



DINOSAUR SUCCESS IN THE TRIASSIC: A NONCOMPETITIVE ECOLOGICAL MODEL

MICHAEL J. BENTON

University Museum, Parks Road,
Oxford OX1 3PW, England, UK

ABSTRACT

The initial radiation of the dinosaurs in the Triassic period (about 200 million years ago) has been generally regarded as a result of successful competition with the previously dominant mammal-like reptiles. A detailed review of major terrestrial reptile faunas of the Permian-Triassic, including estimates of relative abundance, gives a different picture of the pattern of faunal replacements. Dinosaurs only appeared as dominant faunal elements in the latest Triassic after the disappearance of several groups of mammal-like reptiles, thecodontians (ancestors of dinosaurs and other archosaurs), and rhynchosaurs (medium-sized herbivores).

The concepts of differential survival ("competitive") and opportunistic ecological replacement of higher taxonomic categories are contrasted (the latter involves chance radiation to fill adaptive zones that are already empty), and they are applied to the fossil record.

There is no evidence that either thecodontians or dinosaurs demonstrated their superiority over mammal-like reptiles in massive competitive take-overs. Thecodontians arose as medium-sized carnivores after the extinction of certain mammal-like reptiles (opportunism, latest Permian). Throughout most of the Triassic, the thecodontians shared carnivore adaptive zones with advanced mammal-like reptiles (cynodonts) until the latter became extinct (random processes, early to late Triassic). Among herbivores, the dicyodont mammal-like reptiles were largely replaced by diademodontoid mammal-like reptiles and rhynchosaurs (differential survival, middle to late Triassic). These groups then became extinct and dinosaurs replaced them and radiated rapidly (opportunism, latest Triassic). The late Triassic extinctions may be linked with floral and climatic changes. Explanations of dinosaur success based on the competitive superiority of their thermoregulation or locomotory capability are unnecessary in this model.

INTRODUCTION

THE TRIASSIC period (225 to 190 million years ago) is one of the most important in the history of terrestrial vertebrate life. Throughout most of the Triassic, the mammal-like reptiles (synapsids) dominated as small to large-sized herbivores and carnivores, but towards the end of the period they virtually disappeared. Within an apparently short space of time, dinosaurs radiated from being at first rather rare unimportant animals to occupying nearly all terrestrial niches at the end of the Triassic. They

achieved large size very early in the radiation and ruled on land for the next 120 million years.

The pattern of transition from mammal-like reptiles to dinosaurs has been described by many authors (e.g., Cox, 1967, 1973a; Crompton, 1968; Robinson, 1971; Romer, 1972; Colbert, 1973; Bakker, 1975a,b, 1977, 1980; Halstead, 1975; Charig, 1980). These authors have assumed that the mammal-like reptiles declined gradually in importance during the middle and late Triassic, and that dinosaurs and their ancestors, the thecodontians, rose to dominance at the same time.

Conflict between mammal-like reptiles and dinosaurs is the usual cause proposed for this. Dinosaur and thecodontian superiority has been traced to their improved locomotory capability (Bakker, 1968, 1971; Ostrom, 1969; Charig, 1972, 1979, 1980; Sill, 1974; Hotton, 1980), or to an advanced thermoregulatory physiology, either a "warm-blooded" endothermy (Bakker, 1971, 1972, 1975a,b, 1977, 1980) or a "cold-blooded" inertial homeothermy (Spotila, Lommen, Bakken, and Gates, 1973; Halstead, 1975; Benton, 1979a,b; Hotton, 1980). None of these explanations has gained universal approval, and they are all untestable speculations. Nevertheless, this "competitive model" is presented in all current textbooks and popular works dealing with the subject.

In order to examine this transition in detail, it is necessary to distinguish the *pattern* of historical events, which may be assessed on the basis of the known fossil record, from the *process* by which we seek to explain the pattern. It is my intention, first, to present the basic data on the relative abundance of different reptile groups through the Triassic and to analyze the data, with clear statements of their limitations. Second, I will test against the data the fit of different models for the replacement of synapsids by thecodontians and dinosaurs. The currently accepted model involves direct competition between an individual mammal-like reptile species and an individual thecodontian or dinosaur species, in which the latter animal tended to come off best. In the long term, then, the dinosaur genera, families, and orders became established and replaced the mammal-like reptile orders. We may term this the "differential survival hypothesis." The alternative view, that which is presented here, is that the mammal-like reptiles as a group became extinct because of climatic and floral changes, and the dinosaurs radiated initially into empty adaptive zones. This may be termed the "opportunistic replacement hypothesis."

A simple classification of the reptile groups involved is given in Table 1.

STRATIGRAPHY OF THE TRIASSIC REPTILE BEDS

The relative dating (stratigraphy) of the reptile beds within the Triassic period is

complex and unsatisfactory. The Triassic is divided into several stages on the basis of marine molluscs (ammonites), and there are clearly major problems in trying to assign terrestrial deposits to these stages, since Triassic ammonites and reptiles are rarely found associated. Attempts are now being made, however, to correlate the standard ammonite stages with zones based on spores and pollen (Anderson, 1980; Schopf and Askin, 1980). A summary of the main reptile beds of the Triassic, based on the work of Cox (1967, 1973b), Sill (1969), Colbert (1975), Olsen and Galton (1977), Anderson and Cruickshank (1978), Bonaparte (1978), Cooper (1982) and many others, is given in Fig. 1. The terms "Formation," "Series," and "Zone" are used for the different reptile beds according to local custom, and they may be regarded as roughly equivalent. A "Group" includes several Formations, and a "Member" is a subdivision of a Formation.

There has been some controversy over the correct placement of the Santa Maria Formation and the Ischigualasto Formation, which are assigned here to the Carnian or Norian stages of the Upper Triassic. Romer (1970, 1975) argued that these were Middle Triassic in age, but the close resemblance of elements in their faunas to those of the German Mittelkeuper, the Lossiemouth Sandstone Formation of Scotland, parts of the Chinle Formation and Dockum Group of the western United States, and the Maleri Formation of India now places them firmly in the Upper Triassic. Full details will be given elsewhere.

METHODS OF ANALYSIS

The basic approach in the present analysis was to plot numbers of individuals within major faunas against time, rather than numbers of genera or families against time. The latter approach (diversity analysis) is useful in the calculation of rates of evolution. It says little, however, about the composition of faunas, and may give an erroneous impression of the importance of different groups. For example, according to diversity charts of Triassic reptiles (e.g., Colbert, 1966; Crompton, 1968; Robinson, 1971; Moody, 1977; Charig, 1979), thecodontians were dominant in the late Triassic faunas of South America (5-10 genera), whereas

TABLE 1

Classification of the major terrestrial reptile groups of the late Permian and Triassic
 Modified from Romer (1966) and Anderson and Cruickshank (1978).

Subclass Anapsida (no skull openings behind eye)	
Infra-order Pareiasauria	medium to large herbivores
Subclass Synapsida ("mammal-like reptiles")	
ORDER THERAPSIDA (advanced mammal-like reptiles)	
Suborder Dinocephalia	herbivores and carnivores
Suborder Anomodontia	
Infra-order Endothiodontia	medium to large herbivores
Infra-order Dicynodontia	small to large herbivores
Suborder Theriodontia	
Infra-order Gorgonopsia	small to medium carnivores
Infra-order Scaloposauria	small carnivores
Infra-order Therocephalia	small to medium carnivores
Infra-order Cynodontia	
Superfamily Cynognathoidea	small to medium carnivores
Superfamily Diademodontoidea	small to medium herbivores
Superfamily Tritylodontoidea	small to medium herbivores
Infra-order Bauriamorpha	small to medium herbivores
Infra-order Ictidosauria	small carnivores
Subclass Diapsida (two skull openings behind eye)	
ORDER RHYNCHOSAURIA (beaked herbivores)	small to medium herbivores
ORDER THECODONTIA (dinosaur ancestors)	small to large carnivores
Suborder Proterosuchia	
Suborder Phytosauria	
Suborder Aetosauria	(medium herbivores)
Suborder Pseudosuchia	
ORDER CROCODYLIA (crocodiles)	medium to large carnivores
ORDER SAURISCHIA ("lizard-hipped" dinosaurs)	
Suborder Theropoda	
Infra-order Coelurosauria	small to medium carnivores
Infra-order Carnosauria	medium to large carnivores
Suborder Sauropodomorpha	
Infra-order Prosauropoda	medium to large herbivores
ORDER ORNITHISCHIA ("bird-hipped" dinosaurs)	
Suborder Ornithopoda	small to medium herbivores

rhynchosaurs were not important (1 genus). Abundance data show that the reverse was the case, however, for each thecodontian genus is represented by only a few specimens, and the single rhynchosaur genus by several hundred.

Numbers of specimens have been extracted from many hundreds of descriptive taxonomic papers, from museum records, and from correspondence with numerous local experts. Because of the novelty of these numbers and because of their basic importance to an analysis of faunal change, they are listed, in summary form, in the Appendix. The numbers have been then converted to percentages of total faunal content, rounded to the nearest 10 per cent. Animals represented by only one or two specimens

have been combined with close relatives for the purpose of the analysis.

For the sake of clarity, amphibians and small "lizard-like" reptiles (e.g., procolophonids, younginids, prolacertids, sphenodontids) have generally been omitted because they usually represent minute proportions of the total faunal count, are usually differentially preserved and underrepresented, and enter into food chains (involving fish and invertebrates) that cannot be considered here. Percentages have been calculated only for larger faunas (total numbers of individuals ranging from 70 to 1000, and averaging 200) and these form the central part of the results given below. However, some smaller faunas have been considered in comparison with better-known ones. Unfortunately, it was

not possible to obtain numerical data for the Russian and Chinese formations, nor for some of the German faunas.

Reptile footprint faunas are not considered here because of a lack of published numerical data about them, and the difficulty of obtaining such without extensive fieldwork. They appear, however, to reveal the same story as the body fossils (Haubold, 1971).

The analysis suffers from certain limitations of the data that are common to all paleoecological studies. The niche of a fossil reptile is usually hard to define, since direct evidence of diet and habits is rare. Also, the fossilized sample rarely corresponds to a true ecological community, and preservational bias clearly tends to emphasize medium-to-large water-side animals in the Triassic. Collector bias may lead to over-representation of the rarer animals from any particular formation. This will reduce the percentage of commoner animals in the analysis, however, and thus any major trends that are detected will probably be real.

The results are presented in the form of relative abundance polygons for major taxa, based on the main faunas. Small drawings show the relative sizes and shapes of the animals for selected faunas. The text is restricted to a brief outline of major faunal changes and to comments on relevant, less well-known faunas that are not shown in the figures. It was considered desirable to indicate the pre-Triassic situation, and this has been done by offering histograms of the well-known middle to late Permian Beaufort Group faunas of South Africa, which immediately predate the *Lystrorhynchus* Assemblage Zone faunas.

FAUNAL ANALYSES

Southern Africa/South America Area

(including Antarctica, China, India (part),
Russia)

The combined area of southern Africa and South America presents the best sequence of reptile faunas from the late Permian to the earliest Jurassic. It is best to start by summarizing events there first. Five important phases of faunal replacement, each of which ended with major extinctions, may be

distinguished. These phases are roughly equivalent to some of the stratigraphic chronofaunas, or empires, established for the "middle" and late Permian, and the early, middle, and late Triassic by various authors (Olson, 1952, 1971; Romer, 1970, 1972, 1973, 1975; Bakker, 1977; Anderson and Cruickshank, 1978).

The "middle" Permian **Tapinocephalid Empire** (Anderson and Cruickshank, 1978) was dominated by small dicynodonts and medium-to-large dinocephalians and pareiasaurs as herbivores, and by dinocephalians, therocephalians, and gorgonopsians as small-to-large carnivores. It is best represented by the *Tapinocephalus* Zone (= Dinocephalian Assemblage Zone + *Priesterognathus/Diictodon* Assemblage Zone, Keyser and Smith, 1979) of South Africa (Fig. 2). Closely comparable faunas occur on the Russian platform (Zones I-III).

The late Permian **Dicynodontid Empire** (Anderson and Cruickshank, 1978) was dominated by small to large dicynodonts and "endothiodonts" as herbivores, with a few remaining pareiasaurs. Carnivores were medium-to-large gorgonopsians and small-to-medium scaloposaurians, therocephalians, and early cynodonts. The dinocephalians were all extinct, and dicynodonts represented 80 to 90 per cent of all animals present. The best-known representatives of this empire are in the *Cistecephalus* Zone (= *Tropidostoma microtrema* Assemblage Zone + *Aulacephalodon baini* Assemblage Zone) and *Daptocephalus* Zone (= *Dicynodon lacerticeps* Assemblage Zone) of South Africa (Figs. 2, 3). Comparable faunas occur in Scotland (Hopeman Sandstone Formation of Elgin), the Russian platform (Zone IV, with the oldest thecodontian, *Archosaurus*), and China and India (Anderson and Cruickshank, 1978, p. 44). The Permian ended with decreasing faunal diversity and the extinction of many groups of plants, marine invertebrates, and reptiles, possibly in response to the global reduction in marginal seas as Pangaea united (Newell, 1967; Schopf, 1974).

