

TRIASSIC ENVIRONMENTS, CLIMATES AND REPTILE EVOLUTION

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ABSTRACT

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A consideration of all the available data on Triassic vertebrate faunas, and their stratigraphic location reveals a relatively sudden extinction event among the last of the mammal-like reptiles and the herbivorous rhynchosaurs in the Norian of the Upper Triassic. This event was apparently quickly followed by the radiation of the dinosaurs, also in the Norian. This conclusion suggests that competition was not the main factor in the initial success of the dinosaurs, but opportunistic radiation following the extinction of major reptile groups. A global review of Triassic sedimentary facies shows that there were climatic and floral changes towards the end of the Triassic. It is envisaged that increasing aridity in the later Triassic, resulting from plate motions and particularly affecting Gondwanaland and southwestern Laurasia, brought about floral changes and then the reptile extinctions. With the rapid evolution of new floras of conifers and bennettitaleans, the dinosaurs came to dominate all terrestrial faunas within the space of only a few million years.

INTRODUCTION

The Triassic Period (225–190 million years ago) documents important faunal changes from mammal-like reptile communities at the start to dinosaur-dominated communities at the end. The transition has been seen as largely competitive in earlier accounts, with dinosaur dominance ascribed to improved locomotory ability (Ostrom, 1969; Bakker, 1971; Charig, 1972, 1980) or advanced thermoregulatory physiology, whether “warm-blooded” (Bakker, 1971, 1975, 1980), or “cold-blooded” (Robinson, 1971; Halstead, 1975; Benton, 1979a, b). Detailed analysis of all well-documented terrestrial lowland reptile faunas of the Triassic has revealed a rather sudden extinction event among the last of the mammal-like reptiles and the herbivorous rhynchosaurs, in the late Triassic (?middle Norian), which was followed by an apparently rapid radiation of the dinosaurs within a period of 1–2 m.y. These new results divert the search for causes of the dinosaur radiation from intrinsic to extrinsic factors, such as climatic or floral change.

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The aim of this paper is to summarize the available evidence on the environments of Triassic reptiles and to test the suggestion that the eventual extinction of major elements of the mammal-like reptile and rhynchosaur faunas may have been connected with climatic change.

TRIASSIC PALAEOGEOGRAPHY

It is well known that all continents were grouped together as the super-continent Pangaea during the Triassic (actually from the late Carboniferous to early Jurassic). Tethys existed as an embayment separating Eurasia from Gondwanaland and opening eastwards into the ancestral Pacific. Plate reconstructions show that in the early Triassic Pangaea was near-symmetrically located with respect to the equator and both north and south poles were situated in the ocean (the former off eastern Siberia and the latter off southern Africa). Throughout the Triassic, Pangaea moved northwards so that South Africa, for example, went from latitude 55–70°S to 35–50°S, and Britain moved from 15–20°N to 30–35°N. As will be seen later, Triassic sedimentary facies closely reflect latitudinal position and facies changes through the Triassic can be related to changing palaeolatitudes.

Although the concept of Pangaea is still basically correct, recent palaeomagnetic data show that some of the continental blocks of eastern Asia were adrift in the eastern Tethys or proto-Pacific (McElhinny et al., 1981). Of particular note with respect to Triassic facies, discussed later, is the occurrence of the Kolyma block (northeastern Siberia) and the Sikhote Alin block in low palaeolatitudes (33°N in the late Permian), rather than polar latitudes (70–80°N) as depicted in most reconstructions (e.g. Smith and Briden, 1977).

The Triassic is well known as a period dominated by continental processes. Relative to the Palaeozoic, global sea level was low (Hallam, 1977; Vail et al., 1977). Marine deposits are only well-developed along the western sea-board of North America (Cordilleran “geosyncline”), in the Pacific “geosynclines” of eastern Asia, and along the northern and southern shorelines of Tethys. Much of the Pangaeian landmass was subjected to weathering and erosion with deposition taking place in relatively localized regions. Non-marine Triassic sediments are extensively developed in southern Africa, South America, western and eastern North America, and western Europe, including Greenland. They also occur in Antarctica, Australia, India and the U.S.S.R.

In some cases, the Triassic sediments occupy broad intracratonic basins or covered lowland plateaus, as in South Africa, Brazil, western North America and on the Russian and Siberian platforms. Elsewhere, the Triassic sediments occur within relatively narrow fault-bounded basins. These are particularly well developed in the eastern North American–western European region, and in Argentina. Triassic sequences are rarely complete, stratigraphic breaks are common, and correlation within and between basins is often difficult.

TRIASSIC REPTILE FAUNAS AND STRATIGRAPHY

Triassic reptiles are known from all continents (Fig.1). The most important terrestrial sequences occur in the Karoo Basin of South Africa (*Lystrosaurus* Assemblage Zone, *Kannemeyeria* Assemblage Zone, Elliot Formation, Clarens Formation), and they have yielded many thousands of specimens (Kitching, 1977). Middle to late Triassic faunas of South America have also produced abundant material (Chañares Formation and Santa Maria Formation of Brazil, Ischigualasto Formation and Los Colorados Formation of Argentina: Bonaparte, 1978). Other well-studied Triassic Southern Hemisphere faunas include those from India (Panchet, Yerrapalli, Maleri Formations), China (Lower Lufeng Series, etc.), Antarctica (Fremouw Formation), Zambia (N'tawere Formation), Tanzania (Manda Formation), and Australia (Rewan Formation).

