

The Relationships and Early Evolution of the Diapsida

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SYNOPSIS

Living reptiles fall into several natural groupings: turtles, crocodiles, lizards and snakes. The last three groups have, or their ancestors had in the past, two openings in the skull behind the eye – the diapsid condition – and fossil evidence strongly supports their association into the Subclass Diapsida. The diapsids arose 300 million years (My) ago and evolved as two major lineages during the Permo-Triassic (215–285 My ago): the Archosauromorpha [Pterosauria, Prolacertiformes, Archosauria, Rhynchosauria] and the Lepidosauromorpha [Younginiformes, *Sphenodon*, Squamata (early ‘lizards’, lizards, amphisbaenians, snakes)]. A new classification of these groups is presented here on the basis of a cladistic analysis. There was a succession of diapsid radiations in the Permo-Triassic, including some bizarre gliding and swimming forms. Ecologically, the thecodontians and rhynchosaurs were important in the middle and late Triassic when they partly took over major carnivore and herbivore niches from mammal-like reptiles. All these groups died out in the late Triassic (220 My ago) and the dinosaurs subsequently radiated opportunistically world-wide into all major terrestrial niches. The assumption of competition between mammal-like reptiles and various diapsid groups during the Triassic is not supported here.

INTRODUCTION

Reptiles with two temporal arches – the diapsid condition – have had a confused taxonomic history. Osborn (1903) coined the name Diapsida to include lizards, snakes, *Sphenodon*, crocodiles, dinosaurs, thecodontians and pterosaurs, as well as pelycosaur, procolophonids, ichthyosaurs and *Mesosaurus*. Williston (1925) removed the last four groups from the Subclass Diapsida, but also placed the lizards and snakes in his Subclass Parapsida with *Mesosaurus* and the ichthyosaurs. All of these forms have only an upper temporal opening, but Broom (1925) argued strongly that lizards and snakes were true diapsids that had lost the lower temporal bar. Since then, Romer (1933, 1956, 1966, 1971) has maintained the view that the diapsids really consist of two subclasses – the Lepidosauria (basal ‘eosaurians’, lizards, snakes, *Sphenodon*, rhynchosaurs) and the Archosauria (thecodontians, crocodiles, pterosaurs, dinosaurs), each of which probably had a separate origin.

New studies on early diapsid reptiles have shown that they probably all derived from a single ancestral stock, and that there was a series of adaptive radiations of diapsids during the Permo-Triassic (215–285 My ago). The initial radiations were of small terrestrial, aquatic and gliding forms that made little impact on a world dominated by the mammal-like reptiles. However, diapsids achieved larger size and greater abundance during a multiphase replacement of the mammal-like reptiles in the Triassic which culminated in the successful radiation of the dinosaurs.

In this paper, new work on the classification and evolution of early diapsids is reviewed. The application of a cladistic methodology to the classification of all well known early diapsids has produced a scheme of relationships already hinted at by several authors, but rather different from the standard notion (e.g. Romer, 1966). A consideration of the composition and stratigraphic position of the major Permo-Triassic reptile faunas has suggested an interpretation of the diapsid take-over different from the usual competitive models.

CLASSIFICATION OF THE DIAPSIDA

All reptiles from the Permo-Triassic that have been called "diapsid" at one time or another were considered and an attempt was made to include all but the most scrappy specimens in a review of their relationships. At first, it was expected that Romer's "archosaurs" and "lepidosaurs" (Romer, 1966) would not appear as distinct groups, but that the Subclass Diapsida would contain several major lineages radiating in the Permian (Benton, 1982). However, there is strong evidence for two lines that diverged in the mid- to late Permian – the Prolacertiformes (*Protorosaurus*, *Prolacerta*, etc.) and the Younginiformes (*Youngina*, tangasaurids). The Prolacertiformes show close relationships with the rhynchosaurs of the Triassic and with the archosaurs and pterosaurs. This assemblage is the Archosauromorpha (von Huene, 1946). The Younginiformes show close relationships with the "early lizards" of the Permian and Triassic, as well as with subsequent Squamata and Sphenodontidae. This assemblage is the Lepidosauromorpha (Gauthier, in press). The Archosauromorpha and Lepidosauromorpha share numerous derived characters, some of which were absent in the late Permian *Claudiosaurus* and the gliders *Weigeltia* and *Coelurosaururus*. Some archosauromorphs could not be confidently placed (*Notosuchus*, *Malerisaurus*, *Triophosaurus*); others could have been archosauromorphs or lepidosauromorphs (*Heleosaurus*, *Montjurosuchus*),

and some "lepidosaurs" could not be clearly placed at all (*Claraziidae*, *Champosauridae*, *Pleurosauridae*).

A cladistic methodology was used in this study. An attempt was made to determine shared derived characters between various genera or families as an indication of closest relationship. Closely related animals, of course, share numerous primitive characters, but these do not help to resolve taxonomic questions. This kind of analysis was possible since the lowest operational units (usually genera) are well defined because of the relative incompleteness of the record of fossil reptiles, and because many characters may be recorded.

Many problems typical of such taxonomic exercises were encountered: assessment of true homology of characters as opposed to parallelism or convergence; ancestral groups which display few derived characters; rapidly radiating stocks which contain many genera going in different directions and possessing few shared derived characters; highly modified groups that stand in isolation which may have lost numerous characters considered to be diagnostic of their large monophyletic group of relatives; and lack of key characters in poorly preserved fossil material. Several of the early diapsid taxa could not be placed confidently since they appeared to share derived characters with two or more separate groups – e.g. the Proterosuchidae – or because of the absence of critical characters in the fossils or descriptions – e.g. *Protorosaurus*, *Heleosaurus*, *Mesosuchus* and the "Paliguaniidae".

The results of the study are presented in the form of a cladogram (Fig. 1; full details to be published elsewhere), which is a tentative statement of relationships that is readily open to testing and modification by future work. The classification given below is based closely on the cladogram, but several conventions are used in order to avoid: the mechanical problems of a proliferation of new taxon and category names for all dichotomies; the stability problems of introducing new taxa, and particularly fossil taxa, to an established classification (or of revised opinions regarding relationships); and the problem of confusing other biologists with constantly changing and unfamiliar classifications. These conventions (sequencing, indented lists, plesions) have been discussed by Patterson & Rosen (1977), Eldredge & Cracraft (1980) and Wiley (1981). Extinct taxa are indicated by daggers (†). No new taxonomic names are introduced here, although some less familiar ones are reinstated. The names "Eosuchia", "Protorosauria" and "Rhynchocephalia" have no agreed meaning and are applied to variable assortments of unrelated forms. They are not used here.