The Triassic Period opened with the *Lystrorhynchid Empire* (Anderson and Cruickshank, 1978). The dominant medium-to-large herbivore was the dicynodont *Lystrorhynchus*, and carnivores were small-to-medium

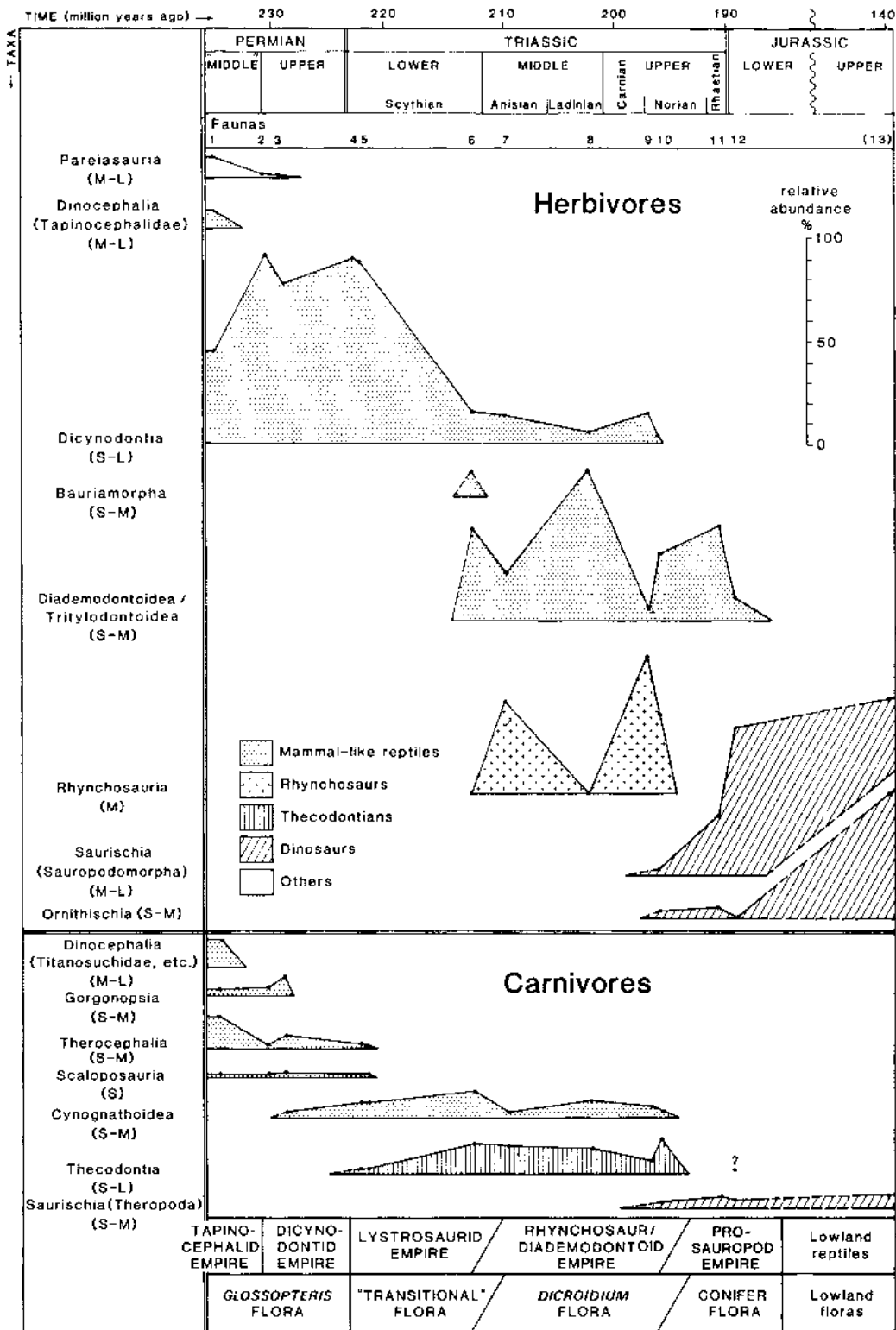


FIG. 2. THE RELATIVE ABUNDANCE OF THE MAJOR GROUPS OF TERRESTRIAL REPTILES IN THE LATE PERMIAN AND TRIASSIC OF SOUTHERN AFRICA, SOUTH AMERICA, AND RELATED AREAS

The time-scale (upper horizontal axis) is drawn to scale for the late Permian and Triassic, and stratigraphic assignments of faunas are based on Fig. 1. Faunas come from the following formations: 1,

therocephalians and cynodonts, and the first well-known thecodontian, *Proterosuchus* (*Chasmatosaurus*). The type example of this empire is the *Lystrosaurus* Assemblage Zone of South Africa (Figs. 2, 3), and nearly identical faunas occur in Russia, China, India (Panchet Formation), Australia (?Rewan Formation), and Antarctica (Fremouw Formation).

The subsequent *Cynognathus* Zone (= *Kannemeyeria* Assemblage Zone) was transitional to the next phase of ecological replacement (see Fig. 2). Medium-sized and large dicynodonts were still important herbivores, but small-to-medium herbivorous cynodonts (diademodontoids) became abundant. Thecodontians were beginning to diversify, and they include the rare *Erythrosuchus*, the first of a series of massive carnivores, which did not oust the mammal-like reptiles, however, since advanced cynodonts (e.g., *Cynognathus*) had radiated as medium-sized predators.

The **Rhynchosaur/Diademodontoid Empire** (= *Kannemeyeriid/Diademodontid* Empire, Anderson and Cruickshank, 1978) lasted from the Anisian to the Norian. The main characteristic of the faunas [Manda (*sensu stricto*), Santa Maria, Ischigualasto; Figs. 2, 3] is the remarkable dominance of each by a medium-sized rhynchosaur (40–60% of all individuals). When rhynchosaurs were absent (e.g., Chañares Formation, Fig. 2), their place was taken by diademodontoids. Some large dicynodonts were present, and the carnivores consisted of cynodonts and thecodontians, the latter finally taking over completely in the Norian faunas. The Norian faunas also had rare dinosaurs and "paracrocodyles." Thus, by a slow process, thecodontians had finally replaced mammal-like reptiles as carnivores by late Triassic times, in all but a few small insectivore adaptive zones but nevertheless both groups were extinct by the end of the

Norian. Other less well-known faunas that fit in here are the N'tawere Formation of Zambia (intermediate between the *Cynognathus* Zone and Manda Formation), the Puesto Viejo and Rio Mendoza Formations of Argentina (like the *Cynognathus* Zone), the Yerrapalli Formation of India (like the Manda Formation), and Zones V and VI of Russia (like the *Cynognathus* Zone). The Maleri Formation of India and Lossiemouth Sandstone Formation of Scotland share the dominance of a rhynchosaur with these southern faunas, but they have other influences and will be discussed later as part of the northern area.

The **Prosauropod Empire** (= Melanorosaurid/Plateosaurid Empire, Anderson and Cruickshank, 1978) was dominated by dinosaurs as medium-to-large herbivores and carnivores. They appeared abundantly first in the Rhactian and earliest Jurassic in the southern hemisphere [South Africa (Elliot, Clarens Formations, Figs. 2, 3), Zimbabwe (Forest Sandstone), South America (upper Los Colorados Formation, El Tranquilo Formation), India (Dharmaram Formation), and China (Lower Lufeng Series)] at the same time, where some achieved vast size (*Melanorosaurus* from the Elliot Formation, 12 m long). Early ornithischians (e.g., *Fabrosaurus*, *Heterodontosaurus*) probably fed on low plants. The coelurosaurs were small carnivores, but larger predator niches were not filled until somewhat later—so-called carnosaurs from the late-Norian and Rhaetian of Germany and England are represented by a jaw and isolated teeth (*Teratosaurs*, *Palaeosauriscus*).

A typical late Jurassic fauna (Tendaguru Formation, Tanzania) is shown on the extreme right of Fig. 2 in order to indicate later developments (data from Russell, Béland, and McIntosh, 1980). The main changes are the replacement of palaeopods by giant

"*Tapinocephalus* Zone," South Africa; 2, "*Cistecephalus* Zone," South Africa; 3, "*Daoptocephalus* Zone," South Africa; 4, "*Lystrosaurus* Zone," South Africa; 5, Fremouw Formation, Antarctica; 6, "*Cynognathus* Zone," South Africa; 7, Manda Formation, Tanzania; 8, Chañares Formation, Argentina; 9, Santa Maria Formation, Brazil; 10, Ischigualasto Formation, Argentina; 11, Elliot Formation, South Africa; 12, Lower Lufeng Series, China. Original data are given in the Appendix. The Tendaguru Formation fauna from Tanzania (Upper Jurassic, 13) is added for comparison (data from Russell et al., 1980). The lowland floras (Anderson and Anderson, 1970; Retallack, 1977) and corresponding faunal empires (Anderson and Cruickshank, 1978; this work) are given at the foot of the chart. L, large; M, medium; S, small.

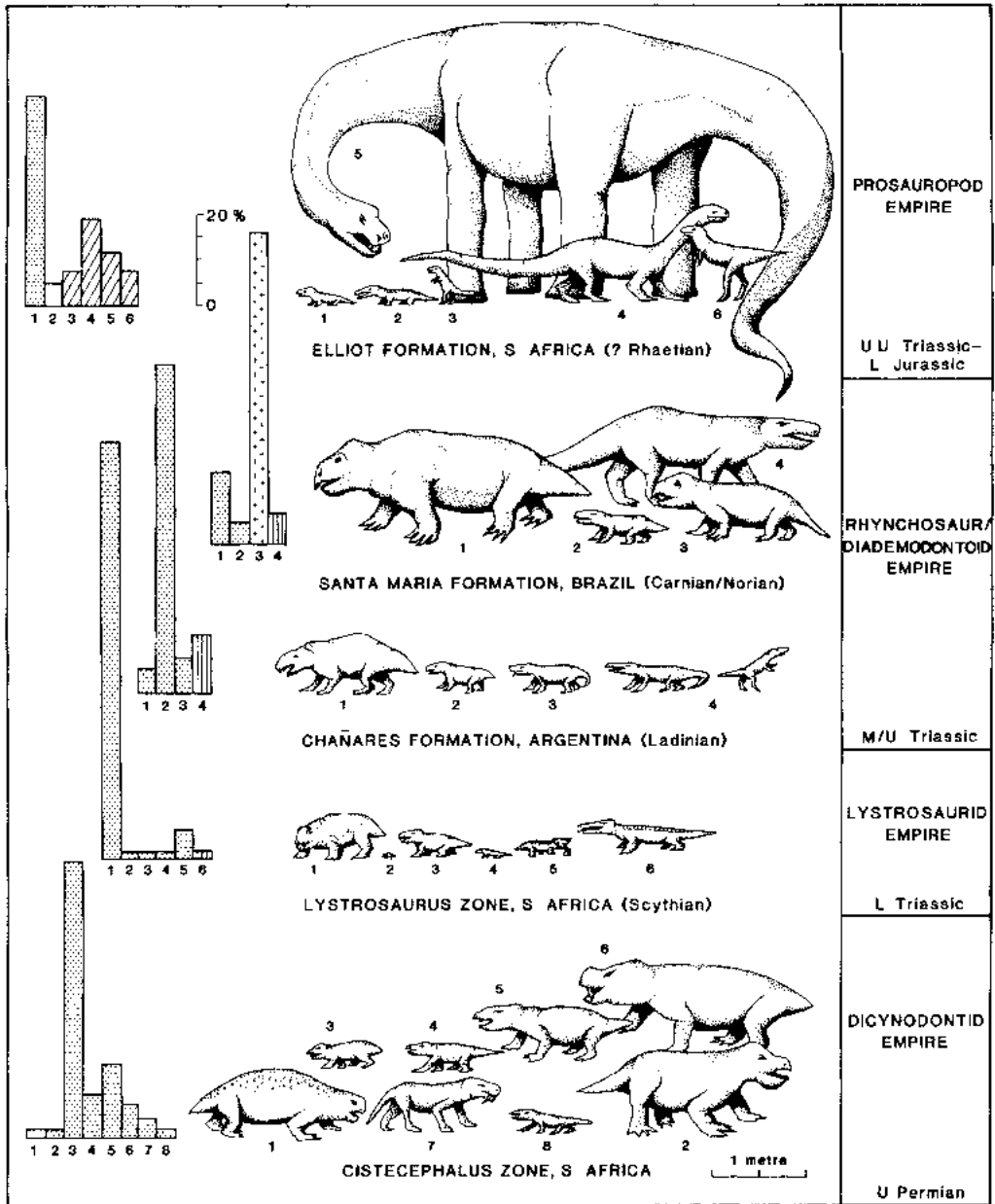


FIG. 3. REPRESENTATIVE FAUNAS OF THE FOUR LOWLAND REPTILE EMPIRES OF THE LATE PERMIAN AND TRIASSIC OF SOUTHERN AFRICA, SOUTH AMERICA, AND RELATED AREAS

The histograms show the relative abundance of each genus or group of related genera (data in Appendix). Histogram shading scheme, same as in Fig. 2. Sketches show the appearance and size of the animals in question (all drawn to scale).

Cistecephalus Zone [Herbivores: pareiasaur *Pareiasaurus* (1), endothiodont (2), dicynodonts *Diictodon*, *Emydops*, *Pristerodon* (3), *Cistecephalus* (4), *Tropidostoma* (5), *Aulacephalodon* (6); carnivores: gorgonopsians (7), scaloposaurians and therocephalians (8)].

Lystrosaurus Zone [Herbivores: dicynodonts *Lystrosaurus* (1), *Myosaurus* (2); carnivores: therocephalian *Moschorhinus* (3), cynodonts *Galesaurus* (4), *Thrinaxodon* (5), thecodontian *Chasmatosaurus* (6)].

Chañares Formation [Herbivores: dicynodont *Dinodontosaurus* (1), diademodont *Massetognathus* (2); carnivores: cynodont *Protelesodon* (3), thecodontians (4)].

Santa Maria Formation [Herbivores: dicynodonts *Stahleckeria*, *Dinodontosaurus* (1), diademodont *Traversodon* (2), rhynchosaur *Scaphonyx* (3); carnivores: thecodontians (4)].

sauropods and the relative increase in importance of diverse ornithischian dinosaurs.

North America and Europe

The sequence of Empires that is so well developed in South Africa, South America, and many other areas, breaks down when we try to classify the faunas from the middle to late Triassic of the United States and parts of Europe. The differences do not indicate separate areas of faunal development (e.g., Gondwanaland and Laurasia, Colbert, 1971) because many elements are shared between north and south (Romer, 1970; Charig, 1971; Cox, 1973a). Many of the peculiarly northern animals indicate more aquatic faunas.

The Scythian Buntsandstein of Germany and the lower Moenkopi Formation of Arizona are dominated by amphibians and *Chirotherium* trackways, probably produced by carnivorous thecodontians. Other animals include small procolophonids, eosuchians, and rhynchocephalians (Schmidt, 1928) (Figs. 4, 5). The early Ladinian upper Moenkopi Formation of Arizona and the late Ladinian Lettenkohl of Germany are also dominated by amphibians, together with a few obscure thecodontians. Some of the amphibians are present also in the typical empires already described, and some occur only here (e.g., *Mastodonsaurus*). We may name a freshwater Scythian-Ladinian **Capitosaurid/Mastodonsaurid Empire** for these European and American faunas, although capitosaurids also occur as rare elements in the Lystrosaurid Empire. These amphibians are present also in the early Ladinian Bromsgrove Sandstone Formation of the English Midlands, but it also has a small rhynchosaur and elements of the marine Nothosaurid/Mixosaurid Empire (Anderson and Cruickshank, 1978) of the German Muschelkalk (nothosaur, macrocnemid, Walker, 1969). The late Ladinian Sol'lets Series (Zone VII) of Russia has similar amphibians, but also some dicynodonts (Battail, 1980).