Northern Hemisphere faunas occur in various formations in Russia, Germany and neighbouring central Europe (divisions of the Mittelkeuper and Rhaetic), Switzerland, Scotland and England. In the United States, there are late Triassic faunas in the Atlantic States (Newark Group), Arizona (Popo Agie Formation, Chinle Formation), New Mexico and Texas (Dockum Group).

Triassic stratigraphy is complex and correlation of the reptile beds has hitherto been largely based on comparisons of the included tetrapods because of the general absence of more appropriate zonal fossils. Ammonites have been used to establish standard zones in the marine Triassic of the Alps and elsewhere (Tozer, 1967, 1979). However, few tetrapod faunas may be correlated with ammonite zones, and we must rely on palynological zonation, when available (Anderson, 1981; Schopf and Askin, 1980), or the vertebrates themselves. The last technique is not satisfactory, but can sometimes locate a formation to a particular stage (accuracy of ± 5 m. y).

The stratigraphic position of most of the Triassic reptile-bearing formations (Fig.2) is agreed by a consensus of authors (e.g., Romer, 1972; Cox, 1973b; Colbert, 1975; Anderson and Cruickshank, 1978; Benton, 1983) and details will not be repeated here. The Chinle Formation, the Dockum Group and the Newark Group of North America, for example, have been correlated with the German Mittelkeuper by means of palynology, and precise age dates have been obtained from associated volcanic layers (Cornet and Traverse, 1975; Olsen and Galton, 1977).

However, the position of the rhynchosaur-bearing beds of South America, and related formations, is controversial. Romer (1960, 1972, 1975) long maintained a middle Triassic age for these, while other authors have placed some as high as Norian. As an example, Romer (1972, 1975) preferred a Ladinian (or possibly Carnian) age for the Ischigualasto Formation; Stipanovic (1967), Cox (1973b), and Bonaparte (1978) argued for a Carnian assignment, and Anderson and Cruickshank (1978) and Benton (1983) preferred an early Norian position.

