boundary. Measured against the radiometric scale of Palmer (1984), this interval covers roughly 24 MY. This is equivalent to a net sedimentation rate of 0.02 mm/year. In contrast, the correlative parts of the exposed portions of most other Late Triassic continental deposits, such as the Chinle Formation in Arizona, United States, and the Newark Supergroup of eastern North America would have much faster net sedimentation rates (500 m/5 MY = 0.10 mm/year for the Chinle and 6600 m/20 MY = 0.31 mm/year for the entire Late Triassic part of the Newark Basin of the Newark Supergroup). The relative thinness of the Keuper and the very slow average sedimentation rates compared to other Triassic continental sequences are very important, because in principally fluvial and “deltaic” sequences, such as the Keuper, sedimentation rates are not constant at all. In general, as the mean sedimentation rate drops, the variance in sedimentation rates measured over shorter intervals increases, and the completeness of the record decreases (Sadler 1981; Sadler and Dingus 1982; Schindel 1982; Rettallack 1984).

The intervals of the Keuper that are composed largely of sandstone, such as the crucial and richly fossiliferous Schilfsandstein (km2) and the Blasen-sandstein (km3), are fluvial and represent one or a few sedimentation packages, each deposited very rapidly. This strongly suggests that, in comparison to other continental areas, the sedimentation rate fluctuated to extremes (viewed over a short time interval), and large intervals of time are represented by few or no sediments in the Keuper. As previously mentioned, Hahn’s paleomagnetic data from the Schilfsandstein indicate at least that sandstone unit is time-transgressive. Thus, fossil assemblages from vertically adjacent Keuper units may be separated by comparatively large hiatuses, and fossils from the same lithologic units need not be contemporaneous.

In addition, there is a regionally recognized unconformity above the Upper Gipskeuper (km3 = Kieselsandstein and Rote Wand), the so-called Haupt Unconformity (Schroeder 1982). In Eastern Europe, all of the pre-km4 sediments are truncated by this slightly angular unconformity so that (for example) in northern Poland, km4 sediments rest on pre-Triassic rocks (Schroeder 1982). The strongly episodic sedimentation rates, coupled with a low total accumulation rate and the presence of the basal km4 unconformity, make correlation with the vastly thicker and more complete continental Mesozoic sequences in other areas difficult. Applying Alpine stage designations to the correlative continental areas is, therefore, even more difficult.

Correlation outside the Germanic Basin of km5, the youngest Germanic Basin Triassic (Rhaetian of older works), is extremely uncertain, because correlation of these mixed marine, paralic, and continental rocks with the Alpine Late Norian (Rhaetian) is itself uncertain. This is all the more confusing because at least some of the classic German "Rhaetian" horizons have proved to be earliest Jurassic (Achilles 1981). We designate these Triassic beds only as latest Norian.

Palynological correlation

Pollen and spore assemblages provide perhaps the most direct means of correlation among the Germanic Basin Triassic, the Alpine Triassic, and continental rocks of other areas. Correlation by pollen and spores in the Triassic largely depends on the recognition of taxa with ranges limited to a portion of the system in Europe. Of the several hundred presumably valid morphospecies that have been described, only a fraction have ranges limited to less than two stages (Fisher and Dunay 1981). The upper and lower limits of these ranges represent the basic data for correlation with other areas. Triassic palynoflorules from Antarctica, Australia, India, southern Africa, and South America are radically different from all more northern assemblages, regardless of the details of correlation (Anderson and Anderson 1970; Dolby and Balme 1976). The megafossil florules from the same southern areas are equally different from the northern florules, which makes paleobotanical correlation of these areas with those of the Germanic Basin and the Alpine Triassic all the more uncertain. Fortunately, there are several areas where marine rocks interfinger with plant- and palynomorph-bearing sections, and these can be tied to the European section (Retallack 1977, 1979).

For the Early and Middle Triassic, we accept the correlations of Anderson and Anderson (1970) and Anderson and Cruickshank (1978), which are based principally on pollen and spore and megafossil plant assemblages. It is necessary to revise the correlations of the Late Triassic and Early Jurassic, however.

The first problem is to differentiate those vertebrate assemblages of Carnian and Norian age. In Anderson and Anderson (1970) and Anderson and Cruickshank (1978) (followed by Benton in Chapter 24), most of the Late Triassic assemblages of the world are considered Norian or early Norian in age. Recent work suggests that most of these are Carnian assemblages.

Recent work on the exposed portions of the Chinle Formation and Dockum Group of the western North American Triassic has failed to locate any palynoflorules that indicate an age younger than latest Carnian–early Norian or older than middle Car-

nian (Ash et al. 1978; Dunay and Fisher 1979; Ash 1980; Chapter 9). We believe that the supposedly Norian assemblages discussed by Chatterjee (Chapter 10) are also Carnian. Those portions of the Newark Supergroup that until recently have produced the bulk of the vertebrates have likewise proved to be middle and late Carnian in age (Hope and Patterson 1970; Cornet 1977a,b; Cornet and Olsen 1985). Younger, much less fossiliferous sequences make up the bulk of the Newark, however.

The Maleri Formation of India and correlative formations were first thought to be Norian in age (Chatterjee 1980), but recent palynological work by Kumaran and Maheswari (1980) on the Tiki Formation has suggested a Carnian age. On the basis of the presence of the rhynchosaur *Hyperodapedon huxleyi* (Ghosh and Mitra 1970; Chatterjee 1980; Cooper 1981; Benton 1983) in both formations, the Tiki Formation correlates with the Maleri. Likewise, the vertebrate-rich Ischigualasto Formation of Argentina is best viewed as Carnian, not Norian, on the basis of megafossil plants and palynomorph assemblages (Bonaparte 1982).

The Early Jurassic formations of Europe present the greatest challenge to correlation. Where lateral correlations can be established with certainty, the rocks are almost entirely marine; where continental rocks are present, their correlation to the stage level is very tentative. Terrestrial vertebrates are virtually absent, and the pollen and spore assemblages are not as well studied as those of the Late Triassic. Nonetheless, pollen and spore assemblages provide the best link with continental areas outside the European marine Jurassic.

Unfortunately, palynological characterization of the Triassic–Jurassic transition is not well established, even in Europe. The transition between the Late Triassic of the Germanic Basin and the European Liassic is marked by change in the relative abundance of taxa, but by surprisingly few extinctions or originations of pollen and spore taxa marking the boundary (Morbey 1975; Schuurman 1979; Fisher and Dunay 1981; Visscher and Brugman 1981). In many areas, this change in relative abundance consists of a dramatic increase in the percentage of the conifer palynotaxon *Corollina*, especially *C. meyeriana* (Visscher, Schuurman, and Van Erve 1980; Alvin 1982). However, even in Europe, *Corollina* does not consistently increase through the boundary at various localities (Cornet 1977a). In fact, the European section appears to straddle an Early Jurassic boundary between a northern palynological province, in which *Corollina* may be absent or only a minor part of palynoflorules, and a southern province, in which *Corollina* is strongly dominant (Hughes 1973; Pederson and Lund 1980; Alvin 1982; Olsen and Galton 1984; Cor-

net and Olsen 1985). The later Early Jurassic is characterized by a number of diagnostic taxa, but they are fewer than the characteristic taxa of divisions of the Triassic. The recognition of the Triassic–Jurassic boundary by the extreme dominance of *Corollina* probably reflects relative abundance of the *Corollina* producers, the cheirolepidaceous conifers (Cornet 1977a; Alvin 1982) that replaced the older, more diverse plant assemblage.

The only region in which both adequate palynological data and adequate terrestrial vertebrate assemblage are in direct association is the Newark Supergroup of eastern North America. Here, the upper Newark Supergroup has produced abundant palynoflorules, which, based on all the available evidence, correlate with those of the European Lias. *Corollina meyeriana* becomes strongly dominant a few meters below the oldest extrusive basalts in all Newark basins, and this is where the Triassic–Jurassic boundary has been placed by Cornet (1977a) and Cornet and Olsen (1985). The overlying extrusive basalt flows consistently give K–Ar and $^{40}\text{Ar}/^{39}\text{Ar}$ dates on the younger side of the Triassic–Jurassic boundary (Armstrong and Besancon 1970; Cornet, Traverse, and McDonald 1973; Armstrong 1982; McHone and Butler 1984; Seideman et al. 1984). In strata higher in the Newark section, palynomorph taxa characteristic of the Early Jurassic occur, just as they do in Europe (Cornet 1977a).

Unfortunately, the taxonomic diversity within Newark Supergroup palynoflorules of Jurassic age is very low. Cornet (1977a) has been forced to divide the more than 2000 m of post-Triassic Newark Supergroup into three palynologically defined zones, which are largely based on the relative proportion of three *Corollina* species. These are the *Corollina meyeriana* zone, *C. torosus* zone, and the *C. murphii* zone, which he correlates with the Hettangian + Sinemurian, Pliensbachian, and Toarcian, respectively. Whereas it seems certain that at least most of these strata are Early Jurassic, precise correlation with the European Jurassic stages must be regarded as uncertain, even though these are not conflicting data.

The age assessment of three other classic areas with diverse continental vertebrates has recently shifted from the Late Triassic to the Early Jurassic, again principally on the basis of floral remains. The Moenave Formation of the lower part of the Glen Canyon Group of the southwestern United States has produced a palynoflorule dominated by *C. torosus* (Olsen and Galton 1977; Peterson, Cornet, and Turner-Peterson, 1977; Peterson and Pippingos 1979; Chapters 20, 22, and 23). This indicates that most of the Glen Canyon Group, including the vertebrate-rich Kayenta Formation, is Jurassic in age.

Likewise, beds in the Tuli Basin of Zimbabwe and Botswana equivalent to the Clarens Formation of the Karoo Basin have produced a palynoflora dominated by *Corollina intrareticulatus*, known otherwise only from Late Sinemurian to Tithonian age sediments of Argentina (Volkheimer 1971; Aldiss, Benson, and Rundel 1984). Interbedded basalt flows and the older flows of the Drakensberg Basalts from the Karoo Basin of South Africa give K–Ar dates of 169–193 MY (Fitch and Miller, 1971; Cleverly, 1979; Bristow and Saggerson, 1983; Aldiss et al., 1984). These basalts appear to be somewhat younger than those of the Newark Supergroup and fall well within the Early Jurassic in all the current radiometric scales (Busbey and Gow 1984). Finally, the “Dark Red Beds” and possibly the underlying “Dull Purplish Beds” of the Lower Lufeng of Yunnan, China appear to be Early Jurassic on the basis of floral remains (Cui 1976; Sigogneau-Russell and Sun 1981; Chapter 21).