The Carnian to mid-Norian Keuper formations of Germany (Gipskeuper, Schilfsandstein, Lehrbergstufe, Biasensandstein) are dominated by the amphibian *Metoposaurus* and the fresh-water fish-eating phytosaurs (*Mystriosuchus*, *Phytosaurus*, *Palaeorhinus*), and we may identify this as a fresh-water and low-land **Metoposaur/Phytosaur Empire**. Other faunas that are dominated by these two forms are the early Norian Popo Agie Formation of Wyoming (see Figs. 4, 5; rarer elements: large thecodontian, large dicynodont: Dawley, Zawiskie, and Cosgriff, 1979), the early to middle Norian Dockum Group (see Figs. 4, 5; rarer elements: aetosaurs *Desmatosuchus* and *Typhothorax*, obscure *Trilophosaurus*, unnamed rhynchosaur), and the early to middle Norian Chinle Formation lower fauna (see Figs. 4, 5; rarer elements: aetosaurs *Desmatosuchus* and *Typhothorax*, dicynodont *Placerias*, Colbert, 1972b). The thecodontians, dicynodonts, and rhynchosaurs are probably southern influences, but the aetosaurs appear to be more important. They are present mainly in the northern hemisphere (a few specimens in the Ischigualasto and Los Colorados Formations of Argentina) and are restricted to the Norian and Rhaetian. They occur in the Metoposaur/Phytosaur Empire and subsequently in some prosauropod faunas of the latest Triassic.

The early Norian Maleri Formation of India (Fig. 6) contains a perfect mix of elements of the Rhynchosaur/Diademodontid Empire and the Metoposaur/Phytosaur Empire. The reptiles and ostracods clearly point to strong northern affinities, although India is normally assumed to have been joined to Africa in the Triassic (Sohn and Chatterjee, 1979). The early Norian Lossiemouth Sandstone Formation of Elgin (see Fig. 6) has no mammal-like reptiles, but the rhynchosaur *Hyperodapedon* and the thecodontian *Ornithosuchus* are closely comparable to South American forms. The Elgin fauna shows no particular affinities with the then neighboring German and North American faunas except for cosmopolitan forms. These transi-

Elliot Formation [Herbivores: tritylodont *Tritylodon* (1), prosauropod dinosaurs *Massospondylus* (4), *Euskelosaurus* (5), ornithischian dinosaurs *Fabrosaurus*, *Heterodontosaurus* (6); carnivores: "crocodiles" (2), coelurosaur dinosaur *Syntarsus* (3)].

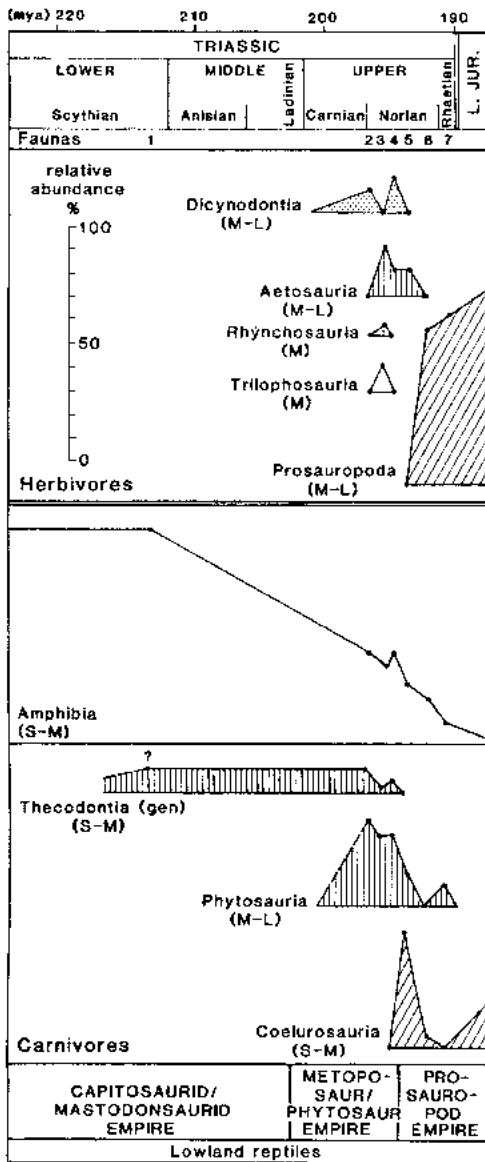


FIG. 4. THE RELATIVE ABUNDANCE OF THE MAJOR GROUPS OF TERRESTRIAL REPTILES IN THE TRIASSIC OF NORTH AMERICA AND EUROPE

The time-scale is the same as in Fig. 3 (mya = millions of years ago), and stratigraphic assignments of faunas are based on Fig. 1. Thecodontia (gen) includes all thecodontians except phytosaurs and aetosaurs. Faunas come from the following formations: 1, Buntsandstein, Germany; 2, Popo Agie Formation, Wyoming; 3, Dockum Formation, Texas, New Mexico; 4, Chinle Formation (lower fauna), Arizona; 5, Chinle Formation (upper fauna), Arizona; 6, Knollenmergel, Germany; 7, Rhaetian, Germany. Original data, in Appendix. Figures for faunas 1 and 7 are esti-

tional faunas link the quite different contemporary faunas of the Norian of Germany and South America.

Dinosaur-dominated faunas appear first in Germany and North America just before the typical Prosauropod Empire of Gondwanaland described above. The German Stubensandstein (middle Norian) contains various saurischians: small carnivorous coelurosaurs (*Procompsognathus*) and larger herbivorous palaeopods like *Plateosaurus*, as well as remnant amphibians (*Cyclotosaurus*), phytosaurs and aetosaurs (*Aetosaurus*). The succeeding late Norian Knollenmergel also has amphibians, and abundant *Plateosaurus* (see Figs. 4, 5). Equivalent faunas occur in France and England (Bristol), and in the Rhaetian of the same countries. The upper part of the Chinle Formation (middle Norian) has abundant specimens of the coelurosaur *Coelophysis*, as well as remaining *Metoposaurus*, phytosaurs, and aetosaurs (see Figs. 4, 5; Colbert, 1974a). The succeeding Glen Canyon Group yields a few dinosaurs and the earliest Jurassic (?) Portland Formation of the eastern United States contains medium-large herbivorous prosauropods, phytosaurs, and "paracrocodyles." These German and United States formations may be included in the Prosauropod Empire, although they lack the giant *Melanorosaurus* and have a few hangers from the Metoposaur/Phytosaur Empire.

DISCUSSION

*Triassic Ecological Replacements:
Faunal Dynamics*

The data from northern and southern faunas are summarized in Fig. 7. We may now assess various explanations that have been given for the following events in the Triassic:

- (a) a replacement of gorgonopsian mammal-like reptiles by thecodontians as medium to large carnivores (late Permian to earliest Scythian) (Fig. 2);
- (b) a replacement of cynodont mammal-like reptiles by thecodontians as carnivores (early Norian);

mated from less accurate counts than the others. The new lowland reptile empires established here are given at the foot of the chart.

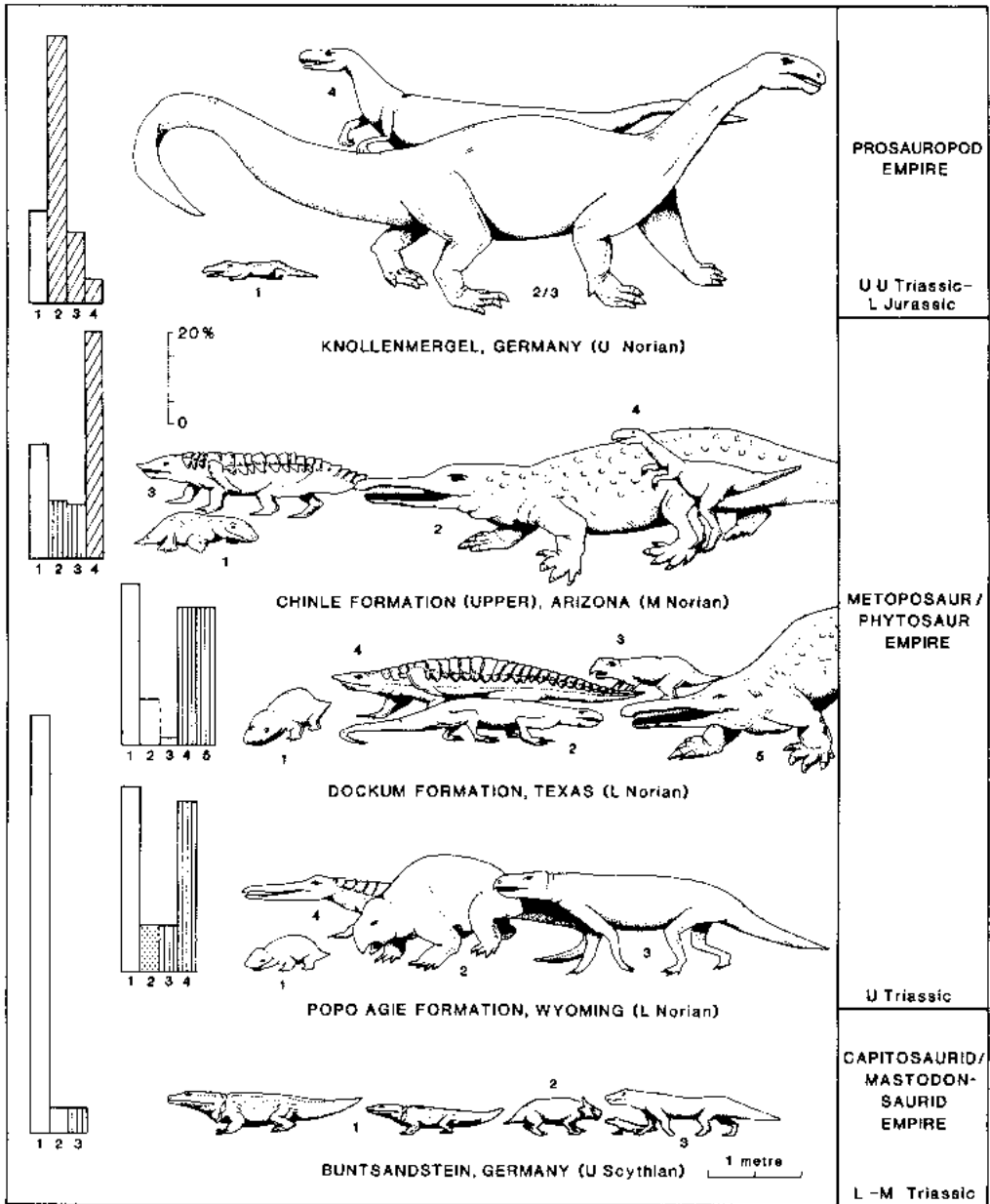


FIG. 5. REPRESENTATIVE FAUNAS OF THE THREE LOWLAND REPTILE EMPIRES OF THE TRIASSIC OF NORTH AMERICA AND EUROPE

Conventions as in Fig. 3. Buntsandstein [Herbivore: procolophonid *Sclerosaurus* (2); fish-eaters: amphibians *Mastodonsaurus*, *Parotosaurus* (1); carnivores: thecodontians (3)].

Popo Agie Formation [Herbivore: dicynodont *Placerias* (2); fish-eater: amphibian *Metoposaurus* (1); carnivores: thecodontian *Rauisuchus* (3), phytosaurs *Palaeorhinus*, *Angistorhinus* (4)].

Dockum Formation [Herbivores: *Trilophosaurus* (2), rhynchosaur (3), aetosaurs *Desmatosuchus*, *Typothorax* (4); fish-eater: amphibian *Metoposaurus* (1); carnivores: phytosaurs *Phytosaurus*, *Ruitodon* (5)].

Chinle Formation (upper fauna) [Herbivore: aetosaur *Typothorax* (3); fish-eater: amphibian *Metoposaurus* (1); carnivores: phytosaur *Phytosaurus* (2), coelurosaur dinosaur *Coelophysis* (4)].

Knollenmergel [Herbivores: prosauropod dinosaurs *Plateosaurus* (2), *Gresslyosaurus* (3); fish-eater: amphibian *Cyclotosaurus* (1); carnivore: coelurosaur dinosaur *Halticosaurus* (4)].

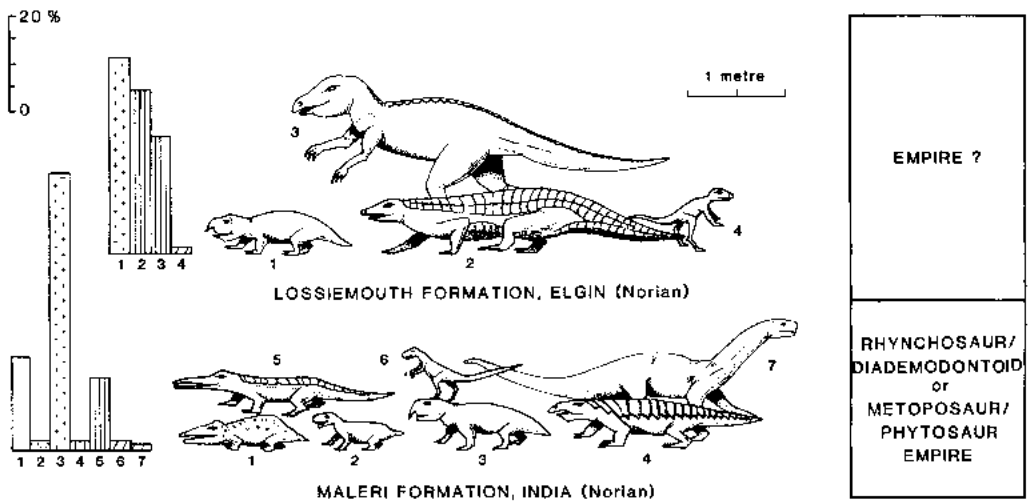


FIG. 6. THE FAUNAS OF THE LOSSIEMOUTH SANDSTONE FORMATION (SCOTLAND) AND MALERI FORMATION (INDIA)

Conventions as in Fig. 3. Lossiemouth Sandstone Formation [Herbivores: rhynchosaur *Hyperdapedon* (1), aetosaur *Stagonotepis* (2); carnivores: thecodontian *Ornithosuchus* (3), coelurosaur dinosaur *Saltopus* (4)].

Maleri Formation [Herbivores: diademodont *Exaeretodon* (2), rhynchosaur *Paradapedon* (3), aetosaur *Typothorax* (4), prosauropod dinosaur (7); fish-eater: amphibian *Metoposaurus* (1); carnivores: phytosaur *Parasuchus* (5), coelurosaur dinosaur (6)].

- (c) a replacement of dicynodont mammal-like reptiles by rhynchosaurs, diademodontoids, and aetososaurs as the dominant herbivores (Anisian to early Norian);
- (d) a replacement of thecodontians, dicynodonts, rhynchosaurs and diademodontoids by dinosaurs (middle to late Norian).

There are problems in scaling up ecological concepts of competition between individuals and species to explain large-scale replacements in the past. At the level of individual organisms, the outcome of each interaction may be explained by a particular cause. Further, if members of one species repeatedly replace those of another, the former species can be said to have positive differential survival when compared with the one it is replacing. Individuals and species may be subject to selection at different levels in a hierarchy of evolution (microevolution and macroevolution respectively: Eldredge and Gould, 1972; Stanley, 1975), and reasons for each extinction and replacement may be found. This deterministic approach may not be valid in seeking explanations for larger-

scale replacements. In such cases, it has been argued (e.g., Schopf, 1979) that we should adopt a stochastic point of view, in which origination and extinction are considered to be random with respect to taxonomic group. Nevertheless, I believe that it is still worthwhile to seek particular explanations for certain large-scale replacement events in the past, and that the fossil record contains the data to test these explanations.