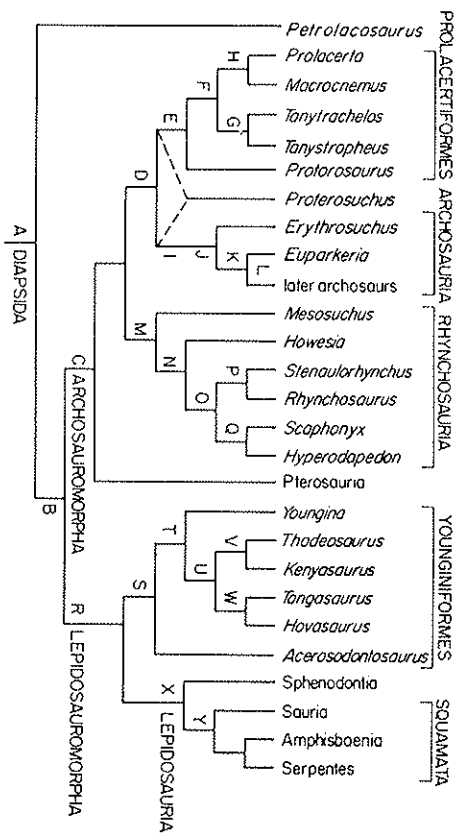


FIG. 1. The relationships of the Perno-Triassic diapsid reptiles. Shared derived characters at each dichotomy are summarized below (full details: Benton, in preparation).

- A. Diapsida. Superior temporal fenestra; shape of bones in temporal region; suborbital fenestra; shape of palate bones around fenestra; true Jacobson's organ; olfactory bulbs of brain on stalks; one or more nasal conchae; Huxley's foramen at end of extracolumella.
- B. Archosauromorpha + Lepidosauromorpha. Reduced lacrimal; ventromedial flanges on parietal; absence of "caniniform" maxillary teeth; reduced quadratojugal; quadrate exposed in lateral view; quadrate emarginated; stapes slender; reduction in pterygoid teeth; no parasphenoid teeth; retroarticular process; ulna lacks well developed olecranon; acetabulum rounded; femur sigmoidal and slender; distal articular surfaces on femur level; femur longer than humerus.
- C. Archosauromorpha. Premaxilla extends up behind naris; nares close to mid-line and elongate; quadratojugal mainly behind lower temporal fenestra; loss of tabulars; stapes rod-like and without foramen; vertebrae not notochordal; dorsal transverse processes project; cleithrum absent; no entepicondylar foramen; loss of perforating foramen in carpus; lateral tuber on calcaneum; complex concave-convex articulation between astragalus and calcaneum; fifth distal tarsal lost; fifth metatarsal hooked in one plane.
- D. Prolacertiformes + Archosauria. Long snout and narrow skull; nasals longer than frontals; post-temporal fenestrae small or absent; recurved teeth; parasphenoid/basisphenoid parietal plates in side wall of braincase; long thin tapering cervical ribs with anterior process.
- E. Prolacertiformes. Lower temporal bar incomplete; 7-12 elongate cervical vertebrae; cervical vertebrae have long low neural spines; short ischium.
- F. Prolacertidae + Tanystraphidae. Quadratojugal much reduced or absent; (?) partially streptostylic quadrate.
- G. Tanystraphidae. Very long neck with 12 cervical vertebrae; post-dorsal bones; fifth metatarsal very short.
- H. Prolacertidae. Squamosal has terratridate shape; choanae and bones of palate very long; mid-line gap in palate between pterygoids and long cultriform process of parasphenoid.
- I. Archosauria. Antorbital fenestra; orbit triangular; teeth laterally compressed; fourth rochanter.
- J. Archosauria (excluding *Proterochasius*). Skull is high; antorbital fenestra close to naris; loss of supratermporal; lateral mandibular fenestra; coronoid reduced or absent; scapula very tall

- and narrow; coracoid small and glenoid faces largely backwards; deltopectoral crest of humerus extends far down shaft; distal end of humerus reduced in width; hand is short; patris has strong anterior tuber; iliac blade has small anterior process; ischium has large postero-ventral process; tarsus contains only four elements.
- K. *Euparkeria* and later archosaurs. Antorbital fenestra large and lies in a depression; parietal foramen absent; otic notch well developed; posterior border of lower temporal fenestra is kinked forward; dentition thecodont; pelvis markedly three-rayed; hind-limbs brought in under body; rotation between astragalus and calcaneum; dermal armour.
- L. Later archosaurs. Postparietals absent; pterygoids meet medially; palatal teeth absent; presence of pleurosphenoid (?); presacral inter-centra absent.
- M. Rhynchosauria. Downturned premaxilla bearing acrodont teeth or no teeth; single median naris; fused parietals; three proximal tarsals.
- N. Rhynchosauroidae. Premaxilla beak-like and toothless; parietal foramen absent; teeth ankylothecondont; batteries of functional teeth on maxilla and dentary.
- O. Rhynchosauridae. Loss of supratermporal; interlocking groove and blade jaw apparatus; central large and united with astragalus.
- P. Rhynchosaurinae. Two grooves on maxilla; occipital condyle set well forward; single row of teeth on pterygoid.
- Q. Hyperodapedoninae. Skull broader than long; jugal large and ridged; single longitudinal groove on maxilla; no teeth on lingual side of maxilla; no teeth on pterygoid; lower jaw deep; dentary has only one or two rows of teeth; coracoid has no posterior process; humerus about as long as femur.
- R. Lepidosauromorpha. Post-frontal in border of upper temporal fossa; accessory inter-vertebral articulations; cervical centra short; dorsal ribs single-headed; co-ossification of paired sternal plates; specialized sternal rib connections.
- S. Younginiformes. Distinctive sutures on parietal for frontal and post-frontal; reduced rod-like quadratojugal below temporal fenestra; dorsal neural spines high and rectangular; entepicondyle of humerus well developed; lateral centrale loses contact with third distal carpal.
- T. Younginoidae. Short neck, 4-5 cervicals; (?) specialized inter-vertebral articulations; radius longer than shaft of ulna (Currie, 1982).
- U. Tangasauridae. Humerus as long as, or longer than, femur; scapula low and mainly ventral; coracoid as large as scapula; fifth distal tarsal not a discrete element (Currie, 1982).
- V. Kenyasaurine. 19-28 pairs of caudal ribs and transverse processes present, all of which taper distally (Currie, 1982).
- W. Tangasaurinae. Neural spines high; 9-12 pairs of caudal ribs; anterior caudal ribs expanded distally; haemal spines large and plate-like; presacral inter-centra do not ossify until animal is mature (Currie, 1982).
- X. Lepidosauria. Determinant growth; specialized articulating surfaces of long bones (bony epiphyses); specialized joint between ulna and ulnare; lacrimal reduced or absent; post-parietal and tabular absent; supratermporal course of notochord; median hypocentral occipital condyle; thyroid fenestra in pelvis; fusion of astragalus and calcaneum; loss of centrale; loss of distal tarsals 1 and 5; hooking of 5th metatarsal in two planes.
- Y. Squamata (living). Mid-line skull roof bones often fused; post-frontal and postorbital often fused; or one missing; pterygoids do not reach vomers; pterygoids do not meet in the mid-line; supratermporal situated deep between squamosal and parietal above quadrate; specialized articulation surface for dorsal wing of quadrate; squamosal reduced to slender bar or absent; no lower temporal bar; no quadratojugal; quadrate ramus of pterygoid reduced and no suture between quadrate and pterygoid; quadrate has tympanic conch; mesokinosis; fenestra rotunda; vidian canal; ossification of braincase anterior to otic capsule; pre-articular fused with articular; vertebrae usually procoelous; all ribs holocaphalous; dorsal intercentra seldom developed; hypapophyses on cervical vertebrae; no true sacral ribs; loss of entepicondylar foramen in humerus; fenestration of anterior margin of scapulo-coracoid (as well as some soft-part characters). Fossil 'squamates' show selections of these derived characters.