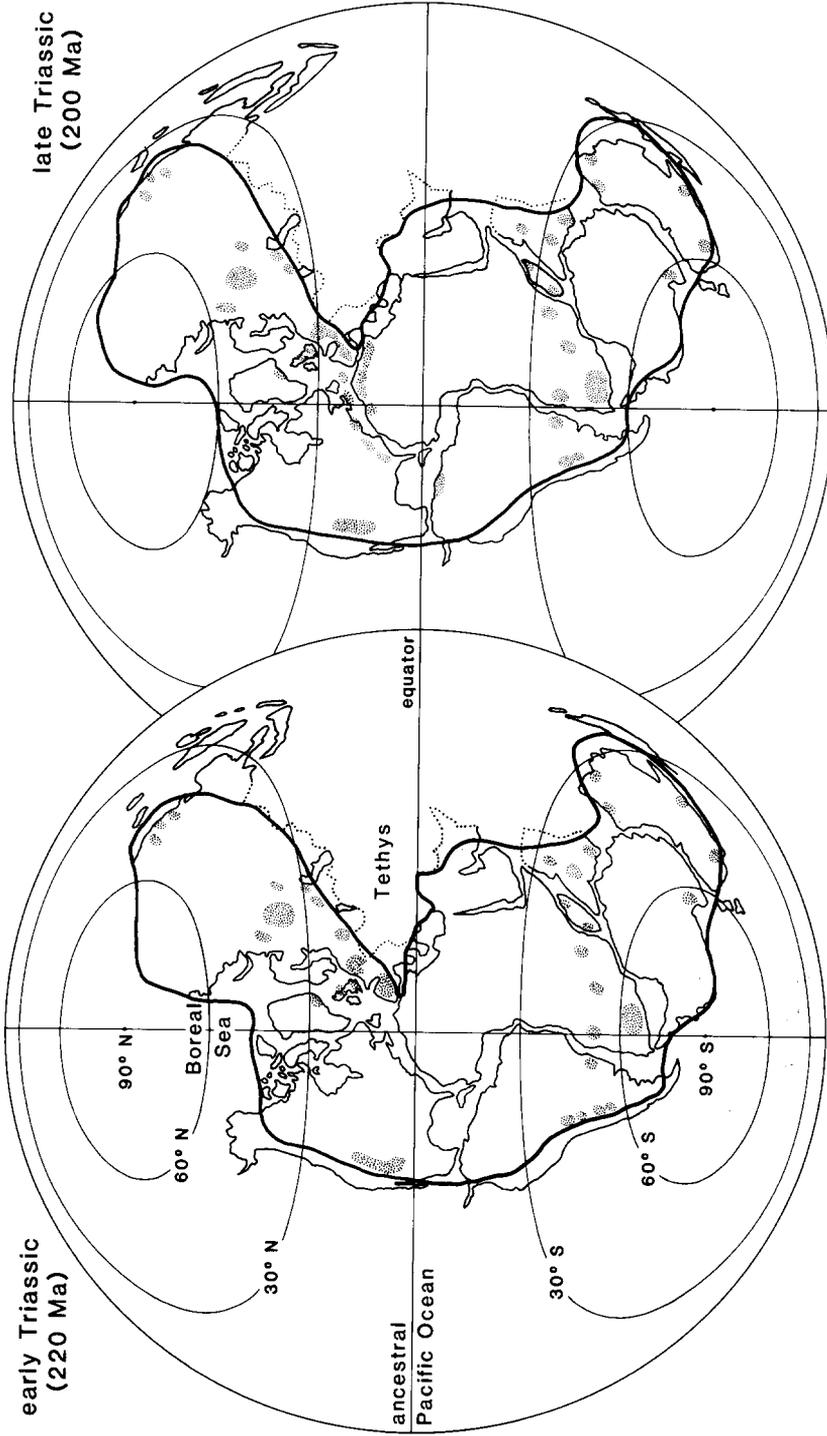


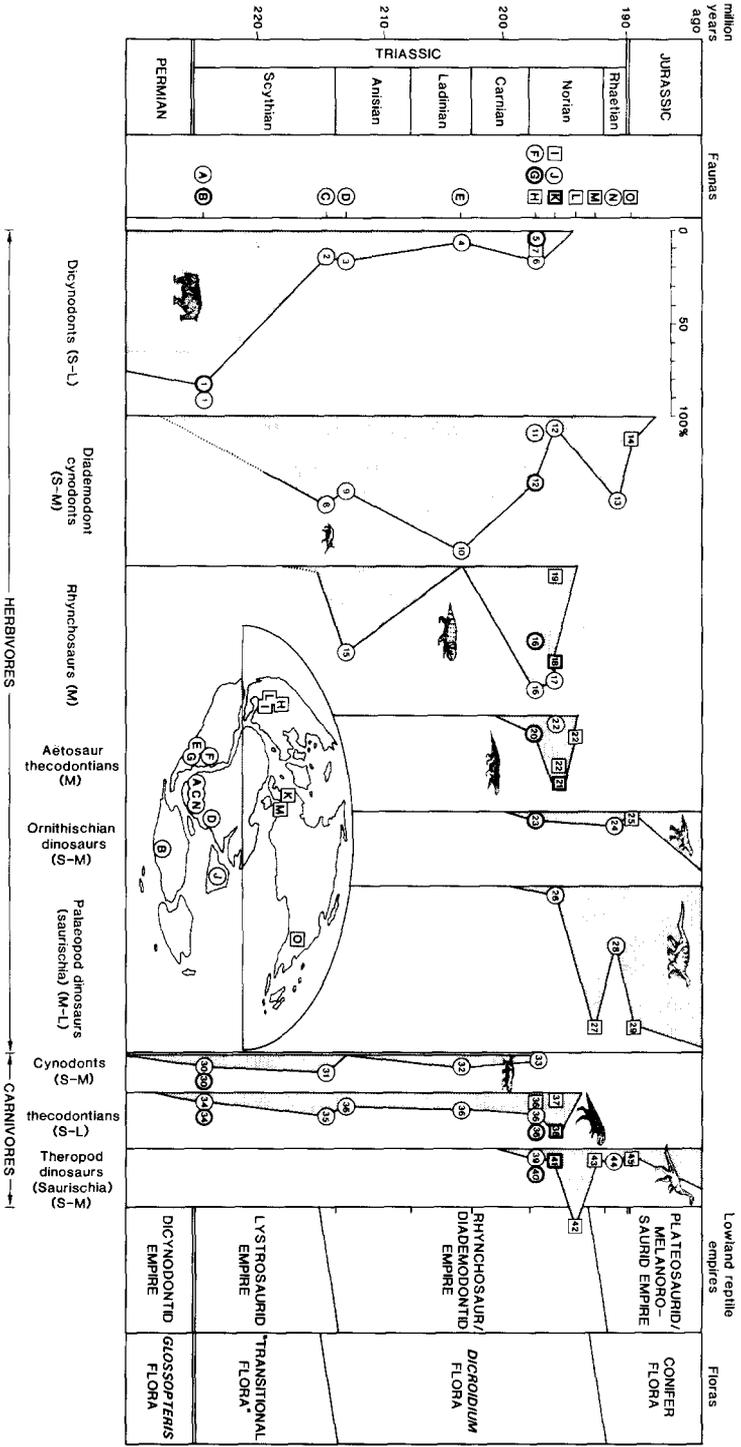
Fig. 1. Plate configurations and approximate location of shoreline for early and late Triassic times. Also shown are the principal areas of outcrop of Triassic non-marine sediments. Note the changes in palaeolatitude from the early to late Triassic. Continental positions based on Smith and Briden (1977).

The evidence from the reptiles certainly favours a position in the late Triassic for the Santa Maria and the Ischigualasto Formations. They share nearly identical rhynchosaurs with the early Norian Lossiemouth Sandstone Formation of Elgin, Scotland and the Maleri Formation of India. The Ischigualasto Formation has an aetosaur (present elsewhere in the palynologically dated Norian of Germany and North America), an ornithosuchid (comparable to *Ornithosuchus* from the Lossiemouth Sandstone Formation), advanced thecodontians and early dinosaurs. The Ischigualasto Formation is probably early Norian in age, and the Santa Maria Formation may be of the same age or a little older.