Two more deposits that must be mentioned are the Evergreen Formation and the Marburg Sandstone of Australia. Dated as late Early Jurassic on the basis of palynoflorules dominated by *Corollina classoides* and *Tsugaepollenites* spp. (de Jersey and Paten 1964; Reiser and Williams 1969), these units have produced the youngest known labyrinthodont amphibians, *Siderops* and *Austropelor* (Family Chigutisauridae) (Warren and Hutchinson 1983). At least one group of labyrinthodonts, it seems, survived the Triassic (Chapter 1).

Correlation by vertebrates

Although correlation by pollen and spores provides the best link between the Early Mesozoic of Europe and areas of wholly continental deposition, the vertebrate evidence is in good agreement. For example, the portion of the Newark Supergroup that is assigned to the Late Triassic on the basis of pollen and spores contains reptiles and amphibians characteristic of the Middle and Upper Keuper. In addition, many vertebrate taxa characteristic of the Jurassic portion of the Newark are absent from the German Keuper (Olsen and Galton 1977, 1984; Cornet and Olsen 1985). The osseous remains of phytosaurs and their referred footprints, for instance, extend to the very top of the palynologically defined Late Triassic in the Newark Basin, and they extend to the very top of the Keuper (Rhaet = km5) as well. No phytosaurs have ever been found in the part of the Newark thought to be Jurassic on the basis of pollen and spores, and phytosaurs have never been found in the disputed or undisputed Jurassic sediments anywhere else in the world. Phytosaurs are absent from the Glen Canyon Group (Olsen and Galton 1977) [the phytosaur-bearing Rock Point Member is now assigned to the Chinle Formation (Pippingos and

O'Sullivan 1978)], the Upper Stormberg Group of southern Africa, and also the Lower Lufeng [the one possible specimen is now lost and regarded as questionable (Chapter 21)]. The tetrapod assemblages from these units, now correlated with the Early Jurassic, are distinctly different from the classic Late Triassic assemblages (Olsen and Galton 1977, 1984; Attridge, Crompton, and Jenkins 1985).

It should be stressed that not all authors agree with an Early Jurassic age for many of these continental strata (Colbert 1958; Busbey and Gow 1984; Chapter 1), and it must be admitted that these assignments are by no means certain [see reviews by Clark and Fastovsky (Chapter 23) and Sues (Chapter 22)]. However, there is considerable published evidence independent of the vertebrates that supports an Early Jurassic age for these strata. A counter-argument presenting positive evidence to the contrary has yet to be presented, in our view.

Both Newark Supergroup and Chinle-Dockum assemblages dated as late Carnian by pollen and spore assemblages yield distinctive vertebrate assemblages dominated by the advanced phytosaur *Rutiodon* and the labyrinthodont amphibian *Metoposaurus* (Olsen, McCune, and Thomson 1982). Such an assemblage is not present in the Germanic Keuper. Instead, the youngest *Metoposaurus* assemblages in km3 contain *Paleorhinus*-type phytosaurs [*Parasuchus* of Chatterjee (Chapter 10)]. The *Paleorhinus*-type phytosaurs also occur with *Metoposaurus* in the Chinle Formation and the Dockum Group in beds with middle Carnian pollen and spores, and these beds occasionally contain *Rutiodon* as well. The hypothesis that the *Rutiodon*-*Metoposaurus* assemblage is represented by the post-km3 unconformity in Europe is used here, but must be tested by additional work.

The Lossiemouth beds of Scotland present an additional problem because there are no independent means to assess the age of the vertebrates. Walker (1961) assigned a Norian age based on the close relationship of the aetosaur *Stagonolepis* to *Aetosaurus* from the German Stubensandstein, of Norian age. Recently, however, Baird and Olsen (1983) have reported the Lossiemouth procolophonid *Leptopleuron* (*Telerpeton*) from the late Carnian Wolfville Formation of the Newark Supergroup. The Nova Scotian form may even be conspecific with that from Scotland. In addition, the Lossiemouth beds have produced the type species of the rhynchosaur *Hyperodapedon*, thus suggesting correlation with the Maleri and Tiki formations. Rhynchosaurids are as yet unknown in beds regarded on other grounds as younger than Carnian. In addition, *Stagonolepis*-like aetosaurs occur in both Carnian and Norian beds in the Newark Supergroup (Olsen et al. 1982; Baird and Olsen 1983) and Ar-

gentina (Bonaparte 1982). We therefore prefer, on balance, to regard the Lossiemouth beds as Carnian (Fig. 25.1).

Two important continental assemblages have even more uncertain ages than those discussed thus far: the fissure-fills of Great Britain and the Los Colorados Formation of Argentina. The classic fissure fillings of Great Britain have been traditionally divided into two suites (Robinson 1957): a supposedly Norian suite dominated by sauropsids, especially *Kuehneosaurus* and other reptiles, and a Rhaeto-Liassic suite dominated by mammals and tritylodonts. One of the latter fissure fillings yields the tritylodont *Oligokyphus* and marine invertebrates indicating a Pliensbachian age (Kuehne 1956). One fissure contains both *Oligokyphus* and the mammal *Morganucodon*, and other fissure fills containing *Morganucodon* have also produced a "Rhaeto-Liassic" plant assemblage (Pacey 1978; Marshall and Whiteside 1980) dominated by cheirolepidaceous conifers. Recently, all these "Rhaeto-Liassic" fissures have been regarded by a number of authors as more definitely Early Jurassic, probably early Sinemurian (Evans 1980; Kermack, Mussett, and Rigney 1981). The mammal *Kuehneotherium* has been considered characteristic of the younger fissure fills, but Fraser and Walkden (1984) and Fraser, Walkden, and Stewart (1985) reported this mammal in association with *Kuehneosaurus*, thus blurring the faunal distinction between the two sets of fissures. The two sets of fissures also share very similar sphenodontids (Pacey 1978; Fraser and Walkden 1983). Thus, it is unclear what range of ages can be assigned to these assemblages, although at least some are regarded as Early Jurassic in age and some just as certainly as late Norian in age (Marshall and Whiteside 1980). For the purposes of our range chart (Fig. 25.2), we regard all the Jurassic fissures listed by Kermack, Mussett, and Rigney (1973), except the Neptunian dike described by Kuehne (1956), as Hettangian, and all the others as Norian.

The La Esquina local fauna of the Los Colorados Formation of Argentina poses a major problem because the assemblage contains elements typical of both Late Triassic and Early Jurassic faunas, and there are no other associated forms of age-correlative data. Specifically, it is the only assemblage known to contain tritheledonts, tritylodonts, protosuchid crocodiles, and sphenosuchids together with stagonolepidids and raiusuchids (Bonaparte 1982). It has not been documented in the published literature that this assemblage represents a single faunal horizon. If it does not represent a mixture of Late Triassic and Early Jurassic horizons, this fauna may be truly transitional, and, in the absence of contrary evidence, we list it here as Norian.

The correlations of the early Mesozoic areas

discussed above with the European type area are shown in Figure 25.1. The ranges of families of tetrapods through the Triassic and Early Jurassic based on these correlations are shown in Figure 25.2. We cannot overemphasize the importance of precise correlations to the pattern of originations that we discuss in the following section.

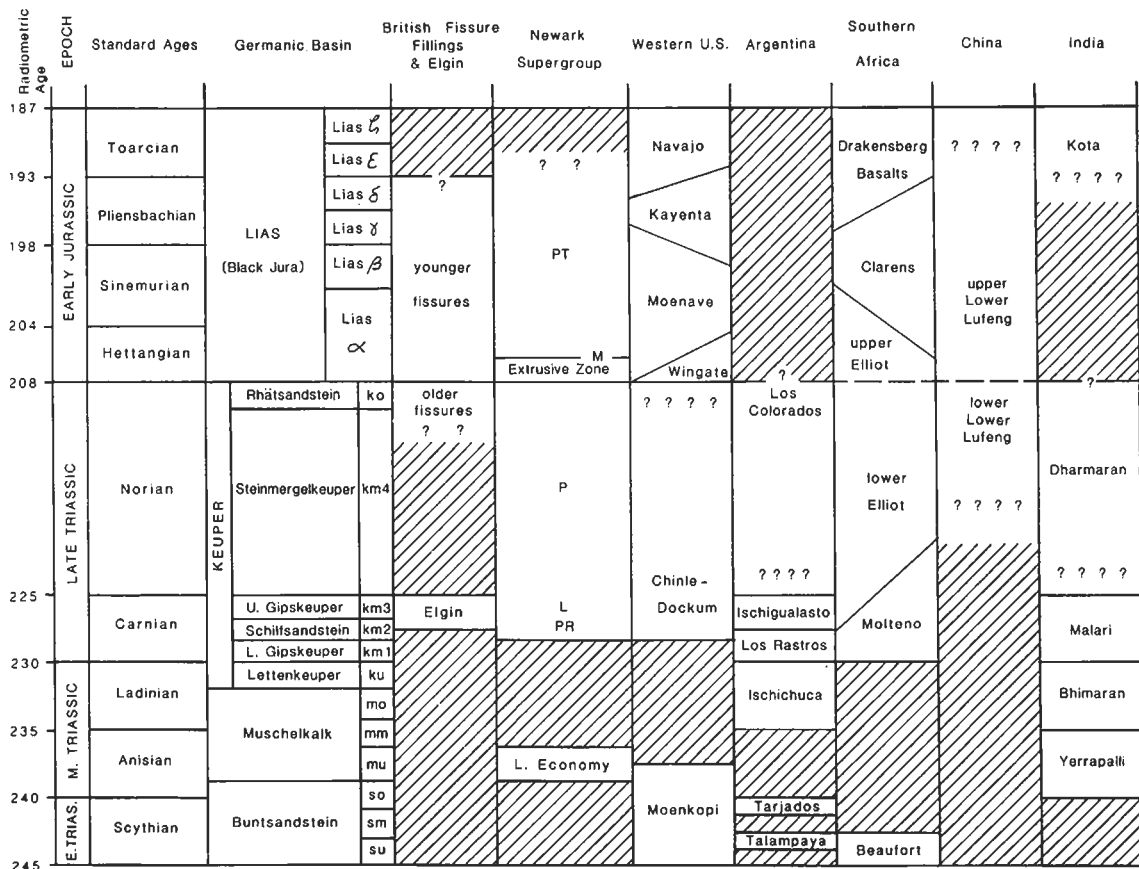
Patterns of diversity, origination, and extinctions in the Early Mesozoic

Every method that expresses some metric of diversity, extinctions, or originations over an interval of time has its own advantages, disadvantages, and implicit assumptions. In fact, choice of the metric may determine the kind of pattern that the analysis of raw data reveals. The main assumption of most

simple metrics is that there is an even distribution of taxa within an interval. In most cases, this is exactly what we do not know because we have selected the shortest reliably correlated interval of time as a unit of resolution.