Classification of the Permo-Triassic Diapsids

- Subdivision Diapsida Osborn 1903
- plesion †*Petrolacosauridae* Peabody 1952 *Petrolacosaurus*
 - plesion †*Galesphyridae* Currie 1981 *Galesphyrus*
 - plesion †*Weigeltisauridae* Romer 1933 *Weigeltisaurus*, *Coelurosaurus*
 - plesion †*Claudiosauridae* Carroll 1981 *Claudiosaurus*
- Infradivision Neodiapsida nov.
- Neodiapsida, *inertae sedis*
 - †Family *Heleosauridae* Haughton 1924 *Heleosaurus*
 - †*Laerthius*
 - †Family *Kuehneosauridae* Romer 1966 *Kuehneosaurus*, *Kuehneosuchus*, *lanosaurus*
 - †Family *Monjurosuchidae* Endo 1940. *Monjurosuchus*
 - †Family *Thalattosauridae* Merriam 1904 *Astrophosaurus*, *Thalattosaurus*
- Cohort Archosauriformes Huene 1946
- Archosauriformes, *inertae sedis* †*Notosuchus*
 - plesion †*Pterosauria* Owen 1840 (Kaup 1834)
 - plesion †*Trilophosauridae* Gregory 1945 *Trilophosaurus*
 - plesion †*Rhynchosauria* Osborn 1903 (Gervais 1839)
- Suborder Mesosuchia Haughton 1924
- Family *Mesosuchidae* Haughton 1924 *Mesosuchus*
 - Suborder *Rhynchosauroida* Nopcsa 1928 (Gervais 1839)
 - Family *Howesidae* Watson 1917 *Howesia*
 - Family *Rhynchosauridae* Huxley 1887 (Cope 1870)
 - Subfamily *Rhynchosaurinae* Nopcsa 1923 *Senaulorhynchus*, *Rhynchosaurus*
- Subfamily *Hyperodapedontinae* Charterjee 1969 *Hyperodapedon*, *Scaphonyx*
- plesion †Proclacertiformes Camp 1945
- Proclacertiformes, *inertae sedis* ?*Cososaurus*, *Malerasaurus*
- Family *Protosauridae* Baur 1889 (Cope 1871) *Protosaurus*
 - Family *Proclacertidae* Parrington 1935 *Proclacerta*, *Macroceramus*, ?*Boreopriza*, ?*Kadimakara*
 - Family *Tanystrophiaeidae* Romer 1945 (Gervais 1839) *Tanystrophia*, *Tanystrochilus*
- Incertae sedis (Proclacertiformes or Archosauria)
- †Family *Proterosuchidae* Huene 1908 *Chamaesaurus*, *Proterosuchus*, *Chamaesuchus*, etc.
- Superorder Archosauria Cope 1869
- plesion †Thecodontia Owen 1859
- Suborder *Erythrosuchia* Goodrich 1930
- Family *Erythrosuchidae* Watson 1917 *Erythrosuchus*, *Vishkavia*, *Gargania*, *Shansisuchus*, etc.
- Suborder *Pseudosuchia* Zittel 1887–1890
- Family *Euparkeriidae* Huene 1920 *Euparkeria*
 - (Suborder *Parasuchia* Huxley 1875)
 - (?Suborder *Ornithosuchia* Bonaparte 1971)
 - (?Suborder *Lagosuchia* Charterjee 1982)
 - (plesion †*Saurischia* Seeley 1888)

- (plesion †*Ornithischia* Seeley 1888)
 - (Order *Crocodylia* Gemelin 1788)
 - (Class *Aves* Linnaeus 1758)
- Cohort *Lepidosauriformes* Benton 1983
- Lepidosauriformes*, *inertae sedis*, †*Palaeagama*, †*Biomosaurus*, †*Kudnu*, †*Coburnifer*
 - plesion †*Younginiformes* Romer 1933
 - plesion †*Acerosodontosaurus*
 - Superfamily *Younginoidea* Currie 1982
 - Family *Younginidae* Broom 1914 *Youngina*
 - Family *Tangasauridae* Camp 1945 (Piveteau 1926)
 - Subfamily *Kenyasaurinae* Currie 1982 *Kenyasaurus*, *Thalassaurus*
 - Subfamily *Tangasaurinae* Piveteau 1926 *Tangasaurus*, *Hovasaurus*
- plesion †*Saurosternidae* Haughton 1924 *Saurosternon*
- Superorder *Lepidosauria* Haekel 1866 (Duméril & Bibron 1839)
- Order *Sphenodontia* Williston 1925
- Family *Sphenodontidae* Cope 1870 *Sphenodon*, *Brachyrhinodon*, *Clerosaurus*, *Homonosaurus*, *Toxolophosaurus*, etc.
 - ?Family *Saphreosauridae* Baur 1895 *Saphrosaurus*
 - plesion †*Gephyrosauridae* Evans 1980 *Gephyrosaurus*
 - Order *Squamata* Oppel 1811
 - (Suborder *Sauria* Macartney 1802)
 - (Suborder *Amphisbaenia* Gray 1844)
 - (Suborder *Serpentes* Linnaeus 1758)
- Diapsida, *inertae sedis*
- ?†Family *Charaziidae* Peyer 1936
 - (†Family *Champsosauridae* Cope 1876)
 - (†Family *Pleurosauridae* Lydekker 1888)

An evolutionary tree of the early diapsids is also given (Fig. 2) — this incorporates the data from the cladistic analysis, as well as stratigraphic information.

PERMO-TRIASSIC DIAPSIDS AND FAUNAL EVOLUTION

Origin of the Diapsids

The earliest known diapsid is *Petrolacosaurus* from the late Carboniferous of Kansas [Fig. 3(A)]. *Petrolacosaurus* was 60–70 cm long and it had a long neck and was probably an agile terrestrial reptile that may have fed on large insects and other arthropods. It shows typical diapsid characters — two temporal fenestrae, suborbital fenestra in the palate, relatively small skull, long limbs, locked tibio-astagal joint (Reisz, 1981). In the late Carboniferous and early Permian, several major lines of reptiles were diverging (Pelycosauria, Protorothyrididae, Caporhinae, Diapsida), and the diapsids seem to show closest relationship to the protorothyrids.