A fauna in equilibrium may be perturbed, and individual species become extinct as a result of the influx of new forms or by environmental change. These possible outcomes are termed differential survival ("competitive") ecological replacement and opportunistic ecological replacement, respectively.

(1) *Differential survival* ("competitive") replacement may result when a group of native animals and a group of invaders occupy similar adaptive zones. If they compete, the invader may succeed and the native become extinct, and this fact could be recorded in the fossil record. If, however, the native repulses the invader, this is unlikely to be recorded (Marshall, 1981).

(2) *Opportunistic replacement* arises when ex-

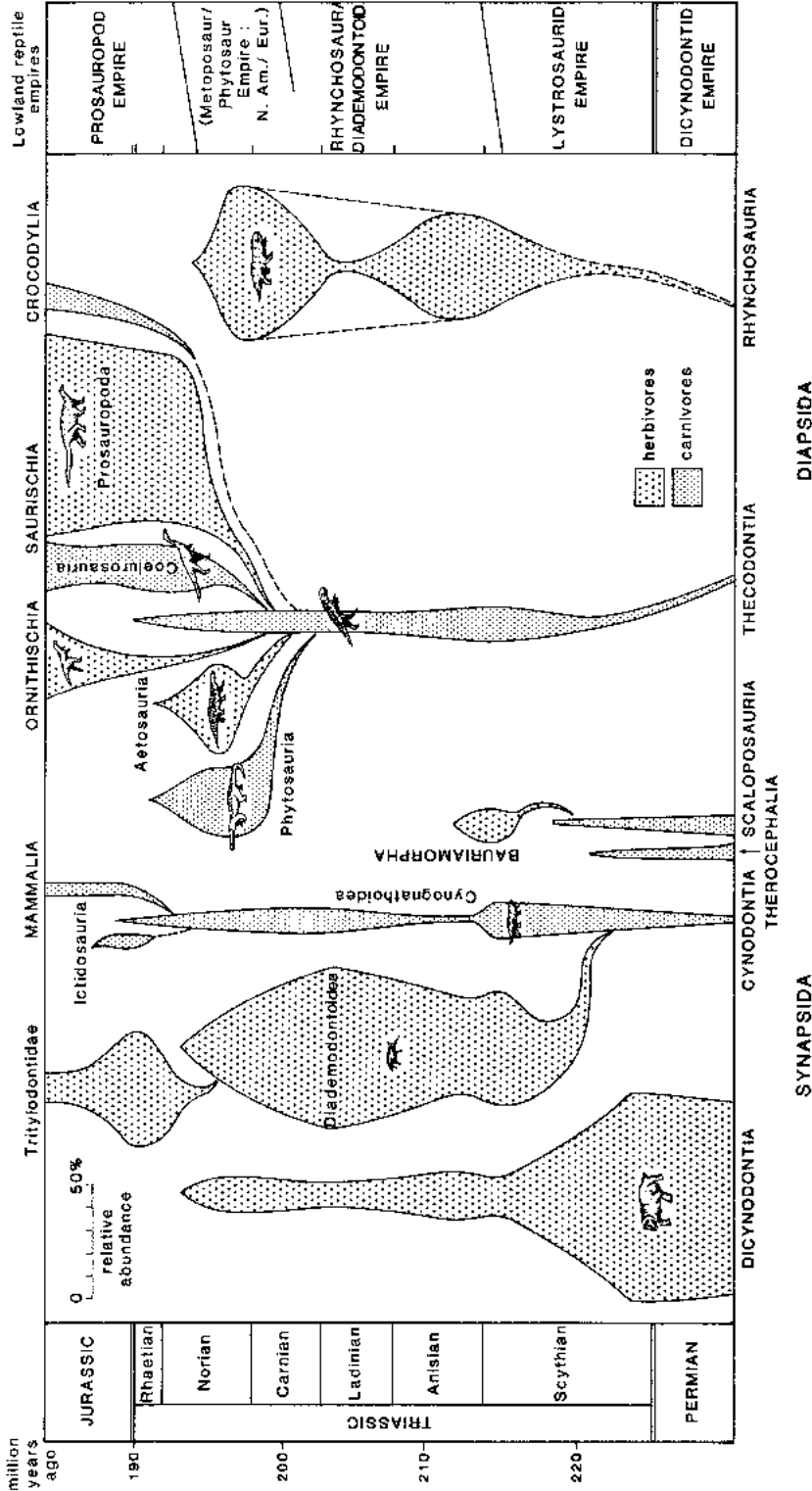


FIG. 7. PHYLOGENETIC CHART OF THE MAJOR GROUPS OF TERRESTRIAL REPTILES OF THE TRIASSIC, SHOWING THE MAJOR EXTINCTION EVENTS DURING THE LATE NORIAN

Based on all major faunas for which data were available (Appendix). The time-scale and faunal correlations are based on data given in Fig. 1. The width of each balloon is intended to correspond exactly to the relative abundance of the group at different times in the Triassic.

tion is caused by some factors unconnected with the new incumbents of the adaptive zone who just "happened along" at the appropriate time. This has been termed "passive replacement" by Marshall (1981, p. 146).

Whole families or orders of animals may become extinct and others may become established in their place by a summation of interspecific interactions in three ways:

(1) positive differential survival of all species in a particular group, giving the predecessor group a high extinction rate and the successor group a high origination rate;

(2) opportunistic replacement displayed by all species in a group after the extinction of another group;

(3) a random mixture of (1) and (2).

When put in these terms, it seems most unlikely that examples of pure differential survival of a family or order based on interspecific competition could be demonstrated in the fossil record. Such explanations are normally adduced in cases of the long-term dwindling of one taxon, and the concomitant rise of another that occupied similar adaptive zones. It would be hard to prove that random effects and external factors were not involved. On the other hand, sudden worldwide extinctions of whole families or orders, which are potentially demonstrable in the fossil record, do point to some environmental change or other external cause.

We may attempt to distinguish purely differential survival replacement from purely opportunistic replacement in the fossil record by an examination of the relative abundance over time of the groups in question. A differential survival hypothesis for the replacement of group A by group B would be suggested by the following pattern:

- (1) A will tend to decrease in abundance, and B will increase in abundance over time;
- (2) the rate of replacement should be gradual (in paleontological terms, this would imply a time span of more than one million years, say, and often more than 10 to 20 million years);
- (3) A and B will be found together, and either could be dominant in any particular formation; and
- (4) the replacement will not necessarily be

associated with climatic or floral change.

An opportunistic hypothesis for the replacement of group A by group B would be suggested by the following pattern:

- (1) B will appear or radiate only *after* the extinction of A;
- (2) the rate of replacement should be rapid (in paleontological terms, this would imply a time span of less than one million years, and possibly a few thousands or tens of thousands of years, if such stratigraphic accuracy were possible);
- (3) A and B will not be found together, or B may be unobtrusively present when A is dominant; and
- (4) the replacement will be associated with climatic or floral change.

With these criteria in mind, we may examine events (a) through (d) mentioned above:

(a) The appearance and radiation of thecodontians as medium to large carnivores at the end of the Permian and the beginning of the Triassic was sudden and followed the extinction of mammal-like reptiles such as the Gorgonopsia. This was in part opportunistic replacement. Cynodonts arose in late Permian times and their radiation and that of the thecodontians was matched by decreasing abundance of therocephalians and sceloposaurians, so that competition may have been involved between carnivores of small to medium size.

(b) The supposed replacement of cynodonts by thecodontians in the early Norian may be more apparent than real. The two groups arose in the late Permian and evolved side by side for thirty million years. Members of both groups are found together in similar proportions in many faunas, and they must have occupied rather different adaptive zones. The cynodonts became extinct in the middle Norian, and the thecodontians survived a little longer. We can hardly link the extinction of the cynodonts with the rise of the thecodontians, and neither differential survival nor opportunism can be proposed as an explanation.

(c) The replacement of dicynodonts by rhynchosaurs, diademodontoids, and aetosaurs was never quite completed. The rhy-

chososaurs and diademodontoids achieved dominance first in various middle Triassic faunas, but the dicynodonts did not become extinct. Aetosours were important herbivores in certain late Triassic faunas, but they were often present with dicynodonts. All four groups became extinct about the same time in the middle Norian. We are evidently dealing with partial replacement by differential survival. The rhynchosaurs will be further discussed below.

(d) The rise of the dinosaurs was rapid in middle-late Norian times. It followed the extinction of thecodontians, dicynodonts, rhynchosaurs and diademodontoids, and appears to have been associated with climatic and floral changes. These will be discussed below. It is suggested here that the initial radiation of dinosaurs was an opportunistic occupation of empty adaptive zones.

Most, if not all, previous authors have implicitly accepted that the replacement of mammal-like reptiles by thecodontians, and then by dinosaurs, was a competitive process throughout. It has been assumed that archosaur characters were superior to those of the synapsids. For example: "In the competition with Triassic archosaurs, the retention of sprawling locomotion, and possibly the lack of efficient heat-loss mechanisms in therapsids caused their extinction" (Bakker, 1971, p. 656).

Charig (1980) has given the best account of how the competitive model is supposed to have operated. He has described the faunal replacement of carnivorous mammal-like reptiles by thecodontians as accelerating rapidly up to the beginning of the late Triassic, when the latter group triumphed. Synapsids and rhynchosaurs, however, were dominant as herbivores until the middle of the late Triassic. Then, selection pressure on competing thecodontian carnivores caused some of them to adapt to a herbivorous diet (aetosours). "The more intense competition between the many carnivorous archosaurs in the late Triassic and the greater selection pressure which it engendered led to the perfection of the 'fully improved' limb posture in the sauropodomorph line [see Table 1]. . . . These had a great advantage over the few surviving herbivorous therapsids, the rhynchosaurs and the other groups of archosaurs

which. . . were not yet 'fully improved' in their locomotor adaptations" (p. 209).

There is no question that thecodontians and dinosaurs had a semi-erect or erect limb pose that was better adapted for supporting weight than was the sprawling limb pose of the early synapsids. It can be argued that it was also better adapted for fast locomotion. Middle and late Triassic cynodonts were highly advanced in their dentition, however, and they also had an obligatory erect hindlimb gait (Kemp, 1980). It is also more likely that these middle and late Triassic synapsids were endothermic than that the thecodontians and dinosaurs of that time were (Brink, 1956; McNab, 1978; Benton, 1979a; Baur and Friedl, 1980). The middle and late Triassic rhynchosaurs, normally classed with the synapsids as losers in the competition with archosaurs, had a semi-erect hindlimb gait (Benton, 1981). Scenarios that attempt to explain complex replacement processes by reference to single characters are likely to be gross oversimplifications. The differential survival hypotheses for dinosaur success tend to be intangible and they are untestable in their present form.

As a preliminary to the development of an opportunistic replacement hypothesis for the achievement of dominance by the dinosaurs, we must consider briefly the climatic changes in the Triassic, the Triassic floras, the role of the rhynchosaurs, and the evidence for the earliest dinosaurs.

Environments of Triassic Reptiles

In the Triassic, all continents were united as the "super-continent" Pangaea, and worldwide faunal similarities existed during this time. There were apparently no polar ice caps, the surface temperatures of the earth were generally higher, and climates around the world were more uniform than today. Fluvial, lacustrine, and aeolian depositional environments were dominant, and in the middle Triassic, thick evaporite (halite) sequences filled basins in northeastern North America, western Europe, and north Africa (Frakes, 1979). Pangaea drifted north during the Triassic (Smith and Briden, 1977), and the combined area of South Africa and South America, for example, moved from latitudes 60-70° to 40-50°. The northward

drift moved this continental mass into warmer, more arid climatic zones during the course of the Triassic (Kremp, 1977), and this shift must have influenced the faunas. Northern areas (Europe, North America) did not move so far in latitude because of rotations occurring near the equator, and their climates probably did not change so much during the Triassic.

An analysis of the sedimentology of important Triassic reptile sites (Tucker and Benton, in press) shows that nearly all are from lowland situations, and these may be classified into three groups:

- (1) moist, warm, equable lakeside and riverside;
- (2) seasonal (monsoon?) floodplains with waterside vegetation and dry sandy or savannah-like interchannel areas;
- (3) largely semi-arid to arid acolian environments with transitory lakes and pools.

Most early Triassic reptile beds may be classed as forming in environment no. 1. There was increasing aridity in the late Scythian and middle Triassic in many areas, but in the early late Triassic most reptile beds appear to belong to the humid monsoonal environment no. 2. Finally, there was a major arid to semi-arid phase at the end of the Triassic, and many reptile faunas of that time experienced environment no. 3.

Triassic Floras

Triassic megaplants are even more sporadic in occurrence than are the reptiles, and they are very rarely associated with them. However, some patterns of floral replacement do emerge, and it is argued here that they were very important in influencing reptile faunal change.

The widespread *Glossopteris* Flora of Gondwanaland disappeared towards the end of the Permian, and was replaced initially by a "transitional flora" (Anderson and Anderson, 1970) in the latest Permian and early Scythian. Representative floras come from various localities in India, Australia, and New Zealand. During this time, such groups as psilopsids, lycopods, and equisetaleans (horsetails) became less abundant, and the pteridosperm (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 (Schopf and Askin, 1980). Representatives come from various localities in Australia, New Zealand, India, South Africa, Zimbabwe, Argentina, and Brazil (Anderson and Anderson, 1970; Retallack, 1977). *Dicroidium* and its relatives (e.g., *Xylopteris*, *Johnstonia*) were abundant in a range of habitats from broadleaf forest and heath to xerophytic woodland. Other elements of the *Dicroidium* Flora include equisetaleans (e.g., *Neocalamites*), filicaleans (ferns, e.g., *Cladophlebis*), "cycadophytes" (e.g., *Taeniopteris*), Ginkgoales (e.g., *Baiera*), and conifers (e.g., *Podozamites*) (Anderson, 1974; Retallack, 1977).

Northern hemisphere floras of the middle to late Triassic are generally dominated by "cycadophytes," ferns, and conifers, and contain no seed ferns. Examples occur in England, Germany, Russia, and the Carnian-Norian Chinle Formation of Arizona (including the petrified forest — with 50 species of macroplants, including fungi, lycopods, sphenopsids, ferns, conifers, ginkgos, cycads, and bennettitaleans; Ash, 1980).