A metric of diversity is particularly sensitive to the distribution of originations and extinctions through the time interval considered. For example, it is not really useful simply to give the total number of taxa present in the interval, because some of the taxa go extinct or have their origin during that interval. What we really want is the average number of taxa per million years per interval. To know this accurately we would have to know the actual duration of taxa at the million year scale, which we do not. However, if we assume that on the average, taxa go extinct or originate at the middle of the stage,

Figure 25.1. Correlation of Early Mesozoic deposits considered in this chapter with the Standard Ages and with the standard section for the Triassic of the Germanic Basin. Germanic Basin correlation from Brinkmann (1960), Gall, Durand, and Muller (1977), and Brenner and Villinger (1981). Radiometric scale from Palmer (1984). Explanation of abbreviations follows. Germanic Basin Section: su–so, mu–mo, ku, km1–km4, and ko are standard abbreviations for subdivisions of Germanic Triassic. Newark Supergroup: PT, Portland Formation (Hartford Basin) faunule; M, McCoy Brook Formation faunule; P, Passaic Formation (Newark Basin)–New Haven Arkose (Hartford Basin) faunules; L, Lockatong Formation (Newark Basin)–New Oxford Formation (Gettysburg Basin)–Cow Branch Formation (Dan River Basin) faunules; PR, Pekin Formation (Deep River Basin)–Richmond Basin–Taylorsville Basin faunules.



Family	stages										
	S	A	L	C	N	H	S	P	T	Ael	B
1 Trematosauridae	XXXXX										
2 Uranocentrodontidae	XXXXX										
3 Benthosuchidae	XXXXX										
4 Indobrachyopidae	XXXXX										
5 Rytidosteidae	XXXXX										
6 Dissorophidae	XXXXX										
7 Lystrosauridae	XXXXX										
8 Myosauridae	XXXXX										
9 Cynognathidae	XXXXX										
10 Diademodontidae	XXXXXXXXXX										
11 Erythrosuchidae	+XXXXXXXXXX										
12 Brachyopidae	XXXXXXXXXX										
13 Ctenosauriscidae		XXXXX									
14 Shansiodontidae		XXXXX									
15 Proterosuchidae	+XXXXXXXXXXXXXXXX										
16 Kannemeyeriidae	XXXXXXXXXXXXXXXXXXXXXXXX										
17 Traversodontidae	XXXXXXXXXXXXXXXXXXXXXXXX										
18 Stahleckeriidae		XXXXXXXXXXXXXXXXXXXX									
19 Rhynchosauridae		XXXXXXXXXXXXXXXXXXXX									
20 Chiniquodontidae			XXXXXXXXXXXX								
21 Metoposauridae			XXXXXXXXXXXX								
22 Proterochampsidae			XXXXXXXXXXXX								
23 Lagosuchidae	S	A			N	H	Sin	P	T	Ael	B
24 Erpetosuchidae					XXXXX						
25 Scleromochlidae					XXXXX						
26 Capitosauridae					XXXXXXXXXX						
27 Procolophonidae	+XXXXXXXXXXXXXXXXXXXXXXXX										
28 Mastodonsauridae					XXXXXXXXXXXXXXXXXXXXXXXX						
29 Rausuchidae					XXXXXXXXXXXXXXXXXXXXXXXX						
30 Trilophosauridae					XXXXXXXXXXXXXXXXXXXXXXXX						
31 Tanystropheidae					XXXXXXXXXXXXXXXXXXXXXXXX						
32 Plagiosauridae					XXXXXXXXXXXXXXXXXXXX						
33 Ornithosuchidae					XXXXXXXXXXXX						
34 Stagonolepididae					XXXXXXXXXXXX						
35 Phytosauridae					XXXXXXXXXXXX						
36 Kuehneosauridae					XXXXXXXXXXXX						
37 Drepanosauridae					XXXXX						
38 Endennosauridae					XXXXX						
39 Prolacertidae	XXXXXXXXXXXXXXXXXXXXXXXX				XXXXXXXXXXXX						
40 Proganochelyidae					XXXXXXXXXXXX						
41 Kuehneotheriidae					XXXXXXXXXXXX						
42 Haramiyidae					XXXXXXXXXXXX						
43 Tritheledontidae	S	A	L	C			Sin	P	T	Ael	B
44 Gephyrosauridae							XXXXXXXXXXXX				
45 Melanorosauridae							XXXXXXXXXXXXXXXXXXXX				
46 Heterodontosauridae							XXXXXXXXXXXXXXXXXXXX				
47 "Scelidosauridae"							XXXXXXXXXXXX				
48 Anchisauridae							XXXXXXXXXXXXXXXXXXXXXXXX				
49 Chigutisauridae							XXXXXXXXXXXXXXXXXXXXXXXX				
50 Procompsognathidae							XX				
51 Fabrosauridae							XX				
52 Sphenodontidae							XX				
53 Stegosuchidae							XX				
54 Sphenosuchidae							XX				
55 "Dimorphodontidae"							XX				
56 "Eudimorphodontidae"							XX				
57 Morganucodontidae							XX				
58 Tritylodontidae							XX				
59 Megalosauridae							XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX				
60 Casichelyidae								XXXXXXXXXXXXXXXXXXXXXXXXXXXX			
61 Cetiosauridae									XXXXXXXXXXXXXXXXXXXXXXXX		

Figure 25.2. Cumulative distribution of tetrapods through the Triassic and Early Jurassic, based on the correlations in Figure 25.1. Distributional data from Anderson and Anderson (1970) and Anderson and Cruickshank (1978) for the Early and Middle Triassic and from Kitching and Raath (1984), Olsen, McCune, and Thomson (1982), and Olsen and Galton (1977, 1984) for the Late Triassic and Early Jurassic.

Notes on the families. Please note here that (1) "family" is a very arbitrarily erected hierarchical category; (2) "families" are not strictly comparable among groups; (3) they are often paraphyletic. Our justification for using them is that they often form cohesive morphologic, taxonomic, and stratigraphic units. This cannot, unfortunately, be said of most lower-level groups. We include the Poposauridae within the Rausuchidae. *Vulcanodon* is included in Melanorosauridae, although Cooper (1984) suggests it should belong in a new family along with *Barapasaurus*, which we include here within the Cetiosauridae. We give the age of *Vulcanodon* as Sinemurian, which is the oldest range for the pollen taxa found in inter-Drakensberg Basalt sediments (Aldiss, Benson, and Rundel 1984), although we recognize it could well be younger. The oldest ornithischians (from the Carnian Ischigualasto Formation and the Newark Supergroup) are included in the "fabrosaurids," although, in our opinion, they cannot really be assigned to a family. *Scelidosaurus* from the English Lias and *Scutellosaurus* are almost certainly thyreophorans, but they cannot be placed in either the Ankylosauria or Stegosauria. Therefore, we place them in the group "Scelidosauridae." Fabrosaurids are known from the Early Cretaceous in the form of *Echinodon*. We include the Saltoposuchidae (including *Terrestrisuchus*) in the Sphenosuchidae. We also regard *Hallopus* from the Morrison Formation as a possible sphenosuchid. Stegomo-

the average diversity per million years turns out to be exactly equal to the average number of taxa at risk per interval as defined by Van Valen (1984). This average number of taxa per million years per interval is equal to the number of originations plus the number of extinctions per interval divided by two, with that value added to the total number of taxa that survive the previous interval and survive through the interval under consideration. The measures of diversity, extinction, origination, and turnover that we use are given in Table 25.1.

We define originations and extinctions as first appearances and last appearances, respectively, within a selected interval. Origination and extinction rates present a problem similar to that of diversity. If originations and extinctions in an interval are distributed through its length, then normalization to the length of an interval is appropriate. This method thus gives the “density” of originations or extinctions during that interval as if they occurred randomly through it. However, if the originations and extinctions are concentrated in a short part of the stage, normalization will mask the origination or extinction “event.” Furthermore, large differences in interval length could make curves of different data sets artificially look similar. For these reasons, we also calculate the probability of extinction per taxon per time interval and the proportion of origination. These are calculated according to the method used by Hoffman and Ghiold (1985); the probability of

extinction is equal to the number of taxa that have their last appearances during an interval divided by the *total* number of taxa at risk during that interval. The latter is equal to the number of taxa surviving from the previous interval plus the originations during that interval. This is preferable to the similar method of Van Valen (1984) in which the number of extinctions is divided by the *average* number of taxa at risk, because the latter method often results in probabilities greater than one. The proportion of originations is equal to the number of first appearances within an interval divided by the number of taxa entering the stage.

Normalizing raw origination and extinction rate to numbers per million years makes the choice of calibrated scales particularly important, because the lengths of the stages of the Triassic and Early Jurassic vary greatly. For example, the Norian is two to five times the length of the average Mesozoic stage, depending on which time scale is used. Fortunately, most modern scales reflect reasonably similar relative durations for the stages of the Triassic and Early Jurassic [Armstrong 1982; Odin and Letolle 1982; Harland 1982 (Norian added to Rhaetian); Palmer 1984]. We have chosen to use Palmer’s (1984) scale because it is the most recent and seems to reflect best the relative duration of the stages as represented by the relative thickness of marine and continental sequences assigned to each stage. We recognize that this approach exacerbates the prob-

Table 25.1 *Measures of diversity, extinctions, originations, and turnover used*

T	= total number of taxa
E	= number of extinctions
O	= number of originations
C	= number of taxa continuing (taxa that both enter from a previous interval and survive into the next interval)
E_n	= number of taxa entering an interval from the previous interval
D	= duration of an interval in millions of years
Average number of taxa	= $(E + O)/2 + C$
Extinction rate = normalized extinction rate	= E/D
Origination rate = normalized extinction rate	= O/D
Turnover rate	= $(E + O)/D$
P_e	= probabilistic extinction rate = E/T
P_o	= probabilistic origination rate = O/E_n
P_t	= probabilistic turnover rate = $(E + O)/E_n$

Caption to Fig. 25.2 (*cont.*)

suchidae = Protosuchidae; a representative of this family may occur in the Morrison Formation and does occur in the Early Cretaceous of Mongolia (J. Clark pers. comm.). We regard *Dyoplax* as indeterminate. All of the British fissure fillings that seem to be Jurassic we place within the Hettangian, except for the one Neptunian dike containing *Oligokyphus* (Kuehne 1956), but we recognize that they could be younger.

lems already outlined with correlating the continental assemblages with the marine stages, because most of the isotopically dated sections must themselves be correlated with the marine stages through sometimes convoluted and uncertain paths.