Diapsids are not known from the early Permian (except for one

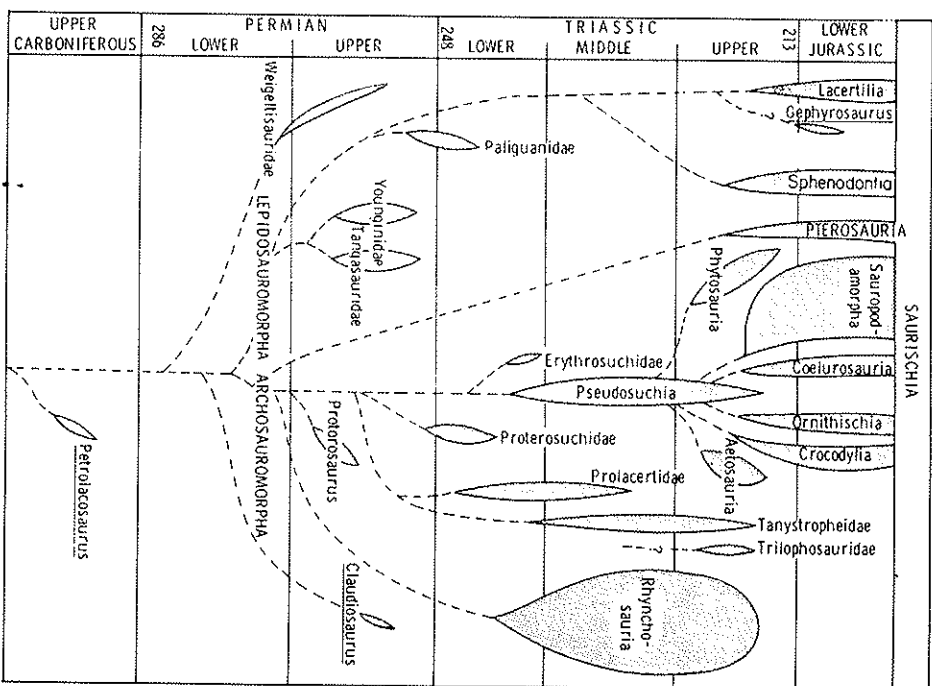


FIG. 2. Phylogenetic tree of the Permian-Triassic diapsid reptiles. Data on relationships are taken from the cladogram (Fig. 1). Stratigraphic information from Anderson & Cruickshank (1978) and Tucker & Benton (1982). Age dates from Harland *et al.* (1982). The spindles are drawn to indicate the known stratigraphic range of each group, and the width represents the relative abundance (a subjective measure of numbers of individuals and numbers of genera present in typical faunas at particular times) - data from various sources, reviewed in Benton (1983a). Dotted lines connecting groups indicate uncertainty about relationships.

possible fragment), but several forms have been found in later Permian faunas of Germany, England, Russia, Tanzania, South Africa and Malagasy. In most of these, the diapsids are represented by only one or two specimens, but they are abundant in the Malagasy fauna.

Late Permian: the Lower Sakamena Formation, Malagasy

The Lower Sakamena Formation (?late Permian: ?Tatarian) of the region between Mount Eliva and Ranohira, south-west Malagasy, has yielded hundreds of fossil reptile specimens. The reptiles consist of the procolophonid *Bavariasaurus*, isolated bones of mammal-like reptiles (dicynodont, theriodont), and the diapsids *Coelurosaurus*, *Claudiosaurus*, *Aerosodontosaurus*, *Thadeosaurus* and *Hovasaurus* [Fig. 3(B)-(E)]. Associated fossils include plants (equisetals, cycads and coniferopsids typical of the *Glossopteris* Flora), bivalves, crustaceans, fish (*Atherostoma*) and the amphibian *Rhinesuchus*. There were probably several environmentally controlled faunas (Currie, 1981). The overwhelming dominance of the faunas by diapsids is remarkable in view of their rarity in faunas of similar age in South Africa, where mammal-like reptiles (dicynodonts, gorgonopsians) were abundant.

Coelurosaurus (*Daedulosaurus*) was a small, 30 cm long animal with hugely expanded dorsal ribs. It has been suggested that these ribs were joined by a membrane, as in the living lizard *Draco* (Carroll, 1978; Evans, 1982). *Coelurosaurus*, represented by only three or four specimens, had a short skull, with pleurodont teeth and a large orbit. The trunk and tail were long, and the ribs were up to 16 cm long. A close relative is known from the late Permian of England and Germany (*Weigelisaurus*).

Claudiosaurus, a 60 cm long animal with a small head, a long neck, and heavy paddle-like hands and feet, has been interpreted as a plesiosaur ancestor by Carroll (1981). The 20 or so specimens certainly show adaptations for swimming in the hands and feet, but the interpretation of *Claudiosaurus* as an early member of the nothosaur/plesiosaur group is less certain. Carroll (1981) notes several features in which *Claudiosaurus* could be seen as intermediate between a younginiform and a nothosaur, but many of these are general aquatic adaptations. *Claudiosaurus* is a diapsid, and it probably classifies as sister-group to the Archosauromorpha + Lepidosauromorpha.

The other three Malagasy diapsids are younginiforms. *Aerosodontosaurus* (Currie, 1980) was probably 60-70 cm long, but the single known specimen is incomplete. It had a generalized "younginid" skull with pointed teeth. *Thadeosaurus* (Carroll, 1981), based on about 10 specimens, was also a terrestrial animal with heavy limbs. The skull is poorly

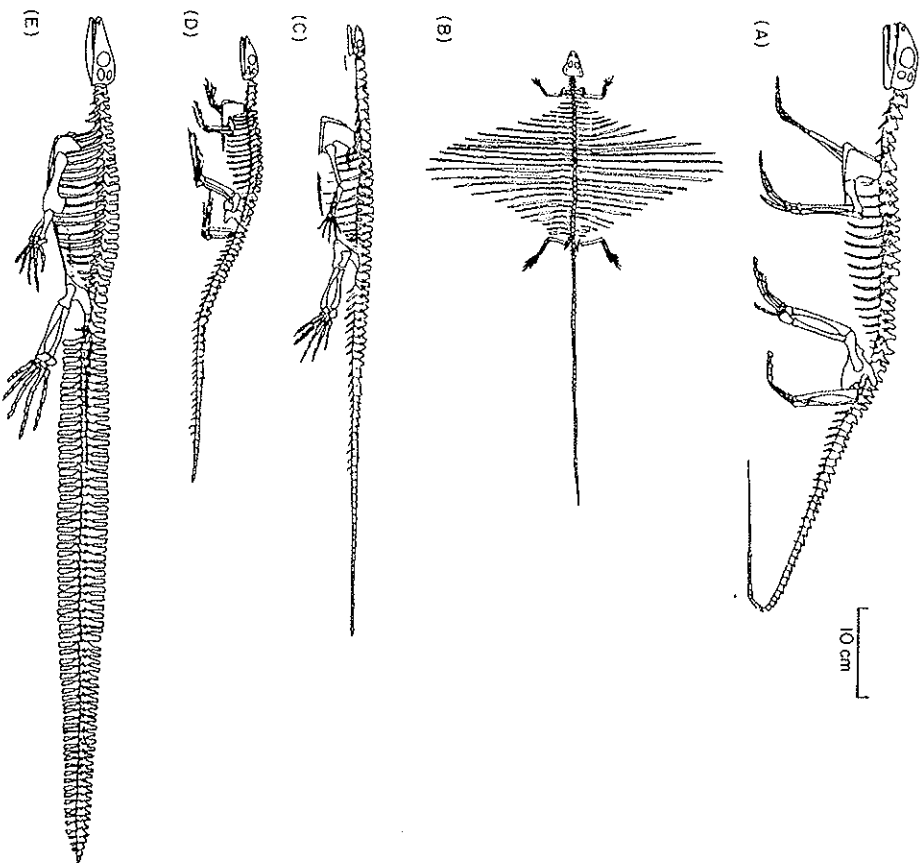


FIG. 3. Diapsid reptiles of the late Carboniferous and late Permian. (A) *Petrolacosaurus* from the late Carboniferous of Kansas. (B) *Coelurosaurus*. (C) *Claudioisaurus*. (D) *Thalassurus*. (E) *Hovasaurus* from the Lower Sakamena Formation of Madagascar. (A, after Reisz, 1981; B, after Carroll, 1978 and Evans, 1982; C, D, after Carroll, 1981; E, after Currie, 1981.)