Dicroidium and its relatives disappeared by the end of the Norian, except for a few localities in the Rhaetian of Queensland (de Jersey, 1975; Retallack, 1977). It did not survive into the Jurassic, although some other seed ferns (e.g., *Lepidopteris*, *Pachypteris*) continued through the Mesozoic Era. A new worldwide flora, dominated by diverse conifers and bennettitaleans, took over in the Rhaetian and Jurassic (Anderson and Anderson, 1970; Barnard, 1973; Hughes, 1976; Miller, 1977), with well-known representatives in Argentina, Yorkshire (England), Greenland, and Germany.

The Role of the Rhynchosaurus

The importance of the rhynchosaurus in Triassic faunas was stressed by Romer (1960, 1963, 1970, 1972, 1975) and this significance has also been emphasized here. In view of recent disagreement about the diets of rhynchosaurus and because of the importance attached to them in this analysis, in influencing the early radiation of dinosaurs, they will now be discussed further.

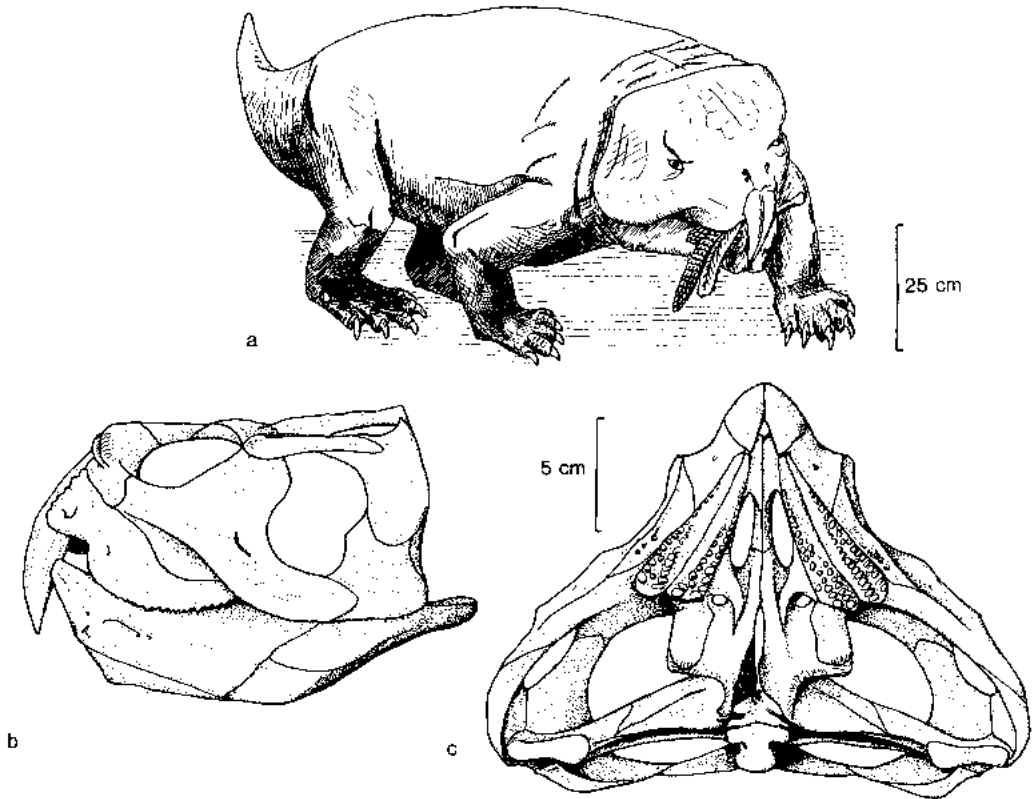


FIG. 8. RHYNCHOSAURS

(a) Reconstruction of the South American rhynchosaur *Scaphonyx*; (b) side view of the skull of the Scottish rhynchosaur *Hyperodapedon*; (c) palatal view.

Rhynchosaurs probably derived from the basal diapsid stock during the Permian, and they share some thecodontian and some primitive eosuchian features (Cruickshank, 1972; Carroll, 1977). The earliest so-called rhynchosaurs, *Noteosuchus* from the *Lystrosaurus* Assemblage Zone, and *Mesosuchus* and *Howesia* from the *Kannemyeria* Assemblage Zone, are rare small lizard-like animals. The first ecologically important rhynchosaur is *Stenaurorhynchus* from the Manda Formation, and it appears in surprising abundance and is much advanced over its supposed ancestors. The important Norian rhynchosaurs are *Scaphonyx* from South America (Argentina and Brazil), *Paradapedon* from India, and *Hyperodapedon* from Elgin, Scotland. These approximately contemporary animals are all medium to large in size, they all dominate their respective faunas, they all display identical adaptations, and they all appear to

have become extinct throughout the world at the same time, the middle Norian. This is an important point that was not evident when the rhynchosaurs were considered to be mainly middle Triassic in age, with a few late survivors in Scotland and India (Romer, 1975).

Rhynchosaurs were squat quadrupedal animals with sprawling limbs and large claws (Fig. 8a). Their heads were large and triangular in top view. In side view (Fig. 8b), several characteristic points are evident: they had large eyes, curved, pointed bony "tusks," a curved roller-like upper tooth row, and a deep boat-shaped lower jaw. In palatal view (Fig. 8c), the small conical teeth are seen to be arranged in dense rows on the maxilla, separated by a central groove. The lower jaw cut like a penknife blade upwards into the groove, but there was little back and forwards motion of the jaw and no sideways

chewing movement. The deeply rooted teeth and the bone at the crest of the lower jaw were worn to a blade that fitted snugly into the groove, and the upper teeth were worn only at the side of the groove.

It has been suggested that rhynchosaurs ate plant material (Huene, 1939; Romer, 1960, 1963; Sill, 1971) or molluscs (Burckhardt, 1900; Chatterjee, 1974, 1980). The latter interpretation does not seem likely because of the lack of wear on the upper teeth in most specimens, and the inappropriateness of the shearing jaw action for dealing with hard-shelled animals. Also in favor of a herbivorous diet is the barrel-shaped body (that would accommodate a large gut for the slow digestion of plants), the large numbers of these animals present in all faunas, and the absence of abundant fossil mollusc shells. The plant materials suggested by Romer (1963) and Sill (1971) as forming the rhynchosaur diet include the "fruit" of lycopsids, sphenopsids, and ferns, artichoke-like bennettitaleans, seed-ferns, and cycad rhizomes. Rhynchosaurs are rarely found with plant remains, but their rapid spread, massive local dominance, and subsequent apparently rapid extinction suggest that important elements of their diet may have had a similar history. The Triassic plant record suggests a parallel in the distribution of the *Dicroidium* Flora for the southern continents. Rhynchosaurs probably could not rear up on their hind legs, and would have had to feed at a height no greater than 1 m. This limitation would have restricted their diet to *Dicroidium*, equisetaleans, ginkgos, and the fallen leaves or fruits of cycads and conifers.

The Rise of the Dinosaurs

Dinosaurs are thought to have arisen from three or more thecodontian lineages (Charig, 1979). They are classified in two orders: the Saurischia and the Ornithischia. Their early history is uncertain because of their rarity until the late Norian (Cox, 1976). The oldest so-called dinosaur, *Avipes*, from the late Ladinian of Germany, is represented by three incomplete metatarsals. The earliest certain dinosaurs occur in the Ischigualasto and Santa Maria Formations, as well as at Elgin, and in India, as very unimportant elements of the rhynchosaur-domi-

nated faunas. These dinosaurs (*Staurikosaurus*, *Pisanosaurus*, *Ischisaurus*, *Herrerasaurus*, *Saltopus*) are represented by fragmentary remains (a total of less than 15 specimens) and their exact relationships are uncertain (Bonaparte, 1978; Galton, 1973). Many so-called dinosaurs of this age, and earlier, have been described (e.g., *Poposaurus* from Wyoming and elsewhere; *Triassoolestes* from Argentina; *Ornithosuchus* from Elgin; *Spondylosoma* from Santa Maria), but these are now classified as advanced thecodontians (Bonaparte, 1978; Galton, 1977; Galton and Cluver, 1976).

It seems that dinosaurs became ecologically important in the north in places where rhynchosaurs and *Dicroidium* were absent (Germany, North America). The extinction of both rhynchosaurs and *Dicroidium*, and the worldwide extension of the conifer flora thereafter permitted the new large dinosaurs to migrate south and radiate even more extensively. In all cases, it seems that they were occupying empty adaptive zones that were unsuitable for rhynchosaurs and synapsids. The extinction of these two groups following the floral changes were probably crucial factors in the rapid rise to domination of the dinosaurs.

A Model for Triassic Tetrapod Faunal Replacements, and Some Predictions Based on It

The replacement of mammal-like reptiles by dinosaurs during the Triassic may be seen as a four-stage model:

- (1) Thecodontians replace gorgonopsians as medium-to-large predators at the end of the Permian, following an extinction event. Opportunism.
- (2) Thecodontians and cynodonts radiate during the Triassic. Thecodontians eventually take over after the cynodonts become extinct in the middle Norian. Random processes.
- (3) Rhynchosaurs and diademodontoids compete successfully with dicynodonts in the middle and late Triassic and are dominant plant-eaters in most areas. Their rise is matched by the rise of the *Dicroidium* Flora. Differential survival.
- (4) Dinosaurs radiate rapidly with the new worldwide conifer and bennettitalean flora in the middle and late

Norian after the extinction of the rhynchosaurs, diademodontoids, dicynodonts, thecodontians, and aetosaurs. Connected with climatic and floral changes. Opportunism.

The following predictions may be made from the last part of this model, and they may be tested by further fossil finds:

- (1) Large synapsids or rhynchosaurs will not be found associated with large dinosaurs.
- (2) Large synapsids and rhynchosaurs will always be found to occur in older deposits than those containing ecologically important dinosaurs.
- (3) Rhynchosaurs will be associated with *Dicroidium* floras, and dinosaurs with

conifer floras, in the southern hemisphere.

ACKNOWLEDGMENTS

I thank the following for checking numbers for the graphs: J. M. Anderson, J. F. Bonaparte, S. Chatterjee, E. H. Colbert, A. R. I. Cruickshank, J. W. Kitching and A. D. Walker. A. R. I. Cruickshank, T. S. Kemp, A. L. Panchen, M. E. Tucker, R. M. Tucker, A. D. Walker, and W. A. Wimbledon kindly read and commented upon the manuscript at various stages. The artwork was produced by Christine Cochrane and David Houghton, and I am extremely grateful to them. This study was carried out during tenure of Natural Environment Research Council post-graduate award GT4/78/GS/120.

LIST OF LITERATURE

- ANDERSON, H. M. 1974. A brief review of the flora of the Moltena Formation (Triassic), South Africa. *Palaeontol. Afr.*, 17: 1-10.
- ANDERSON, H. M., and J. M. ANDERSON. 1970. A preliminary review of the uppermost Permian, Triassic and lowermost Jurassic of Gondwanaland. *Palaeontol. Afr., Suppl.*, 13: 1-22, Charts 1-22.
- ANDERSON, J. M. 1980. World Permo-Triassic correlations: their biostratigraphic basis. In M. M. Cresswell and P. Vella (ed.), *Gondwana Five*, p. 3-10. A. A. Balkema, Rotterdam.
- ANDERSON, J. M., and A. R. I. CRUICKSHANK. 1978. The biostratigraphy of the Permian and Triassic: Part 5. A review of the classification and distribution of Permo-Triassic tetrapods. *Palaeontol. Afr.*, 21: 15-44.
- ASH, S. R. 1980. Upper Triassic floral zones of North America. In D. L. Dilcher and T. N. Taylor (ed.), *Biostratigraphy of Fossil Plants*, p. 153-170. Dowden, Hutchinson & Ross, Stroudsburg.
- BAKKER, R. T. 1968. The superiority of dinosaurs. *Discovery, Peabody Mus., Yale*, 3(1): 11-22.
- . 1971. Dinosaur physiology and the origin of mammals. *Evolution*, 25: 636-658.
- . 1972. Anatomical and ecological evidence of endothermy in dinosaurs. *Nature, Lond.*, 238: 81-85.
- . 1975a. Dinosaur renaissance. *Sci. Am.*, 232 (4): 58-78.
- . 1975b. Experimental and fossil evidence for the evolution of tetrapod bioenergetics. In D. M. Gates and R. B. Schmerl (eds.), *Perspectives of Biophysical Ecology*, p. 365-399. Springer Verlag, New York.
- . 1977. Tetrapod mass extinctions — a model of the regulation of speciation rates and immigration by cycles of topographic diversity. In A. Hallam (ed.), *Patterns of Evolution as Illustrated by the Fossil Record*, p. 439-468. Elsevier, Amsterdam.
- . 1980. Dinosaur heresy—dinosaur renaissance: why we need endothermic archosaurs for a comprehensive theory of bioenergetic evolution. In R. D. K. Thomas and E. C. Olson (eds.), *A Cold Look at the Warm-Blooded Dinosaurs*, p. 351-462. Westview Press, Boulder.
- BARNARD, P. D. W. 1973. Mesozoic floras. In N. F. Hughes (ed.) *Organisms and Continents through Time. Spec. Pap. Palaeontol.*, 12: 175-187.
- BATTAIL, B., 1980. Problèmes de corrélation du Trias continental russe avec le Trias continental gondwanien. *Mém. Soc. Géol. France*, 139: 11-14.
- BAUR, M. E. and R. R. FRIEDL. 1980. Application of size-metabolism allometry to therapsids and dinosaurs. In R. D. K. Thomas and E. C. Olson (eds.), *A Cold Look at the Warm-Blooded Dinosaurs*, p. 253-286. Westview Press, Boulder.
- BENTON, M. J. 1977. *The Elgin Reptiles*. The Moray Society, Elgin.
- . 1979a. Ecological succession among Late Palaeozoic and Mesozoic tetrapods. *Palaeogeog., Palaeoclimatol., Palaeoecol.*, 26: 127-150.
- . 1979b. Ectothermy and the success of dinosaurs. *Evolution*, 33: 983-997.
- . 1981. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and rela-