The Newark Group of the eastern United States and the Glen Canyon Group of Arizona are late Norian to earliest Jurassic in age from palynology and radiometric evidence (Olsen and Galton, 1977). Closely similar dinosaur faunas occur in the Stormberg Beds (Elliot and Clarens Formations) of South Africa, the Forest Sandstone of Zimbabwe, the El Tranquilo Formation and upper Los Colorados Formations of Argentina, the Dharmaram Formation of India, the Lower Lufeng Series of China, the Stubensandstein, Knollenmergel, Rhaetian, and lowest Liassic of Germany (and Central Europe), and the fissure fillings of the Bristol area, England. These are all placed in the latest Norian, Rhaetian, or earliest Jurassic (Romer, 1972; Anderson and Cruickshank, 1978; Bonaparte, 1978). In this paper, the Rhaetian stage is used in its normal sense, although some stratigraphic evidence suggests that it should be combined with the late Norian as a new stage, the Sevastian (Tozer, 1979; Hallam, 1981).

TRIASSIC FLORAS

Triassic megaplants are sporadic in occurrence, and they are only rarely associated directly with the tetrapods. However, major patterns of floral change have been described. The widespread *Glossopteris* flora of southern continents disappeared before the end of the Permian, and it was replaced initially by a "transitional flora" (Anderson and Anderson, 1970) in the latest Permian and early Scythian. During this time, such groups as psilopsids, lycopods and horsetails became less abundant, and the seed-fern *Dicroidium*, and its relatives rose in importance. The *Dicroidium* flora dominated lowland environments of the Southern Hemisphere from late Scythian to late Norian times (Anderson, 1974; Retallack, 1977; Schopf and Askin, 1980). Northern Hemisphere floras of the same time are dominated by "cycadophytes", ferns and conifers and they contain no seed-ferns (e.g. the "petrified forest" of Arizona; Ash, 1980). The *Dicroidium* flora was replaced by a world-wide conifer/bennettitalean flora in the Rhaetian and early Jurassic (Anderson and Anderson, 1970; Barnard, 1973).



GLOBAL TRIASSIC TERRESTRIAL FACIES

Triassic of Africa

The *Lystrosaurus* Assemblage Zone (early Scythian) of South Africa consists of reddish-maroon, purple and green mudrock, interbedded with sandstones and some coal seams. The sandstones include lenticular feldspathic units (<30 m thick) with basal mud-pebble conglomerates, in which the vertebrate bones frequently occur. These sandstones were mostly deposited in fluvial channels and the mudrocks on river floodplains and in shallow lakes. The environment was evidently a warm temperate lowland region with seasonal rainfall and floods (Kitching, 1968, 1977 p. 23; Anderson and Anderson, 1970, chart 1). From fossil plant occurrences, coniferous-like forests existed and a variety of plants in coal-forming swamps. The *Kannemeyeria* Assemblage Zone (late Scythian) is a similar fluvial-floodplain-lacustrine sequence of sandstones and mudrock, but the presence of calcretes and replaced gypsum suggests a drier and hotter climate (Hotton, 1967; Anderson and Anderson, 1970; Kitching, 1977; Cruickshank, 1978; Grine et al., 1979).

Fig. 2. Changes in abundance of major terrestrial reptile groups during the Triassic. Percentage composition of fauna is based on numbers of identifiable individuals of a genus. Information was obtained from the literature, museum records and correspondence with local experts. Animals represented by only one or two specimens were combined with close relatives. Omitted groups are rare or small lizard-like forms that do not affect the overall pattern. Amphibians and mainly fish-eating phytosaurs are also omitted. Histogram percentage scale indicated. Broad adaptive zones of the animals are shown: *S* = small (length <1 m); *M* = medium (length 1–2 m); *L* = large (length >2 m). Southern Hemisphere faunas are shown by circles, Northern Hemisphere by squares, and localities are indicated on a palaeogeographic map. Where two different faunas come from the same stratigraphic horizon in the same hemisphere, then the genera corresponding to these faunas are distinguished by light and heavy circles or squares. Stratigraphic and floral information from references cited in text.

Major faunas shown are: *A*, *Lystrosaurus* Zone, South Africa; *B*, Fremouw Formation, Antarctica; *C*, *Cynognathus* Zone, South Africa; *D*, Manda Formation, Tanzania; *E*, Chañares Formation, Argentina; *F*, Santa Maria Formation, Brazil; *G*, Ischigualasto Formation, Argentina; *H*, Popo Agie Formation, Wyoming; *I*, Dockum Formation, Texas; *J*, Maleri Formation, India; *K*, Lossiemouth Formation, Elgin, Scotland; *L*, Upper Chinle Formation, Arizona, *M*, Knollenmergel, Germany; *N*, Elliot Formation, South Africa; *O*, Lower Lufeng Series, China.

Major genera are: 1 = *Lystrosaurus*; 2 = *Kannemeyeria*; 3 = *Tetragonias*; 4 = *Dinodontosaurus*; 5 = *Ischigualastia*; 6 = *Stahleckeria*; 7 = *Placerias*; 8 = *Diademodon*; 9 = *Scalenodon*; 10 = *Massetognathus*; 11 = *Traversodon*; 12 = *Exaeretodon*; 13 = *Tritylodon*; 14 = *Bienotherium*; 15 = *Stenaulorhynchus*; 16 = *Scaphonyx*; 17 = *Paradapedon*; 18 = *Hyperodapedon*; 19 = rhynchosaur (unnamed); 20 = *Aetosauroides*; 21 = *Stagonolepis*; 22 = *Typothorax*; 23 = *Pisanosaurus*; 24 = *Fabrosaurus*, *Heterodontosaurus*; 25 = *Tatisaurus*; 26 = "unnamed anchisaur"; 27 = *Plateosaurus*; 28 = *Thecodontosaurus*, *Euskelosaurus*; 29 = *Lufengosaurus*; 30 = *Thrinaxodon*; 31 = *Cynognathus*; 32 = *Probelesodon*; 33 = *Belesodon*; 34 = *Chasmatosaurus*; 35 = *Erythrosuchus*, *Euparkeria*; 36 = various thecodontians; 37 = *Poposaurus*; 38 = *Ornithosuchus*; 39 = *Staurikosaurus*; 40 = *Herrerasaurus*, *Ischisaurus*; 41 = *Saltopus*; 42 = *Coelophysis*; 43 = *Halticosaurus*; 44 = *Syntarsus*; 45 = *Lokousaurus*.