known, but *Thalassurus* shows close similarities with *Kenyasaurus* and with the tangasaurid *Hovasaurus*. *Hovasaurus* is the most abundant reptile known from the Lower Sakamena Formation, being represented by more than 300 specimens (Currie, 1981). The skeleton shows clear aquatic adaptations: large paddle-like hands and feet; long and deep tail with high neural spines and long haemaphophyses; and ballast pebbles in the body cavity. An adult was 30–35 cm long (snout–vent length) with a 50–60 cm tail, but a series of juveniles is known, the smallest of which had a total length of about 20 cm.

Early Triassic: the *Lystrosaurus* and *Cynognathus* Zones, South Africa

Diapsid reptiles are known from the late Permian of South Africa (e.g. the lepidosauromorphs *Youngina*, *Palaegama*, *Sarostemon*). The first archosauromorph, the proterosuchid *Archosaurus*, is known from the late Permian (Tatarian) of European Russia, but the Archosauromorpha only became well known in the Triassic.

The *Lystrosaurus* Zone (= *Lystrosaurus* Assemblage Zone of Keyser & Smith, 1979; lowest Scythian) is heavily dominated by the dicynodont *Lystrosaurus* (over 90% of all specimens collected), but four diapsids are present: *Prolacerta*, *Proterosuchus*, *Paliguana* and *Notosuchus* [Fig. 4(A)–(C)]. *Prolacerta* was a 60 cm long quadruped with a low skull, very long neck, long slender limbs and a deep tail (Gow, 1975). The teeth are recurved and pointed, and the lower temporal bar is broken – *Prolacerta* has been regarded as an early lizard (Robinson, 1967; Wild, 1980), but the archosauromorph features shared with thecodontians and rhynchosaurs are overwhelming. The broken lower temporal bar character, often regarded as a diagnostic squamate feature, occurs in many unrelated groups, and is a parallelism (*Coelurosaurus*, *Claudiosaurus*, *Prolacertiformes*, the sphenodontids *Cleosaurus* and *Planocephalosaurus*, (?) nothosaurs and plesiosaurs). *Proterosuchus* (*Chasmatosaurus*), a varanid-shaped carnivore with a 25 cm skull, has frequently been placed at the foot of the archosaur radiation on the basis of its antorbital fenestra. The snout is long and narrow, the teeth are sharp and recurved, and the orbit is high and archosaur-like (Cruickshank, 1972). However, there are numerous prolacertiform characters: the downturned snout tip, elongate snout and palatal bones, long inter-pterygoid vacuity, elongate cervical vertebrae, and broad and deep haemaphophyses. Its taxonomic position is uncertain. *Paliguana*, a small reptile, is known only from its 2.5 cm long skull which shows some lizard-like features (squamosal reduced, no lower temporal bar, quadrate with conch-like tympanic notch), but it lacks key lepidosaur and squamate characters. *Notosuchus*, redescribed as the earliest rhynchosaur (Carroll, 1976), could belong anywhere among primitive archosauromorphs. Elements of the *Lystrosaurus* Zone fauna have been found in Antarctica, Australia, China, Russia and India. In most of these, diapsids were minor elements – small insectivores and small to medium-sized carnivores – comprising only about 1% of all specimens known in each fauna.

The *Cynognathus* Zone (= *Kammejeria* Assemblage Zone of Keyser & Smith, 1979; late Scythian) has yielded some more significant diapsids: the thecodontians *Erythrosuchus* and *Euparkeria* [Fig. 4(D), (E)], and the

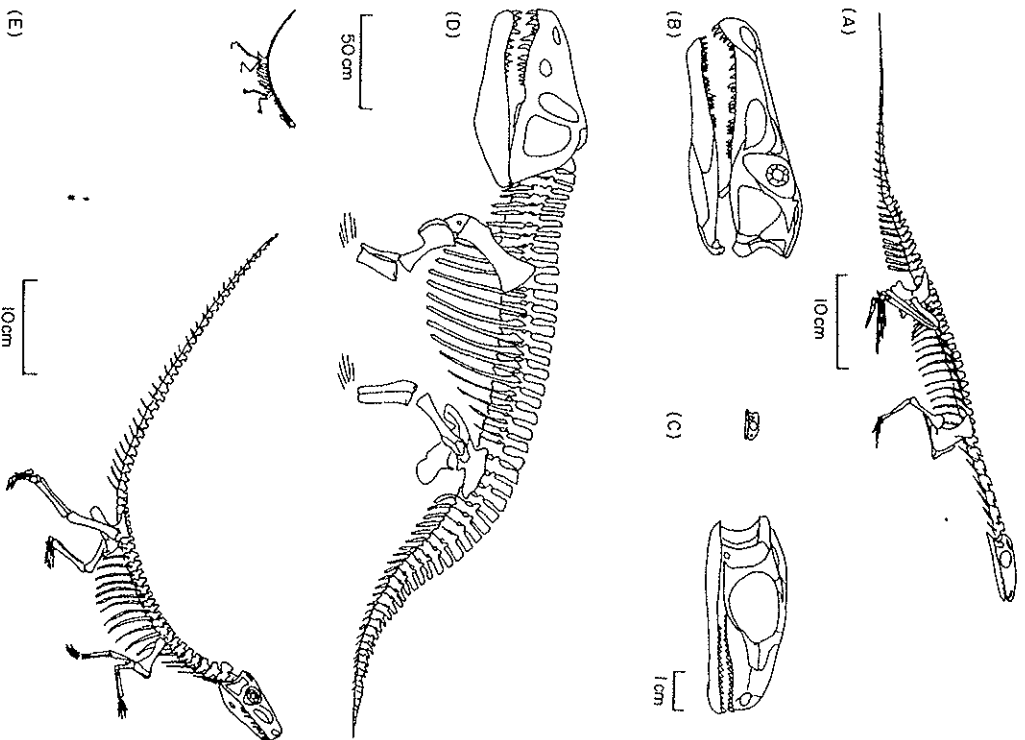


FIG. 4. Diapsid reptiles of the early Triassic. (A) *Prolaerta*, (B) *Chamaeleosaurus* and (C) *Paliguana* from the *Lystrosaurus* Zone of South Africa. (D) *Erythrosuchus* and (E) *Euparkeria* from the *Cynognathus* Zone of South Africa. Note the scales: *Paliguana* and *Euparkeria* are shown at two sizes. (A, after Gow, 1975; B, after Cruickshank, 1972; C, after Carroll, 1975; D, after von Huene, 1956; E, after Ewer, 1965.)

rhynchosaurs. *Mesosuchus* and *Howesia*. *Erythrosuchus*, a 5 m long heavily-built quadruped with a massive 1 m long skull, must have been a prodigious carnivore, preying on the contemporary herbivorous dicynodonts and smaller mammal-like reptiles and amphibians. *Erythrosuchus* is often classed with protosuchids, but it shows numerous advanced characters shared with later thecodontians that are absent in *Proterosuchus* (Fig. 1: J). Close relatives of *Erythrosuchus* are known from Russia and China. *Euparkeria*, a small 65 cm long quadruped and facultative biped shows more advanced features in the skull and hind-limbs. The teeth are thecodont and relatively large. The early rhynchosaurs, *Mesosuchus* and *Howesia*, are inadequately known at present. Of these small animals, *Howesia* is more of a typical rhynchosaur, with multiple rows of deeply rooted teeth. Thecodontians were clearly important carnivores in the *Cynognathus* Zone fauna (14% of all specimens found).