- tionships. Ph.D. Thesis, Univ. Newcastle-upon-Tyne.
- BONAPARTE, J. F. 1972. Annotated list of the South American Triassic tetrapods. In S. H. Haughton (ed.), *Proc. Pap. 2nd Gondwana Symp. (Pretoria)*, 1970, p. 665-682. Scientia, Pretoria.
- . 1975. Nuevos materiales de *Lagosuchus talampayensis* Romer (Thecodontia-Pseudosuchia) y su significado en el origen de los Saurischia. *Acta Geol. Lilloana*, 13: 5-90.
- . 1978. El Mesozoico de América del Sur y sus Tetrapodos. *Opera Lilloana*, 26: 1-596.
- BRINK, A. S. 1956. Speculations on some advanced mammalian characteristics in the higher mammal-like reptiles. *Palaeontol. Afr.*, 4: 77-97.
- . 1963. Two cynodonts from the N'tawere Formation in the Luangwa Valley of Northern Rhodesia. *Palaeontol. Afr.*, 8: 77-96.
- BURCKHARDT, R. 1900. On *Hyperodapedon gordonii*. *Geol. Mag.* (4) 7: 486-492, 529-535.
- CARROLL, R. L. 1977. The origin of lizards. *Linn. Soc. Symp. Ser.*, 4: 359-396.
- CASE, E. C. 1932. A collection of stegocephalians from Scurry County, Texas. *Contr. Mus. Palaeontol. Univ. Michigan*, 4: 1-56.
- CHARIG, A. J. 1971. Faunal provinces on land: evidence based on the distribution of fossil tetrapods, with especial reference to the reptiles of the Permian and Mesozoic. In F. A. Middlemiss, P. F. Rawson, and G. Newall (eds.), *Faunal Provinces in Space and Time. Geol. J. Spec. Iss.*, 4: 111-128.
- . 1972. The evolution of the archosaur pelvis and hind-limb: an explanation in functional terms. In K. A. Joysey and T. S. Kemp (eds.), *Studies in Vertebrate Evolution*, p. 121-155. Oliver & Boyd, Edinburgh.
- . 1979. *A New Look at the Dinosaurs*. Heinemann, London.
- . 1980. Differentiation of lineages among Mesozoic tetrapods. *Mém. Soc. Géol. France*, 139: 207-210.
- CHARIG, A. J., and H.-D. SUES. 1976. Proterosuchia. In O. Kuhn (ed.), *Handbuch der Paläoherpetologie*, Vol. 13, p. 11-39. Gustav Fischer, Stuttgart.
- CHATTERJEE, S. 1974. A rhynchosaur from the Upper Triassic Maleri Formation of India. *Phil. Trans. R. Soc. Lond.*, B, 267: 209-261.
- . 1980. The evolution of rhynchosaurs. *Mém. Soc. Géol. France*, 139: 57-65.
- CHATTERJEE, S., and T. R. CHOWDHURY. 1974. Triassic Gondwana vertebrates from India. *Indian J. Earth Sci.*, 1: 96-112.
- CHEMNIN, S. 1974. Capitosaurid amphibians from the Upper Luangwa Valley, Zambia. *Palaeontol. Afr.*, 17: 33-55.
- . 1977. A new brachyopid, *Batrachosuchus concordii* sp. nov., from the Upper Luangwa Valley, Zambia, with a redescription of *Batrachosuchus browni* Broom, 1903. *Palaeontol. Afr.*, 20: 87-109.
- CHOWDHURY, T. R. 1970. Two new dicynodonts from the Yerrapalli Formation of central India. *Palaeontology*, 13: 132-144.
- COLBERT, E. H. 1947. Studies of the phytosaurs *Machaeropsophus* and *Rutiodon*. *Bull. Am. Mus. Nat. Hist.*, 88: 53-96.
- . 1948. Triassic life in the south-western United States. *Trans. N. Y. Acad. Sci.*, (2) 10: 229-235.
- . 1966. *The Age of Reptiles*. W. W. Norton, New York.
- . 1970. Fossils of the Connecticut Valley; the age of dinosaurs begins. *State Geol. Nat. Hist. Surv. Conn., Bull.*, 96: 1-32.
- . 1971. Tetrapods and continents. *Q. Rev. Biol.*, 46: 250-269.
- . 1972a. *Lystrorhynchus* and Gondwanaland. *Evol. Biol.*, 6: 157-177.
- . 1972b. Vertebrates from the Chinle Formation. *Bull. Mus. N. Ariz.*, 47: 1-11.
- . 1973. Continental drift and the distributions of fossil reptiles. In D. H. Tarling and S. K. Runcorn (eds.), *Implications of Continental Drift for the Earth Sciences*, p. 395-412. Academic Press, London.
- . 1974a. The Triassic paleontology of Ghost Ranch. *New Mexico Geol. Soc. Guidebook, 25th Field Conf.*, 175-178.
- . 1974b. *Lystrorhynchus* from Antarctica. *Am. Mus. Novitates*, 2535: 1-44.
- . 1975. Early Triassic tetrapods and Gondwanaland. *Mém. Mus. Nat. Hist. Nat.*, A, 88: 202-215.
- COLBERT, E. H., and J. W. COSGRIFF. 1974. Labyrinthodont amphibians from Antarctica. *Am. Mus. Novitates*, 2552: 1-30.
- COLBERT, E. H., and J. W. KITCHING. 1975. The Triassic reptile *Procolophon* in Antarctica. *Am. Mus. Novitates*, 2566: 1-24.
- , and —. 1977. Triassic cynodont reptiles from Antarctica. *Am. Mus. Novitates*, 2611: 1-29.
- , and —. 1981. Scaloposaurian reptiles from the Triassic of Antarctica. *Am. Mus. Novitates*, 2709: 1-22.
- COOPER, M. R. 1982. A mid-Permian to earliest Jurassic tetrapod biostratigraphy and its significance. *Arnoldia Zimbabwe*, 9: 77-103.
- COX, C. B. 1964. On the palate, dentition, and classification of the fossil reptile *Endothiodon* and related genera. *Am. Mus. Novitates*, 2171: 1-25.
- . 1965. New Triassic dicynodonts from South

- America, their origins and relationships. *Phil. Trans. R. Soc. Lond.*, B, 248: 457-516.
- . 1967. Changes in terrestrial vertebrate faunas during the Mesozoic. In W. B. Harland et al. (eds.), *The Fossil Record*, p. 77-89. Geol. Soc., London.
- . 1968. The Chañares (Argentina) Triassic reptile fauna. IV. The dicynodont fauna. *Breviora*, 295: 1-27.
- . 1969. The problematic Permian reptile *Eumotatorius*. *Bull. Br. Mus. Nat. Hist. (Geol.)*, 18: 167-196.
- . 1972. The pectoral region and habits of a new digging dicynodont. In K. A. Joysey and T. S. Kemp (eds.), *Studies in Vertebrate Evolution*, p. 173-189. Oliver & Boyd, Edinburgh.
- . 1973a. Triassic tetrapods. In A. Hallam (ed.), *Atlas of Palaeobiogeography*, p. 213-233. Elsevier, Amsterdam.
- . 1973b. Gondwanaland Triassic stratigraphy. *An. Acad. Brasil. Ciênc.*, 45: 115-119.
- . 1976. Mysteries of early dinosaur evolution. *Nature, Lond.*, 264: 314.
- CROMPTON, A. W. 1955. On some Triassic cynodonts from Tanganyika. *Proc. Zool. Soc. Lond.*, 125: 617-669.
- . 1968. The enigma of the evolution of mammals. *Optima*, 18: 137-151.
- CRUICKSHANK, A. R. I. 1972. The proterosuchian thecodonts. In K. A. Joysey and T. S. Kemp (eds.), *Studies in Vertebrate Evolution*, p. 89-119. Oliver & Boyd, Edinburgh.
- DAWLEY, R. M., J. M. ZAWISKIE, and J. W. COSGRIFF. 1979. A rauisuchid thecodont from the Upper Triassic Popo Agie Formation of Wyoming. *J. Paleontol.*, 53: 1428-1431.
- DE JERSEY, N. J. 1975. Miospore zones in the lower Mesozoic of southeastern Queensland. In K. S. W. Campbell (ed.), *Gondwana Geology*, p. 159-172. Australia National Univ. Press, Canberra.
- ELDRIDGE, N., and S. J. GOULD. 1972. Punctuated equilibria: An alternative to phyletic gradualism. In T. J. M. Schopf (ed.), *Models in Paleobiology*, p. 82-115. Freeman, Cooper, San Francisco.
- FRAKES, L. A. 1979. *Climates throughout Geologic Time*. Elsevier, Amsterdam.
- GALTON, P. M. 1973. On the anatomy and relationships of *Efraasia diagnostica* (Huene) n. gen., a prosauropod dinosaur (Reptilia: Saurischia) from the Upper Triassic of Germany. *Paläontol. Z.*, 47: 229-255.
- . 1976. Prosauropod dinosaurs (Reptilia: Saurischia) of North America. *Postilla*, 169: 1-98.
- . 1977. On *Staurikosaurus pricei*, an early saurischian dinosaur from the Triassic of Brazil, with notes on the Herrerasauridae and Poposauridae. *Paläontol. Z.*, 51: 234-245.
- GALTON, P. M., and M. A. CLIVER. 1976. *Anchisaurus capensis* (Broom) and a revision of the Anchisauridae (Reptilia, Saurischia). *Ann. S. Afr. Mus.*, 69: 121-159.
- GOW, C. E. 1975. The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. *Palaeontol. Afr.*, 18: 89-131.
- . 1977. *Owenetta* in perspective. *Palaeontol. Afr.*, 20: 115-118.
- GRINE, F. E., and B. D. HAHN. 1978. Allometric growth in the Diademodontinae (Reptilia: Therapsida): A preliminary report. *Palaeontol. Afr.*, 21: 161-166.
- HALSTEAD, L. B. 1975. *The Evolution and Ecology of the Dinosaurs*. Peter Lowe, London.
- HAUBOLD, H. 1971. Ichnia amphibiorum et reptiliorum fossilium. In O. Kuhn (ed.), *Handbuch der Paläoherpetologie*, Vol. 18, p. 1-124. Gustav Fischer, Stuttgart.
- HAUGHTON, S. H. 1924. The fauna and stratigraphy of the Stormberg Series. *Ann. S. Afr. Mus.*, 12: 323-495.
- HOTTON, N., III. 1980. An alternative to dinosaur endothermy: the happy wanderers. In R. D. K. Thomas and E. C. Olson (eds.), *A Cold Look at the Warm-Blooded Dinosaurs*, p. 311-350. Westview Press, Boulder.
- HUENE, F., VON. 1908. Die Dinosaurier der europäischen Triasformation mit Berücksichtigung der aussereuropäischen Vorkommnisse. *Geol. Paläontol. Abh., Suppl.*, 1: 1-419.
- . 1926. Notes on the age of the continental Triassic beds in North America, with remarks on some fossil vertebrates. *Proc. U. S. Natl. Mus.*, 69 (18): 1-10.
- . 1932. Die fossile Reptil-ordnung Saurischia, ihre Entwicklung und Geschichte. *Monogr. Geol. Paläontol.*, 4: 1-361.
- . 1939. Die Lebensweise der Rhynchosauriden. *Paläontol. Z.*, 21: 232-238.
- . 1940. The tetrapod fauna of the Upper Triassic Maleri beds. *Palaeontol. Indica*, 32: 1-42.
- . 1942a. *Die fossilen Reptilien des südamerikanischen Gondwanalandes*. C. H. Beck, München (1935-1942).
- . 1942b. Die Anomodontier der Ruhuhu Gebietes in der Tübinger Sammlung. *Palaeontographica*, A, 94: 154-184.
- . 1942c. Die Fauna der Panchet-Schichten in Bengalen. *Zentralbl. Miner. Geol. Paläontol.*, 1942 (B): 354-360.
- . 1950. Die Theriodontier des ostafrikanischen Ruhuhu-Gebietes in der Tübinger Sammlung. *N. Jahrb. Geol. Paläontol. Abh.*, 92: 47-136.
- . 1959. Saurians in China and their relations.

- Vertebr. Palasiat.*, 3: 119-123.
- HUGHES, N. F. 1976. *Palaeobiology of Angiosperm Origins*. Cambridge Univ. Press, Cambridge.
- KEMP, T. S. 1980. Aspects of the structure and functional anatomy of the Middle Triassic cynodont *Luangwa*. *J. Zool.*, Lond., 191: 193-239.
- KEYSER, A. W., and R. M. H. SMITH. 1979. Vertebrate biozonation of the Beaufort Group with special reference to the Western Karoo Basin. *Ann. Geol. Surv. S. Afr.*, 12: 1-35.
- KITCHING, J. W. 1977. The distribution of the Karoo vertebrate fauna. *Mem. Bernard Price Inst. Palaeontol. Res.*, 1: 1-131.
- . 1978. The stratigraphic distribution and occurrence of South African fossil Amphibia in the Beaufort Beds. *Palaeontol. Afr.*, 21: 101-112.
- KREBS, B. 1976. Pseudosuchia. In O. Kuhn (ed.), *Handbuch der Paläoherpétologie*, Vol. 13, p. 40-98. Gustav Fischer, Stuttgart.
- KREMP, G. O. W. 1977. The positions and climatic changes of Pangaea and five southeast Asian plates during Permian and Triassic times. *Paleo-databanks*, 7: 1-21.
- KUTTY, T. S. 1971. Two faunal associations from the Maleri Formation of the Pranhita-Godavari Valley. *J. Geol. Soc. India*, 12: 63-67.
- KUTTY, T. S., and T. R. CHOWDHURY. 1972. The Gondwana sequence of the Pranhita-Godavari Valley, India, and its vertebrate faunas. In S. M. Haughton (ed.), *Proc. Pap. 2nd Gondwana Symp. (Pretoria, 1970)*, p. 303-308. Scientia, Pretoria.
- MARSHALL, L. G. 1981. The great American interchange—an invasion-induced crisis for South American mammals. In M. H. Nitecki (ed.), *Biotic Crises in Ecological and Evolutionary Time*, p. 133-229. Academic Press, New York.
- McNAB, B. K. 1978. The evolution of endothermy in the phylogeny of mammals. *Am. Nat.*, 112: 1-21.
- MILLER, C. N. 1977. Mesozoic conifers. *Bot. Rev.*, 43: 217-280.
- MOODY, R. 1977. *A Natural History of the Dinosaurs*. Hamlyn, London.
- NEWELL, N. D. 1967. Revolutions in the history of life. *Geol. Soc. Am. Spec. Pap.*, 89: 63-91.
- OLSEN, P. E., and P. M. GALTON. 1977. Triassic-Jurassic tetrapod extinctions: are they real? *Science*, 197: 983-986.
- OLSON, E. C. 1952. The evolution of a Permian vertebrate chronofauna. *Evolution*, 6: 181-196.
- . 1971. *Vertebrate Paleozoology*. Wiley-Interscience, New York.
- OSTROM, J. H. 1969. Terrestrial vertebrates as indicators of Mesozoic climates. *Proc. N. Am. Paleontol. Conv.*, D: 347-376.
- RAATH, M. A. 1969. A new coelurosaurian dinosaur from the Forest Sandstone of Rhodesia. *Arnoldia*, 4 (28): 1-25.
- . 1980. The theropod dinosaur *Syntarsus* (Saurischia: Podokesauridae) discovered in South Africa. *S. Afr. J. Sci.*, 76: 375-376.
- RETAILLACK, G. J. 1977. Reconstructing Triassic vegetation of eastern Australasia; a new approach for the biostratigraphy of Gondwanaland. *Alcheringa*, 1: 247-277.
- ROBINSON, P. L. 1958. Some new vertebrate fossils from the Panchet Series of West Bengal. *Nature, Lond.*, 182: 1722-1723.
- . 1971. A problem of faunal replacement on Permo-Triassic continents. *Palaeontology*, 14: 131-153.
- ROMER, A. S. 1960. Explosive evolution. *Zool. Jahrb.*, 88: 79-90.
- . 1963. La evolución explosiva de los rincosaurios del Triasico. *Rev. Mus. Argent. Cienc. Nat., Cienc. Zool.*, 8: 1-14.
- . 1966. *Vertebrate Paleontology*. Univ. Chicago Press, Chicago.
- . 1970. The Triassic faunal succession and the Gondwanaland problem. In *Gondwana Stratigraphy, IUGS Symp., Buenos Aires, 1967*, p. 375-400. UNESCO, Paris.
- . 1971. The Chañares (Argentina) Triassic reptile fauna. IX. The Chañares Formation. *Breviora*, 377: 1-8.
- . 1972. Tetrapod vertebrates and Gondwanaland. In S. H. Haughton (ed.), *Proc. Pap. 2nd Gondwana Symp. (Pretoria, 1970)*, p. 111-124. Scientia, Pretoria.
- . 1973. Middle Triassic tetrapod faunas of South America. *Act. IV Congr. Latin. Zool. (1970)*, 2: 1101-1117.
- . 1975. Intercontinental correlations of Triassic Gondwana vertebrate faunas. In K. S. W. Campbell (ed.), *Gondwana Geology*, p. 469-473. Australia National Univ. Press, Canberra.
- RUSSELL, D., P. BÉLAND, and J. S. MCINTOSH. 1980. Paleocology of the dinosaurs of Tendaguru (Tanzania). *Mém. Soc. Géol. France*, 139: 169-175.
- SAWIN, H. J. 1947. The pseudosuchian reptile *Typhothorax meadei*. *J. Paleontol.*, 21: 201-238.
- SCHMIDT, M. 1928. *Die Lebewelt unserer Trias*. Rau, Öhringen.
- SCHOPF, J. M., and R. A. ASKIN. 1980. Permian and Triassic floral biostratigraphic zones of southern land masses. In D. L. Dilcher and T. N. Taylor (eds.), *Biostratigraphy of Fossil Plants*, p. 119-152. Dowden, Hutchinson & Ross, Stroudsburg.
- SCHOPF, T. J. M. 1974. Permo-Triassic extinctions: relation to sea-floor spreading. *J. Geol.*, 82: 129-143.