The succeeding non-reptiliferous Molteno Formation (?Carnian) is largely sandstone deposited by braided, low-sinuosity streams which built an alluvial wedge northwards into a lowland area of floodplains and lakes (Anderson, 1974; Turner, 1975). Thin coal seams and plant beds reflect periods of lush vegetation in a generally warm and humid climate. Towards the top of the South African Trias, the Rhaetian Elliot Formation is largely a red bed sequence of fluvial sandstones and purple, red and locally green mudrocks. Some calcrete horizons occur, suggesting semi-arid conditions (seasonal rainfall less than 500 mm). Aeolian sandstones in the upper Elliot reflect a drier climate still (Anderson and Anderson, 1970; Thulborn, 1978; J.W. Kitching and M.A. Raath, pers. comm.).

The Clarens Formation of the lowest Jurassic shows a continuation of the semi-arid climate with playa-lake mudrocks and evaporites and aeolian sandstones (Beukes, 1972). The Forest Sandstone of Zimbabwe, also of late Triassic/early Jurassic age, shows a similar trend of increasing aridity (Attridge, 1963; Raath, 1969).

Although there are few vertebrate localities in North Africa, it is worth noting that Triassic sediments are well developed from the Carnian and are chiefly of the red bed type: fanglomerates, sandstones and red marls, with halite and sulphate beds from the latest Triassic into the Liassic.

Sequences in southwestern Morocco and those in eastern North America (see below), close by at the time, suggest a warm and rather moist climate in the earlier late Triassic, becoming hotter and drier throughout northwestern Africa (and much of the eastern U.S.) in the latest Triassic and into the Jurassic (Van Houten, 1977).

Triassic of Antarctica

The most complete Triassic occurs in the Transantarctic Mountains. The vertebrate-bearing Fremouw Formation (early Scythian) is a grey sandstone—mudrock sequence with plant beds and coals. Sedimentation took place in well-vegetated floodplains and within rivers of variable discharge (Elliot et al., 1970; Kitching et al., 1972; Collinson et al., 1981). Coals also occur in the middle and late Triassic of Antarctica so that this area, located within mid to high latitudes throughout the Triassic, was predominantly mild and wet.

Triassic of South America

Many vertebrate fossils have been collected from the Santa Maria Formation of the Parana Basin, Brazil, and from various formations in intermontane basins located in western Argentina. The Santa Maria Formation (late Carnian or early Norian) is in part a typical red bed sequence of fluvial sandstone interbedded with floodplain mudrocks; some of the latter contain calcareous concretions which are probably calcrete. However, plant fossils

are locally abundant (Bortoluzzi and Barberena, 1967), so that substantial vegetation clearly existed at times. The best sequences in northwestern Argentina are contained within the Cacheuta and Ischigualasto basins but there is little detailed work on the sediments. Also there is much complex Tertiary faulting so that correlation between basins is difficult. Sequences in the various basins show a similar pattern of basal coarse clastics passing up into mudrocks with coal seams and plant beds. In the higher parts, red mudrocks and sandstones occur, together with some gypsum (Bonaparte, 1969, 1978; Sill, 1969). Changes in sedimentary facies in these basins reflect climatic changes from moist, warm, equable conditions in the middle Triassic and Carnian through to semi-arid and arid conditions in the Norian and later Triassic.

Triassic of North America

Triassic continental sediments occur extensively in the western part (Arizona, Colorado, Utah and Wyoming), marginal to marine sediments of the Cordilleran "miogeocline". The Scythian—Ladinian Moenkopi Formation consists of red beds of fluvial and lacustrine origin, with some gypsum in the upper part (Stewart et al., 1972). These non-marine deposits pass westwards into red beds of tidal flat and sabkha origin (Reif and Slatt, 1979).

The Norian Chinle Formation broadly consists of a lower bentonitic part, chiefly of variegated mudrocks, and upper red beds. Perennial to temporary lacustrine deposition dominated, with floodplains and river channels subordinate. Fossil molluscs suggest fresh water, and indeed the vertebrate fauna itself, dominated by fish, metoposaur amphibians and phytosaurs, indicates no shortage of water. Plant life flourished in the Chinle, with cycadophytes and ferns closely associated with the lakes, lowland forests with ferns and *Araucarioxylon*, and an inferred upland conifer community, where small thecodontians and dinosaurs lived. Climates were hot, but moist (Colbert, 1948, 1974; Gottesfeld, 1972). Aeolian sediments in the overlying Wingate Formation (latest Triassic) imply a dry semi-arid climate and this clearly persisted through deposition of the Kayenta Formation (red beds) and into the aeolian Navajo Sandstone (lowest Jurassic). Changes in sedimentary facies through the Triassic in western North America thus suggest an early hot, semi-arid phase (Moenkopi), giving way to a hot but more humid period (Chinle) and then increasing aridity towards the uppermost Triassic and into the Jurassic.