Middle Triassic: the Grenzbitumenzone, Switzerland

During the Middle Triassic, diapsids radiated in several adaptive zones: the rhynchosaurs became dominant herbivores in the Manda Formation, Tanzania; pseudosuchian thecodontians of various kinds appeared (rauisuchids, proterochampsids, lagosuchids, etc.) and became the dominant carnivores world-wide, although the cynognathoid mammal-like reptiles continued to diversify at the same time.

One exceptional middle Triassic diapsid fauna is that of the Grenzbitumenzone (Anisian-Ladinian boundary) of Monte San Giorgio, Tessin, Switzerland. The largely aquatic fauna contains early ichthyosaurs, nothosaurs, placodonts and the diapsids *Macrocnemus*, *Tanystrophiens*, *Ticinosaurs*, *Askepiasaurus*, *Clarazia* and *Heschleria*, as well as fish and marine invertebrates (Kuhn-Schnyder, 1974) (Fig. 5).

Macrocnemus and *Tanystrophiens* are classed as prolacertiforms. *Macrocnemus* was a small lizard-like animal, with a 7 cm skull, very like *Prolaerta* in certain features, and with long light limbs. *Tanystrophiens*, represented by a series of juvenile to adult skeletons, is the most remarkable reptile present. Adults were up to 6 m long, of which half was made up of an elongate neck. The 12 cervical vertebrae were up to 30 cm long, and the neck was clearly not enormously flexible. Despite its bizarre appearance, *Tanystrophiens* shows prolacertiform features in the skull and limbs. Wild (1973) has suggested that *Tanystrophiens* fed on insects as a juvenile, when the neck was relatively much shorter, and on fish as an adult.

Ticinosaurs, a 2.5 m long rauisuchid thecodontian with large teeth, a long neck and long limbs, must have been a fearsome predator (Krebs,

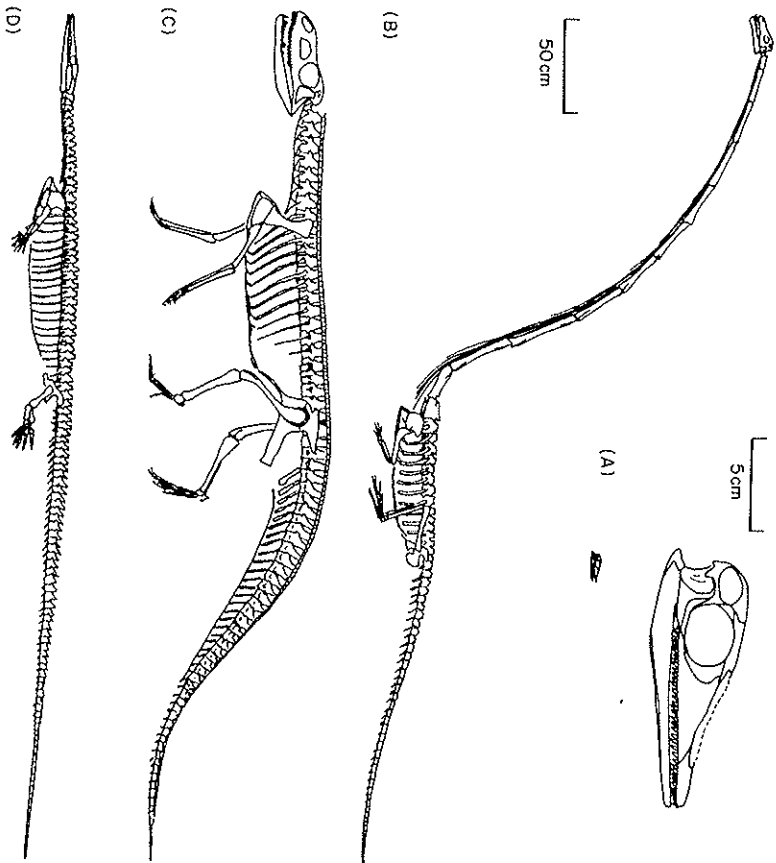


FIG. 5. Diapsid reptiles of the middle Triassic. (A) *Macrocnemus*, (B) *Tanystrophia*, (C) *Teiusuchus* and (D) *Akephosaurus* from the Grenzbitumenzone of Switzerland. Note the scales: *Macrocnemus* is shown at two sizes (A, after Kuhn-Schayder, 1974; B, after Wild, 1973; C, after Krebs, 1965; D, after Kuhn, 1952.)

1965). *Akephosaurus*, a 2.5 m long reptile with a long narrow skull, very long neck, trunk and tail and tiny limbs, was probably a good swimmer (Kuhn, 1952). *Akephosaurus* was clearly a diapsid, but it cannot be confidently placed in the Lepidosauria, as has often been done. Finally, *Clazzia* and *Heschleria*, both poorly known, had broad skulls, heavy grinding teeth, long bodies and reduced limbs. These were aquatic forms, but they cannot confidently be identified as 'lepidosaurs' (Romer, 1966), or even as diapsids at present.

Late Triassic: the Lossiemouth Sandstone Formation, Scotland

By the middle of the late Triassic (Carnian – Norian), several faunas are known around the world in which rynchosaurs and/or aetosaurs were

dominant herbivores, and pseudosuchians and/or phytosaurs were dominant carnivores (e.g. Santa Maria Formation, Brazil; Ischigualasto Formation, Argentina; Maleri Formation, India; Lossiemouth Sandstone Formation, Scotland; Dockum Group, Texas; Chinle Formation, Arizona). In the southern-continent and American faunas of this age, mammal-like reptiles were still significant elements: dicynodonts and diademodontoids as herbivores, and cynognathoids as carnivores. However, these are absent from the Lossiemouth Sandstone Formation, which consists of the procolophonid *Leptopleuron*; a selection of becdontians: the aetosaur *Stagonolepis*; the pseudosuchians *Ornithosuchus*, *Erpetosuchus* and *Scelerosuchus*; the primitive coelurosaur dinosaur *Saltopus*; the rynchosaur *Hyperodapedon*, and the sphenodontid *Brachyrhinodon* (Fig. 6).