- 1979. Evolving paleontological views on deterministic and stochastic approaches. *Paleobiology*, 5: 337-352.
- SILL, W. D. 1969. The tetrapod-bearing continental Triassic sediments of South America. *Am. J. Sci.*, 267: 805-821.
- 1971. Functional morphology of the rhycho-saur skull. *Forma Functio*, 4: 303-318.
- 1974. The anatomy of *Saurosuchus galilei* and the relationships of the rauisuchid thecodonts. *Bull. Mus. Comp. Zool.*, 146: 317-362.
- SIMMONS, D. J. 1965. The non-therapsid reptiles of the Lufeng Basin, Yunnan, China. *Fieldiana: Geol.*, 15: 1-93.
- SMITH, A. G., and J. C. BRIDEN. 1977. *Mesozoic and Cenozoic Paleogeographic Maps*. Cambridge Univ. Press, Cambridge.
- SOHN, I. G., and S. CHATTERJEE. 1979. Fresh-water ostracodes from late Triassic coprolite in central India. *J. Paleontol.*, 53: 578-586.
- SPOTILA, J. R., P. W. LOMMEN, G. S. BAKKEN, and D. M. GATES. 1973. A mathematical model for body temperatures of large reptiles: implications for dinosaur ecology. *Am. Nat.*, 107: 391-404.
- STANLEY, S. M. 1975. A theory of evolution above the species level. *Proc. Natl. Acad. Sci., USA*, 72: 646-650.
- TUCKER, M. E., and M. J. BENTON. In press. Triassic environments, climates, and reptile evolution. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*
- WALKER, A. D. 1961. Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus* and their allies. *Philos. Trans. R. Soc. Lond.*, B, 244: 103-204.
- 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Philos. Trans. R. Soc. Lond.*, 248: 53-134.
- 1969. The reptile fauna of the "Lower Keuper" Sandstone. *Geol. Mag.*, 106: 470-476.
- WELLES, S. P. 1947. Vertebrates from the Upper Moenkopi Formation of Northern Arizona. *Univ. California Publ., Bull. Dept. Geol. Sci.*, 27: 241-294.
- WESTPHAL, F. 1976. Phytosauria. In O. Kuhn (ed.), *Handbuch der Paläoherpetologie*, 13: 99-120. Gustav Fischer, Stuttgart.

Appendix

The composition by genera of late Permian and Triassic reptile faunas. See Figs. 2-7.

The faunas are arranged by geographic area and relative age. Numbers of specimens recorded (No.) for each genus are given. These are summarized by combining similar genera and the percentage composition of well-represented faunas is calculated. Genera are grouped into families and orders. Abbreviations: ANPH, Amphibia; BAUR, Daurianomorpha; COEL, Coelurosauria; CROC, Crocodylia; CYNO, Cynodontia; DIAD, Diapsidodontoidae; DICY, Dicyodontia; DINO, Dinoccephalia; END, Endothiodontia; EOS, Eosuchia; GORG, Gorgonopsia; IXC SED, Incertae sedis; MAMM, Mammalia; MESO, Mesosauria; MILL, Millerosauria; ORN, Ornithischia; PAR, Pareiasauria; PHOC, Protosphenia; PROS, Prosauroptera; RHA, Rhynchosauria; SCAL, Scalopsauria; SQUAM, Squamata; THER, Therodontia; THER, Theroccephalia; TRI, Triphosouria; TRIT, Tritylodontidae; YOLV, Younginidae. The taxonomic positions of the major groups may be found in Table 1.

SOUTH AFRICA

TAPINOCEPHALUS ZONE

(Tapinocephalus Assemblage Zone - Pristerognathus/Dicroidon Assemblage Zone) Karoo Basin, South Africa
 Figures based on Cox (1969) and Kitching (1977, 1978, pers. comm.).

	No.		No.
AMPH	Rhinesuchus 22	Riebeckosaurus	1
PAR	Bradyosaurus 72	Tapinocephalus	14
	Embrithosaurus 8	Keratonecephalus	8
IXC SED	Eumotosaurus 11	Phososaurus	6
MILL	Elliotemithia 1	Mormosaurus	3
	Provia 1	DICY Dicroidon	c. 400
IXC SED	Anningia 1	GORG Aelurosaurus	5
DIRD	Anteosaurus 40	Arctognathus	1
	Paranteosaurus 1	Bronnosaurus	1
	Jonkeria 35	Koarcrops	4
	Tilanosuchus 44	Galesuchus	2
	Struthiocephalus 28	Gorgonops	6
	Struthiocephaloides 5	Nyctaeognathus	1
	Struthionops 1	Hipposaurus	3
	Taurocephalus 1	THER Pristerognathus	84
	Nosclips 17	Scymnosaurus	25
	Delphinocephalus 5	Alopecodon	10
	Criciocephalus 4	Lycosuchus	0
	Avenantia 1	SCAL Ictiocephalus	5

SUMMARY

	No.	%
PAR	Bradyosaurus 80	10
IXC SED	Eumotosaurus 11	1
DINO	Anteosaurus, Jonkeria 76	9
	Titanosuchus 44	5
	Struthiocephalus, Nosclips, Tapinocephalus 89	10
DICY	Dicroidon c. 400	47
GORG	Aelurosaurus, Gorgonops, etc. 25	3
THER	Pristerognathus 84	10
	Scymnosaurus, etc. 41	5
SCAL	Ictiocephalus 5	0
	853	

CISTECEPHALUS ZONE

(Troglodonta microloema Assemblage Zone - Anticephalodon Assemblage Zone) Karoo Basin, South Africa
 Figures based on Cox (1964) and Kitching (1977, 1978, pers. comm.).

	No.		No.
AMPH	Rhinesuchus 20	Aelurosaurus	10
PAR	Pareiasaurus 21	Arctops	9
	Antiodon 4	Arctognathus	5
MESO	Notosuchus 1	Cerdocolus	1
YOLV	Galosphyrus 1	Cynosaurus	15
	Belcosaurus 1	Gorgonops	13
END	Endothiodon 36	Lycanops	14
DICY	Brachyrhiniasuchus 5	Scythognathus	4
	Erydops 14	Seylacops	4
	Pekerydops 15	Clelandina	2
	Pristirodon 20	Dinogorgon	3
	Tropidostoma 40	Prorubidgea	1
	Cistecephalus 435	Rubidgea	2
	Dicroidon 12	Lemnosaurus	2
	Dicynodon 82	Lycocodon	3
	Kingoria 4	THER Eucatherapsia	2
	Oudenodon 190	SCAL Holmeseria	4
	Rhachiocephalus 26	Ictidosuchoides	22
	Anticephalodon 75	Petracynodon	11
GORG	Aelurosaurus		7

SUMMARY

Note: Kitching (1977) does not enumerate all specimens of the extremely abundant dicynodonts. Numbers of indeterminate specimens (indet.) mentioned by him are added to the appropriate groups, and a further adjustment is made in order to bring the percentages close to those given by Keyser and Smith (1979).

	No.	indet.	total %	
PAR	Pareiasaurus	25	6	31
END	Endothiodon	36		36
DICY	Erydops, Pristirodon, Dicroidon	66	+597 (+2000)	2853
	Cistecephalus	435		435
	Tropidostoma, Oudenodon	230	+306 (+ 150)	686
	Rhachiocephalus, Anticephalodon	101	+ 87 (+ 150)	318
GORG	Lycanops, Gorgonops, Cynosaurus	93	+ 74	167
THER + SCAL		39		39
				4375

DAPTOCEPHALUS ZONE

(Dicynodon lacerticeps Assemblage Zone) Karoo Basin, S Africa
 Figures based on Gow (1975, 1977) and Kitching (1977, 1978, pers. comm.).

	No.		No.
AMPH	Lydekkerina 95	Arctognathus	4
	Uranocentrodon 6	Arctops	2
	Rhinesuchus 14	Cynosaurus	21
PAR	Pareiasaurus 15	Ictiocephalus	2
	Antiodon 2	Lycanops	5
PROS	Owenetta 7	Paragalierhinus	1
	Sponyllolestes 1	Scylacosuchus	72
MILL	Millerella 17	Bronniccephalus	2
	Millerosauria 1	Clelandina	1
	Milleropsis 8	Dinogorgon	2
YOLV	Youngina 15	Gorgonathus	22
	Palaeagama 1	Lycosaurus	5
	Uranosternon 1	Prorubidgea	11
DICY	Pekerydops 75	Rubidgea	9
	"Daptocephalus" 64	Sycosaurus	1
	Dicynodon 2150	Rubidgeia	2
	Dicroidon 7	Ictidobrinus	1
	Dianomodon 4	THER Meschorhinus	19
	Kingoria 72	Whaitesia	54
	Oudenodon 73	SCAL Ictidosuchops	23
	Propeltamodon 2	Tetracynodon	10
	Petersonodus 15	CYNOS	11
GORG	Aelurosaurus 2	Paratriloxodon	72
	Cynosaurus 21	Procyonosuchus	35

SUMMARY

Note: Kitching (1977) does not enumerate all specimens of the extremely abundant dicynodonts. Numbers of indeterminate specimens (indet.) mentioned by him are added to the appropriate groups, and a further adjustment is made in order to bring the percentages close to those given by Keyser and Smith (1979).

	No.	indet.	total %	
PAR	Pareiasaurus	17	+ 2	19
DICY	Dicroidon, Pekerydops, etc.	5	+600	605
	Oudenodon, etc.	91	+100	191
	Dianomodon, Dicynodon, "Daptocephalus"	220	+100	320
GORG	Cynosaurus, Prorubidgea, etc.	80	+ 30	110
THER	Whaitesia	73	+ 17	90
SCAL	Ictidosuchops	33		33
CYNOS	Procyonosuchus	38		38
				1406

LYSTROSOSAURUS ZONE

(Lystrosaurus Assemblage Zone) Karoo Basin, South Africa
 Figures from Anderson and Anderson (1970) and Kitching (1977, 1978, pers. comm.).

	No.		No.
AMPH	Rhytidosteus 10	Kestrosaurus	1
	Pneumatostega 2	PRUC Procolophon	100?
	Uranocentrodon 5	Owenetta	1
	Lydekkerina 180	EOS Prolacerta	7
	Broomulus 1	Palliguena	1
	Putterillia 3	Notosuchus	1
	Limoiketes 1	DICY Lystrosaurus	c. 1060
	Micropholis 30	Myosaurus	10

THEC	Moschorhinus	8	Thrinaxodon, etc.	c.70	
SCAL	Oliviera	2	Chasmatosaurus	1	
	Regisaurus	1	Proterosuchus	13	
	Scaloposaurus	10	JNC SED	Aenigmastropheus	1
CYN	Galesaurus	11			

SUMMARY

	No.	%
DICY Lytrosaurus	1000	90
THEC Moschorhinus	8	1
SCAL Scaloposaurus, etc.	13	1
CYN Thrinaxodon, etc.	81	7
THEC Chasmatosaurus	13	1
	1115	

CYNOGNATHUS ZONE

(-Kannemeyeria Assemblage Zone) Karoo Basin, South Africa
 Figures from Guine and Hahn (1978), Kitching (1977, 1978, pers. comm.) and Krebs (1976, p. 71).

	No.		No.
AMPH Parotosuchus	29	Kannemeyeria	21
Trematosuchus	3	Bauria	16
Microposaurus	2	Sesamodon	3
Batrachosuchus	7	CYN Trilobodon	2
PROC Tholegnathus	8	Cynognathus	18
EOS Palaeorodon	1	DIAD Diademodon	60
RHYN Mesosuchus	3	Trirachodon	10
		Hovesia	2
DICY Kombuaria	2	THEC Erythrosuchus	9
		Euparkeria	13

SUMMARY

	No.	%
DICY Kannemeyeria, etc.	23	16
BAUR Bauria, etc.	19	12
CYN Cynognathus	18	12
DIAD Diademodon	60	40
Trirachodon	10	6
THEC Erythrosuchus	9	6
Euparkeria	13	8
	152	

ELLIOT FORMATION

(-Red Beds) Karoo Basin, South Africa
 Figures based on Anderson and Anderson (1970), Galton and Cluver (1976), Houghton (1924), Kitching (pers. comm.), and Haath (1980).