In eastern North America, the Triassic sediments occupy basins which formed in the later part of the period. In the southernmost, Deep River Basin of North Carolina, coals and grey lacustrine mudrocks are interbedded with playa red beds containing calcrete, tufa and chert. These facies alternations are thought to result from a generally hot climate with extended periods of high rainfall alternating with periods of aridity (Wheeler and

Textoris, 1978). In the Newark and Hartford basins of Connecticut and New Jersey, again wet-dry climatic fluctuations gave rise to perennial lakes on the one hand and braided streams with calcrete soils on the other.

Further north persistent aridity is demonstrated by aeolian sandstones in the Bay of Fundy basin (Hubert and Mertz, 1980) and halite in the sub-surface off Newfoundland (Jansa et al., 1980). The general pattern for the late Triassic along the eastern U.S. is thus one of long-term climatic fluctuations of humid to semi-arid in the south and central part, and persistent semi-arid/arid conditions in the north.

Triassic of Europe and Greenland

The classic continental Triassic sequences of Britain, France and Germany consist of fluvatile and aeolian sandstones, halite and gypsum deposits and lacustrine-playa mudstones. In the early Triassic ("Bunter") extensive highland regions supplied much coarse detritus to braided stream networks and alluvial fans, and finer material to floodplain-playa complexes. A mid-Triassic marine transgression from Tethys covered much of Germany and extended into the southern North Sea, depositing shallow-marine lagoonal and tidal flat carbonates of the Muschelkalk. By the later Triassic ("Keuper"), upland relief had been subdued and fluvial and aeolian sandstones and playa-lacustrine marls with halite of marine derivation were the principal facies, often in fault-bounded basins. Marine conditions returned in the very latest Triassic, with the Rhaetian transgression. Throughout the Triassic of western Europe, the climate appears to have been hot and dry, with little rainfall. Desert conditions persisted until the latest Triassic, when humidity increased, in part due to the Rhaetian transgression. Seasonal and longer-term climatic fluctuations, of mean temperature and rainfall, have been detected within the "Keuper" (Anisian-Norian) desert sediments (Wills, 1976; M.E. Tucker, 1978; R.M. Tucker, 1981).

In the Jameson Land Basin of east Greenland, sabkha, playa-lake and aeolian sediments comprise the Middle Triassic Gipsdalen Formation (Clemmensen, 1978), and these give way to fresh-water lacustrine deposits, with coals in the Upper Triassic and lowest Jurassic.

Triassic of Australasia

In the U.S.S.R. continental and marine Triassic is particularly well-developed in easternmost Siberia. The dominantly fluvatile sediments contain many coal seams and plant beds. Coral reefs occur within marine limestones. Although on many continental reconstructions easternmost Siberia is part of Pangaea and close to the Triassic north pole, it is now known that this area consisted of several blocks adrift in eastern Tethys—proto-Pacific, at low latitudes. The warm and moist climate which clearly existed would have been that of a large island situated in a tropical oceanic

realm — comparable to that of Hawaii or the Philippines. Fluvatile and lacustrine deposits without coals but with some aeolian sandstones, do occur in the northern part of the Siberian platform. A relatively dry, semi-arid climate, similar to that of the dry mid-latitude steppe, has been inferred for this area (Nalivkin, 1973). Red beds were deposited over parts of the Russian platform.

Facies of the Scythian Panchet Formation in India are similar to those of the equivalent *Lystrosaurus* Assemblage Zone in southern Africa. Middle and upper Triassic red beds succeed in the Yerrapalli and Maleri formations. Fluvatile sandstones and floodplain mudrocks, together with fresh-water molluscs, in these formations have been taken to indicate a monsoon-type climate of high temperatures and distinct wet and dry seasons (Robinson, 1971).

In Australia, the Triassic only occurs in the southeastern part, and of palaeoclimatic note there are coal seams and fresh-water mollusc beds, as well as red beds. A generally mild, at times pluvial climate has been suggested with some extended arid periods (Retallack, 1977).

FACIES ANALYSIS AND PALAEOCLIMATOLOGY

From the preceding brief review of global Triassic non-marine sediments three major reptile-bearing sedimentary facies associations can be identified: A, fluvio-lacustrine sandstones and mudrocks with coal seams and abundant plant material; B, fluvio-lacustrine sandstones and mudrocks with rare coals, some red beds and calcretes, occasional gypsum, plant material common; and C, fluvio-lacustrine red beds with calcrete, playa mudrocks, gypsum and halite deposits and aeolian sandstones.

Facies association A was deposited under a mild and moist temperate regime, in mid to high latitudes. Perennial rivers and broad floodplains, fresh-water lakes, swamps and forests were typical. The abundant rainfall would have been supplied by stormy westerly winds, travelling over the vast proto-Pacific ocean. The lower Triassic of southern Africa, South America and India, much of the Triassic of Antarctica and Australia and the late Triassic of Greenland, all pertain to facies association A.