We also calculate measures of turnover for all the sets of data. The normalized turnover rate is equal to the sum of originations plus extinctions divided by the duration of the stage. This is equivalent to the "density" of total change. The probabilistic turnover rate is equal to the total number of originations and extinctions divided by the number of taxa entering an interval. This can be greater than one because a taxon can both originate and become extinct within a single interval.

The global tetrapod data

For the global tetrapod data (Figs. 25.2, 25.3, and Table 25.2), we feel justified in working only at the levels of family and stage. At present, identification of taxa at the genus and species level is problematic among different geographic areas and formations. Some taxa are surely synonymous with others elsewhere, whereas others thought to be synonymous are not: Determinations vary with individual workers, much material has not been restudied for years, and it is difficult for individual workers to study firsthand all of the necessary material in collections around the world. (Except as noted, we accept the generic and specific identification of other authors.) On the other hand, we recognize the prob-

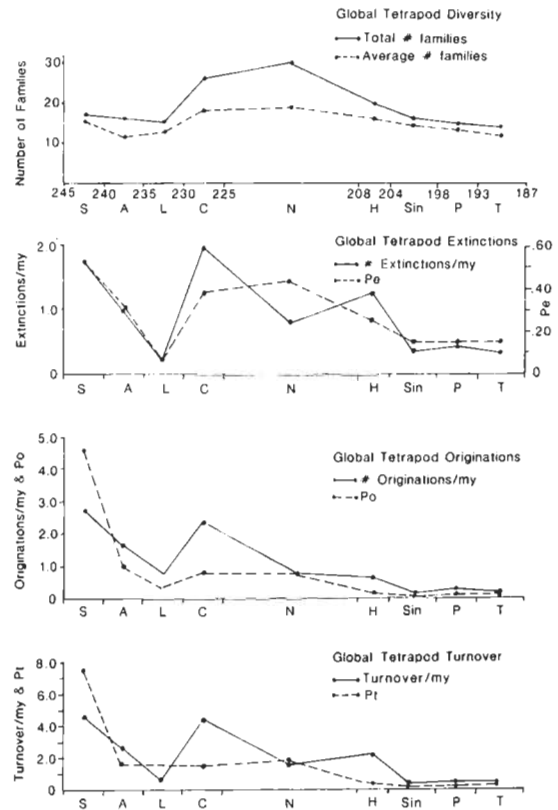


Figure 25.3 Taxic curves for global tetrapod distribution at the stage level. Data derived from Table 25.2 and Figure 25.2.

Table 25.2 Diversity, extinction, origination, and turnover data for global tetrapods^a

Stage	S	A	L	C	N	H	Sin	P	T
No. of families	17	16	15	26	30	20	16	15	14
No. of extinctions	9	5	1	10	13	5	2	2	2
No. of originations	14	8	4	12	14	3	1	1	1
No. continuing	3	5	10	7	5	12	13	12	10
No. entering	3	8	11	14	16	17	15	14	13
Av. no. of families	14.50	11.50	12.50	18.00	18.50	16.00	12.5	13.50	11.50
Duration of stage (MY)	5	5	5	5	17	4	6	5	6
Extinction rate	1.80	1.00	0.20	2.00	0.76	1.25	0.33	0.40	0.33
Origination rate	2.80	1.60	0.80	2.40	0.78	0.75	0.17	0.20	0.17
Turnover rate	4.60	2.60	0.80	4.40	1.58	2.10	0.50	0.60	0.50
P_e	0.53	0.31	0.07	0.38	0.43	0.25	0.13	0.13	0.14
P_o	4.67	1.00	0.36	0.86	0.88	0.18	0.07	0.07	0.08
P_t	7.67	1.63	0.45	1.57	1.93	0.47	0.20	0.21	0.23

^aAbbreviations: S, Scythian; A, Anisian; L, Ladinian; C, Carnian; N, Norian; H, Hettangian; Sin, Sinemurian; P, Pliensbachian; T, Toarcian.

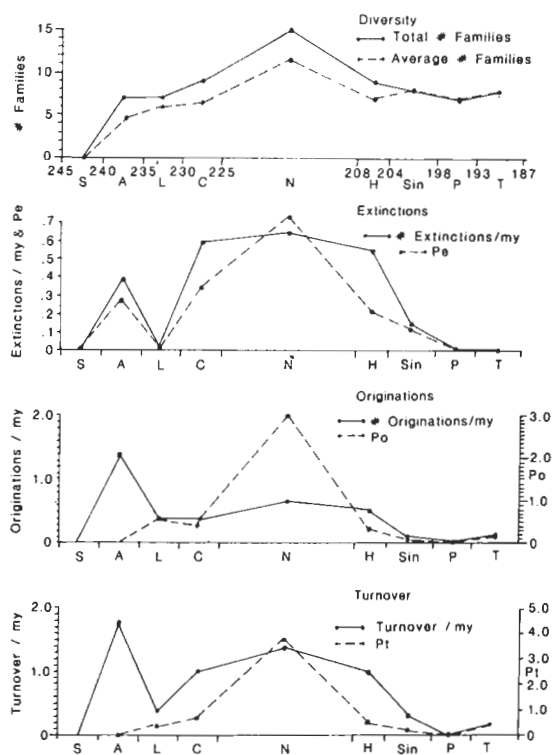


Figure 25.5 Taxic curves for the Germanic Basin based on Table 25.3 and Figure 25.4. Note that Anisian levels are almost certainly an artifact.

Newark Supergroup tetrapods

The Newark Supergroup diversity, origination, and extinction data, viewed at the stage level, are comparable to those of the world (Figs. 25.6, 25.7 and Table 25.4). Comparisons must be limited, however, to the Carnian through Toarcian because, apart from a single Anisian assemblage, older and younger rocks are not known in the Newark (Olsen, McCune, and Thomson, 1982). Like the global data, the Newark extinction rate and probability of extinction for the Norian are lower than for the Carnian. At the stage level, the Newark data, like those of the world, show no evidence of a major extinction at the Triassic–Jurassic boundary. In fact, the Newark data seem to show either a major extinction in the Carnian or only a drop in extinction rates into the Jurassic.

The bulk of the Newark, quite unlike all other described Early Mesozoic deposits, consists of repetitive and periodic (in thickness) sedimentary cycles (Van Houten 1969; Olsen, 1984a,b; Olsen and Imbrie in prep; Chapter 6). These cycles were formed by the rise, fall, and evaporation of very large lakes and appear to have been responses to climatic changes controlled by astronomical variation in the earth's orbit. These pervasive cycles allow the estimation of time between successive fossil assemblages and allow a time scale to be applied to individual Newark Supergroup sections at a $\pm 10,000$ year scale (discussed in more detail in Chapter 6). However,

Table 25.3 Diversity, extinction, origination, and turnover data for Germanic Basin^a

Stages	S	A	L	C	N	H	Sin	P	T
No. of families	0	7	7	9	15	9	8	7	8
No. of extinctions	0	2	0	3	11	2	1	0	0
No. of originations	0	7	2	2	12	2	1	0	1
No. continuing	0	0	5	4	0	5	7	7	7
No. entering	0	0	5	7	6	7	7	7	7
Av. no. of families	0	4.50	16.00	6.50	11.50	7.00	8.00	7.00	7.50
Duration of stage (MY)	5	5	5	5	17	4	6	5	6
Extinction rate	0	0.40	0	0.60	0.65	0.50	0.17	0	0
Origination rate	0	1.40	0.40	0.40	0.71	0.50	0.17	0	0
Turnover rate	0	2.80	0.40	1.00	1.36	1.00	0.34	0	0.17
P_e	0	0.29	0	0.33	0.73	0.22	0.13	0	0
P_o	0	0	0.40	0.29	2.00	0.29	0.14	0	0.14
P_t	0	0	0.40	0.71	3.83	0.57	0.29	0	0.17

^aFor abbreviations see Table 25.2.

correlation between basins, with some notable exceptions, cannot yet be resolved any better than at a two-million-year level. Therefore, although we have applied a time scale for the Newark sections divided into millions of years, we actually examine them over two-million-year intervals (Fig. 25.8 and

Table 25.5). We have used the palynologically placed Triassic–Jurassic boundary in the Newark to fit Palmer's (1984) isotopic scale to the lacustrine cycle-based Newark time scale (see also Chapter 6). The stage boundaries as defined in the Newark on paleontological grounds fall very close to the iso-

Figure 25.6 Distribution of skeletal remains of tetrapods from the Newark Supergroup based on correlations presented in Cornet and Olsen (1985) and faunal lists in Olsen (1980a, in press).