Stagonolepis, a 2.7 m long quadruped with short limbs, a shovel-snouted skull and extensive dermal armour, was a relatively abundant herbivore that may have fed on tubers and roots (Walker, 1961). *Ornithosuchus*, represented by several individuals, ranging in size up to 3.5 m long, was a bipedal or quadrupedal carnivore with heavy jaws (Walker, 1964). It could probably have fed on *Stagonolepis* and *Hyperodapedon*. *Erpetosuchus*, a small carnivore with an 8 cm skull, is poorly known. *Scelerosuchus* was also tiny (25 cm long) and is remarkable for its relatively large skull and very long limbs which may have been adapted for rapid running over sand. *Saltopus*, the small dinosaur, is known from only one incomplete skeleton without a skull. These last three genera probably fed on juvenile *Stagonolepis* and *Hyperodapedon*, as well as *Leptopleuron* and *Brachyrhinodon*.

The rynchosaur *Hyperodapedon*, a 1.3 m long animal with strong digging claws on the foot, a beaked premaxilla, and strong slicing dentition, could have fed on a variety of tough vegetation (Benton, 1983b). The small sphenodontid *Brachyrhinodon* had a very short snout, and is the only lepidosauromorph known from Elgin.

Latest Triassic: the Knollenmergel, Germany

Some time between the early and the middle Norian (220–225 My ago: Harland, Cox, Lewellyn, Pickton, Smith & Walters, 1982) the majority of the early archosauromorphs and the remaining mammal-like reptiles disappeared: rynchosaurs, thecodontians, dicynodonts, diademodontoids and cynognathoids. They were replaced world-wide by dinosaurs as medium to very large-sized herbivores (prosauropods, ornithischians) and carnivores (coelurosaur), which dominated all terminal Triassic terrestrial faunas.

A typical early dinosaur fauna is that of the Knollenmergel (late

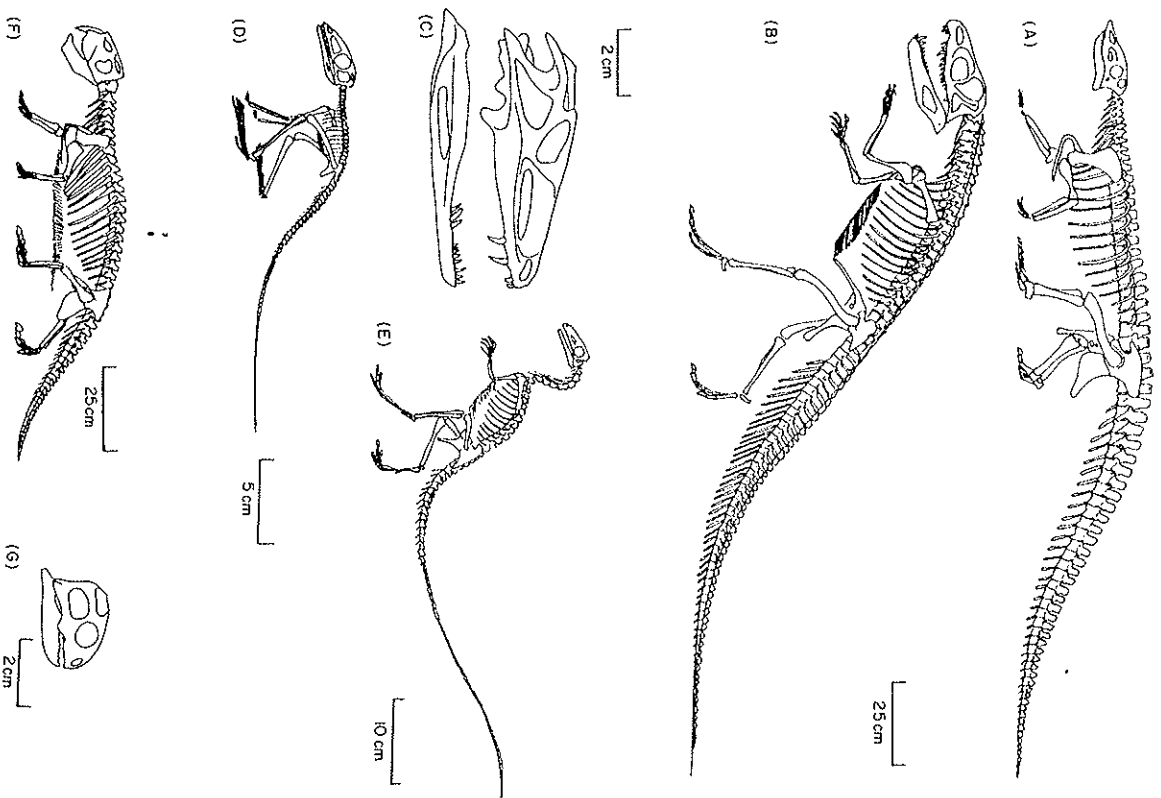


FIG. 6. Diapsid reptiles of the late Triassic: (A) *Stagonolepis*, (B) *Ornithosuchus*, (C) *Epitetrasuchus*, (D) *Sclerozuchus*, (E) *Sclerops*, (F) *Hyperodapedon* and (G) *Brachyrhinodon* from the Lossiemouth Sandstone Formation of Elgin, Scotland. Note the scales: (A), (B) and (F) are drawn to the same scale as are (C) and (G). (A, after Walker, 1961; B, after Walker, 1964; C, D, E, after von Huene, 1956; F, original; G, after von Huene, 1956.)

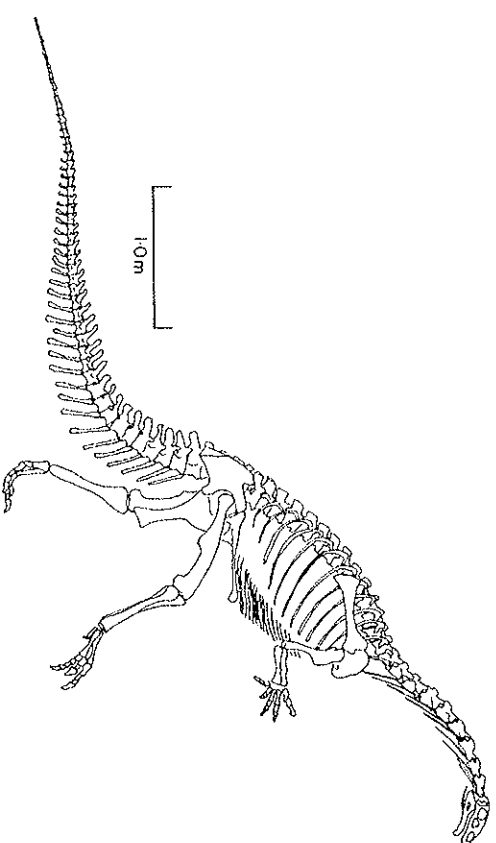


FIG. 7. Diapsid reptile of the latest Triassic: *Plateosaurus* from the Knollenmergel, south-west Germany (after von Huene, 1956).