Facies association B was deposited in a warm to hot climate with variable rainfall, probably extended humid periods alternating with much drier periods. Environments were dominantly river channel and floodplain and fresh-water lake, but coal developed during pluvial phases and calcretes and gypsum at times of semi-aridity. Vegetation varied from abundant to sparse. Sediments of this type occur broadly in the middle and early late Triassic of southern Africa, South America and India, in some parts of the Australian Triassic, and in the Triassic of the eastern U.S.S.R. This facies association developed between the mid-high latitude mild and moist environment and the mid-low latitude hot and dry deserts (facies association C), so the facies association contains elements of both climatic zones. Somewhat similar

sedimentary facies occur in the southern basins of eastern North America, but in these cases the region was located in equatorial to low latitudes so that rainfall was derived from convergence of the trade winds. Long-term climatic fluctuations in facies association B regions could have resulted from migrations of the boundary between the climatic zones, or from astronomical effects on climate.

Facies association C was deposited under a hot subtropical arid/semi-arid climate with rare or erratic rainfall. The environment was basically a desert, with alluvial fans and ephemeral streams, sand seas, playas, sabkhas and salt lakes. Sediments of this type are well developed in the uppermost Triassic of southern Africa and South America, in the Upper Triassic—Liassic of North Africa and northeastern U.S.A., in western Europe through most of the Triassic, and in the mid-Triassic of Greenland. These regions were located in low-mid latitudes and were affected by trade winds, as evidenced by aeolian sandstones. The importance of seasonal migration of the intertropical convergence zone (I.T.C.) (the zone where the trades converge), has been stressed by Robinson (1973) and demonstrated by Clemmensen (1979) in Greenland. There, aeolian sandstones record a dominant ENE trade wind and a subordinate ESE trade. Early to middle Triassic sedimentary facies of western North America, which was also in low latitudes, show some features of a hot, semi-arid climate, such as gypsum horizons, but thick lacustrine sequences and abundant fossil plants suggest significant precipitation. This could be related to equatorial westerlies, bringing moisture from the proto-Pacific while extended arid periods could have resulted from times of trade-wind dominance.

From the distribution of sedimentary facies, it is clear that, compared with the position today and at other times during the geological record, the equatorial humid belt was poorly developed in the Triassic and that the subtropical hot and arid belt occupied an expanded low to mid latitude location (15–50°). The mid to high latitude temperate zone extended to at least 70° and cold, high latitude environments did not exist. These conditions arose from the unique arrangement of continent and ocean at this time. Having one large landmass produced continentality effects: hot summers, cool winters and lower rainfall. These conditions would have existed in central Eurasia and Gondwanaland, and in the region of eastern North America—western Europe. A most important consequence of having a vast open ocean is that heat transfer from low latitudes to the poles is much more efficient. High latitude ocean water would have been much warmer than now, and this together with the absence of land and land-locked seas at the poles would have precluded the formation of polar ice caps. Global temperatures would have been higher too from albedo effects: ice and snow have a high albedo so that their absence at the poles together with a reduced cloud cover would have led to increased heat absorption there. Thus, continentality, oceanic polar heat transfer and albedo effects all contributed to produce a relatively high average global temperature, more equable global temperatures and generally lower rainfall, compared with other geological periods.

REPTILE FAUNAL REPLACEMENT DURING THE TRIASSIC

Mammal-like reptiles, rhynchosaurs and thecodontians

Many authors have described the major aspects of reptile evolution during the Triassic (e.g. Cox, 1967, 1973a; Robinson, 1971; Romer, 1972; Colbert, 1973; Bakker, 1975, 1977, 1980; Charig, 1980), but these accounts have lacked quantitative evidence of the faunal replacements. During the present study, counts of the numbers of individual skeletons collected from all major terrestrial faunas of the Triassic were assembled. Information was obtained occasionally from published accounts, but most had to come from unpublished sources (museum records, field records of local experts, etc.). The information is summarised in Fig.3 and the original data are given in Benton (1983).

Information could not be assembled for faunas from Russia and for very few faunas from China or Germany. The numbers used clearly suffer from preservation and collector bias, but the faunas selected are large (number of individuals = 100–2000), and the trends are so great that there can be little doubt that they are real.

The late Permian of South Africa is characterised by faunas dominated by dicynodonts and other mammal-like reptiles — the Dicynodontid Empire (Anderson and Cruickshank, 1978). During this time the *Glossopteris* Flora was dominant. The Permian ended with decreasing faunal diversity and the extinction of many groups of plants, marine invertebrates and reptiles. This left a restricted fauna at the beginning of the Triassic — the Lystrosaurid Empire (Anderson and Cruickshank, 1978), represented by the *Lystrosaurus* Assemblage Zone of South Africa, the Fremouw Formation of Antarctica, the Panchet Formation of India, and equivalents in China, Russia and Australia. The Lystrosaurid Empire was dominated by the dicynodont *Lystrosaurus*, with rare thecodontian carnivores. Dicynodonts decreased in abundance and herbivorous diademodontid cynodonts radiated towards the end of the Scythian (*Kannemeyeria* Assemblage Zone of South Africa; Puesto Viejo Formation of Argentina; Ehrmayin Formation of China). Thecodontians achieved large size, but did not oust the mammal-like reptiles as carnivores since advanced cynodonts radiated at this time. These interim faunas correlate with a “transitional flora” (Anderson and Anderson, 1970).