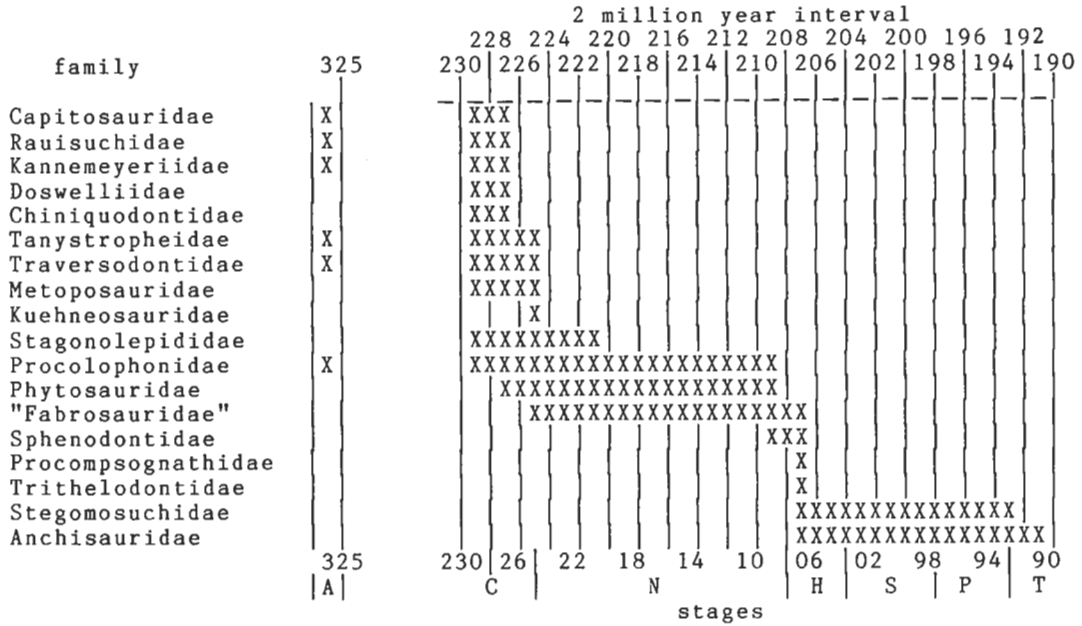


Table 25.4 Diversity, extinction, origination, and turnover data for Newark tetrapods at the stage level^a

Stages	C	N	H	Sin	P	T
No. of families	13	5	6	2	2	1
No. of extinctions	9	3	4	0	1	0?
No. of originations	6	1	4	0	0	0?
No. continuing	1	1	0	2	1	1?
No. entering	6?	4	2	2	2	1?
Average no. of taxa	8.5?	3	4	2	1.5	1?
Duration of state	5	17	4	6	5	6
Extinction rate	1.8	0.2	1	0	0.2	0?
Origination rate	1.2	0.1	1	0	0	0?
Turnover rate	2.0	0.3	2	0	0.2	0?
P_e	0.69	0.60	0.67	0	0.50	0?
P_o	1.00?	0.25	0.50	0	0	0?
P_t	2.50	1.00	4.00	0	0.50	0?

^aFor abbreviations see Table 25.2.

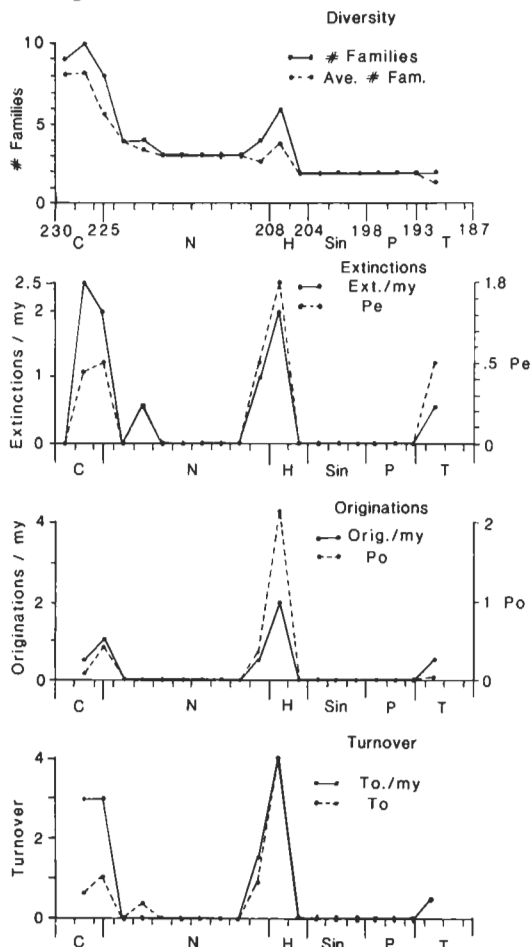
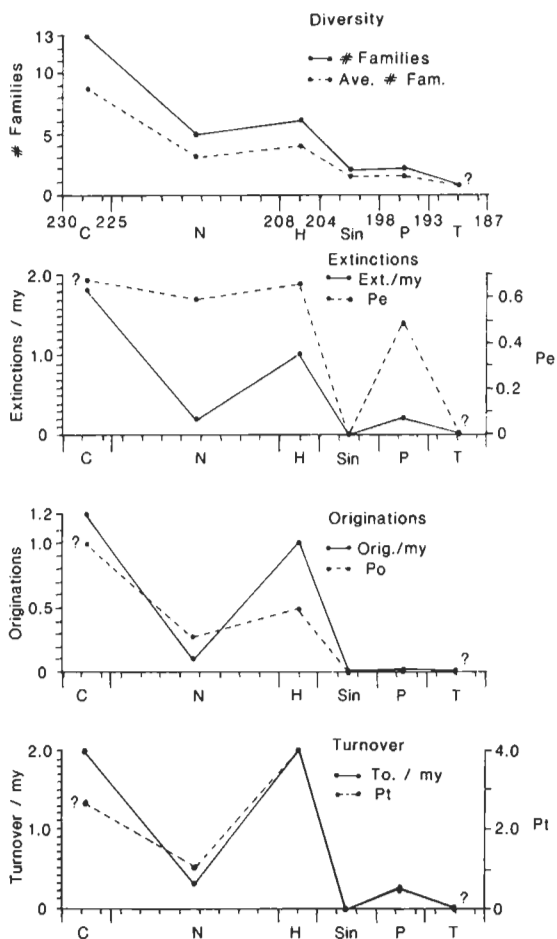
topically defined stage boundaries; any of the current isotopic scales work equally well, however. This is discussed in detail in Olsen (1984a).

Viewed at the two-million-year level rather than the stage level, Newark tetrapod diversity clearly peaked between 230 and 225 MY and between 210 and 204 MY (Fig. 25.8). These intervals correspond to the late Carnian and the late Hettangian. Extinctions are gathered in two similarly placed, well-defined peaks. The general pattern resembles that for the stage level, but the extinctions appear to be concentrated in the Carnian and at the Triassic–Jurassic boundary. Either the extinctions are really concentrated where they appear to be or

the pattern is an artifact of poor sampling in intervals between the two peaks. In this case we can argue the latter. For example, tetrapod bones are exceedingly rare throughout the Newark Jurassic. The diversity and extinction peaks in the early Hettangian are due to the recent discovery of a rich early Hettangian bone assemblage in Nova Scotia (Olsen and Baird 1982); only a few of the vertebrates in this tetrapod assemblage are known elsewhere in the Newark, but more of these Nova Scotian taxa are known from Middle and Late Jurassic rocks in other regions. If taxa known to persist through the Hettangian (specifically sphenodontids, stegomomuchids/protosuchids, “procompsognathids,” and “fabrosaurids”) are inserted through the rest of the Newark Jurassic (even though they are not recorded), the Hettangian diversity and extinction peaks between 208 and 206 MY disappear, and only the late Norian peaks (between 210 and 208 MY) remain.

Figure 25.7 Taxic curves for skeletal remains of tetrapods from the Newark Supergroup at the stage level based on the data in Figure 25.6 and Table 25.4. Question marks show estimates that cannot be directly calculated from the data in figures and tables. They represent minimum values. Abbreviations as in Table 25.1 and Figure 25.3 except as follows: Ave. # Fam., average number of families; Ext./my, extinctions/MY; Orig./my, originations/MY; To./my, Turnover/MY.

Figure 25.8 Taxic curves for skeletal remains of tetrapods from the Newark Supergroup sampled at the two-million-year level based on the data in Figure 25.6 and Table 25.5. Abbreviations as in Figure 25.7.



Newark tetrapod ichnotaxa

A good proxy of tetrapod diversity is reflected in the abundant tetrapod ichnotaxa from the Newark. Ichnofossil assemblages are directly tied to one of the repetitive facies of the lacustrine cycles, and, therefore, a similar environment is sampled through the entire Newark. At individual sites, tracks can be very common, so both sample size and distribution are much less problematic for Newark tracks than for bones. Because the ichnotaxa generally reflect larger cursorial tetrapods, they should be an excellent indicator of major tetrapod extinctions. Comparison among pedal skeletons of tetrapods suggests that ichnogenera and even ichnospecies correspond more or less to families of tetrapods based on skeletal remains (Chapter 20).

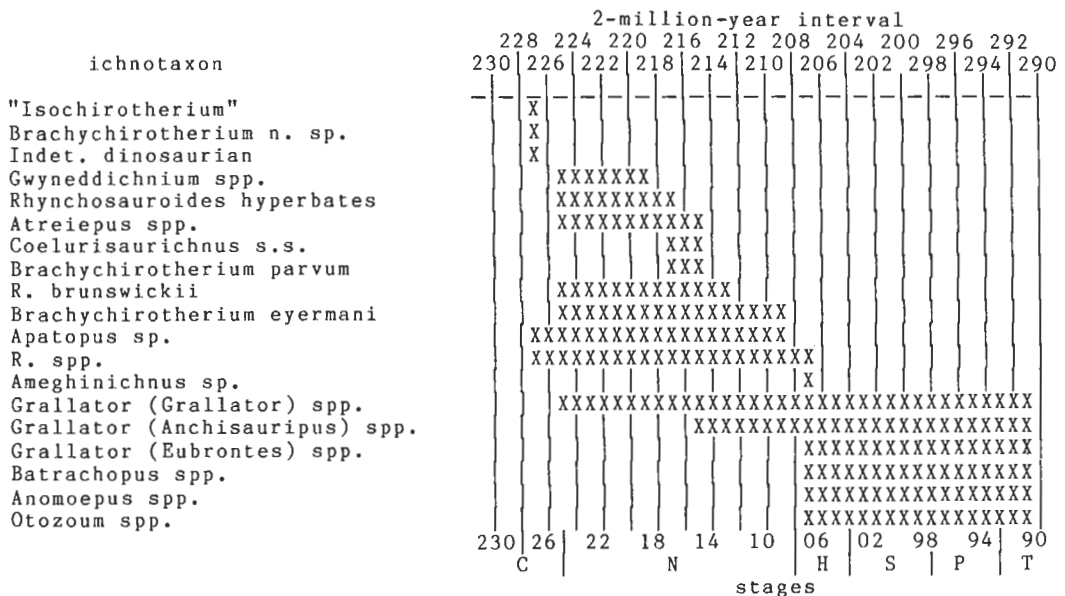
Viewed at the stage level, ichnotaxic diversity drops into the Jurassic (Figs. 25.9, 25.10, and Table 25.6). The probability of extinction is highest in the Norian and drops dramatically into the Jurassic. However, as in all other stage level comparisons, this Norian peak is not seen in the normalized extinction curve. The same data viewed over two-million-year intervals (Fig. 25.11 and Table 25.7) show a strong rise of diversity into the middle Norian, with a drop afterward. Extinctions show three peaks: one in the Carnian between 228 and 226 MY, one in the middle Norian between 216 and 214 MY, and one in the latest Norian between 210 and 208 MY. There are no extinctions after the Hettangian in the footprint data. The first and last extinction peaks correspond exactly to the peaks seen in the skeletal data; the mid-Norian peak in the footprint data does not.