It has been suggested elsewhere (Tucker & Benton, 1982; Benton, 1983a) that the rise of the dinosaurs need not have been the result of prolonged and successful competition with mammal-like reptiles and thecodontians, as has been assumed (e.g. Charig, 1979, 1980; Bonaparte, 1982). There is evidence that the elements of the intermediary "pre-dinosaur" faunas of the late Triassic died out as a result of floral and/or climatic changes. The dinosaurs, already present as small to medium-sized, but rare, faunal elements (e.g. *Sclerops*) radiated rapidly to fill empty ecological space. It seems clear that the dinosaurs achieved their dominance and large size in 2–3 My or less. There is no evidence for sustained competition throughout the Triassic between "inferior" mammal-like reptiles and "superior" archosaurs, whatever the "superior" feature of the latter group is – improved locomotory capability (Ostrom, 1969; Bakker, 1971; Charig, 1972, 1979, 1980), endothermy (Bakker, 1971, 1975), or ectothermic inertial homeothermy (Spotila, Lommen, Bakker & Gates, 1973; Benton, 1979).

Norian) of south-west Germany. A few turtles (*Proganochelys*) are present, as well as abundant specimens of the dinosaur *Plateosaurus* (Fig. 7). This large prosauropod (5–10 m long) had a relatively small skull with peg-like teeth, a long neck and tail and heavy limbs. It was probably quadrupedal and facultatively bipedal. The "Knollenmergel" has also yielded remains of the coelurosaurs *Halticosaurus* and *Pterospodylus*.

Late Triassic/Early Jurassic: the Bristol fissures, England

The Triassic–Jurassic fissures in the region of Bristol, south-west England, and south Wales have yielded a fascinating sample of small animals from typical early dinosaur faunas. The exact ages of the fissures are hard to determine, and there were probably several generations of infilling in the Norian, Rhaetian and early Jurassic. Great interest has focused on these fissures for the early mammal-like reptiles and mammals that they have yielded (*Oligokyphus*, *Haramiya*, *Thomasia*, *Eozostrodon*, *Morganucodon*, *Kuehneotherium*) and the small reptiles. The dominance of small reptiles is probably the result of preservational sorting – dependent on which animals fell into the fissures – rather than an indication of a specialized “upland” fauna (cf. Robinson, 1957; Tarlo, 1962).

The diapsids present (Fig. 8) include the phytosaur or aetosaur *Rileyia*, the prosauropod dinosaur *Thecodontosaurus*, and a selection of other undescribed archosaurs (Marshall & Whiteside, 1980; D. I. Whiteside, pers. comm.; N. C. Fraser, pers. comm.). Several sphenodontids and lizards also await description. Two sphenodontids with broken lower temporal bars have been described; *Cleosaurus* (Swinton, 1939; Robinson, 1973) and *Planocephalosaurus* (Fraser, 1982), with tiny 2–3 cm long skulls. A remarkable gliding animal, *Kuehneosaurus* (Robinson, 1962), is also represented by several specimens – it has a high 3 cm long skull and expanded dorsal rib, giving a span of 25–30 cm. *Kuehneosaurus* has been called a lizard, but it lacks most squamate and lepidosaur characters. It is not even certain that it is a lepidosauriform. *Gephyrosaurus* (Evans, 1980, 1981), a 25–30 cm long lizard-like animal, is probably the sister-group of the Squamata. Some jaw fragments with batteries of broad herbivorous teeth have also been described: *Triacuspisaurus* and *Varioidens*, which may or may not have belonged to diapsids.

CONCLUSIONS :

Recent work on Permo–Triassic diapsids has shed new light on their relationships and evolution. The taxonomic and evolutionary aspects that have been touched upon here, are discussed in more detail elsewhere (Benton, 1983b, in preparation). The new taxonomic outline presented here may be tested and modified by redescriptions of old material, and by the discovery of new specimens. The views expressed on faunal evolution in the Permo–Triassic and the opportunistic radiation of the

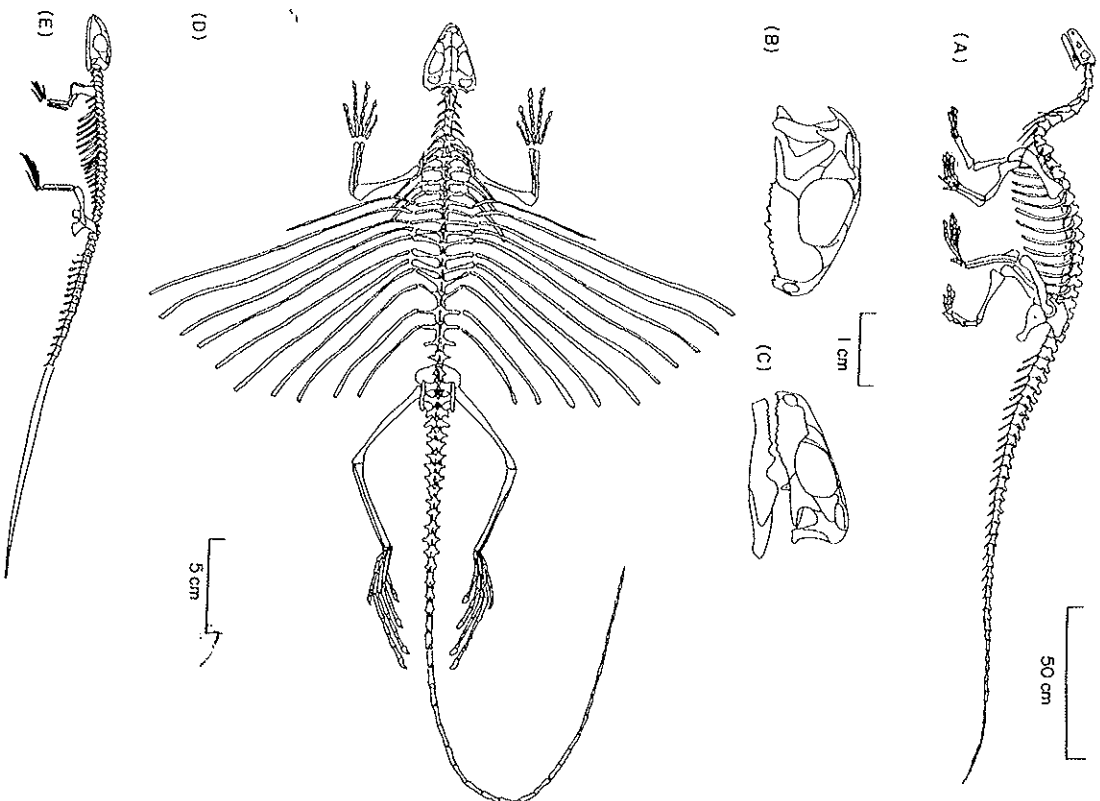


FIG. 8. Diapsid reptiles of the late Triassic/early Jurassic. (A) *Thecodontosaurus*, (B) *Cleosaurus*, (C) *Planocephalosaurus*, (D) *Kuehneosaurus* and (E) *Gephyrosaurus* from the fissures of the Bristol region, England, and south Wales. Note the different scales. (A, after von Huene, 1956; B, after Robinson, 1973; C, after Fraser, 1982; D, after Robinson, in Romer, 1966; E, after Evans, 1981.)

dinosaurs in the mid-late Norian are also cast in a testable form — the discovery of significant numbers of medium to large mammal-like reptiles or rhynchosaurs together with prosauropod dinosaurs in the same fauna would disprove the hypothesis and suggest that competition was involved.

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