The middle and early late Triassic are characterised by what is termed here the Rhynchosaur/Diademodontid Empire (Anisian—early Norian). Representative faunas include those from the Manda Formation of Tanzania, the Yerrapalli Formation of India, the Chañares Formation and Santa Maria Formation of Brazil, and the Ischigualasto Formation of Argentina. Dicynodonts were rare, while rhynchosaurs were the dominant herbivores in many Southern Hemisphere faunas. When absent, as in the Chañares Formation, their place was taken by herbivorous diademodontid cynodonts. Carnivores were cynodonts and thecodontians, the latter finally taking over completely

in the Norian faunas. These later faunas also had rare dinosaurs and "paracrocodyles". The Rhynchosaur/Diademodontid Empire of southern continents is matched in space and time by the *Dicroidium* flora (Retallack, 1977).

Northern faunas of this time have a different aspect, possibly caused to some extent by environmental differences. The Carnian to mid-Norian Keuper formations of Germany were dominated by the amphibian *Metoposaurus* and the fresh-water fish-eating phytosaurs (also thecodontians). Other faunas dominated by these two forms occur in the Popo Agie Formation of Wyoming, the Dockum Group of New Mexico and Texas, and the Chinle Formation of Arizona, and we may name a northern Metoposaur/Phytosaur Empire in the Norian. Some of these faunas also include abundant herbivorous aetosaurs, an aberrant group of thecodontians, rare thecodontians, rhynchosaur and dicynodonts, all closely comparable with contemporary forms in southern continents. Close north-south faunal links in the Norian are confirmed by the Lossiemouth Sandstone Formation of Elgin and the Maleri Formation of India. Both contain abundant rhynchosaur and thecodontians that are very like South American forms. Both contain aetosaurs and the Maleri contains a phytosaur, which compares closely with German and North American forms. Both have primitive small dinosaurs.

Radiation of the dinosaurs

During the middle Norian, major groups of reptiles became extinct worldwide: dicynodonts, diademodontids, rhynchosaur, aetosaurs, other thecodontians (except phytosaurs). Because of the vagaries of the fossil record, the only good middle to late Norian faunas are the upper part of the Chinle Formation of Arizona and the Stubensandstein and Knollenmergel of Germany. The Upper Chinle still contains metoposaurs, phytosaurs and aetosaurs, but also large numbers of the medium-sized bipedal carnivorous dinosaur *Coelophysis*. The Stubensandstein (a little younger) contains similar small carnivores (*Procompsognathus*), larger herbivorous prosauropod dinosaurs (*Plateosaurus*), as well as remnant amphibians, phytosaurs and aetosaurs. Of the older elements, only phytosaurs continued after that time.

Widespread dinosaur faunas occur in the Rhaetian and lowest Jurassic. These include the Elliot and Clarens Formations of South Africa, the Forest Sandstone of Zimbabwe, the Upper Los Colorados Formation of Argentina, the Dharmaram Formation of India, the Lower Lufeng Series of China, the Glen Canyon Group of Arizona, the Newark Group of the eastern United

Fig.3. The major terrestrial reptile-bearing formations of the Triassic. Stratigraphic assignments are based on various sources discussed in the text. The familiar divisions of the Beaufort Group of South Africa are used here, although they have been redefined recently (Keyser and Smith, 1979). The Rhaetian is tentatively retained as a stage between the Norian and Hettangian (Lower Jurassic). *F.* = Formation; *L.* = Lower; *M.* = Middle; *Ser.* = Series; *Sst.* = Sandstone; *U.* = Upper; *Z.* = Zone.

States, and various formations in Germany, France and Britain. These are dominated by large prosauropod dinosaurs (*Plateosaurus*, *Thecodontosaurus*, *Melanorosaurus*), smaller bipedal carnivorous dinosaurs and small herbivorous mammal-like reptiles (tritylodonts) that radiated briefly. The late Norian, Rhaetian, and early Jurassic dinosaur deposits may be named the Prosauropod Empire. This had world-wide extent, and it arose at the same time as the spread to southern continents of the new Conifer/Bennettitalean Flora (Barnard, 1973).

The transition period from faunas dominated by mammal-like reptiles, rhynchosaurs and aetosaurs, as medium and large herbivores, to dinosaur-dominated faunas seems to have been the middle Norian. It cannot be said whether large dinosaurs dominated first in the northern or southern hemisphere because of the absence of middle and late Norian faunas in the south. However, the timing of the changeover suggests a connection with the climatic and floral changes, outlined above, that occurred at that time.

The standard explanation for the initial success of the dinosaurs has been that they competed successfully with mammal-like reptiles and thecodontians. We suggest that competition was not the main factor, but simply wholesale extinction of several groups of terrestrial reptiles which left adaptive zones empty for exploitation. Extinction and opportunistic radiation are suggested by these facts:

- (1) dinosaurs radiated only *after* the extinction of mammal-like reptiles, rhynchosaurs and thecodontians;
- (2) the rate of replacement was geologically rapid;
- (3) mammal-like reptiles and rhynchosaurs are not found together with dinosaurs (except for very rare examples that could hardly have been in competition);
- (4) the extinction and replacement are associated with climatic and floral changes.

The scenario that we envisage involves increasing aridity in the later Triassic, of the Gondwana landmass and southwestern Laurasia, as plate motions brought South America and southern Africa into low latitudes. This occasioned floral changes to a range of plants more adapted to arid conditions. The large mammal-like reptiles and rhynchosaurs, dependent on bush lowland vegetation, died out. New floras of conifers and bennettitaleans radiated worldwide, and with them the dinosaurs came to dominate all terrestrial faunas as large herbivores and medium-sized predators within the space of 1–2 million years.

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