In the actual sections, the first footprint faunules of Jurassic aspect ("Connecticut Valley" aspect) occur in a stratigraphic interval just above the palynologically placed Triassic–Jurassic boundary (Chapter 6). Although the tracks and palynoflorules come from different localities in the same basin (Newark Basin), they are almost certainly correlative within 400,000 years, based on an estimate of possible error in sedimentation rates in sedimentary cycles (Olsen 1984a; Chapter 6). The palynofloral boundary comes from within 60 m of the oldest lava flow in the basin and the oldest Jurassic-aspect track assemblage appears within the last meter below the basalt. Unfortunately, the 1,000-m (about 8-MY) interval between the palynologically fixed Triassic–Jurassic boundary and the youngest well-known Norian assemblage is very poorly sampled for footprints. All other intervals in the Newark, except the oldest Newark Carnian and Anisian age strata, have been relatively densely sampled in either the Newark or Hartford Basins. Thus, it is possible that this 1,000-m gap is wholly responsible for the mid-Norian peak in the extinctions of ichnotaxa, which could have occurred at any time within the unsampled interval.

Overview of tetrapod data

When the tetrapod data of the world are viewed at the stage and family level, there does not appear to be any sign of a major set of extinctions at the Triassic–Jurassic boundary, but there is a peak of extinctions in the Carnian. The same pattern holds for the Newark Supergroup tetrapod data, for the

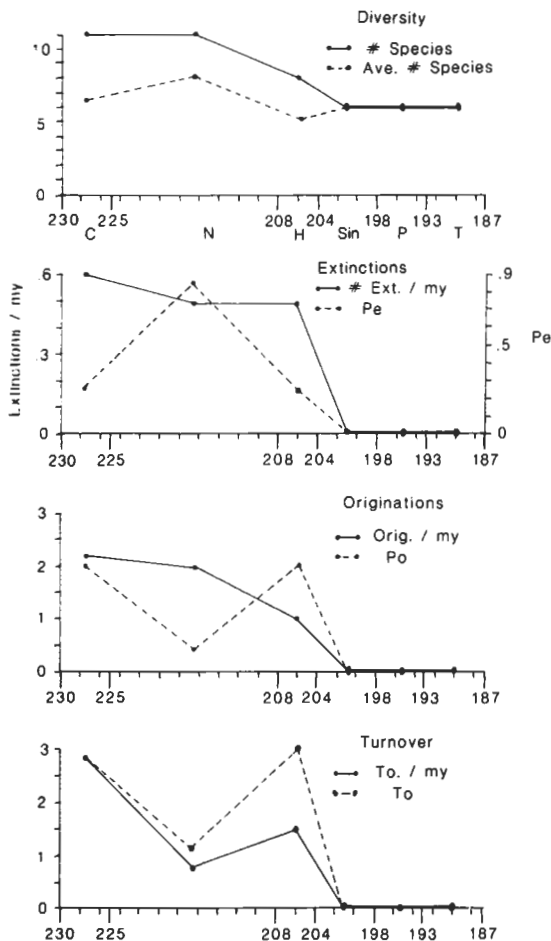
Figure 25.9 Distribution of vertebrate ichnotaxa in the Newark Supergroup.



Carnian to Early Jurassic data of the Germanic Basin, and for the Newark ichnotaxa data, all at the stage level. However, when the Newark track and skeletal data are viewed on a two-million-year sampling interval, the two data sets show strong concentrations of extinctions in the Carnian and in the latest Norian. The way in which the high Norian extinctions disappear in the skeletal data and the high Carnian extinctions disappear in the track data when both are subjected to sampling at the stage interval demonstrates that, no matter what the real pattern of extinctions might be, the stage level is an inappropriate level of analysis for seeking major concentrations of extinctions. It tends to decrease the significance of highly concentrated intervals of extinction and turn several small sets of extinctions spread over the stage into a major extinction event. This is true no matter what metric of diversity and extinction is used.

If we extend this line of reasoning to the global

Figure 25.10 Taxic curves for footprints from the Newark Supergroup at the stage level based on the data in Figure 25.9 and Table 25.6. Abbreviations as in Figure 25.7.



data, it seems clear that although at face value there is no evidence of a major tetrapod extinction at the end of the Triassic, the stage level of analysis may mask the real pattern.

Newark pollen and spores

The pollen and spore record of the Newark is known at a finer level than any other category of fossils, largely due to the work of Bruce Cornet and his associates (Cornet et al. 1973; Cornet and Traverse 1975; Cornet 1977a,b; Cornet and Olsen 1985). Pollen and spore records for the Newark Supergroup, correlated to the nearest two million years, are given in Cornet and Olsen (1985). These records provide a completely independent data set to compare with the Newark track and skeletal records. The Newark palynomorph record detailed by Cornet and Olsen consists of 121 “species” sampled from more than a hundred localities. Palynomorphs have the advantages of usually being very abundant in individual samples and of having relatively high morphological and hence high taxonomic diversity. Assemblages occur in all nonmetamorphosed gray and black fine clastics of the Newark, and species counts and identifications based on separate samples are highly reproducible. Their disadvantage is that their taxonomy is a parataxonomy such as that for footprints; they are organ taxa, and a palynomorph species or genus does not necessarily correspond to an equivalent taxonomic level in whole organisms. A pollen cone of one conifer might produce two or three easily recognized pollen species, or several conifer species might produce only a single morphotype of pollen grain. Nonetheless, if used consistently, the available record is legitimately compared within and between formations, and as a record of plant diversity, palynomorphs are unsurpassed in the Newark.

We must qualify these statements, however, by noting that Cornet and Olsen’s (1985) work is only a first attempt to correlate the palynological records of the various basins of the Newark Supergroup and provide a cumulative range chart for the entire supergroup at such a fine level. We believe that this record will be subject to change, but, at the present, it is still more refined than all the other classes of data.

At the stage level, pollen and spore diversity and extinction patterns show a resemblance to the global tetrapod data and a very strong resemblance to the Newark tetrapod and footprint data (Figs. 25.12, 25.13, and Tables 25.8 and 25.9). Especially noteworthy is the high diversity in the Carnian and Norian and the high probability of extinction in Norian in both the Newark track and pollen records.

As was true for the Newark track and skeletal data, the diversity and extinction curves viewed on

Table 25.6 Diversity, extinction, origination, and turnover data for Newark ichnotaxa at the stage level^a

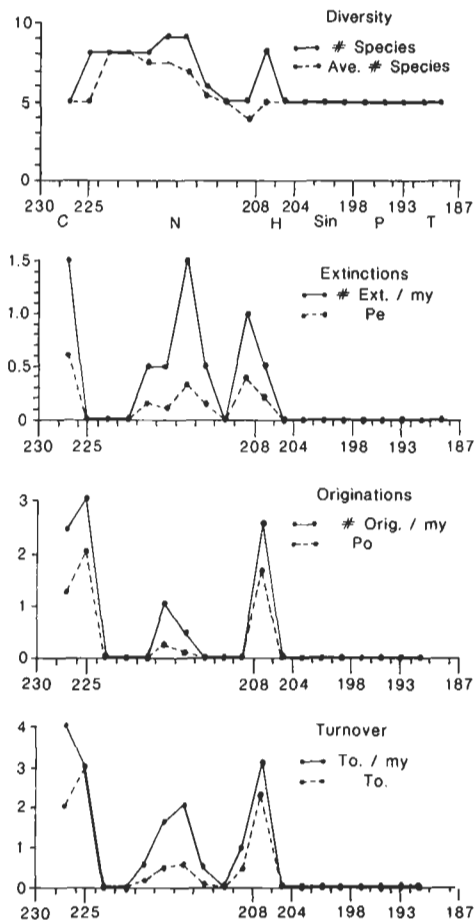
	C	N	H	S	P	T
No. of forms	11	11	8	6	6	6
No. of extinctions	3	9	2	0	0	0
No. of originations	8	3	4	0	0	0
No. continuing	1	2	2	6	6	6
No. entering	4	8	2	6	6	6
Average no. of ichnotaxa	6.5	8	5	6	6	6
Duration of stage	5	17	4	6	5	6
Extinction rate	0.6	0.5	0.5	0	0	0
Origination rate	2.2	0.2	1	0	0	0
Turnover rate	2.8	0.7	1.5	0	0	0
P_e	0.27	0.82	0.25	0	0	0
P_o	2.00	0.38	2.00	0	0	0
P_t	2.75	1.30	3.00	0	0	0

^aFor abbreviations see Table 25.2.

a two-million-year level look rather different than they do at the stage level (Fig. 25.14). In particular, the Carnian high in diversity is all contained in the first two million years of the Newark record, and the rest of the Carnian through Norian record of diversity is relatively flat, with one peak in the late Norian (214–212 MYA). The Jurassic record is of uniformly low diversity. It is of some interest that the Carnian high in palynomorph diversity, extinctions, and originations falls very close to those seen in the Newark skeletal and footprint curves. Likewise, the terminal Norian peak in pollen and spore extinctions is also apparent in the Newark footprint and skeletal assemblages. The terminal Norian extinction peak corresponds to the palynologically defined Triassic–Jurassic boundary within the Newark. However, like the Newark skeletal data, the palynomorph extinction curves show no peak in the mid-Norian such as we see in the curves for the footprints. We avoid consideration of the apparent periodicity exhibited by the data in Figure 25.14 at this time.

The correspondence between the Newark palynomorph, skeletal, and track extinction curves suggest that they may be causally related. Taken at face value, there really is a terminal Triassic extinction event and perhaps also one in the Carnian. We consider these patterns robust only where the taxonomic data can be examined on finer levels than the stage, for at the stage level these patterns become much less clear. The absence of a peak in extinctions in the Norian in all three data sets when examined at the stage level is an artifact.

Figure 25.11 Taxic curves for tetrapod footprints from the Newark Supergroup sampled at the two-million-year level based on the data in Figure 25.9 and Table 25.7. Abbreviations as in Figure 25.7.