	No.		No.
AMPH Capitosaurus	2	Heterodontosaurus	2
CROC Erythrochampsia	1	Lycorhinus	1
Orthosuchus	1	Lanaosaurus	1
Sphenosuchus	1	Abrictosaurus	1
COEL Syntarsus	9	CYN Trithelodon	1
PROS Euskelosaurus, etc.	10	Pachygenelus	6
Plateosaurus	3	TRIT Tritylodon	c.60
Thecodontosaurus	5	MANN Erythrotherium	1
Massospondylus	c.20	Megazostrodon	1
ORN Fabrosaurus	2		

SUMMARY

	No.	%
CROC Erythrochampsia undescr.	6	5
COEL Syntarsus	9	7
PROS Euskelosaurus, etc.	13	10
Massospondylus, etc.	25	19
ORN Fabrosaurus, etc.	8	6
CYN Pachygenelus, etc.	7	5
TRIT Tritylodon	60	46
MANN Megazostrodon, etc.	2	2
	130	

CLARENS FORMATION

(-Cave Sandstone) Karoo Basin, South Africa
 Figures based on Anderson and Anderson (1970), Galton and Cluver (1976), Houghton (1924) and Kitching (pers. comm.). The vertebrates occur in the lower part of the formation. The total fauna is too small (n=27) for the calculation of percentages.

	No.		No.
CROC Notochampsia	1	Massospondylus	6
Orthosuchus	1	Gryponyx	1?
Pedeticosaurus	1	ORN Heterodontosaurus	6
COEL Syntarsus	1	CYN Pachygenelus	3
PROS Anchisaurus	1	TRIT Tritylodon	1
Aristosaurus	3	ICTID Diarthrogathus	2

ZAMBIA

N'TAWERE FORMATION

(Luangwa Valley, Zambia)

Figures from Brink (1963), Churnin (1974, 1977), Cox (1972), Cruickshank (pers. comm.) and Kitching (pers. comm.). There are two faunas (lower and upper), but both are too small (n=4, 7) for the calculation of percentages.

	No.		No.
AMPH Batrachosuchus	1	AMPH Parotosaurus	2
Labyrinthodonts	7	THEC undescribed	?
DICY Dolichuramus	1	DICY ?Sangusaurus	1
Kannemeyeria	1	?Zambiasaurus	2
CYN Diademodon	1	CYN Luangwa	2

TANZANIA

MANDA FORMATION

(Ruhuhu region, Tanzania)

Figures from Anderson and Anderson (1970), Crompton (1956), Cruickshank (pers. comm.), Huene (1939, 1942b, 1950) and Krebs (1976).

	No.		No.
AMPH Parotosaurus	3	undescribed	9
metoposaur	1	CYN Aleodon	1
RHYN Stenaulorhynchus	c.55	Theroposodon	1
THEC Parringtonia	1	DIAD Cricodon	2
Staginosuchus	4	Scalenodon	c.20
undescribed	12	undescribed	8
DICY Tetragonias	10		

SUMMARY

	No.	%
RHYN Stenaulorhynchus	55	40
THEC Staginosuchus, etc.	17	14
DICY Tetragonias	19	15
CYN Theroposodon, etc.	2	2
DIAD Scalenodon, etc.	30	24
	123	

ZIMBABWE

FOREST SANDSTONE FORMATION

(Zaobuzi Valley, Zimbabwe)

Figures from Kitching (pers. comm.) and Raath (1969).

	No.	%
COEL Syntarsus	30	42
PROS Massospondylus	40	56
Euskelosaurus	2	2
	72	

ANTARCTICA

FREMOW FORMATION

(Reardmore Glacier, Antarctica)

Figures from Colbert (1972a, 1974b, pers. comm.), Colbert and Cosgriff (1974) and Colbert and Kitching (1975, 1977, 1981).

	No.		No.
AMPH Austrobrachyops	2	DICY Lytrosaurus	70+
Cryptobatrachus	9	Nyasaurus	3
Massospondyl	1	SCAL Ericoalacerta	2
EOS Prolacerta	7	Pedaeosaurus	1
PROC Procolophon	11	Rhigosaurus	1
THEC undescribed	73	CYN Thrinaxodon	14

SUMMARY

	No.	%
THEC undescribed	37	2
DICY Lytrosaurus, etc. (x100)	173	89
SCAL Ericoalacerta, etc.	4	2
CYN Thrinaxodon	14	7
	194	

ARGENTINA

PUESTO VIEJO FORMATION

(Puesto Viejo Basin, Argentina)

Figures from Bonaparte (1972, 1978, pers. comm.). The total fauna is too small (n=10) for the calculation of percentages.

	No.		No.
DICY Kannemeyeria	4	DIAD Pascualignathus	5
CYN cynognathus	1		

RIO MENDOZA FORMATION

(Cachuta Basin, Argentina)

Figures from Bonaparte (1972, pers. comm.). The total fauna is too small (n=45) for the calculation of percentages.

	No.		No.
DICY Vincoeria	5	DIAD Andes-cynodon	c.40
CYN Crotopodon	1	Ruscotodon	1

CACHEUTA FORMATION

(Cachuta Basin, Argentina)

Figures from Bonaparte (pers. comm.). The total fauna is too small (n=20) for the calculation of percentages.

	No.		No.
AMPH Pelorocephalus	c.19	THEC Cuyosuchus	1

CHAÑARES FORMATION

(Ichigualasto Basin, Argentina)

Figures from Bonaparte (1975, pers. comm.), Cox (1968) and Romer (1971, 1972).

	No.		No.
THEC Chanaresuchus	c.15	DICY Chanaria	1
		Dinodontosaurus	10
		CYN Prohansagathus	c.5
		Prolesodon	15
		DIAD Massetognathus	72
		Negagnomphodon	4
		Luperosuchus	1

SUMMARY

	No.	%
THEC Chanaresuchus, etc.	32	13
DICY Dinodontosaurus, etc.	11	5
CYN Prolesodon, etc.	30	8
DIAD Massetognathus, etc. (100, Bonaparte, pers. comm.)	176	74
	259	

ISCHIGUALASTO FORMATION

(Ichigualasto Basin, Argentina)

Figures from Bonaparte (1972, 1978, pers. comm.), Cox (1965), Krebs (1976), Romer (1972, 1975) and Sill (1971).

	No.		No.
AMPH Pelorocephalus	1	COEL/ Herrerasaurus	c.5
		PROS Ichisaurus	2
RHYX Scaphonyx	50	ORN Pisanosaurus	1
THEC Proterochamps	5	DICY Ichigualastia	5
		CYN Chiniquodon	3
		DIAD Exaeretodon	c.40
		Proexaeretodon	1
		Ichignathus	1

SUMMARY

	No.	%
RHYX Scaphonyx	50	39
THEC Aetosauroides, etc.	22	17
COEL/PROS Herrerasaurus, etc.	7	5
ORN Pisanosaurus	1	1
DICY Ichigualastia	5	4
CYN Chiniquodon	3	2
DIAD Exaeretodon, etc.	42	32
	130	

LOS COLORADOS FORMATION

(Ichigualasto Basin, Argentina)

Figures from Bonaparte (1972, 1978, pers. comm.). All genera are from the upper beds, except Jachaleria. The total fauna is too small (n=37) for the calculation of percentages.

	No.		No.
THEC Neoaetosauroides	3	PROS Riojasaurus	c.20
		Coloradia	1
		DICY Jachaleria	1
		CYN Chalmira	1
		TRIT cf. Tritylodon	2
COEL indet.	1		

EL TRANQUILLO FORMATION

(El Tranquillo Basin, Argentina)

Figures from Bonaparte (pers. comm.). The total fauna is too small (n=12) for the calculation of percentages.

	No.		No.
PROS Plateosaurus	c.5	Mussasaurus (young)	7

BRAZIL

SANTA MARIA FORMATION

(Parana Basin, Brazil)

Figures from Bonaparte (pers. comm.), Cox (1965), Galton (1977), Huene (1942a), Krebs (1976) and Romer (1973).

	No.		No.
PROS Gandelaria	1	DICY Barysma	1
RHYX Scaphonyx	150	Dinodontosaurus	26
THEC Nopletosuchus	1	Stahleckeria	6
		CYN Chiniquodon	3
		Belesodon	4
		Therioherpeton	1
		Massetognathus	1
		Traversodon	9
COEL/PROS Staurikosaurus	1		

SUMMARY

	No.	%
PROS Gandelaria	1	0
RHYX Scaphonyx	150	68
THEC Nopletosuchus, etc.	16	7
CROC Cerritosaurus, etc.	2	1
COEL/PROS Staurikosaurus	1	0
DICY Dinodontosaurus, etc.	33	15
CYN Belesodon, etc.	8	4
DIAD Traversodon, etc.	10	5
	220	

INDIA

PANCHET FORMATION

(Damodar Valley, India)

Figures from Anderson and Anderson (1970), Colbert (1975), Huene (1942c) and Robinson (1958). The total fauna is too small (n=34) for the calculation of percentages.

	No.		No.
AMPH Goniatylops	3	PROS undescribed	1
		THEC Chasmatosaurus	4
		DICY Lytosaurus	c.24

YERRAPALLI FORMATION

(Pranhita-Godavari Valley, India)

Figures from Chatterjee (1980), Chowdhury (1970), and Kutty and Chowdhury (1972). The total fauna is too small (n=13) for the calculation of percentages.

	No.		No.
AMPH Parotosaurus	1	stagonolepid	21
		brachyopid	1
RHYX Mesodapedon	2	Wadnosaurus	4
THEC erythrosuchid	21	DIAD tetradactyl	21
		rausuchid	

MALERI FORMATION

(Pranhita-Godavari Valley, India)

Figures from Chatterjee (1974, 1980, pers. comm.), Chatterjee and Chowdhury (1974), Huene (1940) and Kutty (1971).

	No.	%	
AMPH Metoposaurus	18	19	
EOS Malerisaurus	2	2	
RHYX Paradedon	55	57	
THEC Typothorax (?)	2	2	
		Parasuchus	14
		COEL podokesaur	2
		PROS archisaur	1
		DIAD Exaeretodon	2
			96

CHINA

LYSTROSOSAURUS ZONE EQUIVALENT

(Sinkiang, China)

Figures from Charig and Sues (1976) and Huene (1959). The data are not sufficient for the calculation of percentages.

	No.	DICY	Lystrosaurus	No.
PROC Santalsaurus	1			20+
THEC Proterosuchus	4			

LOWER LUFENG SERIES

(Yunnan, China)

Figures from Huene (1959) and Simmons (1965).

	No.		No.
SQAM Pulegia	1	PROS Lufengosaurus	c.100
THEC ?Pachysuchus	1	?Sinosauros	2
?Strigosuchus	1	ORN Tatisaurus	1
?Dibothrosuchus	1	TRIT Bienotherium	c.10
CROC ?Pistygnothus	1	Lufengia	1
?Microchampsia	1	MAHM Sinocodon	c.6
COEL Lukousaurus	2	Kozostrodon	1
indet.	3		

SUMMARY

	No.	%
?THEC Dibothrosuchus, etc.	3	2
CROC ?Microchampsia, etc.	2	1
COEL Lukousaurus, etc.	5	4
PROS Lufengosaurus, etc.	100	82
ORN Tatisaurus	1	1
TRIT Bienotherium, etc.	11	10
	122	

NORTH AMERICA

MOENKOPI FORMATION

(Arizona, USA)

Figures from Welles (1947). There are two faunas (lower, upper), but neither is large enough (n=1, 20+) for the calculation of percentages.

	No.	No.	
Lower Fauna (Mpatki Member)			
AMPH Stanocephalosaurus	1		
Upper Fauna (Holbrook Member)			
AMPH Hadrokkosaurus	c.14	TRIL Anisodontosaurus	1
Cycloptosaurus	3	THEC Arizonaosaurus	2
Rhadalognathus	1		
indet.	?		

POPO AGIE FORMATION

(Wyoming, USA)

Figures from Dawley et al. (1979) and Huene (1926).

	No.	est. %
AMPH Metoposaurus	?	40+
THEC Paleorhinus	?	
Angistorhinus	?	40+
?Rutiodon	1	
Poposaurus	2	5
Heptasuchus	1	5
DICY Placerias	2	10

DOCKUM FORMATION

(Texas, New Mexico, USA)

Figures from Case (1932), Colbert (pers. comm.), Sawin (1947), and Westphal (1976). The Dockum Formation is divided into a lower, middle and upper fauna, but detailed information on the composition of each is not readily available, and the figures are combined.

	No.	est. %
AMPH Metoposaurus	25+	35
TRIL Trilophosaurus	?	10
RBYN undescribed	4	2
THEC Desmatosuchus	5	2
Typothorax	15+	22
Paleorhinus	?	30
Angistorhinus	?	
Poposaurus	1	1

CHINLE FORMATION

(Arizona, USA)

Figures from Colbert (1947, 1948, 1972b, 1974a, pers. comm.). There is a lower and an upper fauna.

Lower fauna	No. est. %	Upper fauna	No.	est. %	
AMPH Metoposaurus	?	40	AMPH Metoposaurus	?	25
THEC Typothorax	c.10	?	THEC Typothorax	?	10
Desmatosuchus	?	10	Phytosaurus	?	15
Rutiodon	?	30	COEL Coelophysus	100+	50
Phytosaurus	?				
Hesperosuchus	1	5			
DICY Placerias	c.45	15			

GLEN CANYON GROUP

(Arizona, USA)

Figures from Colbert (pers. comm.) and Galton (1976). The faunas are too small (n=8, c.20, 4) for the calculation of percentages.

	No.
CROC Proterosuchus	8

KAYENTA FORMATION

	No.
THEC cf. Desmatosuchus	c.2
ORN Scutelloosaurus	2
COEL? Dilophosaurus	2
TRIT cf. Tritylodon	10+

NAVAJO FORMATION

	No.
CROC Proterosuchus	1
PROS Ammosaurus	2
COEL Segisaurus	1

NEWARK GROUP (PORTLAND FORMATION)

(Atlantic States, USA)

Figures from Colbert (1970, pers. comm.) and Galton (1976). The fauna is too small (n=9) for the calculation of percentages.

	No.	No.	
PROC procnophorid	1	PROS Anchisaurus	2
THEC Stegosus	2	Ammosaurus	2
CROC Stegobosuchus	1	indet.	1

SCOTLAND

LOSSIEMOUTH FORMATION

(Biggar, NE Scotland)

Figures from Walker (1961, 1964, pers. comm.) and Benton (1977, 1981).

	No.	No.	
PROC Leptopteron	c.30	ORN Ornithosuchus	12
BUS Brachyphiodon	c.10	ERPE Erpetosuchus	23
RBYN Hyperodapedon	35	SELC Scleromochlus	7
THEC Stagonolepis	30	COEL Saltopus	1

	No.	%
RBYN Hyperodapedon	35	40
THEC Stagonolepis	30	35
ORN Ornithosuchus, etc.	21	24
COEL Saltopus	1	1
	87	

GERMANY

KNOLLENMERGEL

(Germany, France)

Figures from Huene (1908, 1932).

	No.	est. %
AMPH Cycloptosaurus	c.15	20
COEL Plagosaurus	4	5
PROS Plateosaurus	50+	60
Cresslyosaurus	10+	15