Marine invertebrates

The end of the Triassic is one of the commonly cited intervals in which a mass extinction of invertebrates is supposed to have occurred. Raup and Sepkoski (1982, 1984) summarized the marine data and showed a very important extinction in the Norian. They also showed major extinctions in the Carnian and in the Rhaetian. Raup and Sepkoski (1982), however, normalized the extinction rates to time by dividing the number of extinctions in the stage by its length in millions of years. Neither the post-Paleozoic stage lengths used nor their sources were given by Raup and Sepkoski. The source used, however, seems to have been Armstrong (1978), in which the Carnian, Norian, and Rhaetian are given equal durations of 5 MY. As pointed out by Odin and Letolle (1982) and others, this is unreasonable, as

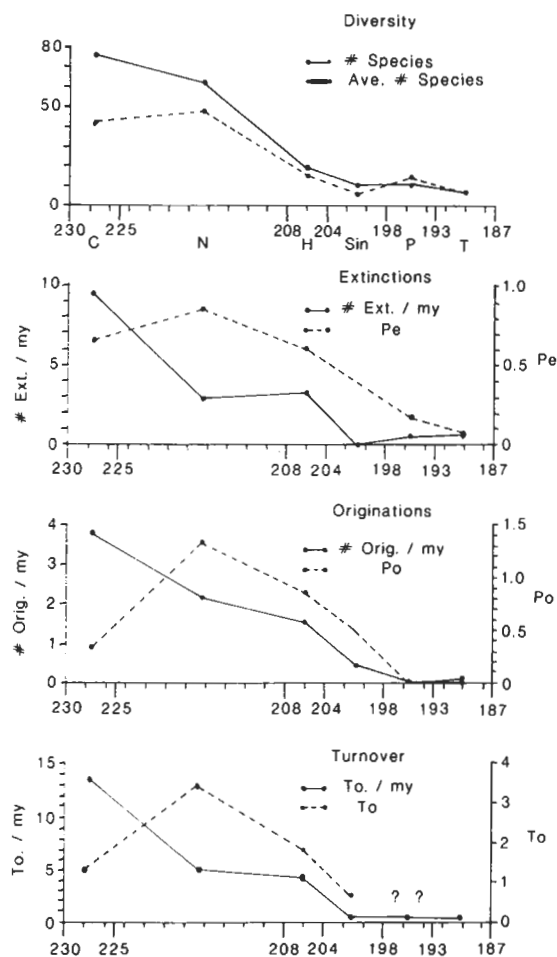
discussed in the first part of this chapter. The very thin Rhaetian record, the very thick Norian record, and the presence of only one ammonite zone in the Rhaetian compared to six in the Norian and five in the Carnian (Tozer 1967) all militate against arbitrarily using equal stage lengths. Using Raup and Sepkoski's (1982) data (from their graph) and normalizing it to Palmer's (1984) time scale, the Norian has an extinction rate of about four families per million years, which is not significant by their own standard. The Carnian extinction is just barely significant by their measure (95 percent confidence level).

On the other hand, Raup and Sepkoski (1984) use percent extinction, which is equal to the probability of extinction [as defined by Hoffman and Ghiold (1985)] multiplied by 100. Raup and Sepkoski (1984) used the Harland (1982) time scale, which still recognizes the Rhaetian as a stage and gives 7 MY to the Carnian, 6 MY to the Norian, and 6 MY to the Rhaetian. It is not important to their major points that the Norian and Rhaetian are given equal lengths by Harland. However, if we combine the Norian and Rhaetian extinctions, the result is an extinction that appears more important than that of the Maastrichtian. This, however, represents a deliberate loss of resolution, as the 2-MY analysis shows. If we consider the Norian and Rhaetian data separately, we cannot know if the extinctions are concentrated at a short interval within a stage or are distributed through it. The Norian seems to be a long stage, and the Rhaetian (if recognized) would be a short one; therefore, if the extinctions were randomly distributed through the stages, the extinctions would definitely be more concentrated in the Rhaetian than in the Norian. According to Hallam (1981), who combines the Rhaetian with the Norian, there were a large number of extinctions distributed through the Norian with, however, a major concentration at the end of the stage, just at the Triassic-Jurassic boundary. If this is so, then the peak in the Norian (without the Rhaetian) extinctions of Raup and Sepkoski (1984) must be spread through that interval, and the "Rhaetian" (i.e., our terminal Norian) and Carnian concentrations of extinctions are the most significant of the Triassic. Viewed in this way, the marine invertebrate data agree strongly with our curves for Newark pollen, tetrapod skeletons, and footprints.

Causes

Two levels of cause can be addressed here: (1) taxa responsible for the observed patterns; (2) processes responsible for taxonomic changes. The first can be derived from an examination of the data that make up the curves. However, at this time, we can only speculate about the second because to imply processes we need to correlate events external to the taxonomic curves in time. Such correlation is even

Figure 25.13 Taxic curves for pollen and spores from the Newark Supergroup at the stage level based on the data in figure 25.12 and Table 25.8. Question marks show estimates that cannot be directly calculated from the data in figures and tables. They represent minimum values. Abbreviations as in Figure 25.7.



more tentative than the stratigraphic correlation that underlies the global continental tetrapod taxic curves.

The extinction peak that occurs at the end of the Carnian reflects the last known occurrences of a variety of synapsids (the Stahleckeriidae, Kannemeyeriidae, Traversodontidae, Chiniquodontidae), labyrinthodont amphibians (Metoposauridae, Capitosauridae), and nondinosaurian archosaurs and archosauromorphs (Rhynchosauridae, Erpetosuchidae, Scleromochlidae, Proterochampsidae). Norian assemblages differ from Carnian assemblages not only in lacking these taxa, but also by having the first definite records of pterosaurs, Sphenosuchidae (including *Terrestriuchus* and *Saltoposuchus*), Protosuchidae, Melanosauridae, Anchisauridae (including Plateosauridae), Proganochelyiidae, Tritylodontidae, Morganucodontidae, Kuehneotheriidae, Haramiyidae, and Tritheledontidae. The latter mammals and therapsids are known only from the youngest Norian (what was called Rhaetian).

Unfortunately, early Norian vertebrate assemblages are very poorly known, and, therefore, it is difficult to place much faith in the peak of Carnian extinctions. Furthermore, it is not at all clear whether these extinctions really were concentrated at a single peak within the Carnian.

Despite these problems, it is possible to show that the extinctions that characterize the middle Carnian in the pollen record predate the vertebrate extinctions by perhaps 2 MY. The very diverse vertebrate assemblages of the Petrified Forest Mem-

ber of the Chinle Formation (Chapter 12) and the correlative Lockatong and Wolfville vertebrate assemblages of the Newark Supergroup include almost all of the typically Carnian families. These assemblages are associated with late Carnian palynoflorules that have a relatively low diversity and are definitely younger than the highly diverse middle Carnian assemblages. No period of major palynofloral extinctions seems to characterize the end of the late Carnian vertebrate assemblages. Unlike the Triassic–Jurassic boundary assemblages, the floral and faunal extinctions do not appear synchronous, and there is no need to look for a common cause.

At the Triassic–Jurassic boundary, the Plagiosauridae, Mastodontosauridae, Procolophonidae, Kuehneosauridae [although see Estes (1983)], Triphosauridae, Tanystropheidae, Phytosauridae, Rauisuchidae (including Poposauridae), Ornithosuchidae, and Stagonolepididae became extinct. This is the same number of families that became extinct at the end of the Carnian. In contrast to the Carnian–Norian extinctions, however, the Hettangian is distinguished only by the appearance of the Tritheledontidae and Heterodontosauridae (not including the problematic South American *Pisanosaurus*), very rare taxa with very poorly defined times of origin. The Tritheledontidae occur definitely only in the Upper Stormberg Group of Africa and the Newark Supergroup of Nova Scotia, Canada, and the Heterodontosauridae are known only from the Stormberg Group and the Kayenta Formation of the southwestern United States. These are listed as Hettangian through Toarcian only because they are dat-

Table 25.8 Diversity, extinction, origination, and turnover data for palynomorphs of the Newark Supergroup^a

	C	N	H	S	P	T
No. of species	75	61	20	11	11	9
No. of extinctions	48	50	12	0	2	3?
No. of originations	19?	35	9	3	0	0?
No. continuing	12?	4	6	5	11	6?
No. entering	56?	26	11	6	0	3?
Average no. of spp.	45.5?	46.5	16.5	6.5	12	7.5?
Duration of stage	5	17	4	6	5	6
Extinction rate	9.6	2.9	3	0	0.4	0.5?
Origination rate	3.8?	2.1	1.5	0.5	0	0?
Turnover rate	13.4	5.0	4.5	0.5	0.4	0.5?
P_c	0.64	0.82	0.60	0	0.17	0.40?
P_o	0.34?	1.35	0.82	0.50	0	0?
P_t	1.20?	3.27	1.91	0.50	U	1.00?

^aFor abbreviations see Table 25.2.

Table 25.9 Diversity, extinction, origination, and turnover data for Newark Supergroup palynomorphs

Time interval (MY)	228	226	224	222	220	218	216	214	212	210	208	206	204	202	200	198	196	194	192	190
No. species	62	29	27	35	34	30	31	45	31	33	20	8	8	8	11	11	11	11	11	11
No. of extinctions	36	2	0	2	4	1	0	14	7	22	12	0	0	0	0	0	0	0	0	2
No. of originations	7	3	0	8	1	0	2	12	0	9	9	0	0	0	3	0	0	0	0	0
No. continuing	19	24	27	25	29	29	29	21	24	10	6	8	8	8	8	11	11	11	11	9
No. entering	55	26	27	27	33	30	29	31	31	34	14	8	8	8	8	11	11	11	11	11
Average no. spp.	40.5	26.5	27	30	31.5	29.5	30	44	27.5	25.5	16.5	8	8	8	9.5	11	11	11	11	10
Extinction rate	18	1	0	1	2	0.5	0	7	3.5	11	6	0	0	0	0	0	0	0	0	1
Origination rate	4	1.5	0	4	0.5	0	1	6	0	4.5	4.5	0	0	0	1.5	0	0	0	0	0
Turnover rate	22	2.5	0	5	2.5	0.5	1	13	3.5	15.5	10.5	0	0	0	1.5	0	0	0	0	1
P_e	0.58	0.07	0	0.06	0.12	0.03	0	0.31	0.23	0.67	0.60	0	0	0	0	0	0	0	0	0.78
P_o	0.13	0.12	0	0.03	0.03	0	0.06	0.39	0	0.26	0.64	0	0	0	0.37	0	0	0	0	0
P_t	0.78	0.19	0	0.37	0.15	0.03	0.07	0.84	0.23	0.91	1.50	0	0	0	0.38	0	0	0	0	0.18

able only to within the “Early Jurassic.” As far as the tetrapod skeletal record goes, the Early Jurassic, quite unlike the Norian, is distinguished *only by a lack of taxa* characteristic of the previous stage (Norian).

Of considerable interest is certain evidence that suggests that the taxa that become extinct at the end of the Norian may have persisted right up to the Triassic–Jurassic boundary, rather than becoming extinct over a longer span. The fissure fillings of Great Britain seem to include assemblages in which “typical” Triassic elements (such as procolophonids) are mixed with others (such as mammals) found in fissures known to be Jurassic on the basis of floral remains and invertebrates. The same sort of mixture occurs in the St. Nicolas-de-Port assemblage (Sigogneau–Russell, Cappetta, and Taquet 1979; Sig-

ogneau–Russell 1983). In addition, a mixed assemblage appears to occur in the Los Colorados Formation of Argentina. The very tentative picture that emerges is one in which the Triassic–Jurassic boundary is characterized by the extinction of at least ten families over what is beginning to look like a very short period of time, perhaps less than 500,000 years. This certainly counts as a mass extinction, at least at the family level. How many genera and species were included within these families at their times of extinction is very much an open question.

The Newark Supergroup ichnological picture is somewhat muddled. All of the ichnotaxa that became extinct at the close of the Triassic are thought to have been produced by families that became extinct at the very end of the Triassic [ichnogenus *Apatopus* = “skeletal” family Phytosauridae (but see Chapter 4); *Brachychirotherium* = ?Stagonolepididae + Rausuchidae; *Procolophonichnium* = Procolophonidae]. The ichnotaxic extinctions appear to occur within 1,000 m (about 4 MY) of the Triassic–Jurassic boundary, but those 1,000 m are unsampled. Sampling this gap could show that

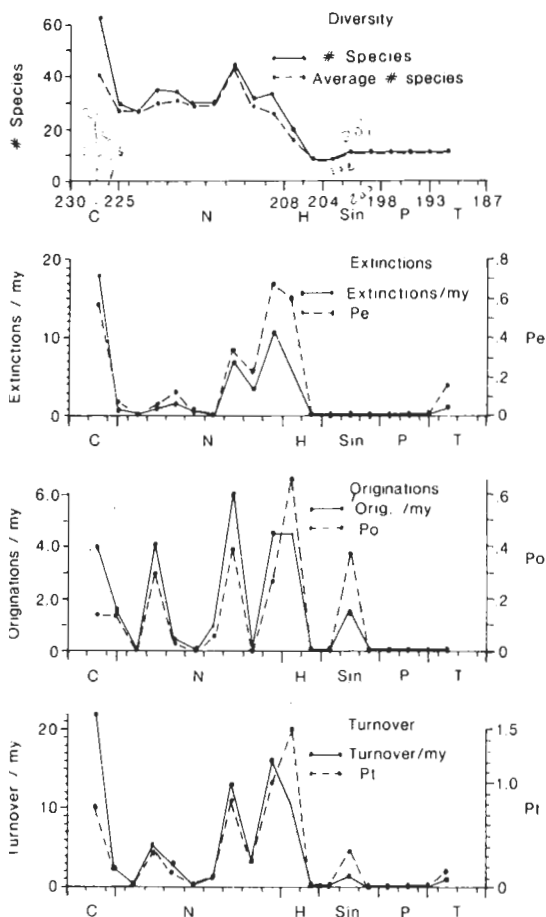
1. The extinctions remain concentrated at the mid-Norian.
2. They are spread out over the interval.
3. They combined with the latest Norian extinction.

If the last is true, the latest Norian extinctions in the footprint data would show a nearly complete turnover in composition, with only the theropod dinosaur tracks continuing unabated. Conversely, the latest Norian extinctions and originations could be spread through this gap, and this could eliminate any concentration of turnover or extinction.

Three ichnogenera characterize the Newark Jurassic (*Batrachopus*, *Anomoepus*, and *Otozoum*), but only *Batrachopus* is definitely known from the earliest Jurassic beds. Whether these forms occur in the 1,000-m unsampled interval below remains to be seen. If the Newark ichnotaxa characteristic of the Norian, such as *Procolophonichnium* sp., *Rhynchosauroides brunswickii*, *Chirotherium lulli*, *Brachychirotherium* spp., and *Atreipus* (Chapter 6), disappear just below the palynologically defined Triassic–Jurassic boundary and if *Batrachopus* occurs below the boundary, the ichnological situation will closely resemble what we see in the skeletal record. In the Newark, however, it will be possible to document the amount of time that the ichnological transition takes and to demonstrate its relationship to the palynological transition. These questions are answerable within the Newark and clearly deserve attention.

Should the Newark Supergroup ichnological picture prove to be as we have outlined above, the

Figure 25.14 Taxic curves for pollen and spores from the Newark Supergroup sampled at the two-million-year level based on the data in Figure 25.12 and Table 25.9. Abbreviations as in Figure 25.7.



timing of the extinctions of skeletal taxa and ichnotaxa and the rise to dominance of the *Corollina* producers would seem close indeed. A change in floral biogeographic patterns can also be tentatively associated with this Triassic–Jurassic transition. Apparently, the rise to dominance of the cheirolepidaceous conifers (and bennettitales) and *Corollina* was marked by the extinction of the distinctive Gondwana macrofloral associations dominated by *Dicroidium* and *Thinnfeldia* and the Ipswich–Onslow microfloral assemblage. Unfortunately, it is beyond the current level of biostratigraphic resolution to know if this biogeographic change was really synchronous with the Triassic–Jurassic boundary. It is very tempting to correlate, in a tentative fashion, the homogenization of the world floras with the vertebrate extinctions at the boundary. This homogenization was maintained over a long interval in the Jurassic of what seem to be very low turnover rates, compared to the Triassic, in both tetrapods at a familial level and microflora at a specific level.

If the terminal Norian invertebrate extinctions prove to be synchronous with the tetrapod extinctions and the floral transition (and there is no evidence that they are not), and if these changes can be shown to occur in a relatively short period of time, then the magnitude of these events would indeed compare with the largest of the major Phanerozoic extinction events as Benton (Chapter 24) and Colbert (1958) have suggested.

If there really is a mass extinction at the Triassic–Jurassic boundary that involves plants, tetrapods, and invertebrates, it is appropriate to seek a common cause and perhaps to look at hypotheses relating this event to others in the Phanerozoic record. Hallam (1981) has hypothesized a causal link between a major terminal Norian regression and a Hettangian marine anoxic event. Bakker (1977) has proffered a major regression as the cause of Triassic extinctions as well. On the other hand, because there is a very large impact structure (Manicouagan) known to be of an age that is close to the Triassic–Jurassic boundary, it is also tempting to associate the extinctions with a bolide impact, as Alvarez et al. (1980) have proposed for the Cretaceous. These hypotheses warrant detailed analysis because all seem plausible mechanisms to explain the observed patterns. However, the bolide impact and the anoxic event model are not mutually exclusive, because the former could cause the latter. At least in the case of the Manicouagan impact, we can look for conclusive evidence in the Newark Supergroup sections; the Fundy Basin was only 500 km away from the impact site in eastern Canada.

However, some of the basic questions still remain unanswered:

1. Over what time period do these extinctions occur?
2. What is the magnitude of the tetrapod extinctions at lower taxonomic levels?
3. How do the Triassic–Jurassic extinctions compare in detail with the “background” rates of extinction through the Early Mesozoic at the same level of resolution?
4. How well do the floral, tetrapod, and invertebrate extinctions correlate within single sections and over larger, even global areas?

The answers to these questions are not yet available and cannot be sought at the standard level of resolution of stage and family. The next step is to look for specific rock units that have characteristics appropriate to these specific questions.

Conclusions

Methodological conclusions

It is crucial to recognize that stratigraphic correlation predetermines the patterns of taxonomic curves on a scale larger than the single section. In this particular study, differences in correlation of Early Mesozoic continental assemblages of the world produce the major differences between our extinction curves and those of Benton (Chapter 24). Without some level of certainty in these correlations, studies of worldwide diversity, extinctions, and originations cannot be expected to yield consistent or meaningful results.

The interval over which worldwide patterns are generally examined is that of the stage. At the stage level, it is impossible to distinguish long intervals of uniform but somewhat high extinction from unified extinction events. An extinction event must be defined in terms of time, but the lengths (4–17 MY) of early Mesozoic stages are too great to qualify as a single “event.” From our examination of the Newark data at the stage and two-million-year level, we conclude that the stage level is simply too coarse. As a consequence, it is probably inappropriate to put much faith in taxic curves compiled at the stage level.

Different metrics of diversity, extinction, and origination can yield different results when applied to the same data. A suite of metrics is always desirable because each has its particular assumptions of the distribution of extinctions or originations through the interval. We rarely know which assumptions are valid.

At this time, for Early Mesozoic continental rocks, the most reliable level of analysis is clearly the basin or the series of tightly correlated basins in which there are ways to apply a chronostratigraphic scale with a level of resolution finer than that of the stage. A uniform sampling interval of at most two

million years is desirable. At present only the Newark Supergroup meets these requirements.

Diversity and periods of major extinctions in the Triassic and Early Jurassic

All of the curves of diversity suggest higher average diversity in the Late Triassic than in the Early Jurassic. This is visible at all levels of analysis in the marine invertebrates and terrestrial tetrapods of the world, as well as in subsets of those records and in Newark Supergroup pollen and spores. Particularly high levels of diversity appear to typify the Carnian.

Of the more detailed analyses of the Newark Supergroup and the marine invertebrates as studied by Hallam (1981), there seem to be two particularly important periods of extinctions: one in the Carnian and one in the late Norian. The latter seems to coincide with the Triassic–Jurassic boundary. These events are not discernible in the global tetrapod record and can only be seen in data sets compiled at a level finer than that of the stage.

The coincidence among the Newark footprint, skeletal, and pollen and spore records and the record of the marine invertebrates at a fine level of resolution seems to reflect a major extinction event at or very near the Triassic–Jurassic boundary. It also suggests a period of (perhaps less concentrated) extinctions in the Carnian. The Carnian is probably better considered a period of very rapid turnover, because originations are also high at the same time. However, the terminal Norian extinction event was not matched by high origination rates, and the net result was a drop in diversity. In contrast to the Triassic, the Early Jurassic was characterized by very low turnover rates.

The Carnian tetrapod extinctions do not seem to have been synchronous with the floral changes, but the late Norian tetrapod extinctions may have been. The latter also may correlate with the major marine invertebrate extinctions. Unfortunately, at this time, it is not possible to be more precise about either the potential correspondence among these extinctions or their relation to external, perhaps causal, events.

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